

Table S1: Overview of nodulation genes identified by forward and/or reverse genetics. Lj: *Lotus japonicus*, Mt: *Medicago truncatula*, Ms: *Medicago sativa*; Gm: *Glycine max*, Ps: *Pisum sativum*; Pv: *Phaseolus vulgaris*, As: *Astragalus sinicus*, Ag: *Alnus glutinosa*, Cg: *Casuarina glauca*, Dg: *Datisca glomerata* and Pan: *Parasponia andersonii*.

receptor complexes	gene name	description	symbiosis	references
LysM-RLK	LjEPR3	Exopolysaccharide receptor	-/Nod	(Kawaharada et al., 2015)
LysM-RLK	MtLYK3, LjNFR1	Rhizobium LCO receptor	AM/Nod	(Radutoiu et al., 2003; Limpens et al., 2003; Smit et al., 2007; Broghammer et al., 2012)
LysM-RLK	LjNFRe	Epidermis specific rhizobium LCO receptor	-/Nod	(Murakami et al., 2018)
LysM-RLK	MtLYK9, LjCERK6, PsLYK9	CO receptor	AM/-	(Bozsoki et al., 2017; Leppyanen et al., 2017; Gibelin-Viala et al., 2019)
LysM-RLK	MtNFP, LjNFR5, PanNFP1	Rhizobium LCO receptor	-/Nod	(Madsen et al., 2003; Arrighi et al., 2006; Op den Camp et al., 2011b; Broghammer et al., 2012)
LysM-RLK	MtLYR3	LCO receptor, induced in nodules	-/Nod	(Fliegmann et al., 2013; Fliegmann et al., 2016)
Flotilin	MtFLOT2, MtFLOT4	Scaffold of LysM-type LCO receptors, required for nodule formation and infection	-/Nod	(Haney and Long, 2010; Haney et al., 2011)
Rho-like Small GTPase	LjROP6	Interacts with LjNFR5. Controls infection	-/Nod	(Ke et al., 2012)
NFR5-interacting cytoplasmic kinase	LjNiCK4	Promotes nodule organogenesis	-/Nod	(Wong et al., 2019)
E3-ligase	MtPUB1	Interacts with MtLYK3, negative regulator	-/Nod	(Mbengue et al., 2010)
E3-ligase	LjPUB13	Interacts with LjNFR5, positive regulator	-/Nod	(Tsikou et al., 2018)
Symbiotic receptor kinase	MtDMI2, LjSYMRK, MsNORK	LRR-RLK, essential for LCO signalling	AM/Nod	(Stracke et al., 2002; Endre et al., 2002)
SYMRK interacting protein HMGR	MtHMGR1	3-hydroxy-3-methylglutaryl coenzyme A reductase involved in mevalonate pathway	AM/Nod	(Kevei et al., 2007; Venkateshwaran et al., 2015)
SYMRK interacting protein SIP1	LjSIP1	ARID/BRIGHT DNA binding domain containing protein	-/Nod	(Zhu et al., 2008)
MAP kinase kinase	LjSIP2	Interacts with LjSYMRK.	-/Nod	(Zhu et al., 2008; Chen et al., 2012)

MAP kinase	LjMPK6	MAP kinase. Target of LjSIP2. Targets LjLHK1	-/Nod	(Yin et al., 2019)
E3-ligase	LjSINA4	Interacts with LjSYMRK, negative regulator of rhizobium infection.	-/Nod	(Den Herder et al., 2012)
E3-ligase	LjSIE3	Interacts with LjSYMRK, involved in nodule formation	-/Nod	(Yuan et al., 2012)
Lectin nucleotide phosphohydrolase	LjLNP	Essential for LCO signalling	AM/Nod	(Yuan et al., 2012; Roberts et al., 2013)
Nod factor hydroloase	MtNFH1	LCO hydrolase	-/AM	(Cai et al., 2018a)
Nuclear signalling				
Calcium-dependent protein kinase	MtCPK3	Controls nodulation efficiency	-/Nod	(Gargantini et al., 2006)
Calcium ATP-ase	MtMCA8	Essential for LCO induced perinuclear calcium oscillations	AM/Nod	(Capoen et al., 2011)
Cyclic nucleotide-gated Ca ²⁺ channel	MtCNGC15a, MtCNGC15b, MtCNGC15c	Essential for LCO induced perinuclear calcium oscillations	-/Nod	(Charpentier et al., 2016)
Nucleoporin	LjNUP85	Essential for LCO induced perinuclear calcium oscillations	AM/Nod	(Saito et al., 2007)
Nucleoporin	LjNUP133	Essential for LCO induced perinuclear calcium oscillations	AM/Nod	(Kanamori et al., 2006)
Nucleoporin	LjNENA	Required for rhizobium and mycorrhizal infection	AM/Nod	(Groth et al., 2010)
Potassium channel	MtDMI1, LjPOLLUX	Essential for LCO signalling	AM/Nod	(Ané et al., 2004; Imaizumi-Anraku et al., 2005)
Potassium channel	LjCASTOR	Essential for LCO signalling	AM/Nod	(Imaizumi-Anraku et al., 2005)
Calcium Calmodulin dependent kinase	MtDMI3, LjCCAMK	Essential for LCO signalling	AM/Nod	(Mitra et al., 2004; Lévy et al., 2004; Tirichine et al., 2006)
Transcriptional regulators				
CYCLOPS transcription factor	MtIPD3, LjCYCLOPS, MtIPD3L	Essential for LCO signalling. Interacts with CCaMK	-/Nod	(Messinese et al., 2007; Yano et al., 2008; Singh et al., 2014; Jin et al., 2018)
NODULE INCEPTION transcription factor	MtNIN, LjNIN, PsSYM35, CgNIN	Nodule Inception transcription factor, essential for nodule formation	-/Nod	(Schauser et al., 1999; Borisov et al., 2003; Marsh et al., 2007; Clavijo et al., 2015)

NIN-LIKE PROTEIN	MtNLP1, LjNRSYM1	Represses NIN upon physical interaction	-/Nod	(Nishida et al., 2018; Lin et al., 2018)
Nuclear Factor YA transcription factor	MtNF-YA1, LjNF-YA1, PvNF-YA1, MtNF-YA2, LjCBFA22, LjCBFA01	Direct target of NIN, forms complex with NF-YB and NF-YC subunits. Essential for nodule development and infection	-/Nod	(Combier et al., 2006; Soyano et al., 2013; Rípodas et al., 2019)
Nuclear Factor YB transcription factor	MtNF-YB16, LjNF-YB1, PvNF-YB7	Direct target NIN, forms complex with NF-YA and NF-YC subunits.	-/Nod	(Soyano et al., 2013; Baudin et al., 2015; Rípodas et al., 2019)
Nuclear Factor YC transcription factor	MtNF-YC1, MtNF-YC2 / PvNF-YC1	Involved in rhizobium infection and nodule development. Forms complex with NF-YA and NF-YB subunits.	-/Nod	(Zanetti et al., 2010; Mazziotta et al., 2013; Baudin et al., 2015; Rípodas et al., 2019)
AP2-ERF transcription factor	MtERN1, MtERN2	Essential for nodule formation, and AM symbiosis	-/Nod	(Middleton et al., 2007; Cerri et al., 2016)
AP2-ERF transcription factor	LjERF1	Involved in nodule formation	-/Nod	(Asamizu et al., 2008)
AP2-ERF transcription factor	MtEFD	Essential for nodule development	-/Nod	(Vernié et al., 2008; Asamizu et al., 2008)
GRAS-type transcriptional regulator	MtNSP1, LjNSP1, PanNSP1	Essential for nodule formation	-/Nod	(Smit et al., 2005; Heckmann et al., 2006b; van Zeijl et al., 2018)
GRAS-type transcriptional regulator	MtNSP2, LjNSP2, PanNSP2	Essential for nodule formation	AM/Nod	(Kalo et al., 2005; Heckmann et al., 2006a; van Zeijl et al., 2018)
GRAS-type transcriptional regulator	MtSymSCL1	Role in nodule number regulation	-/Nod	(Kim and Nam, 2013)
bHLH transcription factor	GmbHLHm1 (GmSAT1)	Essential for nodule functioning	AM/Nod	(Chiasson et al., 2014)
bHLH transcription factor	MtbHLH1	Involved in nodule vasculature patterning	-/Nod	(Godiard et al., 2011)
bHLH transcription factor	MtbHLH476	Direct target of CRE1-dependent cytokinin signaling regulating nodulation	-/Nod	(Ariel et al., 2012)
BOP-type transcriptional regulator	MtNOOT1, MtNOOT2, LjNBCL1, PsCOCH	Regulator of nodule development	-/Nod	(Couzigou et al., 2012; Magne et al., 2018a; Magne et al., 2018b)
aminopetidase P1	LjAPP1	Interactor of LjNBCL1. Negative regulator of nodulation	-/Nod	(Liu et al., 2018)

C2H2 transcription factor	MsZPT2-1	Regulator of nodule development	-/Nod	(Frugier et al., 2000)
C2H2 transcription factor	MtRSD	Regulator of symbiosome development	-/Nod	(Sinharoy et al., 2013)
NAC transcription factor	MtNAC969	Antagonistically regulates root abiotic stress response and nodule senescence	-/Nod	(De Zélicourt et al., 2012)
MYB transcription factor	LjIPN2	Interacting protein of NSP2	-/Nod	(Kang et al., 2014)
MYB transcription factor	GmCND	Controls nodule Development	-/Nod	(Libault et al., 2009)
MADS box transcription factor	GmNMHC5	Positive regulator of nodulation. Sucrose-responsive	-/Nod	(Liu et al., 2015)
KNOX homeodomain transcription factor	MtKNOX3, MtKNOX4, MtKNOX5	Functions in nodule differentiation	-/Nod	(Azarakhsh et al., 2015; Di Giacomo et al., 2016)
WOX homeobox transcription factor	MtWOX5	auxin responsive marker for nodule meristem. Acts upstream of systemic regulator NODULATION3	-/Nod	(Osipova et al., 2012)
bZIP transcription factor	LjASTRAY	negative regulator of nodule formation	-/Nod	(Nishimura et al., 2002a)
AP2 transcriptional repressor	GmNNC1	negative regulator of nodule formation	-/Nod	(Wang et al., 2014; Wang et al., 2019a)
Infection related				
LRR-tye RLK	LjRINK1	Involved in infection thread formation	-/Nod	(Li et al., 2019)
Actin-related protein component	LjARPC1	ACTIN-RELATED PROTEIN COMPONENT1 essential for rhizobium infection	-/Nod	(Hossain et al., 2012)
Annexin	MtANN1	Induced during symbiotic associations; marker for pre-infection	-/Nod	(de Carvalho-Niebel et al., 1998; Niebel et al., 1998; De Carvalho-Niebel et al., 2002)
Cystathionine- β -Synthase	MtCBS1	Required for rhizobium infection	-/Nod	(Sinharoy et al., 2016)
Devil-type peptide	MtDVL	Controls nodulation	-/Nod	(Comber et al., 2008)
Deubiquitinating enzyme	LjAMSH1	Required for rhizobium infection and nodule organogenesis	-/Nod	(Matolepszy et al., 2015)
DNA topoisomerase VI subunit A	LjSUNERGOS1	Required for rhizobium infection	-/Nod	(Yoon et al., 2014)

