Ajit Varma · Ram Prasad
Narendra Tuteja *Editors*

Mycorrhiza - Eco-Physiology, Secondary Metabolites, Nanomaterials

Fourth Edition

Springer

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Foreword

The pressure on plant production systems is steadily increasing. At first, areas which could be used for the cultivation of plants are getting smaller because more and more space is used for other anthropogenic activities. Secondly, environmental constraints like soil erosion, salinization, or flooding lead to periodical yield losses and finally to the decision to give up a particular region for plant production. Thirdly, the use of pesticides becomes difficult, because the application of more and more compounds is not permitted anymore or they have lost their effectiveness. The development of new agents is time and cost intensive, and it is questionable if there will be enough of such new agents to substitute the compounds which are disappearing from the market. Under these circumstances, the application of plant-interacting microorganisms in plant production systems becomes more and more a realistic alternative and might be the only chance in the future to produce enough food for a growing world population. Among such microorganisms, mycorrhizal fungi fill a particular position. With their hyphae colonizing at the same time the root and the surrounding soil, they connect the inside and the outside of the plant. In this so-called mycorrhizosphere, they bring together all physical, chemical, and biological factors of the terrestrial environment with the physiology of the plant.

The book "Mycorrhiza: Eco-Physiology, Secondary Metabolites, Nanomaterials" gives an excellent overview of the current state of the art from basic to applied mycorrhizal research. It covers different types of interactions including those between the orchid mycorrhizal fungus *Piriformospora indica* and non-orchid plants. Several chapters describe more basic aspects but nevertheless important for application. Carbon flux in mycorrhizal plants has more and more to be the basis for predicting the outcome of mycorrhizal interactions. Functional diversity must be managed for an adapted application in the field. Also, plant–fungus signaling needs a better understanding. Most chapters, however, describe where and how mycorrhizal fungi can be used in plant production under difficult conditions and show in this way how broad the possibilities for application can be. I therefore congratulate the editors that they brought together so many different facets of basic and applied mycorrhizal

research. I also congratulate you on holding this book in your hand and ask you to read at least some of the highly interesting chapters.

Erfurt, Germany
20 March 2017

Philipp Franken

Preface

German pathologist A.B. Frank (1885) coined the term Mycorrhiza which literally means fungus roots. These fungi aid in the productivity of plants *via* the formation of dynamic associations with plant roots. Mycorrhiza is considered a fundamental part of the root colonization and stabilization of plants on terrestrial habitats. The symbiotic associations formed are an important subject to evaluate various opportunities using modern tools of biotechnology. The possibilities of genetically manipulating these associations have led to the optimization of plant productivity in ecosystems with minimal risk of environmental damage.

This volume of the mycorrhiza book gives exemplary insight into the advancements in mycorrhizal studies. This edition extensively illuminates the ecophysiological aspects, secondary metabolite production, and interaction of mycorrhiza with nanomaterials. The ability of mycorrhiza to provide resistance against various abiotic and biotic stresses has been explored in various parts of this edition. In addition to providing resistance, mycorrhizas are known to increase secondary metabolite production of plants. Therefore, various studies have been conducted to elucidate the mycorrhiza-induced increase of secondary metabolites in various economically important and medicinal plants. Interaction studies of nanomaterials with mycorrhiza have also been a subject of recent interest.

It is hoped that this new edition will interest readers in the latest outcomes of mycorrhiza research and also encourage young researchers to prove the challenging field of these studies.

This volume consists of 18 chapters covering the diverse mycorrhizal associations by 57 eminent academicians and subject specialists.

We are grateful to the many people who helped to bring this volume to light. We wish to thank Hanna Hensler-Fritton, Isabel Ullmann, and Man-Thi Tran Springer Heidelberg, for generous assistance and patience in finalizing the volume. Finally, special thanks go to our families, immediate, and extended, not forgetting those who have passed away, for their support or their incentives in putting everything together. Editors in particular are very thankful to Dr. Ashok K. Chauhan, Founder President of the Ritnand Balved Education Foundation (an umbrella organization of

Amity Institutions), New Delhi, for the kind support and constant encouragement received. Special thanks are due to my esteemed faculty colleagues and dear student Ms Diksha Bhola and other technical staff.

