Emerging Functions of Nodulin-Like Proteins in Non-Nodulating Plant Species

Nicolas Denancé[1,2,*], Boris Szurek[3] and Laurent D. Noël[1,2]

[1]INRA, Laboratoire des Interactions Plantes-Microorganismes (LIPM), UMR 441, F-31326 Castanet-Tolosan, France
[2]CNRS, Laboratoire des Interactions Plantes-Microorganismes (LIPM), UMR 2594, F-31326 Castanet-Tolosan, France
[3]Institut de Recherche pour le Développement, UMR Résistance des Plantes aux Bioagresseurs (RPB) IRD-Cirad-UM2, F-34394 Montpellier Cedex 5, France
*Corresponding author: E-mail: ndenance@toulouse.inra.fr; Fax, +33-5-6128-5061.

Plant genes whose expression is induced in legumes by *Rhizobium* bacteria upon nodulation were initially referred to as nodulins. Several of them play a key role in the establishment of symbiosis. Yet, nodulin-like proteins are also found in non-nodulating plant species such as Arabidopsis, rice, maize or poplar. For instance, 132 are predicted in the *Arabidopsis thaliana* Col-0 genome. Recent studies now highlight the importance of nodulin-like proteins for the transport of nutrients, solutes, amino acids or hormones and for major aspects of plant development. Interestingly, nodulin-like activities at the plant–microbe interface are also important for pathogens to enhance their fitness during host colonization. This work presents a genomic and functional overview of nodulin-like proteins in non-leguminous plant species, with a particular focus on Arabidopsis and rice.

Keywords: Amino acid • Arabidopsis • Nodulin • Nutrient • Pathogen • Rice • Sugar • Transporter.

Abbreviations: ENODL, early nodulin-like; MFS, major falicitator superfamily; NIP, NOD26-like intrinsic protein; PITP, phosphatidylinositol transfer protein; PLD, phospholipase D; TAL, transcription activator-like.

Introduction

Bacteria of the genus *Rhizobium* interact with legume plants to form a highly specific nitrogen-fixing symbiotic organ called a nodule (Crespi and Frugier 2008). This organogenesis results from the molecular dialog between *Rhizobium* bacteria and leguminous plants, involving plant flavonoids and bacterial lipochitooligosaccharidic molecules called Nod factors (Stacey et al. 2006). Consequently, bacteria colonize root tissues and their hosts form nodules where bacteria differentiate into nitrogen-fixing bacteroids that are beneficial to the plants (Kereszt et al. 2011). Nodulin-encoding genes were first defined as legume genes that are specifically expressed during the

development of symbiotic root nodules (Legocki and Verma 1980). Twenty-nine *Medicago truncatula* genes whose expression is induced during the interaction with *R. meliloti* were referred to as nodulin genes (*MtN1–MtN29*) (Gamas et al. 1996). *Early Nodulin* (*ENOD*) genes correspond to nodulin genes whose expression can be induced by purified Nod factors only, such as *ENOD12* in *Pisum sativum* and *M. truncatula* (Scheres et al. 1990, Pichon et al. 1992).

Interestingly, homologs of nodulin genes are found in the genome of several plants that are unable to nodulate, pointing to a possible ancestral role for nodulin-like genes in plant physiology. This work provides an overview of the distribution and known functions of nodulin-like proteins in non-leguminous plants. The function of most of the nodulin-like genes studied to date deals with the transport of various solutes throughout plant development. Finally, several nodulin-like proteins are also involved in the interaction of plants with pathogenic microbes, highlighting the implication of solute transport in plant innate immunity.

Seven Nodulin-Like Families are Present in Non-Leguminous Plant Species

A keyword search using 'nodulin' as a query against The Arabidopsis Information Resource (TAIR; http://www.arabidopsis.org/) and AmiGO (http://amigo.geneontology.org/cgi-bin/amigo/go.cgi) databases or in the literature identified 132 nodulin-like genes corresponding to seven distinct families (**Fig. 1A**) in the *Arabidopsis thaliana* Col-0 genome: *MtN3/saliva/SWEET*, *MtN21/EamA-like/UMAMIT*, *Early Nodulin-Like*, *Major Facilitator Superfamily*, *Sec14p-nodulin* domain proteins, *NOD26-like intrinsic proteins* and *Vacuolar Iron Transporter/nodulin-like* family. Furthermore, an ortholog of at least one member for each of these seven families was identified from the available genomes of dicot and monocot species when using Arabidopsis nodulin-like gene IDs as queries. These observations indicate that these nodulin-like families belong to

