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

Running title: “Regulation of root morphogenesis in arbuscular mycorrhizae”

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1 **Abstract**

2 • *Background* Arbuscular mycorrhizae (AMs) form a wide-spread root-fungus symbiosis that
3 improves plant phosphate (Pi) acquisition and modifies the physiology and development of host
4 plants. Increased branching is recognized as a general feature of AM roots, and has been
5 interpreted as a means of increasing suitable sites for colonization. Fungal exudates, which are
6 involved in the dialogue between AM fungi and their host during the pre-colonization phase,
7 also play a well-documented role in lateral root (LR) formation. In addition, the increased Pi
8 content of AM plants, in relation to Pi-starved controls, as well as changes in the delivery of
9 carbohydrates to the roots and modulation of phytohormone concentration, transport and
10 sensitivity, are probably involved in increasing root system branching.

11 • *Scope* This review discusses the possible causes of increased branching in AM plants. The
12 differential root responses to Pi, sugars and hormones of potential AM host species are also
13 highlighted and discussed in comparison to those of the non-host *Arabidopsis thaliana*.

14 • *Conclusions* Fungal exudates probably are the main compounds regulating AM root
15 morphogenesis during the first colonization steps, while a complex network of interactions
16 governs root development in established AMs. Colonization and high Pi act synergistically to
17 increase root branching and sugar transport towards the arbusculated cells may contribute to LR
18 formation. In addition, AM colonization and high Pi generally increase auxin and cytokinins and
19 decrease ethylene and strigolactones levels. With the exception of cytokinins, which seem to
20 mainly regulate the root-to-shoot biomass ratio, these hormones play a leading role in governing
21 root morphogenesis, with strigolactones and ethylene blocking LR formation in the non-
22 colonized, Pi-starved plants, and auxin inducing them in colonized plants, or in plants grown
23 under high Pi conditions.

24
25 **Key words:** arbuscular mycorrhizae, root branching, lateral roots, fungal exudates, phosphate,
26 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 cooperative 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 less than 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

1 known to be one of the most prevalent evolutionary adaptations of land plants to P
2 deficiency (Vance *et al.*, 2003; Hodge *et al.*, 2009). In Pi-limiting conditions, intraradical
3 development of the fungus can occur over more than 80% of the root length (Harrison,
4 2005) while high Pi conditions decrease colonization (Balzergue *et al.*, 2011). A wide
5 range of plants, the so-called 'responsive' plants, increases their P status and growth upon
6 colonization (Smith and Read, 2008; Smith and Smith, 2012). In addition, plants generally
7 lower the root-to-shoot biomass ratio (Scannerini *et al.*, 2001; Smith and Read, 2008;
8 Smith and Smith, 2012) because the increased sink strength of the roots induces plants to
9 enlarge their photosynthetic organs, according to both the physiological requirements of the
10 fungal partner and the improved mineral nutrition (Feddermann *et al.*, 2010).

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

1 in monocots and in herbaceous and woody dicots, although differences exist in the order of
2 the roots involved (Berta *et al.*, 1995; Scannerini *et al.*, 2001; table 1).

3 In this paper, the possible causes of increased branching in AM plants have been
4 reviewed in light of the recent findings on RSA regulation. These causes may be both
5 direct and indirect; the former include the production and action of AM fungal exudates,
6 while the latter are mainly related to increased mineral nutrition and modulation of
7 hormone balance. As reported above, Pi is a key element in AM symbiosis. Moreover, Pi
8 availability has clearly been shown to influence root morphogenesis (Jones and Ljung,
9 2012; Niu *et al.*, 2013). Therefore, a large part of this review has been focused on the
10 possible involvement of Pi in AM-induced root development. The role of other minerals,
11 including nitrogen (N), in AM symbiosis is still unclear. Although it is widely recognized
12 that AM fungi are involved in plant N uptake, the quantitative contribution of the
13 colonization to the plant N levels is still controversial as it has been demonstrated in some
14 plants but not in others (Smith and Smith, 2011). Therefore, despite the well-known effect
15 of N on root development (Jones and Ljung, 2012), the role of N in AM root
16 morphogenesis is still impossible to assess and, for this reason, has not been covered in this
17 paper. The mechanisms that could be responsible for root morphogenesis in mycorrhizal
18 plants and the responses to Pi in AM-host species have been discussed and compared with
19 those of the non-host arabidopsis (*Arabidopsis thaliana*). This plant has been the subject of
20 an enormous amount of research on the molecular mechanisms that govern RSA and it
21 therefore represents an invaluable starting point and term of comparison for all studies on
22 root morphogenesis, although the results on arabidopsis cannot be transferred directly to
23 AM host plants.

24 FUNGAL EXUDATES

1 AM fungal exudates directly modify root system development. The establishment of
2 AM depends on a coordinated exchange of signals between symbiotic fungi and their hosts,
3 and it has recently been demonstrated that AM germinating spores or mycorrhized roots
4 release active symbiotic signals, often called Myc-factors, which are perceived by the host
5 plants (Maillet *et al.*, 2011; Mukherjee and Ané, 2011). These active molecules are
6 released, even in the absence of the host, and are not only symbiotic signals that stimulate
7 mycorrhiza formation, but also plant growth regulators, that are able to modify root
8 development as has been demonstrated for different plant species (Maillet *et al.*, 2011;
9 Mukherjee and Ané, 2011).

