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REVIEW

Strigolactones, signals for parasitic plants and arbuscular mycorrhizal fungi

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Abstract Although strigolactones play a critical role as rhizospheric signaling molecules for the establishment of arbuscular mycorrhizal (AM) symbiosis and for seed germination of parasitic weeds, scarce data are available about interactions between AM fungi and strigolactones. In the present work, we present background data on strigolactones from studies on their seed germination activity on the parasitic weeds *Orobanche* and *Striga*, the importance of nitrogen and phosphorus for this seed germination activity, and what this could mean for AM fungi. We also present results on the susceptibility of plants to AM fungi and the possible involvement of strigolactones in this AM susceptibility and discuss the role of strigolactones for the formation and the regulation of the AM symbiosis as well as the possible implication of these compounds as plant signals in other soil-borne plant–microbe interactions.

Keywords Arbuscular mycorrhiza · Parasitic plants · *Orobanche* · *Striga* · Strigolactones

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Introduction

The arbuscular mycorrhiza (AM) association is widely distributed in the plant kingdom (more than 80% of plant species form AM), and this ubiquity is probably a consequence of its ancestral character and the coevolution of the two partners (plant and fungi). Fossil records have revealed that the origin of AM dates back at least 460 million years, and this origin coincides with the appearance of the first terrestrial plants. This suggests that the colonization of land by plants from the water was assisted by ancestral AM fungi (Simon et al. 1993; Redecker et al. 2000).

The close coevolution of plants and AM fungi over time has resulted in a sophisticated system of relationships in which the processes of recognition, penetration, and establishment of the fungi in roots are highly regulated. Despite the central role of the AM symbiosis in agriculture and natural ecosystems, the mechanisms that regulate the formation and functioning of AM are still largely unknown. Nevertheless, recent discoveries regarding the activity of signal molecules and regulatory genes that mediate the communication between AM fungi and the plant root represent an important advance in knowledge about the AM symbiosis.

The relationship of plant roots with the parasitic weeds *Striga* and *Orobanche* is a known case in which major parallelism with the AM signaling pathway has been observed (Bouwmeester et al. 2007; López-Ráez et al. 2008a). In this sense, part of the signaling mechanism of AM fungi–root interactions seems to have been adapted by the parasitic plants to establish, in this case, a parasitic relationship with the root. The discovery of the parallelism between AM fungi and parasitic weeds in their signaling with roots constitutes a milestone in AM research. The fact

that the same host-derived compounds—strigolactones—that can induce the germination of seeds of parasitic plant weeds also induce hyphal branching of AM fungi (Akiyama et al. 2005) has opened up new lines in AM research. Strigolactones are apocarotenoids derived from the plant secondary metabolism and together with flavonoids, terpenoids, and plant hormone regulators are implicated in the molecular dialogue between AM fungi and plants, suggesting that plant secondary metabolites play an essential role in the regulation and development of AM (Akiyama 2007).

From branching factors to strigolactones

In the last decade, numerous authors have reported that roots of AM host plants release signal molecules responsible for hyphal branching in AM fungi (branching factors, BFs). In 1999, Nagahashi and Douds developed an in vitro bioassay for hyphal branching that facilitated the chemical analysis of these compounds and revealed that these factors are widely distributed in all mycotrophic plants tested so far but absent from AM nonhost plants (Buée et al. 2000; Nagahashi and Douds 2000). BFs were found to be of low molecular weight (Giovannetti et al. 1996) and of lipophilic nature (Buée et al. 2000; Nagahashi and Douds 2000). Their concentration in root exudates was described as low and regulated by biotic factors that traditionally have been reported as regulators of mycorrhization, such as the level and the availability of phosphorus in the soil (Nagahashi and Douds 2000).

The first compound characterized as a BF was isolated from root exudates of *Lotus japonicus* cultivated in hydroponic culture and was identified by spectroscopic analysis as the strigolactone 5′-deoxystrigol (Akiyama et al. 2005). Moreover, the natural strigolactones 5-deoxystrigol, sorgolactone and strigol, and the synthetic strigolactone analog, GR24, induced extensive AM hyphal branching of the AM fungus *Gigaspora margarita* at picogram to nanogram levels (Akiyama et al. 2005), supporting the conclusion that strigolactones are branching factors.

Strigolactones

Strigolactones are a group of apocarotenoids that are produced in plants, exuded by roots and act as signaling compounds in the rhizosphere. At least nine strigolactones (strigol, strigyl acetate, 5-deoxystrigol, orobanchol, orobanchyl acetate, sorgolactone, *epi*-orobanchol, solanacol, and sorgomol) have been identified and structurally characterized in the root exudates of AM host and nonhost plant species, and several novel strigolactones have been isolated, but the chemical structure of these has not yet been elucidated (Rani et al. 2008).

