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REVIEW

Nitrogen and carbon/nitrogen dynamics in arbuscular mycorrhiza: the great unknown

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Abstract Many studies have established that arbuscular mycorrhizal fungi transfer N to the host plant. However, the role and importance of arbuscular mycorrhiza (AM) in plant N nutrition is still uncertain, as are the C/N interactions within the symbiosis. Published reports provide differing, and often contradictory, results that are difficult to combine in a coherent framework. This review explores questions such as: What makes the difference between a positive and a negative effect of AM on plant N nutrition? Is the mycorrhizal N response (MNR) correlated to the mycorrhizal growth response (MGR), and how or under which conditions? Is the MNR effect on plant growth C mediated? Is plant C investment on fungal growth related to N needs or N benefit? How is the N for C trade between symbionts regulated? The patternless nature of current knowledge is made evident, and possible reasons for this are discussed.

Keywords Arbuscular mycorrhiza · Nitrogen · Carbon · Mycorrhizal growth responses · Symbiosis cost-benefit

Introduction

Arbuscular mycorrhiza (AM) is a widespread symbiotic association formed between plants and fungi, and arguably one of the most important symbioses between living organisms. The AM symbiosis is generally considered to be mutualistic, having multiple non-nutritional effects on the host plant that may determine increased survival and fitness (e.g., protection against pathogens or toxic minerals, or resistance to drought (Pozo and Azcón-Aguilar 2007; Wehner et al. 2010). However, the main mycorrhizal benefit to the plant is generally considered to be improved nutrition, in exchange for which the plant provides the fungal partner with carbon (C). AM fungi are obligate symbionts, obtaining all their C from host plants (Ferrol and Pérez-Tienda 2009). The C expended by the plant to support the growth and maintenance of the fungus is generally considered to be the cost of the symbiosis for the plant.

Although AM have long been considered primarily responsible for improved plant phosphorus (P) nutrition (Smith and Smith 2011a), numerous works have established that AM fungi can also transfer N to the host plant, from both inorganic and organic N sources (e.g., Johansen et al. 1994; Hawkins et al. 2000; Mäder et al. 2000; Leigh et al. 2009). Estimates of the amounts of N transferred by hyphae to the host plant, in two-compartment studies where access to one compartments by the root is prevented while allowing access to fungal hyphae, have been found to be considerable, ranging from 20 to 74 % of the total N uptake of mycorrhizal plants (George et al. 1992; Frey and Schuepp 1993; Mäder et al. 2000; Tanaka and Yano 2005; Leigh et al. 2009; Fellbaum et al. 2014). This has led to an increased search for the mechanisms behind N uptake by AM fungi and transfer to the plant. A model has been proposed according to which the N taken up by extra-radical mycelia (ERM) is metabolized into arginine, which is then translocated into vacuoles and along the hyphae towards the intra-radical mycelia (IRM), where it is converted into ammonium and transferred to the plant (Bago et al. 2001; Govindarajulu et al. 2005; Jin et al. 2005; Cruz et al. 2007; Tian et al. 2010).

Plant ammonium (NH_4^+) transporters (AMTs) specifically expressed in arbuscule-containing cortical cells of mycorrhizal roots have recently been identified in *Medicago*

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truncatula, *Lotus japonicus*, *Glycine max*, and *Sorghum bicolor* (Gomez et al. 2009; Guether et al. 2009; Kobae et al. 2010; Koegel et al. 2013). These transporters are likely to be involved in the transport across the periarbuscular membrane of NH_4^+ delivered by the fungus and are consistent with the existence of a mycorrhizal N uptake pathway (Guether et al. 2009; Kobae et al. 2010; Pérez-Tienda et al. 2014). The *M. truncatula* MtPt4 phosphate transporter is also located at the periarbuscular membrane, and is essential for symbiotic phosphate transfer into the host cell. *MtPt4* loss-of-function mutants show premature arbuscule degeneration and failed symbiosis but if the plants are N deprived, the arbuscule lifespan does not differ from that of wild-type plants, clearly indicating the importance of N to AM establishment and regulation and a role of AM fungi on plant N nutrition (Javot et al. 2011).

However, much of the essential information on the role and importance of AM fungi in plant N nutrition, and on AM N dynamics, is still missing. Published reports have provided differing, and often contradictory, results that are difficult to combine in a coherent framework. This review offers an overview of the absence of patterns in current knowledge and discusses its possible causes. Here, changes in total plant N content as a result of mycorrhization (compared to non-mycorrhizal (NM) controls under the same growth conditions) are referred to as mycorrhizal N response (MNR), changes in plant growth as mycorrhizal growth response (MGR), and changes in total P content as mycorrhizal P response (MPR). Studies in which the plants were also associated with N-fixing bacteria have not been considered, as well as those with plants grown in multi-compartment systems where the plant + AM fungi have access to an additional source of nutrients, not accessible to NM plants.

AM fungi may have important roles in soil N cycling (Veresoglou et al. 2012). This can be expected to be determinant to their importance to plant N nutrition in the field. However, the studies focusing on this AM fungal role do not provide information on the parameters which are the focus of the present review, and there is no information available that allows to link the AM fungal role on soil N cycling and the analysis of N balance and C/N trade and dynamics of the symbiosis. This question was therefore not considered in the present review.

The controversial beneficial role of AM in plant N nutrition

Although clear evidence exists for a role of AM fungi in transferring N to host plants, reports of negative and neutral MNR have led to questioning of the beneficial role of AM in plant N nutrition (Johnson 2010; Smith and Smith 2011b), even though positive MNR have been found in many studies, including in the field (Table 1). Contradictory responses to mycorrhization have also been observed for P (e.g., Clark and Zeto 1996; Jackson et al. 2002; Smith et al. 2004; Li et al. 2006, 2008; Grace et al. 2009; Antunes et al. 2012) but, in contrast to N, the important beneficial role of AM in plant P nutrition has never been questioned. Rather, the importance of AM for plant P nutrition has been considered to be conditional and depends on different factors including P availability.

