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Review

Jasmonates in arbuscular mycorrhizal interactions

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Abstract

The mutualistic interaction between plants and arbuscular mycorrhizal (AM) fungi is believed to be regulated from the plant side among other signals by the action of phytohormones. Evidences for this are based mainly on application experiments and determination of phytohormone levels in AM roots by comparison to non-mycorrhizal roots. In case of jasmonates, additional proof is given by reverse genetic approaches, which led to first insights into their putative role in the establishment and functioning of the symbiosis. This review summarizes the current data about phytohormone action in AM roots and the role of jasmonates in particular.

Keywords: *Medicago truncatula*; *Glomus* species; *Hordeum vulgare*; Allene oxide cyclase; Jasmonic acid; Phytohormones

Contents

1. Introduction

Arbuscular mycorrhizas (AMs) are the most common type of mycorrhizas (Smith and Read, 1997), formed between roots of more than 80% of the terrestrial plant species and fungi from the phylum Glomeromycota (Schüssler et al., 2001). The fungus is able to grow into the root cortex

Abbreviations: AM, arbuscular mycorrhiza(l); AOC, allene oxide cyclase; AOS, allene oxide synthase; JA, jasmonic acid; LOX, lipoxygenase; OPDA, 12-oxo-phytodienoic acid; PT, phosphate transporter.

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by forming intraradical hyphae which are subsequently differentiated into highly branched structures, the arbuscules, within cortex cells. Both intraradical hyphae and arbuscules are responsible for exchange of nutrients between the plant and the fungus. The plant supplies the fungus with carbohydrates, whereas the fungus assists the plant with the acquisition of phosphate and other mineral nutrients from the soil (Harrison, 1997, 1998). The beneficial effects of the AM symbiosis result from a complex molecular dialogue between the two symbiotic partners (Harrison, 1999). Some processes occurring in this interaction are known to be mediated by phytohormones. The present overview will summarize the data related to the involvement of phytohormones in the regulation of AM symbiosis, concentrating on the role of jasmonates. Thereby, our own results obtained in a project funded through "MolMyk" DFG priority program will be reflected. For further aspects of the role of phytohormones in mycorrhizal interaction other reviews may be considered (Barker and Tagu, 2000; Ludwig-Müller, 2000; Vierheilig, 2004; Vierheilig and Piché, 2002).

2. Phytohormones in AM interactions

Phytohormones such as cytokinins (CK), gibberellins (GA), ethylene (ET), abscisic acid (ABA), auxins, and jasmonic acid (JA) are assumed to participate in the communication between AM fungus and plant (Ludwig-Müller, 2000), but their precise role in the interaction is still unknown. Evidence for phytohormone function in the establishment of AM comes mainly from application experiments or from altered endogenous levels observed during mycorrhization (Barker and Tagu, 2000; Bothe et al., 1994; Regvar et al., 1996). Since salicylic acid (SA) is active in the establishment of the systemic acquired resistance of plants following pre-infection with a pathogen, SA has also been analyzed in the interaction of plants with AM fungi and will be included in this overview (Table 1). Data about involvement of brassinosteroids in AM are not available to date.

2.1. Cytokinins (CK)

AM plants accumulate more CK than non-mycorrhizal plants in both shoots and roots (Allen et al., 1980; Drüge and Schönbeck, 1992; van Rhijn et al., 1997). The levels increase, however, only in a very late phase of mycorrhization (Danneberg et al., 1992). Suppressed expression of two pathogenesis-related (PR) genes was detected in mycorrhizal roots accompanied by increased levels of a zeatin riboside-like CK (Ginzberg et al., 1998). Moreover, several CK-inducible early nodulin (ENOD) genes were found to be up-regulated (van Rhijn et al., 1997). It is unclear, however, whether the altered CK level is due to plant or fungal production. It was assumed that the increase in CK levels could be due to increased phosphate nutrition in AM roots resulting in CK production, presumably synthesized in the additional root primordia (Barker and Tagu, 2000). The increased flux of CK to the shoot may enhance shoot growth, whereas root growth remains unaffected by increased CK (Allen et al., 1980; Drüge and Schönbeck, 1992).

