Chapter 15
Root Allies: Arbuscular Mycorrhizal Fungi Help Plants to Cope with Biotic Stresses

María J. Pozo, Sabine C. Jung, Ainhoa Martínez-Medina, Juan A. López-Ráez, Concepción Azcón-Aguilar, and José-Miguel Barea

15.1 Introduction

Microbial populations living at the root–soil interfaces, the rhizosphere, are immersed in a framework of interactions known to influence plant growth and health and soil quality, key issues for agroecosystem sustainability (Barea and Azcón-Aguilar 2012). Rhizosphere microbes, mainly bacteria and fungi, have different trophic/living habits and establish a variety of saprophytic or symbiotic relationships with the plant, either detrimental or beneficial. They are able to affect plant growth and to influence plant responses to biotic and abiotic stresses (Barea et al. 2005). Some of the mutualistic microorganisms are known to enter the root system of their hosts adopting an endophytic lifestyle, which benefit both the plant and the microbial endophyte. These endophytic microorganisms include (1) plant mutualistic symbionts, such as N_2-fixing rhizobial and actinorhizal bacteria and mycorrhizal fungi; (2) root endophytic fungi; and (3) certain plant growth-promoting rhizobacteria (Barea et al. 2005). The growth of beneficial endophytic microbes inside plant roots requires mutual recognition and substantial coordination of plant and microbial responses. Defense mechanisms are coordinated by the plant immune system which allows the plant to distinguish non-self alien organisms by recognizing structurally conserved microbe-associated molecules, collectively termed *m*icrobe-*a*ssociated *m*olecular *p*atterns (MAMPs). Then different signal molecules including phytohormones such as salicylic acid (SA) and jasmonic acid (JA) orchestrate the plant defense response (Pieterse et al. 2009).

M.J. Pozo (✉) • S.C. Jung • A. Martínez-Medina • J.A. López-Ráez • C. Azcón-Aguilar • J.-M. Barea
Department of Soil Microbiology and Symbiotic Systems, Estación Experimental del Zaidín (CSIC), Professor Albareda 1, 18008 Granada, Spain
e-mail: mariajose.pozo@eez.csic.es; mjpozo@eez.csic.es; sabine.jung@eez.csic.es; ammedina@cebas.csic.es; juan.lopezraez@eez.csic.es; concepcion.azcon@eez.csic.es; jmbarea@eez.csic.es

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Like pathogens, beneficial organisms are confronted with the innate immune system of the roots and colonization success essentially depends on the evolution of strategies for immune evasion. The modulation of plant defense responses by microbial symbionts aids establishing the delicate balance between the two partners and may result in an enhanced defensive capacity of the plant (Pozo and Azcón-Aguilar 2007; Zamioudis and Pieterse 2012). Moreover, this activated defense is often also expressed in aboveground plant tissues, thereby providing the plant with an induced systemic resistance effective against a broad spectrum of plant pathogens (Pozo and Azcón-Aguilar 2007; van Wees et al. 2008).

Well-known examples of beneficial endophytic soil fungi are the mycorrhizal fungi, common components of the soil microbial biomass which establish mutualistic symbioses with most terrestrial plants, including economically important crop species (Smith and Read 2008). Mycorrhizal symbioses can be found in almost all ecosystems worldwide to improve plant growth and health through key ecological processes (Azcón-Aguilar et al. 2009). Most of the major plant families form arbuscular mycorrhizal (AM) associations, the most common mycorrhizal type (Smith and Read 2008). The AM symbiosis increases plant growth; enhances available soil nutrient uptake; increases plant resistance to drought; protects plants against a wide range of belowground attackers such as soilborne fungal and bacterial pathogens, nematodes, or root-chewing insects; and, as reported during the last decade, induces resistance against shoot pathogens (Whipps 2004; Pozo and Azcón-Aguilar 2007; Gianinazzi et al. 2010; Jeffries and Barea 2012; Jung et al. 2012). Therefore, the AM fungi, a major group of plant mutualistic endophytic microorganisms, can be considered as “root allies” which support plants to cope with biotic stresses. Because of their role in enhancing plant resistance to potential deleterious organisms, including microbial pathogens, nematodes, phytopathogenic insects, and parasitic plants (Jung et al. 2012), these microorganisms will be the target endophytic symbiont of this chapter. Accordingly, we will first summarize some key concepts related to (1) the biology and ecology of AM fungi, (2) the biology and functions of the AM symbiosis, and (3) how the AM symbiosis can be managed, as a low-input biotechnology, to help sustainable environmentally friendly agro-technological practices. Then, and as the main information core of this article, we will summarize and discuss the impact of AM on plant resistance to biotic stresses and the underlying mechanisms. Special emphasis will be devoted to the role of plant defense mechanisms, as experimental evidences support that mycorrhizal interactions can effectively stimulate the host’s defensive capacity. This can lead to a primed state of the plant, thereby boosting defense mechanisms triggered upon attack by potential enemies, not only locally in the roots but also in aboveground tissues.

