Chapter 10
The Role of Arbuscular Mycorrhizas in Organic Farming

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Abstract Arbuscular mycorrhizal fungi (AMF) are ubiquitous in natural and agricultural ecosystems. AMF enhance uptake of nutrients by plants, particularly phosphorus (P), and may also improve plant drought avoidance and disease control. AMF may also be necessary for the long-term sustainability of ecosystems, particularly due to their role in the maintenance of soil structure, and plant community structure and diversity. In agricultural systems, high colonisation of roots by AMF is favoured by the absence of mineral fertilisers that supply readily soluble P, minimal soil disturbance, avoidance of non-host plants and bare fallows, and, perhaps, a high degree of plant diversity and minimal use of biocides. Colonisation by AMF is often higher on organic farms than conventional farms and there is some evidence of an increase in species diversity of AMF on organic farms. These differences appear primarily due to the lack of fertilisers containing readily soluble P on organic farms. Yet high colonisation by AMF is not an inevitable outcome of organic farm management and colonisation may be limited on some organic farms by high rates of tillage or residual high soil available P. There is some indication that organic farms can develop a community of AMF with an increased capacity to enhance plant P uptake. However, AMF do not substitute for fertiliser inputs as the nutrients taken up by the fungi primarily originate from the finite pool of soil available nutrients and their removal in farm products must be matched by inputs from off-farm sources. Indeed, high colonisation by AMF may be considered an indicator of low soil available P. As AMF depend on host photosynthate for energy, high levels of colonisation may reduce plant growth under some environmental or farm management conditions. For instance, monocultures, high soil fertility, and high rates of tillage may stimulate development of less beneficial communities of AMF. The need for inoculants containing AMF on organic farms is unknown, but they may prove beneficial if bare fallows or weed-free crops of non-hosts are regularly included in the rotation. Overall, the

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H. Kirchmann, L. Bergström (eds.), *Organic Crop Production – Ambitions and Limitations*, DOI 10.1007/978-1-4020-9316-6_10,

high abundance of AMF that often results from organic management suggests an important role for the fungi in the functioning of organic farming systems.

Keywords Arbuscular mycorrhizal fungi · Organic farming · Farming systems · Phosphorus · Sustainability

10.1 Introduction

Organic farming is often promoted as a superior alternative to conventional farming. The origins and current practices of organic farming are diverse (Kirchmann et al., 2008), but for the purposes of this review a number of alternative farming systems will be termed "organic" (biodynamic, organic, biological organic). Whilst the beliefs that determine the farm management practices permitted in organic farming may sometimes differ from the scientifically-based principles that underlie conventional farming (Kirchmann et al., 2008), in practice organic and conventional farming systems differ in two key aspects: (i) The replacement on organic farms of processed readily soluble fertilisers with leguminous crops and fertilisers which are generally less processed and less soluble (Watson et al., 2002; Kirchmann and Ryan, 2004). Fertiliser inputs also tend to be lower on organic farms and in some instances no fertiliser may be applied. (ii) The replacement on organic farms of the manufactured chemical biocides permitted on conventional farms with what are considered "natural" alternatives.

Arbuscular mycorrhizas are formed by a close association between roots and arbuscular mycorrhizal fungi (AMF), which are ubiquitous in natural and agricultural ecosystems. AMF have long fascinated agricultural researchers due to their ability to enhance host plant uptake of nutrients, especially phosphorus (P) (Koide and Mosse, 2004). Increasingly, AMF are being shown to influence host plants in other ways which include aiding with drought avoidance and providing a degree of disease control. There is now also evidence that AMF may be necessary for the long-term sustainability of agricultural systems due to their interactions with other components of the soil biological community, and their role in the maintenance of soil structure and, in permanent vegetation, plant community structure and diversity.

Thus AMF may be viewed as intermediaries between soil nutrients and host plants, and thereby as biological regulators of plant nutrient uptake. However, while host plant P uptake may be greatly enhanced by AMF (Smith and Read, 1997), when P is readily available to plants due to high soil available P or application of fertilisers containing readily soluble P, the occurrence of AMF may be greatly reduced (Smith and Read, 1997). This characteristic of AMF appears consistent with the view of proponents of organic farming that plants should not be "force-fed" readily soluble inorganic nutrients, instead acquiring nutrients in more desirable amounts and ratios by means of an active, nurtured, soil biological community (Kirchmann and Ryan, 2004).

In this chapter we attempt to characterise the role of AMF in organic farming by reviewing the relatively small literature that examines directly the role of AMF on organic farms as well as the much larger literature on the role of AMF in conventional farming systems. The chapter begins with a brief overview of the structure and function of AMF. The various methods for quantifying abundance, community diversity and structure, and function of AMF are then described. The effect on AMF of farm management (organic and conventional) is then reviewed, followed by consideration of the impacts on AMF of agronomic practices. The role of AMF on organic farms at scales ranging from individual plants through to the whole agricultural system is then discussed and the necessity for inoculation considered.

10.2 Arbuscular Mycorrhizas – Structure and Function

Mycorrhizas are currently classified into seven types based on morphology (Peterson et al., 2004). In this review we consider only one type – arbuscular mycorrhizas. Whilst other types of mycorrhizas are present in agricultural systems, notably ectomycorrhizas and ericoid mycorrhizas, the plants which form these mycorrhizas are generally much less common than those which form arbuscular mycorrhizas and there is almost no published work on the role of these other mycorrhizas in organic farming systems.

Arbuscular mycorrhizas are formed by fungi classified in the new phylum *Glomeromycota* (Schüβler et al., 2001). There are 198 described species of AMF (Schüβler, 2006), although this may be a gross underestimate owing to the small number of rigorous taxonomic studies. Eleven genera of AMF, placed into four orders, are currently recognised; *Glomus, Gigaspora, Scutellospora, Acaulospora, Kuklospora, Entrophospora, Pacispora, Diversispora, Paraglomus, Archaeospora* and *Intraspora* (Schüβler, 2006; Sieverding and Oehl, 2006). In addition, the genus *Glomus* is now considered nonmonophyletic and may soon be split into a number of new genera (Schwarzott et al., 2001). This on-going revision means most of the studies referred to in this chapter contain out-dated taxonomy. None-the-less, their findings remain useful when considering the role of AMF in agricultural systems.

AMF are obligate symbionts and cannot grow without being in association with a host root from which they attain all their energy (carbon) needs (Ho and Trappe, 1973; Pfeffer et al., 1999). This characteristic has resulted in an inability to utilise axenic culture for large scale inoculum production. AMF are believed to use between 4 and 20% of host plant photosynthate (Graham, 2000). When AMF colonise a root they penetrate through the epidermis and intraradical hyphae move from cell to cell or through intercellular spaces (Peterson et al., 2004). In some cells the hyphae form structures with fine branches known as arbuscules which allow exchange of carbon and nutrients with the host plant (Peterson et al., 2004). AMF may also form intraradical or extraradical lipid-filled vesicles, which seem to act as storage structures or, perhaps, propagules (Peterson et al., 2004). The fungi extend extraradical hyphae into surrounding soil and these absorb nutrients up to 11 cm away from the root (Jakobsen et al., 1992a; Leake et al., 2004). The distribution of the hyphae in soil, hyphal growth rate, the distance over which nutrients are transported and nutrient uptake per unit of mycorrhizal root can all differ with species of AMF (Jakobsen et al., 1992a,b). Spores are typically formed from the extraradical hyphae. AMF can constitute a significant portion of the soil microbial biomass (Olsson et al., 1999). For instance, Rillig et al. (2002) found that extraradical hyphae of AMF constituted greater than 50% of the total fungal hyphal length in annual grassland soil.

The extraradical hyphae of AMF, if undisturbed, form a common mycorrhizal network (CMN) of interconnected hyphae and host roots. CMNs may allow movement of nutrients between linked plants, although carbon flow is generally considered to be one way, from the host plant to the fungus (Pfeffer et al., 2004). While such processes are thought to be important in mediating the outcomes of plant competition, the extent to which interplant transfers occur in the field is not known (He et al., 2003; Leake et al., 2004).

Arbuscular mycorrhizas are formed in the majority of angiosperm families and are commonly found in most crop and pasture plants, in particular legumes and cereals (Newman and Reddell, 1987), as well as in many tree crops (Cuenca and Meneses, 1996; Graham et al., 1997; Mamatha et al., 2002). Hence AMF are ubiquitous in agricultural systems (Abbott and Robson, 1977; Talukdar and Germida, 1993; Sjöberg et al., 2004). A small number of crops are non-hosts for AMF including brassicas and some lupin species (Plenchette et al., 1983; Trinick, 1977).

AMF have traditionally been considered to be non-host specific as most species will colonise most host plants (e.g. Klironomos, 2003). However, the impact of AMF on host plant nutrient uptake, soil aggregation and even the relationship between plant species diversity and productivity can differ between species of AMF (Graham et al., 1997; Graham and Abbott, 2000; Klironomos et al., 2000; Piotrowski et al., 2004). The impact of a particular species of AMF on plant growth can also vary greatly between plant species (Klironomos, 2003) or crop cultivars and host plant species can affect AM fungal population growth rates and hence AM fungal community structure (Bever, 2002).

AMF are best known for their ability to enhance host plant P uptake, as well as uptake of other nutrients, although other benefits for the host plant may also occur. When benefits for the host plant outweigh carbon costs, host plant growth may be enhanced. Most studies of AMF have concentrated on their ability to enhance host plant P uptake under conditions of low P availability. Whilst agricultural systems in industrialised countries tend to present a high P soil environment, organic farms are often an exception (e.g. Derrick and Dumaresq, 1999; Ryan et al., 2000). Hence, AMF may be of particular importance in organic farming.

10.3 Assessing Abundance, Community Diversity and Structure, and Function of AMF

Crucial to advancing our understanding of the role of AMF in agricultural systems is the development of techniques for measuring the occurrence and function of AMF.