2.2. Gibberellins (GA)

There are only few data about a possible involvement of GA in AM interaction. Inoculation of *Bouteloua gracilis* with *Glomus fasciculatus* resulted in significantly increased

Table 1
Survey about the data available concerning phytohormone action in mycorrhizal roots

Phytohormone	Effects of application on mycorrhization rate	Endogenous content in mycorrhizal roots (compared to non-mycorrhizal roots)	References
Cytokinin	+	↑	Allen et al. (1980) and García-Garrido and Ocampo (2002)
Gibberellin	+ −	↑ ↓	Allen et al. (1982) and Slezack et al. (2000)
Ethylene	−	↑/−	Geil et al. (2001), Geil and Guinel (2002) and Dugassa et al. (1996)
Abscisic acid	n.d.	↑ (in roots) ↓ (in shoots)	Bothe et al. (1994), Danneberg et al. (1992), Meixner et al. (2005) and Allen et al. (1982)
Auxin	+, Enhanced fungal growth	Young roots: free IBA ↑ Old roots: conjugated IBA ↑ Free IAA: no changes	Kaldorf and Ludwig-Müller (2000), Fitze et al. (2005), Meixner et al. (2005) and Danneberg et al. (1992)
Salicylic acid	−, No effects	↓	Blilou et al. (1999), Blilou et al. (2000a), Blilou et al. (2000b), Ludwig-Müller et al. (2002) and Medina et al. (2003)
Jasmonic acid	+ (Low concentrations) − (High concentrations)	↑	Regvar et al. (1996), Ludwig-Müller et al. (2002), Hause et al. (2002), Vierheilig and Piché (2002), Stumpe et al. (2005) and Meixner et al. (2005)

The effects on mycorrhization rate are given as "+" and "−" for increasing and decreasing rates, respectively. ↑ and ↓ represent the changes determined after extraction of whole root systems.

GA activity in leaves as demonstrated by a *Hordeum vulgare* half seed bioassay (Allen et al., 1982). In AM roots, however, a tendency for decreased activity was found. On the other hand, *Glomus mosseae* was shown to be capable to synthesize at least two gibberellin-like substances (Barea and Azcón-Aguilar, 1982).

2.3. Ethylene (ET)

Only few studies are published, which include the gaseous hormone ET. Decreased colonization of *Medicago sativa* by *G. mosseae* in response to ethylene was first reported by Azcón-Aguilar et al. (1981) using application of ethrel. The addition of ethylene gas inhibited also the colonization of *Poncirus trifolata* by *G. ramisporohora* (Ishii et al., 1996), and of *Pisum sativum* and *Allium porrum* by *G. aggregatum* (Geil and Guinel, 2002; Geil et al., 2001). Application of 5.5 ppm ethylene to the growth substrate led to characteristic changes in root morphology of *P. sativum* and a marked reduction in the root colonization. Whereas the number of appressoria formed was not affected, abnormal, swollen and highly branched appressoria have been found leading to a reduction of fungal entry into the root tissue (Geil et al., 2001). This effect was dependent on the ET concentration used. Whereas at higher concentrations (0.6 μl/l) root and shoot growth and mycorrhization were reduced, at lower concentrations (0.3 μl/l) root length was reduced without effect on colonization (Geil and Guinel, 2002). In *Linum usitatissimum* roots inoculated with *G. intraradices* ET formation is increased (Dugassa et al., 1996), which was not detected in *Lycopersicon esculentum* inoculated with *G. mosseae* (Vierheilig et al., 1994). It was proposed that ethylene biosynthesis is repressed by increased phenolics in AM *Solanum tuberosum* roots, thus enabling the symbiosis to develop (McArthur and Knowles, 1992). Increased phosphate uptake in the fully colonized plant may counter this effect, enabling the plant to restrict further fungal colonization (Barker and Tagu, 2000).

2.4. Abscisic acid (ABA)

Reports about the endogenous level of ABA in mycorrhizal plants are controversial. A strong increase in ABA level was shown for mycorrhizal roots of *Zea mays* (Bothe et al., 1994; Danneberg et al., 1992) and *Glycine max* (Meixner et al., 2005). Interestingly, this increase has been detected not only in the mycorrhizal root but also in the shoot, suggesting a systemic response. Roots of *B. gracilis* inoculated with *G. fasciculatus* exhibited decreased ABA levels in leaves but unchanged levels in roots (Allen et al., 1982). A reduction of ABA in leaves may reflect the consequence of mycorrhiza on improved water relations of drought stressed plants (Barker and Tagu, 2000; Ruiz-Lozano, 2003).