A

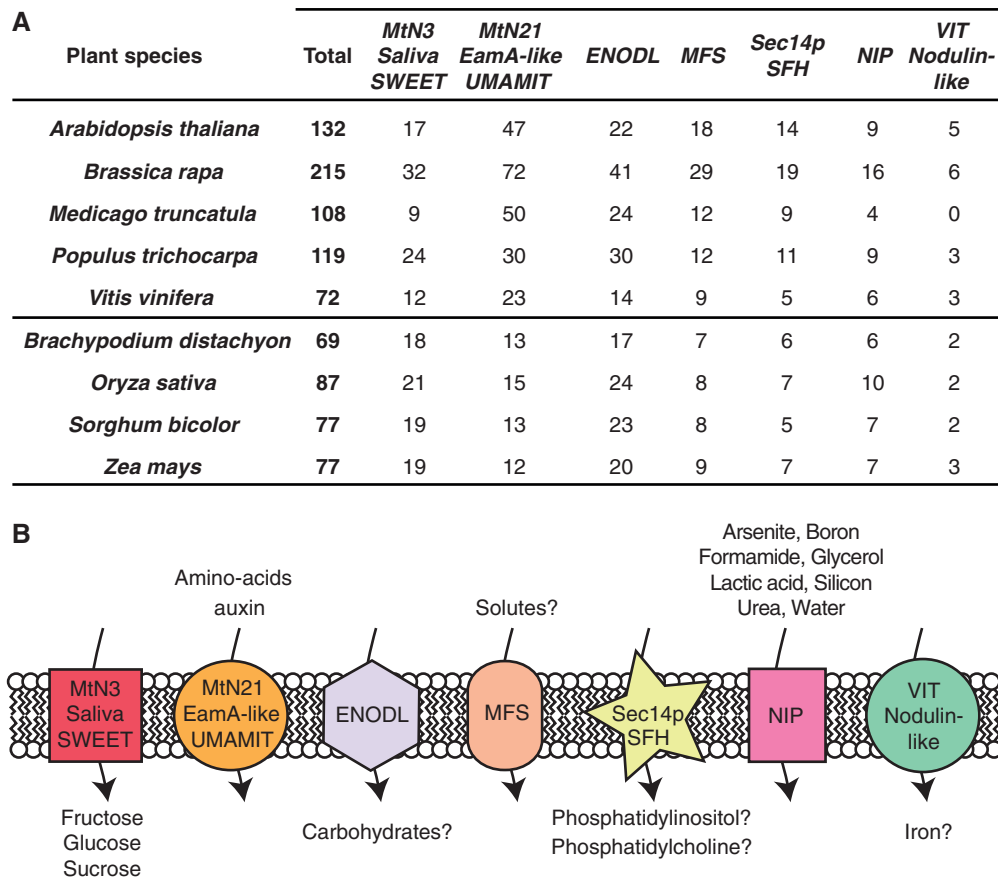| Plant species	Total	MtN3 Saliva SWEET	MtN21 EamA-like UMAMIT	ENODL	MFS	Sec14p SFH	NIP	VIT Nodulin-like
Arabidopsis thaliana	132	17	47	22	18	14	9	5
Brassica rapa	215	32	72	41	29	19	16	6
Medicago truncatula	108	9	50	24	12	9	4	0
Populus trichocarpa	119	24	30	30	12	11	9	3
Vitis vinifera	72	12	23	14	9	5	6	3
Brachypodium distachyon	69	18	13	17	7	6	6	2
Oryza sativa	87	21	15	24	8	7	10	2
Sorghum bicolor	77	19	13	23	8	5	7	2
Zea mays	77	19	12	20	9	7	7	3

B

Fig. 1 The seven nodulin-like protein families in plants: gene occurrence and schematic representation of their demonstrated or putative transported substrates. (A) Occurrence of nodulin-like gene family members in selected monocot and dicot plants. The number of nodulin-like genes of each family was determined via a literature-based search and genome mining. See **Supplementary Table S1** for further details on gene IDs. (B) Nodulin-like proteins are transmembrane proteins with demonstrated or proposed ('?') transporter activity. The type of membrane is not specified and the transport direction (import, export) is represented arbitrarily.

the *Viridiplantae* core genome (**Fig. 1A**; **Supplementary Table S1**). Thus, nodulin-like families expanded long before the speciation of legumes. Gene nomenclature and orthology between Arabidopsis, rice and seven other plant species have been compiled in **Supplementary Table S1** and **Figs. S1–S4**, respectively. Besides their historical role in nodulation, nodulin-like proteins achieve broader functions. The present review outlines their role in non-leguminous plants, with a particular focus on Arabidopsis and rice.