15.2 Nature and Functions of Arbuscular Mycorrhizal Fungi: The AM Symbiosis

The AM fungi establish the so-called AM symbiosis with most vascular plants where both partners exchange nutrients and obtain important benefits. The soilborne AM fungi colonize the root cortex biotrophically and then develop an external mycelium, a bridge connecting the root with the surrounding soil microhabitats (Smith and Read 2008). In this section, the most significant aspects of the available information on the biology and ecology of AM fungi and the biology, functions, and management of the AM symbiosis are summarized.

15.2.1 Biology and Ecology of AM Fungi

The AM fungi are ubiquitous soilborne microbial fungi, whose origin and divergence dates back more than 450 million years (Redecker et al. 2000; Bonfante and Genre 2008; Schüßler and Walker 2011). Molecular analyses and fossil records indicate that AM associations evolved as a symbiosis, facilitating the adaptation of plants to the terrestrial environment and suggesting that AM fungi played a crucial role in land colonization by plants (Schüßler and Walker 2011). Actually, the primitive roots developed in association with AM fungi and coevolved with them to build up the mycorrhizal root systems of extant vascular plants (Brundrett 2002). As a consequence of this coevolution, the AM relationship became an integral component of plant ecology in both natural and agricultural ecosystems (Brundrett 2002).

Because of their very peculiar evolutionary history, underground lifestyle, and genetic makeup, AM fungi are endowed with unusual biological traits (Parniske 2008; Bonfante and Genre 2008; Barea and Azcón-Aguilar 2012). AM fungi develop a typically aseptate and coenocytic mycelial network containing hundreds of nuclei sharing the same cytoplasm and produce very large multinucleate spores having abundant storage lipids and resistant thick walls containing chitin (Smith and Read 2008). Among other important characteristics, AM fungi are asexual, unculturable, and obligatorily biotrophic microbes (Schüßler and Walker 2011). The character of obligate symbionts, unabling them to complete their life cycle without colonizing a host plant, has hampered the study of the biology and the biotechnological applications of AM fungi (Bago and Cano 2005).

The AM fungi belong to the phylum *Glomeromycota* (Schüßler et al. 2001; Schüßler and Walker 2011). Different polymorphic DNA-sequence variants are distributed among different nuclei in the same coenocytic hypha or spore (Rosendahl 2008; Sanders and Croll 2010; Schüßler and Walker 2011). Thus, from a taxonomic point of view, there are difficulties for defining clear species concepts of individuals and also boundaries within populations. However, molecular phylogenetic and evolutionary analyses are substantially contributing to our knowledge on AM fungi speciation. Diversity studies based on molecular approaches allowed us to ascertain that individual fungal strains exhibit little host specificity, while a single plant can be colonized by many different AM fungal species within the same root. A certain degree of host preference (functional compatibility) was evidenced to occur and this has been shown to play an important role in regulating the diversity, stability, and productivity of agroecosystems (Jeffries and Barea 2012).

Undoubtedly, the more relevant biological characteristic of AM fungi is their capacity to form AM associations with members of all phyla of land plants, whatever their taxonomic position, life form, or geographical distribution (Smith and Read 2008).

15.2.2 Biology and Functioning of AM Symbiosis

The information generated during the last years on the cellular and molecular events taking place during AM establishment and the ecophysiological and molecular components of AM functioning have recently been reviewed (Bonfante and Genre 2008; Parniske 2008; Smith and Read 2008; Gianinazzi-Pearson et al. 2009; Barea and Azcón-Aguilar 2012).

