

# The Biocontrol Effect of Mycorrhization on Soilborne Fungal Pathogens and the Autoregulation of the AM Symbiosis: One Mechanism, Two Effects?

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## 1 Introduction

The establishment of the AM in the roots of more than 80% of all land plants is the result of a complex exchange of signals between the host plant and AMF. Many reports are available that once the AMF has penetrated the host root and established its intraradical organs of nutrient exchange between the AMF and the plant, a number of physiological and morphological changes occur in the host plant.

The importance of most of these changes is still unclear, although the most prominent results of mycorrhization are, among others, an improved nutrient status of the host plant (Smith and Read 1997) and a bioprotective effect of mycorrhization against soilborne fungal pathogens (Singh et al. 2000; Azcón-Aguilar et al. 2002; Xavier and Boyetchko 2004; St-Arnaud and Elsen 2005; St-Arnaud and Vujanovic 2007).

In the legume–*Rhizobium* interaction, once a plant has formed nodules, further nodulation is suppressed in other parts of the root system by a long-distance signal exchange, which means that the nodulation is autoregulated (see reviews in Oka-Kira and Kawaguchi 2006; Kinkema et al. 2006).

In recent years, it has been reported that once plants are colonized by AMF, further root colonization by AMF is regulated (reviewed by Vierheilig 2004a,b). In analogy to the rhizobial autoregulatory mechanism in legume plants, this phenomenon with AMF has been named “autoregulation of mycorrhization”. Recently, it has been suggested that the bioprotective effect of mycorrhization and the autoregulation of mycorrhization are possibly two sides of the same coin. It seems plausible that an already mycorrhizal plant develops just one mechanism to repulse further colonization by fungi, not discriminating between AMF and soilborne pathogenic fungi (Vierheilig and Piché 2002; Vierheilig 2004a,b).

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In this chapter, we want to discuss the data accumulated on the mycorrhizal autoregulation and on the bioprotective effect of mycorrhization in order to highlight possible similarities between both processes

## **2 The Biocontrol Effect of Mycorrhization on Soilborne Fungal Pathogens**

Most data about bioprotection of mycorrhization are available for soilborne fungal pathogens. Numerous studies show a clear localized protective effect (reviewed by Singh et al. 2000; Azcón-Aguilar et al. 2002; Xavier and Boyetchko 2004; St-Arnaud and Vujanovic 2007) while recently a systemic protective effect with different soilborne fungal pathogens has also been reported (Cordier et al. 1998a; Pozo et al. 2002; Khaosaad et al. 2007).

In this review, we want to give a short overview about the different aspects involved in mycorrhizal biocontrol. More details can be obtained from several excellent recent reviews on this subject (Whipps 2004; Xavier and Boyetchko 2004; Azcon-Aguilar et al. 2002; Singh et al. 2000), but we will provide some new data relevant to the field.

### ***2.1 Factors Affecting Bioprotection Through Mycorrhization***

Apart from abiotic factors affecting the biocontrol efficacy of the AMF, such as temperature, soil moisture and soil P-content (for details see Singh et al. 2000), the bioprotective effect against soilborne fungal pathogens seems to depend on several biotic factors such as the host genotype, the AMF isolate and the degree of mycorrhization.

#### **2.1.1 The Host Genotype**

In a number of studies, it has been demonstrated that depending on the host genotype the degree of AM root colonization and the plant growth effect of mycorrhization can vary, and it has been suggested that the AM development and its effect on the host plant are at least partially under the genetic control of the host (Lackie et al. 1987; Hetrick et al. 1993; Vierheilig and Ocampo 1990, 1991). The host genome also seems to affect the protective effect provided by the AMF, as the host genotype seems to result in a differing bioprotective response by the mycorrhizal association. Depending on the genotype, mycorrhizal strawberry showed a different susceptibility to *Phytophthora fragariae* (Mark and Cassels 1996).

