Chapter 4
Signaling Events During the Establishment of Symbiosis Between Arbuscular Mycorrhizal Fungi and Plant Roots

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Abstract The most prevalent microorganism association in terrestrial plants is the symbiosis between arbuscular mycorrhizal fungi (AMF) and plant roots. This implies that the genetic background for establishing this symbiosis was developed in the early phases of land plant evolution. A symbiosis faces several challenges, such as penetrating plant cells and overcoming their defense mechanisms. At the same time, it must activate some developmental pathways for symbiotic structures along with membrane transporters required to exchange nutrients and metabolites between two partners. This chapter discusses the response of plants to fungal signals, the function of receptor molecules, and other actors that play a crucial role in the signaling pathways. Ultimately, these pathways result in the expression of symbiosis-specific genes and the formation of symbiosis-specific structures.

Keywords Arbuscule · Mycorrhizal fungi · Mycorrhizal symbiosis · Common symbiotic pathway · Ca^{2+} signaling pathway · Strigolactones · Phosphate acquisition · Plant immune response

4.1 Introduction

The most prevalent microorganism association in terrestrial plants is the symbiosis between arbuscular mycorrhizal fungi (AMF) and plant roots. This implies that the genetic background for establishing this symbiosis was developed in the early periods of land plant evolution. A symbiosis faces several challenges, such as penetrating plant cells and overcoming their defense mechanisms. At the same time, it must activate some developmental pathways for symbiotic structures along

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with membrane transporters required to exchange nutrients and metabolites between two partners. This chapter will discuss the response of plants to fungal signals, the function of receptor molecules, and other actors that play a crucial role in the signaling pathways. Ultimately, these pathways result in the expression of symbiosis-specific genes and the formation of symbiosis-specific structures.

4.2 The Common Symbiotic Pathway

Evidence from two significant beneficial plant–microbe interactions, namely, arbuscular mycorrhiza symbiosis (AMS) and root nodule symbiosis (RNS), revealed the molecular components that transduce the microorganism-derived signals to the plants, resulting in the establishment of a compatible plant-microbe symbiosis. Genetic and mutagenic approaches using legume species that are able to form both AMS and RNS interactions indicated that there are single plant mutations that could block the penetration of both bacteria and fungi to the root. These studies led to the hypothesis that AMS and RNS depend on a shared genetic toolkit as the apparatuses of a common symbiosis pathway (CSP). This pathway is believed to operate downstream of the perception of fungal and rhizobial signals but upstream of the activation of the plant's response to the symbiotic bacteria or fungi.

4.2.1 Receptors and Associated Proteins in the CSP

The initial step in establishing a compatible interaction between legumes and rhizobia is associated with a molecular dialog between two partners. This dialogue requires receptors on the plant side to sense the microorganism's signals.

SYMRK SYMBIOSIS RECEPTOR-LIKE KINASE (SYMRK), a leucine-rich repeat (LRR) receptor-like kinase (Does Not make Infections2, DMI2), constitutes the entry point of CSP and is essential for both RNS and AMS. SYMRK functions as a downstream module of Nod Factor Receptors (NFRs) and Myc Factor Receptors (MFRs) and is a principal component of symbiotic signaling that is functionally conserved. SYMRK is widespread in plant kingdoms but has been subjected to some diversification during evolution (Markmann et al. 2008). *Arabidopsis* lacking RNS or AMS contains SYMRK homologs, ShRK1 and ShRK2 (Shiu and Bleecker 2003), which promote the reproduction ability of the obligate biotroph, oomycete *Hyaloperonospora arabidopsis* (Hpa), within plant cells (Ried et al. 2019). This indicates a widespread function of SYMRK in the interactions between plants and microbes and an overlap between the signaling events related to intracellular symbionts and pathogens.

The knockout mutations of SYMRK abolish the formation of infection threads and inhibit nodulation, while overexpression of the full-length SYMRK or its kinase

domain results in the appearance of spontaneous nodules in the absence of rhizobia (Saha et al. 2014; Ried et al. 2014). This suggests that the kinase domain of SYMRK plays a determining role in nodulation. Many plant RLKs, such as SYMRK, are characterized by the presence of tyrosine (Tyr) in the "gatekeeper" position close to the hinge region of the kinase domain. This gatekeeper Tyr in SYMRK (Y^{670}) is essential for orchestrating epidermal/cortical responses in RNS (Saha et al. 2016) and is predominantly auto-phosphorylated in vitro and in planta (Samaddar et al. 2013).

The extra-cytoplasmic region of SYMRK consists of three leucine-rich repeats (LRRs) and a malectin-like ectodomain (MLD) (Chiu and Paszkowski 2020). Both LRRs and MLD elements are linked via the GDPC motif that is conserved in the majority of MLD-LRR RLKs. This area is cleaved to release the MLD without symbiotic stimulation. Although the truncated version of SYMRK (SYMRKΔMLD that lacks the MLD) is subject to high turnover, it is able to strongly and specifically associate with NFR5 and transduce the signal to downstream targets (Antolín-Llovera et al. 2014). However, the role of MLD release in the function of SYMRK in the AM symbiosis is obscure.

HMGR1 SYMRK interacts, through its cytoplasmic domain, with the enzyme HMGR1 (3-Hydroxy-3-Methylglutaryl CoA Reductase 1), a mevalonate (MVA) biosynthetic enzyme. It has been postulated that symbiotic signal perception by SYMRK leads to the induction of HMGR1, resulting in the localized formation of MVA. This MVA signal is then transmitted to the nucleus, which activates cation channels, thereby initiating nuclear-associated Ca^{2+} spiking (Venkateshwaran et al. 2015). Our knowledge of the players acting between the plasma membrane and the nucleus is extremely limited, and it must be determined whether the signal transition from the cytosol to the nucleus is solely mediated through MVA and its derivatives. Ca^{2+} spiking or Ca^{2+} oscillation is a key component of the interaction between plants and microbes. This is one of the most common events discriminating mutations of the CSP and is used in screening various mutants defective in establishing symbiosis.

4.2.2 Components of Ca^{2+} Signaling Pathway

Nuclear Pore Complexes The downstream components of the SYM pathway are localized in the nucleus, suggesting the trafficking of signaling molecules through the nuclear envelope. The involvement of several nucleoporins (NUPs), e.g., NUP85, NUP133, and NENA, in symbiotic signaling has been evidenced in genetic studies (Kanamori et al. 2006; Saito et al. 2007; Groth et al. 2010). Mutations in these nucleoporins lead to defective Ca^{2+} spiking and aborted symbiosis (Parniske 2008). It has been proposed that NUPs likely contribute to the protein translocation between the nuclear envelope's inner membrane and outer membrane (Tamura and Hara-Nishimura 2013).

Ion Channels The ion channels and the calcium pump that are localized in the nuclear envelope and necessary for generating calcium (Ca^{2+}) spiking have been identified in model legume plants. These transporters include (1) CASTOR and POLLUX (DMI1 in *Medicago truncatula*) that are potassium-permeable channels (Charpentier et al. 2008), (2) a PII-type Ca^{2+}-ATPase (MCA8) (Capoen et al. 2011), (3) and the Ca^{2+} channel, cyclic nucleotide gated channel 15 (CNGC15) (Charpentier et al. 2016). These three components (CASTOR/POLLUX, MCA8, and CNGC15) interact together and generate Ca^{2+} oscillation in the nucleus. It has been assumed that a cyclic nucleotide (CN) binds to and triggers the activation of CNGC15, leading to the release of Ca^{2+}. The mobility of potassium (K^+) ions that balances the transmembrane charge is mediated by CASTOR/POLLUX, whereas the return of Ca^{2+} to the store is mediated by MCA8. Since CASTOR/POLLUX, MCA8, and CNGC15 are localized to both the outer and inner nuclear membranes, Ca^{2+} spiking is produced on one or simultaneously on both sides of the nuclear envelope (Charpentier 2018).

Decoding Ca^{2+} Signature In the nucleoplasm, CCaMK (DMI3), a Ca calmodulin-dependent protein kinase, is potentially involved in decoding Ca^{2+} oscillations (Miller et al. 2013). CCaMK binds to and phosphorylates another nuclear protein, CYCLOPS (Interacting Protein of DMI3, IPD3) (Yano et al. 2008). Together with other transcription factors, CYCLOPS (IPD3) regulates the expression of symbiotic genes (Oldroyd 2013) (Fig. 4.1).

