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REVIEW

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Meeting a non-host: the behaviour of AM fungi

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Abstract Arbuscular mycorrhizal (AM) fungi are obligately biotrophic organisms that live symbiotically with the roots of most plants. The establishment of a functional symbiosis between AM fungi and host plants involves a sequence of recognition events leading to the morphological and physiological integration of the two symbionts. The developmental switches in the fungi are triggered by host signals which induce changes in gene expression and a process leading to unequivocal recognition between the two partners of the symbiosis. It has been calculated that about 80% of plant families from all phyla of land plants are hosts of AM fungi. The remaining plant species are either non-mycorrhizal or hosts of mycorrhizas other than the arbuscular type. Non-host plants have been used to obtain information on the factors regulating the development of a functional symbiosis. The aim of this present review is to highlight present-day knowledge of the fungal developmental switches involved in the process of host/non-host discrimination. The following stages of the life cycle of AM fungi are analysed in detail: spore germination, presymbiotic mycelial growth, differential branching pattern and chemotropism, appressorium formation, root colonization.

Introduction

The establishment of a functional symbiosis between arbuscular mycorrhizal (AM) fungi and host plants involves a sequence of recognition events leading to the morphological and physiological integration of the two symbionts. Developmental switches in the fungi are triggered by host signals which induce changes in gene expression and a process leading to unequivocal recognition between the two partners of the symbiosis (Smith and Read 1997).

When growing in natural plant ecosystems and encountering plant roots, AM fungi discriminate against the many surrounding non-hosts (Read 1991; Giovannetti et al. 1994). The aim of this review is to highlight current knowledge of the key events of the AM fungi life cycle and to discuss the developmental switches in the fungi involved in the process of host/non-host discrimination.

Which plants are non-hosts of AM fungi?

It has been calculated that about 80% of plant families from all phyla of land plants are hosts of AM fungi. Non-mycorrhizal plant families have been described among these non-hosts, and non-mycorrhizal species and genera have been reported in mycorrhizal families (Hirrel et al. 1978; Trappe 1987). Experimental data obtained in a 3-year study showed the occurrence of all the different types of mycorrhizas in a Mediterranean plant ecosystem on the isle of Brioni (Croatia). The survey showed arbuscular mycorrhizas in about 75% of plant species, whith the remaining 25% represented by non-mycorrhizal plants (7%) or plants hosting mycorrhizas other than the arbuscular type (18%) (Matosevic 1996).

An interesting, thorough survey of all the data collected on non-mycorrhizal species in different geographical areas by Tester et al. (1987) details the occurrence of mycorrhizas in non-mycorrhizal families. Since many reports concerned field-collected samples, the authors stressed the importance of the method to be used for assessing the mycorrhizal status of any plant species, i.e. "... to grow plants in pot-cultures ensuring exposure of the roots to infective propagules".

Most hosts of non-arbuscular mycorrhizas never establish functional arbuscular mycorrhizal symbioses in nature. Plants of the Orchidaceae, Ericaceae, Monotropaceae and Pyrolaceae have been reported as exclusive

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hosts of orchid, ericoid, arbutoid, and monotropoid mycorrhizas, respectively. Among ectomycorrhizal plants, only a few genera have been found to be hosts also of arbuscular mycorrhizal fungi, e.g. *Eucalyptus, Alnus, Populus, Fraxinus* (Malajczuck et al. 1981; Lapeyrie and Chilvers 1985; Chilvers et al. 1987; Gonçalves and Martins-Loução 1996). Root colonization by *Glomus*–type vesicles and hyphae, not always coupled with arbuscules, has been reported in *Abies, Pseudotsuga* and *Tsuga* (Càzares and Smith 1992, 1996). Further studies using different experimental approaches to ascertain the mycorrhizal status of Pinaceae would be useful.

Fungal developmental switches in the presence of non-hosts

AM fungi are obligate biotrophs living symbiotically in the roots of host plants. For the establishment of the symbiosis, the key events in the life cycle of AM fungi are spore germination and the pre-symbiotic mycelial growth phase, differential hyphal branching, appressorium formation, root colonization and arbuscule development (Giovannetti et al. 1994). This sequence does not occur when AM fungi are challenged with non-host roots and thus the life cycle of these obligate symbionts is interrupted. Detailed analyses of the behaviour of fungal symbionts in the presence of non-hosts improved our understanding of the cellular and molecular plant responses to AM fungi and the development of a functional symbiosis (Gianinazzi-Pearson et al. 1996).

The developmental switches in the life cycle of AM fungi affected by the presence of non-host plants are discussed in the following sections.

