Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Plant Biology

Cross-interference of plant development and plant–microbe interactions

Edouard Evangelisti, Thomas Rey and Sebastian Schornack

Plant roots are host to a multitude of filamentous microorganisms. Among these, arbuscular mycorrhizal fungi provide benefits to plants, while pathogens trigger diseases resulting in significant crop yield losses. It is therefore imperative to study processes which allow plants to discriminate detrimental and beneficial interactions in order to protect crops from diseases while retaining the ability for sustainable bio-fertilisation strategies. Accumulating evidence suggests that some symbiosis processes also affect plant–pathogen interactions. A large part of this overlap likely constitutes plant developmental processes. Moreover, microbes utilise effector proteins to interfere with plant development. Here we list relevant recent findings on how plant–microbe interactions intersect with plant development and highlight future research leads.

Addresses
Sainsbury Laboratory, University of Cambridge, Cambridge CB2 1LR, UK

Corresponding author: Schornack, Sebastian (sebastian.schornack@slcu.cam.ac.uk)

Current Opinion in Plant Biology 2014, **20**:118–126

This review comes from a themed issue on **Biotic interactions**

Edited by **Makoto Hayashi** and **Martin Parniske**

For a complete overview see the Issue and the Editorial

Available online 10th June 2014

http://dx.doi.org/10.1016/j.pbi.2014.05.014

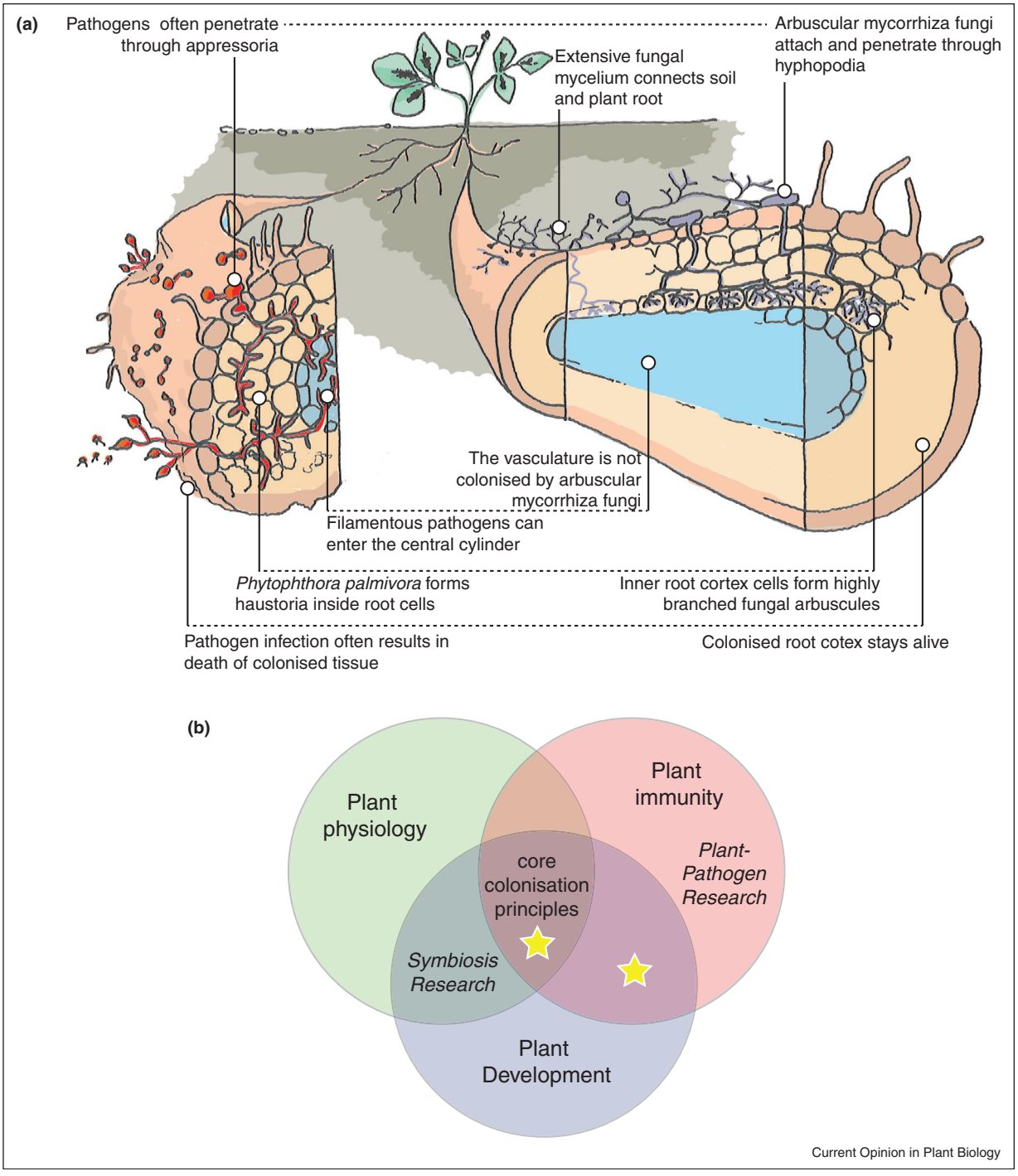
Introduction

Plants' success in conquering land can in part be attributed to their ability to team up with filamentous microorganisms. The oldest land plant fossils from the Rhynie chert give evidence of fungal structures inside plant cells [1] and more than 70% of all existing higher plants are colonised by arbuscular mycorrhizal (AM) fungi [2]. The fungal partner provides mineral nutrients such as phosphorus. Conversely, plants provide carbohydrates generated through photosynthesis. Plant carbohydrates are also attractive to root-infecting filamentous pathogens such as fungi and oomycetes. Pathogenic oomycetes such as *Phytophthora palmivora* and beneficial fungi represent extreme opposites but nevertheless share common root colonisation principles (Figure 1a) and therefore provide means to identify more general plant processes required for both, pathogenic and beneficial interactions [8]. Traditionally, plant–pathogen research has focussed on immune suppression strategies while symbiosis research revealed a strong contribution of cellular and developmental processes for microbial colonisation, especially through studies of interactions between nitrogen-fixing bacteria and legume roots leading to the development of dedicated organs, the root nodules [3]. More recently, the contribution of developmental processes intersecting with plant–pathogen interactions gained growing interest in order to elucidate core colonisation principles (Figure 1b). Changes in root development are visible through reprogramming of colonised plant tissues resulting in significant morphological and structural alterations and the formation of specific cellular interfaces for nutrient exchange, collectively termed symbiosomes [4•] (Box 1). Here we specifically highlight plant components that support a cross-interference of development and plant–microbe interactions and also discuss recent findings that microbial effector proteins can modulate plant development processes.