4.3 Signaling in the AMS

The AM fungi and the host plants must communicate at the molecular levels to establish symbiosis. First, the host root produces signaling molecules and releases them into the rhizosphere. Then, these signaling molecules induce the germination of fungal spores and branching of the fungal hyphae and subsequently induce the fungus to produce and release fungal factors responsible for the modifications in the host roots' gene expression.

4.3.1 Establishment of Symbiosis

The AMF spores may germinate without receiving any signal from plants. After germination, the germ tube extends simultaneously with the consumption of triacylglyceride and glycogen reserves to support growth. However, if the fungus fails to find a host root, the hyphal growth will cease to prevent the depletion of spore reserves. This allows the fungus to re-germinate and find a root of the host plant. In contrast, germ tube growth increases significantly near a root, and the hyphae undergo profuse branching, indicating the presence of specific signaling molecules

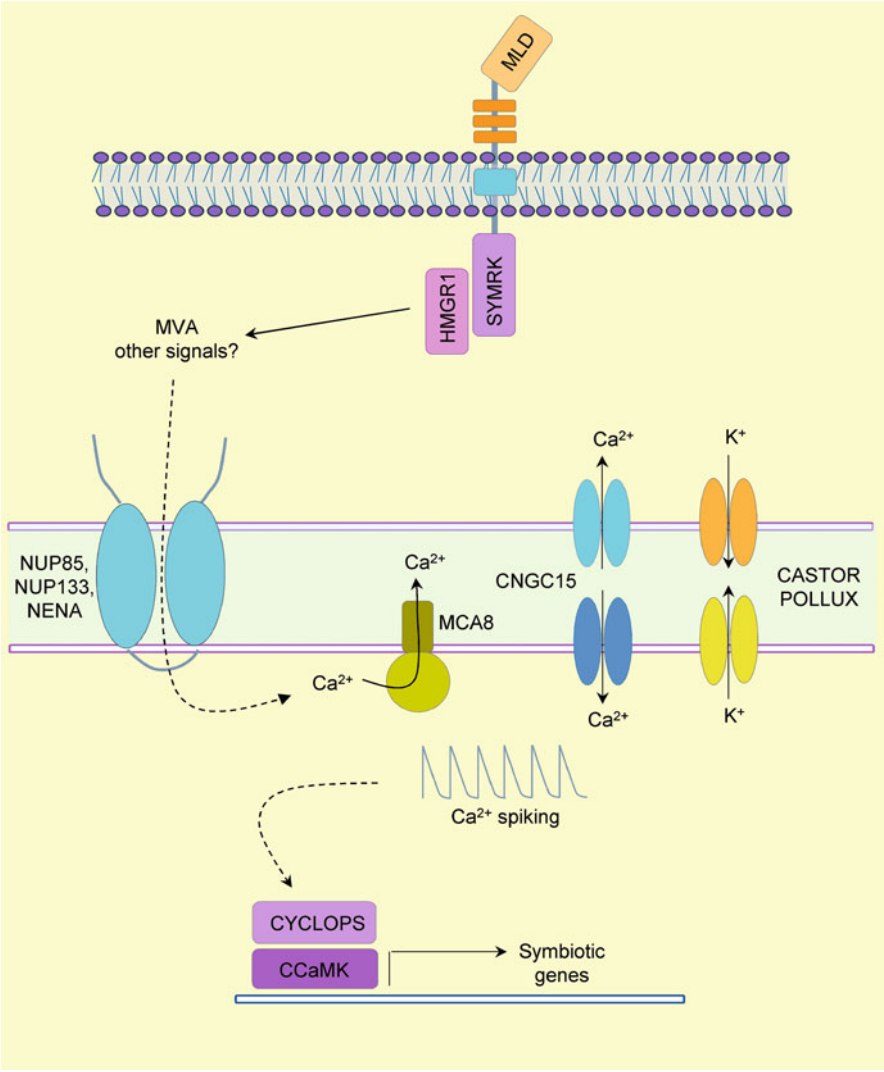


Fig. 4.1 The common signaling pathway. SYMRK is a common receptor complex member involved in the RNS and AMS signaling. The truncated form of SYMRK (the SYMRK version that remains after MLD release, SYMRK-ΔMLD) percepts NFR or MFR signal and produces MVA, as a second messenger, after its interaction with HMGR1. MVA, its derivative, or other unknown signals transduce the message to the nucleus through a nuclear pore complex (NUP85, NUP133, and NENA). Ca^{2+} spiking is initiated through a coordinated function of three transporter proteins, CASTOR/POLLUX (K^+ channels), MCA8 (Ca^{2+}-ATPase), and CNGC15D (Ca^{2+} channel). Ca^{2+} signal activates CCaMK, a Ca calmodulin-dependent protein kinase, leading to the phosphorylation and activation of its downstream target, CYCLOPS. As a transcription factor, CYCLOPS interacts with other transcriptional regulators (mostly RNS and AMS-specific), binds to the upstream elements of the symbiotic gene, and activates their transcription

(e.g., strigolactones (SLs); see below) in the exudate of host roots. This extensive branching, which maximizes the possibility of contact with the root, is accompanied by a significant increase in respiratory activity, which persists until spore reserves are depleted. Indeed, the signals from host plants result in initiating the "presymbiotic growth phase" in that the fungus is committed to starting an association with plant roots (Harrison 2005). Subsequently, the fungal hyphae form an appressoria-like structure named "hyphopodium" that attaches to the root epidermis and acts as the point of entry for the fungus into the root epidermis (Murray et al. 2013). At this phase, the AM hyphae produce fungal factors (Myc factors) that increase the expression of several symbiotic plant genes and Ca^{2+} spiking (Genre et al. 2013).

Following the formation of the hyphopodium, a specific structure called the "pre-penetration apparatus" (PPA) forms in the epidermal and outer root cortical cell. This structure is a broad cytoplasmic bridge that guides the hypha toward the cortical cells (Genre et al. 2008). Fungal hyphae enter the cell and begin to form arbuscules in the inner roots of cortical cells. A plant-derived membrane subsequently surrounds the intracellular hyphae and arbuscules. The "periarbuscular membrane," which separates the arbuscules from the symplasm of the plant cell, contains specific transporters required for the exchange of metabolites between two partners (Balestrini and Bonfante 2005) (Fig. 4.2).

4.3.2 Strigolactones

It has been demonstrated that SLs serve as the initial point of communication between the fungus and the root of the host plants before direct physical contact. SLs are a group of apocarotenoids, the products of oxidative cleavage of carotenoid precursors (Giuliano et al. 2003). They were first identified in the rhizosphere of parasitic plant hosts, allowing their seeds to germinate in close proximity to their hosts (Cook et al. 1966). Later, SLs were identified as the root signals that allow AM fungi to form a symbiotic association with a host (Akiyama et al. 2005; Akiyama and Hayashi 2006).

The natural SLs have a tricyclic lactone structure containing an ABC-ring and a D-ring butenolide group coupled with an enol-ether bridge. Based on the stereochemistry of the B–C-ring junction, the natural SLs are classified into two groups, strigol and orobanchol (canonical SLs). Both of these groups possess a conserved R-configuration at the C-2 position that connects the D-ring to the core and is liable for different bioactivities of different SLs. Conversely, non-canonical SLs generally lack the typical ABC-rings but comprise an enol-ether bridge and D-ring moieties, such as methyl carlactonoate (MeCLA), avenaol, and zealactone (Mashiguchi et al. 2021) (Fig. 4.3).