AM fungi can colonize plant roots from three main types of soil-based propagules: spores, fragments of mycorrhizal roots, and extraradical hyphae, all of them producing a more or less well-developed mycelial network expanding in the soil. When a hypha from an asymbiotic, soil-based AM mycelium approaches a host root, an exchange of signaling molecules between both symbionts takes place (Parniske 2008; Gianinazzi-Pearson et al. 2009; Genre and Bonfante 2010). This molecular dialogue activates specific signaling pathways affecting fungal development and plant gene expression. Several plant regulatory genes are involved in reprogramming processes from a direct cell-to-cell contact on the root surface to the intracellular accommodation of the fungal symbiont. When finally a hypha contacts the plant root, it adheres to epidermal cells forming a characteristic fungal structure called appressorium (or hyphopodium). This event marks the initiation of the symbiotic phase which ends with the production of the characteristic treelike structures, termed “arbuscules,” that the fungus develops within the root cortical cells. The arbuscules, which give name to the symbiosis, are the structures where most of the nutrient exchange between the fungus and the plant is thought to occur (Smith and Read 2008).

Following root colonization, AM fungi form extensive mycelial networks outside the root—the extraradical mycelium (ERM)—where spores are developed completing their life cycle. The ERM results in a tridimensional structure specialized in the acquisition of mineral nutrients from soil, particularly those whose ionic forms have poor mobility or are present in low concentration in the soil solution, as it is the case with phosphate and ammonia (Barea and Azcón-Aguilar 2012). Through the activities of the interlinked and extensive soil ERM, AM fungi affect the distribution and movement of nutrients within the soil ecosystem (Richardson et al. 2009). The major flux is the transfer of carbon from plant to fungus (and thereby to the soil) and the reciprocal movement of phosphate and ammonium from fungus to plant. In addition to the uptake of nutrients, the AM symbiosis improves plant performance through increased protection against environmental stresses, whether they be biotic (e.g., pathogen and herbivore attack) or abiotic (e.g., drought, salinity, heavy metals toxicity, or presence of organic pollutants), and also enhances soil structure through the formation of hydro-stable aggregates necessary for good soil tilth (Barea and Azcón-Aguilar 2012). The ecological, physiological, and molecular basis of AM functioning and their implications in enabling the plant to cope more effectively with natural or anthropogenic environmental stress, either biotic or abiotic, have been the subject of diverse experimental and review studies during the last decade (Barea and Azcón-Aguilar 2012).

15.2.3 Managing the AM Fungi and Symbiosis

Nowadays, it is well accepted that AM associations, which helped plants to thrive in hostile environments such as those prior to their origin and during their evolution, continue helping plants to develop in stressed environments (Barea et al. 2011). This is fundamental because adverse conditions, particularly exacerbated in the current scenario of global climate change, generate a great array of stress situations affecting the stability of both natural and agricultural ecosystems. Plants must be able to cope with these stresses. Consequently, adaptive strategies should be developed in order to increase their resilience to overcome negative impacts. AM establishment can be considered one of these adaptive strategies, through their ability to increase host tolerance to environmental constraints (Barea et al. 2011; Jeffries and Barea 2012).

In nonagricultural situations, as plant diversity has been related to AM diversity, maintenance of a sustainable mixed plant population depends on the maintenance of a diverse AM fungi population and vice versa (Maherali and Klironomos 2007). Thus, it is relevant to recognize that the activity and diversity of mycorrhizal fungi are key elements linking biodiversity and ecosystem functioning (Read 1998).

On the other hand, the increasing demand for low-input agriculture has resulted in greater interest in the manipulation and use of beneficial soil microorganisms. Thus, management of native populations of AM fungi is recognized as a sustainable strategy in agriculture because it can reduce the use of chemicals and energy in agriculture leading to a more sustainable production, while minimizing environmental degradation (Jeffries and Barea 2012). These biological interventions are becoming more attractive as the use of chemicals for fumigation and disease control is progressively discouraged and fertilizers have become more and more expensive (Atkinson 2009).

Because of the importance of the AM symbiosis in sustainable agriculture or restoration of ecosystems management, the development of techniques for AM inoculant production and inoculation has become a focal point of research. The difficulty in culturing obligate symbionts such as AM fungi in the absence of their host plant is a major obstacle for massive inoculum productions (Baar 2008). Despite these problems, the beneficial effects of AM fungi on plant growth have led to their development as bioinoculants for forestry, agriculture, and horticulture (Ijdo et al. 2011), and several companies worldwide are producing AM inoculum products which are now commercially available (Gianinazzi and Vosátka 2004; Vosátka et al. 2008; Ijdo et al. 2011).

15.3 Disease Control by AM Fungi

As stated, AM symbiosis implies important changes in the plant physiology. As a consequence, the association may impact the plant interaction with other organisms. Many studies have shown the protective effect of colonization by AM fungi against infections by microbial pathogens and other deleterious organisms in different plant systems (reviewed in Whipps 2004; Jung et al. 2012). This bioprotection has been termed mycorrhiza-induced resistance (MIR) (Pozo and Azcón-Aguilar 2007). In this section, we will summarize the main conclusions from recent studies about MIR, schematized in Fig. 15.1.

