

11

Arbuscular Mycorrhizal Fungi and the Form and Functioning of the Root System

David Atkinson

11.1 Introduction

That micro-organisms such as arbuscular mycorrhizal fungi (AMF) can influence the functioning of the plant root system has been known since mycorrhizas were first identified in the nineteenth century (Frank 1887; Hiltner 1904). Their value in aiding plants in the absorption of phosphorus has often resulted in this being identified as their most important characteristic. Koide (1991) commented “I have assumed that the most important effects on the host plant due to mycorrhizal infection is an increase in phosphorus acquisition” and “much of the variation in response can be attributed to variation in the magnitude of the phosphorous deficit”. He did however also acknowledge “there are ... effects of infection which are apparently not directly related to improved phosphorus nutrition”. Information on the effects of AMF on root system form are of more recent lineage. For many years it was considered that AMF did not affect the development of the root system (Harley and Smith 1983). This assumption is understandable as the modifications of which we are now aware are of a subtle nature (Berta et al. 2002). The types of modification are however of a form usually predicted as important to enhancing a plant’s ability to access sparsely soluble nutrients such as phosphate (Silberbush and Barber 1983). However it is now clearly established that AMF can and do modify root form and that such effects may, under some conditions, be independent of phosphate supply (Atkinson et al. 1994).

For much of the period since their discovery AMF have been viewed as a component in the plants acquisition of resources from the soil. Against this background they have too often been seen as necessary only under conditions where the plants need extra capacity to source such nutrients. On this basis they are commonly seen as “an extra” for the plant, useful under nutrient limiting conditions but unnecessary at other times. However the relation between AMF and plants is an ancient one; AMF were a significant factor in the ability of plants to grow on land. As such the mycorrhizal state should be regarded as normal (Dunsiger et al. 2003). This historical

David Atkinson: SAC, West Mains Road, Edinburgh, EH9 3JG, UK

perspective recognises a key role for AMF in helping to link the performance of a plant to its environment and in regulating plant growth in line with environmental conditions. In this role a major function of AMF becomes the provision of information on its environment to the plant, with this role being as important as that of resource acquisition.

This chapter details the ways in which AMF may influence the form of the plant root system both through effects on root growth, branching and death and how they influence the functioning of the root system both as a means of the acquisition of resources such as nutrients but also as a source of information which causes the plant to modify its growth so as to adapt better to prevailing environmental conditions.

11.2

AMF Infection and Whole Plant Functioning

AMF exert their primary effects on the functioning of the root system but they are of interest because these root system effects modify the ability of the plant or crop as a whole to cope with an environment which is commonly sub-optimal. While effects of AMF on plant growth mediated through improved nutrient supply have been known for many years (Harley and Smith 1983) the significance of infection and its value in a range of practical situations remains a matter for detailed experimentation. Large numbers of papers are published every year on this topic. Although it remains important to identify the effects of AMF on the physiology of individual roots and whole root systems it matters also to explore the limits of such effects at a whole-plant level. These may become manifest either through a whole plant performance which might otherwise only have been achieved by the supply of large amounts of external resources, e.g. fertilisers, pesticides, irrigation, etc. or through a performance which greatly exceeds that able to be achieved by non-mycorrhizal individuals of the same species. Basic growth and development studies thus remain important to help scale the impact of AMF on function. The results of some recent studies are detailed in Table 11.1 as a means of indicating some remaining key practical information gaps. Examples have been selected to show issues in cereals, legumes and perennial species. Together these show refinement in understanding of conditions in which AMF work. Several studies (Galal et al. 2003; Setua 1999) show that AMF can be effective on both growth and production even when P fertilisers are being applied or when the soil P status is significant. The impact of AMF are influenced by a range of environmental characteristics, e.g. light intensity (Zhu and Smith 2001) and CO₂ concentration (Jifon et al. 2002) and nutrition (Melloni et al. 2001; Song et al. 1999). When carbon supply becomes limiting the impact of AMF

Table 11.1. The effect of AMF on nutrition and whole plant performance

Plant species	Experimental conditions	Effects on nutrition and growth	Reference
Wheat	Effects of P levels to 7 mg/kg and rhizobium co-inoculation	Rhizobium increased AMF effect on growth. AMF increased P uptake at highest levels	Galal et al. (2003)
Wheat	Effect of P levels to 100 mg/kg and G intraradices on high/low P seeds	At low light AMF no effect P uptake. High light AMF increased P AMF eliminated high P seed advantage	Zhu and Smith (2001)
Barley	Effect of P levels to 48 mg/kg on soils with salinity to 17 d S m ⁻¹ and G intraradices	Both AMF and P increased growth in saline soils. AMF P, Fe, Zn increased	Mohammad et al. (2003)
Maize	Effect of P levels to 40 mg/kg on acid and alkaline soils and G intradices	Infection varied from 48 to 68% and increased weight but P only on acid soil. Cu, Mn, Zn both soils	Ozcan and Taban (2000)
Bean	Effect of organic and mineral fertiliser, <i>Glomus</i> spp and Rhizobium	Dual inoculation inc AMF infection, yield and weight in control and organic treatment, N and P in all treatments and Mg in organic	Aryal et al. (2003)
Bean	Effect <i>G mosseae</i> and <i>G spurcum</i> on soils (a) PH5, 4 mg P kg ⁻¹ (b) PH7, 8 mg P kg ⁻¹	<i>G mosseae</i> increase growth and P in higher PH soil	Izaguirre-Mayoral et al. (2000)
Chick Pea	Acid soil with soluble P to 50 mg/kg or rock P to 200 mg/kg and <i>G clarum</i>	AMF inoculation doubled infection and increased P, K, Mg and micro-nutrients regardless of P treatment	Alloush et al. (2000)
Casuarina	Effect of range of AM species on soil with 3 kg P ha ⁻¹	AM colonisation varied from 60 to 71%. Growth increased most by <i>G fasciculatum</i> (2×) as was P uptake	Sempavalan et al. (2001)
Eucalyptus	Effects of variation in AM spore numbers and P to 30 ppm	Efficiency of inoculation best at zero P, growth best at medium spore numbers and P. P uptake best high spore numbers	Sastry et al. (2000)
Citrus	Effects CO ₂ levels on high P soil with G intraradices	At ambient CO ₂ AMF reduced growth (-18%). At elevated CO ₂ increased growth (+15%)	Jifon et al. (2002)
Mulberry	Effects of P treatment to 180 kg/ha on alluvial soil with <i>Glomus</i> sp ^s	<i>G mosseae</i> increased growth and P uptake in low P treatment became equal to high P	Setua et al. (1999)

on growth is negative, a point emphasised by Muthukumar and Udaiyan (2000) who found a negative correlation between root carbohydrate and AM infection. However it is also clear that AMF do influence the ability of plants to grow in difficult conditions such as saline soils (Mohammad et al. 2003) and acid soils (Ozcan and Taban 2000) and through mechanisms beyond “just P supply”. The effectiveness of AM is clearly influenced by the fungal partner (Sempavalam et al. 2001), the efficiency of the infection process (Izaguirre-Mayoral et al. 2000) and the impact of other organisms. These whole plant studies confirm that many long standing key issues in relation to the functioning of AMF remain unsolved at a practical level (Koide 1985). The definition of the circumstances under which AMF will have a critical role in growth or survival, their interaction with other micro-organisms, e.g. *Rhizobium* (Galal et al. 2003; Aryal et al. 2003) and the means by which AMF modify a plants interaction with its environment will ultimately influence the need to either add AMF, through inoculation, or to manage the soil so as to promote AMF infection. These issues provide the scale and scope for the subsequent sections of this review.

11.3

AMF and Root Form and Function

The effect of AMF on nutrient supply was reviewed by Koide (1991) who focused on the role of AMF in enhancing phosphorus absorption, especially under conditions in which P supply was limiting, i.e. when potential demand from the plant is likely to be greater than potential soil supply. AMF have the ability to modify both the supply and demand elements of this balance. Most of the research focus to date has related to effects on supply. The ability of AMF to influence both elements of the balance leads to the variation in response illustrated in Table 11.1. AMF can and do increase P accumulation. This may be used for current or future growth. The past and current focus upon P is a consequence of its being a key element needed for plant growth, an element frequently limiting in relation to availability in soils and because of its limited mobility and restricted availability: an aspect where the enhancement of root surface area, which occurs with AMF infection, but which is also aided by microbial products, is likely to have the greatest effect.

