Chapter 9

Priming Plant Defence Against Pathogens by Arbuscular Mycorrhizal Fungi

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Abstract Root colonisation by arbuscular mycorrhizal fungi (AMF) can improve plant resistance/tolerance to biotic stresses. Although this bioprotection has been amply described in different plant systems, the underlying mechanisms remain largely unknown. Besides mechanisms such as improved plant nutrition and competition, experimental evidence supports the involvement of plant defence mechanisms in the observed protection. During mycorrhiza establishment, modulation of plant defence responses occurs upon recognition of the AMF in order to achieve a functional symbiosis. As a consequence of this modulation, a mild, but effective activation of the plant immune responses may occur, not only locally but also systemically. This activation leads to a primed state of the plant that allows a more efficient activation of defence mechanisms in response to attack by potential enemies.

9.1 Introduction

Mutually beneficial interactions between plants and microbes are frequent in nature. Common benefits for the plant are improved plant nutrition and/or increased capability to cope with adverse conditions. In the case of arbuscular mycorrhizal (AM) associations, the symbioses alter plant physiology, leading to a better mineral nutrition and to increased resistance/tolerance to biotic and abiotic stresses. Although it should be noted that the ability to enhance plant resistance/tolerance differs among AM fungal isolates and can be modulated by environmental conditions, general trends emerge from the multiple studies dealing with mycorrhiza-induced resistance in different pathosystems. Enhanced resistance/tolerance to soil-borne pathogens has been widely reported in mycorrhizal plants (Whipps 2004). Although it is clear that the symbiosis may also impact plant interactions

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with aboveground attackers, the outcome of those interactions is less clear and seems to depend largely on the attacker lifestyle (Pozo and Azcón-Aguilar, 2007). This finding points to a differential regulation of plant defence signalling pathways. In this chapter, we summarise the information available regarding mycorrhiza-induced resistance (MIR) with special emphasis on the involvement of plant defence mechanisms.

9.2 Mycorrhiza-Induced Resistance Against Pathogens

Most studies on protection by AM against soil-borne diseases report reductions in incidence and/or severity of root rot or wilting caused by fungi such as *Rhizoctonia*, *Fusarium* or *Verticillium*, and root rot caused by oomycetes including *Phytophthora*, *Pythium* and *Aphanomyces*. A comprehensive review of these studies was compiled by Whipps (2004). Similarly, a reduction in deleterious effects caused by parasitic nematodes, such as *Pratylenchus* and *Meloidogyne*, is common in mycorrhizal plants (de la Peña et al. 2006; Li et al. 2006). Because of the common localisation in the root of both attackers and AM fungi, it is generally difficult to discern the local or systemic character of the protection. However, the use of split-root experimental systems, allowing physical separation between AM fungi (AMF) and pathogens, has revealed reductions in pathogen infection and in disease symptoms in the non-mycorrhizal parts of root systems of mycorrhizal plants. Systemic protection at the root system level has been demonstrated against *Phytophthora* and *Ralstonia* in tomato (Cordier et al. 1998; Pozo et al. 2002; Zhu and Yao 2004), *Gaeumannomyces* in wheat (Khaosaad et al. 2007) and recently against plant parasitic nematodes in banana plants (Elsen et al. 2008). Such effectiveness against a diverse range of attackers, including nematodes, oomycetes, bacteria and fungi, confirms the broad spectrum character of the induced resistance associated with the AM symbiosis.

