Physiological and Molecular Plant Pathology 102 (2018) 36–45

Contents lists available at ScienceDirect

Physiological and Molecular Plant Pathology

journal homepage: www.elsevier.com/locate/pmpp

AMF: The future prospect for sustainable agriculture

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ARTICLE INFO

Article history:
Received 19 August 2017
Received in revised form
29 October 2017
Accepted 17 November 2017
Available online 21 November 2017

Keywords:
Arbuscules
Mycorrhiza
Phosphorus
Signaling
Strigolactones
Systems biology

ABSTRACT

A wide range of association exists in nature of which symbiotic association is the most evolutionary conserved where both the partners are mutually benefited. However, these associations of the plants with microorganisms are both harmful as well as beneficial. Hence the key to survival for plants is to promote beneficial symbiotic associations and prevent the intruding pathogens. In this review, we focus on the beneficial role of mycorrhiza, a heterogeneous group of fungi primarily associated with plant roots. Out of these associations, one group of root obligate mycorrhiza provides the host plant with water nutrients and importantly protects from pathogens, called Arbuscular mycorrhiza fungi (AMF). This association helps in improving the nutrient supply like nitrogen and phosphorus to the plants and in turn, the fungus gets 20% of the fixed carbon from the plants. The nutrient transfer is established by the help of structures called arbuscules and the release of 'Myc factors' by fungus and strigolactones by plant root exudates induces the symbiotic reactions. A coordination of these two factors, in turn, switches on the downstream signaling cascades that further strengthens the association. In the course of research over the years several genes like novel transporters or receptor kinases have been identified that favors the association and in turn helps in dissecting the cellular responses. In this review, we discuss the current status of several studies, which unravel the contributions of partners involved in these symbiotic associations and can be exploited for improvement of agricultural crops in diverse environmental conditions.

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https://doi.org/10.1016/j.pmpp.2017.11.007
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1. Introduction

Mycorrhiza refers to the association between plant roots and biotrophic mycorrhizal fungi, these mycorrhizal fungi form a network of filaments associated with plant roots and enable roots to absorb the nutrients from the soil. Moreover, this fungus-plant alliance stimulates plant growth and accelerates root development. Mycorrhiza is classified into five groups based on their morphological characteristics as arbuscular, arbutoid, ectoericoid, monoptropoid and orchid [1]. Arbuscular mycorrhiza (AM) is the most common variety of mycorrhizal fungi, these are microscopic and branched forms found in the cortical cells of root [2]. These AM fungi are found in 80% of vascular plants and involved in diverse roles from accelerating the nutrient uptake to improve plant development and improve soil health and properties thereby influencing the ecosystem. Previously, it has been shown that fungal-host interaction can produce microbe-associated molecular patterns (MAMPs), exopolysaccharides, volatile organic compounds (VOCs), Myc factors, and Nod factors [3]. Moreover, VOCs have demonstrated ability to modulate root system architecture favoring symbiotic associations and also modulate Nod factor signaling pathway enabling AMF colonization [4]. The initiation of AMF symbiosis with host plant involves varieties of plant genes, hormones etc and of these strigolactones and fungal-derived lipochito-oligosaccharides have been identified as key players [5]. In addition, *NSP1* and *NSP2* and DELLA proteins like *SLR1* (S-locus-related gene 1) are known to play a role the development of arbuscules and AMF infection [6]. Furthermore, it can also be said that a thorough identification and characterization of the fungal effectome can be of immense help in understanding the interaction of the fungus and the plants [7]. In this review, we have compiled and summarized the current knowledge regarding AMF symbiosis in plants. We present an overview of different phases of AM association with plant roots, the role of AM in nutrient absorption and phytohormone signaling. This review shades light on AMF as primary biotic soil component, which is important for efficient ecosystem functions. Information presented here can be used to improve plant AMF symbiosis and these improvements open a new avenue to employ AMF as bio-fertilizers for sustainable agriculture systems.

2. Perception of fungal signals by plants

Plants response to the infection is organism dependent and the detection of the pathogen-derived elicitors triggers the signaling cascade before being suppressed by AM symbiosis. The Myc (mycorrhization) factors which are fungus-derived soluble compounds induce the expression of mycorrhizal-responsive genes that finally triggers phenotypic changes in the roots. Researches have shown that SYM genes that are common for both bacterial and fungal endosymbioses are induced upon colonization by AM and perception of the Myc factors by the roots suggesting a conserved and concerted gene signaling cascade operating in response to colonization by bacteria or fungi [8,9] (Fig. 1).

2.1. Initial symbiotic phase

Appressoria formation establishes the cell to cell contact between the plants and the fungus thereby signifying the onset of symbiosis and also suggesting that a contact has been established between the plant root and the fungus [10]. These are flattened, elliptical hyphal tips whose onset triggers changes in fungal gene expression profile. Though the appresoria formation signifies the attachment, but for the fungus to propagate and penetrate into the host cell requires the coordinated action of the intact host cells [11].

2.2. Penetration of AMF

The fungal penetration into the host plant occurs by the use of either i. a penetration hypha ii. Infection peg originating from the appresorium that forcefully penetrates the cell iii. By synthesis of enzymes that can help dissolve the cell wall. Previous researches in lotus have shown that the fungal invasion of the host occurs by formation of an epidermal cleft between the two nearby rhizodermal cells through which the fungus enters and then slowly moves to the exodermal cells [9]. Additionally, the fungus can penetrate the roots directly as observed for *Medicago truncatula* [8]. Besides these various researches have also demonstrated the synthesis of various cell wall degrading enzymes like cellulases, xyloglucanases and pectolytic enzymes including polygalacturonase thereby suggesting that fungal colonization of plant roots involves both mechanical and enzymatic mechanisms along with coordination from the host machinery to allow successful penetration [10]. Initiation of fugal symbiosis is marked by the induction of Mycorrhizal Induced Small Secreted Protein7 (*MiSSP7*). Hartig net a symbiotic structure that favors the nutrient exchange between the plant and fungus is also facilitated by *MiSSP7* by coordinately regulation of genes involved in remodeling of the cell wall and auxin homeostasis. Hence it is an important fungal effector protein needed for symbiosis establishment. *XHT1*, an endotransglucosylase/hydrolase gene identified from *M. truncatula* was also shown to help fungal penetration to establish symbiotic association by modifying the cell wall structure of plants [12] (Fig. 1).

