Communication in the Rhizosphere, a Target for Pest Management

Juan Antonio López-Ráez, Harro Bouwmeester, and Maria J. Pozo

Abstract The industrial agriculture has given rise to an excessive use and misuse of agrochemicals causing environmental pollution. Therefore, it is urgent to find alternatives that are more environmentally friendly than chemical fertilizers and pesticides for disease control. The key to achieve successful biological control strategies is the knowledge of the ecological interactions that occur belowground. The rhizosphere constitutes a very dynamic environment harbouring the plant roots and many organisms. Plants communicate and interact with those organisms through the production and release of a large variety of secondary metabolites into the rhizosphere. Thus, they use these metabolites to defend themselves against soil-borne pathogens, which can adversely affect plant growth and fitness, but also to establish mutualistic associations with beneficial soil microorganisms. However, despite the importance of these plant-organism interactions the mechanisms regulating them remain largely unknown.

We review here chemical communication that takes place in the rhizosphere between plants and other soil organisms, and the potential use of this molecular dialogue for developing new biological control strategies against deleterious organisms. We focus on the knowledge of the root parasitic weed germination stimulants – strigolactones – to develop more efficient control methods against this pest.

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Finally, we illustrate this with an exciting example: the use of the mutualistic arbuscular mycorrhizal symbiosis for controlling root parasitic weeds by reducing the production of strigolactones in the host plant.

Keywords Rhizosphere • Chemical communication • Signalling • Biological control • Strigolactones • Arbuscular mycorrhizal fungi • Root parasitic plants • Soil-borne pathogens

Abbreviations

AM	arbuscular mycorrhiza
AHL	N-acyl homoserine lactone
PGPF	plant growth promoting fungi
PGPR	plant growth promoting rhizobacteria
QS	Quorum sensing

1 Introduction

Plants are living organisms that continuous and reciprocally communicate with other organisms in their environment. However, unlike animals plants cannot speak, see, listen or run away, and therefore they largely rely on chemicals as signalling molecules to perceive environmental changes and survive. Thus, plants use flower colour and volatiles to attract pollinators, use chemicals to defend themselves against enemies such as pathogens and herbivores, but they also use signalling molecules to establish mutualistic beneficial associations with certain microorganisms such as bacteria and fungi (Fig. 1). Microorganisms can affect plant growth and development, change nutrients dynamics, susceptibility to disease, tolerance to heavy metals, and can help plants in the degradation of xenobiotics (Morgan et al. 2005). As a result, these plant-microorganism interactions have considerable potential for biotechnological exploitation. A nice example of this complex and precisely regulated signalling takes place underground, where plants use the roots to communicate and interact with other organisms in the so-called rhizosphere.

The term rhizosphere derives from the Greek words *rhiza*, which means root, and *sphere*, meaning field of influence (Morgan et al. 2005). The rhizosphere is the narrow soil zone surrounding plant roots that contains a wide range of organisms and is highly influenced by the roots, the root exudates and by local edaphic factors (Bais et al. 2006; Badri et al. 2009). Originally, the root system was thought only to provide anchorage and uptake of nutrients and water. However, it has been shown that roots are chemical factories that mediates numerous underground interactions

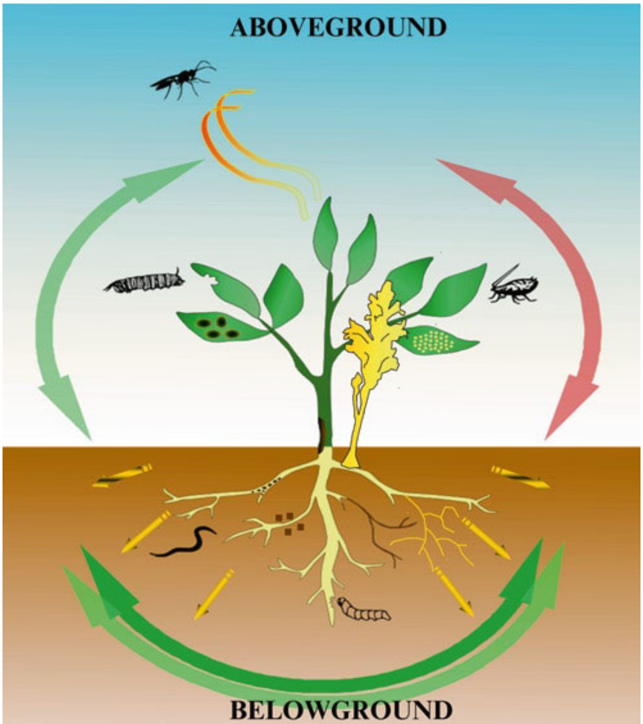

Fig. 1 Plant interactions with other organisms. Positive and negative interactions occurring aboveground and belowground in the rhizosphere. *Yellow arrows* indicate root exudates (Adapted from Pozo and Azcón-Aguilar 2007)

(Badri et al. 2009). Plants produce and exude through the roots a large variety of chemicals including sugars, amino acids, fatty acids, enzymes, plant growth regulators and secondary metabolites into the rhizosphere some of which are used to communicate with their environment (Siegler 1998; Bertin et al. 2003; Bais et al. 2006). Moreover, the release of root exudates together with decaying plant material provides carbon sources for the heterotrophic soil biota. On the other hand, microbial activity in the rhizosphere affects rooting patterns and the supply of available nutrients to plants, thereby modifying the quantity and quality of root exudates (Barea et al. 2005). Of special interest in this rhizosphere communication are the so-called secondary metabolites, which received this name because of their presumed secondary importance in plant growth and survival (Siegler 1998). These metabolites include compounds from different biosynthetic origins and have been shown to be of ecological significance because they are important signals in several mutualistic and pathogenic plant-organism interactions (Estabrook and Yoder 1998; Siegler 1998; Bertin et al. 2003; Bais et al. 2006).

2 Interactions in the Rhizosphere

In the rhizosphere some of the most complex chemical, physical and biological interactions between plant roots and other organisms occur influencing plant fitness. Among these relationships we can find root-root, root-microbe and root-insect interactions. Many of these interactions have a neutral effect on the plant. However, the rhizosphere is also a playground for beneficial microorganisms establishing mutualistic associations with plants, and a battlefield for soil-borne pathogens which establish parasitic interactions (Raaijmakers et al. 2009).