Information about mycorrhizal effects on aboveground diseases is scarce and apparently less conclusive. Early reports associated AM symbioses with enhanced susceptibility to viruses (see Whipps 2004 for review). In line with those studies, it was proposed that mycorrhizal plants are more susceptible to shoot pathogens (Shaul et al. 1999). However, recent studies dealing with pathogens of different lifestyles have reported a more complex reality. Biotrophic pathogens, such as powdery mildew and rust fungi (*Blumeria*, *Oidium*, *Uromyces*), seem to perform better in mycorrhizal plants, although increased tolerance was often observed in terms of plant mass and yield (Gernns et al. 2001; Whipps 2004). Concerning hemibiotrophs, the impact of the symbiosis varies from no effect to reduction of the disease, for example against *Colletotrichum orbiculare*, the causal agent of anthracnose in cucumber (Lee et al. 2005; Chandanie et al. 2006). Finally, several studies have observed a positive effect of the symbiosis on plant resistance to other shoot pathogens. In tomato, AM reduced disease symptoms caused by a phytoplasma and conferred protection against the necrotrophic fungus *Alternaria solani* (Lingua et al. 2002; Fritz et al. 2006; de la Noval et al. 2007). Similarly, colonisation by

Glomus mosseae reduces disease symptoms and proliferation of *Pseudomonas syringae* in tomato leaves (J. García-Andrade and M.J. Pozo, unpublished results). Liu and coworkers have recently shown increased resistance of mycorrhizal *Medicago* to the shoot bacterial pathogen *Xanthomonas campestris* (Liu et al. 2007).

9.3 Effects of AM Symbioses on Phytophagous Insects

Interaction with herbivorous insects is also altered in mycorrhizal plants, as the symbiosis has an impact on the growth and/or survival of those insects. Again, while the symbiosis consistently reduces attacks by root-feeding insects, effects on foliar-feeding ones are more variable. A detailed analysis of published studies allowed Gange (2006) to reach important conclusions, despite the diversity in experimental approaches and systems analysed. In general, AM reduce the incidence of generalist chewing insects, while sap-feeding or specialist insects show increases in performance on mycorrhizal plants (Gange 2006). Such a pattern may indicate that the final outcome of the interaction is largely determined by the insect lifestyle and the degree of specialisation. While generalist insects are sensitive to plant defence mechanisms, specialist herbivores are likely to be able to circumvent the defences of their host plant and remain undetected. As a result, generalists may be affected by the enhanced defence capacity of mycorrhizal plants, while specialists will circumvent the defences and may benefit from improved nutritional status of the mycorrhizal host plant. Despite these general trends, the outcome depends on the plants and organisms involved in each specific interaction. For example, although several works reported increased performance of sap-feeding insects in mycorrhizal plants (Gange 2006), colonisation by *G. mosseae* significantly reduced the performance of potato aphids in tomato (Guerrieri et al. 2004). The scheme in Fig. 9.1 summarises the general effects of AM on different plant attackers.

9.4 Mechanisms of Mycorrhiza Induced Resistance

There is experimental evidence that plant protection by AM results from a combination of mechanisms acting at different levels (Azcón-Aguilar and Barea 1996). The most widely accepted mechanisms to explain mycorrhiza-induced protection are the improvement of plant nutrition and the compensation by the symbiosis of the damage caused by the pathogen. However, studies including nutrient-supplemented controls have shown that mycorrhizal effects cannot be regarded as a mere consequence of improved phosphorus nutrition (Shaul et al. 1999; Fritz et al. 2006; Liu et al. 2007). Another important factor is competition between AMF and pathogens for photosynthates and, in the case of root pathogens, for colonisation sites (Cordier et al. 1998). Mycorrhizal establishment also induces changes in root system

