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THE EVOLUTION OF SYMBIOTIC PLANT–MICROBE SIGNALLING

Michael R. Clear and Erik F. Y. Hom

Department of Biology, Center for Biodiversity & Conservation Research, University of Mississippi, University, MS, USA

Abstract: Plants form beneficial symbioses with a variety of different microbes. Among these, the root associated arbuscular mycorrhizal fungi, ectomycorrhizal fungi, rhizobial, and actinobacterial symbioses are some of the best understood. The successful establishment of these symbioses relies on a complex, coordinated signal exchange that arose from hundreds of millions of years of coevolution between plants and their associated microbes. Despite the diversity of these microbial symbionts, common signalling mechanisms were evolved that include the manipulation of host immunity and the use of similar plant- and microbe-derived signals and receptors. Owing to the plethora of information on these diverse symbioses, their signalling mechanisms are rarely reviewed together and even less so within an evolutionary context. We provide an overview of what is known regarding the evolution of these signals in an effort to highlight knowledge gaps in our understanding of plant–microbe symbiosis.

Keywords: evolution, plant–microbe interactions, symbiosis, mycorrhiza, rhizobia, *Frankia*, signalling, algae, fungi

1 Introduction

The transition of plants from a predominantly aquatic to terrestrial lifestyle was a pivotal transformation in earth's history. This lifestyle shift brought with it a number of challenges related to nutrient and water acquisition and volatile environmental changes. In order to overcome these, the earliest land plants, the bryophytes, entered into mutualisms with arbuscular mycorrhizal fungi (AMF) (Edwards et al., 2015; Lenton et al., 2016; Nelson et al.,

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2018). In order to distinguishing between AMF and potential pathogens, plants evolved a complex signal exchange with AMF. In turn, AMF evolved signals to perceive suitable hosts. Genetic evidence suggests that many of the signalling components in land plants were present in advanced Charophyceae algae, some of which were already terrestrial (Stebbins and Hill, 1980; McCourt et al., 2004; Delaux et al., 2012a, 2015; Delwiche and Cooper, 2015; Harholt et al., 2016). This pre-existing infrastructure was utilised for a variety of plant–microbe symbioses ranging from AMF to rhizobia (Delaux et al., 2012a, 2013b). Decades of research have revealed many of the intricacies of crosstalk signalling between plants and their symbiotic microbes yet many unanswered questions remain regarding the specific roles that these signals play and how they relate to host specificity. Given the prevalence of plant–microbe mutualisms and their ability to facilitate growth under rapidly changing and stressful environments, there has been a growing emphasis on deciphering the dialogue between plants and microbes in order to encourage beneficial mutualisms and foster new ones in the face of a global climate change (Ambrosio et al., 2017; Basu et al., 2018).

AMF-plant mutualisms occur in 80–90% of all extant plant species, having evolved ~480 million years ago (Ma) (Martin et al., 2017; Lutzoni et al., 2018; Strullu-Derrien et al., 2018) (Figure 1), and suggest how other subsequent plant–microbe associations might have begun (Wang and Qiu, 2006; Humphreys et al., 2010). In addition to AMF, plants associate with a wide range of microbial symbionts from root-associated fungi and bacteria to endophytic bacteria and fungi that live within leaf surfaces. Ectomycorrhizal fungi (EMF) form mutualisms with ~2% of plant species in which the fungus does not penetrate the plant cell wall and evolved ~220 Ma from various saprotrophic lineages (Eastwood et al., 2011; Floudas et al., 2012; Kohler et al., 2015; Martin et al., 2017; Lutzoni et al., 2018; Strullu-Derrien et al., 2018). These surface-level interactions activate and suppress immunity similar to AMF during host infection yet utilise distinct signalling mechanisms. More recently (~100 Ma) (Soltis et al., 1995; Raymond et al., 2004; Werner et al., 2014), AMF-associated angiosperms evolved symbioses with two types of nitrogen-fixing bacteria, rhizobia, and actinobacteria (from the genus *Frankia*) that allowed these plants to colonise areas with limited bioavailable nitrogen. Today, over 70% of legumes form symbioses with rhizobia (Sprent, 2007; Divakar et al., 2015).

These four types of root-associated symbioses (AMF, EMF, rhizobia, and *Frankia*) employ a common strategy for the infection of their plant hosts. First, microbes suppress innate immunity, followed by a manipulation of plant hormone signalling. In turn, plants secrete compounds for the recruitment of mutualistic microbes existing within the proximity of plant roots. Microbial symbionts respond by excreting compounds that induce physiological changes in the plant through molecular machinery that is both conserved

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Figure 1 The endosymbiotic structures formed by the four major microbial-plant symbioses ((a) AMF, (b) EMF, (c) Rhizobia, and (d) *Frankia*). (a) AMF symbioses appeared between 440 and 530 million years ago (Ma) (Remy et al., 1994; Brundrett, 2002; Edwards et al., 2015; Lenton et al., 2016; Martin et al., 2017; Lutzoni et al., 2018; Strullu-Derrien et al., 2018). AMF form an intracellular structure termed an arbuscule in which fungal hyphae (blue) penetrate the cell wall of the plant (dark green) yet remain surrounded by a peri-arbuscular membrane. (b) EMF are believed to have evolved several times over the period from 140 to 300 Ma (Eastwood et al., 2011; Floudas et al., 2012; Kohler et al., 2015; Martin et al., 2017; Lutzoni et al., 2018; Strullu-Derrien et al., 2018). EMF do not penetrate the cell walls of plant cells but instead infiltrate the apoplast region between individual cells, forming the 'Hartig Net.' The Hartig Net is composed of multiple layers of plant cells with EMF integrated within the apoplast (note: only the top layer is depicted). (c) Rhizobia evolved ~100 Ma (Soltis et al., 1995; Raymond et al., 2004; Werner et al., 2014). Nodules are typically formed through a temporary structure, termed symbiosome (depicted in red), that allows the rhizobia to penetrate the plant cell wall and enter into the cytoplasm. Rhizobia that enter the cytoplasm remain enveloped in a plant-derived membrane (depicted in red). (d) *Frankia* also arose ~100 Ma (Soltis et al., 1995; Raymond et al., 2004; Werner et al., 2014), however, they utilise a different method for nodulation. Filamentous *Frankia* (depicted in cyan) enter the plant cell via an infection thread, which continues into the plant cytoplasm. Bacterial hyphae branch off from the infection thread and form terminal fixation threads where nitrogen fixation and nutrient exchange takes place within the nodule.

and unique to certain symbioses. In this article, we synthesise what is known about the signalling mechanisms for these most well-studied plant–microbe symbioses towards reconstructing a narrative for the coevolution of these symbioses where possible. Our aim is to highlight what is known and bring to light gaps in the literature that limit a holistic understanding of how these symbioses coevolved.

2 Four Major Types of Interactions

The consortium of microbes associated with a plant is enormously complex and includes thousands of commensal, potentially pathogenic, and beneficial microbes (Vandenkoornhuyse et al., 2015). The best studied beneficial symbionts are AMF, EMF, rhizobia, and *Frankia*, but there is also a growing body of research regarding endophytic fungi and bacteria that grow in and on the surface of leaves (Arnold et al., 2003; Arnold and Engelbrecht, 2007; van der Heijden et al., 2015; Shaffer et al., 2017). Coevolution within the individual plant ecosystem or holobiont is complex and occurs not only between plant–symbiont but also between symbiont–symbiont and even symbiont–plant–symbiont. However, for this article, we focus on comparing bipartite, coevolved strategies between plants and their microbial symbionts as there seems to be an incomplete synthesis in this space. For a framework for assessing holobiont coevolution, we refer the reader to Hassani et al. (2018) or recent reviews of leaf-associated fungi and bacteria by Wagner et al. (2016) and Stone et al. (2018).

2.1 Arbuscular Mycorrhizal Fungi (AMF) Physiology and Evolution

AMF are obligate biotrophs that fall within the Glomeromycotina subphylum of the Mucoromycota (Spatafora et al., 2016). Glomeromycota represent over 1000 species yet only ~300 have been described by morphology (Oehl et al., 2011; Redecker et al., 2013). This relatively small group of fungi form obligate endosymbioses with a diverse range of plants spanning over 200 000 species and generally have low host specificity (Johnson and Jansa, 2017). AMF symbioses appear to have emerged around the same time that bryophytes (moss, liverworts, and hornworts) diverged from a single lineage of single-celled algal charophytes ~440–530 Ma (Remy et al., 1994; Brundrett, 2002; Edwards et al., 2015; Lenton et al., 2016; Martin et al., 2017; Lutzoni et al., 2018; Strullu-Derrien et al., 2018) (Figure 1). Bryophytes lack a root structure making nutrient acquisition limited. It is hypothesised that early bryophytes overcame this limitation by entering into symbioses with AMF. In AMF-symbiosis, the fungus penetrates the plant cell wall (but not the plasma membrane) and forms an intricately branched 'arbuscule'

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structure inside the cortex of a cell (Figure 1). Some early fossil records confirm this hypothesis as fossils from ~407 Ma show structures that appear to be arbuscule like (Krings et al., 2012; Pressel et al., 2014; Strullu-Derrien et al., 2014). Further, empirical data confirm that Glomeromycota and some primitive Mucoromycota are capable of forming mutualistic symbioses with extant liverworts under environmental elevated CO_2 conditions similar to the mid-Palaeozoic atmospheric concentrations (Field et al., 2012).

AMF colonization begins with fungal perception of plant-derived signals such as strigolactones and flavonoids that initiate spore germination, hyphal branching, and the production of fungal-symbiotic signals (Buee et al., 2000; Akiyama et al., 2005; Besserer et al., 2006). AMF symbiotic signals are a mixture of effector proteins and chitin-derived compounds such as short-chained chitin oligosaccharides (COs) and lipo-chitin oligosaccharides (LCOs) (Maillet et al., 2011). Plant perception of LCOs activates calcium oscillations within the plant nucleus through a well-conserved set of genes part of what is referred to as the 'common symbiosis signalling pathway' (CSSP) (Delaux et al., 2013b) (Figure 2). Activation of the CSSP suppresses innate immunity and facilitates hyphal attachment to the root surface followed by penetration of the plant cortical cells using a pre-penetration apparatus. The specialised arbuscule structure optimised for nutrient exchange is then formed. After arbuscule formation, the CSSP is no longer active and plant–fungal communication is conducted using alternative signalling and nutrient pathways beyond the scope of this article (for a recent review see: Choi et al. (2018)).