The relationship between a plant's ability to absorb an immobile nutrient such as P has been reviewed by Nye and Tinker (1997) and Newman and Andrews (1973) among others. Where soil P availability is low, root length can be a good predictor of P availability to the plant (Silberbush and Barber 1983). In some models root hair length has also been incorporated as a variable (Jungk 1987). P inflow has been shown to be low in species with

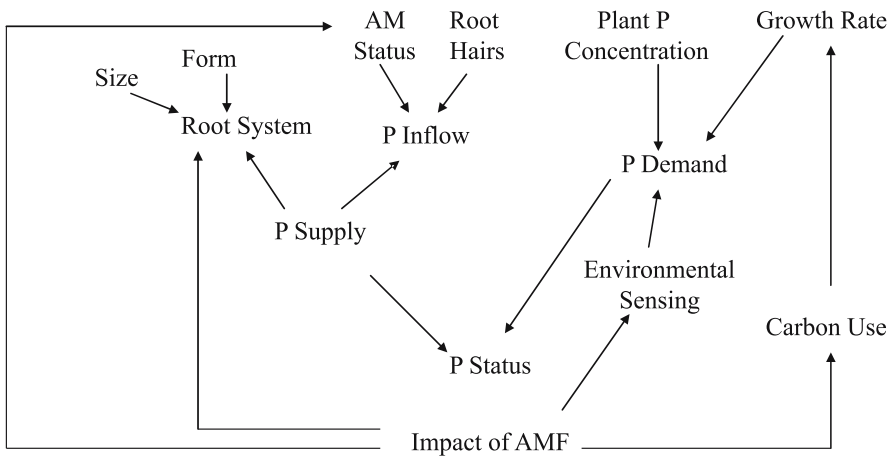


Fig. 11.1. Factors influencing the impact of AMF infection. The P status of the plant is a result of demand and supply. AMF can influence both of these. Modified from Koide (1991)

short root hairs, e.g. onions, intermediate in species with medium (approximately 0.25 mm) root hairs, e.g. tomato and high in species with long (greater than 0.4 mm) root hairs, e.g. rape, ryegrass. Too many appraisals are based on assessments without AMF presence or without consideration of AMF. Common species with short root hairs, e.g. onion are those which are highly mycotrophic while those with long root hairs, especially when associated with high root length density, tend not to be greatly infected with AMF, a factor ignored in much of the earlier literature. As an example of a resource dominated model the relationship between plant P requirement and the potential role of AMF is summarised in Fig. 11.1. AMF impact both the supply and demand sides of the balance. P demand is a function of the addition of new dry matter and the minimum concentration of P within it. AMF need carbon for their growth and maintenance so that under conditions of restricted C supply, e.g. Jifon et al. (2002), AMF reduce plant growth. They may also, through their role in sensing the environment, reduce growth so that growth is better related to environmental capacity (Dunsiger et al. 2003). The role of AMF in influencing supply has been more extensively studied (Aikil and Ruotsalainen 2002). AMF can influence the size of the root system, the form or architecture of the root system, the survival of individual roots, the ability of a length of root to absorb P from the soil and the availability of P from the soil for absorption. Many of these interact; e.g. to interpret the significance of AMF effects on root methodology it is helpful to review the variables which can be used to describe a plant root system as these infer related groups of properties (Atkinson 1992). Root systems can be described in terms of:

1. Quantitative parameters, e.g. length
2. Structural elements, the way individual roots are connected, e.g. morphology or architecture
3. Temporal aspects, when growth and death occur

These aspects are now reviewed against their contribution to resource acquisition.

11.3.1 Root System Size

As the development and maintenance of AMF use resources which might otherwise have been devoted to root system development, it is inevitable that they interact. Azcon and Ocampo (1981) found that the response to AMF infection was inversely related to root system size in wheat. Similarly in tomato Bryla and Kordis (1990) found that root density was negatively related to AMF infection. Fitter (1977) reported decreases in root length as a consequence of AMF infection. It has been suggested that some of these effects may be a consequence of an increased P status as this is also known to reduce root weight (Schjorring and Jensen 1984). In contrast Ortas et al. (2002) found that *G. clarum* infection increased root length in citrus while Bagayoko et al. (2000) found that P and AMF together increased root growth. A number of studies, e.g. Hooker et al. (1992) and Atkinson et al. (2003) have found AMF to have no significant effect on root weight or length. Effects of AMF on both root mass and length and their functional significance thus vary with, at times, other factors having a greater effect than AMF. On the basis that the natural status for most plant species is to be infected with AMF, just as most plants have chloroplasts, it is unsurprising that there will be situations where AMF are associated with both increases and decreases in root system size and others where treatments have no influence. A focus on AMF as a “treatment” is the product of a reductionist approach (Read 2002) rather than one which aims to place AMF in a wider ecological contest.

11.3.2 Root and Root System Morphology

Awareness that AMF can influence the form and architecture of the root system is a relatively recent discovery. That ectomycorrhizas influence root system form has long been known, with the shorter root tips visually obvious (Harley and Smith 1983). While the modifications to the root system

caused by AMF can be extensive they cannot be quantified without careful analysis. With AMF frequently the root system is more highly branched, i.e. a greater number of smaller diameter high order roots. Demonstrating conclusive effects requires the comparison of infected and non-infected plants and the use of image analysis techniques (Hooker et al. 1992, 1998; Hooker and Atkinson 1992). The subject has been reviewed by Atkinson et al. (1994) and Berta et al. (2002).

Previous reviews have emphasised the importance of effects on root system morphology for both the ability of the root system to function in absorption and the energy needed to construct a root system. Berta et al. (1993) found, in *Allium porrum*, that infection with *Glomus* E3 led to a root system with more shorter, more branched adventitious roots of greater diameter but with a relatively unchanged overall pattern. A more branched root system can lead to a range of arrangements in the soil. A herring-bone form, with effectively many branches arising from a central axis, can be effective in soil exploration but has a significant cost in terms of carbon resources (Berta et al. 1993). Mycorrhizal plants, e.g. *Vitis vinifera* (Schellenbaum et al. 1991) and *Platanus acerifolia* (Tisserant et al. 1991) develop a resource efficient random rooting pattern. It seems clear that, while the scope to vary branching within an individual species is not unlimited, the branching pattern actually produced can be influenced by a range of factors of which AMF may well be one of the more significant. Berta et al. (1993) suggested that the scope for modification was greater in dicot species than in grasses. A much branched root system can be both a response to a limited soil nutrient supply and a strategy for maximising infection. The relative importance of this will vary between situations. Schellenbaum et al. (1991) suggested the differences in branching between control and AMF infected roots increased with increasing root order. The number of laterals developed per unit root length were increased by 125%, 185% and 230% for increasing root orders. Hooker et al. (1992) reported a similar effect with the branching of secondary roots increased by 81% and that of tertiary roots by 616% in poplar. Here the level of AMF infection seemed to influence branching. Twenty-three percent infection by *Scutellespora calospora* resulted in a 40% increase in lateral production while a 52% infection by *G. caledonium* gave a 60% increase in branching. The effect of AMF infection with *Glomus* E3 on poplar is shown in Table 11.2 using data from Hooker et al. (1992). This study used a soil whose fertility was such that neither AMF or nutrient additions influenced total growth. While the addition of phosphorous had a small effect on branching, an increase of 32% compared to the control for the branching of secondary roots, this effect was smaller than that induced by AMF, 81%, and less pronounced in respect of the branching of tertiary or quaternary roots. Forbes et al. (1996) assessed the effect of AMF infection on *Plantago lanceolata*. In this species AMF re-

Table 11.2. The effect of AMF (*Glomus E3*) or a high phosphate treatment on the number of lateral roots produced from the various root orders and the contribution to the length of the root system of those laterals. Data from Hooker et al. (1992)

Treatment	Root order							
	1°		2°		3°		4°	
	No	(%)	No	(%)	No	(%)	No	(%)
Control	342	(59)	356	(38)	18	(3)	0	(0)
<i>Glomus E3</i>	336	(21)	646	(58)	129	(18)	21	(2)
High Nutrient	315	(35)	469	(62)	32	(3)	0	(0)
LSD	197	(15)	178	(14)	70	(9)	30	(2)

duced branching, at 21 °C by around 15%. Temperature also changed both branching and infection. Infection was 52% at 15 °C but only 36% at 27 °C. Higher root orders were more heavily colonised. At 27 °C colonisation increased from < 30% in secondary roots to 50% in quaternary roots. The combination of these effects meant that while at 15 °C > 50% of total root length was colonised, at 21 and 27 °C < 40% was colonised (Atkinson et al. 2003).