### 2.1.2 The AMF

In an overview on studies on the bioprotective effect of mycorrhization listing the host plant, the pathogen, the AMF, and the effect of mycorrhization (Singh et al. 2000; Whipps 2004), we can see that more than 80% of the studies on the bioprotective effect of mycorrhization have been performed with the genus *Glomus*, whereas only about 14% were performed with the genus *Gigaspora*, while there are almost no studies available using other AM genera. Moreover, within the genus *Glomus*, nearly half of the studies were performed with *G. mosseae* (25%) and *G. fasciculatum* (23%) and 8% each with *G. etunicatum* and *G. intraradices*. This means that data on a bioprotective effect of mycorrhization originate mostly from the genus *Glomus*, and within this genus from two species.

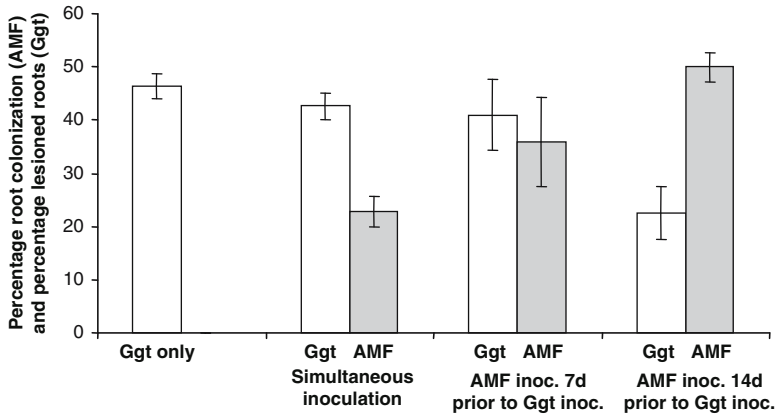
From a few studies comparing the bioprotective effect of AMF species, we can conclude that depending on the AMF species the bioprotective effect differs, e.g., *Glomus intraradices* has been reported not to protect clover against nematode infection (Habte et al. 1999) and was not effective in reducing disease symptoms produced by *Phytophthora parasitica* infection in tomato (Pozo et al. 2002). In contrast, root colonization by *G. mosseae* resulted in a clear protective effect against nematodes and *P. parasitica* infection (Habte et al. 1999; Pozo et al. 2002).

As some AMF exhibit a clear bioprotective effect, whereas other AMF do not affect the plant–pathogen interaction in terms of bioprotection, more comparative studies are definitely needed involving a greater variety of AMF.

### 2.1.3 The Degree of Mycorrhization

After plant inoculation with an AMF, the first signs of root colonization are visible after a few days. Thereafter, AM root colonization can increase drastically until it reaches a final plateau (e.g., for tomato and soybean around 60%; Vierheilig et al. 1994; Wyss et al. 1991). In several studies, a local bioprotective effect has been linked with a high degree of AM root colonization, whereas intermediate and low levels of AM root colonization showed no bioprotective effect. Apparently a critical level of AM root colonization is needed to provide bioprotection for mycorrhizal plants. In mycorrhizal tomato plants a bioprotective effect against *P. parasitica* (Cordier et al. 1998b) and *Fusarium oxysporum* (Caron et al. 1986a,b), and in wheat plants against *Gaeumannomyces graminis* (Graham and Menge 1982), could only be observed when roots were heavily colonized by the AMF; low mycorrhization levels resulted in no bioprotection.

In a recent report it has been demonstrated that not only the local, but also the systemic, bioprotective effect of mycorrhization depends on the degree of AM root colonization (Khaosaad et al. 2007). Moreover, the critical level of AM root colonization in barley to provide local and systemic bioprotection against *G. graminis* seems to be similar (Fig. 1; Khaosaad et al. 2007).



