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The Interplay Between Roots and Arbuscular Mycorrhizal Fungi Influencing Water and Nutrient Acquisition and Use Efficiency

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7.1 Introduction

Since plants colonized the terrestrial environment, they have made a living through an intimate and usually mutualistic partnership with mycorrhizal and other root-inhabiting fungi. In fact, the mycorrhizal symbiosis enabled plants to conquer the land 450–500 million years ago. Plant roots, specialized organs with a gravitropic response, a protective root cap, and root hairs, evolved much later, around 415 million years ago (Kenrick and Strullu-Derrien 2014). Plant roots therefore (co-)evolved within the constraints imposed by mycorrhizal fungi, and some plant species still cannot make it on their own (without mycorrhizal fungi, Rodriguez and Redman 2008). The mycorrhizal symbiosis has been a great success, as the overwhelming majority of land plants form mycorrhizal associations. Even though nonmycorrhizal plants are known, a complete loss of capacity to be colonized by mycorrhizal fungi is exceptional and occurs in plants that have evolved the alternative resource acquisition strategies (Maherali et al. 2016; Werner et al. 2018). Examples from this category of nonmycorrhizal plants are carnivorous plants (Droseraceae), parasitic plants (Orobanchaceae, Santalaceae), and plants that form cluster roots or dauciform roots (Proteaceae and Cyperaceae). A few other families are also largely nonmycorrhizal, including Caryophyllaceae and agronomically important Brassicaceae.

Compared to the long history of the mycorrhizal symbiosis, agriculture is a recent phenomenon, starting around 12 000 years ago. Agriculture has allowed the species *Homo sapiens* to construct and expand its own niche, in terms of appropriation of carbon and nutrients. It allowed the human population to grow to more than 7.8 billion people. The need to ensure sufficient food of sufficient quality to all humans requires further intensification of agriculture; however, we have to recognize that we need *sustainable or ecological intensification* to achieve this (Struik and Kuyper 2017). The challenge is how knowledge of this permanent partnership between crops and arbuscular mycorrhizal fungi

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(AMF) can be harnessed to contribute to ecological intensification. Addressing that question forces us to sail between the Scylla of a phytocentric perspective (where mycorrhizal fungi are seen as just extensions of the root system of the plant, neglecting the fact that fungal fitness matters as much as plant fitness) and the Charybdis of looking at mycorrhizal fungi with disregard for roots and forgetting how mycorrhizal fungi lead a dual life in both soil and roots. In that middle ground, we have to understand how the mycorrhizal symbiosis affects the structure and functioning of roots. Phrased from the opposite perspective, we need to understand how evolution (due to the selection of favourable crop traits) has modified mycorrhizal functioning. As Bonfante and Genre (2015) eloquently worded it: in the middle ground, we have to understand both fungish and plantish in our study of the interplay between both organisms.

To give an example: the Green Revolution that allowed spectacular yield increases of major (mycorrhizal) cereal crops was enabled by the introduction of dwarfing genes into these cereals, together with enhanced resistance against or tolerance of pathogens and pests. Both types of genetic modification could unintentionally have affected mycorrhizal functioning because of underlying changes in the hormonal regulatory pathways. Strigolactones, a class of plant hormones, started as internal plant hormones in early (still aquatic) plants regulating simple developmental processes. Later, they were also exuded and played an additional role in the communication with AMF (and subsequently also in the interaction with parasitic plants of the family Orobanchaceae, Andreo-Jimenez et al. 2015). Other plant hormones (auxin, gibberellin, and abscisic acid) also modify mycorrhizal functioning (Pozo et al. 2015; Lanfranco et al. 2018).

Modern crop breeding has not resulted in novel crops that have abandoned the mycorrhizal symbiosis. However, over ecological times, our current (unsustainable) agricultural practices could have made the symbiosis less important or less efficient (Verbruggen and Kiers 2010). Will such ecological changes ultimately translate into evolutionary changes that make ecological intensification more difficult? Answers to that question have ranged from a decisive “no” to a somewhat cautious “yes”. Ryan and Graham (2002) claimed that AMF do not play a crucial role in the nutrient acquisition and growth of plants in production-oriented agricultural systems, due to management that reduces mycorrhizal benefits (high levels of fertilizers, use of fungicides, disturbance through tillage, rotations with nonmycorrhizal plants, wrong cultivar selection by including less responsive cultivars, etc.). Observations of negative growth responses to mycorrhiza in the major crops under controlled conditions have strengthened this opinion (Smith and Smith 2011). However, a growth depression of (facultatively) mycorrhizal plants can be effective in weed suppression (Veiga et al. 2011). Ryan and Graham (2002) also referred to exceptions to their general conclusion, viz. when the mycorrhizal symbiosis makes a major contribution to soil structure (not treated here, but see the review by Rillig and Mummey (2006), and also Chapter 3) or when enhancing micronutrient concentrations (see Section 7.5). In a recent review, when Ryan and Graham looked at the literature published in the intervening 16 years, they came to a similar conclusion (Ryan and Graham, 2018). They concluded that the yield benefits of maintaining high abundance and diversity of AMF in agro-ecosystems have often been overstated because of an unwarranted view that high colonization levels and/or high species richness are needed for high yields. On the other side of the spectrum, Thirkell et al. (2017) expressed cautious optimism when they referred to mycorrhizal fungi as our sustainable saviours. Other claims that mycorrhizal fungi act as biofertilizer, bioregulator, or biocontrol agent (Rouphael et al. 2015; Berruti et al. 2016; Bitterlich et al. 2018) are also expressions of the prime importance of the arbuscular mycorrhizal symbiosis for ecological intensification. However, we wish to state from the outset that the term biofertilizer is misleading. Contrary to N_2-fixing rhizobia that add nitrogen to the agro-ecosystem, AMF scavenge, but do not mine for, nutrients and therefore have no effect on the total pool of nutrients (Lambers et al. 2008). In fact, under conditions of very low P availability, a scavenging strategy is not successful and a mining strategy through the exudation of carboxylates by nonmycorrhizal plants contributes to P acquisition much better (Parfitt 1979). However, in cases of a legacy of high fertilizer application, the superior scavenging activities of mycorrhizal fungi allow them to use residual soil P, giving the false impression that there is no need for P replacement.

In this chapter, we evaluate arbuscular mycorrhizal functioning in agriculture (especially cropland) and look at the challenges ahead for intensification based on ecological principles. We will consider mycorrhizal function in relation to plant roots. We assume a basic background knowledge of the arbuscular mycorrhizal symbiosis among the readers of this chapter. Our focus is on nutrients and water, and the efficiency of both acquisition and subsequent use is discussed. We will not deal with the role of mycorrhizal fungi in creating and maintaining soil structure (but see Chapter 3) or conferring tolerance/resistance to pathogens and herbivores. In the latter case, both nutritional and hormonal effects are important.

