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Review

Transport of polyols in higher plants

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Abstract – Polyols are reduced forms of aldose and ketose sugars. The most frequently found polyols in plants are mannitol, sorbitol and galactitol as well as the ubiquitous cyclitol, *myo*-inositol. In contrast to *myo*-inositol, mannitol and sorbitol are direct products of photosynthesis in mature leaves, in parallel with sucrose. They serve similar functions such as translocation of carbon skeletons and energy between source and sink organs. As the metabolic pathways and functions of polyols have been extensively reviewed during the past years, this review focuses on the most recent data obtained on transport of polyols and discusses some important points regarding membrane transport events. Some polyols are subjected to long-distance transport as shown by their occurrence in the harvested phloem sap. In some species like celery, phloem loading has been shown to occur from the apoplasmic compartment and specific carriers are involved. In Rosaceae, the pathway for transport of polyols has been a matter of debate (apoplastic vs. symplasmic) but some conclusions may have to be reassessed. Increased transport of polyols, both in the phloem and the xylem occurs frequently as a result of salt or drought stress. The recent cloning of a H^+/mannitol transporter in celery and putative Na^+/*myo*-inositol transporters in *Mesembryanthemum crystallinum* are the first steps in a better understanding of polyol transport in plants. © 2001 Éditions scientifiques et médicales Elsevier SAS

mannitol / plant / polyols / sorbitol / transport

AOS, activated oxygen species / PCMBS, para-chloromercurybenzenesulfonic acid / SE/CC complex, sieve element/companion cell complex

1. INTRODUCTION

Polyols (often named sugar alcohols) are the reduced form of aldose and ketose sugars. The carbon chain of polyols can be either linear (acyclic polyols or alditols) or arranged in a ring (cyclic polyols or cyclitols). The term 'polyol' refers to compounds with three or more carbons, each of them bearing an OH group. Thus the simplest alditol is glycerol. Alditols are named according to the number of carbon atoms they contain. This review will mainly focus on the most common six carbon alditols (hexitols) with some information on inositol in plants. Among the most common alditols, mannitol is derived from mannose, sorbitol (glucitol) from glucose, and galactitol (dulcitol) from galactose.

Polyols are common in many organisms from prokaryotes [12] to eukaryotes. Alditols (glycerol, arabitol, erythritol, mannitol) are produced by several fungi that cause human infections or plant diseases [15]. Mannitol is also found in brown algae [60]. In contrast, in the red algal genera *Bostrychia*, galactitol and sorbitol are synthesized [34]. In higher plants, seventeen alditols are listed and at least thirteen different alditols have been identified in angiosperms [40]. The three most frequent hexitols in angiosperms are galactitol, sorbitol and mannitol. Galactitol is especially present in the Celestraceae (spindle tree) and the Scrophulariaceae (*Antirrhinum*, *Digitalis*). Sorbitol is common in the Rosaceae such as apple, pear, peach and plum, and is also found in the Plantaginaceae. Mannitol, the most widely distributed hexitol, is present in over 100 higher plant species distributed among several families including the Rubiaceae (coffee), Oleaceae (privet, ash, olive), and Apiaceae (celery, carrot, parsley) [40]. Mannitol is also commonly present in root parasitic angiosperms such as *Orobanche*, *Striga* and *Thesium* [24, 30, 53] The

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presence of polyols in several members of the same family could be used as a taxonomic trait [56].

Inositol, the simplest cyclohexane hexitol, is an ubiquitous cellular component in a wide variety of organisms. It normally occurs as a bound form. Phosphatidylinositol is the third most abundant phospholipid in most eukaryotic cells and plays a structural role in membranes [21]. Moreover, inositol phosphates are essential in signal transduction in cells. Inositol is the substrate for the production and accumulation of methylated derivatives like D-ononitol (1-D-4-*O*-methyl-*myo*-inositol) and D-pinitol (1-D-3-*O*-methyl-*chiro*-inositol). These cyclitols are found in common ice plant (*Mesembryanthemum crystallinum*) and in other plants such as tropical legumes (pigeonpea), mangrove fern (*Acrostichum aureum* L.), maritime pine (*Pinus pinaster*) and mistletoes [62, 75]. In plants, galactinol is the basic substrate for the raffinose series and is synthesized from UDP-glucose and inositol [44]. However, according to recent data indicating that raffinose synthesis occurs in intermediary cells of source leaves, galactinol should not be considered as a translocated molecule [74].

In contrast with inositol, mannitol and sorbitol are primary photosynthetic products in mature leaves [70] (see *figure 1* for mannitol synthesis). High productivity and high photosynthetic rates in celery are linked to the synthesis of mannitol which represents an additional sink for photosynthetically fixed CO_2 [55].