One of the reasons for questioning AM beneficial effects on N nutrition is the relative mobility of N forms in the soil (Smith and Smith 2011a, b). This has found support in a study comparing nutrient uptake in soils with patchy and uniform nutrient distributions, where a significant AM effect was observed on P but not on N acquisition (Cui and Caldwell 1996), but there are many evidences that do not support this hypothesis. Although NH_4^+ has lower mobility than NO_3^-, cases of positive MNR in plants supplied with NO_3^- (Vaast and Zasoski 1992; Cuenca and Azcón 1994) or with NH_4NO_3 (Vaast and Zasoski 1992) but not with NH_4^+ have been reported. In addition, cases of positive MNR but negative or neutral MPR, or of more strongly positive MNR than MPR, have been reported (Barea et al. 1989; Sylvia and Neal 1990; Syvertsen and Graham 1990; Vaast and Zasoski 1992; Jongen et al. 1996; Clark and Zeto 1996; Goicoechea et al. 1997; Hartwig et al. 2002; Atul-Nayyar et al. 2009), indicating that in some cases AM may be more important for N than for P. Furthermore, both MNR and MPR have been found to be negative or neutral in some studies (Hays et al. 1982; Cooperband et al. 1994; Fay et al. 1996; Douds et al. 1998, 2008; Hawkins et al. 1999; Leigh et al. 2009; Blanke et al. 2011; Büscher et al. 2012), indicating a general absence of beneficial AM effects on plant nutrition. The hypothesis that high mobility of N ions in the soil prevents AM benefiting N nutrition is also not supported by the fact that ectomycorrhiza improves the host plant's N nutrition, which is considered their major nutritional role. Moreover, the fact that most of AM plants are herbaceous, with higher growth rates and higher nutritional needs than the woody plants that form ECM, may reinforce a possible beneficial role of AM in N uptake.

Another argument that has led to question the beneficial effect of AM on plant N nutrition is that increased N uptake by AM plants may be a consequence of increased growth due to higher uptake of P, and not a direct AM effect on N uptake. Some studies seem to support this view. Hamel and Smith (1991) reported that the positive MNR observed in soya and corn plants disappeared when AM plants were compared with NM controls with comparable P status, and Ibijbijen et al. (1996) observed that both MPR and MNR varied with P but not N levels. However, this is not supported by cases of stronger positive MNR than MPR (Barea et al. 1989; Sylvia and

Table 1 Mycorrhizal N response (MNR), mycorrhizal growth response (MGR), mycorrhizal P response (MPR), mycorrhizal effects on plant N and P concentrations, and N sources used, in all reviewed reports presenting at least MNR and MGR, or data on plant weight and total N contents which allowed to calculate MNR and MGR. In some cases, plant N or P content was not reported by the authors, but the reported values of plant N or P concentrations and weights allowed to extrapolate the effect on total nutrient content. The effects were considered positive or negative when a significant difference in either direction on the respective parameters was reported by the authors, according to their statistical analysis. It should be noted that this review is not a meta-analysis. This table is intended as a way of presenting the very extensive literature included in this review indicating what type of results can be found on each reference

Plant sp.	Fungal sp.	N source	MNR	M% NR	MGR	MPR	M% PR	Reference
C3 grasses								
Psathyrostachys juncea	*Glomus clarum*, *Glomus claroideum*, *Glomus intraradices*	Soil + NH_4^+	Neutral to positive	Neutral to positive	Neutral to positive	Neutral to positive	Neutral	Atul-Nayyar et al. 2009
Lolium perenne	*G. fasciculatum*,	NO_3^- Aspartate Serine	Positive (shoot)	n.d.	Positive (shoot)	n.d.	n.d.	Cliquet et al. 1997
Oriza sativa	*Rhizophagus irregularis*, *Funelliformis mossae*	NH_4^+	Negative to neutral	Neutral to positive	Negative to neutral	Negative to neutral	Positive	Corrêa et al. 2014
Agropyron desertorum	Soil	Soil + NO_3^-	Neutral	Neutral (shoot)	Neutral	Positive	Positive (shoot)	Cui and Caldwell 1996
Hordeum vulgare	*G. mossae*	NO_3^- + NH_4^+	Negative to neutral	Neutral	Negative to neutral	Negative to neutral	Neutral	Fay et al. 1996
Lolium perene	*G. intraradices*	NH_4NO_3	Positive	Neutral	Positive	Positive	Negative	Hartwig et al. 2002
Triticum estivum	*G. mossae*	NO_3^-	Neutral	Neutral	Neutral	Neutral	Neutral	Hawkins et al. 1999
Anthoxanthum odoratum	*Gigaspora gigantea*, *Gigaspora decipiens*, *Archaeospora trappei*, *Glomus* sp.	Soil + NO_3^- Soil + NH_4^+ Soil + glycine Soil + urea Soil + chitin	Neutral	Neutral	Neutral	n.d.	n.d.	Reynolds et al. 2005
Linum usitatissimum	*G. mossae*, *G. intraradices*	NH_4NO_3	Positive		Positive	Positive		Walder et al. 2012
Oryza sativa	*Glomus caledonium*	Soil + urea	Positive	Positive	Neutral	Positive	Positive	Xiao et al. 2010
Oryza sativa	Soil	Soil	Neutral to positive (shoot)	n.d.	Neutral (shoot)	Neutral to positive (shoot)	n.d.	Youpensuk et al. 2006
C4 grasses								
Zea mays	*Glomus etunicatum*, *Glomus diaphanum*, *G. intraradices*	Soil	Neutral to positive (shoot)	Negative to neutral (shoot)	Positive	Neutral to positive (shoot)	Negative, neutral or positive (shoot)	Clark and Zeto 1996
Sorghum bicolor	*G. etunicatum*	Urea	Neutral	Negative, neutral and positive (shoot)	Neutral to positive	Positive	Neutral to positive (shoot)	Fonseca et al. 2001
Z. mays	*G. intraradices*	Soil	Positive	Neutral (shoot)	Positive	Positive	Positive (shoot)	Hamel and Smith 1991
Bouteloua gracilis	*G. fasciculatus*	Soil + NH_4^+	Negative	Neutral to positive	Negative to neutral	Negative to neutral	Neutral to positive	Hays et al. 1982
Brachiaria arrecta	*G. clarum*	Soil	Neutral to positive	Neutral to positive (shoot)	Neutral to positive	Neutral to positive	Neutral to positive (shoot)	Ibijbijen et al. 1996
Sorghum vulgare	*G. clarum*	Soil	Neutral to positive	Neutral (shoot)	Neutral to positive	Neutral to positive		Ibijbijen et al. 1996

Table 1 (continued)

