New Phytologist

Review

Tansley insight

The impact of domestication and crop improvement on arbuscular mycorrhizal symbiosis in cereals: insights from genetics and genomics

Author for correspondence:
Uta Paszkowski
Tel: +44 1223 748981
Email: up220@cam.ac.uk

Received: *1 November 2017*
Accepted: *19 February 2018*

Ruairidh J. H. Sawers[1], M. Rosario Ramírez-Flores[2], Víctor Olalde-Portugal[2] and Uta Paszkowski[3]

[1]Laboratorio Nacional de Genómica para la Biodiversidad/Unidad de Genómica Avanzada, Centro de Investigación y de Estudios Avanzados, Instituto Politécnico Nacional (CINVESTAV-IPN), Irapuato, C.P. 36821 Guanajuato, México; [2]Departamento de Biotecnología y Bioquímica, Centro de Investigación y de Estudios Avanzados (CINVESTAV-IPN), Irapuato, C.P. 36821 Guanajuato, México; [3]Department of Plant Sciences, University Cambridge, Cambridge, CB2 3EA, UK

Contents

New Phytologist (2018)
doi: 10.1111/nph.15152

Key words: arbuscular mycorrhizal (AM) symbiosis, cereal, crop, phytohormones, plant breeding.

Summary

Cereals (rice, maize, wheat, sorghum and the millets) provide over 50% of the world's caloric intake, a value that rises to > 80% in developing countries. Since domestication, cereals have been under artificial selection, largely directed towards higher yield. Throughout this process, cereals have maintained their capacity to interact with arbuscular mycorrhizal (AM) fungi, beneficial symbionts that associate with the roots of most terrestrial plants. It has been hypothesized that the shift from the wild to cultivation, and above all the last *c*. 50 years of intensive breeding for high-input farming systems, has reduced the capacity of the major cereal crops to gain full benefit from AM interactions. Recent studies have shed further light on the molecular basis of establishment and functioning of AM symbiosis in cereals, providing insight into where the breeding process might have had an impact. Classic phytohormones, targets of artificial selection during the generation of Green Revolution semi-dwarf varieties, have emerged as important regulators of AM symbiosis. Although there is still much to be learnt about the mechanistic basis of variation in symbiotic outcome, these advances are providing an insight into the role of arbuscular mycorrhiza in agronomic systems.

I. Introduction

Concern regarding the sustainability of current agricultural practices and the nutritional quality of the food we produce has for some time promoted interest in the potential benefit of arbuscular mycorrhizal (AM) symbiosis in farming systems. While AM symbiosis dates back over 450 million years, agriculture is a relatively recent development. Our major crops were domesticated

within the last *c.* 10 000 years, and modern varieties are the product of the last *c.* 50 years of intensive breeding for high input farming systems (Fig. 1). It has been hypothesized that the dramatic shift from the wild to cultivation has negatively affected the capacity of crop plants to benefit from interactions with AM fungi (discussed in Sawers *et al.*, 2008; Schmidt *et al.*, 2016). Environmental differences between natural and cultivated systems (e.g. nutrient input; resource homogeneity; fungicide, pesticide and herbicide application; tillage; crop rotation and fallows) affect the rhizosphere microbial community (Pérez-Jaramillo *et al.*, 2016). The question remains, however, as to what extent artificial selection acting on the plant host genome has directly, or indirectly, affected their interactions with AM fungi or other soil microbes. Have modern crop varieties lost the 'responsiveness' genes required to benefit fully from mutualistic symbioses? (Sawers *et al.*, 2008). Characterization of the rhizosphere microbiome has revealed a significant effect of the plant genotype on the microbial community (Peiffer *et al.*, 2013). Furthermore, common-garden studies have found differences in the composition of the rhizosphere microbiome between cereals and their wild relatives, although, to date, these studies have not had the resolution to specifically quantify AM fungi (Bulgarelli *et al.*, 2015; Szoboszlay *et al.*, 2015; Shenton *et al.*, 2016). While there may be heritable differences in the diversity and extent of AM colonization between crops and their wild relatives, such differences may not necessarily be correlated with differences in plant response (Lehmann *et al.*, 2012; Sawers *et al.*, 2017). Here, we discuss how advances in the understanding of these molecular mechanisms can generate hypotheses as to the impact of domestication and breeding on AM symbiosis. We focus on the role of plant hormones as both regulators of AM symbiosis and as targets of selection in plant breeding. We also discuss the possible mechanistic basis of differences in cereal response to AM symbiosis.