So far, strigolactones released by roots have been identified to stimulate seed germination of the harmful parasitic plants witchweed (*Striga*) and broomrape (*Orobanche*, including the new taxonomic genus *Pheliphanche*; Bouwmeester et al. 2007; López-Ráez et al. 2008a) and to induce hyphal branching of AM fungi (Fig. 1; Akiyama et al. 2005; Besserer et al. 2006). Such hyphal branching in the vicinity of roots is thought to be an essential step for further root colonization by the AM fungi (Buée et al. 2000; Nagahashi and Douds 1999, 2000).

This potentially important role during the establishment of the AM symbiosis and the fact that more than 80% of all land plant families form an association with these symbiotic fungi (Smith and Read 1997) suggest the presence of strigolactones in nearly all plants. This ubiquity of strigolactones has also recently been suggested from their role as a new class of plant hormones regulating shoot branching (Fig. 1; Gómez-Roldán et al. 2008; Umehara et al. 2008).

Strigolactones in AM nonhost plants

Although most land plants are hosts for AM fungi, some plant families, e.g., the Brassicaceae, the Chenopodiaceae, and lupins (an exception in the mycorrhizal host family of the Leguminosae), are reported as AM nonhost plants (Smith and Read 1997). The mechanism responsible for the nonsusceptibility of these plants to AM fungi is controversial. Some data have provided evidence that root exudates of some AM nonhost plants contain compounds inhibitory to AM fungi, whereas other data indicate that root exudates of other AM nonhost plants lack essential signals for root colonization by AM fungi (reviewed by Giovannetti and Sbrana 1998; Vierheilig et al. 1998; Vierheilig and Bago 2005).

Recent data indicate that the lack of signals essential for AM root colonization could be at least one factor determining the nonsusceptibility of these plants to AM fungi. By testing the effect of root exudates from a wide range of AM nonhost plants on *Striga* and *Orobanche*, it could generally be observed that seed germination in these parasitic plants was not stimulated but that, exceptionally, a low level of seed germination stimulation occurred (Berner and Williams 1998; Fernández-Aparicio et al. 2009a; Lendzemo et al. 2009a; Steinkellner et al. 2007). This could be either due to the absence or to reduced levels of seed germination-stimulating compounds (possibly strigolactones) in these root exudates.

To our knowledge, none of the root exudates of AM nonhost plants tested so far on AM fungi have exhibited a