Plant–microbe interactions intersect with plant development

Alterations of plant development by filamentous microorganism can often result in striking phenotypes and altered plant physiology. Examples are the induction of lateral roots by *Aphanomyces euteiches* [5] and AM fungi [6], or the vascularisation of companion cells in *Verticillium longisporum*-infected *Arabidopsis thaliana* [7]. Mutants allow us to pinpoint processes with common effects on beneficial and detrimental interactions. Table 1 lists mutants, which have been characterised initially by their symbiosis phenotypes and subsequently found to have developmental phenotypes. Knowledge on how these mutants affect interactions with pathogens is still limited but testing them using suitable root pathogens is likely to reveal some common processes [8]. Unsurprisingly, the mutated genes are quite often involved in hormone signalling and thus have been also hit in screens for developmental alterations. Examples include *Medicago truncatula sickle*, *CRE1* and *DELLAs*. *SICKLE* encodes an *Arabidopsis* EIN2 orthologue, an essential component of ethylene signalling. The *sickle* plants display triple response phenotypes affecting both above-ground and below-ground plant organs and are highly susceptible to the filamentous necrotrophs *Rhizoctonia solani* and *Phythophthora medicaginis* but conversely form numerous nodules and are hyper-colonised by AM fungi [9]. The

Figure 1



Commonalities and contrasts of pathogenic and symbiotic microbe interactions with plant roots. **(a)** Structural similarities and differences in *Medicago truncatula* root colonisation between a filamentous oomycete pathogen (left) and arbuscular mycorrhiza fungi (right). **(b)** Growing research interest (indicated by stars) focusses on core colonisation principles requiring the integrated study of plant physiology, plant immunity and plant development and of developmental aspects of plant–microbe interactions, a traditional topic of symbiosis research.

cytokinin receptor *MtCRE1* promotes invasion by both pathogenic and symbiotic bacteria [10,11] but its importance for filamentous microbes has not been assessed yet. The use of *della* mutants recently enabled identification of gibberellic acid (GA3) as a repressor of accommodation structure formation in *M. truncatula* and *Pisum sativum* [12••,13•]. Strikingly, a dominant negative DELLA protein rescues *cyclops*, a common symbiosis pathway

Box 1 Symbiosomes, different or all the same?

Symbiosomes are specialised intracellular interfaces formed by filamentous microorganisms inside plant cells [4•]. Their core structure is a plant cell wall-piercing microbial hypha engulfed by the plant protoplast. Symbiosomes have been termed haustoria of fungi and oomycetes, invading hyphae of fungi such as *Colletotrichum* sp. and *Magnaporthe oryzae*, coils of *Piriformospora indica* and other fungi and arbuscules of AM fungi. Symbiosome shape varies greatly and factors influencing it are not fully understood. Nevertheless, they are all assumed to have two main functions: nutrient transfer and microbial effector delivery. Extensive branching of symbiosomes is likely attributable to efficient nutrient and information exchange and often assigned to beneficial symbiosis. Whether fossil symbiosome-like structures serve mutual nutrient exchange or are extensive one-way pathogenic haustoria will remain unresolved.

Plant and microbe are separated by a specialised membrane termed extrahaustorial membrane (EHM), periarbuscular membrane (PAM) or extrainvasive hyphae membrane (EIHM) depending on the microorganism. PAMs in rice and legumes harbour phosphate transporters which are absent from the remaining plasma membrane [51,52]. Conversely, EHMs of pathogenic fungi and oomycetes are lacking numerous transmembrane proteins including immune receptors. Notably, membrane adhering proteins are still present [53,54]. Differences in symbiosome membrane protein composition [53] compared to the plasma membrane often are attributed to presence of a sealing neckband structure, found in many obligate biotrophs. Absence of a neckband at the PAM and EHMs of *Phytophthora* species highlights the need for further research into membrane protein separation mechanisms. Mechanisms resulting in formation and decoration of symbiosome membranes largely remain elusive. Exclusive PAM integration of the MtPt4 phosphate transporter has been attributed to repolarisation of secretion timed with MtPt4 promoter activation during arbuscule formation [55]. Another open question is the point of new membrane material deployment. The neck, the oldest part of a symbiosome, shows accumulation of plant endomembrane compartments and callose deposition. However, candidate vesicle-fusion sites can be traced all over haustoria and the fine branches of arbuscules [53,56]. Future work using photo-convertible fluorescent probes will shed light on temporal and spatial changes in symbiosome membrane processes.

mutant thus bypassing symbiosis signalling and supporting the hypothesis of GA signalling repression by this pathway. Notably, DELLA proteins are also known to bind JAZ proteins [14], repressors of the jasmonate pathway. Hence contribution of jasmonate-related defence responses depending on GA and dominant negative DELLA proteins might provide further clues about the role of hormonal balance in regulation of mycorrhizal symbiosis. Since hormonal pathways link development to immunity, it remains to be untangled whether specific microbes interfere with them to suppress immunity or to alter development.

Plant–microbe interactions utilise similar chemical signatures

Chitin-derived microbial signals are triggers of plant symbiotic responses [15•]. Interestingly, similar but not identical chitin-derived signals are also perceived by peripheral plant immune receptors. Chitin-binding LysM domain-containing receptor-like kinases are key players in both symbiosis and defence. Numerous activities ranging from immune suppression upon perception of symbiotic signatures in *Arabidopsis*, cell death induction upon ectopic expression in *Nicotiana benthamiana* leaves [16] and involvement in symbiotic [17] to pathogenic interaction with filamentous microbes [18••] have been assigned to them. The finding that a LysM receptor of the symbiosis-incapable *Arabidopsis* perceives symbiotic Nod-factors to suppress immunity [19] shows that specificity of signal integration from LysM receptors and their downstream targets are not fully resolved. It is therefore possible that chitin-derived signals of plant origin may also play a role in developmental processes.

Cutin is a structural component of above-ground organs. However, plant cutin monomers have been shown to be a crucial signal for infection structure formation by filamentous pathogens [20]. Recently this was extended to pathogenic oomycetes (*P. palmivora* and *A. euteiches*) and beneficial AM fungi [21•,22]. A mutant of *M. truncatula* RAM2, a glycerol-3-phosphate acyltransferase, failed to display appressorium formation by the filamentous plant pathogen *P. palmivora* as well as arbuscule development by beneficial AM fungi. The altered seed coat of *ram2* mutants points to its involvement in development [22].

Essential components of specific plant–microbe interactions gain additional roles

Studies of core symbiosis players, the receptor kinase SymRK and the Calcium and calmodulin dependent kinase CCaMK revealed their unexpected involvement in responses to pathogen and mechanical cues. SymRK is important for root hair resistance to mechanical stresses [23]. CCaMK was proposed to cope with stress triggered by penetration events of mycorrhizal fungus and the pathogenic fungus *Colletotrichum trifolii* [24]. CCaMK is presumed to be the main sensor of the nuclear calcium spiking triggered specifically by endosymbionts [25]. However, this protein is also a major regulator of bacterial communities associated with rice roots in natural environments [26] suggesting sources other than endosymbionts may be producers of CCaMK-read calcium signatures. A possible mechanism underlying fine-tuning of root microbiome by CCaMK is its role in abscisic acid (ABA) signalling and reactive oxygen species homeostasis recently demonstrated in rice leaves [27•]. Overexpression of wheat CCaMK in *Arabidopsis* resulted in plants which were less susceptible to ABA during germination and seedling growth [28]. Thus, CCaMK although initially implied only in symbiosis might have additional functions. This is supported by the presence of CCaMK/DMI3 in Charophyta, since AM fungal mycorrhiza has not been reported from these green algae [29].

