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A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants

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Abstract

The beneficial effects of mycorrhizae on plant growth have often been related to the increase in the uptake of immobile nutrients, especially phosphorus (P). In this review the mechanisms for the increase in the uptake of P by mycorrhizae and the sources of soil P for mycorrhizal and non-mycorrhizal plants are examined.

Various mechanisms have been suggested for the increase in the uptake of P by mycorrhizal plants. These include: exploration of larger soil volume; faster movement of P into mycorrhizal hyphae; and solubilization of soil phosphorus. Exploration of larger soil volume by mycorrhizal plants is achieved by decreasing the distance that P ions must diffuse to plant roots and by increasing the surface area for absorption. Faster movement of P into mycorrhizal hyphae is achieved by increasing the affinity for P ions and by decreasing the threshold concentration required for absorption of P. Solubilization of soil P is achieved by the release of organic acids and phosphatase enzymes. Mycorrhizal plants have been shown to increase the uptake of poorly soluble P sources, such as iron and aluminium phosphate and rock phosphates. However, studies in which the soil P has been labelled with radioactive ^{32}P indicated that both mycorrhizal and non-mycorrhizal plants utilized the similarly labelled P sources in soil.

Introduction

Certain soil microorganism colonise roots of higher plants and form symbiotic relationships. Whereas nodulating bacteria play an important role in nitrogen fixation (e.g. Rhizobia in legumes), symbiotic associations formed by fungi with roots, and known as mycorrhizae (Gr myces = fungus, rhizo = roots) are of particular importance in the uptake of phosphorus (P).

Mycorrhizae are widespread under natural conditions and occur in nearly all soils, from mine spoils (Jasper et al., 1989) to agricultural soils (Abbott and Robson, 1982). They are formed by most vascular plants except for a few belonging mainly to the Chenopodiaceae, Crucifereae, Cyperaceae, Juncaceae and Proteaceae (Harley and Harley, 1987; Newman and Reddell, 1987). Depending upon the plant and fungal species involved, mycorrhizae are grouped into two major types. Ectomycorrhizae, characterised by dense mycelial sheaths around the roots and intercellular hyphal invasion of the root cortex, are limited to mostly temperate forest trees. Endomycorrhizae, where the fungi form external hyphal networks in the soil and grow extensively within the cells of the cortex, are formed by nearly all other plants. Specific types of endomycorrhizae are formed by members of the Ericaceae (Ericoid mycorrhizae) and the Orchidaceae (Orchidaceous mycorrhizae), but the type of mycorrhizae which is widespread are the vesicular-arbuscular (VA) mycorrhizae.

The effect of mycorrhizae in increasing plant growth has been well documented by many workers for many plant species (see reviews by Gianinazzi-Pearson et al., 1981; Smith, 1980; Tinker, 1978). The beneficial effect of mycorrhizae on plant growth has mostly been attributed to an increase in the uptake of nutrients, especially phosphorus (P). Recently Hetrick (1989) in an excellent review on the acquisition of phosphorus by mycorrhizal fungi states 'a growing body of circumstantial evidence suggests that mycorrhizal fungi or their accompanying microflora may improve soil phosphorus availability by solubilizing inorganic forms of phosphorus or by mineralization of organic phosphorus'. The overall aim of this review is to examine the effect of mycorrhizae on the uptake of P by plants. The mechanisms for the increased uptake of P by mycorrhizae and the sources of soil P for mycorrhizal and non-mycorrhizal plants will be examined in detail. In order to understand the mechanisms for increased uptake of P by mycorrhizal plants, firstly, the reaction between P and soil, the distribution of different forms of P in soil and the movement of P to plant roots will be examined.

Reactions of phosphorus in soil

When soluble phosphate fertilizers are added to soil, the concentration of P in the soil solution rises initially and then decreases. The decrease in the solution concentration of P continues for a long time without reaching a true equilibrium (Barrow, 1985; White, 1982). The process of removal of P from soil solution is generally termed phosphate 'fixation' or 'retention' (Bache, 1964). The process is rapid initially and then becomes slower with time and involves both inorganic sorption and precipitation and organic immobilization reactions.

The initial rapid decrease in the concentration of P in soil solution has been related to the adsorption of phosphate ions by various soil constituents. Various complex models have been proposed to describe the chemical mechanisms involved in this adsorption process (Barrow, 1985; White, 1982). Briefly, the phosphate ions are closely and chemically bonded to the surface of soil clay minerals and iron (Fe) and aluminium (Al) oxides by specific chemical bonds. The reaction may be regarded as partly a displacement of water molecules and partly a displacement of hydroxyl ions, so that the negative charge conveyed to the surface by the adsorbing anion is usually lower than the charge of the anion (Bolan and Barrow, 1984). In calcareous soils similar reactions have been found to occur with calcium carbonate concretions (Freeman and Rowell, 1981; Mattingly, 1975).

The slow reactions which follow the initial adsorption reactions are considered to be very important in the availability of P fertilizers (Barrow, 1980) and various explanations have been suggested for the slow reaction. Firstly, the reaction has been associated with the formation of amorphous coatings containing P on the surface of the adsorbents (Rajan and Fox, 1972). Secondly, it has been suggested that molecular rearrangement of the adsorbed P occurs leading to the development of a new more strongly adsorbed phase on the surface (Munns and Fox, 1976). Thirdly, the absorbent dissolves leading to the precipitation of amorphous and crystalline phosphate (Van Riemsdijk and Lyklema 1980). Fourthly, it has been suggested that the reaction involves solid-state diffusion of P, with the general idea that P adsorbed initially onto the surface diffuses into deeper layers (Barrow, 1985; McLaughlin et al., 1977). Whereas the first three suggestions have been based on a pragmatic approach, the last reason is based on mechanistic approach. The important difference between the pragmatic and mechanistic models is that the latter attempts to take into account the change in surface charge of soils with P adsorption. This model has been used to examine not only the effect of concentration and time on P adsorption but also the effect of pH and temperature on both adsorption and desorption of P by soils (Barrow, 1985). The slow decrease in the concentration of P in soil solution has also been associated with the immobilization of added P by microorganisms to organic P (Anderson, 1980). This process is very active in soils low in initial P status and organic matter content. In these soils, with continued cultivation and fertilizer application the organic matter builds up and causes immobilization of added P (Walker and Syers, 1976). Under these conditions more than 30% of the added P has been found to be immobilized into organic P (Barrow, 1969; Donald and Williams, 1954). However, in permanent pastures and in farming systems where P deficiency is not extreme and where there is little long-term change in the organic-matter content of soils, accumulation of organic P is less important (Oniani et al., 1978). When tropical soils are cleared and cultivated, soil organic matter declines dramatically and requires fertilizer application to build up the organic matter (Sanchez, 1976).