2.5. Auxins

Mycorrhizal roots exhibit morphological characteristics like increasing number of lateral/fine roots during early growth phases similar to auxin-treated roots. Therefore, a role of auxins in the AM interaction was proposed (Ludwig-Müller, 2000). Initially, application of indole-3-acetic acid (IAA) or of the auxin transport inhibitor tri-iodo-benzoic acid (TIBA) was shown to increase mycorrhization rates (Gunze and Hennessy, 1980; Müller, 1999). Later on, a putative role of auxins in AM symbiosis was strengthened by measurements of endogenous contents of free and conjugated auxins. In *Z. mays* inoculated with *G. intraradices*, an early increase in synthesis of indole-3-butyric acid (IBA) leading to increased levels in free IBA was found, whereas in later phases the free IBA content was constant (Kaldorf and Ludwig-Müller, 2000). This contrasts data obtained for free IAA, which is not increased in mycorrhizal roots of *Z. mays*, *Nicotiana tabacum* and *A. porrum* (Danneberg et al., 1992; Shaul-Keinan et al., 2002), but are elevated in mycorrhizal roots of *G. max* (Meixner et al., 2005).

In case of conjugated auxins, the fraction of conjugated IBA increased in older mycorrhizal roots compared to non-mycorrhizal roots (Kaldorf and Ludwig-Müller, 2000). Ester conjugates of IAA and IBA were found only in low amounts and they did not increase in AM colonized roots, whereas the levels of IAA and IBA amide conjugates increased in later phases of mycorrhization (Fitze et al., 2005). These results may reflect a complex control mechanism to regulate the levels of free and conjugated auxins, which are induced during early stages of the formation of an AM symbiosis (Fitze et al., 2005). On one hand, auxins may facilitate the colonization of a host by increasing the number of lateral/fine roots during early growth phases and thus stimulating the mycorrhizal root colonization (Ludwig-Müller, 2000). On the other hand, auxins could affect growth of AM fungi directly, since it has been reported that auxins strongly affect growth of *G. fistulosum* in vitro (Gryndler et al., 1998).

2.6. Salicylic acid (SA)

SA exogenously applied to inoculated *Oryza sativa* roots reduced root colonization at the onset of symbiotic interaction, but showed no effect on appressoria formation. This excludes a direct inhibitory effect of SA on the fungal growth (Blilou et al., 2000b). Application of SA to leaves of *Cucumis sativus* plants, however, did not affect mycorrhization (Ludwig-Müller et al., 2002). Nevertheless, altered SA accumulation in mycorrhizal plants indicated that SA might be involved in the susceptibility of plants to AM fungi. In mycorrhiza-defective (Myc^-) mutants of *P. sativum*, the SA accumulation was enhanced, whereas in Myc^+ plants the SA accumulation was low (Blilou et al., 1999) or only transient (Blilou et al., 2000a,b). Analysis of transgenic NahG (overexpressing bacterial salicylate

hydroxylase that inactivates SA) and CSA (constitutive SA biosynthesis) *N. tabacum* plants revealed an inverse correlation between SA levels and the degree of root colonization after inoculation with *G. intraradices* or *G. mosseae* (Medina et al., 2003). NahG plants with low SA content showed increased rates of root colonization and higher numbers of infection units and arbuscules, whereas CSA plants with high SA content showed less root colonization. These effects of modulated SA levels were no longer detectable after the level of final root colonization was reached. Therefore, enhanced SA levels may delay root colonization, but did not affect the maximal degree of root colonization (Medina et al., 2003).

2.7. Jasmonic acid (JA)

Conclusions for a possible involvement of JA in mycorrhization were drawn first from application experiments. Treatment of *A. sativum* with low concentrations of JA (5 μM, once per week) stimulated mycorrhizal development (Regvar et al., 1996). Treatment of leaves of *Tropus majus*, *Carica papaya* and *Cucumis sativus* with high concentrations of JA (0.05–5 mM, every second day), however, reduced the mycorrhization of the respective roots drastically (Ludwig-Müller et al., 2002). This suggests a concentration-dependent effect of JA on mycorrhizal plants. Possibly, the JA homeostasis within the plant may control the mycorrhization (see below). The establishment of AM in *H. vulgare* roots was shown to be accompanied by the accumulation of putrescine and agmatine amides of 4-coumarate and ferulate, respectively. Both compounds also accumulated upon treatment of non-mycorrhizal *H. vulgare* roots with jasmonates (Peipp et al., 1997). More recent results revealed that in roots of mycorrhizal plants JA levels are increased in comparison to roots of non-mycorrhizal controls (Hause et al., 2002; Meixner et al., 2005; Stumpe et al., 2005; Vierheilig and Piché, 2002). This implies a possible role of jasmonates in AM formation and will be discussed below.