The pathways of SLs biosynthesis have been investigated, and the enzymes and genes involved have been primarily characterized (Mashiguchi et al. 2021). It has been observed that the carotenoid precursor is subjected to isomerization and

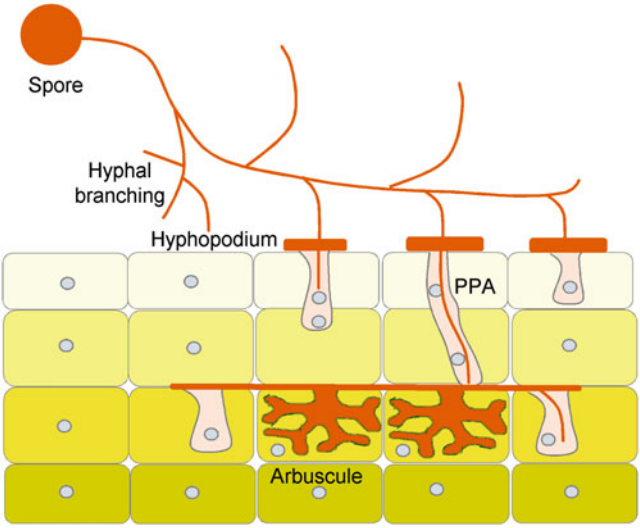


Fig. 4.2 An illustration of the root colonization process by AM fungi. The germination of a resting spore leads to the formation of a short mycelium. The perception of plant exudates induces hyphal branching. Fungi produce and release factors in response to changes in their metabolism. These fungal exudates (Myc factors) are perceived by the root, where they trigger calcium spiking through the activation of the common SYM pathway. In the meantime, a specific fungal structure, "hyphopodium," is formed and adheres to the root surface. This triggers the formation of a particular structure in the epidermal cell outer cortical cell named pre-penetration apparatus (PPA). The intercellular hyphae develop along the root axis, and highly branched arbuscules are formed and occupy the inner cortex cells

cleavage and generates carlactone. The latter compound is the precursor of various SLs (Mori et al. 2020; Wakabayashi et al. 2019, 2020) (Fig. 4.4).

4.3.2.1 Response of AM Fungus to SL

Sub-nanogram levels of SLs in root exudates enhance spore germination and promote AM hyphal branching, most likely by activating lipid metabolic pathways (Lanfranco et al. 2018). SLs detection by AM fungus results in the induction of its oxidative metabolism, ATP production, and generation of the necessary energy for stimulation of growth and hyphal branching and preparation of AM fungus to establish symbiosis (Lanfranco et al. 2018). SLs augment the fungal-derived production of biochemical signals, such as chitin oligomers (COs; see below) (Genre et al. 2013), which induce the Ca^{2+} spiking in plants as the first indication of the interaction between two partners (Bonfante and Genre 2015). Applying COs to plants enhances the expression of an SLs biosynthesis gene (CCD7) and other symbiotic marker genes (Giovannetti et al. 2015), suggesting a synergistic effect of SLs and COs in the establishment of communication between two partners.

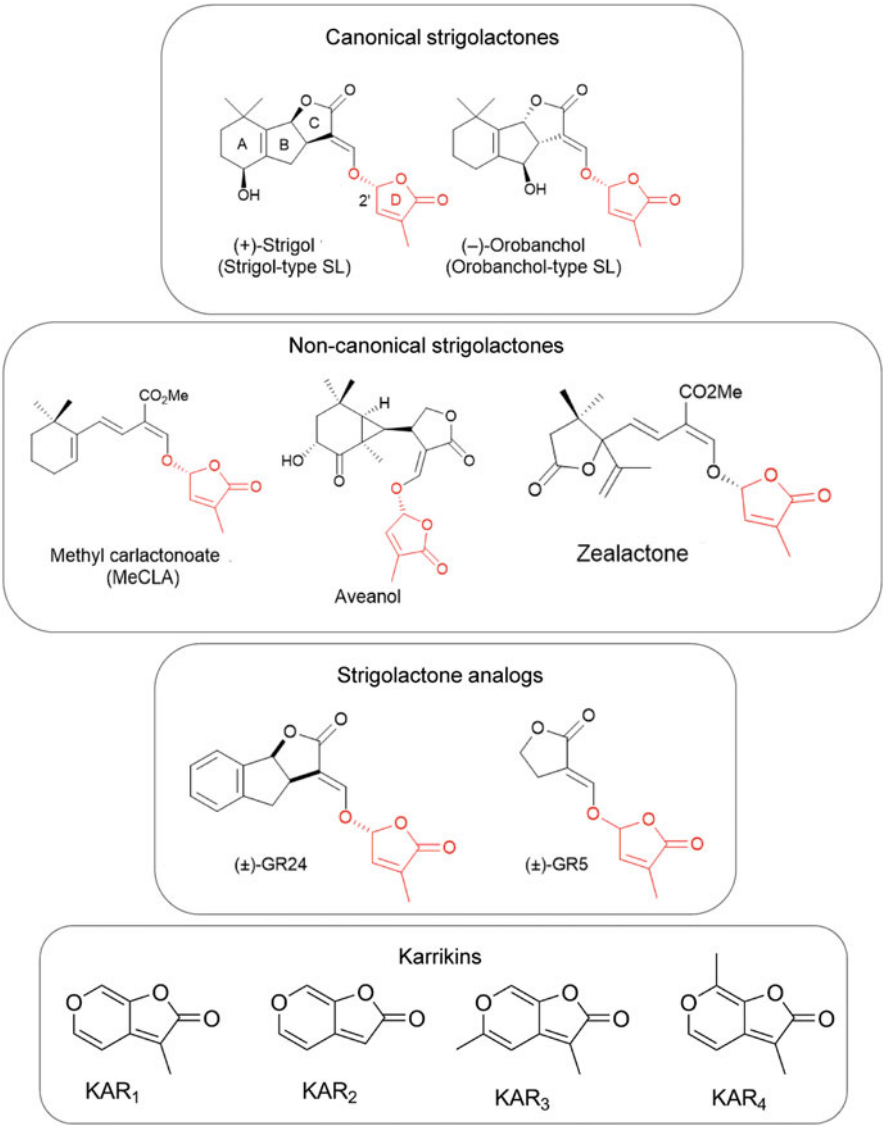
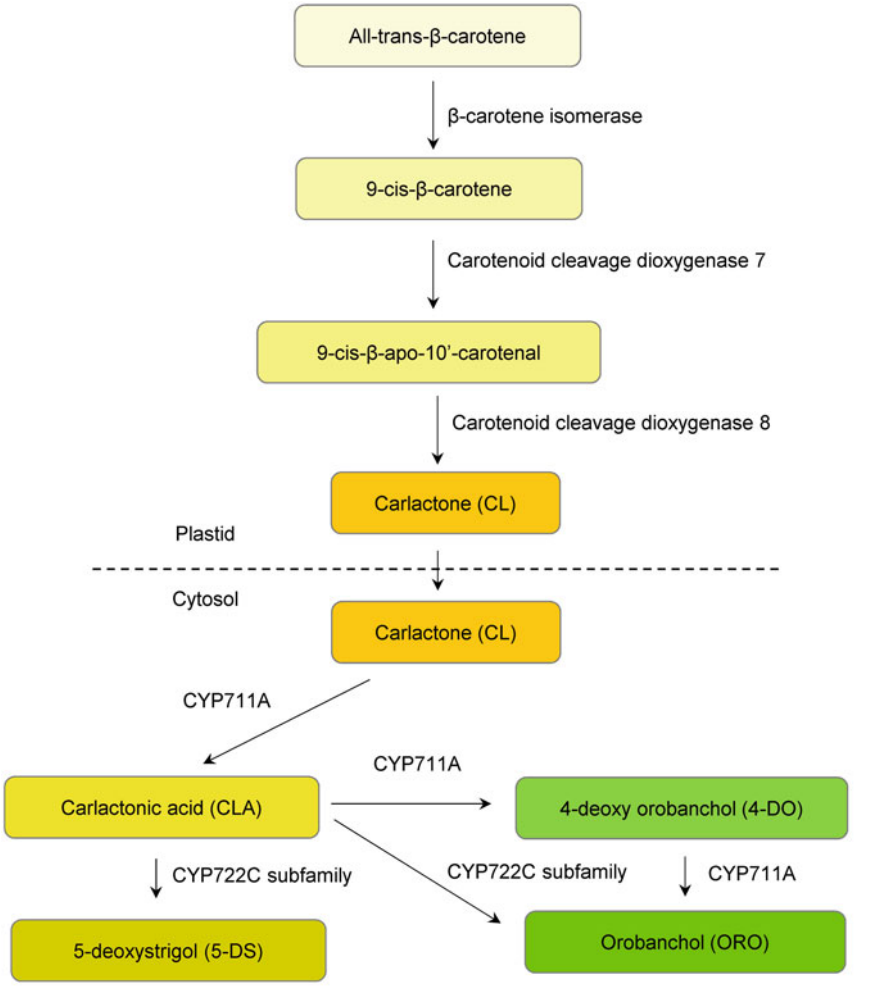