7.2 A Trait-based Approach towards Mycorrhizal Root Systems

Trait ecology is currently a very active and promising field of research, both for ecologists and agronomists (Garnier et al. 2016). The strength of an above-ground trait approach has been shown in the general validity of the leaf economics spectrum, a gradient along which plants can be described from having acquisitive to conservative traits (Reich 2014). Reich hypothesized substantial trait coordination above-ground and below-ground, and this would allow a generalized plant economics spectrum. However, the current literature has shown that trait coordination is not universal (Weemstra et al. 2016; Laliberté 2017). A clear example is provided by specific root length (SRL; root length per unit root biomass). SRL was hypothesized to be equivalent to specific leaf area (SLA; leaf area per unit leaf biomass). Theoretical arguments showed that a high SRL would be beneficial under conditions of both high nutrient availability (as predicted by comparison with SLA) and limited nutrient and water availability, where exploration growth is more efficient than exploitation growth. Two major explanations can be forwarded why trait correlation did not occur. Firstly, roots fulfil a diversity of functions – they need to acquire nutrients of very different mobility. They also need to acquire nutrients and water, and transport them to above-ground tissues. Water availability is often not highest at sites where nutrient concentrations are highest. Secondly, and more importantly for our arguments, plant roots evolved in a mycorrhizal world, and the mycorrhizal symbiosis may impose constraints on economic optimality.

Table 7.1 Shifts in plant trait values due to arbuscular mycorrhizal symbiosis.

Traits	Shift due to mycorrhizal symbiosis	References
Leaf and root nutrient status	Increases, as mycorrhizal plants often have higher nutrient (especially phosphorus) concentrations; shift towards acquisitive side	See Section 7.4
Specific Leaf Area (SLA)	Possibly positive	Zhang et al. (2018)
Root : shoot ratio	Declines; shift towards the acquisitive side; however, after allometric correction (larger plants generally have lower R : S ratios), the effect is unlikely to be significant	Veresoglou et al. (2012)
Decomposability	Increases; shift towards acquisitive side	Schädler et al. (2010)
Specific root length (SRL)	Generally decreases; shift towards conservative side	Berta et al. (1993); see below
Root diameter	Increases; shift towards conservative side	See below
Root tissue density (RTD)	Increases; shift towards conservative side?	See below
Root hairs	Fewer and shorter root hairs; shift towards conservative side	Shao et al. (2018); see below
Root branching	Enhanced branching, shift from herringbone to dichotomous branching with increased fractal dimension; shift towards acquisitive side	Berta et al. (1993) and Yang et al. (2014); see below
Foraging precision	Declines; shift towards conservative side	Johnson and Biondini (2001) and Li et al. (2014); see below

Even though several authors have indicated how plants (notably trees) with different mycorrhizal associations fit into the hypothetical plant economics spectrum, there has been less attention paid to how the mycorrhizal symbiosis has an effect on the expression of root traits (compared to a nonmycorrhizal plant of the same species). Friesen et al. (2011) pointed out that microbes mediate plant functional traits. Table 7.1 provides examples on how the arbuscular mycorrhizal symbiosis modifies plant traits and how such changes could fit in a general economics spectrum.

These changes (Table 7.1) indicate that above-ground traits shift towards the acquisitive side when plants are mycorrhizal, whereas below-ground traits generally shift towards more conservative trait expression in the mycorrhizal plants. The shift in root traits towards the more conservative side benefits the mycorrhizal fungus as it maintains control over the plant. Fungal control has been shown in studies where mycorrhizal fungi dominated P uptake even in the absence of a growth benefit because, under the mycorrhizal condition, the plant P transporters were downregulated (Smith et al. 2011). From a mycocentric perspective, the shift towards a more branched root system may equally benefit the mycorrhizal fungus because a higher branching frequency decreases the chance that the plant root outgrows the growth of the mycorrhizal fungus inside the root. At the same time, the increased nutrient status equally benefits the fungus, as a higher nutrient status translates into higher photosynthesis rates and these would increase carbon flux to, and alleviate carbon limitation of, the fungus.

Bayliss (1970) proposed that plants with few and short root hairs and plants with thick root systems (low SRL) derived more benefit from the mycorrhizal symbiosis than plants with abundant and long root hairs and with thin root systems (high SRL). Data by Schweiger et al. (1995) provided confirmation of that hypothesis. From a fungal fitness perspective, a decline in abundance and length of root hairs would be advantageous, as this reduction maintains mycorrhizal control over nutrient uptake. Over the evolutionary time-scale, there has been a tendency of plants to develop thinner roots (higher SRL) and this has reduced both dependency on, and benefits derived from, mycorrhizal fungi (Ma et al. 2018). Thinner roots provide less cortical space for colonization by mycorrhizal fungi. As thinner roots reduce the cortical volume more than the diameter of the stele (Valverde-Barrantes et al. 2016), this evolutionary trend should result in increases in root tissue density (RTD), as the density of the lignified cells of the stele is higher than that of the cortex. Stele rather than cortex was a major determinant of variation in RTD in the study by Hummel et al. (2007). There may, however, be limits to reduction of root diameter (and hence options for plants to forego the mycorrhizal symbiosis). Transport through roots (or mycorrhizal hyphae) obeys the Hagen–Poiseuille law, which states that flow rates scale with the fourth power of diameter. However, uptake rates scale with surface, so with the second power of diameter. Thinner roots would thereby face constraints in balancing water acquisition and subsequent transport through the roots towards aboveground tissues (Kong et al. 2017).

Mycorrhizal fitness would be enhanced if cortical volume increases more than the volume of the stele, as mycorrhizal colonization should increase with an increase in the relative cortical volume. There are only few data to test this hypothesis. Both Kong et al. (2014) and Valverde-Barrantes et al. (2016) noted a positive correlation between cortex-to-stele ratio and mycorrhizal colonization. However, Berta et al. (1993) studied the effects of AMF on root traits of leek (*Allium porrum*) and noted similar increases in cortex and stele.

A final trait may be foraging precision of (mycorrhizal) roots, usually expressed as the relative increase in root proliferation in nutrient-patches compared to nonenriched patches. Chen et al. (2018b) posited that high precision is associated with an acquisitive strategy (and in line with that, they found higher precision among arbuscular mycorrhizal trees than among ectomycorrhizal ones, and higher precision among arbuscular mycorrhizal herb species than among arbuscular mycorrhizal trees). They also suggested that roots with lower RTD may be more precise than roots with higher RTD. That hypothesis would seemingly contradict the earlier observation that root diameter is a major determinant of RTD, with thin roots having higher RTD because of lower cortical volume. However, in addition to the cortex-to-stele ratio, RTD is also determined by the degree of lignification, and more acquisitive plants contain less lignin and hence have lower RTD. The balance between the two opposing processes needs further study. Data by Johnson and Biondini (2001) showed about twice as high precision by dicotyledonous herbs as by grasses in the nonmycorrhizal condition. In an intercropping field experiment, where plants were likely mycorrhizal, Li et al. (2014) noted that foraging precision was lower by two legumes (chickpea [*Cicer arietinum*] and faba bean [*Vicia faba*]) than by two cereals (common wheat [*Triticum aestivum*] and maize [*Zea mays*]). The discrepancy has not been explained.