3. Biosynthesis of jasmonates

Jasmonic acid (JA) and its derivatives, commonly termed jasmonates, are hormonal regulators involved in plant responses to abiotic and biotic stresses as well as in plant development (Creelman and Mullet, 1997; Wasternack and Hause, 2002). The role of jasmonates is well established as part of a complex signal transduction pathway activated upon wounding of leaves by insects (Schilmiller and Howe, 2005) and interaction of plants with microorganisms (Pozo et al., 2004). Levels of endogenous jasmonate increase upon wounding or pathogen attack and are followed by activation of genes involved in plant defense responses such as those coding for proteinase inhibitors, enzymes of phytoalexin synthesis, vegetative storage proteins, thionins and defensins (Devoto and Turner, 2005; Lorenzo and Solano, 2005). It is less understood, however, how the rise of jasmonates is regulated. Usually, the elevation of jasmonate levels is correlated with the activation of genes coding for JA biosynthetic enzymes (Wasternack and Hause, 2002). In *L. esculentum*, *Arabidopsis thaliana* and *Medicago truncatula*, most genes encoding enzymes of JA biosynthesis are also JA-inducible (Isayenkov et al., 2005; Stenzel et al., 2003a; Strassner et al., 2002) suggesting a feed forward regulatory loop. However, the rise in JA precedes the accumulation of corresponding mRNAs, and enzymes of JA biosynthesis occur constitutively in *L. esculentum*, *M. truncatula* and *A. thaliana* leaves (Hause et al., 2000; Isayenkov et al., 2005; Stenzel et al., 2003b).

JA and its derivatives are lipid-derived signals. They are synthesized by the octadecanoid pathway, where 12-oxophytodienoic acid (OPDA) is a central intermediate (Fig. 1). The initial reaction is the 13-lipoxygenase (13-LOX)-catalyzed insertion of molecular oxygen into position 13 of α-linolenic acid (α-LeA) most likely released from plastid membranes. The resulting (13-*S*)-hydroperoxy linolenic acid (13-HPOT) is the substrate for at least seven different pathways (Feussner and Wasternack, 2002). Only the conversion of 13-HPOT by an allene oxide synthase (AOS) specifically for this substrate leads finally to JA. 13-HPOT is converted by the 13-AOS into an unstable allene oxide that is further processed by an allene oxide cyclase (AOC). 13-AOSs are CYP450 enzymes located in the plastids. They have been cloned as single or multi-copy genes from various plant species and were grouped as the subfamily *CYP74A* (Feussner and Wasternack, 2002). The unstable allene oxide can hydrolyze non-enzymatically into α- and γ-ketols or racemic OPDA. Under cellular conditions presumably most of the allene oxide is converted by an AOC, forming exclusively the *cis*-(+)-enantiomer (9*S*,13*S*) of OPDA, which represents that enantiomeric structure present in the naturally occurring jasmonates. Therefore, the AOC is regarded to be of special importance in JA biosynthesis.

The AOC was cloned from a variety of plant species including *L. esculentum* (Ziegler et al., 2000), *A. thaliana* (Stenzel et al., 2003b) and *M. truncatula* (Isayenkov et al., 2005). In all these species, AOC protein is located in plastids. In *A. thaliana* AOC protein occurs constitutively in all leaf tissues (Stenzel et al., 2003b). By contrast, in *L. esculentum AOC* is specifically expressed in all vascular bundles and the surrounding parenchymatic cells (Hause et al., 2000, 2003). Noteworthy, the occurrence of AOC in vascular tissue of *M. truncatula* is similar to that in tomato. The AOC protein was found to occur constitutively in all vascular tissues of *M. truncatula* including the root central cylinder (Isayenkov et al., 2005).