Forms of phosphorus in soils

Various approaches have been used to categorise the diverse forms of P in soil. These are based on (1) the nature of P compounds in the soil, (2) chemical fractionation and (3) isotropic exchange. Similar approaches have been used to identify the sources of soil P for mycorrhizal and non-mycorrhizal plants; hence, it is appropriate to examine these approaches in detail.

Nature of phosphorus compounds

The various forms of P compounds present in soils are broadly categorized into inorganic and organic P (Dalal, 1977; Larsen, 1967). Relative distribution of these two forms in soils depends on various factors which include type of vegetation, fertilizer history, microbial activity, cultivation and soil type (Anderson, 1980; Dalal, 1977; Hedley et al., 1982a).

Inorganic P (Pi) can occur in soil solution, adsorbed onto the soil surfaces or precipitated as discrete minerals. Although soil solution Pi constitutes only a small proportion of total P (<1%), plants derive most of their immediate P requirements from this source. Most of the Pi is adsorbed onto the soil surfaces or precipitated as Fe and Al phosphates in acid soils and as Ca and Mg phosphates in alkaline and calcareous soils. Relative distribution and plant availability of these forms depend mainly on soil pH (Sample et al., 1980). Evidence for the existence of these compounds in soils is often presented based on results of selective fractionation schemes (Chang and Jackson, 1957). Organic P occurs both as soluble P in soil solution, as insoluble P adsorbed onto soil particles or as a component of soil organic matter (Anderson, 1980). Although more than 30 organic P compounds have been isolated from soils, inositol phosphate, phospholipids and nucleic acid are the predominant compounds (Barrow, 1961; Dalal, 1977). These organic P compounds are easily degraded in soil and the plant availability of these compounds has been demonstrated under aseptic conditions using solution cultures (Martin, 1973). In soils, organic P is generally mineralised to inorganic P before it becomes plant-available. Mineralization is caused either by simple autolysis or by enzymatic dephosphorylation (Cosgrove, 1977). The rate of mineralization of organic P is frequently limited by the rate of supply of inorganic P. A low C:N ratio of organic matter favours immobilization of added P to organic P (Dalal, 1977).

Chemical fractionation

Inorganic P can be fractionated into Ca, Fe and Al forms (Chang and Jackson, 1957). This fractionation is based on consecutive extraction with different chemical extractants, each designed to remove a particular form of P. The orginal fractionation scheme has been modified by many workers (e.g. Sharply and Smith, 1985; Williams et al., 1967). The underlying assumption in all these schemes is that inorganic P consists of varying proportions of three distinct classes of compounds, namely phosphates of Fe, Al and Ca, some of which could be occluded within the coatings of Fe oxides and hydrated oxides. This separation was found to be satisfactory for stable phosphate minerals, such as variscite, strengite and apatite. However, the fractionation scheme cannot differentiate between individual compounds within a class. Thus, for example, different Ca compounds such as octacalcium phosphate, hydroxyapatite, fluoroapaptite, if all present, will be grouped together in the Ca phosphate class. However, in soils added P rarely forms these stable compounds and forms mostly meta-stable compounds. For example, Norrish and Rosser (1983) have analysed discrete phosphate grains in several cultivated and uncultivated soils with an electron microprobe and shown that the composition of precipitated soil P was quite variable and consisted of Fe, Al, Si and in some cases Ca, intimately mixed with P. None of the grains examined showed compositions similar to stable end products. The fractionation scheme is satisfactory for stable end-products but could not distinguish between meta-stable end products. Also this fractionation scheme cannot differentiate adequately between precipitated and sorbed forms of P (Williams et al., 1967).

Isotopic exchange

Equilibrium of phosphate between solution and solid forms has been described by rate of reactions (Barrow, 1983). There is an initial, relatively rapid rate of reaction followed by a slow reaction which continues for a long time (Barrow and Shaw, 1975). Exchange with P isotope (^{32}P) or with chloride-saturated anion-exchange resin (Amer et al., 1955; Vaidyanathan and Talibudeen, 1968) has been used to differentiate between these two rates of reaction. The fraction of soil P which undergoes rapid exchange with ^{32}P is termed 'labile' phosphate which mostly includes the recently adsorbed phosphate. The slowly equilibriating phosphate is termed 'non-labile' phosphate which includes occluded (penetrated) phosphate, precipitated phosphate and organic phosphate (Olsen and Khasawneh, 1980). However, Nye and Tinker (1977) argued that there is no definite limit to the amount exchanged and given sufficient time most of the soil phosphate would exchange. Since these two fractions vary with the time of equilibrium with ^{32}P, standard conditions are used to obtain relative values amongst soils.

It is believed that in short-term experiments plants utilize mostly the labile P (White, 1976). However, there is an equilibrium between these fractions in soil, and change in one fraction due to plant uptake can alter another fraction which is in chemical equilibrium with it. For example, Hedley et al. (1983) showed that under P deficiency conditions, rape plants (*Brassica napus*) were capable of depleting non-labile P as well as labile (resin-exchangeable) P.

Supply of soil phosphorus to plants

Nutrient ions reach the surface of roots by three processes (Barber, 1984). These include: (1) root interception; (2) mass flow and (3) diffusion.

Root interception is the process by which the nutrients are absorbed when the root surface comes in direct contact with a nutrient. Maximum quantity of nutrient supplied by root interception can be calculated from the amount of nutrient present in a volume of soil equal to root volume. Since the volume of root depends on the plant species and presence of mycorrhiza, the quantity of nutrient absorbed by this process also depends upon these factors. Mass flow is the movement of nutrient to the root surface in the convective flow of water during the absorption of water by plant. The amount of nutrient taken up by this process is calculated from the amount of water uptake and the concentration of nutrient in soil solution. It is generally agreed that nutrient ions, such as nitrate, chloride, sulphate, calcium and magnesium which are less readily retained by soils than phosphate and potassium are supplied by mass flow.