The effect of AMF on activity in root apices has been discussed by Berta et al. (2000, 2002). When colonised by AMF adventitious roots showed determinant growth. All root apices show a reduction in root diameter, root cap size, the distance between initials and the differentiated zone and in mitotic activity. In AMF colonised plants the percentage of active apices decreased faster than in non-infected plants. In tomato (Berta et al. 2000) the nuclei of AMF infected cortex cells were large with more de-condensed chromatin. Ploidy varied between the nuclei of AM and control roots with nuclear polyploidisation and AMF colonisation strongly correlated. Polyploidy is usually associated with high metabolic activity.

Given the variation which occurs in the magnitude and type of AMF effects on morphology a range of mechanisms are possible. Currently there is no clear consensus as to the mechanism for the effects. Traditionally it had been suggested that the primary mechanism was to improve phosphorus nutrition (Amijee et al. 1989). However the data of Hooker et al. (1992) where the effects of AMF infection were compared directly with those of a series of high P treatments (Table 11.2) suggest that factors beyond improved P nutrition may be important and that the effects of AMF cannot be explained solely in terms of P effects.

AMF induced modifications to root system development and architecture may modify plant function. That the AMF infected root system is commonly made up of more smaller diameter high order roots is likely to impact on root longevity and turnover. This is reviewed in the next section. This

form of root system is appropriate to the exploitation of scarce resources especially where the availability of resources is transient. High order roots which are more heavily colonised allow the fungi to be placed close to nutrient sources whilst the shorter life of high order roots reduces the carbon maintenance expenditure on roots in areas where nutrients have been depleted (Eissenstat et al. 2000): roots of small diameter have shorter lives.

A major area where the effects of AMF infection on root system form may be important is in relation to the impact of plant pathogens. AMF have been shown to reduce the severity of infection by pathogens with some consequences for changes in the root system (Hooker et al. 1994). Salami (1999) found that inoculation with *G. etunicatum* reduced the impact of *Phytophthora infestans*. The effect was greatest when AMF infection occurred in advance of, or simultaneously with, the impact of the pathogen. Similarly Elwan et al. (2002) found that AMF could reduce the impact of *Rhizoctonia* on cotton and Yao et al. (2002) found that *G. etunicatum* reduced the impact of *Rhizoctonia* on potato by 77% so increasing yield by 140%. Karagiannidis et al. (2002) found that *G. mosseae* eliminated the pathogenic effects of verticillium wilt in both egg plant and tomato.

Most of the AMF pathogen interactions studied have been in relation to *Phytophthora*. As *Phytophthora* usually infects roots behind the tip the increased branching produced by AMF infection might be assumed to increase susceptibility. Norman et al. (1996) tested this. In non-mycorrhizal plants increased branching does increase infection. In AMF infected plants increased branching reduced infection by *Phytophthora* as a result of a modified pattern of exudate production. The effect of AMF is influenced by both time and the extent of colonisation. Henry and Kosola (1999) found the extent of colonisation in one-week-old roots increased with the age of a plant in the grass *Andropogon gerardii*. Colonisation was not generally affected by soil P status although in low P status soils it increased with increasing root age. Atkinson et al. (2003) found that environmental factors such as temperature influence the percent colonisation and the length of individual tertiary roots.

A key need in studies of the effects of AMF on root morphology has been to distinguish effects due to plant size from those due to AMF. Bressan and Vasconcellos (2002) assessed the effect of inoculation with *G. etunicatum* and *G. clarum* and P levels varying from 0 to 200 mg/kg on maize. They found AMF increased root weight, the number of first and second order laterals and P concentration but decreased root-shoot ratio and the number of root hairs. Root weight was significantly correlated with root colonisation. High P levels reduced AMF colonisation. Fusconi et al. (2001) assessed the effect of AMF on the root meristem of *Allium porrum*. They found that the effects of AMF could appear similar to those of improved P nutrition. However at a detailed level AMF blocked meristem activity leading to more

Table 11.3. The effect of AMF infection on the components of root system development (derived from Atkinson et al. 1994)

Process	Effect of AMF	Consequence for root system
Mitotic cycle in root apice cells	Lengthened especially interphase: metaphase increases with increasing colonisation	Modified architecture
Meristematic activity	Blocked by colonisation	Modified root system form
All death in apical meristem	No of abscised apices increased	Short roots
Variation in size of root apices	Diameter and base of meristem and meristem length increased	Larger root apices and thicker roots
Prim ordeal formation	Increased	More numerous and more branched roots. Shorter lived roots

inactive apices and meristems in metaphase. A high supply of P lengthen the mitotic cycle but without blocking the apices, thus resulting in slowed but continued root growth. The effects of AMF on root morphology are summarised in Table 11.3.

11.3.3 Root Longevity

Several recent studies have assessed the effect of AMF on root longevity. Until recently it was assumed that most of the root system survived at least as long as the leaves. Black et al. (1998), Atkinson and Watson (2000) and Watson et al. (2000) showed that, for tree crops and a range of agricultural species, the longevity of many roots could be measured in days rather than weeks. In pea and oats less than 50% of roots survive over seven days. In *Lolium perenne* only 15% of new roots survive over 21 days in warm soils. Soil temperature markedly influences survival (Forbes et al. 1997). Effects of AMF thus needs to be set in the context of a range of other factors which can change root longevity in a major way and the impact of environmental variables such as temperature.

Hooker et al. (1992, 1995) assessed the effect of AMF infection on poplar. They found that infected roots lived a shorter period of time than did control roots. They attributed this to the more pronounced root branching in mycorrhizal poplar. In contrast, with clover, Atkinson et al. (2003) found longevity to be increased in mycorrhizal roots (Fig. 11.2). In *Lolium perenne* AMF had no effect on survival which was lower than that in clover, 40% at 20 days compared to 80% (Fig. 11.3).

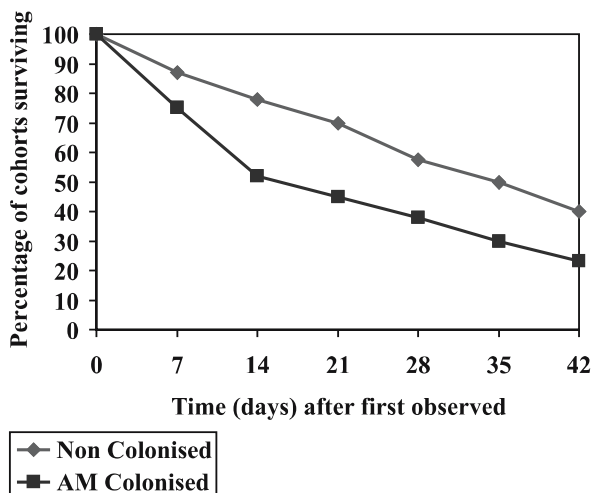


Fig. 11.2. The impact of AMF colonisation on root survival in *Trifolium repens* AM – colonised. Reproduced from Atkinson et al. (2003)

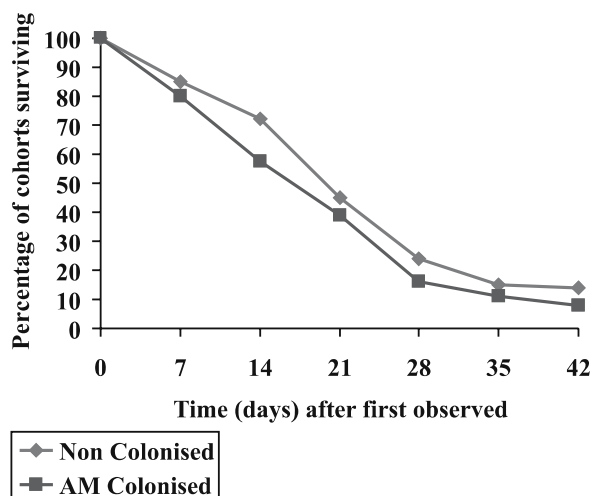


Fig. 11.3. The impact of AMF colonisation on root survival in *Lolium perenne*. Reproduced from Atkinson et al. (2003)