**Fig. 1** The local effect of sequential inoculation by the AMF *G. mosseae* on severity of take-all disease caused by *G. graminis* (Ggt) was studied. In the compartment system described by Vierheilig et al. (2000a), barley plants were sequentially inoculated with the AMF *G. mosseae*. This resulted in a differing AM root colonization at the end of the experiment. When plants were inoculated with Ggt, AM root colonization ranged from 0% (simultaneous inoculation),  $10 \pm 1\%$  (AMF inoculation 7 days prior to Ggt inoculation) to  $18 \pm 2\%$  (AMF inoculation 14 days prior to Ggt inoculation). At the time of harvest (14 days after Ggt inoculation), roots were scored for root browning (for more details, see Khaosaad et al. 2007). Data represent mean  $\pm$  SE ( $n = 5$ )

The sequence of inoculation has also been suggested as an important factor in mycorrhizal bioprotection. In general, it has been postulated that the inoculation has to be prior to inoculation with the soilborne pathogen (Singh et al. 2000; Azcón-Aguilar et al. 2002; Xavier and Boyetchko 2004). However, this aspect is probably closely linked with the degree of mycorrhization. The earlier the AMF colonizes the root, the higher the mycorrhization level will be before a pathogen infection.

## 2.2 Mechanisms of Mycorrhization-mediated Bioprotection

A number of mechanisms have been suggested to be involved in the bioprotective effect of mycorrhization against soilborne fungal pathogens, but hard data are not yet available for all of them. Classically, four major groups of mycorrhizal mode of action mechanisms that mediated bioprotection have been considered: (1) direct competition, (2) mechanism mediated by alteration in plant growth, nutrition and morphology, (3) biochemical and molecular changes in mycorrhizal plants that induce pathogen resistance, and (4) alterations in the soil microbiota and development of pathogen antagonism. Although some of the suggested mechanisms might play no role, it is generally agreed that bioprotection through

mycorrhization is the result of a combination of several of mechanisms and not of a single mechanism.

## 2.2.1 Direct Competition

### 2.2.1.1 Competition for Infection Sites

A competition effect at the infectional level has also been suggested. The AMF might occupy infection sites on the root surface needed by the pathogen to penetrate the root, or cells in the root already occupied by the AMF cannot be colonized any further by the pathogen (Cordier et al. 1998a,b).

### 2.2.1.2 Carbon Competition

Not only the growth of symbiotic AMF but also of pathogenic fungi depends on carbon from photosynthesis. Thus, it has been suggested that the carbon availability in mycorrhizal plants could explain the biocontrol effect of mycorrhization. Once a plant is colonized by AMF, due to the carbohydrates used by the symbiotic AM fungus, less carbon could be available for a root colonizing fungal pathogen (Singh et al. 2000; Azcón-Aguilar et al. 2002; Xavier and Boyetchko 2004).

Different AMF have been reported to exhibit a different carbon sink strength in mycorrhizal roots (Lerat et al. 2003a, 2003b) and, thus, should exhibit a different biocontrol effect. Interestingly, in a split-root system of tomato with one side colonized by the AMF *G. mosseae* (BEG 12), disease symptoms produced by *P. parasitica* on the other side of the split-root system were reduced (Cordier et al. 1998a; Pozo et al. 2002). This would point towards a certain carbon sink strength of the AMF *G. mosseae* (BEG 12). However, *G. mosseae* (BEG 12) has been shown in different plant systems not to exhibit any carbon sink strength. Moreover, despite its high carbon sink strength the AMF *G. intraradices* did not provide bioprotection against *P. parasitica* (Pozo et al. 2002; Lerat et al. 2003a).

From these data, it seems that carbon competition between AMF and a pathogen can be discarded as a factor involved in mycorrhizal bioprotection.

### 2.2.1.3 Direct Competition/Inhibition in Soil

Some experimental evidence has been reported about possible mechanisms of direct action of AM fungi against pathogens in soil (St-Arnaud et al. 1995; Filion et al. 1999; García-Garrido and Ocampo 1989). Nevertheless, at the present time, the production of antibiotics or inhibitory compounds by AM fungi has not been proven.