Diffusion is the movement of nutrient towards a root surface caused by concentration gradient. In the absence of mass flow, continued uptake of nutrient ions by roots reduce the concentration of available nutrients at the root surface causing a concentration gradient perpendicular to the root surface. When a concentration gradient exists, there is a net movement from the zone of higher concentration in the soil solution to the zone of lower concentration in the root surface. The amount of nutrient supplied by diffusion process depends on the rate of diffusion which in turn is affected by the properties of the ions in question and of the soil. Surface adsorption reactions and the tortuous nature of the soil water film retard the rate of diffusion of various ions in soil. For example, the rate of diffusion of phosphate ions is much lower in soil (10^{-11} to $10^{-8}\,cm^2\,s^{-1}$) than in free water ($0.89\times$

10^{-5} cm^2 s^{-1}) (Barber, 1984). The lower the diffusion coefficient for a given nutrient, the greater will be the reduction in concentration at the root surface. In the case of phosphate, most of the plant requirement is obtained by the diffusion process. Plant roots of annual crops have a volume less than 1% of the soil volume (Barber, 1984). Hence, the maximum amount of P supplied by root interception is less than 1% of the available P in soil and this amount is usually a small percentage of the plant requirement. The amount of P moving to the root by mass flow depends on the concentration of P in soil solution. Since the concentration of P in soil solution remains low (0.05–0.3 μg P mL^{-1}; Ozanne, 1980) the amount of P supplied by mass flow also accounts for only a small percentage of the P used by the plant. Hence, it suggests that in many soils diffusion is the mechanism for the supply of most of the P absorbed by the plant. Phosphate which is adsorbed strongly by the soil has a low value of effective diffusion coefficient (D_e) in soil. The low value creates a steep concentration gradient and hence only phosphate in soil near the root zone (diffusion zone) reach the root. All factors which govern the rate of diffusion of P to root and the extent of root growth determine the availability of P to plants growing in soil. These factors include both soil (moisture content, tortuosity, buffering capacity, temperature) and plant factors (root length, mycorrhizal infection). The overall supply of P to plants in a soil system can be represented as in Fig. 1. In a short period, the adsorption-desorption process mostly determines the concentration of P in soil solution which in turn determines the rate of diffusion of P from the surface of the soil particles to the surface of the roots. Other processes such as solid-state diffusion, desorption, precipitation–dissolution and immobilization–mineralization operate over longer periods of time (Murrman and Peech, 1969).

Mechanisms for increased uptake of phosphorus by mycorrhizal plants

In many studies involving mycorrhizae, the mycorrhizal association usually increased the growth of plants solely by enhancing the uptake of nutrients especially P (Abbott and Robson, 1982; Harley and Smith, 1983; Kucey et al., 1989; Mosse, 1973; Tinker, 1978). Various mechanisms have been suggested to account for this increased nutrient uptake.

The contribution of mycorrhizal associations in the efficient uptake of P by plants is illustrated in Fig. 2. The increase in plant growth by mycorrhizal association is largely due to increased absorption of nutrients from soil solution. It has often been reported that the rate of uptake by mycorrhizal plants is faster than that by non-mycorrhizal roots (Sanders and Tinker, 1973; Smith et al., 1985; Son and Smith, 1988). For

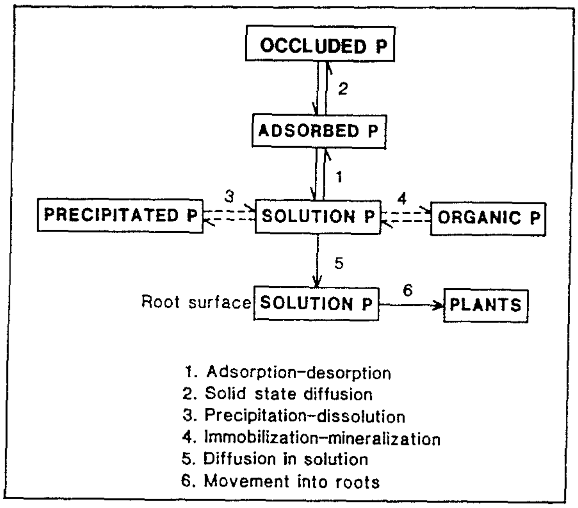

Fig. 1. Schematic representation of supply of phosphorus to plant roots in soil systems.

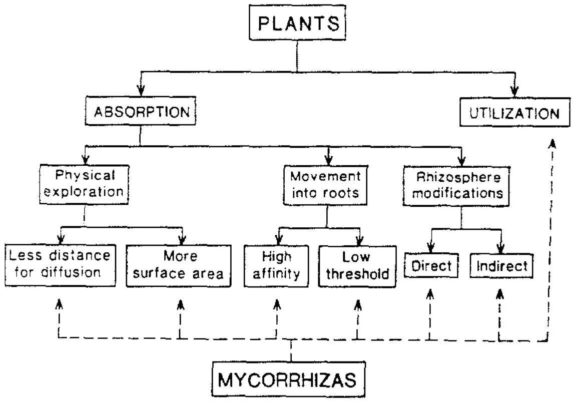

Fig. 2. Possible mechanisms by which mycorrhizal fungi increase the uptake of phosphorus by plants from soil (modified from Barrow, 1978).

example, Sanders and Tinker (1973) observed that the rate of inflow of P into mycorrhizal roots was much higher (17×10^{-14} moles cm^{-1} s^{-1}) than that of non-mycorrhizal plants (3.6×10^{-14} moles cm^{-1} s^{-1}). Assuming that the difference in the rate of inflow was caused by mycorrhizal hyphae they calculated the rate of inflow of P into hyphae to be six times (18×10^{-14} moles cm^{-1} s^{-1}) the rate of the root hair. An increase in absorption of P by mycorrhizal plants could be brought about by: increased physical exploration of the soil; increased movement into mycorrhizal fungus hyphae; modification of the root environment; increased storage of absorbed P; efficient transfer of P to plant roots; and efficient utilization of P within the plant. Each of these processes will be considered in turn.

Physical exploration of soil

Mycorrhizal fungi in association with plant roots seem likely to increase P uptake by more thorough exploration of soil volume thereby making 'positionally unavailable' nutrients 'available'. This is achieved by decreasing the distance for diffusion of phosphate ions and by increasing the surface area for absorption (Tinker, 1978).

Diffusion zone

Phosphorus in soil solution has been shown to reach plant roots mainly by the diffusion process. Sanders and Tinker (1973) concluded that the extensive hyphal growth of mycorrhiza effectively 'short-cricuits' the distance for diffusion and thereby increases the uptake. Hattingh et al. (1973) found that VA mycorrhizal fungus hyphae could intercept labelled P placed 27 cm from a mycorrhizal root, whereas it remained unavailable to non-mycorrhizal roots. Similarly, when onion roots were prevented from entering the soil zone in which ^{32}P had been placed, Rhodes and Gerdemann (1975) observed that only mycorrhizal plants contained radioactivity. Owusu-Bennoah and Wild (1980) showed that the radius of the depletion zone for P around mycorrhizal onion roots was twice that for non-mycorrhizal roots. Calculations of Gerdemann (1968) estimated that mycorrhizae would increase P uptake 60-fold when diffusion limits the uptake, whereas the increase would only be 10-fold when diffusion is not limiting uptake.

