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Chapter

Mycorrhizal Association and Plant Disease Protection: New Perspectives

Julio Alves Cardoso Filho

Abstract

Soil fungi of the phylum Glomeromycota and plants form arbuscular mycorrhizal (AM) symbiosis. The AM fungi, during the symbiosis, establish a sink for plant photosynthate by utilizing it for biomass and metabolic energy, while the AM plants obtain nutrients and water through the AMF hyphae. The benefits of AM symbiosis on plant fitness include better mineral nutrition, especially those that are immobile in soil solution (e.g., phosphorus, copper, and zinc), and higher tolerance of mycorrhizal plants to abiotic stresses, such as drought, salinity, high soil temperature, presence of heavy metals, and others abiotic factors. Recent studies have revealed that AMF can suppress pests and plant diseases by the activation of defense regulatory genes. The knowledge of the mechanisms behind the induction of resistance by mycorrhizal symbiosis (mycorrhizal-induced resistance [MIR]) remains unknown. This chapter describes the current advanced status of the role of MIR in plant disease protection.

Keywords: plant defense, arbuscular mycorrhizas, mycorrhizal-induced resistance

1. Introduction

Mycorrhizas are complex symbioses formed by several components that determine the rate of colonization, such as the incidence of propagules, and the effects and functions of symbiosis on plants and ecosystems [1]. Mycorrhizal fungi improve the host plant's resistance to environmental stresses, while the host plant provides carbon in the photosynthates form, for fungal growth and reproduction [2–4]. Arbuscular mycorrhizas (AMs) are beneficial interactions formed by plant roots and soil fungi of the phylum Glomeromycota [1]. The regulation of mycotrophism determines the response of the host plant, and biotrophism controls the degree of colonization and production of propagules, guaranteeing the survival and evolution of this group of fungi [5, 6]. AM is the most widespread form of mycorrhizal association and is of great ecological and economic importance [7–9]. AMs are compartmentalized biological systems. Thus, they suffer from the influence of the environment and numerous edaphic factors of each component that directly or indirectly control the establishment, the functioning, and the occurrence of AM [10–15]. AM symbiosis is generally inhibited under high fertility and favored by low fertility, where colonization and sporulation are generally maximal. Phosphorus (P) fertilization in the soil optimizes plant growth and reduces colonization [16].

The protection against soil-borne pathogens has been reported in mycorrhizal plants [17–24]. The differential expression of several genes involved in plant defense against pathogen attack has been observed and may play a fundamental role in colonization [25–27]. This modulation seems to occur not only locally but also systemically [28]. This phenomenon, called "priming," results in an induction of basal resistance mechanisms upon subsequent pathogen attack [28-31]. In symbiotic systems, microbial-associated molecular patterns (MAMPs) from AM fungi are perceived and elicit a transient defense response, which later undergoes suppressed induction at the early stages of AM [32]. The absence of a hypersensitive response (HR) after AM fungi recognition may reflect a non-activation, a low level of defense response, or suppression of the plant defense system [30, 31]. The phenylpropanoid biosynthetic pathway, widely known for the action of phytoalexins, involves a series of enzymes that can be regulated at the transcriptional level by biotic and abiotic stimuli and is influenced by mycorrhization [30, 31]. In signaling the localized induction of defense genes considered specific, two types of mechanisms may be involved: acid endochitinase PR4 and β 1,3-endoglycanase EG488 and the systemic suppression of the expression of genes encoding these enzymes and those involved in the phenylpropanoid metabolism [32]. The expression of genes related to the plant defense system is systemically suppressed during the establishment of AM symbiosis [33]. However, the expression of other genes is locally induced, and the modulation of these responses depends on external factors, such as the phosphate level [34, 35].

In this chapter, we want to discuss new perspectives and updates on mycorrhizainduced resistance (MIR).

2. Resistance of plants to microorganisms

The plant defense system is multi-component, acting in a dynamic and coordinated manner, at the appropriate time and place and with adequate magnitude [36–39]. Plant resistance would be its ability to delay or prevent the colonization of its tissues by a phytopathogen, characterized by its dynamic and coordinated nature in a sequence of logical events, immediately after the pathogen contacts its tissues [40]. The growing development of technologies aimed at agriculture and increases in the use of inputs, especially pesticides, have contributed to increased agricultural productivity and adverse effects on the environment and human health. New plant protection measures have been highlighted; such as the induction of resistance (IR) has been used to control pests and diseases [41–43].