The conversion of OPDA is catalyzed by the OPDA reductase 3 (OPR3). This enzyme exhibits specificity for *cis*-(+)-OPDA which is converted to 3-oxo-2-(2′-pentenyl)-

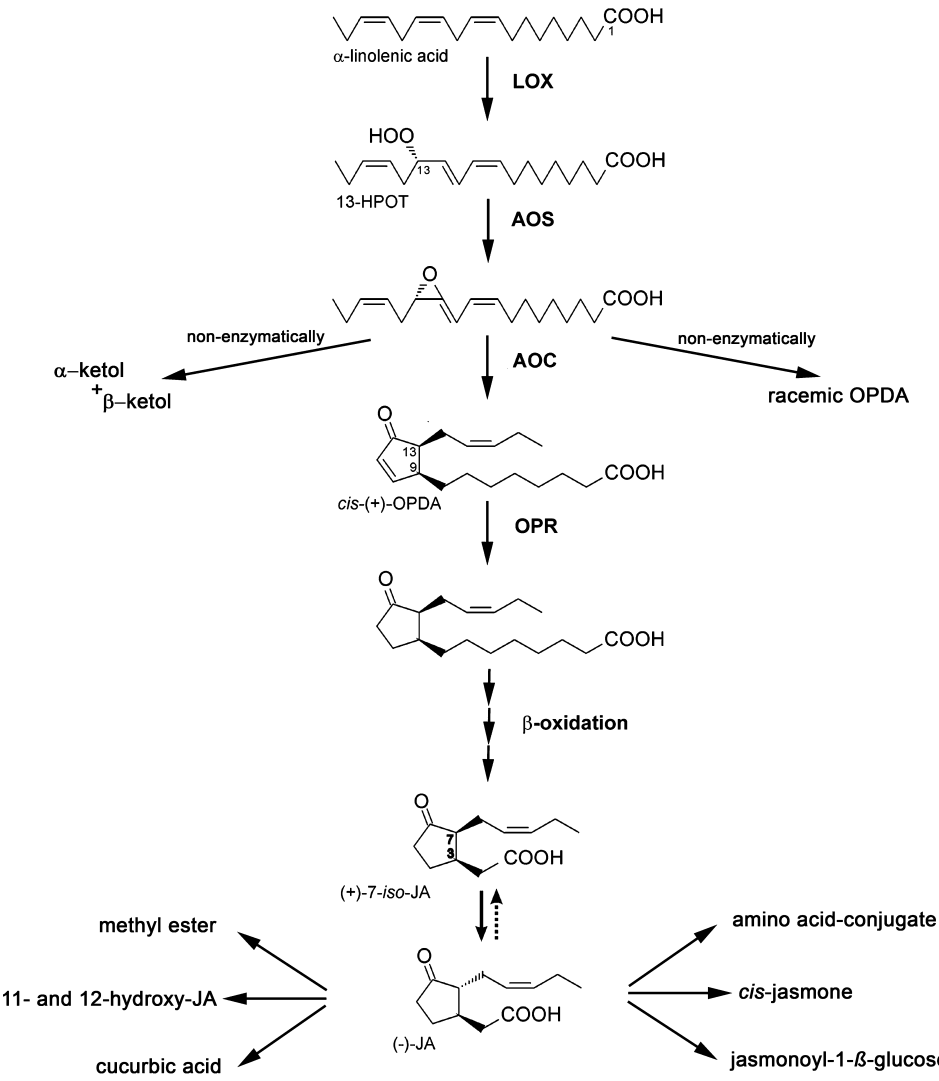

Fig. 1. Metabolic scheme of jasmonate biosynthesis and derived pathways. The enzymes involved are: 13-lipoxygenase (LOX), 13-allene oxide synthase (AOS), allene oxide cyclase (AOC), and oxophytodienoic acid reductase 3 (OPR). The different metabolic steps converting JA are indicated by arrows and the respective end products.

cyclopentane-1-octanoic acid (OPC-8). The OPR3 carries a peroxisomal target sequence and was localized in peroxisomes (Strassner et al., 2002). In the final steps of JA biosynthesis, the carboxylic acid side chain is shortened in three cycles of β-oxidation by acyl-CoA oxidase (ACX), multifunctional proteins (MFP) and 3-ketoacyl-CoA thiolase (KAT). These processes take place also in peroxisomes.

JA is not the only cyclopentanone compound occurring in plants. At least six metabolic conversions of JA can take place leading to various compounds as shown in Fig. 1 (for review, see Delker et al., 2006). This raises the question whether JA or its metabolites exhibit different biological activities. At least for amino acid-conjugates of JA a biological function is highly probable: Several JA-dependent responses are affected in mutant plants missing the capability to produce JA-Ile conjugate indicating at least partial differences in signal transduction of JA- and JA-Ile (Staswick and Tiryaki, 2004).