It has been observed that greater responses to mycorrhizal infection occurred in coarse-rooted plant species than in fine-rooted species (Baylis, 1970; Crush, 1973; Hall, 1977), in high-P-adsorbing soil than in low-P-adsorbing soil (Sainz and Arines, 1988a; Yost and Fox, 1979) and in soils than in solution cultures (Howeler et al., 1982). These observations provide further evidence that mycorrhizal infection increases P uptake by decreasing the distance that phosphate ions must diffuse to plant roots.

Absorption surface

The increase in absorption of P by mycorrhizal plants has been attributed to increases in surface area for absorption (Abbott and Robson, 1977; Sanders and Tinker, 1973). The diameter of root hairs is commonly larger than 10 μm (Barley, 1970) compared to 2–4 μm diameter of hyphae of mycorrhizal fungi. The fineness of hyphae has two-fold advantages. Firstly, it increases the surface area of hyphae for greater absorption of nutrients. Secondly, it enables the entry of hyphae into pores in soils and organic matter that cannot be entered by root hairs and thereby increases the area of exploration (Bjorkmann, 1949). However, the generally noticed lower root:shoot ratio for mycorrhizal plants than for non-mycorrhizal plants cannot be related to the increases in uptake of P by mycorrhizal plants being due to increases in the total surface area of mycorrhizal roots (Hayman and Mosse, 1972).

Movement into mycorrhizal hyphae

It has often been observed that mycorrhizal roots on a unit-weight basis absorbed much higher amounts of P than did non-mycorrhizal plants both in solution cultures (Cress et al., 1979) and in soils (Bolan et al., 1987). This suggests that mycorrhizal fungus hyphae have higher affinity for phosphate ions and lower threshold concentration for absorption than do plant roots.

Affinity

Cress et al. (1979) observed that at a concentration in solution of 1 μM P, mycorrhizal roots absorbed almost twice as fast as did non-mycorrhizal plants. They suggested that the increasing number of absorption sites contributed by the hyphal surface area did not appear to be a major factor for increasing absorption. Consequently, the increase in absorption rate was due primarily to an increase in the affinity for absorption. Similarly Howeler et al. (1982) suggested that the increase in P uptake by cassava plants inoculated with a fungus in flowing-solution culture where diffusion was not limiting uptake, might be due to higher affinity for phosphate in mycorrhizal roots than in non-mycorrhizal roots.

Threshold concentration

It has been observed that plant species differ in the minimum concentration of P they can induce at the surface of their roots; that is, the threshold concentration below which there is little net absorption of P varies between plant species (Barber, 1980). However, differences in threshold concentration between mycorrhizal and non-mycorrhizal plants have not yet been experimentally observed.

Mosse et al. (1973) observed that in some soils only mycorrhizal plants could take up ^{32}P labelled phosphorus. Non-mycorrhizal plants could take up P only when the concentration of P in soil solution was increased. They suggested that mycorrhizal roots have a lower threshold concentration for absorption than non-mycorrhizal roots. Howeler et al. (1982) recently observed that inoculation of cassava plants with a mycorrhizal fungus responded to low levels of applied P and thereby overcame the sigmoidal response obtained for non-mycorrhizal plants. They attributed this to the lower threshold concentration for absorption from soil solution by mycorrhizal plants.

Bolan et al. (1983) observed that there was often a clearly marked threshold level of P application below which the plants took up little P and grew poorly. This threshold effect led to a sigmoidal response curve which occurred when non-mycorrhizal plants were grown in soils with high P sorption capacities such as sub-soils or iron hydroxide-amended soils. Inoculation with a VA mycorrhizal fungi eliminated the threshold, even when large amounts of iron hydroxides were present.

Sainz and Arines (1988a) observed that in a high P-fixing acid soil non-mycorrhizal red clover plants did not reach a measurable yield resulting in sigmoidal response when small amounts of P were added. However, mycorrhizal plants produced 4 times higher yields than non-mycorrhizal plants at these levels of P and attained maximum yields at lower concentration of P in soil solution (14 μg P mL^{-1}) than did non-mycorrhizal plants (25 μg P mL^{-1}). Lower threshold concentration for absorption of P in mycorrhizal plants could also result from the exploration of a larger soil volume.

Modification of root environment

Modification of root environment (rhizosphere) by mycorrhizal fungi could be brought about by active (direct means) or passive (indirect means) mechanisms. Although the effect of rhizosphere modifications on P uptake by plant species has been examined extensively (Gardner et al., 1983; Hoffman et al., 1989; Deist et al., 1971), the effect of mycorrhizal fungi on the rhizosphere has received less attention.

Direct modification

Solubilization of mineral phosphates by ectomycorrhizal fungi has been shown in growth media (Bowen and Theodorou, 1973; Rosendhal, 1942). This may partly be due to high acid production in the presence of readily available carbohydrates in the media. Routein and Dawson (1943) proposed that exudation of hydrogen ions, chelating compounds or phosphatase by ectomycorrhizal fungi could have solubilizing effects on poorly soluble phosphates. Similarly Allen et al. (1981) suggested that an increase in uptake of P by ectomycorrhizal plants from calcium phytates was due to increased phosphatase activity. However, calcium phytates can easily be mineralized by other microorganisms.

Harley (1989) suggested that production of phosphatases by ectomycorrhizal fungi is important in the solubilization of organic phytates, which constitute a large fraction of total phosphate in humic soils. These enzymes are many times more active than those on non-mycorrhizal roots (Barlett and Lewis, 1973; Mitchell and Read, 1981; Williamson and Alexander, 1975). Similarly, ectomycorrhizae have been shown to produce large amounts of calcium oxalate (Cromack et al., 1973; Lapeyrie et al., 1987; Lapeyrie, 1988; Malajczuk and Cromack, 1982) which may be involved in the chelation of Fe and Al and thereby release P for plant uptake (Graustein et al., 1977; Treeby et al., 1989).

There is little experimental evidence for direct chemical modification of P availability by endomycorrhizal plants (Abbott and Robson, 1982; Gianinazzi-Pearson and Gianinazzi, 1978). Parfitt (1979) suggested that the increased uptake of P from goethite – phosphate complexes by mycorrhizal plants might be due to increased production of citrate and other organic compounds. Similarly, Jayachandran et al. (1989) have observed that in the presence of synthetic chelates (EDDHA) mycorrhizae caused greater uptake of P than in the absence of these chelates, whereas non-mycorrhizal plants were unable to take advantage of the P released by chelation. They suggested that siderophore production by mycorrhizal fungi or other soil microbes could significantly increase P availability in low-pH soils and that this is a feasible mechanism by which mycorrhizal plants could acquire P sources unavailable to non-mycorrhizal plants.