II. Recruitment of plant metabolites and hormones as signals in AM symbiosis

The establishment and maintenance of AM symbiosis requires an exchange of multiple chemical signals between fungus and plant. The current catalogue of signalling molecules includes the butenolides strigolactone (Akiyama *et al.*, 2005; Besserer *et al.*, 2006) and karrikin, *N*-acetylglucosamine (GlcNAc)-based chitinaceous molecules (Maillet *et al.*, 2011; Genre *et al.*, 2013; Nadal *et al.*, 2017), and the phytohormones auxin and gibberellin (Floss *et al.*, 2013; Etemadi *et al.*, 2014; Yu *et al.*, 2014; Takeda *et al.*, 2015). Mutation in either the synthesis or perception of any one of these signals is sufficient to disrupt AM symbiosis. Interestingly, many AM symbiotic signals also play a role in plant growth and development: strigolactones regulate plant architecture; karrikins are involved in seed dormancy, photomorphogenesis and leaf development; GlcNAcylation modifies protein activity, and is essential throughout development; auxin and gibberelin play multiple roles throughout the life cycle of the plant. It has been proposed that AM signalling and regulatory molecules have been co-opted from ancestral functions in plant development, requiring co-evolution between fungal and plant partners (Bonfante & Genre, 2015). These central regulators of plant development have also been targeted in more recent times, during the processes of crop domestication and improvement. How might such selection have indirectly affected AM symbiosis?

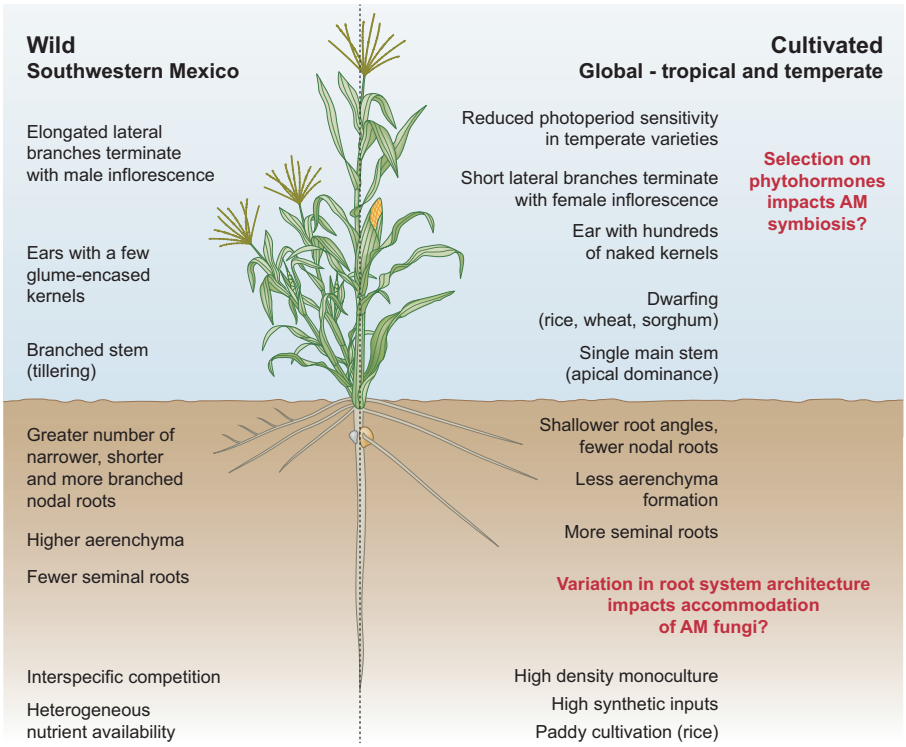


Fig. 1 The effect of domestication and breeding on cereal morphology. Morphological differences between modern cereal varieties and their wild relatives, illustrated through the example of wild teosinte (*Zea mays* ssp. *parviglumis*; left) and cultivated maize (*Zea mays* ssp. *mays*; right). Characteristic differences in above-ground plant morphology are given in the upper portion of the figure. Below-ground differences are shown in the lower portion – although the root system architecture is more variable, and wild and cultivated varieties are less strongly differentiated (Burton *et al.*, 2013; Schmidt *et al.*, 2016). Additional notes are given on the distribution and differences in environment, and differences characteristic of other cereals. AM, arbuscular mycorrhiza.

