REVIEW / SYNTHÈSE

Strigolactones: a cry for help in the rhizosphere

Juan A. López-Ráez, María J. Pozo, and José M. García-Garrido

Abstract: Arbuscular mycorrhizal (AM) symbiosis is a beneficial symbiosis established between fungi of the phylum Glomeromycota and over 80% of terrestrial plants, including most agricultural and horticultural crop species. AM symbiosis improves the nutritional status and fitness of the host plant and enables the plant to perform better under stressful conditions. As a result, when plants are growing under unfavourable conditions, they try to recruit their AM fungal partner in the soil. Symbiosis establishment requires a complex chemical dialogue between the two partners, in which signalling molecules such as the strigolactones play a key role. Under deficient nutrient conditions, the host plant increases the production of strigolactones to promote fungal development and symbiosis establishment (a "cry for help"). As a clue to host presence in the rhizosphere, strigolactones are also detected by other organisms, particularly root parasitic plants, and therefore promote a parasitic interaction. We review here the role of strigolactones and their interaction with other phytohormones during AM symbiosis, paying special attention to the implications of the chemical communication that takes place in the rhizosphere. Finally, we point out the potential use of this molecular dialogue as a target for developing new biological control strategies against deleterious organisms such as root parasitic weeds.

Key words: strigolactones, rhizosphere communication, arbuscular mycorrhizal fungi, phytohormones, root parasitic plants, biological control.

Résumé : Les mycorhizes arbusculaires constituent (MA) une symbiose bénéfique établie entre des champignons du phylum Glomeromycota et plus de 80 % des plantes terrestres, incluant la plupart des espèces de plantes agricoles et horticoles. La symbiose MA améliore le statut nutritif et l'adaptation de la plante hôte et lui permet de mieux performer sous des conditions stressantes. C'est pourquoi, lorsque la plante pousse sous des conditions peu favorables, elle tente de recruter le champignon MA partenaire dans le sol. La mise en place de la symbiose nécessite un dialogue chimique complexe entre les deux partenaires, au cours duquel des molécules de signalisation comme les strigolactones jouent un rôle déterminant. Sous des conditions de nutrition déficientes, la plante hôte augmente sa production de strigolactones pour stimuler le développement du champignon et la mise en place de la symbiose (« un appel à l'aide »). Comme indication de la présence de la plante dans la rhizosphère, d'autres organismes peuvent aussi détecter les strigolacctones, surtout les plantes parasites des racines et ainsi établir une interaction parasitaire accrue avec la plante. Les auteurs révisent le rôle des strigolactones et leurs interactions avec d'autres phytohormones au cours de la symbiose MA, en apportant une attention spéciale à l'implication de la communication chimique qui prévaut dans la rhizosphère. Finalement, ils soulignent le potentiel de l'utilisation de ce dialogue, comme cible pour développer de nouvelles stratégies de lutte biologique contre les organismes délétères comme les plantes parasites des racines.

Mots-clés : strigolactones, communication dans la rhizosphère, champignons mycorhiziens arbusculaires, phytohormones, plantes parasites des racines, lutte biologique.

[Traduit par la Rédaction]

Introduction

Plants are living organisms that continuously and reciprocally communicate with other organisms in their environment. This communication relies on chemicals as signalling molecules to perceive environmental changes. Plants use these chemical signals not only to defend themselves against enemies such as pathogens and herbivores aboveground and belowground, but also to establish mutually beneficial associations belowground with certain microorganisms such as bacteria and fungi (Morgan et al. 2005; Raaijmakers et al. 2009; López-Ráez et al. 2011*a*). Beneficial associations with soilborne partners in the rhizosphere are known to affect plant growth and development, maintain the nutrient cycling, provide resistance to diseases, improve tolerance to heavy metals, and interfere in the degradation of xenobiotics (Morgan et al. 2005).

Received 4 April 2011. Accepted 4 July 2011. Published at www.nrcresearchpress.com/cjb on xx August 2011.

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doi:10.1139/B11-046

One of the best studied and known beneficial plant–microorganism associations that takes place in the rhizosphere is that established with arbuscular mycorrhizal (AM) fungi (Barea et al. 2005; Parniske 2008; Smith and Read 2008; Bonfante and Genre 2010). AM symbiosis is a mutualistic association between fungi of the phylum Glomeromycota and the vast majority of land plants, including most agricultural and horticultural crop species, and it is the most widely distributed symbiosis in the world (Parniske 2008; Smith and Read 2008). This association dates back to about 460 million years ago, and the appearance of AM symbiosis has been postulated to be a key step in the evolution of terrestrial plants (Smith and Read 2008). AM fungi are obligate biotrophs and depend entirely on the plant to obtain carbon and complete their life cycle. They colonize the root cortex of the host plant and form specialized tree-like subcellular structures called arbuscules, which are involved in nutrient exchange between the two partners. Externally, AM symbiosis gives rise to the formation of hyphal networks that facilitate the acquisition of nutrients beyond the area of nutrient depletion, thereby assisting the plant in the acquisition of mineral nutrients (mainly phosphorous) and water (Parniske 2008). Therefore, AM symbiosis positively affects plant growth and enhances the recycling of nutrients (Morgan et al. 2005; Parniske 2008; Bonfante and Genre 2010). Moreover, the AM symbiosis has nonnutritional effects such as the improvement of soil quality by stabilizing soil aggregates and preventing erosion (Gianinazzi et al. 2010). AM symbiosis also provides tolerance against different types of abiotic stresses such as drought, salinity, or heavy metals and enhances the ability of the plant to cope with biotic stresses (Pozo and Azcón-Aguilar 2007; Parniske 2008). Altogether, these benefits highlight the potential use of AM fungi as biofertilizers and bioprotection agents for the sustainable management of agricultural ecosystems (Gianinazzi et al. 2010).