Fig. 4.3 Structures of SLs and SL-related compounds. Naturally occurring SLs are classified into canonical and non-canonical SLs. Canonical SLs possess ABC rings that link to the D-ring via an enol–ether bond. Canonical SLs are further classified into strigol and orobanchol types by the stereochemistry of the B/C-ring junction. In non-canonical SLs, such as methyl carlactonate 3 (MeCLA), avenaol 4, and zealactone 5, the D-ring and an enol–ether bond are conserved, whereas the typical ABC-ring structure is absent. GR24 is a widely used synthetic SL analog. Karrikins (KAR) are smoke-derived chemicals that can induce seed germination of weeds



	Arabidopsis	Rice	Pea	Petunia
β-carotene isomerase	AtD27	D27		
Carotenoid cleavage dioxygenase 7 (CCD7)	MAX3	HTD1/D17	RMS5	DAD3
Carotenoid cleavage dioxygenase 8 (CCD8)	MAX4	D10	RMS1	DAD1
CYP711A (A Cytochrome p450 family member)	MAX1	OsMAX1		PhMAX1
CYP722C subfamily	Was found in *Vigna unguiculata* (cowpea); *Solanum lycopersicum* (tomato); *Gossypium arboreum* (cotton); *Lotus japonicas* (Wakabayashi et al., 2019, 2020; Mori et al., 2020)			

Fig. 4.4 The pathways involved in the biosynthesis of SL. The carotenoid precursor undergoes isomerization by plastid-localized β-carotene isomerase (D27) and oxidation by carotenoid cleavage dioxygenases 7 (CCD7) and 8 (CCD8) to produce carlactone (CL) as the precursor of various SLs. CL is further oxidized in the cytosol by the CYP711A family to yield carlactonic acid (CLA). Some members of the CYP711A and CYP722C families can produce orobanchol (ORO), a canonical SL, from CLA, while GaCYP722C and LjCYP722C are responsible for the generation of 5-deoxystrigol, a strigol-type canonical SL (5-DS). The following table details the enzymes of *Arabidopsis*, rice, pea, and petunia

Finally, SLs regulate the expression of several proteins secreted by the fungal partner (Tsuzuki et al. 2016) that positively regulate host plant colonization during presymbiotic and symbiotic stages (see below). Mutations that lead to defects in the biosynthesis and export of SLs reduce AMF hyphal branches and causes significantly lower colonization rates than wild-type plants. After establishing the AM fungus in the root, SL biosynthesis is reduced, presumably as a mechanism to prevent the plant from becoming over-colonized (Koltai et al. 2010; Lanfranco et al. 2018).

The effect of SLs on the AM fungus depends on its concentration and structural features. The structure-activity relationship of SLs has been comprehensively studied for a variety of physiological functions, including as an endogenous hormone in the suppression of shoot branching and as a regulator of plant–plant interactions in the stimulation of parasitic plant seed germination (Boyer et al. 2012; Zwanenburg and Pospíšil 2013; Zwanenburg et al. 2013; Sanchez et al. 2018) or as a hyphal branching agent for AM fungi (Akiyama et al. 2010). Compared to their function in plants, the structural requirements for an optimal effect of SLs on hyphal branching differ. This may be due to the action of distinct receptor molecules in these three primary functional effects of SLs. The function of SLs as endogenous plant hormones requires receptors with α,β-hydrolase activity, which belongs to the D14 clade in higher plants (Waters et al. 2017).

In contrast, its function for seed germination stimulation in parasitic plants depends on its perception by phylogenetically distinct proteins, D14-like receptors (Lumba et al. 2017). The nature of receptor molecules in the AMF is obscure. No homologs of the D14 proteins have been identified within the only available genome of AM fungi belonging to *Rhizophagus irregularis* (Tisserant et al. 2013).

4.3.2.2 SL Signal Perception by AMF

The mechanisms of SLs perception and signal transduction in AM fungi are widely unknown. The synthetic SL (GR24) evokes a rapid increase in the intracellular Ca^{2+} concentration in the fungus (Moscatiello et al. 2014), which is a characteristic response to stress factor (Zhivotovsky and Orrenius 2011), suggesting that AM fungi primarily sense SLs as foreign molecules.

Previous studies suggest that SLs are perceived by both the AM fungi and their associated bacterial communities (Lanfranco et al. 2018). It has been observed that *Candidatus Glomeribacter gigasporarum* (*Ca*Gg), the endobacterium of *G. margarita*, improves the efficiency of the fungus in responding to SLs. In addition, the bacterial scavenging system specifically metabolizes excess ROS generated due to the SLs-mediated increase in fungal respiration. Thus, the fungal microbiota plays a crucial role in the presymbiotic phase of this AM fungus (Salvioli et al. 2016).

4.3.2.3 SLs Signaling Pathway and AMF

Intriguingly, SLs do not appear to act as endogenous signals in plants during AM development, as the development of arbuscules is unaffected in SL-deficient or export mutants (Liao et al. 2018). Furthermore, SL-insensitive D14 rice mutants devoid of the SL receptor do not exhibit a decrease in AM colonization (Yoshida et al. 2012). These results imply that the effect of SL released into the rhizosphere is limited to the early association stage, i.e., the presymbiotic stage.

4.3.3 Karrikins and Karrikin-Like Signals

In contrast to the unaffected AMF colonization in the SL receptor rice mutant *d14*, in *max2/rms4/d3*, another mutant of the SL signaling pathway, AM development is severely reduced (Yoshida et al. 2012). MAX2/RMS4/D3 is an F-box protein that forms a complex with D14 (SL receptor) and a repressor protein, SMXL6/7/8, resulting in its degradation as the initial step in the activation of SL-responsive genes (Lumba et al. 2017; Rehman et al. 2021; Fig. 4.5). This suggests that an element downstream of the SL signaling pathway, and not its receptor, is involved in the AM signaling in plants. Furthermore, D14L (DWARF 14 LIKE) was identified as an essential factor for establishing rice AM association because, in the *d14l* rice mutant, the transcriptional response to AMF is completely absent, implying the role of D14L in AMF recognition (Gutjahr et al. 2015a, b).

Relationship with Karrikins Pathway D14L is homologous to *Arabidopsis* KAI2 (KARRIKIN INSENSITIVE), a receptor for Karrikins, butanolide molecules derived from wildfire smoke and responsible for post-fire germination of seeds (Waters et al. 2012). The Karrikins signaling pathway has been identified in *Arabidopsis* and shares some common elements with SL signaling (De Cuyper et al. 2017; Fig. 4.5). In this pathway, activation of KAI2 leads to the recruitment of MAX2 and the removal of a negative regulator, SMAX1 (Suppressor of MAX2-1) (De Cuyper et al. 2017; Hull et al. 2021). SMAX1 in rice has been identified as an AM association suppressor that negatively regulates root colonization and symbiotic gene transcription (Choi et al. 2020).