III. Phytohormones are regulators of AM symbiosis and targets of plant breeding

The artificial selection of cereal crops has resulted in a loss of seed dormancy, greater apical dominance, changes to photoperiod sensitivity and flowering time, increased seed number and size, and loss of shattering. Breeding efforts during the 'Green Revolution' have seen the widespread adoption of semi-dwarf varieties of wheat, rice and sorghum, generated by targeting plant hormones (Hedden, 2003). Selection on the morphology of the aboveground portion of the plant can affect root system architecture (Burton *et al.*, 2013; Gaudin *et al.*, 2014), with possible implications for AM colonization (Schmidt *et al.*, 2016). At the molecular level, pleiotropic effects related to selection on hormone signalling can be predicted to include an impact on AM symbiosis. In semi-dwarf varieties of wheat and rice, gibberelic acid (GA) signalling is attenuated, by reduced sensitivity or synthesis (Box 1; Hedden, 2003). In maize, variation in GA signalling is related to differences in photoperiod sensitivity and flowering time between tropical and temperate maize (e.g. Romero Navarro *et al.*, 2017). Considerable insight has been obtained since the first report of GA as a negative regulator of AM symbiosis (El Ghachtouli *et al.*, 1996). Exogenous application of GA or a disruption of genes encoding the GA-sensitive DELLA repressor proteins results in a reduction in AM colonization (Floss *et al.*, 2013; Yu *et al.*, 2014; Takeda *et al.*, 2015). In *Medicago truncatula*, the effect of exogenous GA can be suppressed by the introduction of degradation-resistant mutant versions of the DELLA protein (Floss *et al.*, 2013). Analogous degradation-resistant DELLA proteins are produced by the dominant semi-dwarfing alleles present in modern wheat varieties (Box 1). To date, the effect of dwarfing alleles on AM colonization has not been characterized. Auxin indole-acetic acid (IAA) has been shown to promote AM colonization (Etemadi *et al.*, 2014). Auxin signalling has been a target of selection during cereal improvement, notably in relation to floral morphology. Again, it is not known how differences in auxin signalling between cereal crops and their wild relatives affects AM colonization.

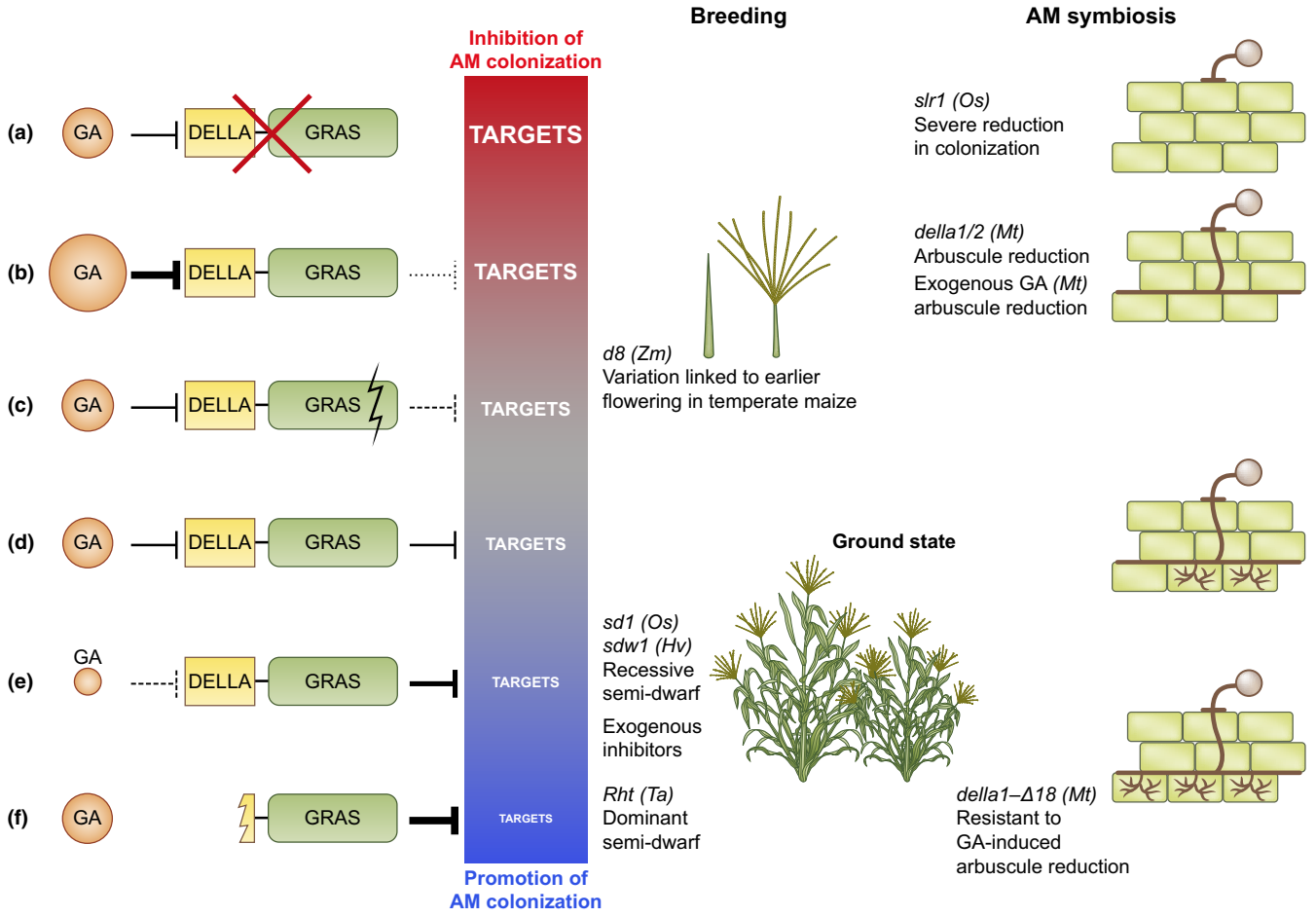
IV. Variations in host response to AM symbiosis