Abundance of AMF is most commonly assessed by estimating the percentage of root length colonised after roots have been cleared and stained (see Giovannetti and Mosse, 1980; Grace and Stribley, 1991; Brundrett et al., 1996). Strong correlations between changes in this measure and changes in plant growth or nutrient uptake have been observed in some studies (e.g. Ryan and Angus, 2003). However, when many studies are compared, the degree of change between plants or treatments in the percentage of root length colonised is not a particularly good indicator of host plant growth response, that is, mycorrhiza function (McGonigle, 1988; Jakobsen et al., 2001; Lekberg and Koide, 2005a). Factors responsible for this could include other limitations on plant growth or changes in root length confounding changes in the percentage of root length colonised. In addition, measuring the abundance of AMF as the percent of root length colonised treats mycorrhizas as a single entity taking no account of the diversity of species that can be present in the roots of one plant (Clapp et al., 1995), their spatial variation or physiological state. An attempt is sometimes made to elucidate the latter parameter by noting the occurrence of arbuscules, vesicles and hyphae (e.g. Johnson, 1993; Egerton-Warburton and Allen, 2000). However, in the absence of a more reliable, but equally simple, measure of mycorrhiza function, the percentage of root length colonised is often used as a surrogate.

The abundance of AMF is also commonly assessed by estimating the density of spores in soil. Spores are sieved from soil, identified, and counted under a microscope (e.g. Cuenca and Meneses, 1996). As it can be difficult to distinguish viable spores from dead spores, or determine the age of viable spores, this measure provides an assessment of the "accumulated sporulation history" (Hijri et al., 2006) which may not reflect the species currently colonising roots (Clapp et al., 1995). Also, spore counts may not reflect the relative abundance of species of AMF, as species can differ in rate and timing of sporulation (Oehl et al., 2003). Species which rarely sporulate may be absent and non-sporulating species will not be represented (Rosendahl and Stukenbrock, 2004).

Community diversity and structure of AMF is a particularly important parameter as it can be greatly changed by agricultural practices (Oehl et al., 2003) and species of AMF from the same soil can differ greatly in their impact on plant growth (Klironomos, 2003). Community diversity and structure has also traditionally been assessed by spore counts (Brundrett et al., 1996). While this method has the drawbacks mentioned above, communities of AMF can be usefully investigated (e.g. Oehl et al., 2004), with the exception of non-sporulating species. Establishing trap cultures can refine this method. Trap cultures involve growing plants in field soil in a glasshouse, with spores then being regularly sampled and identified (e.g. An et al., 1993). The longer the time before samples are taken the greater the number of species that will be confidently identified (e.g. Oehl et al., 2004). However, which of the identified species is actually colonising roots in the field at any point in time is unknown. While this issue could be investigated through careful description of colonisation morphology (Abbott, 1982; Rangeley et al., 1982), the development of molecular methods to identify individual species of AMF in roots now shows much promise (e.g. Hijri et al., 2006). However, not all molecular methods detect a wide range of AM fungal diversity (e.g. Helgason et al., 1998), and care must be taken with interpretation of results.

The impact of AMF on host plant growth and nutrition has been commonly assessed under glasshouse conditions using sterilised soil and single strain inoculants of AMF. The large growth benefits from AMF observed in these circumstances are often not found under field conditions (Rangeley et al., 1982; Fitter, 1985). In a meta-analysis of experiments examining the contribution of AMF to agricultural plants in non-sterile soils, Lekberg and Koide (2005a) found mycorrhizal benefit was substantially greater in the glasshouse (95% CI 84–304%) than the field (95% CI 35–83%). Possible reasons for this difference include the presence in field experiments of more variable and extreme environmental conditions (Gavito et al., 2005; Ryan et al., 2005), other beneficial or pathogenic soil organisms (Daniels Hetrick et al., 1988), or higher soil nutrient availability (Ryan and Graham, 2002). Unfortunately, assessment of mycorrhiza function in the field has many difficulties. In particular, the methods used to produce non-mycorrhizal controls, or treatments with reduced colonisation (e.g. fungicides, long bare fallow, tillage) also affect other soil organisms (Khasa et al., 1992; Ryan et al., 2002), soil nutrient availability (Thompson, 1990) and other parameters (Hulugalle et al., 1998). Thus, care must be taken with extrapolating results from glasshouse studies to field conditions and in the interpretation of results of field experiments.

10.4 Mycorrhizas and Organic Farming

A small number of studies have compared the abundance and diversity of AMF between organic (or low-input) and conventional farms or treatments. Across a broad range of agriculturally utilised host plants, agricultural systems and locations, the degree of colonisation of roots by AMF, spore density and species diversity of AMF are all generally reported as higher on the organic farms (Table 10.1; Limonard and Ruissen, 1989). For instance, Fig. 10.1 shows the results of a survey of dairy farms in SE Australia. Colonisation of clover (*Trifolium* spp.) by AMF was higher on the organic or biodynamic farm in 16 of the 19 pairs (Ryan, 1998; Ryan et al., 2000). Similarly in the UK, Eason et al. (1999) sampled grassland sites on organic and conventional farms and found colonisation by AMF of pasture roots and spore density were both higher, on average, for the organic sites (Table 10.2). For crops, the differences in colonisation reported between organic and conventional farms can be much larger than those reported for pastures (e.g. Sattelmacher et al., 1991; Ryan et al., 1994). Whilst colonisation by AMF is usually lower on conventional farms for both crops and pastures, it is rarely completely absent and above 10% of root length, and sometimes greater than 50% of root length, is usually colonised.

The higher abundance of AMF on organic farms is most commonly attributed to the absence of readily soluble P fertilisers and/or lower soil available P (especially in the Australian studies), minimal use of biocides and more diverse rotations (Table 10.1). However, of the papers referred to in Table 10.1, only the two sets

Table 10.1 Studies which compared the impact of organic and conventional farm management on variables related to AMF

Location	System	Plants present	Variables measured	Farm management under which variable was higher	Characteristics of organic system considered by authors as responsible for differences	Reference
Canada	Cropping	Flax	Root colonisation (%)	Organic	Lower soil P	Entz et al. (2004)
Pennsylvania, USA	Cropping	Maize, soybean	Community structure (measures including species density and Shannon index made using spores from field)	No difference	n.a.[a]	Franke-Snyder et al. (2001)
California, USA	Intensive horticulture	Lettuce	Root colonisation (%)	Organic	No use of biocides and P and N fertilisers, more diverse rotation	Miller and Jackson (1998)
			Spore density	No difference		
California, USA	Orchard	Apple	Root colonisation (%)	Organic	More weeds, no pesticide use	Werner (1997)
California, USA	Horticulture	Strawberries	Root colonisation (%)	Organic	No fumigation, low soil fertility	Werner et al. (1990)
Denmark	Cropping	Wheat	Clonal diversity and population genetic structure (PCR on single spores)	No difference	n.a.[a]	Stukenbrock and Rosendahl (2005)
Northern Germany	Cropping	Cereal rye	Root colonisation (%)	Organic	No use of fertilisers and agrochemicals, more diverse rotation	Sattelmacher et al. (1991)
Basel, Switzerland (DOK experiment)	Cropping	Various	Root colonisation (%)	Organic	Lower soil P	Mäder et al. (2000)

Table 10.1 (continued)

Location	System	Plants present	Variables measured	Farm management under which variable was higher	Characteristics of organic system considered by authors as responsible for differences	Reference
Basel	Cropping	Grass, clover	Root colonisation (%)	Organic	Lower soil P	Oehl et al. (2004)
			Spore density	Organic	Lower soil P	
			Number of species (spores extracted from field and spores present in trap cultures)	Organic	Lower soil P	
			Community diversity (Shannon index using spores from field)	Organic	Lower soil P	
United Kingdom	Pasture	Pasture	Root colonisation (%)	Organic	Not known	Eason et al. (1999)
			Spore density	Organic	Not known	
Brazil	Orchard	Apple	Spore density	Conventional	Not known	Purin et al. (2006)
			Number of species (spores from field)	Organic	Not known	
			Community diversity (Shannon index using spores from field)	Conventional	Not known	
SE Australia	Crop-livestock	Wheat	Root colonisation (%)	Organic	No use of readily soluble P fertiliser	Dann et al. (1996), Ryan et al. (1994, 2004)
SE Australia	Permanent dairy pastures	White clover, ryegrass	Root colonisation (%)	Organic	No use of readily soluble P fertiliser	Ryan et al. (2000), Ryan and Ash (1999)

[a] n.a. = not available.