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Chapter 1
Carbon Fluxes in Mycorrhizal Plants

Veronika Řezáčová, Tereza Konvalinková, and Jan Jansa

Abstract Although declared as a research priority more than 40 years ago, the knowledge about the magnitude and mechanisms of carbon (C) fluxes between plants and their mycorrhizal fungal symbionts remains fragmentary. In spite of a number of experiments with isotopically labeled C documented rapid and directed C transfer from the host plant to its mycobionts, the molecular mechanisms and their regulation involved in such a transport remain largely unknown. It seems that in many arbuscular mycorrhizal (AM) symbioses, the C costs remains well below 10% of the C fixed photosynthetically by the host plants. Higher values were detected in the past only under specific situations such as in young plants, under low light intensities, and/or for particular partner combinations, involving very costly (in terms of C demand) and little nutritionally beneficial AM fungi such as *Gigaspora* sp. Ecological context of the common mycorrhizal networks in terms of redistribution of symbiotic C costs and nutritional benefits on one hand and C movement through soil food webs beyond mycorrhizal hyphae on the other are briefly discussed in this chapter, and further research challenges and open knowledge gaps with respect to C fluxes in mycorrhizal plants are outlined.

1.1 Introduction

Mycorrhiza is one of the most common inter-species interactions on Earth, involving great majority (>90%) of plant species (Smith and Read 2008) and several groups (and functional guilds) of soil fungi (Nguyen et al. 2016; Prasad et al. 2017). This interaction involves bidirectional flows of matter between the symbiotic partners, exchanging mineral nutrients such as nitrogen (N) and phosphorus (P) for the reduced carbon (C) originating from plant photosynthesis (Ferrol et al. 2002). Several different types of the mycorrhizal symbiosis evolved during the history, involving different (often disjunctive) groups of symbiotic partners at both plant and fungal sides (Cairney 2000). Yet, the main function (nutrient for C

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trading) is stunningly uniform across the different mycorrhizal types, with some remarkable deviations from this general pattern such as plant-bound C fluxing in orchid protocorms or mycoheterotrophic plants (Leake and Cameron 2010; Bever 2015).

Most efforts in mycorrhizal research have so far been dedicated to uncovering principles and diversity in nutritional and/or growth benefits the symbiosis confers to the plants or how the diversity of taxa and functions in the fungal communities affects the productivity/stability/diversity of the plant communities and vice versa (van der Heijden et al. 1998; Johnson et al. 2004; Munkvold et al. 2004; Cavagnaro et al. 2005). Less efforts have been dedicated to the role of mycorrhizas in sustainable soil use and in establishing and maintaining soil physical properties (e.g., aggregate stability, water conductivity, etc.) and to non-nutritional benefits such as improved biotic resistance of the plant (Newsham et al. 1995; Rillig 2005; Rillig et al. 2015). Comparatively, very little efforts have so far been invested into quantification of C fluxes in the mycorrhizal symbiosis, and to the underlying molecular mechanisms (Slavíková et al. 2017). The purpose of this chapter is to synthesize current knowledge on the influence of mycorrhiza on the C fluxes between atmosphere, plant, mycorrhizal fungi, and the soil. In this chapter, we focus mainly on the arbuscular mycorrhizal (AM) symbiosis, which is pertinent to most (>60%) plant species on Earth and also for most agricultural systems (Jemo et al. 2014; Sochorová et al. 2016), acknowledging similarities and differences between the different mycorrhizal types.

