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REVIEW

Regulation of root morphogenesis in arbuscular mycorrhizae: what role do fungal exudates, phosphate, sugars and hormones play in lateral root formation?

Anna Fusconi*

Department of Life Sciences and Systems Biology, Università di Torino, Viale Mattioli 25, 10125 Turin, Italy
** For correspondence. E-mail anna.fusconi@unito.it*

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• *Background* Arbuscular mycorrhizae (AMs) form a widespread root–fungus symbiosis that improves plant phosphate (Pi) acquisition and modifies the physiology and development of host plants. Increased branching is recognized as a general feature of AM roots, and has been interpreted as a means of increasing suitable sites for colonization. Fungal exudates, which are involved in the dialogue between AM fungi and their host during the pre-colonization phase, play a well-documented role in lateral root (LR) formation. In addition, the increased Pi content of AM plants, in relation to Pi-starved controls, as well as changes in the delivery of carbohydrates to the roots and modulation of phytohormone concentration, transport and sensitivity, are probably involved in increasing root system branching.
• *Scope* This review discusses the possible causes of increased branching in AM plants. The differential root responses to Pi, sugars and hormones of potential AM host species are also highlighted and discussed in comparison with those of the non-host *Arabidopsis thaliana*.
• *Conclusions* Fungal exudates are probably the main compounds regulating AM root morphogenesis during the first colonization steps, while a complex network of interactions governs root development in established AMs. Colonization and high Pi act synergistically to increase root branching, and sugar transport towards the arbusculated cells may contribute to LR formation. In addition, AM colonization and high Pi generally increase auxin and cytokinin and decrease ethylene and strigolactone levels. With the exception of cytokinins, which seem to regulate mainly the root:shoot biomass ratio, these hormones play a leading role in governing root morphogenesis, with strigolactones and ethylene blocking LR formation in the non-colonized, Pi-starved plants, and auxin inducing them in colonized plants, or in plants grown under high Pi conditions.

Key words: Arbuscular mycorrhizae, root branching, lateral roots, fungal exudates, phosphate, sugars, auxin, cytokinins, ethylene, strigolactones, *Arabidopsis thaliana*.

INTRODUCTION

In almost all natural and agricultural environments, the majority of plant species (perhaps 90 %) form mycorrhizae, with the most common type being represented by arbuscular mycorrhizae (AM; Smith and Read, 2008; Smith and Smith, 2012). To be mycorrhizal can therefore be considered the norm rather than the exception for plants (Hodge *et al.*, 2009). In an AM association, the Glomeromycota fungus inhabits the root cortex tissue, where it obtains sugars from the plant. In turn, the intraradical fungus transfers to the cortical cells mineral nutrients taken up from the soil by the extraradical mycelial network, which extends beyond the root depletion zone (Harrison, 2005; Smith and Smith, 2012). The name of this type of mycorrhiza comes from arbuscules, which are highly dichotomously branched hyphae that develop inside the cortical cells. They are the site in which phosphate (Pi), the most studied mineral nutrient involved in AM symbiosis, is delivered to the root and they contribute, together with intercellular hyphae, to the transfer of carbon compounds to the fungus (Helber *et al.*, 2011). Plants and fungi are both able to detect variations in the resources supplied by their partner, and symbiosis, which is stabilized through 'reciprocal rewards', is favoured for the most co-operative symbionts (Kiers *et al.*, 2011).

Phosphorus (P) is one of the most important elements for plants. However, it is also one of the least available of all essential nutrients in the soil. It is normally taken up by roots in the form of Pi. The concentration of Pi in plant cells exceeds by 2000-fold that of soil solutions, which is usually <2 μM (Vance *et al.*, 2003). Phosphate acquisition has a significant impact on plant growth and health, and Pi-starved plants show a range of adaptive responses, including a combination of growth, developmental and metabolic processes (Péret *et al.*, 2011), in order to sustain growth in such a limiting condition. Moreover, Pi availability is a key factor in the establishment of AM symbiosis, which is known to be one of the most prevalent evolutionary adaptations of land plants to P deficiency (Vance *et al.*, 2003; Hodge *et al.*, 2009). In Pi-limiting conditions, intraradical development of the fungus can occur over >80 % of the root length (Harrison, 2005) while high Pi conditions decrease colonization (Balzergue *et al.*, 2011). A wide range of plants, the so-called 'responsive' plants, increase their P status and growth upon colonization (Smith and Read, 2008; Smith and Smith, 2012). In addition, plants generally lower their root:shoot biomass ratio (Scannerini *et al.*, 2001; Smith and Read, 2008; Smith and Smith, 2012) because the increased sink strength of the roots induces plants to enlarge their photosynthetic organs, according to both the physiological requirements of the fungal partner and the improved mineral nutrition (Feddermann *et al.*, 2010).

Root system architecture (RSA) is frequently modified following AM interactions (Scannerini *et al.*, 2001; Hodge *et al.*, 2009; Table 1). The total root length may increase, as happens for example in the grape (*Vitis vinifera*; Schellenbaum *et al.*, 1991), or not increase, as in the tomato (*Solanum lycopersicum*; Berta *et al.*, 2005), and the number and length of the roots also change according to the different associations, with modifications to the lateral roots (LRs) being more frequent than those to the main roots (Table 1). A common effect of mycorrhization is an increase in LR development, perhaps in order to increase the suitable sites for colonization (Harrison, 2005; Table 1); this gives rise to a more branched root system, which was formerly recognized in colonized leek plants (Berta *et al.*, 1990). Two landmark papers subsequently confirmed the important role of AM symbiosis in LR formation. Paszkowski and Boller (2002) showed that the genetic defect in the *lrt1* mutant of maize (*Zea mays*), which lacks LRs, is partly overcome when AM colonization was established, while Oláh *et al.* (2005) showed that branching in *Medicago truncatula* is directly induced by AM germinating spores. Despite the considerable differences in root architecture, increased branching has been shown to occur in monocots and in herbaceous and woody dicots, although differences exist in the order of the roots involved (Berta *et al.*, 1995; Scannerini *et al.*, 2001; Table 1).

In this paper, the possible causes of increased branching in AM plants have been reviewed in light of the recent findings on RSA regulation. These causes may be both direct and indirect; the former include the production and action of AM fungal exudates, while the latter are mainly related to increased mineral nutrition and modulation of hormone balance. As reported above, Pi is a key element in AM symbiosis. Moreover, Pi availability has clearly been shown to influence root morphogenesis (Jones and Ljung, 2012; Niu *et al.*, 2013). Therefore, a large part of this review has been focused on the possible involvement of Pi in AM-induced root development. The role of other minerals, including nitrogen (N), in AM symbiosis is still unclear. Although it is widely recognized that AM fungi are involved in plant N uptake, the quantitative contribution of the colonization to the plant N levels is still controversial as it has been demonstrated in some plants but not in others (Smith and Smith, 2011). Therefore, despite the well-known effect of N on root development (Jones and Ljung, 2012), the role of N in AM root morphogenesis is still impossible to assess and, for this reason, has not been covered in this review. The mechanisms that could be responsible for root morphogenesis in mycorrhizal plants and the responses to Pi in AM-host species have been discussed and compared with those of the non-host arabidopsis (*Arabidopsis thaliana*). This plant has been the subject of an enormous amount of research on the molecular mechanisms that govern RSA and it therefore represents an invaluable starting point and term of comparison for all studies on root morphogenesis, although the results on arabidopsis cannot be transferred directly to AM host plants.