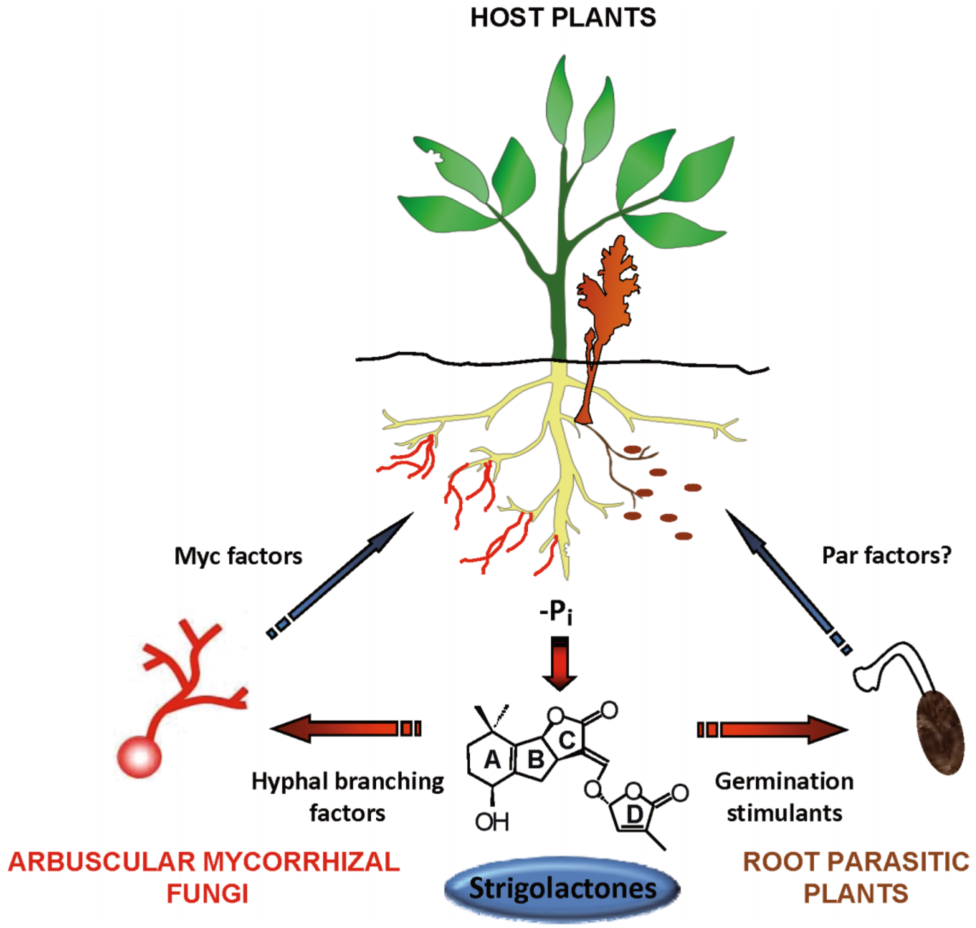
Chemical communication during early stages of AM symbiosis: the role of strigolactones

AM symbiosis establishment and functioning require a high degree of coordination between the two partners based on a finely regulated molecular dialogue (Paszkowski 2006; Hause et al. 2007; Requena et al. 2007). This AM fungus – plant host communication starts in the rhizosphere with host plant production and exudation of signalling molecules that are recognized by the AM fungus and stimulate hyphal growth. Among these signalling molecules, the strigolactones have arisen as essential cues (Akiyama et al. 2005; Bouwmeester et al. 2007) (Fig. 1), although other compounds such as the flavonoids and the hydroxy fatty acids have also been reported as hyphal growth stimulators (Scervino et al. 2005; Nagahashi and Douds 2011). Experimental evidence of strigolactone relevance in AM symbiosis has been provided by the clear reduction in mycorrhizal colonization of mutant plants with impaired strigolactone biosynthesis (Gómez-Roldán et al. 2008; Vogel et al. 2010). Interestingly, strigolactones were first described as germination stimulants of seeds of the root parasitic plants of the family Orobancheaceae (Cook et al. 1972; Bouwmeester et al. 2003) (Fig. 1), which are some of the most damaging agricultural pests worldwide (Gressel et al. 2004; Joel et al. 2007; Parker 2009) (see below). In addition to their role as signalling molecules in the rhizosphere, strigolactones have recently been described as a new class of plant hormones that regulates aboveground and belowground plant architecture (Gómez-Roldán et al. 2008; Umehara et al. 2008; Kapulnik et al. 2011; Ruyter-Spira et al. 2011). Strigolactones are derived from the carotenoids through sequential oxidative cleavage by carotenoid cleavage dioxygenases (CCD7 and CCD8), and thus belong to the apocarotenoid class, to which the phytohormone abscisic acid (ABA) also belongs (Matusova et al. 2005; López-Ráez et al. 2008; Rani et al. 2008). Strigolactones have been detected and analyzed in the root extracts and exudates of a wide range of monocotyledonous and dicotyledonous plant species, indicating their broad spectrum of action and importance in nature (Xie et al. 2010).