Foraging precision by AMF has also been studied. Because these fungi react negatively to increased P availability, foraging precision is likely more important in case of organic than inorganic patches containing N and P (Wang et al. 2016).

Trait approaches to AMF are in their infancy. A trait that currently receives limited attention is architecture of the mycelium, notably the difference between thin hyphae and runner hyphae. Hyphal architecture (the balance between thin, short-lived hyphae/hyphal networks, and much thicker, unbranched, and long-lived runner hyphae) is both a species trait (Friese and Allen 1991) and also dependent on soil fertility (Olsson et al. 2014). Under high P and high C availability, AMF reduce the amount of runner hyphae (and hence become more explorative and less acquisitive). There are only very few publications of the fractal geometry of the mycelium. Juge et al. (2009) noted, *in vitro*, a final fractal dimension of 1.62, similar to the dimension of highly branched root systems. Mycorrhizal plants exhibited a higher fractal dimension of the root system than nonmycorrhizal plants, and the effect was more pronounced during drought (Yang et al. 2014). The interplay between changes in the root and hyphal branching is likely caused by phytohormonal changes (Pozo et al. 2015).

A potentially interesting fungal trait is colonization rate. Graham and Abbott (2000) showed that trait expression was independent of soil fertility and that fungal species that showed high colonization rate (called aggressive colonizers) at low (limiting) P supply also showed high rates at high (nonlimiting) P supply. There was also some evidence that aggressive colonizers generally resulted in a lower and often negative growth response.

7.3 Acquisition and Use of Water by Arbuscular Mycorrhizal Plants

Many studies have shown that under drought mycorrhizal benefit tends to increase compared to the conditions of normal water supply (Augé et al. 2015, 2016). These studies showed increased photosynthesis, stomatal conductance, and transpiration by mycorrhizal compared to nonmycorrhizal plants. The meta-analysis by Augé et al. (2016) showed a 49% increase in carbon exchange rate, a 28% rise in stomatal conductance, and a 26% increase in transpiration, compared with nonmycorrhizal plants. Because the increases in photosynthesis were larger than the increases in transpiration, the net effect was positive. Under less favourable conditions, the effect on photosynthesis was larger than under more favourable conditions (72% versus 30%), whereas the effects on stomatal conductance and transpiration did not change. The authors noted the somewhat troubling effect of changes in photosynthesis over time; in contrast to the initial studies (during the 1980s and 1990s) that reported a mycorrhizal effect on photosynthesis of more than 70%, this effect declined to 30–40% in the most recent decade. Stomatal conductance and transpiration rate did not show a consistent trend over time. It could be possible, therefore, that beneficial mycorrhizal effects on photosynthesis decline over time, if these results were not due to research bias (the use of experimental conditions, treatments, or plant and mycorrhizal fungal species that are conducive to a positive outcome) or publication bias (the tendency to publish significant and positive results rather than nonsignificant outcomes).

Understanding the mechanisms by which the mycorrhizal symbiosis enhances plant performance under drought has lagged behind. Often, the intuitive argument is used that mycorrhizal hyphae, by virtue of their small diameter, have both better access to soil water in small pores and provide better hyphal contact with the water film. However, water transport through mycorrhizal hyphae may be relatively slow due to the physical constraints of small hyphal diameter according to the Hagen–Poiseuille law. Even though most nutrients are taken up through the mycorrhizal mycelium (up to 100%; Smith et al. 2011), Ruth et al. (2011) estimated that the combined direct and indirect hyphal contribution to total plant water uptake was around 20%.

Augé et al. (2001, 2004) argued that to understand relations between soil, water, and the mycorrhizal association we should look at pathways through which the symbiosis improved hydraulic properties of soil as well as plant-related pathways. They demonstrated that the first pathway, whereby mycorrhizal fungi improve soil structure, is as important as the plant-related pathway. They noted that a nonmycorrhizal mutant of bean (*Phaseolus vulgaris*) showed equally increased stomatal conductance as the mycorrhizal wild type. Mycorrhizal effects on soil hydraulic properties have been reviewed by Bitterlich et al. (2018) who pointed out that the mycorrhizal enhancement of soil structure improved water retention and also mobility of water, i.e. hydraulic conductivity. These changes influence the way plants with and without mycorrhiza experience drought, even under equal drought treatments. A further soil-related mycorrhizal effect could be hydraulic redistribution, which may help sustain hyphal activity during drought (Allen 2007).

Plant-related mechanisms are associated with both nutritional (enhanced uptake of K and P) and phytohormonal effects. As the mycorrhizal enhancement of stomatal conductance occurred both with and without a positive mycorrhizal growth response, it is likely that phytohormonal changes play a major role (Augé et al. 2015). Not only are mycorrhizal plants better able to withstand drought, the recovery from drought is also faster in mycorrhizal than nonmycorrhizal rice (*Oryza sativa*) (Ruiz-Sánchez et al. 2010).

Water limitation (physiological drought) can also be caused by high concentration of salt (salinity stress). The mechanisms by which AMF can alleviate growth reduction due to excess salinity are similar to the mechanisms by which mycorrhizal plants cope with drought (Evelin et al. 2009; Chandrasekaran et al., 2014). Like in the case of water shortage, mycorrhizal plants show morphological and physiological effects in roots. Mycorrhizal plants then maintain photosynthesis and stomatal conductance for a longer time, show higher water-use efficiency (the ratio between photosynthesis and transpiration), and production of osmoprotectants (Santander et al. 2017). Some of these effects are regulated by phytohormones. However, shifts in the balance between K uptake and Na uptake (and hence a more favourable K : Na balance in shoots and roots) are likely the major mechanism of coping with high salinity.

7.4 Acquisition and Use of Nutrients by Arbuscular Mycorrhizal Plants

The arbuscular mycorrhizal symbiosis is first and foremost known for its beneficial effects on uptake of immobile (diffusion-transported) nutrients. The hyphal network extends beyond the depletion zone of plant roots (and root hairs), thereby increasing access to these nutrients. The beneficial effects are especially noted with P, but also with diffusion-limited cations Zn, Cu, Fe, Mn, K, and NH_4^+. Beneficial effects on uptake of other plant nutrients e.g. (NO_3^-, Ca, and Mg) have been reported, but these play a minor role. Other beneficial effects of the mycorrhizal symbiosis have been reported, and sometimes they are a consequence of the improved plant nutritional status. Because of the mechanism of extension of the hyphal network beyond the depletion zone, one could expect there is a positive correlation between the extent of the extraradical network and uptake of immobile nutrients. This relationship was found by Munkvold et al. (2004), who compared a number of different strains of the same mycorrhizal fungus, and noted a significant linear correlation between the hyphal length density and P acquisition.