2.1 Parasitic Interactions

As mentioned above, the rhizosphere is not only the playground for mutualistic associations, but also a battlefield where parasitic interactions between plants and soil-borne pathogens take place (Raaijmakers et al. 2009). In most agricultural ecosystems, these negative interactions are economically important as they cause important limitations in the production of marketable yield. It has long been understood that the development of disease symptoms is not solely determined by the pathogen responsible, but is also dependent on the complex interrelationship between host, pathogen and prevailing environmental conditions. Negative interactions with plant roots include pathogenesis by bacteria, true fungi or oomycetes, invertebrate herbivory and parasitism between plants (Agrios 2005; Bais et al. 2006). Among them, fungi and oomycetes, nematodes and parasitic plants are major players in the rhizosphere exerting a serious threat to world agricultural production. Comparatively, fewer bacteria are considered as soil-borne plant pathogens, with some exceptions such as *Ralstonia solanacearum* (causing bacterial wilt of tomato), the enteric phytopathogen *Erwinia carotovora*, responsible of the bacterial soft rot, and *Agrobacterium tumefaciens*, the causal agent of crown gall disease (Hirsch et al. 2003; Genin and Boucher 2004; Badri et al. 2009).

2.1.1 Fungi and Oomycetes

Soil-borne fungal plant pathogens are important determinants in the dynamics of plant populations in natural environments and in agriculture. Fungi and oomycetes are the most important soil-borne microbial plant pathogens, causing economically important losses. They can cause complete destruction of plants and even the total loss of yield (Otten and Gilligan 2006). More than 8,000 species of fungi are known to cause diseases of plants, and most plants are susceptible to several fungal pathogens. The majority of soil-borne fungi are necrotrophic, implying that they do not require a living cell to obtain nutrients. They normally use enzymes and toxins to kill host tissue before hyphal penetration and infection. The most harmful root pathogenic fungi include the genera *Fusarium* spp, *Verticillium* spp and *Rhizoctonia solani*, which affect crops such as barley, wheat, maize, potato and tomato all over the world (Priest and Campbell 2003; Garcia et al. 2006).

The oomycetes include a unique group of biotrophic and hemibiotrophic plant pathogens that gain their nutrients from living cells, and are considered as non-true fungi. Indeed, although they are physiologically and morphologically similar to fungi they belong to different phylogenetical groups. The oomycetes are phylogenetically more closely related to brown algae than to fungi and, in contrast to fungi, they contain cellulose in their cell wall instead of chitin (Raaijmakers et al. 2009). However, despite being only distantly related to fungi, the oomycetes have developed very similar infection strategies. These pathogens establish intimate relations with their hosts by forming an organ called haustorium, which is used to obtain nutrients from the plant, redirecting host metabolism and suppressing host defences. The oomycetes include some of the most destructive plant pathogens worldwide, particularly in the genera *Phytophthora* and *Phytium*, that affect important crops such as potato, tomato, lettuce and soybean (Raaijmakers et al. 2009).

2.1.2 Nematodes

Nematodes are small and complex worm-like eukaryotic invertebrates that rank among the most numerous animals on the planet (Perry and Moens 2006). Most nematodes in soil are free-living and consume bacteria, fungi and other nematodes, but some can also parasitize plant roots being important crop pests in agricultural ecosystems. Some feed on the outside of the root (ectoparasites), some penetrate and move inside the root (endoparasites), and some set up a feeding site in the interior of the root and remain there for reproduction (sedentary endoparasites). Upon infection, nematodes cause important changes in root cells in order to complete their life cycle. Although the parasitism is rarely fatal for the infected plant, there are substantial consequences of the interaction such as stunted growth, chlorosis and poor yields. The most economically important groups of nematodes are the sedentary endoparasites, which include the genera *Meloidogyne* (root-knot nematodes) and *Heterodera* and *Globodera* (cyst nematodes). They are particularly important in tropical and subtropical regions (Bird and Kaloshian 2003; Williamson and Gleason 2003).

Root-knot nematodes are obligate biotrophic pathogens found in all temperate and tropical areas that have evolved strategies for infesting thousands of plant species such as cereals, tomato, potato and tobacco (Caillaud et al. 2008). These root pathogens must locate and penetrate a root, migrate into the vascular cylinder and establish a permanent feeding site, known as giant cells. Unlike root-knot nematodes, cyst nematodes are only able to infect a few plant species, principally soybean and potato, and are more destructive as they migrate and travel intracellularly through the root (Fuller et al. 2008). In both cases, these events are accompanied by extensive signalling between the nematode and the host.

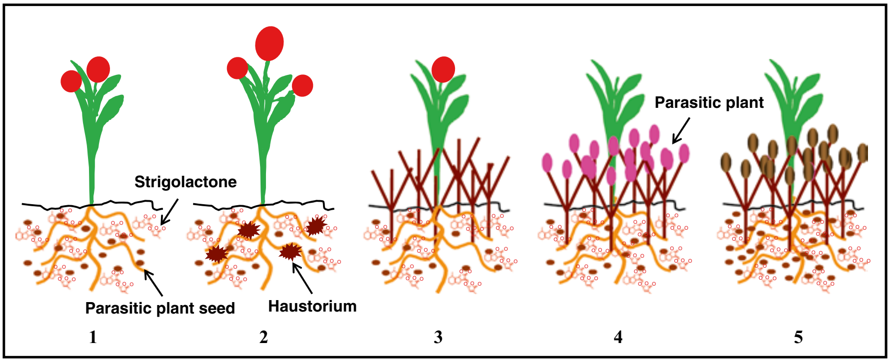

Fig. 2 Life cycle of root parasitic plants. (**a**) Seeds are buried in the soil and perceive the germination stimulants exuded by the roots of the host plant, strigolactones, and germinate. **(b)** The germinated seeds form a haustorium by which they attach to the host root, establishing a xylem-xylem connection. (**c**) The parasitic plant develops, and the shoots emerge from the soil. There is areduction of host growth. (**d**) Parasitic plant flowering and crop yield reduction. (**e**) Production of mature seeds that end up in a new generation of seeds in the soil (Redrawn from Sun et al. 2007)

2.1.3 Root Parasitic Plants

Root parasitic plants of the family Orobancheaceae, including the *Striga*, *Orobanche* and *Phelipanche* genera are some of the most damaging agricultural pests, causing large crop losses. These obligate root parasites attach to the roots of many plant species and acquire nutrients and water from their host through a specialized organ called haustorium (Estabrook and Yoder 1998; Bouwmeester et al. 2003). *Striga* is a hemiparasite, which means that it obtains nutrients from its host but it can also perform its own photosynthesis. It infects important crops such as maize, sorghum, pearl millet, finger millet and upland rice, causing devastating losses in cereal yields in Africa (Gressel et al. 2004). On the other hand, the holoparasitic (lacking chlorophyll and being completely dependent on their host) *Orobanche* and *Phelipanche* spp. affect important agricultural crops in more temperate climates such as southern Europe, Central Asia and the Mediterranean area parasitizing legumes, tobacco, crucifers, sunflower and tomato (Joel et al. 2007).