2.3. Mature phase: signaling

Paris and *Arum* are two main types of AM symbioses with Paris type symbolized by fungal coils that develop directly from cells with no intercellular phase while the AM type, on the contrary, is characterized by arbuscule, a tree-like fungal structure formation [13]. The formation of arbuscule is key feature of AM symbiosis as they represent extreme intimacy and serve as the site of nutrient transfer [14]. Analysis of the M. truncatula mutant stunted arbuscule (str) identified another transporter that is induced by AM symbiosis *STR2*. It has been shown that *STR1* heterodimerizes *STR2* and the resultant complex was found in the peri-arbuscular membrane suggesting that they are necessary for the development of arbuscules and hence AM symbiosis (Zhang et al., 2010).

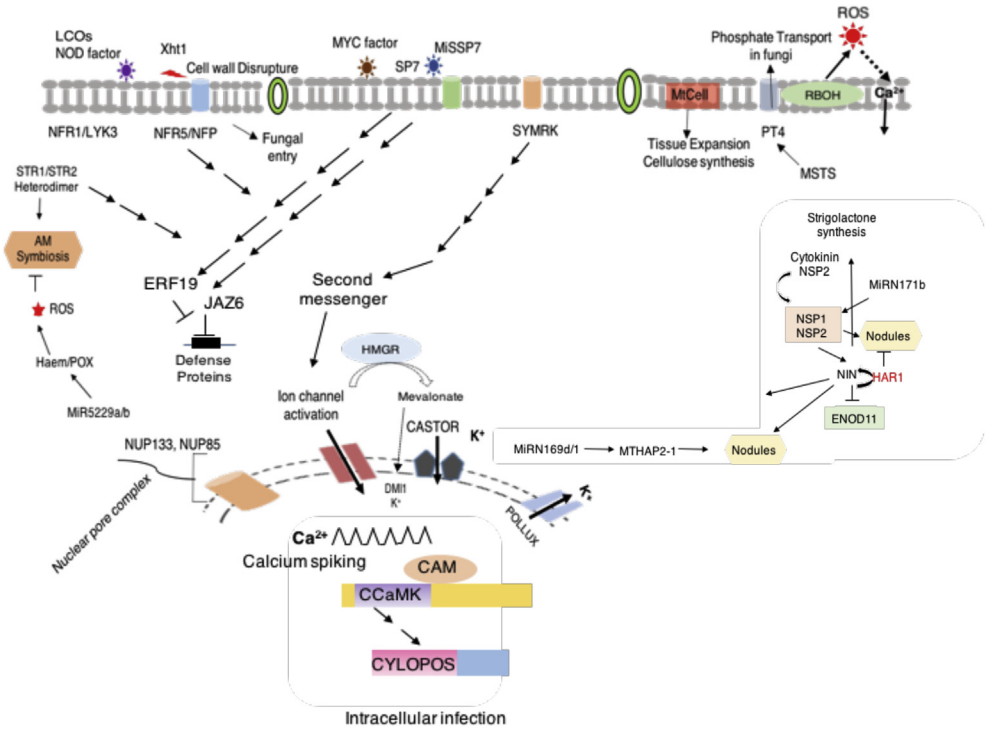

Fig. 1. A model of gene regulation during plant and mycorrhiza interaction. The figure summarizes how the plants sense and perceive mycorrhizal signal through the involvement of various proteins like NOD factors, SYMRK, calcium signaling proteins etc. This model is a summary of the information done on different plants combined into one to give a detailed information of the complexity of the signaling network in plant mycorrhizal interaction.

The host cell undergoes tremendous changes after arbuscule formation, but the arbuscucle collapses after 2–4 days preparing the host cortical cells to host another arbuscule [11,15]. Arbuscule formation probably is initiated when the host cell perceives a sugar gradient developed between the outer cell layers and the vascular tissue. Proteins of SYM pathway like *LjCASTOR*, *LjSYM15*, *LjNup 133* and *LjSYM* 24 plays a crucial role in arbuscule development [16]. Root nodule colonization by AMF begins with the recognition of Nod-factors by *NFR1* and *NFR5* (LysM receptor kinases). Induction of the receptor kinases connects the symbiotic signaling pathway to SYMRK. Researches have shown that silencing of *Nfr1* or *Nfr5* leads to impaired nitrogen fixation. Further, it has been identified that Myc-LCO receptors bears structural analogies to *NFR1*/*LYK3* and *NFR5*/*NFP* and also can perform the same function [17,18]. *SYMRK* (symbiosis receptor-like kinase) in addition to acting as co-receptors during Nod signaling they also play a pivotal role as a coreceptor for interaction with the specific receptor. Moreover, it has also been shown that SYMRK interacts with mitogen-activated protein kinase kinase (*MAPKK*) as well as 3-hydroxy-3-methylglutaryl-CoA reductase (*HMGR*) thereby suggesting that they can play an important role in coordinating signals between ion channels associated with the nucleus as well as membrane-bound receptors. Another key gene that could have a direct role in mycorrhizal symbiosis establishment is *CYCLOPS* that is phosphorylated by *CCaMK* (Calcium and calcium/calmodulin-dependent serine/threonine-protein kinase). However, the exact function played by *CYCLOPS* is still unknown [19]. NUP133 and NUP85 are important nucleoporin proteins that are involved in calcium spiking in the common symbiosis pathway (CMP) [12,20] (Fig. 1). Thus it can be concluded that the arbuscular formation and accommodation of intracellular structures is a complex physiological process that involves a coordinated network of many genes.