15.3.1 Protection Against Soilborne Pathogens

AM symbioses are able to reduce the damage caused by many soilborne pathogens on a variety of crop species. Although there are some examples of protection against pathogenic bacteria, most reports focus on harmful fungi and oomycetes, including major pathogens from the genera *Fusarium*, *Rhizoctonia*, *Verticillium*, *Phytophthora*, *and Pythium* (Whipps 2004; Jung et al. 2012). A reduction of the detrimental effects by parasitic nematodes has also been reported in AM plants (Pinochet et al. 1996; De La Peña et al. 2006; Li et al. 2006; Elsen et al. 2008; Vos et al. 2011; Hao et al. 2012). There are, however, relatively few studies on the impact of AM fungi on root-feeding insects, and these mostly focus on members of the genus *Otiorhynchus*, or weevils (Koricheva et al. 2009). The larvae of these insects are rhizophagous, whereas the adults feed on the foliage of the same plant. A clear protective effect of AM fungi on these pests has been reported (Gange 1996, 2001; Koricheva et al. 2009).

Several mechanisms operate simultaneously in the alleviation of the damage caused by soilborne pathogens. For example, AM fungi have been proven to directly compete with soilborne pathogens and nematodes for space and nutrients (Azcón-Aguilar and Barea 1996; Cordier et al. 1998; Filion et al. 1999; Norman and

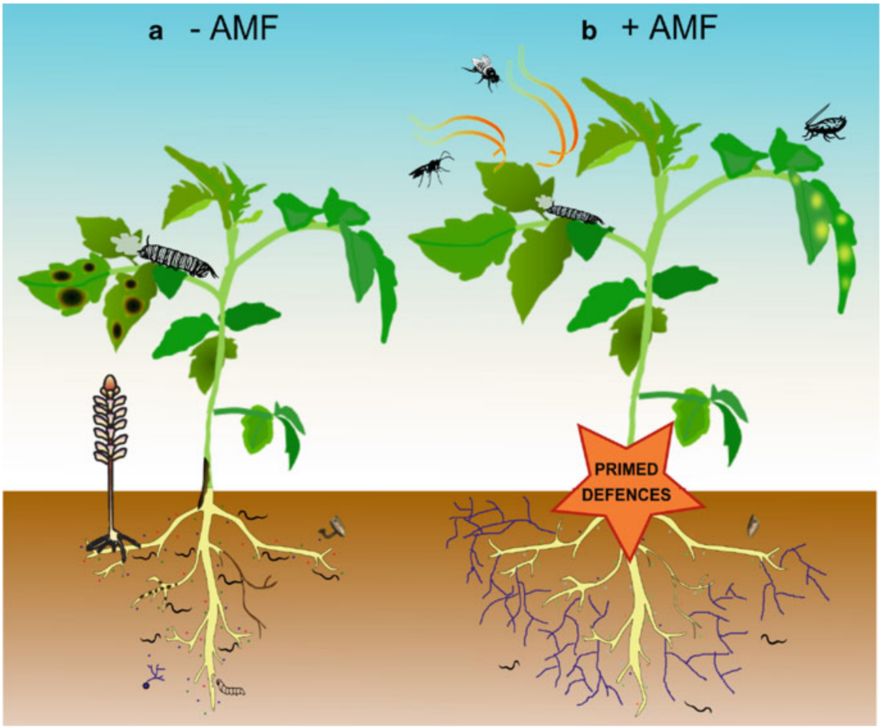

Fig. 15.1 (**a**) Non-mycorrhizal plant (−AMF). Absence of root colonization by AMF leads to stronger development of symptoms in response to necrotrophic pathogens and more damage upon feeding by chewing insects in roots and shoots when compared to mycorrhizal plants. Release of strigolactones (SLs) as part of the root exudates induces branching of AMF hyphae to promote mycorrhization but also induces germination of Orobanchaceae seeds which then parasitize the host plants' root system. (**b**) Mycorrhizal plant (+AMF). Growth promotion is often observed due to improved acquisition of mineral nutrients through the AM fungal hyphal network (represented in *blue*). Changes in the root exudate patterns repel nematodes and induce changes in the soil microbial community, possibly attracting antagonists of pathogens, and a reduced release of SLs minimizes the risk of infection by root parasitic plants. Priming of plant defenses leads to a general reduction of the incidence and/or damage caused by soilborne pathogens, nematodes, and chewing insects. In aboveground plant parts, viral and fungal biotrophs, as well as phloem-feeding insects, perform better on mycorrhizal plants. In contrast, the primed jasmonate-regulated plant defense mechanisms restrict the development of necrotrophic pathogens and the performance of phytophagous insects. Indirect defenses, such as the release of volatiles, are boosted and parasitoids are efficiently attracted