DNA topoisomerase VI RHL1	LjVAG1	Required for the ploidy-dependent cell growth of rhizobial-infected cells	-/Nod	(Suzaki et al., 2014)
E3 ubiquitin ligase	MtLIN / LjCERBERUS	Essential for rhizobium infection	-/Nod	(Kiss et al., 2009; Yano et al., 2009)
Long coiled-coil protein	MtRPG	Essential for rhizobium infection	-/Nod	(Arrighi et al., 2008)
SCAR/WAVE protein	MtNAP1 / LjNAP1	Essential for rhizobium infection, involved in actin rearrangement or nucleation	-/Nod	(Yokota et al., 2009; Miyahara et al., 2010)
p53 inducible RNA	LjPIR1	Essential for rhizobium infection, involved in actin rearrangement or nucleation	-/Nod	(Yokota et al., 2009)
Pectate lyase	LjNPL	Essential for rhizobium infection	-/Nod	(Xie et al., 2012)
Peroxidase	MtRIP1	Rhizobium-induced peroxidase	-/Nod	(Cook et al., 1995; Ramu et al., 2002)
Rapid alkalization factor (RALF) peptide	MtRALF1	Controls nodulation	-/Nod	(Combiér et al., 2008)
Vapyrin	MtVPY	Essential for rhizobium infection and arbuscule formation	AM/Nod	(Pumplin et al., 2010; Murray et al., 2011)
Nodule & symbiosome development				
Symbiosome localized esterase	MtENOD8	Localized to symbiosome membrane.	-/Nod	(Coque et al., 2008)
Early nodulin	GmaENOD93, Dg93	Nodule-induced.	-/Nod	(Kouchi and Hata, 1993; Okubara et al., 2000)
Ankyrin-repeat membrane protein	LjIGN1	Membrane protein, required for persistence of nitrogen-fixation in nodules.	-/Nod	(Kumagai et al., 2007)
Methionine-rich membrane protein	LjSEN1, GmNOD21	Legume-specific, exclusively expressed in infected nodule cells, essential for symbiosome differentiation.	-/Nod	(Delauney et al., 1990; Hakoyama et al., 2012a)
Small membrane localised protein	MtNAD1	Required to repress defense responses in nodules.	-/Nod	(Wang et al., 2016)
Stress up-regulated Nod 19	MtN19	Nodule-induced, possible target of miR398b.	-/Nod	(Gamas et al., 1996)
Small peptide	LjALOG	Controls nodulation efficiency.	-/Nod	(Lei et al., 2018)

Remorin	MtSYMREM1, LjSYMREM1	Symbiotic remorin, interact with SYMRK and LCO LysM-RK receptors.	AM/Nod	(Lefebvre et al., 2010; Tóth et al., 2012)
Signal peptidase	MtDNF1	Required for symbiosome formation.	-/Nod	(Wang et al., 2010)
Phosphatidylinositol phospholipase C-like	MtDNF2	Required for bacteroid persistence.	-/Nod	(Bourcy et al., 2013)
t-SNARE syntaxin	MtSYP132	Gene encoding two splice variants, of which one is essential for symbiosome and arbuscule formation.	-/Nod	(Catalano et al., 2007; Huisman et al., 2016; Pan et al., 2016)
v-SNARE syntaxin	LjSYP71	Ambiguous expressed. Commits essential function in nodules	-/Nod	(Hakoyama et al., 2012b)
v-SNARE syntaxin	MtVAMP721d, MtVAMP721e	Essential for symbiosome and arbuscule formation	AM/Nod	(Ivanov et al., 2012)
Systemic signaling				
CLV1-type LRR-receptor kinase	MtSUNN, LjHAR1, GmNARK	Systemic control of nodulation.	AM/Nod	(Krussel et al., 2002; Nishimura et al., 2002b; Searle et al., 2003; Schnabel et al., 2005; Müller et al., 2019)
CL11-type LRR-receptor kinase	LjKLV	Systemic control of nodulation	-/Nod	(Miyazawa et al., 2010)
CLV2-type LRR-receptor	LjCLV2 / PsSYM28	Systemic control of nodulation	-/Nod	(Krusell et al., 2011)
CLE peptide	MtCLE12, MtCIE13	Responsive to cytokinin, controls nodule development	AM/Nod	(Mortier et al., 2010; Mortier et al., 2012; Müller et al., 2019)
CLE peptide	LjCLE-RS1, LjCLE-RS2	Systemic control of nodulation, binds to LjHAR1	-/Nod	(Okamoto et al., 2009; Okamoto et al., 2013)
CLE peptide	GmRIC	Systemic control of nodulation	-/Nod	(Ferguson et al., 2014)
CEP peptide receptor	MtCRA2	Controls lateral root and nodule development	-/Nod	(Mohd-Radzman et al., 2016)
CEP peptide	MtCEP1	Systemic control of nodulation	-/Nod	(Djordjevic et al., 2015; Mohd-Radzman et al., 2016)
Kelch repeat-containing F-box protein	LjTML	Systemic control of nodulation, acts downstream of CLE-RS signalling	-/Nod	(Takahara et al., 2013)
Arabinosyl transferase	MtRDN1, LjPLENTY, PsNOD3	Systemic control of nodulation	-/Nod	(Yoshida et al., 2010; Schnabel et al., 2011)

Essential for ethylene mediated signalling	MtSKL1, LjEIN2-1, LjEIN2-2, PanEIN2	Negative regulator of symbiotic and pathogenic microbial associations	-/Nod	(Penmetsa et al., 2008; Miyata et al., 2013; van Zeijl et al., 2018)
Hormones				
Histidine kinase Cytokinin receptor	MtCRE1 / LjHK1	Essential for nodule formation.	-/Nod	(Gonzalez-Rizzo et al., 2006; Murray et al., 2007)
C3HC4-type RING finger protein	LjCZF1	Interacts with LjLHK1, controls nodulation efficiency.	-/Nod	(Cai et al., 2018b)
Isopentenyltransferase	LjIPT3	Adenylate isopentenyltransferase IPT3.	AM/Nod	(Chen et al., 2014)
Cytokinin oxidase / dehydrogenase	MtCKX1	Direct target of CRE1-dependent cytokinin signaling, regulating nodulation.	-/Nod	(Ariel et al., 2012)
Cytokinin oxidase / dehydrogenase	LjCKX3	Direct target of CRE1-dependent cytokinin signaling, regulating nodulation	-/Nod	(Reid et al., 2016)
Cytokinin type-A Response Regulator	MtRR4, MtRR9, MtR11	Responsive to cytokinin, control nodule development.	-/Nod	(Op den Camp et al., 2011a; Ariel et al., 2012)
Tryptophan Amino- transferase Related protein	LjTAR1	LCO responsive. Involved in auxin biosynthesis.	-/Nod	(Nadzieja et al., 2018)
Carotene Hydroxylase	GmBCH1, GmBCH2, GmBCH3	involved in nodule development	-/Nod	(Kim et al., 2013)
Carotene isomerase	MtDWARF27	essential for strigolactone biosynthesis, LCO responsive	-/Nod	(Liu et al., 2011; Van Zeijl et al., 2015)
Carotenoid cleavage dioxygenase	MtCCD7, LjCCD7	essential for strigolactone biosynthesis, involved in nodulation and mycorrhization	AM/Nod	(Liu et al., 2013; Van Zeijl et al., 2015)
Carotenoid cleavage dioxygenase	MtCCD8, PsRMS1	essential for strigolactone biosynthesis, involved in nodulation and mycorrhization	AM/Nod	(Gomez-Roldan et al., 2008; Foo and Davies, 2011; Foo et al., 2013; Breakspear et al., 2014)
Jasmonate-Zim- domain	AsJAZ1	Interacts with LB	-/Nod	(Li et al., 2015)
Ammonium transporter	LjAMT1;1	Ammonium transporter 1, involved in nodule functioning	-/Nod	(Rogato et al., 2008; Straub et al., 2014)
Ammonium transporter	MtAMT1;3	Ammonium transporter 1; involved in nodule functioning	-/Nod	(Straub et al., 2014)

Anion transporter	LjN70 / GmN70	Localizes at symbiosome membrane of nodules and has transport preference for nitrate	-/Nod	(Vincill et al., 2005)
Aquaporin	MtAQP1, GmNOD26	Expressed in infected nodule cells	AM/Nod	(Miao and Verma, 1993)
Divalent metal transporter	GmDMT1	Nodule specific expression	-/Nod	(Kaiser et al., 2003)
Class 1 hemoglobin	PanHB1	Class I hemoglobin, commits symbiotic function in <i>Parasponia</i>	-/Nod	(Appleby et al., 1983; Sturms et al., 2010; van Velzen et al., 2018)
Class 2 hemoglobin	LjLB1, LjLB2, LjLB3	Class II symbiotic hemoglobins, essential for nodule functioning	-/Nod	(Ott et al., 2005; Wang et al., 2019b)
Transporters				
Iron-activated citrate transporter	MtMATE67, LjMATE1, GmFRD3a, GmFRD3b	Required for nitrogen-fixation	-/Nod	(Takanashi et al., 2013; Kryvoruchko et al., 2018)
Nitrate transporter	MtNIP/LATD	Controls rhizobium infection and lateral root organ formation	-/Nod	(Bagchi et al., 2012)
Oligopeptide transporter	GmYSL1	Involved in remobilization of iron from the nodule	-/Nod	(Brear et al., 2013)
Potassium transporter	LjKUP1	Nodule specific expression	-/Nod	(Desbrosses et al., 2004)
Phosphate transporter	GmPT7	Required for nodule formation	-/Nod	(Chen et al., 2019)
Sucrose transporter	MtSUT1-1	Induced upon mycorrhization	AM/Nod	(Doidy et al., 2012)
Sucrose transporter	MtSUT4-1, LjSUT4	Induced upon mycorrhization	AM/Nod	(Reinders et al., 2008; Doidy et al., 2012)
Sucrose transporter	MtSWEET11, MtSWEET12, LjSWEET3	Nodule specific expression	-/Nod	(Kryvoruchko et al., 2016; Sugiyama et al., 2016)
Sulfate transporter	LjSST1	Essential for nodule functioning	-/Nod	(Krusell et al., 2005)
Zinc transporter	GmZIP1	Nodule specific expression	-/Nod	(Moreau et al., 2002; Krusell et al., 2005)
Enzymes				
Carbonic anhydrase	MsCA1, LjCA1, GmCA1	Nodule enhanced expression, catalyzes interconversion of CO ₂ and water to bicarbonate and protons	-/Nod	(Kavroulakis et al., 2000; Fliemetakis et al., 2003; Aivalakis et al., 2004)

Cysteine protease	LjCYP1, LjCYP2, LjCYP4, PsCYP15A	Involved in nodule and arbuscule senescence	AM/Nod	(Goetting-Minesky and Mullin, 1994; Vincent and Brewin, 2000; Deguchi et al., 2007)
Glutamate synthase	MtNADH-GOGAT, MsNADH-GOGAT	NADH-dependent glutamine oxoglutarate aminotransferase essential enzyme in nitrogen metabolism in nodules	-/Nod	(Vance et al., 1995; Glevarec et al., 2004)
Glutamine synthetase	MtGS2	Plastid localized enzyme essential enzyme in nitrogen metabolism in nodules	-/Nod	(Melo et al., 2003)
Glutamine synthetase	GmGS1-2	Cytosolic enzyme essential enzyme in nitrogen metabolism in nodules	-/Nod	(Guan et al., 1996; Morey et al., 2002)
Glycinamide ribonucleotide synthetase	GmPURD	nodule enhanced expression, enzyme acts in nitrogen metabolism	-/Nod	(Schnorr et al., 1996)
Glycinamide ribonucleotide transformylase	GmPURN	Nodule enhanced expression, enzyme acts in nitrogen metabolism	-/Nod	(Schnorr et al., 1996)
Homocitrate synthase	LjFEN1	Can compensate homocitrate deficient rhizobia in nodules	-/Nod	(Hakoyama et al., 2009b)
NADH-malate dehydrogenase	MsMDH, GmMDH	Involved in metabolism of malate	-/Nod	(Miller et al., 1998; Imsande et al., 2001)
NADPH oxidase	MtRBOHA, PvRBOHB	Expressed in rhizobium containing nodule cells and arbusculated cells	AM/Nod	(Marino et al., 2011; Montiel et al., 2012; Arthikala et al., 2014; Belmondo et al., 2016)
Nicotianamine synthase	LjNAS2	Nodule specific expression	-/Nod	(Hakoyama et al., 2009a)
Phosphoenolpyruvate carboxylase	GmPEPC7	Involved in metabolism of C4 dicarboxylic acids	-/Nod	(Nakagawa et al., 2003)
Subtilisin-like protease	AgAG12, CgCG12	Nodule enhanced expression	AM/Nod	(Ribeiro et al., 1995)
Subtilisin-like protease	LjSBTS	Expression strongly enhanced in nodules and mycorrhizal roots	AM/Nod	(Kistner et al., 2005)
Sucrose synthase	MtSUCS1, AgSUS1	GT1 Sucrose synthase	-/Nod	(van Ghelue et al., 1996; Hohnjec et al., 1999)
Uricase	GmNOD35	Essential enzyme in nitrogen metabolism in nodules	-/Nod	(Nguyen et al., 1985)