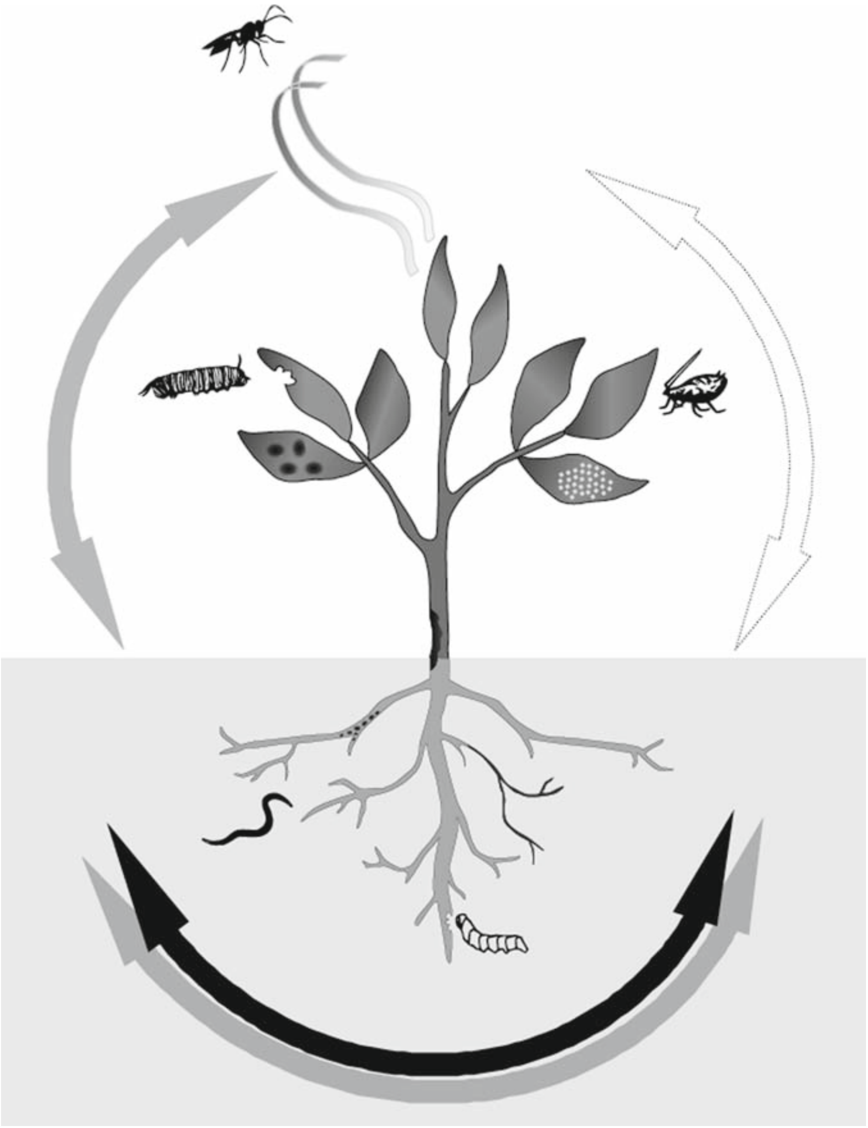

Fig. 9.1 Spectrum of efficiency of mycorrhiza-induced resistance (MIR). AM symbioses generally reduce incidence and/or damage caused by soil-borne pathogens, nematodes and root-chewing insects (*bottom*). The protection results from the combination of local and systemic mechanisms (represented by a *double arrow*). In aboveground tissues, MIR is effective against necrotrophic pathogens and generalist chewing insects (*left*). Indirect defence responses are also enhanced: parasitoids are more attracted by volatiles released by AM plants. Viral and fungal biotrophs, as well as phloem-feeding insects, perform better on mycorrhizal plants (*right*). *Solid* and *open arrows* indicate increased resistance or susceptibility, respectively, of mycorrhizal plants. Drawing by J. Perez-Tienda. Reproduced with permission from Pozo and Azcón-Aguilar (2007)

architecture and morphology. These changes may alter the dynamics of infection by the pathogen, although direct evidence for such a correlation is lacking. An additional level of complexity is the fact that mycorrhization determines important changes in rhizosphere microbial populations, and these changes may lead to the stimulation of components of the microbiota with antagonistic activity toward certain root pathogens (Barea et al. 2005). Finally, the contribution of plant defence mechanisms has been highlighted in different studies, and this will be the main focus of this chapter.