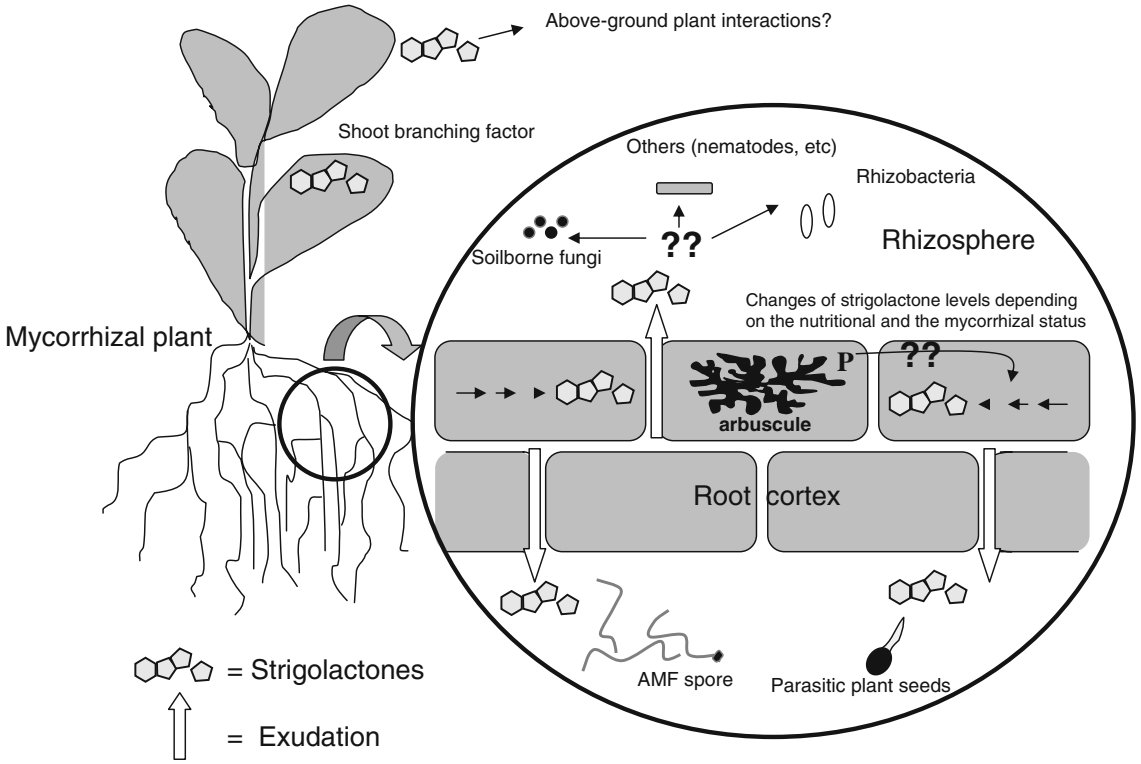

Fig. 1 Strigolactones have been identified as phytohormones involved in shoot branching and as signaling compounds for AMF and parasitic weeds. There is evidence that strigolactone levels in plants are affected by the nutritional status (e.g., P) of the plant. Moreover, strigolactone levels are altered after mycorrhization, indicating their possible role in the regulation of mycorrhization. No data are available yet how these alterations of the strigolactone levels are regulated by the nutritional and/or mycorrhizal status of the plant. Due to their ubiquity in plants, a more general signaling role of strigolactones in below-ground (e.g., soil-borne fungi apart from AMF, rhizobacteria) and even in above-ground plant interactions cannot be excluded

hyphal branching activity (Buée et al. 2000; Nagahashi and Douds 2000). As strigolactones are suggested to be the compounds responsible for hyphal branching in AM fungi, this would indicate an absence or reduced levels of strigolactones in those root exudates. Recently, however, hard analytical data have been provided showing the presence of strigolactones in the root exudates of the two AM nonhost plants *Arabidopsis thaliana* (Brassicaceae) and lupin (Fabaceae; Goldwasser et al. 2008; Yoneyama et al. 2008). This still leaves open the possibility that strigolactone levels are reduced in these plants. In fact, when comparing the effect of root exudates of carrot, tobacco, and *A. thaliana* on *Orobanche* seed germination, Westwood (2000) reported reduced levels of seed stimulating compounds in root exudates of *A. thaliana*. Moreover, Yoneyama et al. (2008) recently reported that strigolactone levels in root exudates of the AM nonhost plant lupin are reduced by a factor 1,000 compared to strigolactone levels in root exudates of the AM host plant *Trifolium pratense*. These data indicate that, among other reasons, the nonhost status of AM nonhost plants could be at least partially determined by the reduced levels of compounds with an AM hyphal branching activity (strigolactones) in their root exudates.

Strigolactones and other compounds with a seed germination activity

Data on the presence of strigolactones in root exudates are only available from a small range of plant species as these compounds occur at very low amounts and are highly unstable, which makes their analytical detection and identification extremely difficult (Bouwmeester et al. 2003, 2007; López-Ráez et al. 2008a; Steinkellner et al. 2007). Another rather simple and inexpensive option to detect the presence of strigolactones is the use of a bioassay based on the germination of *Striga* or *Orobanche* seeds. Seeds of these parasitic plants do not germinate in absence of a seed stimulant, whereas germination is highly sensitive to strigolactones. However, in this context, it has to be kept in mind that germination of *Striga* and *Orobanche* seeds is not only stimulated by strigolactones but also by isoflavones and sesquiterpene lactones (Bouwmeester et al.

2007) as well as other yet unidentified chemical compounds (Fernández-Aparicio et al. 2008). Thus, *Striga* or *Orobanche* seed germination can only be considered an indication for the presence of strigolactones, and the presence of other compounds with seed germination activity cannot be excluded.

There are first indications for the interaction of strigolactones with other parasitic weed-stimulating compounds. In bioassays, the strigolactone analog GR24 is generally used as a positive control for the viability of tested *Orobanche* or *Striga* seeds. By mixing root exudates from cowpea plants with a GR24 solution, it was observed that the *Striga* seed germination activity of this combination was significantly greater than the GR-24 treatment alone (Lendzemo et al. 2009b). This indicates that compounds are present in these root exudates that exhibit a strong synergistic stimulatory effect on *Striga* seed germination when in combination with the strigolactone analog GR24.

As mentioned above, *Striga* and *Orobanche* seed germination-stimulating compounds are not only found in root exudates of host plants for these parasitic plants but they can also occur in root exudates of nonhost plants from different plant families (Berner and Williams 1998; Fernández-Aparicio et al. 2009a; Lendzemo et al. 2009a; Steinkellner et al. 2007). For example, seed germination of *Striga hermonthica* is clearly stimulated not only by root exudates of its host sorghum but also by nonhost plants such as cucumber and bean (Lendzemo et al. 2009a). These data tend to support the hypothesis about the ubiquitous presence of strigolactones in the plant kingdom.