Numerous roles have been attributed to polyols. Polyols are osmotically active solutes notably in response to abiotic stress, i.e. they can accumulate at high levels inside a cell to compensate for reduced cell water potential [57]. Their hydroxyl groups could effectively replace water in establishing hydrogen bonds in case of limited water availability and therefore protect enzyme activities and membranes.

Despite the numerous functions attributed to polyols, investigations have been mostly limited to their metabolism and physiological roles (reviewed in [42, 46, 55, 70]) but very little is known about the mechanisms of their transport inside the plant. Therefore we will focus on the transport of polyols in plants at the whole plant level (long-distance transport in the phloem and xylem) with emphasis on phloem loading. The membrane transport of polyols will be described and finally the possible modification of polyol transport by stress will be discussed and some examples of other types of transport involving polyols described.

2. LONG-DISTANCE TRANSPORT OF POLYOLS IN PLANTS

2.1. Evidence for long-distance transport of polyols in plants

As previously indicated, the synthesis of polyols considered as primary photosynthesis products occurs mainly in the source leaves. The absence of the corresponding synthesis enzymes in sink organs where polyols were detected, is also in favour of long-distance transport of those compounds. This has been clearly shown for mannitol and sorbitol [17, 42, 43, 47].

Another proof of long-distance transport is the detection of polyols in the phloem sap of polyol producers (*table I*). An extensive survey of the presence of polyols in phloem sap was conducted in the 70s [80] and later by Bieleski [3] and Lewis [40]. *Myo*-inositol was frequently found. However, *myo*-inositol was never a major translocated compound, in marked contrast with other polyols that can represent a major portion of the carbon molecules in the sap. For example, sorbitol accounts for 60 to 90 % of the carbon exported from the leaf with a phloem sap concentration of 560 mM in peach tree [48]. In celery, mannitol accounts for between 10 and 60 % [13] of the carbon exported from mature leaves, with phloem sap concentrations of 150–300 mM [31]. However, sucrose is still present in significant amount in those species. It was shown in celery that production, accumulation and metabolism of sucrose and mannitol change in intensity throughout leaf development [17]. In the light, both sucrose and mannitol are exported with a faster rate for sucrose. In the dark, mannitol remained as the predominant substrate translocated when the sucrose pool is low or depleted [16].

The role of *myo*-inositol as a translocated compound has not been considered intensively. Its action in signalling [9, 62] and in the protection of auxin by conjugation during long-distance transport [11] was reported. Whereas most of the information given so far concerned linear or cyclic hexitols, there is some evidence of translocation of other polyols. For example, the seven carbon volemitol (D-glycero-D-manno-heptitol), found in the genus *Primula*, was detected in the phloem exudate as the main translocated carbohydrate with sucrose [29]. Therefore, volemitol is an important phloem translocated in certain species with a possible cryoprotectant effect.

2.2. Phloem loading of polyols

While the presence of polyols in the phloem sap has been clearly demonstrated, the route of entry into the