## **2.2.2 Mechanism Mediated by Alteration in Plant Growth, Nutrition and Morphology**

### **2.2.2.1 Improved Nutrient Status/Root Damage Compensation**

It has been suggested that the improved nutrient status of mycorrhizal plants makes them more tolerant to damage caused by pathogens and carbon drain from the plant to the pathogen. However, there is strong evidence that the nutritional effect of the AM symbiosis is only one among several aspects of the mycorrhizal effect on pathogens (Trotta et al. 1996). Moreover, it has been suggested that the nutrient uptake by the fine extraradical mycelium of the AMF could compensate for a pathogen-reduced root system (Singh et al. 2000).

### **2.2.2.2 Morphological Alterations of the Root**

Due to mycorrhization, the morphology of the root changes (Berta et al. 1995; Copetta et al. 2006), but no clear correlation with a bioprotective effect of mycorrhization has yet been found. In basil, the root fresh weight, the total root length, the number of root tips and the degree of branching was altered differently depending on the root-colonizing AMF (Copetta et al. 2006). Linking these alterations of the root parameters with data on a bioprotective effect of the different AMF could show whether morphological alterations of the root due to mycorrhization are really involved in the bioprotective effect of mycorrhization.

### **2.2.3 Biochemical and Molecular Changes in Mycorrhizal Plants that Induce Resistance to Pathogens**

Several physiological and biochemical alterations of the host after mycorrhization have been reported. Some are possibly linked with a protective effect of the mycorrhizal plant against pathogens, e.g. the induction of hydrolytic enzymes (Pozo et al. 1999), enhanced levels of PR proteins, the accumulation of phytoalexins (Harrison and Dixon 1993; Morandi 1996; Larose et al. 2002) and callose (Cordier et al. 1998b), the accumulation of salicylic acid (Blilou et al. 2000a, 2000b; Medina et al. 2003) and reactive oxygen species (Salzer et al. 1999). During AM development, there is evidence that these defensive responses occur (García-Garrido and Ocampo 2002) and that they are strongly stimulated when a subsequent challenge with a pathogen takes place. Possibly the mechanisms of plant defence are activated faster and to a greater extent in mycorrhizal plants when challenged by a pathogen compared to nonmycorrhizal plants, and it has been suggested that AM colonization acts as a priming system for the process of pathogen resistance (Azcón-Aguilar et al. 2002; Pozo and Azcon-Aguilar 2007). In this respect, elevated JA levels occurring upon mycorrhization, likely associated with a fully established mycorrhiza, may mediate the enhanced defence status of the mycorrhizal plant (Vierheilig and Piché 2002; Hause et al. 2007; Vierheilig 2004a).

However, the importance of each component of the plant resistance response in the bioprotective effect of AM against soil pathogens and the signaling pathway that control these responses are unknown.

As the whole metabolism of the plant is altered by mycorrhization, alterations of the root exudation pattern are no surprise. These alterations could act on the pathogen indirectly, through an altered pH in the rhizosphere and/or directly through an altered composition of the exudates with reduced levels of stimulatory compounds and/or the presence of inhibitory compounds. Changes of the pH in the rhizosphere of the mycorrhizal plant (Bago et al. 1996; Villegas et al. 1996) have been reported before, however, no data are available yet how these pH changes of the rhizosphere affect root pathogens.

There are a number of reports on root exudates and AMF (see recent reviews by Jones et al. 2004; Nagahashi and Douds 2005; Vierheilig and Bago 2005), and more and more data are accumulated that exudates of mycorrhizal plants affect bacteria (Sood 2003), fungi (Norman and Hooker 2000; Lioussanne et al. 2003; Scheffknecht et al. 2006, 2007) and nematodes (Ryan and Jones 2004) differently than exudates from nonmycorrhizal plants.

### **3 The Mycorrhizal Autoregulation**

In recent years, more and more data have been accumulated that once plants are colonized by AMF, in order to limit the energy costs of the AM symbiosis further root colonization by AMF is suppressed. This mechanism has been named “autoregulation of mycorrhization” (Vierheilig 2004a; Garcia-Garrido and Vierheilig 2007).

