Mechanisms and Impact of Symbiotic Phosphate Acquisition

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Phosphorous is important for life but often limiting for plants. The symbiotic pathway of phosphate uptake via arbuscular mycorrhizal fungi (AMF) is evolutionarily ancient and today occurs in natural and agricultural ecosystems alike. Plants capable of this symbiosis can obtain up to all of the phosphate from symbiotic fungi, and this offers potential means to develop crops less dependent on unsustainable P fertilizers. Here, we review the mechanisms and insights gleaned from the fine-tuned signal exchanges that orchestrate the intimate mutualistic symbiosis between plants and AMF. As the currency of trade, nutrients have signaling functions beyond being the nutritional goal of mutualism. We propose that such signaling roles and metabolic reprogramming may represent commitments for a mutualistic symbiosis that act across the stages of symbiosis development.

Phosphorous is crucial for life by virtue of its unique chemistry. Phosphate is capable of chemical bonds that confer remarkable stability but at the same time facile manipulation (Westheimer 1987). Stable phosphodiester bonds enable the encoding of genetic information in nucleic acids. On the other hand, rapid and reversible transfer of phosphoryl groups onto proteins by kinases and phosphatases allow the regulation of cellular signaling processes and core metabolism (e.g., via ATP, GTP) (Westheimer 1987; Hunter 2012; Kamerlin et al. 2013). Phosphates also build phospholipid bilayers in membranes, enabling compartmentalization, electrophysiology, and signaling between organelles, cells, tissues, and organisms.

Plants acquire phosphate mainly in the form of inorganic orthophosphate (Pi) by the roots (Schachtman et al. 1998; Raghothama 1999; Marschner 2011). However, a substantial amount of phosphate in the soil remains inaccessible, precipitated with cations, or assimilated into organic compounds by microorganisms (Schachtman et al. 1998). Thus, a depletion zone of nutrients develops rapidly around the roots. To obtain the Pi necessary for growth, plants evolved intricate and coordinated responses to enhance Pi acquisition, while simultaneously conserving and remobilizing internal Pi stores (Raghothama 1999; Chiou and Lin 2011). Apart from direct uptake, plants also engage in an underground resource exchange, acquiring Pi via the indirect symbiotic pathway (Smith et al. 2003; Smith and Read 2008). Therefore, in the rhizosphere, the narrow region of soil surrounding the roots, plants, and microorgan-

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isms interact and reciprocally influence each other's fitness and biomass.

In this review, we explore the role of and our current understanding on symbiotic phosphate acquisition, from the underlying molecular mechanisms to the physiological, ecological, and agricultural implications; outline existing knowledge gaps and finally, propose that like other symbioses, metabolic reprogramming and dependency of both symbionts is crucial in the signaling and stability of a mutually beneficial symbiosis.

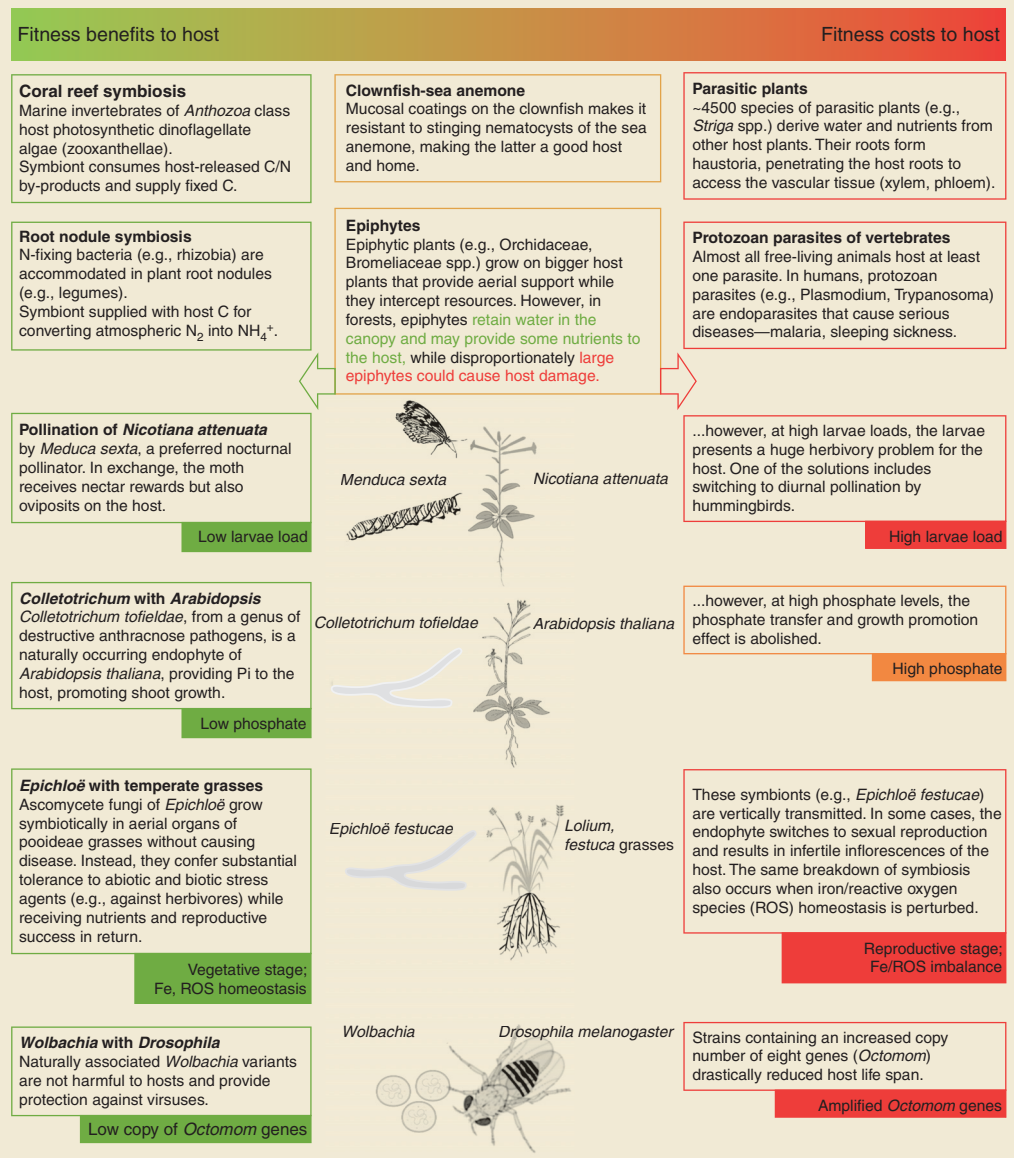
SYMBIOSIS AS THE NORM

In natural and agricultural ecosystems, plants exist in intimate associations with a plethora of microorganisms. Symbiosis, *sensu* de Bary (1879), is the rule (de Bary 1879; Oulhen et al. 2016). Bacteria, archaea, fungi, oomycetes, metazoans, and viruses reside in the rhizosphere (Vorholt 2012; Philippot et al. 2013), and the corresponding symbiotic outcomes exist along a spectrum—with respect to their effect on the host—from parasitism, to commensalism, to mutualism (Box 1 describes some of these associations). Adding to this is the growing nuance that symbiotic outcomes are context-dependent—the same host–symbiont combination can be mutually beneficial in one case, but parasitic in another (see Box 1 for details on how symbioses between the same agents shift across different conditions). For *Arabidopsis thaliana*, the fungus *Colleotrichum toefieldiae* has been shown be a beneficial endophyte only under nutrient-scarce (Pi-limiting) conditions (Hiruma et al. 2016).

Among the multitude of associations plants engage in, the symbiotic relationship with arbuscular mycorrhizal fungi (AMF) is one of the most ubiquitous, ancient, and ecologically important (Remy et al. 1994; Redecker et al. 2000; Bidartondo et al. 2011; Strullu-Derrien et al. 2018). Around 71% of extant plants engage with and accommodate AMF in their roots (Wang and Qiu 2006; Brundrett and Tedersoo 2018). Recent phylogenomics approaches reveal that subsequent losses of the symbiosis in non-AM species appear to be associated with loss of symbiotic genes, although the drivers remain unknown (Favre et al. 2014; Delaux et al. 2015; Bravo et al. 2016). In the roots, highly branched tree-like structures eponymously known as arbuscules develop intracellularly for bidirectional nutrient exchange in the cortex (Fig. 1). This association involves extensive membrane biogenesis via dichotomous hyphal branching concomitant to invaginations of cortex cells; resulting in a symbiotic interface for signal and nutrient exchange without disrupting the host membrane integrity (Marx et al. 1982; Bonfante 2001). AMF are well known for their role in plant Pi acquisition, as the fungal hyphae are able to extend beyond the rhizosphere's depletion zone, mobilize and translocate nutrients, chiefly Pi, from regions inaccessible by roots in exchange for plant-fixed carbon in the form of sugars and fatty acids (FAs). Up to 22% of the photosynthetically fixed carbon is traded for symbiotic Pi, which could supply all (100%) of plant phosphate uptake (Jakobsen and Rosendahl 1990; Smith et al. 2003, 2011; Yang et al. 2012; Bravo et al. 2017; Jiang et al. 2017; Keymer et al. 2017; Luginbuehl and Oldroyd 2017; Roth and Paszkowski 2017).