3. Role of mycorrhiza in plant nutrition

3.1. Phosphorus absorption

Symbiotic relations established between AM and host plant offers major advantages like it provides an effective pathway by which is phosphorus is scavenged from the soil and directly transferred to the root and also it helps reduce the effect of P deletion from the rhizosphere and thereby help plant P nutrition. Symbiosome is the site for mutual nutrient exchange between the host plant and the fungi which is the arbuscules for AM and plant interaction. Not much is known about the structural composition of the periarbuscular membrane a key interface for the symbiotic interaction. The nutrient exchange between the host and the microbe is a tightly controlled process mediated by membrane transport proteins like as phosphate transport and the P-type H^+-ATPase [21]. Recent studies on live cell imaging of periarbuscular membrane have identified two domains: arbuscule branch domain' comprising of MtPT4 phosphate transporter specific for symbiosis and arbuscule trunk domain consisting of MtBcp1 a copper binding protein [15]. Previous researches on *Broomsedge*, a dominant grass has shown that mycorrhizal inoculated plants were able to survive under low Pi and exhibited higher phosphorus use efficiency in comparison to the non-mycorrhizal plants. These observations suggested that mycorrhizal inoculation helps maintain the nutrient homeostasis through alteration in the uptake of nutrients their allocation and use [22]. The expression of Pi transporters (PiTs) gets reduced in the mature regions of the root and the decline in expression can be possibly due to higher P supply and AM colonization [23]. Over the year's researchers have identified Pi transporters from different plant species: two in rice (*OsPT11* and *OsPT13*) [24,25]; three in solanaceous species (*StPT3*/*LePT3*; *StPT4*/*LePT4* and *StPT5*/*LePT5*) [26] and one each from wheat, maize and

barley [27]. The signal transduction components are in response to Pi starvation are conserved in plants that can host AM. Analysis of promoters of several AM-induced PiTs has identified several cis-acting elements including P1BS located near the AM-specific motif, MYCS suggesting that both of them are required for the activation of the AM-induced PiT promoters [28]. *miR399* transcript accumulated at higher levels in AM roots accompanied by a reduced expression of *PHO2* suggesting that the expression of *PHO2* should be kept low to sustain AM symbiosis [29]. Previous researchers in tomato have identified miR395 to be induced only by AM colonization while miR172 is induced by both AM inoculation as well as by high P concentration indicating that they might serve as a link between direct uptake and AM mediated pathways [30]. *Mt4*, a noncoding RNA and a Pi starvation-induced phosphatase gene has been identified to be downregulated in response to AM symbiosis [31]. Sugar signaling mediated by Suc has been recently identified to be interconnected to Pi starvation responses. Previous reports on the bean (*Phaseolus vulgaris*) have shown that sucrose accumulation leads to the induction of miR399 and these in turn lads to physiological changes [32]. Not only the mycorrhizal fungi benefits by getting carbon from the host plant but they are also benefited by lipid transfer which is otherwise absent in the fungi [33]. This has been confirmed in *Lotus japonicas* with studies carried out with mutants deficient in lipid biosynthesis genes like *KASI* (β-keto-acyl ACP synthase I) and *GPAT6* (glycerol 3-phosphate acyl transferase) that inhibits fungal development and accumulation of 16:1ω5 FAs in the fungi [34]. Identification of transcription factor *RAM1* (REQUIRED FOR ARBUSCULAR MYCORRHIZATION 1) that is necessary for induction of lipid biosynthesis pathway in plants colonized with fungal arbuscules has further validated the hypothesis that lipids are another carbon source that is transferred to the fungi from plants for the synthesis of their lipids [35,36].

3.2. Nitrogen absorption

Plant growth is also affected by the depletion of nitrogen from the soil and the mycorrhiza can help uptake nitrogen from the soil and transfer to plants as well as provide means to increase the utilization of different forms of nitrogen. Moreover, the AM fungi can uptake nitrogen directly and transfer it to the host roots. Recent researches have shown that when the hyphae are supplied with nitrate and ammonium the nitrates are absorbed by active transport coupled to protonated-symport mechanism while NH^+_4 is taken up by antiport mechanism with a H^+ efflux. When ammonium is the sole N source its assimilation could result in the loss of carbon for the fungus due to its increased consumption in the roots. Arginine has been implicated to play an essential role in nitrogen transfer between fungal and plant cells during periods of ammonium feeding and are finally absorbed by the fungal systems through NH^+_4 assimilation GS/GOGAT cycle has been found in AM fungi that play a role in the conversion of accumulated N and incorporation into amino acids. Of the two functional isoforms of glutamine synthetase (GS) identified in R. irregularis GiGS1 and GiGS2, the former is constitutively expressed in the ERM while the latter is inducible by NO^-_3. These observation helps suggest that GiGS1has a vital role in N assimilation during N deprivation while GiGS2 under N abundance [37]. Extraradical mycelium uptakes inorganic nitrogen incorporates into amino acids, translocated as arginine to the fungal structures and then finally transported to the plant's ammonium [38,39]. This hypothesis is further validated by transcript abundance of key enzymes involved in nitrogen assimilation and arginine catabolism [38]. The fungal cells are able to maintain a lower concentration of ammonia in the cytoplasm that can be assimilated and transported to the plant roots mediated either by protein interaction or by passive efflux of the reduced form instead of Amt proteins (ammonia transporter) [40]. Based on previous researches several hypotheses have been proposed for the transfer of ammonia from fungal to plant cells i. Nitrogen from the soil is taken up in the inorganic form and then incorporated and stored as arginine ii. Absorbed N is assimilated by the AM fungi through GS/GOGAT, asparagine synthase and the urea cycle iii. The transportation of the stored arginine to intraradical mycelium can be done together with PolyP or can be done bidirectionally as well iv. Finally, the nitrogen released from the stored arginine is transferred to the plants as NH^+_4 which is then incorporated in the roots as other free amino acids [38–40]. The expression of ammonium transporters from AM fungus *Rhizophagus irregularis, GintAMT1* is inversely related to the NH^+_4 concentration while *GintAMT2* is constitutively expressed under N limiting conditions. However, the expression of nitrate transporters is suppressed when NH4+ is available a phenomenon known as N catabolite repression and also regulates the expression of ammonium transporters in fungi [41]. Glutamine has been reported to repress the expression of NH^+_4 in ectomycorrhizal fungi [42]. Researches have shown that GATA transcription factors play a crucial role in N catabolite repression and further analysis of *GintAMT2* showed the presence of GATA core sequences [43]. *RiPTR2* a putative dipeptide transporter identified from *Rhizophagus irregularis* has also been recently suggested to play a vital role in the reabsorption of peptides from the apoplast [44]. The nitrogen uptake can probably take place at the arbuscule involving several plant-encoded nitrogen transporters found in the periarbuscular plant membrane [11]. In addition to providing the balance between N mineralization to plants demand for N, it also helps in recycling the plant residue into living biomass thereby significantly affecting the microbial community in the soil [45,46].