FUNGAL EXUDATES

The AM fungal exudates directly modify root system development. The establishment of AM depends on a co-ordinated exchange of signals between symbiotic fungi and their hosts, and it has recently been demonstrated that AM germinating spores

TABLE 1. *Responses of the root system of different plant species to arbuscular mycorrhizal (AM) colonization.*

Plant	AM fungus	Culture condition (d)	Main roots			First-order LRs			Second-order LRs			Third-order LRs			Total root length	%AMF	References
			no.	l	rb	no.	l	rb	no.	l	rb	no.	l	rb			
Allium porrum	*Glomus* sp. strain E3	a (105)	>	<	>	–	<	–	–	–	–	–	–	–	=	69	Berta *et al.* (1990, 1993)
Olea europaea	*Glomus mosseae*	b (180)	>	=	=	>	>	>	>	>	>	>	–	–	>	29–42	Citernesi *et al.* (1998)
Oryza sativa	*Glomus intraradices*	a (42)	=	>	>	> [1, 2]	>	–	> [2]	–	–	–	–	–	–	30–50	Gutjahr *et al.* (2009*a*)
Platanus acerifolia	*Glomus fasciculatum*	b (77)	=	=	=	=	<	–	>	>	>	>	=	>	>	79	Tisserant *et al.* (1992, 1996)
Populus 'Beaupré'	*Scutellispora calospora*	b (115)	–	=	>	–	>	=	–	>	=	–	=	–	=	8	Hooker *et al.* (1992)
	Glomus sp strain E3; *G. caledonium*		–	=	=	–	>	>	–	>	>	–	=	–	=	22; 28	
Prunus cerasifera	*Glomus intraradices*	a (75)	–	=	>	–	=	>	–	=	>	–	=	–	>	80	Berta *et al.* (1995)
	Glomus mosseae		–	=	>	–	=	>	–	=	=	–	=	–	>	70	
Vitis vinifera	*Glomus fasciculatum*	b (56)	=	<	>	>	=	>	>	<	>	>	=	–	>	90	Schellenbaum *et al.* (1991)

Main roots, primary or adventitious roots; LRs, lateral roots; no., number; l, length; rb, root branching; %AMF, percentage of AM fungal colonization.
Culture conditions: a, sand/nutrient solution; b, soil. The experiment's duration in days is given in parentheses.
[1], large lateral roots; [2], fine lateral roots.
> or <, increased or reduced in relation to the non-mycorrhizal controls; =, not significantly different from the non-mycorrhizal controls; –, not detected.

or mycorrhized roots release active symbiotic signals, often called Myc-factors, which are perceived by the host plants (Maillet *et al.*, 2011; Mukherjee and Ané, 2011). These active molecules are released, even in the absence of the host, and are not only symbiotic signals that stimulate mycorrhiza formation, but also plant growth regulators, that are able to modify root development, as has been demonstrated for different plant species (Maillet *et al.*, 2011; Mukherjee and Ané, 2011).

Germinating spores of *Gigaspora margarita*, *G. rosea* and *Glomus intraradices* (recently reassigned to *Rhizophagus irregularis*) as well as exudates from germinating spores (GSEs) of *G. intraradices* have been demonstrated to stimulate LR formation significantly and increase the total length of the root system in *M. truncatula* (Oláh *et al.*, 2005; Mukherjee and Ané, 2011). This stimulation is neither associated with the inhibition of primary root (PR) elongation nor with a change in root geotropism, as happens following auxin administration (Oláh *et al.*, 2005). Furthermore, GSE from *G. intraradices* increases the number of large LRs (the preferred sites for AM colonization) in rice (*Oryza sativa*) and the total number of LRs in maize, thus pointing to an effect of these exudates not only on the dicots, but also on the monocots (Mukherjee and Ané, 2011).

Recently, Myc-factors have been purified from exudates of carrot (*Daucus carota*) roots colonized by *G. intraradices* and from germinated spores of the same AM fungus, and have been characterized as a mixture of simple sulfated and non-sulfated lipochito-oligosaccharides (LCOs) composed of four or five glucosamine residues, with a strong structural similarity to rhizobial Nod-factors, even though simpler in structure (Maillet *et al.*, 2011). Synthetic LCOs, obtained via bacterial genetic engineering, have been shown to stimulate AM colonization in plant species of diverse families (Fabaceae, Asteraceae and Umbelliferae) (Maillet *et al.*, 2011).

The comprehension of the molecular processes required for AM signalling has mostly been derived from genetic studies of mutants defective in rhizobium–legume symbiosis. 'Common' symbiotic (Sym) genes, which control the Nod-factor signalling pathway that leads to nodulation, but which are also required for the formation of mycorrhizae, have been identified in the model legume *M. truncatula* (Catoira *et al.*, 2000). Two components of this common Sym pathway, *DMI1* and *DMI2*, are also involved in the LR formation induced by GSE in *M. truncatula* (Oláh *et al.*, 2005; Mukherjee and Ané, 2011). Non-sulfated and sulfated Myc-LCOs have been shown to elicit LR formation in the same plant by a Myc and a Nod pathway, respectively. However, using the *nsp1* (*nodulation signaling pathway1*) mutant to allow branching induction exclusively through the Myc pathway, it has been observed that the required concentrations of both sulfated and non-sulfated Myc-LCO were about 100-fold higher than those required to elicit the same response by the Nod pathway (Maillet *et al.*, 2011). Moreover, GSE-induced restructuring of the root architecture in rice does not require *CASTOR* or *POLLUX* (*DMI1* orthologues), thus pointing to another uncharacterized pathway that is independent of the Sym pathway (Gutjahr *et al.*, 2009*a*; Mukherjee and Ané, 2011).

Therefore, although AM fungal exudates have been shown to increase the production of LRs in both monocots and dicots, some aspects of the response have not yet been fully clarified. It is possible that the common Sym pathway elicited by Myc-LCOs may only be active in plants that form both nodules and AMs. An additional or alternative pathway, which mediates AM signalling in a Sym-independent manner, could exist (Mukherjee and Ané, 2011; Ortu *et al.*, 2012). It is also likely that signals of fungal origin other than LCOs may be involved in eliciting LR development (Bonfante and Requena, 2011; Genre *et al.*, 2013).

PHOSPHATE AVAILABILITY

Arbuscular mycorrhizal colonization is generally studied in plants grown in low Pi media, because this condition favours colonization (Harrison, 2005; Balzergue *et al.*, 2011). As a consequence, the non-colonized control plants frequently have lower tissue Pi concentrations than the colonized counterparts (Smith and Read, 2008) and are subjected to Pi starvation. Therefore, besides the direct effect of exudates on branching, the increased Pi tissue content of AM plants, which follows colonization, may be involved in modifying RSA.

Influence of Pi availability on the root system architecture

Morphogenetic root adaptation to the low-Pi environment includes an increase in the root:shoot biomass ratio (Table 2), because of an increased proportion of photosynthates being allocated to the roots (Hermans *et al.*, 2006; Karthikeyan *et al.*, 2007), and the development of a specific RSA to maximize the acquisition of external Pi (see, for example, Vance *et al.*, 2003; Hermans *et al.*, 2006; Hammond and White, 2008).

The effects of Pi starvation on root development in arabidopsis, which like other Brassicaceae (DeMars and Boerner, 1996) is unable to form functional AM associations, have been studied in detail over the last 10 years. In this species, PR growth is reduced remarkably in response to a low Pi condition (Table 2), because of the inhibition of cell elongation and progressive differentiation of the apical cells which lose meristematic status (Sánchez-Calderón *et al.*, 2005). The LR density generally increases (see, for example, Williamson *et al.*, 2001; López-Bucio *et al.*, 2002; Jiang *et al.*, 2007; Mayzlish-Gati *et al.*, 2012), although a reduction in the number of LRs per plant has sometimes been reported (Devaiah *et al.*, 2009; Mayzlish-Gati *et al.*, 2012). Elongation of the LRs is, in contrast, controversial, as longer (Williamson *et al.*, 2001) or shorter (Nacry *et al.*, 2005; Sánchez-Calderón *et al.*, 2005) LRs have been observed. The reprogramming of root development under Pi deprivation in arabidopsis leads to a shallow and superficial root system, and this model of the root system is recognized as an important adaptation strategy to optimize the absorption of Pi. The highest Pi concentration in the soil, in fact, is usually found near the soil surface, and a superficial and shallow phenotype allows plants to forage for the available Pi in the topsoil (Vance *et al.*, 2003; Hammond and White, 2008).