Strigolactones and AM hyphal branching

The mechanism by which strigolactones induce branching of AM fungi is still poorly understood. The findings that strigolactones are produced at low levels are active at nanomolar concentrations and can show multiple functions, support the idea that a receptor-mediated signaling mechanism is involved, analogous to plant hormone perception. In fact, recent results showing that strigolactones control plant shoot branching (Gómez-Roldán et al. 2008; Umehara et al. 2008) confer the character of phytohormone-like compounds to these substances. In earlier studies, a semi-purified exudate fraction of carrot root organ culture was shown to induce the expression of mitochondrial fungal genes, increase mitochondrial respiration, and prompt mitochondrial reorganization before fungal branching (Tamasloukht et al. 2003). In later studies, the application of the strigolactone analog GR24 strongly and rapidly stimulated cell proliferation and changes in mitochondrial density and shape in different AM fungi (Besserer et al. 2006). These effects were associated with a rapid increase in fungal mitochondrial oxidative metabolism, NADH concentration, NADH dehydrogenase activity, and ATP content of the fungal cell, all of which did not require new gene expression (Besserer et al. 2008, 2009). These data suggest the existence of an active mechanism for strigolactone perception and signaling amplification (Bouwmeester et al. 2007). Since these events were not observed with other germination stimulants of parasitic weeds (Besserer et al. 2006), they might be interpreted as strigolactone-specific responses. Whether strigolactones depend on a similar mechanism of perception and signal transduction pathway activation, mediated by mitochondria, in parasitic plant seeds as in AM fungi remains an unresolved question. Future studies targeting the characterization of strigolactone receptors, including plant receptors, should provide some answers to the question of whether there exists a common mechanism of action for these compounds and therefore give new insights into the biological significance of these molecules in rhizosphere signaling.

Strigolactones are unlikely to be the only BFs that stimulate AM fungal growth, and there are reports of the separation of a number of active branching compounds from root exudates of carrot (Nagahashi and Douds 2000, 2007). In addition, different active fractions from a carrot root exudate can induce morphologically distinct hyphal branching patterns in the same AM fungus, and different fungi can respond to the same fraction with a distinct morphological branching pattern (Nagahashi and Douds 2007). This indicates the presence of multiple BFs in carrot root exudates that could promote different reactions in different AM fungi. Since a root exudate will not contain only one strigolactone but a mixture of different strigolactones, BFs in exudates inducing distinct morphological branching patterns could be different strigolactones.

Although induced AM hyphal branching activity has been reported for root exudates of a wide range of AM host plants, such as tomato, tobacco, carrot, sorghum, maize, pea, alfalfa, *Medicago truncatula*, and *L. japonicus* (Nagahashi and Douds 1999, 2000; Buée et al. 2000; Akiyama et al. 2005; Besserer et al. 2006; Gómez-Roldán et al. 2008; López-Ráez and Douds 2008b), analytical data have so far only provided for the presence of strigolactones in root exudates of tomato, sorghum, pea, and *L. japonicus*. However, this strongly indicates that the AM hyphal branching activity of root exudates is due to strigolactones (Akiyama et al. 2005; Besserer et al. 2006; Gómez-Roldán et al. 2008; López-Ráez et al. 2008a, b). Since different strigolactones have been detected in root exudates of AM plants, but all exudates induce hyphal branching, it can be concluded that strigolactones are general branching signals for AM fungi. Nevertheless, as already mentioned, the presence of other compounds in root exudates able to activate

hyphal branching cannot be excluded, but no analytical data are available yet as to their nature.

AM hyphal branching activity versus seed germination activity

At first sight, there seems to exist some contradiction between effects of root exudates on AM hyphal branching and on *Striga* or *Orobanche* seed germination. Root exudates of tomato, a well-described host for AM fungi, exhibit an AM hyphal branching activity (Nagahashi and Douds 2000; López-Ráez et al. 2008b) but do not seem to stimulate seed germination of all *Orobanche* species or of *S. hermonthica* (Fernández-Aparicio et al. 2009a; Lendzemo et al. 2009a). However, the presence of strigolactones in tomato root exudates has been analytically demonstrated (López-Ráez et al. 2008b), and tomato root exudates do induce germination of *O. ramosa* seeds (Fernández-Aparicio et al. 2009a; López-Ráez et al. 2008b). A possible explanation for these apparently contradictory results is that not all strigolactones stimulate the germination of all *Orobanche* species but that a certain *Orobanche* seed-stimulating specificity exists.

A species-specific seed-stimulating activity of different strigolactones could also explain why seeds of *S. hermonthica* do not germinate in presence of tomato root exudates. Moreover, when comparing stimulation of *Orobanche* and *Striga* seed germination by GR24, *Striga* seeds seemed to be more insensitive to the synthetic analog (Matusova et al. 2004; Juan Antonio López-Ráez, personal communication) and thus possibly need higher concentrations of strigolactones in the root exudates to germinate. This should be kept in mind when using the *Striga*/*Orobanche* seed germination bioassay for the detection of strigolactones. On the one hand, the absence of a seed germination induction does not necessarily mean that no strigolactones are present, but the strigolactones present may have no or low levels of seed germination activity for the tested plant parasite, or seed germination inhibitors may be present. On the other hand, an induction of seed germination activity does not necessarily mean that strigolactones are present, but this effect may be due to other seed germination-stimulating compounds which do not have an effect on AM fungi.