REFERENCES

- Aivalakis, G., Dimou, M., Flietakis, E., Plati, F., Katinakis, P., and Drossopoulos, J. B. (2004). Immunolocalization of carbonic anhydrase and phosphoenolpyruvate carboxylase in developing seeds of *Medicago sativa*. *Plant Physiol. Biochem.* **42**:181–186.
- Ané, J.-M., Kiss, G. B., Riely, B. K., Penmetsa, R. V., Oldroyd, G. E. D., Ajax, C., Lévy, J., Debellé, F., Baek, J.-M., Kalo, P., et al. (2004). *Medicago truncatula* DMI1 required for bacterial and fungal symbioses in legumes. *Science* **303**:1364–1367.
- Appleby, C. A., Tjepkema, J. D., and Trinick, M. J. (1983). Hemoglobin in a nonleguminous plant, parasponia: possible genetic origin and function in nitrogen fixation. *Science* **220**:951–953.
- Ariel, F., Brault-Hernandez, M., Laffont, C., Huault, E., Brault, M., Plet, J., Moison, M., Blanchet, S., Ichanté, J. L., Chabaud, M., et al. (2012). Two direct targets of cytokinin signaling regulate symbiotic nodulation in *Medicago truncatula*. *Plant Cell* **24**:3838–3852.
- Arrighi, J.-F., Barre, A., Ben Amor, B., Bersoult, A., Soriano, L. C., Mirabella, R., de Carvalho-Niebel, F., Journet, E.-P., Ghérardi, M., Huguet, T., et al. (2006). The *Medicago truncatula* lysine motif-receptor-like kinase gene family includes *NFP* and new nodule-expressed genes. *Plant Physiol.* **142**:265–279.
- Arrighi, J.-F., Godfroy, O., de Billy, F., Saurat, O., Jauneau, A., and Gough, C. (2008). The *RPG* gene of *Medicago truncatula* controls *Rhizobium*-directed polar growth during infection. *Proc. Natl. Acad. Sci. U. S. A.* **105**:9817–9822.
- Arthikala, M.-K., Sánchez-López, R., Nava, N., Santana, O., Cárdenas, L., and Quinto, C. (2014). RbohB, a *Phaseolus vulgaris* NADPH oxidase gene, enhances symbiosome number, bacteroid size, and nitrogen fixation in nodules and impairs mycorrhizal colonization. *New Phytol.* **202**:886–900.
- Asamizu, E., Shimoda, Y., Kouchi, H., Tabata, S., and Sato, S. (2008). A positive regulatory role for LjERF1 in the nodulation process is revealed by systematic analysis of nodule-associated transcription factors of *Lotus japonicus*. *Plant Physiol.* **147**:2030–2040.
- Azarakhsh, M., Kirienko, A. N., Zhukov, V. A., Lebedeva, M. A., Dolgikh, E. A., and Lutova, L. A. (2015). KNOTTED1-LIKE HOMEODOMAIN 3: a new regulator of symbiotic nodule development. *J. Exp. Bot.* **66**:7181–7195.
- Bagchi, R., Salehin, M., Adeyemo, O. S., Salazar, C., Shulaev, V., Sherrier, D. J., and Dickstein, R. (2012). Functional assessment of the *Medicago truncatula* NIP/LATD protein demonstrates that it is a high-affinity nitrate transporter. *Plant Physiol.* **160**:906–916.
- Baudin, M., Laloum, T., Lepage, A., Rípodas, C., Ariel, F., Frances, L., Crespi, M., Gamas, P., Blanco, F. A., Zanetti, M. E., et al. (2015). A Phylogenetically Conserved Group of Nuclear Factor-Y Transcription Factors Interact to Control Nodulation in Legumes. *Plant Physiol.* **169**:2761–2773.

- Belmondo, S., Calcagno, C., Genre, A., Puppo, A., Pauly, N., and Lanfranco, L. (2016). The *Medicago truncatula* MtRbohE gene is activated in arbusculated cells and is involved in root cortex colonization. *Planta* **243**:251–262.
- Borisov, A. Y., Madsen, L. H., Tsyganov, V. E., Umehara, Y., Voroshilova, V. A., Batagov, A. O., Sandal, N., Mortensen, A., Schauser, L., Ellis, N., et al. (2003). The Sym35 gene required for root nodule development in pea is an ortholog of Nin from *Lotus japonicus*. *Plant Physiol.* **131**:1009–1017.
- Bourcy, M., Brocard, L., Pislariu, C. I., Cosson, V., Mergaert, P., Tadege, M., Mysore, K. S., Udvardi, M. K., Gourion, B., and Ratet, P. (2013). *Medicago truncatula* DNF2 is a PI-PLC-XD-containing protein required for bacteroid persistence and prevention of nodule early senescence and defense-like reactions. *New Phytol.* **197**:1250–1261.
- Bozsoki, Z., Cheng, J., Feng, F., Gysel, K., Vinther, M., Andersen, K. R., Oldroyd, G., Blaise, M., Radutoiu, S., and Stougaard, J. (2017). Receptor-mediated chitin perception in legume roots is functionally separable from Nod factor perception. *Proc. Natl. Acad. Sci. U. S. A.* **114**:E8118–E8127.
- Breakspear, A., Liu, C., Roy, S., Stacey, N., Rogers, C., Trick, M., Morieri, G., Mysore, K. S., Wen, J., Oldroyd, G. E. D., et al. (2014). The Root Hair “Infectome” of *Medicago truncatula* uncovers changes in cell cycle genes and reveals a requirement for auxin signaling in rhizobial infection. *Plant Cell* **26**:4680–4701.
- Brear, E. M., Day, D. A., and Smith, P. M. C. (2013). Iron: an essential micronutrient for the legume-rhizobium symbiosis. *Front. Plant Sci.* **4**:359.
- Broghammer, A., Krusell, L., Blaise, M., Sauer, J., Sullivan, J. T., Maolanon, N., Vinther, M., Lorentzen, A., Madsen, E. B., Jensen, K. J., et al. (2012). Legume receptors perceive the rhizobial lipochitin oligosaccharide signal molecules by direct binding. *Proc. Natl. Acad. Sci. U. S. A.* **109**:13859–13864.
- Cai, J., Zhang, L.-Y., Liu, W., Tian, Y., Xiong, J.-S., Wang, Y.-H., Li, R.-J., Li, H.-M., Wen, J., Mysore, K. S., et al. (2018a). Role of the Nod Factor Hydrolase MtNFH1 in Regulating Nod Factor Levels during Rhizobial Infection and in Mature Nodules of *Medicago truncatula*. *Plant Cell* **30**:397–414.
- Cai, K., Yin, J., Chao, H., Ren, Y., Jin, L., Cao, Y., Duanmu, D., and Zhang, Z. (2018b). A C3HC4-type RING finger protein regulates rhizobial infection and nodule organogenesis in *Lotus japonicus*. *J. Integr. Plant Biol.* Advance Access published July 26, 2018, doi:10.1111/jipb.12703.
- Capoen, W., Sun, J., Wysham, D., Otegui, M. S., Venkateshwaran, M., Hirsch, S., Miwa, H., Downie, J. A., Morris, R. J., Ané, J.-M., et al. (2011). Nuclear membranes control symbiotic calcium signaling of legumes. *Proc. Natl. Acad. Sci. U. S. A.* **108**:14348–14353.
- Catalano, C. M., Czymmek, K. J., Gann, J. G., and Sherrier, D. J. (2007). *Medicago truncatula* syntaxin SYP132 defines the symbiosome membrane and infection droplet membrane in root nodules. *Planta* **225**:541–550.

- Cerri, M. R., Frances, L., Kelner, A., Fournier, J., Middleton, P. H., Auriac, M.-C., Mysore, K. S., Wen, J., Erard, M., Barker, D. G., et al. (2016). The Symbiosis-Related ERN Transcription Factors Act in Concert to Coordinate Rhizobial Host Root Infection. *Plant Physiol.* 171:00230.2016.
- Charpentier, M., Sun, J., Martins, T. V., Radhakrishnan, G. V., Findlay, K., Soumpourou, E., Thouin, J., Véry, A.-A., Sanders, D., Morris, R. J., et al. (2016). Nuclear-localized cyclic nucleotide-gated channels mediate symbiotic calcium oscillations. *Science* 352:1102–1105.
- Chen, T., Zhu, H., Ke, D., Cai, K., Wang, C., Gou, H., Hong, Z., and Zhang, Z. (2012). A MAP kinase kinase interacts with SymRK and regulates nodule organogenesis in *Lotus japonicus*. *Plant Cell* 24:823–838.
- Chen, Y., Chen, W., Li, X., Jiang, H., Wu, P., Xia, K., Yang, Y., and Wu, G. (2014). Knockdown of LjIPT3 influences nodule development in *Lotus japonicus*. *Plant Cell Physiol.* 55:183–193.
- Chen, L., Qin, L., Zhou, L., Li, X., Chen, Z., Sun, L., Wang, W., Lin, Z., Zhao, J., Yamaji, N., et al. (2019). A nodule-localized phosphate transporter GmPT7 plays an important role in enhancing symbiotic N fixation and yield in soybean. *New Phytol.* 221:2013–2025.
- Chiasson, D. M., Loughlin, P. C., Mazurkiewicz, D., Mohammadidehcheshmeh, M., Fedorova, E. E., Okamoto, M., McLean, E., Glass, A. D. M., Smith, S. E., Bisseling, T., et al. (2014). Soybean SAT1 (Symbiotic Ammonium Transporter 1) encodes a bHLH transcription factor involved in nodule growth and NH₄⁺ transport. *Proc. Natl. Acad. Sci. U. S. A.* 111:4814–4819.
- Clavijo, F., Diedhiou, I., Vaissayre, V., Brottier, L., Acolatse, J., Moukouanga, D., Crabos, A., Auguy, F., Franche, C., Gherbi, H., et al. (2015). The *Casuarina NIN* gene is transcriptionally activated throughout *Frankia* root infection as well as in response to bacterial diffusible signals. *New Phytol.* 208:887–903.
- Combiér, J.-P., Frugier, F., de Billy, F., Boualem, A., El-Yahyaoui, F., Moreau, S., Vernié, T., Ott, T., Gamas, P., Crespi, M., et al. (2006). MtHAP2-1 is a key transcriptional regulator of symbiotic nodule development regulated by microRNA169 in *Medicago truncatula*. *Genes Dev.* 20:3084–3088.
- Combiér, J.-P., Küster, H., Journet, E.-P., Hohnjec, N., Gamas, P., Niebel, A., Plantes, I., Cnrs-inra, U. M. R., and Tolosan, F.-C. (2008). Evidence for the involvement in nodulation of the two small putative regulatory peptide-encoding genes MtrALFL1 and MtDVL1. *Mol. Plant. Microbe. Interact.* 21:1118–1127.
- Cook, D., Dreyer, D., Bonnet, D., Howell, M., Nony, E., and VandenBosch, K. (1995). Transient induction of a peroxidase gene in *Medicago truncatula* precedes infection by *Rhizobium meliloti*. *Plant Cell* 7:43–55.
- Coque, L., Neogi, P., Pislariu, C., Wilson, K. A., Catalano, C., Avadhani, M., Sherrier, D. J., and Dickstein, R. (2008). Transcription of ENOD8 in *Medicago*

truncatula nodules directs ENOD8 esterase to developing and mature symbiosomes. *Mol. Plant. Microbe. Interact.* **21**:404–410.