2.1 Non-host resistance in plants

Land plants are sessile, and despite not having an adaptive immune system similar to animals, they are resistant to most microorganisms that attack them in an attempt to invade their tissues [44]. This phenomenon characterizes resistance as a rule and susceptibility to some microorganisms. This recognition of non-adapted pathogens by non-host plants at the cellular level is called non-host resistance (NHR) [45]. Non-host resistance (NHR) is, by definition, the resistance displayed by all genotypes of a plant species to all genotypes of a pathogen species, being considered the most common and effective form of resistance to diseases that occur in nature

[46]. Several genes appear to control the NHR in a given plant species; in addition, the number of genes involved is related to the specific genotype of the analyzed plant [46]. NHR "resistance" refers to the inability of a pathogen to complete its asexual or sexual life cycle on that host plant species [47]. NHR is a tool for breeding against the induction factors of biotic and abiotic stresses, aiming at the development of durable genetic resistance [48]. NHR is an elaborate defense system that protects plants against invasion by non-pathogenic or pathogenic organisms and involves physical and biochemical mechanisms [49, 50]. These defenses include a combination of preformed and inducible mechanisms [51] that act as a physical barrier to penetration and as a toxic barrier [52]. The first line of plant defense is the structural and biochemical mechanism that is present even before the inoculum deposition, called constitutive or passive [53]. The barrier imposed by the cuticle and cell wall is considered an important factor of NHR. The cuticle is structurally variable between plant species; is composed of cutin, waxes, and hydrocarbons; and is closely associated with the cell wall of the epidermal cells [54]. Others mechanisms are activated from the recognition of the pathogen, by the host plant that is active, inducible, or post-formed, and can also be structural and biochemical [55]. Among the biochemical post-formed responses is the accumulation of reactive oxygen species (ROS), phytoalexins, pathogenesis-related (PR) proteins, and HR [56]. However, most defense mechanisms are activated in response to infection by the pathogen [57]. During initial contact with the pathogen, pathogen-associated molecular patterns (PAMPs) [58], such as chitin and glucans in fungi, flagellin, and elongation factor Tu in bacteria, are recognized by the plant through pattern recognition receptors (PRRs) [59]. Recognition of PAMPs triggers signaling events and basal resistance, called PAMP-activated immunity (PTI) [60]. Pathogens have evolved effectors that interfere with different signaling processes involved in plant defense, suppressing PTI, promoting virulence, and triggering effector-activated susceptibility (ETS) [61]. Plants, in turn, acquired resistance (R) genes that detect pathogen-specific effectors, resulting in effector-activated immunity (ETI) [62]. ETI is a version of PTI, typically involving HR, a form of programmed cell death that limits colonization by the pathogen [60]. HR is mediated by the accumulation of ROS, which, in addition to having a toxic effect on the pathogen, can act as secondary messengers for the activation of defense responses [63–67]. Mitogen-activated protein kinases (MAPKs) modulate the activity of transcriptional regulators and phytohormones [68]. Salicylic acid (SA), ethylene, and jasmonic acid are the main hormones involved in signaling. Other hormones, such as abscisic acid and cytokinins, have also emerged as participants in signaling pathways for defense [69, 70]. As a result of the recognition of the pathogen by the host and the consequent activation of signal transduction pathways, several defense mechanisms are formed to limit the infection [71–78]. All plant species are capable of constitutively biosynthesizing chemical compounds with potential defensive function, suggesting that this ability is an evolutionary trait [79]. A feature of antimicrobial compounds is that some are found on the plant surface or accumulated in cells close to the host surface, especially vacuoles or organelles in epidermal cells, and released by hydrolytic enzymes after attack by the microorganism [80].

2.2 Host resistance in plants

The microorganisms that manage to overcome the mechanisms of RNH become pathogens of the plant species and need to act against the host resistance that the plant has [81]. Plants also have a surveillance system that detects/monitors the presence or activity of effector molecules within their tissues and cells. This surveillance system has specific receptors (R proteins) encoded by the plant's R genes [82]. The typical R proteins with nucleotide-binding and leucine-rich domains (NLRs) have an ATPase-binding domain (NB—nucleotide-binding ATPase) and a TIR (toll interleukin-1 receptor) or CC (coiled-coil) domain forming the TIR-NB-LRR or CC-NB-LRR proteins, respectively [82]. The NB domain serves ATP binding and hydrolysis/signaling cascade, and the LRR domain is responsible for activation/ autoinhibition. In the LRR domain, the N-terminal activates the modulation, while the C-terminal is related to recognition specificity [83–85]. Proteins from the NLR genes in their inactive form (absence of the effector cognate) are located in the host cell cytoplasm bound to the plasma membrane, endoplasmic reticulum, or tonoplast. In the presence of the effector, the cognate can move to the nucleus, interacting with transcription factors or with other cytoplasmic proteins to start the signaling chain for the expression of defenses [86–89]. Effector detection triggers a signaling cascade that culminates in the expression of defense and HR genes to contain the pathogen's advance, resulting in race-specific resistance, the ETI immune response, also known as vertical resistance. ETI is one of the main components of host resistance [90, 91]. ETI is activated by the direct or indirect interaction between one or more effectors and one or more NLR proteins. In the Decoy model, where the NLR detects changes in a protein that mimics the target, the effector apparently does not have a defined biological function [92, 93]. In the Guard model, during infection, a modification of the target protein (monitored) occurs by the action of the effector releasing the R protein (monitor), thus allowing it to initiate the signaling cascade that leads to the induction of ETI [94]. Resistance conferred by R genes depends on the effector for virulence or adaptability of the pathogen and its evolutionary potential [95]. From the point of view of resistance durability, for resistance conferred by R genes (qualitative resistance), the evolutionary pressure on the pathogen conferred by quantitative resistance is significantly reduced, thus constituting a source of durable resistance [96]. In summary, resistance mediated by R genes is specific to certain races of the pathogen and effective against biotrophic and hemibiotrophic parasites. On the other hand, quantitative resistance provides a means for controlling biotrophic, hemibiotrophic, and necrotrophic pathogens, being effective against several races of a pathogen, providing broad-spectrum resistance, or in some specific cases, effective against several pathogens [97–103].