2.2 Ectomycorrhizal Fungi (EMF) Evolution and Physiology

EMF are known to provide a number of ecosystem services such as carbon sequestration, nutrient mobilization, and plant–plant communication through common mycorrhizal networks (Courty et al., 2010; Clemmensen et al., 2013). Like AMF, EMF establish symbiotic structures with plant roots and help their host plant obtain nutrients (notably water, nitrogen, and phosphorus) and prevent infection by unwanted pathogens. The Ectomycorrhizae are made up of over 20 000 species from the Basidiomycota, Ascomycota, and Zygomycota fungal phyla (Brundrett, 2009) and typically associate with woody plants. Phylogenetic analyses show that EMF evolved multiple times from various saprotrophic lineages as far back as ~180 Ma (Kohler et al., 2015) (Figure 1). Similar to their saprotrophic ancestors, EMF have a diverse array of degradation enzymes that breakdown organic molecules into their smaller nitrogen and phosphorus components; however, many have lost most of their cell-wall degrading enzymes (Plett and Martin, 2011; Kohler et al., 2015). The loss of cell-wall degrading enzymes necessary for saprotrophy appears to be critical for the formation of beneficial EMF-plant

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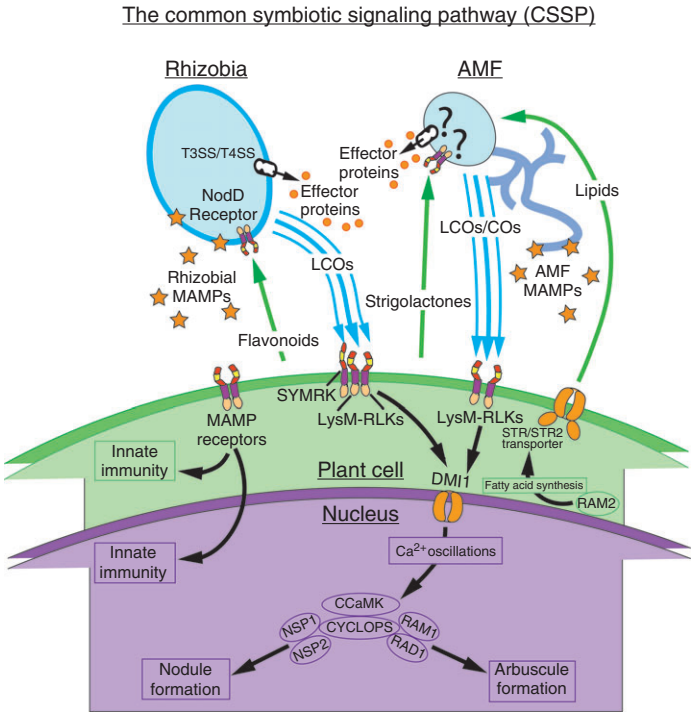

Figure 2 Major signals and receptors involved in the formation of plant-AMF and plant-rhizobia symbioses. Plants perceive MAMPs that are either secreted or located on the surface of rhizobia and AMF through MAMP (LysM-RLK) receptors. Effector proteins are small, secreted proteins that are produced by plant mutualists and pathogens to suppress innate immunity often via interference with plant-hormonal signalling (arrows not drawn). Nodulating plants produce flavonoid compounds that are perceived by rhizobia through a NodD (LysM-RLK) receptor. Rhizobia release a combination of Nod factors and effector proteins; effector proteins are secreted through type III and IV secretion systems (T3SS and T4SS) and often alter plant hormone signalling patterns in a way that suppresses innate immunity. Plants produce strigolactones that are perceived by an unknown receptor(s) in AMF (indicated by a question mark). AMF secrete Myc factors and likely effector proteins through yet unidentified secretion systems (indicated by a question mark). Plants perceive Nod and Myc factors through Nod and Myc factor-specific (LysM-RLK) receptors located on the cell membrane. Activation of Nod/Myc factor receptors initiates the common SYM pathway by signalling a potassium channel (DMI1) in the nuclear membrane that triggers calcium oscillations within the cells of the plant host. These calcium oscillations are perceived by a calcium/calmodulin-dependent protein kinase (CCaMK) and distinct calcium spiking patterns activate GRAS transcription factors that lead to the formation of specialised endosymbiotic structures known as arbuscules (AMF) or nodules (rhizobia). AMF, arbuscular mycorrhizal fungi; MAMP, microbial-associated molecular pattern; LysM-RLKs, LysM receptor-like kinases; LCOs, lipochitin-oligosaccharides; COs, chitooligosaccharides.

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symbioses, as nearly all of the cellulose-degrading enzymes have been lost in sequenced EMF (Kohler et al., 2015; Martin et al., 2016).

Despite the diversity of EMF, the symbiotic structures they form are extremely similar. Initially, EMF make hyphal contact with lateral plant roots followed by the release of aquaporins and effector proteins that facilitate the formation of a network of fungal hyphae in between plant cells within the apoplast known as the 'Hartig net' (Navarro-Ródenas et al., 2015) (Figure 1). Eventually, a thick layer of hyphae forms on the surface of the root to form the mantle. EMF-plant structures have been identified in the fossil record dating back as early as 41–56 Ma (Lepage et al., 1997; Beimforde et al., 2011), even though the EMF symbiosis appears to have arisen multiple times over the course of an extended period between of 140 and 300 Ma from various saprotrophic lineages (Eastwood et al., 2011; Floudas et al., 2012; Kohler et al., 2015; Martin et al., 2017; Lutzoni et al., 2018; Strullu-Derrien et al., 2018).

2.3 Rhizobia Evolution and Physiology

Greater than 70% of legumes and one nonlegume from the genus *Parasponia* form symbioses with nitrogen-fixing bacteria, termed rhizobia (Sprent, 2008; Van Nguyen and Pawlowski, 2017). Rhizobia are a polyphyletic group that come from 15 genera in 8 different families (Remigi et al., 2016). Two competing hypotheses exist regarding the evolution of plant-rhizobia symbioses. The first assumes that there are multiple origins of this symbiosis given the phylogenetic distance between legumes and *Parasponia* (Geurts et al., 2012; Behm et al., 2014). However, a more recent hypothesis suggests that nitrogen-fixing symbioses evolved from a single angiosperm lineage that was already in association with AMF (Werner et al., 2014); this cryptic adaptation was identified in the rosids I clade originating ~100 Ma and is believed to have been able to form stable nodulation with rhizobia. The formation of stable nitrogen-fixing symbioses with rhizobia is believed to have been subsequently lost and regained multiple times, resulting in the host-symbiont specificity commonly observed (Oldroyd et al., 2011). The degree to which coevolution played a role in the evolution of rhizobia is much debated as the ability to nodulate may have been driven by plant selection of beneficial symbionts, or plants may have cultivated symbioses with rhizobia through the formation of nodules. Given the strong evidence of widespread horizontal gene transfer (HGT) within the rhizobia and the discordant speciation between legumes and rhizobia, plant-driven coevolution seems unlikely to be the primary driver.

Plants stimulate rhizobial growth by excreting flavonoids as a means of recruiting suitable nitrogen-fixing symbionts (Figure 2). In response, rhizobia release effector proteins generally referred to as nodulation (Nod) factors and a cocktail of LCOs (with the exception of *Bradyrhizobia* discussed in the following text). Nod factors and effector proteins activate the same CSSP in

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plants required for the establishment of AMF symbioses. Plant activation initiates root growth and the formation of young nodules. Rhizobia then enter nodules through a transient, specialised structure known as the 'symbiosome' that becomes a nutrient exchange interface between the rhizobia and the plant (Figure 1).

2.4 Actinobacteria (*Frankia*)

Filamentous, nitrogen-fixing bacteria within the genus *Frankia* form nodules with a broad diversity of actinorhizal plants including >260 species within the Fagales, Rosales, and Cucurbitales orders (Dawson, 2007) as opposed to rhizobia which only associate with legumes and *Parasponia*. Generally, *Frankia* use similar signalling mechanisms to rhizobia to induce symbioses with the exception of clusters I and III *Frankia*, which lack the core *nodABC* nodulation genes. The actual signals are unknown but cluster I and III species have been shown to produce hydrophilic, chitinase-resistant molecules that induce Ca^{2+} spiking characteristic of CSSP activation (Chabaud et al., 2015). This evidence suggests that cluster I and III *Frankia* are secreting compounds that act as Nod factors that are structurally distinct from chitin-based LCOs. The proposed mechanism of cluster I and III symbiotic signalling likely involves the CSSP given that LysM receptor-like kinases (LysM-RLKs) within the CSSP are activated by a variety of compounds other than LCOs such as peptidoglycans and polysaccharides (Willmann et al., 2011). Despite some work in this area, the identity of these *Frankia*-derived signals and their corresponding plant receptors remain unknown (Nguyen and Pawlowski, 2017).

Actinorhizal plants belong to the Fabales clade (same as legumes and *Parasponia*) further strengthening the hypothesis that nodule-forming plants arose from a single predisposed lineage of angiosperms ~100 Ma (Soltis et al., 1995; Doyle, 1998, 2011) (Figure 1). Nodulation proceeds similarly to rhizobial nodulation. However, actinobacteria form a thread-like structure, termed a 'fixation thread', instead of a symbiosome in order to penetrate the epidermis and transit into the nodule (Figure 1). Unlike symbiosomes, fixation threads remain intact once inside the plant cell; instead of opening, the cell wall thins to allow the transfer of nutrients between the host and symbiont (Holmer et al., 2017). Behm et al. (2014) argue that fixation threads found in the *Parasponia*-rhizobia mutualisms are a younger interaction therefore represent a more ancestral infection mechanism than symbiosomes.