However, these changes are not universal, and vary from plant to plant and from genotype to genotype. Many plant species, including many of the potential hosts of AM fungi belonging to both mono- and dicots, do not exhibit an arabidopsis-like response (Forde and Lorenzo, 2001; Ramaekers *et al.*, 2010). Primary root elongation increases under Pi starvation in many dicots, including horse gram (*Macrotyloma uniflorum*; Anurada and Narayan, 1991), Chinese milk vetch (*Astragalus sinicus*), alfalfa (*Medicago sativa*), lettuce (*Lactuca sativa*),

TABLE 2. *Responses of the root system of different plant species to phosphate (Pi) deprivation.*

Plant species	Culture conditions (d)	Main root length	Main/lateral root number	Lateral root length	Main root branching	Root:shoot ratio	References
Allium porrum.	a (105)	$>^{(3)}$	$<^{(3)}$	–	<	–	Trotta *et al.* (1991)
Arabidopsis thaliana Col-0	b (17)	$<^{(1)}$	$>^{(5)}$	–	>	>	López-Bucio *et al.* (2002)
Brassica cultivars	a (21)	$<^{(1)}$	–	>	–	–	Akhtar *et al.* (2009)
Gossipium hirsutum	a (20)	$=^{(1)}$	$<^{(5)}$	<	–	>	Price *et al.* (1989)
Hordeum vulgare	a (21)	$=^{(2)}$	–	<	<	>	Drew (1975)
Lepidium sativum	c (5)	$=^{(1)}$	$<^{(5)}$	–	–	–	Wiersum (1958)
Linum usitatissimum	c (5)	$>^{(1)}$	$>^{(5)}$	–	–	–	Wiersum (1958)
Nicotiana tabacum	b (28)	$>^{(4)}$	$<^{(5)}$	–	<	>	A. Fusconi (unpubl.)
Phaseolus vulgaris	a (35)	$=^{(6)}$	$<^{(5)}$	=	<	>	Borch *et al.* (1999)
Raphanus sativus	c (5)	$=^{(1)}$	$=^{(5)}$	–	–	–	Wiersum (1958)
Trifolium repens	d (19)	$>^{(3)}$	$>^{(5)}$	>	–	–	Dinh *et al.* (2012)
Triticum aestivum	d (14)	$=^{(2, 3)}$	$<^{(5)}$	=	–	>	Aðalsteinsson and Jensén (1989, 1990)
Zea mays	d (16)	$=^{(3)}$	$<^{(3)}$	<	=	>	Mollier and Pellerin (1999)

Culture conditions: a, sand/nutrient solution; b, agarized medium; c, moistened filter paper; d, hydroponic. The experiment's duration in days is given in parentheses.

Type of root: $^{(1)}$, primary; $^{(2)}$, seminal; $^{(3)}$, adventitious; $^{(4)}$, basal; $^{(5)}$, lateral roots; $^{(6)}$, not specified.

$>$ or $<$, increased or reduced in relation to the Pi-sufficient plants, $=$, not significantly different from the Pi-sufficient plants; –, not detected.

marigold (*Tagetes patula*), tomato (Yoneyama *et al.*, 2012) and some of the dicot species listed in Table 2. The same occurs for the adventitious roots of leek (*Allium porrum*) and rice monocots (Trotta *et al.*, 1991; J. Zhou *et al.*, 2008; Arite *et al.*, 2012). These modifications probably facilitate soil exploration for these plants, because a sustained root growth allows plants to encounter areas of higher Pi availability (Berta *et al.*, 1993; Borch *et al.*, 1999; Ramaekers *et al.*, 2010). However, the PR length is not influenced to any extent by Pi availability in other species (Li *et al.*, 2012; Table 2). On the contrary, the total root length frequently decreases (Drew, 1975; Trotta *et al.*, 1991; Borch *et al.*, 1999) and, unlike arabidopsis, plants grown in low Pi media frequently show a low degree of branching, although there are some exceptions (Table 2). The opposite occurs when the plants grow in Pi-rich soils or become colonized with AM fungi. In the latter case, increased branching frequently coincides with an enhancement of Pi acquisition by AM plants (see, for example, Tisserant *et al.*, 1996). A high Pi content and AM colonization therefore seem to act synergistically to increase root branching in most plant–fungus associations, thus pointing to a role for Pi signalling in root response to colonization.

Pi perception and response

Plants can detect and respond to both the local variations in the external Pi concentration and the endogenous Pi status (Thibaud *et al.*, 2010; Chiou and Lin, 2011; Hammond and White, 2011).

Local signalling is involved in the increased density of LRs in regions of the soil with high Pi availability and the reduced activity of the PR meristem of arabidopsis (Hammond and White, 2011). The latter seems to rely on the combined activity of PDR2 (Phosphate Deficiency Response 2), a P_5-type ATPase, and the multicopper oxidases LPR1/LPR2 (Low Phosphate Root 1/2) in the root tip, once changes in external Pi have been sensed (Ticconi *et al.*, 2009; Chiou and Lin, 2011). It is not likely that a mechanism for sensing the Pi concentration around the root is involved in the difference between the root morphogenesis of AM and non-AM plants, because these plants grow in the same medium under experimental conditions. Moreover, since Pi in functional AM symbiosis is directly delivered to the cortical tissue by the fungus, bypassing the epidermis (Grace *et al.*, 2009; Smith and Smith, 2011, 2012), the external and internal Pi status are uncoupled.

Systemic signalling regulates many plant responses to Pi starvation, as has been demonstrated through experiments in split-root systems with high and low Pi (Branscheid *et al.*, 2010; Hammond and White, 2011). A growing number of transcription factors that participate in the plant Pi deficiency signalling cascade have been described in arabidopsis and cereals, and some of them (such as MYB62, WRKY75, ZAT6 and AtBHLH32 of arabidopsis, MYB2P-1 of rice, and PTF1 of rice and maize) have been shown to be involved in changes in root growth (Chen *et al.*, 2007; Rouached *et al.*, 2011; Dai *et al.*, 2012; Li *et al.*, 2012).

A central role in the systemic signalling of Pi in arabidopsis is played by the MYB transcription factor PHR1, a key transcriptional activator, which binds to the P1BS element (PHR1 Binding Sequence) present in the promoter region of a sub-set of Pi starvation-inducible genes (Rubio *et al.*, 2001; Hammond and White, 2011; Smith *et al.*, 2011). MicroRNAs of the 399 family (miR399) are induced by PHR1 in arabidopsis, and function as signalling molecules transported from the shoot to the roots; they suppress *PHO2* expression, leading to activation of Pi uptake and translocation (Pant *et al.*, 2008; Chiou and Lin, 2011). However, the transcription of *PHR1* is not directly influenced by Pi starvation, and the activity of PHR1 is regulated post-translationally through sumoylation by SIZ1, a Small Ubiquitin-like Modifier (SUMO) E3 ligase (Miura *et al.*, 2005). The PHR1–miR399–PHO2 pathway in arabidopsis is not involved in the remodelling of RSA under Pi deprivation, which is instead regulated, independently of PHR1, by SIZ1, which acts as a negative regulator of Pi starvation-dependent signalling through the control of auxin patterning and the regulation of auxin-responsive genes (Miura *et al.*, 2011).

Components of the Pi starvation signalling pathway in arabidopsis are conserved in AM host species (Smith *et al.*, 2011).

Two homologous genes of *AtPHR1*, *OsPHR1* and *OsPHR2*, have been isolated in rice; both are involved in the Pi starvation signalling pathway (J. Zhou *et al.*, 2008). The overexpression of *OsPHR2* increases sensitivity to Pi starvation, and causes enhanced root elongation, a typical trait stimulated by Pi starvation in rice under flooding conditions, suggesting, unlike in arabidopsis, a direct involvement of *OsPHR2* in Pi-dependent RSA remodelling (J. Zhou *et al.*, 2008). Moreover, PHR2 does not seem to be the only regulator of miR399 in rice. The level of the latter depends to a great extent on the plant Pi status and not on *PHR2* expression, and *PHO2* does not seem to be the target of miR399 (J. Zhou *et al.*, 2008), thus showing further differences in relation to arabidopsis.

The PHR1–miR399–PHO2 pathway has not been explored to any great extent in AM-colonized plants. It has been shown that the level of miR399 is up-regulated in Pi-depleted tissues (Chiou and Lin, 2011) and, consistently, in tobacco and *M. truncatula*, higher levels are found in non-colonized Pi-starved plants than in Pi-sufficient plants. However, surprisingly, AM-colonized roots that grow under low Pi display levels of miR399 similar to, or higher than, non-AM controls, despite the increased tissue Pi concentration that occurs following fungus uptake (Branscheid *et al.*, 2010). It has been hypothesized that an unknown mycorrhizal signal leads to the increased synthesis of miR399 in the shoots, which upon phloem transport accumulates as a mature molecule in the mycorrhizal roots. MicroR399 should keep the expression of *PHO2* in the roots low; otherwise, the increased level of PHO2 in response to symbiotic Pi uptake would lead to the suppression of AM-induced Pi transporter genes (Branscheid *et al.*, 2010; Smith *et al.*, 2011).

