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REVIEW ARTICLE

Functional genomics and signaling events in mycorrhizal symbiosis

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The symbiotic association between plant and arbuscular mycorrhizal fungi is an evolutionary conserved association that resulted from co-evolutionary events where both partners benefit from each other. Different plant genes, hormones, and miRNAs regulate this symbiotic association at different levels. Of those, the most important signaling molecules that play critical roles in symbiotic association are plant-derived strigolactones and fungal-derived lipochito-oligosaccharides. These molecules regulate the symbiotic association at the initial stage of symbiosis. Subsequent signaling events of these two molecules activate downstream signaling cascades to develop a proper symbiotic relationship between plants and fungi.

Keywords: mycorrhiza; strigolactone; calcium signaling; nutrient transporter; arbuscules; miRNA

Abbreviations: SL, strigolactone; CCD, carotenoid cleavage dioxygenase; ABA, abscisic acid; NCED, 9-cis-epoxycarotenoid cleavage dioxygenase; TB, teosinte branched; AM, arbuscular mycorrhiza; DMI, does not make infection; CCaMK, calcium and calmodulin-like protein kinase; STR, symbiosis-induced transporter; SYM, symbiosis; HRGP, hydroxyproline-rich glycoprotein; AGP, ADP-glucose pyrophosphorylase; NUP, nucleoporin; PT, phosphate transporter; MST, monosaccharide transporter; AMT, ammonium transporter; SCWC, stochastic calculus of wrapped compartments; IBA, indole-3-butyric acid; IAA, indole-3-acetic acid; DGT, diageotropic; BSH, bushy; GA, gibberellic acid; JA, jasmonic acid; SA, salicylic acid; LNP, lectin nucleotide phosphohydrolase; CPK, calcium-dependent protein kinase; miRNA, microRNA; HAP, haem peroxidase

Introduction

A major event in the life of the planet occurred around 400–500 myr ago, when plants colonized the land habitat (Selosse & Le Tacon 1998). The roots of those plants were colonized by an ancient group of fungi known as Glomeromycota or arbuscular mycorrhizal fungi (AMF; Bonfante & Genre 2008; Tisserant et al. 2013). The AMF are considered as obligated symbionts (Colard et al. 2011; Tisserant et al. 2012). Evidence to support this scenario was primarily based on phylogenetic information in fossil records (Remy et al. 1994). Humphreys et al. (2010) demonstrated that a mutualistic relationship between the AMF and a member of the most ancient clades of land plants promotes carbon uptake, growth, and sexual reproduction in the plant (Humphreys et al. 2010). They are important for plant growth, nutrition, protection from pathogens, diversity, nutrient cycling, and sustainable ecosystem (Sanders & Croll 2010). Different tool kits of mycorrhizal symbiosis are conserved in basal land plant (Delaux et al. 2013). A key goal in mycorrhizal research is to understand the molecular basis of the establishment, regulation, and functioning of the symbiosis. The symbiotic association induces important physiological changes in both partners that led to the reciprocal benefit from each other, and these events resulted from several modifications in plant and fungal partners (Herre et al. 1999; Perotto et al. 2014). However, there is lack of sufficient knowledge in the genomic, metabolomic, and proteomic events of the fungal side that needs to focus more on understanding the AMF symbiosis event efficiently.

The AMF symbiosis starts with the germination of fungal spores. The establishment of symbiosis includes hyphal branching, appressorium development, colonization, formation of intracellular arbuscules, and concomitant production of extraradical mycelium (Akiyama et al. 2005). At the molecular level, signals are exchanged between two partners, leading to a stage-specific pattern of gene expression and hormonal signaling. The corresponding gene products could be responsible for the morphological and physiological changes necessary for the integration of two partners into one association (Harrier 2001; Gutjahr & Parniske 2013).

Research on the mycorrhizal symbiosis is driven by its fundamental importance for plant growth and development (Miransari 2010; Franzini et al. 2013; Willmann et al. 2013). In spite of great importance being given to mycorrhizal symbiosis, much of basic biology of fungal partner is still lacking (Sanders & Croll 2010). The basic information on AMF, such as ploidy, meiosis, recombination events, and segregation, and other events that play a major role in symbiosis needs to be understood thoroughly. Even some findings are more particular to specific fungal phylum and conventional model of evolution, and Mendelian genetics are difficult to apply in studying inheritance, segregation, gene expression, and genomics of the fungal partner (Bever et al. 2008; Oehl et al. 2011).

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In this section we discussed current advances in functional genomics, nutrient uptake, hormonal signaling, calcium signaling events, and the role of miRNAs in mycorrhizal symbiosis. The AMF are obligated symbionts of the plants that grow toward the root of the plant and subsequently penetrate through it. Upon penetrating the root, it passes through the first layer of the cells and subsequently spread toward the root cortex (Sanders & Croll 2010). The fungi penetrate the cell wall of cortical cells and invaginate the host cell membrane and form a branched structure known as arbuscule (Gianinazzi-Pearson 1996; Veiga et al. 2013; Rich et al. 2014). The arbuscules are involved in the bidirectional exchange of nutrients between the host plant and the fungus (Smith & Smith 2011; Smith & Smith 2012). The hyphae of fungus grow out of the root into the soil and act as an extension of the root system that helps in nutrient uptake (Karandashov & Bucher 2005). In contrast to nutrient uptake, fungi take carbohydrates from the plant partner by using its arbuscules (Schuszler et al. 2006). The extraradical hyphae colonizes the adjacent root and forms a belowground hyphal network thus connecting many different plants within the ecosystem (Bonfante & Requena 2011).

Symbiotic events

Strigolactones (SLs) are plant root exudates and are popularly known as a germination stimulant of AMF spore (Akiyama et al. 2005; Besserer et al. 2006; Bhattacharya et al. 2009; Prandi et al. 2011; Quain et al. 2014; Waldie et al. 2014). These SLs are now considered as a novel class of plant hormones that inhibits shoot branching (Scaffidi et al. 2014; Waldie et al. 2014). All the SLs contain a tricyclic lactone ring (ABC part) that connects via an enol ether bridge to a butenolide group (D ring; Figure 1; Yoneyama et al. 2009; Akiyama et al. 2010; Xie et al. 2013). These compounds have one or two methyl groups on the A ring and one or more hydroxyl or acetyl-oxyl group on the A/B ring (Xie et al. 2007). The 5-deoxystrigol is considered as the most common precursor of various SLs and their derivatives (Figure 1; Besserer et al. 2006; Rath et al. 2006).

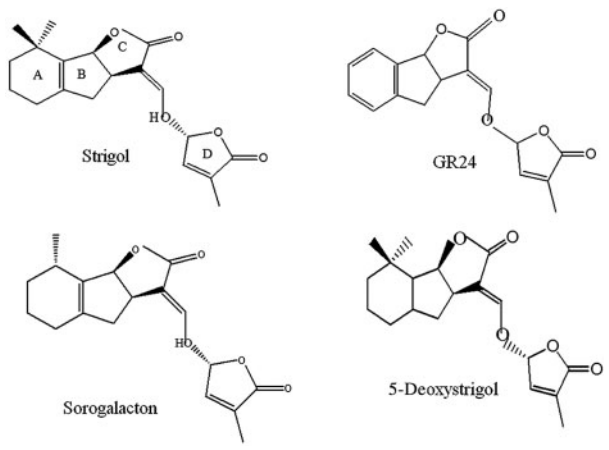

Figure 1. Chemical structure of strigolactones and their derivatives. The related strigolactone precursor and their derivative compounds involved in arbuscular mycorrhizal symbiosis signaling event. The compound 5-deoxystrigol is considered as the common precursor of strigolactone and its derivatives.

It is proposed that SLs originate from the carotenoid biosynthetic pathway (Matusova et al. 2005). The carotenoid cleavage dioxygenase 7 and 8 (CCD7 and CCD8) play significant roles in SL biosynthesis (Figure 2; Domagalska & Leyser 2011; Delaux et al. 2013). Matusova et al. (2005) suggested that plant hormone abscisic acid derived from the carotenoid biosynthetic pathway is involved in the regulation of SLs production (Matusova et al. 2005; López-Ráez et al. 2010). The ABA-deficient mutant in maize (viviparous14, *vp14*) and tomato (*notabilis*), with a null mutation in the gene encoding the 9-cis-epoxycarotenoid cleavage dioxygenase (NCEDs) induced a low level of germination in *Striga hermonthica* and *Phelipanche ramosa* seeds (Tan et al. 1997; Seo & Koshiba 2002; Lefebvre et al. 2006; Bouwmeester et al. 2007). A reduction in SLs in the root exudates of tomato mutant *notabilis* was confirmed by LC-MS/MS analysis (López-Ráez et al. 2010). But it is not clear, whether the reduction in SL production was due to mutation in NCEDs or due to reduced levels of ABA.