Strigolactone perception by the fungus, through an as yet uncharacterized receptor, engages its metabolism and induces the so-called presymbiotic stage. This stage is characterized by a profuse hyphal branching of the germinating spores, increasing the probability of contact with the root and that of establishing symbiosis (Akiyama et al. 2005; Besserer et al. 2006). In some cases, it has been shown that strigolactones can also stimulate spore germination in certain AM fungi (Besserer et al. 2006). In addition, it has been suggested that they might act as the chemoattractant that directs the growth of the AM hyphae to the roots (Sbrana and Giovannetti 2005). In agreement with their role as signalling molecules in the rhizosphere, strigolactones are short-lived owing to a labile ether bond that spontaneously hydrolyzes in watery environments (Akiyama and Hayashi 2006). Therefore, strigolactones are perceived only when a partner is nearby and the AM hyphal germ tube grows and ramifies intensively through the soil towards the host root (Bouwmeester et al. 2007). Despite the importance of strigolactones in the initiation of AM symbiosis, it is unknown whether they also play a role in subsequent steps of the symbiosis. Since these signalling molecules are classified as plant hormones, and they are ubiquitous in plants, it is tempting to speculate about their potential involvement in other plant–microorganism interactions in the rhizosphere. Indeed, it has been recently shown that strigolactones positively affect nodulation — another well-studied beneficial symbiosis that takes place in the rhizosphere between legumes and rhizobia — although not directly via an effect on the bacteria (Soto et al. 2010). Therefore, the functions of the strigolactones described until now represent the tip of the iceberg, as these signalling molecules might have wider biological roles in the rhizosphere than those presently known.

As in the nodulation process, a Myc factor analogous to the rhizobial Nod factor is thought to be produced by the metabolically active fungus and would be involved in fungus – host plant signalling (Fig. 1). This Myc factor was previously described as a diffusible molecule that induces molecular responses in the host root and is required for successful AM fungal colonization (Parniske 2008), although it is not clear yet whether the production of this Myc factor is induced by strigolactones. The chemical nature of the elusive Myc factor has remained unknown for a long time. However, very recently, Maillet and co-workers have shown that AM fungi produce and secrete a mixture of sulphated and

Fig. 1. Rhizosphere communication among plants, arbuscular mycorrhizal (AM) fungi, and root parasitic plants. Under phosphate-limiting conditions, plants produce and release strigolactones into the rhizosphere to communicate with AM fungi, promoting hyphal branching and the establishment of the mutualistic association. When a host root is present, AM fungi release the so-called Myc factors, which are recognized by the host plant. However, strigolactones can be abused by root parasitic plants of the family Orobancheaceae as an indicator of host presence, resulting in seed germination and establishment of a parasitic interaction. Similarly to the AM signal (Myc factor), it has been suggested that, in the presence of a host root, the germinating parasitic seeds would produce Par factors. Redrawn from Bouwmeester et al. (2007).



nonsulphated simple lipochitooligosaccharides that have structural similarities with rhizobial Nod factors (Maillet et al. 2011). Since AM symbiosis is more ancient than nodulation, the authors suggest that the Nod-factor-derived signalling pathway likely evolved from the AM association. Interestingly, Maillet and co-workers have shown that the Myc factors are not only symbiotic signals that stimulate AM establishment but also plant growth regulators affecting root development (Maillet et al. 2011).

Biological relevance of strigolactones in the AM symbiosis: phosphate availability

As mentioned above, one of the primary roles of AM fungi in the symbiotic relationship with plants is the supply of water and mineral nutrients, mainly phosphorous and nitrogen (Harrison 2005; Karandashov and Bucher 2005). In many areas of the world, the concentration or availability of these essential mineral nutrients in the soil is low, resulting in an important negative impact on plant growth and fitness. Phosphorous, which is taken up from the soil as phosphate, is one of the least available of all essential nutrients in soils because of its low mobility, resulting in phosphate depletion in the rhizosphere. Moreover, the majority of the applied phosphorous may be fixed in the soil because of its interaction with other ions, becoming unavailable to plants (Raghothama 2000).