Strigolactones and AM root colonization

The activity of strigolactones in inducing hyphal branching of AM fungi has been clearly demonstrated. Hyphal branching is considered to be an important event in host root recognition by AM fungi (Giovannetti and Sbrana 1998; Buée et al. 2000; Nagahashi and Douds 2000) since the branching response increases "...the probability of encounter with a site on the root suitable for colonization..." (Douds and Nagahashi 2000). This would mean that reduced levels of strigolactones should result in reduced hyphal branching in the root vicinity which could result in reduced root colonization by AM fungi.

Pea mutants deficient in strigolactones have recently been identified (Gómez-Roldán et al. 2008). Inoculation of these mutants with AM fungi resulted in drastically reduced root colonization compared to root colonization of wild-type plants. This observation seems to reinforce the hypothesis that the level of strigolactones in plants affects AM development. Moreover, root colonization partially recovered when the strigolactone analog GR24 was applied, indicating that the reduced AM fungal root colonization was linked to the reduced strigolactone levels (Gómez-Roldán et al. 2008). This represents the first direct proof that strigolactones play an important role in processes involved in AM root colonization.

However, these results raise new questions. If strigolactones are essential for root colonization by AM fungi, plants deficient in strigolactones should show no root colonization at all. This could mean that either the pea mutants were not completely strigolactone deficient but only had drastically reduced levels of strigolactones, thus allowing limited root colonization, or that compounds other than strigolactones exhibit a favorable effect on root colonization, thus compensating the reduced strigolactone levels. Moreover, in the absence of strigolactones, some spores germinating in close proximity to growing roots could initiate root colonization without a branching phenomenon. Another question that still needs to be answered is whether the restored root colonization in the strigolactone-deficient pea mutants after GR24 application is due to stimulation of AM fungal spore germination or due to enhanced branching of hyphae? Since strigolactones can stimulate spore germination of AM fungi (Besserer et al. 2006, 2008), this phenomenon could be responsible for the recovery of AM development in the strigolactone-deficient pea mutants treated with GR24. However, application of GR24 to the growth substrate of the mutant pea plants should result in a profuse branching of the AM fungal hyphae in the substrate, independent of the presence or absence of roots in close vicinity (Fig. 2). This could mean that branching by itself is an important step in the AM fungus–plant interaction and that branching does not have to occur close to the roots of a host plant. To summarize, although there are some data confirming the importance of strigolactones for root colonization by AM fungi, further studies are needed to elucidate the exact mechanisms through which this may occur.