As mentioned above, several of these mechanisms may be operative simultaneously, with individual contributions depending on environmental conditions, timing of the interaction and partners involved (Azcón-Aguilar and Barea 1996; Whipps 2004). A key factor in the induction of resistance seems to be the extension of root colonisation by AMF. Studies comparing different mycorrhizal colonisation levels conclude the requirement of a well-established AM symbiosis for local and systemic induced resistance (Slezack et al. 2000; Khaosaad et al. 2007). However, there are reports on biocontrol of pathogens in non-AM species by co-culture with mycorrhizal plants. Whether this effect is related to induced resistance or to microbial interactions in the soil remains to be elucidated (St-Arnaud et al. 1997).

9.5 Modulation of Plant Defence Responses in Mycorrhizal Plants

During interactions with microorganisms, plants are able to recognise microbe-derived molecules and tailor their defence responses according to the type of micro-organism encountered. The molecular dialogue established between both partners will determine the final outcome of the relationship, ranging from parasitism to mutualism, usually through highly coordinated cellular processes (Bais et al. 2004; Pozo et al. 2005; see Chapter 2 by Provorov and Vorobyov). A tight control in the regulation of plant defence mechanisms appears to be a key aspect in AM fungal colonisation and compatibility with the host (Gianinazzi-Pearson 1996). Remarkably, a correlation between mycorrhiza-induced protection and the ‘autoregulation of mycorrhization’ has been proposed (Vierheilig et al. 2008). The autoregulation is manifested as a reduction in root colonisation by AMF once plants are already mycorrhizal. Mechanisms operating in such autoregulation may also impact plant interactions with pathogenic fungi (Vierheilig et al. 2008).

There is evidence for the accumulation of defensive plant compounds related to mycorrhization, although to a much lower extent than in plant–pathogen interactions (Gianinazzi-Pearson et al. 1996). Accumulation of reactive oxygen species, activation of phenylpropanoid metabolism and accumulation of specific isoforms of hydrolytic enzymes such as chitinases and glucanases has been reported in mycorrhizal roots. However, these reactions are generally localised, suggesting a role in AM establishment or control of the symbiosis (Dumas-Gaudot et al. 2000;

García-Garrido and Ocampo 2002; Pozo et al. 2002). It should be noted that the pattern of PR protein accumulation and the expression of defence-related genes varies during interactions with different AMF (Pozo et al. 1999; Pozo et al. 2002; Gao et al. 2004).

Concerning aboveground effects, transcriptional regulation of defence-related genes and accumulation of insect antifeedant compounds have been reported in shoots of mycorrhizal plants (Gange 2006; Liu et al. 2007). Liu and co-workers (2007) described a complex pattern of changes in gene expression in roots and shoots associated with mycorrhizal colonisation in *Medicago truncatul*a. Defence-related genes were among those with altered expression levels, and the authors correlated that finding with increased resistance to shoot pathogens. Furthermore, the volatile blends released by AM plants can be more attractive to aphid parasitoids than those from non-mycorrhizal ones, as shown in tomato plants (Guerrieri et al. 2004). These results indicate that not only direct, but also indirect, plant defence mechanisms may be modulated in mycorrhizal plants. There is also evidence for systemic repression of plant defence associated with AM symbioses: a delay in the accumulation of PR proteins in response to some defence-related stimuli has been observed in mycorrhizal tobacco (Shaul et al. 1999; Dumas-Gaudot et al. 2000). Altogether, experimental evidence confirms the systemic modulation of plant defence in AM. This modulation may explain the pattern of enhanced resistance/susceptibility of mycorrhizal plants to diverse pests on the basis of the different signalling pathways involved in the plant response to particular attackers. In addition, it would explain the fact that AM can modulate the effectiveness of chemically-induced plant resistance (Sonnemann et al. 2005).

9.6 Priming of Defence Mechanisms in Mycorrhizal Plants

With the exception of the limited activation of plant defence discussed above, a direct activation of defences has not been observed in mycorrhizal plants. This contrasts with the systemic acquired resistance (SAR) triggered in plants after infection with necrotising pathogens. Indeed, systemic accumulation of PR proteins, salicylic acid or expression of marker genes associated with SAR has not been reported in tissues of mycorrhizal plants. This is also the case for systemic resistance achieved after colonisation by other beneficial organisms, such as certain rhizobacteria and other beneficial fungi (Van Wees et al. 2008). Despite the vital character of defence responses, constitutive expression of defence is too costly for the plant. Thus, beneficial micro-organisms have developed the ability of enhancing resistance not through a direct activation of defence, which would be too expensive for the plant in the absence of challenging attackers, but through priming of the defence mechanisms.