- Couzigou, J.-M., Zhukov, V., Mondy, S., Abu el Heba, G., Cosson, V., Ellis, T. H. N., Ambrose, M., Wen, J., Tadege, M., Tikhonovich, I., et al. (2012). NODULE ROOT and COCHLEATA maintain nodule development and are legume orthologs of Arabidopsis BLADE-ON-PETIOLE genes. *Plant Cell* **24**:4498–4510.
- de Carvalho Niebel, F., Lescure, N., Cullimore, J. V., and Gamas, P. (1998). The Medicago truncatula MtAnn1 Gene Encoding an Annexin Is Induced by Nod Factors and During the Symbiotic Interaction with Rhizobium meliloti. *Mol. Plant. Microbe. Interact.* **11**:504–513.
- De Carvalho-Niebel, F., Timmers, A. C. J., Chabaud, M., Defaux-Petras, A., and Barker, D. G. (2002). The Nod factor-elicited annexin MtAnn1 is preferentially localised at the nuclear periphery in symbiotically activated root tissues of Medicago truncatula. *Plant J.* **32**:343–352.
- Deguchi, Y., Banba, M., Shimoda, Y., Chechetka, S. A., Suzuri, R., Okusako, Y., Ooki, Y., Toyokura, K., Suzuki, A., Uchiumi, T., et al. (2007). Transcriptome profiling of Lotus japonicus roots during arbuscular mycorrhiza development and comparison with that of nodulation. *DNA Res.* **14**:117–133.
- Delauney, A. J., Cheon, C. I., Snyder, P. J., and Verma, D. P. (1990). A nodule-specific sequence encoding a methionine-rich polypeptide, nodulin-21. *Plant Mol. Biol.* **14**:449–451.
- Den Herder, G., Yoshida, S., Antolín-Llovera, M., Ried, M. K., and Parniske, M. (2012). Lotus japonicus E3 ligase SEVEN IN ABSENTIA4 destabilizes the symbiosis receptor-like kinase SYMRK and negatively regulates rhizobial infection. *Plant Cell* **24**:1691–1707.
- Desbrosses, G., Kopka, C., Ott, T., and Udvardi, M. K. (2004). Lotus japonicus LjKUP is induced late during nodule development and encodes a potassium transporter of the plasma membrane. *Mol. Plant. Microbe. Interact.* **17**:789–797.
- De Zélicourt, A., Diet, A., Marion, J., Laffont, C., Ariel, F., Moison, M., Zahaf, O., Crespi, M., Gruber, V., and Frugier, F. (2012). Dual involvement of a Medicago truncatula NAC transcription factor in root abiotic stress response and symbiotic nodule senescence. *Plant J.* **70**:220–230.
- Di Giacomo, E., Laffont, C., Sciarra, F., Iannelli, M. A., Frugier, F., and Frugis, G. (2016). KNAT3/4/5-like class 2 KNOX transcription factors are involved in Medicago truncatula symbiotic nodule organ development. *New Phytol.* Advance Access published September 1, 2016, doi:10.1111/nph.14146.
- Djordjevic, M. A., Mohd-Radzman, N. A., and Imin, N. (2015). Small-peptide signals that control root nodule number, development, and symbiosis. *J. Exp. Bot.* **66**:5171–5181.
- Doidy, J., van Tuinen, D., Lamotte, O., Corneillat, M., Alcaraz, G., and Wipf, D. (2012). The Medicago truncatula sucrose transporter family: characterization

and implication of key members in carbon partitioning towards arbuscular mycorrhizal fungi. *Mol. Plant* **5**:1346–1358.

- Endre, G., Kereszt, A., Kevei, Z., Mihacea, S., Kaló, P., and Kiss, G. B. (2002). A receptor kinase gene regulating symbiotic nodule development. *Nature* **417**:962–966.
- Ferguson, B. J., Li, D., Hastwell, A. H., Reid, D. E., Li, Y., Jackson, S. A., and Gresshoff, P. M. (2014). The soybean (*Glycine max*) nodulation-suppressive CLE peptide, Gm RIC 1, functions interspecifically in common white bean (*Phaseolus vulgaris*), but not in a supernodulating line mutated in the receptor Pv NARK. *Plant Biotechnol. J.* **12**:1085–1097.
- Flemetakis, E., Dimou, M., Cotzur, D., Aivalakis, G., Efrose, R. C., Kenoutis, C., Udvardi, M., and Katinakis, P. (2003). A *Lotus japonicus* β -type carbonic anhydrase gene expression pattern suggests distinct physiological roles during nodule development. *Biochimica et Biophysica Acta (BBA) - Gene Structure and Expression* **1628**:186–194.
- Fliegmann, J., Canova, S., Lachaud, C., Uhlenbroich, S., Gascioli, V., Pichereaux, C., Rossignol, M., Rosenberg, C., Cumener, M., Pitorre, D., et al. (2013). Lipo-chitooligosaccharidic symbiotic signals are recognized by LysM receptor-like kinase LYR3 in the legume *Medicago truncatula*. *ACS Chem. Biol.* **8**:1900–1906.
- Fliegmann, J., Jauneau, A., Pichereaux, C., Rosenberg, C., Gascioli, V., Timmers, A. C. J. J., Burlet-Schiltz, O., Cullimore, J., and Bono, J.-J. (2016). LYR3, a High-affinity LCO-Binding Protein of *Medicago truncatula*, interacts with LYK3, a Key Symbiotic Receptor. *FEBS Lett.* **590**:1477–1487.
- Foo, E., and Davies, N. W. (2011). Strigolactones promote nodulation in pea. *Planta* **234**:1073–1081.
- Foo, E., Yoneyama, K., Hugill, C. J., Quittenden, L. J., and Reid, J. B. (2013). Strigolactones and the regulation of pea symbioses in response to nitrate and phosphate deficiency. *Mol. Plant* **6**:76–87.
- Frugier, F., Poirier, S., Satiat-Jeunemaitre, B., Kondorosi, A., and Crespi, M. (2000). A Krüppel-like zinc finger protein is involved in nitrogen-fixing root nodule organogenesis. *Genes Dev.* **14**:475–482.
- Gamas, P., Niebel, F. de C., 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.
- Gargantini, P. R., Gonzalez-Rizzo, S., Chinchilla, D., Raices, M., Giammaria, V., Ulloa, R. M., Frugier, F., and Crespi, M. D. (2006). A CDPK isoform participates in the regulation of nodule number in *Medicago truncatula*. *Plant J.* **48**:843–856.

- Gibelin-Viala, C., Amblard, E., Puech-Pages, V., Bonhomme, M., Garcia, M., Bascaules-Bedin, A., Fliegmann, J., Wen, J., Mysore, K. S., Signor, C., et al. (2019). The Medicago truncatula LysM receptor-like kinase LYK9 plays a dual role in immunity and the arbuscular mycorrhizal symbiosis. *New Phytol.* **223**:1516–1529.
- Gievarec, G., Bouton, S., Jaspard, E., Riou, M.-T., Cliquet, J.-B., Suzuki, A., and Limami, A. M. (2004). Respective roles of the glutamine synthetase/glutamate synthase cycle and glutamate dehydrogenase in ammonium and amino acid metabolism during germination and post-germinative growth in the model legume Medicago truncatula. *Planta* **219**:286–297.
- Godiard, L., Lepage, A., Moreau, S., Laporte, D., Verdenaud, M., Timmers, T., and Gamas, P. (2011). MtbHLH1, a bHLH transcription factor involved in Medicago truncatula nodule vascular patterning and nodule to plant metabolic exchanges. *New Phytol.* **191**:391–404.
- Goetting-Minesky, M. P., and Mullin, B. C. (1994). Differential gene expression in an actinorhizal symbiosis: evidence for a nodule-specific cysteine proteinase. *Proc. Natl. Acad. Sci. U. S. A.* **91**:9891–9895.
- Gomez-Roldan, V., Fermas, S., Brewer, P. B., Puech-Pagès, V., Dun, E. A., Pillot, J.-P., Letisse, F., Matusova, R., Danoun, S., Portais, J.-C., et al. (2008). Strigolactone inhibition of shoot branching. *Nature* **455**:189–194.
- Gonzalez-Rizzo, S., Crespi, M., and Frugier, F. (2006). The Medicago truncatula CRE1 cytokinin receptor regulates lateral root development and early symbiotic interaction with Sinorhizobium meliloti. *Plant Cell* **18**:2680–2693.
- Groth, M., Takeda, N., Perry, J., Uchida, H., Dräxl, S., Brachmann, A., Sato, S., Tabata, S., Kawaguchi, M., Wang, T. L., et al. (2010). NENA, a Lotus japonicus Homolog of Sec13, Is Required for Rhizodermal Infection by Arbuscular Mycorrhiza Fungi and Rhizobia but Dispensable for Cortical Endosymbiotic Development. *Plant Cell* **22**:2509–2526.
- Guan, C., Ribeiro, A., Akkermans, A. D., Jing, Y., van Kammen, A., Bisseling, T., and Pawlowski, K. (1996). Nitrogen metabolism in actinorhizal nodules of Alnus glutinosa: expression of glutamine synthetase and acetylornithine transaminase. *Plant Mol. Biol.* **32**:1177–1184.
- Hakoyama, T., Watanabe, H., Tomita, J., Yamamoto, A., Sato, S., Mori, Y., Kouchi, H., and Sukanuma, N. (2009a). Nicotianamine synthase specifically expressed in root nodules of Lotus japonicus. *Planta* **230**:309–317.
- Hakoyama, T., Niimi, K., Watanabe, H., Tabata, R., Matsubara, J., Sato, S., Nakamura, Y., Tabata, S., Jichun, L., Matsumoto, T., et al. (2009b). Host plant genome overcomes the lack of a bacterial gene for symbiotic nitrogen fixation. *Nature* **462**:514–517.
- Hakoyama, T., Niimi, K., Yamamoto, T., Isobe, S., Sato, S., Nakamura, Y., Tabata, S., Kumagai, H., Umehara, Y., Brossuleit, K., et al. (2012a). The integral

membrane protein SEN1 is required for symbiotic nitrogen fixation in lotus japonicus nodules. *Plant Cell Physiol.* **53**:225–236.

Hakoyama, T., Oi, R., Hazuma, K., Suga, E., Adachi, Y., Kobayashi, M., Akai, R., Sato, S., Fukai, E., Tabata, S., et al. (2012b). The SNARE protein SYP71 expressed in vascular tissues is involved in symbiotic nitrogen fixation in Lotus japonicus nodules. *Plant Physiol.* **160**:897–905.