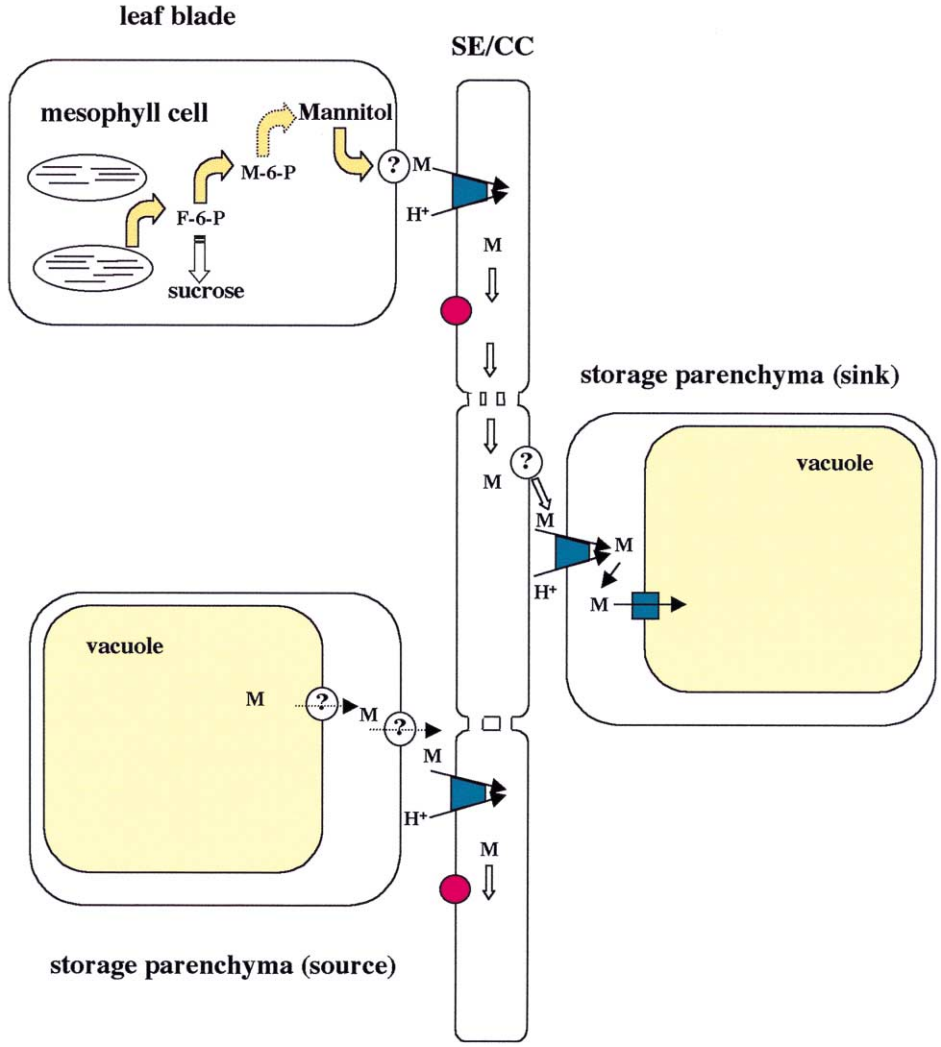

Figure 1. The mannitol transport pathways in celery leaves and petioles. Mannitol is synthesized from fructose-6-P (F-6-P) through mannose-6-P (M-6-P) and mannitol-1-P (not shown in the figure) in mesophyll cells. Several data indicate that mannitol exits the cells to the apoplasm before being loaded in the phloem. The exact nature of this step (diffusion, facilitated diffusion or other system) is not known (question mark). Loading in the SE/CC complex occurs certainly through a cotransport H^+/mannitol (cone symbol, [13, 67]) as indicated by expression profile of AgMaT1 in source leaves [52]. Mannitol is then transported in the SE/CC complex and is unloaded to be stored in the storage parenchyma cells of young petioles at the sink stage. The exit pathway from the phloem is not known (question mark). Most of the data concerning the storage of mannitol comes from the work of the group of Keller [27, 35]. Keller [35] demonstrated that the uptake of mannitol at the plasma membrane level is occurring through cotransport with protons and this was later confirmed by Salmon et al. [67]. Low but detectable expression of AgMaT1 in storage parenchyma [52] could indicate that this transporter is implicated in this step. This will deserve further investigations as Keller [35] reported that mannitol uptake is sensitive to PCMBS whereas AgMaT1 is not [52]. Entry of mannitol in the vacuole occurs by facilitated diffusion [28] in accordance with the absence of a significant gradient in mannitol concentration between the vacuole and the cytosol [36]. Mature petioles are source organs and mannitol originally stored in the vacuole of storage parenchyma cells is reloaded into the SE/CC complex. Although the exit pathway from mesophyll cells is unknown, uptake into the phloem occurs through a H^+/mannitol cotransport as originally demonstrated by Daie [13] and later confirmed by Salmon et al. [67] and the cloning of *AgMaT1* from a celery phloem cDNA library by Noiraud et al. [52]. Unloading in other organs such as roots has not been investigated so far. The circles represent the H^+/sucrose cotransporter expression [51].

phloem has been a matter of debate (a situation quite reminiscent of the one existing for phloem loading of sucrose several years ago). In peach tree, the pathway for phloem loading has been addressed recently [48]. Sucrose and sorbitol are both found in the phloem sap and sucrose concentration was slightly higher than the

Table I. Occurrence of several polyols in the phloem sap of plant may indicate their long-distance transport. These data were not included in the former list of polyols transported in plants [80].