10 Germinating spores of *Gigaspora margarita*, *Gi. rosea* and *Glomus intraradices*
11 (recently reassigned to *Rhizophagus irregularis*) as well as exudates from germinating
12 spores (GSE) of *G. intraradices* have been demonstrated to significantly stimulate LR
13 formation and increase the total length of the root system in *M. truncatula* (Oláh *et al.*,
14 2005; Mukherjee and Ané, 2011). This stimulation is neither associated with the inhibition
15 of primary root (PR) elongation nor with a change in root geotropism, as happens following
16 auxin administration (Oláh *et al.*, 2005). Furthermore, GSE from *G. intraradices* increases
17 the number of large LRs (the preferred sites for AM colonization) in rice (*Oryza sativa*)
18 and the total number of LRs in maize, thus pointing to an effect of these exudates not only
19 on the dicots, but also on the monocots (Mukherjee and Ané, 2011).

20 Recently, Myc-factors have been purified from exudates of carrot (*Daucus carota*)
21 roots colonized by *G. intraradices* and from germinated spores of the same AM fungus and
22 have been characterized as a mixture of simple sulphated and non-sulphated
23 lipochitooligosaccharides (LCOs) composed of four or five glucosamine residues, with a
24 strong structural similarity to rhizobial Nod-factors, even though simpler in structure
25 (Maillet *et al.*, 2011). Synthetic LCOs, obtained via bacterial genetic engineering, have

1 been shown to stimulate AM colonization in plant species of diverse families (Fabaceae,
2 Asteraceae and Umbelliferae) (Maillet *et al.*, 2011).

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

19 Therefore, although AM fungal exudates have been shown to increase the production
20 of LRs in both monocots and dicots, some aspects of the response have not yet been fully
21 clarified. It is possible that the common Sym pathway elicited by Myc-LCOs may only be
22 active in plants that form both nodules and AMs. An additional or alternative pathway,
23 which mediates AM signaling in a Sym-independent manner, could exist (Mukherjee and
24 Ané, 2011; Ortu *et al.*, 2012). It is also likely that signals of fungal origin other than LCOs
25 may be involved in eliciting LR development (Bonfante and Requena, 2011; Genre *et al.*,
26 2013).

1
2 PHOSPHATE AVAILABILITY
3

4 Arbuscular mycorrhizal colonization is generally studied in plants grown in low Pi
5 media, because this condition favours colonization (Harrison, 2005; Balzergue *et al.*,
6 2011). As a consequence, the non-colonized control plants frequently have lower tissue Pi
7 concentrations than the colonized counterparts (Smith and Read, 2008) and are subjected to
8 Pi starvation. Therefore, besides the direct effect of exudates on branching, the increased Pi
9 tissue content of AM plants, which follows colonization, may be involved in modifying
10 RSA.

11
12 *Influence of Pi availability on the root system architecture*

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

18 The effects of Pi starvation on root development in arabidopsis, which like other
19 Brassicaceae (DeMars and Boerner, 1996) is unable to form functional AM associations,
20 have been studied in detail over the last 10 years. In this species, PR growth is reduced
21 remarkably in response to a low Pi condition (table 2), because of the inhibition of cell
22 elongation and progressive differentiation of the apical cells which lose meristematic status
23 (Sánchez-Calderón *et al.*, 2005). Lateral root density generally increases (see, for example,
24 Williamson *et al.*, 2001; López-Bucio *et al.*, 2002; Jiang *et al.*, 2007; Mayzlish-Gati *et al.*,
25 2012), although a reduction in the number of LRs per plant has sometimes been reported
26 (Devaiah *et al.*, 2009; Mayzlish-Gati *et al.*, 2012). Elongation of the LRs is, in contrast,

1 controversial as longer (Williamson *et al.*, 2001) or shorter (Nacry *et al.*, 2005; Sánchez-
2 Calderón *et al.*, 2005) LRs have been observed. The reprogramming of root development
3 under Pi deprivation in arabidopsis leads to a shallow and superficial root system, and this
4 model of root system is recognized as an important adaptation strategy to optimize the
5 absorption of Pi. The highest Pi concentration in the soil, in fact, is usually found near the
6 soil surface and a superficial and shallow phenotype allows plants to forage for the
7 available Pi in the topsoil (Vance *et al.*, 2003; Hammond and White, 2008).

8 However, these changes are not universal and vary from plant to plant and from
9 genotype to genotype. Many plant species, including many of the potential hosts of AM
10 fungi belonging to both mono- and dicots, do not exhibit an arabidopsis-like response
11 (Forde and Lorenzo, 2001; Ramaekers *et al.*, 2010). Primary root elongation increases
12 under Pi starvation in many dicots, including horse gram (*Macrotyloma uniflorum*;
13 Anurada and Narayan, 1991), chinese milk vetch (*Astragalus sinicus*), alfalfa (*Medicago*
14 *sativa*), lettuce (*Lactuca sativa*), marigold (*Tagetes patula*), tomato (Yoneyama *et al.*, 2012)
15 and some of the dicot species listed in table 2. The same occurs for the adventitious roots of
16 leek (*Allium porrum*) and rice monocots (Trotta *et al.*, 1991; Zhou J. *et al.*, 2008; Arite *et*
17 *al.*, 2012). These modifications probably facilitate soil exploration for these plants, because
18 a sustained root growth allows plants to encounter areas of higher Pi availability (Berta *et*
19 *al.*, 1993; Borch *et al.*, 1999; Ramaekers *et al.*, 2010). However, the PR length is not
20 influenced to any extent by Pi availability in other species (Li *et al.*, 2012; table 2). On the
21 contrary, the total root length frequently decreases (Drew 1975; Trotta *et al.*, 1991; Borch
22 *et al.*, 1999) and, unlike arabidopsis, plants grown in low Pi media frequently show a low
23 degree of branching although there are some exceptions (table 2). The opposite occurs
24 when the plants grow in Pi-rich soils or become colonized with AM fungi. In the latter
25 case, increased branching frequently coincides with an enhancement of Pi acquisition by
26 AM plants (see, for example, Tisserant *et al.*, 1996). A high Pi content and AM

1 colonization therefore seem to act synergistically to increase root branching in most
2 plant/fungus associations, thus pointing to a role of Pi signaling in root response to
3 colonization.