The above data suggest that differences exist in the Pi signalling pathway of AM-host species in relation to arabidopsis. However, at present, little is known about the molecular components that are involved, especially in relation to root morphogenesis. In this respect, a possible breakthrough is represented by the recent identification and characterization of LjMAMI (*Lotus japonicus* Meristem and Arbuscular Mycorrhiza Induced; Volpe *et al.*, 2012). This is a transcription factor that is phylogenetically related to PHR1, which is upregulated to a great extent in arbusculated root cells and in root apices. Its downregulation, in RNA interference transgenic hairy roots lines, has been shown to cause an important reduction in branching under low Pi. Interestingly, the wild-type phenotype is restored by AM colonization (Volpe *et al.*, 2012, 2013). Hence, unravelling the pathway involved in the LjMAMI action would shed light on the relationship between AM symbiosis, Pi assimilation and root development.

Apart from Pi itself, the role of which has been questioned (Chiou and Lin, 2011), and miRNAs, there may be other signals involved in the modification of RSA in response to low Pi and AM colonization. These include changes in the delivery of carbohydrates, mainly sucrose, to the roots and modulation of the phytohormone concentration, transport and sensitivity.

SUGAR SIGNALLING

Sugars, including both sucrose and hexoses, play an important role in root system morphogenesis, and act as both a metabolite and a signalling molecule by regulating the expression of Pi starvation-induced genes and RSA. They are required for Pi starvation responses, and influence the root morphology of arabidopsis (reviewed by Hammond and White, 2008, 2011; Rouached *et al.*, 2010; Puig *et al.*, 2012) and the formation of cluster roots in the non-mycorrhizal species *Lupinus albus* (K. Zhou *et al.*, 2008).

Arabidopsis seedlings are generally cultivated on growth media supplemented with sucrose (see, for example, López-Bucio *et al.*, 2002; Pérez-Torres *et al.*, 2008; Richter *et al.*, 2009), and the growth of seedlings on sucrose-free medium greatly suppresses the development of LRs; the addition of sugar, in contrast, increases LR density (Jain *et al.*, 2007; Karthikeyan *et al.*, 2007). Moreover, direct contact between the aerial tissues and sucrose in the growth media has been shown to promote the emergence of LR primordia (MacGregor *et al.*, 2008). The use of the mutant *hps1* (*hypersensitive to phosphate starvation1*) of arabidopsis, which overexpresses the *SUC2* (*Sucrose Transporter2*) gene and shows a high sucrose accumulation in the plant tissues because of enhanced sucrose uptake, has also shown that an elevated sucrose level alone is sufficient to enhance LR formation (Lei *et al.*, 2011). Some studies have suggested that sucrose may be involved in the transport of auxin from the shoot to the root, which is critical for LR formation, and in increasing the responsiveness of the root system to auxin (Jain *et al.*, 2007).

Although photosynthetic carbon assimilation is reduced under Pi deficiency, increased sucrose biosynthesis has been witnessed in the leaves of some plants, such as arabidopsis, common bean (*Phaseolus vulgaris*), barley (*Hordeum vulgare*) and soybean (*Glycine max*) (Hammond and White, 2008). Additionally, a sustained and, in some cases, an increased translocation of mobile carbohydrates, primarily sucrose, has been observed via the phloem to the roots (Hammond and White, 2008). This increased sucrose flux has been related to the changes in root phenotype because the two events occur close to each other in time (Rouached *et al.*, 2010). However, the sucrose concentration increases in the roots of some, but not all, plant species. It remains unchanged in arabidopsis roots (Ciereszko *et al.*, 2001) while it increases in common bean, especially in the meristematic and elongation root zones (Ciereszko *et al.*, 1998). In the latter plant, unlike in arabidopsis, the PR length is similar in both Pi-starved and Pi-sufficient plants, and branching decreases under Pi starvation (Borch *et al.*, 1999). The high sugar level in the root apical zone possibly sustains the PR meristem activity and elongation, despite the unfavourable, low Pi conditions. The different sucrose distribution observed between the common bean and arabidopsis may be related to the different and specific redistribution of root growth in these two species, in response to Pi-limiting conditions.

When plants are colonized by AM fungi, they have to pay the price of sugars for Pi (Smith and Read, 2008). An increased import of sucrose into roots has in fact been reported for mycorrhizal plants, and this is induced, at least in part, by signals released from the fungus (Gutjahr *et al.*, 2009*b*; Helber *et al.*, 2011). It has been demonstrated, over a range of herbaceous and woody plants, that up to 20 % more photosynthate is transported to the roots of AM plants than to the non-AM control roots (Smith and Read, 2008).

The exchange of carbon and Pi in the roots is closely correlated, with the carbon allocation being controlled locally in relation to the Pi homeostasis of the cell (Fitter, 2006; Kiers *et al.*, 2011). The mechanism of Pi transfer in arbusculated cells has

been studied extensively, while the reciprocal carbon transfer process is less known. A fungal high-affinity Monosaccharide Transporter 2 (MST2) from *Glomus* sp., which has been shown to be required for colonization functionality and arbuscular development, has recently been characterized (Helber *et al.*, 2011). Expression analysis has shown that the activity of MST2 is closely correlated with that of the plant Pi transporter PT4, which is located in the periarbuscular membrane; both proteins are downregulated by sufficient Pi availability. These results made Helber *et al.* (2011) suggest that the arbuscule interface is the main site where the Pi/carbon exchange is modulated.

These data together indicate that, following AM colonization, in addition to the increased transport of sucrose to the root, a change in the route of photosynthates also occurs, with sugars being diverted towards the arbusculated cortex cells. Because sugar has proven to induce LR formation, it is tempting to speculate that the changed sugar partitioning and pathway that occur in AM roots could be involved in increased branching. However, the data on sugar distribution are still limited to just a few species. Further studies on the effects of exogenous sugar on root branching, on the sugar root distribution and on the expression and localization of the genes involved in the sugar signalling cascade (see Hammond and White, 2011) are therefore needed for potential AM-hosting plants under different levels of Pi nutrition, and in colonized vs. non-colonized plants.

PHYTOHORMONES

Plant hormone levels have been reported to change during AM development, and almost all hormones have been proposed as important regulators of the symbiosis (Hause *et al.*, 2007; Ludwig-Müller, 2010; Foo *et al.*, 2013). Moreover, many of these hormones have been shown to be involved in root morphogenesis under Pi starvation (reviewed by Rouached *et al.*, 2010; Chiou and Lin, 2011; Hammond and White, 2011; Sato and Miura, 2011; Niu *et al.*, 2013). Therefore, hormonal regulation of RSA following AM colonization is to be expected. However, the data on the changes in hormonal concentration, following AM colonization, are often contradictory. There is very little literature on the correlation between the altered hormonal levels in AM plants and root morphogenesis, and the molecular mechanisms involved are almost unknown.

The possible involvement of auxin, which is recognized as essential for LR formation, and that of cytokinin (CK) and ethylene (ET), the effects of which are well documented on RSA, are dealt in this section, taking into account the interactions of these hormones with Pi starvation. The role played by strigolactones (SLs), a novel class of hormones, is also discussed in relation to the regulation of AM root morphogenesis and the plant responses to Pi.

Auxin

Auxin is a major regulator of plant growth and developmental processes. In the roots, it positively regulates the size of the root apical meristem by promoting cell division antagonistically to CK, and it is involved in the regulation of cell elongation with ET (Muday *et al.*, 2012; Vanstraelen and Benková, 2012). Moreover, it is the main regulator of each LR formation step (Fukaki and Tasaka, 2009; De Smet, 2011). Elevated levels of auxin, either due to exogenous application or to enhanced biosynthesis, are sufficient to increase LR formation, while mutations that reduce auxin signalling, such as *solitary root1* of arabidopsis, cause a strong reduction in LR formation (revised by Ivanchenko *et al.*, 2008). Since AM colonization increases root branching, the involvement of auxin in the RSA regulation of mycorrhizal plants has been suggested (Ludwig-Müller, 2010; Hanlon and Coenen, 2011; Sukumar *et al.*, 2013).