3 Plant Hormone Signalling

An overwhelming number of plant and microbial-derived signals and their perception mechanisms have been identified (for review see: Venturi and

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Keel, 2016). While a variety of signals appear to be relevant to plant–microbe signalling, strigolactones, and flavonoids are some of the best studied plant-derived signals while LCOs, COs, and effector proteins are the most well-understood microbial-derived cues. The majority of symbioses involving AMF, rhizobia, and *Frankia* have evolved to require the CSSP pathway in plants to perceive these microbial-derived signals and alter plant hormonal signalling in order to form the proper endosymbiotic structures (Delaux et al., 2013b) (Figure 2). As discussed in the following section, plants use this same pathway to distinguish between fungal and bacterial symbionts that result in completely different endosymbiotic structures. The mechanism behind how specific symbionts are perceived by the CSSP remains one of the primary outstanding questions.

3.1 Algal Ancestors Contain the Building Blocks for the Common Symbiosis Signalling Pathway (CSSP)

As mentioned earlier, the CSSP is a shared signalling pathway present in nearly all land plants and used by both AMF, rhizobia, and actinobacteria to modify plant hormone signalling and regulate root growth (Figure 2). Briefly, the CSSP is induced by microbial derived LCOs and COs (Genre et al., 2013) and perception of these microbial signals by plants occurs via LysM-RLKs that, in turn, activate a symbiosis receptor kinase, SYMRK, which is referred to as DMI2 in *Medicago truncatula* (Stracke et al., 2002). SYMRK activates the potassium channel (DMI1) on the nuclear membrane to produce Ca^{2+} oscillations. These Ca^{2+} signals are decoded by calcium/calmodulin-dependent protein kinase (CCaMK) that leads to the phosphorylation of the transcriptional regulators CYCLOPS (in *Lotus japonicus*) or IPD3 (in *M. truncatula*) (Ané et al., 2004; Levy et al., 2004). CYCLOPS/IPD3 regulates one or more of four downstream "GRAS"-domain transcriptional factors (Hirsch and Oldroyd, 2009) required for arbuscular (RAM1 and RAD1) or nodulation (NSP1 and NSP2) specific symbioses (Gobbato et al., 2012; Delaux et al., 2013a; Singh et al., 2014; Xue et al., 2015) (Figure 2). The CSSP has been the subject of a number of recent reviews and the reader is recommended to consult Oldroyd (2013) and MacLean et al. (2017) for further details.

Comparative genomics have revealed the degree to which the CSSP is conserved across terrestrial plants and their algal ancestors. A complete set of CSSP-related orthologues (LysM-RLK, DMI1, DMI2, CCaMK, and IPD3) were identified in bryophytes (Delaux et al., 2015). Homologues for LysM-RLK and IPD3 were identified in select charophytes and a DMI2 orthologue was identified in a single charophyte. Perhaps most surprising, potential DMI1 and CCaMK homologues were found in charophytes as well as a few chlorophytes (Delaux et al., 2015). The selectivity filter domain of the DMI1 potassium channel appears to have originated in chlorophytes but

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was significantly refined within the charophytes to the form represented in extant terrestrial plants (Delaux et al., 2015). Additional homologues downstream of CCaMK were identified in chlorophytes (e.g., an ABC transporter, a H^+-ATPase (HA), and a phosphate transporter (PT)) although more were found in charophytes (all four of the GRAS transcription factors, two ABC transporters, HA, and PT). Despite the presence of these downstream components in algal ancestors, the majority of downstream components only appear in the bryophytes (Delaux et al., 2015). Regardless, this genetic evidence strongly suggests that fungal–algal interactions likely predated the establishment of terrestrial bryophyte-AMF interactions.

Taken together, much of the CSSP predates terrestrial land plants and several microbes have tapped into this signalling pathway to establish beneficial symbioses. Mosses show highly diverged CSSP genes relative to those of land plants, which show extremely high conservation, and transformation with moss CCaMK could not rescue AMF colonization in *M. truncatula* null mutants (Wang et al., 2010). The divergent loss of crucial CSSP genes likely represents a secondary loss (Field and Pressel, 2018) and confirms the importance of the CSSP as mosses do not form AMF symbioses. Current evidence suggests that while the CSSP is required for AMF, rhizobial, and actinobacterial-plant symbioses, it is not required for EMF-plant symbioses. In fact, downstream components of the CSSP are absent in many of the EMF-specific species within the Pinaceae family potentially due to genome streamlining (Garcia et al., 2015).

However, the CSSP is present in other EMF-associated plants within and outside of the Pinaceae family (Garcia et al., 2015). This means that the CSSP could have been used in early EMF-plant associations and may be partly required in some EMF-plant associations. For example, the glycerol-3-phosphate acyltransferase (RAM2; Venkateshwaran et al., 2013) involved in fatty acid biosynthesis that central to the CSSP is present in most EMF associating plants including those within the Pinaceae that lack most of the CSSP, suggesting that fatty acids may still play a role in EMF symbioses (Garcia et al., 2015). To date, the importance of the CSSP to the evolution of EMF symbioses remains unclear.

4 Suppression of Plant Immunity

While plant symbiotic signalling and innate immunity have commonly been studied as distinct entities, they must work in concert for the establishment of beneficial endosymbioses (for a detailed review, see: Desaki et al. (2018) and Plett and Martin (2018)). Plant-immune responses are triggered by the detection of common signatures of plant-associated microbes termed 'microbe-associated-molecular-patterns' (MAMPs) that include flagellin,

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peptidoglycan, chitin, and their molecular derivatives. Although AMF, rhizobia, and actinobacteria secrete LCOs, these compounds are not classified as MAMPs because plant perception of LCOs typically results in the formation of specialised endosymbiotic structures (arbuscules and nodules) instead of a prolonged innate immune response (Hacquard et al., 2017). While plant immune responses are often pathogen-specific, there are common characteristics that indicate the activation of plant immunity; typically, the secondary signalling compounds jasmonic acid, ethylene, and salicylic acid are produced and reactive oxygen species (ROS) accumulate in infected areas (Plett and Martin, 2018). As will be discussed below, so-called 'symbiotic' signals have been shown to induce some of the same physiological changes associated with innate immunity. Understanding the connections between symbiosis and immunity should yield insights into how plants distinguish between beneficial symbionts and pathogens as well as how these signals coevolved.

The origins of plant immunity have been traced back to a superfamily of Nod-like receptor (NLR) proteins that were present in early charophyte algae and remain conserved across gymnosperms and angiosperms but lost in grasses (Yue et al., 2012; Gao et al., 2018). The presence and diversification of NLRs in the Charophyceae suggests that these proteins may have been used to sense algal pathogens (Gao et al., 2018). This is not surprising as algae and early embryophytes interact with a plethora of microbes. Some algae are known to have tight mutualistic symbioses with bacteria (Croft et al., 2005; Droop, 2007; Geng and Belas, 2010; Seymour et al., 2017; Hom et al., 2015) as well as antagonistic symbioses (Rasconi et al., 2012; Knack et al., 2015). The work by Gao and colleagues highlights the importance of ancestral algal immunity on the evolution of advanced plant immune responses (for a detailed discussion, see: Ortiz and Dodds (2018)). Future work may illuminate the physiological responses of algae to microbial contact that go beyond the mere presence of receptor proteins.

4.1 AMF and Plant Immunity

Immune responses are known to be triggered upon initial AMF contact, followed by immune suppression during later stages of arbuscule formation (Kapulnik et al., 1996; Fester and Hause, 2005; Fouad et al., 2014; Benhiba et al., 2015; Mo et al., 2016; Sarkar et al., 2016). Some receptors associated with MAMP perception appear to play a dual role in activating plant immunity when faced with a pathogen and in establishing symbiotic arbuscules when associated with AMF. The LysM receptor in rice, OsCERK1, is well known to perceive LCOs produced by AMF (Carotenuto et al., 2017), while its homologue in *Arabidopsis* is associated with triggering host immunity in response to chitin perception (Miya et al., 2007; Shimizu et al., 2010). This raises the question as to how OsCERK1 distinguishes between AMF and

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pathogens. OsCEBiP is a coreceptor protein that is required for pathogenic chitin perception but that does not affect AMF colonization (Kaku et al., 2006; Shimizu et al., 2010), suggesting that a yet unidentified membrane protein coreceptor may be required for distinguishing AMF-specific LCOs.

The idea that plants rely on a numerous LysM-RLK receptors to perceive different extracellular signals is not new. Bozsoki et al. (2017) identified additional receptors in *M. truncatula* and *Lotus japonicus* that bind distinctly to chitin and result in the activation of innate immunity while being unaffected by LCO production, by AMF, or rhizobia. Desaki et al. (2018) further reviews what is known about the role of specific LysM-RLK receptors used in distinguishing between pathogens and specific beneficial symbionts. There are some cases where pathogens appear to have coopted the CSSP machinery associated with AMF and nitrogen-fixing bacteria in order to avoid host immunity. Recent work has documented the necessity of various CSSP genes (SYMRK, NUP133, SEC13, and POLLUX) in *Arabidopsis thaliana* required for successful life cycle completion by the mildew pathogen *Hyaloperonospora arabidopsidis* (Ried et al., 2018). It has yet to be determined whether *H. arabidopsidis* has truly coopted the signalling machinery utilised by AMF or if this is a snapshot in the coevolutionary arms race in which *H. arabidopsidis* is evolving into a pathogen from initially being a mutualist. At this point, the role of plant immunity in the formation of AMF symbioses remains unclear. What is known is that an immune response is triggered but subsequently suppressed when arbuscules form. Moreover, immune suppression is linked to the activation of specific LysM-RLK receptors responsible for the perception of AMF-derived LCOs and COs.