Indirect modification

The relative abilities of mycorrhizal and non-mycorrhizal plants to absorb P from a soil solution can have different effects on the equilibrium of P in the soil. If the mycorrhizal roots can deplete the concentration of P in soil solution faster or to a lower concentration than can non-mycorrhizal roots, there would be greater desorption of adsorbed phosphate into soil solution (Nye, 1977; Nye and Tinker, 1977). Hayman and Mosse (1972) suggested that a possible explanation for the increase in uptake of P by mycorrhizal plants from poorly soluble phosphate was that mycorrhizal roots had a larger area of close contact with surfaces where phosphate ions were dissociating chemically. If these ions were taken up more effectively by external hyphae, more ions would dissociate chemically to restore the equilibrium. However, there is no experimental evidence for this effect of endomycorrhizae in increasing the availability of P to plants.

Accumulation of calcium near a root zone will depress the concentration of P in soil solution near the root surface and presumably reduce uptake. Barrow (1978) suggested that one of the beneficial effects of mycorrhizae in some soils is that they permit P to be taken up from outside this zone of calcium accumulation. Increased uptake of P from rock phosphate by some plant species have been attributed to their increased abilities to utilize calcium from rock phosphates (Deist et al., 1971). Similarly increased uptake of calcium by mycorrhizal plants (Ross, 1971; Ross and Harper, 1970) may be a possible reason for increase in P uptake from poorly soluble calcium phosphate by mycorrhizal plants.

Differences between mycorrhizal and non-mycorrhizal plants in the absorption of anions and cations (Buwalda et al., 1983) may lead to differences in rhizosphere pH. Such changes in rhizosphere pH may change the availability of adsorbed P to plants (Hedley et al., 1982b). It has been observed that mycorrhizal plants utilize NH_4^+–N more efficiently than non-mycorrhizal plants (Smith et al., 1985). Absorption and assimilation of ammonium by extramatrical hyphae of mycorrhizae would have further consequences in the rhizosphere. It seems probable that H^+ extrusion, which is an inevitable consequence of ammonium assimilation in cells (Bolan et al., 1989; Raven and Smith, 1976) would occur from the hyphae as well as from the roots (Raven et al., 1978). This could reduce the pH around an infected root and thereby affect the availability of slowly soluble P sources such as rock phosphates.

It has been observed that the colonization of plant roots with mycorrhizal fungi has both synergistic and antagonistic effects on the rhizosphere microflora (Ames et al., 1984; 1987; Meyer and Linderman, 1986). Consequently the changes in rhizosphere microflora indirectly affect the availability of both organic and inorganic P sources to plants (Azcon et al., 1976; Hetrick et al., 1988).

Storage of absorbed phosphorus

Mycorrhizal hyphae can store larger amounts of absorbed P than plant roots, thus facilitating the continued movement of P into the hyphae. Inorganic phosphate absorbed by hyphae is stored in three forms: soluble orthophosphate (Harley and Loughman, 1963); soluble polyphosphate (Loughman and Ratcliff, 1984; Martin et al., 1983); and polyphosphate granules (Chilvers and Harley 1980; White and Brown, 1979). In addition to storage in these three forms, there is a continued movement of phosphate during absorption into the host tissue which involves 10% of that being absorbed (Strullu et al., 1986). The bulk of the phosphate is stored as polyphosphates, mainly in granular form (up to 40% of total P). Phosphate in solid form, and located within the hyphal vacuoles, is eminently suited to fulfil the role of a storage reserve in an osmotically inactive form. As pointed out by Strullu et al. (1981; 1982) vacuolar granules containing phosphate and Ca occur in both ectomycorrhizae and endomycorrhizae. Polyphosphates are synthesised by an inducible polyphosphate kinase.

Evidence for the production of polyphosphate was obtained from physiological studies. For example, phosphate uptake is frequently related to oxygen uptake (Harley, 1981). Since polyphosphate formation depends on an ATP requiring polyphosphate kinase, he attributed the relationship between P uptake and oxygen uptake to oxidative phosphorylation. Similarly, Strullu et al. (1986) observed that divalent cations increased the rate of uptake of P. This has been attributed to the formation of polyphosphate resulting in a decrease in the solution concentration of P rather than to a cation effect on the electrochemical properties of the cell wall. Recently, direct evidence for the accumulation of polyphosphate has been obtained from cytochemical studies involving electron microscope, electron microprobe analysis using wavelength dispersion and nuclear magnetic resonance and chemical extraction studies (Harley, 1989).

Transfer of phosphorus to roots

Woolhouse (1975) summarized the transfer of inorganic P between the mycorrhizal fungus and the host plant into three steps: 1. active transport into fungus outside the root; 2. passive transport from fungus at the fungus-root interface; and 3. active transport into root. In contrast to Pi, the transfer of cations such as Zn involves reverse order of active and passive steps, i.e. passive uptake into the fungus from the soil solution, active extrusion and passive uptake into the host at the interface (Smith and Gianinazzi, 1988).

The increase in P uptake by mycorrhizal plants can also be explained in terms of the rate of transfer of P between mycorrhizal fungus hyphae and plant root hairs. The concentration of inorganic P inside the hyphae is approximately 1000 times higher than that in soil solution (Gianinazzi-Pearson and Gianinazzi, 1986), so P must be absorbed actively against an electrochemical potential. The difference in concentration of P between the fungus and the host determines the direction and rate of transport. Translocation of P within the hyphae occurs passively down a concentration gradient between the P source in the external hyphae and a sink in the root. Cytoplasmic streaming is involved in the movement of P within the hyphae (Harley and Smith, 1983). A high concentration of P in the fungus is maintained by the hydrolysis of polyphosphate. Polyphosphate is broken down by polyphosphatases or by reversal of polyphosphate kinase (Capaccio and Callow, 1982; Cox et al., 1980). Recently, Smith and Gianinazzi-Pearson (1988) have proposed that bidirectional transfer of Pi and carbohydrates occurs between the root and the hyphae at the fungus-root interface which involves both passive and active transfer processes.

Utilization of phosphorus within plants

Bowen (1973) suggested that, although increased uptake may be a major part of nutrient response in mycorrhizal association, it is not the only response, i.e. it is possible that a mycorrhizal plant may use its nutrients more efficiently than a non-mycorrhizal plant. The only evidence for this effect is that of Lambert et al. (1979) who noticed that one maize line grew better when infected with a mycorrhizal fungus and produced more dry weight at any concentration of P in plant tissue than did non-mycorrhizal plants. Even this observation cannot be taken as evidence for increased utilization of P within mycorrhizal plants because enhanced uptake of other nutrients by mycorrhizal plants may cause a decrease in P concentration due to internal dilution.