This evidence demonstrated a significant overlap between the AM signaling and karrikins pathways; however, the endogenous ligand of D14L/KAI2 that initiates this response is unknown. KAI2 also responds to the N-substituted phthalimides (cotylimides) (Tsuchiya et al. 2010) and non-naturally occurring SLs (Flematti et al. 2016). Since these compounds are not found naturally in plants, it has been hypothesized that D14L/KAI2 recognizes a "yet-to-be-identified karrikin-like" (KL) ligand (Morffy et al. 2016). KAI2 proteins are evolutionarily conserved in the plant kingdom and are also found in plants not associated with fire-prone habitats (Ahmad et al. 2022). It has been suggested that the main function of D14L/KAI2

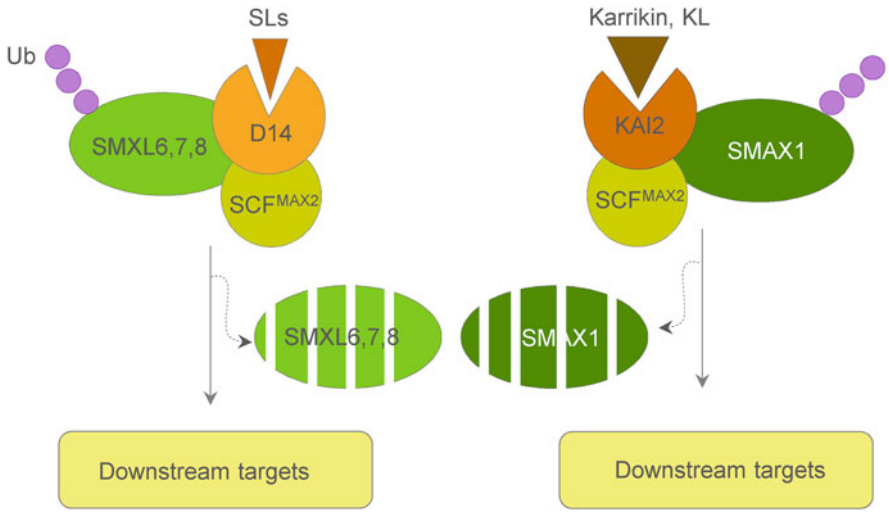


Fig. 4.5 A model of SL signaling and hypothetic KAR signaling. (A) The SL receptor AtD14 binds and hydrolyzes the SL, triggering the formation of a D14–SCF^{MAX2}–SMXL6/7/8 complex, which targets SMXL6/7/8 for ubiquitination and degradation. This leads to the de-repression of unknown TFs and activates the expression of downstream targets. (B) KAR, or a putative KAI2 ligand, is perceived through KAI2. The ligand–receptor interaction triggers the formation of a KAI2–SCF^{MAX2}–SMAX1 complex to induce the ubiquitination and degradation of SMAX1, which then activates downstream responses

signaling is related to AM presymbiotic signaling, while its effect on post-fire germination is the secondary role (Ho-Plágaro et al. 2021). Consistent with the observations on the disrupted AMF association in SMAX1, LCO responsiveness was eliminated, and CO responsiveness was diminished in *d14l* mutants (see below).

4.3.4 Other Plant Signals

Some other carotenoid-derived metabolites, including blumenols (C13), mycorradicins (C14), and zaxinone, have been shown to be involved in AM association and contribute to the AMF colonization at different stages of this process (Table 4.1).

4.3.5 Plant Hormones

In contrast to a direct role for SLs in the rhizosphere, other phytohormones' role in regulating the structure and function of the AM symbiosis is much more complex. In a mycorrhizal root, both local and systemic responses to the phytohormones occur,

Table 4.1 Some identified (or hypothetical) signaling molecules (other than hormones) from plants with a regulatory role in the AM symbiosis

Potential signaling molecules	Role in AM symbiosis
Blumenols (C_{13} cyclohexenone derivatives)	They are highly accumulated in AM roots; reduced synthesis of blumenols decreases transcript levels of AM markers and increases the number of degenerating arbuscules (Floss et al. 2008a)
Mycorradicins (C14 polyenic dicarboxylic acids)	They are massively accumulated in mycorrhizal roots and are responsible for the characteristic yellow color of strongly colonized roots; mycorradicins contribute to the decay and reemergence of arbuscules, but they are not directly involved in the regulation of the number of active arbuscules (Floss et al. 2008b)
Zaxinone	They are natural apocarotenoid synthesized by a carotenoid cleavage dioxygenase (*zas*) and regulates plant architecture and root growth (Wang et al. 2019). The *zas* mutant displays less colonization than wild-type plants; this phenotype is not rescued by an exogenous supply of zaxinone, while the exogenous synthetic SL analog (GR24) rescues the mycorrhizal phenotype in the *zas* mutant (Votta et al. 2022). *ZAS* orthologs have not been found in genomes of non-host species, including *A. thaliana* (Vallabhaneni et al. 2010). In rice, *OsZAS* is induced during the early stages of the interaction (7 days post-inoculation), and zaxinone content is increased before fungal penetration inside the root (Wang et al. 2019). The *zas* mutant, however, is unable to increase the level of SLs at 7 days post-inoculation with AMF (Votta et al. 2022)
N-acetylglucosamine-like compound) (GlcNAc) (a hypothetical compound)	The plant N-acetylglucosamine exporter, NOPE1 (NO PERCEPTION1), contributes to the excretion of N-acetylglucosamine (GlcNAc)-like compounds, thus influences transcription of genes related to the presymbiotic stage; the root exudates derived from the *nope1* mutant could not induce the transcriptional responses before the physical contact, hyphopodium is not formed, and, subsequently, root penetration by fungal hyphae is inhibited (Nadal et al. 2017)
Coumarins	As a signal in the presymbiotic chemical dialog, it promotes fungal metabolism and stimulates pre-penetration development and metabolism in AMF. Overexpression of genes involved in coumarin production (e.g., scopoletin) and secretion mitigates the incompatibility in the non-host plant, *Arabidopsis* (Cosme et al. 2021)
Flavonoids	These compounds contribute to the signaling, establishment, and regulation of mycorrhizal association in legumes (Singla and Garg 2017), supported by an RNAi silencing study in soybeans (Salloum et al.

(continued)

Table 4.1 (continued)

Potential signaling molecules	Role in AM symbiosis
	2018). Some flavonoids (e.g., apigenin) induce AMF spore germination and hyphal branching (Scervino et al. 2006, 2007). Some flavones (e.g., quercetin and luteolin) improve AMF symbiosis (Steinkellner et al. 2007)
2-hydroxy fatty acids	2-hydroxytetradecanoic acid (2OH-TDA) and 2-hydroxydodecanoic acid (2OH-DDA) induce a hyphal growth response in *Gigaspora gigantean* (Nagahashi and Douds Jr 2011)
Cutin monomers	They are necessary for the formation of hyphopodium and the development of arbuscular because a mutation in the genes responsible for the synthesis of cutin monomers (*ram1* and *ram2*; see below) shows a defect in the formation of these structures (Gobbato et al. 2012; Keymer et al. 2017). Although roots do not contain cutin, the use of cutin compounds as a specific cue for the fungus is likely related to the evolution of AMF in early land plants that have interactions similar to mycorrhizas in their rhizomes as modified stems (Brundrett 2002)

which are necessary to activate the fungus metabolism in the early phase of the interaction but control it and the late stages, i.e., the arbuscule turnover, to guarantee the favorable mutualistic association. As is well-known for other plant developmental processes, phytohormones do not act independently, but a cross-talk between phytohormones regulates AM development and arbuscule formation (Gutjahr 2014; Liao et al. 2018). A summary of information concerning the phytohormones involved in AM symbiosis regulation is provided in Tables 4.2 and 4.3.

4.4 Fungal Signals

SLs have been observed to induce the release of signals by the AM fungus. Due to methodological constraints in applying genetic approaches to AM fungi, the signaling molecules released by AM fungi to establish or regulate symbiosis have not been exhaustively investigated.

4.4.1 Myc-LCOs and COs

The function of lipo-chitooligosaccharide (LCO) as signaling molecules derived from rhizobia (Nod-LCO) in the nodule organogenesis and bacterial colonization has been well documented (Murray 2011). Similarly, branched hyphae of AMF

Table 4.2 The effect of five major phytohormones (auxin, gibberellic acids, cytokinins, abscisic acid, and ethylene) and the mechanisms for their action on the AM establishment and functionality