Although root parasitic plants parasitize different hosts in different parts of the world, their lifecycles are very similar and involve germination in response to a root host stimulus, radicle growth towards the host root, and attachment and penetration through the haustorium (Fig. 2). Upon vascular connection, the parasitic plant obtains nutrients and water from the host plant, negatively affecting plant fitness and crop yield. After emergence from the soil, parasitic plants will flower and produce new ripe seeds that are shattered increasing the seed bank (Fig. 2) (Bouwmeester et al. 2003; López-Ráez et al. 2009). Parasitic weeds are difficult to control because most of their life cycle occurs underground and therefore new control strategies that focus on the initial steps in the host-parasite interaction are required (López-Ráez et al. 2009).

2.2 Mutualistic Beneficial Associations

The rhizosphere generally helps the plant by maintaining the recycling of nutrients, providing resistance to diseases and to improve tolerance to toxic compounds. When plants lack essential mineral elements, such as phosphorous or nitrogen, symbiotic relationships can be beneficial and promote plant growth. Thus, plants biologically interact with other organisms to establish mutualistic associations which rely on a mutual fitness benefit. Mutualism is very ancient, indeed is thought to have driven the evolution of much of the biological diversity present today (Thompson 2005). In addition, mutualism plays a key role in ecology being very important for the correct functioning of the terrestrial ecosystem. Microorganisms that positively affect plant growth and health include the plant growth-promoting rhizobacteria (PGPR) and plant growth-promoting fungi (PGPF), the nitrogen-fixing *Rhizobium* bacteria (rhizobia), and the mycorrhizal fungi (mycorrhiza). The PGPR are non-symbiotic beneficial rhizosphere bacteria that are known to participate in many important ecosystem processes, such as nitrogen fixation, nutrient cycling, seedling growth, phytohormone production, and biological control of plant pathogens (Barea et al. 2005; Raaijmakers et al. 2009). The most commonly genera described as including PGPR are *Pseudomonas* and *Bacillus*. The PGPF include rhizospheric non-symbiotic beneficial fungi from the Deuteromycetes, e.g. *Trichoderma*, *Gliocladium* and non-pathogenic *Fusarium oxysporum* (Raaijmakers et al. 2009). These ubiquitous soil fungi are effective in controlling a broad range of phytopathogenic fungi by competition, antibiosis and mycoparasitism (Raaijmakers et al. 2009).

Other beneficial microorganisms, the endophytes, establish mutualistic symbiosis with plants by colonizing the root tissues and promote plant growth and plant protection (Barea et al. 2005). Although new endophytic microbes which colonize roots and promote plant growth are being found such as the fungus *Piriformospora indica* (Varma et al. 1999), the best studied examples of rhizosphere mutualism are those established with rhizobia bacteria and mycorrhizal fungi.

2.2.1 Rhizobia

Rhizobia are free-living soil bacteria which colonize plant roots (endosymbionts) establishing a mutualistic relationship with most of the plant legume species worldwide (Sprent 2009). The two partners cooperate in a nitrogen-fixing symbiosis of major ecological importance because in many environments nitrogen limits plant growth (Masson-Boivin et al. 2009). Legume-rhizobia symbiosis is a classic example of mutualism, where rhizobia supply ammonia (NH_4^+) or amino acids to the plant and in return receive organic acids (principally malate and succinate) as a carbon and energy source, proteins and sufficient oxygen to facilitate the fixation process (Fig. 3a). Fixed nitrogen is a limiting nutrient in most environments, with the main reserve of nitrogen in the biosphere being the molecular nitrogen in the atmosphere. Molecular nitrogen cannot be directly assimilated by plants, but it

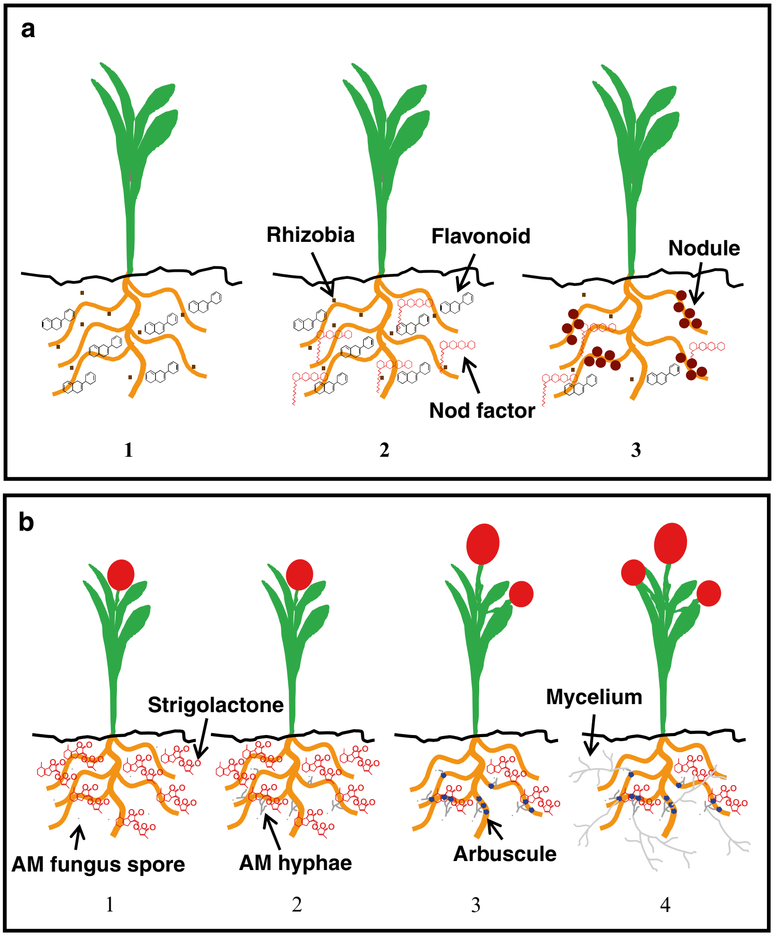

Fig. 3 Scheme of signalling and establishment of plant-microorganism mutualistic associations in the rhizosphere. (**a**) Molecular signalling and nodulation process during rhizobia-legume association; *1* Production of flavonoids by the host plant under low nitrogen conditions. *2* Flavonoids are perceived by the bacteria and induce the production of the bacterial Nod factors. 3 Nod factors are recognized by the host plant and initiate the symbiotic program for nodulation. (**b**) Molecular signalling and mycorrhizal establishment between plants and arbuscular mycorrhizal (AM) fungi; *1* Under phosphate deficient conditions plants release the signalling molecules strigolactones. *2* Strigolactones are perceived by germinating spores of AM fungi and induce hyphal branching and growth towards the host root. *3* AM hyphae produce Myc factors which are perceived by the host plant initiating the symbiotic program. *4* AM fungus colonizes the host root forming arbuscules and develops an external mycelia network. AM symbiosis and nodulation increase plant fitness and crop production