4. Stimulation of phytohormones production

4.1. ABA

The development of fungal colonization in the host plant is a complex process that involves well-orchestrated changes in morphology as well as gene expression changes leading to a significant alteration in signaling cascades. The AM fungi also produce compounds that are similar to plant hormones like auxins, cytokinins (CKs) that helps in the growth and development of the plant. Similar to plants where ABA is synthesized by MEP and mevalonate pathway the fungi also use the mevalonate pathway and makes use of different precursors of ABA [47,48]. Some studies have shown the role of ABA in mycelium production and growth. Exogenous application of ABA to *Ceratocystis fimbriata* showed a slight increase in growth while in *M. oryzae*, ABA stimulated the production of appresoria as well as it increased germination as well [49]. The role of ABA in plant-fungal symbiosis was substantiated by research carried out with ABA-deficient mutant *sitiens* in tomato. It has been shown that the arbuscular morphology of *Glomus intraradices* (indicated by reduced alkaline phosphatase activity) exhibited reduced frequency and intensity of root colonization. The fungal activity was restored upon exogenous application of ABA. Researches carried out with transgenic plants, ABA-deficient mutant, *notabilis* or ABA and ethylene biosynthesis inhibitors supported the idea that ABA deficiency hampers mycorrhizal intensity/hyphal colonization, reduces arbuscular formation and increasing the levels of ethylene probably due to the increase in the expression of defense-related genes and modification of cell walls [50,51].

4.2. Ethylene

Unlike ABA, the increase of ethylene negatively affects the plant growth and the negative effect can be alleviated by controlling the

ethylene levels. Moreover, ethylene also negatively affects the AM colonization especially under P deprivation and this has been observed in *Pisum sativum*. Studies conducted using inhibitors of ethylene biosynthesis like aminoethoxyvinylglycine had a positive influence on symbiosis [52,53]. In *Solanum tuberosum*, ethylene production is decreased due to the synthesis of phenolic compounds in the roots facilitating symbiotic association and further development gets inhibited due to enhanced P uptake resulting from symbiotic association [54] suggesting the specificity of mycorrhizal symbiosis. Hence it can be concluded that the plants that are mycotropic produce some compounds that inhibit the negative regulators of AM symbiosis. Recent studies have shown that similarity exists between mycorrhizal and N symbiosis like both *Sinorhizobium meliloti* and *G. intraradices* induces the expression of *ENOD11* (Medicago truncatula Early Nodulin) [55] (Fig. 1). Analysis of the *ripening inhibitor* (*rin*) mutant, MADS-box transcription factor that inhibits ripening and ethylene-overproducing mutant *epinastic* in tomato displayed the inverse effects of ethylene on mycorrhizal colonization [56].

4.3. Strigolactones

Strigolactones are sesquiterpenes lactones newly identified plant hormones from parasitic weeds that affect fungal symbiosis [57–59]. Strigolactones synthesized in the carotenoid pathway and synthesis of these molecules dependent on the strategies used by the plants in the absorption of nutrients [60,61]. These compounds are involved in various physiological and cellular processes like inducing hyphal branching, respiratory processes in fungi by regulating the activity of mitochondria and lipid catabolism and thereby inducing the expression of Myc factors [62]. Strigolactones are produced and used in very low concentration indicating the presence of strong receptors in the fungus and are regulated by ethylene and ABA suggesting an active hormonal crosstalk [63,64]. Recent researches conducted with two strigolactones insensitive mutants from rice and peas of an orthologous F-box protein that is responsible for protein degradation through SCF (Skp, Cullin, F-box containing complex) complex have shown that AM symbiosis is highly reduced [65,66]. Nodulation signaling pathway 1 (*NSP1*) and *NSP2* encoding two GRAS domain transcription factors are associated with nodulation signaling and LCO signaling associated with AMF until recently when it has been shown to be associated with strigolactone biosynthesis [19] (Fig. 1 and Fig. 2). However, defining the role for this hormone in AM symbiosis requires further analysis. Formononetin is another group of signal molecules that promote AM colonization by enhancing fungal sporulation. Increased sporulation thereby helps to boost the inoculum potential of the AM fungi. Moreover, it has also been seen that in addition to promoting AM formation they also trigger plant growth like stomatal activity, photosynthesis and shoot growth as observed in Russet Norkotah potatoes. Further, it also increases the yield of potato tuber and the formation of extraradical hyphae [67].