Other mycorrhizal associations (e.g., ectomycorrhizal, ericoid, arbutoid) exist but the arbuscular mycorrhizal symbiosis (also known as vesicular-arbuscular mycorrhiza [VAM] symbiosis) is unique as being a monophyletic fungal lineage that coevolved with land plants and maintained a wide host range (Peterson and Massicotte 2004; Smith and Read 2008; Martin et al. 2016). Structures strikingly similar to extant arbuscules have been identified in fossils dating as far back as the Rhynie Chert (Remy et al. 1994; Taylor et al. 1995; Redecker et al. 2000; Strullu-Derrien 2018; Strullu-Derrien et al. 2018). Although it is uncertain whether the symbiosis >400 million years ago (mya) was more parasitic or mutualistic, the ancient occurrence coupled with broad modern-day phylogenetic distribution of this symbiosis indicate its importance in the evolution of land plants (Humphreys et al. 2010; Field et al. 2015). Indeed, occurrence of AM symbiosis predates the evolution of true roots and has thus been attributed to the successful terrestrial colonization of plants from algal predecessors. Coevolution of plant (and roots)

BOX 1. THE SYMBIOSIS SPECTRUM



on Palaeozoic palaeosols alongside with AMF profoundly shaped terrestrial landscapes and, today, AM symbiosis remain an important aspect of global biogeochemical cycles (Retallack 1997; Raven and Edwards 2001; Brundrett 2002; Hetherington and Dolan 2018; Mills et al. 2018).

Mechanisms Underlying Establishment of Arbuscular Mycorrhizal Symbiosis

AM colonization occurs asynchronously across the root system, but follows a set of distinct stages as illustrated in Figure 2, and detailed in recent

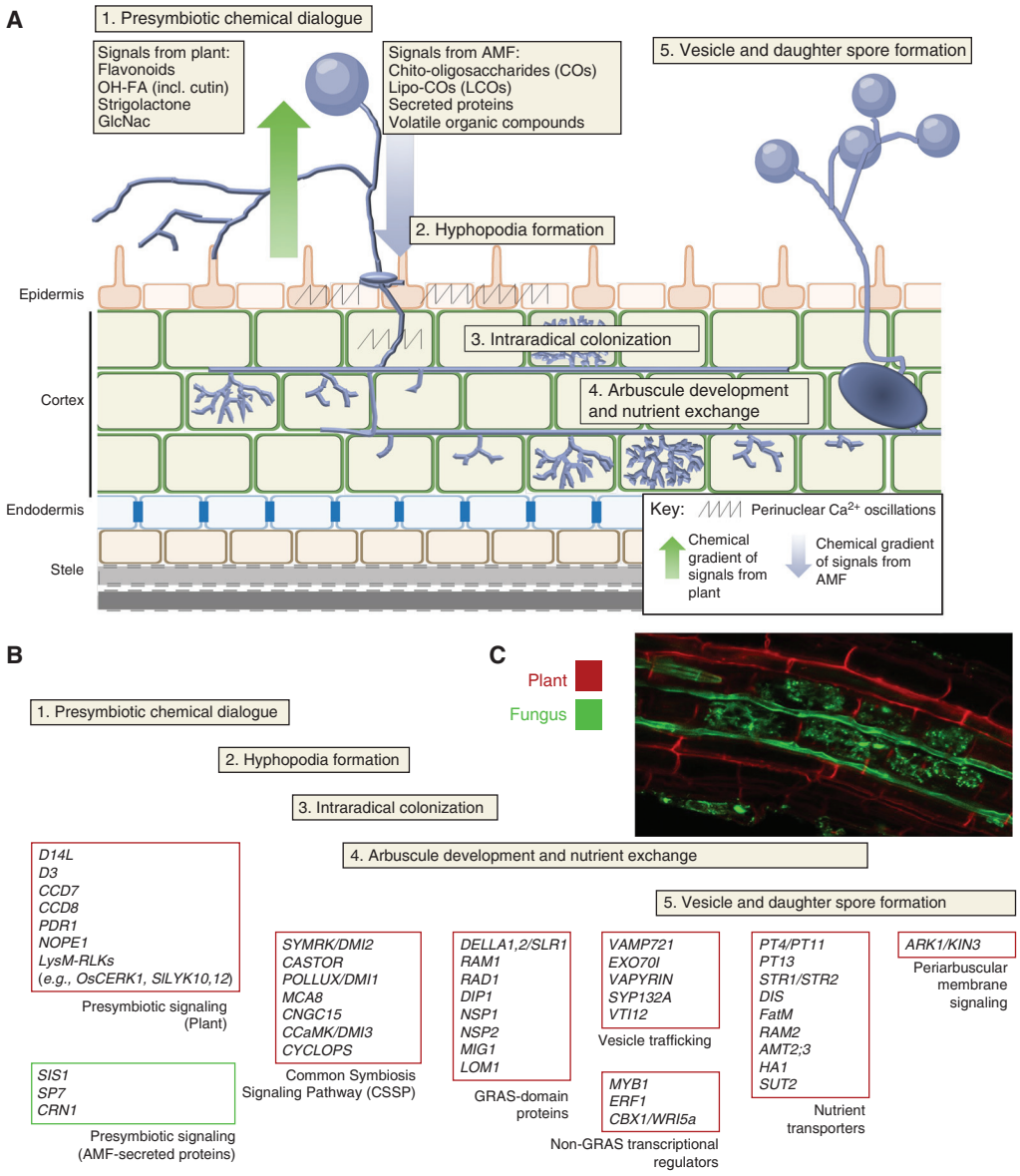


Figure 1. Mechanisms underlying establishment of arbuscular mycorrhizal symbiosis for nutrient transfer. (*A*) Signaling steps during arbuscular mycorrhizal (AM) symbiosis can be divided into five distinct stages beginning with precontact signaling mediated by diffusible molecules that reprogram both host and symbiont to commit to symbiosis, leading to contact and plant accommodation of arbuscular mycorrhizal fungi (AMF) intraradical hyphae inside the roots. At the cortex, precise regulation of cell biology leads to the development of arbuscules—the site of main nutrient exchange. A successful symbiosis enables the fungus to complete its life cycle by producing daughter spores that can then reinfect the same, as well as other hosts. In all cases, the symbiosis is asynchronous, so every stage is occurring in the host roots. (*B*) Molecular actors in the symbiosis. A list of key genes that have been identified to be required for the various stages of symbiosis signaling, divided according to their known roles (see MacLean et al. 2017 for an exhaustive list). (*C*) Fungal accommodation structures in roots stained with Alexa Fluor 488 wheat germ agglutinin showing intraradical spread of AMF and fully developed arbuscules (in green) in lateral roots of 5 weeks old (4 weeks postinoculation) rice (*Oryza sativa*). Plant cell walls are stained with propidium iodide (in red).

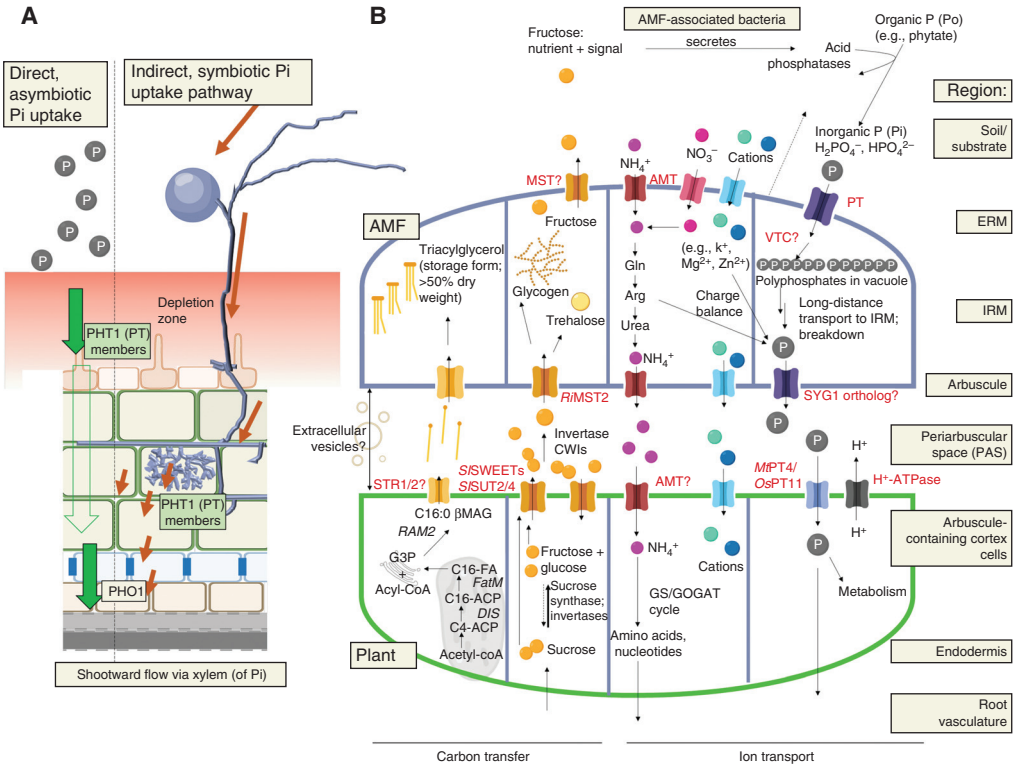


Figure 2. Mechanisms of phosphate acquisition in plants. All arbuscular mycorrhizal (AM) host plants are capable of direct and indirect uptake of inorganic orthophosphate (Pi). (*A*) Direct uptake occurs via the asymbiotic route where plant phosphate transporters (PTs) are directly involved in the uptake of Pi from the soil into the root and eventually translocate the net flux toward the shoot. However, limited accessibility of Pi rapidly builds a depletion zone of Pi (red gradient). Plant PTs (also known as PHT1 in the literature) belong to the phosphate: H^+-symporter (PHS) family in the major facilitator superfamily (MFS) and comprise 12 transmembrane domains (TMDs) with a conserved GGDYPLSATIxSE signature in TMD4. (*B*) Indirect, symbiotic pathway. The long hyphae of arbuscular mycorrhizal fungi (AMF) enable them to extend outside of the depletion zone for Pi uptake via fungal PTs, as well as via another symbiotic relationship between AMF hyphae and its associated microbiome that secretes acid phosphatases to solubilize organic phosphate (P) into Pi. Pi taken up by AMF is assimilated as polyphosphates into the vacuole and moved over long distances into the intraradical mycelium. At the arbuscule, polyphosphates are broken down into Pi for release into periarbuscular space, where plant PTs (including but not limited to the *OsPT11/MtPT4* type) expressed in the arbuscule and localized to the plant periarbuscular membrane (PAM) takes up Pi with the help of H^+-ATPases. Apart from Pi, the plant receives other nutrients as well, including N (as NH_4^+) and metal ions. Bidirectional exchange is a hallmark and also a functional necessity in AM symbiosis. In return, plants provided reduced, organic carbon in the form of sugars and more importantly fatty acids (FAs) to the AMF. AMFs are FA auxotrophs as they lack genes for long-chain FA biosynthesis. De novo FA synthesis is regulated in arbuscule-containing cortex cells via WRI5b/ERF1/WRI5a/CBX1 (transcription factors), to produce FA in a pathway involving DIS (FA synthase), FatM (acyl transferase), and RAM2 (GPAT6). PAM-localized lipid transporter candidates STR/STR2 then shuttles the FA into the periarbuscular space for the AMF. Circles denote nutrients and the known/proposed/unknown transporters are indicated in red.