Molecular studies have confirmed that quantitative, rather than qualitative, differences in the defence mechanisms determine plant resistance or susceptibility to a pathogen (Nimchuk et al. 2003). Indeed, a rapid and strong activation of defence mechanisms is crucial for success in controlling attackers. Accordingly, preconditioning of plant tissues for a quick and more effective activation of defence upon attack has important ecological fitness benefits and seems to be a common feature of the plant's immune system (Conrath et al. 2006). This boost of basal defences, known as priming, seems to be successfully triggered by certain beneficial micro-organisms (Pozo et al. 2005; Van Wees et al. 2008), including AMF (Pozo and Azcón-Aguilar 2007).

Several studies point to priming as a main mechanism operating in MIR, indicated by stronger defence reactions triggered in the mycorrhizal plant upon attack. Mycorrhizal transformed carrot roots displayed stronger defence reactions at challenge sites by *Fusarium* (Benhamou et al. 1994). Mycorrhization also amplified the accumulation of the phytoalexins rishitin and solavetivone in *Rhizoctonia*-infected potato plantlets, while AMF themselves did not alter the levels of these compounds (Yao et al. 2003). Priming for callose deposition seems to be the mechanism involved in the protection achieved by *G. intraradices* against *Colletotrichum* in cucumber (Lee et al. 2005). Furthermore, colonisation by AMF systemically protects root systems. This was first illustrated for tomato plants against *Phytophthora parasitica* infection (Cordier et al. 1998; Pozo et al. 2002). Only mycorrhizal plants formed papilla-like structures around the sites of pathogen infection in non-mycorrhizal regions with 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* infection (Cordier et al. 1998; Pozo et al. 1999; Pozo et al. 2002). Mycorrhizal protection of grapevine roots against *Meloidogyne incognita* has also been associated with primed expression, ubiquitously throughout the whole root system, of a chitinase gene, *VCH3*, in response to the nematode (Li et al. 2006). These different observations illustrate that primed responses are not restricted to AMF colonised areas, but they occur in the whole root system.

To investigate whether mycorrhizal colonisation leads to systemic priming of defence in aerial tissues, we compared the response of non-mycorrhizal plants or plants colonised by either *G. mosseae* or *G. intraradices* to the application in the shoots of different defence-related stimuli. Gene expression and enzymatic activities were monitored in a time course experiment after shoot treatment with jasmonic acid (JA), ethylene (ET) or salicylic acid (SA). Transcript profiling of leaves of mycorrhizal and non-mycorrhizal plants 24 h after treatment with JA revealed a stronger induction in mycorrhizal plants, particularly in *G. mosseae* colonised plants, of JA-regulated genes, including typical defence-related JA responsive genes such as those coding for proteinase inhibitors (Fig. 9.2; A. Verhage and M.J. Pozo, unpublished results). Our results show different defence-related gene regulation patterns in mycorrhizal plants, and point to a prominent role of priming for JA-dependent responses in AM-induced resistance.