In agreement with the important role of AM fungi in the acquisition of mineral nutrients, and especially phosphorous, it was observed that root exudates produced by plants grown under phosphate-limited conditions are more stimulatory to AM fungi than exudates produced under adequate phosphate nutrition (Nagahashi and Douds 2004). Later on, it was shown that phosphate deficiency has a significant stimulatory effect on the production and exudation of strigolactones by the plant roots (Yoneyama et al. 2007*a*, 2007*b*; López-Ráez et al. 2008). In addition, in tomato the increase in the strigolactones solanacol, orobanchol, and the didehydro-orobanchol isomers 1 and 2 under phosphate starvation correlated with an increased induction of hyphal branching of germinating spores of the AM fungus *Gigaspora margarita* (López-Ráez et al. 2008). More recently, Balzergue and co-workers showed that the regulation of AM symbiosis by phosphate involves not only early and local events, but also systemic signalling (Balzergue et al. 2011). The authors, using split-root systems, found a systemic downregulation of strigolactone production induced by high-phosphate conditions. Interestingly, AM colonization could not be restored after exogenous strigolactone application, suggesting the existence of additional signals during early AM fungus – host plant communication. Therefore, further research is required to elucidate the mechanisms by which the chemical signalling between host plants and AM fungi is regulated to further optimize this mutually beneficial association.

Role of other phytohormones in AM symbiosis establishment

AM symbiosis is regulated according to plant and fungal characters, and phytohormones are believed to orchestrate the modifications that take place in the host plant. Numerous studies support the hypothesis that a delicate balance between hormones and nutrient availability (phosphorous, carbon, and nitrogen) is probably important in the regulation of mycorrhizal formation and functioning (Ludwig-Müller 2000). Phytohormones regulate physiological processes of plants, participate in interactive plant–environment processes, and signal the interactions with microbes, including both pathogens and mutualistic symbionts (Weyers and Paterson 2001; Wolters and Jurgens 2009; Dodd et al. 2010). As plant hormones are usually multifunctional molecules and excellent plant growth regulators, it is not surprising that they participate in AM developmental processes involving mutual recognition and root morphological and physiological adjustments to support the fungus. Indeed, a combination of genetic, molecular, and cellular studies have shown that the functional symbiosis appears to occur at the end of a series of plant-controlled checkpoints, where different classes of phytohormones play an essential role (Paszkowski 2006; Hause et al. 2007; Requena et al. 2007; López-Ráez et al. 2010*b*) (Fig. 2). Although there remain large gaps in our knowledge of how plant hormones control and regulate the establishment and functioning of AM symbiosis, we can summarize their involvement as follows: (*i*) they redirect assimilates towards the root tissue colonized by the fungus and regulate mycorrhizal plant growth; (*ii*) they are involved in the formation of fungal structures and the establishment of functional symbiosis; and (*iii*) they regulate defence mechanisms and stress alleviation in mycorrhizal plants. For simplification, the plant hormones related to the AM symbiosis have been grouped into two major classes: isoprenoids and non-isoprenoids.

Isoprenoids

Especially relevant is the role of isoprenoid plant hormones in relation to functional mycorrhization. On the basis of our current findings as well as previous data, it is possible to speculate that, at least in relation to tomato, the interaction of three end products from different branches of the isoprenoid metabolism — strigolactones, ABA, and gibberellins (GAs) — is necessary to regulate AM formation and functioning (García-Garrido et al. 2010; López-Ráez et al. 2010*a*) (Fig. 2). Two plant apocarotenoids with hormonal capabilities, specifically ABA and strigolactones, play an essential role in relation to mycorrhizal roots. The importance of strigolactones in the normal development of mycorrhizal colonization has been described earlier, and for ABA, besides its stress protection function in mycorrhizal plants, recent research has indicated that it is even more important in the establishment of AM symbiosis. Analysis of AM fungus colonization in the ABA-deficient tomato mutant *sitiens* showed that ABA is necessary to complete the arbuscule formation process, enhance its functionality, and promote sustained colonization of the plant root (Herrera-Medina et al. 2007) (Fig. 2). In addition, comparative analysis of two ABA-deficient tomato mutants has highlighted both quantitative and qualitative differences in the pattern of AM fungus colonization (Martín-Rodríguez et al. 2010). On one hand, the highly limited fungal colonization of *sitiens* in terms of mycorrhizal intensity and arbuscule formation was closely correlated with its ABA biosynthesis deficiency. On the other hand, *notabilis* plants, with a less-pronounced ABA deficiency in the roots, showed lower mycorrhizal intensity only at the end of the mycorrhization process (Martín-Rodríguez et al. 2010). Recently, a lower ABA content in leaves of mycorrhizal compared with those of control plants was observed (Fiorilli et al. 2011). Interestingly, Fiorilli and co-workers suggested that this mycorrhizal-induced ABA reduction could be associated with a lower susceptibility to the pathogen *Botrytis cinerea*.