Another link between microbial accommodation and development is provided by MLO proteins. MLO has been

Table 1

Examples of mutants impaired symbiosis and defects in development. *Abbreviations*: *Aa, Alternaria alternata*; Ae, *Aphanomyces euteiches*; API, altered primordia invasion; *Bc, Botritys cinerea*; BTB/POZ, BR-C, ttk and bab/Pox virus and Zinc finger; CCaMK, calcium and calmodulin dependent kinase; ccd8, carotenoid cleavage dioxygenase; CEP1, C-terminus encoded peptide; CRE1, cytokinin receptor 1; Ct, *Colletotrichum trifolii*; EIN2, ethylene insensitive 2; Gm, *Glycine max*; GPAT, glycerol phosphate acyl transferase; HAR, hypernodulated abberant root; LATD, lateral deficiency; LCO, lipochitooligosaccharide; Lj, *Lotus japonicus*; Lot1, low nodulation and trichome distortion; LRI, lateral root induction; LRR-RLK, leucine rich repeat receptor-like kinase; LysM-RLK, lysine motif RLK; Mt, *Medicago truncatula*; NAP1, Nck-Associated Protein1; NARK, Nodule Autoregulation Receptor Kinase; NFP, Nod factor perception; NSP, Nod signalling pathway; PIR1, 121F-specific p53 inducible RNA 1; *Pm, Phytophthora medicaginis*; *Pp*, *Phytophthora palmivora*; PRAF, PH, RCC1 and FYVE;*Ps, Pisum sativum*; RAM2, required for arbuscular mycorrhiza2; RDN1, root determined nodulation; RIT, required for infection thread; ROP9, Rho-related GTPases 9; Rs, *Ralstonia solanacearum*; *R. solani*, *Rhizoctonia solani*; Sl, *Solanum lycopersicum*; SUNN, super numeric nodule; SymRK, symbiotic receptor kinase; Va, *Verticillium albo-atrum*.

Gene/locus	Protein	Rhizobial symbiosis	Fungal symbiosis	Pathogen	Development	Refs
MtSUNN/LjHAR1/GmNARK	LRR-RLK Clavata	Repress	Repress	Susceptibility to *Va*	Root growth	[57–60]
MtCRE1	Cytokinin receptor	Nodulation	?	Susceptibility to *Rs*	Repression of LRI	[10,11,61]
MtRAM2	GPAT	Not involved	Promote	Susceptibility to *Pp* and *Ae*	Seed coat	[21•,22]
Mtsickle	EIN2	Repress	Repress	Susceptibility to Pm and *R. solani*, resistance to *Va*	Plant growth, root hairs	[9,60,62]
CCaMK	Kinase	Required	Required	Susceptibility to *Ct*	Repress ABA signalling, ROS homeostasis	[24,26,27•,28,63]
Slccd8	CCD	?	Promote	Resistance to *Bc* and *Aa*	Strigolactones synthesis	[64]
MtNFP	LysM-RLK	Required	LCO signalling, LRI	Resistance to *Ae*, *Ct* and *Va*	Not involved	[17,18••,59,65]
MtROP9	Rac1 small G protein	Infection Thread	Repress	Resistance to *Ae*	Root and root hairs	[66]
SymRK	LRR-RLK	Required	Required	?	Root hair touch response	[23]
MtNSP1	GRAS transcription factor	Required	Promote	?	Strigolactones synthesis	[67,68]
MtNSP2	GRAS transcription factor	Required	Promote	?	Strigolactones synthesis	[68]
LjLot1	?	Infection Thread	Not involved	?	Trichome, pollen tube	[69]
OsD3	F-Box	?	Required	?	Strigolactone signalling	[70]
LjBRUSH	?	Temperature dependent	?	?	Defect depending on temperature	[71]
LjnsRING	RING protein	Required	?	?	Shoot, root growth	[72]
MtRDN1	Unknown function	Repress	?	?	Root	[73]
LjKLAVIER	LRR-RLK	Repress	?	?	Meristem, vasculature, shoot growth and flowers	[74]
MtCEP1	Signalling peptides	Promote	?	?	Repression of LRI, inducer of cortical division	[75]
MtZR1	PRAF protein	Promote	?	?	Root	[76]
MtLATD	Nitrate transporter	Infection Thread and nodulation	?	?	LRI, root hairs, ABA response, root meristem	[77–79]

Table 1 (*Continued*)

Gene/locus	Protein	Rhizobial symbiosis	Fungal symbiosis	Pathogen	Development	Refs
LjNAP1/MtRIT	SCAR/WAVE	Infection Thread	?	?	Pollen tube, trichome, seed coat	[80,81]
LjPIR1	SCAR/WAVE	Infection Thread	?	?	Pollen tube, trichome	[81]
LjCRINKLE	?	Infection Thread	?	?	Pollen tubes, root hairs, trichome, pods	[82,83]
MtAPI	?	Infection Thread	?	?	Root hairs	[84]
Ljsym74-3 Ljsym80	?	Infection Thread	?	?	Root hairs	[85]
MtNOOT/PsCOCHLEATA	BTB/POZ-ankyrin domain	Nodule meristem identity	?	?	Leaf and flower development	[86]

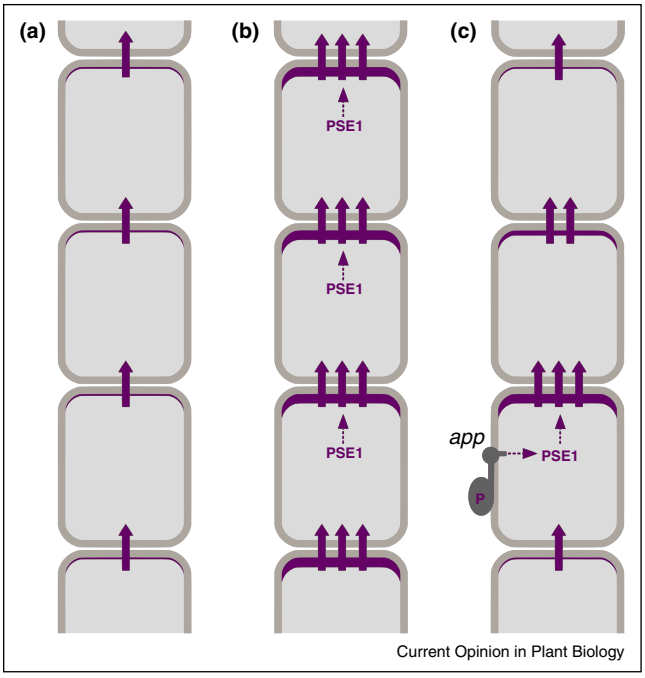
initially described as an essential component for barley colonisation by the biotrophic pathogen *Blumeria graminis* [30]. However, some mutants of MLO homologs are affected in AM fungus colonisation, display aberrant root development [31] and are crucial for pollen tube reception during fertilisation [32]. These examples support the general concept that similar functional principles and genetic elements can be employed in plant processes of development as well as plant–microbe interactions. It is thus exciting to explore the numerous development mutants available in symbiosis plant systems for their effects on beneficial or detrimental interactions.