It is hard to predict the impact of artificial selection on the outcome of AM symbiosis (i.e. the net benefit to each partner), and it will be informative to test empirically the effect of mutation or allelic substitution at candidate loci. For example, while attenuated GA signalling in semi-dwarf crop varieties might favour increased AM colonization, this may, or may not, be to the benefit of the plant, depending on the environmental conditions. The mechanistic and genetic basis of variation in plant response to AM colonization remains poorly characterized. The quantification of root-internal fungal structures is often used as an indication of the fungal contribution to host nutrition and benefit to the plant host. When compared among diverse varieties, however, the abundance of arbuscules is a poor predictor of plant response (e.g. Sawers *et al.*, 2017). When phosphorus is limiting, plant AM response is well correlated with phosphate uptake (Jakobsen *et al.*, 2001; Sawers *et al.*, 2017), focusing attention on the plant-encoded PHT1 proteins that take up phosphate from the peri-arbuscular space into the host cells. Complete *PHT1* gene families have now been characterized from all major cereal crops (Box 2), opening the door to the study of functional diversity. To date, however, variation in the *PHT1* family has not been linked to differences in plant response, either among modern breeding lines or between wild and domesticated varieties. In a study aimed at quantifying mycorrhizal phosphate uptake using radio-labelling, a single teosinte accession in the study performed comparably to a panel of six maize inbred lines (Svane, 2013). Under a given set of conditions, the extent of root-external hyphae may be more important than the level of root-internal colonization in driving variation in symbiotic outcome (Jakobsen *et al.*, 2001). The balance between root-internal and root-external fungal development can differ depending on the host genotype, indicating that involvement of plant genetic factors, although this mechanism has not been characterized (Sawers *et al.*, 2017). The signalling molecules and plant hormones discussed above in the context of pre-symbiotic signalling and root-internal fungal development might also act to regulate the growth of the root-external mycelium. It may be significant that in the absence of arbuscule formation in *Medicago truncatula della1/della2* mutants, root-internal hyphae were observed to hyper-proliferate (Floss *et al.*, 2013). In conjunction with this, carbohydrates and lipids delivered to the fungus as a carbon source have the potential to act as developmental regulators. A further intriguing possibility is that plant encoded small RNAs move from host to fungus, regulating fungal gene expression and development (e.g. Helber *et al.*, 2011).

V. Outlook

The availability of complete genome sequences for a number of major cereal crops has allowed the identification of the molecular machinery required for AM symbiosis. Although many of these genes were first characterized in *Medicago* or *Lotus*, significant new components have been isolated directly through forward genetic approaches in cereal species (e.g. Gutjahr *et al.*, 2015; Nadal *et al.*, 2017), reflecting differences in gene copy number, and illustrating the importance of using multiple 'models' in the study of complex biological processes. With a greater understanding of the mechanisms underlying the regulation of AM symbiosis, it is becoming possible to formulate specific hypotheses which address long standing questions regarding the effect of plant breeding on AM symbioses, and their potential application in agricultural systems. To draw robust conclusions about the differences between domesticated plants and their wild relatives, it will be important to better sample diversity, using genomic information to take population structure into account. Ideally, plant response will be evaluated in mature field-grown plants, assessing a broad range of traits, including yield components and grain quality, in conjunction with a characterization of the AM community and colonization. Implementing field trials using crop wild-relatives poses logistic problems. In addition, comparisons between wild relatives and domesticated varieties are complicated by their range of morphological and phenological differences. The development of crop wild-relative introgression stocks (modern varieties carrying a small, known component of a wild-relative genome) will greatly

Box 1 Gibberellic acid is both a regulator of arbuscular mycorrhizal (AM) symbiosis and a target of plant breeding