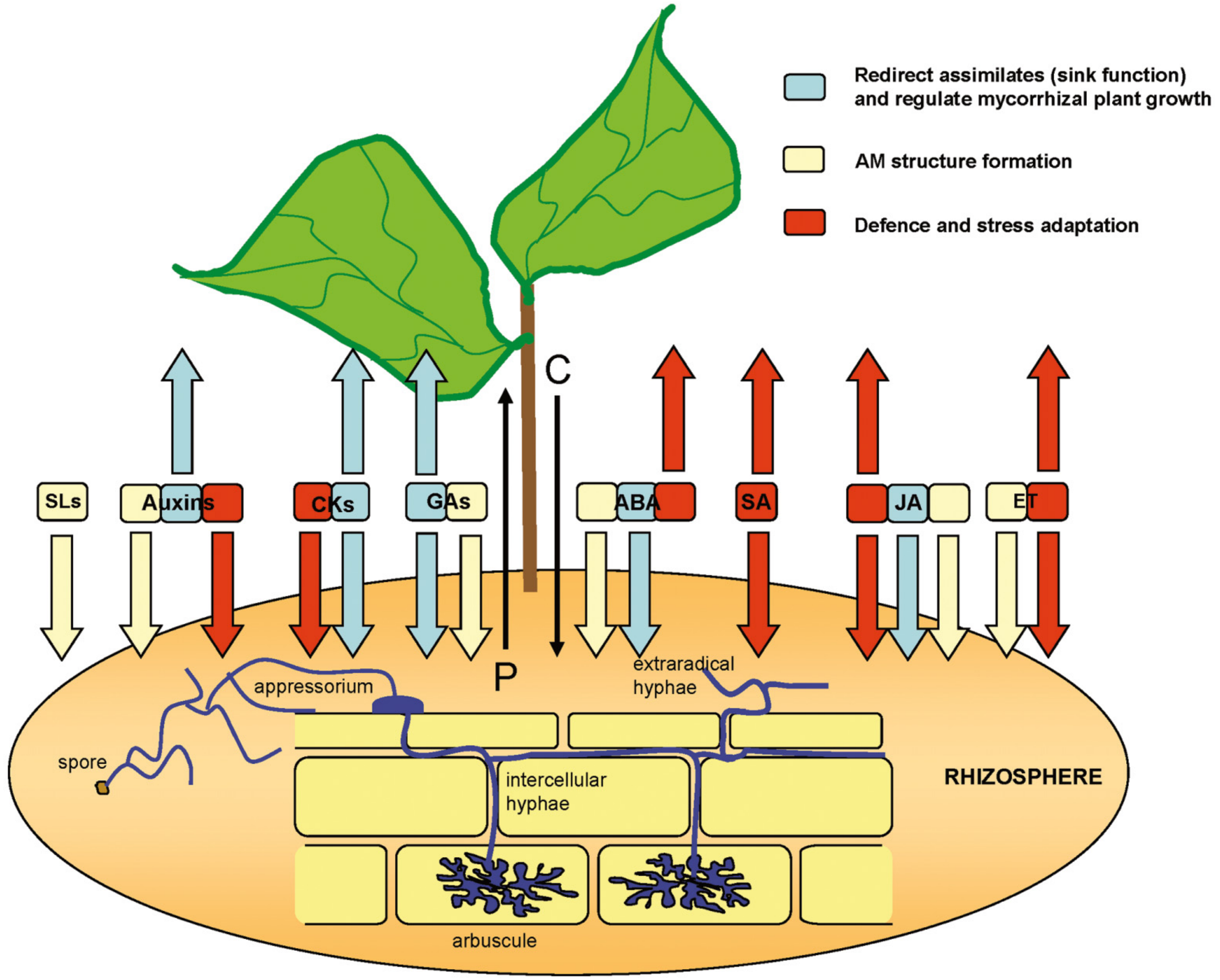
The third type of isoprenoid-derived plant hormone relevant to AM formation is GAs (Fig. 2). Little information exists on the role of these phytohormones during AM development. One study has reported the accumulation of GAs in mycorrhizal roots (Shaul-Keinan et al. 2002), and another has described a negative effect of gibberellic acid application on arbuscule formation (El Ghachtouli et al. 1996). More recently, a direct role for GAs in mycorrhization of tomato plants has been suggested, since at least four different genes associated with the metabolism of these plant hormones were upregulated in mycorrhizal plants (García-Garrido et al. 2010). Interestingly, in agreement with this observation, earlier studies reported the production of GA-like substances from AM fungi (Barea and Azcón-Aguilar 1982).

