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Review: Arbuscular mycorrhizas as key players in sustainable plant 5 phosphorus acquisition: An overview on the mechanisms involved*

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2019

Abstract

Phosphorus (P) is a poorly available macronutrient essential for plant growth and development and consequently for successful crop yield and ecosystem productivity. To cope with P limitations plants have evolved strategies for enhancing P uptake and/or improving P efficiency use. The universal 450-million-yr-old arbuscular mycorrhizal (AM) (fungus-root) symbioses are one of the most successful and widespread strategies to maximize access of plants to available P. AM fungi biotrophically colonize the root cortex of most plant species and develop an extraradical mycelium which overgrows the nutrient depletion zone of the soil surrounding plant roots. This hyphal network is specialized in the acquisition of low mobility nutrients from soil, particularly P. During the last years, molecular biology techniques coupled to novel physiological approaches have provided fascinating contributions to our understanding of the mechanisms of symbiotic P transport. Mycorrhiza-specific plant phosphate transporters, which are required not only for symbiotic P transfer but also for maintenance of the symbiosis, have been identified. The

present review provides an overview of the contribution of AM fungi to plant P acquisition and an update of recent findings on the physiological, molecular and regulatory mechanisms of P transport in the AM symbiosis. 45 Keywords: arbuscular mycorrhiza, arbuscular mycorrhizal fungi, phosphate transporter, phosphorus nutrition, phosphorus signalling 48 Abbreviations: arbuscular mycorrhizal (AM), inorganic phosphorus (Pi), phosphorus 49 (P) 50 51

Key concepts

#claim/arbuscular_mycorrhiza; #finding/symbiosis; #claim/arbuscular_mycorrhizal; #claim/phosphate_transporter; #mycelium; #glomus; #claim/arbuscular_mycorrhizal_fungi; #symbioses; #depletion_zone; #plant_growth; #plant_root; #astragalus_sinicus; #rhizophagus_irregularis; #hyphal_network

Quote

> These mutants displayed the same mycorrhizal phenotype than the M. truncatula PT4 mutants, that is, a reduced colonization level and stunted arbuscules, which supports the idea that symbiotic Pi transfer is required for maintenance of the symbiosis

Key points

- Professor José Miguel Barea, who recently passed away
- Phosphorus (P) is one of the most important nutrients for plant growth and development, as it is a central component of nucleic acids and phospholipids
- Another widespread strategy engaged by plants to overcome P deficiency is the formation of a mutualistic symbiotic interaction, referred as arbuscular mycorrhiza, with some soil-borne fungi belonging to the subphylum Glomeromycotina within the phylum
- Afterwards, orthologous of GvPT were identified in Rhizophagus irregularis (GintPT), Glomus mosseae (GmPT) and Gigaspora margarita (GigmPT)

- Cytoplasmic streaming is likely driven by water flow mediated by a fungal plasma membrane aquaporin, as suppression of host transpiration and knockdown of the Rhizophagus clarus aquaporin RcAQP3, which is highly expressed in the intraradical mycelia and mediates water transport across the plasma membrane, decelerated polyphosphate translocation [1]
- These mutants displayed the same mycorrhizal phenotype than the M. truncatula PT4 mutants, that is, a reduced colonization level and stunted arbuscules, which supports the idea that symbiotic Pi transfer is required for maintenance of the symbiosis

Synopsis

Fungal Pi transporters

The first AM fungal Pi transporter, GvPT, was described in 1995 in Glomus versiforme [2], a homolog of the Saccharomyces cerevisiae Pho84p.
Genes encoding the H+-ATPases generating the proton-motive force driving the uptake of Pi across the membrane of the extraradical mycelia have been identified in G. mosseae and R. irregularis [3], [4].
Afterwards, orthologous of GvPT were identified in Rhizophagus irregularis (GintPT), Glomus mosseae (GmPT) and Gigaspora margarita (GigmPT).
These transporters were found to be expressed in the extraradical mycelium, and in the arbuscules where the Pi flux is expected to be directed towards the plant cell [5], [6], [7], [8], [9].
Functional characterization of the full complement of the Pi transporters is needed to understand their specific role in the different fungal structures

Fungal Pi metabolism and translocation

Pi is transformed into ATP in the mitochondria and polymerized into polyphosphate, lineal polymers of three to thousands of Pi residues connected by high-energy bonds, in the vacuoles [10].
Polyphosphate is translocated from the extraradical to the intraradical mycelia via cytoplasmic streaming and/or along a motile tubular vacuole system [11], [12].
Cytoplasmic streaming is likely driven by water flow mediated by a fungal

plasma membrane aquaporin, as suppression of host transpiration and knockdown of the Rhizophagus clarus aquaporin RcAQP3, which is highly expressed in the intraradical mycelia and mediates water transport across the plasma membrane, decelerated polyphosphate translocation [1-1].
The intraradical mycelium-expressed vacuolar Pi transporter PHO91 might mediate Pi export to the cytosol [13].
It has been proposed that a plasma membrane VTC complex polymerizes cytosolic Pi into polyphosphate and exports it to the periarbuscular interface, which will be hydrolysed by a plant acid phosphatase [14].
Further studies are required to uncover the mechanisms of polyphosphate breakdown and Pi efflux from the arbuscules

The periarbuscular membrane

Symbiotic P uptake by a mycorrhizal plant occurs at a specialized interface formed in arbuscule-colonized cortical cells.
Pumplin and coworkers (2012), by expressing MtPT4 and other plasma membrane proteins from promoters active at different phases of the symbiosis, demonstrated that trafficking of these transporters occurs by default.
It was shown that proper targeting into the periarbuscular membrane is achieved by precise temporal regulation of gene expression, coincident with arbuscule formation.
This is coupled with a transient reorientation of the secretory pathway, favouring fusion with developing periarbuscular membrane rather than with the plasma membrane, and with changes in the protein cargo entering the secretory system of the arbuscule-colonized cortical cell [15]

Mycorrhiza-induced transporters

Putative Pi transporters mediating the acquisition of the Pi delivered by the fungus to the periarbuscular space were initially identified by their specific- or increased-expression in mycorrhizal roots relative to non-mycorrhizal plants.
HA1 isoforms of M. truncatula and rice have been shown to be essential to generate the proton gradient required for Pi uptake by the Pi transporters localized in the periarbuscular membrane, as disruption of the genes in Mtha

and Osha mutants leads to impaired Pi transport via the mycorrhizal pathway [16]

These mutants displayed the same mycorrhizal phenotype than the M. truncatula PT4 mutants, that is, a reduced colonization level and stunted arbuscules, which supports the idea that symbiotic Pi transfer is required for maintenance of the symbiosis.
The G. margarita Pi transporter GigPT1, that is expressed both in the extraradical and intraradical mycelium, has been shown to be a transceptor, indicating that Pi sensing is important for the fungus [8-1]
These findings indicate that a flow of nutrients across the symbiotic interface is required to sustain arbuscule within the cortical cell.
Given that Pi fertilization increases plant stress tolerance and productivity, and that AM fungi increase plant nutrition and plant tolerance to multiple stresses, the optimized application of AM fungi in sustainable agriculture will be crucial for developing more P-efficient farming systems and to counteract the negative impacts of climate change

Findings

- That is why AM fungi were suggested to play a key role in land colonization by plants. This plant-fungus association has proven to be an evolutionary successful strategy, since more than 80% of all terrestrial plant species live in symbiosis with AM fungi [17]

Builds on previous research

- Although both paralogs are expressed in arbuscule-containing cells, the PT5 ones are also expressed in noncolonized cortical cells [6-1]. The findings that the tomato LePT3, LePT4 and LePT5 transporters are simultaneously expressed in arbuscule-containing cells [6-2], [18], that symbiotic Pi transport was not affected in a null allele of the tomato LePT4 and that the expression of the other mycorrhiza-inducible transporters of tomato LePT3 and LePT5 remained unchanged in the mutant line suggest

that there might exist functional redundancy between the three mycorrhiza-associated Pi transporters [19]

Future work

- Further studies are required to uncover the mechanisms of polyphosphate breakdown and Pi efflux from the arbuscules.
- On the plant side, the Pi transporters mediating Pi flow through the mycorrhizal pathway have been identified and they are useful markers for a functional mycorrhiza. On the fungal side, the Pi transporters involved in acquisition have been characterized, but further studies are required to understand the specific roles of the full complement of the fungal Pi transporters. A new function, as Pi sensors, has emerged for the fungal and AM-inducible plant Pi transporters. Despite these advances, a full understanding of the regulatory mechanisms of symbiotic Pi flow remains to be achieved. In the future work, it would be of interest to identify the fungal players mediating Pi release from the arbuscules and to go further on the understanding of the mechanisms controlling the amount of Pi transferred to the plant, the interplay between direct and mycorrhizal pathways and the role of Pi and other nutrients in regulating the maintenance of the symbiosis. On the fungal side, despite the difficulties for the genetic manipulation of AM fungi, recent genome sequencing and the development of host-induced and virus-induced gene silencing techniques of AM fungal genes will accelerate our knowledge of Pi metabolism and transport in the arbuscule.

References

Paszkowski_MechanismsImpactSymbioticPhosphateAcquisition_2019

Mechanisms and Impact of Symbiotic Phosphate Acquisition

Chai Hao Chiu; Uta Paszkowski

2019

Abstract

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.

Key concepts

#arbuscular_mycorrhizal; #claim/symbiosis; #arbuscular_mycorrhizal_fungi; #fatty_acids; #GRAS; #metabolism; #claim/symbioses; #transcription_factor; #extracellular_vesicles; #rhizophagus_irregularis; #glomus; #lotus_japonicus; #depletion_zone; #reactive_oxygen_species; #petunia_hybrida; #arabidopsis_thaliana; #saccharomyces_cerevisiae; #solanum_tuberosum

Quote

> This suggests that the Ca2+-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 arbuscular mycorrhizal fungi downstream of Ca2+ oscillations

Key points

- Phosphorous is crucial for life by virtue of its unique chemistry
- This suggests that the Ca2+-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 arbuscular mycorrhizal fungi (AMF) downstream of Ca2+ oscillations
- 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
- 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
- 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

Synopsis

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 ([20]).
It was recently demonstrated that C delivered from the plant to fungus is 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). Ospt13 mutants, despite having reduced colonization and stunted arbuscule development, have wild-type levels of OsPT11 transcripts and symbiotic Pi uptake ([21]).

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.
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 ([22]).
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 ([23]; [21-1]; [24]; [25]; [26]; [27], [28]; [29]; [30]).
Experiments such as those in [31]), [32]), and [33]) 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.
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 ([34]; [35]; [36]; [37]; [38]), as well as transkingdom gene transfer for putative effector-like proteins with an extended phenotype on the plant ([39]).
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.
AMF colonization steadily increases in wildtype plants, suggesting that symbiosis signaling down-regulates certain aspects of the PSR to favor fungal accommodation over exclusionary defense.
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

Study subjects

8 genes

- Reproductive stage; Fe/ROS imbalance. Strains containing an increased copy number of eight genes (Octomom) drastically reduced host life span. Amplified Octomom genes on Palaeozoic palaeosols alongside with AMF profoundly shaped terrestrial landscapes and, today, AM symbiosis remain an important aspect of global biogeochemical cycles ([40]; [41]; [42]; [43]; [44])

150000 genes

- 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 ([45]). In addition, singlenucleus sequencing of AMF revealed that genetic diversity can be generated via internuclear recombination in a dikaryotic stage (two distinct mating loci) ([46])

Data analysis

- #method/pearson

Findings

- Up to 22% of the photosynthetically fixed carbon is traded for symbiotic Pi, which could supply all (100%) of plant phosphate uptake ([47]; Smith et al 2003, 2011; [21-2]; [28-1]; [48]; [29-1]; [49]; [50])
- In rice, AMF contributes up to 70% of the P acquired by the plant ([21-3])

Counterpoint to earlier claims

- 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 ([51]; [52]). Although the role of SPX-MFS3 in mediating vacuolar Pi efflux in rice is contested ([53]; [52-1]), 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 ([52-2])

Contributions

- 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 ([54]; [55]; [56], [57]; [58]) and infection attempts in maize roots were found to be inversely proportional to shoot Pi status ([59]). This regulation is systemic, as split-root experiments demonstrated that high Pi on one side suppressed AM symbiosis globally ([55-1]; [60]; [56-1]). 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 ([55-2]). 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 ([60-1]; [56-2]), indicating that reduced SLs in the rhizosphere is insufficient to explain the suppressive effect. However, perinuclear Ca2+-oscillations were still generated in response to AMF hyphopodia under high Pi levels ([57-1]). This suggests that the Ca2+-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 Ca2+ 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 ([61]; [62]; [63]). It is, however, a challenge to uncouple intrinsic AMF responses from plant/exudatemediated responses in a plant-AMF coculture system.

Future work

- Following arbuscule senescence, vesicles often emerge as lipid storage bodies and could be crucial for subsequent rounds of infection affected in ark1 mutants ([22-1]). 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.

References

Bonfante_FutureRootsPastIdeasScientists_2018

The future has roots in the past: the ideas and scientists that shaped mycorrhizal research

Paola Bonfante

2018

Abstract

Review 983 most plant species. According to [64]), 72% of vascular plants are arbuscular mycorrhizal (where Glomeromycotina fungi form inter-/intracellular hyphal networks within the roots), 2.0% are ectomycorrhizal (where fungi of the Ascomycota or Basidiomycota produce a mantle surrounding the root tip as well as an intercellular hyphal network between the root epidermal and cortical cells), 1.5% are ericoid mycorrhizal (where mostly Ascomycota form coils inside the epidermal cells of the thin roots of Ericales) and 10% are orchid mycorrhizal (where mostly Basidiomycota colonize the cortical cells of orchid protocorms and roots). Just 8% of plants are completely nonmycorrhizal, and 7% have inconsistent nonmycorrhizal–arbuscular mycorrhizal associations. The State of the World's Plants report ([65]) lists about 391 000 species of vascular plants currently known to science; therefore, we can conclude that the number of mycorrhizal plant species ranges from 320 000 to 340 000, also taking into account that many nonvascular plants, like liverworts, interact with mycorrhizal fungi. All these plants associate with more than 50 000 fungal species ([66]) and appear equally successful in colonizing different environments, from alpine and boreal zones to tropical forests and grasslands.

Key concepts

#finding/arbuscular_mycorrhizal; #claim/mycorrhizal_fungi; #phytologist; #new_phytologist; #symbiosis; #chitin; #biology; #cell_wall; #symbioses; #glomus; #plant_root; #vascular_plant; #plant_species; #lotus_japonicus; #cenococcum_geophilum; #rhizophagus_irregularis; #allium_porrum; #monotropa_hypopitys; #ornithogalum_umbellatum; #pisum_sativum; #hyphal_network

Quote

> Irrespective of the huge number of descriptions, many years were required before researchers produced an experimental demonstration of the role played by these endophytic fungi we identify as arbuscular mycorrhizal fungi

Key points

- The aim of this review is to draw up a map of the ideas that changed mycorrhizal research, searching for topics that were central in the 19th century, became seminal in revealing the biological meaning of mycorrhizal associations along the decades, and are still crucial today in the 'omics' era
- Ó 2018 The Author New Phytologist Ó 2018 New Phytologist Trust other scientific fields, the most recent molecular studies of mycorrhizal biology were developed on the shoulders of work by researchers in the past
- Thanks to a protocol that allowed him to produce ectomycorrhizal symbioses under sterile conditions, he examined the competition for available nitrogen between soil microorganisms and plant roots and suggested that ectomycorrhizal fungi primarily facilitate nitrogen uptake
- The discovery that GR24 treatment led to an increase in the release of chitin oligomers ([67]) by arbuscular mycorrhizal fungi and, subsequently, to amplification of the calcium spiking response, offered the first experimental evidence of the interaction between the signalling molecules released by the fungal and plant partners ([68])
- In the absence of molecular data, ultrastructural observations have allowed researchers to look beyond the hedge: the deep reorganization of the cortical cells following the fungal colonization suggested a reprogramming of the molecular plant machinery that has been largely confirmed by RNA-sequencing studies in all the mycorrhizal symbioses ([69]; [70]; [71]; [72]; [63-1]; [73])

Synopsis

Signalling: a central question of our time?