Due to the fact that in roots a recent AM root colonization cannot be distinguished from a prior AM root colonization, and that in roots it is extremely difficult to distinguish one AMF from another, split-root systems have been used to study the mycorrhizal autoregulation. Split-root systems of plants were inoculated on one side with an AMF and, when the symbiosis was well established, the other side was inoculated with the same or another AMF. In these experiments with different AM host plants, such as barley (Vierheilig et al. 2000a, 2000b), alfalfa (Catford et al. 2003, 2006) and soybean (Meixner et al. 2005, 2007), it could be clearly shown that AM precolonization on one side of a split-root system systemically suppresses AM root colonization on the other side of the root system. The mechanisms which are actually controlling this autoregulatory effect are still unknown.

#### **3.1 Carbon Competition**

Carbon availability in mycorrhizal plants could explain the reduced root colonization in already mycorrhizal plants. Once one side of a split-root system is colonized by AMF, due to the carbohydrates used by the symbiotic AM fungus, less carbon

could be available for a later root colonizing AMF on the other side of the split-root system.

Testing the carbon sink strength of several AMF in split-root systems of barley and sugar maple, it could be demonstrated that different AMF exhibit a different carbon sink strength in mycorrhizal roots (Lerat et al. 2003a; b). The *G. mosseae* strain BEG 12 for example showed no carbon sink strength, whereas *G. intraradices* and *Gigaspora rosea* were strong carbon sinks. With carbon availability as the controlling factor this would mean that with *G. mosseae* there is no or only a weak autoregulatory effect, whereas with the two other fungi mycorrhization is clearly autoregulated.

Interestingly the degree of autoregulation was similar with *G. mosseae*, *G. intraradices* and *Gigaspora* (Vierheilig et al. 2000b), thus discarding the competition for carbon as the regulatory factor of mycorrhizal autoregulation.

### 3.2 Regulation by P-Levels

An improved P-status has been suggested as another possible factor affecting further AM root colonization of already mycorrhizal plants (Pearson et al. 1993). Mycorrhization could increase the P-level of the plant and thus suppress further root colonization by AMF. An experiment with a split-root system of barley with one side mycorrhizal showed that on the non-mycorrhizal side of the split-root system P-levels were similar as in the split-root system of the non-mycorrhizal control plant.

However, in the pre-colonized root system further root colonization was suppressed, whereas without pre-colonization no suppression of root colonization could be observed (Vierheilig et al. 2000b). In the experimental system studying mycorrhizal autoregulation, this excludes P as a potential suppressive factor of further root colonization in mycorrhizal plants. Moreover, in a P-application experiment it could be demonstrated that in split-root systems the improved P-status and the observed suppressive effect following mycorrhization can not be linked (Vierheilig et al. 2000b).

## 4 The Mycorrhizal Biocontrol Effect and the Mycorrhizal Autoregulation: One Mechanism, Two Effects?

Above we describe characteristics of the biocontrol effect of mycorrhization and of the mycorrhizal autoregulation. Once a plant is mycorrhizal it seems to control further root colonization by AMF and pathogenic fungi. Although compared to mycorrhizal biocontrol, only a few data are available on mycorrhizal autoregulation, both effects seem to share certain similarities. Below we want discuss these similarities.

### **4.1 Systemic Effects**

A systemic effect of mycorrhization has been reported from mycorrhizal bioprotection and mycorrhizal autoregulation. Both systemic effects were studied in split-root systems.

Precolonization of one side of a split-root systems resulted in a clear suppression of different soil-borne fungal pathogens on the other side of the split-root system (Cordier et al. 1998a; Pozo et al. 2002; Khaosaad et al. 2007).

A similar systemic suppressive effect on AM root colonization was observed. When the first side of a split-root system was colonized by different AMF, AM root colonization on the other side was drastically decreased. Further studies are needed to verify whether the two systemic phenomena share the same mechanism.