Non-isoprenoid phytohormones

Some non-isoprenoid plant hormones are also believed to play an important role in the AM symbiosis. Among them, jasmonic acid and its derivates (herein referred as jasmonates, JAs) have received special attention, although experimental data are highly controversial (Hause et al. 2007; Gutjahr and Paszkowski 2009; Hause and Schaarschmidt 2009; López-Ráez et al. 2010*b*). Indeed, increased JAs levels have been described in medicago and tomato plants upon mycorrhizal colonization (Hause et al. 2002; Meixner et al. 2005; López-Ráez et al. 2010*b*), while they remained unaltered in *Nicotiana attenuata* (Riedel et al. 2008). In addition, studies using reverse genetics approaches with plant mutants affected in JA biosynthesis or signalling have suggested positive and negative regulatory roles for JA on the symbiosis (Herrera-Medina et al. 2008; Isayenkov et al. 2005; Tejeda-Sartorius et al. 2008). In any case, it has been proposed that JAs affect mycorrhizal establishment by interfering in host cell wall expansion and arbuscule development (Isayenkov et al. 2005; Gutjahr and Paszkowski 2009).

Auxins and ethylene have also arisen as important hormones in the AM association. A role for auxin signalling

Fig. 2. Simplified model of the regulation of arbuscular mycorrhizal formation and functioning of plant hormones in belowground and aboveground development of the host plant. The role of plant hormones can be summarized as the follows: (*i*) they redirect assimilates towards the root tissues colonized by the fungus and regulate the growth of the mycorrhizal plant; (*ii*) they are involved in the formation of fungal structures and the establishment of a functional mycorrhiza; and (*iii*) they regulate defence mechanisms and stress alleviation in mycorrhizal plants. Interestingly, multiple functions can be envisaged for a particular hormonal group. Conversely, hormones that participate in similar functions interact to coordinate and regulate the different responses. ABA, abscisic acid; CKs, cytokinins; ET, ethylene; GAs, gibberellins; JA, jasmonic acid; SA, salicylic acid; SLs, strigolactones.



within the host root during the early stages of AM formation has been shown (Ludwig-Müller 2010; Hanlon and Coenen 2011) (Fig. 2). Since auxins are involved in regulating plant root architecture, they could be responsible for lateral root formation on the host plant, favoring AM colonization. However, upon colonization this hormone seems to play a less important role in fungal development, although its signalling would be required for mycorrhizal formation (Hanlon and Coenen 2011). As for JAs, responses of root auxin to AM colonization appear to vary with host species (Ludwig-Müller 2010). Regarding ethylene, some findings suggest that it might act as a negative regulator of mycorrhizal intensity (Fig. 2). Exogenous application of ethylene has been observed to restrict the spread of the AM fungus along the root's axis, although the movement of the fungus towards the inner cortex, where arbuscules are formed, did not appear to be impeded (Geil et al. 2001). Moreover, a high inhibition of mycorrhizal colonization was detected in the ethylene-affected tomato mutants *epinastic* (an ethylene overproducer) and *Never ripe* (with a low sensitivity to ethylene) (Zsögön et al. 2008). These results are in agreement with those reported by Mukherjee and Ane (2011), where early symbiotic gene expression and root development associated with the application of exudates from germinating spores of AM fungi were negatively regulated by ethylene in rice and medicago plants (Mukherjee and Ane 2011).

Hormonal cross-talk and its potential relevance in AM symbiosis

Since plant hormones are involved in a variety of processes and mostly function in combination, the hormone balance in both metabolism and signalling terms is critical for short- and long-term responses. This also applies to the isoprenoid-derived hormones regulating mycorrhization. Recently, a reduction in strigolactone production by several tomato ABA-deficient mutants, including the mutant *sitiens*, compared with wild-type plants has been reported (López-Ráez et al. 2010*a*). The results showed a correlation between ABA levels and strigolactone production and suggested that ABA plays a role in the regulation of strigolactone biosynthesis. This fact agrees with the reduced AM colonization observed in *sitiens* (Herrera-Medina et al. 2007; Martín-Rodríguez et al. 2010) and suggests that the effect of ABA in the AM symbiosis might be mediated through strigolactone production. Some degree of cross-talk between strigolactones and GA signalling can also be envisaged during AM symbiosis (Rochange 2010). This possibility is supported by the observation that, as for strigolactone-deficient mutants, GA-deficient mutants display a greatly enhanced shoot branching (Silverstone et al. 1997), while the tomato mutant *procera* DELLA, with a constitutive response to GA, exhibits reduced outgrowth of basal lateral buds (Bassel et al. 2008). Moreover, recent data suggest that there is a similarity between strigolactones and GAs at the hormone receptor level. In this sense, analysis of a putative strigolactone receptor in rice showed that this protein is a member of the alpha/beta-fold hydrolase superfamily (Arite et al. 2009), which shares similarities with proteins identified as receptors, such as the GA receptor GID1 (Hirano et al. 2008).

Hormonal cross-talk during AM establishment also applies to other hormones. Indeed, it is known that ABA deficiency induces ethylene production (Herrera-Medina et al. 2007), and it has been suggested that one of the mechanisms by which ABA regulates susceptibility to fungal infection might be the negative modulation of the ethylene pathway (Herrera-Medina et al. 2007; Martín-Rodríguez et al. 2010, 2011). With regards to the strigolactones, it was shown that auxin can locally induce the expression of the biosynthetic gene *CCD8* in the root tip, which would result in an increased production of these signalling molecules (Bainbridge et al. 2005). More recently, Rutyer-Spira and co-workers proposed that strigolactone's regulation of root architecture, which could facilitates AM interaction, depends on the auxin status of the plant and that strigolactones are able to modulate local auxin levels (Ruyter-Spira et al. 2011).