Auxin is involved in the AM host–fungus interaction. The addition of auxin has been shown to increase spore germination and hyphal growth, and to influence the infection rate and percentage of colonization (Ludwig-Müller, 2010). Moreover, auxin was shown to be required within the host roots for the early stages of AM formation, e.g. during pre-symbiotic signal exchange (Hanlon and Coenen, 2011), in part through the control of the SL levels (Foo *et al.*, 2013).

The auxin level in plant tissues increases in different plant–fungus associations (Ludwig-Müller, 2010), probably independently of fungus production (Jentschel *et al.*, 2007; Ludwig-Müller, 2010). The concentration of indole-3-acetic acid (IAA), the major endogenous auxin, has been observed to increase in the AM roots of leeks with colonization and applied Pi (Torelli *et al.*, 2000). In both situations, this high IAA concentration is closely related to the observed RSA modifications, which consist of more numerous, more branched and shorter adventitious roots (Berta *et al.*, 1990; Trotta *et al.*, 1991). However, colonization does not increase IAA systemically. In fact, in soybean roots grown in a split-root system, IAA only accumulated in the roots growing on the inoculated side, and remained low on the other side as in controls (Meixner *et al.*, 2005).

Arbuscular mycorrhizal colonization in maize (Kaldorf and Ludwig-Müller, 2000; Fitze *et al.*, 2005) and in *M. truncatula* (Ludwig-Müller and Güther, 2007) increases the IBA (indole-3-butyric acid) concentration. When maize is inoculated with *G. intraradices*, the IBA synthesis increases, as does the free IBA, and this occurs along with a significant increase in the percentage of fine LRs (reviewed by Kaldorf and Ludwig-Müller, 2000). The hormone IBA is known to contribute to the regulation of RSA (Overvoorde *et al.*, 2010) and is recognized as an important regulator of auxin activity. It acts as a storage form of IAA and may be converted to IAA, thus contributing to the formation of IAA gradients that are required for root development (reviewed by Simon and Petrášek, 2011). Moreover, the root phenotype of AM plants could be mimicked through the application of exogenous IBA (Kaldorf and Ludwig-Müller, 2000). Therefore, an increased IBA concentration might be involved in AM root morphogenesis.

An important auxin homeostasis mechanism involves the formation of auxin conjugates, as free IAA comprises only up to 25 % of the total amount of IAA, depending on the tissue and plant species (Ludwig-Müller, 2011). In most cases, IAA can be converted to ester conjugates with sugars or to amide conjugates with amino acids, and a fraction of these conjugates may be hydrolysed back to free IAA (Ludwig-Müller, 2011). The levels of amide conjugates of IAA and IBA have been shown to increase in the roots of maize inoculated with *G. intraradices* (Fitze *et al.*, 2005), and the increased formation of these conjugates is in line with the accumulation of transcripts for a putative IAA-amido synthetase and an auxin-responsive GH3-like protein in tomato mycorrhizal roots, mainly in arbuscule-

containing cells (Fiorilli *et al.*, 2009). However, the function of auxin conjugates in AM roots is currently unclear. They are possibly involved in the development of colonization and the control of fungus morphogenesis, as suggested by Fiorilli *et al.* (2009), while their involvement in root morphogenesis is unclear, as they play a negative role in root branching (Quint *et al.* 2009).

The proper transport of auxin, which leads to the formation of concentration gradients, is required for the regulation of the sequential steps of LR formation, which include priming of pericycle cells, acquisition of founder cell identity, cell cycle reactivation and primordium development (Dubrovsky *et al.*, 2011). Indole-3-acetic acid moves passively through the vascular tissues and actively, in a polar manner, across plant cells, depending on specific influx and efflux protein carrier proteins. Among these proteins, PIN efflux proteins are the main regulators of polar auxin transport in the root apical zone (Finet and Jaillais, 2012). Efflux PIN3 and PIN7 proteins have been shown to be involved in the correct positioning and extension of the competent pericycle zone for LR initiation (Dubrovsky *et al.*, 2011), while the rearrangement of PIN1 polarity, mediated by endocytic recycling of the PIN1 protein, redirects the auxin flux into the developing LR (Ruyter-Spira *et al.*, 2011). Once bound to its receptor, auxin promotes the degradation of AUX/IAA transcription repressors. This allows ARFs (Auxin Response Factors) to activate the transcription of genes related to LR initiation and development (for reviews, see, for example, Fukaki and Tasaka, 2009; Péret *et al.*, 2009; Overvoorde *et al.*, 2010; Finet and Jaillais, 2012). This mechanism is conserved between dicot and monocot plants (Dubrovsky *et al.*, 2011; Smith and De Smet, 2012), and is therefore operative in the potential hosts of AM fungi.

Phosphate starvation interferes with auxin gradient formation and sensitivity. Studies on arabidopsis have shown that during Pi starvation response, auxin accumulates in the PR meristem, and this is connected with the cessation of PR elongation. Coincidentally, auxin accumulates in the LR primordia and this is followed by LR elongation, with SIZ1 involved in the negative regulation of Pi starvation-induced RSA remodelling through the modifications of auxin accumulation (Miura *et al.*, 2011). In addition, enhanced auxin sensitivity has been detected in Pi-deprived arabidopsis plants. This has been correlated to a higher expression of the auxin receptor gene *TIR1*. A higher TIR1 level may thus activate LR formation, although the free auxin content in Pi-deprived seedlings is quite similar to that present in seedlings grown on high Pi (Pérez-Torres *et al.*, 2008; Chiou and Lin, 2011).

The above-reported data indicate that, in addition to the variations in auxin concentration which have been found in a number of colonized AM plants, the regulation of auxin transport and sensitivity to auxin may be equally important for AM root morphogenesis. Different signal molecules, such as sucrose (Jain *et al.*, 2007; Hammond and White, 2011) and hormones including ET, CKs and SLs (see below), gibberellins (Gou *et al.*, 2010), jasmonate (Sun *et al.*, 2009; 2011) and abscisic acid (ABA; Shkolnik-Inbar and Bar-Zvi, 2010), and other substances, such as nitric oxide (Calcagno *et al.*, 2012; Chen and Kao, 2012) and flavonoids (Harrison and Dixon, 1994; Abdel-Lateif *et al.*, 2012), could influence mycorrhizal RSA by altering the auxin and PIN protein synthesis and/or distribution. However, there is still no evidence in favour of a changed sensitivity/response to auxin in relation to both Pi starvation and AM colonization in AM-hosts. Differential expression of genes involved in auxin signalling has been shown between Pi-starved and Pi-sufficient maize plants (Li *et al.*, 2012), and the induction of putative ARFs has been found during AM symbiosis in maize, rice and *M. truncatula*, but not in *L. japonicus* (reviewed by Formey *et al.*, 2013). However, comparative transcriptomic analysis among these plant species has not detected any common orthologous auxin-specific genes involved in root development of AM-colonized plants (Formey *et al.*, 2013).

All these data point to the probable involvement of auxin in AM root branching. Furthermore, they could also indicate the existence of different regulations of auxin homeostasis and response pathways, possibly on the basis of the plant species, as suggested by Formey *et al.* (2013).

Cytokinins

Cytokinins play a crucial role in regulating the proliferation and differentiation of plant cells, and also control many developmental processes. They are recognized as essential regulators of the plant root system, as they are involved, antagonistically to auxin, in the control of the size of the root apical meristem, and in the rate of root growth and LR organogenesis (Sakakibara, 2006; Werner *et al.*, 2010; Marhavý *et al.*, 2011). They can redirect assimilates and induce invertases, thus contributing directly to the plant carbon redistribution (Ludwig-Müller, 2010). Cytokinin receptors are essential for the establishment of symbiosis with rhizobial bacteria (Gonzalez-Rizzo *et al.*, 2006), and CKs are thought to be involved, like auxin, in the repression of defence responses of the host during the establishment of symbiosis (Ludwig-Müller, 2010). However, recent studies have suggested that CKs might not be involved to any great extent in the regulation of mycorrhizal development (see Foo *et al.*, 2013).