Type of polyol	Plant species	Method of determination	Reference
Pinitol	*Medicago sativa*	Aphid honeydew	[9]
Ononitol	ibid	ibid	ibid
Myo-inositol	ibid	ibid	ibid
Ononitol	*Mesenbryanthemum crystallinum*	Phloem exudate (EDTA) following salt stress	[49]
Myo-Inositol	ibid	ibid	ibid
Mannitol	*Apium graveolens*	Phloem exudate	[31]
Volemitol	*Polyanthus*	Phloem exudate (EDTA)	[29]
Sorbitol	*Prunus persica*	Aphid stylectomy	[48]

sorbitol concentration. The measured sorbitol sap content was very close to the estimated concentration of sorbitol inside the other tissues: this absence of a concentration gradient indicated that energy was not required for sorbitol loading and this could occur by a symplasmic pathway through plasmodesmata. This was also noted in *Populus deltoides* [65]. Leaf infiltration with PCMBS has been used to demonstrate the existence of an apoplastic step in phloem loading [5]. The rationale of the effect of PCMBS infiltration is as follows: if a sugar is taken up from the apoplast and if this uptake is sensitive to PCMBS, then infiltration of PCMBS in the apoplasmic compartment of a leaf prevents phloem loading of the sugar considered. This leads to a decrease in sugar content of the phloem sap collected from the treated leaf. However several points have to be considered for the correct interpretation of such data. The entry of water in the phloem is an important determinant of sap flow. Taking into account recent data showing that water uptake through aquaporins (water channels) is also highly sensitive to PCMBS [18], the decrease in phloem transport by PCMBS might also be due to a decrease in the water transport leading to a reduced sap flow. Moreover, if the uptake system for the sugar is not sensitive to PCMBS, no conclusion can be drawn from such experiments. The action of PCMBS depends on the transporter considered but also on the ability of PCMBS to infiltrate the apoplasmic spaces. Concerning sugar loading in peach trees, infiltration of PCMBS in the leaf apoplast reduced export of both sucrose and sorbitol. This was in agreement with an apoplastic step in phloem loading [48]. Several data showing uptake of radiolabelled sorbitol in *Prunus* leaf discs from the external medium were also in agreement with an apoplastic loading [4].

In olive tree, where carbon export from the leaves occurs in the forms of stachyose (a member of the raffinose family) and mannitol, synthesis of raffinose in intermediary cells, from galactinol and sucrose, has been considered as a polymer trap mechanism to explain symplasmic phloem loading [25]. The synthesized oligosaccharides are effectively too large to diffuse back through the plasmodesmata connecting intermediary cells and mesophyll cells but they can pass to the sieve tube [74]. However, this mechanism can operate in olive tree though the phloem loading of mannitol may not be symplasmic. It is obvious that further studies are needed to definitely answer that question [25]. The fact that mannitol membrane transport is not sensitive to PCMBS [14, 35, 67] argues against the use of PCMBS as indicator of apoplastic phloem loading. In parsley [26], sucrose and mannitol are exported from mature leaves, and uptake of exogenously supplied sucrose in leaf discs was PCMBS-sensitive, whereas uptake of mannitol was not (a situation similar to the one noted for celery, another member of the Apiaceae, [67]). Following infiltration of leaves with 2 mM PCMBS, recovery of both labelled sucrose and mannitol was not changed as compared to control, uninfiltrated plants. This would indicate that phloem loading occurred symplasmically, at least for sucrose. However taking into account the limitations of the PCMBS infiltration method, more work is needed to fully understand the pathway for phloem loading of polyols. Different mechanisms may exist according to species but in some cases, phloem loading of polyols clearly occurs apoplasmically as described for celery (see following section). Cloning of polyol transporters may help resolve these contradictions: in *Cucurbita* where polymer trapping is involved in phloem loading, a sucrose transporter cDNA has nevertheless been cloned [64] and shown to be expressed in the phloem.

2.3. Phloem unloading of polyols

Unloading of polyols has been even less studied than loading. Berüter and Feusi [2] followed the uptake to radiolabelled sorbitol in the apple fruit. A comparison was made between uptake in excised tissue discs and in cortex tissue from intact fruit. The authors concluded on the existence of a transport system at the plasma membrane of parenchyma cells together with a system at the tonoplast level. However the transport system at the tonoplast level could only be detected in intact fruits, suggesting that the integrity of the plasma membrane is partly lost when working

with excised discs. Depending on the uptake conditions, sorbitol uptake was not or slightly sensitive to PCMBS.

3. MEMBRANE TRANSPORT OF POLYOLS: CELERY AS A MODEL PLANT

As already indicated, data on polyol transport are rather scarce except in one case, celery, where the different membrane transport steps described in *figure 1* have been investigated. Celery may therefore be considered as a model plant for the studies of mannitol transport both in source and sink organs. Transport experiments were run in celery, mainly because of the possibility to strip phloem strands from leaf petioles. The seminal work by Daie [13] established that mature petioles of celery act as a source organ where the sugars initially stored in the storage parenchyma cells are reloaded into the phloem for long-distance transport to sink organs (mainly young immature leaves). Daie [14] demonstrated that radiolabelled sucrose inoculated into the fleshy petiole was transported to the phloem. Moreover, uptake of radiolabelled sucrose in isolated phloem strands, suggested that phloem loading is apoplastic. As phloem strands are rather homogenous (SE/CC complex + phloem parenchyma) especially when compared to leaf discs also used to study phloem loading in other species, they represented a very interesting model. Although they were certainly initially chosen in order to study sucrose phloem loading, the presence of mannitol in the phloem sap of celery was rapidly acknowledged and studies were then also conducted on mannitol transport.