Microbial effectors can alter plant development mechanisms

Filamentous plant microbes have evolved small secreted molecules termed effectors which interfere with host cell metabolism in order to support colonisation. Recent genome sequencing of the AM fungus *Rhizophagus irregularis* enabled identification of potential effectors. Homology-based and sequence-based searches uncovered Crinkler (CRN) effector-encoding genes [33••]. First identified in *Phytophthora infestans*, CRNs were soon recognised as an ancient family with predominant nuclear localisation [34] also present in fungi. Some pathogen CRNs trigger cell death when overexpressed as mature proteins in *N. benthamiana* [35] but the underlying functional mechanisms remain to be elucidated. It will be interesting to see whether CRNs of symbiotic AM fungi carry similar activities. Further recent work on effectors highlighting their importance for plant immune suppression and promotion of plant susceptibility [36–38] will not be discussed in detail here.

An increasing number of studies from non-filamentous pathogens reports effectors interfering with plant development and plant hormone physiology not directly related to defence [39,40]. Striking recent examples are insect-transmitted phytopathogenic *Phytoplasma* effectors that interfere with plant development [41]. SAP54 alters floral development, resulting in leaf-like flowers similar to those of *Phytoplasma*-infected plants [42••]. SAP11 binds and destabilises *Arabidopsis* TCP transcription factors which control plant development and promote the expression of jasmonate biosynthesis genes [43]. TENGU leads to dwarfism and witches' broom symptoms in *Arabidopsis*, while auxin-related genes are being downregulated [44]. Exciting data by Okazaki *et al.* show that the symbiotic bacterium *Bradyrhizobium elkanii* induces the symbiotic accommodation program in a type III secretion system dependent manner likely mediated by bacterial effectors [45••]. Finally, plant–parasitic nematodes interfere with auxin transport during root infection [46]. The beet cyst nematode *Heterodera schachtii* delivers the effector protein Hs19C07 which interacts with auxin influx carrier LAX3 to control feeding site development in *Arabidopsis* [47].

Figure 2



Model of *Phytophthora parasitica* PSE1 activity. **(a)** In wild-type plants auxin flux (thick arrows) is established through polar localisation of PIN auxin efflux carriers (blue crescents). **(b)** Overexpression of PSE1 in plant roots stabilises PINs in the membrane and interferes with their recycling, resulting in overall root growth and morphology changes. **(c)** In natural root infections PSE1 is expressed in *P. parasitica* appressoria (*app*) and injected in the first penetrated cell and only locally stabilises PINs resulting in a far less dramatic tissue-wide effect.

Knowledge on filamentous effectors interfering with tissue or organ development is now emerging too. The *Phytophthora parasitica* effector PSE1 interferes with auxin partitioning during root infection in *Arabidopsis*. Expression of PSE1 in plants resulted in root curling and aberrant root hair phenotypes. It is conceivable that PSE1 interferes with stability or endocytosis cycling of auxin efflux carriers [48••] (Figure 2). Often, the most challenging part is to show that perturbations described through mutants also occur during microbial colonisation of wild-type plants as these effects can often be limited to a single cell. A recent study reports that the smut fungus *Ustilago maydis* utilises Tin2 to stabilise the maize kinase ZnTTK1 resulting in higher anthocyanin biosynthesis for the cost of lignin biosynthesis. This may lead to altered cell wall composition thereby affecting penetration and migration of the fungus as well as changes in vascular tissue characteristics [49•]. In summary, it is exciting to see that effectors provide a handle to pinpoint elements of plant development which might not be traceable using knock-out approaches; however, their significance needs to be scrutinised. Pharmacological approaches to modulate development can have effects in addition to the process of interest. In analogy, single plant target studies cannot always explain the full phenotype caused by an effector. Thus, future effector multi-target research and awareness of technical limitations of effector studies are important.

Concluding remarks

While historically plant–pathogen research and symbiosis research did not have much common ground, both communities are merging into one. The growing demand for disease resistant crops which retain the ability for sustainable bio-fertilisation through use of symbiotic microbes demands research into possibilities to tweak interactions towards beneficial outcomes. One emerging feature is the modulation of plant development by microbial effectors. Unravelling plant target processes will provide inroads to establish genetic control of pathogens while keeping unwanted developmental defects in check.

Certainly, numerous questions remain to be answered. Symbiosomes (Box 1) are at the heart of symbiosis and therefore pose an interesting target to tweak interaction outcomes. Comparative approaches will reveal whether interaction-type specific symbiosome membrane decorations exist and can be exploited to prevent formation of haustoria while maintaining beneficial arbuscules. Genome sequencing of *R. irregularis* gave access to predicted symbiotic effector inventories [33••,50••]. Their comparison with pathogen effector sets and further sequencing will soon allow delineation of the 'must have' equipment for symbiosis. Effector gene repertoires of filamentous pathogen genomes are subject to frequent changes to escape perception by the plant immune system and to adapt to new host environments. It will be interesting to see whether effector repertoires of different *R. irregularis* isolates vary as much as in some filamentous pathogens.

Acknowledgements

We apologise to those authors whose work was not emphasised. We are indebted to Uta Paszkowski for commenting on an earlier draft of this manuscript. The authors acknowledge funding from the Gatsby Charitable Foundation (GAT3273/GLD). SS also acknowledges funding by the Royal Society and the University of Cambridge institutional HEIF funds as well as motivational support by Dr. Féi Mão.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Remy W, Taylor TN, Hass H, Kerp H: **Four hundred-million-year-old vesicular arbuscular mycorrhizae**. *Proc Natl Acad Sci U S A* 1994, **91**:11841-11843.

2. Wang B, Qiu Y-L: **Phylogenetic distribution and evolution of mycorrhizas in land plants**. *Mycorrhiza* 2006, **16**:299-363.

3. Oldroyd GED, Murray JD, Poole PS, Downie JA: **The rules of engagement in the legume-rhizobial symbiosis**. *Annu Rev Genet* 2011, **45**:119-144.

4. • Parniske M: **Intracellular accommodation of microbes by plants: a common developmental program for symbiosis and disease?** *Curr Opin Plant Biol* 2000, **3**:320-328.

This pioneering review suggests common and contrasting principles in microbial accommodation in plants.