The biosynthesis of SL is usually boosted under phosphate-limiting conditions (López-ráez & Bouwmeester 2008; Yoneyama et al. 2010; Czarnecki et al. 2013; Yamada et al. 2014). A pair of GRAS-type transcription factors, nodulation signaling pathway (SNP) 1 and 2, play important roles in the regulation of SL biosynthesis under low phosphate condition (Liu et al. 2011). Both of these factors are indispensable for nodule formation in legumes. The GRAS and SNP genes are required for appropriate regulation of DWARF27 gene that encodes β-carotene isomerase (Alder et al. 2012; Waters et al. 2012). The β-carotene isomerase catalyzes the first committed step in SL biosynthesis (Alder et al. 2012). It is reported that F-box protein D3/MAX2/RMS4 interacts with α/β-hydrolase family receptor D14/DAD2/HTD2 to perceive SL signaling (Kagiyama et al. 2013; Nakamura et al. 2013). Once SL binds to D14/DAD2/HTD2, it undergoes conformational changes promoting its interaction with D3/MAX2/RMS4 that leads to the activation of E3-ligase-mediated protein degradation, permitting the SL responses (Gutjahr & Parniske 2013; Kagiyama et al. 2013; Nakamura et al. 2013). The F-box protein D3/RMS4 is also required for AM colonization in rice and pea (Yoshida et al. 2012; Foo, Yoneyama, et al. 2013; Gutjahr 2014). Early reports suggest the role of D27 and D14 genes in SL biosynthetic pathway as well as in the early phase of symbiotic association (Liu et al. 2011; Delaux et al. 2013). The *Arabidopsis* BRANCHED1 (BRC1), encoding a TCP transcription factor, is closely related to TEOSINTE BRANCHED1 (TB1) of maize that acts downstream of auxins and SLs (Dun et al. 2009).

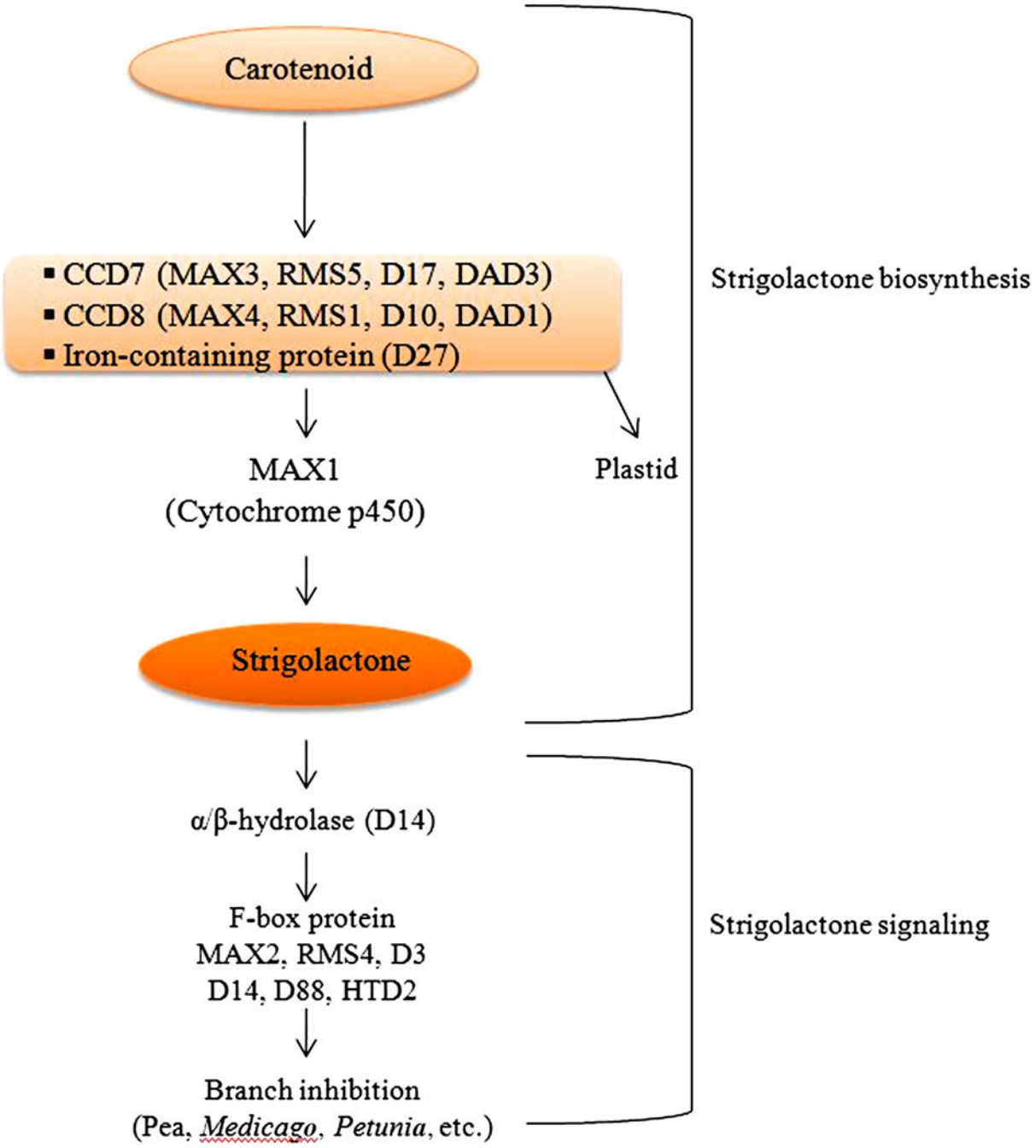

Figure 2. Biosynthetic pathway of strigolactone biosynthesis. Biosynthesis of strigolactone and its related molecules involved in mycorrhizal symbiosis signaling event starts from the carotenoid molecule of plant. Different genes involved in this process are indicated in figure. Study shows that loss of function mutant of different genes involved in biosynthetic process fails to synthesize SL molecule properly and resulted in abnormal/altered or no mycorrhizal symbiosis.

Successful symbiosis with AM fungi relies on the fine-tuning and appropriate control of host gene expression and its physiological responses (Bhattacharya et al. 2009; Bonfante & Requena 2011; Chabaud et al. 2011). A molecular dialog is established between the host plant and the AM fungus that prepares both the partners for subsequent root colonization (Balzergue et al. 2013; Geurts & Vleeshouwers 2012). The communication and signal exchange start prior to the initial cell-to-cell contact between the two symbionts. The plant root exudes SLs that carry out the stimulatory effect on fungus and lead to its proper growth and development. The fungal hyphae in turn produce diffusible molecules known as 'Myc factors' that are perceived by plant roots (analogous to the rhizobial Nod factors; Kosuta et al. 2003; Akiyama et al. 2005; Balzergue et al. 2013; Delaux & Guillaume 2013; Gutjahr & Paszkowski 2013). The perception of Myc factor by the host cell triggers rapid and transient elevation in the intracellular calcium ion, alteration in the cellular architecture, and transcriptional reprogramming in the root

(Delaux & Guillaume 2013; Gutjahr & Paszkowski 2013; Bucher et al. 2014). Besides the role of Myc factor, AM fungi also secrete lipochitooligosaccharides that stimulate the formation of AM symbiosis (Maillet et al. 2011; Herrbach et al. 2014).

Cytological studies show that the nuclear division that occurs in the nuclei within the germination hyphae is necessary for the symbiotic hyphal growth (Requena et al. 2000). Earlier it was demonstrated that *GmTOR2* gene from *Glomus mossae*, a homolog of *Saccharomyces cerevisae,* controls cell cycle arrest in response to nutrient starvation (Requena et al. 2000). Requena et al. (2000) also suggested a possible role of *GmGIN1* of *G. mossae* in the signaling event during spore germination before symbiosis. The genes encoding germin-like, nodulin 26-like, and four other proteins of unknown function are activated at the appressorium stage suggesting their role in the early stage of mycorrhizal colonization (Brechenmacher et al. 2004). Other genes encoding cell wall protein PsENOD12A and C1p serine protease are activated in pea root during appressoria formation (Cathy et al. 1999). A proline-rich protein which is encoded by ENOD11 activates the epidermal cells before, during pre-penetration apparatus formation (PPA), and at the late stage of mycorrhizal development, and even in arbuscule-containing cells. Three ion channel genes of *Medicago truncatula* DMI1 (does not make infection 1), DMI2, and DMI3 are required for the induction of pre-penetration apparatus in plants (Genre et al. 2005; Siciliano et al. 2007; Genre & Bonfante 2010). A novel IPD3 protein interacts with the DMI3 protein, involved in pre-penetration apparatus formation (Messinese et al. 2007). Using mutants of *Lotus japonicus*, five genes, namely CASTOR, POLLUX, NUP85, NUP133, and CYCLOPS, were identified from legumes required for the development of the mycorrhizal symbiosis in the plant roots (Figure 3; Banba et al. 2008; Charpentier et al. 2008; Gutjahr et al. 2008; Yano et al. 2008; T. Hayashi et al. 2014). All these genes are common to *Rhizobium*-legume symbiosis as well as mycorrhizal symbiosis and are induced at early stage of signal transduction. The genes necessary for mycorrhizal formation in rice were also well investigated (Sanders & Croll 2010). The putative orthologs of CASTOR, POLLUX, CCaMK (DMI3), and CYCLOPS in rice and legumes are necessary for mycorrhiza