In a physiological sense, utilization of a nutrient may be expressed in terms of unit dry matter per unit nutrient in the dry weight (Marschner, 1986). It has been generally observed by many workers that mycorrhizal plants produce less dry weight at a given P concentration in shoots than non-mycorrhizal plants when soluble phosphates have been added (Abbott and Robson, 1977; Howeler et al., 1982; Paiurunan et al., 1980; Stribley et al., 1980). These findings have led to the conclusion that mycorrhizal plants may use more carbon for purposes other than growth of photosynthate tissue. Stribley et al. (1980) suggested that weight loss in mycorrhizal plants was associated with the drain of energy by the fungus. However, lower dry weight of mycorrhizal plants than non-mycorrhizal plants per unit concentration of P in plant tissue may also result from the luxury consumption of P due to faster supply of P to mycorrhizal plants than to the non-mycorrhizal plants. When the rate of growth is slower than the rate of supply of phosphorus, accumulation of P may occur in the plant tissue.

Sources of phosphorus for mycorrhizal and non-mycorrhizal plants

Attempts have been made to identify the 'sources' of soil P from which mycorrhizal and non-mycorrhizal plants obtain their P requirements. Three approaches have been used to identify the sources of soil P for mycorrhizal and non-mycorrhizal plants. These include: (1) use of radioactive tracers; (2) comparison of different phosphate fertilizers; and (3) fractionation of soil phosphorus. These three approaches are discussed in detail.

Use of radioactive tracers

Radioactive P (^{32}P) has been used to differentiate the sources of soil P between mycorrhizal and non-mycorrhizal plants. This involves labelling the soil with ^{32}P and then comparing the specific activity of P absorbed by mycorrhizal and non-mycorrhizal plants. A lower value for the specific activity of P in mycorrhizal plants would indicate that the mycorrhizal fungus helped plants to take up P that was not labelled by the added ^{32}P. It is assumed that in short-term incubation, ^{32}P exchanges only with the 'labile' fraction of soil P. In most of such studies similar specific activities have been observed for both mycorrhizal and non-mycorrhizal plants (Table 1).

The only conclusion that can be drawn from these observations is that both mycorrhizal and non-mycorrhizal plants absorb similarly labelled P (Bolan et al., 1984; Tinker, 1975) from soil. However, such results have led to further conclusions such as that mycorrhizal and non-mycorrhizal plants obtain their P requirements from the same 'sources' (Hayman and Mosse, 1972), 'fractions' (Mosse et al., 1973), 'pools' (Owusu Bennoah and Wild, 1980), or 'forms' (Powell, 1975) of P from the soil. Such conclusions are based on the assumption that soil contains different 'forms' of P which differ in their ability to exchange with added ^{32}P. However, there are difficulties in the use of ^{32}P for making such conclusions. Firstly, isotopic exchange is a continuing process (Barrow and Shaw, 1975; Jose and Krishnamoorthy, 1972) and it has been observed that given sufficient time added ^{32}P exchanges with even the 'slowly exchangeable' P (Nye and Foster, 1958). Secondly, Olsen and Watanabe (1970) suggested that there may be P in soil which is accessible to ^{32}P but not to plants and, hence, the use of ^{32}P labelling does not necessarily distinguish between forms of P which differ in their availability to plants. Using ^{32}P, Bolan et al. (1984) have attempted to differentiate between the 'fractions' of soil P taken up by mycorrhizal and non-mycorrhizal plants and those extracted by various chemical extractants. They examined the effect of a mycorrhizal fungus on the uptake of P which has reacted with a soil amended with iron hydroxide ($Fe(OH)_3$) and subsequently labelled with ^{32}P. Mycorrhizal plants took up more P than did non-mycorrhizal plants and addition of $Fe(OH)_3$ had little effect on the amount of P in the shoots. In contrast for non-mycorrhizal plants, adding $Fe(OH)_3$ decreased the amount of P in the shoots. However, the specific activity of P in the mycorrhizal and non-mycorrhizal plants did not differ significantly and there was no effect of adding $Fe(OH)_3$ on the specific activity of P in either mycorrhizal or non-mycorrhizal plants. Similarly, although there

Table 1. Comparisons of specific activities (SA) of phosphorus in mycorrhizal (+M) and non-mycorrhizal (−M) plants grown on soils labelled with radioactive (P^{32}) phosphorus

Host plant	Growth conditions	Observations	Conclusions	Reference
Trifolium subterraneum *Lolium perenne*	4 weeks P incubation with iron oxide amended soil	SA same for +M and −M and for chemical extracts	similarly labelled P	1
Allium cepa	4 weeks P incubation; 8 weeks growth	SA same for +M and −M plants	same sources of P	2
Paspalum notatum *Centrosema pubescens* *Melinus minutiflora*	4 weeks P incubation 8 weeks growth;	for Melinus SA same for +M and −M; for Paspalum, Centrosema −M took up no P	same fractions of P; +M has lower threshold P	3
Allium cepa	P not completely mixed; 3 weeks growth	SA for +M less than −M plants	+M took up more P	4
Allium cepa *Trifolium pratense*	4 weeks P incubation; 6 weeks growth 2 weeks P incubation	SA same for +M and −M plants SA for +M less than −M plants	same pools of p +M solubilized P	5
Agrostis sp.	13 weeks growth; 3 harvests	SA same for +M and −M; SA decreased with time	same pools of P	6
Allium cepa *Trifolium pratense*	4 weeks P incubation; 10 weeks growth	SA same for +M and −M; SA decreased with time	same forms of P	7
Allium cepa	5 weeks growth 4 harvests	SA same for +M and −M; SA decreased with time	similarly labelled P	8

References: 1. Bolan et al. (1984); 2. Hayman and Mosse (1972); 3. Mosse et al. (1973); 4. Owusu-Bennoah and Wild (1979); 5. Owusu-Bennoah and Wild (1980); 6. Pichot and Binh (1976); 7. Powell (1975); 8. Saunders and Tinker (1971).

was a difference in the amount of P extracted by different chemical extractants, the specific activity of P in these extracts remained the same as that of the plants. This suggests that most of the P in soil was uniformly labelled and differences in the availability of soil P between mycorrhizal and non-mycorrhizal plants or between different extractants are not reflected by difference in labelling. It therefore follows that lack of difference in specific activity between mycorrhizal and non-mycorrhizal plants does not eliminate the possibility that mycorrhizal plants can obtain P that is unavailable to non-mycorrhizal plants. Direct evidence for the difference in the source of soil P between mycorrhizal and non-mycorrhizal plants can be obtained by using labelled organic and inorganic P compounds.