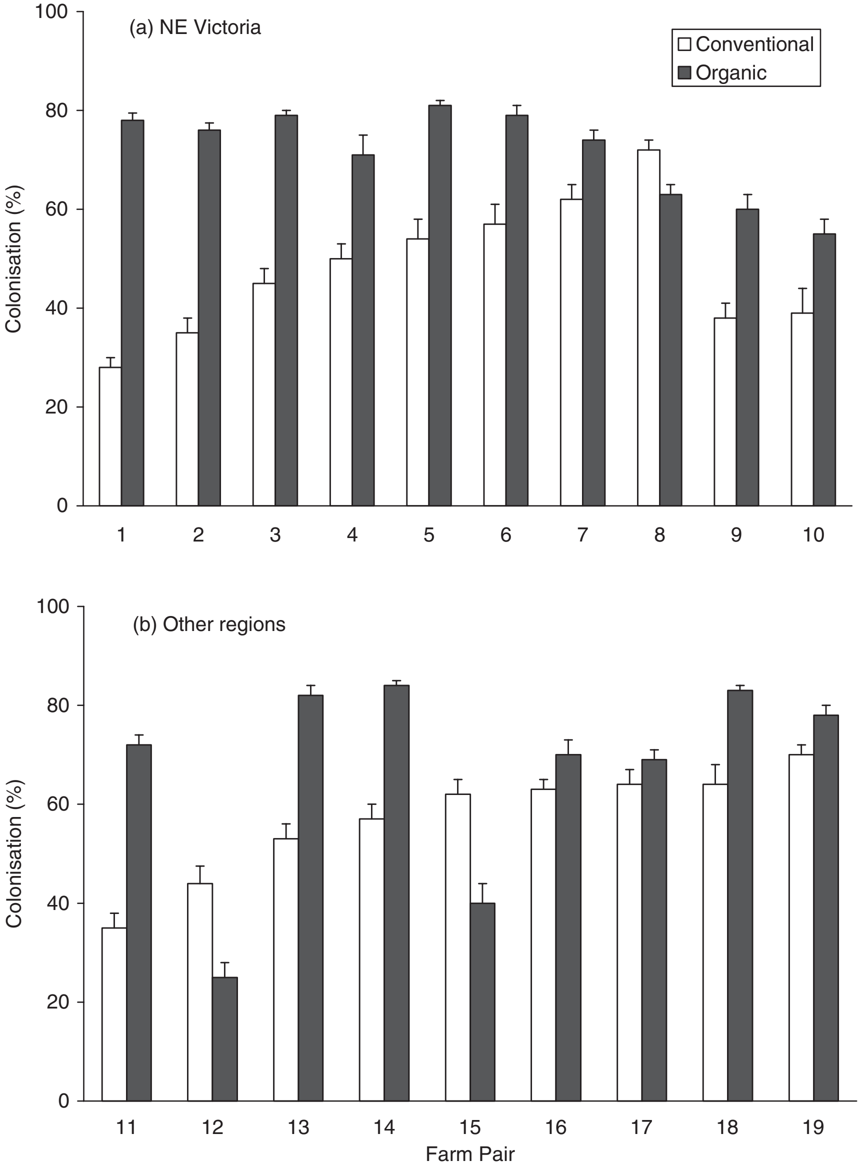

Fig. 10.1 The percentage of clover (*Trifolium* spp.) root length colonised by AMF on 19 biodynamic or organic dairy farms paired with a conventional neighbour located in (**a**) NE Victoria (Ryan et al., 2000) or (**b**) elsewhere in SE Australia (Ryan, 1998) (n = 20, mean ± SE)

Table 10.2 Soil extractable P, percentage of root length colonised by AMF and density of spores of AMF in soil from 13 conventional and 10 organic grassland sites in the United Kingdom (Eason et al., 1999)

Farm management	Soil extractable P (mg kg^{-1})	Colonisation by AMF (%)	Spore density (no. per gram dry soil)
Conventional	5.4	40.4	12.1
Organic	2.0	63.6	34.4
Significance	$P < 0.001$	$P < 0.001$	$P < 0.001$

of studies based in SE Australia included experimental investigation of the factors responsible for the differences in AMF. In addition, only a very few studies have investigated the functioning of the communities of AMF that develop on organic farms and their impact on plant nutrition or growth (Scullion et al., 1998; Eason et al., 1999; Muckle, 2003). We now examine the reasons behind the higher occurrence of AMF on organic farms through an examination of the effects of agricultural practices on AMF. The implications for plant and agricultural system function of the high occurrence of AMF on organic farms is then explored.

10.5 The Impacts of Agricultural Practices on AMF

The impacts of common agricultural practices on the abundance, community diversity and structure, and function of AMF have been examined in many review papers and books (e.g. Bethlenfalvay and Linderman, 1992; Smith and Read, 1997; Gosling et al., 2006). We will focus on areas relevant to understanding the role of AMF in organic farming and refer to other more detailed reviews as appropriate.

10.5.1 Mineral Fertilisers

Phosphorus, nitrogen (N), and potassium (K) are the nutrients most commonly applied as readily soluble fertilisers on conventional farms. On organic farms, biological N fixation by legumes is generally relied upon to supply N (e.g. Ryan et al., 2000; Ryan et al., 2004), although some N may also be supplied from composts or manures. Potassium is present in significant concentrations in manure and may also be applied on organic farms in other forms such as rock K (Watson et al., 2002). If P fertilisers are applied on organic farms they tend either to be relatively insoluble minerals such as rock phosphate or organic materials such as chicken manure or composts. Inputs of P on organic farms tend to be lower than those on conventional farms. Thus, over time, a decline in total and soil extractable P tends to occur on organic farms (Tables 10.2, 10.3; Penfold et al., 1995; Nguyen et al., 1995; Løes and Øgaard, 1997; Derrick and Dumaresq, 1999; Ryan et al., 2000; Oehl et al., 2002; van Diepeningen et al., 2006).

Table 10.3 Farming system, nutrient inputs, diversity of AMF and P budget for the DOK experiment. An identical seven year crop rotation was maintained in all farming systems

Treatment	Type of fertiliser or manure	Biocides	N	P	K	Species of AMF (field spores)[b]	Species of AMF (spores from 20 month trap cultures)[b]	P budget (1977–1988) (kg P ha^{-1} yr^{-1}) [c]
			Inputs (kg ha^{-1} yr^{-1}) [a]					
Mineral-conventional	Mineral	Synthetic	124	41	254	15	22	-5.0
Conventional	Manure, slurry plus mineral	Synthetic	154	39	258	15	24	3.8
Bio-organic	Manure, slurry	No synthetic	88	25	139	19	30	-5.7
Bio-dynamic	Manure, slurry, biodynamic preparations	No synthetic	91	22	159	17	26	-7.8
Control	No fertiliser		0	0	0	18	24	-20.9

[a] Mean nutrient inputs since 1985 (Oehl et al., 2004).

[b] Oehl et al. (2004).

[c] Oehl et al. (2002).

Readily soluble P fertiliser is often thought responsible for the lower occurrence of AMF on conventional farms (Table 10.1). While very low P supply will impede colonisation by AMF (e.g. Kelly et al., 2005), abundant P has been shown many times to reduce colonisation (Smith and Read, 1997), possibly due to a reduction in exudation of carbohydrates by roots (Graham et al., 1981). The reduction in colonisation limits the cost to the plant of supporting the AMF. Thus, readily soluble P fertiliser is most commonly reported to decrease colonisation by AMF and the density of spores in soil (Dann et al., 1996; Smith and Read, 1997; Miller and Jackson, 1998; Kahiluoto et al., 2000; 2001). The resulting increase in soil extractable P may lower colonisation levels for many years, even if no further fertiliser is added (Dekkers and van der Werff, 2001). If soil extractable P is very high, as may occur in conventional intensive horticultural systems, colonisation by AMF may be negligible (Ryan and Graham, 2002). Poorly soluble P fertilisers permitted on organic farms, such as rock phosphate, are generally reported to not reduce colonisation by AMF (Dann et al., 1996), although if applied at a rate high enough to increase soil available P presumably a negative impact on AMF would result.

In agricultural systems, negative correlations are often found between soil extractable P (or plant P status) and the percentage of root length colonised by AMF or spore density (e.g. Mårtensson and Carlgren, 1994; Cuenca and Meneses, 1996; Ryan et al., 2000). For instance, Fig. 10.2 shows high pasture foliar P strongly correlated to low colonisation by AMF of clover (*Trifolium* spp.) roots using data from 19 biodynamic or organic dairy farms paired with a conventional neighbour in SE Australia (Ryan, 1998; Ryan et al., 2000). However, even in low P soils, P-fertiliser does not always reduce colonisation by AMF (Xavier and Germida, 1997), especially if the soil is strongly P-fixing (Kabir and Koide, 2002) or the P is quickly immobilised by the microbial community. A decline in the community diversity of AMF with increasing soil extractable P, assessed by spore counts, was also reported by Cuenca and Meneses (1996), but was not found by Kahiluoto et al. (2001).

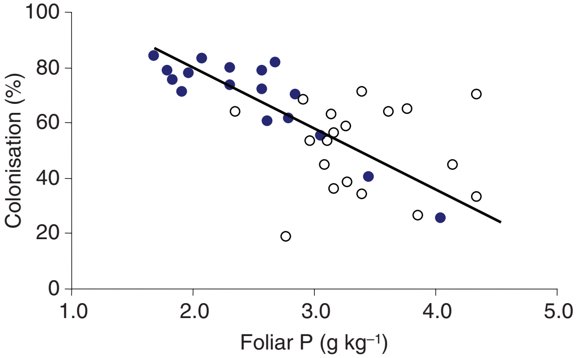

Fig. 10.2 The relationship between the percentage of clover (*Trifolium* spp.) root length colonised by AMF and whole pasture foliar P concentration for 19 biodynamic or organic dairy farms (●) paired with a conventional neighbour (○) located in SE Australia (Ryan, 1998; Ryan et al., 2000) (n = 20)

In SE Australia a series of studies clearly show readily soluble P fertiliser as the primary factor responsible for lowered colonisation by AMF on both irrigated permanent dairy pastures (Figs. 10.1 and 10.2; Ryan and Ash, 1999; Ryan et al., 2000) and conventional dryland livestock-cropping farms (Ryan et al., 1994; Dann et al., 1996). For instance, Ryan et al. (2000) compared colonisation by AMF of dairy pastures in two adjacent fields; the biodynamic field had received no P fertiliser for several decades while the conventional field had received regular applications of readily soluble P fertiliser. A strip in the conventional field had not received P fertiliser for 10 years and colonisation by AMF was higher than in the rest of the field and similar to the colonisation level in the adjacent biodynamic field. Thus the other practices of the conventional farmer, such as use of N fertiliser and biocides, and use of conventional livestock medicines, apparently had a minimal impact on colonisation level. Similarly, a glasshouse experiment undertaken by Ryan et al. (1994) suggested that readily soluble P fertiliser, but not N fertiliser, herbicides, seed fungicide dressings, wheat (*Triticum aestivum* L.) variety or soil pH, was responsible for lower colonisation by AMF on a conventional wheat farm compared with an organic neighbour. However, in these two examples, biocide inputs on the conventional farms were relatively small and for the cropping farms, rotations and tillage regimes were similar on the organic and conventional farms.

The impact on AMF of N fertiliser in agricultural systems is variable and generally does not match in magnitude the impacts of P fertiliser (e.g. Baltruschat and Dehne, 1989; Furlan and Bernier-Cardou, 1989; Ryan et al., 1994; Ryan and Ash, 1999). However, a number of recent studies in natural ecosystems have shown a shift in mycorrhizal community structure or decrease in the abundance of AMF in response to N fertiliser (e.g. Egerton-Warburton and Allen, 2000; Bradley et al., 2006). For instance, in coastal sage scrub vegetation in California, USA, Egerton-Warburton and Allen (2000) found high N was associated with displacement of the larger spored *Scutellospora* and *Gigaspora* species by small-spored *Glomus* species. The impact of K fertiliser on AMF has been little investigated, but has been reported to stimulate spore production (Furlan and Bernier-Cardou, 1989).