4. Occurrence of jasmonates in mycorrhizal roots

Colonization of various plants with mycorrhizal fungi leads to increased endogenous levels of jasmonates within the roots. This was shown for *H. vulgare* (Hause et al., 2002), *Cucumis sativus* (Vierheilig and Piché, 2002), *M. truncatula* (Stumpe et al., 2005) and *G. max* (Meixner et al., 2005). The increase in jasmonate levels of mycorrhizal roots compared to non-mycorrhizal roots differed widely among various plant species. Whereas in *M. truncatula* the basal level was relatively low and increased two to three times in mycorrhizal roots (Stumpe et al., 2005), in *H. vulgare* and *C. sativus* an up to 5-fold and 14-fold increase, respectively, was found in response to mycorrhization (Hause et al., 2002; Vierheilig and Piché, 2002). In all cases, however, the content of JA increased steadily. This contrasts upstream components of the LOX pathway, which were not altered by AM in *M. truncatula* (Stumpe et al., 2005), and to OPDA that remained at unchanged levels

in AM roots of each plant analyzed so far (Hause et al., 2002; Stumpe et al., 2005). The amino acid conjugate of JA, JA-Ile, however, increased transiently in the early phase of colonization of *H. vulgare* (Hause et al., 2002).

There is no approach to localize directly the site of JA accumulation within plant tissues so far. Therefore, an indirect method by analyzing the temporal and spatial expression of JA biosynthetic genes was used in *H. vulgare* and *M. truncatula* (Hause et al., 2002; Isayenkov et al., 2005). The expression of these genes can be taken as indicator for elevated JA levels (Maucher et al., 2000; Stenzel et al., 2003a). In addition, the occurrence of a protein encoded by a JA responsive gene can be taken as marker of elevated JA levels having signaling capacity (Hause et al., 1996). All the analyzed proteins are expressed in arbuscule-containing cells (Fig. 2), whereas cortex cells of non-mycorrhizal roots did not contain any detectable amounts of the respective proteins (Hause et al., 2002; Isayenkov et al., 2005). This spatial and coordinate expression implicates a local rise in JA specifically within arbuscule-containing cells. It is, however, not to exclude that JA or derivatives derived from it, could move into other cells/organs because jasmonates have been shown to act as mobile signals in response to wounding (Schilmiller and Howe, 2005). Nevertheless, due to the dilution of any local JA level by whole tissue extraction, the cell-specific elevation of JA could be noteworthy.

In addition to the putative spatial link between mycorrhization and JA levels, a temporal correlation was found. Increased JA levels occurred after the onset of mycorrhization (Hause et al., 2002). This implies that a fully established mycorrhiza rather than the recognition of the interacting partners or the establishment of the symbiotic interface might cause expression of genes coding for JA biosynthetic enzymes and elevation of JA levels. It was further discussed that enhanced JA levels in mycorrhizal roots could be linked to an increase in the number of collapsed arbuscules (Vierheilig, 2004).

For mycorrhizal *H. vulgare* roots, it has been assumed that the increased JA formation could be due to osmotic stress caused by increased carbohydrate influx from the shoot into mycorrhizal root (Hause et al., 2002). Mycorrhizal roots represent an increased sink compared to non-mycorrhizal roots (Douds et al., 2000). The increased transport of carbohydrates into the root and the glucose-inducible expression of *AOS* and *AOC* (Hause et al., 2000; Maucher et al., 2000) suggest the following scenarios: (i) sugars supplied by source tissues are translocated into sink tissues, where an osmotic stress may occur; (ii) the sugar itself may induce expression of genes coding for