reviews by (Luginbuehl and Oldroyd 2017; MacLean et al. 2017; Choi et al. 2018; Pimprikar and Gutjahr 2018). Presymbiotic molecular dialog involves the reciprocal perception of diffusible molecules: root-released flavonoids, hydroxy-FAs, strigolactones (SLs), and *N*-acetylglucosamine (GlcNAc) derivatives are perceived by AMF (Harrison and Dixon 1993; Larose et al. 2002; Akiyama et al. 2005; Besserer et al. 2006; Steinkellner et al. 2007; Kretzschmar et al. 2012; Wang et al. 2012; Nadal et al. 2017), whereas a cocktail of fungal molecules, including chito-oligosaccharides (COs), lipochito-oligosaccharides (LCOs), proteins, and possibly volatile organic compounds, are perceived by plants (Kloppholz et al. 2011; Maillet et al. 2011; Genre et al. 2013; Sun et al. 2015a,b; Tsuzuki et al. 2016; Carotenuto et al. 2017). These signals trigger perinuclear Ca^{2+} oscillations, cytoskeletal rearrangements, as well as symbiosis gene expression that involve and also transcend the common symbiosis signaling pathway (CSSP) (Kistner et al. 2005; Gutjahr et al. 2008; Parniske 2008; Gutjahr and Parniske 2013; Camps et al. 2015). The CSSP, as its name suggests, represents a conserved signaling pathway for intracellular symbiont accommodation, from which arose the nodulation symbiosis in the eurosids ~100 mya (Parniske 2008). Meanwhile, host perception triggers hyphal growth and branching in AMF. Hyphopodia, a swollen, branched fungal structure forms upon contact at the root surface. The penetration hypha invades the rhizodermal cell layer, whereby the plant directs the route of growth for the fungi, eventually forming arbuscules in the cortex (Genre et al. 2005, 2008; Gutjahr and Parniske 2013). Most of the symbiotic nutrient transfer occurs at these highly ramified yet ephemeral structures. Concurrently, lipid storage vesicles and spores emerge as the AMF completes its life cycle and reinfects the roots (Alexander et al. 1988; Kobae and Hata 2010; Kobae and Fujiwara 2014).

MECHANISMS OF PHOSPHATE UPTAKE IN PLANTS

Two pathways for uptake, direct and indirect, exist for plants capable of entering AM symbiosis (Smith et al. 2003, 2011). In the direct uptake pathway, Pi is acquired by low and high H^+/Pi symporters primarily on the epidermis (Mudge et al. 2002; Misson et al. 2004; Shin et al. 2004). These *PHOSPHATE TRANSPORTER1* (PHT1; abbreviated and used henceforth as PT) family transporters are either constitutively expressed or inducible upon Pi starvation, and have overlapping and spatiotemporally complementary functions in Pi uptake (Nussaume et al. 2011; Gu et al. 2016). In the roots, Pi is assimilated and loaded into the xylem via PHO1 transporters toward the shoot (Hamburger et al. 2002; Stefanovic et al. 2011; Arpat et al. 2012), whereas organic forms (ATP, hexose phosphates) move in the phloem (Rausch and Bucher 2002). Figure 2 illustrates the physiological route of direct and indirect Pi uptake, with greater detail on the latter.

Indirect Phosphate Pathway—Uptake by Fungus

In the indirect mycorrhizal pathway, P is acquired by H^+/Pi or Na^+/Pi symporters of the AMF extraradical hyphae (Harrison and Buuren 1995; Maldonado-Mendoza et al. 2001; Tisserant et al. 2012; Kikuchi et al. 2014; Xie et al. 2016). The Pi is imported presumably via the vacuolar transporter chaperone complex (Hothorn et al. 2009) into the tonoplast and translocated as polyphosphates to the intraradical mycelium (IRM) probably driven by mobile tubules in vacuole and/or aquaporin-mediated water flow driving bulk flow (Cox et al. 1980; Solaiman et al. 1999; Rasmussen et al. 2000; Viereck et al. 2004; Kuga et al. 2008; Tani et al. 2009; Hijikata et al. 2010; Kikuchi et al. 2014; Ezawa and Saito 2018).

Organic P sources (Po, e.g., phytate) are abundant in nature and can also be mobilized (Feng et al. 2002; Shibata and Yano 2003), possibly via acid phosphatases secreted either by AMF (Sato et al. 2015), by colonized plant roots (Ezawa et al. 2005), or by AMF-associated bacteria (Kim et al. 1997; Toro et al. 1997; Zhang et al. 2016, 2018; Battini et al. 2017). AMF-associated bacteria have long been hypothesized to solubilize Po to enhance phosphate uptake by

AMF. It was recently demonstrated that C delivered from the plant to fungus is then delivered as fructose to the bacteria, which acts as a nutrient and signal for the latter to secrete acid phosphatases to solubilize Po for uptake by AMF (Fig. 2). Thus, nutrient exchanges also exist between AMF and its microbiome (Zhang et al. 2018). Similarly, AMF-associated bacteria was also shown to be crucial determinants of growth-promoting and suppressive soils (Svenningsen et al. 2018). These recent insights highlight the tripartite association and multitude of interactions that, through AMF symbiosis, determine soil health and productivity.

Breakdown of polyphosphates in the IRM might involve acid and alkaline phosphatases, and this huge negative charge generated by Pi could explain the simultaneous uptake of cations observed (Ezawa et al. 2001; Aono et al. 2004; Kojima and Saito 2004; Kikuchi et al. 2014). More unclear is how Pi from AMF is released at the arbuscular interface, as suggested by presence of phosphatase activities and evidenced by polyphosphate accumulation in *mtpt4* mutants where symbiotic transfer is disrupted (Gianinazzi et al. 1979; Capaccio and Callow 1982; van Aarle et al. 2001, 2002; Javot et al. 2007a).

Taken together, significant knowledge gaps exist regarding the mediators and mechanisms underlying fungal phosphate metabolism. The notorious genetic intractability of AMF, compounded by the presence of hundreds to thousands of coenocytic nuclei per individual, has severely hampered functional characterization of genes involved in symbiosis (Sanders and Croll 2010; but see Helber and Requena 2007). Nonetheless, functional characterization is possible, as exemplified by the charcterization of *Gigaspora margarita* phosphate transceptor *GigmPT* (Xie et al. 2016). Recent efforts in obtaining AMF genomes and transcriptomes of various strains, species, and life stages have greatly facilitated comparative functional analyses (Tisserant et al. 2012, 2013; Lin et al. 2014; Handa et al. 2015; Salvioli et al. 2016; Tang et al. 2016; Kamel et al. 2017; Chen et al. 2018; Kobayashi et al. 2018; Mathieu et al. 2018; Sun et al. 2018a; Zeng et al. 2018). For instance, a list of candidate genes has since been proposed (Ezawa and Saito 2018), including yeast SYG1 orthologs in AMF as putative Pi exporters at the arbuscule (Azevedo and Saiardi 2017). With techniques such as host-induced gene silencing and the careful validation of symbiont-specific gene silencing (and not on hosts), we are witnessing an increasing understanding of AMF genes during symbiosis (Helber et al. 2011; Kloppholz et al. 2011; Tsuzuki et al. 2016; Xie et al. 2016; Sun et al. 2018b; Voß et al. 2018).

Plant Uptake of Symbiotic Pi Requires Specialized Phosphate Transporters

Plant-encoded H^+/Pi symporters are specifically expressed in arbuscule-containing cortex cells and are localized to the plant periarbuscular membrane (PAM) for Pi uptake (Javot et al. 2007a; Yang et al. 2012; Watts-Williams et al. 2015). Arbuscules are believed to be the main site of nutrient transfer, where plants obtain primarily P/N (among other nutrients), while providing carbohydrates and FAs to the fungus. Since the first identification of AM-specific PTs in plants (Rausch et al. 2001; Harrison et al. 2002; Paszkowski et al. 2002), PTs that are specifically expressed or are involved in Pi uptake during symbiosis have been described in an expanded list of angiosperm species, summarized in Table 1 (Gümil et al. 2005; Nagy et al. 2005; Poulsen et al. 2005; Maeda et al. 2006a; Wegmüller et al. 2008; Loth-Pereda et al. 2011; Xie et al. 2013; Walder et al. 2015; Liu et al. 2016a; Sawers et al. 2017). Not all of the identified transporters have been characterized for expression and localization activity, and species-specific differences exist (e.g., expression in other tissues, with roles not limited to symbiotic uptake) as discussed below (see also Table 1). In all of these species, there appears to be at least one phylogenetically conserved PT4/PT11 transporter. These form a clade closely related to *Physcomitrella patens* and *Selaginella moellendorffii* PTs, suggesting an ancient origin and functional conservation (Yang et al. 2012); although a more recent analysis suggests the relationship to be nonorthologous in the nonvascular plants (Delaux et al. 2015). From a phylogenetic perspective, it will