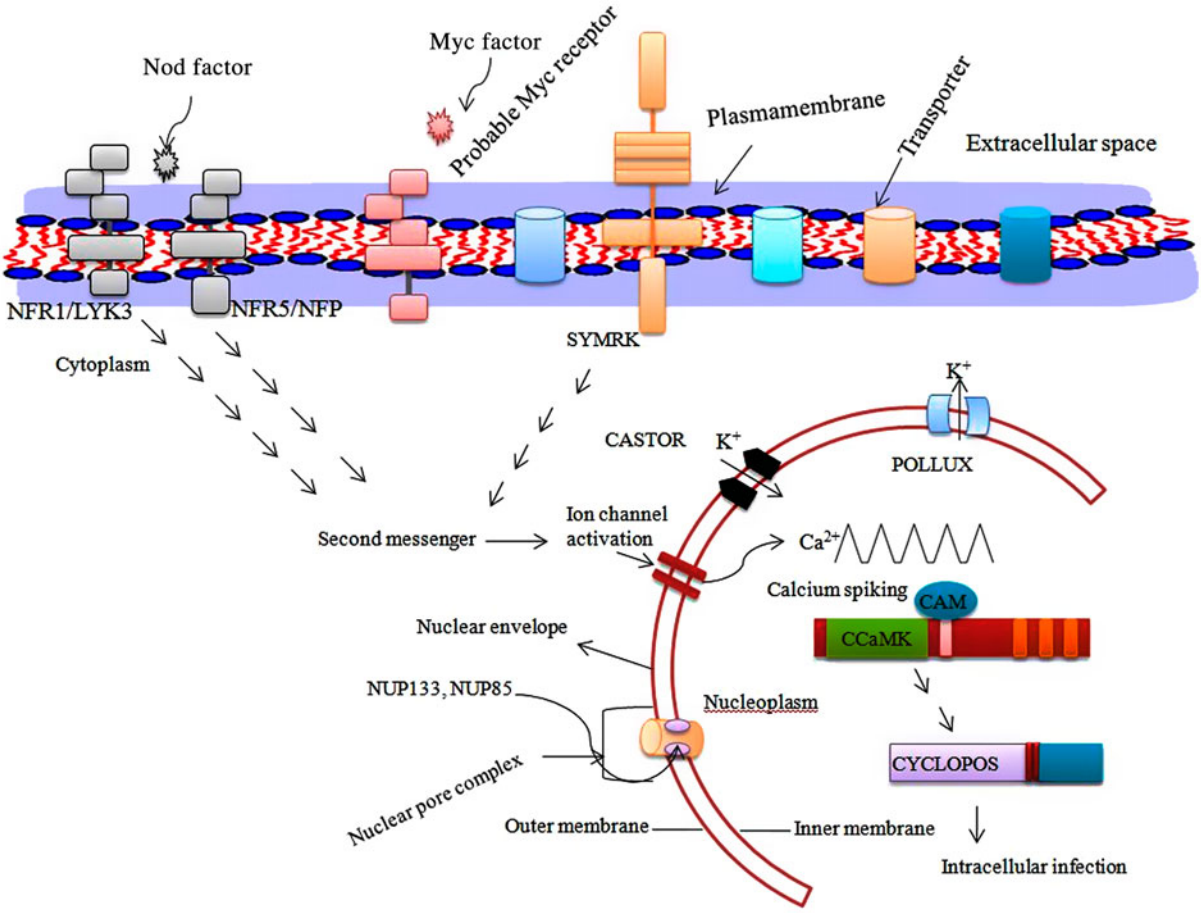

Figure 3. Figure representing perception of arbuscular mycorrhizal Nod/Myc factor by the respective receptor molecule. Upon perception of Nod/Myc signal, receptor molecule passed the signal to downsteam part which in turn activates the second messengers in cytoplasm. The second messengers led to activation of CASTOR, POLLUX or DMI1 like molecules. Upon activation of CASTOR, POLLUX, or DMI1 molecule, K^+ ion released out from nucleoplasm making the cytoplasm hyperpolarized. Once the cytoplasm gets hyperpolarized, perinuclear Ca^{2+} ion enters into the nucleoplasm resulting in Ca^{2+} spiking. The Ca^{2+} ion binds to CCaMK which in turn passes the signal to CYCLOPOS gene responsible for regulation of mycorrhization process.

formation (Figure 3; Banba et al. 2008; Gutjahr et al. 2008). However, a number of other genes are also identified in rice that appear to be specific to mycorrhiza formation (Charpentier et al. 2008; Gutjahr et al. 2008; Yano et al. 2008). These genes are divided into two different groups, AM13 and AM11. These groups of genes are expressed at early stages of symbiosis before arbuscule formation. The genes *AM10*, *11*, *14*, *15*, *18*, *20*, *24*, *25*, *26*, *29*, *31*, *34*, *39*, *42*, and *PT11* are expressed at the later stage of development, and some are in arbusculated cells (Gutjahr et al. 2008). The functions encoded by most of these genes are currently unknown.

Gallou et al. (2012) performed potato microarray analysis that led to finding of changes in transcript level at pre-, early, and late stages in potato root colonization by *Glomus* sp. MUCL41833 (Gallou et al. 2012). Data analysis revealed 526 up-regulated and 132 down-regulated genes during pre-stage, 272 up-regulated and 109 down-regulated during early stages, and 734 up-regulated and 122 down-regulated genes during the late stage of root colonization. The most important class of regulated genes that reported to play a significant role is associated with plant stress and in particular with the *WRKY* transcription factor genes. The *WRKY* transcription factor genes are regulated at the pre-stage in the root colonization process. The expression profiles demonstrated wide transcriptional variation in pre-, early, and late stage of root colonization. It is found that the *WRKY* transcription factor genes are involved in controlling the mechanism of arbuscular mycorrhizal establishment by regulating the plant defense genes.

The mycorrhizal-induced plant genes play major roles in the development of symbiotic phase during mycorrhization process (Balestrini et al. 2007; Koegel et al. 2013). Nowadays, significant progress has been made in identification of related genes involved in symbiosis events (Table 1). Uses of ESTs, cDNA libraries, genomic libraries, and microarray analysis have the potential to screen differentially expressed transcripts. Three different *M. truncatula*-based lectine-like genes are induced in mycorrhizal roots during the colonization process (Wulf et al. 2003a). Expression of transcript corresponding to gene encoding lectin-like glycoprotein *PsNLEC-1* is strongly expressed in root nodules of *Pisum sativum* (Kardailsky et al. 1994; Dahiya et al. 1997). Identification of numerous different lectin-like transcripts is also increased in mycorrhizal roots. This indicates their significant role during the symbiotic process. Toward understanding the molecular aspects of arbuscule development in AM fungi, Gomez et al. (2009) used Affymetrix genechip *Medicago* genome array to document *M. truncatula* transcript profile associated with AM symbiosis and then developed laser micro-dissection (LM) of *M. truncatula* root cortical cells to enable the analysis of gene expression in individual cell types (Gomez et al. 2009). Experiments showed that within the arbuscule, genes associated with urea cycle, amino acid biosynthesis, and cellular autophagy are detected to be potentially much higher than the others. Analysis of gene expression in colonized cortical cells revealed the up-regulation of a lysine motif (LysM) receptor-like kinase (members of the GRAS transcription factor family) and a symbiotic-specific ammonium transporter (Table 1). The rice transcriptome analysis shows that 12 genes are exclusively expressed in mycorrhizal roots (Güimil et al. 2005). These genes are proposed as marker genes for AM symbiosis. Among them, one encodes for putative peroxidase OsAM1 (Table 1). Interestingly, 43% of the mycorrhiza-induced rice gene responds similarly to the infection by fungal pathogens, suggesting the conservation of the transcriptional activation pathway in mycorrhizal symbiosis (Güimil et al. 2005). In addition, about one third of the mycorrhizal responsive genes of rice are matched with homologous sequences of dicotyledonous plants that are up-regulated during AM symbiosis, suggesting a relatively conserved symbiotic mechanism in monocot and dicot plants (Güimil et al. 2005).

Zhang et al. (2010) have performed an experiment with *M. truncatula* mutant, stunted arbuscule (*str*), in which arbuscule development was impaired (Zhang et al. 2010). The AM symbiosis failed, which led to the identification of a second AM symbiosis-induced transporter STR2. The silencing of STR2 by RNA interference resulted in a stunted arbuscule phenotype. They also reported that STR1 and STR2 are co-expressed constitutively in the vascular tissue, and their expression was induced in cortical cells that contained arbuscules (Zhang et al. 2010). The STR1 heterodimerizes with STR2, and the resulting transporter was found in the peri-arbuscular membrane where its activity is necessary for arbuscule development and consequently functional AM symbiosis.