3.1. Transport at the plasma membrane level

The initial studies [13, 14] indicated that sucrose and mannitol were loaded in the phloem via different transporters with kinetics in agreement with H^+/cotransport mechanisms in both cases. Then, in order to demonstrate that those transport activities were occurring at the plasma membrane level and therefore reflected phloem loading per se and not compartimentation in internal stores (e.g. vacuoles), plasma membrane vesicles were purified from phloem strands and the uptake properties of sucrose and mannitol studied [67]. The results confirmed former data by Daie [13] and strengthen the idea that transport occurs through cotransport with protons. Moreover the transport activities in plasma membrane vesicles from phloem strands were clearly higher than in plasma membrane vesicles purified from storage parenchyma cells, indicating that those transport activities were involved in phloem loading [67].

Our understanding of sugar transport in plants has been greatly improved since the initial cloning of monosaccharide and sucrose transporters (reviewed in [76]). Understanding the mechanisms of polyol transport would then require the initial cloning of the corresponding transporters. Cloning the sucrose transporter in celery was a relatively easy task due to the high level of similarity existing among sucrose transporters from different species [51]. In contrast, no information was available on any polyol transporter in plants and orthologues in other species could not be clearly identified (see following section). Therefore an approach combining PCR and heterologous expression in the yeast *Saccharomyces cerevisiae* was followed to clone the mannitol carrier of celery [52]. The cloned cDNA (*AgMaT1* for *Apium graveolens* mannitol transporter 1) gave yeast cells the ability to grow on mannitol. The kinetic properties under those conditions were comparable to the different results obtained in planta. *AgMaT1* encodes a protein with twelve putative transmembrane helices and is a member of the superfamily of transmembrane facilitators [45]. The AgMaT1 protein expressed in yeast cells exhibited a K_m value for mannitol uptake of 275 μM. This affinity correlates well with the K_m value determined in plasma membrane vesicles from phloem tissues [67]. Mannitol uptake was described to occur by cotransport with protons and was, as expected from former results [66], not sensitive to PCMBS. This absence of sensitivity to PCMBS has also been noted for a number of polyol transporters [13, 26, 35, 67] and may well be a feature distinctive from sucrose carriers [39]. AgMAT1 was not able to transport sucrose and was not related to sucrose transporters [52]. Gene expression analysis by northern blots indicated that *AgMaT* was mainly expressed in the sites of phloem loading (mature leaves and phloem of petioles from mature leaves). Gene expression is low in petiole storage parenchyma and almost null in roots. AgMaT1 sequence (protein) did not exhibit high homologies with *myo*-inositol transporters [10], for example. However, several sequences of unknown functions from *Arabidopsis* and sugar beet are clearly related to AgMaT1, but, the presence of mannitol has not been reported in these two species so far. The nature of the substrate of these carriers will be an interesting point to address. A clue may reside in the observation that the celery mannitol dehydrogenase sequence is close to an *Arabidopsis*

sequence involved in pathogen resistance [78]. This and later results in tobacco [32] were taken as an indication that plants, as a defence mechanism against pathogen attack, can degrade mannitol liberated by the pathogen by an induced mannitol dehydrogenase activity. The role of mannitol would be to protect the pathogen from AOS synthesized by the plant. In celery, mannitol dehydrogenase has been localized to the intracellular space (cytoplasm and nucleus, [79]). Therefore, this defence pathway may involve a mannitol transport step inside the plant cells at the time of infection; therefore, the expression of a mannitol transporter could be induced by infection. However, this is still speculative and will have to be examined.

Other transport steps have also been investigated in celery. Keller [35] studied the uptake of mannitol in the parenchyma cells of celery petioles. In these cells, mannitol is stored without modifications whereas sucrose is converted to hexoses before storage [36]. The uptake of radiolabelled mannitol was studied in discs of storage parenchyma. Uptake kinetics appeared biphasic with a saturable component showing an apparent K_m of 1 mM. This confirmed former work [14]. The data were in accordance with a proton cotransport system operating at the plasma membrane of the parenchyma cells (*figure 1*). This system appeared highly specific for mannitol. These results were further confirmed by studies on mannitol uptake in plasma membrane vesicles isolated from parenchyma cells [67]. At the present time, no information is available on the presence of several mannitol transporters in celery (different members of a gene family as reported for sucrose and hexose transporters [76]) and therefore it is not possible to decide whether the same transporter AgMaT1 or a closely related transporter is involved in phloem loading and uptake in parenchyma cells.