The extent to which plants benefit from the mycorrhizal symbiosis depends on the nature of fungus, properties of root system, environmental context, and management. These factors do not act in isolation, and the interactions (including the most complex one, fungus × plant × environment × management) should receive more attention.

Root system characteristics (root hair density and length and root diameter) largely determine the plant benefits arising from the symbiosis (but see Maherali (2014) for a meta-analysis that did not find support for this hypothesis). Plants can therefore be placed in different categories, ranging from those with only minor growth increments under conditions of normal nutrient supply to those with large benefits, in addition to those where plant growth in the nonmycorrhizal condition is hardly possible (Habte and Manjunath 1991; Tawaraya 2003). The latter category includes the members of Alliaceae (onion [*Allium cepa*] and leek) and Solanaceae (bell pepper [*Capsicum annuum*]), as well as cassava [*Manihot esculenta*]. In cases where the mycorrhizal growth response is very low, the mycorrhizal fungi can still be responsible for almost all P uptake (Smith et al. 2011).

Environmental context has an important role; with increasing nutrient availability, the mycorrhizal benefits decline, whereas at declining water availability (i.e. increasing tortuosity – the length of nutrient flow path) mycorrhizal benefits increase. Finally, management of agro-ecosystems is of major importance. Sustainable management should therefore avoid practices that reduce the amount or activity of mycorrhiza, such as excessive disturbance, unbalanced fertilization, overfertilization, use of fungicides, use of nonmycorrhizal crops in a rotation, etc. The latter topic may be particularly relevant considering the increasing area of rapeseed/canola (*Brassica napus*) or fodder radish (*Raphanus sativus*) as (winter) cover crop or as part of a wider crop rotation. Several studies reported decreased mycorrhizal colonization and poorer plant performance of crops after canola, and noted that a crop responsive to mycorrhiza should not be grown after canola (Gavito and Miller 1998; McGonigle et al. 2011).

Normally, benefits of the mycorrhizal symbiosis are shown by comparing plants with and without mycorrhiza at the same soil nutrient status. Because of the very poor performance of some nonmycorrhizal plants, or even the impossibility of growing nonmycorrhizal plants in the field, an alternative approach would be to compare plants whose colonization level has been experimentally reduced, e.g. through rotation cores. Comparisons between mycorrhizal and nonmycorrhizal plants, or between plants with high (“normal”) and low (“experimentally reduced”) mycorrhizal colonization, indicate how much primary production can be increased if we were to manage the mycorrhizal symbiosis well. It is also possible to compare mycorrhizal and nonmycorrhizal plants at the same size, and then assess the attainable fertilizer savings. Such savings are increasingly important, considering that P is a finite, nonrenewable resource. Wang et al. (2020a) observed that under adequate mycorrhizal management, mycorrhizal maize plants fertilized by 30 kg P ha^{-1} performed equally well as plants with reduced mycorrhizal abundance but with a double dose of fertilizer. Assuming that fertilizer savings of 50% were possible for maize globally, we can calculate the economic value of this ecosystem service (Gianinazzi et al. 2010; Chen et al. 2018a) by the mycorrhizal symbiosis: US$1.5 billion annually. Based on yield increases, Kuyper and Giller (2011) calculated that assuming AMF increase P crop uptake by 10%, the ecosystem service provided by AM fungi would be US$2 billion per year in additional crop yield. However, they did not calculate the economic benefits of fertilizer savings at a constant yield.

Even though Ryan and Graham (2002, 2018) questioned the use of mycorrhiza in production agriculture, they did explicitly refer to cases of micronutrient deficiencies where the mycorrhizal symbiosis may be crucial. Awareness of the mycorrhizal role in remedying micronutrient deficiencies has been increasing, with micronutrient deficiencies, notably that of Zn, in human populations being a major health hazard in many (sub-) tropical areas. Awareness of low micronutrient content in crops increased when it became clear that P fertilization increased cereal yield, but decreased plant and especially grain Zn concentrations. This effect was first shown by Lambert et al. (1979) and was due to P fertilization increasing plant size and grain yield without additional Zn uptake (e.g. in maize), resulting in a dilution effect. In soybean (*Glycine max*), the results were even bleaker: Zn concentration was much higher in mycorrhizal compared with nonmycorrhizal plants. However, increased P fertilization of nonmycorrhizal plants had a small beneficial effect on total Zn uptake, but the same P fertilization of mycorrhizal plants resulted in a decline of mycorrhizal colonization of roots and a decrease in Zn uptake, resulting in a more severe negative effect than what could be explained by dilution only. It is likely therefore that the use of P fertilizer in order to achieve yield increases without management of micronutrients and mycorrhizal fungi can result in declining food quality. The study by Ryan et al. (2008) showed a 30–40% decrease in wheat grain Zn concentration due to either P fertilization, or cropping wheat after fallow or in a rotation with nonmycorrhizal crop, implying the crucial role of AMF in Zn acquisition. Moreover, high P fertilization increased concentration of phytic acid in grains, which adversely affected Zn bioavailability in flour.

In addition to biofortification (enhanced content of micronutrients, for instance Zn), the mycorrhizal symbiosis has been implicated in higher production of bio-active compounds with positive health effects for humans (Avio et al. 2018). The same applies to anti-oxidant enzymes – suggesting the specific use of AMF in production of functional foods. However, underlying mechanisms have yet to be elucidated.

Mycorrhiza-related increases in micronutrient content in crops confronts us with a mycorrhizal conundrum that has not yet been explained convincingly. Even though mycorrhizal plants show both increased water-acquisition efficiency and enhanced water-use efficiency (see Section 7.3), there seems to be a disconnect between nutrient-acquisition efficiency and nutrient-use efficiency (the amount of biomass produced per unit of nutrient acquired). Many researchers have noted that the mycorrhizal P responsiveness (relative increases in P uptake) was larger than the mycorrhizal responsiveness based on biomass. An empirical relationship between both parameters was proposed by Van Der Heijden (2002), but without an underlying physiological mechanism. This effect (an increase in P concentration or enhanced P uptake that is not translated into additional biomass) has usually been explained by referring to carbon costs.