1.2 Magnitude of C Flow from Plants to the Mycorrhizal Fungi

Mycorrhizal fungi derive most of their C from their plant hosts, with only a little fraction (if any) of the C originating from the dead organic matter (Olsson and Johnson 2005; Hobbie et al. 2014; Lindahl and Tunlid 2015). Establishment of mycorrhizal symbiosis often increases allocation of C to the roots and further to the mycorrhizal fungi (Slavíková et al. 2017, and references therein), affecting whole plant C balance (Wright et al. 1998) and also the rate of plant photosynthesis, either directly through improved mineral nutrition or indirectly through increased below-ground C sink strength (Fig. 1.1, Douds et al. 2000; Kaschuk et al. 2009; Valentine et al. 2013). Due to the complexity of the interactions between the C and P economies (e.g., nutritional benefits conferred by the mycorrhizal association to the plant may stimulate host plant growth and thus C accumulation under nutrient limiting conditions to a great extent or completely compensate theoretical C allocation to the mycorrhizal fungus in a mycorrhizal plant of the same size as the nonmycorrhizal plant), there are different, partly contradicting concepts for calculation of mycorrhizal costs and benefits, sometimes resulting in conflicting

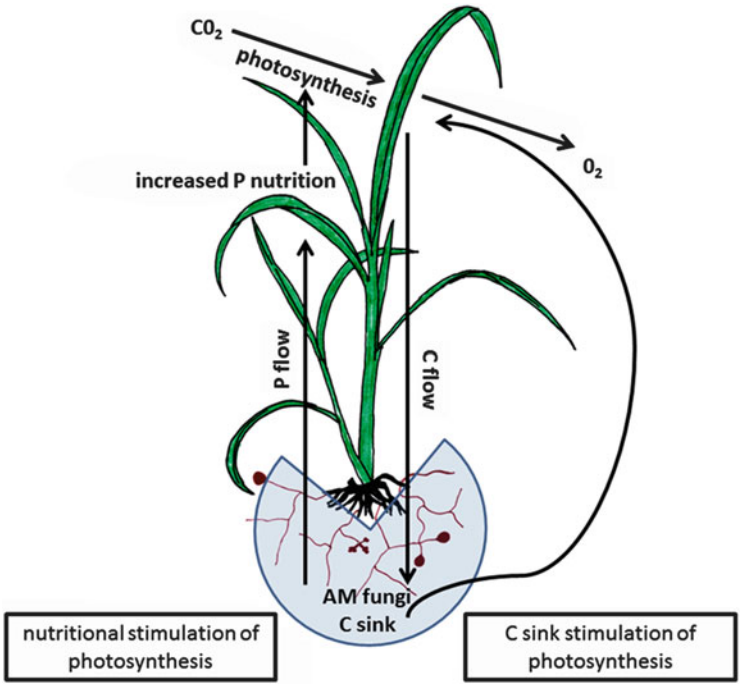

Fig. 1.1 Two possible pathways how establishment of arbuscular mycorrhiza could feed back on the rates/efficiency of photosynthesis of its plant host

predictions (Fitter 1991; Tinker et al. 1994; Landis and Fraser 2008; Correa et al. 2011).

In spite of the wealth of theories and predictions, the flux of C from the plant to the fungus could be quantified, particularly by employing isotopic C labeling, and relative C expenditure to mycorrhizas (e.g., the fraction of plant C budget allocated to the fungus) could be calculated from such data. Previously, mycorrhizal C cost of AM symbiosis was reported to reach between 4 and 20% of the photosynthetically fixed C by the plant (Smith and Read 2008). Yet, the value of 20% has only been recorded once for young cucumber plants under artificial environmental conditions (Jakobsen and Rosendahl 1990), but it has been frequently cited and also widely generalized up to a global ecosystem level (e.g., Brzostek et al. 2014). More recent research by Tomé et al. (2015) and by Slavíková et al. (2017) reported mycorrhizal C expenditure to reach only a few percent of the plant C budget (see Table 1.1 for more details), which is even below the previously reported low end (4%) of the C allocation to AM fungi. Yet, not all studies reported/measured C allocation to all relevant system compartments such as plant, soil, and the respiration losses above- and belowground. From the handful of studies including all relevant system compartments (coincidentally, all employing short-term pulse $^{14}CO_2$ labeling, Table 1.2), we learn that the shoot respiration could reach between 1 and 6%