Box 1 Figure Gibberellic acid (GA) promotes the degradation of DELLA domain repressor proteins, releasing the activity of downstream targets – targets that, broadly, promote elongation growth, but inhibit arbuscular mycorrhizal (AM) colonization. Artificial selection and experimental manipulation have acted on the GA-DELLA module to either relax or strengthen the level of repression acting on the downstream targets (indicated by colour bar, font size and weight of line indicating repression: blue, high repression, low target activity; red, low repression, high target activity; large font, high activity; heavy line weight, high repression). (a) Null mutations in DELLA encoding genes. (b) Increased synthesis/exogenous application of GA. (c) Loss of GRAS domain function. (d) Ground state. (e) Reduced synthesis of GA. (f) Loss of DELLA domain function. Further details and citations given in the text.

The phytohormone gibberellic acid (GA) acts to promote elongation growth and flowering, but to inhibit AM symbiosis. GA acts through a 'release-of-repression' mechanism, promoting the degradation of DELLA domain repressor proteins, and thereby freeing downstream targets for activation (see Van De Velde *et al.*, 2017 for a more detailed discussion). DELLA target repression requires the C terminal GRAS domain, and the action of DELLA interacting proteins. GA-mediated DELLA turnover requires the N-terminal DELLA and TVHYNP motifs. Diploid cereal genomes typically contain a single DELLA encoding gene (in rice, *SLR1;* Yu *et al.*, 2014; in maize, the paralogous gene pair *Dwarf8* and *Dwarf9* are retained following an ancient duplication; in hexaploid bread wheat three paralogous *Rht* genes are present across the A, B and D genomes; Van De Velde *et al.*, 2017). By contrast, three DELLLA encoding genes are present in *Medicago*, and five in *Arabidopsis*. Grass genomes do encode an additional class of DELLA-related proteins that are not found in model dicotyledonous plants, potentially allowing for more subtle control of GA signalling (Van De Velde *et al.*, 2017).

Selection on plant architecture and photoperiod sensitivity in cereals has targeted the GA-DELLA module, to either relax or strengthen the level of repression acting on the downstream targets. The wheat dominant semi-dwarfing alleles *Rht-B1b* and *Rht-D1b* encode degradation-resistant DELLA-proteins, resulting in a constitutive repression of plant growth (Hedden, 2003). Dwarf rice varieties carry a mutation in the GA20Ox enzyme, resulting in reduced GA synthesis (Hedden, 2003). In maize breeding, there has been less selection for dwarf varieties as robust hybrid maize plants can well support high grain weight in ears borne low-down on the plant, in contrast to the panicles of other cereals. Variation in the maize DELLA encoding gene *dwarf8* (*d8*), however, is related to variations in photoperiod sensitivity and flowering time that were significant in the spread of maize from the tropics to temperate regions (e.g. Romero Navarro *et al.*, 2017). GA also plays a key role in the regulation of AM symbiosis. In the model plant *Medicago truncatula*, a mutation of two of the three DELLA encoding genes present in the genome results in a strong reduction in arbuscule formation. In the rice mutant *slender rice1,* a loss-of-function of the single rice DELLA encoding gene, the phenotype is more marked, and all root-internal fungal structures are reduced (Yu *et al.*, 2014).

Box 2 Arbuscular mycorrhizal (AM) associated PHT1 genes have been identified in the major cereal crops