Nodulin-Like Proteins are Transmembrane Proteins with Varied Expression Patterns and Subcellular Localizations

Nodulin-like genes are usually expressed in all Arabidopsis organs (flowers, leaves, roots, stems, etc.) and during various developmental stages (pollen formation, secondary cell wall deposition, germination, senescence, etc.). They can be modulated by external cues (e.g. biotic or abiotic stress, or treatment with hormones or plant immunity elicitors) independently of the family they belong to. Yet, according to the Bio-Analytic Resource for Plant Biology (http://bar.utoronto.ca/welcome.htm), individual nodulin-like genes can have tissue-specific or inducible expression levels that provide hints as to their biological function. Furthermore, the seven nodulin-like protein families correspond to transmembrane proteins predicted to be targeted to distinct cellular membranes (plasmalemma, tonoplast or chloroplast) in Arabidopsis. This suggests that nodulin-like proteins are probably involved in a wide variety of physiological processes.

Nodulin-Like Proteins are Emerging as Proteins with Transporter Activity

The following sections review recent studies that provide hints as to the possible molecular and biological functions of each nodulin-like protein family. In particular, several nodulin-like proteins were recently shown to be bona fide transporters of

various solutes, while others are candidate transporters awaiting experimental validation (**Fig. 1B**).

The MtN3/saliva/SWEET family: glucose, sucrose or fructose transport

MtN3 was originally described as one of the 29 genes induced by *R. meliloti* in *M. truncatula* nodules (Gamas et al. 1996). Because Arabidopsis and rice *MtN3* orthologs function as glucose, sucrose or fructose transporters (Chen et al. 2010, Chen et al. 2012, Chardon et al. 2013, Klemens et al. 2013), and can also be associated with copper and aluminum transport (Yuan et al. 2010), these genes were renamed *SWEET* genes (Sugars Will Eventually be Exported Transporters). The function of the *SWEET* nodulin-like family has been reviewed recently (Chen et al. 2013, Yuan and Wang, 2013). The expression of several Arabidopsis *SWEET* genes is notably strongly induced in response to infection by *Pseudomonas syringae* pv. *tomato* (*Pst*) (*AtSWEET4, 5, 7, 8, 10* and *12*) and *Botrytis cinerea* (*AtSWEET4* and *17*) (Chen et al. 2010), suggesting that the control of SWEET-dependent sugar transport could be important for pathogenicity. Several rice *SWEET* genes are targeted by *Xanthomonas* virulence proteins named TALs (transcription activator-like; Muñoz Bodnar et al. 2013, Schornack et al. 2013), which specifically activate transcription of *OsSWEET* genes during infection to promote disease (Yang et al. 2006, Antony et al. 2010, Romer et al. 2010, Yu et al. 2011, Verdier et al. 2012, Li et al. 2013, Streubel et al. 2013). Interestingly, *OsSWEET14* expression can be induced by distinct TAL proteins from *X. oryzae* pv. *oryzae* (*Xoo*) strains of different geographic origins and genetic lineages (Streubel et al. 2013). This indicates that the ability to induce rice *SWEET* genes and the consecutive release of sugar in the apoplast is critical for bacterial pathogenicity at the early stages of infection. Yet, only clade III *OsSWEET* genes promoted *Xoo* pathogenicity (Streubel et al. 2013), suggesting that members of the other clades are involved in other physiological processes.

The MtN21/EamA-like transporter/UMAMIT family: amino acid and auxin transporters

The MtN21 protein-encoding gene was initially described as nodulin induced during *R. meliloti*–*M. truncatula* symbiosis (Gamas et al. 1996). The name of the EamA-like family derives from protein structure analysis which predicted a drug/metabolite transporter domain characteristic of amino acid exporters in *Escherichia coli*, such as EamA (*O*-acetylserine and cysteine), YdeD (cysteine, asparagine and glutamine) and RhtA (threonine and homoserine) proteins (Franke et al. 2003, Livshits et al. 2003). In the Arabidopsis TAIR database, the entire gene family was recently renamed as Usually Multiple Acids Move In and out Transporters (UMAMIT; **Supplementary Table S1**). So far, none of the 15 MtN21/UMAMIT nodulin-like proteins has been characterized in rice. Arabidopsis AtUMAMIT18/AtSIAR1 (Siliques Are Red 1) was reported to act as a bidirectional amino acid transporter