Comparison of different phosphate fertilizers

The effectiveness of P fertilizers of different solubilities for the growth and P uptake of mycorrhizal plants relative to non-mycorrhizal plants have been compared (Table 2). The basic assumption is that if mycorrhizal fungi modify the availability of poorly soluble P fertilizers then the effectiveness increases with decreasing solubility of added P. Two kinds of experiments have been conducted to measure the relative effectiveness of different P fertilizers between

Table 2. The effectiveness of different phosphate fertilizers for mycorrhizal plants relative to non-mycorrhizal plants

Plant species	Fertilizers	Solubility[a]	Effectiveness[b]	Reference
Bouteloua	Sodium phosphate	High	1.51 (a)	1
(*Bouteloua gracilis*	Calcium phytate	Low	1.01 (a)	
Lavender (*Lavendula spica*)	Rock phosphate	Low	5.00 (a)	2
Tomato	Dicalcium phosphate	Medium	1.56 (a)	4
(*Lycopersicum*	Tricalcium phosphate	Low	5.38 (a)	
esculentum)	Rock phosphate	Low	1.96 (a)	
Oil palm	Rock phosphate	Low	2.20 (a)	5
(*Elaeis sp.*)	Triple superphosphate	High	1.94 (a)	
Leucaena	Potassium phosphate	High	2.91 (a)	6
(*Leucaena leucocephala*	Rock phosphate	Low	4.00 (a)	
Stylosanthes	Rock phosphate	Low	1.32 (a)	7
(*Stylosanthes guyanensis*	Hyperphosphate	Low	1.69 (a)	
Clover (*Trifolium pratense*)	Rock phosphate	Low	5.00 (a)	8
Centrosema (*Centrosema sp.*)	Rock phosphate	Low	3.01 (a)	8
Stylosanthes (*S. guyanensis*)	Rock phosphate	Low	1.39 (a)	8
Sorghum	Superphosphate	High	1.01 (a)	9
(*Sorghum vulgare*)	Rock phosphate	Low	2.38 (a)	
	Monocalcium phosphate	High	1.03 (a)	9
	Tricalcium phosphate	Low	2.80 (a)	
American Elm (*Ulmus americana*)	Rock phosphate	Low	5.52 (a)	13
Soybean	Monocalcium phosphate	High	1.56 (a)	14
(*Glycine max*)	Aluminium phosphate	Medium	1.78 (a)	
	Iron phosphate	Low	5.35 (a)	
	Rock phosphate	Low	2.11 (a)	
Pueraria	Rock phosphate	Low	1.45 (a)	16
(*Pueraria sp.*)	Rock phosphate	Low	9.95 (a)	
Stylosanthes	Rock phosphate	Low	1.11 (a)	16
(*Stylosanthes sp.*)	Rock phosphate	Low	1.52 (a)	
Sub-clover	Potassium phosphate	High	1.24 (b)	3
(*Trifolium*	Iron phosphate	Medium	1.85 (b)	
subterraneum)	Iron phosphate	Low	5.84 (b)	
Ryegrass	Potassium phosphate	High	1.11 (b)	3
(*Lolium perenne*)	Iron phosphate	Medium	1.19 (b)	
	Iron phosphate	Low	3.43 (b)	
Sub-clover	Superphosphate	High	1.51 (b)	10
(*Trifolium*	Calciphos	Medium	1.49 (b)	
subterraneum)	Rock phosphate	Low	1.45 (b)	

Table 2. Continued

Plant species	Fertilizers	Solubility[a]	Effectiveness[b]	Reference
White clover	Sodium phosphate	High	1.14 (b)	11
(*Trifolium repens*)	Rock phosphate	Low	1.51 (b)	
White clover (*T. repens*)	Rock phosphate	Low	3.75 (b)	12
Ryegrass (*L. perenne*)	Rock phosphate	Low	3.01 (b)	12
Lucerne	Sodium phosphate	High	2.00 (b)	15
(*Medicago sativa*)	Tricalcium phosphate	Low	1.52 (b)	

[a] based on percentage of total fertilizer P soluble in water. High >50%, medium 10–50% and low <10%.

[b] Calculated from the ratio of:
(a) yield of mycorrhizal:non-mycorrhizal plants at a particular level of P;
(b) fertilizer P required for non-mycorrhizal:mycorrhizal plants to produce 50% of maximum yield.

References: 1. Allen et al. (1981); 2. Azcon et al. (1976); 3. Bolan et al. (1987); 4. Daft and Nicolson (1967); 5. Gianinazzi-Pearson and Gianinazzi (1989); 6. Manjunath et al. (1989); 7. Mosse (1977); 8. Mosse et al. (1976); 9. Murdoch et al. (1967); 10. Pairunan et al. (1980); 11. Powell and Daniel (1977); 12. Powell et al. (1980); 13. Rosendahl (1942); 14. Ross and Gilliam (1973); 15. Smith and Daft (1977); 16. Waidyanatha et al. (1979).

mycorrhizal and non-mycorrhizal plants. One involves comparing the yield and P uptake at a particular level of added P and the other involves comparing the amount of P required to produce a certain yield using complete P response curve. In most of the studies in which comparisons have been made at a single level of P application between different P fertilizers, the increase in plant growth due to mycorrhizal infection was found to be larger with poorly soluble P than with soluble P. This led to the conclusion that mycorrhizal plants solubilize the poorly soluble P. However, in these experiments, although the total amount of P added was the same for different fertilizers, the amount of soluble P added varied. It has been consistently shown that the response to mycorrhizal infection depends upon the amount of soluble P added to soil (Stribley et al., 1980), and hence these experiments do not respresent a true comparison of the effectiveness of different fertilizers between mycorrhizal and non-mycorrhizal plants. To overcome this problem, responses to mycorrhizal infection have been compared over a range of P levels between different P fertilizers.

Pairunan et al. (1980) found that although mycorrhizal plants are better than non-mycorrhizal plants in getting P from poorly soluble rock phosphate, the increase in P uptake from rock phosphate was the same as that from soluble P fertilizers. Similarly, Barrow et al. (1977) observed that the increase in the uptake of P by mycorrhizal plants from P that had reacted with soil was the same as that from freshly applied P. These experiments provide no conclusive evidence for the solubilization of insoluble fertilizers by mycorrhizae.