4 *Pi perception and response*

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

9 Local signaling is involved in the increased density of LRs in regions of the soil with
10 high Pi availability and the reduced activity of the PR meristem of arabidopsis (Hammond
11 and White, 2011). The latter seems to rely on the combined activity of PDR2 (Phosphate
12 Deficiency Response 2), a P₅-type ATPase, and the multicopper oxidases LPR1/LPR2
13 (Low Phosphate Root 1/2) in the root tip, once changes in external Pi have been sensed
14 (Ticconi *et al.*, 2009; Chiou and Lin, 2011). It is not likely that a mechanism for sensing the
15 Pi concentration around the root is involved in the difference between the root
16 morphogenesis of AM and non-AM plants, because these plants grow in the same medium
17 under experimental conditions. Moreover, since Pi in functional AM symbiosis is directly
18 delivered to the cortical tissue by the fungus, bypassing the epidermis (Grace *et al.*, 2009;
19 Smith and Smith, 2011; 2012), the external and internal Pi status are uncoupled.

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

1 changes in root growth (Chen *et al.*, 2007; Rouached *et al.*, 2011; Dai *et al.*, 2012; Li *et al.*,
2 2012).

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

17 Components of the Pi-starvation signaling pathway in arabidopsis are conserved in
18 AM host species (Smith *et al.*, 2011). Two homologous genes of *AtPHR1*, *OsPHR1* and
19 *OsPHR2*, have been isolated in rice; both are involved in the Pi-starvation signaling
20 pathway (Zhou J. *et al.*, 2008). The overexpression of *OsPHR2* increases sensitivity to Pi
21 starvation, and causes enhanced root elongation, a typical trait stimulated by Pi starvation
22 in rice under flooding conditions, suggesting unlike in arabidopsis a direct involvement of
23 *OsPHR2* in Pi-dependent RSA remodeling (Zhou J. *et al.*, 2008). Moreover, PHR2 does
24 not seem to be the only regulator of miR399 in rice. The level of the latter depends to a
25 great extent on the plant Pi status and not on *PHR2* expression, and *PHO2* does not seem to

1 be the target of miR399 (Zhou J. *et al.*, 2008) thus showing further differences in relation to
2 arabidopsis.

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

15 The above data suggest that differences exist in the Pi signaling pathway of AM-host
16 species in relation to arabidopsis. However, at present, little is known about the molecular
17 components that are involved, especially in relation to root morphogenesis. In this respect,
18 a possible breakthrough is represented by the recent identification and characterization of
19 LjMAMI (*Lotus japonicus* Meristem and Arbuscular Mycorrhiza Induced; Volpe *et al.*,
20 2012). This is a transcription factor that is phylogenetically related to PHR1, which is up-
21 regulated to a great extent in arbusculated root cells and in root apices. Its down-regulation,
22 in RNA interference transgenic hairy roots lines, has been shown to cause an important
23 reduction in branching under low Pi. Interestingly, the wild type phenotype is restored by
24 AM colonization (Volpe *et al.*, 2012; 2013). Hence, unravelling the pathway involved in
25 the LjMAMI action would shed light on the relationship between AM symbiosis, Pi
26 assimilation and root development.

1 the transport of auxin from the shoot to the root, which is critical for LR formation, and in
2 increasing the responsiveness of the root system to auxin (Jain *et al.*, 2007).

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

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

1 *al.*, 2007; Ludwig-Müller, 2010; Foo *et al.*, 2013). Moreover, many of these hormones
2 have been shown to be involved in root morphogenesis under Pi starvation (reviewed by
3 Rouached *et al.*, 2010; Chiou and Lin, 2011; Hammond and White, 2011; Sato and Miura,
4 2011; Niu *et al.*, 2013). Therefore, hormonal regulation of RSA following AM colonization
5 is to be expected. However, the data on the changes in hormonal concentration, following
6 AM colonization, are often contradictory. There is very little literature on the correlation
7 between the altered hormonal levels in AM plants and root morphogenesis and the
8 molecular mechanisms involved are almost unknown.

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

14 15 *Auxin*

16 Auxin is a major regulator of plant growth and developmental processes. In the roots,
17 it positively regulates the size of the root apical meristem by promoting cell division
18 antagonistically to cytokinin, and it is involved in the regulation of cell elongation with
19 ethylene (Vanstraelen and Benková, 2012; Muday *et al.*, 2012). Moreover, it is the main
20 regulator of each LR formation step (Fukaki and Tasaka, 2009; De Smet, 2011). Elevated
21 levels of auxin, either due to exogenous application or to enhanced biosynthesis, are
22 sufficient to increase LR formation, while mutations that reduce auxin signaling, such as
23 *solitary root1* of arabidopsis, cause a strong reduction in LR formation (revised by
24 Ivanchenko *et al.*, 2008). Since AM colonization increases root branching, the involvement
25 of auxin in the RSA regulation of mycorrhizal plants has been suggested (Ludwig-Müller,
26 2010; Hanlon and Coenen, 2011; Sukumar *et al.*, 2013).