Table 1. List of symbiotic phosphate transporters in plants identified to date

Species	Gene	Mutant phenotype	P transport activity demonstrated?	Transcript/promoter or protein localization or expression pattern	References
Oryza sativa	*OsPT11*	Reduced % root length colonization (RLC) and % arbuscules (A) Stunted arbuscules Abolished symbiotic Pi transport	Yes; ^{33}P uptake in yeast *pho84*	Arbuscules (promoter:*uidA* reporter for GUS staining; GUS) PT11-GFP to PAM	Paszkowski et al. 2002; Kobae and Hata 2010; Yang et al. 2012
	OsPT13	Same as *pt11* mutants, but functional symbiotic Pi uptake	Does not complement	Arbuscules (GUS)	
Zea mays	*ZmPT6*	Phenocopies *ospt11* in sterile culture Transcomplementation with chive nurse plants increases %RLC but not %A; % RLC WT-like in soil, reduced %A	Complements *pho84* growth	Arbuscules (in situ hybridization; ISH)	Glassop et al. 2005; Willmann et al. 2013; Liu et al. 2016a; Sawers et al. 2017; Liu et al. 2018
	ZmPT9	p35S:PT9 lines in *Lotus* hairy roots reduced %RLC	Complements *pho84* growth	*Colonized regions* (pZmPT9-GFP; *Lotus* hairy roots)	
	ZmPT2,4, 7, 11		n.d.	Induced by low Pi or AMF	
Brachypodium distachyon	*BdPT3, 13*	All n.d.	All n.d.	Both root-specific and AM-specific	Hong et al. 2012
	BdPT7, 12			Both AMF-induced; also expressed in shoots	
Sorghum bicolour	*SbPT10, 11*	n.d. (*SbPT10*: Putative OsPT11 function)	n.d.	Both highly induced	Walder et al. 2015; Watts-Williams et al. 2018
	SbPT8, 9, 11	n.d. (*SbPT9*: putative OsPT13 function)	n.d.	Both have modest AMF-induction	
Medicago truncatula	*MtPT4*	Phenocopies *ospt11* Transcomplementation with leek nurse plants increases %RLC but not stunted arbuscules Phenotype rescued with N-starvation; dependent on AMT2;3	Yes; P uptake in *pam2* and NS219 mutants	Arbuscules (GUS, hairy roots) Immunolocalization onto PAM; surrounding branches	Harrison et al. 2002; Javot et al. 2007; Breuillin-Sessoms et al. 2015; Floss et al. 2017

Continued

Table 1. *Continued*

Species	Gene	Mutant phenotype	P transport activity demonstrated?	Transcript/promoter or protein localization or expression pattern	References
Lotus japonicus	*LjPT3*	RNAi (hairy roots): reduced %RLC and %A; reduced growth and Pi uptake; co-inoculation of AMF and rhizobia gave necrotic nodules	Yes; ^{32}P uptake in *pam2*	Arbuscules (ISH)	Maeda et al. 2006
	LjPT4	RNAi (hairy roots): reduced colonization, stunted arbuscule morphology, reduced root P content	n.d.	Arbuscules and root tips (GUS, hairy roots)	Volpe et al. 2016
Astralagus sinicus	*AsPT4*	Phenocopy *ospt11*	Does not complement MB192	Both: Arbuscules (GUS, hairy roots, and ISH)	Xie et al. 2013
		Required for symbiotic Pi uptake (total shoot P levels, not $^{32/33}$P)	Complements; transport Pi		
	AsPT1	Phenocopy *ospt13*; *As-PT1OE* increases colonization in hairy roots			
Glycine max	*GmPT10, 11*	n.d.	Yes; ^{32}P uptake in *pam2*	Branch domains of arbuscules (prom: GFP, hairy roots)	Tamura et al. 2012; Inoue et al. 2014
	GmPT7	n.d.	n.d.	Mature noncollapsing arbuscules, root tips, LR primordia, vein endings of senescent leaves (GUS, hairy roots)	
Solanum tuberosum	*StPT3*	n.d.	Yes, ^{32}P uptake in *pam2*	All: Arbuscules (GUS, hairy roots); *PT3* is also expressed in asymbiosis and shoots	Rausch et al. 2001; Karandashov et al. 2004; Nagy et al. 2005
	StPT4	n.d.	*Pam2* data unclear; n.d. for PT5		
	StPT5	n.d.		*PT4 and PT5* AMF-induced and root-specific	
Solanum lycopersicum	*LePT3*	n.d.	n.d.	All are AMF-induced	Nagy et al. 2005; Balestrini et al. 2007; Xu et al. 2007
	LePT4	Dispensable for Pi uptake and symbiosis	*pam2* data unclear	*PT4*: Arbuscules (GUS, hairy roots)	
	LePT5	n.d.	n.d.	*LePT1* to *5* all detected in LCM of arbuscules	
Petunia hybrida	*PhPT3, 4, 5*	All n.d.	n.d.	AMF induced; PT4 might be AM-specific	Wegmüller et al. 2008

Continued

Table 1. *Continued*

Species	Gene	Mutant phenotype	P transport activity demonstrated?	Transcript/promoter or protein localization or expression pattern	References
Solanum melongena	*PT4, 5*	All n.d.	n.d.	Root-specific, AMF-specific	Chen et al. 2007
Capsicum frutescens	*PT3*			Induced by AMF, also expressed in shoots	
Nicotiana tabacum	*PT2*			Root-specific, induced by AMF and Pi starvation	
Populus trichocarpa	*PtPT10*	All n.d.	No growth complementation of *pho84* for *PT10*; others n.d.	Root-specific, AM-specific	Loth-Pereda et al. 2011
	PtPT9, 12			Induced by AM and ECM; also in senescing autumn leaves	
Vitis vinifera	*VvPT1*, *VvPT2*	n.d.	n.d.	Both are root-specific (not in leaves at least), AM-specific	Valat et al. 2018

Phosphate transporters (PTs) highlighted in yellow are specifically induced during arbuscular mycorrhizal (AM) symbiosis and phylogenetically cluster with the OsPT11/MtPT4 clade; while other PTs may also be involved in Pi uptake at the arbuscule during symbiosis but have low levels of expression during asymbiosis; or expression in other tissues. Where subsequent functional characterization was conducted, the phenotypes and observations are listed in the respective columns; for mutant phenotypes, complementation of P uptake/transport in yeast mutants; as well as expression/localization pattern of the transcript/protein where investigated. Nonstably transformed plants are indicated "hairy roots" in parentheses to indicate *Agrobacterium rhizogenes*–mediated transformation of root organ culture.

AMF, Arbuscular mycorrhizal fungi; ECM, ectomycorrhizal; LCM, laser capture microdissection; n.d., not determined; WT, wild type.

be exciting to investigate the existence of functional conservation in symbiotic pteridophytes and bryophytes to better understand how the symbiotic transporters were recruited.

Inside plant cells, excess Pi is stored in vacuoles while a net flux toward the shoot occur via *PHO1*-mediated xylem loading. The remobilization of vacuolar Pi stores, best understood in non-AM hosts *Arabidopsis*, is important for Pi homeostasis, and recent work have identified vacuolar Pi transporters (VPTs; also PHT5 family members) that possess both SYG1/PHO81/XPR1 (SPX) and major facilitator family (MFS) domains, to primarily mediate vacuolar influx (Liu et al. 2016b; Xu et al. 2019). Although the role of SPX-MFS3 in mediating vacuolar Pi efflux in rice is contested (Wang et al. 2015; Xu et al. 2019), a recent study revealed that intriguingly, an ancestral plasma membrane-localized glycerol-3-phosphate transporter (GlpT; at least in *Escherichia coli*) is instead directed to the plant tonoplast and mediates vacuolar Pi efflux in rice, *Marchantia polymorpha* and *P. patens* (Xu et al. 2019). These studies have since advanced our understanding on how Pi shuttles in and out of the vacuolar stores. However, how Pi is specifically partitioned and transported from the ports of entry (epidermis or cortex during asymbiosis and symbiosis, respectively) into the endodermis remains to be elucidated, although most models suggest nutrients to move via apoplastic, symplastic, or a *trans*-cellular pathway coupling both mechanisms for inward radial movement of nutrients.

Energetics of Nutrient Transfer

Nutrients exchanged at the symbiotic interface, regardless of their direction, identity, precursor, and subsequent assimilation pathways, traverse the same cell membranes. Because the membrane potential is negative inside relative to the outside, both parties require cation/proton channels to power the transport of neutral and negatively charged molecules across membranes. Accordingly, the periarbuscular space has been described as an acidic compartment, and H^+-ATPases were proposed to provide the proton gradient and electrochemical energy (Gianinazzi-Pearson et al. 2000; Guttenberger 2000; Ferrol et al. 2002; Krajinski et al. 2002; Ramos et al. 2009). Indeed, H^+-ATPases have since been demonstrated to be necessary for transport of phosphate, arbuscule development, and fungal colonization in both *Medicago* and rice (Krajinski et al. 2014; Wang et al. 2014).

Recent modeling and biophysical descriptions of nutrient exchange at the arbuscule suggest that the main classes of nutrient traded to our knowledge is relatively comprehensive, although the underlying mechanistic understanding is unclear (Dreyer et al. 2018). Using either minimal transporter networks for P/C exchange (Schott et al. 2016), or without transporter identity but simply first principles of thermodynamics and H^+-ATPase-powered transport as the sole assumptions (Dreyer et al. 2018), P (or P/N) trade for C at the interface was shown to be sufficient as the general minimal model to which more nutrients can be added. These models reveal that AMF is likely to unload Pi via hitherto elusive H^+/Pi symporters because it is energetically favorable and ensures increased reward in the form of increased C flux (Dreyer et al. 2018). Whereas for the plant, although electroneutral transport of C (as hexoses or FAs) is not the most energetically favorable, it enables additional P uptake as long as C is not limiting. Importantly, these models show that even when viewed from a competitive perspective, the relative ease of access to P or C stores by each party (i.e., self-interest), is sufficient to drive a robust mutualistic exchange.