4.2 EMF and Plant Immunity

EMF appear to have evolved separately from AMF and rhizobia/actinobacteria. While EMF have retained a small number of cellulases, they appear to have lost a great number of extracellular degradative enzymes present in their saprotrophic fungal counterparts (Plett and Martin, 2011; Kohler et al., 2015). This reduction appears crucial to the formation of stable symbioses as plants have evolved so-called 'damage-associated-molecular-patterns' (DAMPs) that detect cell wall fragments such as oligogalacturonides, galacturonic acid, and hyaluronan fragments (Land, 2003). Similarly, AMF have very few if any cell wall modifying enzymes (Tisserant et al., 2013; Kohler et al., 2015); rhizobia and *Frankia* have some active cellulases and endoglucanases that are required for the formation of infection threads and/or the establishment of a healthy nodule (Robledo et al., 2008, 2011). Following the initial phases of plant colonization, the activation of plant immunity by EMF is quickly attenuated (Duplessis et al., 2004; Plett et al., 2014b, 2015). However, Plett et al. (2014b) found that ethylene and jasmonic acid production (immune response markers, see above) was increased in

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Populus during later stages of EMF infection by *Laccari bicolor*. The authors hypothesise that this enhanced host immunity during late-stage colonization may be induced to limit the number of fungi able to inhabit the roots so as avoid overtaxing the plant host. Stimulation of plant immunity during late-stage colonization in AMF has not been reported, although the appropriate studies have not been conducted to see if plants use similar methods to restrict colonization in AMF symbioses.

4.3 Rhizobia and Plant Immunity

The relationship between symbiotic signalling and innate plant immunity is probably best understood with the rhizobia-plant endosymbiosis. Recent studies have shown that rhizobia-specific LCOs and COs (Nod factors) stimulate the *upregulation* of genes associated with innate immunity (Libault et al., 2010; Nguyen et al., 2012; Rose et al., 2012). However, the precise mechanism of plant immunity activation and the compounds associated with activation are not yet understood. There are also numerous examples of Nod factors that are required for the *attentuation* of an immune response. For example, Nod factor deficient rhizobia (*nodC* mutants) were shown to increase the amount of salicylic acid, a secondary signalling compound associated with plant immunity (Martínez-Abarca et al., 1998). Nod factor additions have also been associated with the reduction of ROS accumulation in *M. truncatula* (Shaw and Long, 2003) as well as the reduction of a general innate immune response brought on by the exogenous addition of the MAMP, flg22, to *Arabidopsis* (Liang et al., 2013). Taken together, these findings show a clear link between the Nod factors produced by rhizobia and the manipulation of plant immunity. The catch-all term 'Nod factors' refers to a complex cocktail of compounds that may mask the distinct effects of individual compounds that may also elicit responses at different timescales. The potentially paradoxical interaction between Nod factors and plant immunity may simply be due to shared sensing machinery (gene sharing/pleiotropy (Piatigorsky, 2007)) for immune activation and nodulation initiation and perhaps the result of rhizobia having evolved from a pathogen that was able to suppress plant immunity. Effector proteins are also known to play an important role in the suppression of plant immunity (see Section 9).

4.4 *Frankia* and Plant Immunity

To date, we know little about the regulation of plant immunity with respect to actinobacteria-plant symbioses. However, an important group of smallsecreted hydrophilic, chitinase-resistant compounds is associated with the establishment of Nod-independent nodule formation (Chabaud et al., 2015; Cissoko et al., 2018) as well as the conservation and expression of *nad1*, a gene associated with defence response in legume nodules, in

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actinorhizal plants (Wang et al., 2016). Plant innate immunity may play a role in actinorhizal nodulation, but the mechanisms remain to be elucidated. The production of other compounds associated with the suppression of plant immunity such as Nod factors and effector proteins by *Frankia* cluster II species is discussed in Sections 8.5 and 9, respectively.

5 Strigolactones

Strigolactones are synthesised by plants and serve a number of functions for internal and external plant signalling (Smith, 2014). The effect of strigolactones has been assessed on many plant developmental processes including leaf elongation, thickening, senescence, outgrowth, lateral root formation, and primary root growth (for a detailed review, see: Waters et al. (2017)). Both low phosphate and low carbon conditions increase strigolactone production, although low phosphate leads to increased lateral root formation (Ruyter-Spira et al., 2011; De Cuyper et al., 2015) while low carbon leads to increased primary root growth; both these responses appear to be well conserved across plants. Low phosphate conditions have also been shown to increase the amount of strigolactones secreted by plants into the surrounding soil and is expected to impact neighbouring plants and microbes (Akiyama et al., 2005; Kohlen et al., 2011).

The discovery by Akiyama et al. (2005) that strigolactones can stimulate hyphal branching in AMF kicked off countless studies assessing the role of strigolactones in plant–microbe interactions. To date, strigolactones have been shown to stimulate growth in AMF, *Frankia*, and rhizobia, although the role of strigolactones in EMF-plant associations is still not well understood (reviewed by Holmer et al. (2017)). In the following sections, we discuss the evolution of strigolactone production and perception within plants as well as strigolactone perception by plant symbionts.

5.1 Evolution of Strigolactone Production and Perception in Plants

Strigolactones are carotenoid-derived terpenoid lactones that serve as intracellular and intercellular signals for symbiotic signalling and the control of hormone production. Strigolactone production in plants requires a carotenoid isomerase, two carotenoid cleaving dioxygenases, CCD7 and CCD8, a cytochrome P450 (Alder et al., 2012; Zhang et al., 2014), and an ABC-transporter, PDR1 (Kretzschmar et al., 2012). Chlorophyte algae do not appear to have CCD7 or CCD8 orthologues and do not exhibit physiological changes in response to strigolactone additions (Delaux et al., 2012b). However, a recent study has shown that strigolactone-like compounds are

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produced by *Trebouxia arboricola*, a common green-algal symbiont in lichens (Smýkalová et al., 2017) suggesting that the ancestral origins of plant strigolactones may stem from algae earlier than previously thought (Delaux et al., 2012a). Some advanced charophytes such as *Nitella hyalina*, *Nitella pseudoflabellata*, and *Chara corallina* have been shown to produce and respond to the strigolactone and sorgolactone, while other charophytes such as *Spirogyra* sp. and *Coleochaete scutata* are notably incapable of producing strigolactone-like compounds (Delaux et al., 2012b). The lack of a clear CCD8 orthologue in *Nitella* paired with strigolactone production in these Charophytes indicates a CCD8-independent pathway for strigolactone production. Further studies are needed to explore alternative strigolactone production pathways and to elucidate the origins of strigolactone production and potential interspecies strigolactone signalling. While alternative pathways appear to be crucial to some algal ancestors, there does not appear to be an alternative strigolactone production pathway in angiosperms (Gomez-Roldan et al., 2008; Umehara et al., 2008). Basal land plants including liverworts and mosses appear to use a canonical strigolactone production pathway, as they contain CCD7 and CCD8 orthologues and are capable of producing strigolactones; they also respond to exogenous strigolactone additions (Proust et al., 2011; Delaux et al., 2012b).

Much less is understood about how plants perceive strigolactones that they produce or that are produced by other plants. Strigolactone perception in angiosperms requires the α/β-hydrolase superfamily protein, D14 (Arite et al., 2009). However, D14 orthologues have only been identified in spermatophytes, suggesting an alternative receptor protein in basal land plants. The karrikin receptor, KAI2, appears to function as an alternative strigolactone receptor (Scaffidi et al., 2014) and is well conserved across all land plants and a number of charophytes (Bythell-Douglas et al., 2017). The presence of KAI2 orthologues in early charophytes raises the question as to the role they played in early algal ancestors and suggests that karrikin-like compounds, such as strigolactones, were important signals well before the evolution of land plants.

5.2 AMF Perception of Strigolactones

In addition to increasing hyphal branching, strigolactones have been shown to increase nuclear division (Akiyama et al., 2005; Besserer et al., 2006, 2008), the production of short-chain COs (Genre et al., 2013), and induce expression of a putative effector protein (RiSIS1) in AMF (Tsuzuki et al., 2016). In general, increased plant strigolactone production is associated with the early stages of AMF colonization that is reduced following successful colonization (López-Ráez et al., 2011, 2015). It is believed that most AMF can respond to low concentrations of strigolactones; for example, *Gigaspora margarita* has been shown to respond to extremely low concentrations (10 nM) of the

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synthetic strigolactone GR24 (Besserer et al., 2006). However, AMF responses to strigolactones are often concentration-dependent (Akiyama et al., 2005), and were astutely noted by Holmer et al., 2017 to be codependent on the presence of flavonoids (Besserer et al., 2008). Thus far, it has been difficult to link specific strigolactone-induced signals with AMF physiological changes because the mechanisms for AMF strigolactone perception are still unknown despite this is too extreme attempts to identify AMF strigolactone receptors (Tisserant et al., 2012, 2013). In large part, the difficulties associated with determining AMF signal receptors stem from the apparent obligate symbiotic nature of these fungi, making it impossible to grow these AMF independently and thus practically difficult to generate mutant libraries for screening. However, the recent discovery of the essential role of lipids in symbiotic signalling (Bravo et al., 2017; Jiang et al., 2017; Keymer et al., 2017; Luginbuehl and Oldroyd, 2017; Rich et al., 2017) (discussed in Section 7) may make it technically feasible to culture these lipid-auxotrophic AMF apart from their plant hosts.

Although strigolactone signalling is not absolutely required for AMF colonization, it is beneficial: strigolactone-knockout mutants typically show less colonization than their strigolactone-producing counterparts (Gomez-Roldan et al., 2008; Koltai et al., 2010; Gutjahr et al., 2012). It is unclear whether increased colonization is due to: (i) increased recruitment of AMF from the surrounding soil, (ii) increased production of COs/effector proteins that lead to an increased symbiotic response, or (iii) increased plant growth in direct response to strigolactone self-stimulation. It is generally believed that this last reason is less likely as mycorrhizal recruitment has been linked to the presence of the strigolactone exporter (PDR1), suggesting that strigolactones are primarily acting as signalling mechanisms for fungi during the symbiont recruitment stage as opposed to phytohormones (Kretzschmar et al., 2012). However, this does not rule out the possibility that plants are responding to their own secreted strigolactones. It has yet to be assessed if PDR1 is conserved in early bryophytes or algal lineages, but this may shed light on the role of strigolactones in ancestral land plants as the current hypothesis is that they are used only as phytohormones and not as symbiotic signals (Delaux et al., 2012b).