3. Plant priming for enhanced defense

To compensate for their sessile life and face a broad range of biotic and abiotic stresses, plants have evolved survival and adaptation strategies, such as inducing some stress memory or stress imprinting [104]. In plants, the IR is frequently associated with the accumulation of antimicrobial pathogenesis-related (PR) proteins and with the so-called priming of cells [89]. Priming for enhanced defense is a cellular process in biological and chemical IR immunity, including systemic acquired resistance (SAR), induced systemic resistance (ISR), and herbivore-induced resistance [105–109]. Plants maintain immune memory through priming, in the absence of such specialized cells [110, 111].

3.1 Epigenetic molecular mechanism of priming

3.1.1 Memory of plant immunization

Advances in the knowledge of epigenetic regulation in the plant multiple generation stress memory have provided new procedures and approaches for breeding crops and sustainable germplasm banks for future climate challenges [112, 113]. Plant stress memory is described under two categories: mitotic stress memory, or somatic memory, and meiotic stress memory, or transgenerational memory [114–116]. Plant stress memory associated with the inheritance of SAR is likely to be epigenetic [117, 118]. In plants, defense priming and SAR are associated with epigenetic modifications of histones, DNA methylation, increased signaling enzymes, and an accumulation of pattern recognition receptors (PRRs) at cell membranes [119, 120]. In summary, strategies exploiting epigenetic variations appear promising for crop resistance breeding [121–124].

4. Mycorrhiza-induced resistance: new perspectives

The effects of AM symbiosis on plant interactions with other organisms, such as the induction of resistance against plant pathogens, seem to result from the combination of multiple mechanisms that may operate simultaneously [125]. A proposed hypothesis is that colonization of roots by AM fungi primes defense mechanisms, leading to mycorrhiza-induced resistance (MIR) [126] by the activation of MAMP-triggered immunity (MTI) [127]. MIR is a low-cost type of induced resistance that may be among the reasons to explain why root associations with AM fungi have been conserved during evolution and are widespread among species [128, 129]. MIR includes a priming of defense-related plant genes and shares more elements with the ISR induced by rhizobacteria [130, 131]. The plant can restrict AMF colonization once the plant is already mycorrhizal, a phenomenon known as autoregulation [132]. The mechanisms operating in such autoregulation may also affect plant interactions with phytopathogens [133]. However, the molecular mechanisms that regulate the formation and establishment of AM symbiosis and the modulation of plant defense responses during MIR are still not understood [134]. According to Fiorilli et al. [135], who elucidate the molecular mechanisms underlying the establishment of AM symbiosis, we need to investigate the changes in transcripts and proteins in roots and leaves during the double (plant-AM fungus) and tripartite (plant-AM fungus-pathogen) interactions [136, 137]. The recognition of friend versus foe is still incompletely understood in signaling between the host plant and the pathogen interaction [138-141]. Another critical challenge is to elucidate the biological roles of receptor-like kinases (RLK) mediated by endocytosis in the plant interaction with microbes, aiming to elucidate the molecular mechanisms by which pathogens and non-pathogen microorganisms can reprogram the RLK trafficking [142, 143]. Besides, the role of MIR against viruses and foliar phytopathogens stays in the speculative field. In some cases, the susceptibility to the foliar pathogen is related to mycorrhizal plants compared with non-mycorrhizal plants. However, it is linked with the higher amounts of plant phosphorus available to viruses for their multiplication in infected and colonized plants [144, 145]. Recent advances indicate that the beneficial effects of MIR may not be related to mycorrhizal plant nutrition [140]. Thus, knowing the

mechanisms of AM symbiosis physiology regulation under different environmental conditions is required to understand the MIR context of AM fungi-host plant dependency.

5. Conclusions and future prospects

MIR is a low-cost type of IR and has a positive effect from an ecological point of view. However, still, open questions require particular attention, among which is why infection by AM fungi does not elicit a defense response in roots. Besides, the role of MIR against viruses and foliar phytopathogens stays in the speculative field. Thus, knowing the mechanisms of AM symbiosis physiology regulation during MIR is required for their applications in sustainable agriculture.

Conflicts of interest

The author declares no conflict of interest.

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