3.2. Transport at the tonoplast level

In celery, mannitol is transiently stored in the vacuoles of the parenchyma cells of fleshy petioles from mature leaves [36]. However, taking into account that the vacuole represents 90 % of the cell volume, mannitol concentration was similar in the cytoplasm and in the vacuole. Uptake studies of radioactive mannitol in purified vacuoles or tonoplast vesicles demonstrated that this step occurred by passive diffusion (*figure 1*) [27]. Therefore, the active step of mannitol storage in petioles is located at the plasma membrane level. Although hexoses (glucose and fructose) are also stored in the same vacuoles, this tonoplastic mannitol transport system is specific for mannitol [27].

4. POLYOL TRANSPORTERS IN OTHER ORGANISMS

The first polyol transport system described was the phosphotransferase system from *Escherichia coli* [38]. In prokaryotes, phosphotransferase systems are multienzyme complexes that achieve phosphorylation and transport of the phosphorylated substrates. Such systems have not been described in eukaryotes so far. Nevertheless, the transmembrane domain of the complex (the permease) identified in prokaryotes does not share significant homologies with celery sequences (AgMaT1).

In the yeast *S. cerevisiae*, two *myo*-inositol transporters (*ITR1* and *ITR2*) have been cloned [50] and were identified as members of the sugar transporter superfamily. However, no transport system for acyclic polyols has been described so far, although transport activities for mannitol have been reported in strains growing on mannitol ([59]; Noiraud and Lemoine, unpubl. results). The completion of the genome sequencing for several yeasts such as *Saccharomyces cerevisiae* should help identify such transporters.

Recently, two closely related transporters (MITR1 and MITR2) were cloned from *Mesembryanthemum crystallinum* [10]. They show sequence homologies to yeast *myo*-inositol transporters and MITR1 restored the growth on inositol and Na^+ of a yeast strain mutated at endogenous inositol transporters. These results are in agreement with MITR1 and MITR2 being Na^+/*myo*-inositol symporters. Peptide antibodies raised against the two proteins indicated the presence of MITR1 in all organs and of MITR2 in leaves. Both transporters were mainly located at the tonoplast level but a minor plasma membrane location was also seen [10].

A sorbitol permease has been described in human erythrocytes [37] and could be a facilitated diffusion system as described in renal epithelial cells. A neutral solute channel with a broad specificity has also been described in rat liver [73]. This channel is related to aquaporins and is therefore called AQP9. It mediates the uptake of a wide range of neutral molecules (including water) when expressed in *Xenopus* oocytes. Interestingly, several polyols (mannitol, sorbitol, xylitol, erythritol, threitol and glycerol) where shown to enter oocytes through AQP9. The occurrence of such

systems in plants which seem to be equipped with a number of water channels (as inferred from the sequencing of the *Arabidopsis* genome, [72]) will be a very interesting point to address.

5. MODIFICATION OF POLYOLS TRANSPORT DURING STRESS

Numerous studies have indicated an increase in polyol content following stress (mainly drought or salt stress, [42, 57]). The following section will discuss those data in relation to long-distance transport. As polyol synthesis occurs in mature leaves, an increase in the concentration in sink organs is certainly related to an increased transport of polyols. There are only a few examples where transporter expression has been studied during stress. In *Arabidopsis*, salt or water stress induces the specific expression of a proline transporter (ProT2) [61]. In contrast, the expression of other amino acid transporters decreased, indicating that transport of proline was favoured under stress. It seems therefore that transport of osmolytes, and polyols in particular, represents a major event when plants have to adapt to stress conditions.

In peach tree seedlings subjected to drought stress, Escobar-Gutiérrez et al. [22] demonstrated that sorbitol synthesis increased in leaves as did sorbitol content in the phloem sap. This increase in phloem sap was correlated with the up-regulation of sorbitol synthesis. In contrast, Lo Bianco et al. [41], studying the effect on drought stress also in peach trees, concluded that sorbitol accumulation in sinks was mainly due to a reduction of sorbitol utilization (reduction in sorbitol dehydrogenase activity, SDH). This reduction of sorbitol utilization and demand would eventually lead to a reduction in sorbitol export from mature leaves. Such contradictions could be explained by major differences in the applied stress (duration and intensity).