Fertiliser regime may be a major determinant of differences in AMF in the biodynamic, bio-organic and conventional (DOK) field experiment established near Basel, Switzerland, in 1978 (Mäder et al., 2000, 2002; Oehl et al., 2002, 2003, 2004; Hijri et al., 2006). At this site, two conventional farming treatments (mineral fertilisers only, mineral fertilisers plus farmyard manure) two organic farming treatments (bio-dynamic and bio-organic), and a non-fertilised control are subjected to identical seven year rotations, crop varieties and tillage. The treatments differ primarily in the type and amount of nutrients added and in the use of synthetic pesticides (Table 10.3). Fertiliser inputs of N, P and K have all been higher in the conventional treatments (Table 10.3). Colonisation by AMF was 30–60% higher in roots from the organic treatments than the conventional treatments (Mäder et al., 2000). Species richness of AMF, as assessed by spore abundance, was slightly higher in the organic treatments (Table 10.3) and spores of *Acaulospora* species and *Scutellospora* species were more abundant in the organic treatments (Oehl et al., 2004). While Oehl et al. (2004) concluded that higher P inputs and higher soil extractable

P in the conventional treatments (Oehl et al., 2002) were responsible for the lower colonisation and diversity of AMF, higher inputs of N and K, and lower inputs of organic matter, could also have played a role (Table 10.3).

Hijri et al. (2006) examined the diversity of AMF in five agricultural field sites, including the DOK experiment, using variable regions of ribosomal RNA genes to identify species of AMF within colonised roots. Whilst a high species diversity of AMF was found throughout the DOK experiment, low diversity and a complete absence of AMF in the genera *Acaulospora, Scutellospora, Gigaspora* and *Paraglomus* was found at two sites; a conventional intensively managed maize (*Zea mays* L.) monoculture and a leek (*Allium porrum* L.) field which had been managed organically for six years. Of the five field sites, the organic leek field had the highest soil P, due to a history of high P additions prior to conversion (soil N not given), while the maize site had the highest annual inputs of fertiliser P and N. Thus, it appears high availability of P, and perhaps N, may lower the diversity of AMF and over-ride any positive impacts from other organic management practices, including elimination of the biocides permitted in conventional farming systems.

There is some evidence that the communities of AMF that develop in frequently fertilised soils may be less beneficial to host plant growth. For instance, Johnson (1993) found use of fertiliser for eight years raised soil N from 1.6 to 8.6 mg kg^{-1} and extractable soil P from 26.5 to 62.2 mg kg^{-1} and caused the relative abundance of *Gigaspora* and *Scutellospora* species to decrease. The fertiliser addition also created a community of AMF less effective at promoting plant growth, as assessed by an indicator plant inoculated with soil from the different fertiliser treatments. These results suggest that organic farms may develop more effective communities of AMF than conventional farms due to presenting a lower P environment. This conclusion is supported by Scullion et al. (1998) who inoculated leek and white clover (*Trifolium repens* L.) growing in four soil types with spores of AMF isolated from pasture on organic or conventional farms. Shoot weight was greater with organic farm inocula in two of the four soils for leek (41 and 530%) and one of the four soils for clover (9%), although the higher colonisation levels produced by the organic inocula may have contributed to these results as well as differences in effectiveness. Overall, organic inocula were superior to conventional inocula in soil of lower P status. Similarly, Eason et al. (1999) compared growth in a low P soil of leek and white clover inoculated with spores from 13 conventional and 10 organic grassland sites (Table 10.4). The organic sites had, on average, lower soil extractable P (Table 10.2). The mean increase in yield was greater with organic inocula than the conventional inocula (Table 10.4), although some highly effective inocula were obtained from conventional farms and some relatively ineffective inocula from organic farms (Eason et al., 1999). Non-sporulating AMF and species that had not recently sporulated would have not been represented in the inocula in either study.

In summary, the prohibition of readily soluble P fertilisers in organic farming may be largely responsible for the higher levels of colonisation by AMF on organic farms and may also contribute towards a higher species diversity of AMF and development of communities of AMF with a greater ability to enhance host plant P-uptake. However, research which controls for the other management differences

Table 10.4 The response to inoculation with spores of AMF sieved from 13 conventional and 10 organic grassland sites in the United Kingdom for white clover (*Trifolium repens* L.) and leek (*Allium porrum* L.) grown in an irradiated low P soil ($n = 3$ per site, mean and range). Approximately 1000 spores were placed in each pot (Eason et al., 1999)

	Farm management	Total shoot weight (mg)	Shoot P content (mg)	Colonisation by AMF (%)
Clover	Conventional	9.4 (8.2–11.4)	7.6 (4.9–11.0)[a]	55 (0–68)
	Organic	10.3 (8.6–12.3)	8.2 (5.7–10.2)[a]	63 (44–73)
	Significance	$P < 0.05$	*ns*	*ns*
Leek	Conventional	0.39 (0.16–0.93)	0.97 (0.05–2.26)	57 (34–77)
	Organic	0.55 (0.16–1.22)	1.48 (0.37–3.30)	64 (53–76)
	Significance	$P < 0.05$	*ns*	*ns*

[a] From the third of three cuts.

between organic and conventional farms is required to confirm the impacts of fertiliser regime on diversity and function of AMF.

10.5.2 Organic Matter Amendments

Organic farmers are encouraged to apply organic amendments such as composts to the soil and plough in green manure crops and thus may apply greater amounts of organic carbon to soils (e.g. van Diepeningen et al., 2006). The impact of organic matter on colonisation by AMF seems to reflect the ease with which P is mineralised, which is highly dependent on the quality of the organic matter amendment (Smith et al., 2006). High levels of colonisation by AMF can occur after addition of high rates of compost if soil extractable P remains low (e.g. Gaur and Adholeya, 2000, 2002). Indeed an increase in extraradical hyphal length in response to organic matter addition is often noted (Gryndler et al., 2006). However, if the organic matter addition results in a rapid mineralisation of P it will act in the same manner as a readily soluble P fertiliser and have a negative impact on colonisation by AMF (Sáinz et al., 1998). Research is required to investigate the release of P and N from manure on AMF abundance and diversity.

10.5.3 Biocides

The effect of biocides, including fungicides, on AMF is complex and studies show impacts on abundance and function of AMF ranging from negative through to positive (see review by Johnson and Pfleger, 1992; and e.g. Sreenivasa and Bagyaraj, 1989; Plenchette and Perrin, 1992; Ryan et al., 1994; Udaiyan et al., 1999). For instance, Udaiyan et al. (1999) investigated the impact of six pesticide drenches at recommended rates on mycorrhizas of three cereals under field conditions. All pesticides reduced colonisation by AMF, but the impact of each pesticide often differed between host plants. The impact of the pesticides on spore density also differed between host plants with sporulation by AMF colonising *Panicum miliaceum* L. being stimulated by most of the pesticides. In contrast, Plenchette and Perrin (1992) found fungicides had minimal effect on the percentage of length of root colonised by AMF when applied after colonisation was already well established. The impact of biocides on community structure and diversity of AMF is essentially unknown, although one study does suggest that the decrease in host plant diversity that results from the use of herbicides can cause a decrease in the diversity of AMF (Feldmann and Boyle, 1999.

Thus it appears the prohibition on organic farms of many of the biocides permitted on conventional farms could contribute towards enhanced colonisation by AMF in some situations. However, biocides approved for organic farms may also be quite toxic (Edwards-Jones and Howells, 2001). For instance, Sreenivasa and Bagyaraj (1989) found copper oxychloride decreased colonisation by AMF, as well as spore density and, in particular, number of infective propagules. As noted by Gosling et al. (2006), for both conventional and organic farms there is a lack of studies, both short-term and long-term, which examine the impact of commercial biocide application regimes on AMF. Such regimes could involve several different biocides being added alone or in combination during the crop lifecycle. In a commercial context, the substantial yield benefits that can accrue from successful control of weeds, pests and diseases may outweigh any detrimental effects on AMF.

10.5.4 Tillage

Tillage or soil disturbance may reduce levels of colonisation by AMF, or reduce the effectiveness of colonisation, by disrupting the CMN (Miller, 2000). It is hypothesised that the ability to tap into an intact CMN allows fast colonisation of new roots and fast uptake of nutrients early in the season. As well as disrupting the CMN, excessive tillage or soil disturbance can greatly reduce subsequent colonisation by AMF (Mulligan et al., 1985) due to the destruction of inoculum (Jasper et al., 1991; Boddington and Dodd, 2000). However, in situations where inoculum concentrations are initially very high, sufficient inoculum may remain following tillage to ensure high levels of colonisation are quickly produced (Jasper et al., 1991). For instance, in the organic wheat crop examined by Ryan et al. (1994), 60% of root length was colonised 11 weeks after sowing even though the soil had been inverted with a mouldboard plough, left as a bare fallow for seven months, and then cultivated twice prior to sowing.

Tillage is known to have a significant effect on community structure of AMF. A number of recent studies have found that *Glomus* species predominate in cropping soils and it has been suggested that tillage may favour this genus (Land and Schönbeck, 1991; An et al., 1993; Helgason et al., 1998; Ezawa et al., 2000; Daniell et al., 2001; Jansa et al., 2002). For instance, Jansa et al. (2003) used PCR markers to examine roots of maize crops grown in an experiment established in 1987 and cropped continuously using a number of tillage treatments. Whilst tillage had little impact on *Gigaspora* species, colonisation by *Scutellospora* species was dramatically higher in no-tillage plots and there was an increased incidence of *Glomus* species in the tilled plots. Boddington and Dodd (2000) found soil disturbance caused the spore density of *Scutellospora* species to be greatly reduced; spore density of *Glomus* species was also reduced, while *Acaulospora* spore density was unaffected. Tillage may also reduce the species diversity of AMF (Menéndez et al., 2001). However, in Sweden, little difference was found in spore numbers or species diversity of AMF between semi-natural grassland and ploughed fields (Sjöberg et al., 2004).