The plant PHT1 proteins are proton:phosphate symporters belonging to the major facilitator superfamily. Characterization of the *PHT1* rice family identified the divergent gene *OsPT11* (hereafter *PT* will be used to abbreviate the longer *PHT1*) to be specifically expressed in AM plants (Paszkowski *et al.*, 2002). Functional characterization of *OsPT11*, and the orthologous gene *MtPT4* of *Medicago truncatula*, has indicated that the encoded protein is localized to the peri-arbuscular space, providing the primary route for mycorrhizal phosphate into the host cells (Javot *et al.*, 2007; Yang *et al.*, 2012). Intriguingly, mutation of either *OsPT11* or *MtPT4* results in a drastic reduction in AM colonization, suggesting that plant phosphorus uptake represents a point of regulation of the symbiosis (Javot *et al.*, 2007; Yang *et al.*, 2012). The availability of whole genome sequence data has revealed other cereals which carry single copy orthologs of *OsPT11* (Box 2 Table). In common with rice, the sorghum gene *SbPT11* is specifically expressed in the roots of AM colonized plants. In maize and millet, however, the genes *ZmPt6* and *SiPT9*, respectively, although greatly induced by AM colonization, are also significantly expressed in noncolonized plants when phosphorus is limiting (Nagy *et al.*, 2006; Ceasar *et al.*, 2014; Liu *et al.*, 2016a; Sawers *et al.*, 2017). Mutation of *ZmPt6* results in reduced productivity in field-grown plants, although colonization is still observed, in contrast to the absence of colonization in loss-of-function mutants of either *OsPT11* or *MtPT4* (Willmann *et al.*, 2013). Cereals possess a number of additional mycorrhiza-associated PT genes which are not found in model dicotyledonous plants (dicots). A group defined by the rice gene *OsPT13* is represented by two genes in sorghum and millet, and five genes in maize. The functional characterization of *OsPT13* has shown that the gene, although expressed at relatively low levels, is required for normal symbiotic development, although not for the uptake of mycorrhizal phosphate *per se* (Yang *et al.*, 2012). Expression analyses have revealed that the various *OsPT13* homologues of sorghum, millet and maize show diverse patterns of regulation, with the genes *SbPT9*, *SbPT10*, *ZmPt4* and *ZmPt11* most strongly induced by AM colonization. A second group of AM associated PT genes not represented in model dicots consists of the barley gene *HvPT8*, the wheat *TaPTmyc*, maize *ZmPt2*, sorghum *SbPT8* and millet *SiPT8*. There is no *HvPT8* ortholog in rice, and, to date, members of this group have been described only from Panicoid (maize, sorghum and millet) and Pooid cereals (wheat and barley). Apart from the characterization of transcriptional responses to AM colonization, there has been little functional study of the majority of these genes, and their importance and role in the regulation of AM symbiosis remains to be determined.

Box 2 Table PHT1 transporters associated with arbuscular mycorrhizal (AM) symbiosis

	'*OsPT11*' group	'*OsPT13*' group	'*HvPT8*' group	
Medicago	*MtPT4**	–	–	Javot *et al.* (2007)
Rice	*OsPT11**	*OsPT13*^{7}*	–	Paszkowski *et al.* (2002), Yang *et al.* (2012)
Maize	*ZmPT6*$^{+}$	*ZmPT4*$^{+}$, *ZmPT5*$^{-}$, *ZmPT10*, *ZmPT11*$^{+}$, *ZmPT12*	*ZmPT2*$^{+}$	Willmann *et al.* (2013), Liu *et al.* (2016a), Sawers *et al.* (2017)
Sorghum	*SbPT11**	*SbPT9*$^{+}$, *SbPT10**	*SbPT8*$^{+}$	Walder *et al.* (2015)
Millet	*SiPT9*$^{+}$	*SiPT10*$^{\times}$, *SiPT11*$^{\times}$	*SiPT8**	Ceasar *et al.* (2014)
Wheat	*TaPT11**	*TaPT14*	*TaPT8*$^{+}$	Teng *et al.* (2017)

*, AM-specific; +, AM-induced; –, AM-repressed; ×, not detected in AM plants (roots).

facilitate this evaluation (Liu *et al.*, 2016b). A further challenge in the field evaluation of AM response is the need to control the native AM community in order to establish a baseline level of plant performance. In this context, the identification of mycorrhiza resistant mutants in cereal species provides an attractive alternative means of estimating the performance baseline (Gutjahr *et al.*, 2008, 2015; Willmann *et al.*, 2013). By combining mapping resources and mycorrhizal resistant mutants, it will be possible to characterize the genetic architecture of plant response in both domesticated varieties and their wild relatives.

Acknowledgements

R.S. and M.R-F. are supported by the Mexican Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) project 'Impacto de los Hongos Micorrízicos Arbusculares Nativos en el Rendimiento de Maíz'. Research in the laboratory of U.P. is supported by the Biotechnology and Biological Sciences Research Council (BBSRC) grants BB/N008723/1 and BB/P003419/1.

ORCID

Uta Paszkowski http://orcid.org/0000-0002-7279-7632

References

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

Besserer A, Puech-Pagès V, Kiefer P, Gomez-Roldan V, Jauneau A, Roy S, Portais J-C, Roux C, Bécard G, Séjalon-Delmas N. 2006. Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. *PLoS Biology* **4**: e226.

Bonfante P, Genre A. 2015. Arbuscular mycorrhizal dialogues: do you speak "plantish" or "fungish"? *Trends in Plant Science* **20**: 150–154.

Bulgarelli D, Garrido-Oter R, Münch PC, Weiman A, Dröge J, Pan Y, McHardy AC, Schulze-Lefert P. 2015. Structure and function of the bacterial root microbiota in wild and domesticated barley. *Cell Host & Microbe* **17**: 392–403.

Burton AL, Brown KM, Lynch JP. 2013. Phenotypic diversity of root anatomical and architectural traits in *Zea* species. *Crop Science* **53**: 1042–1055.