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

7 The auxin level in plant tissues increases in different plant-fungus associations
8 (Ludwig-Müller, 2010), probably independently of fungus production (Jentschel *et al.*,
9 2007; Ludwig-Müller, 2010). The concentration of indole-3-acetic acid (IAA), the major
10 endogenous auxin, has been observed to increase in the AM roots of leeks with
11 colonization and applied Pi (Torelli *et al.*, 2000). In both situations, this high IAA
12 concentration is closely related to the observed RSA modifications, which consist of more
13 numerous, more branched and shorter adventitious roots (Berta *et al.*, 1990; Trotta *et al.*,
14 1991). However, colonization does not increase IAA systemically. In fact, in soybean roots
15 grown in a split-root system, IAA only accumulated in the roots growing on the inoculated
16 side, and remained low on the other side as in controls (Meixner *et al.*, 2005).

17 Arbuscular mycorrhizal colonization in maize (Kaldorf and Ludwig-Müller, 2000;
18 Fitze *et al.*, 2005) and in *M. truncatula* (Ludwig-Müller and Güther, 2007) increases the
19 IBA (indole-3-butyric acid) concentration. When maize is inoculated with *G. intraradices*,
20 the IBA synthesis increases, as does the free IBA, and this occurs along with a significant
21 increase in the percentage of fine lateral roots (reviewed by Kaldorf and Ludwig-Müller,
22 2000). IBA is known to contribute to the regulation of RSA (Overvoorde *et al.*, 2010) and
23 is recognized as an important regulator of auxin activity. It acts as a storage form of IAA
24 and may be converted to IAA, thus contributing to the formation of IAA gradients that are
25 required for root development (reviewed by Simon and Petrášek, 2011). Moreover, the root
26 phenotype of AM plants could be mimicked through the application of exogenous IBA

1 (Kaldorf and Ludwig-Müller, 2000). Therefore, an increased IBA concentration might be
2 involved in AM root morphogenesis.

3 An important auxin homeostasis mechanism involves the formation of auxin
4 conjugates, as free IAA comprises only up to 25% of the total amount of IAA, depending
5 on the tissue and plant species (Ludwig-Müller, 2011). In most cases, IAA can be
6 converted to ester conjugates with sugars or amide conjugates with amino acids, and a
7 fraction of these conjugates may be hydrolyzed back to free IAA (Ludwig-Müller, 2011).
8 The levels of amide conjugates of IAA and IBA have been shown to increase in the roots of
9 maize inoculated with *G. intraradices* (Fitze *et al.*, 2005), and the increased formation of
10 these conjugates is in line with the accumulation of transcripts for a putative IAA-amido
11 synthetase and an auxin-responsive GH3-like protein in tomato mycorrhizal roots, mainly
12 in arbuscule-containing cells (Fiorilli *et al.*, 2009). However, the function of auxin-
13 conjugates in AM roots is currently unclear. They are possibly involved in the development
14 of colonization and the control of fungus morphogenesis, as suggested by Fiorilli *et al.*
15 (2009), while their involvement in root morphogenesis is unclear, as they play a negative
16 role in root branching (Quint *et al.* 2009).

17 The proper transport of auxin, which leads to the formation of concentration
18 gradients, is required for the regulation of the sequential steps of LR formation, which
19 include priming of pericycle cells, acquisition of founder cell identity, cell cycle
20 reactivation and primordium development (Dubrovsky *et al.*, 2011). Indole-3-acetic acid
21 moves passively through the vascular tissues and actively, in a polar manner, across plant
22 cells, depending on specific influx and efflux protein carrier proteins. Among these
23 proteins, PIN efflux proteins are the main regulators of polar auxin transport in the root
24 apical zone (Finet and Jaillais, 2012). Efflux PIN3 and PIN7 proteins have been shown to
25 be involved in the correct positioning and extension of the competent pericycle zone for LR
26 initiation (Dubrovsky *et al.*, 2011), while the rearrangement of PIN1 polarity, mediated by

1 endocytic recycling of the PIN1 protein, redirects the auxin flux into the developing LR
2 (Ruyter-Spira *et al.*, 2011). Once bound to its receptor, auxin promotes the degradation of
3 AUX/IAA transcription repressors. This allows ARFs (Auxin Response Factors) to activate
4 the transcription of genes related to LR initiation and development (for reviews, see e.g.:
5 Fukaki and Tasaka, 2009; Péret *et al.*, 2009; Overvoorde *et al.*, 2010; Finet and Jaillais,
6 2012). This mechanism is conserved between dicot and monocot plants (Dubrovsky *et al.*,
7 2011; Smith and De Smet 2012), and is therefore operative in the potential hosts of AM
8 fungi.

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

19 The above-reported data indicate that, in addition to the variations in auxin
20 concentration which have been found in a number of colonized AM plants, the regulation
21 of auxin transport and sensitivity to auxin may be equally important for AM root
22 morphogenesis. Different signal molecules, such as sucrose (Jain *et al.*, 2007; Hammond
23 and White, 2011) and hormones including ethylene, cytokinins and strigolactones (see
24 below), gibberellins (Gou *et al.*, 2010), jasmonate (Sun *et al.*, 2009; 2011) and abscisic acid
25 (Shkolnik-Inbar and Bar-Zvi, 2010), and other substances, such as nitric oxide (Calcagno *et*
26 *al.*, 2012; Chen and Kao, 2012) and flavonoids (Harrison and Dixon, 1994; Abdel-Lateif *et*

1 *al.*, 2012), could influence mycorrhizal RSA by altering the auxin and PIN protein
2 synthesis and/or distribution. However, there is still no evidence in favor of a changed
3 sensitivity/response to auxin in relation to both Pi starvation and AM colonization in AM-
4 hosts. Differential expression of genes involved in auxin signaling has been shown between
5 Pi-starved and Pi-sufficient maize plants (Li *et al.*, 2012) and the induction of putative
6 ARFs has been found during AM symbiosis in maize, rice and *M. truncatula*, but not in *L.*
7 *japonicus* (reviewed by Formey *et al.*, 2013). However, comparative transcriptomic
8 analysis among these plant species has not detected any common orthologous auxin-
9 specific genes involved in root development of AM-colonized plants (Formey *et al.*, 2013).