Upon development of hypopodium on the outer wall of root epidermal cells, both the plant and fungal partner enters into a novel developmental program that culminates fungal accommodation inside the root cell lumen that lead to fully functional symbiosis. It is reported that initiation of an accommodation program strongly correlates with the activation of SYM pathway (Gutjahr et al. 2008). As symbiosis occurs, it undergoes significant changes in the morphological organization of host cells to accommodate fungal partners. This includes the creation of new interface compartments within the host cell. The genes encoding both ADP-glucose pyrophosphorylase (AGP) and a hydroxyproline-rich glycoprotein (HRGP) are supposed to play important roles in this process. These genes are induced in mycorrhizal roots of *M. truncatula* and maize, respectively, and the transcripts are specifically localized in arbusculated cells (Balestrini et al. 1997; Van Burren et al. 1999). Many of the ESTs that are identified by Grunwald et al. (2004) belong to the gene product involved in cell wall modification. One encodes an extensin-like glycoprotein that belongs a to large protein family characterized by hydroxy-proline rich motifs. Using a cDNA array, Liu et al. (2003) reported the induction of *MtCell* gene during symbiosis. It suggested that *MtCell* is localized in the periarbuscular membrane and is involved in assembling the cellulose/

Table 1. Table showing list of genes and their roles during mycorrhizal symbiosis process.

Symbiotic Genes	Gene product	Function	Phenotype	References
Genes involved in strigolactone biosynthesis and signaling				
CCD7	Carotenoid cleavage dioxygenase	Strigolactone synthesis	Reduced colonization	(Gomez-Roldan et al. 2008)
CCD8	Carotenoid cleavage dioxygenase	Strigolactone synthesis	Reduced colonization	(Gomez-Roldan et al. 2008)
D27	Carotenoid isomerase	Strigolactone synthesis	Not tested	(Alder et al. 2012)
PDR1	ABC Transporter	Strigolactone transport	Reduced colonization	(Kretzschmar et al. 2012)
NCED	9-cis-epoxycarotenoid cleavage dioxygenase	Strigolactone synthesis	Not studied	(López-Ráez et al. 2010)
D14/DAD2/HTD2	β-hydrolase family receptor	Perceive strigolactone signaling	Not studied	(Zhou et al. 2013)
DWARF53 (D53)	class I Clp ATPase	Repressor of strigolactone synthesis	Insensitive to strigolactone signaling	(Zhou et al. 2013)
DWARF3 (D3)	F-box protein	Strigolactone response	Defects in fungal colonization	(Yoshida et al. 2012)
DWARF14	Hydrolase family protein	Strigolactone response	Higher AM fungal colonization	(Yoshida et al. 2012)
Genes involved in symbiotic events				
GINI	Hedghog protein	Germination of fungal spore	Not studied	(Requena et al. 2002)
EARLY NODULINE ENOD12	Serine protease	Signal transduction in SYM8 pathway	Not studied	(Albrecht & Lapeyrie 1998)
DMI2	Receptor like kinase	Myc-LCOs signaling	Reduced colonization	(Maillet et al. 2011)
LNP	Lectin nucleotide phosphohydrolase	Nod factor binding protein	Nodulation	(Roberts et al. 2013)
NUP85	Nucleoporin	Nuclear trafficking	Reduced colonization	(Kanamori et al. 2006)
NUP133	Nucleoporin	Nuclear trafficking	Reduced colonization	(Saito et al. 2007)
NENA	Nucleoporin	Nuclear trafficking	Reduced colonization	(Groth et al. 2010)
NSP2	GRAS transcription factor	Transcription factor	Reduced colonization	(Maillet et al. 2011)
RAM1	GRAS transcription factor	Transcription factor	No hypopodium	(Wang et al. 2012)
RAM2	GPAT	Cutin monomer biosynthesis	No hypopodium	(Gobbato et al. 2012)
VAPYRIN	MSP and ANK repeat containing protein	Unknown	No arbuscules	(Pumplin et al. 2010)
VAMP72	Exocytotic vesicle associated membrane protein	Formation of periarbuscular membrane	Stunted arbuscules	(Ivanov et al. 2012)
SbtM1	Subtilisin-like protease	Unknown	Reduced colonization and reduced arbuscules	(Takeda et al. 2009)
SbtM3	Subtilisin-like protease	Unknown	Reduced colonization and reduced arbuscules	(Takeda et al. 2009)
STR1	Half ABC transporter	Unknown	Reduced colonization and stunted arbuscules	(Gutjahr et al. 2012)
STR2	Half ABC transporter	Unknown	Reduced colonization and stunted arbuscules	(Gutjahr et al. 2012)
DELLA	DELLA	Transcriptional Regulator	Arbuscle formation	(Floss et al. 2013)
Genes involved in calcium signaling				
DMI1	Cation channel	Calcium spiking PPA formation	Reduced colonization Fails to assemble PPA	(Ané et al. 2004) (Genre et al. 2005)
DMI3	Calcium/calmodulin dependent protein kinase	Calcium spiking	No colonization	(Catoira et al. 2000; Capoen et al. 2011)
IPD3	Coiled-coil domain containing protein	Interacts with DMI3	No arbuscules	(Horváth et al. 2011)
MCA8	Calcium pump	Calcium spiking	Reduced colonization	(Capoen et al. 2011)

Table 1 (*Continued*)

Symbiotic Genes	Gene product	Function	Phenotype	References
CASTOR, POLLUX, and CYCLOPOS	Ion channel	Calcium spiking	Impaired in calcium spiking	(Charpentier et al. 2008)
	Coiled coil motif with nuclear localization signal	Interacts with CCaMK in nucleus	Impaired in AM colonization	(Yano et al. 2008; Singh et al. 2014)
Genes involved in nutrient uptake				
PT4	Phosphate transporter	Symbiotic phosphate uptake	Reduced symbiotic phosphate uptake	(Javot et al. 2007)
PT10	Phosphate transporter	Symbiotic phosphate uptake	Not studied	(Tamura et al. 2014)
PT11	Phosphate transporter	Symbiotic phosphate uptake	Reduced symbiotic phosphate uptake	(Paszkowski et al. 2002)
AMT2	Nitrate transporter	Symbiotic nitrate uptake	Not studied	(Guether et al. 2009)
Genes involved in hormonal regulation				
DGT	Cyclophilin	Gravitropism and lateral root formation	Lack presymbiotic root branching	
PCT	Negative regulator of polar auxin transport	Cotyledon formation	Stimulated presymbiotic root branching	(Hanlon & Coenen 2011)
BSH	SNF5 type protein	Auxin signaling	Reduced mycorrhizal colonization	(Foo 2013)
DELLA	Della protein	Gibberellin signaling	Reduced mycorrhizal colonization	(Foo, Ross, et al. 2013)
SPR2	Fatty acid desaturase	Biosynthesis of jasmonic acid	Reduced mycorrhizal colonization	(Li et al. 2002)
miRNA in mycorrhizal symbiosis				
miR5229a/b	microRNA5229a/b	Targets Haem-Peroxidase	Arbuscules development	(Branscheid et al. 2011)
miR171h	microRNA171h	Targets NSP2	Increase root colonization and arbuscules formation	(Lauressergues et al. 2012)
miR169	microRNA169	Targets BCP1	Arbuscules development	(Pumplin & Harrison 2009)
miR5204	microRNA5204	Targets GRAS transcription factor	Decrease in mycorrhizal colonization via GRAS cleavage	(Gobbato et al. 2012)
miR160f	microRNA160f	Targets auxin response factor gene family	AM symbiosis	(Branscheid et al. 2011)
miR160c	microRNA60c	Targets auxin response factor gene family	AM symbiosis	(Branscheid et al. 2011)
miR5282	microRNA5282	Targets Glutathione s-transferase	Involved in ROS mediated mycorrhization	(Wulf et al. 2003b)
miR399	microRNA399	Targets PHO2 phosphate transporter	Involved in cellular phosphate homeostasis	(Branscheid et al. 2010)
miR159b	microRNA159b	Targets Erf transcription factor	Targeted silencing led to deformed arbuscules	(Devers et al. 2013)

hemicelluloses matrix at the interfaces. This *Mtcell* gene is associated with expanding tissue and cellulose synthesis.

An extracellular protein, expansin, with the possible role in cell wall loosening is up-regulated during intracellular colonization of AM fungi during early stage of mycorrhizal interactions. This indicates that these classes of proteins are involved in cell wall loosening and could be crucial in accommodating the AM fungus inside cortical cells. The mutational analysis of *Mt-xht1* gene shows a systemic modification of cell wall structure to enable fungal penetration to the roots (Balestrini & Bonfante 2014). The cytoskeleton of host cell undergoes a massive change during the invasion of cortical cells and undergoes transient rearrangement, presumably to enable the development of arbuscular interfaces. This re-organization is induced by signals before mycorrhizal penetration to the host cells. The activation in α-tubulin promoter and accumulation of enhanced mRNA of β-tubulin gene occur during a cellular modification stage in arbuscule-containing cells (Zampieri et al. 2010). The β-tubulin gene also modulated during the symbiosis process (Rhody et al. 2003).