Spore germination

Since the first experimental work of Barbara Mosse in 1959, it has been possible to germinate AM fungi in axenic culture in the absence of the host (Mosse 1959). This suggests that host-derived signals are not essential for the germination of AM fungal propagules.

No conclusive data have been obtained on the effects of host roots or root exudates on spore germination. Depending on the experimental conditions and both the plant and fungus, host roots either positively affect germination or have no effect (Powell 1976; Daniels and Trappe 1980; Graham 1982; Tommerup 1984; Gemma and Koske 1988; Becard and Pichè 1989; Gianinazzi-Pearson et al. 1989; Suriyapperuma and Koske 1995; Giovannetti et al. 1993a; Schreiner and Koide 1993a). Inhibitory effects on spore germination by non-host root extracts have been shown; living non-host roots or root exudates do not influence this developmental stage, although contrasting results were obtained with *Brassica* spp. root factors (Ocampo and Azcòn 1980; Azcòn and Ocampo 1984; El-Atrach et al. 1989; Gianinazzi-Pearson et al. 1989; Avio et al. 1990; Bécard and Piché 1990; Vierheilig and Ocampo 1990a, b; Schreiner and Koide 1993a).

Table 1 Germination percentages of *Glomus mosseae* sporocarps in the presence of roots of different plant species. All values are not significantly different from control ($P = 0.01$) (C. Logi, unpublished data)

Plant species	Germination percentage
Host of arbuscular mycorrhizas	
Ocimum basilicum	94.3
Host of arbuscular and ectomycorrhizas	
Alnus glutinosa	94.0
Hosts of ectomycorrhizas	
Abies alba	83.6
Pinus nigra	98.2
Host of arbutoid mycorrhizas	
Arbutus unedo	94.0
Host of ericoid mycorrhizas	
Vaccinium myrtillus	98.0
Nonmycorrhizal plants	
Brassica oleracea	78.0
Brassica napus	94.0
Beta vulgaris	92.0
Dianthus caryophyllus	94.0
Eruca sativa	91.0
Nasturtium officinale	93.8
Spinacia oleracea	96.0
Control	92.3

Spore germination of *Glomus mosseae* in vivo in the presence of host or non-host roots was neither stimulated by host roots nor inhibited by non-host roots (Table 1). Thus, at least at the stage of spore germination, AM fungi are unable to discriminate between hosts and non-hosts.

Pre-symbiotic mycelial growth

Research on the growth of AM fungi in axenic culture has shown that many factors affect pre-symbiotic mycelial growth. Negative effects were observed in the presence of particular inorganic and organic compounds in the culture media, and hyphal length was generally increased by unsterile soil or flavonoids (Mosse 1959, 1962; Hepper 1979, 1983, 1984; Gianinazzi-Pearson et al. 1989; Bécard et al. 1992; Morandi et al. 1992).

Many authors have reported increased hyphal growth, both in vitro and in vivo, in response to root exudates or volatiles from host plants, before physical contact between the symbionts (Mosse 1962; Mosse and Hepper 1975; Graham 1982; Hepper 1984; Carr et al. 1985; Mosse 1988; Bécard and Piché 1989; Gianinazzi-Pearson et al. 1989; Tsai and Phillips 1991; Nair et al. 1991; Giovannetti et al. 1993a; Poulin et al. 1993; Schreiner and Koide 1993c; Ishii et al. 1997). As to whether AM fungi are able to discriminate against non-hosts during the pre-symbiotic growth stage there is no evidence for the release of inhibitory compounds by living non-host roots, and non-hosts appear to lack factors capable of hyphal growth promotion (Glenn et al. 1985, 1988; Gianinazzi-Pearson et al. 1989; Avio et al. 1990; Bécard and Piché 1990; Vierheilig and Ocampo 1990a, b; Koske and Gemma 1991; Giovannetti et al. 1993a; Schreiner and Koide 1993c; Giovannetti et al. 1994).

Differential branching pattern and chemotropism

It is now widely accepted that host roots, as well as promoting hyphal growth in AM fungi, also induce changes in hyphal growth pattern and morphology by increasing branching and inducing short, branched hyphal fans (Mosse and Hepper 1975; Graham 1982; van Nuffelen and Schenck 1984; Elias and Safir 1987; Bécard and Fortin 1988; Mosse 1988; Giovannetti et al. 1993b, 1994; Smith and Read 1997). Such differential hyphal morphogenesis can be detected in vivo as early as 24 h after challenging the fungal mycelium with host roots (Giovannetti et al. 1993b; Giovannetti 1997). Differential branching has been described also in hyphae of *Gigaspora* spp. as they approach host root exudates in vitro (Nagahashi et al. 1996) and in hyphae of *Glomus mosseae* growing on membranes bearing host root exudates (Logi 1997).