becomes available through the biological nitrogen fixation process that only some prokaryotic cells (diazotrophs), including rhizobia, have developed (Masson-Boivin et al. 2009).

In rhizobial plants, nitrogen fixation takes place in special organs known as nodules. On the roots of host plants, principally in the root hairs, rhizobia colonize intracellularly by triggering the formation of an infection thread structure that elongates, ramifies and penetrates inside the emerging nodule. Then, they become internalized in plant cells via an endocytosis-like process. Once reached the central tissue, known as symbiosome, release the rhizobia in these cells where they multiply and differentiate morphologically into bacteroids. Within the nodules the host plant provides the bacteria with the carbohydrates they need. In return, the bacteroids by the action of the enzyme nitrogenase fix the atmospheric nitrogen from the atmosphere into a plant usable form (NH_4^+). Then, the NH_4^+ is converted into amides or ureides which are translocated to the plant xylem (Masson-Boivin et al. 2009).

2.2.2 Mycorrhiza

Fungi are eukaryotic, filamentous, multicellular and heterotrophic organisms that produce a network of hyphae called mycelium which absorbs nutrients and water from the surrounding substrate. Mycorrhiza is a symbiotic, generally mutualistic symbiosis established between certain soil fungi and the roots of most vascular plants, including agricultural and horticultural crop species (Smith et al. 2006; Smith and Read 2008). Mycorrhizas are commonly grouped into two categories based on their colonization style. They are considered either ectomycorrhiza if they colonize host plant roots extracellularly or endomycorrhiza, if they colonize intracellularly. Ectomycorrhiza are typically formed between the roots of around 10% of plant families, mostly woody plants, and fungi belonging to the Basidiomycota, Ascomycota, and Zygomycota (Bonfante and Genre 2010). Ectomycorrhizas consist of a hyphal sheath, or mantle covering the root tip and a hartig net of hyphae surrounding the plant cells within the root cortex. Endomycorrhiza include the arbuscular mycorrhizal (AM) symbiosis, the ericoid mycorrhiza established with members of the family Ericaceae and the orchid mycorrhiza, a symbiotic relationship between fungi and the roots of plants of the family Orchidaceae (Smith and Read 2008).

Among them, the AM symbiosis is the most common form of mycorrhizal symbiosis and consists of an association established between certain soil fungi of the phylum Glomeromycota – which is widely distributed throughout the world – and over 80% of terrestrial plants, including most agricultural and horticultural crop species (Smith et al. 2006; Parniske 2008). This association is considered to be older than 400 million years and it has been postulated to be a key step in the evolution of terrestrial plants (Smith et al. 2006). AM fungi are obligate biotrophs and therefore they depend entirely on the plant to complete their life cycle (Fig. 3b). They colonize the root cortex forming specialized and tree-like subcellular structures called arbuscules for nutrient exchange (Parniske 2008). Through the symbiosis, the fungus obtains carbohydrates from the host plant for which, in return, the fungus assists the plant in the acquisition of mineral nutrients (mainly phosphorous) and water, hence improving plant fitness (Fig. 3b). AM symbiosis gives rise to the formation of mycorrhizal networks that offer a number of advantages for the acquisition of nutrients such as fungal hyphae extension beyond the area of nutrient depletion and increase of the surface area for the absorption of nutrients. Moreover, some mycorrhizal fungi can access forms of nitrogen and phosphorous that are not available to non-mycorrhizal plants, for example when bound in organic forms (Morgan et al. 2005). Thus, AM symbiosis contributes to global phosphate and carbon cycling and influences primary productivity in terrestrial ecosystems (Fitter 2005). Besides improving the nutritional status, the symbiosis enables the plant to perform better under stressful conditions (Pozo and Azcón-Aguilar 2007; Parniske 2008). Therefore, AM symbiosis plays a crucial role in agriculture and natural ecosystems.

In summary, the rhizosphere is an environment influenced by the plant root exudates where both pathogenic and beneficial interactions between plant and other organisms constitute a major influential force on plant growth and fitness, soil quality and ecosystem dynamics.

3 Molecular Dialogue in the Rhizosphere

All the different interactions reported above are based on molecular communication occurring belowground. Plants produce and release enormous amounts of chemicals into the rhizosphere through their roots in order to communicate and interact with their environment. Root exudates can be divided into two classes of compounds: high-molecular weight such as polysaccharides and proteins, and low-molecular weight compounds including amino acids, organic acids, sugars, phenolics, and other secondary metabolites (Bais et al. 2006). Although the functions of most of the compounds present in root exudates have not been determined so far, it has been determined that several of them are essential to establish plant interactions with other organisms in the rhizosphere. Equally, chemical signals secreted by the rhizospheric organisms are also involved in early steps of host recognition and colonization, and necessary for the establishment of the association. These signalling molecules are important in both negative and positive interactions (Bais et al. 2006).

3.1 Communication Between Plants and Parasites

In plant-plant interactions, plants secrete phytotoxins such as the flavonoids cathechins and benzoflavones, and sorgoleone that reduce the establishment, growth, or survival of susceptible plant neighbours, a phenomenon known as allelopathy, from the Greek words *allele* (mutual) and *pathy* (harm or suffering), to avoid competition with other plant species (Weir et al. 2004). Plants also produce germination stimulants of seeds the root parasitic plants of the genera Orobancheaceae – strigolactones – which are essential for the establishment of a negative association (Bouwmeester et al. 2003) (see Sect. 6).