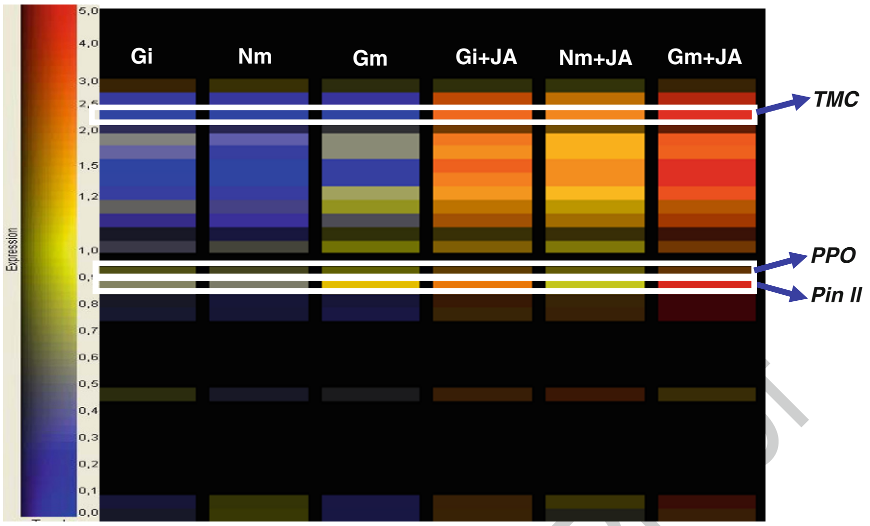

Fig. 9.2 Primed expression of JA-responsive genes in mycorrhizal plants. Induction of gene expression in tomato leaves upon treatment with methyl jasmonate (*+JA*) as a defence inducer was compared in non-mycorrhizal (*NM*) and mycorrhizal plants colonised by either *Glomus mosseae* (*Gm*) or *G. intraradices* (*Gi*). Transcriptomic analysis was performed using Affymetrix GeneChip® tomato Arrays, including probe sets for about 10,000 tomato genes. The heat map depicts a cluster of JA responsive genes with primed expression in mycorrhizal plants, including those coding for the defence-related tomato proteins multicystatin (*TMC*), polyphenol oxidase (*PPO*) and proteinase inhibitor II (*PIN II*). The expression values are represented following the colour scale on the left, ranging from blue (low expression level) to red (high expression level). Note that primed expression upon treatment was more pronounced in *G. mosseae* (*Gm+JA*) than in *G. intraradices* (*Gi+JA*) colonised plants

9.7 Signalling Pathways Involved in Mycorrhiza Priming of Defence

Plant defence mechanisms are tightly regulated through an interconnected network of signalling pathways in which JA, ET and SA play major roles. Priming is often manifested as a sensitisation of the tissues to one or some of the signalling molecules (Conrath et al. 2006). Salicylic acid coordinates defence mechanisms are generally effective against biotrophic pathogens, whereas JA regulates wounding responses and resistance against necrotrophs (Ton et al. 2002; Glazebrook 2005). Nevertheless, there is some overlap in their spectrum of efficiency, especially concerning pathogens with intermediate lifestyles (Thaler et al. 2004; Pozo et al. 2005). Insect feeding guilds also determine the response they trigger in the plant. Generalist chewing insects, but not phloem-feeding ones, cause wounding and trigger JA-regulated responses (Heidel and Baldwin 2004; De Vos et al. 2005). These signalling pathways are not independent: intensive interactions ranging from synergism to antagonism shape a complex regulation network, in which trade-offs between SA and JA pathways are well documented (Bostock 2005; Beckers and Spoel 2006; Koornneef and Pieterse 2008).

As obligate biotrophs, AMF share similarities with biotrophic pathogens (Paszkowski 2006). Coherently, transcriptional profiling comparing plant responses during interactions with AM and pathogenic fungi showed that plant responses to AMF overlap more with those induced by the hemibiotroph *Magnaporthe grisea* than with those by the necrotroph *Fusarium moniliforme* (Güimil et al. 2005). Thus, AMF sensitivity to SA-regulated defences is likely. Indeed, exogenous SA application delays mycorrhizal colonisation, and plant mutants altered in endogenous SA levels point to a role of this pathway in the control of the AM symbiosis (García-Garrido and Ocampo 2002). It is plausible that AMF partially repress SA-dependent defence responses in the host in order to achieve a compatible interaction. A suppression of SA responses is also necessary for the establishment of the *Rhizobium*–legume symbiotic association (Stacey et al. 2006). In the case of mycorrhizal plants, such attenuation could explain the delay in systemic accumulation of PR proteins upon treatment with SA or analogs (Shaul et al. 1999; Dumas-Gaudot et al. 2000) and the reported enhanced susceptibility of mycorrhizal plants to viruses and certain biotrophic pathogens (Pozo and Azcón-Aguilar 2007). How would attenuation of plant defence fit with the widespread and mutualistic character of AM associations? A possible explanation may be by compensation via other defence signalling pathways.