When mycelium is grown in the presence of non-host roots, neither non-mycorrhizal plants nor plants hosting mycorrhizas other than the arbuscular type emit volatiles or exudates able to elicit differential branching in AM fungal hyphae. Moreover, in plant species able to induce hyphal branching fungus also developed appressoria, suggesting that these two morphogentic events are related (Giovannetti et al. 1994).

Among the compounds released in root exudates, flavonoids have been suggested to be involved in stimulation of pre-contact hyphal growth and branching (Gianinazzi-Pearson et al. 1989; Siqueira et al. 1991), which is consistent with their role as signalling molecules in other plant-microbe interactions. However, maize plants unable to produce chalcone synthase, a key enzyme in flavonoid biosynthesis, were found to develop arbuscular mycorrhizas, suggesting that such compounds are not essential to the symbiosis (Bécard et al, 1995).

Directional growth of AM fungal hyphae towards host roots has also been reported (Mosse and Hepper 1975; van Nuffelen and Schenck 1984; Mugnier and Mosse 1987). The ability to locate host roots by chemotropic growth has been shown in aerial hyphae of *Gigaspora gigantea* (Koske 1982; Gemma and Koske 1988). Further studies of the mechanisms of host location by AM fungal hyphae are needed to ascertain whether contact with host roots is the result of passive chance encounters or fungal ability to locate the source of the stimulus.

Appressorium formation

The formation of appressoria is the most significant sign of fungal recognition of a potential host plant (Staples and Macko 1980). This important stage of the fungus life cycle has been studied only recently, mainly in connection with factors affecting appressorium formation (Lackie et al. 1987; Garriock et al. 1989; Giovannetti et al. 1993a). Appressoria are formed in the presence of host roots as early as 36 h after the beginning of the plant-fungus interaction (Fig. 1). Differentiation of these structures is followed rapidly by root penetration, colonization and arbuscule formation, which in host plants may occur as early as 48 h after the beginning of the interaction (Giovannetti and Citernesi 1993; Giovannetti 1997). Investigation of signals inducing the formation of infection structures has shown that, even in the presence of host root exudates, thigmotropic stimuli in the form of nylon, silk, cellulose, polyamide or glass threads did not elicit the differentiation of appressoria (Giovannetti et al. 1993a). However, specific topographical signals may be involved in mediating appressorium formation, as shown in other biotrophic fungi (Hoch et al. 1987; Teruhne et al. 1993). In fact, hyphal growth is frequently orientated along epidermal grooves and appressoria are formed over clinal and anticlinal wall junctions between adjacent epidermal cells (Garriock et al. 1989; Giovannetti et al. 1993a).

Many investigations of infection structure formation on non-host plant roots found no appressoria formation (Powell 1976; Malajczuck et al. 1981; Glenn et al. 1985, 1988; Avio et al. 1990; Parra-Garcia et al. 1992; Giovannetti et al. 1993a, 1994). There are some reports of abortive entry points and/or slight root colonization on roots of non-hosts growing alone or together with host plants, although details of appressoria were not given (Morley and Mosse 1976; Trinick 1977; Ocampo 1980, 1986; Bedmar and Ocampo 1986).

It is important to note that the term "appressorium" has been used in some reports to describe hyphal tip enlargements produced on non-host roots or dead host wall fragments (Tommerup 1984; Nagahashi and Douds 1997). However, the morphological characteristics of these structures resemble the "swellings" noted by Glenn et al. (1985, 1988) and Giovannetti et al. (1993a, 1994), which are also formed on host and dead non-host roots (Figs. 2–4) Moreover, appressoria have been defined also as hyphal apices attached to the root surface, regardless of whether they are swollen (Tommerup 1984). This controversy indicates the need for a clearcut definition of "appressoria" in AM fungi to avoid misinterpretation of experimental data.

Some nodulation mutants of pea (*Pisum sativum* cvs. Frisson, Finale, Sparkle) completely devoid of mycorrhizal infection (Myc^{-1} Nod^{-} phenotype) were considered as potentially useful model systems for studying the mechanisms of non-host discrimination by AM fungi (Duc et al. 1989). Unfortunately, the early recognition events in these mutants are the same as in other