Nutrient uptake

A major *breakthrough* in AMF symbiosis was achieved when the Pi transporter gene was characterized from *Glomus versiforme* extraradical hyphae involved in Pi uptake from soil (Harrison & van Buuren 1995). This Pi gene was induced at the transcriptional level in the presence of lower amount of Pi. Later the PT homolog GmosPT was reported from *the Glmous mosseae* that plays a similar role in Pi transport (Benedetto et al. 2005). The phosphate transporter genes encoding alkaline phosphatases were also described in *Glomus intraradices* and *G. margarita* (Tisserant et al. 1993; Aono et al. 2004). The transcript level of these genes are higher in the mycorrhizal root than in the germinating spore and external hyphae, suggesting their significant role in nutrient exchange with the host plant (Aono et al. 2004). The phosphate transporter *MtPT4* gene from *M. truncatula* is located in the periarbuscular membrane, at the interface between arbuscules and the invaginated plant cell membrane, generally assumed as the site of nutrient exchange (Harrison et al. 2002). A gene *Mtha1* encodes the plasma membrane H^+ ATPase up-regulated in *M. truncatula* during AM symbiosis, and *Mtha1* transcript get accumulated in arbuscule-containing cells (Wulf et al. 2003a; Krajinski et al. 2014). Karandashov and Bucher (2005) demonstrated the role of phosphate transporter *StPT3* gene (Karandashov & Bucher 2005). They reported that *StPT3* is expressed in root cells harboring various mycorrhizal structures. The cell-to-cell contact between the partner is required to induce the phosphate transport system by Pi transporters (Güimil et al. 2005). The redundancy within the mycorrhiza-inducible Pi transporter pathways ensure that Pi transfer is evolutionary robust and relatively insensitive to mutation (Nagy et al. 2005). At present, it is confirmed that several Pi transporter genes were strongly induced during AM colonization process (Figure 4). These genes are *OsPT11* (*Oryza sativa* phosphate transporter11), *LePT4* (*Lycopersicon esculentum PT4*), *PtPT8* (*Populus*

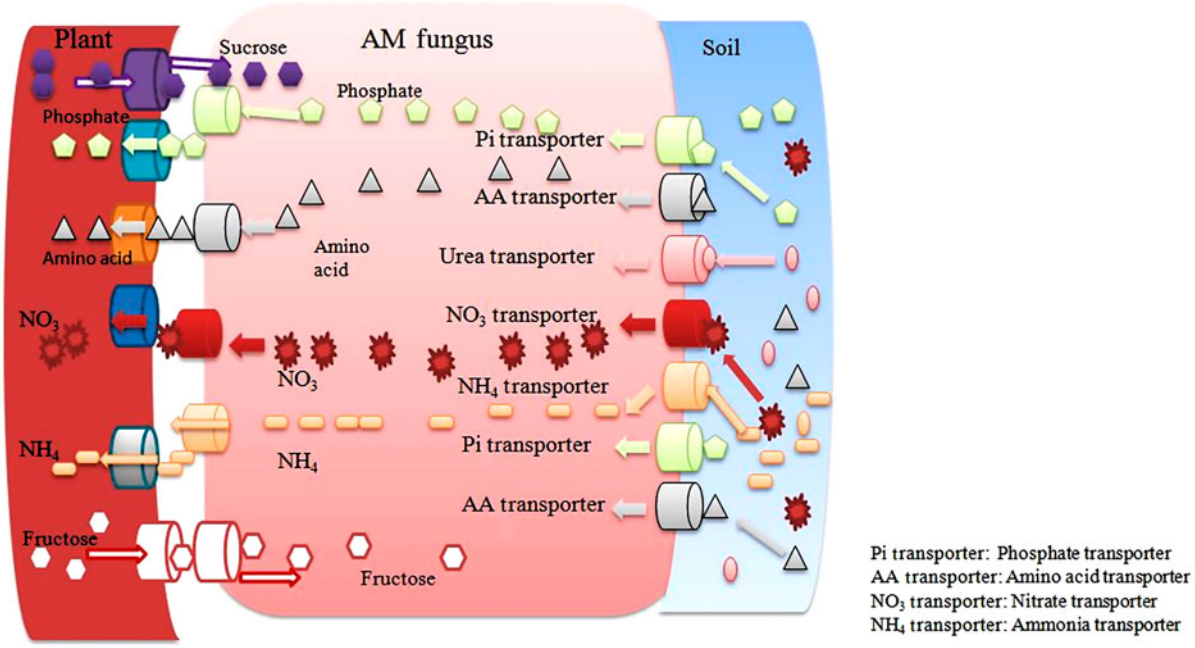

Figure 4. Figure depicting soil, mycorrhiza and plant interfaces involved in nutrient uptake during mycorrhizal symbiosis process. The fungi receive different nutrient supplement from soil and transports them to its symbiotic plant partner. Nutrient transfer from soil by mycorrhizal fungus occurred via different transporter molecules. Different transporter molecules involved in this process are phosphate, amino acids, urea, ammonia and nitrate transporters. Similarly, fungus receives its carbon source like fructose, sucrose etc. from host plant via specialized transporter molecule in exchange of nutrient supply.

trichocarpa PT8), *PtPT10* (*Populus trichocarpa PT10*), *StPT4* (*Solanum tuberosum PT4*), *StPT5* (*Solanum tuberosum PT5*), *LePT4* (*Lycopersicon esculentum PT4*), *PhPT4* (*Petunia hybrid PT4*), *PhPT5* (*Petunia hybrid PT5*), *LjPT3* (*L. japonicus PT3*), *GmPT7* (*Glycine max PT7*), *GmPT11* (*Glycine max PT11*), *GmPT10* (*Glycine max PT10*), *ZmPT6* (*Zea maize PT6*). The organic phosphate molecule delivers to the host plant via the mycorrhizal-induced phosphate transporter genes (Balestrini et al. 2007). The fungal partner activates part of the low Pi adaptation system of the plant partner by secreting phosphatases and improves the overall efficiency of Pi uptake. Many other plant Pi transporters and one fungal Pi transporter were identified in arbusculated cells (Loth-Pereda et al. 2011). The *MtPT4* is essential for the acquisition of Pi delivery by AM fungi. The loss of *MtPT4* function led to the premature death of arbuscules in *M. truncatula* plant, and fungus was unable to proliferate within the host root and thus symbiosis was terminated (Javot et al. 2007).

The monosaccharide transporter (MST2) from *Glomus* sp. with a broad substrate spectrum that functions at several symbiotic root location are demonstrated very well (Büttner & Sauer 2000; Schuszler et al. 2006; Helber et al. 2011; Slewinski 2011). The plant cell wall sugar can efficiently outcompete the Glc uptake capacity of MST2, suggesting that they can serve as the alternative carbon source (Figure 4; Helber et al. 2011). The *MST2* expression is closely correlated with that of mycorrhizal-specific phosphate transporter 4 (PT4). The reduction of *MST2* expression using host-induced gene silencing resulted in impaired mycorrhiza formation, malformed arbuscules, and reduced *PT4* expression. This finding highlighted the symbiotic role of MST2 and supported the hypothesis that the exchange of carbon for phosphate is tightly regulated (Figure 4). During the symbiotic phase, C metabolisms of both partners are significantly modified at the level of gene expression (Balestrini & Lanfranco 2006). Ravnskov et al. (2003) reported an up-regulation of the sucrose synthase gene which led to hypothesize that the sucrose synthase plays a major role in generating sink strength (Ravnskov et al. 2003). In 1996, Harrison reported a high expression of sugar transporter gene (*Mtst1*) in arbuscule-containing cells as well as the adjacent surrounding colonized area (Harrison 1996).