5. Djébali N, Jauneau A, Ameline-Torregrosa C, Chardon F, Jaulneau V, Mathé C, Bottin A, Cazaux M, Pilet-Nayel M-L, Baranger A *et al.*: **Partial resistance of *Medicago truncatula* to *Aphanomyces euteiches* is associated with protection of the root stele and is controlled by a major QTL rich in proteasome-related genes**. *Mol Plant Microbe Interact* 2009, **22**:1043-1055.

6. Oláh B, Brière C, Bécard G, Dénarié J, Gough C: **Nod factors and a diffusible factor from arbuscular mycorrhizal fungi stimulate lateral root formation in *Medicago truncatula* via the DMI1/DMI2 signalling pathway**. *Plant J* 2005, **44**:195-207.

7. Reusche M, Thole K, Janz D, Truskina J, Rindfleisch S, Drübert C, Polle A, Lipka V, Teichmann T: ***Verticillium* infection triggers VASCULAR-RELATED NAC DOMAIN7-dependent de novo xylem formation and enhances drought tolerance in Arabidopsis**. *Plant Cell Online* 2012, **24**:3823-3837.

8. Rey T, Schornack S: **Interactions of beneficial and detrimental root-colonizing filamentous microbes with plant hosts**. *Genome Biol* 2013, **14**:121.

9. Penmetsa RV, Uribe P, Anderson J, Lichtenzveig J, Gish J-C, Nam YW, Engstrom E, Xu K, Sckisel G, Pereira M *et al.*: **The *Medicago truncatula* ortholog of Arabidopsis EIN2, sickle, is a negative regulator of symbiotic and pathogenic microbial associations**. *Plant J* 2008, **55**:580-595.

10. Gonzalez-Rizzo S, Crespi M, Frugier F: **The *Medicago truncatula* CRE1 cytokinin receptor regulates lateral root development and early symbiotic interaction with *Sinorhizobium meliloti***. *Plant Cell* 2006, **18**:2680-2693.

11. Moreau S, Fromentin J, Vailleau F, Vernié T, Huguet S, Balzergue S, Frugier F, Gamas P, Jardinaud MF: **The symbiotic transcription factor MtEFD and cytokinins are positively acting in the *Medicago truncatula* and *Ralstonia solanacearum* pathogenic interaction**. *New Phytol* 2014, **201**:1343-1357.

12. •• Floss DS, Levy JG, Levesque-Tremblay V, Pumplin N, Harrison MJ: **DELLA proteins regulate arbuscule formation in arbuscular mycorrhizal symbiosis**. *Proc Natl Acad Sci U S A* 2013, **110**:E5025-E5034.
The authors demonstrate that GA signalling is crucial for the formation of intracellular accommodation structures by AM fungi in both dicots and monocots. In addition, DELLA activity in the vascular tissue and endodermis is sufficient to enable arbuscule formation in the inner cortex.

13. • Yu N, Luo D, Zhang X, Liu J, Wang W, Jin Y, Dong W, Liu J, Liu H, Yang W *et al.*: **A DELLA protein complex controls the arbuscular mycorrhizal symbiosis in plants**. *Cell Res* 2014, **24**:130-133.
This manuscript describes a possible link between GA signalling and symbiosis by reporting the possible presence of the DELLA protein SLR1 in complexes containing GRAS-type transcription factors DIP1 and RAM1, the latter of which previously has been implicated in symbiosis signalling.

14. Hou X, Lee LYC, Xia K, Yan Y, Yu H: **DELLAs modulate jasmonate signaling via competitive binding to JAZs**. *Dev Cell* 2010, **19**:884-894.

15. • Genre A, Chabaud M, Balzergue C, Puech-Pagès V, Novero M, Rey T, Fournier J, Rochange S, Bécard G, Bonfante P *et al.*: **Short-chain chitin oligomers from arbuscular mycorrhizal fungi trigger nuclear Ca^{2+} spiking in *Medicago truncatula* roots and their production is enhanced by strigolactone**. *New Phytol* 2013, **198**:190-202.
This manuscript reports short chain chitin oligomers (CO4/5) as inducers of calcium spiking in root organ cultures. Calcium spiking was induced in a symbiosis-pathway dependent manner, but independent of the receptor of lipochito-oligosaccharidic Nod factors.

16. Pietraszewska-Bogiel A, Lefebvre B, Koini MA, Klaus-Heisen D, Takken FL, Geurts R, Cullimore JV, Gadella TW: **Interaction of *Medicago truncatula* lysin motif receptor-like kinases, NFP and LYK3, produced in *Nicotiana benthamiana* induces defence-like responses**. *PLoS One* 2013, **8**:e65055.

17. Czaja LF, Hogekamp C, Lamm P, Maillet F, Martinez EA, Samain E, Dénarié J, Küster H, Hohnjec N: **Transcriptional responses toward diffusible signals from symbiotic microbes reveal MtNFP- and MtDMI3-dependent reprogramming of host gene expression by arbuscular mycorrhizal fungal lipochitooligosaccharides**. *Plant Physiol* 2012, **159**:1671-1685.

18. •• Rey T, Nars A, Bonhomme M, Bottin A, Huguet S, Balzergue S, Jardinaud MF, Bono JJ, Cullimore J, Dumas B *et al.*: **NFP, a LysM protein controlling Nod factor perception, also intervenes in *Medicago truncatula* resistance to pathogens**. *New Phytol* 2013, **198**:875-886.
The authors show that a receptor assumed to be exclusively involved in root nodule symbiosis also contributes to disease severity by the root-pathogenic oomycete *A. euteiches*.

19. Liang Y, Cao Y, Tanaka K, Thibivilliers S, Wan J, Choi J, Kang C Ho, Qiu J, Stacey G: **Nonlegumes respond to rhizobial Nod factors by suppressing the innate immune response**. *Science* 2013, **341**:1384-1387.

20. DeZwaan TM, Carroll AM, Valent B, Sweigard JA: ***Magnaporthe grisea* pth11p is a novel plasma membrane protein that mediates appressorium differentiation in response to inductive substrate cues**. *Plant Cell* 1999, **11**:2013-2030.

21. • Wang E, Schornack S, Marsh JF, Gobbato E, Schwessinger B, Eastmond P, Schultze M, Kamoun S, Oldroyd GED: **A common signaling process that promotes mycorrhizal and oomycete colonization of plants**. *Curr Biol* 2012, **22**:2242-2246.
This manuscript describes a common role for cutin monomers in penetration of *M. truncatula* root tissue by beneficial and detrimental filamentous microorganisms.

22. Gobbato E, Wang E, Higgins G, Bano SA, Henry C, Schultze M, Oldroyd GED: **RAM1 and RAM2 function and expression during arbuscular mycorrhizal symbiosis and *Aphanomyces euteiches* colonization**. *Plant Signal Behav* 2013 http://dx.doi.org/10.4161/psb.26049.