In addition to plant-plant interactions, plants produce and exudate antimicrobial secondary metabolites such as indole, terpenoids, phenylpropanoids including the flavonoids (e.g. rosmarinic acid) which show potent antimicrobial activity against an array of soil-borne pathogens (Bais et al. 2002). Antimicrobial compounds can be classified in two different classes: phytoanticipins, which occur constitutively in healthy plants acting as chemical barriers to fungal pathogens, and phytoalexins, including terpenoids, glycosteroids and alkaloids, that are induced in response to pathogen attack but not normally present in healthy plants (Badri et al. 2009). It has been described that phenylpropanoid levels, a diverse family of organic compounds derived from the amino acid phenylalanine which provide protection against herbivores and pathogens, were significantly higher in roots that were challenged by non-host bacterial pathogens *Pseudomonas syringae* strains compared to host bacterial strains (Bais et al. 2006). Bacterial pathogens able to infect roots and cause disease were resistant to these compounds, suggesting an important role of phenylpropanoids in defense against non-host pathogens (Bais et al. 2006).

Besides functioning as antimicrobial compounds, some secondary metabolites can act as chemoattractants for certain pathogens. For example, it has been shown that before infection establishment, zoospores of the pathogen oomycete *Phytophthora sojae* are chemically attracted by the isoflavones daidzein and genistein secreted by soybean roots (Hirsch et al. 2003). In a large number of pathogenic bacteria, initiation of the production and secretion of virulence factors is controlled by a phenomenon known as quorum-sensing (QS). QS is a cell-cell communication and density-dependent regulatory mechanism which is mainly induced by the small molecules N-acyl homoserine lactones (AHLs) (Bais et al. 2006). The rhizosphere contains a higher proportion of AHL-producing bacteria than bulk soil, suggesting that they play a role in colonization (Bais et al. 2006). It has been also suggested that plants could be using root-exuded compounds in the rhizosphere to take advantage of this bacterial communication system and influence colonizing communities.

On the other hand, the association between plants and nematodes is also subjected to an extensive signalling between the nematode and its host, although the knowledge of the initial signalling molecules is scarce. It was shown that hatching of juveniles of the cyst nematode *Globobera* is controlled by solanoeclepin A, a molecule secreted by the roots of some Solanaceae species such as potato and tomato (Schenk et al. 1999). More recently, it has been reported that Medicago roots released a volatile (dimethyl sulphide) that attract nematodes (Horiuchi et al. 2005). Reciprocally, nematodes secrete cytokinins that play a role in cell cycle activation and in establishing the feeding in the host root.

3.2 Chemical Signalling Between Plants and Mutualists

A functional mutualistic relationship also implies and requires a signal exchange between both partners that leads to mutual recognition and development of symbiotic structures (Siegler 1998). Moreover, this molecular dialogue must be precisely regulated in order to avoid opportunities for malevolent organisms (Hirsch et al. 2003; Bouwmeester et al. 2007). An important number of plant-derived signalling molecules destined to the establishment of beneficial associations with soil microbe partners belong to the class of the secondary metabolites (Siegler 1998; Steinkellner et al. 2007). We will go into detail on a number of them, the flavonoids and the strigolactones, which are key signalling molecules in the interaction rhizobia-legume and in AM symbiosis, respectively.

3.2.1 Communication in Nodulation

Rhizobia-legume symbiosis is an ecologically important mutualistic association because of its implication in nitrogen fixation. The establishment of this symbiosis requires a high degree of coordination between the two partners, which is based on a finely regulated molecular dialogue that orchestrates the complex symbiotic program (Garg and Geetanjali 2007; Badri et al. 2009) (Fig 3a). The chemical communication between the plant and the bacteria starts, before there is any contact between the partners, with the production of flavonoids and isoflavonoids by the host plant (Badri et al. 2009; Faure et al. 2009). More than 4,000 different flavonoids have been identified in vascular plants, but just a small subset of them are involved in this mutualistic interaction (Bais et al. 2006). Host legume-derived flavonoids and related compounds act as chemo attractants for rhizobial bacteria and as specific inducers of rhizobial nodulation genes (*nod* genes), that encode the biosynthetic machinery for a bacterial signal – the lipochitooligosaccharides – that are released into the rhizosphere (Fig. 3a) (Perret et al. 2000; Reddy et al. 2007). These bacterial-derived signals are known as Nod factors, and are specific for different rhizobial strains. In turn, Nod factors are perceived by the host plant which leads to the induction of root hair deformation and several cellular responses such as ion fluxes. This mutual recognition precedes the intracellular infection by the bacteria through the deformed root hair. The infection triggers cell division in the cortex of the root where a new organ, termed nodule, appears as a result of successive processes (Fig. 3a). Finally, in the nodule nitrogen fixation takes place by the bacteria (see Sect. 2.2.1). Interestingly, this signal-detection machinery for interaction with beneficial rhizobia employs common components that are also implicated in the detrimental association with root-knot nematodes (Weerasinghe et al. 2005).

3.2.2 Signalling During Arbuscular Mycorrhizal Symbiosis

In addition to their involvement in the rhizobia-legume symbiosis, flavonoids play a role also in the AM symbiosis, which is also of ecological importance because it contributes to phosphate and carbon cycling. Flavonoids act as stimulants of AM fungi hyphal growth, differentiation and root colonization (Steinkellner et al. 2007). Besides flavonoids, the strigolactones, a recently described new class of plant hormones regulating plant architecture (Gomez-Roldan et al. 2008; Umehara et al. 2008; Koltai et al. 2010; Ruyter-Spira et al. 2011), have been shown to be crucial for a successful root colonization by the AM fungi (Akiyama et al. 2005). Interestingly, strigolactones are present in the root exudates of a wide range of plants and trigger a response only in AM fungi, not in other beneficial fungal species such as *Trichoderma* and *Piriformospora* (Steinkellner et al. 2007).