One of the major questions of the community studying plant– microbe interactions is the nature of the signals exchanged between the partners and how they are perceived. [74]) compiled an exhaustive list of the molecules so far identified as involved in plant–microbe interactions.
The pregerminated spores were stimulated by exudates diffusing from the growing roots in the absence of any physical contact (Fig. 4) The stimulation of hyphal branching was impressive
These observations were nicely confirmed by the group of Manuela Giovannetti in Pisa ([75]), only many years later did other studies identify the plant bioactive molecules that stimulate the branching and metabolism of presymbiotic hyphae in arbuscular mycorrhizal fungi as strigolactones ([76]; [77]).
The discovery that GR24 treatment led to an increase in the release of chitin oligomers ([67-1]) by arbuscular mycorrhizal fungi and, subsequently, to amplification of the calcium spiking response, offered the first experimental evidence of the interaction between the signalling molecules released by the fungal and plant partners ([68-1]).
Looking at the fungal factors, chitin-related molecules seem to be shared by pathogenic and arbuscular mycorrhizal fungi, opening the question of whether they could function in signalling in ectomycorrhizal symbioses

The colonization process: how cellular studies predicted future 'omics' data

If the authors stop to look at the old drawings by G.
At the 1974 Leeds meeting, the different types of interfaces originating during the interaction between Ornithogalum umbellatum and its endogenous arbuscular mycorrhizal fungi were carefully described and listed
They were assigned different numbers: the plant cell wall–fungal wall contact was named IT8, and at the moment of fungal penetration and plant membrane invagination the interface was named IT24.
In the absence of molecular data, ultrastructural observations have allowed researchers to look beyond the hedge: the deep reorganization of the cortical cells following the fungal colonization suggested a reprogramming of the molecular plant machinery that has been largely confirmed by RNA-sequencing

studies in all the mycorrhizal symbioses ([69-1]; [70-1]; [71-1]; [72-1]; [63-2]; [73-1]). Dictyosome Microtubules molecules from minerals to organic compounds), as well as the events that allow new membrane biogenesis, and the regulatory machinery, already belong to the molecular era of mycorrhizal research, as summarized in many recent reviews ([78]; [79]; [80])

The genetics underlying colonization events

At the end of the 1980s the authors already had a good deal of knowledge of mycorrhizal morphology, but a crucial bit was missing: the genetic control that plants exert on entry by the fungus
This important discovery was made in Dijon, when the plant geneticist Gerard Duc, collaborating with two 'mycorrhizal' colleagues, Vivienne Gianinazzi-Pearson and Silvio Gianinazzi, discovered that mutant plants that were not successful in producing active nodules were resistant to mycorrhiza formation.
The authors have learned that many genes control the signalling/early phase, whereas others are directly related to mycorrhizal functioning
Most of these mutants share a similar phenotype: the arbuscules are stunted and not fully developed, suggesting that plant genetic determinants control arbuscule morphology ([81]).
Tailoring the interactions of crop plants and their associated microbiota may provide a crucial advance for sustainable agriculture

Concluding thoughts: chance and needs in mycorrhizal symbioses

A walk through mycorrhizal research from the middle of the 1800s to today reveals that many of the crucial questions the authors are facing were first asked many years ago.
[82]) described the presence of bacteria-like organisms inside the spores of F. mosseae; some years later the author observed similar organisms the first time that the author looked at a mycorrhizal section under the electron microscope ([83]), but the invention of PCR was needed for successful naming of these organisms ([84]; [85])

This is a great time for the mycorrhizal scientific community, because of the powerful tools that are available, and because of a crucial change in the perception of mycorrhizal symbiosis.
In looking to the future of mycorrhizal studies, the authors can learn much by examining their roots in the past – and the author looks forward to future developments in the understanding of these remarkable biological systems

Study subjects

983 most plant species

- . Review 983 most plant species. According to [64-1]), 72% of vascular plants are arbuscular mycorrhizal (where Glomeromycotina fungi form inter-/intracellular hyphal networks within the roots), 2.0% are ectomycorrhizal (where fungi of the Ascomycota or Basidiomycota produce a mantle surrounding the root tip as well as an intercellular hyphal network between the root epidermal and cortical cells), 1.5% are ericoid mycorrhizal (where mostly Ascomycota form coils inside the epidermal cells of the thin roots of Ericales) and 10% are orchid mycorrhizal (where mostly Basidiomycota colonize the cortical cells of orchid protocorms and roots)

391000 species

- Just 8% of plants are completely nonmycorrhizal, and 7% have inconsistent nonmycorrhizal–arbuscular mycorrhizal associations. The State of the World's Plants report ([65-1]) lists about 391 000 species of vascular plants currently known to science; therefore, we can conclude that the number of mycorrhizal plant species ranges from 320 000 to 340 000, also taking into account that many nonvascular plants, like liverworts, interact with mycorrhizal fungi. All these plants associate with more than 50 000 fungal species ([66-1]) and appear equally successful in colonizing different environments, from alpine and boreal zones to tropical forests and grasslands

50000 fungal species

- The State of the World's Plants report ([65-2]) lists about 391 000 species of vascular plants currently known to science; therefore, we can conclude that the number of mycorrhizal plant species ranges from 320 000 to 340 000, also taking into account that many nonvascular plants, like liverworts, interact with mycorrhizal fungi. All these plants associate with more than 50 000 fungal species ([66-2]) and appear equally successful in colonizing different environments, from alpine and boreal zones to tropical forests and grasslands.

Data analysis

- #method/pearson

Findings

- Just 8% of plants are completely nonmycorrhizal, and 7% have inconsistent nonmycorrhizal–arbuscular mycorrhizal associations

Confirmation of earlier findings

- Thanks to the sequencing of new genomes, their study clearly indicated that Mucoromycota constitutes a phylum with three subphyla: Mucoromycotina, Mortierellomycotina, and Glomeromycotina; at least until today, this study unambiguously defines the phylogenetic position of arbuscular mycorrhizal fungi. It is true that our arbuscular mycorrhizal fungi are now relegated from phylum status to a lower subphylum level, but many shared phenotypic features among the three subphyla (e.g. the presence of endobacteria; [85-1]) have provided a good rationale for explaining similarities (hyphal morphology) and dissimilarities (nutritional styles) among these enigmatic fungi
- Despite the emerging understanding of the role of strigolactones, the molecular mechanisms underlying the hyphal branching of arbuscular mycorrhizal fungi, first observed by [86]), remain poorly known ([87]). Data from RNA sequencing of germinated spores of Gigaspora margarita after a treatment with the synthetic strigolactone analogue GR24 confirmed the

findings of [77-1], [88]), revealing the upregulated expression of mitochondrial genes ([35-1]) as well as of some genes related to cell wall components (encoding chitin deacetylase, chitin synthase)

- Gallaud or B. Peyronel and compare them with the beautiful schemes of ectomycorrhizas in the publications by [89]), or with the iconic arbuscules shown by [90]) or by Maria Harrison's group ([28-2]), we will have no doubt of the beauty and richness of the details in the recent publications
- However, many basic points of information (i.e. fungal structure, host anatomy and plant cell specificity) were already correctly identified at the dawn of research on mycorrhizas. The finding that fossils of the Rhynie Chert host fungal structures similar to modern arbuscular mycorrhizal fungi reflects the excellent knowledge of our colleagues of the past ([91])

Contributions

- We can conclude this endless tale by claiming that almost 100 years ago (1923) Beniamino Peyronel, who looked at the coenocytic hyphae running between mycorrhizal roots and the spores of Endogone-like fungi, was not so far from our current views.

References

Bellincampi_et+al_PlantCellWallDynamicsWallrelated_2014

Plant cell wall dynamics and wall-related susceptibility in plantâ€“pathogen interactions

Daniela Bellincampi; Felice Cervone; Vincenzo Lionetti

2014

Abstract

The cell wall is a dynamic structure that often determines the outcome of the interactions between plants and pathogens. It is a barrier that pathogens need to breach to colonize the plant tissue. While fungal necrotrophs extensively destroy the integrity of the cell wall through the combined action of degrading enzymes, biotrophic fungi require a more localized and controlled degradation of the cell wall in order to keep the host cells alive and utilize their feeding structures. Also bacteria and nematodes need to degrade the plant cell wall at a certain stage of their infection process, to obtain nutrients for their growth. Plants have developed a system for sensing pathogens and monitoring the cell wall integrity, upon which they activate defense responses that lead to a dynamic cell wall remodeling required to prevent the disease. Pathogens, on the other hand, may exploit the host cell wall metabolism to support the infection. We review here the strategies utilized by both plants and pathogens to prevail in the cell wall battleground.

Key concepts

#claim/cell_wall; #arabidopsis; #pectin; #movement_proteins; #callose; #plant_cell_wall; #CWDE; #metabolism; #reactive_oxygen_species; #ferulic_acid; #transgenic; #plant_defense; #PGIP; #fusarium; #bacteria; #pathogenic; #pattern_recognition_receptors; #arabidopsis_thaliana; #pattern_recognition; #fusarium_graminearum; #pseudomonas_syringae; #plant_tissue; #DAMP; #sclerotinia_sclerotiorum; #blumeria_graminis; #verticillium_dahliae

Quote

> Pathogens try to escape the plant defenses and sometimes take advantage of the host cell wall metabolism to facilitate their entry into the tissue

Key points

- Phytopathogenic fungi, bacteria, and nematodes infect, grow and reproduce themselves on the plant tissues and, at least at the early stages of infection, require breaking the integrity of the host cell wall
- The cell wall is the battleground where plants and pathogens attempt to prevail by implementing contrasting wall-reinforcing and wall-weakening strategies
- When pathogens start degrading the plant cell wall components, plants are capable of perceiving the loss of wall integrity and subsequently activate the defense signaling pathways
- Pathogens try to escape the plant defenses and sometimes take advantage of the host cell wall metabolism to facilitate their entry into the tissue
- These dynamic processes vary according to the lifestyle of the pathogen and the type of plant pathogen interaction
- While necrotrophy involves a strong and diffused molecular warfare that may provoke extended lesions of the tissue, during biotrophy the battle involves a weaker cell wall degradation mainly localized at the point of penetration and at the level of the feeding apparatus

Synopsis

Phytopathogenic fungi, bacteria, and nematodes infect, grow and reproduce themselves on the plant tissues and, at least at the early stages of infection, require breaking the integrity of the host cell wall.
The loss of CWI induced by pathogens activates a variety of defense responses including a cell wall remodeling required to prevent the disease.
Pathogens produce effector proteins that counteract the plant defenses ([92]) and, sometimes, exploit the host cell wall metabolism to favor the infection process ([93]).
Necrotrophs have a spatial and temporal strategy of attacking the plant cell wall by producing several cell wall degrading enzymes (CWDEs) belonging to multiple families (Figure 1A).
One of the strategies used by plants to limit the degradation of the cell wall

polysaccharides by microbial CWDEs is the production of proteinaceous inhibitors (Figures 1A,B).
Alteration of pectin integrity caused by the expression of PGII from Aspergillus niger in tobacco and Arabidopsis causes a constitutive activation of defense genes and resistance against Botrytis cinerea ([94]).
The transcription factor MYB46 which affect the secondary cell wall biosynthesis ([95]), regulates the expression of genes encoding several cell wall proteins including PMEI and mediates disease susceptibility of Arabidopsis to B. cinerea ([96]).
Arabidopsis and Brachypodium distachyon plants expressing xylan or pectin acetylesterases from A. nidulans activate specific defense responses and are more resistant to B. cinerea and B. sorokiniana ([97]).
The Arabidopsis AtPME3 is induced upon infection with B. cinerea and P. carotovorum and functions as susceptibility factor required for the initial colonization of the host tissue (Raiola et al, 2011).
A PG (LePG) and expansin (LeExp1) cooperatively contribute to cell wall loosening during tomato ripening; their expression is induced by necrotrophic pathogens to successfully infect fruits ([98]).
Biotrophs need to avoid the host defense responses and carefully regulate the cell-wall degradation at the border of their feeding structures to allow fungal accommodation and haustorium function (Figure 2C).
Callose deposition may work in favor of the pathogen by contributing to the stability and function of the haustoria and acting as a barrier that renders haustoria less susceptible to toxic metabolites that are produced by the host and accumulate in the site of infection ([99]).
The expression of endogenous and microbial CWDEs and their inhibitors is a valuable approach for studying the dynamics of the cell wall during plant–pathogen interactions as well as a strategy to improve plant protection.

Contributions

- The cell wall is the battleground where plants and pathogens attempt to prevail by implementing contrasting wall-reinforcing and wall-weakening strategies. When pathogens start degrading the plant cell wall components,

plants are capable of perceiving the loss of wall integrity and subsequently activate the defense signaling pathways. Pathogens try to escape the plant defenses and sometimes take advantage of the host cell wall metabolism to facilitate their entry into the tissue. These dynamic processes vary according to the lifestyle of the pathogen and the type of plant pathogen interaction. While necrotrophy involves a strong and diffused molecular warfare that may provoke extended lesions of the tissue, during biotrophy the battle involves a weaker cell wall degradation mainly localized at the point of penetration and at the level of the feeding apparatus. Perception of cell wall damage as well as the pathogen- and host-induced cell wall remodeling occurs in both cases. The damage of specific cell wall polysaccharides during infection may be perceived by receptors as THE1, ER and WAK1. Plants may also rely on the recognition of CWDEs by LRR-RLPs receptors, as RBPG1 and LeEIX1-2. Cell wall fragments may be released during infection and sensed as damage signals. Analysis of cell wall mutants has shed light on the relationship between cell wall remodeling and plant response to pathogens. The expression of endogenous and microbial CWDEs and their inhibitors is also a valuable approach for studying the dynamics of the cell wall during plant– pathogen interactions as well as a strategy to improve plant protection.

References

Zeng_et+al_HostStagedependentSecretomeArbuscularMycorrhizal_2018

Host- and stage-dependent secretome of the arbuscular mycorrhizal fungus Rhizophagus irregularis

Tian Zeng; Rens Holmer; Jan Hontelez et al.

2018

Abstract

Arbuscular mycorrhizal fungi form the most wide-spread endosymbiosis with plants. There is very little host specificity in this interaction, however host preferences as well as varying symbiotic efficiencies have been observed. We hypothesize that secreted proteins (SPs) may act as fungal effectors to control symbiotic efficiency in a host-dependent manner. Therefore, we studied whether arbuscular mycorrhizal (AM) fungi adjust their secretome in a host- and stage-dependent manner to contribute to their extremely wide host range. We investigated the expression of SP-encoding genes of Rhizophagus irregularis in three evolutionary distantly related plant species, Medicago truncatula, Nicotiana benthamiana and Allium schoenoprasum. In addition we used laser microdissection in combination with RNA-seq to study SP expression at different stages of the interaction in Medicago. Our data indicate that most expressed SPs show roughly equal expression levels in the interaction with all three host plants. In addition, a subset shows significant differential expression depending on the host plant. Furthermore, SP expression is controlled locally in the hyphal network in response to hostdependent cues. Overall, this study presents a comprehensive analysis of the R. irregularis secretome, which now offers a solid basis to direct functional studies on the role of fungal SPs in AM symbiosis.

Key concepts

#claim/allium_schoenoprasum; #claim/arbuscular_mycorrhiza; #claim/effector; #claim/medicago_truncatula; #claim/arbuscular_mycorrhizal; #claim/RNA_seq; #claim/secretome; #claim/host_plant; #claim/symbiosis; #chitin; #result/laser_microdissection; #claim/rhizophagus_irregularis; #claim/nicotiana_benthamiana; #mycorrhizal_fungi; #result/hyphal_network; #pathogenic; #claim/host_range; #biology; #virus_induced_gene_silencing; #endosymbiosis; #next_generation_sequencing; #histoplasma_capsulatum

Quote

> To study whether arbuscular mycorrhizal fungi adjust their secretome depending on the plant host species that they colonize, we analyzed the fungal transcriptome in mycorrhizal roots of three evolutionary distantly related plant species

Key points

- The vast majority of all land plants establish endosymbiosis with arbuscular mycorrhizal (AM) fungi belonging to the fungal subphylum Glomeromycotina ([100])
- Our results reveal that distinct sets of putative effector genes are expressed in extraradical mycelium, intraradical hyphae and in arbuscules
- To study whether AM fungi adjust their secretome depending on the plant host species that they colonize, we analyzed the fungal transcriptome in mycorrhizal roots of three evolutionary distantly related plant species
- The three plant species were inoculated with R. irregularis DAOM197198 and grown under standardized low phosphate conditions (20 IM Pi)
- This host-dependent expression is controlled locally in the hyphal network in response to host-dependent cues. Such host-dependent cues may be specific signals or metabolites of the plant, constitute physical properties of the root system or reflect differences in nutrient conditions that affect fungal development. These results supported our hypothesis that AM secreted proteins (SPs) may act as effectors to control symbiotic efficiency in a host-dependent manner and contribute to the host preferences observed in nature
- host-induced gene silencing (HIGS) has for example been used to silence the putative effector RirG110290, called SIS1, which we show to be most strongly expressed in the intraradical mycelium (IRM) in line with its predicted role in efficient intraradical colonization ([62-1])

Synopsis

Introduction

The vast majority of all land plants establish endosymbiosis with arbuscular mycorrhizal (AM) fungi belonging to the fungal subphylum Glomeromycotina ([100-1]).
Individual AM fungi can colonize a large number of host plants, which indicates that there is a lack of Continuous signal exchange between both partners is needed to establish a functional AM symbiosis.
This dialog starts when fungal spores/hypha perceive plant signals such as flavonoids, hydroxy fatty acids and strigolactones which stimulate germination, hyphal growth and branching or hyphopodium formation ([101]).
These essential signals are perceived by LysM-domain receptor kinase complexes, which activate a highly conserved signaling cascade, called the common symbiotic signaling pathway ([81-1]; [102]; [103])

Results

To study whether AM fungi adjust their secretome depending on the plant host species that they colonize, the authors analyzed the fungal transcriptome in mycorrhizal roots of three evolutionary distantly related plant species.
The authors chose the model legume Medicago truncatula (Medicago), Nicotiana benthamiana (Nicotiana) and the monocot crop Allium schoenoprasum.
The three plant species were inoculated with R. irregularis DAOM197198 and grown under standardized low phosphate conditions (20 lM Pi).
At 7 weeks after inoculation plants were harvested and the mycorrhizal colonization level was determined.
All three plants species were well mycorrhized and showed improved growth when compared to the non-mycorrhized control (Figure 1a–c).
Highest mycorrhizal growth stimulation was observed for Nicotiana.
No differences in colonization strategy were observed, with all three plant species showing an Arum-type infection, forming arbuscules in the cortical cells