Cardoso et al. (2004) noted an apparent paradox that the mycorrhizal symbiosis in many cases increases nutrient-acquisition efficiency but reduces nutrient-use efficiency; however, they disagreed with the conventional explanation that referred to carbon costs. They noted problems with the comparison per se because in some cases plants of very different sizes were compared. In order to correct for differences in plant size, Wang et al. (2020a) compared plants with high and low colonization along a P-availability gradient. They then plotted biomass against the natural logarithm of P content. The slope in this graph can be used as a proxy for nutrient-use efficiency, with a slope = 0 indicating luxury uptake (whereby additional P acquired cannot be used to increase biomass) and a positive slope indicating that additional P acquired is partly converted into biomass. A higher slope for mycorrhizal than nonmycorrhizal plants indicates that the mycorrhizal symbiosis improves nutrient-use efficiency (Elser et al. 2010). In the study of Wang et al. (2020a), a higher slope was associated with plants that had high colonization compared to plants with reduced colonization, implying that nutrient-use efficiency of plants with high (or normal) colonization was actually increased.

Cardoso et al. (2004) applied the double-pot technique and noted that under conditions where P was limiting for both mycorrhizal and nonmycorrhizal plants, P-use efficiency was similar. They therefore suggested that reduced P-use efficiency of mycorrhizal plants could be due to the fact that in certain experiments nonmycorrhizal plants were P-limited, whereas mycorrhizal plants were limited by an unknown factor. However, Stribley et al. (1980a,b) observed that shoots of mycorrhizal leek contained higher P concentration than nonmycorrhizal plants of equal size. Under the assumption that an increase in P concentration was due to carbon invested in the mycorrhizal symbiosis, they calculated carbon costs of around 40–60%, which is much higher than the carbon flux to mycorrhizal fungi that has been commonly reported (around 10%). Physiological studies are recommended to understand the underlying basis for changes in nutrient-use efficiency of mycorrhizal plants. However, as noted above: even if nutrients taken up are not converted to biomass, food quality may still be improved by increased nutrient content.

Theories on carbon costs of the mycorrhizal symbiosis have been regularly invoked to explain conditions in which nonmycorrhizal plants outperform mycorrhizal plants. In several cases, even the term *mycorrhizal parasitism* has been coined to refer to this negative mycorrhizal growth response (Johnson et al. 1997). However, the debate on carbon costs of the mycorrhizal symbiosis has been complicated; in most cases, the term has been used to explain the cases of lower mycorrhizal performance, without any measurement of the actual carbon costs. Carbon costs have sometimes been defined as carbon fluxes to the fungus, but this measurement is biased because larger plants (due to the mycorrhizal benefits) allow a larger flux of carbon below-ground. The issue of carbon costs assumes that carbon is a costly or even limiting element, which is unlikely to be the case in many conditions, with carbon often being available in surplus amounts in the plant. Carbon costs should be evaluated in relation to the carbon gained through enhanced photosynthesis due to alleviating N and/or P limitation. One should therefore compare plants of the same size with and without mycorrhiza. Kaschuk et al. (2009) demonstrated that plants, due to mycorrhizal fungi resulting in enhanced photosynthesis because of sink stimulation, had photosynthesis rates 5–10% higher than equally sized plants without root symbionts. The magnitude of the effect is similar to the amount of carbon (10%) that is invested in the root symbiont.

If carbon costs do not explain negative mycorrhizal responsiveness, there are several other plausible hypotheses that may explain this negative effect. Jin et al. (2017) divided possible explanations in phytocentric and mycocentric. Their list is not complete, and an additional mechanism underlying negative responses is the potential for nutrient immobilization in the mycorrhizal mycelium (Püschel et al. 2016; Wang et al. 2018). This mycorrhizal trap (Kuyper and Kiers 2014) may also explain why the mycorrhizal symbiosis persists and why it is unlikely that facultative mycorrhizal plant species (that can complete their life cycle in the absence of mycorrhiza) would evolve towards becoming nonmycorrhizal. Finally, cases where the mycorrhizal symbiosis impacts on the root traits (see Table 7.1) could also result in a reduced capacity to acquire nutrients and hence in a negative growth response.

7.5 Breeding to Enhance Mycorrhizal Benefits

Crop species differ in the degree to which they depend on, and are responsive to, the mycorrhizal symbiosis (Janos 2007). There is not only variation among different plant species, but also intraspecific variation in responsiveness of wild plants and crops. Table 7.2 provides a list of major crops for which genetic variation in mycorrhizal responsiveness has been demonstrated. Because of the likely genetic basis of this intraspecific variation, (natural) selection has apparently directly or indirectly favoured traits that are associated with the mycorrhizal symbiosis. The existence of variation in responsiveness among crops raises questions about whether it would be desirable to consider plant breeding for mycorrhizal benefits as a component of ecological intensification.

Variation in responsiveness was first described and analysed by Manske (1989), who compared 22 landraces and 22 high-yielding varieties of wheat. Under nutrient-poor conditions, the landraces showed a higher mycorrhizal responsiveness than the modern high-yielding cultivars. The author noted that high responsiveness was correlated with poor plant growth in the nonmycorrhizal condition. The author also made reciprocal crosses between an efficient and a nonefficient cultivar and noted that mycorrhizal responsiveness of the hybrid was different in the reciprocal crosses, suggesting a role of both chromosomal and cytoplasmatic effects.

The question of a genetic basis of mycorrhizal responsiveness gained increased prominence when Hetrick et al. (1992) reported that ancestors and landraces of wheat were more responsive to mycorrhizal fungi than modern cultivars. The authors suggested that differential responsiveness was due to breeding history and stated that selection under fertilized conditions could have reduced the frequency of genes that foster mycorrhizal associations. The authors proposed that the conditions under which cultivar selection took place, i.e. at adequate to high soil fertility, had inadvertently selected against mycorrhizal responsiveness. Their intuitively plausible explanation has initially gained general acceptance, and several papers made a plea for breeding for (enhanced) mycorrhizal

Table 7.2 Major crops for which genetic variation in mycorrhizal responsiveness has been demonstrated.

Plant species	Reference
Allium cepa	Taylor et al. (2015)
Allium fistulosum	Tawaraya et al. (2001)
Allium trihybrid	Galván et al. (2011)
Arachis hypogaea	Quilambo et al. (2005) and Daft (1991)
Avena sativa	Koide and Lu (1992)
Bactris gasipaes	Clement and Habte (1995)
Capsicum annuum	Sensoy et al. (2007)
Carica papaya	Trindade et al. (2001)
Cicer arietinum	Daft (1991)
Cucumis sativus	Rouphael et al. (2010)
Dioscorea rotundata	Dare et al. (2014)
Dioscorea spp.	Dare et al. (2008) and Lu et al. (2015)
Elaeis guineensis	Blal and Gianinazzi-Pearson (1989)
Fragaria vesca	Mark and Cassells (1996)
Glycine max	Khalil et al. (1994) and Salloum et al. (2016)
Helianthus annuus	Turrini et al. (2016)
Hordeum vulgare	Hetrick et al. (1992) and Baon et al. (1993)
Ipomoea batatas	Yooyongwech et al. (2016)
Lactuca sativa	Jackson et al. (2002)
Musa acuminata	Declerck et al. (1995) and Elsen et al. (2003)
Nicotiana tabacum	Janoušková et al. (2007)
Olea europaea	Citernesi et al. (1998)
Oryza sativa	Dhillion (1992) and Gao et al. (2007)
Pennisetum glaucum	Krishna et al. (1985)
Phaseolus vulgaris	Izaguirre-Mayoral et al. (2000)
Pisum sativum	Mårtensson and Rydberg (1994) and Estaún et al. (1987)
Solanum lycopersicum	Bryla and Koide (1990)
Sorghum bicolor	Lendzemo et al. (2006)
Trifolium repens	Hall et al. (1977) and Eason et al. (2001)
Triticum durum	Kapulnik and Kushnir (1991)
Triticum aestivum	Azcón and Ocampo (1981) and Hetrick et al. (1992, 1993, 1995)
Vigna unguiculata	Mercy et al. (1990) and Oruru et al. (2018)
Zea mays	Hall (1978) and Kaeppler et al. (2000)