Infection with AMF can thus increase, decrease or have no influence on root longevity. While plant species is important the extent of root colonisation will also be a significant factor (Table 11.2). Different species are naturally colonised to different extents. Grass species tend to be infected to only a limited extent. Here AMF had little effect on longevity. Clover is naturally well infected and AMF increased longevity. Root morphology, as

discussed above, is influenced by infection to a varying degree in general with increased infection leading to greater branching. Fitter (1985) found that AMF infection reduced branching in clover. In contrast, in poplar where root longevity was reduced (Hooker et al. 1995), AMF resulted in a major increase in root branching (Hooker et al. 1992). Whether AMF influence or decrease root longevity may well be linked to its effect on the degree of branching. Where branching is increased, as in poplar, then mean root longevity falls; where branching is reduced as in clover then mean root longevity increases. This is clearly a sector where more research would be helpful.

11.4 Infection and Root Function

It is clear that the degree of root infection modifies root morphology, survival and functioning, for example, Isobe and Tsuboki (1998). The impact of level of infection and the distribution of infection in different parts of the root system are not however well understood. This and the functioning of the individual hyphae are considered here.

11.4.1 Effects on Infection

Citrus seedlings plants grown with high P (2 mmol/l) showed reduced colonisation, an effect countered if the treatment was applied in an elevated (2×) CO₂ regime. High P, high CO₂ and *G. intraradices* all increased growth but decreased root to shoot ratio. *G. intraradices* reduced starch concentrations in structural roots especially under low P supply (Syvertsen and Graham 1999). Light intensity also influences the contribution of AMF. Olsen et al. (1999) found that when phosphate was more limiting than carbon, then AMF improved crop growth, but not when the reverse occurred. While an increased level of infection is usually associated with an increased growth effect the responsiveness of plants to AMF infection is not always correlated with the levels of infection found (Kaeppeler et al. 2000). Dunsiger (1999) studied the relationship between the length of extra-matrical hyphae in the soil and mycorrhizal colonisation, root and shoot weight. Hyphal length and both percentage infection and root weight were poorly correlated. The relationship with shoot weight was better. The impact of percentage infection may be modified by the functioning of individual hyphae both within the plant and the extra-matrical hyphae.

11.4.2

Hyphae Functioning

Fungal species differ in their ability to access soil P and to transfer it to the plant. Solaiman and Abbott (2003) assessed the effectiveness of AMF in the under-story species of a Jarrah forest. The proportion of root length colonised was positively related to plant biomass in *Phyllanthus colycinus* but not in *Trifolium subterraneum*. In *Phyllanthus colycinus* hyphae accessed more P 2 cm from the root than from greater distances. Drew et al. (2003) assessed the impact of soil structure on the functioning of the extra-matricular hyphae. They found that *G. intraradices* used distant P more than did *G. mosseae* and that P acquisition was not related to the amount of external hyphae. For both fungi more hyphae were produced in a soil medium compared to quartz sand with pore size having a greater impact on *G. intraradices*. The absence of a quantitative link between the level of infection and nutrient uptake was also found by Rubio et al. (2002) in a study using wheat and *G. etunicatum*. Nadian et al. (1998) assessed the impact of soil compaction on AMF infection and functioning. They found that different AMF species were effected by different levels of soil compaction. Compaction to a bulk density of 1.6 mg/m³ had no effect on colonisation percentage but reduced the total length of root colonised.

A factor which has received relatively little attention is the longevity of the extra-matricular hyphae in soil. Using a Rhizotron method Atkinson and Watson (2000) assessed hyphal longevity in a mixed plant community. They found that 60% of the external hyphae visible turned-over in 7 days and that by 21 days less than 10% of hyphae remained. Hyphae appear to be more ephemeral than roots.

11.5

AMF and Resource Acquisition

In the proceeding sections I have discussed the practical impact of AMF on the growth of a range of crop types and the effect on AMF on root system development and the survival of individual roots. Unequivocally an important factor for AMF is that they facilitate the plant gaining resources which would not otherwise be available. This has most substantially been assessed for phosphorus. As this has been substantially reviewed elsewhere, e.g. Harley and Smith (1983), Smith and Smith (1990), Koide (1991) and van der Heijden and Sanders (2002), it is unnecessary to review it again in any detail. A review of AMF effects on functioning, however, would be incomplete without some mention of recent studies on the impact of AMF on the uptake of P. This is important to the supply-side aspects identified in Fig. 11.1.

11.5.1 Effects on Nutrient Uptake from the Soil

Tibbett (2000) suggested that the relatively slow rate of root proliferation within a nutrient rich patch of soil (Hodge et al. 1998) implied that the primary mechanism for acquiring nutrients from such patches was for the plant roots to support a network of mycorrhizal hyphae. The structure of the vegetative mycelia allows rapid colonisation of the area (Boddy 1993). Simard et al. (2002) reviewed literature on the length of mycorrhizal hyphae which could be found in soil and the relative surface they provided for uptake, compared to that provided by a root. They identified a range of hyphal lengths from $1\ 300\ \text{m m}^{-1}$ (Jones et al. 1990) to $8,000\ \text{mm}^{-1}$ (Read and Boyd 1986) and concluded that mycorrhizae could increase the effective root surface area 60-fold. Although these estimates were for ectomycorrhizal fungi, effects of AMF are also substantial (Tisdall and Oades 1979).

Hawkes and Casper (2002) found that shrubs with AMF absorbed more rubidium than non-infected plants but without a change in the volume of soil exploited. This suggested more intensive soil exploitation. Hodge et al. (2000) found that AMF enhanced root development especially within organic patches but did not significantly increase N uptake. P concentration in the plant was increased.

P uptake is affected by a range of factors, e.g. root age, soil temperature and so effects of AMF must be seen in a wider context. Staddon et al. (1999) studied the interaction between CO_2 availability from the atmosphere and AMF infection on P inflow. They found that a range of herbaceous species all responded similarly to elevated ($610\ \mu\text{Mol Mol}^{-1}$) CO_2 . This did not change the percentage root length colonised by AMF but increased the total colonised length, because root length was increased. P inflow was stimulated in total but not on a root length basis. A recent study of the effect of root hairs on the functioning of barley also emphasises the importance of “root” surface area in general, for phosphorus uptake: root hairs and AMF can be seen as alternative evolutionary solutions to the same problem. Both increase plant contact with soil and reduce the length of the external transfer path for nutrients moving to the root. Gahoonia et al. (2001) found that a mutant of the barley variety Pallas, which did not have root hairs, absorbed only half the P of the original variety with root hairs. The original variety absorbed most of the P contained in the 0.8 mm radius root hair zone, produced more acid phosphatase and mobilised more organic P. ‘Root’ surface area is important to P uptake in low P availability soils.

While it is generally accepted that AMF allow the more efficient uptake of labile and sparsely soluble sources of P from the soil it remains unclear as to just how they do this. Whether they make available to the plant P from insoluble mineral sources and from the organic sources, which are

increasingly being recognised as a major component of the soil's total P reserves, or whether the effect is simply due to more efficient uptake, is the key question. The latter has long been the prevailing consensus and recent studies have produced more evidence to support this view. Yao et al. (2001) assessed the ability of *Trifolium pratense* with *G. versiforme* to access P from calcium phosphates varying from CaHPO_4 to $\text{Ca}_{10}(\text{PO}_4)_6\text{F}_2$. AMF promoted the uptake of P but effectiveness was greater for Ca_2P and least for Ca_{10} forms. The external hyphae were efficient at mobilising P from Ca_2P , Ca_8P and AlP . In this study AMF mobilised P, also available to uninfected roots, but were more effective. In addition to organic compounds acting as P sources, Aryal et al. (2003) and Ravnskov et al. (1999) found that organic additions to the soil could influence the functioning of extramatricular hyphae. Hyphal growth of *G. intraradices* was promoted by yeast and bovine serum albumin but depressed by starch and cellulose. P uptake was decreased by cellulose.