4.4. Jasmonic acid, salicylic acid

Though the role of JA in responses of plants to pathogen has long been studied its role in AM colonization needed to be studied. Researches, conducted using exogenous application of JA (or derivatives such as methyl jasmonate) have shown from positive as well as the inhibitory effect on fungal colonization. It has been seen that in transgenic plants, down-regulation of *allene oxide cyclase* gene resulted in delayed AM colonization [68]. This hypothesis of the positive role of jasmonic acid were further validated by observations using JA-deficient *spr2* mutant in tomato which also showed delayed AM colonization, and the activity of fungal colonization was restored by exogenous application of MeJA [69]. Like JA, salicylic (SA) acid also helps to protect plants against biotic stresses and hence its believed that it will be induced during AM symbiosis. This hypothesis is validated with researches carried out in pea roots where increased SA concentration is observed during early stages of AM symbiosis. Researches carried out with transgenic tobacco plants overexpressing bacterial *nahG* gene, which encodes the enzyme salicylate hydroxylase an enzyme that inactivates SA and transgenic CSA (constitutive SA biosynthesis) overexpressing bacterial genes that can convert chorismate to SA (enhanced SA level) have shown that NahG plant showed increased AM colonization than CSA. However, it was noted that root colonization was unaffected at the end of the experiment. These studies suggest that SA can delay the root colonization but does not affect the symbiotic potential [70]. To make an effective conclusion about the roles of these two hormones further studies are required combining molecular, genetic and physiological approaches monitored over the course of colonization in a specific system.

4.5. Cytokinin and brassinosteroids

Previous researches had shown that levels of cytokinin were increased in AM colonized plants but recent studies conducted with cytokinin-insensitive *Medicago truncatula*, *cre1* mutant have suggested that cytokinins may not play an effective role in mycorrhizal development [71]. As previously reported that GA's are produced by AM fungi, so researches were conducted in *Medicago truncatula* to study the expression of GA related genes of which six of them were upregulated when infected with AM fungi and these results were consistent with previous observations from tomato [72]. Moreover, researches have shown increased accumulation of the active form of GA i.e. GA_1 instead of GA_8 in the AM colonized roots but still there are ambiguities regarding the role of the hormone in AM colonization and hence researches needs to be carried out using AM sensitive plants to explore their role in AM symbiosis. In addition to the known phytohormones, brassinosteroids (BRs) are another class of steroidal hormones that are responsible for cell growth and differentiation, responses to various stresses and photomorphogenesis. Several BRs have been identified over the years from different plant species. However not much is known about the contribution of BRs in AM symbiosis. Recent researches conducted with d^X mutants (extreme dwarf) from tomato defective in BR synthesis showed reduced mycorrhization and also a reduction in the level of sugars that acts as an energy source for establishing and sustaining a functional mycorrhiza suggesting that they might have a role in AM symbiosis. *SlSUT2* a sucrose transporter has been identified and known to interact with signaling components of BR metabolic cascade to control mycorrhizal symbiosis [73]. Similarly, expression of *MSBP1* (Membrane steroid-binding protein 1), identified in *Medicago truncatula* as another key player, found necessary for the establishment of AM symbiosis [74]. To further elucidate the role of BRs, studies were carried out using rice mutant *brd2-1* that are defective in the expression of *DIM/DWF1* (*DIMINUTO/DWARF1*) the interacting partners of *SUT2* from tomato. When the wild-type Nipponbare and the mutant plants were treated with *Rhizophagus irregularis*, and the results monitored after 4 weeks of inoculation they showed reduced AM symbiosis. Moreover, gene expression analysis of *SlSUT2* homologs in rice (*OsSUT4*) showed reduced transcript accumulation in the mutants [75]. In a recent study in Arabidopsis with a leaky mutant (lkb) of *DIMINUTO* gene catalyzing the conversion of 24-methylenecholesterol to campesterol showed reduced levels of BR in the vegetative tissues but no difference in AM colonization was observed in comparison to the wild-type. These findings suggest additional experimental

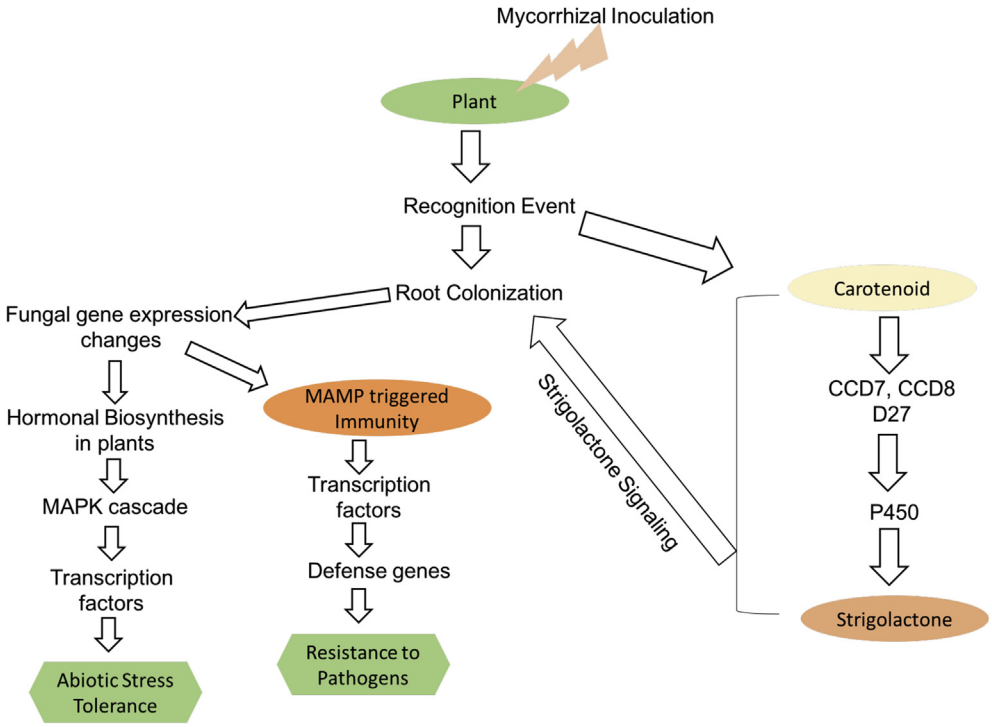

Fig. 2. A schematic Representation of plant's response to mycorrhizal inoculation and induced tolerance to abiotic stress and pathogen attack.

analysis needs to be carried out to elucidate the role of BR more precisely in AM symbiosis.