A number of AM plants accumulate more CKs than non-mycorrhizal plants in both the shoots and the roots (Allen *et al.*, 1980; Drüge and Schönbeck, 1992; van Rhijn *et al.*, 1997; Torelli *et al.*, 2000; Shaul-Keinan *et al.*, 2002). However, the CK concentration in AM-colonized maize plants has been shown to increase only during the late plant growth phase, in relation to non-mycorrhizal controls (Danneberg *et al.*, 1992). Since the main sites of CK synthesis include the root tips (Aloni *et al.*, 2006), the high CK level found may be, in part, a consequence of increased root branching. Cytokinin-like substances have been shown to be produced by axenically grown mycelium of *G. mosseae* (Barea and Azcon-Aguilar, 1982). However, the possible contribution of AM fungi to the regulation of the host CK level is unclear (Barker and Tagu, 2000).

The higher CK content in AM plants is in line with the reduction in the root:shoot biomass ratio, which occurs when colonization is established. In fact, CK functions as a repressor of root development. Larger root systems have been observed in plants that show a reduction in the CK status, such as mutants for genes encoding CK biosynthetic enzymes, transgenic arabidopsis and tobacco plants with enhanced root-specific degradation of CK, or plants treated with anti-CKs (Arata *et al.*, 2010). A low root:shoot biomass ratio is also one of the plant responses to a high Pi status, and a direct correlation has been found between CK concentration and Pi availability/tissue content in different plant species. The CK level decreases in arabidopsis under Pi starvation, along with a decrease in the expression of *CRE1*, a

CK receptor gene (Franco-Zorrilla *et al.*, 2002). The CK and Pi contents are also directly related in some potential AM fungal hosts, such as sunflower (*Helianthus annuus*; Salama and Wareing, 1979), *Plantago major* (Baas and Kuiper, 1989) and leek (Torelli *et al.*, 2000).

Numerous studies have shown that CK acts as a negative regulator of LR initiation (e.g. Fukaki and Tasaka, 2009). Both exogenous CK and the overproduction of CK have been shown to inhibit LR initiation in arabidopsis (López-Bucio *et al.*, 2002; Laplaze *et al.*, 2007). Conversely, mutants in CK receptors or signal transduction and transgenic plants with reduced levels of CK, caused by the overexpression of *CK Oxidase/Dehydrogenase*, which encodes a CK-degrading enzyme, exhibit an increased number of LRs (Laplaze *et al.*, 2007; Bielach *et al.*, 2012).

An important part of the CK-mediated regulation of development involves interaction with the auxin pathway. Thus, an accurate balance between opposing auxin and CK effects is crucial for proper developmental output (Marhavý *et al.*, 2011). Recent results have shown that CK and auxin response maxima barely overlap and are complementary in the root, where LR organogenesis takes place. The zone in which the priming and initiation of LRs occur displays elevated levels of biologically active CKs but a repressed CK response, while enhanced CK responses occur in the pericycle cells between existing LR primordia, perhaps in order to block additional primordia formation (Bielach *et al.*, 2012).

Enhanced CK levels perturb the expression of PIN genes in LR founder cells (Laplaze *et al.* 2007), prevent PIN1 recycling and promote the lytic degradation of PIN1 in vacuoles (Marhavy *et al.*, 2011). This CK action thus prevents the auxin gradient required for LR initiation, but it does not repress the further development of LR primordia (Laplaze *et al.*, 2007). According to Bielach *et al.* (2012), this phase-dependent effect of CK could rely on the robustness and stability of the auxin gradient.

In agreement with the negative role of CK in LR formation, root branching decreases in arabidopsis plants grown under high Pi (and therefore with a high CK content) (López-Bucio *et al.*, 2002; Laplaze *et al.*, 2007). However, the opposite occurs in many plant species, including several AM host plants, which instead exhibit decreased branching when grown under low Pi conditions (Table 2). Nevertheless, a reduction in LR formation, induced by CK, has been documented in different plants. The inhibition of LR primordia formation has been observed after exogenous CK administration in rice (Debi *et al.*, 2005), and RNA interference of the CK receptor MtCRE1 has been shown to increase the number of LRs in *M. truncatula* (Gonzalez-Rizzo *et al.*, 2006).

Taken together, these literature data would seem to point to a primary role for CKs in the regulation of the root:shoot biomass ratio in AM plants. The contradiction between high CK content and high branching found in some potential AM-host plants grown under high Pi or colonized by AM fungi is unclear, as there are very few data on the root distribution of auxin and CK in plants other than arabidopsis, or on the sensitivity to CK and/or the CK–auxin balance.

Ethylene

Ethylene plays an important role in co-ordinating internal and external signals, as well as in several stress responses and interaction of plants with other organisms (Lei *et al.*, 2010; López-Ráez *et al.*, 2010). In AM symbiosis, ET and salicylic acid function as negative regulators of mycorrhizal intensity (Gamalero *et al.*, 2008; Ludwig-Müller, 2010). In fact, a strong ET inhibitory effect has been observed on early symbiotic gene expression, on fungus entry into roots (Mukherjee and Ané, 2011) and on intraradical fungal spread (Martín-Rodríguez *et al.*, 2011). The ET content is increased by a deficiency of ABA, which is in contrast necessary for arbuscule formation and is positively correlated to mycorrhizal establishment (Ludwig-Müller, 2010; Martín-Rodríguez *et al.*, 2011). Accordingly, most papers indicate that ET production is diminished in AM-infected plants (McArthur and Knowles, 1992; Besmer and Koide, 1999; López-Ráez *et al.*, 2010), although a few contradictory results have also been reported (Dugassa *et al.*, 1996).

Ethylene, like auxin and CK, is an important regulator of root morphogenesis. It inhibits root elongation by reducing cell elongation synergistically with auxin (reviewed by Muday *et al.*, 2012). However, it also acts antagonistically to auxin by inhibiting LR formation in the earliest stages of LR initiation, as has been shown through treatments with ET or with the ET precursor 1-aminocyclopropane carboxylic acid (ACC), and in the recent genetic studies on arabidopsis and tomato (reviewed by Fukaki and Tasaka, 2009; Lewis *et al.*, 2011; Muday *et al.*, 2012).

The regulation of ET–auxin interactions plays an important role in root morphogenesis: it has, in fact, been shown that ET and auxin can reciprocally influence and regulate their biosynthesis and response pathway (Stepanova *et al.*, 2007; Vanstraelen and Benková, 2012). The precursor ACC has been found to reduce free IAA and to decrease auxin-induced gene expression in regions where LRs form (Negi *et al.*, 2010; Lewis *et al.*, 2011). In addition, high ET levels increase PIN3 and PIN7 expression, and this increase results in elevated auxin transport, which prevents the localized accumulation of the auxin needed to drive LR formation (Lewis *et al.*, 2011). However, the effects of ET have been shown to depend on its concentration (Pierik *et al.*, 2006). Treatments with low concentrations of ACC have been shown to promote the initiation of new LR primordia by increasing tryptophan-dependent auxin synthesis. Higher doses have, in contrast, been shown to inhibit initiation to a great extent, as reported above, but also to promote the emergence of existing primordia in arabidopsis (Ivanchenko *et al.*, 2008; Fukaki and Tasaka, 2009).

The reduced level of ET generally found in AM plants is therefore in agreement with the increased branching of the colonized roots. It has also been shown that exogenous ACC has a strong inhibitory effect on LR formation in response to germinating spore exudates, in *M. truncatula* and rice (Mukherjee and Ané, 2011). Moreover, a reduced ET level has frequently been shown to occur under high Pi (Borch *et al.*, 1999; Lynch and Brown, 2001; Li *et al.*, 2009).

Ethylene is involved in root development in response to low Pi availability, as has been shown in different plants (Borch *et al.*, 1999; López-Bucio *et al.*, 2002; Ma *et al.*, 2003; Dinh *et al.*, 2012; Niu *et al.*, 2013) including arabidopsis and common bean. Ethylene has shown an opposite effect on the primary/main root length in low and high Pi conditions in these two species. The use of ET inhibitors or mutants has shown that endogenous ET limits PR lengthening in Pi-sufficient conditions, as reported above, while the opposite happens in low Pi

conditions, with ET promoting root extension (Borch *et al.*, 1999; Ma *et al.*, 2003). This happens although Pi-deficient roots of common bean produce twice as much ET g^{-1} dry weight as roots of Pi-sufficient plants (Borch *et al.*, 1999), and increased transcript levels for ET biosynthetic genes have been found in arabidopsis (reviewed by Nagarajan and Smith, 2012). Moreover, in the common bean, endogenous ET decreases LR density in low Pi conditions and increases it in Pi-sufficient conditions (Borch *et al.*, 1999). The use of some ET signalling mutants (such as *etr1*, *ein2* and *ein3*) in arabidopsis has shown that endogenous ET also decreased the LR number and density under low Pi (López-Bucio *et al.*, 2002). A different root sensitivity to ET has thus been considered in relation to Pi availability (Borch *et al.*, 1999; Ma *et al.*, 2003).