5.3 EMF Perception of Strigolactones

Past experiments have shown that synthetic strigolactone additions (i.e. GR24) have had no effect on the hyphal branching characteristics of EMF (Steinkellner et al., 2007). However, strigolactones have been shown to reduce hyphal branching in phytopathogenic fungi when added at relatively high concentrations (Dor et al., 2011). The micromolar concentrations employed by Dor and colleagues is far above the pico- and nanomolar concentrations thought to be secreted by plants and their relevance to natural interactions

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are questionable (Xie et al., 2010). While strigolactones may not affect EMF growth, it is possible that they activate the production of signalling molecules such as effector proteins or LCOs/COs (Genre et al., 2013). EMF-associated species from the *Pinus* genus maintain enzymes required for strigolactone production (CCD7 and CCD8) although they have lost critical genes related to the CSSP (Garcia et al., 2015); this is consistent with the hypothesis that strigolactone acts as a phytohormone but not a symbiotic signal. Future transcriptomic studies following exogenous strigolactone additions (similar to one conducted by Tsuzuki et al. (2016) with AMF) may confirm whether EMF have gene-level responses to strigolactone secretion. Controlling for confounding cosignals in such studies, however, will be critical; for example flavonoids have been shown to increase basidiomycete spore germination (Kikuchi et al., 2007) and are known to be critical cosignals with strigolactones in AMF symbioses (Besserer et al., 2008).

5.4 Rhizobia Perception of Strigolactones

Strigolactones have been shown to increase nodule formation in rhizobium-legume symbioses (Soto et al., 2010) although without apparent effect on rhizobia bacteria, whose growth and *nodC* expression (associated with Nod-factor production) remained unchanged. At least some strigolactones may act on the plant and not directly on their bacterial symbionts. More recent work has shown that strigolactone-silenced plant mutants have significantly less nodules than wild-type controls suggesting that while strigolactones are not required for nodulation, they may impact the number of nodules formed and plant fitness (Foo and Davies, 2011; Liu et al., 2013; De Cuyper et al., 2015). These studies do not, however, address whether strigolactones directly affect rhizobia or indirectly increase nodulation by influencing plant growth. Strigolactones have been shown to increase the motility and swarming ability of rhizobia, which is hypothesised to be responsible in general for the increased rate of nodulation in strigolactone-excreting plants (Tambalo et al., 2014). Peláez-Vico et al. (2016) demonstrated that increased swarming ability of alfalfa-associated rhizobia increased nodule formation, and for the first time showed that strigolactone production decreased in response to successful nodulation. This negative feedback of nodulation-colonization on strigolactone production mirrors the well-established behaviour of AMF colonization on strigolactone production (Lendzemo et al., 2007; Sun et al., 2008; Fernandez-Apricio et al., 2010; López-Ráez et al., 2011; Aroca et al., 2013). As is the case with AMF, potential strigolactone receptors have not been identified in rhizobia. Additional work addressing this question may allow future studies to assess the prevalence of strigolactone receptors in rhizobia as well as potentially track the activation of receptors during pre-symbiotic signalling and nodule formation.

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5.5 *Frankia* Perception of Strigolactones

There is only one study we are aware of supporting strigolactones as a signal involved in the establishment of *Frankia* nodulation. Beauchemin et al. (2012) showed that Casuarina root exudates increased *Frankia* growth and induced hyphal 'curling.' However, the effects of strigolactones were not separated from those potentially caused by flavonoids as the authors were only interested in the effect of bulk exudate applications on plant-*Frankia* symbiosis. The observed response could be due to flavonoids or other compounds present in the root exudates. This is a critical distinction as flavonoids have been directly shown to influence *Frankia* nodulation as is discussed in Section 6.5.

6 Flavonoids

6.1 Evolution of Flavonoid Production and Perception in Plants

Flavonoids are produced by plants and act as both phytohormonal and direct symbiotic signals for microbial recruitment. Flavonoids are produced in plants through the phenylpropanoid pathway. Phenylalanine ammonia lyase (PAL) initiates the synthesis of flavonoids. Plants typically contain five PAL gene homologues but may contain as many as twelve (Raes, 2003; Cochrane et al., 2004; Tsai et al., 2006; Reichert et al., 2009; Huang et al., 2010; Dong and Shang, 2013; De Jong et al., 2015). PAL genes are induced by a variety of factors including environmental stress, pathogen infection, and nutrient deprivation (Dixon and Paiva, 1995; Payyavula et al., 2012). The regulation of auxin signalling within plants is one of the most critical roles of flavonoids (Peer and Murphy, 2007). However, it has been known for decades that flavonoids act as key signals in rhizobia-legume symbioses, triggering rhizobia to produce LCOs and regulating the plant growth during nodule formation (Redmond et al., 1986; Djordjevic et al., 1987; Wasson, 2006). Given the numerous functional roles of flavonoids, it has been difficult to discern their original role (if only one) in ancestral plants although protection against UV radiation is likely (Tripp et al., 2018).

It was previously thought that the phenylpropanoid biosynthetic pathway originated by HGT from bacteria to the first land plants (Emiliani et al., 2009), however, these analyses did not have the advantage of the wealth of sequencing data from streptophyte algae that has been generated in recent years (Ju et al., 2015; Van de Poel et al., 2016). A recent survey of algal genome and transcriptome data identified an orthologue for PAL in the charophyte, *Klebsormidium flaccidum*, and identified a set genes related to the so-called 'genetic toolkit' for phenylpropanoid synthesis (De Vries et al., 2017). To our knowledge, metabolite screenings of *Klebsormidium* have not been conducted to see

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if flavonoid or flavonoid-like compounds are being produced. This may be a fruitful avenue for research as there is some degree of specificity between the types of flavonoids produced and their likely biological role, whether it be for pathogen defence, phytohormonal signalling, or symbiotic signalling. While flavonoids are typically thought of as plant-rhizobia signals, they have been shown to play a modulatory role in the establishment of AMF, EMF, and *Frankia* symbioses as well as with rhizobia.

6.2 AMF Perception of Flavonoids

Flavonoids are generally thought of as pre-symbiotic cues for AMF-plant symbioses as they have been shown to stimulate spore germination and hyphal branching (Tsai and Phillips, 1991; Bécard et al., 1992) and increase overall mycorrhizal colonization (Garg and Singla, 2016). It has also been suggested that flavonoids increase the number of entry points for colonization by the fungus (Scervino et al., 2007). Some studies have evaluated the role of specific flavonoids on particular mycorrhizal-plant symbioses; however, an insufficient number of studies that evaluate the same set of flavonoids across a broad range of AMF-plant interactions, as has been done for rhizobial-plant symbioses (Reddy et al., 2007), prevents general conclusions from being drawn about how flavonoids might influence AMF host specificity.

While flavonoids have been shown to induce hyphal branching and spore germination, the mechanism of flavonoid perception in AMF remains unidentified. Identification of a flavonoid receptor would be important for delineating downstream pathways. At this point, it is unclear whether flavonoids are: (i) primarily perceived by the plant to regulate growth, (ii) inducers of fungal growth that increase the likelihood of plant colonization, (iii) a selective signal that helps the recruitment of symbionts (Ellouze et al., 2012), or (iv) a signal perceived by AMF in order to induce the production of LCO-based signalling compounds (mycorrhizal or 'Myc' factors). It has been suggested that flavonoids are capable of inducing hyphal growth at longer distances than strigolactones thus acting as long-distance signals that increase the probability of plants coming in contact with suitable AMF (Nadal and Paszkowski, 2013).

6.3 EMF Perception of Flavonoids

Similar to AMF, flavonoids can enhance EMF hyphal branching, spore germination, and colonization of plants (Lagrange et al., 2001; Kikuchi et al., 2007; reviewed by Abdel-Lateif et al. (2012)). Flavonoids have also been shown to increase the production of effector proteins by the ectomycorrhizal fungus, *L. bicolor* (Plett and Martin, 2012). Interestingly, the flavonoid, rutin, seems to act as nonspecific signalling molecule that enhances the colonization of

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Pisolithus species on *Eucalyptus* trees (Lagrange et al., 2001) but also enhances the growth of pathogenic fungi (Kalinova and Radova, 2009). This suggests that for EMF, flavonoids may not specifically enhance the recruitment of beneficial fungi as hypothesised for AMF systems. As with AMF, the mechanism of flavonoid perception in EMF is yet unknown.

6.4 Rhizobial Perception of Flavonoids

Flavonoids have long been studied in the context of plant-rhizobial symbioses and most of what is understood about the perception and the physiological changes induced by flavonoids are in reference to rhizobia. As is the case for AMF and EMF, flavonoids are thought of as pre-symbiotic signalling compounds used to recruit compatible rhizobia. Flavonoids are secreted primarily from the elongating root hair zone where nodules are generally found (Zuanazzi et al., 1998). Flavonoids target LysR-type transcriptional regulators in rhizobia, specifically NodD proteins (Honma et al., 1990). In rhizobia, there are typically multiple operons that contain a NodD promoter (Chen et al., 2005). These include genes required for the production and secretion of rhizobia specific LCOs (Oldroyd, 2013; Limpens et al., 2015): the enzymes N-acetylglucosaminyltransferase (NodC), chitooligosaccharide deacetylase (NodB), N-acyltransferase (NodA), and components for an ABC transporter (NodI and NodJ).

There has been extensive work to understand the role of specific flavonoids on plant-rhizobia host specificity (Reddy et al., 2007). Cases in which flavonoid compounds promote endosymbiosis in some instances but antagonise endosymbiosis in others is a consistent pattern across AMF, EMF, and *Frankia* symbioses (Lagrange et al., 2001; Kikuchi et al., 2007; Reddy et al., 2007; Abdel-Lateif et al., 2012; Garg and Singla, 2016). The aforementioned host-symbiont specific signals may be partly responsible for these differences, although the *timing* of flavonoid release may be important in dictating the observed outcomes (Figure 3). Previous studies have shown that more mature roots will secrete different phenolics than younger root tips (Peters and Long, 1988; Zuanazzi et al., 1998), suggesting that signal timing may be critical for proper symbiont recruitment and productive endosymbiosis.