Multiple Evolutionary Trajectories of Plant Phosphate Transporters

With their key roles in symbiosis, plant symbiotic PTs have been studied in considerable detail relative to other transporters. Table 1 summarizes the various symbiotic phosphate transporters identified across a wide range of species to date. Apart from the conserved MtPT4/OsPT11 transporters, individual mycorrhizal plant families also appear to have evolved phylogenetically divergent PTs that may serve redundant or nonredundant roles in symbiosis. In rice,

OsPT11 and *OsPT13* are specifically expressed in arbuscules and serve nonredundant roles in the regulation of symbiosis (Yang et al. 2012). Whereas *OsPT11* belongs to the phylogenetically conserved AM-specific PT, *OsPT13* represents a phylogenetically distant innovation in the monocotyledons (Yang and Paszkowski 2011; Yang et al. 2012). *OsPT11* alone is necessary and sufficient for symbiotic Pi uptake. *OsPT13*, in contrast, does not contribute to symbiotic Pi transport, although it is expressed at the arbuscule, and also failed to display Pi transport activity in yeast *pam2* mutants (Yang et al. 2012). Interestingly, *ospt13* mutants, despite having reduced colonization and stunted arbuscule development, have wild-type levels of *OsPT11* transcripts and symbiotic Pi uptake (Yang et al. 2012). Therefore, whether OsPT13 functions as a nontransporting sensor to monitor Pi levels at the periarbuscular interface—that is, as a transceptor—remains to be shown. Transceptor activity has been identified for yeast *Pho84*, which transports Pi and activates protein kinase A signaling in *A. thaliana* nitrate transporter *NRT1.1*; and more recently has also been suggested for *GigmPT* (Bun-Ya et al. 1991; Giots et al. 2003; Walch-Liu and Forde 2008; Xie et al. 2016).

Neofunctionalization of symbiotic phosphate transporters for asymbiotic roles is also observed in certain plant families or species, and may have thus conferred additional tools for the plant P transport and allocation over evolutionary time. Gene duplication in the Solanaceae gave rise to two orthologs of OsPT11 in tomato and potato (*SlPT4/LePT4* and *SlPT5/LePT5*) (Nagy et al. 2005; Poulsen et al. 2005). *LePT4* is exclusively expressed during symbiosis, but it is dispensable for symbiotic P uptake; whereas *LePT5* is also expressed during asymbiosis and is induced >10-fold during fruit ripening (Xu et al. 2007; Chen et al. 2014). These examples suggest that gene duplications can give rise to new regulation and functions in P partitioning. Similarly, OsPT11/MtPT4 orthologs in maize (*ZmPT6*) and *Brachypodium* (*BdPT7*) accumulate in both mycorrhizal roots and also noncolonized roots and leaves of Pi-starved plants (Nagy et al. 2006; Hong et al. 2012). This raises a question regarding the ancestral state and subsequent evolution of phosphate transporters in the plant kingdom—were the roles of the ancestral phosphate transporter(s) symbiotic, asymbiotic, or both?

Spatial Physiology of Symbiotic Pi Exchange Remains Unclear

One neglected aspect of symbiotic and asymbiotic Pi uptake is the relative contributions of various root types to the overall uptake and assimilation of Pi. Changes in root architecture is one of the common physiological responses investigated in asymbiotic nutrient signaling pathways. In non-AM *A. thaliana*, primary root growth is arrested and lateral root density (LRD) increases (Péret et al. 2014) during Pi starvation. In monocots where genetic architecture of root development is different, changes to the primary embryonic roots of seedling roots are subtle, whereas LRD decreased in maize but increased in rice (Péret et al. 2014; Hochholdinger et al. 2018). More importantly, lateral rooting correlates positively with Pi acquisition under low P conditions (Zhu and Lynch 2004; Gamuyao et al. 2012; Vejchasarn et al. 2016). Where and how phosphate transporters are expressed in different root types, and contribute to Pi uptake, remain to be fully characterized.

AM symbiosis, meanwhile, increases LRD in the leguminous and monocot hosts examined thus far (Oláh et al. 2005; Gutjahr et al. 2009; Maillet et al. 2011; Mukherjee and Ané 2011; Chiu et al. 2018). With AMF preferentially colonizing LRs in both monocots and dicots, this effectively increases the symbiotic interface for nutrient exchange (Gutjahr et al. 2009). Colonization by AMF elicited a fundamental reprogramming of the rice crown root transcriptome, whereby the profiles of secondary cell wall metabolism, hormone, and transport-related genes indicated a switch in functional relationships of root types upon entering symbiosis (Gutjahr et al. 2015). To this end, better physiological characterization of contributions of the various root types to symbiotic Pi uptake will help define an "ideal" root architecture for crop-breeding programs.

Plant Carbon Transfer to AMF in Exchange for Pi

Reciprocal nutrient exchange is a hallmark of this mutualism—in exchange for Pi, plants deliver C to AMF. Most plants are facultative symbionts—they allow AMF colonization and benefit from symbiotic Pi uptake, but can grow axenically without them. On the other hand, AMF, being FA auxotrophs, absolutely rely on plant-fixed carbon to complete their life cycle (Bago and Bécard 2002). Radiolabeling experiments demonstrated that fixed C is transferred to the fungus as hexoses and lipids via the IRM (Shachar-Hill et al. 1995; Solaiman and Saito 1997; Bago et al. 2000, 2002, 2003). *Rhizophagus irregularis* high-affinity monosaccharide transporter *MST2*, for example, is able to transport glucose, mannose, fructose, and is expressed in IRM—suggesting that apart from arbuscules, IRM are possible sites of symbiotic nutrient exchange (Helber et al. 2011; Ait Lahmidi et al. 2016; Roth and Paszkowski 2017). Noteworthy also are *Medicago truncatula della* mutants, where extensive IRM growth suggest hexose transfer but the severe lack of arbuscules and lipid transfer result in the failure of AMF to complete its life cycle (Floss et al. 2013; Yu et al. 2014).

Meanwhile, FAs have emerged as the central form of C required by AMF to complete their life cycle. Substantial amounts of C are stored as triacylglycerols in all fungal structures (Bago et al. 2002), and the central role of lipids for AMF metabolism contrasted starkly against the lack of type I fatty acyl synthase subunits for palmitic acid synthesis from AMF genomes and transcriptomes (Tisserant et al. 2013; Wewer et al. 2014; Tang et al. 2016). Lipid transfer from plants to AMF was conclusively demonstrated via two independent approaches. First, using a synthetic method, *Umbellularia californica* fatty acyl-ACP thioesterase (*UcFatB*) introduced into *Medicago* roots resulted in the production of 12:0FA (lauric acid), which does not occur naturally in *Medicago*. Detection of lauric acid in *R. irregularis* spores demonstrated the existence of lipid transfer (Jiang et al. 2017; Luginbuehl et al. 2017). In addition, isotopolog profiling of FA compositions with ^{13}C-labeled glucose together with fungal-specific 16:1ω5 FA enabled the monitoring of FA transfer. The close mirroring of 16:0 and 16:1 FA, and the impaired 16:1FA accumulation in *Lotus japonicus* FA biosynthesis mutants demonstrated their roles in lipid transfer (Keymer et al. 2017; Brands et al. 2018). *STUNTED ARBUSCULES1* (*STR1*) and *STR2*, both half-size ABC transporters of the G family, are therefore widely hypothesized to transport lipids as 16:0βMAG across the plant PAM (Bravo et al. 2017; Keymer et al. 2017; MacLean et al. 2017), but their direct transport activity remains to be demonstrated, and elucidating transport activity of ABC transporters is nontrivial (Lefevre et al. 2015). Plant carbon nourishment of AMF is reviewed extensively in Luginbuehl and Oldroyd (2017), MacLean et al. (2017), Roth and Paszkowski (2017), and Keymer and Gutjahr (2018).

REGULATION OF ARBUSCULE DEVELOPMENT—THE OLD AND NEW

Transcriptional Regulation of Arbuscule Development

Arbuscules are often considered the "heart of the symbiosis," for the symbiosis culminates in these highly branched structures where nutrient exchange occurs. Years of work by various groups have revealed how the plant coordinates and orchestrates the development of the arbuscule, revealing the transcriptional and traffic control required for a functional nutrient exchange interface to be established. In the meantime, new frontiers of signaling have also emerged.

Trafficking of Plant Symbiotic Transporters

During arbuscule development, root cortical cells undergo significant transcriptional reprogramming, creating a PAM that carries a distinct composition of proteins otherwise contiguous with the plasma membrane. These include the aforementioned symbiosis-specific phosphate, ammonium, sugar, ABCG transporters (e.g., STRs), and H^+-ATPases. How the arbuscule achieves such precise spatiotemporal localization of proteins is not completely under-

stood. For example, MtPT4/OsPT11/GmPT10/GmPT11 specifically localizes to the branch domains of periarbuscular membrane (Kobae and Hata 2010; Tamura et al. 2012). Genetic analyses predominantly in legumes reveal the involvement of polarized exocytosis involving an EXO70I subunit of the EXOCYST complex, v-SNARE: VESICLE ASSOCIATED MEMBRANE PROTEIN (VAMP721d,e) and a splice variant of t-SNARE (*SYNTAXIN OF PLANTS, SYP132*), which are all symbiosis-specific members of big gene families, as well as symbiosis-induced *VAPYRIN* (Feddermann et al. 2010; Pumplin et al. 2010; Murray et al. 2011; Ivanov et al. 2012; Zhang et al. 2015; Huisman et al. 2016; Pan et al. 2016). Systematic promoter analysis in *Medicago* revealed that precise localization is achieved by the timing of gene expression and transient reorientation of the secretory pathway (Pumplin et al. 2012; reviewed in Harrison and Ivanov 2017). Demonstrating the conservation in other AM host species, and identifying the temporal regulators of expression and secretory activity will generate better understanding and potentially useful biological applications.