In addition to phosphate in mycorrhizal associations, the fungal partner assisted the plant partner by providing nitrogen (N) nutrient too (Hodge et al. 2001; Govindarajulu et al. 2005; Matsumura et al. 2013; Kranabetter 2014). Arbuscular mycorrhizal (AM) fungi have access to inorganic or organic forms of nitrogen, such as nitrate, ammonia, and urea. They easily translocate them from the extraradical surface to the intraradical mycelium via respective transporter molecule, where the nitrogen is transferred to the plant without any carbon skeleton (Figure 4) (Pérez-Tienda et al. 2011; Jin et al. 2012; Ellerbeck et al. 2013). However, the molecular form in which N is transferred, as well as the involved mechanism is still under debate. The NH_4^+ seems to be the preferred molecule (Guether et al. 2009). The transcript of *LjAMT2* (Amt/Rh family) is up-regulated in transcriptome analysis of *L. japonicus* root upon colonization with *G. margarita*. This transcript is extensively expressed in mycorrhizal root, but not in the nodule (Guether et al. 2009). The ammonium transporter LjAMT2 transports NH_3 instead of NH_4^+. The ammonium transporter binds to charged ammonium in the apoplastic interface compartment and releases the uncharged NH_3 molecule into the cytoplasm. The role of ammonium transporter LjAMT2 is confirmed by stochastic calculus of wrapped compartment (SCWC) (Variant of stochastic calculus of looping sequence) in mycorrhizal symbiosis (Coppo et al. 2011). The *X-ray* structure study of ammonium transporter revealed the conduction mechanism of Amt/Rh (rhesus) protein that involved in the single- file diffusion of NH_3 molecule (Zheng et al. 2004; Andrade et al. 2005; Lamoureux et al. 2010). However it is suggested that AmtB could be filled with water molecule and the presence of water molecule in the pore lumen indicate, Amt/Rh protein work as plain NH_3 channel (Lamoureux et al. 2010). The Amt/Rh protein also plays variety of permeation mechanism including passive diffusion of NH_3.

Hormonal regulation

The relationship between host root and AM fungi requires continuous exchange of different signals those help them for proper development of symbiosis. The phytohormones are important signaling molecules known to regulate many growth and developmental process in plants (Barker & Tagu 2000; Foo, Yoneyama, et al. 2013; Gutjahr 2014). In maize and *M. truncatula*, level of indole-3-butyric acid (IBA) get increases whereas, level of indole-3-acetic acid (IAA) remains unaltered in mycorrhizal symbiotic plant (Ludwig-Müller et al. 1997; Ludwig-Müller & Güther 2007). In *Glycine max,* IA*A level* present in higher concentration in AM root than in control plant (Meixner et al. 2005). Altered level of auxin and cytokinin was observed in *Solanum lycopersicum* harbored with mycorrhizal symbiont (Torelli et al. 2000; Shaul-keinan et al. 2002). It is speculated that auxin, more particularly IBA may facilitate colonization of host by increasing the number of lateral root during early growth phase of plant development (Kaldorf & Ludwig-Müller 2000; Ludwig-Müller & Güther 2007). The application of inhibitor against IBA, root growth and lateral root induction reduced significantly that led to reduced AM colonization (Kaldorf & Ludwig-Müller 2000). The transcript level of leghemoglobin get up-regulated in AM colonized root, in IAA and IBA treated plant (Frühling et al. 1997; Heidstra et al. 1997). The leghemoglobin play crucial role in N_2 fixation in *Rhizobium*-legume interaction (Heidstra et al. 1997). But, its role in AM symbiosis is unclear. Some of the nitrate transporter genes get down regulated in AM root (Ludwig-Müller & Güther 2007). The endochitnase gene family members are down

regulated in AM colonized as well as an IBA treated plant of *M. truncatula* (Ludwig-Müller & Güther 2007). Hanlon and Coenen (2011) carried out experiment in diageotropic (*dgt*), an auxin-resistant mutant and polycotyledon (*pct*) mutant with hyperactive polar auxin transport. They found that, *G. intraradices* stimulate presymbiotic root branching in *pct* but not in *dgt* root (Hanlon & Coenen 2011). In auxin deficient *bushy* mutant of pea, *bsh* root has reduced mycorrhizal colonization compared to wild-type plant (Foo, Yoneyama, et al. 2013). This mutant also has reduced level of SL content in root due to down-regulation of *PsCCD8* gene (Foo et al. 2005; Johnson et al. 2006). The application of exogenous auxin reverted the effect of *bsh* mutant and reported to have higher mycorrhizal colonization (Symons et al. 2002; Foo 2013).

Beside auxin, other phytohormones like gibberellic acid, cytokinin, jasmonic acid, and salicylic acid also plays significant role in AM colonization (Barker & Tagu 2000; Foo, Ross, et al. 2013; Miransari et al. 2014; Yu et al. 2014). It is reported that GA (gibberellic acid) involved in root nodulation process (S. Hayashi et al. 2014). Floss et al. (2013) demonstrated the role of DELLA protein in gibberellic acid mediated arbuscule formation during mycorrhization process (Floss et al. 2013). The gene expression analysis in GA-related genes are up-regulated in *M. truncatula* as reported earlier in tomato too (Garrido et al. 2010; Ortu et al. 2012). The jasmonic acid has long been implicated in plant systemic response to pathogen attack, that led to question regarding its involvement in the regulation of AM development (Regvar et al. 1996; Hause et al. 2002). But it is found that the application of JA or its derivatives can have ranges of effect in the AM colonization process. The effect may be positive or may be inhibitory depending on the species, nutritional conditions, timing and dosage conditions. Regvar et al. (1996) showed a clear promotion of AM colonization in *Allium* plant by application of low level of jasmonic acid (Regvar et al. 1996). Landgraf et al. (2012) reported increased level of endogenous JA content in plants by repeated wounding, and found that, the resulting plants are able to increase AM colonization (Landgraf et al. 2012). This suggests the positive role of JA in AM development process. This result supported with the report of Isayenkov et al. (2005), where they found down regulation of J*A level* by antisense expression of *allene oxide cyclase* gene and found delay in AM colonization (Isayenkov et al. 2005). Tejeda-Sartorius et al. reported, JA deficient *spr2* mutant of tomato undergoes reduced AM colonization. Later the AM colonization was restored by exogenous application of methyl jasmonate (Li et al. 2002; Tejeda-sartorius et al. 2007). Unlike jasmonic acid, salicylic acid (SA) also act to *coordinate* the plant defense against biotropic pathogen and hence activated during AM colonization (Stacey et al. 2006; Zhang et al. 2013; Foo, Ross, et al. 2013). Blilou et al. (1999) and Herrera-Medina et al. (2003) showed, SA content in plant affect the rate of AM colonization (Blilou et al. 1999; Herrera Medina et al. 2003).

Calcium signaling

The calcium dependent protein kinases are important calcium binding sensor proteins that play significant role in plant growth and development as well as other biotic and abiotic responses (Kanchiswamy et al. 2013). One of the most studied features during early stages of establishment of AM symbiosis is calcium mediated signaling pathway that initiated in host plant by AM fungal diffusible signal. The exudate of germinated fungal spores triggers transient elevation of cytosolic Ca^{2+} level in *Glycine max* (Navazio et al. 2007). The chemical nature of symbiotic signals released by AM fungi, responsible for calcium spiking for AM symbiosis is carried out by 'Myc/Nod' factor (Figures 4 and 5) (Sieberer et al. 2009; Chabaud et al. 2011; Maillet et al. 2011; Genre et al. 2013). The LysM receptor-like kinase NFR1/LYK3 and NFR5/NFP are the strongest candidate genes that function as Nod factor receptor (Figure 4; Broghammer et al. 2012). The *M. truncatula* DOES NOT MAKE INFECTIONS1 (DMI1) and *L. japonicus* CASTOR and POLLUX that encodes for nuclear ion channel are prominent genes required for initiation of Nod and Myc factor induced Ca^{2+} spiking. The *M. truncatula* DMI13 (CCaMK) promotes Ca^{2+} binding during calcium oscillations (Miller et al. 2013). The *L. japonicus* CASTOR and POLLUX as well as *M. truncatula* DMI1 are localizes to the nuclear envelope (Riely et al. 2007; Charpentier et al. 2008). *M. truncatula* Ca^{2+} ATPase MCA8 block Nod factor induced calcium spiking (Capoen et al. 2011). This MCA8 localize in inner and outer nuclear membrane, suggesting their coordinated role in nuclear calcium spiking (Capoen et al. 2011). A study carried out by Venkateshwaran et al. (2012) shown that DMI1 of *M. truncatula* is a close ortholog of *L. japnicus* POLLUX and sufficient enough to carry out symbiosis in the absence of CASTOR and POLLUX (Venkateshwaran et al. 2012). The *L. japonicus castor, pollux* and *castor pollux* double mutant are rescued by presence of DMI1 of *M. truncatula*, confirming its indispensable role in symbiosis. In another case, both Lj-CASTOR and Lj-POLLUX were required for rescuing *dmi1* mutant of *M. truncatula* (Venkateshwaran et al. 2012). When Lj-CASTOR and Lj-POLLUX expressed individually, they failed to rescue *dmi1-4* (Venkateshwaran et al. 2012). This is due to lack of appropriate promotor that control the expression of these genes. The DMI1 contain ADAGNHA and Lj-CASTOR and Lj-POLLUX have ADSGNHA amino acid residues in the selectivity filter. In this sequence, Ala of DMI1 is substituted by a Ser amino acid. When Lj-CASTOR^{S266A} and Lj-POLLUX^{S329A} is replaced by Ala amino acid in exchange of DMI Ser amino acid, the Lj-*castor* and Lj-*pollux* mutant able to rescue the plant (Venkateshwaran et al. 2012). This substitution of Ser to Ala amino acid reduced the potassium conductance. Roberts et al. (2013) reported LNP (LECTIN NUCLEOTIDE PHOSPHOHYDROLASE) as a Nod factor binding protein that act upstream of calcium signaling