Whilst a move towards low-tillage or no-tillage cropping has occurred in agricultural systems around the world, encouraged by benefits for soil structure and reduced soil erosion, such systems usually rely on herbicides for weed control, often making their adoption by organic farmers problematic. In addition, the restrictions on use of biocides on organic farms could result in increased tillage and soil disturbance in order to achieve adequate weed control. Although, in some circumstances, the greater use of pasture leys on organic farms could result in the net amount of tillage being lower on organic farms.

10.5.5 Rotations and Agricultural System

Perhaps the greatest impact of rotation on AMF can occur from a bare fallow. During a bare fallow AMF persist in the soil only as inactive inoculum in the form of spores, hyphae and colonised root segments (Bellgard, 1992; Jasper et al., 1993). Consequently the density of inoculum declines over time (Troeh and Loynachan, 2003) and colonisation is usually reduced in following crops (Thompson, 1987; Kabir and Koide, 2002; Ryan et al., 2002). In some instances this reduction in colonisation has corresponded to reduced crop uptake of P and Zn and a corresponding reduction in crop growth and yield (Thompson, 1987; Kabir and Koide, 2002). Non-host plants such as brassicas may act in the same manner as a bare fallow, providing there is no significant presence of weeds that host AMF (Ryan et al., 2002). The impact of bare fallows and non-hosts can be alleviated by the presence of plants that host AMF. For instance, in Pennsylvania, USA, the replacement of bare fallow with a rye (*Secale cereale* L.) or oats (*Avena sativa* L.) cover crop increased colonisation by AMF, shoot dry weight, shoot height and yield of marketable ears of following sweet corn (*Zea mays* L.) (Kabir and Koide, 2002). Bare fallows and non-host crops may not always have a negative impact on AMF. In western New South Wales, Australia, long fallow cotton (*Gossypium hirsutum* L.) (cotton, alternating with a bare fallow, is sown every other year) had similar colonisation by AMF to continuous cotton (Hulugalle et al., 1998). Low mean annual rainfall may have contributed towards a low rate of inoculum death.

An increase in plant diversity in a field or during the course of a rotation may increase AMF colonisation levels. For instance, in California, USA, Werner (1997) speculated that an increase in weeds was the cause of apple (*Malus domestica*

Borkh.) trees managed organically having higher colonisation than conventionally grown apples. In Indonesia, the density of AMF extraradical hyphae under maize grown in a monoculture was less than when maize was grown in an agroforestry system with a tropical tree legume (Boddington and Dodd, 2000).

Community structure and diversity of AMF can be quickly influenced by host crop and therefore by crop rotations (An et al., 1993; Daniell et al., 2001; Bever, 2002; Troeh and Loynachan, 2003). Thus monocultures of different crops may build up markedly different communities of AMF. For instance, in central Iowa, USA, after three years of cropping, *Glomus albidum* and *G. etunicatum* spores dominated under corn, while *G. constrictum* spores dominated under soybean (*Glycine max* (L. Merrill) (Troeh and Loynachan, 2003). Johnson et al. (1991) also observed distinct communities of AMF in plots with either corn or soybean cropping histories. Further experimentation suggested the communities were detrimental to yield of the crop they proliferated under, but beneficial to the other crop (Johnson et al., 1992).

There is some indication that an increase in plant diversity will lead to an increase in the species diversity of AMF. In a non-agricultural field experiment in Minnesota, USA, as plant diversity increased from one to 16 plant species per plot, sporulation and species numbers of AMF were increased and, in particular, sporulation by larger-spored *Gigaspora* and *Scutellospora* species was increased (Burrows and Pfleger, 2002). These relationships may have been mediated through factors such as midseason soil nitrate concentrations, plant density and specificity between host plants and species of AMF (Burrows and Pfleger, 2002). Feldmann and Boyle (1999) examined the impact on maize of removing all weeds, removing only weeds that host AMF or removing weeds that were non-hosts. The maize monoculture developed the least diverse community of AMF. When maize plants were later inoculated with each community of AMF, the community from the monoculture was the least effective at promoting growth. In western Kentucky, USA, An et al. (1993) found a higher species richness and higher diversity of AMF when crops were rotated than when soybean was continually grown, but only early in the season.

Eight sites in Europe with differing levels of plant diversity were examined by Oehl et al. (2003). Three sites were low-input very species rich grasslands, two sites were treatments in the DOK experiment which were farmed with a seven year rotation involving three years of grass-clover meadow as well as a range of crops, and three sites were high input continuous maize cropping. Spores of AMF were examined in soil samples and in trap cultures. The number of spores and species of AMF declined with decreasing plant diversity. However, strong conclusions can not be drawn from this experiment about the importance of plant diversity as lower plant diversity was correlated with increased farming intensity (i.e. increased inputs of P and N and tillage intensity).

In a farming system trial at the Rodale Institute Experimental Farm in Pennsylvania, USA, 15 years of more diverse rotations in the low-input treatments did not result in any substantial increase in species diversity of AMF (Franke-Snyder et al., 2001) with one species, *Gigapsora gigantean*, accounting for more than 60% of spore volume in most treatments. Franke-Snyder et al. (2001) speculated that the homogenised AMF diversity and failure to develop greater diversity in the low-input treatments reflected very high soil extractable P, 50–90 kg yr^{-1} of N inputs, and mouldboard ploughing of all treatments.

Organic farms do tend to support greater plant diversity than conventional farms (Gabriel et al., 2006) due to the importance of legumes for provision of N and the ensuing requirement for longer pasture leys than conventional farms, higher occurrence of weeds and a strong emphasis on crop rotation for control of weeds, pests and diseases (Watson et al., 2002). It seems high plant diversity could result in an increased species diversity of AMF and, perhaps, a community of AMF more beneficial to plant growth. Other characteristics of rotations likely to favour AMF, such as absence of non-host crops, may more reflect the nature of the agricultural system or preferences of individual farmers than whether a farm is under organic or conventional management.

10.5.6 Summary – The Combined Effect of Agricultural Practices on AMF

The abundance, community diversity and structure, and function of AMF are affected by many agricultural practices. While many studies have not examined farm management practices individually, it does appear that a reduction in abundance and community diversity of AMF is most likely to result from application of fertilisers which readily supply P to plants, as well as tillage and inclusion of bare fallows or non-host crops in rotations. The biocides used on conventional farms, and perhaps organic farms, may reduce abundance of AMF in some circumstances, although their impact on community diversity of AMF is unknown. There is some evidence that a more diverse community of AMF can develop if there is an increase in the diversity of plants within a rotation. Thus, the frequent finding of a higher abundance of AMF on organic farms than conventional farms – and the tendency towards a greater diversity of AMF on organic farms – most likely results from the elimination of readily soluble P fertilisers and the implementation of a more diverse rotation. Also, there is some evidence that less beneficial communities of AMF may develop under conditions of high P availability and in monocultures. However, organic farm management does not guarantee a high abundance of AMF and when factors such as high soil available P, frequent tillage or low crop diversity occur on organic farms the occurrence of AMF may be similar to, or lower than, on conventional farms.

10.6 Impacts of AMF in Agricultural Systems

In regards to agriculture, AMF are best known for their ability to enhance growth of plants due to their ability to increase plant P uptake. We will explore whether high levels of colonisation on organic farms automatically confers an important role for AMF in crop nutrition and growth and whether AMF can be considered as biological fertilisers. The non-nutritional impacts of AMF on host plants and on agricultural system sustainability are then examined.

10.6.1 Host Plant Growth

10.6.1.1 Biomass and Yield

AMF are generally regarded to have a positive effect on growth and yield of crop and pasture plants. A recent meta-analysis of mycorrhizal impact on agricultural plants grown in the field in non-sterilised soil found that inoculation with AMF increased yield by an average of 34% ± 9% (mean ± 95% CI) (Lekberg and Koide, 2005a). McGonigle (1988), using a different data set, found the average yield response of agricultural plants to inoculation in the field to be 37%.

The impact of the indigenous community of AMF on crop growth can be harder to quantify as eliminating or reducing colonisation for the purposes of comparison also changes other factors (e.g. Khasa et al., 1992). For instance, in the meta-analysis carried out by Lekberg and Koide (2005a), an increase in colonisation by AMF due to a shortened bare fallow had a very variable impact on yield with an average increase of 27 ± 21% (mean ± 95% CI). A positive response to increased colonisation was most likely at low soil extractable P ($<5\text{mg kg}^{-1}$) and at sites where inoculum potential was low (<5% root length colonised) (Lekberg and Koide, 2005a). Unfortunately, such sites may be very much over-represented in the literature as studies are often carried out at sites where a response to inoculation is expected (e.g. eroded or reclaimed soils, or subsoils) (Lekberg and Koide, 2005a). The prevalence of such sites in established agricultural systems, especially on organic farms, may not be high as low soil extractable P is likely to correspond to high colonisation by AMF and high inoculum concentrations (e.g. Fig. 10.2). Thus while AMF are most commonly reported to have a beneficial effect on crop growth and yield, currently it is not possible to confidently predict the importance of AMF for a particular situation without experimentation. This situation reflects our limited understanding of how farm management and environmental variables affect the mycorrhizal symbiosis.

For instance, while arbuscular mycorrhizas are traditionally thought of as mutualisms, increasingly AMF are considered to function along a continuum from highly parasitic to highly beneficial (Johnson et al., 1997; Jones and Smith, 2004; Egger and Hibbett, 2004). The reliance of AMF on host photosynthate for all their energy requirements (Ho and Trappe, 1973) means a parasitic impact can occur if no benefits accrue to the plant (Johnson et al., 1997). Indeed, in their meta-analysis, Lekberg and Koide (2005a) found biomass of crops was significantly reduced in 2% of experiments where colonisation by AMF was increased. This could reflect plants not requiring the P supplied by the fungi, which could occur under conditions of high soil P or if other growth limiting factors were present (Jones and Hendrix, 1987; Graham and Eissenstat, 1998; Khaliq and Sanders, 2000; Kahiluoto et al., 2001). Alternatively, parasitic impacts could occur if plant carbon reserves were limited, such as under conditions of low light (Son and Smith, 1988), or if the fungi were unable to supply nutrients for a reason such as low temperatures (Cooper and Tinker, 1981). Under field conditions, seasonal fluctuations in climate and changes in the lifecycle stage of the host plant and AMF may result in the impact of AMF oscillating between beneficial and parasitic (Bethlenfalvay et al., 1982; Pearson and Schweiger, 1993; van der Heijden, 2001; Lerat et al., 2003; Ryan et al., 2005). This makes untangling the impact of AMF on crop growth complicated. For instance, if a crop finishes under dry conditions a mycorrhizal-induced increase or decrease in early biomass could greatly impact on available soil water during grain filling and thereby influence grain yield (e.g. Weber et al., 1993; Ryan et al., 2005).