Plant sp.	Fungal sp.	N source	MNR	M% NR	MGR	MPR	M% PR	Reference
							Neutral to positive (shoot)	
Andropogon gerardii	Mix	Soil + NO_3NH_4	Negative to neutral	Negative to neutral	Neutral	Positive	Positive	Miller et al. 2002
Z. mays (native)	*G. etunicatum*, *G. mossae*, *Glomus pallidum*	Soil	Neutral to positive (shoot)	n.d.	Positive	Neutral to positive (shoot)	n.d.	Quintero-Ramos et al. 1993
Z. mays (hybrid)	*G. etunicatum*, *G. mossae*, *Glomus pallidum*	Soil	Neutral to positive (shoot)	n.d.	Neutral	Neutral to positive (shoot)	n.d.	Quintero-Ramos et al. 1993
Panicum sphaerocarpon	*Gigaspora gigantea*, *Gigaspora decipiens*, *Archaeospora trappei*, *Glomus* sp.	Soil + NO_3^- Soil + NH_4^+ Soil + glycine Soil + urea Soil + chitin	Negative to neutral	Neutral to positive	Negative to neutral	n.d.	n.d.	Reynolds et al. 2005
Z. mays	*G. intraradices*	Peat + fertilizer	Neutral to positive	n.d.	Neutral to positive	Positive	n.d.	Subramanian and Charest 1999
S. bicolor	*G. mossae*, *G. intraradices*	NH_4NO_3	Positive	n.d.	Neutral	Positive	n.d.	Walder et al. 2012
N-fixing forbs								
Medicago sativa	*Glomus fasciculatum*	NO_3NH_4	Positive	n.d.	Neutral	Negative	n.d.	Goicoechea et al. 1997
Glycine max	*G. intraradices*	Soil	Positive	Neutral (shoot)	Positive	Positive	Positive (shoot)	Hamel and Smith 1991
Vicea faba	Roots	NO_3^-	Neutral to positive	Neutral to positive	Positive	Positive	Positive	Jia et al. 2004
Trifolium repens	*G. mossae*	$NO_3^- + NH_4^+$	Positive	Positive	Positive	Neutral	Negative	Jongen et al. 1996
Plantago lanceolata	*Glomus hoi*, *G. intraradices*	Soil + NO_3NH_4	Neutral	Neutral	Neutral	Neutral	n.d.	Leigh et al. 2009
Non-N-fixing forbs								
Allium cepa	*Glomus fasciculatum*	Soil + NH_4^+	Null to positive	Positive	Null to positive	Null to positive.	n.d.	Azcón-Aguilar et al. 1993
Lycopersicum esculentum	Soil	Soil + NH_4^+	Positive (shoot)	Positive (shoot)	Null to positive	Positive (shoot)	Positive (shoot)	Cavagnaro et al. 2006
Fragaria x ananassa	Mix	Soil	Neutral	Neutral	Neutral	Neutral	Neutral	Douds et al. 2008
Solanum >tuberosum	*G. intraradices*	Soil + NO_3NH_4	Neutral	Negative or positive (shoot)	Neutral	Neutral to positive	Neutral to positive (shoot)	Gabriel-Neumann et al. 2011
P. lanceolata	*G. hoy*, *G. mossae*	Unidentified	Negative or positive	n.d.	Negative or positive	Positive	n.d.	Hodge and Fitter 2010
Lactuca sativa	*G. intraradices*	Soil + NO_3NH_4	Negative	Positive	Negative	Negative to neutral	Neutral to positive	Jackson et al. 2002
Lactuca serriola	*G. intraradices*	Soil + NO_3NH_4	Negative	Neutral to positive	Negative	Negative to neutral	Neutral to positive	Jackson et al. 2002
Cucumis sativus	*G. intraradices*, *Glomus* sp.	Soil + NO_3NH_4 + NH_4^+	Neutral	n.d.	Neutral	n.d.	n.d.	Johansen 1999
Capsicum annuum	*G. intraradices*	NO_3^-	Positive	Neutral	Positive	Positive	Neutral	Kim et al. 2002

Table 1 (continued)

Plant sp.	Fungal sp.	N source	MNR	M% NR	MGR	MPR	M% PR	Reference
Pulsatilla patens	Soil inoculum	Soil	Positive	Neutral	Positive	n.d.	n.d.	Moora et al. 2004
Pulsatilla pratensis	Soil inoculum	Soil	Positive	Neutral	Neutral to positive	n.d.	n.d.	Moora et al. 2004
Petunia hybrida	*Rhizophagus irregularis*	Soil + NO_3^-	Negative to neutral	Negative to neutral	Neutral to positive	Neutral to positive	Neutral to positive	Nouri et al. 2014
Pelargonium peltatum	TerraVital Horti-mix, Endorize-Mix (Bio), AMYkor (Tri) commercial inoculums	Compost + fertilizer	Neutral	Neutral	Neutral	n.d.	Neutral to positive	Perner et al. 2007
Helyanthus anuus	*G. etunicatum*, *G. mossae*, *Glomus pallidum*	Soil	Neutral to positive (shoot)	n.d.	Positive	Neutral to positive (shoot)	n.d.	Quintero-Ramos et al. 1993
Salvia lyrata	*Gigaspora gigantea*, *Gigaspora decipiens*, *Archaeospora trappei*, *Glomus* sp.	Soil + NO_3^- Soil + NH_4^+ Soil + glycine Soil + urea Soil + chitin	Negative to neutral	Neutral to positive	Negative to neutral	n.d.	n.d.	Reynolds et al. 2005
P. lanceolata	*Gigaspora gigantea*, *Gigaspora decipiens*, *Archaeospora trappei*, *Glomus* sp.	Soil + NO_3^- Soil + NH_4^+ Soil + glycine Soil + urea Soil + chitin	Neutral	Neutral to positive	Negative	nd	nd	Reynolds et al. 2005
Rumex acetosella	*Gigaspora gigantea*, *Gigaspora decipiens*, *Archaeospora trappei*, *Glomus* sp.	Soil + NO_3^- Soil + NH_4^+ Soil + glycine Soil + urea Soil + chitin	Neutral	Neutral to positive	Negative to neutral	n.d.	n.d.	Reynolds et al. 2005
Solanum lycopersicum	Unidentified	Soil + NH_4^+	Positive	Positive (shoot)	Positive	Positive	Positive (shoot)	Ruzicka et al. 2011
N-fixing shrubs and trees								
Erythrina berteroana	Mix	Soil	Neutral to positive	n.d.	Neutral to positive	Neutral to positive	n.d.	Cooperband et al. 1994
Ceratonia siliqua	*G. intraradices*	Soil + NO_3^-	Neutral to positive	n.d.	Neutral to positive	Positive	n.d.	Cruz et al. 2004
Cajanus cajan	*G. mosseae*	Soil	Positive	Negative to neutral	Positive	Positive	Positive	Wellings et al. 1991
Non-N-fixing shrubs and trees								
Vitis vinifera	*G. mossae*	Soil + urea Soil + NO_3^- Soil + NH_4^+ Soil + NO_3NH_4	Positive	Neutral to positive	Positive	Positive	Neutral to positive	Karagiannidis et al. 2007
Citrus aurantium	*G. intraradices*	Soil + NO_3^-	Positive (leaves)	Positive (leaves)	Neutral	Neutral (leaves)	Neutral (leaves)	Syvertsen and Graham 1990
Coffea arabica	*G. intraradices*	Soil + NO_3^- Soil + NH_4^+ Soil + NO_3NH_4	Neutral to positive	n.d.	Neutral to positive	Null	n.d.	Vaast and Zasoski 1992
Macaranga denticulata	Soil	Soil	Positive (shoot)	n.d.	Positive	Positive (shoot)	n.d.	Youpensuk et al. 2006
Theobroma cacao		Soil	Positive	Positive	Positive	Positive	Positive	Chulan 1991