11.5.2 AMF and Water Relations

While soil water can be considered as a resource in the same way as is P it differs from P in that only a small percentage of the water absorbed by a plant is retained within the plant. Most absorbed water is transpired. In assessing the effects of AMF on water relations a wider range of aspects are therefore of importance.

Over the years during which the effects of AMF have been studied, suggestions have been made that mycorrhizas influence the plants ability to cope with water stress. Following the logic of the role of AMF in improving P supply it is commonly suggested that AMF function by increasing the ability of the plant to absorb water. Whether this occurs remains an open question. It is now clear however that AMF can influence an infected plant's response to water stress in a number of other ways (Fig. 11.4), e.g. through effects on soil aggregation and water holding capacity (Sutton and Sheppard 1976).

Souza et al. (1999) assessed the growth of the tropical grasses *Brachiaria brizantha* and *Stylosanthe guianensis* on a low fertility soil under water stressed conditions. They found that increasing P supply to 300 mg/kg increased drought resistance which was further enhanced by the presence of AMF (*G. etunicatum*). The same fungus had little impact on the performance of *Eucalyptus grandis* seedlings which under some conditions benefited from inoculation with the ectomycorrhizal fungus *Pisolithus tinctorius* (Fernandes et al. 1999). In soyabean Barakah and Heggio (1998) found that the dual inoculation of plants with *Bradyrhizobium*, *Glomus* and *Gigaspora* increased growth by 400% under conditions of water stress which

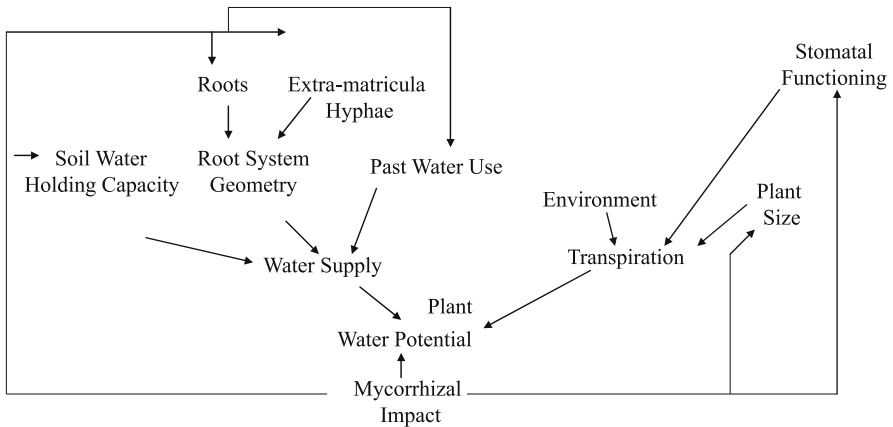


Fig. 11.4. Factors which determine the impact of AMF on plant water potential. The balance of water absorption and transpiration determine plant water potential and water deficits. AMF can influence both of these in a range of ways

increased infection compared to that found under non-stressed conditions. AMF increased NPK concentrations under stressed and non-stressed conditions alike. Similar results were found for barley and wheat by Al-Karaki and Clark (1999) and Al-Karaki et al. (1998). They found that AMF increased growth regardless of soil water potential. Concentrations of P, Mn and Cu were increased by AMF on all soils.

Recent studies on the performance of AMF infected plants under conditions of water stress thus indicate that AMF favourably influence plant response to a limited water supply. The resource acquisition model would assume that AMF would affect a plant's ability to cope with water stress by increasing the plant's ability to obtain water. Whether or not AMF do this, it is now clear that AMF can influence water relations in other ways (Fig. 11.4). AMF influence both the supply and demand sides of the balance. Dunsiger et al. (2003) suggested that AMF influence how a plant responds to a decreasing soil water potential, i.e. increasing water stress, in three ways:

1. In a study of the impact of AMF on the relationship between transpiration and soil water potential they found that AMF infected plants reduced their transpiration more than did non-infected plants as soil water potential decreased. This would reduce plant water stress and permit available soil water to be available for use over a longer period. This relationship is shown in Fig. 11.5. This effect can be mediated in a range of ways including the decreased production of aquaporins (water channels) in the cells of the root cortex or by an increased production of ABA (Steudle 2000).

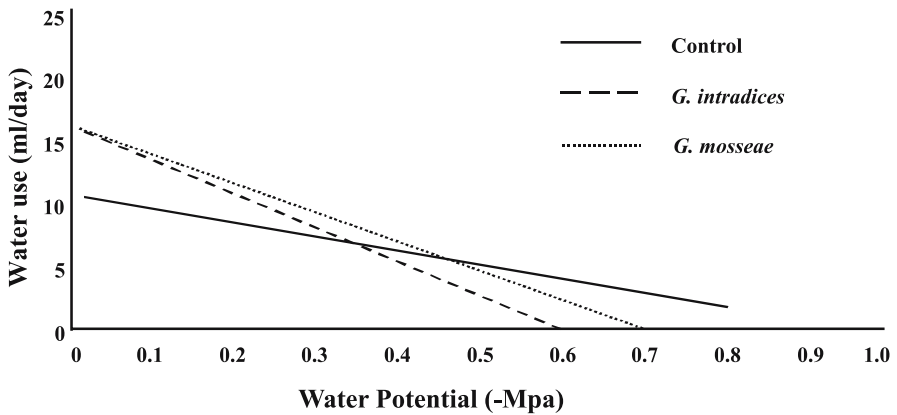


Fig. 11.5. Plant water use compared with soil water potential when inoculated with different mycorrhizal species – one month after inoculation. Trend lines are fitted by linear regression. Reproduced from Dunsiger et al. 2003

- Through an increase in the direct transport of water from the soil by the extra-matricular hyphae as suggested earlier by Safir et al. (1972). Dunsiger et al. (2003) related water removed from a hyphal area in a compartmentalised root box to the length of hyphae found in the soil in that section. The relationship was not good (Fig. 11.6). This does not wholly discount this as a mechanism among a wider range of possibilities. An increased absorption of water, in this way, would not however easily relate to the more conservative pattern of water use described in 1. above.

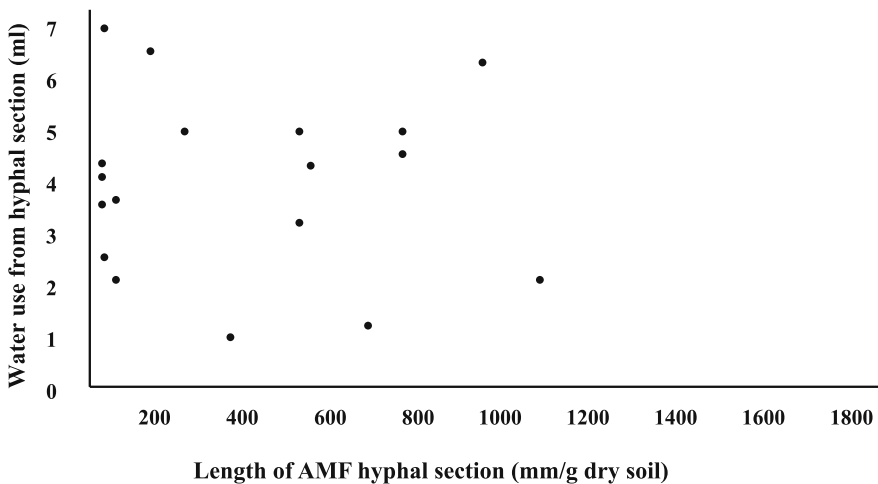


Fig. 11.6. Relationship between AMF hyphal length in the hyphal section of rhizoboxes and water loss from hyphal sections over five days. Reproduced from Dunsiger et al. 2003

3. The most radical suggestion of Dunsiger et al. (2003) was that hyphae signalled a decreasing water availability to the plant which then down-regulated its water use by premature stomatal closure, a feature recorded in their study. Growing plants in a root box, providing a root plus hyphal and hyphal only compartments, showed that the relationship between leaf stomatal conductance and soil water potential in both compartments was less good following the severing of the hyphal connections with the hyphal compartment. While this did not prove the signalling mechanism it did provide support for the hypothesis and suggested signalling as an aspect of the total role of AMF in relation to plant water use. Mechanisms by which roots and soil organisms communicate have recently been discussed by Bais et al. (2004). They suggested that a range of root exudates could, as chemical signals, have a significant role in the infection by symbionts such as AMF, resistance to pathogens and the soil water release characteristics and hydraulic conductivity of rhizosphere soil.