responsiveness in order to harness mycorrhizal benefits in sustainable agriculture (Gosling et al. 2006; Bennett et al. 2013).

Kaeppler et al. (2000) investigated the genetic basis for variation in mycorrhizal responsiveness of inbred lines of maize by characterizing quantitative trait loci (QTL) for mycorrhizal responsiveness. Their study, based on a hypothesized relationship between plant breeding under nutrient-rich conditions and decreased responsiveness to AMF, showed a negative correlation between mycorrhizal responsiveness and performance of nonmycorrhizal maize cultivars under nutrient-poor conditions. The implications of the study were twofold: (i) if this pattern was generally valid, any selection for enhanced mycorrhizal responsiveness could entail selecting plants that perform more poorly under nonmycorrhizal conditions, and (ii) a quest for genetic markers (e.g. QTL) for responsiveness might ultimately pinpoint genes associated with poor performance under nonmycorrhizal conditions. The same conclusions were reached in a genetic analysis of mycorrhizal responsiveness in the trihybrid *A. cepa* × (*Allium fistulosum* × *Allium roylei*), which is used to introgress genes of Welsh onion (*A. fistulosum*) into onion. Galván et al. (2011) observed that (relative) mycorrhizal responsiveness was negatively correlated with growth under the nonmycorrhizal conditions and noted that this relation was almost universal.

In contrast to the studies listed above, Lehmann et al. (2012) performed a meta-analysis and found that new cultivars were more responsive than ancestral cultivars. They suggested that the effect could be due to the fact that most experiments were executed under conditions of low P supply, whereas the new cultivars have usually been bred under conditions of P sufficiency. Under P-sufficient conditions, the plants may have lost the capacity to perform well when nonmycorrhizal, which translates into increased responsiveness. The study also found a strong relation between the year the study was published and mycorrhizal responsiveness, suggesting that research and/or publication bias could impact on the generality of these research findings. Martín-Robles et al. (2018) did not find an impact of domestication on mycorrhizal responsiveness. However, modern crops benefitted only under P-limiting conditions, whereas their ancestors benefitted under a wider range of P availability.

Sawers et al. (2008, 2010) critically reflected on the issue of the genetic basis of mycorrhizal responsiveness and supported claims that a negative correlation between performance of nonmycorrhizal plants and mycorrhizal responsiveness is inevitable and unrelated to the actual mechanisms by which mycorrhizal fungi increase acquisition of nutrients. However, by separating dependence-based and nondependence-based variation in mycorrhizal responsiveness, they tried to save the idea that plant breeding can be based on genetic variation in crops for nondependence-based variation in responsiveness. Apparently, they refrained from drawing the inevitable conclusion that the attempt to breed for mycorrhizal responsiveness is misguided.

As an alternative for breeding for mycorrhizal responsiveness, we could breed plants for enhanced mycorrhizal colonization. The underlying rationale would be that there are generally good correlations between partial colonization and plant performance (Lekberg and Koide 2005). Several studies showed genetic variation in mycorrhizal colonization (maize: An et al. 2010; common wheat and durum wheat: Lehnert et al. 2017; De Vita et al. 2018; subterranean clover [*Trifolium subterraneum*]: Ryan et al. 2016). However, the traits associated with high colonization in sorghum (*Sorghum bicolor*) had low heritability;

hence, the breeding for enhanced mycorrhizal colonization may not be very effective (Leiser et al. 2016). A further caveat might be in order: breeding efforts and plant selection that result in thinner roots, usually caused by a decreased cortex-to-stele ratio, result in lower mycorrhizal colonization. However, thinner plant roots also facilitate increased P uptake.

What has not been attempted in the case of the mycorrhizal symbiosis is whether we can breed for enhanced plant selectivity, whereby plants associate only with a specific subset of mycorrhizal fungi that provide largest benefits. Such breeding has been successfully used in legumes, and soybean (*Glycine max*) has been bred for (i) promiscuity because that would guarantee nodulation and some N_2-fixation without the need for artificial inoculation, which would benefit resource-poor farmers in sub-Saharan Africa, and (ii) high selectivity in order to achieve maximal yield gains under conditions of efficient inoculation, as in Brazil. Even though mycorrhizal fungi are generally considered to be nonspecific (i.e. able to form mycorrhizal symbiosis with a large range of plant species), there are many studies that suggest high selectivity, in terms of either the plant × fungus combination or the benefit that a certain fungus provides to a plant. It would be an interesting set of experiments to test to which extent the breeding of soybean for promiscuity vs. selectivity would produce a variable degree of specificity with respect to AMF. Such breeding, however, is not trade-off free. Enhanced selectivity of crop cultivars for certain mycorrhizal fungi would make crop rotations more complex. A related option that has been suggested, but never tested, is breeding for enhanced discriminatory powers and sanctioning capacity of plants (i.e. to selectively withhold carbon from less beneficial or less cooperative symbionts) (Duhamel and Vandenkoornhuyse 2013).

It is still debated whether plant selectivity and fungal cooperativeness have a hereditary basis. If they have and if plants have sufficient capacity to discriminate, it is hard to understand why many plant individuals are colonized by 10–25 different fungal species rather than harbour a mycorrhizal fungal monoculture in/on their roots, because it is unlikely there would be beneficial effects of fungal species richness.

Plant breeding for mycorrhizal responsiveness could also have unexpected effects. Breeding for pathogen resistance negatively impacted on mycorrhizal colonization in maize (Toth et al. 1990), which may also have an impact on mycorrhizal functioning. Jacott et al. (2017) reiterated the warning that there could be a trade-off between disease resistance and mycorrhizal symbiosis. However, Hohmann and Messmer (2017) were more positive, and suggested beneficial effects through targeted breeding for pathogen suppression, possibly through priority effects or enhanced competition for root space, enhanced nutritional status (a case of tolerance rather than resistance) or because of the capacity of mycorrhizal fungi to modify phytohormone biosynthesis, notably of jasmonic acid and salicylic acid.