Table 1 (continued)

Plant sp.	Fungal sp.	N source	MNR	M% NR	MGR	MPR	M% PR	Reference
	Scutellospora calospora							
Communities								
Grassland community	Soil	Soil	Neutral	n.d.	Neutral	Neutral	n.d.	Büscher et al. 2012
Microcosms with 11 different plant species	*Glomus* sp., *Glomus geosporum*	Soil	Neutral	Positive	Negative	Positive	Positive	van der Heijden et al. 2006
Brachypodium pinnatum + *Prunella vulgaris*	Basle pi, BEG 21, BEG 19	Soil	Positive	Positive	Positive	Positive	Positive	van der Heijden et al. 2003

n.d non-described

BEG is the name of the strains tested as they are referred to in the paper

Neal 1990; Syvertsen and Graham 1990; Vaast and Zasoski 1992; Jongen et al. 1996; Clark and Zeto 1996; Goicoechea et al. 1997; Hartwig et al. 2002; Atul-Nayyar et al. 2009), and especially by cases of positive MNR and neutral MPR (Sylvia and Neal 1990; Syvertsen and Graham 1990; Jongen et al. 1996). Studies where AM N effects were observed on plants grown with the same P and different N supplies, also clearly indicate direct AM effects on N (e.g., Wallace et al. 1982; Hawkins and George 1999; Jackson et al. 2002; Blanke et al. 2005, 2011; Schroeder-Moreno et al. 2011; Corrêa et al. 2014). Also, Cruz et al. (2004) observed positive MGR and MNR under low, but not under high, nutrient conditions, whereas MPR was always positive, indicating that N and P acquisition are influenced by AM in different ways.

The questioning of AM effects on N nutrition appears to derive principally from the fact that the AM symbiosis affects more than one nutrient and that it can be difficult to unravel these multiple effects. Analyzing both plant N and P contents and concentrations can be useful in clarifying them. Table 2 presents a summary of different combinations of possible AM effects on plant N and P content and concentration, and the information provided by them. If both total content and concentration of a given nutrient increase with mycorrhization (e.g., of N), this clearly indicates a positive effect of AM on that nutrient uptake. But if only the content increases, and this is accompanied by an increase in the uptake of another nutrient (e.g., of P), the results become difficult to interpret (Table 2). In these cases, the increased nutrient uptake may be due to a stoichiometric effect, as discussed above. The fact that plant tissue concentration does not increase can also be due to the limited availability of the nutrient in question. For example, if N is growth limiting, the plant will grow according to the N availability, there will be no luxury N uptake, and therefore no N accumulation. Such analyses can be relevant to clarify the previous argument that positive MNR is an indirect effect of increased P uptake and consequential increased growth of AM plants. This argument implies that the growth of NM plants is limited by P. If this is the case, then N accumulation, and therefore higher N concentrations, can be expected in NM plants, which did not have the P limitation to growth relieved by AM. If this is not observed, it indicates a lack of capacity of NM plants for higher N uptake, and therefore any increase in N uptake upon mycorrhization is at least partially due to direct AM effects.

Another relevant point is that because the plant N demands are much higher than those for P, it is likely that N becomes limiting before P. This would explain why the effects of AM on N tend to be less pronounced than those on P. It also suggests that AM effects on N may have been so far underestimated because of overshadowing P effects. In order to clarify the effect of AM on N acquisition, it is therefore essential to know whether the nutrient availability in the

Table 2 Interpretative table of the different combinations of total plant N and P contents and concentrations

			AM effect on plant total content								
			> N			= N			< N		
			> P	= P	< P	> P	= P	< P	> P	= P	< P
AM effect on plant concentration	> N	> P	+ N +P	+ N 0 P	+ N −P	0 N + P	0 N 0 P	0 N −P	−N + P	−N 0 P	0 N 0 P
		= P	+ N ? P	+ N 0 P	+ N −P		0 N 0 P	0 N −P			0 N 0 P
		< P	+ N ? P	+ N 0 P	+ N −P		0 N 0 P	0 N −P			0 N 0 P
	= N	> P	? N + P	+ N 0 P		0 N + P			−N + P	−N 0 P	0 N 0 P
		= P	? N + P	+ N 0 P			0 N 0 P				0 N 0 P
		< P	+ N ? P	+ N 0 P	+ N −P			0 N −P			0 N 0 P
	< N	> P	? N + P			0 N + P			−N + P	−N 0 P	Improbable
		= P	? N + P			0 N + P				−N 0 P	0 N 0 P
		< P	? N ? P	+ N 0 P	+ N −P	0 N + P	0 N 0 P	0 N −P			0 N 0 P

AM effects can be >: AM plants have higher content/concentration than NM plants, =: AM plants have the same content/concentration than NM plants, and <: AM plants have lower content/concentration than NM plants. AM benefit in terms of N and P can be +: positive, 0: neutral −: negative. *Lightly shaded cells*: growth is limited by a factor other than N or P. *Darkly shaded cells*: combination not possible

experimental system is growth limiting or not, namely for N and P. As a rule, this is not taken into consideration in experimental designs or interpretation of results, and nutrient supplies tend to be considered high or low, without considering plant demand.

What makes the difference between a positive and a negative effect of AM on N nutrition?

As previously discussed, AM effects on N uptake and plant growth have been observed to vary from negative to positive

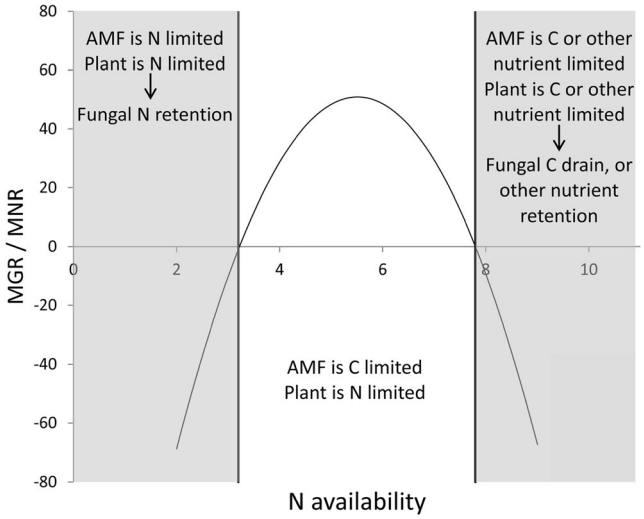

Fig. 1 Hypothesized curvilinear relation between mycorrhizal N (MNR) or growth (MGR) response and N availability. AM will have a positive effect at intermediate N levels, but negative at both high and low. At low N availabilities, both AMF and host plant will be N limited, and negative mycorrhizal effects result from fungal N retention. At intermediate N levels, the AMF will be C limited and the plant N limited, and the plant benefits from increased N uptake leading to increasing growth. At high N levels, both AMF and host plant are either C limited or limited by the availability of a nutrient other than N, and negative mycorrhizal effects may result from either excess C drain or retention of this other nutrient by the AMF. Values in x-axis are uniteless and merely indicative

depending on the experiments performed. The reasons for this variation are not clear. However, it has been repeatedly assumed that AM effects depend on nutrient availability, being negative at high, and positive at low nutrient availabilities (Fig. 1). In accordance with this, increased N uptake in presence of low N supply and neutral or negative effects at high N have been observed in some studies (Cruz et al. 2004; Jia et al. 2004). However, the opposite has also been reported (Wallace et al. 1982; Jackson et al. 2002). Similar results have been obtained for P (Ibijbijen et al. 1996; Müller et al. 1999; Gabriel-Neumann et al. 2011; Watts-Williams and Cavagnaro 2011; Antunes et al. 2012).