4.6. Mycorrhizal inoculation and secondary metabolism in plants

AM symbiosis in plants has been shown to contribute significantly towards synthesis of secondary metabolites as well. Recent researches have focused on the contribution of mycorrhizal inoculation in plant roots on isoprenoid metabolism. Mycorradicin and blumenin, cyclohexenone derivatives of carotenoid origin are two pigments that accumulated in the legumes upon inoculation with mycorrhiza. Analysis of the biosynthetic pathway for mycorradicin have identified the increased accumulation of 1-deoxy-D-xylulose 5-phosphate synthase (DXS) and 1-deoxy-D-xylulose 5-phosphate reductoisomerase (DXR) in mycorrhizal plants and hence identifying that the synthesis takes place throughnon-mevalonate methylerythritol phosphate pathway (MEP pathway). Flavonoids have been suggested to play to play a significant role in the AMF-plant symbiosis either by controlling differentiation of the hyphae, growth of hyphae and colonization of roots [76]. Some flavonoids have been shown to have a stimulatory effect on the AMF interaction on plants and this effect is more obvious in the presence of rhizospheric concentrations of CO_2. In addition, it has been shown that the alteration in the profile of flavonoids in the root extracts is obtained through changes in the expression of genes involved in flavonoid, phenylpropanoid and isoflavoid metabolic pathway [77]. However, recently it has observed that both the accumulation and stimulatory effect of flavonoids are dependent on the genus and species specificity of the AMF. Phytoalexin and medicarpin two flavonoids have been reported to have accumulated in the colonized roots at a later stage. Though the flavonoids have been identified during the early stage of AMF symbiosis initiation but their active participation as a signaling molecule is still questionable but their regulatory role after establishment of AMF symbiosis is undoubted. Phenolic compounds produced by plants have been also identified to play a significant role in the initiation of AM symbiosis but the penetration of the roots and the establishment of AM symbiosis is dependent on the host and the interaction of the host plant with fungus. This observation has been validated by colonization experiments with (AM) fungus Glomus done on clover and sorghum (Sorghum bicolor L.) by using phenolic compounds like p-coumaric acid, p-hydroxybenzoic acid, or quercetin as growth stimulator. Simultaneously, strigolactones that are present in the root exudates of different plants have also been shown to positively influence AMF symbiosis by influencing the AMF establishment, branching of the hypha or the directed growth of the AMF [58,78]. Furthermore, it can also be said that AMF inoculation can serve as a key factor in improving the essential oil (terpenoid) concentration in the medicinal plants. Thus to conclude it can be said that a detailed analysis can lead to designing of new strategies that can result in increased accumulation of secondary metabolites in the roots/leaves of mycorrhizal inoculated plants and thereby play a significant in contributing to human health benefits.

4.7. Mycorrhiza-induced resistance against pathogen attack

Plants treated with mycorrhiza adapt very well to changing environmental conditions. Researches conducted in the last few years have shown that symbiotic associations established between the plants and AMF confers resistance to the plants enabling survival from pathogen attack but the molecular mechanism governing mycorrhiza-induced resistance (MIR) is not well characterized. It has been shown that tomato plants colonized with AMF *Rhizophagus irregularis*, *Funneliformis mosseae* developed increased resistance against *Botrytis cinerea,* early blight disease caused by *Alternaria solani* Sorauer by modulating the oxylipin pathway identified through increased accumulation of vitamins folic acid and riboflavin etc. [79] as well as by changes in the in activities of β-1,3-glucanase, chitinase, phenylalanine ammonia-lyase (PAL) and