Discussion

The authors report a comprehensive and detailed analysis of the expressed SP repertoire of R. irregularis during the interaction with three distantly related host species and during different stages of the interaction.
A subset (~14%) of the SPs show differential expression depending on the host plant
This host-dependent expression is controlled locally in the hyphal network in response to host-dependent cues.
Such host-dependent cues may be specific signals or metabolites of the plant, constitute physical properties of the root system or reflect differences in nutrient conditions that affect fungal development.
These results supported the hypothesis that AM SPs may act as effectors to control symbiotic efficiency in a host-dependent manner and contribute to the host preferences observed in nature

Conclusion

Arbuscular mycorrhizal fungi form the most wide-spread endosymbiosis with plants.
There is very little host specificity in this interaction, host preferences as well as varying symbiotic efficiencies have been observed.
The authors hypothesize that secreted proteins (SPs) may act as fungal effectors to control symbiotic efficiency in a host-dependent manner.
The authors studied whether arbuscular mycorrhizal (AM) fungi adjust their secretome in a host- and stage-dependent manner to contribute to their extremely wide host range.
In addition the authors used laser microdissection in combination with RNA-seq to study SP expression at different stages of the interaction in Medicago.
The authors' data indicate that most expressed SPs show roughly equal expression levels in the interaction with all three host plants.
A subset shows significant differential expression depending on the host plant.
This study presents a comprehensive analysis of the R. irregularis secretome, which offers a solid basis to direct functional studies on the role of fungal SPs in AM symbiosis

Study subjects

3 plant species

- Our results reveal that distinct sets of putative effector genes are expressed in extraradical mycelium, intraradical hyphae and in arbuscules. The vast majority of the expressed effector genes are expressed equally in all three plant species, but in addition a set of host-dependent effector candidates were identified. These putative effector genes are induced in response to local cues determined by the plant

3 host plant species

- These results support the hypothesis that AM effectors may control symbiotic efficiency in a hostdependent manner and offers a comprehensive set of candidate AM effectors for future functional studies. Mycorrhization of three host plant species. To study whether AM fungi adjust their secretome depending on the plant host species that they colonize, we analyzed the fungal transcriptome in mycorrhizal roots of three evolutionary distantly related plant species

3 plant species

- Therefore, we chose the model legume Medicago truncatula (Medicago), Nicotiana benthamiana (Nicotiana) and the monocot crop Allium schoenoprasum (chives, which is closely related to important crops in the Alliaceae family). The three plant species were inoculated with R. irregularis DAOM197198 and grown under standardized low phosphate conditions (20 lM Pi). At 7 weeks after inoculation plants were harvested and the mycorrhizal colonization level was determined

Data analysis

- #method/pca

Findings

- In line with [104]), we found two SPs encoding for acid phosphatases (RirG239030 and RirG190440) that were expressed especially in the ERM. These SPs might be of key importance for phosphate utilization in natural soils, which can consist for up to 80% of organic phosphate ([105])

Confirmation of earlier findings

- Similarly, from the 220 putative effectors predicted by Sezdzielewska Toro and Brachmann (2016), we could only confirm 43 SPs supported by our RNA-seq analyses. For the 78 host-induced SPs identified by [106]) we could confirm most (62) in our RNA-seq analysis
- One important mechanism contributing to this ability is the secretion of acid phosphatases by ERM which can free phosphoryl group from organic phosphate that is otherwise not readily available to most plants ([104-1]). In line with [104-2]), we found two SPs encoding for acid phosphatases (RirG239030 and RirG190440) that were expressed especially in the ERM

Counterpoint to earlier claims

- However, different genome as well as de novo transcriptome assemblies have led to different gene models and predictions ([106-1]; [107]). We identified a set of 338 expressed SPs that were well supported by the available RNA-seq data
- Furthermore, 354 predicted SPs were not found in the DAOM197198w assembly, the majority of which were not classified as expressed SPs based on our criteria. Conversely, we predicted 370 SPs that were not considered by [108])

Data and code

- Additional Supporting Information may be found in the online version of this article
- Additional Supporting Information may be found in the online version

References

Wipf_et+al_TradingArbuscularMycorrhizaMarketFrom_2019

Trading on the arbuscular mycorrhiza market: from arbuscules to common mycorrhizal networks

Daniel Wipf; Franziska Krajinski; Diederik Tuinen et al.

2019

Key concepts

#arbuscular_mycorrhiza; #arbuscular_mycorrhizal; #symbiosis; #phosphate_transporter; #glomus; #fatty_acids; #host_plant; #ammonium; #rhizophagus_irregularis; #ecosystem_service; #pattern_recognition_receptors; #transient_receptor_potential; #pseudomonas_putida; #X_100; #solanum_tuberosum; #petunia_hybrida; #mitogen_activated_protein; #EAAT2; #astragalus_sinicus; #lotus_japonicus; #alzheimer_disease

Quote

> Arbuscular mycorrhizal symbiosis is the fruit of a long coevolution of AMF with their plant partners, in constant interaction with many other components of their environment; as such, it constitutes a major element of plant life, and of agroecological production

Key points

- New Phytologist pathogens – mycorrhiza-induced resistance – which occurs in a wide variety of plant species including important crop species ([109]; [110])
- AMF and plant-growth-promoting rhizobacteria (PGPR) are currently considered as essential actors in agronomic practices because they could help cut down chemical fertilizer and pesticide inputs, and promote the agriculture of the future, based on the implementation of practices that favour the ecosystem services rendered by beneficial microorganisms ([111])
- Arbuscular mycorrhizal symbiosis is the fruit of a long coevolution of AMF with their plant partners, in constant interaction with many other components of their environment; as such, it constitutes a major element of plant life, and of agroecological production
- The growing understanding of the mechanisms underlying AM symbiosis should not overshadow the fact that so far most results have been obtained on a small number of AM fungal species interacting with a small number of plant species
- Future progress will depend on the generalization of current knowledge to different Glomeromycota genera and species, through: (1) a deeper understanding of AM functioning; (2) the selection of AMF strains differing in their ability to provide ecosystem services; (3) the development of new AMF cocktails of synthetic communities covering the broadest possible range of ecosystem services; and (4) the development of technologies allowing AMF cultivation under controlled conditions
- This progress will be a prelude to the development of a future 'ecological engineering of AMF and their associated microorganisms' and its integration into modern plant breeding while taking care of the ecosystem services rendered by these valuable fungi

Synopsis

Nutrient transfer mechanisms between AMF and host plants in AM symbiosis

Improved mineral nutrition is considered as the main benefit of AM symbiosis, especially as regards phosphorus (P) and nitrogen (N) nutrition of mycorrhizal plants: these two essential macroelements are needed in large amounts by plants, and most plants constantly cope with low N and P concentrations in natural environments ([112]).

One-third of the root protein N could be provided by symbiotic AMF ([113])

This N uptake is mediated by various transport systems including transport of inorganic N in the forms of ammonium (NH4+) and nitrate (NO3À), and of organic N in the forms of amino acids and peptides (Figs 1, 2).

It has been proposed that the relative availability of soil N and P determines whether or not mycorrhizal benefits outweigh their costs ([114])

This trade-off model of compromise balance predicts that N fertilization only is of benefit when the plant is limited by P and there will be positive effects from providing C to the roots and the AMF.

Using petunia plants inoculated with R. irregularis, [115]) found that only Pi and nitrate exerted a negative influence on AM root colonization, whereas other major plant nutrients such as potassium, calcium, magnesium, sulfate and iron did not influence mycorrhizal development at elevated concentrations

Symbiotic C transfer to the fungus

AMF provide their host plants greater access to soil nutrients and water that are not directly reachable by/ available to the host roots ([116]).

Experiments carried out on germinating spores of R. irregularis supplied evidence of a natural capacity to incorporate external glucose, but at very low concentrations

This transport was inhibited by high sugar concentrations, suggesting catabolic repression of the hexose transporter(s).

Spore germination and initial hyphal growth during the pre-symbiotic phase do not directly depend on the presence of host roots

These findings highlight the complexity of sugar partitioning in plant– microbe interactions (PMI) in general, especially in AM as regards the obligate biotrophy of AMF.

Investigations of the specific arbuscule-containing-cell transcriptome revealed no specific induction of potential sucrose transporter genes in this cell type, but

increased promoter activity of putative sucrose and hexose transporter genes in cells adjacent to arbuscules or intercellular fungal hyphae ([117])
This shows a role of SUTs in C partitioning rather than direct C supply to the fungus in mycorrhizal roots.
These findings suggest that depending on the Pi supply, the symbiont may be starved for plant lipid C

Mycorrhizal benefits: a mutualism-to-parasitism continuum

Not all AMF are beneficial for the host ([118]; [119]).
Plant DRMs have been characterized in several plants including tobacco, Medicago and Arabidopsis ([120]; [121]; [122]): in the main, structural phospholipids are not integrated in DRMs, except polyphosphoinositides ([123]), which were characterized as players of signal transduction or as controllers of ion transporters and channels functioning ([124]; [125])
This highlights a possible role of DRMs in signalling and/or regulation.
Concerning amino-acid transport in plants, to the knowledge only one lysine- and histidine-specific transporter (LHT) ([126]; [127]) and two oligopeptide transporters (OPTs) ([127-1]) have been reported as being present in plant DRMs

Managing common mycorrhizal networks: a tool toward a sustainable agriculture

The AMF have nearly unrestricted host ranges and can associate with most plant species ([128]) (Fig. 4).
Annual plant species harbour higher AMF diversity than perennial plant species, and half of the currently identified AMF species are specific to one plant species ([129]).
This suggests that the establishment of selected AMF communities in agricultural applications for enhanced crop productivity is no trivial issue.
The extraradical mycelium of one AMF or hyphal fusion of separate mycelia ([130]; [131]) can colonize and further connect neighbouring plants of the same or different species within a community to form common mycorrhizal networks

(CMNs) ([132]).
CMNs can induce plant defence responses and plant communication through a variety of phytohormones such as jasmonic acid, methyl jasmonate and zeatin riboside ([133]) (Fig. 4)

CMNs and plant–plant interactions

CMNs amplify intraspecific competition by altering the distribution of population size classes ([134]), a functional trait reflecting symmetrical or asymmetrical competition ([135]) between young and mature trees.
CMNs showed asymmetrical competition whereas plants with severed CMNs showed symmetrical competition ([134-1]), suggesting that intact CMNs may supply nutrients such as N to large individuals that are highly photosynthetically active and provide the most C to their associated AMF ([136]).
This reciprocal reward could depend on the rate of exchange of fungal mineral nutrients for host plant C ([137]).
CMNs may provide faster mycorrhiza formation, limit the investment of seedlings in the construction costs of hyphal networks, give access to mineral nutrients and water, and could transfer C from one plant to another depending on the plant photosynthetic rates or the intensity of sources and sinks

Plant–CMN–plant interplay and potential for crop pest control

Plant–plant signalling could be involved in food security by reducing pest-related crop losses (Fig. 4).
The CMN helps extend the bioactive zone of allelochemicals in the soil ([132-1]) or changes leaf volatile organic chemicals ([138]).
CMNs represent a considerable potential for crop pest control through this belowground plant– plant signalling mechanism ([139]).
Most cropped soils are tilled, which likely breaks up CMNs. Increasing tillage intensity decreases the mycorrhizal colonization of plants ([140]; [141]; [142]; [143]).
Tillage may change the AMF community composition by positively selecting

more tolerant AMF species and by impacting on the ability of CMNs to transfer defence signals ([144]; Brıgido et al, 2017).
All of these findings highlight the importance of CMNs and the imperative need for further research on their function and role, in the context of agroecological management

AM fungi are not alone: interactions with PGPR

Apart from AMF, plants interact with further mutualistic root microorganisms such as plant-growth-promoting rhizobacteria (PGPR), which can impact plant development and health (Fig. 1).
([145]), that can either be free or attached to the fungal mycelium ([146]; [147])
They stimulate plant development through a variety of mechanisms, namely mobilization of rhizosphere-bound nutrients, fixation of atmospheric di-nitrogen, solubilization of P and synthesis of phytohormones such as IAA (Indole-3-acetic acid) ([148]; [149]).
A few fluorescent pseudomonads act as mycorrhiza-helper bacteria ([150]) by improving mycorrhizal root colonization ([151]) and promoting the growth of extraradical hyphae, and by enhancing spore germination ([152]).
AMF and PGPR are currently considered as essential actors in agronomic practices because they could help cut down chemical fertilizer and pesticide inputs, and promote the agriculture of the future, based on the implementation of practices that favour the ecosystem services rendered by beneficial microorganisms ([111-1])

Conclusion and prospects

Arbuscular mycorrhizal symbiosis is the fruit of a long coevolution of AMF with their plant partners, in constant interaction with many other components of their environment; as such, it constitutes a major element of plant life, and of agroecological production.
Future progress will depend on the generalization of current knowledge to different Glomeromycota genera and species, through: (1) a deeper understanding of AM functioning; (2) the selection of AMF strains differing in their ability to provide ecosystem services; (3) the development of new AMF

cocktails of synthetic communities covering the broadest possible range of ecosystem services; and (4) the development of technologies allowing AMF cultivation under controlled conditions

This progress will be a prelude to the development of a future ‘ecological engineering of AMF and their associated microorganisms’ and its integration into modern plant breeding while taking care of the ecosystem services rendered by these valuable fungi

Study subjects

62 members

- Nitrate is taken up via an energy-dependent uptake process by specific, highly regulated transporters (Fig. 2) belonging to the huge nitrate and peptide transporter families – the NPF (NRT1/PTR family; [153]), NRT2 and NRT3 families ([154]; [155]). In plants, NPF is a large protein family (85, 79 and 62 members in rice, poplar and Arabidopsis, respectively) whose members transport either NO3À with low affinity or di-/tripeptides ([156]), and also nitrite, glucosinolates or phytohormones ([155-1]). In AMF, only one high-affinity transporter belonging to the NRT2 family has so far been described in R. irregularis (GiNT), and it was shown to be expressed in all AMF tissues (spores, extra and intraradical mycelium, arbuscules)

12 genes

- Hence, AMF are assumed to depend on host plants for de novo FA synthesis, another potential reason for the obligate biotrophy of these organisms. The FA auxotrophy of AMF is further supported by the fact that 12 genes related to lipid biosynthesis are exclusively present in the genomes of plants forming AM symbioses ([27-1]). Recent isotope labelling experiments clearly confirmed that R. irregularis cannot synthesize FAs de novo from carbohydrates ([48-1]), which supports the obligate FA auxotrophy of AMF

Builds on previous research

- Nevertheless, only few reports are available about the effects of PGPR on strawberry. [157]) co-inoculated strawberry plants with AMF and Pseudomonas putida, and reported a synergistic effect on plant growth ([157-1]). The same authors highlighted a positive effect of Agrobacterium radiobacter on root colonization. [158]) recently reported an impact of PGPR and AMF co-inoculation on strawberry quality as well as the importance of the strains

Differs from previous work

- Although the influence of Pi availability on the plant proteins that direct lipid fluxes in arbuscules have not been investigated yet, the mycorrhiza-specific GPAT was found to belong to the genes expressed in all mycorrhiza fertilized with low phosphate, but not to the mycorrhiza of the low- or high-P control roots ([60-2]). Moreover, the expression of STR and STR2, which mediate lipid fluxes into AMF, also was repressed by high Pi concentrations ([159],b)
- The similarity of animal proteins involved in neurotransmitter transport with plant members suggests that current knowledge concerning the lipid regulation of neurotransmitter transporters should help to decipher this topic in plants (e.g. [160]). Concerning amino-acid transport in plants, to our knowledge only one lysine- and histidine-specific transporter (LHT) ([126-1]; [127-2]) and two oligopeptide transporters (OPTs) ([127-3]) have been reported as being present in plant DRMs

Contributions

- **Conclusion and prospects**

  Arbuscular mycorrhizal symbiosis is the fruit of a long coevolution of AMF with their plant partners, in constant interaction with many other (abiotic and biotic) components of their environment; as such, it constitutes a major

element not only of plant life, but also of agroecological production. The ecological services provided by AMF are truly broad, and suitable tools and/or markers have to be defined to phylogenetically characterize the OTUs and functionally define their contribution during the interaction. Moreover, quick and reliable tests for evaluating and monitoring their diversity and functionality in agroecosystems are still lacking.

Furthermore, the growing understanding of the mechanisms underlying AM symbiosis should not overshadow the fact that so far most results have been obtained on a small number of AM fungal species interacting with a small number of plant species. In particular, the R. irregularis model strain DAOM 197198, the first AMF whose genome was fully sequenced, is probably the most studied strain in research laboratories. Thus, our understanding of mycorrhizal biology is often limited to a few special cases, and any generalization of these concepts should be based on studies involving additional AMF species. Future progress will depend on the generalization of current knowledge to different Glomeromycota genera and species, through: (1) a deeper understanding of AM functioning; (2) the selection of AMF strains differing in their ability to provide ecosystem services; (3) the development of new AMF cocktails of synthetic communities covering the broadest possible range of ecosystem services; and (4) the development of technologies allowing AMF cultivation under controlled conditions. This progress will be a prelude to the development of a future ‘ecological engineering of AMF and their associated microorganisms’ and its integration into modern plant breeding while taking care of the ecosystem services rendered by these valuable fungi.