10.6.1.2 Mycorrhizal Dependency

The benefit to agricultural crops from the presence of AMF can differ greatly between crop species (Plenchette et al., 1983; Khasa et al., 1992). This effect is termed "mycorrhizal dependency" and is defined as:

$$\frac{\text{weight of the colonised plant} - \text{weight of the uncolonised plant}}{\text{weight of mycorrhizal plant}} \times 100$$

In general, under P limiting conditions, plants with thick roots with few, short, thick root hairs will be most dependent on AMF and plants with finer roots and more, longer and thinner root hairs are likely to be less dependent on AMF as they can adequately access P without AMF (Crush, 1974; Baylis, 1975; Schweiger et al., 1995). Thus, grasses are often less dependent on AMF than legumes (Plenchette et al., 1983). Highly dependent crops include the onion family (*Allium* spp.), flax (*Linum usitatissimum* L.) and most legumes (Owusu-Bennoah and Mosse, 1979; Plenchette et al., 1983; Thompson, 1987; Schweiger et al., 1995; Kahiluoto et al., 2001). For legumes, the high P requirements for adequate nodulation and N-fixation also contribute towards high dependency (Crush, 1974).

Generalising about mycorrhizal dependency at a broad level can be problematic as dependency can vary with crop species and cultivar (Khalil et al., 1994; Hetrick et al., 1996; Xavier and Germida, 1997), species of colonising AMF (Graham and Abbott, 2000; Klironomos, 2003) and with environmental conditions such as the level of soil available P. For instance, mycorrhizal dependency in *Citrus* varies with host genotype (Graham et al., 1997), with high dependency linked to a relatively loose regulation of carbon expenditure on AMF (Jifon et al., 2002). Thus, highly dependent genotypes benefit from AMF at low P supply but are more likely to suffer a growth depression when P is plentiful (Jifon et al., 2002). The retention of an ability to form mycorrhizas in relatively poorly dependent plants such as grasses may indicate AMF influence host plants in areas unrelated to P nutrition, such as disease control (Newsham et al., 1995). On organic farms a reliance on legumes for N fixation, a tendency for more diverse rotations, and low soil available P may mean a greater number of highly dependent crops are grown than on conventional farms.

It has been suggested that modern crop breeding practices, especially the selection of crops under conditions where P is not limiting, may have resulted in modern cultivars generally possessing low mycorrhizal dependency and/or a poor capacity to become colonised by AMF (e.g. Hetrick et al., 1993). If this was the case, older or unimproved cultivars would be more suited to the low soil available P often found on organic farms, both for maximising yield benefits from AMF and obtaining other benefits such as disease control. Evidence for this hypothesis is sparse, with studies generally conducted under glasshouse conditions and often including only a few breeding lines. For instance, Khalil et al. (1994) examined three improved and three unimproved lines of corn and soybean (*Glycine soja* Siebold and Zucc. and *G. max* L.). Colonisation was uniformly high, but considerable variability in mycorrhizal dependency was evident across improved and unimproved lines. However, responsiveness to AMF does appear heritable (Azcón and Ocampo, 1981; Hetrick et al., 1992, 1993, 1996), and organic farmers may benefit from crop selection under low soil available P conditions for high mycorrhizal dependency and a high degree of mycorrhizal colonisation.

10.6.1.3 Impact of Location and Agricultural System

Both environmental and cultural characteristics of an agricultural system may determine the degree of reliance of crops on AMF for nutrient uptake and growth. Crops may be highly reliant on AMF in systems with one or more of the following characteristics: soil low in available nutrients particularly P; soil which causes fertiliser P to quickly become unavailable to crops; favourable conditions for rapid crop growth (i.e. high light levels, warm temperatures and adequate water) (e.g. irrigated summer crops); regular inclusion of dependent crops in rotations; and little addition of fertiliser (e.g. organic farms, developing countries). In particular, temperature may play an important role in delineating levels of colonisation and activity by AMF (Cooper and Tinker, 1981; Koske, 1987; Gavito et al., 2005). However, the impacts of temperature minimum or range are rarely examined in studies of AMF, perhaps due to methodological difficulties in both the field and the glasshouse (Tibbett and Cairney, 2007).

Many agricultural systems in the tropics and subtropics, which are often in developing countries, meet many of these criteria listed above (Khasa et al., 1992; Runge-Metzger, 1995; Lekberg and Koide, 2005b). For instance, in the subtropical NE cropping zone of Australia, low colonisation by AMF following long bare fallows can be associated with poor P and zinc (Zn) nutrition and low yields in following crops; a situation termed *long fallow disorder* (Thompson, 1987, 1994, 1996). Yet when crops are grown after bare fallows or non-host crops in the SE cropping zone of Australia, colonisation by AMF is reduced but growth and yield are often increased, suggesting AMF are generally parasitic in this region (Ryan et al., 2002, 2005; Ryan and Angus, 2003) and high colonisation may be contributing to low yields on organic farms (Kitchen et al., 2003; Ryan et al., 2004). The parasitic impact of AMF in SE Australia, which occurs primarily before anthesis for autumn-sown crops, could reflect soil temperatures below 5 °C reducing the ability of AMF hyphae to transport P, combined with short winter days and low light levels, at a time when AMF carbon demands are at a peak (Ryan et al., 2005).

10.6.2 Host Plant Nutrition

Increased plant uptake of P in the presence of AMF has been shown on many occasions (Smith and Read, 1997; Clark and Zeto, 2000) and is greatest when P is limiting (Schweiger et al., 1995; Smith and Read, 1997). The enhanced uptake is thought to result from the exploration of a greater volume of soil by colonised plants due to the growth of the extraradical hyphae of AMF past the nutrient depletion zones that form around roots (Jakobsen et al., 1992a,b). The enhancement of P-uptake by AMF has often been observed to increase nodulation by rhizobia and thereby indirectly enhance plant N nutrition (Lekberg and Koide, 2005b). Recent work also shows AMF are capable of transferring large amounts of N from the soil to plant roots (Govindarajulu et al., 2005) and there are some reports of AMF increasing host plant N uptake in both legumes and non-legumes (e.g. Gaur and Adholeya, 2002). Nitrogen may be transferred from legumes to non-legumes through the CMN (He et al., 2003).

AMF may also affect plant uptake of other nutrients including sulphur, boron, K, calcium, magnesium, sodium, Zn, copper, manganese, iron, aluminium, silicon and some other trace elements (Clark and Zeto, 2000). The impact of AMF on these elements can be positive, neutral or negative depending on soil type, host plant and other factors. A recent review by Clark and Zeto (2000) concluded that the nutrients most commonly enhanced in host plants by AMF are P, N, Zn and Cu, with K, Ca and Mg enhanced when plants are grown in acidic soils. Mn uptake is often reduced in mycorrhizal plants (Kothari et al., 1991). The tendency of AMF to decrease the root-shoot ratio of the host plant (e.g. Weber et al., 1993) may result in poor host uptake of nutrients in some instances (e.g. Ryan and Angus, 2003). AMF may also alleviate toxicities of some elements (Clark and Zeto, 2000).

Enhanced uptake of P by AMF has traditionally been thought to reflect increased access to soil available P (Bolan, 1991). However, the ability of AMF to access P from poorly soluble P sources is important when considering the role of AMF on organic farms as fertiliser P is often applied in either organic forms (e.g. composts, manure) or in poorly soluble mineral forms (e.g. rock phosphate). Moreover, an ability to increase weathering of P from insoluble forms in soil is the only means by which AMF can aid in the maintenance of a positive P balance for organic farms. If this does not occur, the ability of AMF to enhance plant P-uptake and crop yields also increases losses of P in farm products. AMF can enhance plant uptake of P from organic sources such as phytate due to the production of extracellular phosphatase by extraradical hyphae (Tarafdar and Marschner, 1994; Koide and Kabir, 2000). Recent evidence also suggests hyphae of AMF produce exudates such as citric acid that can aid with solubilisation of poorly soluble forms of inorganic P (Tawaraya et al., 2006). However, the impact of AMF on plant access to organic and insoluble inorganic P in an agricultural context is unknown and may not be large.

The contribution of AMF to crop P uptake has not been directly compared between organic and conventional farms. However, as soil extractable P is generally lower on organic farms than conventional farms and colonisation by AMF correspondingly higher, it should be safe to assume that AMF play a greater role in crop P nutrition on organic farms. A trend towards greater effectiveness in enhancing P uptake for AMF from organic farms was reported by Scullion et al. (1998) and Eason et al. (1999) (Table 10.4). Similarly, Muckle (2003) found P-uptake from root-free mycorrhizal compartments was around 80% higher in soil from organic wheat fields than conventional wheat fields.

Little information is available on the role of AMF on organic farms in the uptake of elements other than P. For organic wheat crops in SE Australia, Ryan et al. (2004) found concentrations in grain of Zn and copper (Cu) were higher, and concentrations of manganese (Mn) and P were lower, than in grain of conventional crops. Colonisation by AMF was 2–3 times higher in the organic crops. A series of related glasshouse and field experiments suggested that higher colonisation by AMF on the organic farms was responsible for the higher Zn and partly responsible for the lower Mn, with other agronomic factors affecting Cu, P and, partly, Mn (Dann et al., 1996; Ryan and Angus, 2003; Ryan et al., 2004). A further study found that the differences in grain Zn bioavailability between the organic and conventional grain were significant for human nutrition (Ryan et al., 2008). Graham et al. (2000) also found lower P and higher Zn concentrations in grain of organic crops of SE Australia in comparison to conventional crops.