lipoxygenase (LOX). Moreover, they have also shown that tolerance to pathogen attack is also mediated by jasmonate signaling [80]. MIR mediated by mycorrhiza is a complicated response mediated by hormonal crosstalk. To study the involvement of jasmonic acid and salicylic acid in MIR against *A. alternata* was studied by estimating the level of enzymes involved in their biosynthesis as well as the intrinsic levels of these hormones. It was observed that the higher levels of these enzymes correlated well with the hormonal levels in the inoculated plants. These observation were further validated by increased expression of genes involved in JA biosynthesis like (*OPR3*) as well as SA responsive genes like PR1 and wound-inducible polypeptide prosystemin [81]. Recently it has been shown that inoculation of potato plants with Rhizophagus irregularis MUCL 41833 enhances defense response against *Rhizoctonia Solani* mediated by *ERF3* thereby suggesting the involvement of ethylene signaling pathway [82]. In addition, to the role played by mycorrhizas in protecting against pathogen attack it has also been shown to provide protection against herbivory. Tomato plants inoculated with *Glomus mosseae* negatively affected the larval performance of chewing caterpillar *Helicoverpa arimigera* by inducing the expression of defense-related genes like LOXD, AOC, PI-I, and PI-II and also activates the JA pathway [83]. Two Corn varieties Gaoyou-115 and Yuenong-9 that are sensitive and resistant to sheath blight disease caused by *Rhizoctonia solani* were used for identifying the role of mycorrhiza in providing protection against the disease. It was observed that pre-inoculation of corn plants with *G. mosseae* increased the disease resistance of corn plants to sheath blight by inducing the accumulation of 2,4-dihydroxy-7-methoxy-2 H-1,4-benzoxazin-3 (4 H)-one (DIMBOA) and defense response mediated by increased accumulation of defense-related genes *PR2a*, *PAL*, and *AOS*, as well as *BX9* [84]. Mycorrhizal inoculation has proven effective in providing protection against pathogen attack in rice as well by enhancing the defense response through the induced accumulation of genes like *OsNPR1*, *OsAP2*, *OsEREBP* and *OsJAmyb*, genes from signaling pathway (*OsDUF26* and *OsMPK6*) and genes that function in calcium-mediated signalling processes like *OsCBP*, *OsCaM* and *OsCML4*. Thus it can be said that the enhanced resistance to blast fungus *Magnaporthe oryzae* can be attributed to increased expression of defense effector and regulatory genes respectively [85,86]. Researches over the years have identified secreted protein 7 (SP7) as an important protein that play a negative role in plants defense machinery. It reduces the plant's defense response by interacting with ERF19. Hence, it can be said that the identification of an effector protein from AMF that suppresses the plants defense response making it more vulnerable to pathogen attack is an important point that needs to be considered when we are exploring the future of a sustainable agriculture using AMF [87] (Fig. 1). Hence it can be said that the defense response inflicted on the plants by mycorrhizal inoculation is highly dependent on the differential effect of the AM fungi on the physiology of the plants, type of the pathogen and finally the ability of the plants to adapt to the changing conditions in response to the biotic stresses [88] (Fig. 2).

4.8. Role of mycorrhiza in abiotic stress response

Osmotic Stresses: Drought, Salinity and Temperature.

Plant growth and productivity are adversely affected by environmental stresses like salt, drought etc. Recent researches have shown that the soil microbiome can be effective in controlling the detrimental effects of abiotic stresses but the mechanism is still not clear. Tolerance to the abiotic stresses involves different aspects like alteration in photosynthetic carbon metabolism, changes in signaling cascade, hormonal crosstalk and antioxidant machinery. To study the role of mycorrhiza in the allocation of carbon resources to different classes of isoprenoids like volatile nonessential isoprenoids (monoterpenes and sesquiterpenes) and the non-volatile essential isoprenoids (abscisic acid, chlorophylls, and carotenoids) the plants were subjected to drought stress and exogenous application of JA. It was observed that the colonization by AM fungi increased the accumulation of essential isoprenoids and proposed that since mycorrhiza itself are a source of nutrient uptake for plants the plants can eventually use the carbon reserve for the synthesis of essential isoprenoids that can be used to facilitate their growth [85]. Inoculation of the Talh tree (*Acacia gerrardii* Benth.) with arbuscular mycorrhizal fungi increased tolerance to the damage caused by salinity stress by upregulating the antioxidant enzymes as well as by modulating the level of osmoprotectants like glycine betaine, proline, and phenols [89]. Experiments done on root colonization with *Funneliformis mosseae* in trifoliate orange seedlings showed that it can alleviate the effects of drought stress by inducing efflux of hydrogen peroxide in taproot and lateral roots [90]. GintAQPF1 and GintAQPF2 two aquaporin genes identified from Glomus intraradices were shown to have positive correlation with survival under drought stress [91]. Moreover, another effect of AMF induced drought tolerance is achieved through osmotic adjustments mediated by accumulation of compounds like proline, chlorophyll, carotenoids [92]. AMF inoculation in plants also enables survival under drought by enhancing the water content through improved water absorption of water by the hyphae and in turn reducing the ROS accumulation. Enzymatic and non-enzymatic antioxidants have also been proposed to be involved but the exact mechanism is not yet understood [93]. Aquaporin accumulation modulating water transport and mobilization of N compounds, signaling molecules, or metalloids in response to mycorrhizal inoculation in drought-stressed maize plants have been proven effective in conferring drought tolerance [94]. AM fungi have been reported to improve drought tolerance by increasing the water use efficiency, stomatal conductance or by upregulating the abundance of glycoproteins like glomalin [95]. A similar effect of increased salt/high temperature tolerance was observed due to increase in antioxidant enzymes, ascorbic acid content and attenuated the metabolic heat flux and fatty acid desaturation in leaves when salt sensitive barley (*Hordeum vulgare*) cultivar Ingrid was inoculated with mycorrhiza [96–98]. Trehalose, a carbohydrate reserve in AMF has been proven to extend protection against abiotic stresses like heat or chemical stress [99].

4.9. Heavy metal stresses

In addition to providing protection against osmotic stresses, mycorrhiza inoculation has also been reported to provide protection against heavy/transition metal contamination like arsenic or copper and cadmium [100–102] by increasing the uptake of nutrients like nitrogen and phosphorus [103] or by regulating the osmoprotectants (Fig. 2). There are several mechanisms involved in the AMF induced cleaning of heavy metals from soil like i. dilution of the metal by promoting the growth of plants ii. synthesis of organic acids by the roots that prevents the entry of the heavy metals iii. Selective action of the plasma membrane iv. chelation of the heavy metal ions by the metallothionin or by v. immobilization and retention of the meal ions by the hyphae or the roots. In addition, researches have also shown that glomalin, a glycoprotein produced by the AMF can also help in decontaminating the soil [104,105].