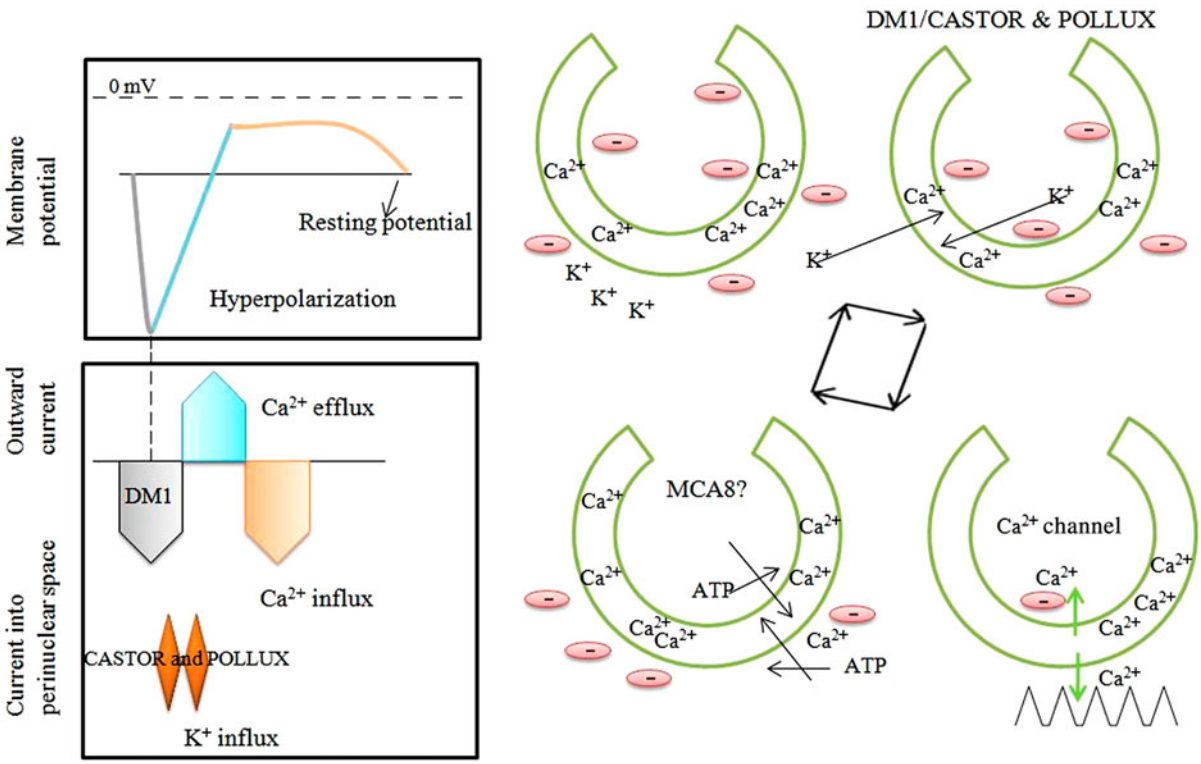

Figure 5. The calcium spiking events by DMI1, POLLUX and CASTOR genes during arbuscular mycorrhizal symbiosis as proposed by Venkateshwaran et al. (2012). They proposed that an unknown secondary messenger activates cation channels like DMI1 or CASTOR-POLLUX. The CASTOR and POLLUX responsible for permeation of K^+ ion in favor of their concentration gradient from cytoplasm to perinuclear space. The permeation of K^+ by DMI1, CASTOR and POLLUX lead to hyperpolarization of nuclear membrane. Upon hyperpolarization, hyperpolarized mediated gated Ca^{2+} channels get activated. This leds to flow of perinuclear Ca^{2+} ions to cytoplasm and nucleoplasm giving rise to Ca^{2+} spike and calcium mediated signaling. As Ca^{2+} enters into cytoplasm and nucleoplasm, it reduces the hyperpolarization of cytoplasm. This led to closure of hyperpolarization mediated Ca^{2+} channels. Once calcium mediated signaling is over, Ca^{2+} ions pumped out from cell by Ca^{2+} mediated ATPase, MCA8 resulting in resting potential of cell. Figure prepared as hypothesized by Venkateshwaran et al. (2012).

event (Roberts et al. 2013). The LNP acts in the early stage of symbitic signaling process.

Campos-Sariano et al. (2011) reported expression of seventeen calcium-dependent protein kinase (CPK) genes of rice representative of four distinct phylogenetic groups (Campos-Soriano et al. 2011). Among them *OsCPK18* and *OsCPK4* are transcriptionally activated in response to AM fungus *G. intraradices*. The *OsCPK18* and *OsCPK4* gene expression was also up-regulated by fungal produced diffusible molecules. The laser micro-dissection study revealed expression of *OsCPK18* in cortical cells, and not in epidermal cells of *G. intraradices* inoculated rice root, suggesting preferential role of this gene in root cortex. The rapid activation of *OsCPK18* expression in response to AM inoculation reflects its roles in perception of AMF signaling. The *OsCPK18* gene might be considered as a marker gene of the pre-symbiotic phase. This finding will provide a better understanding of the signaling mechanism process during AM symbiosis and will greatly facilitate their molecular dissection. In *L. japonicas,* it is reported that seven common symbiotic genes (SYMRK, CASTOR, POLLUX, SYM3, SYM6, SYM15, and SYM24) are required for both fungal and bacterial entry into root epidermal or cortical cells (Stracke et al. 2002; Kaneko et al. 2005).

miRNA in mycorrhizal symbiosis

MicroRNAs (miRNAs) are small non-coding RNA gene product of about 22 nt long that are processed by dicer from precursor with a characteristic hairpin secondary structure (Chen et al. 2010; Ameres & Zamore 2013; Martin et al. 2014). The miRNAs are typically inactivate developmentally important mRNA by inhibiting their translation or bringing to their cleavage and degradation (Ossowski et al. 2008; Warthmann et al. 2008; Djuranovic et al. 2012). Devers et al. (2011) suggested the important role of miRNA in AM symbiosis (Devers et al. 2011). They studied miRNA mediated mRNA cleavage in root cell reprogramming during AM symbiosis. High throughput (Illumina) sequencing of small RNAs and dendrogram tag of *M. truncatula* roots led to annotation of 243 novel miRNAs. An increased accumulation of several novel and conserved miRNAs in mycorrhizal roots suggests their significant roles during AM symbiosis. The dendrogram analysis led to identification of 185 root transcript as mature miRNA. Several of identified miRNA targets are known to be involved in root symbiosis. Increased accumulation of specific miRNA and miRNA mediated cleavage of symbiosis relevant genes indicated that miRNAs are important part of

regulatory network that lead to the development of symbiosis (Devers et al. 2011). They found higher up-regulation in miR5229a/b and miR5229a/b in mycorrhizal roots and are highly abundant in arbuscule containing cells, suggesting their specific role during arbuscule development. Still no target gene has predicted for this miRNA, but prediction suggests a transcript encoding a haem peroxidase could be a target for this miRNA. It might be suggested that induction of miR5229a/b suppresses the haem peroxidase leading to locally increased hydrogen peroxide accumulation in cells with degenerate arbuscules. Lauressergues et al. (2012) reported that miR171h modulates arbuscular mycorrhizal colonization in *M. truncatula* by targeting NSP2 gene (Lauressergues et al. 2012). Induction of miR169d/I also reported in mycorrhizal roots. The miR169 target the transcription factor MtHAP2-1, that reported to play important role in nodule differentiation by restricting MtHAP2-1 expression in the nodule meristematic zone (Combier et al. 2008). The miRNA* sequences of miRNA169 family also strongly induced in mycorrhizal roots that can target Mtbcp1 gene. The Mtbcp1 encodes for protein specifically accumulating in periarbuscular membrane and speculated that the miR169* accumulating in mycorrhizal roots are involved in restricting the *MtBcp1* expression in arbuscule containing cells (Pumplin & Harrison 2009). The miR169* was detected in mycorrhizal colonized phloem, however the function of miRNA169* is yet to elucidate. The miR5204 appears to be phosphate responsive and located around individual arbuscules. They hypothesized that presence miR5204 correlates with phosphate concentration of distinct phosphate containing arbuscule. The miR160f and mycorrhizal induced miR160c predominantly localized in the phloem and targets several transcripts of auxin response factor (ARF) gene family.