Studies using ^{15}N to evaluate AM fungal N uptake and transfer to the plant have also produced contradictory results. While some have found that increased N inputs reduce N transport by AM fungal to hosts (Johansen et al. 1994; Hawkins and George 1999; Mäder et al. 2000), others report the opposite (Hawkins and George 2001; Tu et al. 2006; Schroeder-Moreno et al. 2011). It remains therefore unclear whether and how N availability affects AM fungal contributions to plant N. A possible explanation for these discrepancies is that MNR may be higher at intermediate N levels, and differences in results depend on where in the gradient of AM effects the observations are being made (Fig. 1). This has been observed for ectomycorrhizal plants (Corrêa et al. 2008). Curvilinear responses have been modeled for AM (Gange and Ayres 1999; Janos 2007), and some experimental evidence exists to support this interpretation (Bååth and Spokes 1989). However, when this was investigated in rice, by testing mycorrhizal responses over a range of N supplies going from severely growth limiting to non-growth limiting, no evidence of curvilinear responses to mycorrhization was observed (Corrêa et al. 2014). Further studies are needed using other experimental systems, with other AMF and, namely, with plants presenting more positive responses to AM than rice.

Whereas positive effects of AM on nutrient uptake are extensively reported and well understood, negative effects are not. Negative MNR has been proposed to result from fungal N retention (Johansen 1999; Nouri et al. 2014; Corrêa et al. 2014) Negative MNR may result from fungal N retention (Johansen 1999; Nouri et al. 2014; Corrêa et al. 2014). Since the fungal partner also has N needs, it can be expected to replenish them and provide the plant with only the N that is available in excess (Alberton et al. 2005; Corrêa et al. 2012). The fact that the C:N ratio of fungi is lower than that of plants may mean that under limiting N availability, the fungus works as the first N sink (Nordin et al. 2004). Nevertheless, negative MNR may not necessarily imply decreased N transport to the plant by the fungal partner. There is evidence that the mycorrhizal P uptake pathway operates, and AM-inducible P transporter genes are expressed, even in plants that present negative MPR. The contribution of the AM P uptake pathway has been observed to be related to the degree of colonization and expression of AM-inducible P transporter genes, but not to plant responsiveness (Smith et al. 2004; Javot et al. 2007; Grace et al. 2009; Fellbaum et al. 2014). This may be related to the fact that mycorrhization seems to inhibit direct P uptake by the root (Smith and Smith 2011b), a mechanism that is still unknown for N. It is also important to consider that the form of N available may be determinant for MNR. Under monoxenic conditions and when only one N source is available, ammonium uptake rates by *Glomus intraradices* tend to be higher than those of nitrate. However, in nature several forms of inorganic and organic N are simultaneously available at very distinct concentrations, and no information is available on the AM fungal N preferences under these conditions (Cruz et al. 2013).

Relation between MNR and MGR: can MNR be responsible for different MGR?

AM can have a wide variety of effects on plant growth, and positive MGR has been assumed to occur at low, but not at high, nutrient availabilities. This has sometimes been observed (Ibijbijen et al. 1996; Graham et al. 1997; Yoshida and Allen 2001; Fonseca et al. 2001; Ning and Cumming 2001; Cruz et al. 2004), but not always (Smith et al. 1986; Müller et al. 1999; Jackson et al. 2002; Klironomos 2003; Bi et al. 2003; Wright et al. 2005; Hodge and Fitter 2010). Different underlying causes of this variability are possible. One

possibility would be that MGR could be correlated with nutrient effects. However, the correspondence between MGR and MNR or MPR is frequent but it does not always occur (Table 1) (Smith et al. 1986; Barea et al. 1989; Wellings et al. 1991; Clark and Zeto 1996; Douds et al. 1998; Müller et al. 1999; van der Heijden et al. 2006; Xiao et al. 2010; Ryan et al. 2012; Büscher et al. 2012). On the other hand, positive effects of mycorrhization follow the same trend if not the same magnitude, for total N and P contents in a large number of reported cases, making it hard to tell whether MGR is MNR- or MPR-related. The effect on P is sometimes stronger or clearer than on N (Smith et al. 1986; Wellings et al. 1991; Clark et al. 1999; Karagiannidis et al. 2007), but other times it is less pronounced (Vaast and Zasoski 1992; Jongen et al. 1996; Clark and Zeto 1996; Hartwig et al. 2002). However, a meta-analysis has indicated that although MGR is most positive when plants are P limited rather than N limited, with N-fertilization being the most important factor in predicting MGR (Hoeksema et al. 2010). The relation between MGR and MNR is therefore not clear and may depend on factors still unknown. In the absence of other stresses, positive MGR seems to always be a consequence of higher nutrient uptake by AM plants and relief of nutrient limitation to plant growth (Hamel and Smith 1991; Ibijbijen et al. 1996; Cruz et al. 2004; Jia et al. 2004; Karagiannidis et al. 2007; Ruzicka et al. 2011). Interpretation of negative MGR is less consensual, as is discussed below.

Is a negative MGR C mediated?

A classical assumption behind cost-benefit analyses and interpretation of changes in MGR and mycorrhizal symbiotic function is that variations in MGR depend on the balance between C supplied by the host plant and nutrient received. Growth depressions of AM plants have been suggested to occur if the C cost to the plant exceeds the benefit from increased N and/or P uptake and resulting increased photosynthesis (Fitter 2006; Johnson 2010), and negative MGR is conventionally considered to be caused by an excessive C drain by the fungus (Johnson et al. 1997; Smith and Smith 2011b). However, there is increasing evidence that negative MGR is not always associated with the C costs of the symbiosis (Graham and Abbott 2000; Li et al. 2008; Grace et al. 2009; Smith and Smith 2011b).