Despite showing similar responses to ET, the morphogenesis of the root system of the common bean and arabidopsis under low Pi is quite different (Borch *et al.*, 1999; López-Bucio *et al.*, 2002), thus showing a different responsiveness to ET also from species to species. Transcriptomic analyses, in agreement, have shown both up- and downregulation of *ET Response Factor* genes in a variety of plant species on the basis of the Pi availability (reviewed by Nagarajan and Smith, 2012). In arabidopsis, according to López-Bucio *et al.* (2002), ET is not involved in the LR response to low Pi. When auxin is applied simultaneously with ACC, the latter is unable to prevent auxin stimulation of LR formation in arabidopsis (Ivanchenko *et al.*, 2008), which is consistent with a dominant role for auxin on ET. In contrast, root morphogenesis of the common bean under low Pi is probably under the main control of ET. This plant, in these conditions, decreases the number of LRs without any significant change in the main root length and therefore reduces root branching, as happens in many non-colonized potential AM hosts. This leads to the hypothesis that the different degree of branching found for non-colonized and colonized AM-host plants depends on a switch from one state dominated by ET and found in Pi-starved, non-colonized plants to another one that is controlled by auxin, when colonization has been established.

Strigolactones

Among the hormones that can affect RSA, SLs have been the subject of a great deal of interest in recent years, although their effects have only been analysed in a few species. Strigolactones are terpenoid lactones (for a review, see Seto *et al.*, 2012) which play different roles in plants. They act as stimulants for the germination of seeds of root parasitic plants, such as *Orobanche* spp. and *Striga* spp. (Cook *et al.*, 1966), and hence play a negative role on the plant that exudes them. At the same time, they are rhizosphere signals that induce hyphal branching (Akiyama *et al.*, 2005) and spore germination of some AM fungi (Besserer *et al.*, 2006); inside the root, they seem to promote AM colonization, thus favouring the establishment of symbiosis with AM fungi (reviewed by Foo *et al.*, 2013). This may be related to an SL-induced fungal production of short chain chitin oligomers, which, after perception, have been shown to activate the Sym-dependent signalling pathway involved in the initial stages of fungal root colonization in *M. truncatula* (Genre *et al.*, 2013). Besides their role in plant interactions, SLs act as phytohormones: they are thought to be synthesized mainly in the lower parts of the stem and in the roots and move acropetally towards the shoot apex (Kohlen *et al.*, 2011). They have been shown to inhibit shoot branching and to regulate root development and its architecture (Ruyter-Spira *et al.*, 2011; Seto *et al.*, 2012; Brewer *et al.*, 2013). Several genes, isolated from both mono- and dicots, are involved in the synthesis, starting from carotenoids, or the signalling of SLs. The biosynthetic genes include *MAX1* (*More Axillary Growth1*), *MAX3* and *MAX4* of arabidopsis, *RMS1* (*Ramosus1*) and *RMS5* of pea (*Pisum sativum*), *D10* (*Dwarf10*), *D17* and *D27* of rice, and *DAD1* (*Decreased Apical Dominance1*) and *DAD3* of petunia. The only SL signalling genes described so far are *MAX2/D3/RMS4* and *AtD14/OsD14/DAD2* (reviewed by Arite *et al.*, 2009; Janssen and Snowden, 2012; Seto *et al.*, 2012; Waters *et al.*, 2012; Yoshida *et al.*, 2012). It has recently been suggested that the binding of DAD2 to SLs allows an interaction with MAX2, which leads to ubiquination and degradation of downstream signalling proteins (Janssen and Snowden, 2012).

Analysis of SL-deficient and signalling mutants and the use of the synthetic SL analogue GR24 have shown that endogenous SLs have little impact on PR length in rice (Arite *et al.*, 2012) and tomato (Koltai *et al.*, 2010), as well as in arabidopsis under optimal growth conditions (Ruyter-Spira *et al.*, 2011). Nevertheless, SLs stimulate PR lengthening in arabidopsis under carbohydrate starvation, because of an increased meristem cell number and size of the transition zone (Ruyter-Spira *et al.*, 2011). Endogenous SLs increase the lengthening of the crown roots of rice, as demonstrated by the shorter crown roots of the *d10-1* (*max4*) synthesis mutant and the *d14* signalling mutant and the rescuing of the defect in the *d10-1* mutant but not in *d14* with application of GR24 (Arite *et al.*, 2012), thus pointing to a general role for SLs on root lengthening. In addition, SLs negatively regulate LR density in arabidopsis by affecting both LR initiation and elongation (Kapulnik *et al.*, 2011*a*; Ruyter-Spira *et al.*, 2011).

The morphological responses of the root to SLs involve a reduction in auxin transport, through changes in the regulation of the auxin efflux, which may affect the auxin optimum required for LR formation (Koltai *et al.*, 2010; Ruyter-Spira *et al.*, 2011). An enhanced expression of *PIN1* has in fact been found in stems of arabidopsis *max* mutants (Bennett *et al.*, 2006), while, in the same plant, a GR24 treatment has been shown to cause a reduction in PIN1/3/7–green fluorescent protein intensities in the provascular tissue of the PR (Ruyter-Spira *et al.*, 2011).

The SL content increases under low Pi. Increased SL levels in *M. truncatula* in this condition have been shown to be related to an important upregulation of the *Mt-D27* synthetic gene (Liu *et al.*, 2011). An inverse correlation between SL synthesis and Pi supply has been demonstrated in different plants, including pea, tomato, wheat (*Triticum aestivum*) and arabidopsis (Balzergue *et al.*, 2011; Kohlen *et al.*, 2011; Liu *et al.*, 2011; Yoneyama *et al.*, 2012). Nevertheless, the amount of SLs in the latter, a non-host for AM fungi, is low compared with that of plants forming AMs (Westwood, 2000). In agreement with the decreased SL levels observed in high Pi conditions, fully established AM colonization lowers SL production in mono- and dicots (López-Ráez *et al.*, 2011), although the contribution of SLs to the regulation of AM symbiosis by Pi is still poorly understood (Balzergue *et al.*, 2011).

The enhanced crown root elongation observed under Pi starvation in rice is in line with the enhanced production of SLs in these conditions, and is supported by a lack of crown root elongation in

d10-1 and *d14-1* mutant seedlings (Arite *et al.*, 2012). The effects of SLs under low Pi on root elongation are thus similar to those of ET in rice. Unfortunately there are no data on the effect of SLs on branching in this plant.

In arabidopsis, unlike in rice, the PR length and the branched RSA do not seem to be affected much by SLs. In fact, increased root branching has also been found in *max* mutants in low Pi conditions (Mayzlish-Gati *et al.*, 2012). It is known that the responses to low Pi in arabidopsis are associated with induction of the transcription of the auxin receptor *TIR1* (Pérez-Torres *et al.*, 2008). It has recently been shown that such an induction does not occur in the SL signalling mutant *max2-1* and is reduced in the synthetic *max4-1* mutants relative to the wild type (Mayzlish-Gati *et al.*, 2012). Although this indicates the involvement of SLs in the increased sensitivity to auxin in low Pi conditions, differences between *max2-1* and the wild type in terms of RSA are moderate under Pi starvation. Thus, according to the authors, the possibility exists that as yet unknown factors, such as MAX2-independent auxin responses, may dominate the root morphogenesis of arabidopsis in some stages of development (Mayzlish-Gati *et al.*, 2012).