Haney, C. H., and Long, S. R. (2010). Plant flotillins are required for infection by nitrogen-fixing bacteria. *Proc. Natl. Acad. Sci. U. S. A.* **107**:478–483.

Haney, C. H., Riely, B. K., Tricoli, D. M., Cook, D. R., Ehrhardt, D. W., and Long, S. R. (2011). Symbiotic rhizobia bacteria trigger a change in localization and dynamics of the Medicago truncatula receptor kinase LYK3. *Plant Cell* **23**:2774–2787.

Heckmann, A. B., Lombardo, F., Miwa, H., Perry, J. A., Bunnewell, S., Parniske, M., Wang, T. L., and Downie, J. A. (2006a). Lotus japonicus nodulation requires two GRAS domain regulators, one of which is functionally conserved in a non-legume. *Plant Physiol.* **142**:1739–1750.

Heckmann, A. B., Hebelstrup, K. H., Larsen, K., Micaelo, N. M., and Jensen, E. Ø. (2006b). A single hemoglobin gene in Myrica gale retains both symbiotic and non-symbiotic specificity. *Plant Mol. Biol.* **61**:769–779.

Hohnjec, N., Becker, J. D., Pühler, A., Perlick, A. M., and Küster, H. (1999). Genomic organization and expression properties of the MtSucS1 gene, which encodes a nodule-enhanced sucrose synthase in the model legume Medicago truncatula. *Mol. Gen. Genet.* **261**:514–522.

Hossain, M. S., Liao, J., James, E. K., Sato, S., Tabata, S., Jurkiewicz, A., Madsen, L. H., Stougaard, J., Ross, L., and Szczyglowski, K. (2012). Lotus japonicus ARPC1 is required for rhizobial infection. *Plant Physiol.* **160**:917–928.

Huisman, R., Hontelez, J., Mysore, K. S., Wen, J., Bisseling, T., and Limpens, E. (2016). A symbiosis-dedicated SYNTAXIN OF PLANTS 13II isoform controls the formation of a stable host--microbe interface in symbiosis. *New Phytol.* Advance Access published 2016.

Imaizumi-Anraku, H., Takeda, N., Charpentier, M., Perry, J., Miwa, H., Umehara, Y., Kouchi, H., Murakami, Y., Mulder, L., Vickers, K., et al. (2005). Plastid proteins crucial for symbiotic fungal and bacterial entry into plant roots. *Nature* **433**:527–531.

Imsande, J., Berkemeyer, M., Scheibe, R., Schumann, U., Gietl, C., and Palmer, R. G. (2001). A soybean plastid-targeted NADH-malate dehydrogenase: cloning and expression analyses. *Am. J. Bot.* **88**:2136–2142.

Ivanov, S., Fedorova, E. E., Limpens, E., De Mita, S., Genre, A., Bonfante, P., and Bisseling, T. (2012). Rhizobium--legume symbiosis shares an exocytotic pathway required for arbuscule formation. *Proceedings of the National Academy of Sciences* **109**:8316–8321.

Jin, Y., Chen, Z., Yang, J., Mysore, K. S., Wen, J., Huang, J., Yu, N., and Wang, E. (2018). IPD3 and IPD3L Function Redundantly in Rhizobial and

Mycorrhizal Symbioses. *Front. Plant Sci.* **9**:267.

- Kaiser, B. N., Moreau, S., Castelli, J., Thomson, R., Lambert, A., Bogliolo, S., Puppo, A., and Day, D. A. (2003). The soybean NRAMP homologue, GmDMT1, is a symbiotic divalent metal transporter capable of ferrous iron transport. *Plant J.* **35**:295–304.
- Kalo, P., Gleason, C., Edwards, A., Marsh, J., Mitra, R. M., Hirsch, S., Jakab, J., Sims, S., Long, S. R., Rogers, J., et al. (2005). Nodulation signaling in legumes requires NSP2, a member of the GRAS family of transcriptional regulators. *Science* **308**:1786–1789.
- Kanamori, N., Madsen, L. H., Radutoiu, S., Frantescu, M., Quistgaard, E. M. H., Miwa, H., Downie, J. A., James, E. K., Felle, H. H., Haaning, L. L., et al. (2006). A nucleoporin is required for induction of Ca²⁺ spiking in legume nodule development and essential for rhizobial and fungal symbiosis. *Proc. Natl. Acad. Sci. U. S. A.* **103**:359–364.
- Kang, H., Chu, X., Wang, C., Xiao, A., Zhu, H., Yuan, S., Yang, Z., Ke, D., Xiao, S., Hong, Z., et al. (2014). A MYB coiled-coil transcription factor interacts with NSP2 and is involved in nodulation in *Lotus japonicus*. *New Phytol.* **201**:837–849.
- Kavroulakis, N., Fłemetakis, E., Aivalakis, G., and Katinakis, P. (2000). Carbon metabolism in developing soybean root nodules: the role of carbonic anhydrase. *Mol. Plant. Microbe. Interact.* **13**:14–22.
- Kawaharada, Y., Kelly, S., Nielsen, M. W., Hjuler, C. T., Gysel, K., Muszyński, A., Carlson, R. W., Thygesen, M. B., Sandal, N., Asmussen, M. H., et al. (2015). Receptor-mediated exopolysaccharide perception controls bacterial infection. *Nature* **523**:308–312.
- Ke, D., Fang, Q., Chen, C., Zhu, H., Chen, T., Chang, X., Yuan, S., Kang, H., Ma, L., Hong, Z., et al. (2012). The small GTPase ROP6 interacts with NFR5 and is involved in nodule formation in *Lotus japonicus*. *Plant Physiol.* **159**:131–143.
- Kevei, Z., Loughnon, G., Mergaert, P., Horváth, G. V., Kereszt, A., Jayaraman, D., Zaman, N., Marcel, F., Regulski, K., Kiss, G. B., et al. (2007). 3-Hydroxy-3-Methylglutaryl Coenzyme A Reductase1 Interacts with NORK and Is Crucial for Nodulation in *Medicago truncatula*. *Plant Cell* **19**:3974–3989.
- Kim, G.-B., and Nam, Y.-W. (2013). A novel GRAS protein gene MtSymSCL1 plays a role in regulating nodule number in *Medicago truncatula*. *Plant Growth Regul.* **71**:77–92.
- Kim, Y.-K., Kim, S., Um, J.-H., Kim, K., Choi, S.-K., Um, B.-H., Kang, S.-W., Kim, J.-W., Takaichi, S., Song, S.-B., et al. (2013). Functional implication of β -carotene hydroxylases in soybean nodulation. *Plant Physiol.* **162**:1420–1433.
- Kiss, E., Oláh, B., Kaló, P., Morales, M., Heckmann, A. B., Borbola, A., Lózsa, A., Kontár, K., Middleton, P., Downie, J. A., et al. (2009). LIN, a novel type of

- U-box/WD40 protein, controls early infection by rhizobia in legumes. *Plant Physiol.* **151**:1239–1249.
- Kistner, C., Winzer, T., Pitzschke, A., Mulder, L., Sato, S., Kaneko, T., Tabata, S., Sandal, N., Stougaard, J., Webb, K. J., et al. (2005). Seven *Lotus japonicus* genes required for transcriptional reprogramming of the root during fungal and bacterial symbiosis. *Plant Cell* **17**:2217–2229.
- Kouchi, H., and Hata, S. (1993). Isolation and characterization of novel nodulin cDNAs representing genes expressed at early stages of soybean nodule development. *Mol. Gen. Genet.* **238**:106–119.
- Krusell, L., Krause, K., Ott, T., Desbrosses, G., Krämer, U., Sato, S., Nakamura, Y., Tabata, S., James, E. K., Sandal, N., et al. (2005). The Sulfate Transporter SST1 Is Crucial for Symbiotic Nitrogen Fixation in *Lotus japonicus* Root Nodules. *The Plant Cell* **17**:1625–1636.
- Krusell, L., Sato, N., Fukuhara, I., Koch, B. E. V., Grossmann, C., Okamoto, S., Oka-Kira, E., Otsubo, Y., Aubert, G., Nakagawa, T., et al. (2011). The *Clavata2* genes of pea and *Lotus japonicus* affect autoregulation of nodulation. *Plant J.* **65**:861–871.
- Krusell, L., Madsen, L. H., Sato, S., Aubert, G., Genua, A., Szczyglowski, K., Duc, G., Tabata, S., de Bruijn, F., Pajuelo, E., et al. (2002). Shoot control of nodule organogenesis and root development is mediated by a serine/threonine receptor kinase. *Nature* **420**:422–426.
- Kryvoruchko, I. S., Sinharoy, S., Torres-Jerez, I., Sosso, D., Pislariu, C. I., Guan, D., Murray, J., Benedito, V. A., Frommer, W. B., and Udvardi, M. K. (2016). MtSWEET11, a Nodule-Specific Sucrose Transporter of *Medicago truncatula*. *Plant Physiology* **171**:554–565.
- Kryvoruchko, I. S., Routray, P., Sinharoy, S., Torres-Jerez, I., Tejada-Jiménez, M., Finney, L. A., Nakashima, J., Pislariu, C. I., Benedito, V. A., González-Guerrero, M., et al. (2018). An Iron-Activated Citrate Transporter, MtMATE67, Is Required for Symbiotic Nitrogen Fixation. *Plant Physiol.* **176**:2315–2329.
- Kumagai, H., Hakoyama, T., Umehara, Y., Sato, S., Kaneko, T., Tabata, S., and Kouchi, H. (2007). A novel ankyrin-repeat membrane protein, IGN1, is required for persistence of nitrogen-fixing symbiosis in root nodules of *Lotus japonicus*. *Plant Physiol.* **143**:1293–1305.
- Lefebvre, B., Timmers, T., Mbengue, M., Moreau, S., Hervé, C., Tóth, K., Bittencourt-Silvestre, J., Klaus, D., Deslandes, L., Godiard, L., et al. (2010). A remorin protein interacts with symbiotic receptors and regulates bacterial infection. *Proc. Natl. Acad. Sci. U. S. A.* **107**:2343–2348.
- Lei, Y., Su, S., He, L., Hu, X., and Luo, D. (2018). A member of the ALOG gene family has a novel role in regulating nodulation in *Lotus japonicus*. *J. Integr. Plant Biol.* Advance Access published August 21, 2018, doi:10.1111/jipb.12711.
- Leppyanen, I. V., Shakhnazarova, V. Y., Shtark, O. Y., Vishnevskaya, N. A., Tikhonovich, I. A., and Dolgikh, E. A. (2017). Receptor-Like Kinase LYK9 in

Pisum sativum L. Is the CERK1-Like Receptor that Controls Both Plant Immunity and AM Symbiosis Development. *Int. J. Mol. Sci.* **19**.