Similar to strigolactones, flavonoids are known to act as symbiotic signals as well as key plant–plant signalling compounds. Flavonoids have been shown to modulate auxin transport (Mathesius et al., 1998; Brown, 2001; Wasson, 2006), which is hypothesised to be important for successful nodulation (Deinum et al., 2012). In turn, auxin transport is thought to be regulated by cytokinin signalling (Pernisova et al., 2009; Ruzicka et al., 2009; Marhavý et al., 2011, 2014). During nodulation, both cytokinin signalling in the cortex of the root and auxin transport are increased. Recent work by Ng et al. (2015) found that the flavonoid, naringenin, affects endogenous

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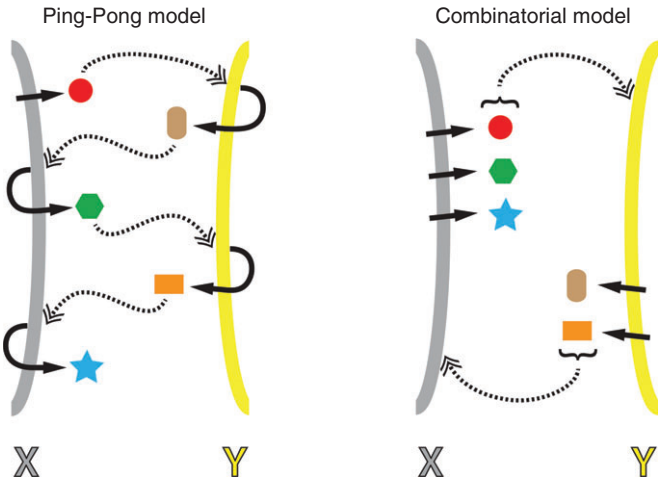

Figure 3 Two models for how multiple symbiotic signals between plant and microbes could be exchanged. The 'Ping-Pong' Model illustrates how the perception of an initial signal from symbiont X might activate signal secretion from symbiont Y, which in turn stimulates the production of a secondary signal in symbiont X, and so forth. This type of exchange implies a signalling order and the existence of time lags between signals required for the formation of symbioses. The Combinatorial Model depicts how different combinations of multiple signals are simultaneously released and perceived by symbionts X and Y that may be required for the establishment of symbioses. These models are not mutually exclusive and plant–microbe signal exchange is likely to possess aspects of both models (e.g., signal 'cocktails' could be released and perceived in a ping-pong fashion, and result in reciprocal cascades of events).

plant signalling during nodulation. This was confirmed in a nonnodulating *M. truncatula* mutant lacking the cytokine receptor *cre1*. Applications of naringenin restored auxin transport and restored nodulation in this mutant. This work demonstrated that flavonoids behave similarly to cytokinins as endogenous signals during nodulation suggesting that they may act as more than simply plant-rhizobia signals.

6.5 *Frankia* Perception of Flavonoids

RNAi silencing of chalcone synthase, the first enzyme of flavonoid biosynthesis, dramatically reduces *Frankia* nodulation with the wetland plant *Casuarina glauca* (Abdel-Lateif et al., 2013), in support of the long-held hypothesis that flavonoids play a fundamental role in *Frankia*-plant symbioses (Van Ghelue et al., 1997; Hughes et al., 1999). Unlike rhizobia, a systematic analysis of how specific flavonoids affect *Frankia* nodulation has not been done. While it is apparent that some flavonoids affect *Frankia*

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nodulation, it is unclear whether flavonoid perception induces secondary signal production by *Frankia* or if it simply alters the surface components of the bacterium (Beauchemin et al., 2012).

7 Lipid Signalling

It was previously thought that AMF only receive carbohydrates from their plant partners, although it was recently found that AMF lack the core fatty acid synthase genes and require the transfer of lipids from the plant host in order to grow (Bravo et al., 2017; Jiang et al., 2017; Keymer et al., 2017; Luginbuehl and Oldroyd, 2017; Rich et al., 2017) (Figure 2). Two lipid synthesis enzymes, FatM and RAM2, in conjunction with an ABC transporter, are required for lipid transfer (Bravo et al., 2017). Given the importance of plant-AMF lipid transfer, it would be beneficial to identify 'symbiotic lipid' genes and determine their degree of conservation within basal plant and algal lineages. Such work may shed additional light on early photoautotroph interactions prior to terrestrialization. It is curious that AMF are lipid auxotrophs, and yet AMF symbiosis is based on the release of lipid-modified symbiotic signals from AMF (LCOs/Myc factors) to the plant host. The machinery related to LCO/Myc factor biosynthesis is still uncharted, with unconvincing fungal homologues for the NodA N-acyl transferase used to transfer fatty acyl chains and generate LCOs from COs (Poinsot and Couderc, 2017). Nonetheless, fatty acyl chains for LCOs likely derive from the lipids transferred from the plant host. For AMF to use a nutritional component supplied from a plant host for symbiotic signalling may be a form of a 'hand shake' or 'honest signal' (Maynard-Smith, 1991) that ensures partner fidelity and serves to distinguish beneficial symbionts from pathogens. Recent work has shown that lipids can be transferred not only to beneficial symbionts but also to the fungal pathogens such as *Golovionomyces cichoracerum* (Jiang et al., 2017). Jiang et al. (2017) show that lipid transfer is required for plant colonization by this fungal pathogen. Such pathogens do not, however, signal back to the plant host with LCOs/Myc factors. As mentioned previously, RAM2 has been shown to be conserved in the Pinaceae family where other genes related to the CSSP have been lost (Garcia et al., 2015). This indicates that lipid transfer may also be involved in EMF symbioses.

8 Microbial LCO and CO Production

8.1 Plant Perception of LCOs

Plant perception of LCOs both activates the common CSSP and has a role in activating plant innate immunity (for recent review: Zipfel and Oldroyd

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(2017)). LCOs are perceived by three extracellular LysM receptor-like kinases located on the cell membrane. While these three genes are only present in land plants, LysM-RLK orthologues are present in some advanced charophytes (Delaux et al., 2015) suggesting that algal ancestors may have been able to recognise chitin-like compounds. LCO perception has been best studied in the legumes, *L. japonicus* and *M. truncatula*, where the formation of rhizobial symbioses is dependent on the LysM-RLKs LjNFR1 and LjNFR5 with *L. japonicus*, and MtLYK3 and MtNFP with *M. truncatula*. LjNFR1/MtNFP and LjNFR5/MtLYK3 enhance mycorrhizal symbioses, but they are nonessential for legumes to form arbuscules. Legumes may be independent of these receptors because of alternative LysM-RLKs that have arisen through gene duplication or other receptors used for plant perception of mycorrhizal-derived COs. COs have been shown to be produced by mycorrhizae along with LCOs and will enhance AMF colonization although they do not influence lateral root growth. Analysis of LCO perception in nonlegumes is illuminating as OsCERK1 is a chitin and LCO receptor required for the activation of the immune response and AMF endosymbiosis in rice (Miyata et al., 2014). Recent work has documented that the NFR5/NFP orthologues, OsNFR5/OsRLK2, can activate OsCERK1 during AMF colonization but are not required (Miyata et al., 2016). Further work is needed to identify additional coreceptors that aid the plant in distinguishing between mutualistic LCO signals and those from fungal pathogens.

8.2 AMF LCO/CO Production and Compatibility

Early research on AMF-plant signalling referred to AMF signals generically as Myc factors, although recent work has started to differentiate Myc factors more concretely as LCOs, COs, and/or various effector proteins. AMF increase the production of LCOs and COs, which are more formally referred to now as 'Myc factors', in response to the perception of secondary plant-derived metabolites such as strigolactones and flavonoids (see Sections 5.2 and 6.2) (Genre et al., 2013). LCOs and COs both initiate similar Ca^{2+} oscillations via activation of the CSSP (Sun et al., 2015b) and increase the rate of AMF colonization, however, only LCOs have been shown to stimulate lateral root formation (Maillet et al., 2011). While the importance of LCO and CO secretion in the establishment of AMF-plant symbioses is well understood, the genetic mechanisms in fungi responsible for the production of LCOs and COs have not been identified. In addition, the isolated effect of LCOs versus COs has not been established in AMF symbioses, yet there appears to be a type of synergy that occurs between them as different Ca^{2+} spiking signatures are observed when LCOs and COs are present as opposed to when they are added separately (Sun et al., 2015b).

Distinct Myc-factor receptors have not been fully identified in plants; knockout mutants of all known rhizobia LCO receptors did not compromise

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AMF colonization of *L. japonicus* (Amor et al., 2003; Rasmussen et al., 2016). However, recent work silencing the orthologue of *NFP* in the nonlegume *Solanum lycopersicum* did prevent AMF colonization (Buendia et al., 2016). It is possible that the orthologue present in *S. lycopersicum* represents a more ancestral LCO receptor that was subsequently duplicated during the divergence of legumes. This work underscores the difficulty of identifying specific LysM-RLKs critical for AMF symbioses in legumes given extensive redundancy.

8.3 EMF LCO/CO Production?

It has yet to be determined whether LCOs and COs play a role in the establishment of EMF-plant symbioses (Martin et al., 2016). If LCOs/COs are found in pine-EMF symbioses they must function independently of the CSSP and the canonical LysM-RLK receptors since CSSP genes including NFP are absent in some species of the Pinaceae family (Garcia et al., 2015). However, as discussed in Martin et al. (2016), the multiple origins of EMF decrease the likelihood of a single, common symbiotic mechanism.

8.4 Rhizobia LCO Production and Compatibility

Rhizobia-derived Nod factors are made up of LCOs but lack the COs included in Myc factors. Nonetheless, Nod-factor LCOs are structurally very similar to AMF-LCOs with the exception of a few different decorations and side chains that in part contribute to rhizobial host specificity (Dénarié et al., 1996; Long, 2001). The *nodABC* genes are responsible for LCO production in rhizobia (Rodpothong et al., 2009). *NodIJ* encodes for genes responsible for exporting the LCOs (Aoki et al., 2013). Rhizobial plant host ranges have been correlated with the composition of LCOs produced (Relić et al., 1993).