23. Esseling JJ, Lhuissier FG, Emons AM: **A nonsymbiotic root hair tip growth phenotype in NORK-mutated legumes: implications for nodulation factor-induced signaling and formation of a multifaceted root hair pocket for bacteria**. *Plant Cell* 2004, **16**:933-944.

24. Genre A, Ortu G, Bertoldo C, Martino E, Bonfante P: **Biotic and abiotic stimulation of root epidermal cells reveals common and specific responses to arbuscular mycorrhizal fungi**. *Plant Physiol* 2009, **149**:1424-1434.

25. Miller JB, Pratap A, Miyahara A, Zhou L, Bornemann S, Morris RJ, Oldroyd GED: **Calcium/calmodulin-dependent protein kinase is negatively and positively regulated by calcium, providing a mechanism for decoding calcium responses during symbiosis signaling**. *Plant Cell Online* 2013 http://dx.doi.org/10.1105/tpc.113.116921.

26. Ikeda S, Okubo T, Takeda N, Banba M, Sasaki K, Imaizumi-Anraku H, Fujihara S, Ohwaki Y, Ohshima K, Fukuta Y *et al.*: **The genotype of the calcium/calmodulin-dependent protein kinase gene (CCaMK) determines bacterial community diversity in rice roots under paddy and upland field conditions**. *Appl Environ Microbiol* 2011, **77**:4399-4405.

27. • Shi B, Ni L, Zhang A, Cao J, Zhang H, Qin T, Tan M, Zhang J, Jiang M: **OsDMI3 is a novel component of abscisic acid signaling in the induction of antioxidant defense in leaves of rice**. *Mol Plant* 2012, **5**:1359-1374.
Here, DMI3, a classical common symbiosis pathway component is reported to have additional functions in ABA signalling and reactive oxygen species homeostasis in leaves.

28. Yang C, Li A, Zhao Y, Zhang Z, Zhu Y, Tan X, Geng S, Guo H, Zhang X, Kang Z *et al.*: **Overexpression of a wheat CCaMK gene reduces ABA sensitivity of *Arabidopsis thaliana* during seed germination and seedling growth**. *Plant Mol Biol Rep* 2010, **29**:681-692.

29. Delaux PM, Séjalon-Delmas N, Bécard G, Ané J-M: **Evolution of the plant–microbe symbiotic 'toolkit'**. *Trends Plant Sci* 2013, **6**:298-304.

30. Büschges R, Hollricher K, Panstruga R, Simons G, Wolter M, Frijters A, van Daelen R, van der Lee T, Diergaarde P, Groenendijk J *et al.*: **The barley Mlo gene: a novel control element of plant pathogen resistance**. *Cell* 1997, **88**:695-705.

31. Chen Z, Noir S, Kwaaitaal M, Hartmann HA, Wu M-J, Mudgil Y, Sukumar P, Muday G, Panstruga R, Jones AM: **Two seven-transmembrane domain MILDEW RESISTANCE LOCUS O proteins cofunction in Arabidopsis root thigmomorphogenesis**. *Plant Cell* 2009, **21**:1972-1991.

32. Kessler SA, Shimosato-Asano H, Keinath NF, Wuest SE, Ingram G, Panstruga R, Grossniklaus U: **Conserved molecular components for pollen tube reception and fungal invasion**. *Science* 2010, **330**:968-971.

33. •• Lin K, Limpens E, Zhang Z, Ivanov S, Saunders DGO, Mu D, Pang E, Cao H, Cha H, Lin T *et al.*: **Single nucleus genome sequencing reveals high similarity among nuclei of an endomycorrhizal fungus**. *PLoS Genet* 2014, **10**:e1004078.
This manuscript demystifies the long lasting hypothesis that nuclei of a single AM fungus isolate are markedly different in their genetic setup. The authors also report CRN proteins as potential effector candidates of *R. irregularis*. Overall the repertoire of effectors seems to be small compared to filamentous pathogens.

34. Schornack S, Damme M van, Bozkurt TO, Cano LM, Smoker M, Thines M, Gaulin E, Kamoun S, Huitema E: **Ancient class of translocated oomycete effectors targets the host nucleus**. *Proc Natl Acad Sci U S A* 2010, **107**:17421-17426.

35. Stam R, Howden AJM, Delgado-Cerezo M, Amaro MM, Motion TM, Pham GB, Huitema EJ: **Characterization of cell death inducing *Phytophthora capsici* CRN effectors suggests diverse activities in the host nucleus**. *Front Plant Sci* 2013, **4**:387.

36. McLellan H, Boevink PC, Armstrong MR, Pritchard L, Gomez S, Morales J, Whisson SC, Beynon JL, Birch PRJ: **An RxLR effector from *Phytophthora infestans* prevents re-localisation of two plant NAC transcription factors from the endoplasmic reticulum to the nucleus**. *PLoS Pathog* 2013, **9**:e1003670.

37. Caillaud M-C, Asai S, Rallapalli G, Piquerez S, Fabro G, Jones JDG: **A downy mildew effector attenuates salicylic acid–triggered immunity in Arabidopsis by interacting with the host mediator complex**. *PLoS Biol* 2013, **11**:e1001732.

38. Kloppholz S, Kuhn H, Requena N: **A secreted fungal effector of *Glomus intraradices* promotes symbiotic biotrophy**. *Curr Biol* 2011, **21**:1204-1209.

39. Kay S, Hahn S, Marois E, Wieduwild R, Bonas U: **Detailed analysis of the DNA recognition motifs of the *Xanthomonas* type III effectors AvrBs3 and AvrBs3Δrep16**. *Plant J* 2009, **59**:859-871.

40. Block A, Guo M, Li G, Elowsky C, Clemente TE, Alfano JR: **The *Pseudomonas syringae* type III effector HopG1 targets mitochondria, alters plant development and suppresses plant innate immunity**. *Cell Microbiol* 2010, **12**:318-330.

41. Sugio A, MacLean AM, Kingdom HN, Grieve VM, Manimekalai R, Hogenhout SA: **Diverse targets of phytoplasma effectors: from plant development to defense against insects**. *Annu Rev Phytopathol* 2011, **49**:175-195.

42. •• MacLean AM, Sugio A, Makarova OV, Findlay KC, Grieve VM, Toth R, Nicolaisen M, Hogenhout SA: **Phytoplasma effector SAP54 induces indeterminate leaf-like flower development in Arabidopsis plants**. *Plant Physiol* 2011, **157**:831-841.
This is one of the publications from the Hogenhout lab which demonstrate the exciting interference of Phytoplasma effectors with plant development processes resulting in the production of leaf-like flowers that are similar to those produced by Phytoplasma-infected plants.

43. Sugio A, Kingdom HN, MacLean AM, Grieve VM, Hogenhout SA: **Phytoplasma protein effector SAP11 enhances insect vector reproduction by manipulating plant development and defense hormone biosynthesis**. *Proc Natl Acad Sci U S A* 2011, **108**:1254-1263.