A symbiotic program has to be activated in the host plant to achieve a successful mutualistic interaction upon recognition of the AM fungal partner (Reinhardt 2007). This program should allow a redistribution of nutrients and active physical accommodation of the fungal symbiont inside root cells (Genre et al. 2005). Both aspects may be regulated by jasmonates (Hause et al. 2007). Roots of mycorrhizal plants are associated with higher levels of endogenous JA as compared to non-mycorrhizal ones. The increase occurs after the onset of mycorrhization, and is probably related to fully established mycorrhizas (Hause et al. 2002). Elevated levels of basal JA production could be related to the increased resistance of mycorrhizal plants to certain pathogens and insects. In line with this hypothesis, experimental evidence linking the JA pathway to primed deposition of callose and enhanced resistance to oomycetes (Hamiduzzaman et al. 2005) argues for a role of JA signalling in the primed papillae formation observed in mycorrhizal tomato root systems upon infection with *Phytophthora* (Cordier et al. 1998). Recently, a central role for JA in systemic immunity has also been proposed in *Arabidopsis* (Truman et al. 2007). It is tempting to speculate that JA also serves as endogenous signal in MIR.

It is noteworthy that parallels exist between rhizobacteria and mycorrhiza-induced resistance. Like MIR, rhizobacteria-mediated ISR is mainly effective against necrotrophic pathogens and is based on priming of JA regulated responses (Verhagen et al. 2004). ISR by other beneficial organisms also seems to be associated with priming of JA-inducible responses (Pozo et al. 2005; Van Wees et al. 2008). Thus, modulation of plant defence mechanisms and conditioning of plant tissues for a more efficient activation of JA responses may be a common feature of beneficial interactions.

In summary, we propose that a functional mycorrhiza implies partial suppression of SA-dependent responses in the plant, compensated by an enhancement of those that are JA-regulated. This would result in priming of JA-dependent defence mechanisms (Pozo and Azcón-Aguilar 2007). Experimental evidence supports such a hypothesis: AM induced systemic protection against take-all disease is independent of systemic accumulation of salicylic acid (Khaosaad et al. 2007), and AM symbiosis primes tomato plants for a stronger activation of JA-dependent defence responses (Fig. 9.2). This defence regulation model is coherent with the spectrum of effectiveness described for MIR: increased susceptibility to biotrophs, and increased resistance to necrotrophs and generalist chewing insects (summarised in Fig. 9.1).

9.8 Conclusions

Mycorrhizal symbioses have an important impact on plant interactions with pathogens and insects. The association generally leads to reduction of damage caused by soil-borne pathogens, but effects on shoot-targeting organisms depend greatly on the attacker lifestyle. Mycorrhiza-induced resistance (MIR) in aboveground tissues seems effective against necrotrophic pathogens and generalist chewing insects, but not against biotrophs. Instead of constitutive activation of plant defence, MIR is associated with priming for an efficient activation of defence mechanisms upon attack. The spectrum of MIR efficiency correlates with a potentiation of JA-dependent plant defences. This low-cost type of induced resistance may be among the reasons to explain why root associations with AMF have been conserved during evolution and are widespread among plant species.

There is growing awareness about the importance of soil microbiota in natural and man-made ecosystems. Indeed, progresses in basic knowledge of plant interactions with mycorrhizal fungi, identification of markers associated with induced resistance, as well as the generation of predictive models for the outcome of particular interactions, may have important practical implications regarding the effectiveness of AMF in the biological control and integrated management of pests and diseases.

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