capable of importing glutamine, histidine and aspartate into yeast and *Xenopus* oocytes and exporting glutamine, valine, citrulline and isoleucine into yeast culture medium (Ladwig et al. 2012). AtUMAMIT18 may be required for releasing amino acids from the phloem to the apoplasmic space, making them subsequently available for import into adjacent cells of the endosperm and the embryo. In roots, AtUMAMIT18 is thought to be involved in amino acid loading into the xylem (Ladwig et al. 2012). AtUMAMIT5/AtWAT1 (Walls Are Thin1) is a tonoplast-localized protein required for proper secondary cell wall formation in stem fibers (Ranocha et al. 2010). A loss-of-function mutant displayed reduced stem size, was deficient in tryptophan and its derived auxin production, lacked auxin basipetal transport and displayed a deregulation of the expression of many auxin-related genes, including some involved in auxin biosynthesis and transport, and to the response to auxin (Ranocha et al. 2010). In accordance with these features, Ranocha et al. (2013) recently demonstrated that AtUMAMIT5/AtWAT1 acted as a vacuolar auxin export facilitator in isolated Arabidopsis vacuoles, in yeast and in *Xenopus* oocytes. Additionally, *wat1* mutants exhibited enhanced vascular immunity suspected to result from a hormonal shift in roots (less auxin, more salicylic acid) likely to modify sap composition and constitute a hostile environment for xylem-colonizing pathogens (Denancé et al. 2013).

The early nodulin-like (ENODL) family: carbohydrate transporters?

In Arabidopsis, 22 ENODL family members (AtENODL1–AtENODL22) were identified through several proteomic and genomic studies (**Supplementary Table S1**) (Borner et al. 2002, Borner et al. 2003, Khan et al. 2007, Mashiguchi et al. 2009). These proteins are related to phytocyanins, i.e. blue copper proteins that bind a single copper atom and function as electron transporters. Yet, the amino acid residues needed for copper binding are missing in AtENODL proteins, suggesting the involvement of this protein family in other processes (Greene et al. 1998, Mashiguchi et al. 2004). AtENODL1, 13–15 and 17 were identified in a phosphoproteomic analysis of plasma membranes treated with elicitors of plant immunity (Benschop et al. 2007), suggesting a role in this process. As regards AtENODL9, it accumulates to high levels in mature sieve elements that participate, together with companion cells, in phloem loading/unloading and solute transport. *atenodl9* mutants had a delayed bolting, and the number and biomass of the siliques were strongly reduced, albeit that their vegetative development was not impaired significantly (Khan et al. 2007). Since carbohydrate signaling affects the vegetative to reproductive stage shift and floral initiation, it is tempting to attribute a role in carbohydrate transport to AtENODL9, but further experimental evidence is required to support such a function.

The major facilitator superfamily: transporters of unknown solutes?

The major falicitator superfamily (MFS) is composed of 74 families of uniporters, symporters or antiporters of various compounds that are found ubiquitously in all three kingdoms of living organisms. Among them, a few members carry the IPR010658 domain, which is a well-conserved region within plant nodulin-like proteins. Their transporter activity was deciphered in bacteria and demonstrated for various substrates such as mono- and polysaccharides, phosphate, nitrate, drugs or ions (Reddy et al. 2012). Although no transport activity of an MFS nodulin-like protein has been reported so far in plants, some gene expression data sets suggest their potential involvement. For instance, *AtMFS4* and *AtMFS5* expression is induced upon treatment with karrikins, a class of signaling molecules which trigger seed germination (Nelson et al. 2010). Interestingly, karrikins are structurally similar to strigolactones which stimulate the initiation of symbiosis by arbuscular mycorrhizal fungi in legumes (Akiyama et al. 2005, Besserer et al. 2006, Waters et al. 2013). Expression of *AtMFS10*, which encodes a plasmodesmal protein, increases during infection by the oomycete *Hyaloperonospora arabidopsidis* (Fernandez-Calvino et al. 2011, Hok et al. 2011). Collectively, these data suggest that some MFS nodulin-like proteins might be important for plant responses to symbiotic or pathogenic microbes.

The Sec14p-nodulin domain family: phosphatidylinositol or phosphatidylcholine transport?

Sec14p-nodulin domain proteins share homologies with ScSec14p, a Golgi-associated phosphatidylinositol transfer protein (PITP) that regulates lipid trafficking in yeast (Bankaitis et al. 1990, Cleves et al. 1991). Proteins related to Sec14p are found exclusively in eukaryotes, including plants (Jouannic et al. 1998, Vincent et al. 2005). AtSFH4– AtSFH6 were identified in the phosphoproteome of plasma membranes treated with flg22 and xylanase elicitors (Benschop et al. 2007). Mutants of *AtSFH1/COW1/SRH1/ PITP1* (*Can Of Worms 1/Short Root Hair 1*) and *OsSNDP1* (Sec14-nodulin domain protein), a close ortholog of *AtSFH1*, display abnormal root hair morphology, indicating that these genes are required for correct root hair elongation (Bohme et al. 2004, Vincent et al. 2005, Huang et al. 2013). PITPs can bind phosphatidylcholine and deliver it to phospholipase D (PLD). Therefore AtSFH1 could transport phosphatidylcholine to a PLD for hydrolysis. In this case, loss of *AtSFH1* function is thought to interfere with PLD activity and thus to impair the correct membrane trafficking process that is essential for root hair tip growth (Bohme et al. 2004, Vincent et al. 2005). Like all proteins with Sec14-domains, rice OsSNDPs share all three conserved residues corresponding to E207, K239 and G266 in yeast Sec14p. These residues are critical for

phosphatidylinositol transport activity (Huang et al. 2013), suggesting that rice OsSNDPs could be active proteins.