Table 1.1 Mycorrhizal carbon (C) costs as a fraction of the total C budget of a host plant reported for various combinations of fungal and plant partners at different environmental contexts and assessed by different approaches

Reference	Plant-fungal partner combination			Isotope	Length of labeling period	Length of chase period	Above-ground respiration assessed	Below-ground respiration assessed	Mycorrhizal cost (% of recorded C budget)	Note
	Host plant species	AM fungal species as reported	Current AM fungal name							
Pang and Paul (1980)	*Vicia faba*	*Glomus mosseae*	*Funneliformis mosseae*	^{14}C	48 h	4.5 days	–	+	11[a]	C in all measured compartments allocated to AM minus NM roots and belowground respiration
Paul and Kucey (1981)	*Vicia faba*	*Glomus mosseae*	*Funneliformis mosseae*	^{14}C	48 h	96 h	+	+	4	Fraction of the whole assimilated C in mycorrhizal hyphae and fungal respiration
Kucey and Paul (1982)	*Vicia faba*	*Glomus mosseae*	*Funneliformis mosseae*	^{14}C	48 or 8 h	96 or 116 h	+	+	3.5–4.2	C in all measured compartments allocated into mycorrhizal respiration and biomass
Snellgrove et al. (1982)	*Allium porrum*	*Glomus mosseae*	*Funneliformis mosseae*	^{14}C	30 min	48 h	+	+	7	Total fixed C in roots of AM minus NM plants
Koch and Johnson (1984)	*Citrus aurantium*, *Poncirus trifoliata* × *Citrus sinensis*	*Glomus intraradices*	*Rhizophagus intraradices*	^{14}C	8.5 min	2 h	–	–	6–10	Difference of the total assimilated C to the half-roots between AM and NM parts in split-root system × 2

Harris et al. (1985)	*Glycine max*	*Glomus fasciculatum*	*Rhizophagus fasciculatus*	^{14}C	16 h	68 h	+	+	8–17	Total photosynthate allocated into AM biomass, AM respiration, root exudates + soil of AM plants (deduced from comparison of dually colonized (mycorrhizal + *Rhizobium*) vs. NM and NM + *Rhizobium* plants)
Douds et al. (1988)	*Poncirus trifoliata* × *Citrus sinensis*	*Glomus intraradices*	*Rhizophagus intraradices*	^{14}C	10 min	2 h	–	–	5.6–7.8	% assimilated C allocated to roots of AM minus NM plants
Wang et al. (1989)	*Panicum coloratum*	*Gigaspora margarita*		^{11}C	100–120 min	200 min	–	–	>3.9	In the short-term study focused on ^{11}C fluxes was not possible to calculate %C in all measured compartments. The authors quote that allocation to mycorrhizal part of the roots was probably more than 3.9% higher than to the nonmycorrhizal roots

(continued)

Table 1.1 (continued)

Reference	Plant-fungal partner combination			Isotope	Length of labeling period	Length of chase period	Above-ground respiration assessed	Below-ground respiration assessed	Mycorrhizal cost (% of recorded C budget)	Note
	Host plant species	AM fungal species as reported	Current AM fungal name							
Jakobsen and Rosendahl (1990)	*Cucumis sativus*	*Glomus fasciculatum*	*Endogone arenacea*	^{14}C	16 h	80 h	+	+	20	% of assimilated C consumed by fungal biomass and its respiration
Peng et al. (1993)	*Citrus volkameriana*	*Glomus intraradices*	*Rhizophagus intraradices*	None			+[b]	+	7[a]	% C of the net C assimilation flow into root and soil respiration (AM minus NM)
Pearson and Jakobsen (1993)	*Cucumis sativus*	*Scutellospora calospora, Glomus caledonium, Glomus* sp.	*Scutellospora calospora, Funneliformis caledonium, Glomus* sp.	^{14}C	16 h	70 h	–	+	8.5–18.6[a]	% of assimilated C allocated by AM minus NM plants to belowground (roots, ERM, belowground respiration)
Wright et al. (1998)	*Trifolium repens*	Field AM fungal community		None			+[b]	+	15	% of the net amount of CO_2 assimilated by AM plants respired by AM minus NM roots
Johnson et al. (2002a)	Grassland—24 plant species	Field AM fungal community		^{13}C	3.5 h	24 h	+[d]	+	3.9–6.2	% of the fixed C passed through the ERM—no accumulation of ^{13}C observed in the substrate