In soybean plants subjected to high temperature, pinitol accumulated in the different organs in the plants [28]. As pinitol synthesis occurs mainly in leaves [28], this result suggested that an increase in pinitol translocation was also induced by high temperatures. Interestingly, no such pinitol accumulation was observed when plants were subjected to low temperatures. The protective effect of pinitol appeared stress-specific.

A slightly different modification of transport is observed in the water-stressed *Vigna umbellata* plants which accumulate D-ononitol in their leaves [75]. However, the activity of the key enzyme involved in ononitol synthesis from *myo*-inositol (*myo*-inositol 6-*O*-methyltransferase) increases in the stems but not in the leaves. This suggests that ononitol synthesis is increased in stems during drought stress, then is subsequently transported to the leaves where it accumulates. In that case, long-distance transport occurs from stem to leaves, a rather unusual situation.

Recently, Bohnert and coworkers [49] reported that *myo*-inositol could be a signal during the adaptation to salt stress in *M. crystallinum*. In seedlings, feeding of *myo*-inositol to roots led to an enhanced transport of Na^+ together with inositol from roots to leaves via the xylem. The transport of Na^+ did not occur in seedlings not fed with inositol which showed no increase in the synthesis of inositol under stress conditions. *Myo*-inositol would serve as a leaf-to-root signal promoting sodium uptake and salt adaptation [49]. The expression of MITR1 and MITR2 (two putative Na^+/*myo*-inositol transporters) was in accordance with a role in such transport during salt stress [10]. Then, the authors discussed this transport in relation to compartmentation of sodium in an halophyte plant. In animal cells, *myo*-inositol would be also a compatible osmolyte. Up-regulation of a *myo*-inositol transporter (SMIT) in human macrophages subjected to hypersomotic stress has been reported [20]. In *Fraxinus excelsior* plants subjected to a drought stress, the mannitol content of the leaf xylem sap increased [54] indicating that modification of polyol transport also occurs in the xylem. Whereas the changes in the enzyme activities related to polyol metabolism have been well documented in the case of salt stress [69, 70], almost nothing is known about the evolution of the expression of polyol transporters under such conditions (except for *myo*-inositol). This mainly results from the absence of cloned sequences for polyol transporters so far. In celery plants subjected to severe salt stress, the expression of the sucrose carrier AgSUT1 decreased in all organs [51]. Although the authors did not measure the changes in the mannitol transporter expression, one might suspect that transport of mannitol is favoured over that of sucrose in case of salt stress, confirming previous information [69].

6. OTHER TYPES OF POLYOL TRANSPORT

6.1. Polyol transport in xylem

The presence of sugars in the xylem has been reported, especially during dormant periods. One typical example is the high amounts of sucrose of the xylem sap of maple trees (*Acer saccharum*) that is exploited to collect maple syrup. Sorbitol content also

increased in the xylem sap of several apple trees when subfreezing temperatures were applied during the dormant season [66, 77]. This is rather common during dormant periods and does not seem to be related to long-distance transport but rather to a redistribution of sugar between xylem sap and cells surrounding the vessels [68]. Mannitol content of the xylem sap of *F. excelsior* has been reported to increase in response to drought stress [54]. However, the transport mechanism implicated in these phenomena are far from being understood.

6.2. Polyol transport in parasitic angiosperms

Several hemiparasitic angiosperms have been shown to synthetize polyols [58]. Examples are *Thesium humile*, *Striga hermonthica* and *Orobanche ramosa* [58] which damage cereal and legume cultures under warm climates. Several studies indicate that polyols are transported in the phloem of parasite. For example, $^{14}CO_2$ assimilation in *Thesium humile* is quickly followed by the detection of labelled mannitol in the roots of this chlorophyllous parasite [24]. Taking into account that the host plants do not synthesize mannitol, mannitol metabolism is a potential target for the control of these parasites [63]. However, nothing is known on the mannitol transport pathway in the parasite, but this could also represent a potential target. A slightly different situation is found in the case of mistletoe. It has been shown that this parasite can take polyols in the host xylem sap, and, as mistletoe can grow on a number of different species, the profile of polyols in the parasite is host-dependent [62].