The NOD26-like intrinsic protein (NIP) family: arsenite, boron, formamide, glycerol, lactic acid, silicon, urea or water transporters

NIPs, also referred to as NLMs (NOD26-like major intrinsic proteins), are proteins homologous to GmNOD26, an aquaporin abundantly found in peribacteroid membranes in soybean root nodules (Fortin et al. 1987). NIPs transport various substrates such as water (AtNIP1;1), glycerol (AtNIP1;1, AtNIP1;2 and AtNIP6;1), lactic acid (AtNIP2;1), arsenite (AtNIP1;1, AtNIP1;2 and AtNIP5;1), formamide (AtNIP1;6), boron (AtNIP5;1, AtNIP6;1 and AtNIP7;1) and urea (AtNIP6;1) (Li et al. 2011, Mitani-Ueno et al. 2011, and references therein). In rice, OsNIP2;1 transports silicon, which can have a protective role against powdery mildew infection (Fauteux et al. 2006, Ma et al. 2006).

Vacuolar iron transporter/nodulin-like proteins: iron transporters?

The yeast *ScCCC1* (Ca^{2+}-sensitive cross-complementer1) gene encodes an iron/manganese transporter involved in the vacuolar accumulation of these metals (Li et al. 2001). AtVIT1 (vacuolar iron transporter1; At2g01770), an Arabidopsis ortholog of ScCC1, localizes to the tonoplast, mediates iron sequestration in vacuoles and controls iron homeostasis in seeds (Kim et al. 2006). The Arabidopsis genome contains five nodulin-like proteins with similarity to ScCC1 and AtVIT1 (**Supplementary Table S1**; Gollhofer et al. 2011). While the expression of *AtNodulin-like21/AtCCCL1* (*CCC1-like1*), *AtNodulin-like1/ AtCCCL2* and *AtNodulin-like2/AtCCCL3* was first reported as increased upon iron deficiency in roots (Garcia et al. 2010), decreased expression of these genes after Fe depletion was later reported (Gollhofer et al. 2011). *AtNodulin-like3 and 4* gene expression was insensitive to the treatment (Gollhofer et al. 2011). Thus, the exact molecular function of these putative transporters remains unclear.

Conclusions

Whenever nodulin-like protein functions were reported in Arabidopsis or rice, they were shown to transport a whole range of compounds or to be associated with their transport (**Fig. 1B**). The presence of members of seven nodulin-like families in the core genome of plants indicates that nodulin-like proteins acquired important biological functions prior to the speciation of legumes and the recruitment of nodulin-like proteins for nodulation. In particular, the transporter function of nodulins in both symbiotic and pathogenic interactions suggests that the control of molecular fluxes at the plant–microbe interface is critical for the outcome of these interactions. Microbes have learnt how to subvert these transporters to increase their fitness, as exemplified by the pathogenic bacterium *Xanthomonas* which induces the expression of the *SWEET* sugar

transporters using TAL virulence proteins. The investigation of the functions of nodulin-like protein in non-leguminous plants is just emerging. Future studies will shed new light on how nodulin-like proteins are involved in plant development and plant–microbe interactions.

Supplementary data

Supplementary data are available at PCP online.

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Disclosures

The authors have no conflicts of interest to declare.

References

Akiyama, K., Matsuzaki, K. and Hayashi, H. (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature* 435: 824–827.

Antony, G., Zhou, J., Huang, S., Li, T., Liu, B., White, F. et al. (2010) Rice *xa13* recessive resistance to bacterial blight is defeated by induction of the disease susceptibility gene *Os-11N3*. *Plant Cell* 22: 3864–3876.

Bankaitis, V.A., Aitken, J.R., Cleves, A.E. and Dowhan, W. (1990) An essential role for a phospholipid transfer protein in yeast Golgi function. *Nature* 347: 561–562.

Benschop, J.J., Mohammed, S., O'Flaherty, M., Heck, A.J., Slijper, M. and Menke, F.L. (2007) Quantitative phosphoproteomics of early elicitor signaling in *Arabidopsis*. *Mol. Cell. Proteomics* 6: 1198–1214.

Besserer, A., Puech-Pagès, V., Kiefer, P., Gomez-Roldan, V., Jauneau, A., Roy, S. et al. (2006) Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. *PLoS Biol.* 4: e226.