### **4.2 The Degree of Mycorrhization**

In several studies it has been reported that a local bioprotective effect depends on the degree of AM root colonization (Graham and Menge 1982; Caron et al. 1986; Cordier et al. 1998b).

In analogy to a local bioprotective effect by mycorrhization, the systemic bioprotection also seems to depend on a critical level of AM root colonization. This has been reported recently in a study with mycorrhizal barley plants and the soil-borne pathogen *G. graminis*. Once one side of a split-root system of barley was extensively colonized by the AMF *G. mosseae*, the damage caused by *G. graminis* was clearly reduced on the other side, whereas low levels of AM root colonization on the first side of the split-root system resulted in no protective effect (Khaosaad et al. 2007).

Interestingly, in the same test plant, barley, a similar pattern has been observed for the mycorrhizal autoregulation. Only high levels of AM root colonization on the first side of a split-root system resulted in a significant suppression of further AM root colonization on the other side (Vierheilig 2004b). These data indicate that both phenomena depend on a critical degree of root colonization by AMF.

### **4.3 Alterations of the Root Exudation Pattern**

Alterations of the root exudation pattern have been suggested to be involved in the expression of the mycorrhizal bioprotective effect and these changes have been suggested to be at least partially involved in the altered susceptibility of mycorrhizal plants towards soil-borne microorganisms (Vierheilig and Piché 2002; Vierheilig 2004a). In *in vitro* studies root exudates from mycorrhizal strawberry plants reduced the sporulation of *P. fragariae* (Norman and Hooker 2000) and root

exudates from mycorrhizal potato plants increased hatching of nematodes (Ryan and Jones 2004). Looking at the chemotactic response root exudates collected from non-mycorrhizal tomato roots exhibited a higher attracting effect on zoospores of *P. parasitica* (Lioussanne et al. 2003), whereas in the case of the two plant-growth-promoting bacteria *A. chroococum* and *P. fluorescens*, root exudates from mycorrhizal tomato plants showed a higher attractational effect (Sood 2003). Most recently it was reported that root exudates from mycorrhizal plants show an altered effect on microconidia germination of *F. oxysporum* compared to root exudates from non-mycorrhizal plants (Scheffknecht et al. 2006, 2007).

Interestingly the altered exudation pattern of mycorrhizal plants is not only affecting pathogenic and non-pathogenic soil-organisms but also the AMF itself. Root exudates from mycorrhizal cucumber plants lost their stimulating effect on the hyphal growth of AMF. Moreover, when added to inoculated cucumber plants root exudates from mycorrhizal cucumber plants suppressed AM root colonization (Pinior et al. 1999). This suppressive effect on root colonization was systemic, that means even root exudates from the non-mycorrhizal side of a split-root system of a mycorrhizal plant affected the AM root colonization negatively (Vierheilig et al. 2003). Systemic alterations of root exudates through mycorrhization affecting the soil-borne pathogen *F. oxysporum* have been reported recently (Scheffknecht et al. 2006).

These data show clearly that alterations of the root exudation pattern through mycorrhization do not only affect other soil-borne pathogenic and non-pathogenic organisms, but also the AMF in the soil.

## 5 Conclusions

To summarize, the systemic effect of mycorrhizal biocontrol and mycorrhizal autoregulation, their regulation by the degree of AM root colonization and the alterations by the root exudation pattern do point towards “one mechanism, two effects”.

In 2002 Vierheilig and Piché suggested that plants colonized by AMF while trying to limit their costs of the AM symbiosis by mycorrhizal autoregulation might have acquired bioprotection against pathogenic fungi. It seems plausible that an already mycorrhizal plant develops only one mechanism to repulse colonization by fungi, not discriminating between AM fungi and soil borne pathogenic fungi.

Further studies, including transcriptomic and metabolomic analysis, are needed to study the hypothesis of “one mechanism, two effects” and to elucidate which mechanisms and signalling molecules are decisive for the regulation and functioning of the two effects.

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