Johnson et al. (2002b)	Grassland—24 plant species	Field AM fungal community		^{14}C	3 h	70 h	+[d]	+	3.4	% C allocation of the photosynthetically fixed C by the plant into AM mycelium (incorporation into + release from AM fungi)
Grimoldi et al. (2006)	*Lolium perenne*	*Glomus hoi*		^{13}C	16 h	6–7 h	+	+	4.8–6	% C of daily gross photosynthesis allocated to the AM fungi
Heinemeyer et al. (2006)	*Plantago lanceolata*	*Glomus mosseae*	*Funneliformis mosseae*	^{13}C	3.5 h	2 h	–	+	<1	% C of net photosynthesis allocated to ERM
Drigo et al. (2010)	*Festuca rubra*	Field AM fungal community		^{13}C	16 h	6 days	–	–	8.8–9[a,c]	% of total fixed C in the assessed compartments incorporated into the AM fungi (NLFA)
Lendenmann et al. (2011)	*Medicago truncatula*	*Glomus intraradices, Glomus claroideum, Gigaspora margarita*	*Rhizophagus intraradices, Claroideoglomus claroideum, Gigaspora margarita*	^{13}C	1 h	5 days	–	+	1.7–12.9[a]	% C in all measured compartments allocated belowground (roots, substrate and belowground respiration), difference between AM a NM plants
Calderón et al. (2012)	*Sorghum bicolor*	*Glomus clarum*	*Rhizophagus clarus*	^{14}C	3 h	24 days	+	+	4 (6.8[a])	% photoassimilated C allocated belowground, difference between AM and NM plants

(continued)

Table 1.1 (continued)

Reference	Plant-fungal partner combination			Isotope	Length of labeling period	Length of chase period	Above-ground respiration assessed	Below-ground respiration assessed	Mycorrhizal cost (% of recorded C budget)	Note
	Host plant species	AM fungal species as reported	Current AM fungal name							
Tomé et al. (2015)	*Fragaria ananassa* var. *elsanta*	Mix *Funneliformis mosseae* and *Rhizophagus intraradices*		^{13}C	6 h	1 and 7 days	–	–	1.8–4.3	% of total fixed C allocated to AM fungal mycelium
Slavíková et al. (2017)	*Medicago truncatula*	*Rhizophagus irregularis*		^{13}C	2 h	6 days	+[b]	+	2.3 (2.9)	% of the plant C budget allocated to the AM fungi—comparison between AM and NM plants of C allocation to substrate (or belowground)

Values were estimated with or without including above- and/or below-ground respiration
AM arbuscular mycorrhizal, *NM* non-mycorrhizal, *ERM* extraradical mycelium, *NLFA* neutral lipid fatty acid
[a]Our calculation from the numbers provided in the publication
[b]Dark shoot respiration
[c]Approximate values deduced from graphic presentation of results
[d]Approximate figures of shoot respiration deduced from sequentially harvested pots

Table 1.2 Carbon (C) allocation into different compartments of the arbuscular mycorrhizal (AM) plant-soil system in studies assembling C budgets of the whole plants[a]