Hooker 2000; De La Peña et al. 2006) and to alter root morphology that may change the dynamics of pathogen infection (Schellenbaum et al. 1991; Norman et al. 1996). Colonization by AM fungi can lead to alterations in the quality and quantity of root exudates (Sood 2003; Pivato et al. 2008). These changes impact the microbial community of the mycorrhizosphere and, among other effects, may lead to a shift in its composition favoring certain components of the microbiota with the capacity to antagonize possible root pathogens (Barea et al. 2005; Badri and Vivanco 2009). Altered root exudation may also directly impact microbial pathogens and nematodes (see Jung et al. 2012 for references).

The use of experimental split-root systems has confirmed that the protection by mycorrhiza is manifested in non-colonized areas of the root system (Cordier et al. 1998; Pozo et al. 2002; Zhu and Yao 2004; Khaosaad et al. 2007; Hao et al. 2012). These experiments allowing physical separation of the AM fungi and the aggressor have highlighted the involvement of plant-mediated responses in the enhanced resistance, pointing out a major role for plant defense mechanisms. The plant defense mechanisms involved in root protection have been analyzed (Pozo et al. 2002; Jung et al. 2012) and will be discussed in Sect. 15.4.

15.3.2 Systemic Protection Against Leaf Pathogens

Recent findings have shown the ability of certain beneficial soil fungi for controlling shoot pathogens by eliciting a plant-mediated resistance response. The pathogens' lifestyles have been shown to determine the outcome of the interaction with regard to the biocontrol of shoot diseases by the AM symbiosis (Pozo and Azcón-Aguilar 2007; Jung et al. 2012). Early studies reported a higher susceptibility of AM plants to viruses, and biotrophic pathogens appear to develop better on AM plants, although an increased tolerance was observed in terms of plant productivity (Gernns et al. 2001; Whipps 2004). Regarding to pathogens with a hemibiotrophic lifestyle, the effect of the symbiosis varies from no effect to a reduction of the disease (Lee et al. 2005; Chandanie et al. 2006). In contrast, several studies evidence the positive effect of AM symbiosis on plant resistance against necrotrophic shoot pathogens (Fritz et al. 2006; de la Noval et al. 2007; Møller et al. 2009; Pozo et al. 2010; Campos-Soriano et al. 2012).

Two main plant-mediated mechanisms may be operative in the protective effect of beneficial soil fungi against leaf pathogens. One is the improvement of the nutritional status of the host plants and/or alterations of the source–sink relation that may help a plant overcome a herbivore attack or quickly recover after the attacker has been fought off. The other mechanism involves the activation of the plant defense response by the beneficial microorganisms (Jung et al. 2012). Because of the special interest of this modulation of the plant immune responses and its implications in plant resistance to biotic stresses, the topic is discussed in detail in Sect. 15.4.

15.3.3 Effect on Herbivorous Insects

Insects may be deleterious to plants by directly damaging them through herbivory or acting as vectors for pathogens such as viruses and phytoplasmas. However, they can also have positive effects on plant health acting as natural enemies of pests or as pollinators (Jung et al. 2012). The outcome of the AM-plant–herbivore interaction depends on many factors, such as the AM fungus, host plant, insect species involved, and prevailing environmental factors (Gange 2007; Pineda et al. 2010). Several reviews have tried to compile the published studies dealing with these multitrophic interactions, most of them from an ecological point of view (Gehring and Bennett 2009; Hartley and Gange 2009; Jung et al. 2012). The AM symbiosis can actually influence insect herbivore performance, but the magnitude and direction of the effect depend mainly upon the feeding mode and lifestyle of the insect (Hartley and Gange 2009; Koricheva et al. 2009). The improvement of plant nutrition by the symbiosis may have opposite effects: On the one hand, by improving nutrient and water uptake, mycorrhizas can facilitate the regrowth of tissues after herbivory by promoting plant tolerance through compensation of biomass losses. On the other hand, as nutrition improves, plants may become more nutritive or attractive to insects (Kula et al. 2005; Bennett and Bever 2007; Hoffmann et al. 2011). Furthermore, the induction of defense mechanisms operating in resistance against microbial pathogens may also impact herbivorous insects (Jung et al. 2012). The final impact on insect performance will depend on the interplay between a positive effect derived from the enhanced plant growth and a negative effect derived from the induced resistance in the plant and is depending on the type of the attacking insect. Generalist insects, able to feed on diverse plants and sensible to the plant defense mechanisms, are usually negatively affected by the presence of AM fungi (Gange and West 1994; Fontana et al. 2009). However, specialist insects, which feed from one or only a small number of host species and show a high degree of adaptation to their hosts' defense responses, usually perform better on AM plants, probably because of the improved nutritional quality of the host (Gehring and Bennett 2009; Hartley and Gange 2009). Some even prefer mycorrhizal plants for oviposition to improve growth and development of their offspring (Cosme et al. 2011).