Recently, small anionic lipids—phosphoinositides and phosphatidic acid—have also been shown to possess distinct subcellular distribution during arbuscule development (Ivanov and Harrison 2018). The specific distribution of these anionic lipids known to influence cellular processes ranging from membrane trafficking, signaling, exocytosis, and endocytosis raises questions on their roles in regulating arbuscule development.

Network of GRAS-Domain Proteins May Integrate Host Nutrient and Growth Status

A suite of transcriptional regulators, especially GRAS-domain proteins, have emerged as key players that regulate arbuscule development, possibly through their spatiotemporal expression and combinatorial control of symbiotic gene expression in successive "transcriptional waves" (Gutjahr and Parniske 2013; Luginbuehl and Oldroyd 2017; MacLean et al. 2017; Choi et al. 2018; and detailed in Pimprikar and Gutjahr 2018). Perception of AMF activates the CSSP via CALCIUM/CALMODULIN DEPENDENT KINASE (CCaMK) and via CYCLOPS, a transcription factor (TF) to activate symbiotic gene expression, enabling intraradical accommodation of AMF. DELLA proteins (SLENDER1 in rice), members of the GRAS-domain family, and known transcriptional suppressors of gibberellic acid signaling, form a complex with CCaMK and CYCLOPS essential for arbuscule development (Jin et al. 2016; Pimprikar et al. 2016). This includes REQUIRED FOR ARBUSCULAR MYCORRHIZA1 (RAM1), a GRAS-domain TF that activates *EXO70I*, *FatM*, *RAM2*, *STR1* expression, suggesting a key role of this transcriptional module in orchestrating lipid biosynthesis and membrane biogenesis. Another GRAS-domain protein, REQUIRED FOR ARBUSCULE DEVELOPMENT1 (*Lj*RAD1), interacts with RAM1 and DELLAs in vivo, and is required for arbuscule development at the fine branch stage (Park et al. 2015; Rich et al. 2015, 2017; Xue et al. 2015; Pimprikar et al. 2016). Joining the concert of GRAS-domain proteins regulating arbuscule development is MYCORRHIZA-INDUCED GRAS (MtMIG1), which is also required for arbuscule branching and together with DELLA proteins activate radial cell expansion of the cortex (Heck et al. 2016). Taken together, the pervasive role of GRAS domain TFs (Fig. 1), especially in the case of DELLA proteins, could provide a means for plants to integrate growth, developmental, and nutritional signals via phytohormones with arbuscule development.

Transcriptional Module Regulating Bidirectional Nutrient Exchange

Recently, two independent groups working on different leguminous species identified and functionally characterized *WRINKLED1-like* AP2 TFs that work downstream of RAM1. *CTTC MOTIF-BINDING TRANSCRIPTION FACTOR1 (LjCBX1)* and *Medicago WRINKLED5a (MtWRI5a)* (Jiang et al. 2018; Xue et al. 2018) are TFs that bind to the AW-box motif and regulate the expression of fatty-acid biosynthesis genes, phosphate transporters (*MtPT4/LjPT4*), as well as H^+-ATPases, suggest-

ing the existence of a transcriptional network directly regulating bidirectional nutrient exchange (Jiang et al. 2018; Xue et al. 2018). With the plethora of actors identified in the plant host, we look forward to the identification of the fungal counterparts.

Receptor-Like Kinase Signaling at the Periarbuscular Membrane

In addition to the increasingly complex transcriptional network and nutrient exchange during arbuscule development, recent work characterizing the proteome and transcriptome of mycorrhizal roots and arbusculated cells, respectively, demonstrated for the first time existence of signaling cascades mediated by receptor-like kinases (RLKs) at the PAM (Roth et al. 2018). In rice, *ARBUSCULAR RECEPTOR-LIKE KINASE 1* (*ARK1*), a family of serine/threonine RLK present in AM host species, is a PAM-localized RLK required for sustaining fungal fitness at the latter stages of symbiosis. *OsARK1* is orthologous to *M. truncatula KINASE3* (*MtKIN3*) (Bravo et al. 2016; Roth et al. 2018). Although arbuscule development remained normal, vesicle development of AMF was impaired and symbiosis collapsed over prolonged time periods. The presence of a common mycorrhizal network supported by wild-type plants, however, rescued the *ark1* mutant phenotype. Following arbuscule senescence, vesicles often emerge as lipid storage bodies and could be crucial for subsequent rounds of infection affected in *ark1* mutants (Roth et al. 2018). Whereas the formation of vesicles and daughter spores in AMF reflects fungal fitness, the dearth of knowledge on the mechanisms specifying and underlying these processes invite further studies.

INSIGHT: NUTRIENTS ARE ALSO SIGNALS FOR SYMBIOSIS

Beyond transcriptional and trafficking changes orchestrated in the developing arbuscule, a key insight into regulation of arbuscule development is the regulatory role played by nutrients (Yang and Paszkowski 2011). Functional characterization of symbiotic transporters have revealed the regulatory role of nutrients in arbuscule development. Consistently, mutants of symbiotic PTs (*MtPT4*, *OsPT11*, *OsPT13*), genes involved in lipid biosynthesis/delivery (*OsSTR1,2*, *MtSTR1,2*, *LjFatM*, *DIS*, *RAM2*), as well as H^+-ATPases powering nutrient transfer all result in disrupted nutrient transfer, reduced colonization, stunted arbuscule development, altered arbuscule morphology, and in the case of *mtpt4/ospt11* mutants, increased arbuscule turnover (Javot et al. 2007a; Yang et al. 2012; Xie et al. 2013; Krajinski et al. 2014; Wang et al. 2014; Bravo et al. 2016, 2017; Keymer et al. 2017; Brands et al. 2018). Radiotracer experiments showed that like *mtpt4/ospt11*, symbiotic Pi uptake is also abolished in *mtha1* mutants (Krajinski et al. 2014). Beyond P, uptake of other nutrients is also affected in *mtha1* mutants (Hubberten et al. 2015). The *Rhizobia-Medicago* nodule symbiosis, however, appears unaffected (Krajinski et al. 2014; Wang et al. 2014). Thus, proton gradients established by MtHA1/OsHA1 appear crucial for AM symbiosis development and exchange of neutral and negatively charged nutrients. It will be interesting to investigate whether symbiotic Pi transfer is abolished in lipid transfer mutants, and whether the lack of transfer is a result of plant or fungal signaling.

Interestingly, in the case of *Medicago pt4*, the mutant phenotype is rescued by nitrogen deprivation, in a manner dependent on an ammonium transporter, *MtAMT2-3* (Javot et al. 2011; Breuillin-Sessoms et al. 2015). As *MtAMT2-3* is unable to complement a yeast ammonium transport mutant, it has since been suggested to have a signaling role in arbuscule maintenance—possibly in a similar fashion to *OsPT13* (Yang et al. 2012; Breuillin-Sessoms et al. 2015). Screening for the suppression of the *mtpt4* phenotype revealed the role of MYB1, a MYB-like TF that regulates arbuscule degeneration. The requirement of a MYB1-DELLA-NSP1 complex to degenerate arbuscules lends further support to the theme that GRAS-domain protein complexes have temporal and combinatorial control of arbuscule development (Floss et al. 2017).

Collectively, it appears that nutrient delivery is a signaling requirement. Nonproductive colonization can be detected and terminated by the

plant host, and possibly by the AMF symbiont as well (e.g., undernourishment without FAs). How each party measures the delivery of P/FAs and senses the lack of symbiotic nutrient exchange to terminate arbuscule development is currently unclear. Nonetheless, it is also plausible that H^+/Pi/C fluxes may have a self-organizing feature capable of driving and sustaining transcriptional activities to allow full arbuscule development without requiring a "sensor."

Why Are Arbuscules Transient?

Given the multitude of transport and regulatory activity occurring during symbiosis, the transient nature of arbuscules may appear enigmatic. Arbuscules have short life spans of ~4–15 days before they mature and collapse, leaving the cortical cells competent for reinfection (Toth and Miller 1984; Alexander et al. 1988; Kobae and Hata 2010; Kobae and Fujiwara 2014). As such, in the same plant (and likewise fungus), symbiosis development is highly asynchronous, with new infection units co-occurring alongside fully developed arbuscules and senescing ones.

Here, we propose that rather than being a futile cycle of infection and iterative membrane biogenesis, the transitory nature of an arbuscule may be crucial to its symbiotic nature, from enabling bidirectional uptake in the short term to allowing evolutionary stability in the long run. A substantial amount of membrane phospholipids is generated per arbuscule, which in itself provides an increased surface area for symbiotic nutrient and signal exchange. Phospholipids constitute two of the key currencies of the trade—phosphates and fatty acids. We speculate that the sustained development of a PAM requires commitment by both parties to direct P and C to the interface, which allows the monitoring and policing of symbiotic nutrient exchange, and provides, with the ensuing senescence, a possible second pathway of symbiotic nutrient exchange. This policing could ensure that nonproductive arbuscules (and nonproductive AMF species) become terminated instead of maintained.

Meanwhile, ultrastructural analyses of the periarbuscular space reveal the presence of interkingdom trafficking of extracellular vesicles (EVs) between the plant and AMF (Ivanov et al. 2019; Roth et al. 2019), which invites speculation on the cargo constituents in these EVs. In *Prochlorococcus*, EVs carry organic carbon and nucleic acids with importance in nutrient fluxes in marine ecosystems (Biller et al. 2014). In *Paracoccus*, EVs carry hydrophobic *N*-acylhomoserine lactones for quorum sensing (Toyofuku et al. 2017). In a plethora of human organs, EVs are capable of regulating local and global metabolism and associated cellular processes (Iraci et al. 2016, 2017). In AMF symbiosis, could these EVs be involved in signaling and potential nutrient exchange as well?