Even though it is unlikely plant breeding for mycorrhizal responsiveness would make a major contribution to sustainable agriculture, one might wonder whether we could breed or genetically improve AMF, resulting in enhanced plant benefit. Angelard et al. (2010) showed a fivefold enhancement of growth of rice when inoculated with segregated, but not with crossed lines. However, such very large effects in a crop poorly responsive to the mycorrhizal symbiosis raises a question of why plants did not select such beneficial strains during evolution. Rather than direct genetic improvement of AMF, we could train them to provide enhanced benefits to the desired host(s) and fewer/lesser benefits to the alternate hosts. Observations, however, suggest that this is unlikely to work. The host shifts can generate rapid (genetic or epigenetic) changes in mycorrhizal fungi (Angelard et al. 2014; Rua et al. 2016; Koyama et al. 2017) that would hinder selectivity in terms of host preference and/or benefit.

We may have unintentionally exerted selective pressure on mycorrhizal fungi; by increasing fertilizer doses or by tillage and other disruptive practices, we may have selected more ruderal species that are not necessarily the most beneficial (Verbruggen and Kiers 2010). In many cases, such changes happen over ecological rather than evolutionary times because these disruptive agricultural practices are relatively recent.

A final caveat appears to be in order. Plants have coevolved with their root symbionts for millions of years before the advent of agriculture slightly more than 10 000 years ago. Many agriculturally important crops are now grown outside their area of origin, and this movement of crops has intensified during the last century. Hence, it may be worth asking why natural selection has not enhanced benefits to both plants and microbes beyond the current level, considering that fitness alignment is likely the default state. Denison (2012, 2015) argued that it is extremely unlikely that natural selection would not have favoured genetic improvements free from trade-offs. Denison also pointed out the exception to this general rule, viz. cases where we can deliberately select for the collective traits that are traded-off against the individual fitness benefits. In that case, genetic improvement should start with a primary focus on the selection arena (the current forms of agriculture and their potential for ecological intensification) rather than on the individual crop or microbe species.

7.6 Managing Diversity and Abundance of Mycorrhizal Fungi

It is generally accepted that diversity or species richness, due to niche differentiation, increases ecosystem functioning. Several studies have intended to show that higher mycorrhizal species richness increases plant productivity. However, there is one major issue that needs to be addressed before such a relation can be demonstrated. We should be aware that the consensus pertains to the relationship within one trophic level (mycorrhizal fungal diversity and fungal productivity), not between two trophic levels (mycorrhizal fungal diversity and plant productivity). Powell and Rillig (2018) made the point that we should independently assess the relation between fungal diversity and productivity (a mycocentric question) and between fungal productivity and plant productivity (a phytocentric question). The latter relation would only pertain if the fitness of both partners is aligned and if there are excess resources (both carbon and nutrients) in both partners to be shared.

Several studies have shown a direct relation between fungal diversity and plant productivity of either plant mixtures in grasslands or a single crop. Most of these studies reported the number of fungal species inoculated, not the number of species that survived. Gosling et al. (2016) tested the relationship for a range of one to seven species of AMF and the growth of onion. For most parameters, the relationship saturated at low diversity, i.e.

two or three species. Such numbers are very low indeed, considering that most roots harbour between 10 and 25 species and that numbers of up to 66 species per root of an individual plant have been reported by Davison et al. (2015). Gosling et al. (2016) questioned the importance of agricultural management contributing to the maintenance of high fungal species richness. In other words, should we worry that current management has created impoverished arbuscular mycorrhizal communities? They suggested the conclusion could be premature, and that a lack of a relationship between fungal species diversity and onion biomass was due to experimental conditions. Their study took place in a glasshouse with very little environmental variation, whereby only fungal niche differentiation with respect to overcoming P-limitation would drive the relationship. Under multiple limiting factors, it could still be beneficial for plants to maintain high fungal species richness. Even though their suggestion is relevant (how suitable are our experiments under controlled conditions for understanding mycorrhizal functioning in agro-ecosystems?), it has the disadvantage of shielding the theory against falsification, as the number of factors that allow niche differentiation by AMF can in principle be infinite. We would therefore argue that large fungal redundancy is to be expected, even though Gosling et al. (2016) observed that most plant benefits could actually accrue by inoculation with one species (*Funneliformis caledonium*).

When the biomass of individual fungal species can be determined, e.g. through qPCR, results of experiments can be used to evaluate the importance of complementarity effects (niche differentiation between different fungal species) and selection effects (the increasing likelihood of including species in mixtures that cause above-average productivity). Wagg et al. (2011) grew a legume and a grass in all possible combination of one to four species of AMF in two soils (N-rich and P-poor “low-sand” soil vs. N-poor and P-rich “high-sand” soil). They observed overyielding of both plant species, but with a major role of the selection effect in the high-sand soil, and a major role of complementarity in the low-sand soil. The study by Gosling et al. (2016) provided support for, but did not test, the hypothesis that the selection effect rather than the complementarity effect would drive the diversity–productivity relationship.

Maherali and Klironomos (2007) showed that the relationship was only evident in the case of species of different evolutionary history, likely a proxy for functional differentiation (Powell et al. 2009). When species that belong to the same fungal genus were added, there was no evidence for niche differentiation and yield increase. Their results were confirmed in a meta-analysis by Yang et al. (2017) who showed a lack of relationship between species richness and plant productivity; however, they also noted (i) a positive relationship between family richness and plant productivity, and (ii) a counterintuitive result that phylogenetic diversity correlated negatively with plant response (family richness should be a proxy for phylogenetic diversity). They suggested that the latter negative relationship was due to the nature of available datasets and hence was likely an artefact.

An alternative to using phylogenetic diversity would be to use functional diversity. A link between phylogeny and functional differentiation was shown by Hart and Reader (2002a,b), who noted that members of Glomeraceae are better root colonizers, whereas members of Gigasporaceae are better soil colonizers. The latter group was also less efficient in the carbon-for-phosphorus trade than the first group. The meta-analysis by Yang et al. (2017) confirmed that members of Glomeraceae are better in enhancing P uptake. Powell et al.

(2009), however, showed that the capacity to colonize soils and roots were positively correlated rather than traded-off.