M. loti mutants lacking *nodA* and *nodC* are capable of forming nodules independent of Nod factors with *L. japonicus* through crack entries (Madsen et al., 2010). This suggests that more ancient rhizobial-plant symbioses may have been Nod factor independent yet still activate Ca^{2+} oscillations after entry. To date, the majority of LCO-related signalling studies have focused on legumes as opposed to more basal plant species. It seems probable that multiple LysM-RLK receptors may have arisen due to gene duplication, leading to the muddled view of the role that LCO perception plays in the formation of rhizobial or AMF symbioses. The use of more basal, genetically tractable monocots, dicots, and bryophytes for LCO signalling assessments may help clarify mechanisms involved in LCO perception and shed light on the potential evolution of these mechanisms.

The similarity of AMF and rhizobial LCOs raises the question of how plants activate such different symbiotic processes with such similar chemical cues. One potential answer is that there are unique receptors for each specific

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(or specific class of) LCO. This hypothesis is based on genetic evidence that plants have numerous LysM-RLK receptors; legumes have 21-26 whereas plants that only associate with AMF have 5–9 (Arrighi et al., 2006; Zhang et al., 2007; Lohmann et al., 2010). While unique LysM-RLK receptors may play a role in distinguishing between symbionts, the relationship between the CSSP and innate immunity (Section 4) and the secretion of additional signals such as effector proteins suggest that there is more to microbe-host specificity than just LCO-receptor dynamics (Limpens et al., 2015). Experiments attempting to experimentally evolve nodulation bacteria highlight this complexity and are discussed in Section 11.

Not all rhizobia produce LCOs. Some photosynthetic *Bradyrhizobia* are capable of LCO-independent nodulation (Giraud et al., 2007). Photosynthetic *Bradyrhizobia* are divided into two groups. Group I species contain the canonical *nodABC* genes and produce LCOs while Group II species are able to form nodules on a few plant species but do not possess the *nodABC* genes nor appear to produce LCOs (Chaintreuil et al., 2001; Giraud et al., 2007). Despite missing the genes associated with LCO production, Fabre et al. (2015) showed that crucial components of the CSSP are active during *Bradyrhizobium-Aeschynomene evenia* symbiosis as signal transduction through SYMRK, Ca^{2+} oscillations, and CCaMK are required for nodulation. This study raises the question as to what signals Group II *Bradyrhizobia* produce to trigger the CSSP of hosts. Are there other genes responsible for LCO production beyond the canonical *nodABC* orthologues? Giraud et al. (2007) hypothesised that *nodABC*-lacking *Bradyrhizobium* species use purine derivatives for plant signalling. What additional secondary metabolites might be required for the formation of these endosymbioses? Other nodulating bacteria such as *Frankia* also lack *nodABC* genes, underscoring the importance of identifying other potential signalling mechanisms. Unfortunately, no reverse genetic studies on LysM-RLKs have yet been conducted to identify genes responsible for perception of cluster I/III *Frankia* signals.

8.5 *Frankia*: LCO-Independent Nodulation

Although *Frankia* cluster II species have the highly conserved *nonABC* genes for LCO production, clusters I and III species do not (Tisa et al., 2013) and yet are still able to form nodules through SYMRK signalling and activation of Ca^{2+} oscillations (Gherbi et al., 2008; Franche et al., 2011; Chabaud et al., 2015; Granqvist et al., 2015; Cissoko et al., 2018). However, cluster I and III species appear to secrete water-soluble, low molecular weight compounds (0.5–5 kDa) that are distinct from LCOs (Chabaud et al., 2015). Given that LysM-RLK receptors are capable of binding to peptidoglycan (Willmann et al., 2011) and exopolysaccharides (Kawaharada et al., 2015), it is possible that cluster I and III *Frankia* use alternative signalling molecules to activate the CSSP.

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Recent work has suggested that *nodA* arose first in the basal genus, cluster II Actinobacteria, and was subsequently transferred to rhizobia via lateral gene transfer (Persson et al., 2015). Despite the presence of *nodABC* in cluster II *Frankia*, it is unclear whether nodulation relies on the production of LCOs (Nguyen and Pawlowski, 2017).

9 Microbial Derived Effector Proteins

The role of small secreted proteins, termed 'effector proteins', have long been known to promote infection by plant pathogens through the manipulation of innate plant immunity (reviewed by Rovenich et al. (2014)). However, it was not until genes encoding for small secreted proteins were identified in the first sequenced EMF fungus, *L. bicolor*, and confirmed by a mycorrhizae meta-transcriptomic analysis that their importance in mycorrhizal interactions was illuminated (Martin et al., 2008, 2016; Liao et al., 2014; Garcia et al., 2015; Plett and Martin, 2015). In fact, all known fungal genomes encode for similar small-secreted proteins (Martin et al., 2008, 2016; Kohler et al., 2015; Pellegrin et al., 2015; Kamel et al., 2017). While effector proteins are crucial in the establishment of mutualistic symbioses and fungal pathogenesis, significantly more small-secreted proteins were found to be expressed in symbiotic AMF than in the saprotrophic brown-rot fungus, *Serupla lacrymans*, which has roughly the same percentage of genes dedicated to small secreted proteins (Kohler et al., 2015). *S. lacrymans* is a brown rot fungus that is a member of the same clade that gave rise to the ectomycorrhizal Boletales, consistent with the idea that the loss of decay mechanisms as well as changes in expression patterns of effector proteins may facilitate the path to mutualistic symbiosis (Martin et al., 2008, 2016; Doré et al., 2015). Thus, it appears that effector proteins may play a more significant role in the establishment of beneficial symbioses than in pathogenesis.

Thus far, only two effector proteins have been characterised, SP7 and MiSSP7 in the AMF *R. irregularis* and EMF *L. bicolor*, respectively (Kloppholz et al., 2011; Plett et al., 2014a). SP7 is secreted by *R. irregularis* during the early stages of the colonization of *M. truncatula* (Kloppholz et al., 2011). SP7 is then perceived by a key transcription factor of the internal ethylene signalling pathway of *M. truncatula* (ERF19) resulting in a reduction in ERF19 expression. Decreased ERF19 expression is linked to decreased ethylene production, which is associated with decreased plant immunity; thus SP7 reduces the immune response of *M. truncatula* and increase AMF colonization (Xu et al., 1994; Camehl et al., 2010; Plett et al., 2014b). In the EMF *L. bicolor*, MiSSP7 behaves similarly to SP7 except it impinges on jasmonate instead of ethylene signalling. In *Populus trichocarpa*, *L. bicolor* production of

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MiSSP7 has been shown to reduce jasmonate production and thus reduce immune response (Plett et al., 2011, 2014a).

Effector proteins also play a key role in nodulation. In particular, many nonphotosynthetic bradyrhizobia that do not synthesise LCOs appear to rely on effector protein secretion by the type III secretion system (T3SS) for nodulation with *Aeschynomene* species (Okazaki et al., 2013, 2016). However, many of the photosynthetic *Bradyrhizobium* species found in the natural environment lack both *nodABC* genes and a T3SS. The mechanism by which these bradyrhizobia are capable of nodulating has not yet been identified.

10 Other Signals and Coordination

The majority of plant–microbe endosymbioses rely on 'primary' signals such as strigolactones, flavonoids, LCOs, COs, and effector proteins. However, broader screenings of secondary metabolites involved in plant–microbe signal exchange have yielded a number of other compounds that may play fundamental roles in plant–microbe interactions. In rice, the plant receptor DWARF 14 LIKE (D14L) for karrikin, a compound in smoke, was identified as essential for the establishment of AMF with rice (*Oryza sativa*) (Gutjahr et al., 2015). Karrikin perception induces seed germination in early plant colonisers following fire (Flematti et al., 2004). D14L is conserved in liverworts, suggesting that karrikin signal perception is ancient and may have been important for early AMF-plant signalling. Future work should address how essential D14L may be for the formation of other plant–microbe symbioses.

Beyond karrikin, a number of volatile organic compounds (VOCs) have been associated with plant–microbe symbioses. Several fungal VOCs have been identified as plant growth promoting compounds (Ezquer et al., 2010; Minerdi et al., 2011; Splivallo et al., 2011; Yamagiwa et al., 2011; Paul and Park, 2013; Naznin et al., 2014; Bitas et al., 2015; Ditengou et al., 2015; for review see: Li et al. (2016)). Similarly, a host of bacterial-derived VOCs have been shown to positively promote plant growth (Ryu et al., 2003; Zou et al., 2010; Velázquez-Becerra et al., 2011; Bailly et al., 2014). Only a few studies have attempted to look at the role of fungal-derived VOCs in a plant-symbiont context. Sesquiterpenes are exchanged between EMF and both *Populus* and *Arabidopsis* plants and lead to lateral root growth (Ditengou et al., 2015). A metatranscriptomic analysis by Liao et al. (2014) revealed the upregulation of three gene groups related to terpene synthesis in ectomycorrhizal roots associated with pines when compared to mycelium growing in soil alone. However, sesquiterpene is not essential for the formation of these symbioses and was found to induce a similar response in symbiotic and nonsymbiotic plants (Ditengou et al., 2015). Nonetheless, terpenes may play an important role in fungal–fungal signalling thus influencing the competition for EMF

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colonization of plant roots as terpenes have been recently shown to be important for fungal-bacteria signalling (Schmidt et al., 2017).

Recent work has identified additional plant-derived signals that play a role in AMF symbioses with rice. Nadal et al. (2017) showed that exudates from rice plants lacking the N-acetylglucosamine (GlcNAc) transporter NO PERCEPTION1 (NOPE1) induced a stress response from the model AMF, *R. irregularis*, as opposed to a response more typical of pre-symbiotic signalling. Hyphal branching was unaffected; and there was no attempt to test the degree of arbuscule formation with rice mutants vs. wild-type so the essential function of NOPE1 remains unclear.