AGRICULTURAL SIGNIFICANCE OF SYMBIOTIC PHOSPHATE UPTAKE

Understanding molecular and physiological processes of symbiotic P uptake have translational importance to agriculture where P is often limiting crop growth and supplemented by fertilizers. In all plant species tested, the direct and indirect P uptake pathways appear to be distinct, nonadditive physiological alternatives (Smith 2003; Bucher 2007). Using radioisotopes of $^{32}P/^{33}P$ accessible by AMF hyphae but not plant roots allows the relative contributions of direct and indirect P to be determined. Early radiotracer experiments showed that the indirect pathway can dominate total P uptake, even when the plants (e.g., cucumber, wheat, barley, and tomato) do not display increased biomass or total P increase over the nonmycorrhizal plants (Pearson and Jakobsen 1993; Morel and Plenchette 1994; Ravnskov and Jakobsen 1995; Schweiger and Jakobsen 1999; Zhu et al. 2003; Smith et al. 2004; Yang et al. 2012). In species such as tomato and flax, the mycorrhizal pathway contributed 100% of Pi acquired by the plant (Smith et al. 2004). Such physiological experiments also demonstrate that the quantities of Pi delivered by AMF correlate strongly with the extraradical hyphae abundance, rather than percentage of intraradical structures (Schweiger and Jakobsen 1999; Jakobsen et al. 2001; Yao et al. 2001; Schnepf et al. 2008). Interestingly, a similar correlation between mycorrhizal Pi delivery and ex-

traradical hyphae abundance was also observed in a diversity panel of 30 maize lines (Sawers et al. 2017), and it will be interesting to investigate whether a recent diversity analysis of 14 *Sorghum* accessions produces the same observations (Watts-Williams et al. 2018).

Importantly, these physiological observations imply that in agricultural and natural ecosystems, symbiotic P uptake might be the predominant uptake pathway for AM host species and is therefore crucial for crop nutrition. For example, in rice, AMF contributes up to 70% of the P acquired by the plant (Yang et al. 2012). Second, the nonadditive interaction may explain the lack of simple additive growth/Pi acquisition benefits with AMF observed in physiological experiments. Third, experiments such as those in Sawers et al. (2017), Watts-Williams et al. (2018), and Zhang et al. (2018) suggest that plant genetics, fungal genotypes, and associated bacteria together determine mycorrhizal benefit derived from symbiosis, forming the basis for complex crop-breeding programs in the future (see Toju et al. 2018). Crop-domestication and -breeding programs to date might have selected for AM independence under high Pi, well-fertilized conditions (Martín-Robles et al. 2018). Thus, beyond Pi-directed growth benefits, the additional benefits such as drought, salinity (abiotic stress) tolerance, and resistance to other biotic agents conferred by AMF (Newsham et al. 1995; Herre et al. 2007) should also be considered in modeling and implementing mycorrhizal enrichment as well as plant-breeding programs. Finally, it will be interesting to investigate whether derepressing the direct uptake pathway during symbiosis, if possible, could significantly increase total P uptake or the replacement of Pi fertilizers, and whether it reciprocally affects stages or the extent of AM symbiosis.

Looking forward, significant benefits of symbiotic Pi delivery can be harnessed, considering that modern industrial agricultural practices including the intensive use of fertilizers, fungicides, long fallow periods, and tilling have diminished the contribution of symbiotic Pi to crop nutrition (Sawers et al. 2008, 2018; Pérez-Jaramillo et al. 2016). The nonrenewable and politically tenuous nature of mined rock phosphates as well as pollutive impact of intense fertilizer application in industrial agriculture have led to the growing awareness and drive for more sustainable alternative mechanisms to improve crop P acquisition and P use efficiency (Cordell et al. 2009; Carpenter and Bennett 2011; Elser and Bennett 2011; Steffen et al. 2015).

ECOLOGICAL SIGNIFICANCE OF AM SYMBIOSIS

Empirically, AMF have variable effects on their hosts ranging from growth promotion to growth depression; and conversely AMF proliferation and sporulation varies with host species. Although surprising in deviating from the definition of a pure mutualistic symbiosis, it is less surprising considering that symbiotic trade necessitates costs and benefits, and the fitness benefits need not necessarily manifest as growth increases.

Plants and AMF May Select for More Cooperative Partners

In a mycorrhizal network, one plant can be colonized by multiple AMF species at once, and each AMF species can infect multiple hosts of the same or different plant species (Giovannetti et al. 2004). This has lent the symbiosis to many imaginative metaphors (e.g., "wood-wide web"; underground economy, etc.). Indeed, trade of commodities (nutrients) between multiple actors with different comparative advantages (in harnessing phosphate versus reduced carbon) invites analyses via the biological market theory and other models that allow hypotheses on resource exchange in different contexts to be formulated and tested (Noë and Hammerstein 1995; Kiers et al. 2003; Werner et al. 2014; Walder and van der Heijden 2015; Noë and Kiers 2018). Given the benefits of "cheating" in mutualism, does the plant and fungus select for a more cooperative partner (West et al. 2007; Kiers and Denison 2008)?

Several experiments suggest that a discrimination mechanism for reciprocal exchange exists—plants provided more C to fungal species

that delivered more Pi (Bever et al. 2009; Kiers et al. 2011) and, likewise, AMF species provided more N/Pi to unshaded plants that likely delivered more C (Fellbaum et al. 2014). Collectively, these mechanisms might drive the amplification of size inequality in a network (Merrild et al. 2013; Weremijewicz and Janos 2013; Weremijewicz et al. 2016). However, in contrast to these observations, flax derived more nutrients than sorghum despite contributing less into the mycorrhizal network (Walder et al. 2012). Nevertheless, direct comparisons may be difficult, as the relative costs of C for a C4 plant (sorghum) may be different from that of a C3 plant (flax).

Cheating Partners May Be an Evolutionarily Stable Outcome

Overall, it appears that preferential resource allocation is able to drive evolution of mutualism even when the costs are immense, whereas coexistence of an exploitative partner is possible as a negative feedback in the long run in a mixed colonization situation (Foster and Kokko 2006; Steidinger and Bever 2016). These conclusions may help explain the diversity of plant-AMF interaction outcomes, as well as the evolutionary emergence of mycoheterotrophs that epitomize exploitative plant partners. Ultimately, symbiotic nutrient exchange occurs between a kingdom of plants and a subdivision of Glomeromycotina fungi, notwithstanding other symbioses. The diversity in trade terms is therefore not unexpected, and remains to be characterized across many other combinations and hierarchies with modeling tools.

Less Well-Understood Traits of AMF: Ecological and Agricultural Applications

Moreover, there are several aspects regarding the lifestyle and genetics of AMF that we are only beginning to understand. If and how diversity may lead to functional differences in plant symbiotic uptake is still unknown. Although ecologically successful, AMF only comprise ~300 species in contrast to their broad host range (~200,000 plant species). Its mycelium contains hundreds to thousands of nuclei within one continuous cytoplasm without undergoing formal sexual reproduction but capable of anastomosis. This has led to the long-standing enigma of how AMF of limited morphological diversity, are capable of colonizing roots of disparate genetic diversity over 400 million years (Judson and Normark 1996; Sanders 1999; Corradi and Brachmann 2017). Large-scale sequencing approaches have since revealed some insight into how diversity can be generated in spite of an apparent asexual lifestyle. First, AMF possess massive intraspecific genotypic variation, with the common laboratory strain *R. irregularis* alone possessing a pangenome of 150,000 genes and likely, as a result, considerable phenotypic variation even in a morphologically defined species (Mathieu et al. 2018). In addition, single-nucleus sequencing of AMF revealed that genetic diversity can be generated via internuclear recombination in a dikaryotic stage (two distinct mating loci) (Chen et al. 2018). Although rare in laboratory-cultured strains, how widespread are these processes in natural ecosystems? How functionally important is recombination toward symbiosis and long-term ecological fitness? Can an optimized, highly "cooperative" strain be developed to boost plant symbiotic P uptake?

Symbiont in a Symbiont: A Symbiotic Matryoshka?

In another symbiosis almost as old as AM symbiosis (Naumann et al. 2010; Mondo et al. 2012; Pawlowska et al. 2018), most AMF themselves harbor bacterial endosymbionts in their cytoplasm that are obligate biotrophs, although their function in symbiotic Pi uptake or in forming a tripartite mutualism remains to be fully demonstrated (Bianciotto et al. 2003, 2004; Naumann et al. 2010). Sequenced genomes of *Candidatus* Glomeribacter gigasporum (*Ca*Gg) or the more widespread *Mollicutes*-related endobacteria (MRE) reveal their lack of crucial metabolic pathways and consequent dependency on the fungal host for essential nutrients and energy (Ghignone et al. 2012; Naito et al. 2015; Torres-Cortés et al. 2015). In-

triguingly, MRE form a sister lineage to the *Mycoplasma* groups, which are biotrophic extracellular parasites of animals (Torres-Cortés et al. 2015). Although the endobacteria are unculturable without a host, they are dispensable for AMF survival insofar that the few species of AMF cured of bacteria examined to date can still establish root symbiosis (Lumini et al. 2007; Bonfante 2014; Bonfante and Desirò 2017). The existence of endobacteria dependent on AMF, which themselves are dependent on plants, raises exciting questions on the dynamics and function of the interphylum interactions and nutrient transfer in the plant-fungi-bacteria holobiont. As the fungal–bacterium association is vertically transmitted, pan-global, evolutionarily stable, and ancient, it is likely that they provide fitness benefits to the fungal host (Bianciotto et al. 2004; Mondo et al. 2012; Bonfante and Desirò 2017; Pawlowska et al. 2018). Possible roles of endobacteria have been proposed to include nutrient transfer to and activating metabolic reprograming of AMF to increase success of colonizing host plants (Lumini et al. 2007; Salvioli et al. 2016; Vannini et al. 2016; Venice et al. 2017; Dearth et al. 2018), as well as trans-kingdom gene transfer for putative effector-like proteins with an extended phenotype on the plant (Torres-Cortés et al. 2015).