Limitations

- Furthermore, the growing understanding of the mechanisms underlying AM symbiosis should not overshadow the fact that so far most results have been obtained on a small number of AM fungal species interacting with a small number of plant species. In particular, the R. irregularis model strain DAOM 197198, the first AMF whose genome was fully sequenced, is probably the most studied strain in research laboratories. Thus, our

understanding of mycorrhizal biology is often limited to a few special cases, and any generalization of these concepts should be based on studies involving additional AMF species. Future progress will depend on the generalization of current knowledge to different Glomeromycota genera and species, through: (1) a deeper understanding of AM functioning; (2) the selection of AMF strains differing in their ability to provide ecosystem services; (3) the development of new AMF cocktails of synthetic communities covering the broadest possible range of ecosystem services; and (4) the development of technologies allowing AMF cultivation under controlled conditions. This progress will be a prelude to the development of a future 'ecological engineering of AMF and their associated microorganisms' and its integration into modern plant breeding while taking care of the ecosystem services rendered by these valuable fungi.

Future work

- Tillage may change the AMF community composition by positively selecting more tolerant AMF species and by impacting on the ability of CMNs to transfer defence signals ([144-1]; Brigido et al, 2017). Taken together, all of these findings highlight the importance of CMNs and the imperative need for further research on their function and role, in the context of agroecological management.

References

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Plant carbon nourishment of arbuscular mycorrhizal fungi

Ronelle Roth; Uta Paszkowski

2017

Abstract

of fungal carbon nourishment during AM symbiosis. AM fungal colonization results in increased expression of source-to-sink metabolizing genes Sucrose Transporters (SUTs) and Sugars Will Eventually Be Exported Transporters (SWEETs) as well as genes encoding sucrose metabolizing enzymes Sucrose Synthase and Invertases. ==Fungal uptake of apoplastic hexoses are likely mediated by Monosaccharide Transporter2== (MST2) that is induced around intra-radical hyphae (IH) and arbuscules. Upregulation of MST5/6 in spores and extra-radical mycelia (ERM) suggest that AM fungi may also be able to take up glucose (Glc) from their surrounding. AM-conserved genes, RAM2 and FatM are induced in arbuscule-containing cells and are required for synthesis of the C16:0 fatty acid, b-monoacylglycerol (b-MAG). ABC transporters STR1/STR2 that localize to the peri-arbuscular membrane (PAM) might play a role in the transport of b-MAG into the symbiotic interface from where it is taken up by the fungus and utilized for arbuscule formation.

Key concepts

#arbuscular_mycorrhizal; #sucrose; #metabolism; #rhizophagus_irregularis; #sucrose_synthase; #cell_wall; #functional_analysis

Quote

> Sugars Will Eventually Be Exported Transporters activity may lead to the release of sugars into the interface between the plant and the fungal membrane and thereby fine-tune sugar fluxes and availability in colonized and adjacent non-colonized cortex cells

Key points

- The symbiotic success in arbuscular mycorrhizal (AM) symbioses for over 400 million years has involved host– fungal transactions, underpinned by a tightly regulated reciprocal nutrient exchange based on mutual rewards

- Functional analysis of RiMST2 by knocking down RiMST2 using hostinduced gene silencing (HIGS) led to severely compromised fungal colonisation and abnormal arbuscule morphology [161]. This confirmed the importance of plant carbohydrates for the maintenance of intra-radical hyphae (IH) and arbuscule growth and suggested cell wall monosaccharides as a source of organic C for AM fungi
- Sugars Will Eventually Be Exported Transporters (SWEETs) activity may lead to the release of sugars into the interface between the plant and the fungal membrane and thereby fine-tune sugar fluxes and availability in colonized and adjacent non-colonized cortex cells
- [2-1] Upregulated in cortex cells containing IH and arbuscules; Protein localizes to PM and peri-arbuscular membrane (PAM) [2-2] Upregulated in cortex cells containing IH and arbuscules

Synopsis

Introduction

The symbiotic success in arbuscular mycorrhizal (AM) symbioses for over 400 million years has involved host– fungal transactions, underpinned by a tightly regulated reciprocal nutrient exchange based on mutual rewards.
For AM fungi, forming a successful symbiosis with plants is an obligate requirement to complete their life-cycle, manifested by the production of daughter spores [162].
A role for carbohydrates in sustaining fungal growth during AM symbiosis AM fungi acquire sugar in the form of hexoses, predominantly glucose [163], [17-1], [164].
RiMST2 has promiscuous substrate specificity for hexoses with preference for xylose and is present in extraradical mycelium (ERM), around IH and arbuscules during the interaction with potato and M. truncatula [161-1], indicating that sugar uptake in AM fungi might involve IH in addition to arbuscules, which is supported by earlier radiotracer-based observations (Figure 1, [163-1]).
Addition of xylose induced RiMST2 expression in Current Opinion in Plant Biology 2017, 39:50–56 www.sciencedirect.com

AM fungal colonization results in increased expression of source-to-sink metabolizing genes Sucrose Transporters (SUTs) and Sugars Will Eventually Be Exported Transporters (SWEETs) as well as genes encoding sucrose metabolizing enzymes Sucrose Synthase and Invertases.
Fungal uptake of apoplastic hexoses are likely mediated by Monosaccharide Transporter (MST2) that is induced around intra-radical hyphae (IH) and arbuscules.
Functional analysis of RiMST2 by knocking down RiMST2 using hostinduced gene silencing (HIGS) led to severely compromised fungal colonisation and abnormal arbuscule morphology [161-2].
This confirmed the importance of plant carbohydrates for the maintenance of IH and arbuscule growth and suggested cell wall monosaccharides as a source of organic C for AM fungi.

Gene expression

Promoters of genes encoding distinct members of potato SWEETs were recently shown to be active within and next to arbuscule-hosting cells (Figure 1, Table 1B, [165]).
SWEET activity may lead to the release of sugars into the interface between the plant and the fungal membrane and thereby fine-tune sugar fluxes and availability in colonized and adjacent non-colonized cortex cells.
Knockdown of the tomato sucrose transporter SUT2, but not SUT1 or SUT4, led to increased mycorrhizal colonization and abolished the positive growth response to AMS in tomato, intuitively pointing towards a fungal advantage in the competition for carbohydrates in the absence of functional SUT2 (Figure 1, Table 1B, [3-1]).

Mutant description

Upregulated in vasculature, cortex cells surrounding IH and arbuscules [166]
Induced [165-1].
Upregulated in vasculature, cortex cells containing IH and arbuscules [167]

Induced [2-3] Upregulated in vasculature, cortex cells containing IH and arbuscules [2-4] Upregulated in cortex cells containing IH and arbuscules; Protein localizes to PM and PAM [2-5] Upregulated in cortex cells containing IH and arbuscules [15-1] Induced [168].
[169] Baier et al, Plant Physiology 2010, 152:1000–1014.
[15-2] Harrison Plant Journal 1996, 9:491–503
[169-1] Baier et al, Plant Physiology 2010, 152:1000–1014. [15-3] Harrison Plant Journal 1996, 9:491–503

Increased colonization compared to WT

FatM function appeared to be the result of timing and heightened expression culminating in the increased release of C16:0 free fatty acids from plastids during AM symbiosis (Figure 1, [170])
This points to a fungal requirement of FatM for arbuscule development or for supplying lipids building the PAM [14-1].
It is noteworthy that the different mutant phenotypes share the commonality that the fungus is able to continue intraradical spreading despite a lack of vesicle and spore production
These observations support a hypothesis whereby carbohydrate uptake promote intraradical fungal proliferation, for completion of the fungal life cycle alternative C sources such as FAs are required that are essential for arbuscule development.
Uncovering their function and regulation during AM symbiosis will unleash new insights into organic C nurture of AM fungi and into ancient host-fungal transactions that drive AM symbiosis

Builds on previous research

- This points to a fungal requirement of FatM for arbuscule development or for supplying lipids building the PAM [14-2]. In addition to FatM, the earlier reported Reduced Arbuscular Mycorrhization 2 (RAM2) also belongs to the phylogenetically conserved AM-specific genes [14-3]

References

Saito_RoleCellWallPolyphosphatesPhosphorus_2021

Role of Cell Wall Polyphosphates in Phosphorus Transfer at the Arbuscular Interface in Mycorrhizas

Cuc Thi Nguyen; Katsuharu Saito

2021

Abstract

Arbuscular mycorrhizal fungi provide plants with soil mineral nutrients, particularly phosphorus. In this symbiotic association, the arbuscular interface is the main site for nutrient exchange. To understand phosphorus transfer at the interface, we analyzed the subcellular localization of polyphosphate (polyP) in mature arbuscules of Rhizophagus irregularis colonizing roots of Lotus japonicus wild-type (WT) and H+-ATPase ha1-1 mutant, which is defective in phosphorus acquisition through the mycorrhizal pathway. In both, the WT and the ha1-1 mutant, polyP accumulated in the cell walls of trunk hyphae and inside fine branch modules close to the trunk hyphae. However, many fine branches lacked polyP. In the mutant, most fine branch modules showed polyP signals compared to the WT. Notably, polyP was also observed in the cell walls of some fine branches formed in the ha1-1 mutant, indicating phosphorus release from fungal cells to the apoplastic regions. Intense acid phosphatase (ACP) activity was detected in the periarbuscular spaces around the fine branches. Furthermore, double staining of ACP activity and polyP revealed that these had contrasting distribution patterns in arbuscules. These observations suggest that polyP in fungal cell walls and apoplastic phosphatases may play an important role in phosphorus transfer at the symbiotic interface in arbuscules.

Key concepts

#claim/arbuscule; #arbuscular_mycorrhizal; #method/acid_phosphatase; #claim/cell_wall; #result/polyphosphate; #claim/symbiosis; #method/distilled_water; #lotus_japonicus; #method/phosphate_buffered_saline; #claim/metabolism; #method/transmission_electron_microscopy; #alkaline_phosphatase; #arbuscular_mycorrhizal_fungi; #method/tris_buffered_saline; #glomus; #dynamics; #arbuscular_mycorrhizas; #method/bovine_serum_albumin; #alkaline; #method/wheat_germ_agglutinin; #method/rhizophagus_irregularis; #escherichia_coli

Quote

> We propose a hypothesis for P transfer at arbuscular mycorrhizal fungus-host interface in which polyP is released into the cell walls of fine branches and immediately subjected to hydrolysis by acid phosphatase located in the periarbuscular space

Key points

- Phosphorus is a crucial element for plant growth and development
- To determine whether the HA1 mutation affects P acquisition via the mycorrhizal pathway, we examined the P nutrition of the ha1-1 mutant using a two-compartment system consisting of RHC and HC (Figure 1D)
- Since intense acid phosphatase (ACP) activities were found in periarbuscular space (PAS) around fine branches, the absence of polyP in the fine branch cell walls could be explained by the degradation of polyP in fungal cell walls by apoplastic ACP
- We propose a hypothesis for P transfer at arbuscular mycorrhizal (AM) fungus-host interface in which polyP is released into the cell walls of fine branches and immediately subjected to hydrolysis by ACP located in the PAS

- The liberated Pi is delivered to host cells by symbiotic Pi transporters driven by the H+ gradient generated across the periarbuscular membrane (PAM) by the HA1 H+-ATPase ([23-1]; [21-4]; Willmann et al, 2013; [24-1]; [25-1]; Wang et al, 2014; [171]; [172])
- Because the mechanism of polyP release into the fungal cell wall is unknown and it remains unclear whether the apoplastic ACP can catalyze polyP hydrolysis, we cannot rule out the possibility that polyP is hydrolyzed in AM fungal hyphae and the liberated Pi is exported to the PAS via an unidentified Pi exporter

Synopsis

Introduction

Phosphorus is a crucial element for plant growth and development.
Terrestrial plants absorb P as orthophosphate (Pi) from the soil solution.
Soil Pi is mainly present in immobile forms that are not directly available to plants ([173]).
Host plants can acquire soil Pi via two pathways, the mycorrhizal pathway and the direct pathway.
The mycorrhizal pathway is a route via AM fungal hyphae ([174], [175]).
Pi is directly taken up by plant roots.
The mycorrhizal pathway is usually activated even in non-responsive AM plants, for which AM fungal colonization does not positively affect growth or P nutrition ([174-1], 2004).

Methods

The L. japonicus homozygous ha mutant line with a LORE1 insertion in the HA1 gene and the wild-type (WT) segregant were selected from a heterozygous LORE1 insertion line that was obtained from Lotus Base..
A two-compartment culture system consisting of root-hyphal (RHC) and hyphal (HC) compartments was used to cultivate plants (Figure 1).
The two compartments were separated by a threelayered barrier ([176]) comprising an RHC filter (57 μM opening), a medial mesh (1 mM in thickness; 2

mM opening), and an HC filter (32 μM opening), which prevented plant roots from passing through but allowed AM fungal hyphae to pass.
The inoculated and non-inoculated plants were grown in a growth chamber for 4 weeks.
RHC was supplied with a half-strength Hoagland's solution containing a low concentration of KH_2PO_4 (100 μM)

Results

The authors investigated the effect of the mutation of HA1 on P acquisition through the mycorrhizal pathway.
A L. japonicus homozygous line carrying a LORE1 insertion in exon 8 of the HA1 gene was selected to obtain a ha mutant, ha (Figure 1A).
To determine whether the HA1 mutation affects P acquisition via the mycorrhizal pathway, the authors examined the P nutrition of the ha mutant using a two-compartment system consisting of RHC and HC (Figure 1D).
The positive effects on shoot P content were lower in the ha mutant than in the WT.
These data demonstrate that P transfer from the AM fungus to the host via the mycorrhizal pathway was partially impaired in the ha mutant.

Conclusion

P transfer across the symbiotic interface is an important process in the mycorrhizal pathway.
Since intense ACP activities were found in PAS around fine branches, the absence of polyP in the fine branch cell walls could be explained by the degradation of polyP in fungal cell walls by apoplastic ACP
Supporting this idea, the ha mutant, in which the mycorrhizal pathway was partially suppressed, showed polyP localization in some cell walls of the fine branches.
The authors propose a hypothesis for P transfer at AM fungus-host interface in which polyP is released into the cell walls of fine branches and immediately subjected to hydrolysis by ACP located in the PAS.
Because the mechanism of polyP release into the fungal cell wall is unknown

and it remains unclear whether the apoplastic ACP can catalyze polyP hydrolysis, the authors cannot rule out the possibility that polyP is hydrolyzed in AM fungal hyphae and the liberated Pi is exported to the PAS via an unidentified Pi exporter

Study subjects

35 purple ACP genes

- Several AM-inducible phosphatase genes are candidates for encoding ACPs present in PAS. In soybean, two out of 35 purple ACP genes are upregulated in AM roots ([177]). The AM-inducible soybean purple ACP gene, GmPAP33, is expressed in arbuscule-containing cortical cells and is involved in arbuscule degeneration via phospholipid hydrolysis ([178])

Data analysis

- #method/fishers_exact_test
- #method/pearson
- #method/kolmogorov_smirnov_test
- #method/t_test
- #method/tukeys_hsd_test

Findings

- The positive effects on shoot P content were lower in the ha1-1 mutant (average increase of 268%) than in the WT (average increase of 492%)

Confirmation of earlier findings

- NTP activity localization was similar to ACP activity with signals along the PAM and in small vesicles present in the PAS surrounding fine branches (Figure 7), as previously reported ([179]). To further study the relationship between phosphatase activity and polyP accumulation, we detected phosphatase activity and polyP signals simultaneously by enzyme

cytochemistry using the ELF97 phosphatase substrate and DAPI staining, respectively

Future work

- To further study the relationship between phosphatase activity and polyP accumulation, we detected phosphatase activity and polyP signals simultaneously by enzyme cytochemistry using the ELF97 phosphatase substrate and DAPI staining, respectively. ELF97 forms fine precipitates after hydrolysis of its phosphate ester bond by non-specific phosphatases, emitting yellow-green fluorescence at the site of phosphatase activity ([180]). ACP and NTP activities were visualized in a typical mature arbuscule by single ELF97 staining in WT and ha1-1 roots, respectively (Figure 8A). In the WT, ACP activity was present throughout the arbuscule but was excluded from its central region. NTP activity was detected in arbuscules in the mutant but the central region without phosphatase activity was larger than that in the WT. We performed double labeling of phosphatase activity and polyP. The localization of phosphatase activity (green) and polyP (yellow) was distinct based on different emission colors using a long-pass filter, albeit showing weak and different color signals compared to the single staining (Figure 8B). Double labeling showed that polyP was present in the center of arbuscules, and phosphatase.
- The yeast VTC2, a subunit of VTC complexes, is observed at the cell periphery along the plasma membrane under high Pi conditions, it is localized in vacuoles in a low-Pi medium ([181]). How polyP is released across the fungal plasma membrane and the role of cell wall polyP in fungal physiology are important questions to be explored in future studies.
- Further research, including mutant analysis, is needed to clarify whether these purple ACPs are responsible for ACP activity in PAS.