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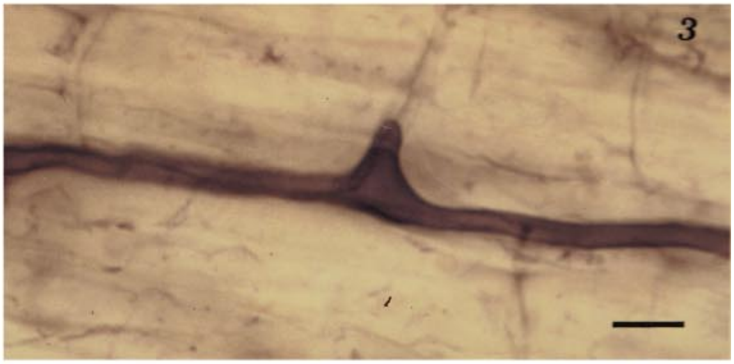
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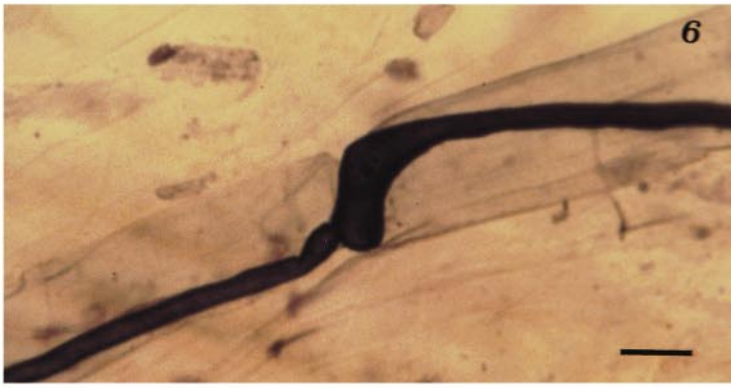
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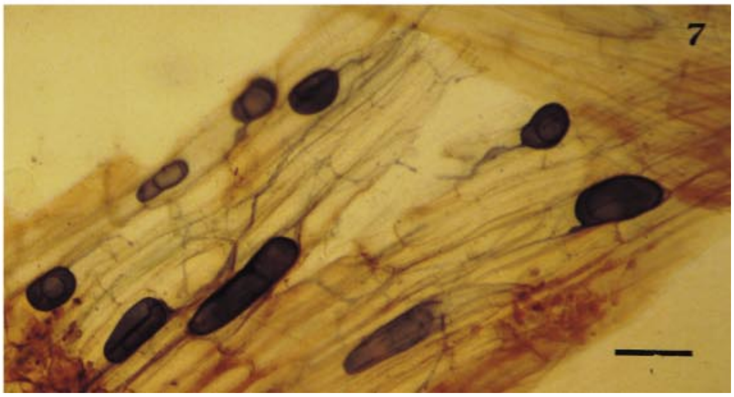
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host plants, and AM fungi undergo the same developmental steps to appressoria formation as in parental cultivars. The subsequent penetration of infection hyphae developing from appressoria (Fig. 5) is hindered in Myc^{-1} mutants by the plant defence response of abnormally, thick cell wall appositions at the sites where appressoria are formed (Gollotte et al. 1993). Thus, AM fungi are able to recognize Myc^{-1} mutant roots as host roots. Interestingly, no pea mutant hindering appressorium differentiation has yet been found and, thus, all the mutants obtained so far are not altered in genes important for host recognition by AM fungi (L. Avio, unpublished results).

Transgenic plants constitutively overexpressing defence-related genes and showing increased resistance to root fungal pathogens, also considered interesting model systems of early symbiotic interactions with AM fungi, are colonized in the same way as normal host plants (Vierheilig et al. 1993, 1995).

In conclusion, appressoria are formed by AM fungi after recognition of host signals at the root surface, regardless of the outcome of the interaction, whereas their development is not elicited on the surface of non-host roots. Non-host roots appear to be unambiguously recognized by AM fungi at this stage of the interaction. The question of whether the activity of antifungal compounds produced by some non-mycorrhizal plants is involved in their lack of susceptibility to AM fungi has not yet been answered (Vierheilig and Ocampo 1990a, b; Koide and Schreiner 1992; Schreiner and Koide 1993a, b).

Root colonization

After the differentiation of appressoria, AM fungi usually colonize host roots by forming intercellular and intracellular hyphae and intracellular arbuscules. Two main anatomical types have been identified in arbuscular mycorrhizas (*Arum* and *Paris*), their occurrence depending on the host plant genome (Smith and Read 1997).