44. Hoshi A, Oshima K, Kakizawa S, Ishii Y, Ozeki J, Hashimoto M, Komatsu K, Kagiwada S, Yamaji Y, Namba S: **A unique virulence factor for proliferation and dwarfism in plants identified from a phytopathogenic bacterium**. *Proc Natl Acad Sci U S A* 2009, **106**:6416-6421.

45. •• Okazaki S, Kaneko T, Sato S, Saeki K: **Hijacking of leguminous nodulation signaling by the rhizobial type III secretion system**. *Proc Natl Acad Sci U S A* 2013, **110**:17131-17136.
The authors report that the root nodule forming bacterium *B. elkanii* has likely adopted type III delivered effectors to activate host symbiosis signalling. Nod-factor deficient *B. elkanii* still induced nodules unless their type III secretion systems were mutated. The absence of root hair curling and infection threads suggests that *B. elkanii* utilises other forms of colonisation.

46. Grunewald W, Noorden G van, Isterdael GV, Beeckman T, Gheysen G, Mathesius U: **Manipulation of auxin transport in plant roots during Rhizobium symbiosis and nematode parasitism**. *Plant Cell Online* 2009, **21**:2553-2562.

47. Lee C, Chronis D, Kenning C, Peret B, Hewezi T, Davis EL, Baum TJ, Hussey R, Bennett M, Mitchum MG: **The novel cyst nematode effector protein 19C07 interacts with the Arabidopsis auxin influx transporter LAX3 to control feeding site development**. *Plant Physiol* 2011, **155**:866-880.

48. •• Evangelisti E, Govetto B, Minet-Kebdani N, Kuhn M-L, Attard A, Ponchet M, Panabières F, Gourgues M: **The *Phytophthora parasitica* RXLR effector Penetration-Specific Effector 1 favours *Arabidopsis thaliana* infection by interfering with auxin physiology**. *New Phytol* 2013, **199**:476-489.
This manuscript describes a filamentous pathogen effector which alters root morphology by interfering with auxin efflux carrier distribution patterns.

49. • Tanaka S, Brefort T, Neidig N, Djamei A, Kahnt J, Vermerris W, Koenig S, Feussner K, Feussner I, Kahmann R: **A secreted *Ustilago maydis* effector promotes virulence by targeting anthocyanin biosynthesis in maize**. *Elife* 2014, **3**:e01355.
The authors report a role for the effector Tin2 in rerouting metabolic pathways to reduce lignin biosynthesis thereby presumably allowing better access of *Ustilago* to vascular tissues.

50. •• Tisserant E, Malbreil M, Kuo A, Kohler A, Symeonidi A, Balestrini R, Charron P, Duensing N, Frey NF dit, Gianinazzi-Pearson V *et al.*: **Genome of an arbuscular mycorrhizal fungus provides insight into the oldest plant symbiosis**. *Proc Natl Acad Sci U S A* 2013, **110**:20117-20122.
Sequencing of *R. irregularis* did not give evidence for cell wall degrading enzymes. It remains to be elucidated what mechanisms arbuscular mycorrhizal fungi use to penetrate root cortex cell walls. No orthologues of bacterial genes coding for enzymes involved in symbiotic lipochito-oligosaccharide factors have been identified, which contradicts the long-standing assumption that rhizobia acquired them from AM fungi.

51. Pumplin N, Zhang X, Noar RD, Harrison MJ: **Polar localization of a symbiosis-specific phosphate transporter is mediated by a transient reorientation of secretion**. *Proc Natl Acad Sci U S A* 2012, **109**:E665-E672.

52. Kobae Y, Hata S: **Dynamics of periarbuscular membranes visualized with a fluorescent phosphate transporter in arbuscular mycorrhizal roots of rice**. *Plant Cell Physiol* 2010, **51**:341-353.

53. Lu Y-J, Schornack S, Spallek T, Geldner N, Chory J, Schellmann S, Schumacher K, Kamoun S, Robatzek S: **Patterns of plant subcellular responses to successful oomycete infections reveal differences in host cell reprogramming and endocytic trafficking**. *Cell Microbiol* 2012, **14**:682-697.

54. Haney CH, Long SR: **Plant flotillins are required for infection by nitrogen-fixing bacteria**. *Proc Natl Acad Sci U S A* 2010, **107**:478-483.

55. Pumplin N, Harrison MJ: **Live-cell imaging reveals periarbuscular membrane domains and organelle location in *Medicago truncatula* roots during arbuscular mycorrhizal symbiosis**. *Plant Physiol* 2009, **151**:809-819.

56. Ivanov S, Fedorova E, Bisseling T: **Intracellular plant microbe associations: secretory pathways and the formation of perimicrobial compartments**. *Curr Opin Plant Biol* 2010, **13**:372-377.

57. Amiour N, Recorbet G, Robert F, Gianinazzi S, Dumas-Gaudot E: **Mutations in DMI3 and SUNN modify the appressorium-responsive root proteome in arbuscular mycorrhiza**. *Mol Plant Microbe Interact* 2006, **19**:988-997.

58. Nishimura R, Hayashi M, Wu GJ, Kouchi H, Imaizumi-Anraku H, Murakami Y, Kawasaki S, Akao S, Ohmori M, Nagasawa M *et al.*:

HAR1 mediates systemic regulation of symbiotic organ development. *Nature* 2002, **420**:426-429.

59. Schaarschmidt S, Gresshoff PM, Hause B: **Analyzing the soybean transcriptome during autoregulation of mycorrhization identifies the transcription factors GmNF-YA1a/b as positive regulators of arbuscular mycorrhization**. *Genome Biol* 2013, **14**:R62.

60. Ben C, Toueni M, Montanari S, Tardin MC, Fervel M, Negahi A, Saint-Pierre L, Mathieu G, Gras MC, Noël D *et al.*: **Natural diversity in the model legume *Medicago truncatula* allows identifying distinct genetic mechanisms conferring partial resistance to Verticillium wilt**. *J Exp Bot* 2013, **64**:317-332.

61. Ariel F, Brault-Hernandez M, Laffont C, Huault E, Brault M, Plet J, Moison M, Blanchet S, Ichanté JL, Chabaud M *et al.*: **Two direct targets of cytokinin signaling regulate symbiotic nodulation in *Medicago truncatula***. *Plant Cell* 2012, **24**:3838-3852.

62. Sun J, Cardoza V, Mitchell DM, Bright L, Oldroyd G, Harris JM: **Crosstalk between jasmonic acid, ethylene and Nod factor signaling allows integration of diverse inputs for regulation of nodulation**. *Plant J* 2006, **46**:961-970.

63. Shi B, Ni L, Liu Y, Zhang A, Tan M, Jiang M: **OsDMI3-mediated activation of OsMPK1 regulates the activities of antioxidant enzymes in abscisic acid signalling in rice**. *Plant Cell Environ* 2014, **37**:341-352.

64. Torres-Vera R, García JM, Pozo MJ, López-Ráez JA: **Do strigolactones contribute to plant defence?** *Mol Plant Pathol* 2014, **15**:211-216.