The degree of root colonization can be considered an indicator of AM fungal biomass and, therefore, of C allocation towards fungal growth, which is presumed to be mostly C limited (Treseder and Allen 2000). Studies of either different plant species with the same AM fungi, or different AM fungal species colonizing the same host plant, and resulting in different colonization levels, allow comparison of potentially different C costs for the hosts. In such studies, degree of AM colonization and MGR have sometimes been found to be positively correlated (Graham and Eissenstat 1994; Graham et al. 1997; Wilson and Hartnett 1998; Graham and Abbott 2000; van der Heijden et al. 2006; Li et al. 2008; Blanke et al. 2011; Maiti et al. 2011) and other times negatively (Graham and Eissenstat 1998; Wilson and Hartnett 1998; Jackson et al. 2002; Veiga et al. 2011; Blanke et al. 2011; Walder et al. 2012; Corrêa et al. 2014). In many cases, no correlation has been found (Edathil et al. 1996; Graham and Abbott 2000; Ryan and Angus 2003; Smith et al. 2004; van der Heijden et al. 2006; Gao et al. 2006; Grace et al. 2009; Busby et al. 2011; Aleklett and Wallander 2012; Büscher et al. 2012; Sikes et al. 2012; Fellbaum et al. 2014). Differences in MGR therefore cannot be unequivocally attributed to differences in AM colonization, so that even if they are sometimes related to C drain by the fungus, this is obviously not always the case. Further research is necessary to determine the underlying reasons for this.

It is, however, important to note that studies usually report percentage of root colonization, which may not correspond to the total fungal biomass or total C allocated towards the fungal partner. Higher degrees of root colonization of a smaller root may correspond to a smaller, or similar, total fungal biomass than in a less colonized larger root and therefore constitute a lower or similar total C investment by the host plant. On the other hand, the C cost to the plant can also vary according to its size, and its capacity for total photosynthesis, i.e., the same amount of C can correspond to a higher percentage of the total assimilated C in a smaller plant, than in a better fed, larger plant. Different cases may therefore be difficult to compare. It should, however, be considered that small, nutrient-limited plants can still assimilate C in excess of what they can use for growth and that the C allocated to the fungus may not constitute a true cost, in the sense of negatively affecting plant growth. This has been observed in both *Piriformospora* associations (Corrêa et al. 2014) and ectomycorrhiza (Corrêa et al. 2008, 2012). It should also be noted that colonization by arbuscules, which are considered beneficial structures for the host by providing the exchange interface, may have a different meaning than colonization by vesicles or spores, which have sometimes been interpreted as solely beneficial for the fungus. However, these differences in colonization are rarely considered.

On the other hand, if MGR is determined by C, differences in C availability due to increased CO_2 or shading would be expected to affect MGR. Shading should increase the C cost of AM by decreasing C availability, and elevated CO_2 should decrease it. However, studies of increased CO_2 or shading have also given contradictory results. Elevated atmospheric CO_2 tends to stimulate AM fungal root colonization, indicating higher C allocation to the AM fungal, but this is not always the case (Alberton et al. 2005; Compant et al. 2010; Büscher et al. 2012). Moreover, this increased fungal C allocation is not always associated with increased growth or nutrient uptake by AM plants (Compant et al. 2010; Büscher et al. 2012). Low light can decrease MGR, as shown by shading experiments (reviewed by Smith et al. 2009), but it has

also been found to not result in negative MGR, even though the C flow to the fungus remained unchanged (Kyllo et al. 2003; Olsson et al. 2010).

In addition, photosynthetic stimulation may also play a role in making C not determinant. The meta-analyses performed by Kaschuk et al. (2009, 2010) demonstrated that legumes are not C limited under symbiotic conditions, and that rates of photosynthesis in AM and rhizobial plants can be sink stimulated above the C costs of the symbioses, allowing plants to take advantage of nutrient supply from their mycosymbionts without compromising the availability of photosynthates for plant growth. However, in all the cases analyzed, the symbioses had either positive or neutral effects on plant yield, and no clue was offered as to the reasons behind negative effects of AM symbioses.

Is the N effect of AM on plant growth direct?

Differences in N uptake between AM and NM plants may be directly responsible for negative MGR. It has been previously hypothesized that negative effects on plant growth could occur as a consequence of fungal N retention (Smith and Smith 2011b), and recent studies have provided evidence supporting this hypothesis. In a recent study, testing AM responses over a gradient of N availabilities, MNR, together with a synergy between N and Zn uptake, were found to explain MGR, and evidence was obtained that a fungal C drain was not associated with negative MGR (Corrêa et al. 2014). In an experiment using wild-type and transgenic potato plants, with either constitutive overexpression or antisense inhibition of a sucrose transporter SUT1, a decrease in biomass was observed in AM SUT1 antisense plants growing under low P which could not be explained by an increased C drain, since these plants allocated less sucrose to the root. However, mycorrhization also resulted in decreased N uptake in these plants, indicating that MGR was more dependent on MNR than on C expenditure on fungal growth (Gabriel-Neumann et al. 2011). As discussed below, higher fungal growth is sometimes accompanied by higher MNR, but at other times not, providing no conclusive evidence of N retention by AM fungi, or C/N exchange reciprocity between partners. It is therefore uncertain whether nutrient retention by AM fungi always occurs, or when it occurs, and how much reciprocity there is in C and N exchange between partners.

Is plant C investment in fungal growth related to N needs or N benefit?

Regulation of N-for-C trade

Connected to the question of C mediation of N effects is the regulation of N-for-C trade in the symbiosis. Investigations of cost-benefit balances have so far mainly focused on C–P trade. This regulation is essential for the symbiosis, but is still poorly understood. Fitter (2006) and Helgason and Fitter (2009) have hypothesized that if the fungus fails to supply the plant with adequate amounts of nutrients, this will reduce C supply to the fungus, and a model of coupled exchange of C for P has been proposed (Bücking and Shachar-Hill 2005). Some studies have provided evidence consistent with these hypotheses. It has been suggested that fungal P and NH_4^+ transporters expressed in arbusculated cells are able to reabsorb P and NH_4^+ released into the periarbuscular apoplast, resulting in competition between plant and fungal cells for nutrients present in the symbiotic interface and suggesting that the fungus may control the amount of nutrients delivered to the host plant (Balestrini et al. 2007; Pérez-Tienda et al. 2011). On the other hand, a linear correlation between C allocation to the ERM and the root P concentration was found in monoxenic cultures (Olsson et al. 2002), and host roots were found to allocate significantly more ^{14}C to *Rhizophagus irregularis* (former *G. intraradices*) hyphae with access to P (Kiers et al. 2011). Similar decision mechanisms appear to be active on the fungal side, with more P being allocated to mycorrhizal roots in presence of a higher sucrose supply (Bücking and Shachar-Hill 2005; Kiers et al. 2011).