The degree of protection also depends on the feeding guild of the attacking herbivore. Phloem-sucking insects produce minimal damage to the plant while feeding and thereby avoid detection by the host's immune system (Walling 2008). Thus, it is unlikely that potentiation of plant defense mechanisms in AM plants may have a significant impact on them. Moreover, they may profit from its higher nutritional value. In fact, higher incidence of phloem-sucking insects in AM plants has been reported (Gange et al. 1999; Goverde et al. 2000). In contrast, leaf chewers and miners are usually negatively affected by AM fungi (Gange and West 1994; Vicari et al. 2002). These insects feed on the leaf tissue and cause massive damage which activates defenses that depend on the plant hormone JA (Howe and Jander 2008). Remarkably, as discussed later on, JA seems to be a key signal in MIR.

15.3.4 Impact on Parasitic Plants

Plants of the genera *Striga* and *Orobanche* can parasitize a number of important crop plants. They attach to the host roots and acquire nutrients and water from them, constituting one of the most damaging agricultural pests (Bouwmeester et al. 2003). Several studies reported that the attachment and the emergence of *Striga* are reduced in AM plants (see López-Ráez et al. 2011b for references). It is known that seeds of these weeds germinate upon perception of strigolactones (SLs), a group of carotenoid-derived signaling molecules that are exuded by the roots of the host plant. These signals are produced by the plant under conditions of phosphate starvation and promote AM hyphal branching and thereby facilitate mycorrhiza establishment (Akiyama et al. 2005; Bouwmeester et al. 2007). Root parasitic plants have intercepted this recruitment system and utilize the signal for the detection of an appropriate host plant. Remarkably, mycorrhization downregulates the level of SLs once a well-established mycorrhiza is achieved, thus reducing the germination rate of weed seeds (Lendzemo et al. 2007; López-Ráez et al. 2011a). This reduction seems to be the underlying reason for the decrease in the incidence and damage of root parasitic plants on mycorrhizal plants (López-Ráez et al. 2012).

In addition to the root parasitic plants, it has been suggested that certain AM fungi may suppress growth of other aggressive agricultural weeds which cause crop yield losses every year (Rinaudo et al. 2010). These authors reported that the presence of AM fungi reduced total weed biomass, because most aggressive weeds are non-mycorrhizal, while the crop plant benefitted from AM symbiosis via enhanced phosphorus nutrition. Overall, these observations indicate that the use or stimulation of AM fungi in agroecosystems may suppress some aggressive weeds and suggest a possible applicability of the AM symbiosis in weed control.

15.4 Overview of Mechanisms Underlying the Impact of AM Fungi on Plant Protection Against Pathogen and Pests

As indicated above, AM fungi may alleviate biotic stresses through a combination of different mechanisms ranging from direct interactions as competition with the agressor to indirect, plant-mediated effects.

Direct effects include competition for carbon, nitrogen, and other growth factors and competition for niches or specific infection sites. Direct competition has been suggested as mechanism by which AM fungi can reduce the abundance of pathogenic fungi in roots (Filion et al. 2003). Presumably, pathogenic and AM fungi exploit common resources within the root, including infection/colonization sites, space, and photosynthates (reviewed in Whipps 2004). Negative correlations between the abundance of AM fungal structures and pathogenic microorganisms have been found in roots and soil (Filion et al. 2003; St Arnaud and Elsen 2005).

Full exclusion of the pathogenic oomycete *Phytophthora* from arbusculated cells was also evidenced (Cordier et al. 1998).