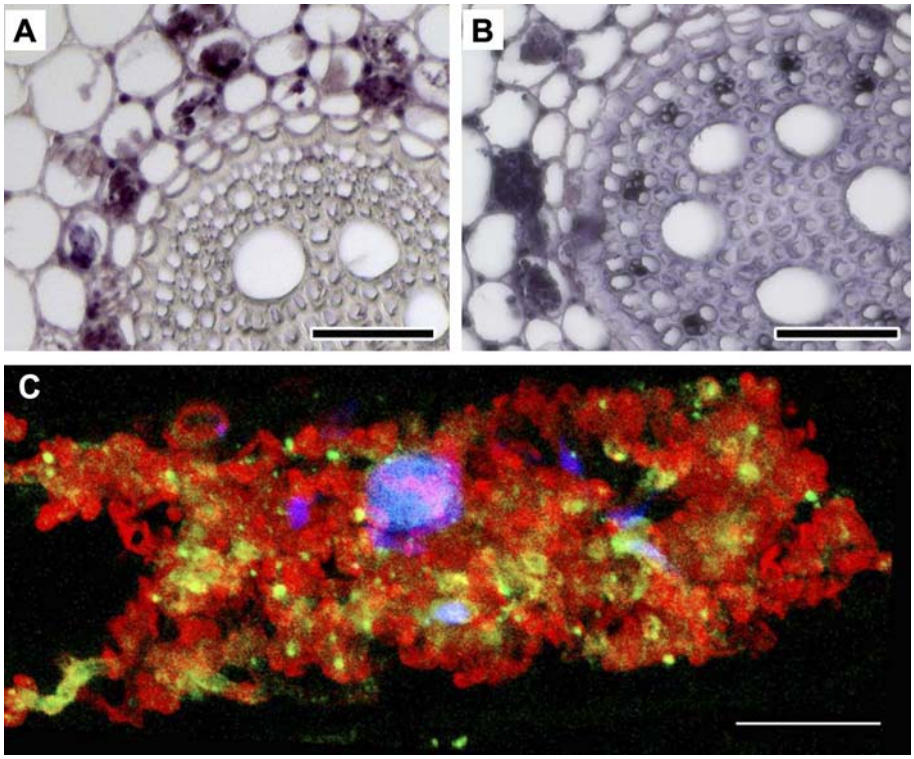

Fig. 2. Occurrence of JA-biosynthetic enzymes and JA-induced proteins in arbuscule-containing cells. Cross sections of a mycorrhizal *H. vulgare* root (A, B) and longitudinal section of a mycorrhizal *M. truncatula* root were immuno labeled with specific antibodies against *H. vulgare* AOS (A), jasmonate-induced protein 23 (JIP-23) of *H. vulgare* (B) and AOC from *L. esculentum* (C), respectively. Immunodecorated proteins were visualized by alkaline phosphatase reaction (dark purple label in A and B) or by a fluorescent dye (green label in C). Note the occurrence of all proteins in arbuscule-containing cells. In C, the arbuscule is stained by fluorescence-labeled wheat-germ agglutinin (red) and nuclei by a DNA-specific dye (blue). Bars represent 50 μm in A, B and 10 μm in C, respectively.

enzymes of JA biosynthesis and finally elevate JA level; and (iii) JA produced in mycorrhizal roots could enhance the sink strength of such roots. In the latter case an extracellular invertase could be the mediator, since its expression is induced in mycorrhizal roots (Schaarschmidt et al., 2006). Extracellular invertases are sensitive to different stress-related stimuli like wounding or application of methyl jasmonate, thereby modulating source-sink relations (Ehness et al., 1997).

5. Effects of modulated jasmonate levels on mycorrhiza

In order to investigate the role of JA in mycorrhization by a reverse genetic approach, the cDNA coding for AOC1 from *M. truncatula* was used in the antisense direction for the transformation of roots of *M. truncatula* (Isayenkov et al., 2005). By partial suppression of *MtAOC1* expression the amount of AOC protein and the endogenous level of JA in mycorrhizal roots could be clearly reduced. To quantify root colonization and symbiotic activity in such transgenic roots colonized by *G. intraradices*, a new method based on quantitative polymerase chain reaction was established (Isayenkov et al., 2004). Using this method, a strong correlation between fungal colonization of the root system and the amounts of fungal rDNA and rRNA could be shown, whereas the transcript levels of the AM-specific phosphate transporter 4 from *M. truncatula* (*MtPT4*) correlate rather with arbuscule formation.

In the *MtAOC1antisense*-transformed roots the reduced JA level was accompanied by a delay in colonization (Isayenkov et al., 2005). The most obvious effect was visible at day 21 post-inoculation: In comparison to roots transformed with the empty vector construct, in *MtAOC1antisense*-transformed roots the amount of fungal rRNA dropped to about 40% and the amount of *MtPT4* transcript to 10% suggesting an effect of decreased JA level in mycorrhizal roots on the colonization rate as well as on arbuscule formation. Noticeably, the well-known positive effect of mycorrhization on plant growth (Smith and Read, 1997) was diminished in these plants (S. Isayenkov and B. Hause, unpublished). Surprisingly, *MtAOC1*-overexpressing roots, which have enhanced JA levels, exhibited also a slightly decreased mycorrhization (C. Mrosk and B. Hause, unpublished). It is tempting to speculate that (i) JA attributes to the homeostasis between plants and AM fungi, and (ii) JA might also contribute to a suppression of colonization. This corresponds to the concentration-dependent effect of JA-application on mycorrhization (see above).