Indeed, impacts of AMF on product quality generally seem related to enhanced grain nutrient concentrations (e.g. Kahiluoto et al., 2001), although Gupta et al. (2002) found inoculation with AMF enhanced oil content and essential oil yield of menthol mint (*Mentha arvensis* L.). For instance, in California, USA, Cavagnaro et al. (2006) compared a tomato (*Lycopersicon esculentum* Mill.) mycorrhizal defective mutant and its mycorrhizal wildtype and found AMF had little impact on yield, but enhanced fruit Zn concentration by around 24%. Although, as fruit P concentration was also enhanced by 41%, the additional Zn may have been bound in forms unavailable to human digestive systems such as phytate (Adeyeye et al., 2000).

10.6.3 Can AMF Substitute for Fertilisers?

AMF are sometimes considered as a biological substitute for P fertiliser. However, AMF can only aid crops in the depletion of a finite pool of P that will eventually need replenishment. In addition, AMF are unlikely to be as efficient as a readily soluble P fertiliser at enhancing plant P uptake as all their energy requirements come from host plant photosynthate (Ho and Trappe, 1973) and P release to the plant may not match the timing of plant P requirements. Comparing the impacts on plant growth of readily soluble P fertiliser and AMF in sterilised soil is essentially a comparison between plants supporting high colonisation in a low P environment (no fertiliser) and plants with low colonisation in a high P environment (plus fertiliser). The results of such comparisons vary (e.g. Rangeley et al., 1982), but the fertilised plants often grow best (Al-Karaki, 2002; Ortas, 2003; Ryan and Angus, 2003), even in soil from organic farms (Dann et al., 1996; Ryan and Ash, 1999).

Thus, the higher abundance and diversity of AMF on organic farms does not mean yields will match those of conventional farms with similar rotations, but higher soil available P and a lower abundance of AMF. For instance, in the DOK experiment, crops yields were 20% lower in the organic treatments due largely to low K supply and disease (Mäder et al., 2002). While colonisation by AMF was 40% higher in the organic treatments (Mäder et al., 2000), P-budgets were negative and yields were maintained using native soil reserves of P or residual P from earlier fertiliser applications (Oehl et al., 2002). In SE Australia, colonisation by AMF was higher in 9 of 10 paired biodynamic and conventional irrigated permanent dairy pastures, but soil extractable P and pasture shoot P were lower and P deficiency appeared responsible for lower milk yields on the biodynamic farms (Table 10.5; Burkitt et al., 2007a,b). Whilst AMF were presumably important for pasture P-uptake on the biodynamic farms, the fungi could not match the P supplied to conventional pastures in readily soluble fertiliser and, more importantly, could not compensate for P lost in farm products. Soil extractable P was declining over time for the biodynamic pastures (Table 10.5; Burkitt et al., 2007a).

Significant imbalances exist in global P management and many developing countries which have agricultural systems with low external inputs (Latin America, Sub-Saharan Africa and Asia) also have P as a constraining factor for increasing yield (Runge-Metzger, 1995) and soils with high P fixation capacities. AMF cannot overcome P shortages in such situations as they primarily provide P to plants from existing pools of soil available P. Thus, limiting inputs of readily soluble P in order to favour AMF may dangerously restrict yields. In both industrialised and developing countries returning some of the P lost from farms in produce, i.e. returning animal wastes, sewage and food wastes (Kirchmann and Ryan, 2004) is important to increase the sustainability of agricultural systems (although often not currently permitted by organic farming regulations). Doing so in a manner not detrimental to

Table 10.5 Nutrient inputs, soil and pasture nutrient concentrations, the percentage of root length colonised by AMF, milk yield and P-budget for 10 paired biodynamic and conventional dairy farms in SE Australia. All sampled fields were under permanent perennial irrigated pasture (Ryan et al., 2000; Burkitt et al., 2007a; b)

Characteristics	Conventional	Biodynamic	Significance
	Superphosphate, diammonium phosphate or urea	No P fertilisers	
N input (kg ha^{-1} yr^{-1})	17	none	–
P input (kg ha^{-1} yr^{-1})	27	none	–
Soil extractable P (mg kg^{-1})	18.0	8.4	$P < 0.002$
Pasture foliar P (g kg^{-1})	3.3	2.4	$P < 0.00001$
Pasture foliar N (g kg^{-1})	20.1	21.1	ns
Clover colonisation by AMF (%)	48	71	$P < 0.0004$
Grass colonisation by AMF (%)	38	48	$P < 0.02$
Milk yield (L yr^{-1} cow^{-1})	4585	3436	$P < 0.001$
P budget (kg P ha^{-1} yr^{-1})	15.9	−7.3	–

the abundance of AMF would allow the other benefits from AMF to be realised, but as this would involve restricting the solubility of P, it may not maximise yields.

10.6.4 Non-nutritional Impacts

The water balance of host plants, both adequately watered and droughted, can be influenced by AMF (Augé, 2001). In particular, AMF are frequently reported to improve drought avoidance, often due to improved P nutrition (Augé, 2001). While a recent review by Augé (2001) concluded that the effects of AMF on the water balance of host plants are often "subtle, transient and probably circumstance and symbiont specific", in terms of plant growth and reproduction, such small effects may still be very significant over time. For instance, Klironomos et al. (2001) showed that the impact of drought on colonisation by five species of AMF isolated from an old-field meadow in Canada differed from positive to negative and suggested that the association of particular plants with particular AMF could confer a competitive advantage at certain times. Perhaps the tendency for higher diversity of AMF on organic farms may confer more advantage in regards to plant water relations than the generally high levels of colonisation.

Many studies have also indicated that AMF can play a role in controlling plant diseases (Whipps, 2004). Most studies involve soil-borne fungal pathogens although bacterial pathogens have also been investigated (Whipps, 2004). For instance, Thompson and Wildermuth (1989) reported an inverse correlation between colonisation by AMF and infection by the fungal pathogen *Bipolaris sorokiniana*. Control of nematodes has also often been shown. While results of studies vary, a degree of control of these three groups of pathogens is generally reported. Foliar pathogens, conversely, are often stimulated by AMF presumably due to improved nutrition and greater physiological activity in mycorrhizal plants (Whipps, 2004). The mechanisms behind disease control by AMF are not well understood and the control is most likely the outcome of interactions between numerous mechanisms (Harrier and Watson, 2004). However, relatively few studies investigate the impact of AMF on pathogens under field conditions, partly due to methodological difficulties with such studies. Certainly, high colonisation by AMF is no guarantee of an agronomically relevant degree of pathogen control (Bødker et al., 2002; Ryan et al., 2002). Overall, the impacts of an enhanced community of AMF, as may occur on organic farms, on pathogen control is likely to be minor compared to its impact on plant nutrition and, perhaps, soil structure.

10.6.5 Agricultural System Sustainability

AMF can be considered as a bridge between plants and the soil ecosystem (Bethlenfalvay and Schüepp, 1994). The contribution by AMF of plant photosynthate to soil carbon pools is substantial. For example, Johnson et al. (2002) found that within 21 h of pulse-labelling a grassland sward, between 5 and 8% of the fixed ^{13}C lost by shoot respiration and translocation was passed through the extraradical hyphae of the colonising AMF through the soil to the atmosphere. AMF also directly impact on other soil organisms and vice versa through a variety of mechanisms and may act synergistically with other soil organisms to aid plant growth (see reviews by Douds and Johnson, 2003; Artursson et al., 2006). While AMF obviously have a large effect on the soil biological community, this is not discussed further in this chapter as the application of this knowledge to management of agricultural systems is currently not possible. Instead we briefly consider the impact of AMF on soil structure, and plant community structure and diversity.

10.6.5.1 Soil Structure

The extraradical hyphae of AMF aid in the maintenance of soil structure by assisting roots in entangling and enmeshing soil particles to form macroaggregates (Tisdall and Oades, 1979; Jastrow et al., 1998). For instance, in Pennsylvania, USA, Kabir and Koide (2002) reported a significant positive linear relationship between the density of AM fungal hyphae and aggregate stability under a sweet corn crop. In organic tomato production, Cavagnaro et al. (2006) found the presence of AMF improved aggregate stability in a poorly structured soil when N was also applied. Hyphal architecture can vary greatly between species of AMF (Jakobsen et al., 1992a) and the impact of AMF on soil aggregation can vary with AMF-host species combinations (Piotrowski et al., 2004). Piotrowski et al. (2004) found hyphal lengths of AMF and root biomass were not positively correlated with aggregation, which suggested that other physiological or architectural mechanisms were also important. One possible mechanism is glomalin.

Glomalin is a fungal protein (or class of protein) that is quantified from soil as glomalin-related soil protein (GRSP) (Wright and Upadhyaya, 1998; Rillig and Mummey, 2006). Glomalin is thought to act as a glue with hydrophobic properties, although actual biochemical evidence for this is not available (Rillig and Mummey, 2006). Several recent studies show GRSP to be positively correlated with water stabile soil aggregates in both natural and agricultural ecosystems (e.g. Rillig et al., 2002). For instance, Wright et al. (1999) found as the number of years of no-tillage increased, so too did aggregate stability and total glomalin, while Wright and Anderson (2000) found aggregate stability and glomalin varied together with crop rotation. Further research is required to better understand both the contribution of AMF to accumulation of GRSP and the impact of GRSP on aggregation and, perhaps, other soil processes. Increased production of GRSP is likely to be a benefit arising from high levels of colonisation by AMF on organic farms and may contribute to higher aggregate stability in soils on organic farms (e.g. Mäder et al., 2002).

10.6.5.2 Plant Community Structure and Diversity

In natural ecosystems AMF appear important in determining plant community structure (Hetrick et al., 1994; Klironomos et al., 2001; O'Connor et al., 2002). For instance, Klironomos (2003) inoculated a single local isolate of AMF onto 64 local plants with growth responses, compared to non-inoculated controls, ranging from −46 to +48%, suggesting no single "mycorrhizal effect", but a series of plant-fungal symbioses with differing effect. It was speculated that a high degree of variation in plant response to AMF may be a large contributor to plant species co-existence (Klironomos, 2003). There is also evidence to suggest that AMF may allow maximum productivity with fewer plant species, as the fungi allow greater access to soil resources (Klironomos et al., 2000). An increased diversity of species of AMF may have a strong positive effect on plant community diversity and productivity (van der Heijden et al., 1998). Thus in situations such as permanent pastures a diverse community of AMF may be more important for maximum yields to be obtained on nutrient-limited organic farms than on conventional farms and may also play a role in the maintenance of high plant diversity.