The discovery of a potentially important mycorrhizal role in plant N nutrition warrants the extension of such a focus to C–N trade (Smith and Smith 2011b). Although there is much less information for N, some evidence of N for C transfer reciprocity between mycorrhizal partners has also been obtained in monoxenic root organ cultures. Increased C supply to the root compartment was observed to result in increased N uptake from the hyphal compartment and transport to the root (Fellbaum et al. 2011). However, monoxenic cultures lack a shoot and sink-source relationships, and in them C allocation to the root is not controlled by the plant nutrient status but is artificially controlled by the experimenters. Unrepresentative conditions of abundant nutrients accompanied by abundant C allocation to the AM fungus may therefore be created, which would offer no light on how normal functioning of whole plants, with normal source-sink relationships, will supply the fungus with more C. Furthermore, reciprocity between N and C supplies is not always observed in monoxenic cultures. Olsson et al. (2005) reported that increasing N in the root compartment decreased ^{13}C allocation to the mycelium, whereas increasing N in the hyphal compartment had no influence on C allocation, indicating that the regulation of C/N exchange may be more complex.

Data obtained from pot experiments have revealed similar contradictions. In a labeling experiment, using a compartmented system, a correlation was observed between the amount of ^{15}N received through an AM fungus and the degree of mycorrhization (Ames et al. 1983), and in a pot experiment where an AM fungus could choose between a shaded and a

non-shaded host, it was observed to allocate more N and P to non-shaded hosts (Fellbaum et al. 2014). However, different observations have been made in several other studies. Variations in amounts of sucrose reaching sink organs, namely roots, did not result in different nutrient uptake by AM plants (Gabriel-Neumann et al. 2011), and increased C allocation towards the fungus as a result of elevated CO_2 was also not rewarded with increased N or P uptake or plant growth (Büscher et al. 2012). In a study of C allocation into ERM in mixed flax and sorghum cultures using stable isotope compositions, Walder et al. (2013) found that flax allocated much less carbon to the AM fungus but gained up to 94 % of the N and P that it provided. In addition, as discussed previously, several studies found no correlation between root colonization and mycorrhizal benefit, in terms of either MGR or MNR (Edathil et al. 1996; Graham and Abbott 2000; Ryan and Angus 2003; Smith et al. 2004; van der Heijden et al. 2006; Gao et al. 2006; Grace et al. 2009; Busby et al. 2011; Aleklett and Wallander 2012; Büscher et al. 2012; Sikes et al. 2012; Fellbaum et al. 2014).

The hypothesis of reciprocity in C/N exchange does not consider that this exchange may change according to the symbiotic partners' needs. As the plant becomes more N limited, more C may become available for growth of its fungal partner. As it receives more C from the plant, the fungus will become less C limited, its N needs will increase, and this could lead to N retention by the mycelium leaving less N available for the plant. Evidence has been found in ECM that increased C allocation towards the fungus, and resulting increase in fungal biomass, could increase competition for nutrients and decrease nutrient allocation to the plant (Alberton et al. 2005; Corrêa et al. 2012). C investment in fungal growth would therefore not be linked to a nutrient gain from the fungus. A similar mechanism has been proposed, and a model has been built, for AM and P (Landis and Fraser 2008), and it was recently reported that this may also be true for AM and N (Corrêa et al. 2014). However, Alberton et al. (2005) observed a less clear pattern in AM than in ECM symbioses. The authors expected that under elevated CO_2, and hence increased C availability for the fungus, there would be increased growth of the fungal partner, accompanied by increased fungal N retention, and decreased plant growth response. However, the AM fungal and host plant response ratios to elevated CO_2 did not differ, indicating a synchronization of benefits between the mycorrhizal partners.

Plant N status can profoundly impact allocation of C to roots, mycorrhiza, and mycorrhizal functions

It is not clear whether increased C allocation towards an AM fungus will be rewarded with increased N uptake to the host plant. However, plant N status can profoundly impact C allocation to AM fungi. The degree of mycorrhization has been repeatedly reported to respond to N supply, indicating that the host plant will change its C investment in fungal growth according to N availability and plant needs. As observed for P (Treseder 2004), increased N supply often reduces the percentage of mycorrhizal root colonization (Jensen and Jakobsen 1980; Chambers et al. 1980; Hays et al. 1982; Hepper 1983; Johnson 1984; Cuenca and Azcón 1994; Bressan 2001; Miller et al. 2002; Jackson et al. 2002; Johnson et al. 2003; Treseder 2004; Jia et al. 2004; Blanke et al. 2005; Becerra et al. 2007; Hodge and Fitter 2010; Liu et al. 2012; Nouri et al. 2014; Corrêa et al. 2014), and Tu et al. (2006), using $^{13}CO_2$, observed decreased belowground C allocation in AM plants with increased N fertilization again suggesting changed C allocation towards AM fungi with the N supply.

Cases of no response of mycorrhizal colonization to N have, however, also been reported (Oliver et al. 1983; Cuenca and Azcón 1994; Johansen et al. 1994; Ibijbijen et al. 1996; Hawkins and George 1999; Jumpponen et al. 2005; Tu et al. 2006; Breuillin et al. 2010; Schroeder-Moreno et al. 2011; Antunes et al. 2012), as have positive responses (Furlan and Bernier-Cardou 1989; Eom et al. 1999; Bressan 2001; Hawkins and George 2001; Tu et al. 2006). In addition, studies have revealed correlations between root colonization and plant tissue N concentrations that were positive (Tu et al. 2006), negative (Miller et al. 2002; Blanke et al. 2005), or neutral (Ibijbijen et al. 1996). Contradictory responses have also been observed for ERM. Decreased ERM with increased N has been observed (Olsson et al. 2005), both in cases where the percentage of colonization also decreased (Hodge and Fitter 2010; Liu et al. 2012) and in others where it did not respond to N (Antunes et al. 2012), but other studies showed no response of ERM to N supply (Hodge and Fitter 2010), or positive responses, both in cases where colonization did not respond to N (Hawkins and George 1999) and where colonization also increased (Eom et al. 1999). Regardless of the direction or variability of the response, however, the fact that N availability can influence AM fungal growth supports a role for interactions between AM and plant N nutrition and warrants further investigation.

In some of the reported cases, mycorrhizal colonization was observed to respond to P but not to N (Smith et al. 1986; Ibijbijen et al. 1996) so that where colonization increases with increasing N supply, it is may actually be responding positively to higher P limitation. In support of this hypothesis, Johnson et al. (2003) found that mycorrhization decreased under N limited growth conditions when N supply was increased, while at high N levels increasing the N supply increased mycorrhization. This highlights the importance of N:P stoichiometry in AM effects on plants.