Major phytohormones	Role in AM symbiosis
Auxin	Auxin acts through numerous mechanisms in regulating AMF symbiosis: (1) Similar to SLs, it regulates early events of the AM association as a part of Pi signaling (Koltai 2015). (2) It controls SLs levels: the *bsh* mutant, with three times less auxin in its roots, shows a significant reduction of SL exudation and low expression level of a key SL synthesis gene (PsCCD8) and defect in AMF colonization; this phenotype is partially restored by the application of GR24 (Foo 2013). (3) It is involved in the post-infection stage of AM symbiosis: exogenous application of auxin analogs stimulates arbuscule formation in the colonized roots (Etemadi et al. 2014); the concentrations of free auxin and auxin conjugates are significantly increased in the mycorrhizal roots (Liao et al. 2015)
Gibberellic acids (GA)	There is evidence of the positive effect of GAs on AM colonization: (1) an increased GA level and upregulation of its biosynthesis and signaling genes is a characteristic of the AM colonized roots (Shaul-Keinan et al. 2002). (2) inhibition of the GA biosynthesis or suppressing of its signaling results in a substantial reduction of hyphal branching and arbuscule formation within the root (Takeda et al. 2015). However, there is evidence showing that GAs act as a negative factor in AM symbiosis: (1) exogenous GAs lead to a substantial reduction of root AM colonization; lower levels of GAs inhibit the arbuscules formation; and higher levels completely inhibit the root colonization (El Ghachtouli et al. 1996). (2) AM colonization and the number of arbuscules are higher in the GA-deficient pea mutant, *na-1* (Foo et al. 2013). (3) Overexpression of the DELLA (Yu et al. 2014) or expression of a non-degradable version of this protein (Floss et al. 2013), a key suppressor in the GA-signaling, results in a significantly increased AM colonization and promotes arbuscule formation. (4) DELLA proteins physically interact with diverse transcriptional regulators in the symbiosis pathway (Pimprikar et al. 2016). (5) GA suppresses Arum-type AM symbiosis but promotes Paris-type AM symbiosis (Tominaga et al. 2020, 2021). These findings suggest the function of mechanisms for precise regulation of the GA biosynthesis and signaling during the establishment of the AM symbiosis
Cytokinins (CK)	Improved levels of CK in both shoots and roots upon mycorrhization have been observed in early studies (Allen et al. 1980), one of the mechanisms for the growth promotion of AM plants. Nevertheless, other studies have observed contradictory results: CK-deficient transgenic tobacco plants (Cosme and Wurst 2013) and CK-overproducing pea mutants (Jones et al. 2015) show higher AM colonization than their wild-type counterparts. Using the root-specific and constitutive expression of CKX (CK oxidase) genes, it has been observed that the shoot CK positively affects AM functioning. At the same time, root CK is responsible for limiting the carbon sink capacity of the fungus to avert fungal parasitism (Cosme et al. 2016)
Abscisic acid (ABA)	ABA treatment induces hyphal branching and promotes fungal spore viability (Mercy et al. 2017). In ABA-deficient mutants, AM colonization, arbuscule formation, and functionality are impaired, suggesting a positive regulation of AM development by ABA (Herrera-Medina et al. 2007). However, ABA seems to modulate the AM symbiosis in a concentration-dependent manner: it stimulates AM colonization at low concentrations. Still, it hampers it at higher levels by impairing the Myc factor-initiated

(continued)

Table 4.2 (continued)

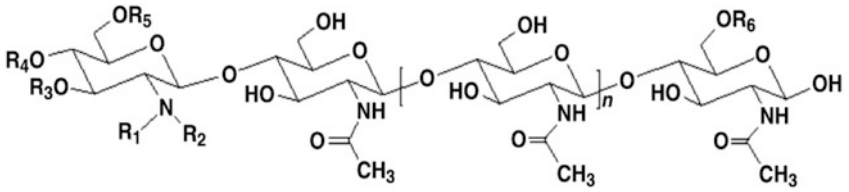
Major phytohormones	Role in AM symbiosis
	symbiotic signaling (Charpentier et al. 2014). In sufficiently AM-colonized roots, the inhibitory effect of ABA observed on the early signaling events could be regarded as a control mechanism for avoiding excess colonization
Ethylene (ET)	ET negatively impacts AM fungal penetration and colonization (Torres Santos et al. 2011). The phenotypes of ET-overproducing and the ET-insensitive mutants of tomato and pea suggest that ET has an inhibitory role in AM colonization (Torres Santos et al. 2011; Foo et al. 2016). However, using mutants with higher sensitivity to ET, it has been shown that ET may mitigate the inhibitory effect of Pi on the AM association (Torres Santos et al. 2016)

Table 4.3 The contribution of three phytohormones (brassinosteroids, salicylic acid, and jasmonic acid) in the AMS

Other phytohormones	Role in AM symbiosis
Brassinosteroids (BRs)	Have a role during AM symbiosis; the tomato biosynthetic mutant (dX) exhibits a lower level of AM colonization (Bitterlich et al. 2014). BR acts likely through inhibition of plant defense or upregulation of invertase (Lin6) (Bitterlich et al. 2014), which is involved in the provision of hexoses to the fungus (Schaarschmidt et al. 2006)
Salicylic acid (SA)	Exogenous application of SA decreases the root colonization at the beginning of the AMF–plant interaction but fails to affect the formation of appressoria (Blilou et al. 2000). The AM-defective (Myc^-) mutants show higher SA accumulation compared with wild (Myc^+) plants (Blilou et al. 1999). The transgenic plant with reduced SA levels is colonized rapidly by AM colonization, while mutants with improved SA levels show a significant delay in AM colonization. However, the ultimate colonization level is not significantly modified (Medina et al. 2003)
Jasmonic acid (JA)	There are reports on both positive and negative effects of JA on AM colonization: JA-deficient tomato *spr2* mutant exhibits a lower colonization rate that could be restored by exogenous application of JA (Tejeda-Sartorius et al. 2008); conversely, an elevated level of AM colonization has been observed in the tomato JA-insensitive mutant *jai*-1 (Herrera-Medina et al. 2008). JA response partially depends on the plant and fungal species (Liao et al. 2018) and is not essential for AM colonization. Still, high levels of JA in the roots have an inhibitory effect on mycorrhization, potentially through the activation of the plant's defense (Gutjahr et al. 2015a, b)

secrete specific signaling molecules, i.e., Myc factors, lipo-chitooligosaccharides (LCOs), and short-chain chitooligosaccharides (CO4/CO5).

Identifying LCOs from AM fungi with a basic structure similar to the Nod-LCO demonstrated that the establishment AMF also implicates LCO-mediated signaling, named Myc-LCOs (Maillet et al. 2011). A generic symbiotic LCO is based on a linear, β(1–4) linked oligomers (tetra- or pentasaccharide) of N-acetyl glucosamine (GlcNAc) with a considerable variation in the N-substitutions (acyl and methyl) and



Fungus species	n	R_1	R_2	$R_{3,4,5}$	R_6
Rhizophagus irregularis	0, 1, 2	C16:0, C18:0, C18:1	H, Me	H	H, S, Fuc, MeFuc
Rhizophagus intraradices	0, 1, 2	C16:0, C18:0, C18:1	H, Me	H	H, MeFuc
Rhizophagus clarus	0, 1, 2	C16:0, C18:0, C18:1	H	H	H, Fuc, MeFuc
Gigaspora rosea	0, 1, 2	C16:0, C16:1, C18:0, C18:1, C18:2, C20:1	H, Me	H	H, S, Fuc, MeFuc, MeFucS

Fig. 4.6 The generic structure of lipo-chitooligosaccharides (LCOs) shows sites of chemical substitutions. (n) denotes the number of residues of chitin oligomers, (R1) represents the type of fatty acid identified as saturated or unsaturated fatty acid, and (R2–R6) are chemical substitutions: hydrogen (H), acetyl (Ac), carbamoyl (Cb), fucosyl (Fuc), fucosyl sulfate (FucS), methylfucosyl (MeFuc), and sulfate (S)

O-substitutions (methyl, carbamoyl, acetyl, fucosyl, and sulfate) (Gough and Cullimore 2011; Rush et al. 2020) (Fig. 4.6). Exogenously applied Myc-LCOs enhance root colonization and activate Ca^{2+} spiking in the host plants (Sun et al. 2015; Camps et al. 2015). Short-chain chitooligosaccharides (COs) are also able to activate Ca^{2+} spiking, implying that both LCOs and short-chain COs contribute to the recognition of host roots (Genre et al. 2013).

4.4.2 Plant Perception of the Fungal Signal

Plant receptors of LCOs released by rhizobia are characterized as lysin motif receptor-like kinases (LysM-RLKs) (Fliegmann et al. 2013). Some Lys-RLKs are necessary for AM colonization and, thus, are the candidate receptors of Myc-COs or Myc-LCOs in various plant species (Buendia et al. 2018; Wu et al. 2022).