Data and code

- DATA AVAILABILITY STATEMENT SUPPLEMENTARY MATERIAL The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the

corresponding author. The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2021.725939/full#supplementary-material

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MacLean_et+al_PlantSignalingMetabolicPathwaysEnabling_2017

Plant Signaling and Metabolic Pathways Enabling Arbuscular Mycorrhizal Symbiosis

Allyson M. MacLean; Armando Bravo; Maria J. Harrison

2017

Abstract

AND CONCLUSIONS
In summary, research over the past few years has enhanced our understanding of the common symbiosis signaling pathway and established direct connections between signaling and downstream events in the colonized cells. Yet, despite these advances, a full understanding of the receptor complexes and signaling molecules that generate input to the pathway, and the transcriptional regulatory networks that control downstream gene expression, remains to be achieved. Currently, GRAS factors dominate the regulatory landscape, yet spatial and temporal details are sparse, and their regulatory roles within

multiprotein complexes remain to be established in a symbiotically relevant context. While the importance of the common symbiosis signaling pathway cannot be denied, new data from rice and maize indicate that additional signaling pathways play significant roles. Whether signaling through the D14L/D3 pathway connects directly to the symbiosis signaling pathway or is necessary to establish an appropriate molecular environment to enable symbiosis remains to be determined. Additionally, the rice and maize data emphasize the importance of studies in a diversity of plant species and provide opportunities for comparisons between hosts with different evolutionary trajectories.

Key concepts

#arbuscular_mycorrhizal; #claim/symbiosis; #GRAS; #arabidopsis; #metabolism; #symbioses; #lysin_motif; #calcium; #gibberellic_acid; #lotus_japonicus; #land_plant; #NSP1; #gibberellin; #leucine_rich_repeat; #pisum_sativum; #solanum_lycopersicum; #arabidopsis_thaliana; #rhizophagus_irregularis

Quote

> Phosphorylated CYCLOPS forms a complex with calcium and calmodulin-dependent kinase, which acts in concert with GRAS transcription factors such as DELLA proteins, to initiate the expression of genes such as Reduced Arbuscular Mycorrhiza 1 that are necessary to accommodate the fungal symbiont

Key points

- Of the many associations formed between plants and microbes, arbuscular mycorrhizal (AM) symbiosis, in which plants and fungi of the Glomeromycota engage, is one of the most widespread and ancient ([128-1])
- Phylogenetic analyses indicate that symbiosis signaling genes are present in the genomes of the closest algal relatives to land plants and the function

of the encoded proteins is conserved, which suggests that these plant ancestors were preadapted for symbiosis (Delaux et al, 2015)
- Phosphorylated CYCLOPS forms a complex with calcium and calmodulin-dependent kinase (CCaMK), which acts in concert with GRAS transcription factors such as DELLA proteins, to initiate the expression of genes such as Reduced Arbuscular Mycorrhiza 1 (RAM1) that are necessary to accommodate the fungal symbiont
- Research over the past few years has enhanced our understanding of the common symbiosis signaling pathway and established direct connections between signaling and downstream events in the colonized cells
- While the importance of the common symbiosis signaling pathway cannot be denied, new data from rice and maize indicate that additional signaling pathways play significant roles
- While this review has focused on events taking place within a plant host, a true understanding of AM symbiosis requires comprehensive knowledge of both symbiotic partners

Synopsis

Of the many associations formed between plants and microbes, arbuscular mycorrhizal (AM) symbiosis, in which plants and fungi of the Glomeromycota engage, is one of the most widespread and ancient ([128-2]).
Phosphorylated CYCLOPS forms a complex with CCaMK, which acts in concert with GRAS transcription factors such as DELLA proteins, to initiate the expression of genes such as RAM1 that are necessary to accommodate the fungal symbiont.
Primacy of CCaMK at the apex of the regulatory transcriptional cascade is underscored by the observation that expression of an activated gain-of-function CCaMK is sufficient to fully complement the severe symbiotic phenotypes exhibited by mutants of genes upstream in the pathway such as dmi1/ pollux, castor, and dmi2/symrk ([182]), thereby uncoupling the requirement for Myc-factor perception and the resulting Ca2+ oscillations to elicit the subsequent downstream transcriptional response necessary to support AM symbiosis.

Genes that have functions outside of the symbiotic context ([183]), for example, M. truncatula DELLA1 and DELLA2 ([184]), D14L (Gutjahr et al, 2015), and NOPE1 (Nadal et al, 2017), as well as several others indicated, are present in AM non-host and host plants and are required for AM symbiosis.

Addressing the topic from different angles and with different approaches, four groups recently provided complementary lines of evidence that collectively demonstrate that the plant provides fatty acids, most likely 16:0 b-monoacylglycerol (16:0 b-MAG) but possibly a derivative, to the fungus and that transfer occurs at the interface with the arbuscule (Figure 3) ([28-3]; [48-2]; Keymer et al, 2017; [185]).

Support the direction of lipid flux toward 16:0 b-MAG and potentially transfer to the periarbuscular space was provided by analyses of M. truncatula loss-of-function mutants of three AM symbiosisconserved proteins, FatM, an acyl ACP-thioesterase, RAM2, a glycerol-3-phosphate acyl transferase (GPAT), and STR, a periarbuscular membrane-resident ABC transporter.

The genes encoding these three proteins are highly induced in colonized cells, and in all three mutants arbuscule development is impaired, fungal lipid levels are low, and symbiosis is not maintained ([186]; Gobbato et al, 2012; [187]; [27-2], [28-4]).

Coupled with the native lipid profiles ([28-5]), the data collectively provide strong evidence that the colonized cell increases fatty acid biosynthesis and redirects flux through lipid metabolism to generate 16:0 b-monoacylglycerols (16:0 b-MAG) and these, or a derivative thereof, are transferred to the periarbuscular apoplast and subsequently accessed by the fungus (Figure 3).

These data reveal that during AM symbiosis, signaling through the common symbiosis signaling pathway triggers the reprogramming of lipid metabolism in the colonized cells to enable production and export of essential fatty acids for the fungus.

The rice and maize data emphasize the importance of studies in a diversity of plant species and provide opportunities for comparisons between hosts with different evolutionary trajectories

Study subjects

1000 plant genes

- The latter two proteins are also required for arbuscule development, which suggests that changes in composition of a transcription factor complex may regulate the transition between the development and degeneration phases of the accommodation program. With several thousand plant genes showing differential expression during AM symbiosis, genetic dissection of the symbiotic program is a daunting task. However, the early single origin of AM symbiosis, the broad taxonomic distribution within the vascular plant lineage, and the observation that all mycorrhizal plants contain the same set of genes for AM symbiosis provided a unique opportunity to use phylogenomics to identify genes conserved for AM symbiosis, which provides a point of focus for reverse genetics analyses

138 AM symbiosisconserved genes

- This evolutionary pattern of conservation in hosts and loss in non-host plants was visualized by constructing phylogenies and exploited to identify genes conserved for AM symbiosis ([188]; [189]; [27-3]). The most stringent analysis identified 138 AM symbiosisconserved genes, of which 15 had known roles in AM symbiosis and mutants in an additional six also revealed their involvement ([27-4]). The 138 AM symbiosis-conserved genes show a variety of molecular functions, but in several cases, they were found to interact or to function at different points of a cellular process or single metabolic pathway, leading to a proposal that the AM conserved genes function in small modules to fine-tune cellular processes for symbiosis ([27-5])

138 AM symbiosis-conserved genes

- The most stringent analysis identified 138 AM symbiosisconserved genes, of which 15 had known roles in AM symbiosis and mutants in an additional six also revealed their involvement ([27-6]). The 138 AM symbiosis-conserved genes show a variety of molecular functions, but in several cases, they were found to interact or to function at different points of a

cellular process or single metabolic pathway, leading to a proposal that the AM conserved genes function in small modules to fine-tune cellular processes for symbiosis ([27-7]). For example, EXO70I, Vapyrin, and SYP132 are AM symbiosis-conserved proteins that modulate exocytosis to enable deposition of the periarbuscular membrane ([190]; [191]; Murray et al, 2011; [192]; [193]; [194])

Findings

- AM fungi obtain their entire carbon supply from the plant, and it is estimated that they acquire up to 20% of the carbon fixed during photosynthesis ([116-1])

Builds on previous research

- The developmental phenotypes exhibited by kai2 mutants that are not related to karrikin perception per se, and broad conservation of KAI2 in basal land plants and species not associated with fire-prone habitats, have led to a hypothesis that the receptor KAI2 recognizes and binds to an as yet unidentified endogenous ligand, presumably a phytohormone that is structurally related to karrikins and strigolactones ([195], [196]; [197]). The observation that D14L is essential for AM symbiosis in rice (Gutjahr et al, 2015), coupled with an earlier report of a rice d3 mutant (homolog of MAX2) that is likewise unable to support AM symbiosis ([198]), suggests this signaling pathway may be involved in AM symbiosis

Contributions

- In summary, research over the past few years has enhanced our understanding of the common symbiosis signaling pathway and established direct connections between signaling and downstream events in the colonized cells. Yet, despite these advances, a full understanding of the receptor complexes and signaling molecules that generate input to the pathway, and the transcriptional regulatory networks that control

downstream gene expression, remains to be achieved. Currently, GRAS factors dominate the regulatory landscape, yet spatial and temporal details are sparse, and their regulatory roles within multiprotein complexes remain to be established in a symbiotically relevant context. While the importance of the common symbiosis signaling pathway cannot be denied, new data from rice and maize indicate that additional signaling pathways play significant roles. Whether signaling through the D14L/D3 pathway connects directly to the symbiosis signaling pathway or is necessary to establish an appropriate molecular environment to enable symbiosis remains to be determined. Additionally, the rice and maize data emphasize the importance of studies in a diversity of plant species and provide opportunities for comparisons between hosts with different evolutionary trajectories.

References

Lanfranco_et+al_PartnerCommunicationRoleNutrientsArbuscular_2018

Partner communication and role of nutrients in the arbuscular mycorrhizal symbiosis

Luisa Lanfranco; Valentina Fiorilli; Caroline Gutjahr

2018

Abstract

New Phytologist potential of mating-related processes has been obtained ([199]). They have a rather long history of taxonomic revisions, which reflects the general difficulty in resolving the earliest branches in the fungal genealogy.

Ribosomal DNA-based phylogenies placed them in the Glomeromycota phylum which is considered a sister group to Dikarya (Schu€ssler et al., 2001). An extensive phylogenomic study, based on kingdom-wide sampling of fungal species and genome-scale sampling of loci, placed AMF in the subphylum Glomeromycotina with a close relationship with Mortierellomycotina ([100-2]).

Key concepts

#arbuscular_mycorrhizal; #symbiosis; #fatty_acids; #metabolism; #chitin; #rhizophagus_irregularis; #symbioses; #volatile_organic_compounds; #lotus_japonicus

Quote

> These results indicate genetic redundancy at the level of MYB1 when Pi is delivered normally

Key points

- Plant roots, under inorganic phosphate (Pi) limiting conditions, release strigolactones (SLs), carotenoid-derived molecules with hormone functions in plants ([200])
- Myc factors LCOs/COs mutants displayed aborted colonization attempts and reduced arbuscules formation, respectively ([198-1]; [201]; [202]), and a rice mutant defective in the karrikin receptor D14-LIKE/KAI2 is characterized by an absence of hyphopodia ([202-1])
- The rice d14l/ kai2 mutant lacks the transcriptional response to fungal germinating spore exudates, indicating that the karrikin receptor complex may be involved in perception of the fungus
- Ectopic expression of MYB1 is associated with a decreased root length colonization, stretches of hyphae without arbuscules and a high incidence of degenerated arbuscules ([203]). These results indicate genetic redundancy at the level of MYB1 when Pi is delivered normally

- An Arabidopsis double mutant defective in PHR1 and PHL1, encoding two redundant master transcriptional regulators of Pi starvation responses, showed an upregulation of plant defence genes leading to an atypical composition of a synthetic bacterial community at low as well as high Pi conditions. These results are in line with the observation that Arabidopsis roots induce defence genes when colonized at high Pi conditions by the fungal endophyte C. tofieldiae ([204]), which promotes plant growth under low-Pi conditions by translocating Pi to the host ([205]), reminiscent of what occurs in AM symbiosis
- The characterization of putative AMF effectors and the identification of factors involved in the perception of plant signals, nutrient uptake, transport and metabolism will be an active field of research and should involve AMF species-comparisons to foster an understanding of AMF functional diversity

Synopsis

Plant exudates activate the fungus

AMF and plants rely on reciprocal recognition before physical contact ([101-1]; [68-2]).

SLs are plant-derived, they do not appear to play an important role at the host side because rice mutants defective in the alpha-beta hydrolase SLs receptor D14, are not perturbed in AM colonization ([198-2]; [202-2]).

The rice d14l/ kai mutant lacks the transcriptional response to fungal germinating spore exudates, indicating that the karrikin receptor complex may be involved in perception of the fungus.

It is not yet clear whether a karrikin-like compound of fungal or plant origin acts as ligand of the D14L receptor in plant–AMF recognition ([202-3]; [200-1]).

Identification of the NOPE1 substrate will add an exciting new aspect to plant biology in general, as GlcNac-based signalling molecules are currently only known from bacteria and fungi but not – to the knowledge – from plants

Fungal chitin-based molecules elicit symbiotic plant responses

AMF use GlcNAc-based molecules as pre-contact signals to activate symbiotic responses in the host plant such as calcium spiking, lateral root formation, starch accumulation and gene expression ([206]; [207]; [208]; [67-2]; [209]; [210]).
These so called 'Myc Factors' include lipo-chito-oligosaccharides (MycLCOs, Maillet et al, 2011) and short chitin tetra- and pentamers (Myc-COs; [67-3]) (Fig. 2).
SLs biosynthesis gene LjCCD7, was upregulated following exposure to these VOCs, suggesting that SLs may act as mediators of such a response ([211])

An emerging role for fungal effectors in AM symbiosis

In addition to GlcNAc-containing molecules, other AMFproduced factors contribute to interkingdom communication.
Kamel et al (2017) identified a small set of SPs, shared by R. irregularis and G. rosea, with similar expression patterns in the different host plants
These genes, which have been referred to as the AM symbiotic core secretome, encode proteases or protein with unknown function.
RiPEIP1 expression in Oidiodendron maius, an ericoid endomycorrhizal fungus, for which transformation protocols are available, led to enhanced colonization capacity compared to the O. maius WT strain ([212])
Because it encodes a four-transmembrane domain protein, RiPEIP1 does not fit to the canonical definition of effectors; further studies are needed to define the mechanism of action of RiPEP1 and its specific role in the process of AM colonization.
The interference with RNA metabolism of the host plant can be envisaged for the so-called RALPH (RNase-Like Proteins associated with Haustoria) the secreted avirulence effectors described in the obligate biotroph pathogenic fungus Blumeris graminis ([213])

Nutritional and regulatory roles for key metabolites in the AM symbiosis

After the AM symbiosis has been established, both symbionts benefit from nutrient supply by the other partner.
Accumulating evidence indicates that the exchanged nutrients function as nourishment, and act as signals that can drastically influence AM development.
AM development is strongly linked to symbiotic function

AMF receive lipids as well as carbohydrates from the host

Based on stable isotope labelling experiments, it has long been established that AMF receive carbohydrates and glucose from the plant ([214]; Trepanier et al, 2005).
[29-2]) measured lipid transfer in nontransgenic plants by isotopolog profiling of 16:0 and 16:1 FAs. Transgenic Medicago roots carrying UcFatB synthesized lauric acid and it was detected in the spores of colonizing R. irregularis ([48-3]; [185-1]), unequivocally demonstrating that lauric acid containing lipids were transferred from the host to AMF.
STR together with its complex partner STR2 ([186-1]) is considered a good candidate transporter for lipid transfer across the PAM ([215]; [28-6]; [216])
Taken together, these recent findings indicate that AMF are entirely dependent on lipid supply by the plant for their growth, development and reproduction.
These findings change the view on the energy balance of the symbiosis, in which the burden of organic carbon compound biosynthesis is more significantly shifted towards the plant than was assumed previously

Mechanisms of phosphate transfer from AMF to plant hosts

Phosphorus (P) is a major macronutrient limiting for plant growth. It occurs in soils predominantly as dihydrogen phosphate ion (H2PO4À, Pi; [217]).
AM-inducible PT genes have been identified in different host plants ([218]; [219]; Paszkowski et al, 2002; [220]; [221]; [23-2]; [222]; [223]; [224]; [21-5]; [225]; [24-2]; [226]; [227]; [31-1])
They are homologues of the yeast PHO84 and belong to the Phosphate

transporter 1 (Pht1) class ([228]) of the plant H+/Pi symporters.
This suggests that PT4 is involved in root architecture responses to low Pi, in addition to symbiotic Pi uptake

Phosphate status influences AM development

When a fungal PT or plant PT genes essential for symbiosis are mutated or silenced arbuscule development is affected ([23-3]; [21-6]; [227-1]; [229]) by accelerated arbuscule turnover ([23-4]).
An Arabidopsis double mutant defective in PHR1 and PHL1, encoding two redundant master transcriptional regulators of Pi starvation responses, showed an upregulation of plant defence genes leading to an atypical composition of a synthetic bacterial community at low as well as high Pi conditions
These results are in line with the observation that Arabidopsis roots induce defence genes when colonized at high Pi conditions by the fungal endophyte C. tofieldiae ([204-1]), which promotes plant growth under low-Pi conditions by translocating Pi to the host ([205-1]), reminiscent of what occurs in AM symbiosis.
High Pi treatment led to downregulation of 29 putative secreted proteins, including the SLs-induced putative secreted protein (SIS1) ([63-3]), pointing to an effect of the reduced SLs production of the plant