The relationship between different plant species, their stomata and soil water potentials have always been complex in practice (Hsiao et al. 1976). That AMF do not have a simple controlling role is to be expected. The results obtained through recent research do however suggest that AMF infected plants are more acutely coupled to the soil environment and so are better equipped to deal with stressful situations, i.e. their use of a potentially scarce resource is better coupled to availability. This must require an improved ability to sense the environment and so implies a role for AMF beyond more resource acquisition.

11.6 Conclusions

With the development of the breadth of current experimental work on AMF we became aware of the range of aspects of plant and crop development in which they are important. More than perhaps any other rhizosphere organism, AMF are a part of the plant. AMF cannot be regarded as an additive to crops. Many of the agricultural treatments applied in recent years (Dunsiger et al. 2003) have however resulted in a loss of AMF from agricultural soils and from current cropping systems necessitating inoculation so as to restore AMF status to what it would naturally have been. The complexity of fungal-plant structures is illustrated by the recent study of van der Heijden and Kuyper (2001) who found fungus-plant compatibility had a major influence on AMF effectiveness. Plant origin influenced symbiosis effectiveness, mediated through genetic difference in root parameters. Fungal origin had a lesser effect. Miller and Kling (2000) identified the range of

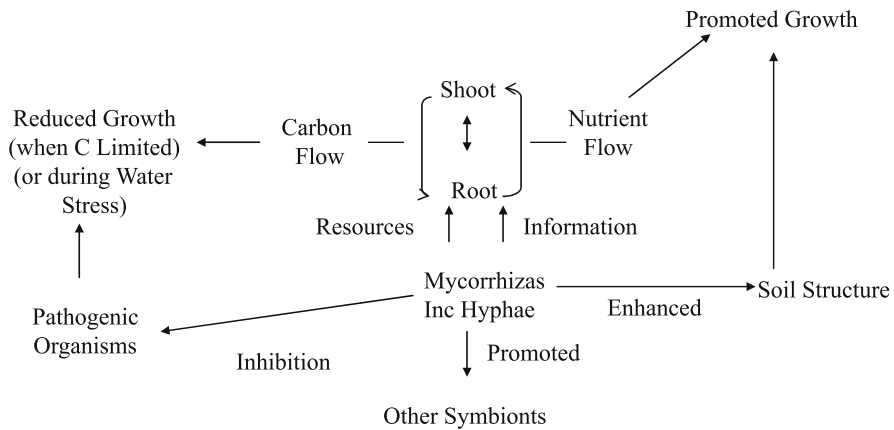


Fig. 11.7. Effects of AM fungi on root form and function

factors which AMF could influence and the range of scales at which they were operational. Currently we can determine the colonisation of a root segment by AMF. With more difficulty the same can be done for an individual root system. We know little of how these parameters vary with time. The information presented here indicates that the amount of fungus, and where it is in the root system, will change with time and may even change over a period of days. Being able to characterise this is one of the major challenges for the future, roots and their AMF symbionts are not physiologically static. In addition, many factors which are influenced by AMF are also influenced by other parameters, e.g. temperature and so the impact of AMF must be viewed against this wider background of environmental conditions. This is summarised in Fig. 11.7 which provides a framework for assessing some of our current gaps in information. While much remains unknown about resource provision, even more remains unknown about information supply. Much of what is needed has a molecular basis. Current developments in this sector are likely therefore to aid the development of a more definite view of the role of AMF in root functioning.

References

- Aikio S, Ruotsalainen AL (2002) The modelled growth of mycorrhizal and non-mycorrhizal plants under constant versus variable soil nutrient concentration. *Mycorrhiza* 12:257–261
- Al-Karaki GN, Clark RB (1999) Varied rates of mycorrhizal inoculum on growth and nutrient acquisition by barley grown with drought stress. *Plant Nutr* 22:1775–1784
- Al-Karaki GN, Al-Raddad A, Clark RB (1998) Water stress and mycorrhizal isolate effects on growth and nutrient acquisition of wheat. *Plant Nutr* 21:891–902

- Alloush GA, Zeto SK, Clark RB (2000) Phosphorus source, organic matter, and arbuscular mycorrhiza effects on growth and mineral acquisition of chickpea grown in acidic soil. *Plant Nutr* 23:1351–1369
- Amijee F, Tinker PB, Stribley D (1989) The development of endomycorrhizal root systems. VII. A detailed study of effects of soil phosphorous on colonisation. *New Phytol* 111:435–446
- Aryal UK, Xu HL, Fujita M (2003) Rhizobia and AM fungal inoculation improve growth and nutrient uptake of bean plants under organic fertilization. *Sustain Agric* 21:29–41
- Atkinson D (1992) Tree root development: the role of models in understanding the consequences of arbuscular endomycorrhizal infection. *Agronomie* 12:817–820
- Atkinson D, Watson CA (2000) The beneficial rhizosphere: a dynamic entity. *Appl Soil Ecol* 15:99–104
- Atkinson D, Berta G, Hooker JE (1994) Impact of mycorrhizal colonisation on root architecture, root longevity and the formation of growth regulators. In: Gianinazzi S, Scheu H (eds) Impact of arbuscular mycorrhizas on sustainable agriculture and natural ecosystems. Birkhauser, Switzerland, pp 89–99
- Atkinson D, Black KE, Forbes PJ, Hooker JE, Baddeley JA, Watson CA (2003) The influence of arbuscular mycorrhizal colonisation and environment on root development in soil. *Eur Soil Sci* 54:751–757
- Azcon R, Ocampo JA (1981) Factors affecting the vesicular – arbuscular infection and mycorrhizal dependency of thirteen wheat cultivars. *New Phytol* 87:677–685
- Bagayoko M, George E, Romheld V, Buerkest A (2000) Effect of mycorrhizae and phosphorus on growth and nutrient uptake of millet, cowpea and sorghum on a West African soil. *J Agric Sci* 135:399–407
- Bais HP, Park SW, Weir TL, Callaway RM, Vivenco JM (2004) How plants communicate using the underground information super highway. *Trends Plant Sci* 9:26–32
- Barakah FN, Heggo AM (1998) Moisture stress, bradyrhizobia, vesicular-arbuscular mycorrhiza and P-fertilizers effects on soybean growth, nutrient content and phosphatase activity under calcareous soil. *Ann Agric Sci (Cairo)* 43:461–475
- Berta G, Fusconi A, Trotta A (1993) VA-mycorrhizal infection and the morphology and function of root system. *Environ Exp Bot* 33:159–173
- Berta G, Fusconi A, Sampo S, Lingua G, Perticone S, Repetto O (2000) Polyploidy in tomato roots as affected by arbuscular mycorrhizal colonisation. *Plant Soil* 226:37–44
- Berta G, Fusconi A, Hooker JE (2002) Arbuscular mycorrhizal modification to plant root systems: scale, mechanism and consequences. In: Gianinazzi S, Schue H, Barea JM, Hesselwandler K (eds) Mycorrhizal technology in agriculture. Birkhauser, Switzerland, pp 71–85
- Black KE, Harbron CG, Franklin M, Atkinson D, Hooker JE (1998) Differences in root longevity of some tree species. *Tree Physiol* 18:259–264
- Boddy L (1993) Saprophytic cord forming fungi: welfare strategies and other ecological aspects. *Mycol Res* 97:641–655
- Bressan W, Vasconcellos CA (2002) Morphological alterations on root system of maize induced by mycorrhizal fungi and phosphorus. *Pesqui Agropecu Bras* 37:509–517
- Bryla DR, Koide RT (1990) Role of mycorrhizal infection in the growth and reproduction of wild vs cultivated plants. II. Eight wild accessions and two cultivars of *Hycopersicon esculentum*. *Oecologia* 84:82–92
- Drew EA, Murray RS, Smith SE, Jakobsen I (2003) Beyond the rhizosphere: growth and function of arbuscular mycorrhizal external hyphae in sands of varying pore sizes. *Plant Soil* 251:105–114
- Dunsiger Z (1999) The influence of arbuscular mycorrhizas on the water relation of trees. PhD Thesis, University of Edinburgh