CERK1 LysM-RLKs receptors, such as OsCERK1 and OsLYK2 from rice, MtLYK9 from *M. truncatula*, PsLYK9 from *Pisum sativum*, and SlLY10 and SlLYK12 from tomato, are mediated in the COs and LCOs signaling (Ho-Plágaro and García-Garrido 2022). This suggests that the contribution of LysM-RLKs receptors is a conserved feature in AM association of host plants. The rice OsCERK1 (Chitin-elicitor receptor kinase 1) is required for COs-induced responses (Zhang et al. 2015), and the AM association is severely impaired in the *Oscerk1* mutant (Miyata et al. 2014).

CEBiP Chitin is a constituent of the fungal cell wall, a long-chain polymer of GlcNAc. The secreted chitinases from plants break down chitin and release COs (Roberts and Selitrennikoff 1988). Thus, it is important to maintain the immunity response, simultaneous with employing strategies for plant-microbe symbioses. In this process, different classes of LysM receptor kinases (LYKs) or different combinations of single receptors could be used to discriminate different GlcNAc molecules and determine the ultimate response: immunity or symbiosis (Miyata et al. 2014). The LysM protein OsCEBiP (Chitin Elicitor binding protein) collaborates with rice OsCERK1 to regulate chitin signaling in this species (Shimizu et al. 2010). Indeed, in addition to AM signaling, CERK1 is also involved in MAMP-triggered immunity (Miyata et al. 2014). This gene was primarily characterized as a receptor necessary for chitin elicitor signaling, and the *Arabidopsis* knockout mutant of AtCERK1 is unable to respond to chitin (Miya et al. 2007).

Contrary to the impaired mycorrhizal phenotype of rice *Oscerk1* mutant, however, AM response is normal in the *Oscebip* mutant (Miyata et al. 2014), suggesting the involvement of CEBiP only in the plant immune response.

MYR1 In rice, OsCERK1 does not seem to bind to CO4 (Chitotetraose) directly (Kaku et al. 2006), but another lysin motif (LysM)-containing receptor kinase (LYKs), OsMYR1, is involved in the perception of the AM signal, CO4 (He et al. 2019). The *Osmyr1-1/Oslyk2-1* mutant shows a decreased AMF colonization, lower level of Ca^{2+} spiking, and reduced transcription of marker genes of AMS compared to wide-type rice plants upon inoculation with *Rhizophagus irregularis* (Zhang et al. 2021). Evidence suggests that OsMYR1 binds to CO4 from symbiotic fungi and subsequently is associated with OsCERK1. Further dimerization and phosphorylation between OsMYR1 and OsCERK1 trigger the symbiosis signaling pathway (He et al. 2019). Indeed, CERK1 is a common receptor of the AMS and immune response pathway (Zhang et al. 2015; Gibelin-Viala et al. 2019). Such dual function for CERK1 depends on its specific interaction with its coreceptors, OsCERK1 or OsMYR1, in response to either pathogenic or symbiotic signals, respectively (Zhang et al. 2021). The dual function of OsCERK1 homologs in both symbiosis and immunity was also observed in other plant species (Gibelin-Viala et al. 2019; Leppyanen et al. 2017).

Collectively, long-chain COs (CO6, CO7, and CO8) are recognized by OsCEBiP and trigger immunity by the formation of the OsCERK1–OsCEBiP complex, whereas short-chain COs (CO4 or CO5) are sensed by OsMYR1 and trigger symbiotic signaling after the formation of OsCERK1–OsMYR1 complex (Liang et al. 2013) (Fig. 4.7).

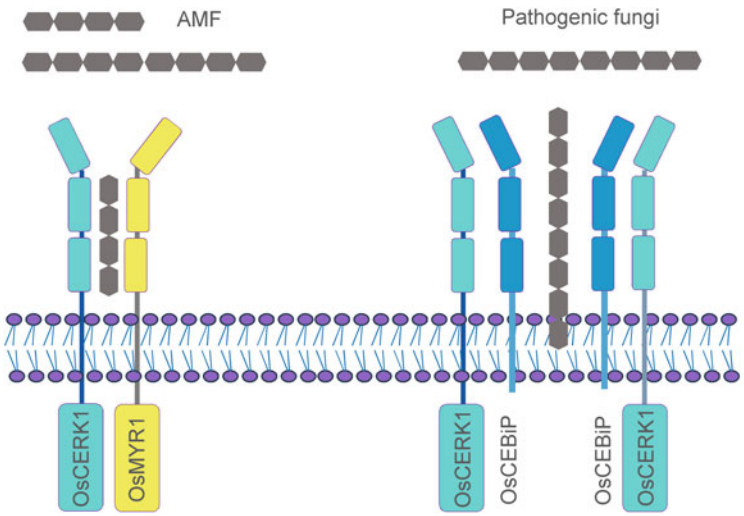


Fig. 4.7 The discrimination of symbiosis and immunity signals through the formation of a specific combination of three different receptors and coreceptors. OsCERK1 acts as a common receptor for both defense and symbiosis pathways that can trigger either of two contrasting signal outputs depending on the context. Symbiotic receptor OsMYR1 binds CO4 (chitotetraose) and subsequently forms a complex with OsCERK1, while long-chain chitins (CO8) bind the MAMP receptor OsCEBiP and then, after the formation of a complex with OsCERK1, triggers immunity response. In the presence of AM fungus, OsCERK1 is mainly allocated to CO4; thus, depletion of OsCERK1 prevents the formation of OsCERK1–OsCEBiP and suppresses immune signaling

4.5 AMF-Activated Genes

After receiving the necessary signals from the fungus and the host plant, the signaling pathway is started, and a wide range of genes are activated as downstream targets to regulate the physiological responses of the plant to the symbiont. A large number of transcription factors and other regulatory proteins are involved in the downstream AMS-specific pathways that are activated in response to CSP induction. Some of the most important molecular players in the AMS are discussed below.

RAM1, RAM2 In searching for molecules specific to the AM signaling pathway, two genes were found, including RAM1 (Reduced Arbuscular Mycorrhization 1) and RAM2 (Wang et al. 2012). Mutations in these genes (*ram1* and *ram2*) are able to form root nodules and also induce hyphal branching in the AM fungi, indicating unaffected strigolactone synthesis in these mutants. However, the root colonization level is severely decreased and associated with a reduction of hyphopodia at the root surface. In addition, *ram2* plants displayed a severe defect in arbuscule formation (Gobbato et al. 2013). Complementation experiments demonstrated that RAM1 encodes a GRAS-type transcription factor responsible for RAM2 expression (Gobbato et al. 2013). RAM2 is a glycerol-3-phosphate acyl transferase (GPAT), which contributes to the synthesis of cutin monomers. The overexpression of RAM2

leads to higher levels of α,ω-dicarboxylic acids and ω-hydroxy fatty acids (Gobbato et al. 2012).

NSP1 and NSP2 In the nodulation pathway, two GRAS-type transcription factors downstream of the Sym pathway have been identified, i.e., NSP1 (Nodulation Signaling Pathway 1) and NSP2 (Kaló et al. 2005; Smit et al. 2005), which are required for both nodulation and mycorrhization (Delaux et al. 2013). Both NSP1 and NSP2 are involved in activating strigolactone biosynthesis through the induction of DWARF27 (Liu et al. 2011). In barley, NSP2 overexpression activates RLK10/NFR5, SYMRK, and CYCLOPS (Li et al. 2022). Interestingly, the NSP2 complex with NSP1 activates strigolactone production (Liu et al. 2011), while the complex of NSP2 with RAM1 leads to the expression of RAM2 responsible for cutin monomer synthesis. Thus, a competition between RAM1 and NSP1 for binding with NSP2 provides a mechanism for the regulation of two different sets of symbiosis-specific genes (Murray et al. 2013). Further evidence on the importance of RAM1 and NSP1 has been provided by Hohnjec et al. (2015), showing that both GRAS-type transcription factors act synergistically in the transduction of diffusible signals and are essential for the presymbiotic transcriptional reprogramming triggered by Myc-LCOs, downstream of the CSP (Hohnjec et al. 2015) (Fig. 4.8).

Given the central role of AMS in P nutrition for plants, a link between Pi deficiency responses and the AMF signaling pathway has been observed in various plant species (Shi et al. 2021; Das et al. 2022). The transcription factors PHR1 and PHR2 are master regulators of the P-starvation response (Sega and Pacak 2019). The PHR2-controlled plant phosphate starvation response is required for pre-contact signaling, gene expression, root colonization, and mycorrhizal phosphate uptake (Shi et al. 2021; Das et al. 2022). Under P-starvation conditions, PHR2 promotes the expression of RAM1 (Shi et al. 2021) and NSP2 (Das et al. 2022), activating the biosynthetic pathway of cutin monomers and SLs, respectively.