Summarizing, mycorrhizal symbiosis establishment implies a fine regulation of phytohormone levels in the host plant. Altered levels of plant hormones, particularly those related to defense and stress responses, may underlay the enhanced tolerance and resistance of AM plants to biotic and abiotic stresses. Thus, defence-related plant hormones likely have a dual function in AM plants. On one hand they act as signals for the maintenance of the AM symbiosis, and on the other they may contribute to stress tolerance of the host plant. In this regard, salicylic acid, JAs, cytokinins, and ethylene may regulate local and systemic defence responses activated during the symbiosis (Hause et al. 2007; Khaosaad et al. 2007; Pozo and Azcón-Aguilar 2007; López-Ráez et al. 2010*b*), while other hormones such as ABA may contribute to stress tolerance in mycorrhizal roots (Ruiz-Lozano et al. 2006).

Strigolactones are also germination stimulants of root parasitic plant seeds

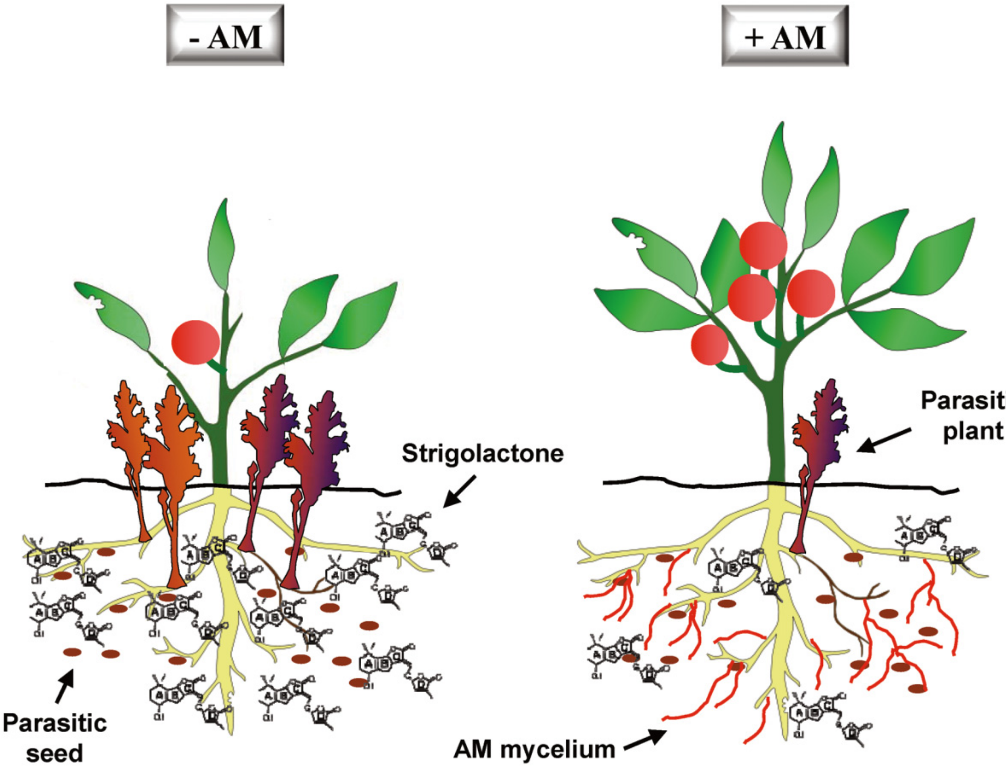
As mentioned above, despite the importance of the strigolactones in AM symbiosis establishment, they were first described as germination stimulants for the seeds of root parasitic plants (Cook et al. 1972; Bouwmeester et al. 2003). Therefore, strigolactones play a dual and important role in the rhizosphere as host detection signals for AM fungi and root parasitic plants (Bouwmeester et al. 2003; Xie et al. 2010) (Fig. 1). As in nodulation and mycorrhization, it has been hypothesized that a Par factor produced by the parasitic plant would be recognized by the host plant before contact (Vieira Dos Santos et al. 2003) (Fig. 1). Root parasitic weeds of the family Orobancheaceae — including *Striga*, *Orobanche*, and *Phelipanche* — affect important crops such as maize, rice, legumes, and tomato and are considered to cause the highest negative impact on food production (Gressel et al. 2004; Joel et al. 2007; Parker 2009). These obligate root parasites attach to the roots of many plant species worldwide and acquire nutrients and water from their host through a specialized organ called a haustorium, negatively affecting plant fitness and crop yield (Estabrook and Yoder 1998; Bouwmeester et al. 2003).