Root colonization by AM fungi also induces changes in the root system architecture, in morphology, and in root exudates (Schellenbaum et al. 1991; Norman et al. 1996; Pivato et al. 2008). These changes may alter the dynamics of infection by the pathogen or impact on the microbial community of the mycorrhizosphere favoring components of the microbiota with the capacity to antagonize root pathogens (Barea et al. 2005; Badri and Vivanco 2009). Changes in root exudation can directly impact microbial pathogens and nematodes (Norman and Hooker 2000; Vos et al. 2011). More recent findings indicate that a primary mechanism of pathogen control occurs through the ability of AM fungi to reprogram plant gene expression (Liu et al. 2007; López-Ráez et al. 2010a; Campos-Soriano et al. 2012). As consequence, alterations in the primary and secondary metabolism of the plant do occur, many of these changes being related to plant defense (Hause et al. 2007; Schliemann et al. 2008; López-Ráez et al. 2010b).

Actually, as other biotrophs, AM fungi are able to trigger plant defense responses at initial stages (Paszkowski 2006). Thus, for a successful colonization, the fungus has to cope with these reactions and actively modulate plant defense responses. This modulation may result in pre-conditioning of the tissues for efficient activation of plant defenses upon a challenger attack, a phenomenon that is called priming (Pozo and Azcón-Aguilar 2007). Priming set the plant is an “alert” state in which defenses are not actively expressed but in which the response to an attack occurs faster and/or stronger compared to plants not previously exposed to the priming stimulus, efficiently increasing plant resistance. Thus, priming confers important plant fitness benefits (Conrath et al. 2006; Walters and Heil 2007) thereby defense priming by AM has a great ecological relevance (Jung et al. 2012).

15.4.1 Modulation of the Host Plant’s Immune System by AM Fungi and Induced Systemic Resistance

Both mutualistic and pathogenic biotroph fungi are initially recognized as alien organisms and the plant reacts with the activation of an immune response. As stated before, the AM fungus has to deal with the plant’s immune system, contend with the defense mechanisms, and overcome them for a successful colonization of the host (Kloppholz et al. 2011; Zamioudis and Pieterse 2012). Once established, the plant has to regulate the level of AM fungal proliferation within the roots to prevent excessive colonization and carbon drainage, thus maintaining the interaction at an equilibrium to limit the colonization by the mutualistic symbionts. Actually, plants possess a feedback system to prevent excessive colonization over a critical threshold, a phenomenon termed autoregulation of the symbiosis (Vierheilig et al. 2008). In summary, from pre-symbiotic stages and throughout a well-established AM association, plant defense mechanisms are tightly regulated to control the symbiosis. As a side effect, this regulation of plant defenses in the root may directly impact root pathogens.

During the early stages of the interaction, the plant reacts to the presence of AM fungi activating some defense-related responses that are subsequently suppressed (García-Garrido and Ocampo 2002). A quick but transient increase of endogenous salicylic acid (SA) occurs in the roots with a concurrent accumulation of defensive compounds, such as reactive oxygen species, specific isoforms of hydrolytic enzymes, and the activation of the phenylpropanoid pathway (reviewed in Jung et al. 2012). These initial reactions are temporally and spatially limited compared to the reaction during plant–pathogen interactions, suggesting a role in the establishment or control of the symbiosis (Dumas-Gaudot et al. 1996; García-Garrido and Ocampo 2002). To promote successful colonization, AM fungi likely have to evade and manipulate the host innate immune system. Indeed, recent studies support that AM fungi can actively suppress plant defense reactions by secreting effector proteins that interfere with the host's immune system (Kloppholz et al. 2011). However, even in later stages of the interaction, the levels of SA and other defense-related phytohormones, such as jasmonic acid (JA), abscisic acid (ABA), and ethylene (ET), may be altered in mycorrhizal roots. These changes may contribute to control the extension of fungal colonization and the functionality of the symbiosis on mutualistic terms (Hause et al. 2007; López-Ráez et al. 2010a). Indeed, regulation of JA has been reported to have a central role in the correct functioning of the AM symbiosis (Hause and Schaarschmidt 2009). As regulation of defense signaling molecules occurs, the plant immunity system is altered in AM plants, and this may play a major role in MIR. Often, this induced resistance is also expressed in aboveground plant tissues, giving rise to a systemic response that is typically effective against a broad spectrum of plant pathogens and even herbivores. The dependence of successful mycorrhization on the control of JA and SA signaling would explain the range of protection conferred by this symbiosis (Pozo and Azcón-Aguilar 2007; Jung et al. 2012). Mycorrhizal plants are more resistant to necrotrophs and chewing insects, which are targeted by JA-dependent defense responses, while frequently being more susceptible to biotrophs, as these are targeted by SA-regulated defenses. This pattern correlates with an activation of JA-dependent defenses and repression of SA-dependent ones in a well-established mycorrhiza. The antagonistic interaction between SA and JA signaling is a conserved mechanism for plant defense regulation (Thaler et al. 2012).