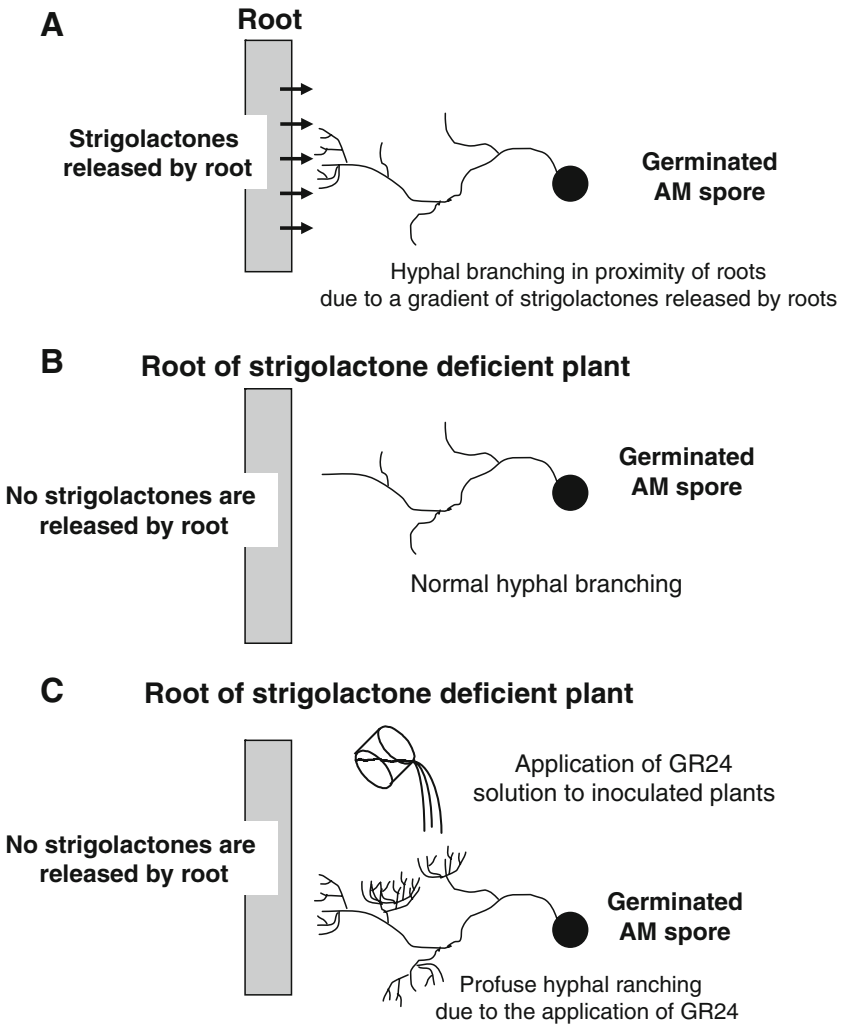

Fig. 2 Strigolactones, released by roots, induce hyphal branching in proximity to the root (**a**). In strigolactone-deficient plants, no strigolactone should be released by roots, and thus, no branching should occur (**b**) resulting in a reduced AM root colonization (Gómez-Roldán et al. 2008). The strigolactone analog GR24 also induces hyphal branching. This means that application of GR24 to AM inoculated plants should result in profuse AM hyphal branching (**c**) independently whether the AM hyphae is in proximity of a root or not. It is not clear yet why this branching, even when in distance to a root, results in an enhanced AM root colonization (Gómez-Roldán et al. 2008)

Strigolactones and the autoregulation of mycorrhization

Recently, a plant-regulatory mechanism of mycorrhization has been described: Once a certain level of root colonization is reached, further root colonization is suppressed (Vierheilig and Piché 2002; Vierheilig 2004a, b). This mechanism has been named autoregulation of mycorrhization (Vierheilig et al. 2000a; Vierheilig and Piché 2002; Vierheilig 2004a, b) since it seems to share some similarities with the autoregulation of nodulation in rhizobial–legume interactions, where once a certain number of nodules have been formed, further nodulation is suppressed (see Caetano-Anollés and Gresshoff 1991). Several studies of the autoregulatory mechanism of mycorrhization have excluded plant phosphorus (Vierheilig et al. 2000b) or the competition for carbon (Lerat et al. 2003a, b) as the regulatory factor of the observed suppression of further root colonization by AM fungi in already mycorrhizal plants.

Data are accumulating that strigolactone levels are altered in mycorrhizal plants and this might be involved in the autoregulation of mycorrhization. In several studies, it has been reported that mycorrhizal plants, such as sorghum and maize, are less susceptible to infection by *Striga* spp. (Lendzemo and Kuyper 2001; Gworgwor and Weber 2003; Lendzemo et al. 2005). Since the absence of compounds inhibitory to *Striga* seed germination has recently been reported in root exudates from mycorrhizal plants (Sun et al. 2008; Lendzemo et al. 2009b), the reduced susceptibility of mycorrhizal plants to *Striga* may be at least partially due to reduced levels of strigolactones, resulting in a lower *Striga* seed germination activity when compared to exudates from nonmycorrhizal control plants (Lendzemo 2004; Lendzemo et al. 2007, 2009b; Matusova et al. 2005; Sun et al. 2008). These data have led Matusova et al. (2005) and Lendzemo et al. (2007) to hypothesize that mycorrhization might downregulate the production of the

AM fungal branching factor (strigolactones). Interestingly, a lower *Striga* seed germination activity was not only reported for compounds released from mycorrhizal roots but also for compounds released from the stem of mycorrhizal plants, indicating that the levels of *Striga* seed germination-stimulating compounds (possibly strigolactones) are reduced systemically in mycorrhizal plants (Lendzemo et al. 2009b).

To our knowledge, there are only a few reports on the effect of root exudates of mycorrhizal plants on AM fungi. Observations from in vitro studies have indicated that AM fungal branching is reduced in the presence of root exudates from mycorrhizal cucumber plants, when compared to exudates from nonmycorrhizal control plants (Pinior 1999; Pinior et al. 1999). However, no quantitative data were presented in the latter studies and no tests have as yet been performed on root exudates from mycorrhizal and nonmycorrhizal plants using the branching assay described by Nagahashi and Douds (1999). Application of root exudates from mycorrhizal cucumber plants to AM fungal-inoculated cucumber plants also resulted in reduced root colonization, suggesting an inhibitory effect of mycorrhizal root exudates on AM development (Pinior et al. 1999; Vierheilig et al. 2003).

The data discussed above indicate that alterations in the levels of strigolactones are involved in the regulation of root colonization by AM fungi of already mycorrhizal plants (autoregulation). This may not be the only mechanism involved.