Ceasar SA, Hodge A, Baker A, Baldwin SA. 2014. Phosphate concentration and arbuscular mycorrhizal colonisation influence the growth, yield and expression of twelve *PHT1* family phosphate transporters in foxtail millet (*Setaria italica*). *PLoS ONE* **9**: e108459.

El Ghachtouli N, Martin-Tanguy J, Paynot M, Gianinazzi S. 1996. First report of the inhibition of arbuscular mycorrhizal infectioin of *Pisum sativum* by specific and irreversible inhibition of polyamine biosynthesis or by gibberellic acid treatment. *FEBS Letters* **385**: 189–192.

Etemadi M, Gutjahr C, Couzigou J-M, Zouine M, Lauressergues D, Timmers A, Audran C, Bouzayen M, Bécard G, Combier J-P. 2014. Auxin perception is required for arbuscule development in arbuscular mycorrhizal symbiosis. *Plant Physiology* **166**: 281–292.

Floss DS, Levy JG, Lévesque-Tremblay V, Pumplin N, Harrison MJ. 2013. DELLA proteins regulate arbuscule formation in arbuscular mycorrhizal symbiosis. *Proceedings of the National Academy of Sciences, USA* **110**: E5025–E5034.

Gaudin AC, McClymont SA, Soliman SS, Raizada MN. 2014. The effect of altered dosage of a mutant allele of *Teosinte branched 1* (*tb1-ref*) on the root system of modern maize. *BMC Genetics* **15**: 23.

Genre A, Chabaud M, Balzergue C, Puech-Pagès V, Novero M, Rey T, Fournier J, Rochange S, Bécard G, Bonfante P *et al.* 2013. 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 Phytologist* **198**: 190–202.

Gutjahr C, Banba M, Croset V, An K, Miyao A, An G, Hirochika H, Imaizumi-Anraku H, Paszkowski U. 2008. Arbuscular mycorrhiza-specific signaling in rice transcends the common symbiosis signaling pathway. *Plant Cell* **20**: 2989–3005.

Gutjahr C, Gobbato E, Choi J, Riemann M, Johnston MG, Summers W, Carbonnel S, Mansfield C, Yang S-Y, Nadal M *et al.* 2015. Rice perception of symbiotic arbuscular mycorrhizal fungi requires the karrikin receptor complex. *Science* **350**: 1521–1524.

Hedden P. 2003. The genes of the Green Revolution. *Trends in Genetics* **19**: 5–9.

Helber N, Wippel K, Sauer N, Schaarschmidt S, Hause B, Requena N. 2011. A versatile monosaccharide transporter that operates in the arbuscular mycorrhizal fungus *Glomus* sp is crucial for the symbiotic relationship with plants. *Plant Cell* **23**: 3812–3823.

Jakobsen I, Gazey C, Abbott LK. 2001. Phosphate transport by communities of arbuscular mycorrhizal fungi in intact soil cores. *New Phytologist* **149**: 95–103.

Javot H, Penmetsa RV, Terzaghi N, Cook DR, Harrison MJ. 2007. A *Medicago truncatula* phosphate transporter indispensable for the arbuscular mycorrhizal symbiosis. *Proceedings of the National Academy of Sciences, USA* **104**: 1720–1725.

Lehmann A, Barto EK, Powell JR, Rillig MC. 2012. Mycorrhizal responsiveness trends in annual crop plants and their wild relatives – a meta-analysis on studies from 1981 to 2010. *Plant and Soil* **355**: 231–250.

Liu Z, Cook J, Melia-Hancock S, Guill K, Bottoms C, Garcia A, Ott O, Nelson R, Recker J, Balint-Kurti P *et al.* 2016b. Expanding maize genetic resources with predomestication alleles: maize-teosinte introgression populations. *Plant Genome* **9**: doi: 10.3835/plantgenome2015.07.0053.

Liu F, Xu Y, Jiang H, Jiang C, Du Y, Gong C, Wang W, Zhu S, Han G, Cheng B. 2016a. Systematic identification, evolution and expression analysis of the *Zea mays PHT1* gene family reveals several new members involved in root colonization by arbuscular mycorrhizal fungi. *International Journal of Molecular Sciences* **17**: 930.

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

Nadal M, Sawers R, Naseem S, Bassin B, Kulicke C, Sharman A, An G, An K, Ahern KR, Romag A *et al.* 2017. An *N*-acetylglucosamine transporter required for arbuscular mycorrhizal symbioses in rice and maize. *Nature Plants* **3**: 17073.

Nagy R, Vasconcelos MJV, Zhao S, McElver J, Bruce W, Amrhein N, Raghothama KG, Bucher M. 2006. Differential regulation of five Pht1 phosphate transporters from maize (*Zea mays* L.). *Plant Biology* **8**: 186–197.