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

15 *Cytokinins*

16 Cytokinins (CKs) play a crucial role in regulating the proliferation and differentiation
17 of plant cells, and also control many developmental processes. They are recognized as
18 essential regulators of the plant root system, as they are involved, antagonistically to auxin,
19 in the control of the size of the root apical meristem, and in the rate of root growth and LR
20 organogenesis (Sakakibara, 2006; Werner *et al.*, 2010; Marhavý *et al.*, 2011). They can
21 redirect assimilates and induce invertases, thus contributing directly to the plant carbon
22 redistribution (Ludwig-Müller, 2010). CK receptors are essential for the establishment of
23 symbiosis with rhizobial bacteria (Gonzalez-Rizzo *et al.*, 2006), and CKs are thought to be
24 involved, as auxin, in the repression of defense responses of the host during the
25 establishment of symbiosis (Ludwig-Müller, 2010). However, recent studies have

1 suggested that CKs might not be involved to any great extent in the regulation of
2 mycorrhizal development (see Foo *et al.*, 2013).

3 A number of AM plants accumulate more CKs than non-mycorrhizal plants in both
4 the shoots and the roots (Allen *et al.*, 1980; Drüge and Schönbeck, 1992; van Rhijn *et al.*,
5 1997; Torelli *et al.*, 2000; Shaul-Keinan *et al.*, 2002). However, the CK concentration in
6 AM-colonized maize plants has been shown to only increase during the late plant growth
7 phase, in relation to non-mycorrhizal controls (Danneberg *et al.*, 1992). Since the main
8 sites of CK synthesis include the root tips (Aloni *et al.*, 2006), the high CK level found may
9 be, in part, a consequence of increased root branching. Cytokinin-like substances have been
10 shown to be produced by axenically-grown mycelium of *G. mosseae* (Barea and Azcon-
11 Aguilar, 1982). However, the possible contribution of AM fungi to the regulation of the
12 host CK level is unclear (Barker and Tagu, 2000).

13 The higher CK content in AM plants is in line with the reduction in the root-to-shoot
14 biomass ratio, which occurs when colonization is established. In fact, CK functions as a
15 repressor of root development. Larger root systems have been observed in plants that show
16 a reduction in the CK status, such as mutants for genes encoding CK biosynthetic enzymes,
17 transgenic arabidopsis and tobacco plants with enhanced root-specific degradation of CK,
18 or plants treated with anti-CKs (Arata *et al.*, 2010). A low root-to-shoot biomass ratio is
19 also one of the plant responses to a high Pi status and a direct correlation has been found
20 between CK concentration and Pi availability/tissue content in different plant species. The
21 CK level decreases in arabidopsis under Pi starvation, along with a decrease in the
22 expression of *CRE1*, a CK receptor (Franco-Zorrilla *et al.*, 2002). The CK and Pi contents
23 are also directly related in some potential AMF hosts, such as sunflower (*Helianthus*
24 *annuus*, Salama and Wareing, 1979), *Plantago major* (Baas and Kuiper, 1989) and leek
25 (Torelli *et al.*, 2000).

1 Numerous studies have shown that CK acts as a negative regulator of LR initiation
2 (e.g. Fukaki and Tasaka, 2009). Both exogenous CK and the overproduction of CK have
3 been shown to inhibit LR initiation in arabidopsis (López-Bucio *et al.*, 2002, Laplaze *et al.*,
4 2007). Conversely, mutants in CK receptors or signal transduction and transgenic plants
5 with reduced levels of CK, caused by the overexpression of *CK Oxidase/Dehydrogenase*,
6 which encodes a CK-degrading enzyme, exhibit an increased number of LRs (Laplaze *et*
7 *al.*, 2007; Bielach *et al.*, 2012).

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

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

22 In agreement with the negative role of CK in LR formation, root branching decreases
23 in arabidopsis plants grown under high Pi (and therefore with a high CK content) (López-
24 Bucio *et al.*, 2002, Laplaze *et al.*, 2007). However, the opposite occurs in many plant
25 species, including several AM host plants, which instead exhibit decreased branching when
26 grown under low Pi conditions (table 2). Nevertheless, a reduction in LR formation,

1 induced by CK, has been documented in different plants. The inhibition of LR primordia
2 formation has been observed after exogenous CK administration in rice (Debi *et al.*, 2005)
3 and RNA interference of the CK receptor MtCRE1 has been shown to increase the number
4 of LRs in *M. truncatula* (Gonzalez-Rizzo *et al.*, 2006).

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

11 *Ethylene*

13 Ethylene (ET) plays an important role in coordinating internal and external signals, as
14 well as in several stress responses and interaction of plants with other organisms (Lei *et al.*,
15 2010; López-Ráez *et al.*, 2010). In AM symbiosis, ET and salicylic acid function as
16 negative regulators of mycorrhizal intensity (Gamalero *et al.*, 2008; Ludwig-Müller, 2010).
17 In fact, a strong ET inhibitory effect has been observed on early symbiotic gene expression,
18 on fungus entry into roots (Mukherjee and Ané, 2011) and on intraradical fungal spread
19 (Martín-Rodríguez *et al.*, 2011). The ET content is increased by a deficiency of ABA,
20 which is in contrast necessary for arbuscule formation and is positively correlated to
21 mycorrhizal establishment (Ludwig-Müller, 2010; Martín-Rodríguez *et al.*, 2011).
22 Accordingly, most papers indicate that ET production is diminished in AM-infected plants
23 (McArthur and Knowles, 1992; Besmer and Koide, 1999; López-Ráez *et al.*, 2010),
24 although a few contrary results have also been reported (Dugassa *et al.*, 1996).