- Dunsiger Z, Atkinson D, Watson CA (2003) Arbuscular mycorrhizal fungi: their role in the ability of crops to cope with stress. In: Proc BCPC Intl Congr Crop Sci and Technol, pp 433–439
- Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. *New Phytol* 147:33–42
- Elwan IM, Omran SEH, Mohamed HZ (2002) Effect of phosphorus and micronutrients fertilization accompanied with VA-mycorrhizal fungi in controlling Rhizoctonia damping-off on the growth and nutritional status of cotton plants. *Ann Agric Sci (Cairo)* 47:1139–1157
- Fernandes MF, Ruiz HA, Neves JCL, Muchovej RMC (1999) Growth and phosphorus uptake by *Eucalyptus grandis* seedlings associated to mycorrhizal fungi in different phosphorus rates and soil water potentials. *Rev Bras Cienc do Solo* 23:617–625
- Fitter AH (1977) Influence of mycorrhizal infection on competition for phosphorous and potassium by two grasses. *New Phytol* 79:199–225
- Fitter A (1985) Functional significance of root morphology and root system architecture. In: Fitter AH, Atkinson D, Reid DJ, Usher MB (eds) Ecological interaction in soil. Blackwell, Oxford, pp 87–106
- Forbes PJ, Ellison CH, Hooker JE (1996) The impact of arbuscular mycorrhizal fungi and temperature on root system development. *Agronomie* 16:617–620
- Forbes PJ, Black KE, Hooker JE (1997) Temperature-induced alteration to root longevity in *Lolium perenne*. *Plant Soil* 190:87–90
- Frank AB (1887) Ueber neue mykorrhiza – former *Ber Dtsch Bot Ges* 5:395
- Fusconi A, Tagliasacchi AM, Berta G, Trotta A, Brazzaventre S, Ruberti F, Scannerini S (2001) Root apical meristems of *Allium porrum* L. as affected by arbuscular mycorrhizae and phosphorus. *Protoplasma* 214:219–226
- Gahoonia TS, Neilsen NE, Priyavadan AJ, Jahoor A (2001) A root hairless barley mutant for elucidating genetics of root hairs and phosphorous uptake. *Plant Soil* 235:211–219
- Galal YGM, El-Ghandour IA, Osman ME, Raouf AMNA (2003) The effect of inoculation by mycorrhizae and *Rhizobium* on the growth and yield of wheat in relation to nitrogen and phosphorus fertilization as assessed by 15 N techniques. *Symbiosis (Rehovot)* 34: 171–183
- Harley JL, Smith SE (1983) Mycorrhizal symbiosis. Academic Press, London
- Hawkes CV, Casper BB (2002) Lateral root function and root overlap among mycorrhizal and non-mycorrhizal herbs in a Florida shrubland, measured using rubidium as a nutrient analog. *Am J Bot* 89:1289–1294
- Henry A, Kosola KR (1999) Root age and phosphorus effects on colonization of *Andropogon gerardii* by mycorrhizal fungi. *Soil Biol Biochem* 31:1657–1660
- Hiltner L (1904) Über neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berücksichtigung der Gründüngung und Brache. *Arb. dtsh. Landwirt. Ges.* 98:59–78
- Hodge A, Stewart J, Robinson D, Griffiths BS, Fitter AH (1998) Root proliferation, soil fauna and plant nitrogen capture from nutrient rich pockets in soil. *New Phytol* 139:479–494
- Hodge A, Robinson D, Fitter AH (2000) An arbuscular mycorrhizal inoculum enhances root proliferation in, but not nitrogen capture from, nutrient-rich patches in soil. *New Phytol* 145:575–584
- Hooker JE, Atkinson D (1992) Application of computer aided image analysis to studies of Am fungi effects on plant root systems architecture and dynamics. *Agronomie* 12:821–824
- Hooker JE, Munro M, Atkinson A (1992) Vesicular – arbuscular mycorrhizal fungi induced alteration in poplar root system morphology. *Plant Soil* 145:207–214
- Hooker JE, Jaizme-Voga M, Atkinson D (1994) Biocontrol of plant pathogens using arbuscular mycorrhizal fungi. In: Gianinazzi S, Schue H (eds) Impact of arbuscular mycorrhizas on sustainable agriculture and natural ecosystems. Birkhuaser, Basel, pp 191–200

- Hooker JE, Black KE, Perry RL, Atkinson D (1995) Arbuscular mycorrhizal fungi in dual alteration to root longevity of poplar. *Plant Soil* 172:327–329
- Hooker JE, Berta G, Lingua G, Fusconi A, Sgorbate S (1998) Quantification of AMF-induced modifications to root system architecture and longevity. In: Varma A (ed) *Mycorrhizal manual*. Springer, Berlin Heidelberg New York, pp 515–531
- Hsiao TC, Acevedo E, Fereres E, Henderson DW (1976) Water stress, growth and osmotic adjustment. *Philos Trans R Soc London* 273:479–500
- Isobe K, Tsuboki Y (1998) The relationship between growth promotion by arbuscular mycorrhizal fungi and root morphology and phosphorus absorption in gramineous and leguminous crops. *Jpn J Crop Sci* 67:347–352
- Izaguirre-Mayoral ML, Carballo O, Carreno L, Mejia MG de (2000) Effects of arbuscular mycorrhizal inoculation on growth, yield, nitrogen, and phosphorus nutrition of nodulating bean varieties in two soil substrates of contrasting fertility. *J Plant Nutr* 23:1117–1133
- Jifon JL, Graham JH, Drouillard DL, Syvertsen JP (2002) Growth depression of mycorrhizal Citrus seedlings grown at high phosphorus supply is mitigated by elevated CO₂. *New Phytol* 153:133–142
- Jones MD, Durall DM, Tinker PB (1990) Phosphorous relationships and production of extramatricular hyphae by two types of willow ectomycorrhizas and different soil phosphorus levels. *New Phytol* 115:259–267
- Jungk A (1987) Soil-root interactions in the rhizosphere affecting plant availability of phosphorus. *J Plant Nutr* 10:1197–1204
- Kaeppler SM, Parker JC, Mueller SM, Senior L, Stuber C, Tracy WF (2000) Variation among maize inbred lines and delimitation of quantitative trait loci for growth of low phosphorus and responsiveness to arbuscular mycorrhizal fungi. *Crop Sci* 40:358–364
- Karagiannidis N, Bletsos F, Stavropoulos N (2002) Effect of *Verticillium* wilt (*Verticillium dahliae* Kleb.) and mycorrhiza (*Glomus mosseae*) on root colonization, growth and nutrient uptake in tomato and eggplant seedlings. *Sci Hortic* 94:145–156
- Koide RT (1985) The nature of growth depressions in sunflower by vesicular-arbuscular mycorrhizal infection. *New Phytol* 99:449–462
- Koide RT (1991) Nutrient supply, nutrient demand and plant response to mycorrhizal infection. *New Phytol* 117:365–386
- Melloni R, Nogueira MA, Freire VF, Cardoso EJBN (2001) Phosphorus levels and arbuscular mycorrhizal fungi on growth and mineral nutrition of Citrus limonia (L.) Osbeck. *Rev Bras Cienc do Solo* 24:767–775
- Miller RM, Kling M (2000) The importance of integration and scale in the arbuscular mycorrhizal symbiosis. *Plant Soil* 226:295–309
- Mohammad MJ, Malkawi HI, Shibli R (2003) Effects of arbuscular mycorrhizal fungi and phosphorus fertilization on growth and nutrient uptake of barley grown on soils with different levels of salts. *J Plant Nutr* 26:125–137
- Muthukumar T, Udaiyan K (2000) Influence of organic manures on arbuscular mycorrhizal fungi associated with *Vigna unguiculata* (L.) Walp. in relation to tissue nutrients and soluble carbohydrate in roots under field conditions. *Biol Fertil Soils* 31:114–120
- Nadian H, Smith SE, Alston AM, Murray RS, Siebert BD (1998) Effects of soil compaction on phosphorus uptake and growth of *Trifolium subterraneum* colonized by four species of vesicular-arbuscular mycorrhizal fungi. *New Phytol* 140:155–165
- Newman EI, Andrews RE (1973) Uptake of phosphorous and potassium in relation to root growth and root density. *Plant Soil* 38:49–69
- Norman JR, Atkinson D, Hooker JE (1996) Arbuscular mycorrhizal fungal induced alteration to root architecture in strawberry and induced resistance to the root pathogen *Phytophthora fragariae*. *Plant Soil* 185:191–198
- Nye PH, Tinker PB (1977) *Solute movement in the soil-root system*. Blackwell, Oxford