Strigolactones and the nutritional status of plants

There are several reports that fertilizer application (specifically P and N) reduces the infestation of crops by *Striga* and *Orobanche* (Abu Irmaileh 1994; Raju et al. 1990; Jain and Foy 1992; Cechin and Press 1993; Mumera and Below 1993; Yoneyama et al. 2001) and this reduced infestation appears to be linked with a reduced exudation of strigolactones at higher nutrient levels (Fig. 1). In fact, while a supply of elements such as K, Ca, or Mg to plants seems to have no effect on the exudation of strigolactones (Raju et al. 1990; Yoneyama et al. 2007a, b), alterations in the P or N status of plants do alter strigolactone exudation. Low P levels clearly resulted in an enhanced exudation of strigolactones in red clover, sorghum (Yoneyama et al. 2007a, b), and tomato (López-Ráez et al. 2008b). This alteration in the strigolactone exudation pattern in presence or absence of P seems rather rapid. When tomato plants were grown for 96 h in a P-deficient nutrient solution, the germination rate of *Orobanche ramosa* was tripled compared to the control plants grown in a nutrient solution with P, indicating an enhanced exudation of the seed germination-stimulating compound/s (López-Ráez et al. 2008b), whereas application of P to red clover cut exudation to half after 24 h (Yoneyama et al. 2007a).

With N, the data are not that clear. Whereas in sorghum, low N levels resulted in a drastic increase in strigolactone 5-deoxystrigol in the root exudates (Yoneyama et al. 2007b) and enhanced N levels resulted in a reduced germination rate of *Striga asiatica* exposed to sorghum root exudates indicating a reduced strigolactone exudation (Raju et al. 1990), the picture was less clear with red clover (Yoneyama et al. 2007a). Although in red clover low N levels induced a certain, but compared to sorghum, low stimulation of *Orobanche minor* seed germination, indicating an enhanced strigolactone exudation by the roots, the exudation of the strigolactone orobanchol was not enhanced (Yoneyama et al. 2007a).

As strigolactones not only stimulate the germination of parasitic weeds but also the hyphal branching of AM fungi (Akiyama et al. 2005), alterations in the exudation pattern of strigolactones due to the nutritional status of the plant should also affect the branching and root colonization by AM fungi. The P status of plants is known to be decisive as to whether a plant is or not colonized by AM fungi (see Smith and Read 1997). Increasing P levels in the growth substrate decrease the level of root colonization and high P levels can even result in a complete absence of AM root colonization (Mosse 1973; Sparkling and Tinker 1978; Stribley et al. 1980; Siqueira et al. 1984; Thomson et al. 1986; Amijee et al. 1989). There are reports that root exudates from tomato plants grown under P-deficient conditions stimulate branching of AM fungi to a greater extent than root exudates from tomato plants grown under P-sufficient conditions (Nagahashi and Douds 2000, 2003; Nagahashi et al. 1996; López-Ráez et al. 2008b). This could mean that at high P levels, the production and exudation of compounds with hyphal branching activity (e.g., strigolactones as shown by López-Ráez et al. 2008b) are reduced and that this results in reduced AM root colonization.

As in the case of high P levels, high N levels have similarly been reported to suppress root colonization by AM fungi (Chambers et al. 1980; Azcón et al. 1982). However, the effect of N on AM root colonization appears to be more complex. There seems to exist an interaction between the effect of P and N on AM root colonization, and in several studies, it has been suggested that AM root colonization is only suppressed when both elements, P and N, are available at higher concentrations (Bååth and Spokes 1989; Sylvia and Neal 1990; Liu et al. 2000; Treseder and Allen 2002; Blanke et al. 2005). Although there is some

information available that the levels of P and N do affect the exudation of strigolactones (Yoneyama et al. 2007a, b; López-Ráez et al. 2008a, b), there is no clear experimental proof to link alterations in the exudation pattern of strigolactones, due to changes of the nutrient status of a plant, directly with enhanced or decreased AM root colonization levels. It is tempting to speculate that strigolactones are the decisive factor affecting the susceptibility of plants to AM fungi. However, factors other than strigolactone exudation might also play a role in the nutritional effect on AM root colonization. At the molecular level, no data are yet available to connect a mechanism of P or N sensing with the strigolactone pathway. Future experiments, combining different P and N levels and targeting the effect of these combinations on AM root colonization, the effect of root exudates on *Orobanche* or *Striga* seed germination and hyphal branching of AM fungi, as well as the quantification of strigolactones in exudates, should clarify how the nutritional status of plants and AM root colonization are linked to strigolactone exudation patterns.

Strigolactones and *Rhizobium*

Considering the function of strigolactones as plant hormones regulating shoot branching and the suggestion that they are ubiquitous in plants (Gómez-Roldán et al. 2008; Umehara et al. 2008), it is feasible to envisage an involvement of strigolactones in the signaling of other plant–microbe interactions in the rhizosphere. However, to date, data on strigolactones released by plants and interacting with other root-inhabiting organisms are scarce (Fig. 1). Similar signaling pathways exist during certain steps of the establishment of AM and rhizobia symbioses in legume plants (Guinel and Geil 2002; Hirsch and Kapulnik 1998; Vierheilig and Piché 2002; Parniske 2008), but nothing is known about a possible function of strigolactones in the *Rhizobium*–legume interaction. As strigolactones are found in all legumes tested so far (Steinkellner et al. 2007; Yoneyama et al. 2008), it would not be surprising that they also play a role during the establishment of the *Rhizobium*–legume symbiosis.