Bohme, K., Li, Y., Charlot, F., Grierson, C., Marrocco, K., Okada, K. et al. (2004) The Arabidopsis *COW1* gene encodes a phosphatidylinositol transfer protein essential for root hair tip growth. *Plant J.* 40: 686–698.

Borner, G.H., Lilley, K.S., Stevens, T.J. and Dupree, P. (2003) Identification of glycosylphosphatidylinositol-anchored proteins in *Arabidopsis*. A proteomic and genomic analysis. *Plant Physiol.* 132: 568–577.

Borner, G.H., Sherrier, D.J., Stevens, T.J., Arkin, I.T. and Dupree, P. (2002) Prediction of glycosylphosphatidylinositol-anchored proteins in *Arabidopsis*. A genomic analysis. *Plant Physiol.* 129: 486–499.

Chardon, F., Bedu, M., Calenge, F., Klemens, P.A., Spinner, L., Clement, G. et al. (2013) Leaf fructose content is controlled by the vacuolar transporter SWEET17 in Arabidopsis. *Curr. Biol.* 23: 697–702.

Chen, L.-Q. (2013) SWEET sugar transporters for phloem transport and pathogen nutrition. *New Phytol.* (in press).

Chen, L.-Q., Hou, B.H., Lalonde, S., Takanaga, H., Hartung, M.L., Qu, X.Q. et al. (2010) Sugar transporters for intercellular exchange and nutrition of pathogens. *Nature* 468: 527–532.

Chen, L.-Q., Qu, X.Q., Hou, B.H., Sosso, D., Osorio, S., Fernie, A.R. et al. (2012) Sucrose efflux mediated by SWEET proteins as a key step for phloem transport. *Science* 335: 207–211.

Cleves, A.E., McGee, T.P., Whitters, E.A., Champion, K.M., Aitken, J.R., Dowhan, W. et al. (1991) Mutations in the CDP-choline pathway for phospholipid biosynthesis bypass the requirement for an essential phospholipid transfer protein. *Cell* 64: 789–800.

Crespi, M. and Frugier, F. (2008) De novo organ formation from differentiated cells: root nodule organogenesis. *Sci. Signal.* 1: re11.

Denancé, N., Ranocha, P., Oria, N., Barlet, X., Rivière, M.-P., Yadeta, K.A. et al. (2013) Arabidopsis *wat1* (*walls are thin1*)-mediated resistance to the bacterial vascular pathogen, *Ralstonia solanacearum*, is accompanied by cross-regulation of salicylic acid and tryptophan metabolism. *Plant J.* 73: 225–239.

Fauteux, F., Belzile, F., Menzies, J.G. and Bélanger, R.R. (2006) The protective role of silicon in the Arabidopsis–powdery mildew pathosystem. *Proc. Natl Acad. Sci. USA* 103: 17554–17559.

Fernandez-Calvino, L., Faulkner, C., Walshaw, J., Saalbach, G., Bayer, E., Benitez-Alfonso, Y. et al. (2011) *Arabidopsis* plasmodesmal proteome. *PLoS One* 6: e18880.

Fortin, M.G., Morrison, N.A. and Verma, D.P.S. (1987) Nodulin-26, a peribacteroid membrane nodulin is expressed independently of the development of the peribacteroid compartment. *Nucleic Acids Res.* 15: 813–824.

Franke, I., Resch, A., Dassler, T., Maier, T. and Böck, A. (2003) YfiK from *Escherichia coli* promotes export of O-acetylserine and cysteine. *J. Bacteriol.* 185: 1161–1166.

Gamas, P., de Carvalho-Niebel, F., Lescure, N. and Cullimore, J. (1996) Use of a subtractive hybridization approach to identify new *Medicago truncatula* genes induced during root nodule development. *Mol. Plant Microbe Interact.* 9: 233–242.

Garcia, M.J., Lucena, C., Romera, F.J., Alcantara, E. and Perez-Vicente, R. (2010) Ethylene and nitric oxide involvement in the up-regulation of key genes related to iron acquisition and homeostasis in Arabidopsis. *J. Exp. Bot.* 61: 3885–3899.

Gollhofer, J., Schläwicke, C., Jungnick, N., Schmidt, W. and Buckhout, T.J. (2011) Members of a small family of nodulin-like genes are regulated under iron deficiency in roots of *Arabidopsis thaliana*. *Plant Physiol. Biochem.* 49: 557–564.

Greene, E.A., Erard, M., Dedieu, A. and Barker, D.G. (1998) MtENOD16 and 20 are members of a family of phytocyanin-related early nodulins. *Plant Mol. Biol.* 36: 775–783.