Recently Bolan et al. (1987) compared three P compounds differing in solubility (KH_2PO_4, colloidal iron phosphate and crystalline iron phosphate) as sources of P to mycorrhizal and non-mycorrhizal subterranean clover and ryegrass. For both species the increase in P uptake with mycorrhizal infection was found to vary with source of P. Greatest benefit from mycorrhizal inoculation was obtained with the least soluble source of iron phosphate. The simplest explanation for the increased uptake by the mycorrhizal plants is that the mycorrhizas explored the soil volume more thoroughly and so found more of the point sources of P. Having found the sources it is possible that they also increased the rate of uptake from the sources by increasing the diffusion gradient either by a closer approach to the source or by achieving a low concentration of phosphate at the surface. A further possibility is that mycorrhizal hyphae may be able to chemically modify the availability of iron phosphate by producing organic compounds with chelating properties, such as citrate.

Fractionation of soil phosphorus

Attempts have been made to fractionate soil P before and after growing mycorrhizal and non-mycorrhizal plants and then to compare the changes in different fractions of soil P between these treatments. This should provide information on the availability of different fractions of P for uptake by mycorrhizal and non-mycorrhizal plants (Swaminathan, 1979). However, as indicated earlier, change in one fraction due to plant uptake can alter another fraction which can make it difficult to identify the sources of soil P for plant uptake.

Sainz and Arines (1988b) measured different fractions of inorganic P after growing both mycorrhizal and non-mycorrhizal plants for 6 months. There were differences in the inorganic P fractions between different mycorrhizal species treatments suggesting that species differ in their ability to take up P. However, since the initial amounts of inorganic P fractions are not given, it is not possible to compare the changes in P fractions between mycorrhizal and non-mycorrhizal plants. Recently, they have shown that both mycorrhizal and non-mycorrhizal plants decreased the concentration of inorganic P in soil but did not affect the concentration of organic P and suggested that both mycorrhizal and non-mycorrhizal plants obtained their P requirement from the same source of P in soil (Sainz and Arines, 1988c).

Conclusions

The rate-limiting steps in the uptake of P by plants from soil are: (1) the diffusion of phosphate ions in the soil solution to the plant roots; (2) the concentration of phosphate at the root surface; and (3) the release of phosphate ions from the soil particles. Infection of plant roots with a mycorrhizal fungus could alter any of these rate-limiting steps and increase phosphate uptake by plants (Figure 3).

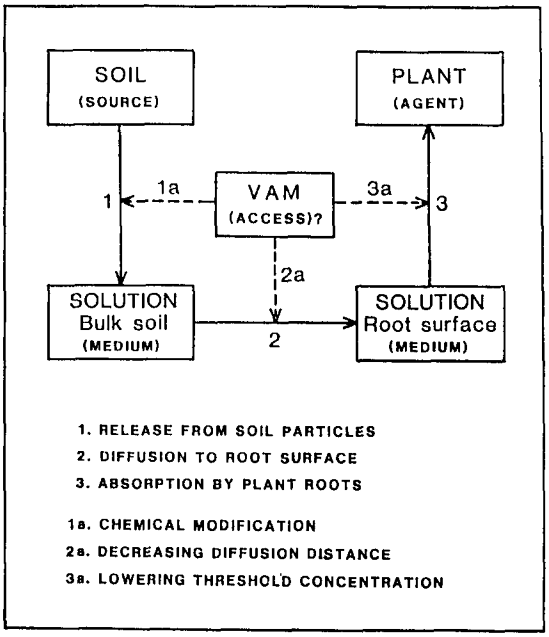

Fig. 3. Rate-limiting steps in the uptake of phosphorus from soil by plants and the effect of vesicular-arbuscular mycorrhizae (VAM) on these rate-limiting steps.

The rate of movement of P to plants is much less compared to the rate of absorption by plant roots, which suggests that the uptake of P is limited by the rate of diffusion of P in soil solution and not by the ability of the roots to absorb from low concentrations in soil solutions. The increase in phosphate uptake by mycorrhizal infection has been generally associated with a decrease in the distance that phosphate ions must diffuse to plant roots. Evidence for this conclusion is many-fold. Firstly, the advantage of mycorrhizal infection has frequently been observed for poorly mobile nutrients such as P and Zn. Secondly, the phosphate depletion zone around mycorrhizal roots is much larger than that around non-mycorrhizal roots. Thirdly, the advantage of mycorrhizal plants in the uptake of phosphate is generally greater for coarse-rooted species with many root hairs. Fourthly, the relative advantage of mycorrhizal plants compared to non-mycorrhizal plants increases with the increasing ability of soil to adsorb phosphate.

There is evidence that plant species differ in their abilities to reduce the concentration of P at the surface of their roots. However, there is no experimental evidence for a difference in threshold concentration of P for absorption between mycorrhizal and non-mycorrhizal plants. The effective conversion of inorganic orthophosphate absorbed by mycorrhizal fungus hyphae to polyphosphate may reduce the efflux of the absorbed phosphate. This may be a possible reason for the lower threshold concentration for absorption by mycorrhizal roots than by non-mycorrhizal roots. The threshold concentration for absorption could be further examined by growing plants in very low, but maintained concentrations of P in solution culture. The low concentration of P could perhaps be achieved by: (a) using ^{32}P-labelled, poorly-soluble phosphate (such as iron phosphate) with different values of solubility products; and (b) adsorbing phosphate onto an iron hydroxide (such as goethite) and placing inside dialysing bags. This approach has been used by Cassman et al. (1979) to examine the phosphate nutrition of rhizobia.

In soils with large capacities to adsorb phosphate, the rate of release of phosphate from soil particles becomes the major limiting step in the supply of P to plants. An increase in the rate of release of phosphate from soil particles by plants may be achieved either by decreasing the concentration of phosphate in soil solution to low values (threshold concentration) or by producing organic compounds (chemical modifications). As discussed earlier, there is no experimental evidence for differences in threshold concentration between mycorrhizal and non-mycorrhizal plants. Production of organic compounds, such as citrate, which can release phosphate from soil particles, has been observed for many plant species. Based on the results from isotopic labelling of soil P and the use of fertilizers differing in their solubilities, chemical modification of rhizosphere has not been favoured as one of the mechanisms for increased uptake of P by mycorrhizal plants. However, recent studies have indicated that these two kinds of approach may not provide unequivocal evidence that both mycorrhizal and non-mycorrhizal plants utilize the same source of P in soils. Direct evidence for chemical solubilization of P by mycorrhizal plants can be obtained by comparing the availability of radioactively labelled inorganic and organic fertilizers between mycorrhizal and non-mycorrhizal plants. Mycorrhizal roots may produce organic compounds such as citrate and oxalate which help in the desorption of adsorbed phosphate or the dissolution of poorly soluble phosphates. Production of these organic compounds by endomycorrhizas and the effect of these compounds on the uptake of P by mycorrhizal plants should be an area of future research.

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