The data point to a specific function of jasmonates in the interaction of roots with mycorrhizal fungi, and the following mechanisms might be involved:

(i) Induction of flavonoid biosynthesis. Flavonoids are assumed to be signals to stimulate the growth of AM fungi (Harrison, 1999). It is well known that application of jasmonates leads to increases in phenylalanine ammonia lyase (PAL) mRNA accumulation and in PAL enzyme activity (Gundlach et al., 1992; Thoma et al., 2003). In *M. truncatula*, transcripts encoding enzymes of the isoflavone biosynthetic pathway, such as PAL and chalcone synthase (CHS), are induced specifically in cells containing arbuscules (Harrison and Dixon, 1994).

(ii) Reorganization of cytoskeleton. An extensive remodelling of the microtubular cytoskeleton was observed in mycorrhizal roots, in arbsucule-containing cells as well as in adjacent non-colonized cortical cells (Bonfante et al., 1996; Genre and Bonfante, 1998). Furthermore, a gene coding for β-tubulin (*MtTubb1*) is transcriptionally upregulated in mycorrhizal roots (Manthey et al., 2004) and in non-mycorrhizal roots upon JA-treatment (S. Isayenkov and B. Hause, unpublished). Moreover, microtubules are known to change their organization in response to application of jasmonates (Koda, 1997; Matsuki et al., 1992).

(iii) Alterations of sink status of roots. The maintenance of mycorrhizal symbiosis requires carbohydrate supply for the fungus. Jasmonates are known to contribute to a redistribution of nutrients (Creelman and Mullet, 1997). As described above, *LIN6*, a gene coding for an extracellular invertase from *L. esculentum*, is inducible by JA (Thoma et al., 2003) and is expressed in mycorrhizal roots (Schaarschmidt et al., 2006). In this context, jasmonates could enhance the sink-strength of mycorrhizal roots and thereby stimulate carbohydrate biosynthesis in the shoots and their transport into the roots.

(iv) Increase in plant fitness. Jasmonates may contribute to a better growth of the plant. This could be mediated by effects on the level of cytokinins, which are well known factors of cell division and growth (Haberer and Kieber, 2002). Interestingly, levels of active cytokinins increased in potato plants upon treatment with JA (Dermastia et al., 1994). Another aspect of plant fitness is the increased resistance of mycorrhizal plants to pathogens and drought stress (Augé, 2001; Cordier et al., 1998). This might be mediated by a JA-induced expression of genes coding for defence-related and vegetative storage proteins (Wasternack and Hause, 2002).

Analyses of transcript and metabolite patterns by microarrays and metabolite profiling, both in wild type and transgenic roots, can help to identify which processes during mycorrhization are mediated by jasmonates. Analyses of transcript profiles of mycorrhizal versus non-mycorrhizal wild type *M. truncatula* roots gave additional information for the transcript accumulation of jasmonate regulated genes, like genes coding for enzymes involved in synthesis of secondary metabolites or defense proteins (Hohnjec et al., 2005). First analyses of the transcript pattern of transgenic *M. truncatula* roots overexpressing or suppressing *MtAOC1*, both non-mycorrhizal and mycorrhizal, revealed a high number of differentially regulated genes with a dependence on the endogenous JA level (C. Mrosk, H. Küster and B. Hause, unpublished). This is also reflected by changes in the pattern of secondary metabolites, which revealed among others a significant decrease

in the level of isoflavonoids in mycorrhizal *AOCsense*-roots in comparison to the empty vector control (C. Mrosk, W. Schliemann and B. Hause, unpublished).

6. Conclusions

Among all phytohormones analyzed in mycorrhizal plants so far, the available data concerning jasmonates provide a strong indication of a crucial role for this hormone in mycorrhizal roots. It was shown that jasmonates affect mycorrhization, possibly in multiple ways. Elevated JA levels occurring upon mycorrhization may enhance the defense status of mycorrhizal tissues, which were shown to be less sensitive to secondary infections by pathogens (Cordier et al., 1998) or to drought and osmotic stress (Augé, 2001). This could be similar to the growth-promoting effect and induced systemic resistance (ISR) described for non-pathogenic rhizobacteria (Pozo et al., 2004). Various elements of ISR have been observed in roots colonized by AM fungi (Hause and Fester, 2005). Whether jasmonates could serve as a putative endogenous signal in mycorrhiza-induced ISR, remains to be elucidated. As a consequence, jasmonates might mediate at least partially the maximal benefit, which mycorrhizal plants have from the symbiotic interaction.

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