25 Ethylene, like auxin and CK, is an important regulator of root morphogenesis. It
26 inhibits root elongation by reducing cell elongation synergistically with auxin (reviewed by

1 Muday et al. 2012). However, it also acts antagonistically to auxin by inhibiting LR
2 formation in the earliest stages of LR initiation, as has been shown through treatments with
3 ET or with the ET precursor 1-aminocyclopropane carboxylic acid (ACC), and in the
4 recent genetic studies on arabidopsis and tomato (reviewed by Fukaki and Tasaka, 2009;
5 Lewis *et al.*, 2011; Muday *et al.*, 2012).

6 The regulation of ET-auxin interactions play an important role in root morphogenesis:
7 it has, in fact, been shown that ET and auxin can reciprocally influence and regulate their
8 biosynthesis and response pathway (Stepanova *et al.*, 2007; Vanstraelen and Benková,
9 2012). ACC has been found to reduce free IAA and to decrease auxin-induced gene
10 expression in regions where LR form (Negi *et al.*, 2010; Lewis *et al.*, 2011). In addition,
11 high ET levels increase PIN3 and PIN7 expression, and this increase results in elevated
12 auxin transport, which prevents the localized accumulation of the auxin needed to drive LR
13 formation (Lewis *et al.*, 2011). However, the effects of ET have been shown to depend on
14 its concentration (Pierik et al. 2006). Treatments with low concentrations of ACC have
15 been shown to promote the initiation of new LR primordia by increasing Trp-dependent
16 auxin synthesis. Higher doses have in contrast been shown to inhibit initiation to a great
17 extent, as reported above, but also to promote the emergence of existing primordia in
18 arabidopsis (Ivanchenko *et al.*, 2008; Fukaki and Tasaka, 2009).

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

25 Ethylene is involved in root development in response to low Pi availability, as has
26 been shown in different plants (Borch *et al.*, 1999; López-Bucio *et al.*, 2002; Ma *et al.*,

1 2003; Dinh *et al.*, 2012; Niu *et al.*, 2013) including arabidopsis and common bean.
2 Ethylene has shown an opposite effect on the primary/main root length in low and high Pi
3 conditions in these two species. The use of ET inhibitors or mutants has shown that
4 endogenous ET limits PR lengthening in Pi-sufficient conditions as reported above, while
5 the opposite happens in low-Pi conditions, with ET promoting root extension (Borch *et al.*,
6 1999; Ma *et al.*, 2003). This happens although Pi-deficient roots of common bean produce
7 twice as much ET g⁻¹ dry weight as roots of Pi-sufficient plants (Borch *et al.*, 1999), and
8 increased transcript levels for ET biosynthetic genes have been found in arabidopsis
9 (reviewed by Nagarajan and Smith 2012). Moreover, in the common bean, endogenous ET
10 decreases LR density in low Pi conditions and increases it in Pi-sufficient ones (Borch *et*
11 *al.*, 1999). The use of some ET signaling mutants (such as *etr1*, *ein2*, *ein3*) in arabidopsis
12 has shown that endogenous ET also decreased the LR number and density under low Pi
13 (López-Bucio *et al.*, 2002). A different root sensitivity to ET has thus been considered in
14 relation to Pi availability (Borch *et al.*, 1999; Ma *et al.*, 2003).

15 Despite showing similar responses to ET, morphogenesis of the root system of the
16 common bean and arabidopsis under low Pi is quite different (Borch *et al.*, 1999; López-
17 Bucio *et al.*, 2002), thus showing a different responsiveness to ET also from species to
18 species. Transcriptomic analyses, in agreement, have shown both up- and down-regulation
19 of *ET Response Factor* genes in a variety of plant species on the basis of the Pi availability
20 (reviewed by Nagarajan and Smith, 2012). In arabidopsis, according to López-Bucio *et al.*
21 (2002), ET is not involved in the LR response to low Pi. When auxin is applied
22 simultaneously with ACC, the latter is unable to prevent auxin stimulation of LR formation
23 in arabidopsis (Ivanchenko *et al.*, 2008), which is consistent with a dominant role of auxin
24 on ET. On the contrary, root morphogenesis of the common bean under low Pi is probably
25 under the main control of ET. This plant, in these conditions, decreases the number of LRs
26 without any significant change in the main root length and therefore reduces root

1 branching, as happens in many non-colonized potential AM hosts. This leads to the
2 hypothesis that the different degree of branching found for non-colonized and colonized
3 AM-host plants depends on a switch from one state dominated by ET and found in Pi-
4 starved, non-colonized plants to another one that is controlled by auxin, when colonization
5 has been established.

6 7 *Strigolactones*

8 Among the hormones that can affect RSA, strigolactones (SLs) have been the subject
9 of a great deal of interest in recent years, although their effects have only been analyzed in
10 a few species. Strigolactones are terpenoid lactones (for a review, see Seto *et al.*, 2012)
11 which play different roles in plants. They act as stimulants for the germination of seeds of
12 root parasitic plants, such as *Orobancha* spp. and *Striga* spp. (Cook *et al.*, 1966), and hence
13 play a negative role on the plant that exudes them. At the same time, they are rhizosphere
14 signals that induce hyphal branching (Akiyama *et al.*, 2005) and spore germination of some
15 AM fungi (Besserer *et al.*, 2006); inside the root, they seem to promote AM colonization,
16 thus favouring the establishment of symbiosis with AM fungi (reviewed by Foo *et al.*,
17 2013). This may be related to a SL-induced fungal production of short-chain chitin
18 oligomers, which, after perception, have been shown to activate the Sym-dependent
19 signaling pathway involved in the initial stages of fungal root colonization in *M. truncatula*
20 (Genre *et al.*, 2013). Besides their role in plant interactions, SLs act as phytohormones:
21 they are thought to be synthesized mainly in the lower parts of the stem and in the roots and
22 move acropetally towards the shoot apex (Kohlen *et al.*, 2011). They have been shown to
23 inhibit shoot branching and to regulate root development and its architecture (Ruyter-Spira
24 *et al.*, 2011; Seto *et al.*, 2012; Brewer *et al.*, 2013). Several genes, isolated from both
25 mono- and dicots, are involved in the synthesis, starting from carotenoids, or the signaling
26 of SLs. The biosynthetic genes include *MAX1* (*More Axillary Growth1*), *MAX3* and *MAX4*