- Lévy, J., Bres, C., Geurts, R., Chalhoub, B., Kulikova, O., Duc, G., Journet, E.-P., Ané, J.-M., Lauber, E., Bisseling, T., et al. (2004). A putative Ca²⁺ and calmodulin-dependent protein kinase required for bacterial and fungal symbioses. *Science* **303**:1361–1364.
- Li, Y., Xu, M., Wang, N., and Li, Y. (2015). A JAZ Protein in *Astragalus sinicus* Interacts with a Leghemoglobin through the TIFY Domain and Is Involved in Nodule Development and Nitrogen Fixation. *PLoS One* **10**:e0139964.
- Li, X., Zheng, Z., Kong, X., Xu, J., Qiu, L., Sun, J., Reid, D., Jin, H., Andersen, S. U., Oldroyd, G. E. D., et al. (2019). Atypical Receptor Kinase RINRK1 Required for Rhizobial Infection But Not Nodule Development in *Lotus japonicus*. *Plant Physiol.* **181**:804–816.
- Libault, M., Joshi, T., Takahashi, K., Hurley-Sommer, A., Puricelli, K., Blake, S., Finger, R. E., Taylor, C. G., Xu, D., Nguyen, H. T., et al. (2009). Large-scale analysis of putative soybean regulatory gene expression identifies a Myb gene involved in soybean nodule development. *Plant Physiol.* **151**:1207–1220.
- Limpens, E., Franken, C., Smit, P., Willemsse, J., Bisseling, T., and Geurts, R. (2003). LysM domain receptor kinases regulating rhizobial Nod factor-induced infection. *Science* **302**:630–633.
- Lin, J.-S., Li, X., Luo, Z. L., Mysore, K. S., Wen, J., and Xie, F. (2018). NIN interacts with NLPs to mediate nitrate inhibition of nodulation in *Medicago truncatula*. *Nat Plants* Advance Access published October 8, 2018, doi:10.1038/s41477-018-0261-3.
- Liu, W., Kohlen, W., Lillo, A., Op den Camp, R., Ivanov, S., Hartog, M., Limpens, E., Jamil, M., Smaczniak, C., Kaufmann, K., et al. (2011). Strigolactone biosynthesis in *Medicago truncatula* and rice requires the symbiotic GRAS-type transcription factors NSP1 and NSP2. *Plant Cell* **23**:3853–3865.
- Liu, J., Novero, M., Charnikhova, T., Ferrandino, A., Schubert, A., Ruyter-Spira, C., Bonfante, P., Lovisolo, C., Bouwmeester, H. J., and Cardinale, F. (2013). Carotenoid cleavage dioxygenase 7 modulates plant growth, reproduction, senescence, and determinate nodulation in the model legume *Lotus japonicus*. *J. Exp. Bot.* **64**:1967–1981.
- Liu, W., Han, X., Zhan, G., Zhao, Z., Feng, Y., and Wu, C. (2015). A Novel Sucrose-Regulatory MADS-Box Transcription Factor GmNMHC5 Promotes Root Development and Nodulation in Soybean (*Glycine max* [L.] Merr.). *Int. J. Mol. Sci.* **16**:20657–20673.
- Liu, Y.-C., Lei, Y.-W., Liu, W., Weng, L., Lei, M.-J., Hu, X.-H., Dong, Z., Luo, D., and Yang, J. (2018). LjCOCH interplays with LjAPP1 to maintain the nodule development in *Lotus japonicus*. *Plant Growth Regul.* **85**:267–279.

- Madsen, E. B., Madsen, L. H., Radutoiu, S., Olbryt, M., Rakwalska, M., Szczyglowski, K., Sato, S., Kaneko, T., Tabata, S., Sandal, N., et al. (2003). A receptor kinase gene of the LysM type is involved in legume perception of rhizobial signals. *Nature* **425**:637–640.
- Magne, K., George, J., Berbel Tornero, A., Broquet, B., Madueño, F., Andersen, S. U., and Ratet, P. (2018a). Lotus japonicus NOOT-BOP-COCH-LIKE1 is essential for nodule, nectary, leaf and flower development. *Plant J.* **94**:880–894.
- Magne, K., Couzigou, J.-M., Schiessl, K., Liu, S., George, J., Zhukov, V., Sahl, L., Boyer, F., Iantcheva, A., Mysore, K. S., et al. (2018b). MtNODULE ROOT1 and MtNODULE ROOT2 are essential for indeterminate nodule identity. *Plant Physiol.* Advance Access published July 19, 2018, doi:10.1104/pp.18.00610.
- Małolepszy, A., Urbański, D. F., James, E. K., Sandal, N., Isono, E., Stougaard, J., and Andersen, S. U. (2015). The deubiquitinating enzyme AMSH1 is required for rhizobial infection and nodule organogenesis in Lotus japonicus. *Plant J.* **83**:719–731.
- Marino, D., Andrio, E., Danchin, E. G. J., Oger, E., Gucciardo, S., Lambert, A., Puppo, A., and Pauly, N. (2011). A Medicago truncatula NADPH oxidase is involved in symbiotic nodule functioning. *New Phytol.* **189**:580–592.
- Marsh, J. F., Rakocevic, A., Mitra, R. M., Brocard, L., Sun, J., Eschstruth, A., Long, S. R., Schultze, M., Ratet, P., and Oldroyd, G. E. D. (2007). Medicago truncatula NIN is essential for rhizobial-independent nodule organogenesis induced by autoactive Calcium/Calmodulin-Dependent Protein Kinase. *Plant Physiol.* **144**:324–335.
- Mazziotta, L., Reynoso, M. A., Aguilar, O. M., Blanco, F. A., and Zanetti, M. E. (2013). Transcriptional and functional variation of NF-YC1 in genetically diverse accessions of Phaseolus vulgaris during the symbiotic association with Rhizobium etli. *Plant Biol.* **15**:808–818.
- Mbengue, M., Camut, S., de Carvalho-Niebel, F., Deslandes, L., Froidure, S., Klaus-Heisen, D., Moreau, S., Rivas, S., Timmers, T., Hervé, C., et al. (2010). The Medicago truncatula E3 ubiquitin ligase PUB1 interacts with the LYK3 symbiotic receptor and negatively regulates infection and nodulation. *Plant Cell* **22**:3474–3488.
- Melo, P. M., Lima, L. M., Santos, I. M., Carvalho, H. G., and Cullimore, J. V. (2003). Expression of the Plastid-Located Glutamine Synthetase of Medicago truncatula. Accumulation of the Precursor in Root Nodules Reveals an in Vivo Control at the Level of Protein Import into Plastids. *Plant Physiology* **132**:390–399.
- Messinese, E., Mun, J.-H., Yeun, L. H., Jayaraman, D., Rougé, P., Barre, A., Lougnon, G., Schornack, S., Bono, J.-J., Cook, D. R., et al. (2007). A Novel Nuclear Protein Interacts With the Symbiotic DMI3 Calcium- and Calmodulin-Dependent Protein Kinase of Medicago truncatula. *Mol. Plant. Microbe Interact.* **20**:912–921.

- Miao, G. H., and Verma, D. P.** (1993). Soybean nodulin-26 gene encoding a channel protein is expressed only in the infected cells of nodules and is regulated differently in roots of homologous and heterologous plants. *Plant Cell* **5**:781–794.
- Middleton, P. H., Jakab, J., Penmetsa, R. V., Starker, C. G., Doll, J., Kaló, P., Prabhu, R., Marsh, J. F., Mitra, R. M., Kereszt, A., et al.** (2007). An ERF transcription factor in *Medicago truncatula* that is essential for Nod factor signal transduction. *Plant Cell* **19**:1221–1234.
- Miller, S. S., Driscoll, B. T., Gregerson, R. G., Gantt, J. S., and Vance, C. P.** (1998). Alfalfa malate dehydrogenase (MDH): molecular cloning and characterization of five different forms reveals a unique nodule-enhanced MDH. *Plant J.* **15**:173–184.
- Mitra, R. M., Gleason, C. A., Edwards, A., Hadfield, J., Downie, J. A., Oldroyd, G. E., and Long, S. R.** (2004). A Ca²⁺/calmodulin-dependent protein kinase required for symbiotic nodule development: Gene identification by transcript-based cloning. *Proc. Natl. Acad. Sci. U. S. A.* **101**:4701–4705.
- Miyahara, A., Richens, J., Starker, C., Morieri, G., Smith, L., Long, S., Downie, J. A., and Oldroyd, G. E. D.** (2010). Conservation in function of a SCAR / WAVE component during infection thread and root hair growth in *Medicago truncatula*. *Mol. Plant. Microbe. Interact.* **23**:1553–1562.
- Miyata, K., Kawaguchi, M., and Nakagawa, T.** (2013). Two distinct EIN2 genes cooperatively regulate ethylene signaling in *Lotus japonicus*. *Plant Cell Physiol.* **54**:1469–1477.
- Miyazawa, H., Oka-Kira, E., Sato, N., Takahashi, H., Wu, G.-J., Sato, S., Hayashi, M., Betsuyaku, S., Nakazono, M., Tabata, S., et al.** (2010). The receptor-like kinase KLAVIER mediates systemic regulation of nodulation and non-symbiotic shoot development in *Lotus japonicus*. *Development* **137**:4317–4325.
- Mohd-Radzman, N. A., Laffont, C., Ivanovici, A., Patel, N., Reid, D., Stougaard, J., Frugier, F., Imin, N., and Djordjevic, M. A.** (2016). Different Pathways Act Downstream of the CEP Peptide Receptor CRA2 to Regulate Lateral Root and Nodule Development. *Plant Physiol.* **171**:2536–2548.
- Montiel, J., Nava, N., Cárdenas, L., Sánchez-López, R., Arthikala, M.-K., Santana, O., Sánchez, F., and Quinto, C.** (2012). A *Phaseolus vulgaris* NADPH oxidase gene is required for root infection by *Rhizobia*. *Plant Cell Physiol.* **53**:1751–1767.
- Moreau, S., Thomson, R. M., Kaiser, B. N., Trevaskis, B., Lou Guerinot, M., Udvardi, M. K., Puppo, A., and Day, D. A.** (2002). GmZIP1 Encodes a Symbiosis-specific Zinc Transporter in Soybean. *Journal of Biological Chemistry* **277**:4738–4746.
- Morey, K. J., Ortega, J. L., and Sengupta-Gopalan, C.** (2002). Cytosolic Glutamine Synthetase in Soybean Is Encoded by a Multigene Family, and the Members Are Regulated in an Organ-Specific and Developmental Manner. *Plant Physiology* **128**:182–193.

- Mortier, V., Den Herder, G., Whitford, R., Van de Velde, W., Rombauts, S., D'Haeseleer, K., Holsters, M., and Goormachtig, S. (2010). CLE peptides control *Medicago truncatula* nodulation locally and systemically. *Plant Physiol.* **153**:222–237.
- Mortier, V., De Wever, E., Vuylsteke, M., Holsters, M., and Goormachtig, S. (2012). Nodule numbers are governed by interaction between CLE peptides and cytokinin signaling. *Plant J.* **70**:367–376.
- Müller, L. M., Flokova, K., Schnabel, E., Sun, X., Fei, Z., Frugoli, J., Bouwmeester, H. J., and Harrison, M. J. (2019). A CLE–SUNN module regulates strigolactone content and fungal colonization in arbuscular mycorrhiza. *Nature Plants* **5**:933–939.
- Murakami, E., Cheng, J., Gysel, K., Bozsoki, Z., Kawaharada, Y., Hjuler, C. T., Sørensen, K. K., Tao, K., Kelly, S., Venice, F., et al. (2018). Epidermal LysM receptor ensures robust symbiotic signalling in *Lotus japonicus*. *Elife* **7**.
- Murray, J. D., Karas, B. J., Sato, S., Tabata, S., Amyot, L., and Szczyglowski, K. (2007). A cytokinin perception mutant colonized by *Rhizobium* in the absence of nodule organogenesis. *Science* **315**:101–104.
- Murray, J. D., Muni, R. R. D., Torres-Jerez, I., Tang, Y., Allen, S., Andriankaja, M., Li, G., Laxmi, A., Cheng, X., Wen, J., et al. (2011). Vapyrin, a gene essential for intracellular progression of arbuscular mycorrhizal symbiosis, is also essential for infection by rhizobia in the nodule symbiosis of *Medicago truncatula*. *Plant J.* **65**:244–252.
- Nadzieja, M., Kelly, S., Stougaard, J., and Reid, D. (2018). Epidermal auxin biosynthesis facilitates rhizobial infection in *Lotus japonicus*. *Plant J. Advance Access published April 20, 2018*, doi:10.1111/tpj.13934.
- Nakagawa, T., Takane, K., Sugimoto, T., Izui, K., Kouchi, H., and Hata, S. (2003). Regulatory regions and nuclear factors involved in nodule-enhanced expression of a soybean phosphoenolpyruvate carboxylase gene: implications for molecular evolution. *Mol. Genet. Genomics* **269**:163–172.
- Nguyen, T., Zelechowska, M., Foster, V., Bergmann, H., and Verma, D. P. (1985). Primary structure of the soybean nodulin-35 gene encoding uricase II localized in the peroxisomes of uninfected cells of nodules. *Proc. Natl. Acad. Sci. U. S. A.* **82**:5040–5044.
- Niebel, F. D. C., Lescure, N., Cullimore, J. V., Gamas, P., and Biologie, L. D. (1998). The *Medicago truncatula* MtAnn1 Gene Encoding an Annexin Is Induced by Nod Factors and During the Symbiotic Interaction with *Rhizobium meliloti*. *Mol. Plant. Microbe. Interact.* **11**:504–513.
- Nishida, H., Tanaka, S., Handa, Y., Ito, M., Sakamoto, Y., Matsunaga, S., Betsuyaku, S., Miura, K., Soyano, T., Kawaguchi, M., et al. (2018). A NIN-LIKE PROTEIN mediates nitrate-induced control of root nodule symbiosis in *Lotus japonicus*. *Nat. Commun.* **9**:499.