AM fungi depend entirely on their plant host to complete their life cycle (Fig. 3b). As for the rhizobia-legume association, AM symbiosis establishment and functioning also require a high degree of coordination between the two partners (Paszkowski 2006; Hause et al. 2007; Requena et al. 2007). The AM fungi-plant host molecular dialogue starts in the rhizosphere with the production of strigolactones by the host plant that induce hyphal branching in germinating spores of AM fungi (Akiyama et al. 2005; Besserer et al. 2006; Parniske 2008). Spores of AM fungi can germinate spontaneously and undergo an initial asymbiotic stage of hyphal germ tube growth, which is limited by the amount of carbon storage in the spore. If a partner is nearby, the hyphal germ tube grows and ramifies intensively through the soil towards the host root (Bouwmeester et al. 2007). It has been suggested that these signalling molecules, later known as strigolactones, may also act as the chemoattractant that directs the growth of the AM hyphae to the roots (Sbrana and Giovannetti 2005). Once the host-derived strigolactones are perceived by the fungus, it engages its catabolic metabolism which results in hyphal branching that will increase the probability to contact the root and establish symbiosis. Similarly to the nodulation process, it has been proposed that a Myc factor analogous to the rhizobial Nod factor and produced by the metabolic active fungus, induces molecular responses in the host root required for a successful AM fungal colonization (Fig. 3b) (Kosuta et al. 2003; Bucher et al. 2009). The chemical nature of the elusive Myc factor, has remained unknown for a long time. However, it has been recently shown to have structural similarities with rhizobial Nod factors (Maillet et al. 2011).

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 strigolactones are considered plant hormones and are ubiquitous in plants, it is tempting to speculate about their involvement in other plant-microorganism interactions in the rhizosphere. Indeed, it has been recently shown that strigolactones positively affect nodulation, although their effect was not due to an effect on the bacteria (Soto et al. 2010). Probably, this just represent the tip of the iceberg of biological roles for the strigolactones, showing the biological and ecological importance of these signalling compounds.

Thus, plants form associations – either beneficial or detrimental – with other organisms in the rhizosphere. Interestingly, most of these interactions are facilitated by a molecular dialogue between the host and the symbionts through chemical cues, which are crucial for the establishment of these belowground associations. However, although some of these signalling molecules have been identified there are still many other unknown factors involved.

4 Regulation of Chemical Communication in the Arbuscular Mycorrhizal Symbiosis

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; Yoneyama et al. 2007). In many areas of the world the concentration or availability of these essential mineral nutrients in the soil is low, which results 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 phosphorus may be fixed in the soil due to the interaction with other ions and hence be unavailable to plants (Raghothama 2000). Similarly, nitrogen availability may be limited due to its loss through volatilization and leaching (Delgado 2002).

In agreement with the important role of AM fungi in the acquisition of mineral nutrients, 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). Moreover, it was shown that phosphate and nitrogen deficiency have a significant stimulatory effect on the production and exudation of strigolactones by plants (Yoneyama et al. 2007; López-Ráez et al. 2008a). Yoneyama and co-workers have suggested that the response of strigolactones production and exudation to nutrient availability varies between groups of plant species (Yoneyama et al. 2007). Thus, legumes, that can establish symbiosis with rhizobia and acquire nitrogen from root nodules, only respond to phosphate deficiency with enhanced strigolactone production to attract AM fungi, whereas in non-leguminous plant species such as tomato both phosphate and nitrogen starvation enhance the production of strigolactones. The strigolactones have been detected in the root exudates of a wide range of plant species including mono- and dicotyledonous, indicating their broad spectrum of action and importance in nature (Bouwmeester et al. 2007; Yoneyama et al. 2008).

Future research is required to elucidate the mechanisms by which the chemical signalling between plants and AM fungi is regulated to further optimize this beneficial mutualistic association.

5 Strigolactones: Ecological Significance in the Rhizosphere

Strigolactones have been recognized as a new class of plant hormones that inhibits shoot branching and hence controls above ground architecture (Gomez-Roldan et al. 2008; Umehara et al. 2008). More recently, it has been suggested that they also affect root growth and root hair elongation (Koltai et al. 2010; Ruyter-Spira et al. 2011), which shows they are even more important components in the regulation of plant architecture than already postulated. Long before the discovery of their function as plant hormones, the strigolactones were described as germination stimulants for the seeds of root parasitic plants *Striga*, *Orobanche* and *Phelipanche* spp (Cook et al. 1972; Bouwmeester et al. 2003) (see Sect. 2.1.3). They are produced and exuded into the rhizosphere by plants in very low amounts, can stimulate the germination of these parasitic plants in nano- and pico-molar concentrations, and are instable in a watery environment and in alkaline soils (Bouwmeester et al. 2007; Yoneyama et al. 2009; Zwanenburg et al. 2009). Strigolactones are derived from the carotenoids (Matusova et al. 2005; López-Ráez et al. 2008a) and all the strigolactones characterized so far are remarkably similar, showing a similar chemical structure (Fig. 4) (Rani et al. 2008; Yoneyama et al. 2009; Zwanenburg et al. 2009). The structural core of the molecules consists of a tricyclic lactone (the ABC-rings) connected via an enol ether bridge to a butyrolactone group (the D-ring). It has been suggested that the biological activity of the strigolactones resides in the enol ether bridge, which can be rapidly cleavage in an aqueous and/or alkaline environment (Yoneyama et al. 2009; Zwanenburg et al. 2009; Akiyama et al. 2010).

An intriguing question was why plants would produce compounds that have such negative consequences (parasitiation by parasitic plants) for the plants themselves. The answer to this question came only few years ago when Akiyama and co-workers demonstrated that these secondary metabolites are involved in signalling between plants and mutualistic AM fungi (Akiyama et al. 2005). We now know that under nutrient deficient conditions 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. 4). The ability to develop AM symbiosis is of great advantage to plants and this, therefore, likely explains why strigolactones are secreted by plants despite the possibility of being abused by root parasitic plants.

Again, a better understanding about how strigolactone signalling is regulated and the possible specificity of different strigolactones seems crucial to further evaluate their importance in the plant-parasitic plant and plant-AM fungus interactions and favor one against another.

6 Control Strategies Against Root Parasitic Plants

As mentioned in Sect. 2.1.3, root parasitic plants are a serious threat to agriculture causing enormous crop losses worldwide. One of the reasons of their devastating effect is that these parasitic weeds are difficult to control because most of their life-cycle occurs underground (Fig. 2). This fact makes the diagnosis of infection difficult and normally only after 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 success (Joel et al. 2007; Rispail et al.