4.6 AMF Association and Plant Immune Response

Every organism acts as a non-self-cue and evokes a response in plants. In general, to distinguish these cues and responding appropriately, plants are able to recognize microbe-associated molecular patterns (MAMPs) from pathogen-associated molecular patterns (PAMPs). Upon activation of the specific immunity response for each type of microorganism, the corresponding signaling cascades are initiated and induce the expression of related defense genes leading to the release of chitinases and accumulation of reactive oxygen species (van der Burgh and Joosten 2019). Microorganisms have developed mechanisms to evade these responses, suppress host immunity, and manipulate host cell physiology (Wang et al. 2022). The "effector proteins" promote the colonization of the host by controlling the plant immune system (Plett and Martin 2018). "Pathogen effector proteins" allow successful infection by suppressing the host defense response (Kamoun 2006).

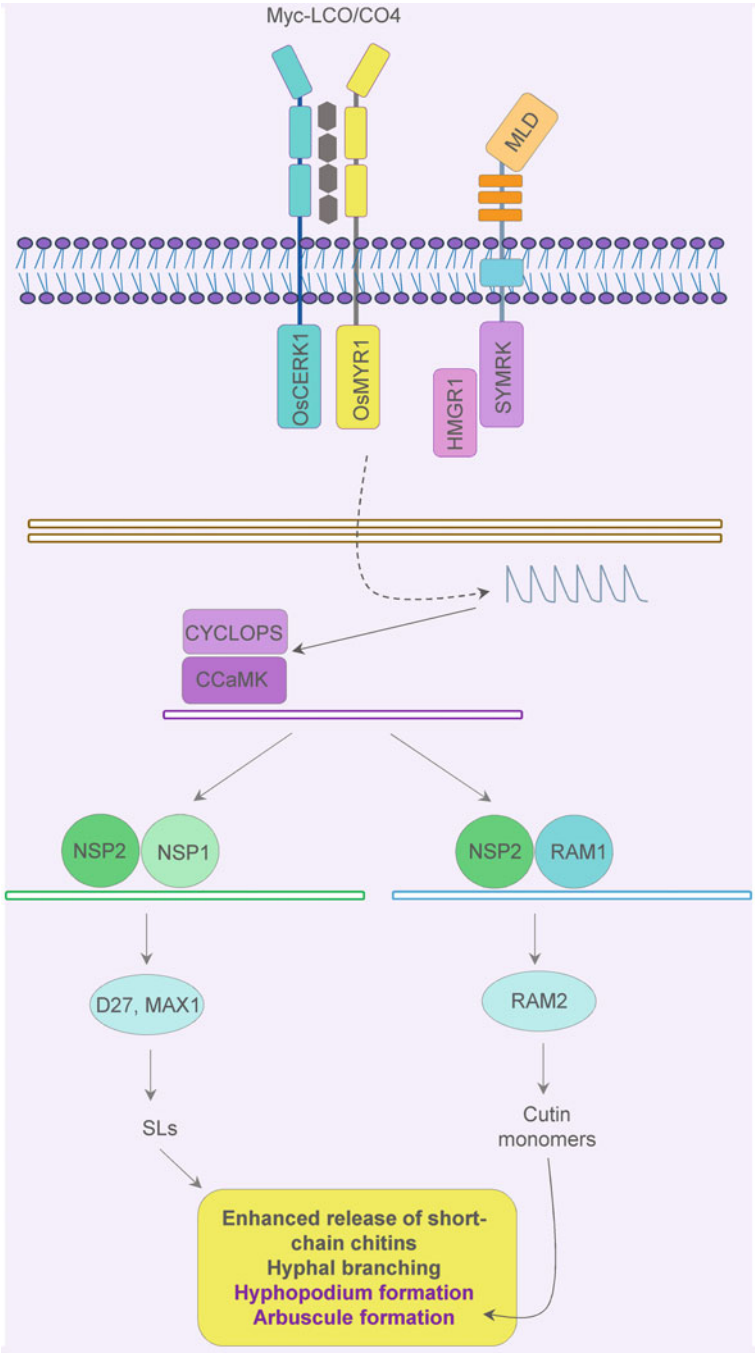


Fig. 4.8 Mycorrhiza-specific signaling. Specific Lys-RLKs detect AM-released Myc factors by forming a heterodimer (OsMYR1/OsCERK1) that leads to the induction of the common symbiosis pathway (CSP). The CSP activates the GRAS transcription factors NSP1, NSP2, and RAM1. NSP1 and NSP2 are involved in elevating strigolactone levels by activating its two biosynthetic genes,

In plant symbiosis, colonization of the host root while avoiding its defense responses is an essential prerequisite for establishing an association. Similar to "pathogen effector proteins," "symbiotic effectors" control the plant immune system, allow successful infection, and promote plant colonization (Kloppholz et al. 2011). Such similarity in the response of plants during infection by symbiotic and pathogenic microorganisms suggests that suppression of plant defense is a conserved feature in plant–microbe interactions.

The secreted effector proteins (SSPs) are involved in subduing the plant defense systems and, thus, facilitating fungal entry into plant cells. Among the predicted SSPs identified in sequencing projects of AM fungi, only a small number of proteins were confirmed to be involved in the AMF–plant interaction.

SP7 SP7 (RP23081 and RP8598) are small, secreted proteins from *Rhizophagus irregularis* that are translocated to the host plant nucleus and interact with the pathogenesis-related transcription factor of plant origin, ETHYLENE-RESPONSIVE FACTOR 19 (ERF19). By counteracting the expression *of ERF19*, SP7 can promote AMF symbiosis (Kloppholz et al. 2011).

SIS1 Another secreted protein, SL-induced putative secreted protein 1 (SIS1) (RP5293), is upregulated in *R. irregularis* and has a role in the colonization of host root (Tsuzuki et al. 2016).

RiCRN1 The third AMF effector, RiCRN1, belongs to the significant pathogen-associated Crinkler (CRN) effector family. CRN effectors are widespread in plant-pathogenic oomycetes and contain an N-terminal motif (LXLFLAK) essential for the effector's intracellular localization. In plant pathogenic oomycetes, CRN enters the plant cell nucleus to exert their function, such as induction of plant cell death (Amaro et al. 2017). RiCRN1 found in *Rhizophagus irregularis* also localizes to the host plant nucleus but, in contrast to other CRN, does not induce plant cell death (Voss et al. 2018). Gene silencing of RiCRN1 (through Host-Induced Gene Silencing, HIGS) results in much smaller arbuscules demonstrating that RiCRN1 expression facilitates AMS and is necessary for symbiosis progression (Voss et al. 2018).

In summary, AMF effector proteins promote symbiosis by impairing the synthesis of plant proteins that are produced upon contact with chitin or its derivatives and are involved in defense, cell death, and immune responses. Despite the lack of host specificity in plant–AMF interactions, there is evidence that fungal SSPs may contribute to host specificity and are likely responsible for variation in symbiosis efficiency among different combinations of AMF species/lines and host plant species/genotypes (Prasad Singh et al. 2019).

Fig. 4.8 (continued) D27 and MAX1. In addition to hyphal branching, the production of short-chain chitin oligomers (CO3-6) by AMF is elevated by SLs leading to the activation of CSP in the initial stages of fungal root colonization. RAM2 expression depends on the formation of a complex between NSP2 and RAM1. Cutin monomers produced by RAM2 promote hyphopodia and arbuscule formation by AMF

4.7 Conclusions

Although our knowledge of signaling pathways in response to AMF has advanced significantly in recent years, several questions remain regarding the nature of the Karrikin-like compound and its biosynthesis, the cause and consequences of the loss of symbiosis ability in non-host plants, and the mechanisms underlying the differential efficiency of specific combinations of plant species/genotypes and AMF species/isolates. However, unlike the legume nodule symbiosis, the diversity of host plants for AMS enables researchers to study and compare plant orders and families for the evolution of signaling pathways and other molecular components, as well as to investigate the diversity and evolutionary changes of symbiotic interactions and their ecological significance during the evolution of terrestrial plants on Earth.

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