Paszkowski U, Kroken S, Roux C, Briggs SP. 2002. Rice phosphate transporters include an evolutionarily divergent gene specifically activated in arbuscular mycorrhizal symbiosis. *Proceedings of the National Academy of Sciences, USA* **99**: 13324–13329.

Peiffer JA, Spor A, Koren O, Jin Z, Tringe SG, Dangl JL, Buckler ES, Ley RE. 2013. Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proceedings of the National Academy of Sciences, USA* **110**: 6548–6553.

Pérez-Jaramillo JE, Mendes R, Raaijmakers JM. 2016. Impact of plant domestication on rhizosphere microbiome assembly and functions. *Plant Molecular Biology* **90**: 635–644.

Romero Navarro JA, Willcox M, Burgueño J, Romay C, Swarts K, Trachsel S, Preciado E, Terron A, Delgado HV, Vidal V *et al.* 2017. A study of allelic diversity underlying flowering-time adaptation in maize landraces. *Nature Genetics* **49**: 476–480.

Sawers RJ, Gutjahr C, Paszkowski U. 2008. Cereal mycorrhiza: an ancient symbiosis in modern agriculture. *Trends in Plant Science* **13**: 93–97.

Sawers RJH, Svane SF, Quan C, Grønlund M, Wozniak B, Gebreselassie M-N, González-Muñoz E, Chávez Montes RA, Baxter I, Goudet J *et al.* 2017. Phosphorus acquisition efficiency in arbuscular mycorrhizal maize is correlated with the abundance of root-external hyphae and the accumulation of transcripts encoding PHT1 phosphate transporters. *New Phytologist* **214**: 632–643.

Schmidt JE, Bowles TM, Gaudin ACM. 2016. Using ancient traits to convert soil health into crop yield: impact of selection on maize root and rhizosphere function. *Frontiers in Plant Science* **7**: 373.

Shenton M, Iwamoto C, Kurata N, Ikeo K. 2016. Effect of wild and cultivated rice genotypes on rhizosphere bacterial community composition. *Rice* **9**: 42.

Svane SF. 2013. *Variation in reponses to mycorrhiza and phosphorus among maize (*Zea mays *L.) genotypes*. MSc Thesis. University of Copenhagen, Denmark.

Szoboszlay M, Lambers J, Chappell J, Kupper JV, Moe LA, McNear DH. 2015. Comparison of root system architecture and rhizosphere microbial communities of Balsas teosinte and domesticated corn cultivars. *Soil Biology and Biochemistry* **80** (Suppl. C): 34–44.

Takeda N, Handa Y, Tsuzuki S, Kojima M, Sakakibara H, Kawaguchi M. 2015. Gibberellins interfere with symbiosis signaling and gene expression and alter colonization by arbuscular mycorrhizal fungi in *Lotus japonicus*. *Plant Physiology* **167**: 545–557.

Teng W, Zhao Y-Y, Zhao X-Q, He X, Ma W-Y, Deng Y, Chen X-P, Tong Y-P. 2017. Genome-wide identification, characterization, and expression analysis of PHT1 phosphate transporters in wheat. *Frontiers in Plant Science* **8**: 543.

Van De Velde K, Ruelens P, Geuten K, Rohde A, Van Der Straeten D. 2017. Exploiting DELLA signaling in cereals. *Trends in Plant Science* **22**: 880–893.

Walder F, Brulé D, Koegel S, Wiemken A, Boller T, Courty P-E. 2015. Plant phosphorus acquisition in a common mycorrhizal network: regulation of phosphate transporter genes of the *Pht1* family in sorghum and flax. *New Phytologist* **205**: 1632–1645.

Willmann M, Gerlach N, Buer B, Polatajko A, Nagy R, Koebke E, Jansa J, Flisch R, Bucher M. 2013. Mycorrhizal phosphate uptake pathway in maize: vital for growth and cob development on nutrient poor agricultural and greenhouse soils. *Frontiers in Plant Science* **4**: 533.

Yang S-Y, Grønlund M, Jakobsen I, Grotemeyer MS, Rentsch D, Miyao A, Hirochika H, Kumar CS, Sundaresan V, Salamin N *et al.* 2012. Nonredundant regulation of rice arbuscular mycorrhizal symbiosis by two members of the *PHOSPHATE TRANSPORTER1* gene family. *The Plant Cell* **24**: 4236–4251.

Yu N, Luo D, Zhang X, Liu J, Wang W, Jin Y, Dong W, Liu H, Yang W, Zeng L *et al.* 2014. A DELLA protein complex controls the arbuscular mycorrhizal symbiosis in plants. *Cell Research* **24**: 130–133.