6.3. Boron transport and polyols

Boron (B) is an essential nutrient for plant growth. Symptoms of B deficiency are mainly brown heart in roots (rutabaga, turnip, radish), hollow stem (cauliflower, broccoli) and seed set decrease [7]. These alterations occur even when B is in ample supply, suggesting impairment of boron mobility within the plant. In species where phloem B mobility is restricted, B accumulates in leaves and is not quickly redistributed to other plant parts [7]. Hence, even a short interruption of B supply can lead to deficiency [19]. In contrast, B is highly mobile in plants that synthesize alditols, such as sorbitol [6], mannitol or galactitol [31]. The complexation of B to sorbitol in the leaves of *Prunus*, *Malus* and *Pyrus* may facilitate B mobilisation by preventing its complexation to insoluble compounds [6]. Subsequently, B-alditol complexes were identified in the phloem sap of celery (*Apium graveolens*) and the extrafloral nectar of peach (*Prunus persica*) [31].

Recently, additional evidence supporting a role for polyols in B mobility has been obtained with transformed plants. Tobacco plants do not produce alditols and B mobility is very restricted in this species. Tobacco plants were genetically engineered to synthesize sorbitol by introducing an apple cDNA encoding NADP-dependent sorbitol-6-phosphate dehydrogenase [1, 8]. They produced sorbitol, showed an increase in phloem B mobility from mature leaves and then were more tolerant to B deficiency, with maintenance of growth and yield [8]. Moreover, sorbitol production was accompanied by an increase in B uptake from the soil resulting in an increase in B content in plant tissue. This shows that polyol concentration in plants affects B uptake and its subsequent distribution within the plant [8]. However, the major question still to be answered is that of the pathway for B transport in the phloem. Does complexation of B to alditols occur in the phloem or in the mesophyll? Different pathways and transporters would then be involved: in the first case, alditol and B are loaded separately in the phloem, whereas in the second case, the complex B-alditols are loaded in the phloem for long-distance transport. In modified tobacco, the use of the ubiquitous *CaMV-35S* promoter led to sorbitol synthesis in all cells including phloem [8]. This is rather in favour of a complexation of B to sorbitol inside the phloem. However, additional work is still needed to understand precisely the transport pathway for sorbitol-B complexes in plants. Nevertheless, these results demonstrated a positive role for polyols also in the long-distance transport of minerals such as B.

7. CONCLUSION

Our understanding of polyol transport in plants is still very scarce, especially compared to the transport of other carbohydrates such as sucrose or hexoses. However, this may reflect a general lack of interest regarding polyols: despite their evident role, from primary photosynthetic products to osmolytes and radical scavengers, few basal studies have been conducted by a limited number of groups. For example, the major enzymes of mannitol synthesis and degradation have only been cloned recently [23, 78]. This is in marked contrast with the increasing number of studies where the positive effects on stress resistance of genetically modifying plants to synthesize polyols have been followed.

However, it is clear that mannitol and sorbitol are translocated in the phloem from their site of synthesis to their site of use, in a way very similar to sucrose in most plants. There is still some controversy on the pathway involved in phloem loading: either symplasmic or apoplasmic. At least in celery where phloem loading has been extensively studied, an apoplasmic loading has been clearly demonstrated. This was recently confirmed by the cloning of a mannitol transporter in celery [52]. This cloning will certainly open new opportunities to run the same studies in other mannitol producers. Only when sufficient data from several species are available can the controversy over the loading pathway be solved.

Unloading pathways are even less understood [27, 36]. In *figure 1*, numerous question marks indicating unknown transporters remain and certainly represent a major challenge for the next years. In fact some of the remaining questions (mainly unloading and exit from mesophyll cells) are common with sucrose transport pathways [76].

The interest in polyols has increased since the availability of plant transformation. Increased resistance to several stresses (salt, drought, cold) has often been related to an increase in polyol synthesis, although the exact mechanisms are still to be discovered. Therefore, it was expected that introducing polyol production would increase the resistance to stress of genetically modified plants. Some positive results have been reported, although the actual polyol concentration was not very high [71]. This strategy used the ubiquitous promoter *CaMV-35S*; therefore synthesis of polyols occurred in all cells of the plant, a situation clearly different from the one noted in natural mannitol-synthesizing plants. This could have two major drawbacks: the additional energetic cost of polyol synthesis could have detrimental effects on plant growth (which was noted at least in one case, [33]) and the fine regulation of polyol synthesis and transport was lost. We therefore believe that understanding the regulation of polyol synthesis and polyol transport in stressed plants is a prerequisite before these characteristics can be transferred and exploited efficiently in other plants. Another challenge will be to find whether the transporters related to AgMaT1 in *Arabidopsis* and sugar beet are also involved in polyol transport. This would indicate that polyol metabolism is relevant in many plants: Bieleski [3] recommended that we assume that a polyol is present in a species, unless shown otherwise. The diversity of roles attributed to polyols clearly plead in favour of intensive research on the involved mechanisms.

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