Plant growth responses cannot be predicted by AMF phylogeny

Despite a rather modest morphological variation, AMF show a high level of genetic variability.
With the exception of total spore volume, none of the considered fungal traits was positively correlated with plant performance ([230]).
This suggests that molecular features such as the repertoire of fungal signalling molecules, effectors or the abundance and efficiency of nutrient transport proteins may play a more important role for plant performance than AMF growth and morphology.
Plant growth promotion may not be the only trait that should be considered:

other benefits such as tolerance to abiotic or biotic stresses could provide a different picture
This knowledge will be fundamental to predict the impact of inoculation with specific AMF on plant performance.
These new findings and expected advances in the understanding of AMF genetics and life cycle may even pave the way to genetic strain improvement for applied purposes

Plant responsiveness to AMF is subject to genetic diversity

The AMF, and the plant genotype strongly affects the outcome of the symbiosis ([231]; Fig. 5).
The capacity of the maize lines to profit from the symbiosis in terms of shoot dry weight and shoot Pi content correlated with the amount of associated extraradical hyphae ([31-2]; Fig. 5)
This suggested an influence of plant genetics on fungal growth performance and, an impact of fungal morphology on plant performance when comparisons are based on only one fungal isolate.
Suppression of root colonization at high Pi was more pronounced in the domesticated plants ([232])
Together, this indicates that – at least in the tested species – domestication selected for AM independence at high Pi concentrations, which possibly increased yield in the absence of the fungus-associated carbon drain.
As AMF provide other services to plants such as increased resistance to abiotic stress and certain pathogens, it remains to be investigated whether other stresses would enhance AMresponsiveness of domesticated plants under high Pi fertilization

Perspectives

It is commonly accepted that soil biodiversity promotes multiple ecosystem functions and that the tailored management of soil communities, including AMF, has the potential to enhance agricultural sustainability ([233]).
The full complement of the microbiota living inside AMF certainly deserves

further investigation to define their influence on the metabolism of the fungal host and the potential impact on plant performance.
The characterization of putative AMF effectors and the identification of factors involved in the perception of plant signals, nutrient uptake, transport and metabolism will be an active field of research and should involve AMF species-comparisons to foster an understanding of AMF functional diversity.
It is becoming increasingly clear that despite their large host range, the efficiency of AMF in promoting plant performance differs strongly among fungal species and isolates, and the ability of the plant to respond to the symbiosis depends on the plant genotype.
The identification of the genetic polymorphisms underlying differences in symbiotic performance of plants and AMF will be key to smart breeding for profitable application of the AM symbiosis in sustainable agricultural systems with reduced chemical fertilizer and pesticide input

Study subjects

3 plant species

- Indeed, a comparison of the transcriptomes from R. irregularis and G. rosea, when colonizing three different host plants (the dicotyledon M. truncatula, the monocotyledon Brachypodium distachyon and the liverwort Lunularia cruciata), revealed that the expression of putative SPs can differ depending on the host plant. Among 87 SP genes expressed in the intraradical mycelium of R. irregularis only 33 were expressed in all three plant species ([234]), suggesting that these 33 fulfill core functions, whereas the others may act hostspecifically (Fig. 3). Remarkably, a larger proportion (74%) of host-specific SPs was found in G. rosea with respect to R. irregularis (44%) and this may reflect differences in the their host range

6 isolates of Magnaporthe species

- In plant–pathogen interactions effectors can play a significant role in host specificity ([235]). Regarding SPs, a recent study compared the complete genome sequence of six isolates of Magnaporthe species obtained from

three different host plants. An inventory of SPs showed that many new SPs have evolved in different isolates and, interestingly, some of these SPs are only present in groups of isolates from the same host plant suggesting that the evolution of SPs is under host-directed selection ([236])

3 AM-induced lipid biosynthesis genes

- Surprisingly, it was found that genes encoding the cytosolic fatty acids (FA) synthase subunits, which are responsible for the bulk FA production in fungi, are absent from AMF genomes ([237]; [238]). At approximately the same time it was discovered that legume mutants with stunted arbuscules and with reduced colonization were defective in three AM-induced lipid biosynthesis genes: DISORGANIZED ARBUSCULES (DIS), FatM and REDUCED ARBUSCULAR MYCORRHIZA 2 ([187-1]; [27-8]; [28-7]; [48-4]; [29-3]; [185-2]). DIS encodes a b-keto-acyl-ACP synthase I (KASI), which is specific to genomes of AM-competent gymnosperms and dicots and catalyses FA chain elongation from C4 to C16 ([29-4])

Findings

- A large majority (95%) of R. irregularis secreted proteins (SPs) is conserved in the related species R. clarus, whereas only 194 of 872 (22%) of R. irregularis SPs show similarity with those from Gigaspora rosea, a distantly related AMF (Sezdzielewska Toro & Brachmann, 2016; [234-1])
- A larger proportion (74%) of host-specific SPs was found in G. rosea with respect to R. irregularis (44%) and this may reflect differences in the their host range

Confirmation of earlier findings

- An Arabidopsis double mutant defective in PHR1 and PHL1, encoding two redundant master transcriptional regulators of Pi starvation responses, showed an upregulation of plant defence genes leading to an atypical composition of a synthetic bacterial community at low as well as high Pi conditions. These results are in line with the observation that Arabidopsis

roots induce defence genes when colonized at high Pi conditions by the fungal endophyte C. tofieldiae ([204-2]), which promotes plant growth under low-Pi conditions by translocating Pi to the host ([205-2]), reminiscent of what occurs in AM symbiosis

Future work

- Because it encodes a four-transmembrane domain protein, RiPEIP1 does not fit to the canonical definition of effectors; further studies are needed to define the mechanism of action of RiPEP1 and its specific role in the process of AM colonization.

References

LANFRANCO_et+al_7GeneticsGenomicsDecipherPartner_2021

7 Genetics and Genomics Decipher Partner Biology in Arbuscular Mycorrhizas

LUISA LANFRANCO; GENNARO CAROTENUTO; ANDREA GENRE et al.

2021

Abstract

Differently from model fungi (Neurospora, Aspergillus) and plants (Arabidopsis), the genetics of arbuscular mycorrhizas, intended as the sum of interacting plants and fungi, is therefore a very recent domain of science. Parniske (2004) was one of the first to use the term genetics in his highly quoted review “Molecular genetics of the arbuscular mycorrhizal symbiosis.”

Key concepts

#arbuscular_mycorrhizas; #symbiosis; #host_plant; #GRAS; #glomus; #metabolism; #rhizophagus_irregularis; #lotus_japonicus; #genetics; #biology; #finding/transposable_elements; #gibberellic_acid; #small_rna; #land_plant; #rna_interference_machinery; #triticum_aestivum; #small_interfering_rna

Quote

> Together these results suggest that the karrikin receptor complex plays a role in symbiotic signaling even if the involvement of karrikin-like molecules of fungal or plant origin remains to be investigatedWaters et al 2017)

Key points

- The aim of this chapter is to provide a review of the multiple interactions that are included in the term “arbuscular mycorrhizas” and present an updated view of our knowledge on the molecular genetics of Arbuscular mycorrhizas (AMs), covering the genomes of AM fungi, the cellular and molecular responses of the host plant, as well as the fungal and plant natural variation that contributes to the outcome of this fascinating interaction
- Even if AM host plants can survive if deprived of their fungal symbionts, this condition is virtually unknown in natural ecosystems, where AM fungi are associated as helper microorganisms in most of the environments so far investigated (Davison et al 2015, 2018)
- The expectations of the researchers involved in genome sequencing of Rhizophagus irregularis were first focused on another crucial question: why are AM fungi unculturable? At a first glance, their obligate biotrophy was not explained by genome erosion or any related loss of metabolic complexity in central metabolism

- The AM symbiosis develops in roots where extensive cellular reorganizations and specific metabolic changes occur, which are mirrored by local changes in the transcript profiles as it has been demonstrated by transcriptomic analyses carried out on several plant species
- The detailed characterization of several isolates of R. irregularis at the level of single nuclei has even opened a window on the potentials to genetically manipulate AM fungi (Chen et al 2018)

Synopsis

Genetics and Genomics Decipher Partner Biology in Arbuscular Mycorrhizas

From model fungi (Neurospora, Aspergillus) and plants (Arabidopsis), the genetics of arbuscular mycorrhizas, intended as the sum of interacting plants and fungi, is a very recent domain of science.
Parniske (2004) was one of the first to use the term genetics in his highly quoted review “Molecular genetics of the arbuscular mycorrhizal symbiosis.”.
In this context, the aim of this chapter is to provide a review of the multiple interactions that are included in the term “arbuscular mycorrhizas” and present an updated view of the knowledge on the molecular genetics of AMs, covering the genomes of AM fungi, the cellular and molecular responses of the host plant, as well as the fungal and plant natural variation that contributes to the outcome of this fascinating interaction

A New Look at the Interacting Partners

Arbuscular mycorrhizas (AMs) are traditionally described as the symbiosis resulting from the interaction between the roots of land plants and soil fungi. The colonization processes by Mucoromycotina are still to be defined: these fungi may establish different interactions with plants; some of them establish ectomycorrhizas ([239]) and have been detected mostly by using molecular tools, while morphology suggests that they form characteristic intracellular swellings ([240]).
On the basis of the current data, Glomeromycotina can be defined as a stable

component of the plant microbiota, since they are found in most of the environments so far investigated (Davison et al 2015, 2018), but on the other hand, they host their own microbiota, given by the intracellular endobacteria as well as by the bacteria which are commonly associated to the surface of their extraradical hyphae (Turrini et al 2018).
Mycoviruses can be considered an additional component of the AM microbiome with the potential to influence the biology of AM fungi and their host plant (Ikeda et al 2012)

Lessons from the Genome Sequencing of AM Fungi

The authors' knowledge of the AM symbiosis mainly mirrors a plant-centric view
This is due to (1) the obligate biotrophic status of Glomeromycotina, which cannot be cultivated in the absence of their host plants; (2) their multinuclear condition, i.e., hundreds of nuclei coexist within one continuous cytoplasm; and (3) the absence of observable sexual reproduction and a uninucleated life stage (Chen et al 2018).
All these aspects hamper the use of the classical genetic tools which have, by contrast, allowed to study model fungi like Neurospora or Aspergillus, or their host plants which offer genetically tractable systems.
Clonality still appears to be the prevalent mode of reproduction (Chen et al 2018)

The Biotrophism of AM Fungi

The expectations of the researchers involved in genome sequencing of Rhizophagus irregularis were first focused on another crucial question: why are AM fungi unculturable? At a first glance, their obligate biotrophy was not explained by genome erosion or any related loss of metabolic complexity in central metabolism.
The genome sequencing of four Endogonaceae fungi (Chang et al 2018) has detected the symbiotic signatures already identified in the other mycorrhizal fungi such as large genome size, high repetitive DNA content, and low diversity of plant cell walldegrading enzymes but without elevated small secreted

proteins/secretome ratios.
The genome sequence led to the detection of Mollicutes-related endobacteria (MREs) in D. epigea and in three of the four sequenced Endogonaceae
Their genomes can be read as “metagenomes.” By contrast, G. margarita genome confirmed the presence of Candidatus Glomeribacter gigasporarum, which was already sequenced ([241]).
The intimate contact between bacteria and fungi may have favored horizontal gene transfer (Torres-Cortes et al 2015; Naito et al 2015; Sun et al 2018), potentially leading to an impact on the fungal biology (Salvioli et al 2016)

From Structure to Function

The genome sequencing of AM fungi has so far provided relevant information concerning their genome structure and evolution, even if data from some more distantly related members, such as Archeospora, would be essential to better define their ancient relationships.
A small set of secreted proteins, shared by distantly related AM fungi (Rhizophagus irregularis and Gigaspora rosea), showed similar expression patterns in different host plants ([234-2]).
These genes, described as the AM symbiotic core secretome, encode proteins with unknown function or proteases.
The mechanism of action of RiCRN1 does not involve cell death processes as often described for CRNs from oomycetes
In all these three abovementioned cases, host-induced gene silencing (HIGS) has been used to silence the fungal genes during the symbiotic phase allowing the description of an impaired colonization pattern.
The success of the HIGS approach as a tool to silence fungal genes in the AM symbiosis (Helber et al 2011; Tsuzuki et al 2016) is a strong clue toward the occurrence of such a process

Cellular and Molecular Changes in the Host Plant

In analogy to most root-microbe interactions, AM establishment depends on finely tuned recognition processes (Bonfante and Genre 2015) through signal release and perception between both partners before their physical contact

([242]).
Rice d3 and pea rms mutants displayed important defects in AM colonization and arbuscule formation, respectively ([198-3]; Foo et al 2013; [202-4]); a d14l/kai rice mutant does not stimulate the formation of hyphopodia ([202-5]) and does not respond transcriptionally to AM germinating spore exudates
Together these results suggest that the karrikin receptor complex plays a role in symbiotic signaling even if the involvement of karrikin-like molecules of fungal or plant origin remains to be investigated ([202-6]; Waters et al 2017).
Myc-COs are active in both legumes and non-legumes at very low concentration, down to 10À8 M ([67-4]; Sun et al 2015), and can be considered as universal AM-specific elicitors

The Common Symbiotic Signaling Pathway

The study of Myc factor signaling mechanisms in legumes such as Medicago truncatula and Lotus japonicus has mostly come as a followup of analogous research on symbiotic nitrogen fixation (SNF; Denarieand Cullimore 1993; Maillet et al 2011).
The process of arbuscule accommodation in cortical cells is the most striking feature of AM development and requires a broad reorganization of the host cells in strict coordination with fungal development: hyphal penetration associates with nuclear movement at the center of the cell ([243]), engulfed by a broad PPA (Genre et al 2008)
This anticipates the formation of the arbuscule trunk and the PAM trunk domain (Pumplin and Harrison 2009), characterized by a set of proteins that is analogous to that of the plasma membrane.
In response to CSSP activation, several transcription factors are expressed during either early or later stages of arbuscule formation (Bucher et al 2014; Luginbuehl and Oldroyd 2017; [244]; Pimprikar and Gutjahr 2018), in turn regulating the expression of genes involved in nutrient transfer, primary and specialized metabolism, membrane and cell wall modifications, secretion, and signal transduction (Hohnjec et al 2005; Gaude et al 2012; Hogekamp and Kuster 2013; [245]).
Arbuscule senescence is a regulated process where the host cell remains active

during and after arbuscule collapse and maintains the ability to be colonized again by a new arbuscule

Mycorrhizal Omics

The AM symbiosis develops in roots where extensive cellular reorganizations and specific metabolic changes occur, which are mirrored by local changes in the transcript profiles as it has been demonstrated by transcriptomic analyses carried out on several plant species.
An untargeted metabolomic analysis was recently performed on tomato mycorrhizal roots with the aim to identify key metabolites involved in the mycorrhiza-induced protection against osmotic stresses (Rivero et al 2018).
The analysis of putative targets of selected miRNAs revealed an involvement in P starvation, phytohormone signaling, and defense (Pandey et al 2018).
All these studies convincingly demonstrate that AM fungi have a local and systemic influence on their host plant, since they lead to a deep reorganization of the plant biology acting on multiple transcriptomic, regulatory, and metabolomic pathways

The AM Symbiosis in the Light of Natural Variation

Despite the low morphological variation and their large host range, AM fungal species and isolates show different efficiency in promoting plant performance; on the other hand, the plant genotype has an important role in determining the extent of plant responsiveness to the AM symbiosis (Smith et al 2004).
Concerning the responsiveness to AM fungi, Sawers et al (2017) analyzed the growth response of 30 maize lines upon colonization by F. mosseae; variations in shoot dry weight and shoot Pi content were observed, and, interestingly, these correlated with the amount of extraradical mycelium, suggesting a plantfungus reciprocal effect on growth performances.
Domesticated plants reduced AM fungal colonization more strongly than did wild progenitors in response to increased P availability
On the whole these studies indicate a strong fungal genotype X plant genotype interaction in the mycorrhizal symbiosis.
This variation may have profound impact in natural populations and has to be

considered in agricultural practices where AM fungi are exploited to improve plant health and productivity

Conclusions

Genetics and genomics have recently provided crucial novel information on the biology of arbuscular mycorrhizas.
Phylogenomics analyses based on genomes from host and non-host species are emerging as powerful tools to identify conserved genes required for the AM symbiosis (Bravo et al 2016) and to trace the evolution of the underlying genetic network from basal plants to angiosperms (Delaux et al 2015).
The authors can envisage that the CRISPR/Cas-based genome editing technique will offer an efficient strategy for producing plant genotypes with mutations in genes of interest.
These genes could be selected among those responsible of the molecular dialogue between partners and among those which regulate AM functionality.
In the frame of a more friendly agriculture, these plant genes could be the targets for the development of new crop varieties more susceptible and responsive to the beneficial AM fungi