65. Maillet F, Poinsot V, André O, Puech-Pagès V, Haouy A, Gueunier M, Cromer L, Giraudet D, Formey D, Niebel A *et al.*: **Fungal lipochitooligosaccharide symbiotic signals in arbuscular mycorrhiza**. *Nature* 2011, **469**:58-63.

66. Kiirika LM, Bergmann HF, Schikowsky C, Wimmer D, Korte J, Schmitz U, Niehaus K, Colditz F: **Silencing of the Rac1 GTPase MtROP9 in *Medicago truncatula* stimulates early mycorrhizal and oomycete root colonizations but negatively affects rhizobial infection**. *Plant Physiol* 2012, **159**:501-516.

67. Delaux PM, Bécard G, Combier JP: **NSP1 is a component of the Myc signaling pathway**. *New Phytol* 2013, **199**:59-65.

68. Liu W, Kohlen W, Lillo A, Op den Camp R, Ivanov S, Hartog M, Limpens E, Jamil M, Smaczniak C, Kaufmann K *et al.*: **Strigolactone biosynthesis in *Medicago truncatula* and rice requires the symbiotic GRAS-type transcription factors NSP1 and NSP2**. *Plant Cell* 2011, **23**:3853-3865.

69. Ooki Y, Banba M, Yano K, Maruya J, Sato S, Tabata S, Saeki K, Hayashi M, Kawaguchi M, Izui K *et al.*: **Characterization of the *Lotus japonicus* symbiotic mutant lot1 that shows a reduced nodule number and distorted trichomes**. *Plant Physiol* 2005, **137**:1261-1271.

70. Yoshida S, Kameoka H, Tempo M, Akiyama K, Umehara M, Yamaguchi S, Hayashi H, Kyozuka J, Shirasu K: **The D3 F-box protein is a key component in host strigolactone responses essential for arbuscular mycorrhizal symbiosis**. *New Phytol* 2012, **196**:1208-1216.

71. Maekawa-Yoshikawa M, Müller J, Takeda N, Maekawa T, Sato S, Tabata S, Perry J, Wang TL, Groth M, Brachmann A *et al.*: **The temperature-sensitive brush mutant of the legume *Lotus japonicus* reveals a link between root development and nodule infection by rhizobia**. *Plant Physiol* 2009, **149**:1785-1796.

72. Shimomura K, Nomura M, Tajima S, Kouchi H: **LjnsRING, a novel RING finger protein, is required for symbiotic interactions between *Mesorhizobium loti* and *Lotus japonicus***. *Plant Cell Physiol.* 2006, **47**:1572-1581.

73. Schnabel EL, Kassaw TK, Smith LS, Marsh JF, Oldroyd GE, Long SR, Frugoli JA: **The root determined nodulation1 gene regulates nodule number in roots of *Medicago truncatula* and defines a highly conserved, uncharacterized plant gene family**. *Plant Physiol* 2011, **157**:328-340.

74. Miyazawa H, Oka-Kira E, Sato N, Takahashi H, Wu GJ, Sato S, Hayashi M, Betsuyaku S, Nakazono M, Tabata S *et al.*: **The receptor-like kinase KLAVIER mediates systemic regulation of nodulation and non-symbiotic shoot development in *Lotus japonicus***. *Development* 2010, **137**:4317-4325.

75. Imin N, Mohd-Radzman NA, Ogilvie HA, Djordjevic MA: **The peptide-encoding CEP1 gene modulates lateral root and nodule numbers in *Medicago truncatula***. *J Exp Bot* 2013, **64**:5395-5409.

76. Hopkins J, Pierre O, Kazmierczak T, Gruber V, Frugier F, Clement M, Frendo P, Herouart D, Boncompagni E: **MtZR1, a PRAF protein, is involved in the development of roots and symbiotic root nodules in *Medicago truncatula***. *Plant Cell Environ* 2013, **37**:658-669.

77. Bagchi R, Salehin M, Adeyemo OS, Salazar C, Shulaev V, Sherrier DJ, Dickstein R: **Functional assessment of the *Medicago truncatula* NIP/LATD protein demonstrates that it is a high-affinity nitrate transporter**. *Plant Physiol* 2012, **160**:906-916.

78. Bright LJ, Liang Y, Mitchell DM, Harris JM: **The *LATD* gene of *Medicago truncatula* is required for both nodule and root development**. *Mol Plant Microbe Interact* 2005, **18**:521-532.

79. Liang Y, Mitchell DM, Harris JM: **Abscisic acid rescues the root meristem defects of the *Medicago truncatula latd* mutant**. *Dev Biol* 2007, **304**:297-307.

80. Miyahara A, Richens J, Starker C, Morieri G, Smith L, Long S, Downie JA, Oldroyd GE: **Conservation in function of a SCAR/WAVE component during infection thread and root hair growth in *Medicago truncatula***. *Mol Plant Microbe Interact* 2010, **23**:1553-1562.

81. Yokota K, Fukai E, Madsen LH, Jurkiewicz A, Rueda P, Radutoiu S, Held M, Hossain MS, Szczyglowski K, Morieri G *et al.*: **Rearrangement of actin cytoskeleton mediates invasion of *Lotus japonicus* roots by *Mesorhizobium loti***. *Plant Cell* 2009, **21**:267-284.

82. Tansengco ML, Imaizumi-Anraku H, Yoshikawa M, Takagi S, Kawaguchi M, Hayashi M, Murooka Y: **Pollen development and tube growth are affected in the symbiotic mutant of *Lotus japonicus*, crinkle**. *Plant Cell Physiol* 2004, **45**:511-520.

83. Tansengco ML, Hayashi M, Kawaguchi M, Imaizumi-Anraku H, Murooka Y: **Crinkle, a novel symbiotic mutant that affects the infection thread growth and alters the root hair, trichome, and seed development in *Lotus japonicus***. *Plant Physiol* 2003, **131**:1054-1063.

84. Teillet A, Garcia J, de Billy F, Gherardi M, Huguet T, Barker DG, de Carvalho-Niebel F, Journet EP: **api, A novel *Medicago truncatula* symbiotic mutant impaired in nodule primordium invasion**. *Mol Plant Microbe Interact* 2008, **21**:535-546.

85. Yano K, Tansengco ML, Hio T, Higashi K, Murooka Y, Imaizumi-Anraku H, Kawaguchi M, Hayashi M: **New nodulation mutants responsible for infection thread development in *Lotus japonicus***. *Mol Plant Microbe Interact* 2006, **19**:801-810.

86. Couzigou J-M, Zhukov V, Mondy S, Abu el Heba G, Cosson V, Ellis THN, Ambrose M, Wen J, Tadege M, Tikhonovich I *et al.*: **Nodule Root and cochleata maintain nodule development and are legume orthologs of Arabidopsis blade-on-petiole genes**. *Plant Cell* 2012, **24**:4498-4510.