Reference	Plant–fungal partner combination			Isotope	Length of labeling period	Length of chase period	Recently fixed C allocation (% of total)							
	Host plant species	AM fungal species as reported	Current AM fungal name				Aboveground respiration	Shoot	Roots[b]	Substrate[c]	Belowground respiration[d]	AM fungus		Note
												AM fungal mycelia	AM fungal respiration	
Paul and Kucey (1981)	*Vicia faba*	*Glomus mosseae*	*Funneliformis mosseae*	^{14}C	48 h	96 h	2	40–47	18–19	0.5	28–31	1	3	A
Kucey and Paul (1982)	*Vicia faba*	*Glomus mosseae*	*Funneliformis mosseae*	^{14}C	48 or 8 h	96 or 116 h	1–2.3	41.7–52	16.8–29		22.1–37.9	0.8–0.9	2.8–3.3	A
Snellgrove et al. (1982)	*Allium porrum*	*Glomus mosseae*	*Funneliformis mosseae*	^{14}C	30 min	48 h	2.3–6.3	49.7–60.8	15.7–27.1	2.1–5.3	9.7–23.1			A
Harris et al. (1985)	*Glycine max*	*Glomus fasciculatum*	*Rhizophagus fasciculatus*	^{14}C	16 h	68 h	4–6.3	51–61.2	9.9	1.3–1.8	14.6–16.3	2.7–2.8	4.7–13.7	B
Jakobsen and Rosendahl (1990)	*Cucumis sativus*	*Glomus fasciculatum*	*Rhizophagus fasciculatus*	^{14}C	16 h	80 h	2.5	54.1	13.2	2.3	27	0.8		A
Calderón et al. (2012)	*Sorghum bicolor*	*Glomus clarum*	*Rhizophagus clarus*	^{14}C	3 h	24 days	5	47.9	28.9	6.3	11.9			A

The studies vary in terms of symbiotic partner combinations, plant age, labeling pulse or chase periods, and presence or absence of *Rhizobia* for leguminous hosts

A—carbon allocation into the different compartments as reported by the authors, B—carbon allocation into the different compartments calculated by us from values provided by the authors

[a]Only including studies where all the relevant measurements were made and properly reported

[b]Including nodules and intraradical mycelium for dually colonized leguminous hosts

[c]Including extraradical AM fungal mycelium

[d]Including rhizobial and fungal respiration if the latter is not explicitly provided

photosynthetically fixed C, C allocated to shoots 40–61%, C allocated to roots 10–29%, C allocated to substrate 1–6%, and C allocated specifically to AM fungal mycelium 1–3%; AM fungal respiration reaching 3–14%; and belowground respiration in total reaching 8–38% (Paul and Kucey 1981; Kucey and Paul 1982; Snellgrove et al. 1982; Harris et al. 1985; Jakobsen and Rosendahl 1990; Calderón et al. 2012).

Based on summary of all available literature on the magnitude of C fluxes in AM symbioses, it seems that the average C expenditure of the AM symbiosis may well be under 10% of the plant C budget (see Table 1.1 for more details). For comparison, in ectomycorrhizal symbioses, the magnitude of C allocated to fungal partner oscillates (apparently) around 3–36% of C fixed by photosynthesis (Bryla and Eissenstat 2005 and references therein). Very low (0.4% of the total C fixed by the plant) loss of plant photosynthate to its associated mycorrhizal fungus was, in contrast, reported for mycorrhizal green orchid *Goodyera repens* by Cameron et al. (2008).

The reported values on C allocation to AM fungi range widely. Here, the low number of publications dedicated to mycorrhizal C costs, especially in comparison with the quantity of literature concerning nutritional benefits of mycorrhizas, do not allow to properly uncover the determinants of plant C allocation to AM fungi. However, it seems that the choice of model host plant, AM fungal species and/or their combinations (Pearson and Jakobsen 1993; Lerat et al. 2003; Lendenmann et al. 2011), developmental stage of the symbiosis (Wright et al. 1998), environmental conditions (Slavíková et al. 2017), size and setup of the pots, and the duration of the isotope labeling/chase periods all strongly affect the outcome of quantification of C allocation to the AM fungi (see also Tables 1.1 and 1.2).