Study subjects

30000 genes

- The strain DAOM-197198 was selected for several reasons: it had been hypothesized to possess a very small genome; it easily grows in association with root organ cultures, producing a large amount of noncontaminated fungal material; and – as a last key feature – it does not host endobacteria, thus representing a potentially more amenable scenario. The sequence of its 153-Mb haploid genome showed a repertoire of about 30,000 genes and revealed a low level of polymorphism offering for the first time a reply to the crucial question: do the nuclei of AM fungi possess multiple, highly diverged genomes? The data strongly suggested the inconsistency of such a hypothesis, which was also elegantly refuted by the whole sequence of isolated single nuclei (Lin et al 2014). Mating (MAT)-

related genes were found to be expanded, suggesting the existence of cryptic sex-related processes and opening the possibility that a non-observable mating does not mean absence of sex

3 abovementioned cases

- Although not yet defined, the mechanism of action of RiCRN1 does not involve cell death processes as often described for CRNs from oomycetes. In all these three abovementioned cases, host-induced gene silencing (HIGS) has been used to specifically silence the fungal genes during the symbiotic phase allowing the description of an impaired colonization pattern. These examples also highlight how, in the absence of protocols for stable genetic transformation for AM fungi, genetic manipulation tools developed for the host plants can be successfully applied to study the function of AM fungal genes at least in the in planta phase

3 mycorrhizal genes

- Among the CCaMK/CYCLOPS-regulated transcription factors, the GRAS-domain proteins NSP1 (Nodulation Signalling Pathway 1) and NSP2 play an essential role in Nod factor signaling (Catoira et al 2000; Kaloet al. 2005; Smit et al 2005). Evidence suggests direct roles of NSP1 and NSP2 also in Myc factor signaling: with NSP2 being involved in NS-LCO-induced lateral root growth (Maillet et al 2011) and NSP1 being required for the induction of three mycorrhizal genes in response to NS-LCO (Delaux et al 2013). NSP1 and NSP2 interaction is required for the induction of nodulationspecific promoters (Hirsch et al 2009; [246]) but not crucial for AM symbiosis, suggesting that different GRAS transcription factor complexes regulate distinct groups of genes (Pimprikar and Gutjahr 2018)

Findings

- The genome expansion seems to be strictly correlated with the presence of transposable elements (TE) which, in the case of G. margarita, represent more than 80% of the whole genome

Counterpoint to earlier claims

- Furthermore, Myc-LCOinduced responses were shown to be NFPdependent, indicating the involvement of this receptor in both Nod- and Myc-LCO perception (Op den Camp et al 2011). Although nfp mutants exhibit normal Ca2+ spiking and AM colonization (Maillet et al 2011; [67-5]; [247]), such mutants do not display nuclear Ca2+ spiking in response to Myc-LCOs (Sun et al 2015)

Contributions

- Genetics and genomics have recently provided crucial novel information on the biology of arbuscular mycorrhizas. The genome sequencing of a number of AM fungal species is allowing to identify common features such as the fatty acid auxotrophy but also dispensable species-specific components. The detailed characterization of several isolates of R. irregularis at the level of single nuclei has even opened a window on the potentials to genetically manipulate AM fungi (Chen et al 2018).

  On the plant perspective, phylogenomics analyses based on genomes from host and non-host species are emerging as powerful tools to identify conserved genes required for the AM symbiosis (Bravo et al 2016) and to trace the evolution of the underlying genetic network from basal plants to angiosperms (Delaux et al 2015). We can also envisage that the CRISPR/Cas-based genome editing technique will offer an efficient strategy for producing plant genotypes with mutations in genes of interest. These genes could be selected among those responsible of the molecular dialogue between partners (also considering the presymbiotic steps) and among those which regulate AM functionality. In the frame of a more friendly agriculture, these plant genes could be the targets for the development of new crop varieties more susceptible and responsive to the beneficial AM fungi.

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Synergies between mycorrhizal fungi and soil microbial communities increase plant nitrogen acquisition

Rachel Hestrin; Edith C. Hammer; Carsten W. Mueller et al.

2019

Abstract

Nitrogen availability often restricts primary productivity in terrestrial ecosystems. Arbuscular mycorrhizal fungi are ubiquitous symbionts of terrestrial plants and can improve plant nitrogen acquisition, but have a limited ability to access organic nitrogen. Although other soil biota mineralize organic nitrogen into bioavailable forms, they may simultaneously compete for nitrogen, with unknown consequences for plant nutrition. Here, we show that synergies between the mycorrhizal fungus Rhizophagus irregularis and soil microbial communities have a highly non-additive effect on nitrogen acquisition by the model grass Brachypodium distachyon. These multipartite microbial synergies result in a doubling of the nitrogen that mycorrhizal plants acquire from organic matter and a tenfold increase in nitrogen acquisition compared to non-mycorrhizal plants grown in the absence of soil microbial communities. This previously unquantified multipartite relationship may contribute to more than 70 Tg of annually assimilated plant nitrogen, thereby playing a critical role in global nutrient cycling and ecosystem function.

Key concepts

#arbuscular_mycorrhizal; #finding/organic_matter; #symbiosis; #claim/mycorrhizal_fungus; #result/primary_productivity; #method/NMDS; #claim/brachypodium_distachyon; #organic_material; #terrestrial_ecosystem; #method/terrestrial_plant; #result/ecosystem_function; #nutrient_cycling; #claim/rhizophagus_irregularis; #organic_nitrogen

Quote

> Arbuscular mycorrhizal fungi, and soil microbial communities collected from an N gradient experiment to investigate how multipartite interactions influence plant N acquisition from organic matter and how these relationships respond to long-term N enrichment

Key points

- Nitrogen availability often restricts primary productivity in terrestrial ecosystems
- Plant mesocosms, Arbuscular mycorrhizal (AM) fungi, and soil microbial communities collected from an N gradient experiment to investigate how multipartite interactions influence plant N acquisition from organic matter and how these relationships respond to long-term N enrichment
- Brachypodium distachyon seeds were planted in double-autoclaved sand and gravel with or without spores of the AM fungus Rhizophagus irregularis
- Our results demonstrate that emergent synergies between plants, mycorrhizal fungi, and free-living soil microbes have a highly non-additive effect on plant N acquisition from organic matter
- –0.15 that more than half of the N that AM plants derive from organic matter may be attributed to a synergistic relationship between AM plants and soil microbial communities and that this synergy is disrupted by a history of N enrichment
- Applied to estimates of global plant N uptake, these results suggest that more than 70 Tg of annually assimilated plant N can be attributed to

interactions between AM plants and soil microbes, but that these relationships are sensitive to environmental change[248]

Synopsis

Introduction

Nitrogen availability often restricts primary productivity in terrestrial ecosystems.
Arbuscular mycorrhizal (AM) fungi form symbioses with the majority of terrestrial plants and can substantially enhance plant N acquisition from soil, thereby potentially alleviating plant N limitation and playing an important role in plant productivity and soil nutrient cycling[249],[250],[251],[163-2],[252],[253],[17-2].
Long-term N enrichment disrupts these synergies, resulting in diminished mycorrhizal N acquisition from organic matter
These results have implications for terrestrial nutrient cycling models, agricultural management, and the understanding of ecosystem response to global change

Methods

Brachypodium distachyon seeds were surface sterilized with ethanol and planted in cones filled with 1:1 mixtures of double-autoclaved sand and gravel (v:v) at near-neutral pH.
After ~1 month, plants were transplanted from cones into mesocosms containing a double-autoclaved mixture of sand and gravel.
For treatments with soil microbial inocula, 0.25 g of fresh soil from perennial switchgrass (Panicum virgatum L.) fields that had been fertilized with three different levels of N (0, 28, and 196 kg N ha−1 per year; Kellogg Biological Station Long-Term Ecological Research Site, Hickory Corners, MI) for eight years was added directly to the organic matter[165-2].
For treatments without live soil microbial inocula, 0.25 g of double-autoclaved soil was added to the organic matter to control for any potential effect of abiotic soil components.

Each treatment was replicated seven times; replicates were arranged in a spatially

Results

Plant mesocosms, AM fungi, and soil microbial communities collected from an N gradient experiment to investigate how multipartite interactions influence plant N acquisition from organic matter and how these relationships respond to long-term N enrichment.
Brachypodium distachyon seeds were planted in double-autoclaved sand and gravel with or without spores of the AM fungus Rhizophagus irregularis.
The root systems of plants that had been inoculated with spores were colonized by the fungus.
AM and non-AM plants were transplanted into mesocosms containing a double-autoclaved sand-gravel mixture and a patch of 15N/13C-enriched organic matter (Fig. 1a).
An inoculum of fresh grassland soil containing whole soil microbial communities that had been exposed to an N enrichment gradient for eight years was added to the organic matter in a subset of the mesocosms

Conclusion

Applied to estimates of global plant N uptake, these results suggest that more than 70 Tg of annually assimilated plant N can be attributed to interactions between AM plants and soil microbes, but that these relationships are sensitive to environmental change[248-1].
These findings can be used to constrain Earth system models and improve agricultural management, where organic inputs provide an important supply of N to plants.
Since terrestrial ecosystems are often N-limited, this has implications for global N cycling and net primary productivity[254], [14-4].

Study subjects

7 biologically independent samples

- . Multipartite synergies between AM fungi and soil microbial communities increase plant biomass and N acquisition from organic matter. a Mesocosm design. b Plants acquired more N from organic matter in the presence of AM fungi and soil microbial communities. c Plants grown with both AM fungi and soil microbes acquired more N than expected based on the sum of N acquired by control plants and those grown with AM fungi or soil microbes alone. d AM colonization is associated with greater plant biomass. e AM plants grown with soil microbes derived a greater proportion of their total N from organic matter than control plants and plants grown with AM fungi or soil microbial communities alone. Significance levels are indicated with the following symbols: ·p < 0.1, *p < 0.05, **p < 0.01, ***p < 0.001 and denote the results of a Tukey's HSD test performed on log-transformed data (b, d), an unpaired t test (c), and a Tukey's HSD test performed on untransformed data (e). Error bars represent the standard error (n = 7 biologically independent samples). Relative 15N enrichment of fungal hyphae, plant roots, and plant aboveground tissue. Lowercase letters denote the results of a Tukey's HSD test comparing log-transformed mean δ 15N values of fungal hyphae; uppercase letters denote the results of a Tukey's HSD test comparing mean δ 15N values of plant tissues ($p < 0.05$). Error bars represent the standard error (n = 7 biologically independent samples)

7 biologically independent samples

- Multipartite synergies between AM fungi and soil microbial communities increase plant biomass and N acquisition from organic matter. a Mesocosm design. b Plants acquired more N from organic matter in the presence of AM fungi and soil microbial communities. c Plants grown with both AM fungi and soil microbes acquired more N than expected based on the sum of N acquired by control plants and those grown with AM fungi or soil microbes alone. d AM colonization is associated with greater plant biomass. e AM plants grown with soil microbes derived a greater proportion of their total N from organic matter than control plants and plants grown with AM fungi or soil microbial communities alone. Significance levels are indicated with the following symbols: ·p < 0.1, *p < 0.05, **p < 0.01, ***p < 0.001 and denote the results of a Tukey's HSD test performed on log-transformed data (b, d), an

unpaired t test (c), and a Tukey's HSD test performed on untransformed data (e). Error bars represent the standard error (n = 7 biologically independent samples). Relative 15N enrichment of fungal hyphae, plant roots, and plant aboveground tissue. Lowercase letters denote the results of a Tukey's HSD test comparing log-transformed mean δ 15N values of fungal hyphae; uppercase letters denote the results of a Tukey's HSD test comparing mean δ 15N values of plant tissues ($p < 0.05$). Error bars represent the standard error (n = 7 biologically independent samples). Microbial lipid biomass present in organic matter. Phospholipid fatty acid (PLFA) analysis was used to measure microbial lipid biomass in the organic matter harvested from mesocosms containing AM plants only and both AM plants and free-living soil microbes from grasslands fertilized with 0, 28, and 196 kg N ha−1 per year. Significant differences between total microbial lipid biomass measured through a Tukey's HSD test performed on log-transformed PLFA sums from each treatment are indicated by the following symbols: ·$p < 0.1$, *$p < 0.05$, **$p < 0.01$. Error bars represent the standard error of the mean of total microbial PLFAs measured in each mesocosm type (n = 7 biologically independent samples). Microbial lipid biomass associated with AM fungi, bacteria, and non-AM fungi is indicated in yellow, blue, and orange bars, respectively. Lowercase letters above the upper right-hand corner of each bar denote the results of Tukey's HSD tests performed only for PLFAs of the same subtype (AM fungi, bacteria, or nonAM fungi; $p < 0.05$). N enrichment did not result in a substantial difference in the ratio of fungal:bacterial lipids present in mesocosms containing AM plants and microbial inoculum from grassland fields. However, the ratios of AM fungal:bacterial lipids in these mesocosms were higher than in mesocosms inoculated only with AM fungi, suggesting that the presence of soil microbial communities benefitted the AM fungi in addition to benefitting the plant. It is not clear whether this was a direct benefit to the AM fungi, or whether it was modulated through increased provision of plant photosynthates time of sampling, providing further evidence that N enrichment has a lasting effect on microbial function[167-1], [165-3]. The inhibitory effect that we observed of long-term N enrichment on microbially-mediated plant N acquisition supports these findings and

demonstrates that this legacy effect has implications for plant-biotic synergies and ecosystem primary productivity

7 biologically independent samples

- Relative 15N enrichment of fungal hyphae, plant roots, and plant aboveground tissue. Lowercase letters denote the results of a Tukey's HSD test comparing log-transformed mean δ 15N values of fungal hyphae; uppercase letters denote the results of a Tukey's HSD test comparing mean δ 15N values of plant tissues ($p < 0.05$). Error bars represent the standard error ($n = 7$ biologically independent samples). Microbial lipid biomass present in organic matter. Phospholipid fatty acid (PLFA) analysis was used to measure microbial lipid biomass in the organic matter harvested from mesocosms containing AM plants only and both AM plants and free-living soil microbes from grasslands fertilized with 0, 28, and 196 kg N ha−1 per year. Significant differences between total microbial lipid biomass measured through a Tukey's HSD test performed on log-transformed PLFA sums from each treatment are indicated by the following symbols: ·$p < 0.1$, *$p < 0.05$, **$p < 0.01$. Error bars represent the standard error of the mean of total microbial PLFAs measured in each mesocosm type ($n = 7$ biologically independent samples). Microbial lipid biomass associated with AM fungi, bacteria, and non-AM fungi is indicated in yellow, blue, and orange bars, respectively. Lowercase letters above the upper right-hand corner of each bar denote the results of Tukey's HSD tests performed only for PLFAs of the same subtype (AM fungi, bacteria, or nonAM fungi; $p < 0.05$). N enrichment did not result in a substantial difference in the ratio of fungal:bacterial lipids present in mesocosms containing AM plants and microbial inoculum from grassland fields. However, the ratios of AM fungal:bacterial lipids in these mesocosms were higher than in mesocosms inoculated only with AM fungi, suggesting that the presence of soil microbial communities benefitted the AM fungi in addition to benefitting the plant. It is not clear whether this was a direct benefit to the AM fungi, or whether it was modulated through increased provision of plant photosynthates time of sampling, providing further evidence that N enrichment has a lasting effect on microbial function[167-2], [165-4]. The inhibitory effect that we observed of long-term

N enrichment on microbially-mediated plant N acquisition supports these findings and demonstrates that this legacy effect has implications for plant-biotic synergies and ecosystem primary productivity. Mean relative 13C enrichment of microbial biomass lipids measured through phospholipid fatty acid (PLFA) analysis. Since organic matter was enriched with 13C and plant photosynthates were depleted in 13C, lower PLFA δ 13C values suggest that microbes derived a greater proportion of their C from plant photosynthates. Letters denote the results of a Tukey's HSD test performed on log-transformed data; error bars represent the standard error ($p < 0.01$, $n = 7$ biologically independent samples)

Data analysis

- #method/tukeys
- #method/t_test
- #method/tukeys_hsd_test

Findings

- In the presence of both free-living soil microbial communities and AM fungi, plants derived up to 18% of their total N from organic matter—double the proportion of plant N derived from organic matter when plants grew with free-living soil microbes or AM fungi alone, even after differences in total plant biomass were accounted for (Fig. 1d, e)
- The composition of microbial lipid biomass was significantly different across treatments (Fig. 6, $p < 0.01$)

Builds on previous research

- NanoSIMS data are available from the authors upon request. The data that support the findings of this study are available in Cornell University's digital repository eCommons[169-2]

Differs from previous work

- In some cases, these changes have been decoupled from soil N concentrations measured at the. We expected to find that a lasting inhibitory effect of N enrichment on microbially-mediated plant N acquisition from organic matter would be associated with N-driven decreases in microbial biomass and decomposition activity[161-3], [255], [256], [167-3], [11-1], [12-1]
- The PLFA 16:1ω5 is sometimes used as an indicator of AM fungal biomass, but can also be produced by other microbes[257]. Unlike all other PLFAs measured here, the PLFA 16:1ω5 was depleted in 13C

Future work

- Additional research is necessary in order to evaluate the net effect of AM-microbial synergies and associated plant N acquisition on soil C stocks.