The gene MtGst1 encodes for mycorrhizal symbiosis specific glutathione-s-transferase regulated by miR5282 and candidate miRNA new_miRc_275 (Wulf et al. 2003a). Earlier it has described that *Vitis venifera* miR156 and miR535 regulate squamosa promoter binding transcription factor (Mica et al. 2009). Some other symbiotic related genes that are regulated by miRNA are MtNsp2, a GRAS transcription factor that essential for root nodule development. The GRAS transcription factor is cleaved by miR5204*. In addition, *nsp2-2* mutant show decrease mycorrhizal colonization (Gobbato et al. 2012). Significant modulation of *MtNsp2* transcript levels was reported in mycorrhizal roots that cleaved by miR171h (Branscheid et al. 2011). The second most up-regulated transcript encodes a major facilitator protein PHO2 that is target by miR399 (Kim et al. 2011). The strong transcriptional induction of this major facilitator gene and its regulation by miR399 supports the role of miR399 during cellular phosphate homeostasis regulation in mycorrhizal roots (Branscheid et al. 2011).

Proteomics of mycorrhizal symbiosis

Proteins are *well known* effector molecule of plants that responds to different environmental cues. But very little information's are known about the changes in protein expression in root during AMF symbiosis. In recent year outstanding molecular approaches are used to identify genes and proteins those involved in mycorrhization process. Originally, in 1995 Marc Wilkin coined the term 'proteome' which describes the 'protein complement of genome'. So, it is very important to understand the role of genome complement (proteome) during AMF symbiosis. Although the proteomics study of AMF symbiosis is not significant enough, there are few reports that discussed the proteomic events of AMF symbiosis. Recent report by Abdallah et al. (2014) in *M. truncatula* root membrane proteome study colonized with *Rhizophagus irrgularis* revealed differential expression of 1226 candidate proteins (Abdallah et al. 2014). Among them abscisic acid 8'- hydroxylase 4, 60S ribosomal protein L6, RuBisco large subunit alpha, pre-mRNA processing ribonucleoprotein, translation factor proteins, flotillin like protein 4 are accumulated much higher than others. The abundance of β- barrel domain containing proteins and palmitate modified proteins are also detected significantly. The palmitate modified proteins are involved in membrane trafficking, protein sorting and other signaling cascades. The model plant *M. truncatula* inoculated with AMF *G. mosseae* shows significant modulation in proteome level (Bestel-Corre et al. 2002). Major differentially expressed proteins found when *M. truncatula* colonized with *G. mosseae* are RNA helicase, phytochrome A1, leghemoglobin, nitorgenase iron protein. The leghemoglobin and nitorgenase iron protein are also differentially modulated when *M. truncatula* was treated with nitrogen fixing bacteria *Sinorhizobium meliloti* (Bestel-Corre et al. 2002). This shows that leghemoglobin and nitorgenase iron proteins are indispensible for symbiosis. Some other differentially modulated proteins found during this study are glutathione-s-transferase, cytochrome c-oxidase subunit 6b, polygalacturonase inhibitor protein, myosin heavy chain like protein, profucosidase precursor, elongation factor Tu, enolase, malate dehydrogenase, and superoxide dismutase. The cytochrome c-oxidase is an integral membrane protein that play major role in respiratory metabolism. Induction of cytochrome c-oxidase during mycorrhization could directly relate with mitochondrial respiration in arbuscule containing cells. Dumas-Gaudot et al. (2004) performed an experiment in transferred-DNA (RiT-DNA) transformed root of carrot (*Daucus carota*) and colonized with *G. intraradices* to identify fungal protein involved in arbuscular mycorrhizal symbiosis (Dumas-Gaudot et al. 2004). They reported differential protein expression of NmrA-like protein, oxidoreductase, heat shock protein, ATP synthase β-mitochondrial precursor and MYK15-like protein (Dumas-Gaudot et al. 2004). Fester et al. (2002) also reported the role of MYK15-like protein in proteomic study of wheat (*Triticum aestivum*) root

infected with *G. intraradices* (Fester et al. 2002). The MYK15-like protein is an indicator of strong mycorrhizal colonization (Fester et al. 2002). The molecular mass of MYK15 is 15 kDa and isoelectric point (pI) is 4.5. So, mycorrhizal proteome study above pI 4.5 will automatically subtract this protein and cannot be detected in 2D-gel electrophoresis analysis. We already mentioned that DMI3 plays significant role in mycorrhiza process (Catoira et al. 2000). Study by Amiour et al. (2006) demonstrated that mutation in *DMI3* and *SUNN* modifies the appressorium-responsive root proteome in *M. truncatula* (Amiour et al. 2006). A DMI3 dependent *M. truncatula* increased accumulation of dehydroascorbate reductase, cyclophilin and actin depolymerization factor like proteins those related to signal transduction pathways. The role of actin depolymerization factor can be highly inferred as this protein is highly responsible for cell rearrangement that require for appressorium and arbuscule formation. No changes in proteome level was observed *post* five days of infection in *M. truncatula* mutant TRI22 (hyper-mycorrhizal) and TRV25 (mycorrhizal defective) when inoculated with *G. intraradices* (Amiour et al. 2006). In the wild type *M. truncatula,* infected with *G. intraradices* displayed an increase level of chalcone reductase, glutathione dependent dehydroascorbate reductase and actin depolymerization factor proteins. In TRI22 and TRV25 mutant, glutathione transferase is down regulated at appressorium stage. In the proteomic study of *Lycopersicum esculentum* inoculated with *G. mosseae*, 16 differentially expressed spots are detected during AM colonization stage (Ferrol & Benabdellah 2000). Sequence analysis from the selected bands revealed 69 kDa catalytic subunit of vacuolar type H^+ ATPase. Recorbet et al. (2010) colonized *M.truncatula* root with two *Glomus* (*G. mosseae and G. intraradices*) species and found 42 overlapping protein spots (Recorbet et al. 2010). Some of them are putative groES chaperonin, putative succinate dehydrogenase, putative malate dehydrogenase, leghemoglobin, glutathione and peroxidase.

Beside these proteomics events in mycorrhizal symbiosis, some research group applied toxicity stress to mycorrhiza inoculated plants. Repetto et al. (2003) applied cadmium stress (100 mg Cd/kg substrate) to *G. mosseae* inoculated pea root (*Pisum sativum*) and found differential proteome abundance (Repetto et al. 2003). Some differentially observed spots are vacuolar ATPase β subunit, annexin, short chain alcohol dehydrogenase, profucosidase and pea disease resistance protein (Repetto et al. 2003). In another study, 2 mg Cd/kg was used in *M. truncatula* plant inoculated with *G. irregularis* (Aloui et al. 2011). The mycorrhiza responsive shoot proteome highly accumulated photosynthesis related proteins coupled to reduction in gluconeogenesis/glycolysis and antioxidant process. The mycorrhizal plant treated with Cd metal accumulated molecular chaperons in shoot relative to metal free inoculation (Aloui et al. 2011). When *Pteris vittata,* a mycorrhizal fern inoculated with *G. mosseae* or *Gigaspora margarita* along with 25 ppm/kg arsenic contamination, it resulted into differential accumulation of glyceraldehy*de*-3-phosphate dehydrogenase, phosphoglycerate kinase, and enolase (Bona et al. 2010). These differentially accumulated proteins are majorly glycolytic proteins and plays important roles in arsenic metabolism. Beside this, a putative arsenic transporter gene PgPOR29 also upregulated by arsenic treatment (Bona et al. 2010). The arsenic treatment did not induce any changes in morphological parameters when compared with untreated plants. The plants treated with *G. margarita* showed significant reduction in *P. vitata* frond dry weight relative to *G. mosseae* treated and control plants (Bona et al. 2010). The pine tree *Populus alba* inoculated with *G. intraradices* shows sharp decrease in ATP synthase isoform and enolase protein (Lingua et al. 2012). The grapevine root stock SO4 (selection Oppenheim 4) inoculated with *Glomus* species elicit proteome response opposite of p-starvation (Cangahuala-Inocente et al. 2011). Some highly upregulated protein identified during this study are involved in energy production, signaling, protein synthesis etc. These proteins are 32 subtilisin-like protease, putative signal peptidase, proteasome regulatory subunit S5A, TGF-β receptor-interacting protein 1, putative ATP synthase D chain, ubiquitin carrier protein, and RNA-binding glycine-rich protein. From the overall proteome study of AMF symbiosis, it observed that proteins like leghemoglobin, nitrogenase, enolase, glutathione transgerase, ATPases, and MYK15 are accumulated more than other proteins.

Conclusion and future perspectives

Symbiotic events are evolutionary conserved phenomena present since the days of evolutionary history. Although the core set of symbiotic genes is conserved in both symbiotic partners, conservation of biochemical function seems to be insufficient to understand their biological function. The reverse genetics study will be very useful to understand these events very efficiently. Characterization of different mutants from cereal crops as well as from other important model organisms by applying genomics, proteomics, and other aspects will be very helpful in understanding the conserved evolutionary aspects of symbiotic event. Beside the AM fungal symbiotic research on legume plants, it is very important to shift the focus to other alternative model organism to gain more insight into the different aspects of symbiotic event. Besides this, genomics and proteomics data are increasing enormously from the plant as well as its fungal partner. This will provide most crucial base to understand different genomics and proteomics aspects of symbiosis.

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