A further issue that needs consideration is that of intraspecific diversity (Hazard and Johnson 2018). For reasons poorly understood, some traits are phylogenetically conserved between species but variable within species. Large intraspecific variation in hyphal length (which is directly proportional to enhanced plant P content) was shown by Munkvold et al. (2004) for *Funneliformis mosseae*. Growth responses by test plants to different strains of the same fungus also showed high variability (Koch et al. 2017). Roger et al. (2013) tested the effect of genetic relatedness within one species of AMF, *Rhizophagus irregularis*, on fungal coexistence in the root system and plant performance. They observed that greater relatedness actually increased plant performance compared to more distantly related strains. Considering the large intraspecific diversity of AMF and also the large diversity of arbuscular mycorrhizal fungal species in the same agro-ecosystem, it is unclear how we can generalize the mycorrhizal fungal diversity effects and identify and subsequently manage agro-ecological conditions under which species richness of mycorrhizal fungi is or is not redundant.

Similarly, the effect of arbuscular mycorrhizal fungal networks (connections between different plant species by the same mycorrhizal fungal individual) on productivity of plant mixtures has resulted in contradictory outcomes. Klironomos et al. (2000) showed that the relationship between plant species richness and productivity saturated at lower plant species diversity when plants are mycorrhizal than nonmycorrhizal. They hypothesized that this effect was due to an increased niche overlap (reduced complementarity) of plant species interconnected in a mycorrhizal network. However, Wang et al. (2020b) actually found overyielding when two maize varieties were grown together with the same mycorrhizal fungus, whereas there was no overyielding in the nonmycorrhizal condition. Analysis of their data showed that this finding was due to complementarity effects.

To manage mycorrhizal diversity and abundance in the field, we need to know cases of inoculum limitation, or inefficiency of field inoculum. We also need to understand the extent to which plants function better with a species-rich mycorrhizal inoculum; and whether plants perform better with indigenous or autochthonous inoculum. Most commercial inoculum suppliers provide a few strains of a small number of fungi (especially fungi that can be multiplied easily, and therefore have the typical characteristics of r-selected or ruderal strategies) without too much concern about potential invasiveness and ecosystem effects (replacement of endemic species, or preferential benefit to exotic plants, with a risk of starting a cascade of subsequent plant invasions) in case these fungi "escape". However, recent concerns about this topic have surfaced (Hart et al. 2018; Thomsen and Hart 2018). These authors concluded that the (ruderal) traits selected for successful inocula might also be the traits that enhance invasion success (e.g. high number of propagules produced, strong competitive behaviour towards indigenous species, etc.). Fast colonization, as was shown for so-called aggressive mycorrhizal fungi (Graham and Abbott 2000), may be a further trait of these r-selected species.

Apart from possible risks that exotic AMF escape from managed fields, there is the need to evaluate if indigenous (autochthonous) or exotic (allochthonous) fungi generally function better. In a scenario of plant sanctions or rewards (towards less or more beneficial fungi), it is expected that indigenous strains would perform better. Fitness alignment (a positive correlation between the fitness of the microbial symbiont [microbial biomass] and the fitness of the plant [biomass used as proxy]), was demonstrated for the rhizobium–legumes symbiosis (Friesen 2012). The author concluded that fitness alignment is the default state, and that cases of fitness conflict mainly involve non-coevolved associations. That conclusion is particularly relevant for agriculture, which is only slightly over 10 000 years old, and especially for modern agriculture with exotic crops (crops are commonly grown outside their area of origin in the last one or two centuries), where time for coevolution has been limited. For mycorrhizal symbiosis, evidence is mixed (Rua et al. 2016). Koch et al. (2017) found weak evidence for fitness alignment at best. They referred to evolutionary asymmetry whereby fungal species have their traits highly conserved, but plant responses are highly plastic.

In many cases it appears there is no inherent inoculum limitation in well-managed agro-ecosystems, which raises questions about the efficacy of applying commercial inocula. If agro-ecosystems are poorly managed, it is likely the commercial inocula would deteriorate as well. A meta-analysis by Bowles et al. (2017) showed that less intensive tillage and winter cover cropping similarly increased (by around 30%) AMF colonization of roots of summer annual cash crops. Their data indicate the farmers can manage their agro-ecosystems in ways that enhance or maintain the mycorrhizal symbiosis. However, there could be specific crop production systems where the use of commercial inoculants is likely to be beneficial, such as greenhouse horticulture, soilless cultivation, or the initial growth of plantlets generated *in vitro*. In such systems, the mycorrhizal symbiosis may be more important for protection against pathogens rather than nutritional benefits.

7.7 Conclusions and Outlook

Even though the mycorrhizal symbiosis can still be considered primarily from the nutritional perspective, this chapter also points out the importance of the hormonal crosstalk between plants and mycorrhizal fungi resulting in plant trait modifications that enhance fungal fitness and often also enhance plant fitness. However, the interplay is poorly understood. The differential impact of drought and nutrient scarcity on that crosstalk needs to be further disentangled. Additional physiological research in this area is likely to yield novel insights into the evolution of mycorrhizas and their current ecological functioning.

Several authors have made a plea for a rethinking of our plant breeding activities as a contribution to ecological intensification of agriculture (Lammerts van Bueren et al. 2018). It is likely that this rethinking will also include breeding for traits that relate to more beneficial root symbioses. However, we should be aware of Denison's (2012) plea to take a Darwinian perspective – breeding for mycorrhizal benefits is unlikely to be trade-off free.

It has been noted that elevated atmospheric CO_2 directly impacts on food quality by reducing nutrient content of our foods (Loladze 2014). In this chapter, we have indicated the beneficial effects of arbuscular mycorrhiza not just on the amount of biomass produced but also on food quality, especially micronutrient content. There is some evidence about regulation of nutrient content through stoichiometric homeostasis under a range of environmental conditions. It may therefore be important to investigate whether the mycorrhizal symbiosis would counteract the deterioration of food quality. The topic has been clearly underinvestigated; we found only one paper dealing with that topic (Goicoechea et al. 2016). The authors showed that elevated CO_2 reduced concentrations of almost all macro- and micronutrients in durum wheat (*Triticum durum*), with mycorrhiza making no difference in most cases. Moreover, for copper, iron, manganese, and zinc, mycorrhizal plants even had lower concentrations than nonmycorrhizal plants under elevated CO_2. The role of mycorrhiza in enhancing nutritional quality of the major crops under elevated CO_2 is therefore an important topic for further research that should likely focus on stoichiometry (Elser et al. 2010). Uptake of limiting nutrients to an extent greater than what can be converted to biomass represents luxury consumption, but also contributes to enhanced nutritional quality of food. A degree to which plants exhibit stoichiometric homeostasis (unchanged nutrient concentrations and ratios despite changes in nutrient supply) likely varies for different plant species and different nutrients. It is also unclear to what extent mycorrhizal fungi impact on stoichiometric homeostasis.

Questions about the relation between intraspecific/interspecific diversity of mycorrhizal fungi and plant performance (biomass, yield, and/or nutritional quality) will likely remain in the near future. However, with the current molecular tools, it is possible to determine the persistence and relative abundance of different fungal species in roots, and hence extend our mechanistic knowledge on differential importance of the complementarity vs. selection effects.

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