PERSPECTIVES AND CONCLUSION

Perspective: The Paradox of Phosphate Starvation during AM Symbiosis

Phosphate not only regulates local arbuscule development; it also has well-known systemic regulatory roles in symbiosis signaling. AM colonization is repressed under high Pi supply (Mosse 1973; Branscheid et al. 2010; Balzergue et al. 2011, 2013; Kobae et al. 2016) and infection attempts in maize roots were found to be inversely proportional to shoot Pi status (Braunberger et al. 1991). This regulation is systemic, as split-root experiments demonstrated that high Pi on one side suppressed AM symbiosis globally (Branscheid et al. 2010; Breuillin et al. 2010; Balzergue et al. 2011). The root-to-shoot signal remains elusive. Overexpression of miR399, members of which are well-described systemic Pi-starvation signals, failed to restore AM colonization under high Pi levels (Branscheid et al. 2010). In addition, high phosphate suppresses SL biosynthesis, which attenuates the level of plant-to-fungus signal during presymbiotic signaling. Nevertheless, the exogenous application of a synthetic SL, GR24, failed to restore AM colonization at high Pi levels (Breuillin et al. 2010; Balzergue et al. 2011), indicating that reduced SLs in the rhizosphere is insufficient to explain the suppressive effect. However, perinuclear Ca^{2+}-oscillations were still generated in response to AMF hyphopodia under high Pi levels (Balzergue et al. 2013). This suggests that the Ca^{2+}-oscillation machinery is not affected, but does not rule out Pi-suppression of presymbiotic signals leading to hyphopodia formation, or of the transcriptional activation to accommodate AMF downstream of Ca^{2+} oscillations. Finally, we also cannot rule out intrinsic inhibitory responses of AMF under high Pi. How AMF sense and respond to high Pi and subsequent root colonization dynamics is also relatively unclear. Evidence so far suggest that high Pi treatment may decrease expression of secreted AMF proteins, including STRIGOLACTONE-INDUCED SECRETED PROTEIN1 (SIS1) that positively regulates AMF colonization; as well as cell-cycle regulatory genes, DNA replication, and mitosis-related genes in the IRM but not ERM extraradical mycelium (Kikuchi et al. 2014; Tsuzuki et al. 2016; Sugimura and Saito 2017). It is, however, a challenge to uncouple intrinsic AMF responses from plant/exudate-mediated responses in a plant-AMF coculture system.

In addition, recent work on biotic interactions in the non-AM host *Arabidopsis* illustrates that the continuity from mutualism to parasitism along the symbiosis spectrum (Box 1) can shift with phosphate availability and phosphate starvation signaling. For one, *C. toefieldiae* acts as a Pi-delivering endophyte without causing disease only under Pi limitation. When Pi is abundant, plant defense genes are induced and growth-promoting benefits of the endophyte are abolished (Hiruma et al. 2016). Whereas in mutants of *phr1*, *phl1* where transcriptional phos-

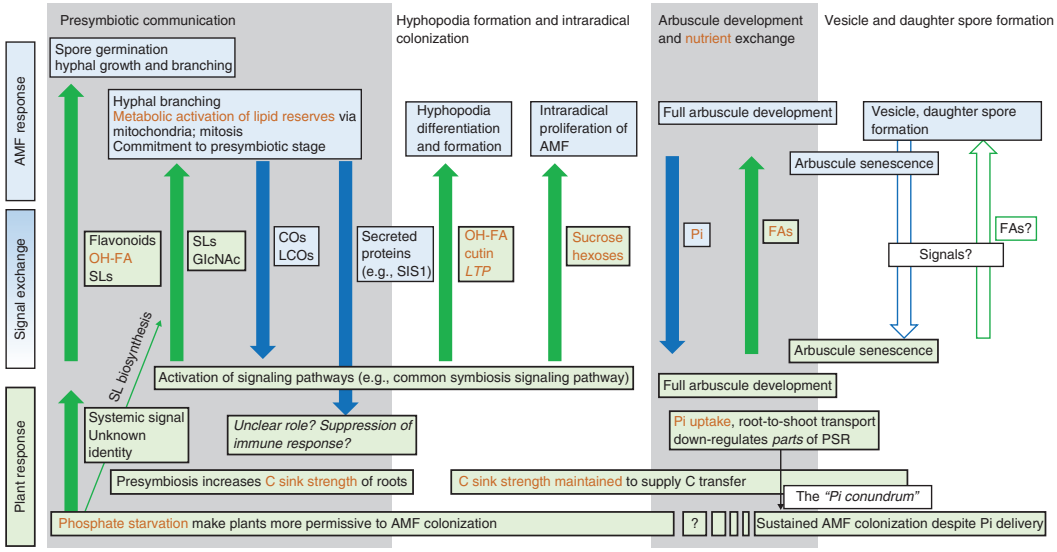


Figure 3. Nutrients play important signaling roles at various stages of symbiosis. The first stages of symbiosis signaling result in substantial reprogramming of both plant and arbuscular mycorrhizal fungi (AMF) metabolism. Crucially, the reprogramming commits the plant to supply AMF with carbon via hydroxyl fatty acids (OH-FA), cutin, and lipid transfer proteins (LTPs) at the presymbiotic and contact stages and via sugars in the intraradical stage. At the heart of the symbiosis, a fully functional bidirectional exchange of Pi and fatty acids is required for signaling as much as nutritional benefit. Together, the plant and fungus elicit, via and as a result of signal exchanges, metabolic changes in the other party. Several gaps in understanding remain—including the nature of signals exchanged in the last stage of symbiosis where arbuscules degenerate, while vesicles and daughter spores form. Importantly, how AMF manages to deliver Pi without down-regulating the entirety of PSR to continue to allow sustained symbiosis development at new, secondary infection sites remains unclear.

phate starvation responses (PSRs) are lost, defense genes were up-regulated and the root microbiota composition was atypical to that of wild-type in a synthetic community setup. This suggests that PSRs, under homeostatic conditions, have regulatory roles on the defense response and correspondingly shape the root microbiome (Castrillo et al. 2017). Finally, in the AM-host maize, high Pi activated defense responses, shifted fungal community, and reduced AMF colonization especially in lateral roots (Yu et al. 2018).

Therefore, during symbiosis, AMF experience a "Pi regulation conundrum" (Fig. 3). PSR promotes AMF colonization, but symbiotic Pi exchange and subsequent mobilization to the shoot could relieve the PSR and activate defense gene expression to terminate symbiosis. Indeed, symbiotic Pi uptake mediated by *MtPT4*/*OsPT11* is required for down-regulating the direct Pi uptake arm of PSR (Harrison et al. 2002; Paszkowski et al. 2002; Javot et al. 2007a; Yang et al. 2012; Watts-Williams et al. 2015). However, AMF colonization steadily increases in wild-type plants, suggesting that symbiosis signaling also down-regulates certain aspects of the PSR to favor fungal accommodation over exclusionary defense. The exact molecular mechanisms mediating the differential regulation of PSR during symbiosis, however, is unclear.

Conclusion: Metabolic Reprogramming and Nutrient Dependency Is a Hallmark of Symbiosis

Symbioses enabled the first eukaryotes to gain complex metabolic capabilities with the establishment of mitochondria and plastids (Mereschkowsky 1905; Margulis 1991); and continued to provide evolutionary innovations to

enable functional and ecological diversity to occupy new niches. The symbiosis between plants and AMF is one of the many symbioses, but it is remarkable for its widespread occurrence, evolutionary success, and our level of mechanistic understanding. Metabolic interdependence has been invoked to explain symbiotic dependence, in particular between sap-feeding insects and obligate symbionts, where the latter provide amino acids, vitamins, and cofactor synthesis in exchange for host-derived sugars (Zientz et al. 2004; Wu et al. 2006; Luan et al. 2015; Wilson and Duncan 2015). Evolutionarily younger, artificial symbioses similarly reveal the gradual evolution of auxotrophy and nutritional interdependence for mutualism to develop. This includes the *Chlamydomonas reinhardtii—Saccharomyces cerevisiae* exchange of carbon and nitrogen (Hom and Murray 2014); *Lobomonas rostrate—Mesorhizobium loti* exchange of carbon for Vitamin B12 (Helliwell et al. 2018); as well as *Synechocystis* PCC6803—*Paramecium bursaria* exchange of carbon for nitrogen (Sørensen et al. 2016), to name a few.

Nutrient interdependency occurs in the AM symbiosis too. Plants, when colonized, can become predominantly reliant on AMF for phosphate nutrition, whereas the fungal symbiont, probably as a result of the readily available C transfer from plants, lost the ability to synthesize fatty acids over evolutionary time. Moreover, on top of long-term evolutionary dynamics, the signaling processes required for successful symbiosis establishment appear to involve nutrient dependency at all stages (Fig. 3). Presymbiotic signaling itself induces transcriptional and metabolic reprogramming in hosts, increasing C flux and C sink strength. On the fungal end, perception of SL, uptake of plant-released fatty acids (e.g., of hydroxyfatty acids, or of cutin), and monosaccharides drive metabolism, although potentially maintaining an altered plant metabolic status for its growth inside the root (Nagahashi et al. 2010; Helber et al. 2011; Wang et al. 2012). Especially at the stage of arbuscule development, it is now clear that sustained nutrient transfer is not just the ultimate goal, but a necessary signal. It will be exciting to unravel exactly how nutrient signals recur and mediate the various stages of symbiosis and vice versa. For one, emerging frontiers such as EVs at the biogenesis and collapse of the arbuscule offer further, yet uncharacterized opportunities for ways to mediate nutrient and signal exchanges between organisms. Understanding how plants, AMF, as well as the AMF-associated microbiome engage in the symbiotic nutrient trade strategies maintained over millions of years will, importantly, help provide solutions for the phosphate challenge modern agriculture faces.

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