According to these data, the involvement of SLs in the responses of the roots to low Pi seems to be greater in rice than in arabidopsis, and in rice it is synergistic with that of ET. Cross-talk between SLs and ET has been described during root-hair elongation in arabidopsis (Kapulnik *et al.*, 2011*b*) and during the germination of seeds of *Striga hermonthica* (Sugimoto *et al.*, 2003). In both cases, an SL effect through ET biosynthesis and signalling has been suggested, and a more general effect of SLs on plant growth mediated by ET has been proposed (Kapulnik *et al.*, 2011*b*; Koltai, 2013). The root morphogenesis of plants under low Pi, characterized by an extension of the main roots and reduced branching, as in many non-colonized AM hosts, may thus be controlled by SLs through the ET pathway. In contrast, the branched root growth of arabidopsis in low Pi conditions, which is only in part mediated by SLs (Mayzlish-Gati *et al.*, 2012) and which has been considered to be independent of ET (López-Bucio *et al.*, 2002), may be mainly directed by auxin. The decreased SL level found in AM-colonized plants (López-Ráez *et al.*, 2011) could negatively influence the ET pathway, and this could in part explain the increased branching of AM-colonized plants.

CONCLUSIONS

Plant responses to AM colonization involve physiological, molecular and morphological mechanisms, including a change in RSA which becomes more branched in relation to the non-colonized controls. In this paper, an overview of the possible mechanisms implicated in AM root morphogenesis and a model of root growth regulation in which fungal exudates, sugars and hormones are the main players in the regulation of mycorrhizal root growth, are provided (Fig. 1).

Fungal exudates induce LR formation in the first stages of plant–fungus interaction (Oláh *et al.*, 2005; Mukherjee and Ané, 2011), possibly to increase the potential sites of

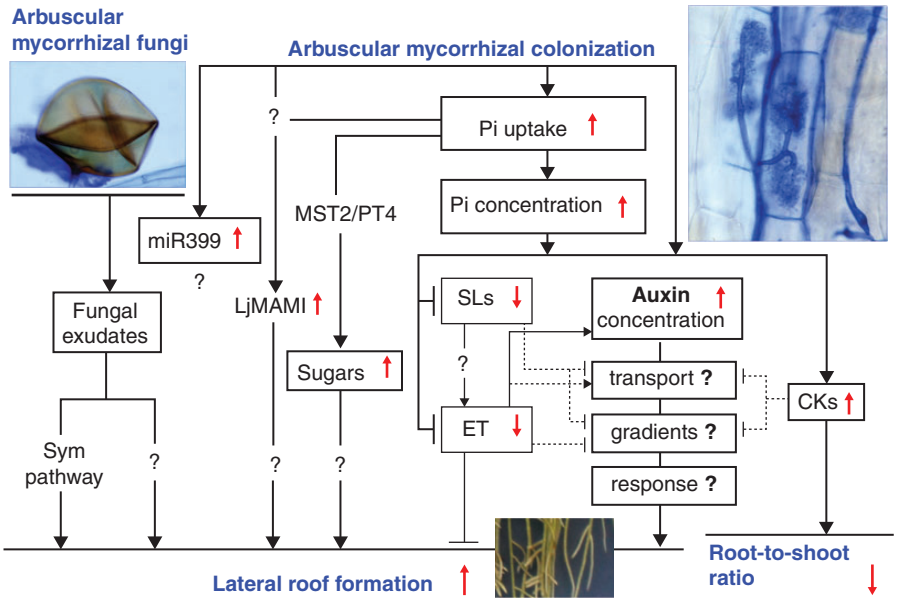

Fig. 1. Schematic drawing of the possible signalling events that lead to increased root branching in arbuscular mycorrhizal (AM) plants. In the first stage of colonization, fungal exudates induce lateral root (LR) formation through the common Sym pathway (*Medicago truncatula*; Oláh *et al.*, 2005) and/or another as yet unknown pathway (*Oryza sativa*; Gutjahr *et al.*, 2009*a*). Increased phosphate (Pi) uptake may change the root architecture through different, integrated mechanisms and probably plays a central role when colonization is established. MicroR399 increases in AM plants (Branscheid *et al.*, 2010); however, the PHR1–miRNA–PHO2 pathway has not been explored to any extent in relation to LR formation. The recently discovered *Lotus japonicus* Meristem and Arbuscular Mycorrhiza Induced (LjMAMI) transcription factor could link the AM symbiosis to Pi nutrition and branching (Volpe *et al.*, 2012). The increased import of sugars into the AM roots and the flux towards the arbusculated cells, sustained by C/Pi exchange (high-affinity Monosaccharide Transporter 2, MST2/Pi transporter, PT4; Helber *et al.*, 2011) could also favour LR induction and growth. Arbuscular mycorrhizal colonization and the resulting increased Pi tissue content act together with hormone homeostasis and signalling. An increased auxin and cytokinin (CK) concentration and reduction in strigolactones (SLs) and ethylene (ET) generally have been found in both AM and Pi-sufficient plants, in relation to Pi-starved, non-colonized, plants (see text). A dominant role for auxin on SL and ET signalling in AM root morphogenesis is thus suspected, with CKs probably being involved in the reduction of the root:shoot ratio, which generally occurs following AM colonization and high Pi nutrition.

colonization. However, questions about the nature of the bioactive molecules and the pathways involved in LR formation are still unclear, particularly for non-legume plants, where a Sym-independent pathway seems to exist (Gutjahr *et al.*, 2009*a*; Mukherjee and Ané, 2011). Fungal exudates may also influence root morphogenesis at later stages of colonization, when, however, others factors probably are the main regulators.

Colonized plants generally show a higher Pi tissue level than the non-colonized, Pi-starved controls. Thus, mycorrhizal RSA relies on one hand on the suppression of the responses to Pi starvation and, on the other hand, on the effects of higher Pi levels, both being mainly mediated by hormonal regulation. Levels of ET and SL frequently increase under low Pi, whereas they decrease in AM-colonized or Pi-sufficient plants. Since they have been shown to reduce root branching, at least in some species, their effects are probably correlated to the loss of the Pi-starved condition. Auxin and CKs, in contrast, tend to increase in mycorrhizal plants. Auxin is recognized to be essential for LR formation. Although regulation of auxin homeostasis and response pathways is still little understood in AM plants and seems to change from plant to plant (Formey *et al.*, 2013), a pre-eminent role for auxin in AM root morphogenesis is likely. High CK levels are possibly involved in decreasing the root:shoot ratio in response to high Pi and colonization, while a possible influence of CKs on branching is unclear, due to their suppressive effects on LR formation.

Apart from hormones, in this review it has been proposed that, in established mycorrhizae, the symbiotic carbon/Pi exchange itself, which occurs mainly in the arbusculated cells (Helber *et al.*, 2011), may regulate AM root morphogenesis. When plants are colonized by AM fungi an increased transport of photosynthates, which are directed towards the fungal sink zones of the root cortex, occurs. Since a relationship exists between elevated sugar levels and enhanced LR formation (Lei *et al.*, 2011), the flux of sugars towards the colonized root cortex may stimulate LR formation. However, further research is required to confirm this hypothesis, as well as for a more detailed understanding of the role of hormones in AM root morphogenesis. There is still limited knowledge on the distribution of hormones and other morphogens, as well as of their complex network of interactions, in AM roots. As far as auxin is concerned, it has been shown that a large number of factors, hormonal or not, converge on the regulation of its synthesis, transport and the downstream signalling pathway. It would not be surprising to find that fungal exudates may also influence AM root morphogenesis through interaction with auxin, in analogy with the Nod-factor during nodule formation (see Kuppusamy *et al.*, 2009). Moreover, among hormones, a possible role in AM root morphogenesis may be played by gibberellins. These latter, in addition to auxin, CKs, ET and SLs, are involved in the root morphogenesis in response to Pi availability (Jiang *et al.*, 2007; Devaiah *et al.*, 2009); however, their behaviour and functions are still unclear in AM plants (Ludwig-Müller, 2010; Foo *et al.*, 2013).

Thus, many issues still have to be clarified in order to confirm (or refute) the assumptions presented herein. Moreover, to gain an overall picture of AM root morphogenesis, efforts should be focused on the search for the genetic determinants that act at the crossroads between mycorrhization and root development. Despite the large amount of molecular data available on mycorrhizae, only a few clues have been found on this topic. Understanding the mechanisms involved in the regulation of miR399 (Branscheid *et al.*, 2010) and the signalling pathway related to the action of LjMAMI (Volpe *et al.*, 2012, 2013) could be instrumental in deciphering the complex network that underlies the AM colonization and the morphogenetic processes. In-depth knowledge of the regulation of AM root morphogenesis could also shed new light on the role of RSA in the physiology of mycorrhizae and in the protection of AM colonization from biotic and abiotic stresses.

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