The importance of N:P stoichiometry in AM benefits

It has been hypothesized that rather than being based on need or availability of one nutrient, be it N, P, or another, the mycorrhizal benefit depends on the relative availabilities of C, N,

and P, i.e., on the stoichiometry of these nutrients (Chen et al. 2009; Johnson 2010). Nutrient limitations are not absolute but relative and interdependent. For example, as N availability increases, and N ceases to be growth-limiting, the probability of P- or C-related growth limitation increases. Resource stoichiometry allows a better prediction of resource exchange and cost:benefit balance, and of the outcome of the mycorrhizal symbiosis, than single resource limitation.

Johnson (2010) hypothesized that AM symbiotic function is determined by the interaction of N and P availability with C supply and demand among host plants and fungi so that changes in AM symbiotic function would be driven by P and N availability, but mediated by C. It was further suggested that this dependency changes according to the trade balance model, in which the host plants may be C or P limited and the AM fungi may be C or N limited. The model considers that the plant only benefits from mycorrhization if P is limiting and does not consider any benefit in terms of N nutrition. N is only considered to the extent that it can increase or decrease photosynthetic efficiency or rate, and therefore C supply to the fungus. The model predicts that under N-limiting conditions (i) photosynthesis, and hence C available for supply to the AM fungus, will decrease, and (ii) the fungus will become N limited, and hence will decrease its C demand. If N is not limiting, the converse applies. Stoichiometry, however, can have much more complex consequences for symbiotic function than those considered in the proposed trade balance model. N limitation has to be considered as a possible scenario for mycorrhizal benefits, in addition to P limitation. Since these two limitations depend on the stoichiometry of the availability of the two nutrients, it becomes difficult to predict in which conditions the mycorrhiza are of benefit and in which they are not. In addition, needs of the fungal partner for N, P, and C add to this complexity.

Correlation between MNR, MGR, and extent of mycorrhizal colonization

The scenarios evoked so far have sometimes positive, sometimes negative. and sometimes neutral MNR, MGR, and effects of N on AM colonization. So, the question arises of whether negative or positive MGR and MNR coincide and whether they are connected to lower or higher root colonization. Only a very limited number of studies could be found which report all responses of mycorrhizal colonization to N addition, MNR, and MGR, and these do not offer any discernible pattern. In some cases, lower N levels resulted in increased colonization and higher MNR and MGR (Cruz et al. 2004), while in others a lower MNR and MGR (Jackson et al. 2002; Corrêa et al. 2014), or higher MNR but no response of MGR (Jia et al. 2004) was reported. In one study, mycorrhization did not respond to N level but resulted in different MNR (Smith et al. 1986). None of the reviewed published reports of positive responses of mycorrhization to N supply report total N content.

Conclusions

Currently available data do not allow construction of a coherent common framework for, or even provide consistent answers to, the main questions concerning N and C/N dynamics in AM. This disarray may derive from a number of factors. One possible cause of the disparate observations is that the reported experiments studied a wide variety of different plant and fungal species, and even plant genera (Table 1). A meta-analysis revealed the host plant functional group to be one of the factors that best explained variations in MGR, together with N fertilization (Hoeksema et al. 2010). This has been repeatedly pointed out as one of the problems in mycorrhizal research, but it of course reflects the fact that AM fungi establish symbioses in a variety of habitats with a wide variety of plant species with various life strategies and resource needs. It is possible that AM interactions between different plant and fungal partners follow different basic premises, and so establish different dynamics. If so, analyzing them together is not likely to lead to a common, consistent conclusion.

Another, and perhaps the simplest, possible reason is that mycorrhizal responses may not be linear, but curvilinear, and more positive at intermediate levels of N (Fig. 1). The most common experimental designs, which consider only the binomials high nutrient/low nutrient, or nutrient source type A/nutrient source type B, are unable to detect possible curvilinearity or to determine where in the gradient of AM effects the observations are being made. The use of gradients of the tested variable, namely the supply of a given nutrient, would be essential to clarify this. This approach has been used in a recent study where mycorrhizal rice responses over a gradient of N availabilities, going from severely limited to non-growth limiting, were tested (Corrêa et al. 2014). In this study, no evidence of curvilinear responses was found. However, this needs to be further tested in other systems, namely using other AM fungi and plants belonging to different functional groups which present more positive responses to AM than rice does.

On the other hand, when testing mycorrhizal effects on a given nutrient, researchers tend to measure that nutrient alone, or almost alone, overlooking possible parallel effects of other nutrients, which could potentially result in different outcomes of the symbiosis. The effect of changing the supply of a single nutrient may in fact result from interactive effects of several nutrients (particularly N, P, and C), due to stoichiometry and co-limitations. It has been previously pointed out that the dynamics of C, N, and P in mycorrhizal systems should be studied in a coordinated fashion because the availability of one of

these elements influences the ability of plants and fungi to acquire the others (Miller et al. 2002; Johnson 2010). However, it is possible that nutrients other than N, P, and C can also be crucial, due to synergies or antagonisms. An example of such a synergy has recently been reported, where AM effects on N uptake led to effects on Zn uptake, which were then responsible for MGR (Corrêa et al. 2014).

In addition, the discovery that co-limitation of plant growth by more than one nutrient may be far more frequent than previously thought has further implications for how mycorrhizal interactions are perceived, as well as comparisons of AM with NM plants. One particularly relevant possible cause of co-limitation is trade-offs in allocation between different acquisition strategies (Craine et al. 2009). In AM plants, a possible trade-off in allocation will be generated when different resources are acquired by the mycorrhizal fungi and the host roots. Since this is not possible in NM plants, the establishment of co-limitations should also be different in AM and NM plants.

Other, more complex and difficult to address questions remain. Mycorrhizal interactions are multi-component systems, encompassing at least two organisms, plant and fungus (in its simplest, laboratory-controlled version), but they have been consistently studied in the same manner as non-mycorrhizal plants, i.e., as comparatively simple isolated organisms. However, with the addition of a new organism to the system, the fungal partner, which both affects nutrient supply to the plant and has its nutrient supply affected by the plant, many other variables and variable interactions enter into play that may influence the possible outcome. This is further complicated by the fact that plants and fungi vary in their chemical composition and resource acquisition abilities.

The need for a mycocentric approach, in addition to the conventional phytocentric approach, in mycorrhizal studies, and the integration of the two, has previously been advocated (Alberton et al. 2005, 2007; Johnson 2010), but rarely adopted. In addition, the mycorrhizal system is probably more complex than the result of the added needs of the plant and fungal partners. It may be too simplistic to expect mycorrhization to change the magnitude but not the quality of the plant response, and the whole may be different from the sum of its parts. The concept of mycorrhizal plants should perhaps be replaced by more appropriate mycorrhizal systems and studied using a systems biology approach. In summary, an understanding of both the C:N:P stoichiometry of the symbiosis (Chen et al. 2009; Johnson 2010), and of other nutrient interactions, is essential to achieve a more predictive understanding of mycorrhizal responses. This should be further combined with a more holistic approach to their study and the adoption of a systems' view of the symbiosis.

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