4.10. Mycorrhiza and sustainable agriculture: A look into the future

In order to feed the growing population and achieve global food security under climate change, we need to have a sustainable

agriculture that is less impacted by the environmental factors. A sustainable agriculture refers to the key components of agriculture conservation that practices the use of continuous cover crops, no tilling and crop rotations [106]. To make use of mycorrhizal technologies for a greener future we need to have a clear understanding of the contribution of mycorrhiza to the causal metabolic pathways that influence the interaction with rhizosphere for maintaining a sustainable agriculture. This also refers to assessing the influence of other factors that affect mycorrhizal contributions to increased yield or health and productivity of crops, soil properties or other agronomic parameters. Given the complexity of interaction, it is vital that we use statistical and other mathematical tools like structural equation modeling that can relate the influence of effective sizes of mycorrhiza in all the causal pathways. To unravel the molecular mechanism of interaction we need to have a systems view of the global plant-mycorrhizal interaction. This can be realized by developing a genome-scale model mimicking the metabolic state of the organism by integrating different omics data, to develop a biological network using different perturbations that can finally lead to interpreting the connection between different network components [107–110]. Consequently, a large dataset can be integrated into one enabling identification of key genes that can be genetically manipulated to increase the plant mycorrhizal interaction. Once the key regulatory genes are identified we can make use of gene editing strategies like TALENs (Transcription Activator Like Effectors Nucleases) technology or the powerful CRISPR-Cas9 (clustered regularly interspaced short palindromic repeats), CRISPR/Cpf1(Clustered Regularly Interspaced Short Palindromic Repeats from *Prevotella* and *Francisella 1*) [111–114] for manipulating the genes overexpressing the genes of interest (Fig. 3). Along with the implementation of systemic approaches for crop improvement another important consideration that needs to be taken into account is that we need to develop strategies that investigate different parameters influencing the effectiveness of mycorrhizal colonization in plants. The data acquired from these experiments will help minimize the interference of other agricultural management policies from interfering with mycorrhizal derived benefit. Additionally, we need to acquire information about the negative influence along with the positive effect of mycorrhizal technology on the plants. A well-documented knowledge about these tradeoffs as well as a complete understanding of the mechanism of interaction will be essential to advance mycorrhizal technology for a better tomorrow.

5. Conclusion

The presence of symbiotic association is a conserved phenomenon that has been documented from times immemorial. Despite the fact that the genes facilitating the symbiotic association between both the partners is conserved but the lack of knowledge about the conservation of biochemical function has made it difficult to understand their function. The present review clearly emphasizes the important role played by mycorrhiza in benefiting the terrestrial ecosystems and it also highlights the fact that the plant species that predominate the terrestrial biomes have been naturally selected and are capable of symbiotic association enabling survival under all adverse atmospheric conditions. The real essence of mycorrhizal association is that it benefits the primary producers by supplying essential nutrients required for growth as well as allowing the movement of energy-rich compounds. Moreover, they also help in plant hormone biosynthesis. In the light of the current scenario what seems to be essential is the identification of the mechanism and nature of interaction and the key genes from fungi as well as the plants that regulate the interaction. Based on the literature-curated on genes involved we have generated a model of signaling cascade (Fig. 1). Another important factor that needs to be considered is what makes the mycorrhizal interaction different from the effect of the pathogenic fungi in plants. Thus to conclude the future researches should be aimed at i. identifying the mechanism of interactions in the natural field conditions ii. explore the

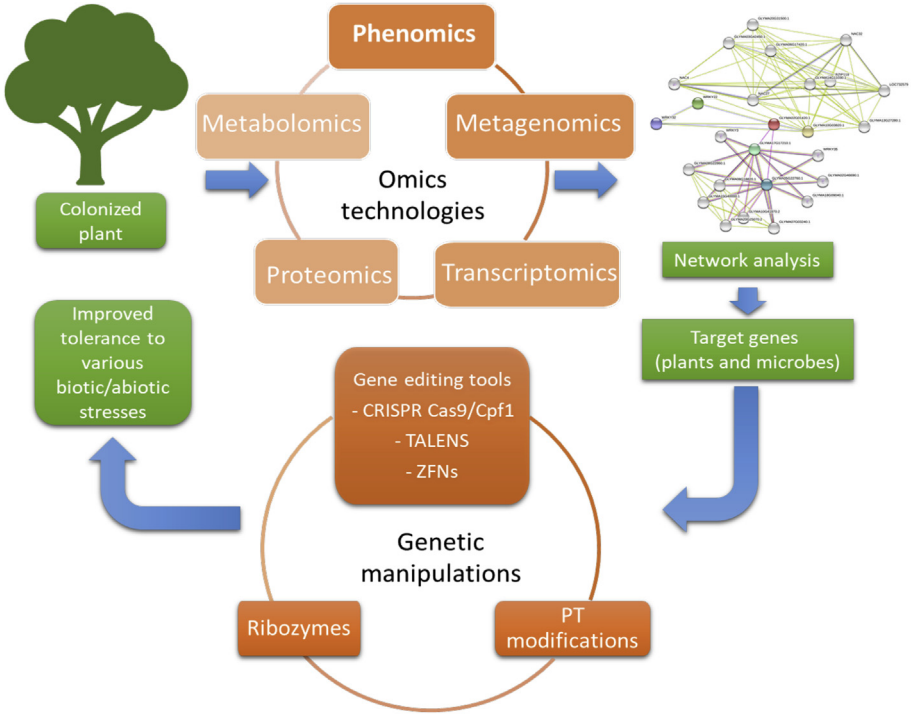

Fig. 3. A systematic overview of the pipeline that needs to be followed for understanding the plant mycorrhizal interactions through systems biology. Here: P: Phenomics, Me: Metagenomics, R: RNAseq, M: Metabolomics, Pr: Proteomics.

beneficial strains of fungus or their combinations that can work in tandem to promote plant growth iii. Study the effect of co-inoculation under stressed conditions iv. identification of the genes that help survival under stressful environments and v. generate transgenic plants overexpressing the target genes and dissect the signaling cascade.

Acknowledgements

The authors would like to acknowledge New Mexico Consortium, Los Alamos for their support. We extend our sincere thanks to Dr. Gargi Chatterjee Basu and Jennifer Jara- Rabara for their help in reviewing the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.pmpp.2017.11.007.

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