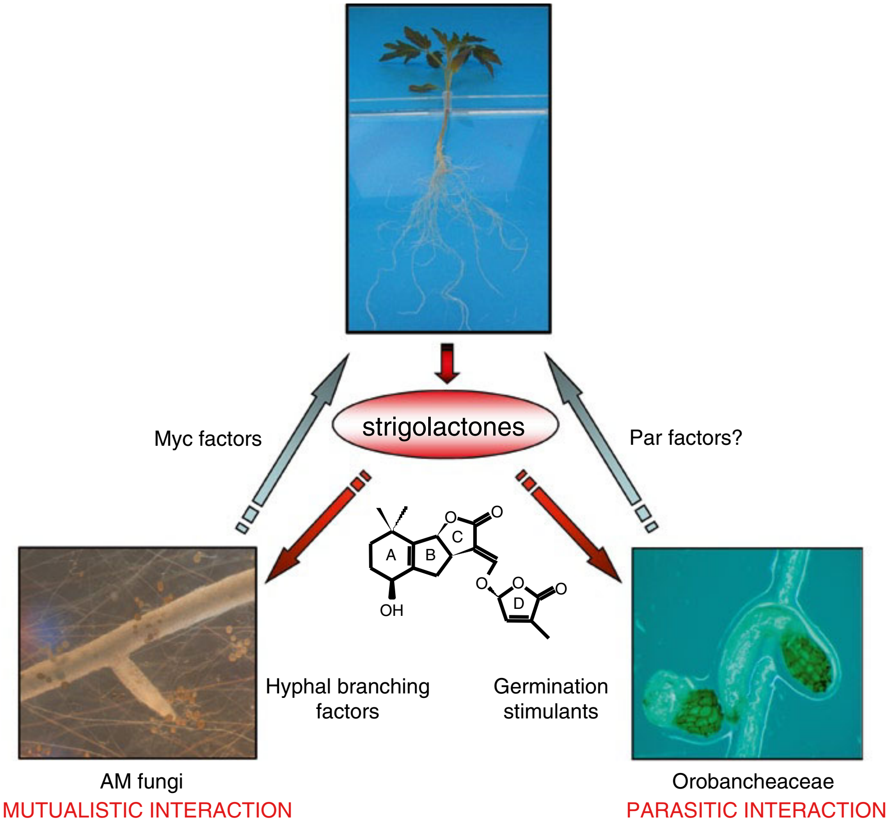

Fig. 4 Underground communication between plants, arbuscular mycorrhizal (AM) fungi and parasitic plants. Plants produce and release strigolactones into the rhizosphere to communicate with AM fungi in order to establish a mutualistic association. As a response, AM fungi release the so-called Myc factors 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 response to the strigolactones, the germinating parasitic seeds would produce Par factors (Modified from Bouwmeester et al. 2007)

2007; Scholes and Press 2008), and the most efficient control method – fumigation – is environmentally hazardous. Therefore, new methods for a more effective control against 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 (Joel et al. 2007; Scholes and Press 2008), the development of more effective control strategies should focus on the initial steps in the host-parasite interaction. Particularly on the germination of the parasitic weed seed stage, which is trigged by the strigolactones (Sun et al. 2007; López-Ráez et al. 2009). In this sense, two general approaches to control root parasitic plants may be envisaged: through enhanced or reduced seed germination.

6.1 Control Through Enhanced Germination

6.1.1 Trap and Catch Crops

This strategy consists in the use of non-host plant species that produce germination stimulants – strigolactones -, inducing suicidal germination of the parasite' seeds. Once germinated, the seeds cannot survive without a suitable host, hence causing a reduction in the parasite seed bank (Zwanenburg et al. 2009). These trap and catch crops can be resistant in a later stage of the parasite lifecycle – trap crops – or harvested before the seeds of the parasite are shed – catch crops – (Bouwmeester et al. 2003; Sun et al. 2007). The effectiveness of catch and trap crops could be increased by the selection of cultivars overproducing germination stimulants (breeding) or through molecular engineering of such overproduction. The latter can potentially be achieved by overexpression of the rate-limiting enzymes from the strigolactone biosynthetic pathway such as CCD7 or CCD8. In addition to the suicidal germination induced by these catch and trap crops with enhanced production of strigolactones, they could favour arbuscular mycorrhizal colonization in the host plant, with the corresponding benefits on plant growth, fitness and yield.

6.1.2 Synthetic Germination Stimulants

An alternative strategy to controlling root parasitic plant infestation through the induction of suicidal germination is the use of synthetic germination stimulants. In this sense, the application at very low concentrations of the strigolactone analogues GR24, GR7 and Nijmegen-1 to *Striga*-infested soils resulted in reduction in the seed population (Johnson et al. 1976; Wigchert et al. 1999). However, one of the limitations of this approach is that these synthetic germination stimulants are rather unstable in the soil. Therefore, more stable compounds or suitable formulations should be developed in order to overcome these stability problems and increase their effectiveness.

6.2 Control Through Reduced Germination

Another approach to avoid root parasitic weed infection is based on the opposite strategy, aimed at reducing seed germination. However, since strigolactones are also AM hyphal branching factors and are involved in plant architecture, the consequences for the AM fungal community in the soil and possible unwanted side-effects on plant architecture should be carefully evaluated before following this approach.

6.2.1 Soil Fertilization

As mentioned above, plants grown under nutrient deficient conditions, specially regarding phosphate and nitrogen, are more active in producing and exuding strigolactones and, therefore, in inducing germination of root parasitic plant seeds (Yoneyama et al. 2007; López-Ráez et al. 2008a). In many areas of the world, the concentration or availability of these essential mineral nutrients are limited in the soil, fact that has a significant impact on plant growth and health. Therefore, the use of fertilisers not only would improve soil fertility, plant fitness and crop yield, but also would reduce strigolactone production by the host plant and hence reduce the infection by parasitic weeds (Fig. 2). Indeed, the application of phosphate to phosphate-deficient soils significantly reduced the population and infestation of the parasites *Orobanche minor* in red clover and *P. aegyptiaca* in tomato plants (Jain and Foy 1992; Yoneyama et al. 2001). However, since strigolactone production in response to nutrient availability differs between plant species, fertiliser rate and composition should be carefully optimised depending on the crop, soil fertility and possibly the parasitic weed species before using this strategy as a control method.

6.2.2 Chemical Inhibitors

Strigolactones are derived from the carotenoids (Matusova et al. 2005; López-Ráez et al. 2008a). Therefore, herbicides that inhibit carotenoid biosynthesis such as fluridone, norflurazon, clomazone and amitrole could be used in very low concentrations as a tool to reduce strigolactone production and ultimately parasitic seed infection (López-Ráez et al. 2009; Jamil et al. 2010). Indeed, it was observed that application of these inhibitors at concentrations that do not cause chlorophyll bleaching to maize, sorghum, cowpea, rice and tomato strongly reduces strigolactone production and *in vitro* germination of *Striga hermonthica* and *Phelipanche ramosa* seeds by the exudates of the treated plants (Matusova et al. 2005; López-Ráez et al. 2008a; Jamil et al. 2010). These results show that treatments with such herbicides may be an effective and relatively cheap method to reduce parasitic weed infestation in the field either alone or in combination with other control strategies.