Although these plants parasitize different hosts in different parts of the world, their life cycles are very similar and start with seed germination in response to the strigolactones (Bouwmeester et al. 2003). After emergence from the soil, the parasitic plants will flower and produce enormous amounts of new ripe seeds that are scattered, increasing the seed bank (Bouwmeester et al. 2003; López-Ráez et al. 2009). These parasitic weeds are difficult to control because most of their life cycle occurs underground, making the diagnosis of infection difficult and possible usually only when irreversible damage has already been caused to the crop. To date, a wide number of approaches such as hand weeding, crop rotation, sanitation, fumigation, solarization, and improvement of soil fertility are being used to control root parasites without the desirable level of success (Joel et al. 2007; Rispail et al. 2007; Scholes and Press 2008), and the most efficient control method — fumigation — is environmentally hazardous. Therefore, new methods for a more effective control of these agricultural pests are required. Since the root parasites affect their host from the moment they attach and exert the greatest damage prior to emergence, the development of more effective control strategies should focus on the early steps in the host–parasite interaction, and particularly on the germination stage which is triggered by the strigolactones (López-Ráez et al. 2009).

Use of AM symbiosis as a control strategy against root parasitic plants

Under nutrient-deficient conditions (mainly phosphate), plants increase the production of strigolactones to attract AM fungi and establish a mutualistic relationship, but the parasitic weeds have evolved a mechanism by which they can abuse this "cry for help" plant signal to establish a negative interaction (Bouwmeester et al. 2007) (Fig. 1). Likely, the ability to develop AM symbiosis is of such great advantage to plants that strigolactones are secreted by plants despite the possibility of being abused by root parasitic plants. The fact that the strigolactones play a dual role in the rhizosphere as signalling molecules for both AM fungi and root parasitic plants (Fig. 1) opens the possibility of potential interactions

Fig. 3. Effect of arbuscular mycorrhizal (AM) symbiosis on control of root parasitic plants. In nutrient-poor soils, plants produce an increased amount of strigolactones. Strigolactones act as germination stimulants of root parasitic plant seeds, leading to greater infection (left). Upon mycorrhizal colonization, plants reduce the production of strigolactones, thus reducing parasitic plant infection and consequently diminishing the deleterious effect of these weeds on plant fitness and yield (right). Redrawn from López-Ráez et al. (2011*a*).



in both biosystems. Remarkably, AM fungal inoculation of maize and sorghum reduced *Striga hermonthica* infection in the field (Lendzemo et al. 2005). Later on, Lendzemo and co-workers proposed that this reduced infection was caused, at least partially, by a reduction in the production of strigolactones in the mycorrhizal plants (Lendzemo et al. 2007). Similarly, colonization of pea by AM fungi in the field induced less germination of seeds of *Orobanche* and *Phelipanche* species than that of noncolonized plants (Fernández-Aparicio et al. 2010). In agreement with these observations, we have recently shown that AM symbiosis in tomato also leads to a reduction in the germination stimulatory activity of tomato exudates for seeds of the root parasite *Phelipanche ramosa* and analytically demonstrated that this reduction was caused by a reduction in the production of strigolactones (López-Ráez et al. 2011*b*). It has been suggested that this strigolactone reduction induced by AM symbiosis might be involved in the regulation of mycorrhization as a plant strategy to avoid excessive mycorrhizal colonization, a phenomenon known as autoregulation (García-Garrido et al. 2009). However, the mechanism by which AM symbiosis reduces strigolactone production is so far unknown. Either a direct effect of mycorrhization on strigolactone biosynthesis or an indirect effect through the improvement of plant nutritional status by the symbiosis are two possible explanations. However, further research is needed to determine the contribution of each of these mechanisms to the phenomenon of autoregulation.

In summary, the results with maize, sorghum, pea, and tomato indicate that the reduction in strigolactone production and exudation induced by AM symbiosis is a conserved phenomenon across the plant kingdom. Since this beneficial association is established by most plant species worldwide, it can potentially be used as an environmentally friendly biocontrol strategy for economically important crops that suffer from these root parasites (Fig. 3). Moreover, these crops would take advantage of all the other well-known benefits of the AM symbiosis, such as a positive effect on plant fitness and tolerance and resistance of plants against biotic and abiotic stresses. However, since strigolactones are also AM hyphal branching factors and are involved in plant architecture, the consequences to the AM fungal community in the soil and possible unwanted side effects on plant architecture should be carefully evaluated before following this approach. Therefore, a better understanding of how strigolactone signalling is regulated and the possible specificity of different strigolactones seem crucial for further evaluating their importance in the host plant – parasitic plant and host plant – AM fungus interactions, to understand how one interaction can be favored over the other.

Acknowledgements

Our research is supported by grants PERG-02–2007–224751 from the Marie Curie program from the European Commission, AGL2009-07691 and AGL2008-00742/AGR from the National R&D Plan of the Ministerio de Ciencia e Innovación (MICINN). J.A.L.-R. was supported by a postdoctoral contract (JAE-Doc) from the Spanish Research Council (Consejo Superior de Investigaciones Científicas).

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