Data and code

- The data that support the findings of this study are available in Cornell University's digital repository eCommons[169-3]. NanoSIMS data are available from the authors upon request. Received: 15 March 2019 Accepted: 28 May 2019
- Supplementary information accompanies this paper at https://doi.org/10.1038/s42003019-0481-8.

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di_Fossalunga;_TradeFieldMolecularDeterminantsArbuscular_2019

To trade in the field: the molecular determinants of arbuscular mycorrhiza nutrient exchange

[Alessandra Salvioli di Fossalunga; Mara Novero]

2019

Abstract

Traditionally, the most popular sentences used to describe the arbuscular mycorrhizal symbiosis sound like: “AM fungi form one of the most widespread root symbioses, associating with 80% of land plants. In this symbiosis, the fungus provides the plant host with mineral nutrients, especially phosphate, receiving in turn carbohydrates.” In the last years, the mycorrhiza research field has witnessed a big step forward in the knowledge of the physiology and the mechanisms governing this important symbiosis, that helped plants colonizing the lands more than 400 MYA. The huge expansion of the -omics studies produced the first results on the fungal side, with genomes and transcriptomes of AM fungi being published. In parallel, the need for more sustainable agricultural practices has boosted the research in the field of the plant symbioses, with the final aim of improving plant productivity employing symbiotic microbes as bioinoculants. Beside all the other (positive) effects that mycorrhizal fungi exert on plants, the nutrient exchange is considered as the keystone, and the core mechanism governing this symbiosis. This review will focus on the molecular determinants underneath this exchange, both on the fungal and the plant side. Coming back to the sentence that claims this symbiosis as based on phosphate provided to the plant in return to carbohydrate, we will find that some concepts of this view still stand, while some others have been partly revolutionized.

Key concepts

#phosphate; #symbiosis; #arbuscular_mycorrhizal_fungi; #phosphate_transporter; #lotus_japonicus; #rhizophagus_irregularis; #mycorrhizal_fungi; #glomus; #aquaporin; #solanum_tuberosum

Quote

> Both carbon and mineral nutrition in the AM symbiosis have been exhaustively reviewed by many Authors, the aim of this review is to provide the reader with a “handy guide” through the current view of the symbiotic transportome

Key points

- Arbuscular mycorrhizal fungi belong to the basal fungal phylum of Glomeromycota [162-1]
- The functional core of this symbiosis is represented by the arbuscule, a complex, highly branched structure formed by the fungus intracellularly, and surrounded by a plant membrane called periarbuscular membrane (PAM) [249-1]
- Major recent breakthroughs in the AM biotrophy, as the discovery of the fungal dependency on host fatty acids, represented a real paradigm shift, and stimulated the researchers to construct an updated scenario of the plant–fungal exchanges to integrate the new findings. Both carbon and mineral nutrition in the AM symbiosis have been exhaustively reviewed by many Authors, the aim of this review is to provide the reader with a “handy guide” through the current view of the symbiotic transportome
- Sawers et al [7-1] showed that the mycorrhizal outcome in terms of growth response of maize plants better correlates with the abundance of the extraradical mycelium than with the accumulation of the mycorrhiza-inducible phosphate transporter ZmPT6
- Volpe et al [167-4] demonstrated that the expression of the mycorrhiza-inducible PT4 from M. truncatula and L. japonicus was not restricted to the PAM and present in the root tips of non-colonized plants
- In the plant-to-fungus direction, recent compelling results requested a real paradigm shift that shook up the mainstream bulk of knowledge: beside sugars, lipids are transferred from the plant to arbuscular mycorrhizal fungi (AMF), and their transfer might represent the key of the fungal obligate biotrophy

Synopsis

Arbuscular mycorrhizal fungi belong to the basal fungal phylum of Glomeromycota [162-2]. They are obligate biotrophs that associate with plant roots forming the mycorrhiza.
Sawers et al [7-2] showed that the mycorrhizal outcome in terms of growth response of maize plants better correlates with the abundance of the extraradical mycelium than with the accumulation of the mycorrhiza-inducible phosphate transporter ZmPT6.
Volpe et al [167-5] demonstrated that the expression of the mycorrhiza-inducible PT4 from M. truncatula and L. japonicus was not restricted to the PAM and present in the root tips of non-colonized plants.
This fungal ability to take up and transfer N is mirrored by the presence of specific plant transporters: several AM-inducible ammonium transporters have been identified in different species such as Lotus japonicus, Glycine max, and Medicago truncatula.
Plants have different families of sucrose transporters (SUTs) that can be involved in the sugar transfer to the colonized roots: in M. truncatula, the expression profiles of MtSUTs are finely tuned by the presence of the fungal symbiont [258], and the three sucrose transporters from tomato are up-regulated in roots colonized by Funneliformis mosseae [259].
M. truncatula antisense lines for the biosynthetic enzyme sucrose synthase (MtSucS1) in roots displayed an abnormal mycorrhizal phenotype, with an impairment of plant growth under phosphate limitation, a reduced mycorrhization and relevant alterations in the morphology and life span of the arbuscules [260].
Monosaccharides are the most likely sugar forms transferred to the fungal symbiont: consistently, plant monosaccharides transporters (MSTs) are finely regulated in roots upon mycorrhizal colonization [261], [262], [263].
Some specific isoforms of the SUT and SWEET transporters showed expression patterns that nicely followed the plant C partitioning: the expression levels of MtSUT2 and MtSUT4-1 positively correlated with the C allocation to the symbiotic partners, and MtSWEET12, MtSWEET15c, and MtSWEET15d were up-regulated in the mycorrhizal roots when the fungus had access to a N source,

but were down-regulated when the host plant was not under N starvation. Some very recent researches well characterized at the molecular level the dynamics of such a fatty acid auxotrophy, and clarified that lipids are likely transferred from the plant host to the fungus at the symbiotic interface (Table 1).
The RAM1 transcription factor has been identified as an early regulator of the mycorrhiza-specific reprogramming, activating on the one hand genes involved in the transfer of FAs to the fungus [264] and the AM-specific phosphate transporter PT4 on the other [265].

Findings

- In mycorrhizal plants, a considerable part (up to 70%) of the overall phosphate uptake can be acquired via the AM pathway [255-1]
- Mycorrhizal colonization increases the root sink strength, with up to 20% of photosynthates transferred to the fungus [266]

Builds on previous research

- Mycorrhizal plants exposed to high environmental heavy metal concentrations exhibited a wide spectrum of behaviors ranging from hyper accumulation to a reduction of the uptake, also including neutral responses (see Shi et al [17-3] for a review). Early reports showed that zinc uptake in maize was positively affected by AM fungi, with an increase of plant growth parameters [267]

Differs from previous work

- Taken together, these data strengthen the vision that the regulation of iron homeostasis might represent a relevant mechanism enabling AM fungi to cope with bacteria in the rhizosphere. Does the plant reward the fungus only with sugars? Early reports showed that sugars can be transported from the plant host to the fungus in the AM symbiosis [268], [269] (Table 1)

Contributions

- The nutrient exchange has surely been the more extensively studied aspect of the arbuscular mycorrhizal symbiosis. Yet, recent findings demonstrated that the scenario depicted in many years of research was far to be conclusive, and that much work is still needed to clarify the mechanics and the implications underneath this flow of nutrients. In particular, some important milestones have been recently placed:

  • In the fungus-to-plant direction, the relevant role of the transfer of nutrients other than P and N has been brought to light, as well as the intricate network of connections that orchestrates the regulation of the nutrient exchange as a whole;

  • In the plant-to-fungus direction, recent compelling results requested a real paradigm shift that shook up the mainstream bulk of knowledge: beside sugars, lipids are also transferred from the plant to AMFs, and their transfer might represent the key of the fungal obligate biotrophy.

  The advancements made in the deciphering of this multifaceted scenario are extremely meaningful for the mycorrhiza scientific community. Nonetheless, they are also

Data and code

- Availability of data and materials Not applicable Funding ASdF and MN received funding from MIUR-Ministero dell'Istruzione dell'Università e della Ricerca, Italy. Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations. Received: 13 December 2018 Accepted: 7 March 2019

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Floss_et+al_DellaProteinsRegulateArbusculeFormation_2013

DELLA proteins regulate arbuscule formation in arbuscular mycorrhizal symbiosis

D. S. Floss; J. G. Levy; V. Levesque-Tremblay et al.

2013

Abstract

Most flowering plants are able to form endosymbioses with arbuscular mycorrhizal fungi. In this mutualistic association, the fungus colonizes the root cortex and establishes elaborately branched hyphae, called arbuscules, within the cortical cells. Arbuscule development requires the cellular reorganization of both symbionts, and the resulting symbiotic interface functions in nutrient exchange. A plant symbiosis signaling pathway controls the development of the symbiosis. Several components of the pathway have been identified, but transcriptional regulators that control downstream pathways for arbuscule formation are still unknown. Here we show that DELLA proteins, which are repressors of gibberellic acid (GA) signaling and function at the nexus of several signaling pathways, are required for arbuscule formation. Arbuscule formation is severely impaired in a Medicago truncatula Mtdella1/Mtdella2 double mutant; GA treatment of wild-type roots phenocopies the della double mutant, and a dominant DELLA protein (della1-Δ18) enables arbuscule formation in the presence of GA. Ectopic expression of della1-Δ18 suggests that DELLA activity in the vascular tissue and endodermis is sufficient to enable arbuscule formation in the inner cortical cells. In addition, expression of della1-Δ18 restores arbuscule formation in the symbiosis signaling pathway mutant cyclops/ipd3, indicating an intersection between DELLA and symbiosis signaling for arbuscule formation. GA signaling also influences arbuscule

formation in monocots, and a Green Revolution wheat variety carrying dominant DELLA alleles shows enhanced colonization but a limited growth response to arbuscular mycorrhizal symbiosis.

Key concepts

#claim/gibberellic_acid; #arbuscular_mycorrhizal; #claim/symbiosis; #result/arabidopsis; #result/reduced_height; #medicago_truncatula; #result/NSP1; #result/biosynthesis; #result/GRAS; #claim/double_mutant; #CCAMK; #lotus_japonicus; #calmodulin; #gibberellins; #method/agrobacterium_rhizogenes; #arabidopsis_thaliana; #CASTOR

Quote

> The Arbuscular mycorrhizal symbiosis is of central importance to plant mineral nutrition, and arbuscules are critical for nutrient exchange between the fungal and plant symbionts

Key points

- Most flowering plants are able to form endosymbioses with arbuscular mycorrhizal fungi
- CYCLOPS/IPD3, a protein of unknown function that interacts with CCAMK, influences cortical colonization, and in Lotus japonicus and rice cyclops mutants, Arbuscular mycorrhizal (AM) fungal hyphae grow into the cortex, but arbuscules are not formed
- A reverse genetic screen that aimed to identify M. truncatula genes involved in AM symbiosis revealed that RNAi knockdown of a DELLA gene resulted in aberrant AM symbiosis
- The AM symbiosis is of central importance to plant mineral nutrition, and arbuscules are critical for nutrient exchange between the fungal and plant symbionts
- It is possible that the site of DELLA action may not be directly in the cortical cells where arbuscules develop, because ectopic expression of

della1-Δ18 in the vascular tissue and endodermis enables arbuscule formation in gibberellic acid (GA)-treated roots and in the della1/della2 mutant
- If the site of action is the vascular tissue and endodermis, DELLA proteins may interact with transcription factors that subsequently move to the cortex; alternatively, DELLA regulation of arbuscule formation may be indirect

Synopsis

Introduction

Most flowering plants are able to form endosymbioses with arbuscular mycorrhizal fungi
In this mutualistic association, the fungus colonizes the root cortex and establishes elaborately branched hyphae, called arbuscules, within the cortical cells.
Transcript profiling and promoter–reporter gene analyses indicate complex changes in plant gene expression in the root cortex during arbuscule development, suggesting that multiple signaling pathways may be involved in arbuscule formation [270], [7-3], [8-2], [9-1], [13-1], [10-1].
Transcriptome analyses reveal substantial alterations in the expression of genes encoding enzymes of gibberellic acid (GA) biosynthesis, degradation, and signaling during AM symbiosis [9-2], [248-2], [254-1], [14-5], [170-1], [271]
Consistent with these alterations, GA levels increase significantly in mycorrhizal roots [272].
The authors' data provide insights into regulation of arbuscule formation and identify a potential mechanism by which the plant can coordinate the symbiosis with its growth and nutrient status

Methods

Plants were grown in a growth chamber under a 16-h light (25 °C)/8-h dark (22 °C) regime at 40% relative humidity in sterile Turface (Profile Products) inoculated with 300 surface-sterilized G. versiforme or G. intraradices spores

per plant, as described [273], and fertilized once a week with modified half-strength Hoagland's solution containing full-strength nitrogen and 20 μM potassium phosphate.
To characterize the AM phenotype in della1/della plants (Fig. 1 A–C, E, and F), 2-d-old seedlings were planted in a sand layer 4 cm below the top of 20.5-cm cones filled with a sterile gravel/filter sand mixture (1:1 ratio) containing 300 surface-sterilized G. versiforme spores.
1D, 2, and 6), spore counting (Table 1), and plant phenotype evaluation (Fig. S4) were performed on plants growing in cones filled with a sterile gravel/sand mixture (1:2 ratio) inoculated with 500 surface-sterilized G. versiforme spores per cone.

Results

A reverse genetic screen that aimed to identify M. truncatula genes involved in AM symbiosis revealed that RNAi knockdown of a DELLA gene resulted in aberrant AM symbiosis.
In DELLA RNAi roots inoculated with Glomus versiforme, hyphal growth into the roots occurred as in wild-type roots, but development in the cortex was altered, and arbuscule formation was markedly reduced (Fig. S1).
There are three DELLA genes in the M. truncatula genome database Mt3.5: MtDELLA1, MtDELLA2, and MtDELLA3.
The encoded proteins share 56–68% identity with DELLA proteins of Arabidopsis (Fig. S2), and MtDELLA1 and MtDELLA2 are orthologs of Pea LA and CRY [16-1], which recently were shown to influence arbuscule formation [274].
To confirm and extend the RNAi results, M. truncatula lines containing Tnt insertions in MtDELLA1 and MtDELLA2 were obtained from a mutant population generated at the Samuel Roberts Noble Foundation.

Conclusion

The AM symbiosis is of central importance to plant mineral nutrition, and arbuscules are critical for nutrient exchange between the fungal and plant symbionts.

It is possible that the site of DELLA action may not be directly in the cortical cells where arbuscules develop, because ectopic expression of della1-Δ18 in the vascular tissue and endodermis enables arbuscule formation in GA-treated roots and in the della1/della mutant.
These experiments establish that DELLA can act from the vascular tissue and endodermis, but in the native situation a contribution from DELLA in the cortex cannot be ruled out.
DELLA proteins influence several other phytohormone-signaling pathways, so responses in the cortex could result from changes in other mobile signaling molecules [275], [276]; alternatively, a temporary restraint of root growth [277] may be necessary to enable arbuscule formation

Study subjects

5 independent samples

- Roots were harvested 7 wk after inoculation. Five independent samples of della1/della2 mutant and wildtype roots were analyzed. GA Treatment

3 SSP mutants

- Several components of the pathway have been identified, and in SSP mutants AM symbiosis is blocked at different stages of development. In three SSP mutants, including those with a mutation in a calcium calmodulin-dependent protein kinase (CCAMK/DMI3), hyphal growth is arrested in the epidermis [161-4], [255-2], [270-1], [168-1]. CYCLOPS/IPD3, a protein of unknown function that interacts with CCAMK, influences cortical colonization, and in Lotus japonicus and rice cyclops mutants, AM fungal hyphae grow into the cortex, but arbuscules are not formed

5 DELLA proteins

- DELLA proteins, a unique group of GRAS transcriptional regulators, are central players in GA signaling and repress GA responses and restrain growth [278], [279]. There are five DELLA proteins in Arabidopsis, two in pea,

and one in rice [18-1], [280], [281], [282], [283], [16-2], [284]. DELLA proteins contain domains typical of other GRAS transcription factors [285], but in addition they contain a unique DELLA domain at the N terminus

Data analysis

- #method/kruskal_wallis_rank_sum_test

Findings

- On average, the arbuscule density in della1/ della2 mycorrhizal roots was 85% lower than in control roots

Confirmation of earlier findings

- In Arabidopsis, a role for DELLA proteins and GA signaling in Pi-starvation signaling has been established, and DELLA proteins regulate a subset of the adaptive responses to Pi starvation, including alterations in root architecture [286]. Here, we demonstrate that in M. truncatula DELLA1 and DELLA2 are required for arbuscule formation, as is consistent with a recent report that arbuscule formation is impaired in a pea cry, la mutant [274-1]
- A link between GA and NSP2 has been reported during nodulation when Nod factor-induced expression of NSP2 was suppressed by GA treatment [287]. Consistent with these data, we found that nodulation in the della1/della2 mutant was reduced significantly (Fig. S9)
- Furthermore, TaPT10 and TaPT11 transcripts, which encode AM-induced phosphate transporters belonging to the MtPT4 subfamily [268-1], also were significantly higher in the Rht1/Rht2 line than in the wild type (Fig. 7 C and D), suggesting an increase in arbuscules numbers. These data are consistent with the effects observed in M. truncatula expressing della1-Δ18, and we observed a similar effect in Maize D8 [288], [269-1], a dominant della mutant

Data and code

- supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1308973110/-/DCSupplemental.

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