- Olsen JK, Schaefer JT, Edwards DG, Hunter MN, Galea VJ, Muller LM (1999) Effects of mycorrhizae established from an existing intact hyphal network on the growth resistance of capsicum (*Capsicum annuum* L) and tomato (*Lycopersicon esculentum* Mill) to five ratios of applied phosphorus. *Austral J Agric Res* 50:223–237
- Ortas I, Ortaka D, Kaya Z (2002) Variation mycorrhizal fungi propagated on different hosts have different effects on citrus growth and nutrient uptake. *Com Soil Sci Plant Anal* 33:259–272
- Ozcan H, Taban S (2000) Effects of VA-mycorrhiza on growth and phosphorus, zinc, iron, copper and manganese concentrations of maize grown in acid and alkaline soils. *Turk J Agric For* 24:629–635
- Ravnkov S, Larsen J, Olsson PA, Jakobsen I (1999) Effects of various organic compounds on growth and phosphorus uptake of an arbuscular mycorrhizal fungus. *New Phytol* 141:517–524
- Read DJ (2002) Towards ecological deliverance – progress and pitfalls in the path towards an understanding of mycorrhizal functions in nature. In: Van der Heijden MGA, Sanders IR (eds) *Mycorrhizal ecology*. Springer, Berlin Heidelberg New York, pp 3–29
- Read DJ, Boyd R (1986) Water relations of mycorrhizal fungi and their host plants. In: Ayres PG, Boddy L (eds) *Water fungi and plants*. CUP, pp 287–303
- Rubio R, Borie F, Schalchli C, Castillo C, Azcon RAA (2002) Plant growth responses in natural acidic soil as affected by arbuscular mycorrhizal inoculation and phosphorus sources. *J Plant Nutr* 25:1389–1405
- Safir GR, Bayer JS, Gerdemann JW (1972) Nutrient status and mycorrhizal enhancement of water transport in soyabean. *Plant Physiol* 49:700–703
- Salami AO (1999) Influence of mycorrhizal biotechnology on disease severity and growth of pepper (*Capsicum annum* Linn). *Int J Trop Plant Dis* 17:51–60
- Sastry MSR, Sharma AK, Johri BN (2000) Effect of an AM fungal consortium and *Pseudomonas* on the growth and nutrient uptake of *Eucalyptus* hybrid. *Mycorrhiza* 10:55–61
- Schellenbaum L, Berta G, Ranirina F, Tisserant B, Gianinazzi S, Fitter AH (1991) Influence of endomycorrhizal infection on root morphology in a micropropagated woody plant species (*Vitis vinifera* L). *Ann Bot* 68:135–141
- Schjorring JK, Jensen P (1984) Phosphorus nutrition of barley, buckwheat and rape seedlings. II. Influx and efflux of phosphorus by intact roots of different P status. *Physiol Plant* 61:584–590
- Sempavalan J, Kumutha K, Santhanakrishnan P (2001) Relative effect of vesicular arbuscular mycorrhizal fungi on growth and nutrient uptake of *Casuarina equisetifolia*. *Madras Agric J* 88:700–703
- Setua GC, Kar R, Ghosh JK, Das NK, Saratchandra B (1999) Response of direct inoculation of VAM on growth, leaf yield and phosphorus uptake in mulberry (*Morus alba*). *Indian J Agric Sci* 69:444–448
- Silberbush M, Barber SA (1983) Sensitivity of simulated phosphorus uptake to parameters used by a mechanistic mathematical model. *Plant Soil* 74:93–100
- Simard SW, Jones MD, Durrall DM (2002) Carbon and nutrient fluxes within and between mycorrhizal plants. In: Van der Heijden MGA, Sanders IR (eds) *Mycorrhizal ecology*. Springer, Berlin Heidelberg New York, pp 34–74
- Smith SE, Smith FA (1990) Structure and function of the interfaces in biotrophic symbiosis as they relate to nutrient transport. *New Phytol* 114:1–38
- Solaiman MZ, Abbott LK (2003) Phosphorus uptake by a community of arbuscular mycorrhizal fungi in jarrah forest. *Plant Soil* 248:313–320
- Song Yong Chun, Zhang Jun Ling, Li Xiao Lin, Feng Gu, Yang Zhi Fu AA (1999) Effect of VA mycorrhizal hyphae links on growth and P nutrient of red clover. *J Chin Agric Univ* 4:26–32

- Souza RF de, Pinto JC, Siqueira JO, Rezende VF (1999) Effects of mycorrhizae and phosphorus fertilizer on growth of *Brachiaria brizantha* and *Stylosanthes guianensis* on soil of low fertility. 3. Dry matter yield under water stress. *Pasturas Tropic* 21:31–35
- Staddon PL, Graves JD, Fitter AH (1999) Effect of enhanced atmospheric CO₂ on mycorrhizal colonisation and phosphorus inflow in 10 herbaceous species of contrasting growth strategies. *Func Ecol* 13:190–199
- Stedle E (2000) Water uptake by plant roots an integration of views. *Plant Soil* 226:45–56
- Sutton JC, Sheppard BR (1976) Aggregation of sand-dune soil by endomycorrhizal fungi. *Can J Bot* 54:326–333
- Syvrtsen JB, Graham JH (1999) Phosphorus supply and arbuscular mycorrhizas increase growth and net gas exchange responses of two Citrus spp. grown at elevated [CO₂]. *Plant Soil* 208:209–219
- Tibbett M (2000) Roots, foraging and the exploitation of soil nutrient patches: the role of mycorrhizal symbiosis. *Func Ecol* 14:397–399
- Tisdall JM, Oades JM (1979) Stabilisation of soil aggregates by the root system of rye grass. *Aust Soil Res* 17:429–441
- Tisserant B, Schellenbaum L, Gianinazzi-Pearson V, Gianinazzi S, Berta G (1991) Influence of infection by an endomycorrhizal fungi on root development and architecture in *Plantanus acerifolia*. *Allinia* 30:171–181
- van der Heijden EW, Kuyper TW (2001) Does origin of mycorrhizal fungus or mycorrhizal plant influence effectiveness of the mycorrhizal symbiosis. *Plant Soil* 230:161–174
- van der Heijden MGA, Sanders I (2002) *Mycorrhizal ecology*. Springer, Berlin Heidelberg New York
- Watson CA, Ross JM, Bagnaresi U, Minotta GF, Roffi F, Atkinson D, Black KE, Hooker JE (2000) Environment-induced modifications to root longevity in *Lolium perenne* and *Trifolium repens*. *Ann Bot* 85:397–401
- Yao Q, Li X, Feng G, Christie P (2001) Mobilisation of sparingly soluble inorganic phosphates by the external mycellium of an arbuscular mycorrhizal fungus. *Plant Soil* 230:279–285
- Yao MK, Tweddell RJ, Desilets H (2002) Effect of two vesicular-arbuscular mycorrhizal fungi on the growth of micropropagated potato plantlets and on the extent of disease caused by *Rhizoctonia solani*. *Mycorrhiza* 12:235–242
- Zhu YG, Smith SE (2001) Seed phosphorus (P) content affects growth, and P uptake of wheat plants and their association with arbuscular mycorrhizal (AM) fungi. *Plant Soil* 231:105–112