1 of arabidopsis, *RMS1* (*Ramosus1*) and *RMS5* of pea (*Pisum sativum*), *D10* (*Dwarf10*), *D17*
2 and *D27* of rice, and *DAD1* (*Decreased Apical Dominance1*) and *DAD3* of petunia. The
3 only SL signaling genes described so far are *MAX2/D3/RMS4*, and *AtD14/OsD14/DAD2*
4 (reviewed by Arite *et al.*, 2009; Seto *et al.*, 2012; Waters *et al.*, 2012; Yoshida *et al.*, 2012;
5 Janssen and Snowden, 2012). It has recently been suggested that the binding of DAD2 with
6 SLs allows an interaction with MAX2, which leads to ubiquitination and degradation of
7 downstream signaling proteins (Janssen and Snowden, 2012).

8 Analysis of SL-deficient and signaling mutants and the use of the synthetic SL-
9 analogue GR24 have shown that endogenous SLs have little impact on PR length in rice
10 (Arite *et al.*, 2012) and tomato (Koltai *et al.*, 2010), as well as in arabidopsis under optimal
11 growth conditions (Ruyter-Spira *et al.*, 2011). Nevertheless, SLs stimulate PR lengthening
12 in arabidopsis under carbohydrate starvation, because of an increased meristem cell number
13 and size of the transition zone (Ruyter-Spira *et al.*, 2011). Endogenous SLs increase the
14 lengthening of the crown roots of rice as demonstrated by the shorter crown roots of the
15 *d10-1(max4)* synthesis mutant and the *d14* signaling mutant and the rescuing of the defect
16 in the *d10-1* mutant but not in *d14* with application of GR24 (Arite *et al.*, 2012), thus
17 pointing to a general role of SLs on root lengthening. In addition, SLs negatively regulate
18 LR density in arabidopsis by affecting both LR initiation and elongation (Kapulnik *et al.*,
19 2011a; Ruyter-Spira *et al.*, 2011).

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

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

12 The enhanced crown root elongation observed under Pi starvation in rice is in line
13 with the enhanced production of SLs in these conditions, and is supported by a lack of
14 crown root elongation in *d10-1* and *d14-1* mutant seedlings (Arite *et al.*, 2012). The effects
15 of SLs under low Pi on root elongation are thus similar to those of ET in rice.
16 Unfortunately there are no data on the effect of SLs on branching in this plant.

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

1 independent auxin responses, may dominate the root morphogenesis of arabidopsis in some
2 stages of development (Mayzlish-Gati *et al.*, 2012).

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

18 19 CONCLUSIONS

20
21 Plant responses to AM colonization involve physiological, molecular and
22 morphological mechanisms, including a change in RSA which becomes more branched in
23 relation to the non colonized controls. In this paper, an overview of the possible
24 mechanisms implicated in AM root morphogenesis and a model of root growth regulation
25 in which fungal exudates, sugars and hormones are the main players in the regulation of
26 mycorrhizal root growth, are provided (Fig. 1).

1 Fungal exudates induce LR formation in the first stages of plant-fungus interaction
2 (Oláh *et al.*, 2005; Mukherjee and Ané, 2011), possibly to increase the potential sites of
3 colonization. However, questions about the nature of the bioactive molecules and the
4 pathways involved in LR formation are still unclear, particularly for non-legume plants,
5 where a Sym-independent pathway seems to exist (Gutjahr *et al.*, 2009a; Mukherjee and
6 Ané, 2011). Fungal exudates may also influence root morphogenesis at later stages of
7 colonization, when, however, other factors probably are the main regulators.

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

21 Apart from hormones, in this paper it has been proposed that, in established
22 mycorrhizae, the symbiotic carbon/Pi exchange itself, which occurs mainly in the
23 arbusculated cells (Helber *et al.*, 2011), may regulate AM root morphogenesis. When
24 plants are colonized by AM fungi an increased transport of photosynthates, which are
25 directed towards the fungal sink zones of the root cortex, occurs. Since a relation exists
26 between elevated sugar levels and enhanced LR formation (Lei *et al.* 2011), the flux of

1 sugars towards the colonized root cortex, may stimulate LR formation. However, further
2 research is required to confirm this hypothesis, as well as for understand in more detail the
3 role of hormones in AM root morphogenesis. There is still limited knowledge on the
4 distribution of hormones and other morphogens, as well as of their complex network of
5 interactions, in AM roots. As far as auxin is concerned, it has been shown that a large
6 number of factor, hormonal or not, converge on the regulation of its synthesis, transport
7 and the downstream signaling pathway. It would not be surprising that fungal exudates also
8 may influence AM root morphogenesis through interaction with auxin, in analogy with the
9 Nod-factor during nodule formation (see Kuppusamy *et al.*, 2009). Moreover, among
10 hormones, a possible role in AM root morphogenesis may be played by gibberellins. These
11 latter, in addition to auxin, CKs, ET and SLs, are involved in the root morphogenesis in
12 response to Pi availability (Jiang *et al.*, 2007; Devaiah *et al.*, 2009); however their behavior
13 and functions are still unclear in AM plants (Ludwig-Müller, 2010; Foo *et al.*, 2013).