Hok, S., Danchin, E.G., Allasia, V., Panabières, F., Attard, A. and Keller, H. (2011) An *Arabidopsis* (malectin-like) leucine-rich repeat receptor-like kinase contributes to downy mildew disease. *Plant Cell Environ.* 34: 1944–1957.

Huang, J., Kim, C.M., Xuan, Y-H., Park, S.J., Piao, H.L., Je, B.I. et al. (2013) OsSNDP1, a Sec14-nodulin domain-containing protein, plays a critical role in root hair elongation in rice. *Plant Mol. Biol.* 82: 39–50.

Jouannic, N., Lepetit, M., Vergnolle, C., Cantrel, C., Gardies, A.M., Kader, J.C. et al. (1998) Isolation of a cDNA from *Arabidopsis*

thaliana that complements the *sec14* mutant of yeast. *Eur. J. Biochem.* 258: 402–410.

Kereszt, A., Mergaert, P. and Kondorosi, E. (2011) Bacteroid development in legume nodules: evolution of mutual benefit or of sacrificial victims? *Mol. Plant Microbe Interact.* 24: 1300–1309.

Khan, J.A., Wang, Q., Sjolund, R.D., Schulz, A. and Thompson, G.A. (2007) An early nodulin-like protein accumulates in the sieve element plasma membrane of Arabidopsis. *Plant Physiol.* 143: 1576–1589.

Kim, S.A., Punshon, T., Lanzirotti, A., Li, L., Alonso, J.M. and Ecker, J.R. (2006) Localization of iron in Arabidopsis seed requires the vacuolar membrane transporter VIT1. *Science* 314: 1295–1298.

Klemens, P.A., Patzke, K., Deitmer, J., Spinner, L., Le Hir, R., Bellini, C. et al. (2013) Overexpression of the vacuolar sugar carrier AtSWEET16 modifies germination, growth, and stress tolerance in Arabidopsis. *Plant Physiol.* 163: 1338–1352.

Ladwig, F., Stahl, M., Ludewig, U., Hirner, A.A., Hammes, U.Z., Stadler, R. et al. (2012) *Siliques Are Red1* from Arabidopsis acts as a bidirectional amino acid transporter that is crucial for the amino acid homeostasis of siliques. *Plant Physiol.* 158: 1643–1655.

Legocki, R.P. and Verma, D.P. (1980) Identification of 'nodule-specific' host proteins (nodulins) involved in the development of rhizobium–legume symbiosis. *Cell* 20: 153–163.

Li, L., Chen, O.S., McVey, W.D. and Kaplan, J. (2001) CCC1 is a transporter that mediates vacuolar iron storage in yeast. *J. Biol. Chem.* 276: 29515–29519.

Li, T., Choi, W.-G., Wallace, I.S., Baudry, J. and Roberts, D.M. (2011) *Arabidopsis thaliana* NIP7;1: an anther-specific boric acid transporter of the aquaporin superfamily regulated by an unusual tyrosine in helix 2 of the transport pore. *Biochemistry* 50: 6633–6641.

Li, T., Huang, S., Zhou, J. and Yang, B. (2013) Designer TAL effectors induce disease susceptibility and resistance to *Xanthomonas oryzae* pv. *oryzae* in rice. *Mol. Plant* 6: 781–789.

Livshits, V.A., Zakataeva, N.P., Aleshin, V.V. and Vitushkina, M.V. (2003) Identification and characterization of the new gene *rhtA* involved in threonine and homoserine efflux in *Escherichia coli*. *Res. Microbiol.* 154: 123–135.

Ma, J.F., Tamai, K., Yamaji, N., Mitani, N., Konishi, S., Katsuhara, M. et al. (2006) A silicon transporter in rice. *Nature* 440: 688–691.

Mashiguchi, K., Asami, T. and Suzuki, Y. (2009) Genome-wide identification, structure and expression studies, and mutant collection of 22 early nodulin-like protein genes in *Arabidopsis*. *Biosci. Biotechnol. Biochem.* 73: 2452–2459.

Mashiguchi, K., Yamaguchi, I. and Suzuki, Y. (2004) Isolation and identification of glycosylphosphatidylinositol-anchored arabinogalactan proteins and novel beta-glucosyl Yariv-reactive proteins from seeds of rice (*Oryza sativa*). *Plant Cell Physiol.* 45: 1817–1829.

Mitani-Ueno, N., Yamaji, N., Zhao, F.J. and Ma, J.F. (2011) The aromatic/arginine selectivity filter of NIP aquaporins plays a critical role in substrate selectivity for silicon, boron, and arsenic. *J. Exp. Bot.* 62: 4391–4398.

Muñoz Bodnar, A., Bernal, A., Szurek, B. and López, C.E. (2013) Tell me a tale of TALEs. *Mol. Biotechnol.* 53: 228–235.