The exploration of mycorrhizal C cost has formerly been restricted by the available methodologies. Using ^{14}C radioisotope to directly trace the C fluxes from plant to mycorrhiza and to the soil was subject to strict health and radiosafety regulations (Schuur et al. 2016). Commercial availability of C sources enriched by stable ^{13}C isotope in the recent decades together with customization of the necessary mass spectrometry instrumentation made the direct C tracing much more available. However, despite the fact that the isotopic pulse-chase labeling enabled significant advances in assessing the C transfers within the plant–soil systems, it still only provides information with regard to the fate of recently fixed plant C, thus inevitably covering only a short period within the plant and/or fungal life cycles (Johnson 2008). This may be particularly short-sighted with respect to the mycorrhizal symbioses in trees and other long-living plants that could accumulate C reserves over long periods of time.

Further, the estimates of the mycorrhizal C costs based on incomplete C budgets (Pang and Paul 1980; Koch and Johnson 1984; Pearson and Jakobsen 1993; Heinemeyer et al. 2006; Drigo et al. 2010; Lendenmann et al. 2011) should be regarded with caution. This is because the gaseous C losses from shoots or roots/soil may reach a significant share of the plant C budget and thus should not be neglected (Lendenmann et al. 2011; Slavíková et al. 2017). Ignoring these C pools automatically leads to overestimation of the mycorrhizal C costs, which obviously was the case in some of the previous studies, although not the study by Jakobsen

and Rosendahl (1990) reporting the highest C costs of AM symbiosis ever (Table 1.1). Provided the rapidity of C fluxes between the plant, AM fungi, and the soil (Johnson 2008), it is sometimes very challenging to distinguish the C allocation to the root biomass, intra- and extraradical AM fungal mycelium and the soil/substrate, and to separate root and hyphal respirations (Heinemeyer et al. 2006). To this end, comparing mycorrhizal and nonmycorrhizal plants seems inevitable, although it is now widely accepted that this may be a source of many artifacts (Smith and Smith 2012). Moreover, depending on the balance between net costs and benefits of the symbiosis, mycorrhizal phenotypes appear to cover a whole continuum of plant responses to AM fungal colonization ranging from positive to neutral to negative (Johnson et al. 1997; Klironomos 2003). For some combinations of symbiotic partners and environmental conditions, mycorrhizal C costs may simply outweight the growth benefits conferred to plants (Johnson et al. 2015), and it may not be possible to produce nonmycorrhizal and mycorrhizal plants of the same size and mineral nutrition (Peng et al. 1993; Graham et al. 1996; Lendenmann et al. 2011). Here, the solution to compare physiology of mycorrhizal and nonmycorrhizal plants may be in using P fertilization to produce mycorrhizal and nonmycorrhizal plants of the same size (Brown and Bethlenfalvay 1987; Baas and Lambers 1988; Slavíková et al. 2017). Another possibility is using plants with a split-root system (Douds et al. 2000).

Peripheral importance has been so far dedicated to fungus-to-plant C transfers, despite they have been shown as a significant component of the overall C budget (at least) in the orchid mycorrhizas. Yet, because up to 10% of plant species are at least partially mycoheterotrophic and receive a net C gain from their fungal symbiont for at least a part of their life (Leake 2005), they should be taken seriously. Clear demonstration of the fungus-to-plant C flux, although much lower than the C flow in opposite direction, was shown by Cameron et al. (2008) who quantified the bidirectional C fluxes by using ^{14}C labeling in green orchid *Goodyera repens* associated with fungus *Ceratobasidium cornigerum*. In ectomycorrhizas, the transfer of amino acid-C from fungus to plant has also been demonstrated (Abuzinadah and Read 1989), although importance of this mechanism for bulk C transfer from fungus to plant is probably low. Yet it may potentially have some impact on the C economy of the mycorrhizal symbiosis (Taylor et al. 2004) and thus should be incorporated in the assessments of mycorrhizal C cost. Such an "up-flow" of C may occur even in arbuscular and ericoid mycorrhizal associations, but have not been demonstrated as yet (Johnson 2008).

1.3 Mechanisms of C Transfer Between the Symbiotic Partners

Although it has been demonstrated many times that there is a fast and directed C transfer between the plants and the AM fungi (e.g., Johnson et al. 2002b; Dilkes et al. 2004; Olsson and Johnson 2005; Kiers et al. 2011), the molecular mechanisms