- Nishimura, R., Ohmori, M., Fujita, H., and Kawaguchi, M. (2002a). A Lotus basic leucine zipper protein with a RING-finger motif negatively regulates the developmental program of nodulation. *Proc. Natl. Acad. Sci. U. S. A.* **99**:15206–15210.
- Nishimura, R., Hayashi, M., Wu, G.-J., Kouchi, H., Imaizumi-Anraku, H., Murakami, Y., Kawasaki, S., Akao, S., Ohmori, M., Nagasawa, M., et al. (2002b). HAR1 mediates systemic regulation of symbiotic organ development. *Nature* **420**:426–429.
- Okamoto, S., Ohnishi, E., Sato, S., Takahashi, H., Nakazono, M., Tabata, S., and Kawaguchi, M. (2009). Nod factor/nitrate-induced CLE genes that drive HAR1-mediated systemic regulation of nodulation. *Plant Cell Physiol.* **50**:67–77.
- Okamoto, S., Shinohara, H., Mori, T., Matsubayashi, Y., and Kawaguchi, M. (2013). Root-derived CLE glycopeptides control nodulation by direct binding to HAR1 receptor kinase. *Nat. Commun.* **4**:2191.
- Okubara, P. A., Fujishige, N. A., Hirsch, A. M., and Berry, A. M. (2000). Dg93, a nodule-abundant mRNA of *Datisca glomerata* with homology to a soybean early nodulin gene. *Plant Physiol.* **122**:1073–1079.
- Op den Camp, R. H. M. O., De Mita, S., Lillo, A., Cao, Q., Limpens, E., Bisseling, T., and Geurts, R. (2011a). A phylogenetic strategy based on a legume-specific whole genome duplication yields symbiotic cytokinin type-A response regulators. *Plant Physiol.* **157**:2013–2022.
- Op den Camp, R., Streng, A., De Mita, S., Cao, Q., Polone, E., Liu, W., Ammiraju, J. S. S., Kudrna, D., Wing, R., Untergasser, A., et al. (2011b). LysM-type mycorrhizal receptor recruited for rhizobium symbiosis in nonlegume *Parasponia*. *Science* **331**:909–912.
- Osipova, M. A., Mortier, V., Demchenko, K. N., Tsyganov, V. E., Tikhonovich, I. A., Lutova, L. A., Dolgikh, E. A., and Goormachtig, S. (2012). WUSCHEL-RELATED HOMEODOMAIN5 Gene Expression and Interaction of CLE Peptides with Components of the Systemic Control Add Two Pieces to the Puzzle of Autoregulation of Nodulation. *Plant Physiol.* **158**:1329–1341.
- Ott, T., van Dongen, J. T., Günther, C., Krusell, L., Desbrosses, G., Vigeolas, H., Bock, V., Czechowski, T., Geigenberger, P., and Udvardi, M. K. (2005). Symbiotic leghemoglobins are crucial for nitrogen fixation in legume root nodules but not for general plant growth and development. *Curr. Biol.* **15**:531–535.
- Pan, H., Oztas, O., Zhang, X., Wu, X., Stonoha, C., Wang, E., Wang, B., and Wang, D. (2016). A symbiotic SNARE protein generated by alternative termination of transcription. *Nat Plants* **2**:15197.
- Penmetsa, R. V., Uribe, P., Anderson, J., Lichtenzweig, J., Gish, J.-C., Nam, Y. W., Engstrom, E., Xu, K., Sckisel, G., Pereira, M., et al. (2008). The *Medicago truncatula* ortholog of *Arabidopsis* EIN2, *sickle*, is a negative regulator of symbiotic and pathogenic microbial associations. *Plant J.* **55**:580–595.

- Pumplin, N., Mondo, S. J., Topp, S., Starker, C. G., Gantt, J. S., and Harrison, M. J. (2010). Medicago truncatula Vapyrin is a novel protein required for arbuscular mycorrhizal symbiosis. *Plant J.* **61**:482–494.
- Radutoiu, S., Madsen, L. H., Madsen, E. B., Felle, H. H., Umehara, Y., Grønlund, M., Sato, S., Nakamura, Y., Tabata, S., Sandal, N., et al. (2003). Plant recognition of symbiotic bacteria requires two LysM receptor-like kinases. *Nature* **425**:585–592.
- Ramu, S. K., Peng, H.-M., and Cook, D. R. (2002). Nod factor induction of reactive oxygen species production is correlated with expression of the early nodulin gene rip1 in Medicago truncatula. *Mol. Plant. Microbe. Interact.* **15**:522–528.
- Reid, D. E., Heckmann, A. B., Novák, O., Kelly, S., and Stougaard, J. (2016). CYTOKININ OXIDASE/DEHYDROGENASE3 Maintains Cytokinin Homeostasis during Root and Nodule Development in Lotus japonicus. *Plant Physiol.* **170**:1060–1074.
- Reinders, A., Sivitz, A. B., Starker, C. G., Gantt, J. S., and Ward, J. M. (2008). Functional analysis of LjSUT4, a vacuolar sucrose transporter from Lotus japonicus. *Plant Mol. Biol.* **68**:289–299.
- Ribeiro, A., Akkermans, A. D., van Kammen, A., Bisseling, T., and Pawlowski, K. (1995). A nodule-specific gene encoding a subtilisin-like protease is expressed in early stages of actinorhizal nodule development. *Plant Cell* **7**:785–794.
- Rípodas, C., Castaingts, M., Clúa, J., Villafañe, J., Blanco, F. A., and Zanetti, M. E. (2019). The PvNF-YA1 and PvNF-YB7 Subunits of the Heterotrimeric NF-Y Transcription Factor Influence Strain Preference in the Phaseolus vulgaris–Rhizobium etli Symbiosis. *Front. Plant Sci.* **10**:221.
- Roberts, N. J., Morieri, G., Kalsi, G., Rose, A., Stiller, J., Edwards, A., Xie, F., Gresshoff, P. M., Oldroyd, G. E. D., Downie, J. A., et al. (2013). Rhizobial and mycorrhizal symbioses in Lotus japonicus require lectin nucleotide phosphohydrolase, which acts upstream of calcium signaling. *Plant Physiol.* **161**:556–567.
- Rogato, A., D’Apuzzo, E., Barbulova, A., Omrane, S., Stedel, C., Simon-Rosin, U., Katinakis, P., Flietakis, M., Udvardi, M., and Chiurazzi, M. (2008). Tissue-specific down-regulation of LjAMT1;1 compromises nodule function and enhances nodulation in Lotus japonicus. *Plant Mol. Biol.* **68**:585–595.
- Saito, K., Yoshikawa, M., Yano, K., Miwa, H., Uchida, H., Asamizu, E., Sato, S., Tabata, S., Imaizumi-Anraku, H., Umehara, Y., et al. (2007). NUCLEOPORIN85 Is Required for Calcium Spiking, Fungal and Bacterial Symbioses, and Seed Production in Lotus japonicus. *the Plant Cell Online* **19**:610–624.
- Schauser, L., Roussis, A., Stiller, J., and Stougaard, J. (1999). A plant regulator controlling development of symbiotic root nodules. *Nature* **402**:191–195.

- Schnabel, E., Journet, E.-P., de Carvalho-Niebel, F., Duc, G., and Frugoli, J. (2005). The *Medicago truncatula* SUNN gene encodes a CLV1-like leucine-rich repeat receptor kinase that regulates nodule number and root length. *Plant Mol. Biol.* **58**:809–822.
- Schnabel, E. L., Kassaw, T. K., Smith, L. S., Marsh, J. F., Oldroyd, G. E., Long, S. R., and Frugoli, J. A. (2011). The ROOT DETERMINED NODULATION1 Gene Regulates Nodule Number in Roots of *Medicago truncatula* and Defines a Highly Conserved, Uncharacterized Plant Gene Family. *Plant Physiol.* **157**:328–340.
- Schnorr, K. M., Laloue, M., and Hirel, B. (1996). Isolation of cDNAs encoding two purine biosynthetic enzymes of soybean and expression of the corresponding transcripts in roots and root nodules. *Plant Mol. Biol.* **32**:751–757.
- Searle, I. R., Men, A. E., Laniya, T. S., Buzas, D. M., Iturbe-Ormaetxe, I., Carroll, B. J., and Gresshoff, P. M. (2003). Long-distance signaling in nodulation directed by a CLAVATA1-like receptor kinase. *Science* **299**:109–112.
- Singh, S., Katzer, K., Lambert, J., Cerri, M., and Parniske, M. (2014). CYCLOPS, a DNA-binding transcriptional activator, orchestrates symbiotic root nodule development. *Cell Host Microbe* **15**:139–152.
- Sinharoy, S., Torres-Jerez, I., Bandyopadhyay, K., Kereszt, A., Pislariu, C. I., Nakashima, J., Benedito, V. A., Kondorosi, E., and Udvardi, M. K. (2013). The C2H2 transcription factor regulator of symbiosome differentiation represses transcription of the secretory pathway gene VAMP721a and promotes symbiosome development in *Medicago truncatula*. *Plant Cell* **25**:3584–3601.
- Sinharoy, S., Liu, C., Breakspear, A., Guan, D., Shailes, S., Nakashima, J., Zhang, S., Wen, J., Torres-Jerez, I., Oldroyd, G., et al. (2016). A *Medicago truncatula* Cystathionine- β -Synthase-like Domain-Containing Protein is required for rhizobial infection and symbiotic nitrogen fixation. *Plant Physiol.* **170**:2204–2217.
- Smit, P., Raedts, J., Portyanko, V., Debellé, F., Gough, C., Bisseling, T., and Geurts, R. (2005). NSP1 of the GRAS protein family is essential for rhizobial Nod factor-induced transcription. *Science* **308**:1789–1791.
- Smit, P., Limpens, E., Geurts, R., Fedorova, E., Dolgikh, E., Gough, C., and Bisseling, T. (2007). *Medicago* LYK3, an entry receptor in rhizobial nodulation factor signaling. *Plant Physiol.* **145**:183–191.
- Soyano, T., Kouchi, H., Hirota, A., and Hayashi, M. (2013). Nodule inception directly targets NF-Y subunit genes to regulate essential processes of root nodule development in *Lotus japonicus*. *PLoS Genet.* **9**:e1003352.
- Stracke, S., Kistner, C., Yoshida, S., Mulder, L., Sato, S., Kaneko, T., Tabata, S., Sandal, N., Stougaard, J., Szczyglowski, K., et al. (2002). A plant receptor-

like kinase required for both bacterial and fungal symbiosis. *Nature* **417**:959–962.