10.6.6 Summary – The Impact of AMF in Agricultural Systems

In agricultural systems where P is limiting plant growth, AMF may make an important contribution to host plant P nutrition, growth and yield. However, this contribution will vary between locations and agricultural systems for reasons that are not yet fully understood. Beneficial impacts of AMF on host plants resulting from enhanced uptake of other nutrients, and improvements in drought avoidance and disease control, may also occur in some instances. AMF may be necessary for maintaining the long-term stability and sustainability of agricultural systems through their influence on other components of the soil biological community, soil structure and, in permanent vegetation, plant community structure and diversity. As organic farms generally support high colonisation levels by AMF, they may harness more of the beneficial impacts of AMF than conventional farms and may benefit from crop breeding programs with a focus on increasing mycorrhizal dependency and the degree to which host plants become colonised. However, AMF do not substitute for external inputs of P and there may be a trade-off between supplying P in a form that maximises yield and the occurrence of AMF.

10.7 Do Agricultural Systems Select for "Weedy" AMF?

As discussed above, in natural ecosystems the host plant growth response to AMF may vary from highly parasitic to highly beneficial and this may be an important contributor to plant species co-existence (Klironomos, 2003). However, agricultural systems in industrialised countries are generally managed with the goal of maximising plant productivity, not diversity, and the long-term relationship between the communities of AMF and their host plants has been disrupted by regular applications of fertiliser and regular reseeding with crop and pasture species selected off-farm for maximum yield under well-fertilised conditions. Under these circumstances, the benefits to AMF from contributing to host plant growth and nutrition and thereby ensuring persistence of host species will be reduced and the fungi may act to maximise their own fitness at the expense of the host plant. Thus, Kiers et al. (2002) suggest that modern agricultural practices will select for less mutualistic, “weedy”, mycorrhizal associations.

There is some evidence that agricultural practices do select for less beneficial AMF, particularly application of fertilisers, maintenance of monocultures and, perhaps, tillage (Johnson et al., 1991, 1992; Johnson, 1993; Scullion et al., 1998; Eason et al., 1999; Feldmann and Boyle, 1999; Menéndez et al., 2001; Kiers et al., 2002). Indeed, a positive plant growth response to inoculation with exotic AMF, even when colonisation by indigenous AMF is high (Owusu-Bennoah and Mosse, 1979; Plenchette et al., 1981; Rangeley et al., 1982; Ortas, 2003), could reflect the exotic AMF not originating under the farm management and host crops present in the target agricultural system.

Characteristics of less beneficial species of AMF could include a tendency to colonise roots slowly, but sporulate rapidly (Oehl et al., 2003), and a tendency for a greater proportion of colonisation to consist of fungal storage structures (vesicles) at the expense of hyphae and arbuscules (Johnson, 1993). Interestingly, Oehl et al. (2003) found more rapid spore formation from isolates of individual species of AMF when they originated from cropped soils in comparison to grassland soils. This suggests that changes in the function of the mycorrhizal community can occur not only through a shift in relative abundance of species, but also through development of ecotypes of individual species of AMF.

Whether organic farms would be susceptible to development of “weedy” communities of AMF is unclear, but certainly the prohibition of readily soluble P fertilisers and a tendency towards higher plant diversity could prove beneficial in this regard. The impact of a community of AMF with reduced benefit for crop growth on other ecosystem-level benefits of AMF, such as improved soil structure is unknown.

10.8 Inoculation with AMF

There is great interest in the use of inoculum of AMF in agricultural systems, based on the assumption that any introduction is likely to be beneficial for crop nutrition, crop yield and agricultural system sustainability (Gianinazzi and Vosátka, 2004). Indeed, there are greater than 33 companies currently engaged in the production of AM fungal inoculum for use in agriculture (Gianinazzi and Vosátka, 2004). However, only a tiny area of agricultural land has been inoculated with AMF. This reflects difficulties with the cheap production and application of large quantities of inoculum, as well as a lack of knowledge about the outcomes of inoculation, meaning reliable prediction of impacts on crop growth cannot be made without experimentation. Some of the issues associated with use of inoculum are briefly discussed below.

10.8.1 Exotic or Indigenous Inoculum?

Schwartz et al. (2006) suggest only local species of AMF be utilised as inoculum and list potential detrimental consequences of exotic inoculum as decreased yields, decreased survival of desirable plant species, increased fitness of noxious weeds, reduced diversity of native AMF and the risk of introduced AMF becoming invasive weeds. However, there is little evidence for most of these negative outcomes, but many reports of beneficial outcomes from inoculation, where the confounding factor of soil fumigation is not involved, which involved exotic strains being inoculated into soil where indigenous AMF were abundant (Owusu-Bennoah and Mosse, 1979; Plenchette et al., 1981; Rangeley et al., 1982; Ortas, 2003). For instance, Mamatha et al. (2002) inoculated 10 year old mulberry (*Morus alba* L.) plants and 1.5 year old papaya (*Carica papaya* L.) plants which had 20–30% of root length colonised by indigenous AMF. For mulberry, an additional 8% of root length becoming colonised corresponded with an increase in fresh leaf yield of 400 kg ha^{-1}, while for papaya an additional 15% of root length becoming colonised corresponded with an additional seven fruits per plant. Similarly, on a soil with low extractable P, inoculation of garlic (*Allium sativum* L.) increased root colonisation from 68 to 85% and increased fresh bulb yield by 23%. When 60 kg ha^{-1} of P was applied, colonisation increased from 25 to 30% and fresh bulb yield increased by 4% (Al-Karaki, 2002). These studies suggest that unless inoculum potential has been recently lowered by a specific circumstance, such as a bare fallow or a non-host crop, there may be little benefit to inoculating with indigenous AMF, as colonisation levely may be little increased. However, inoculation with exotic AMF that substitute for indigenous may provide benefits if the indigenous AMF community has responded to farm management practices with a decline in beneficial impact on host plants.

10.8.2 Possible Problems with Inoculation

The likely incidence of negative outcomes from inoculation is difficult to predict as, presumably, studies showing negative outcomes are less likely to be submitted and accepted for publication. However, it is clear that under some circumstances, such as high soil extractable P, inoculation may cause a decrease in host growth (e.g. Khaliq and Sanders, 2000). As discussed previously, there are also instances where indigenous AMF have either no impact or a negative impact on crop growth. A negative outcome from inoculation has financial implications for farmers.

Lekberg and Koide's (2005a) meta-analysis of studies involving inoculation with AMF showed that even when soil extractable P and inoculum potential were very low there was no guarantee of a beneficial response to inoculation. The reasons for the lack of response in some instances were not known, but perhaps very effective communities of indigenous AMF were present and hence low levels of colonisation did not correlate to low mycorrhizal activity and benefit (see van der Heijden, 2001). For instance, in field experiments, Rangeley et al. (1982) found inoculation increased colonisation but did not benefit growth of white clover on a peat soil with very low extractable P and low colonisation by indigenous AMF. On a brown soil with more abundant P and higher colonisation from indigenous AMF, the inoculated fungi partly replaced the indigenous fungi in roots but growth was increased only when P was also applied (Rangeley et al., 1982).

The length of time the benefits from inoculation persist is rarely investigated, but is important when considering the economic viability of inoculum addition, as is the time taken for a positive effect to occur. For instance, Harinikumar and Bagyaraj (1996) found *Glomus intraradices* persisted for only one season after inoculation and Rangeley et al. (1982) found that a positive effect on white clover growth did not occur until the second year after inoculation.

10.8.3 Inoculum Production

It may be easiest and cheapest to bulk-up inoculum, which consists of spores, hyphae and colonised root segments, on-farm (Douds et al., 2006). However, on-farm inocula are not readily processed for mechanical application and are best suited to labour intensive situations in developing countries or high value horticultural farms where inoculated seedlings are transplanted into the field (Douds et al., 2005) or, perhaps, inoculation of established tree crops (Mamatha et al., 2002).

It is worth noting that field-scale inoculation with AMF is always an introduction of more than just the target groups of AMF as the inoculum will contain a range of other bacteria and fungi that are typically not controlled for in experiments and may contribute to the beneficial or parasitic effects of AMF (Daniels Hetrick et al., 1988). While deliberate combined inoculation of AMF with other micro-organisms has been shown to yield beneficial results (Whipps, 2004; Artursson et al., 2006), the range of organisms contained in inoculum is rarely quantified. This could explain some of the variation in outcomes of inoculation. Introduction of disease organisms with inoculants must also be considered.

In conclusion, while many studies show advantages to inoculation with AMF, usually exotic isolates, and particularly when soil available P is low, a beneficial outcome for crop growth and yield from inoculation cannot be guaranteed without on-site testing. Research is required to determine whether organic farms derive the same benefit from inoculation as conventional farms. Perhaps organic farms may benefit most directly after conversion, when soil inoculum levels are likely to be lower. Inoculants may be best utilised when inoculum levels are deficient such as after long bare fallows or non-host crops or, for conventional farms, following soil fumigation. Comparison of economic outcomes between applying inoculum and a change in farming practices to favour AMF should be undertaken before inoculum production and application is commenced.

10.9 How Important are AMF in Organic Farming?

High abundance of AMF on organic farms probably provides many benefits for crop growth and agricultural system stability and sustainability, although these may vary between locations and agricultural systems. However, it is specific components of organic farm management that contribute to this high abundance, notably low inputs of readily soluble P fertilisers and high plant diversity. However, there may be trade-offs between maximising the occurrence and activities of AMF, maximising crop or pasture yields and maintaining a neutral or positive farm P budget. While conventional farms may have a tendency to develop weedy, less beneficial, communities of AMF and hence benefit from inoculation with exotic species of AMF, it is not known if this situation also occurs on organic farms. As stated by Douds and Johnson (2003), a much better understanding of the evolutionary mechanisms responsible for generating beneficial, neutral or parasitic impacts from AMF on host plants in agricultural systems is necessary before the fungi can be effectively managed to maximise desirable outcomes.

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