Many authors have described the colonization of non-host roots with intercellular development of fungal hyphae, often associated with the formation of vesicles (Malloch and Malloch 1981; Taber and Strong 1982; Giovannetti and Lioi 1990; Càzares and Smith 1992; Càzares and Trappe 1993; Guerrero 1996; Treu et al. 1996). Vesicles in arbuscular mycorrhizal host roots usually occur after arbuscule development. In contrast, vesicles in non-host roots have been detected in the absence of arbuscules. Ultrastructural observations of non-host *Brassica* roots colonized by *Glomus mosseae* showed that intracellular colonization occurred only when cells were dead, i.e. when no plasma membrane was present (Glenn et al. 1985). Moreover, AM fungi have been described as being able to colonize different organs or tissues of host and non-host plants and to form swellings and intraradical vesicles (Park and Linderman 1980; Stasz and Sakai 1984; Warner 1984; Giovannetti and Lioi 1990). The absence of both appressoria and arbuscules in these interactions between AM fungi and plant tissues suggests the lack of any recognition event leading to the establishment of a functional symbiosis (Figs. 6, 7) and instead a rather parasitic type of colonization.

In pea mutants forming non-nitrogen fixing or defective nodules (Myc^{-2} Nod$^{+/-}$ phenotype), AM fungi are able to differentiate appressoria, penetrate host roots and develop intercellular hyphae, without completing arbuscule formation (Fig. 8) (Gianinazzi-Pearson and Dénarié 1997). In this kind of root colonization, infected cortical cells lack the ATPase activity usually present in the peri-arbuscular membrane of fully developed functional symbioses (Gianinazzi-Pearson et al. 1991, 1995). This suggests that a further signal is necessary for arbuscule differentiation and that this sig-

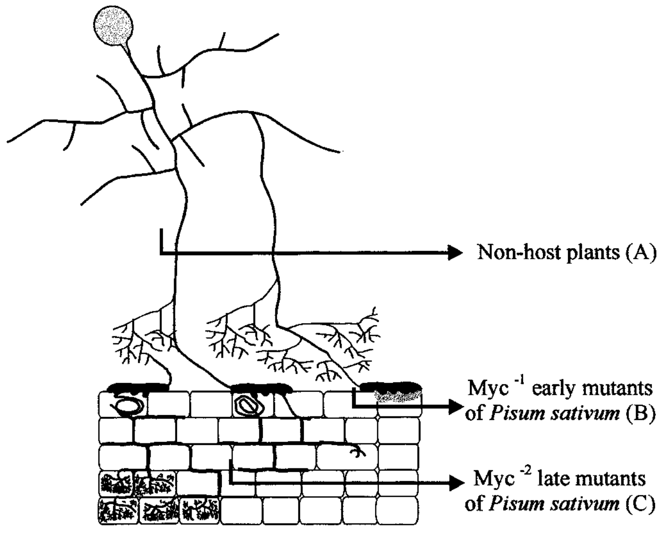

Fig. 8 Scheme representing fungal developmental switches dependent on the plant genome. *A* Non-host plant roots are unable to induce differentiation in AM fungal hyphae. *B* Myc^{-1} early mutants trigger the formation of infection structures, but further developmental steps are hindered by host defence responses. *C* Myc^{-2} mutants trigger appressorium formation, followed by intraradical colonization, but complete arbuscule differentiation is hindered

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Fig. 1 Appressoria and intraradical coils formed by *Glomus mosseae* on the roots of the host *Prunus cerasifera*; *bar* 35 μm

Fig. 2 Hyphal swellings formed by *G. mosseae* on the edge of two contiguous dead epidermal root cells of the non-host *Lupinus albus*; *bar* 28 μm

Fig. 3 Hyphal swelling formed by *G. mosseae* when growing on dead roots of the host *Medicago sativa*; *bar* 18 μm

Fig. 4 Hyphal swelling formed by *G. mosseae* when growing on dead roots of the host *Pisum sativum*; *bar* 23 μm

Fig. 5 Appressoria formed by *G. mosseae* on the root surface of a mycorrhiza-resistant mutant of *Pisum sativum*; *bar* 55 μm

Fig. 6 *G. mosseae* hypha invading dead epidermal root cells of the host *Pisum sativum*; *bar* 18 μm

Fig. 7 Vesicles formed by *Glomus microcarpum* in the roots of the non-host *Arbutus unedo*; *bar* 70 μm nal is lacking as a consequence of a gene mutation in Myc^{-2} pea mutants.

What is non-host for AM symbionts?

The mechanisms which determine the non-host nature of plant species, preventing the establishment of a functional AM symbiosis, are not known at the genetic level. The absence of signals regulating morphogenic changes in AM fungal mycelium, either during pre-contact growth or at the root surface, may explain the "immunity" of non-host plants. Nevertheless, present knowledge of the sequence of fungal development leading to establishment of functional AM symbioses suggests that the non-host nature of plants lies in their inability to trigger expression of fungal genes involved in hyphal commitment to the symbiotic status.

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