The production of specific exopolysaccharides by *Sinorhizobium meliloti* and the exopolysaccharide receptor-like kinase EPR3 is essential for nodule development (Kawaharada et al., 2015). Kawaharada and colleagues found that *Epr3* was induced by LCO perception and used to recognise surface polysaccharides on the rhizobia. These findings document a 'two-stage' mechanism for nodulation (i.e. perception of LCOs followed by recognition of rhizobial exopolysaccharides) and the importance of timing in nodule formation. Modulation of surface exopolysaccharides remains a relatively unexplored avenue responsible for fungal and bacterial host specificity.

The growing list of signalling compounds that are found to be important for plant–microbe symbiosis (e.g. flavonoids, strigolactones, LCOs, effector proteins) suggests that the signalling dialogue between partners may be procedurally complex. For example, do partners 'call-and-respond' using a sequential, ping-pong-like dialogue or are multiple signals simultaneously and combinatorially exchanged (Figure 3) – or is it some combination of these two different modes? The architecture of symbiont crosstalk has implications on short timescales (i.e. hours) relevant to mutualism establishment as well as for the evolution of mutualism since the timing of signal exchange could fundamentally impact host-endosymbiont specificity. There are precedents for the kinetics of signal exchange being a critical determinant of interaction specificity; for example, large differences in mating kinetics have been shown to prevent two strains of the budding yeast, *Saccharomyces cerevisiae*, from mating, thus leading to reproductive isolation (Iwasa and Sasaki, 1987; Leu and Murray, 2006). Differences in the kinetics of plant–microbe signalling may lead to specificity barriers similar to this example, particularly if a ping-pong model of signal exchange applies.

11 Experimental Evolution and Potential Signalling Gaps

While our understanding of plant–microbe signal exchange has dramatically improved in the past 20 years, there are still many gaps in knowledge. Attempts to leverage what we know by experimentally evolving novel

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plant–microbe symbioses have highlighted additional factors that influence the formation of these symbioses (Marchetti et al., 2010, 2014; reviewed in Remigi et al., 2016). Given the propensity of bacteria to undergo HGT and the overwhelming evidence that HGT played a crucial role in the evolution of rhizobia-plant symbioses (Galibert et al., 2001; Masson-Boivin et al., 2009; Wang et al., 2014), several elegant experimental evolution studies have been performed to understand how legume pathogens transformed with *nod* genes from rhizobia might evolve into nodulating bacteria. These studies have resulted in varying degrees of success, but each one has yielded key insights into plant-rhizobial signalling. Marchetti et al. (2010) showed that insertion of a symbiosis plasmid containing *nod* and *nif* genes into the *Mimosa* pathogen, *Ralstonia solanacearum*, was capable of inducing root hair curling, but incapable of forming nodules. However, after ~10–20 generations of *in planta* evolution, virulence regulators were inactivated and nodulation resulted. Subsequent generations yielded optimised strains that initiated a weaker immune response although no nitrogen fixation was observed.

A subsequent study by Marchetti et al. (2014) focused on the experimental evolution of a transformed *R. solanacearum* containing *nod* and *nif* genes. *R. solanacearum* mutants were inoculated into *Mimosa pudica* plants, allowed to colonize the roots, and subsequently isolated in order to be re-inoculated. Four hundred generations of this *ex planta-in planta* (i.e., off plant-on plant) evolution resulted in reduced immune response by the host. Over the course of this experiment, nitrogen fixation was not established due in part to low nodulation efficiencies. Despite the presence of the required *nod* and *nif* genes, extended periods of coevolution may be needed to optimise nodulation for stable and productive endosymbiosis. The results of these evolution experiments raise at least two fundamental questions: (i) what types of coevolved traits are required for successful symbiosis, and (ii) what order might these traits need to coevolve for productive endosymbiosis? The inactivation of virulence factors and attenuation of antagonistic processes seem like a necessary first step. It remains to be seen whether continued *in planta* evolution of evolved *R. solanacearum* lineages could result in nitrogen-fixing clones if given enough time; the evolutionary trajectories that lead to successful nitrogen-fixation would be fascinating to dissect and understand.

Attempts to engineer novel plant–microbe mutualisms may be the best avenue for identifying additional signals required for symbiosis establishment and advancing our ability to reconstruct the coevolution of these ancient mutualisms. To our knowledge, there are no studies that have attempted to genetically engineer alternative fungal symbionts to behave like AMF or EMF. All attempts have thus far been conducted with genetically modified pathogenic α- and β-proteobacteria for the purpose of generating nodulating bacteria. While these studies have been limited to rhizobial–plant interactions, they have nevertheless been instructive and point to the power of using evolution experiments to glean mechanistic insights.

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12 Conclusions and Future Directions

Given the interrelatedness of AMF-, rhizobia-, *Frankia*-, and to a lesser extent, EMF-plant symbiotic signalling, there are some general lessons and several common questions that emerge from the decades of plant signalling research. The role of plant immunity in the establishment of successful symbioses and its interrelatedness with the CSSP remains unclear. As seen across all four symbioses, plant innate immunity appears to be activated during early stage pre-symbiotic signalling but then suppressed during colonization, and in some cases, an immune response is reactivated after successful colonization. To what degree is this initial activation of plant immunity required for successful colonization? Is the activation of immunity the result of MAMP detection or does plant perception of Myc and Nod factors activate CSSP and in turn trigger innate immunity? By answering these questions, we may begin to better understand the coevolution of mutualistic microbes and their pathogenic analogues.

It remains unclear how early beneficial fungal-photoautotroph symbioses were first established. Recent reviews have discussed the strong evidence for ancient AMF-bryophyte symbioses (Martin et al., 2017; Strullu-Derrien et al., 2018) yet phylogenetic analyses suggest that much of the known mechanisms required for plant-AMF symbioses may have existed in much earlier diverging lineages like the charophyte algae (Delaux et al., 2012b, 2013b, 2015). To our knowledge, there have been no systematic studies to examine fungal–algal interactions or the potential nutrient or signal exchanges that can occur between these taxa. Hom and Murray (2014), however, demonstrated an innate potential for fungi to form mutualisms with a chlorophyte alga in an environmental-dependent manner, and ongoing work suggests that the capacity for various fungi and algae to interact may be quite broad (M.R. Clear and E.F.Y. Hom, unpublished data). While Hom and Murray (2014) did not assess the potential exchange of the plant–fungal signals discussed in this article (e.g., Myc factors), their work does highlight the importance of more carefully examining the potential for algal–fungal interactions in nature and as the basis for understanding plant–fungal symbiosis, as well as the importance of the plant–fungal cell–cell interface in symbiosis.

Berbee et al. (2017) examined the evolution of the earliest fungal-photoautotroph interactions and proposed that fungi were interacting with the cell walls of streptophyte algae as early as ~750 Ma. This interpretation is based on phylogenetic work tracing the earliest pectinases to the same age of pectin-containing streptophytes (Parfrey et al., 2011; Chang et al., 2015). This assumption appears reasonable as pectins are largely found only in streptophytes (Sørensen et al., 2011). These phylogenetic analysis were possible because pectinase genes have long been identified in fungi (Kubicek, 2012). Unfortunately, the majority of fungal genes related to plant symbiosis have not yet been identified. Identification of potential

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strigolactone receptors in AMF should be prioritised. While this will likely be a difficult undertaking given that no candidate strigolactone receptors were identified in the *R. irregularis* genome (Tisserant et al., 2013), an affinity proteomics approach (Ziegler et al., 2013) may be feasible given that synthetic strigolactones such as GR24 are readily available.

Efforts to experimentally evolve transformed bacterial pathogens into nodulating and nitrogen-fixing bacteria (Nandasena et al., 2006; Masson-Boivin et al., 2009; Marchetti et al., 2010, 2014) is of significant practical importance as it may help diversify the number of bacteria and agricultural crops capable of fixing nitrogen (Castro et al., 2016). These efforts have also highlighted the shortcomings of the current rhizobia-plant signalling paradigms (Remigi et al., 2016) and strongly suggests similar knowledge gaps exist in our understanding of AMF-plant signalling. In particular, Marchetti et al. (2010) and Tamburini et al. (2014) showed that additional genome modifications are required beyond insertion of the *nod* and *nif* genes associated with symbiotic signalling and nitrogen fixation. Rounds of experimental evolution revealed parallel evolution in genetic regions of unknown function that were potentially related to pathogenicity. However, nodulation rates remained low and nitrogen fixation was never obtained. It remains unclear whether additional signals such as effector proteins, specific LCOs, or yet undefined signals such as lipids are required for optimised nodulation. Future work may benefit from assessing transcriptional changes between transformed bacteria and mutants that have undergone experimental evolution. This may help address the fairly unexplored issue of signal exchange timing and how it may influence nodulation rates.

As our understanding of the AMF genes required for pre-symbiotic signalling improves, it will become more feasible to perform similar experimental evolution studies with mycorrhizal fungi. Clarifying the additional signals involved in pre-symbiotic signalling and the potential effect of signal timing (Figure 3) will be important for addressing the longstanding question of how plants distinguish between pathogens and specific symbionts using the same CSSP. While recent work has continued to highlight the importance of numerous LysM-RLK receptors capable of distinguishing between pathogen-associated chitin and AMF/rhizobia-derived LCOs (Bozsoki et al., 2017), much of the work on signalling has been conducted solely on legumes and the tendency may be to over-generalise these mechanisms for all plants. This may be a poor assumption (Genre and Russo, 2016) as legumes are unique in regards to the large number of LysM-RLKs involved relative to in plants that associate with AMF only (21–26 vs. 5–9) (Arrighi et al., 2006; Zhang et al., 2007; Lohmann et al., 2010). Recent work identifying the importance of CERK1 in both pathogen and AMF recognition by rice plants underscores the existence of more generalised receptors in nonlegume model species (Zhang et al., 2015). Continuing to expand the number of studies utilizing model nonlegume species (Gutjahr et al., 2009; Miyata et al., 2014; Sun

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et al., 2015a; Zhang et al., 2015) in conjunction with increasing the number of sequenced AMF genomes will be key to broadening our understanding of the evolutionary origins of plant–microbe signalling and will begin to shed light on how the mechanisms of symbiotic signalling may have coevolved.

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