6.2.3 Breeding for Low Strigolactone Production Cultivars

The selection of cultivars with low production/exudation of strigolactones could be an attractive strategy to control root parasitic weeds. In this sense, genetic variation for the production of strigolactones has been observed for different crops. We have shown that different cultivars of tomato produce different amounts of strigolactones (López-Ráez et al. 2008b). The tomato mutant *high pigment-2* (*hp-2*^{dg}), which is an important mutant line introgressed into commercial tomato cultivars because of its enhanced levels of carotenoids including lycopene, was less susceptible to *P. aegyptiaca* infection than the corresponding wild-type, which correlated with a reduced production of strigolactones (López-Ráez et al. 2008b). Genetic variation for low germination stimulant production has been also described in sorghum, fact that was used to breed for *Striga* resistant varieties and introduce them into high yielding sorghum cultivars in several African countries (Ejeta 2007). Therefore, selecting programs to breed for cultivars with low strigolactone production is a valid and promising strategy.

6.2.4 Genetic Engineering

Molecular biology techniques targeting one or more of the rate-limiting genes from the strigolactone biosynthetic pathway could be another approach to reduce strigolactone biosynthesis. Indeed, *ccd7* and *ccd8* mutants of several plant species show a reduced production of strigolactones (Gomez-Roldan et al. 2008; Umehara et al. 2008). Moreover, genetic engineering using RNAi technology on *CCD7* and *CCD8* genes induced a significant reduction on strigolactones in tomato, which correlated with a reduction in the germinating activity of *P. ramosa* seeds (Vogel et al. 2010; Kohlen, López-Ráez and Bouwmeester, unpublished). Therefore, molecular engineering may be an important and efficient component of a long-term strategy for parasitic weed control. However, further research is required to completely characterize the biosynthetic pathway of strigolactones in order to select appropriate target genes with temporal or inducible promoters.

6.2.5 Use of Beneficial Microorganisms: Arbuscular Mycorrhizas

The fact that the strigolactones play a dual role in the rhizosphere as signalling molecules for both AM fungi and root parasitic plants (Fig. 4), and that AM symbiosis greatly benefits plant fitness make the strigolactones a suitable candidate to develop environmentally friendly biological control methods against parasitic weeds. Indeed, it was shown that AM fungal inoculation of maize and sorghum led to a reduction in *Striga hermonthica* infection in the field (Lendzemo et al. 2005), and it was 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; Sun et al. 2008) (Fig. 5). A similar effect was observed in pea, where AM colonization reduced seed germination of *Orobanche* and *Phelipanche* species (Fernández-Aparicio et al. 2010). 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 parasite *P. ramosa*, and have analytically demonstrated that this reduction is caused by a reduction in the production of strigolactones (López-Ráez et al. 2011). Moreover, we have also observed that this reduction requires a fully established mycorrhizal association (López-Ráez et al. 2011). The results with maize, sorghum, pea (although not analytically supported) and tomato suggest that the reduction in strigolactone exudation induced by AM symbiosis is conserved across the plant kingdom. As AM fungi colonize roots of most agricultural and horticultural species and are widely distributed around the globe, this environmentally friendly biocontrol strategy can potentially be used in the majority of economically important crops that suffer from these root parasites worldwide. Thus, mycorrhizal

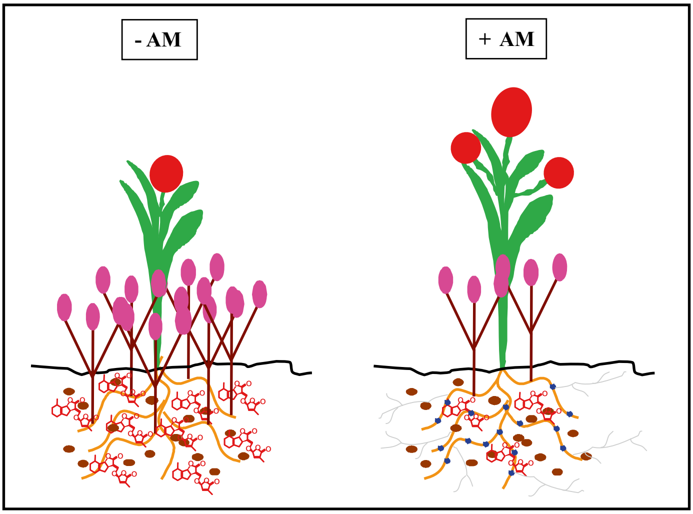

Fig. 5 Effect of arbuscular mycorrhizal (*AM*) symbiosis on root parasitic plant control. Under low phosphorous conditions plants produce an increased amount of strigolactones. These signalling molecules act as germination stimulants of root parasitic plant seeds (*left*). Upon mycorrhizal colonization, 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*)

management through agroforestry, reduced soil disturbance, crop rotation or mycorrhizal inoculation would improve mycorrhizal benefits in agro-ecosystems. In addition, these crops would take advantage of all the other well-known benefits of the AM symbiosis such as positive effect on plant fitness and boost of plant defence mechanisms (Fig. 5). Altogether makes AM symbiosis a suitable and promising tool for the biological control of parasitic weeds.

So far, none of the reported approaches applied alone has led to an optimal solution against root parasitic weeds. Therefore, an integrated approach using several strategies, including the control of seed germination, should lead to an efficient and long-term management of this pest in agriculture.

7 Conclusion

Chemicals fertilizers and pesticides are used to prevent, mitigate or control plant diseases. However, the environmental pollution caused by excessive use and misuse of agrochemicals has led to public concerns about the use of these chemicals in agriculture. Therefore, there is a need to find more environmentally friendly alternatives for disease control. The key to achieve successful biological control is the knowledge on plant interactions in an ecological context. We emphasize here the importance of the chemical communication that occurs in the rhizosphere between plants and other organisms, and the potential use of this molecular dialogue as a target to control soil-borne pathogens and pests. An interesting example is the use of the mutualistic AM symbiosis for controlling root parasitic plant infection by reducing the production of strigolactones by the host plant. This example illustrates the suitability of approaches based on the knowledge of the biological system to target. Further research will expand our knowledge on what is going on underground, and the information generated will help us decipher the regulation of chemical communication in the rhizosphere and may result in the development of new biocontrol strategies against soil pests.

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