Nelson, D.C., Flematti, G.R., Riseborough, J.A., Ghisalberti, E.L., Dixon, K.W. and Smith, S.M. (2010) Karrikins enhance light responses during germination and seedling development in *Arabidopsis thaliana*. *Proc. Natl Acad. Sci. USA* 107: 7095–7100.

Pichon, M., Journet, E.P., Dedieu, A., de Billy, F., Truchet, G. and Barker, D.G. (1992) *Rhizobium meliloti* elicits transient expression of the early nodulin gene *ENOD12* in the differentiating root epidermis of transgenic alfalfa. *Plant Cell* 4: 1199–1211.

Ranocha, P., Denancé, N., Vanholme, R., Freydier, A., Martinez, Y., Hoffmann, L. et al. (2010) Walls are thin 1 (WAT1), an *Arabidopsis* homolog of *Medicago truncatula* NODULIN21, is a tonoplast-localized protein required for secondary wall formation in fibers. *Plant J.* 63: 469–483.

Ranocha, P., Dima, O., Nagy, R., Felten, J., Corratgé-Faillie, C., Novák, O. et al. (2013) *Arabidopsis* WAT1 is a vacuolar auxin transport facilitator required for auxin homeostasis. *Nat. Commun.* 4: 2625.

Reddy, V.S., Shlykov, M.A., Castillo, R., Sun, E.I. and Saier, M.H. Jr (2012) The major facilitator superfamily (MFS) revisited. *FEBS J.* 279: 2022–2035.

Romer, P., Recht, S., Strauss, T., Elsaesser, J., Schornack, S., Boch, J. et al. (2010) Promoter elements of rice susceptibility genes are bound and activated by specific TAL effectors from the bacterial blight pathogen, *Xanthomonas oryzae* pv. *oryzae*. *New Phytol.* 187: 1048–1057.

Scheres, B., van Engelen, F., van der Knaap, E., van de Wiel, C., van Kammen, A. and Bisseling, T. (1990) Sequential induction of nodulin gene expression in the developing pea nodule. *Plant Cell* 2: 687–700.

Schornack, S., Moscou, M.J., Ward, E.R. and Horvath, D.M. (2013) Engineering plant disease resistance based on TAL effectors. *Annu. Rev. Phytopathol.* 51: 383–406.

Stacey, G., Libault, M., Brechenmacher, L., Wan, J. and May, G.D. (2006) Genetics and functional genomics of legume nodulation. *Curr. Opin. Plant Biol.* 9: 110–121.

Streubel, J., Pesce, C., Hutin, M., Koebnik, R., Boch, J. and Szurek, B. (2013) Five phylogenetically close rice *SWEET* genes confer TAL effector-mediated susceptibility to *Xanthomonas oryzae* pv. *oryzae*. *New Phytol.* 200: 808–819.

Verdier, V., Triplett, L.R., Hummel, A.W., Corral, R., Cernadas, R.A., Schmidt, C.L. et al. (2012) Transcription activator-like (TAL) effectors targeting *OsSWEET* genes enhance virulence on diverse rice (*Oryza sativa*) varieties when expressed individually in a TAL effector-deficient strain of *Xanthomonas oryzae*. *New Phytol.* 196: 1197–1207.

Vincent, P., Chua, M., Nogue, F., Fairbrother, A., Mekeel, H., Xu, Y. et al. (2005) A Sec14p-nodulin domain phosphatidylinositol transfer protein polarizes membrane growth of *Arabidopsis thaliana* root hairs. *J. Cell Biol.* 168: 801–812.

Waters, M.T., Scaffidi, A., Flematti, G.R. and Smith, S.M. (2013) The origins and mechanisms of karrikin signalling. *Curr. Opin. Plant Biol.* 16: 667–673.

Yang, B., Sugio, A. and White, F.F. (2006) *Os8N3* is a host disease-susceptibility gene for bacterial blight of rice. *Proc. Natl Acad. Sci. USA* 103: 10503–10508.

Yu, Y., Streubel, J., Balzergue, S., Champion, A., Boch, J., Koebnik, R. et al. (2011) Colonization of rice leaf blades by an African strain of *Xanthomonas oryzae* pv. *oryzae* depends on a new TAL effector that induces the rice nodulin-3 *Os11N3* gene. *Mol. Plant Microbe Interact.* 24: 1102–1113.

Yuan, M., Chu, Z., Li, X., Xu, C. and Wang, S. (2010) The bacterial pathogen *Xanthomonas oryzae* overcomes rice defenses by regulating host copper redistribution. *Plant Cell* 22: 3164–3176.

Yuan, M. and Wang, S. (2013) Rice MtN3/saliva/SWEET family genes and their homologues in cellular organisms. *Mol. Plant* 6: 665–674.