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

26

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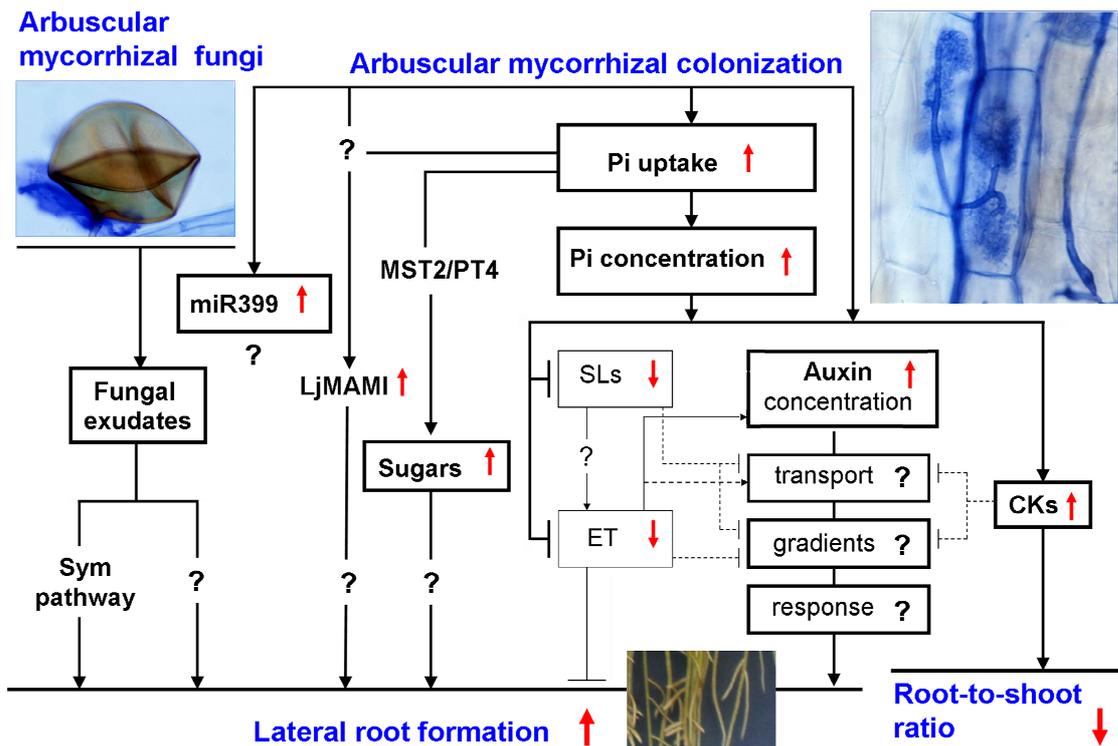
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1
2 Fig. 1. Schematic drawing of the possible signaling events that lead to increased root branching in arbuscular
3 mycorrhizal (AM) plants. In the first stage of colonization, fungal exudates induce lateral root (LR) formation
4 through the common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

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

Plant	AM fungus	Culture condition (days)	Main roots			1 st order LRs			2 nd order LRs			3rd order LRs			Total root length	%AMF	References
			no.	l	rb	no.	l	rb	no.	l	rb	no.	l	rb			
<i>Allium porrum</i>	<i>Glomus sp.</i> strain E3	a (105)	>	<	>	-	<	-	-	-	-	-	-	-	=	69	Berta <i>et al.</i> , 1990; 1993
<i>Olea europaea</i>	<i>Glomus mosseae</i>	b (180)	>	=	=	>	>	>	>	>	>	>	-	-	>	29-42	Citernesi <i>et al.</i> , 1998
<i>Oryza sativa</i>	<i>Glomus intraradices</i>	a (42)	=	>	>	> ^(1,2)	-	-	> ⁽²⁾	-	-	-	-	-		30-50	Gutjahr <i>et al.</i> , 2009a
<i>Platanus acerifolia</i>	<i>Glomus fasciculatum</i>	b (77)	=	=	=	=	<	>	>	<	>	>	=	>	>	79	Tisserant <i>et al.</i> , 1992; 1996
<i>Populus var. Beaupré</i>	<i>Scutellispora calospora</i> ,	b (115)	-	=	>	-	>	=	-	>	=	-	=	-	=	8	Hooker <i>et al.</i> , 1992
	<i>Glomus sp</i> strain E3; <i>G. caledonium</i>		-	=	=	-	>	>	-	>	>	-	=	-	=	22; 28	
<i>Prunus cerasifera</i>	<i>Glomus intraradices</i>	a (75)	-	=	>	-	=	>	-	=	>	-	=	-	>	80	Berta <i>et al.</i> , 1995
	<i>Glomus mosseae</i>		-	=	>	-	=	>	-	=	=	-	=	-	>	70	
<i>Vitis vinifera</i>	<i>Glomus fasciculatum</i>	b (56)	=	<	>	>	=	>	>	<	>	>	=	-	>	90	Schellenbaum <i>et al.</i> , 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. In brackets, the experiment's duration in days. ⁽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.

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

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

Culture conditions: a, sand/nutrient solution; b, agarized medium; c, moistened filter paper; d, hydroponic. In brackets, the experiment's duration in days.

Type of root: ⁽¹⁾, primary; ⁽²⁾, seminal; ⁽³⁾, adventitious; ⁽⁴⁾, basal and, ⁽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.