15.5 Priming for Enhanced Defense by AM Fungi

The induction of resistance after plant root colonization by AM fungi does not necessarily require direct activation of defense mechanisms but can result from a sensitization of the tissue upon appropriate stimulation to express basal defense mechanisms more efficiently after subsequent pathogen attack (Pozo and Azcón-Aguilar 2007; Jung et al. 2012). This priming of the plant's innate immune system is common upon interaction with beneficial microorganisms and has important fitness benefits compared to direct activation of defenses (Van Hulten et al. 2006; Van Wees et al. 2008; Conrath 2009). Several mechanisms have been proposed to mediate the induction of the primed state as a moderate accumulation of defense-related regulatory molecules, such as transcription factors or MAP kinases and chromatin modifications (Pozo et al. 2008; Beckers et al. 2009; Van der Ent et al. 2009; Pastor et al. 2012). For example, rhizobacteria-induced systemic resistance in *Arabidopsis* is related to priming of JA-dependent responses through the accumulation of MYC2, a transcription factor with a key role in the regulation of JA responses (Pozo et al. 2008).

Examples of primed defense responses in AM plants were first observed in root tissues. Mycorrhizal-transformed carrot roots displayed stronger defense reactions at sites challenged by *Fusarium* (Benhamou et al. 1994). In tomato, AM colonization systemically protected roots against *Phytophthora parasitica* infection. Only mycorrhizal plants formed papilla-like structures around the sites of pathogen infection through deposition of non-esterified pectins and callose, preventing the pathogen from spreading further, and they accumulated significantly more PR-1a and basic β-1,3 glucanases than non-mycorrhizal plants upon *Phytophthora* attack (Cordier et al. 1998; Pozo et al. 1999, 2002). Similarly, mycorrhizal potatoes showed amplified accumulation of the phytoalexins rishitin and solavetivone upon *Rhizoctonia* infection, whereas AM fungi alone did not affect the levels of these compounds (Yao et al. 2003). Primed accumulation of phenolic compounds in AM date palm trees has been related to protection against *F. oxysporum* (Jaiti et al. 2007), and priming has also been involved in AM induction of resistance against nematodes (Li et al. 2006; Hao et al. 2012).

However, the primed response is not restricted to the root system as priming of defenses has also been shown in shoots of AM plants (Pozo et al. 2010). Actually, the AM symbiosis induced systemic resistance in tomato plants against the necrotrophic foliar pathogen *Botrytis cinerea*. While the amount of pathogen in leaves of mycorrhizal plants was significantly lower, the expression of some jasmonate-regulated, defense-related genes was higher in those plants (Pozo et al. 2010; Jung et al. unpublished). A primed response of JA-dependent defenses was confirmed by transcript profiling of leaves after exogenous application of JA, since JA-responsive genes were induced earlier and to a higher extend in AM plants (Pozo et al. 2009). The use of tomato mutants impaired in JA signaling confirmed that JA is required for AM-induced resistance against *Botrytis* (Jung et al. 2012), corroborating that MIR is similar to the well-studied rhizobacteria-induced systemic resistance (ISR) in *Arabidopsis* and requires a functional JA signaling pathway for the efficient induction of resistance (Pieterse et al. 1998).

15.6 Conclusions

Arbuscular mycorrhizal fungi are key elements in natural and man-made ecosystems. The establishment of the AM symbiosis with plant roots significantly alters the host plant physiology and has far-reaching consequences for the plant and its biotic interactions. Generally, mycorrhizal symbioses enhance the plant's ability to cope with biotic stresses. Even though the individual outcome always depends on the AMF-plant attacker combination, protective effects against deleterious organisms ranging from microbial pathogens to herbivorous insects and parasitic plants have been widely described.

Experimental evidences confirm that this protection is based not only on improved nutrition or local changes within the roots and the rhizosphere, but that plant defense mechanisms play a key role. Mycorrhizal colonization can prime plant immunity by boosting the plant ability to respond to an attack. In this process, jasmonate signaling appears as a central element. Unveiling the principles behind a successful symbiosis and the functional interplay between plant and fungus is of great interest. Particularly, the identification of defense regulatory elements coordinating mycorrhizal development and mycorrhiza-induced resistance is a major challenge for research. This identification will pave the way to the development of biotechnological strategies for improving mycorrhiza establishment and the use of AMF in the integrated management of pests and diseases.

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