In fact, some recent observations indicate that *Orobanche* plant infection could be partly controlled by the conserved symbiotic pathway that mediates nodulation and AM formation. Nod−Myc− mutant plants of *M. truncatula* and *Pisum sativum* showed altered patterns in their interaction with *Orobanche crenata*, suggesting that parasitic plants have recruited several steps of the symbiotic pathway (Fernández-Aparicio et al. 2009b). Moreover, there are some indications that the release of parasitic weed stimulating compounds (strigolactones) somehow interacts with the rhizobial symbiosis. It has been reported that inoculation with *Rhizobium* decreases *Orobanche* infection in several studies with legumes (Mabrouk et al. 2007a, b, c). This decrease in *Orobanche* infection seems to be at least partially linked to changes in root exudation in the presence of rhizobia. Rhizobial inoculation of legumes reduced seed germination enhancement of *Orobanche* by root exudates of pea (Mabrouk et al. 2007a, b, c) and red clover (Morozov et al. 2000), indicating a reduced release of germination stimulants, possibly strigolactones, or the release of inhibitors by roots in presence of rhizobia. This strongly recalls the reduced seed germination enhancement of root exudates once plants are colonized by AM fungi (Lendzemo 2004; Lendzemo et al. 2007, 2009b; Matusova et al. 2005; Sun et al. 2008).

By mixing root exudates of rhizobial pea plants with the strigolactone analog GR24, Mabrouk et al. (2007c) showed that the reduced parasitic seed germination activity of the root exudates of rhizobial pea plants on *O. crenata* is at least partially due to the presence of seed germination inhibitors in those exudates. This contrasts with the changes in the root exudates of mycorrhizal plants. By mixing root exudates of a mycorrhizal cowpea plant (Lendzemo et al. 2009b) or a mycorrhizal maize plant (Sun et al. 2008) with a GR24 solution, no presence of compounds inhibitory to the germination of *Striga* was observed.

Strigolactones and soil-borne fungi (apart from AM fungi)

Only scarce data are available about interactions between strigolactones and other fungi apart from AM fungi (Fig. 1). While Besserer et al. (2006) observed that in presence of the synthetic strigolactone analogs GR7 and GR24, spore germination of *Glomus intraradices* and *Glomus claroideum* is accelerated and the percentage of germinating spores is increased, Steinkellner et al. (2007) reported that microconidia germination of *Fusarium oxysporum* f.sp. *lycopersici*, a tomato pathogen, is not affected by GR24. In order to analyze more widely the effect of GR24 on fungal growth patterns, the strigolactone analog was applied to a range of fungi: ectomycorrhizal fungi, beneficial fungi such as *Trichoderma* and *Piriformospora indica*, soil-borne pathogens, and the two shoot pathogens *Botrytis cinerea* and *Cladosporium* sp. (Steinkellner et al. 2007). After the application of the compound, none of the tested fungi showed any obvious alterations in growth patterns or a branching reaction similar to that reported for AM fungi.

These data seem to indicate that strigolactones are specific signals for AM fungi and do not play a role in plant interactions with the other rhizospheric flora. However, there are some indications that strigolactones can act

on nonsymbiotic fungi. When applying fractions of maize root exudates containing hyphal branching factors (Buée et al. 2000) to the maize pathogen *Sporisorium reilianum*, the growth pattern of the pathogen was altered (Martinez et al. 2001). Moreover, it was recently reported that GR24 application to *S. reilianum* results in the rapid induction of genes involved in cell division and cell respiration and enhances cell respiration of *S. reilianum* and of *Ustilago maydis*, a close relative of *S. reilianum* (Sabbagh 2008). Thus, Sabbagh (2008) suggested "..... that strigolactones could have a wider biological implication in the rhizosphere than presently known.....".

Conclusion

Although there exists information about strigolactones and their activity on seed germination of parasitic weeds, scarce data are available on AM fungi and strigolactones. These compounds seem to play a role in the AM association, but it is not yet clear at which stages they are involved in the signaling between the plant and the AM fungi. There are clear indications that these compounds are involved in the signaling cascade at the presymbiotic stage (e.g., hyphal branching), before fungal contact with the plant root and there are indications for their implication at later stages when the symbiosis is already established (reduced levels of strigolactones in root exudates once plants are mycorrhizal). However, further studies are necessary to elucidate their exact function during each stage of the AM symbiosis. As these compounds are suggested to be ubiquitous in plants, it is tempting to speculate on a more general signaling role in soil-borne plant–microbe interactions, although data about such a role are still scarce.

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