- Straub, D., Ludewig, U., and Neuhäuser, B.** (2014). A nitrogen-dependent switch in the high affinity ammonium transport in *Medicago truncatula*. *Plant Mol. Biol.* **86**:485–494.
- Sturms, R., Kakar, S., Trent, J., and Hargrove, M. S.** (2010). Trema and parasponia hemoglobins reveal convergent evolution of oxygen transport in plants. *Biochemistry* **49**:4085–4093.
- Sugiyama, A., Saida, Y., Yoshimizu, M., Takanashi, K., Sosso, D., Frommer, W. B., and Yazaki, K.** (2016). Molecular Characterization of LjSWEET3, a Sugar Transporter in Nodules of *Lotus japonicus*. *Plant Cell Physiol.* Advance Access published December 21, 2016, doi:10.1093/pcp/pcw190.
- Suzaki, T., Ito, M., Yoro, E., Sato, S., Hirakawa, H., Takeda, N., and Kawaguchi, M.** (2014). Endoreduplication-mediated initiation of symbiotic organ development in *Lotus japonicus*. *Development* **141**:2441–2445.
- Takahara, M., Magori, S., Soyano, T., Okamoto, S., Yoshida, C., Yano, K., Sato, S., Tabata, S., Yamaguchi, K., Shigenobu, S., et al.** (2013). Too much love, a novel Kelch repeat-containing F-box protein, functions in the long-distance regulation of the legume-Rhizobium symbiosis. *Plant Cell Physiol.* **54**:433–447.
- Takanashi, K., Yokosho, K., Saeki, K., Sugiyama, A., Sato, S., Tabata, S., Ma, J. F., and Yazaki, K.** (2013). LjMATE1: a citrate transporter responsible for iron supply to the nodule infection zone of *Lotus japonicus*. *Plant Cell Physiol.* **54**:585–594.
- Tirichine, L., Imaizumi-Anraku, H., Yoshida, S., Murakami, Y., Madsen, L. H., Miwa, H., Nakagawa, T., Sandal, N., Albrechtsen, A. S., Kawaguchi, M., et al.** (2006). Deregulation of a Ca²⁺/calmodulin-dependent kinase leads to spontaneous nodule development. *Nature* **441**:1153–1156.
- Tóth, K., Stratil, T. F., Madsen, E. B., Ye, J., Popp, C., Antolín-Llovera, M., Grossmann, C., Jensen, O. N., Schübler, A., Parniske, M., et al.** (2012). Functional domain analysis of the remorin protein LjSYMREM1 in *Lotus japonicus*. *PLoS One* **7**.
- Tsikou, D., Ramirez, E. E., Psarrakou, I. S., Wong, J. E., Jensen, D. B., Isono, E., Radutoiu, S., and Papadopoulou, K. K.** (2018). A *Lotus japonicus* E3 ligase interacts with the Nod Factor Receptor 5 and positively regulates nodulation. *BMC Plant Biol.* **18**:217.
- Vance, C. P., Miller, S. S., Gregerson, R. G., Samac, D. A., Robinson, D. L., and Gantt, J. S.** (1995). Alfalfa NADH-dependent glutamate synthase: structure of the gene and importance in symbiotic N₂ fixation. *Plant J.* **8**:345–358.
- van Ghelue, M., Ribeiro, A., Solheim, B., Akkermans, A. D., Bisseling, T., and Pawlowski, K.** (1996). Sucrose synthase and enolase expression in

- actinorhizal nodules of *Alnus glutinosa*: comparison with legume nodules. *Mol. Gen. Genet.* **250**:437–446.
- van Velzen, R., Holmer, R., Bu, F., Rutten, L., van Zeijl, A., Liu, W., Santuari, L., Cao, Q., Sharma, T., Shen, D., et al. (2018). Comparative genomics of the nonlegume *Parasponia* reveals insights into evolution of nitrogen-fixing rhizobium symbioses. *Proceedings of the National Academy of Sciences* **115**:E4700–E4709.
- Van Zeijl, A., Liu, W., Xiao, T. T., Kohlen, W., Yang, W.-C., Bisseling, T., and Geurts, R. R. (2015). The strigolactone biosynthesis gene DWARF27 is co-opted in rhizobium symbiosis. *BMC Plant Biol.* **15**:260.
- van Zeijl, A., Wardhani, T. A. K., Seifi Kalhor, M., Rutten, L., Bu, F., Hartog, M., Linders, S., Fedorova, E. E., Bisseling, T., Kohlen, W., et al. (2018). CRISPR/Cas9-Mediated Mutagenesis of Four Putative Symbiosis Genes of the Tropical Tree *Parasponia andersonii* Reveals Novel Phenotypes. *Front. Plant Sci.* **9**:284.
- Venkateshwaran, M., Jayaraman, D., Chabaud, M., Genre, A., Balloon, A. J., Maeda, J., Forshey, K., den Os, D., Kwiecien, N. W., Coon, J. J., et al. (2015). A role for the mevalonate pathway in early plant symbiotic signaling. *Proceedings of the National Academy of Sciences* **112**:201413762.
- Vernié, T., Moreau, S., de Billy, F., Plet, J., Combiér, J.-P., Rogers, C., Oldroyd, G., Frugier, F., Niebel, A., Gamas, P., et al. (2008). EFD is an ERF transcription factor involved in the control of nodule number and differentiation in *Medicago truncatula*. *Plant Cell* **20**:2696–2713.
- Vincent, J. L., and Brewin, N. J. (2000). Immunolocalization of a cysteine protease in vacuoles, vesicles, and symbiosomes of pea nodule cells. *Plant Physiol.* **123**:521–530.
- Vincill, E. D., Szczyglowski, K., and Roberts, D. M. (2005). GmN70 and LjN70. Anion transporters of the symbiosome membrane of nodules with a transport preference for nitrate. *Plant Physiol.* **137**:1435–1444.
- Wang, D., Griffiths, J., Starker, C., Fedorova, E., Limpens, E., Ivanov, S., Bisseling, T., and Long, S. (2010). A nodule-specific protein secretory pathway required for nitrogen-fixing symbiosis. *Science* **327**:1126–1129.
- Wang, Y., Wang, L., Zou, Y., Chen, L., Cai, Z., Zhang, S., Zhao, F., Tian, Y., Jiang, Q., Ferguson, B. J., et al. (2014). Soybean miR172c targets the repressive AP2 transcription factor NNC1 to activate ENOD40 expression and regulate nodule initiation. *Plant Cell* **26**:4782–4801.
- Wang, C., Yu, H., Luo, L., Duan, L., Cai, L., He, X., Wen, J., Mysore, K. S., Li, G., Xiao, A., et al. (2016). NODULES WITH ACTIVATED DEFENSE 1 is required for maintenance of rhizobial endosymbiosis in *Medicago truncatula*. *New Phytol.* **212**:176–191.

- Wang, L., Sun, Z., Su, C., Wang, Y., Yan, Q., Chen, J., Ott, T., and Li, X. (2019a). A GmNINa-miR172c-NNC1 Regulatory Network Coordinates the Nodulation and Autoregulation of Nodulation Pathways in Soybean. *Mol. Plant* Advance Access published June 12, 2019, doi:10.1016/j.molp.2019.06.002.
- Wang, L., Rubio, M. C., Xin, X., Zhang, B., Fan, Q., Wang, Q., Ning, G., Becana, M., and Duanmu, D. (2019b). CRISPR/Cas9 knockout of leghemoglobin genes in *Lotus japonicus* uncovers their synergistic roles in symbiotic nitrogen fixation. *New Phytol.* Advance Access published July 29, 2019, doi:10.1111/nph.16077.
- Wong, J. E. M. M., Nadzieja, M., Madsen, L. H., Bücherl, C. A., Dam, S., Sandal, N. N., Couto, D., Derbyshire, P., Uldum-Berentsen, M., Schroeder, S., et al. (2019). A *Lotus japonicus* cytoplasmic kinase connects Nod factor perception by the NFR5 LysM receptor to nodulation. *Proc. Natl. Acad. Sci. U. S. A.* Advance Access published June 25, 2019, doi:10.1073/pnas.1815425116.
- Xie, F., Murray, J. D., Kim, J., Heckmann, A. B., Edwards, A., Oldroyd, G. E. D., and Downie, J. A. (2012). Legume pectate lyase required for root infection by rhizobia. *Proceedings of the National Academy of Sciences* **109**:633–638.
- Yano, K., Yoshida, S., Müller, J., Singh, S., Banba, M., Vickers, K., Markmann, K., White, C., Schuller, B., Sato, S., et al. (2008). CYCLOPS, a mediator of symbiotic intracellular accommodation. *Proceedings of the National Academy of Sciences* **105**:20540–20545.
- Yano, K., Shibata, S., Chen, W. L., Sato - The Plant ..., S., and 2009 (2009). CERBERUS, a novel U-box protein containing WD-40 repeats, is required for formation of the infection thread and nodule development in the legume *Wiley Online Library* Advance Access published 2009.
- Yin, J., Guan, X., Zhang, H., Wang, L., Li, H., Zhang, Q., Chen, T., Xu, Z., Hong, Z., Cao, Y., et al. (2019). An MAP kinase interacts with LHK1 and regulates nodule organogenesis in *Lotus japonicus*. *Sci. China Life Sci.* **62**:1203–1217.
- Yokota, K., Fukai, E., Madsen, L. H., Jurkiewicz, A., Rueda, P., Radutoiu, S., Held, M., Hossain, M. S., Szczyglowski, K., Morieri, G., et al. (2009). Rearrangement of actin cytoskeleton mediates invasion of *Lotus japonicus* roots by *Mesorhizobium loti*. *Plant Cell* **21**:267–284.
- Yoon, H. J., Hossain, M. S., Held, M., Hou, H., Kehl, M., Tromas, A., Sato, S., Tabata, S., Andersen, S. U., Stougaard, J., et al. (2014). *Lotus japonicus* SUNERGOS1 encodes a predicted subunit A of a DNA topoisomerase VI that is required for nodule differentiation and accommodation of rhizobial infection. *Plant J.* **78**:811–821.
- Yoshida, T., Fujita, Y., Sayama, H., Kidokoro, S., Maruyama, K., Mizoi, J., Shinozaki, K., and Yamaguchi-Shinozaki, K. (2010). AREB1, AREB2, and ABF3 are master transcription factors that cooperatively regulate ABRE-dependent ABA signaling involved in drought stress tolerance and require ABA for full activation. *Plant J.* **61**:672–685.

- Yuan, S., Zhu, H., Gou, H., Fu, W., Liu, L., Chen, T., Ke, D., Kang, H., Xie, Q., Hong, Z., et al. (2012). A ubiquitin ligase of symbiosis receptor kinase involved in nodule organogenesis. *Plant Physiol.* **160**:106–117.
- Zanetti, M. E., Blanco, F. A., Beker, M. P., Battaglia, M., and Aguilar, O. M. (2010). AC subunit of the plant nuclear factor NF-Y required for rhizobial infection and nodule development affects partner selection in the common bean--*Rhizobium etli* symbiosis. *Plant Cell* **22**:4142–4157.
- Zhu, H., Chen, T., Zhu, M., Fang, Q., Kang, H., Hong, Z., and Zhang, Z. (2008). A novel ARID DNA-binding protein interacts with SymRK and is expressed during early nodule development in *Lotus japonicus*. *Plant Physiol.* **148**:337–347.