Physiological Roles of Polyols in Horticultural Crops

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Sucrose is generally considered the primary photosynthate in plants; however, many horticultural crops, including rosaceous fruit trees, synthesize and use polyols (sugar alcohols). This review describes recent progress in physiological research on the metabolism and transport of sorbitol in rosaceous fruit trees, and of mannitol, another common polyol, in horticultural crops. Studies on various polyols other than sorbitol (in rosaceous fruit trees) and mannitol are then described. Polyols play a role not only in the translocation and storage of photosynthates but also in biotic and abiotic responses in many horticultural crops; therefore, this review also provides insights into the effects of polyol metabolism on the biochemical mechanisms of pathogenicity and environmental stress tolerance, including a novel strategy for engineering stress tolerance.

Key Words: mannitol, polyol, sorbitol, sugar alcohol.

Introduction

Sucrose is generally considered the primary photosynthate in plants; therefore, sucrose synthesis, transport, and catabolism have been well studied. Glucose, fructose, and their phosphate esters, which are metabolites in sucrose catabolism, generally play a role in primary metabolism in plant cells; however, many horticultural crops, including rosaceous fruit trees, synthesize and use polyols (sugar alcohols). Polyols are carbohydrates that are generally formed through the reduction of reducing sugars or their phosphate esters. Polyols are non-reducing carbohydrates of high solubility and are thus suitable as translocatable carbohydrates, similar to sucrose, although a recent study claimed that reducing sugars are transported in the phloem (van Bel and Hess, 2008).

Soluble carbohydrates are used for respiration and macromolecule synthesis in plant cells and also generate cell turgor during the cell enlargement stage of development. Accumulated soluble carbohydrates increase the sweetness of fruit during maturation and ripening. Sucrose phosphate synthase plays a role in the biosynthesis of sucrose in leaves, while sucrose synthase and acid invertase play roles in the metabolism of sucrose in fruit. Cell wall invertase in fruit hydrolyzes sucrose to hexoses to enhance the uptake of sugars into fruit cells. Importantly, Fridman et al. (2004) reported that a single nucleotide polymorphism in the cell wall invertase directly affects sugar accumulation in tomato fruit. This finding indicates the horticultural importance of research into the metabolism and transport of soluble carbohydrates.

Soluble carbohydrates also play a role in abiotic stress responses. Since polyols are involved in osmotic adjustment, the genes for polyol synthesis have been used to enhance abiotic stress tolerance using transformation techniques. Interestingly, there is evidence that the role of polyols in abiotic stress tolerance is not solely osmotic adjustment. Recent interesting work has shown the important role of polyols in pathogenicity. This review describes recent progress in physiological research and genetic engineering regarding sorbitol in rosaceous fruit trees and other polyols in horticultural crops. It also describes the role of polyols in pathogenicity and abiotic stress tolerance. Myo-inositol is not considered here because it is common in plant cells, where it plays a primary role, and has also been well studied.

1. Physiological studies of sorbitol metabolism and transport in rosaceous fruit trees

Sorbitol is a primary photosynthate and a major soluble carbohydrate in the phloem of rosaceous fruit trees (Moing et al., 1997a). Sorbitol 6-phosphate dehydrogenase (S6PDH), also called aldose 6-phosphate reductase, is a key enzyme in sorbitol biosynthesis in source leaves. S6PDH converts glucose 6-phosphate to sorbitol 6-phosphate, which is then converted to sorbitol.
by sorbitol 6-phosphate-specific phosphatase (Zhou et al., 2003). A key enzyme in the sorbitol metabolic pathway in fruit is believed to be NAD-dependent sorbitol dehydrogenase (SDH), which catalyzes the oxidation of sorbitol to fructose. Other important components are the sorbitol transporters, which play a role in membrane transport of sorbitol. Sorbitol metabolism and transport are important not only in sugar accumulation into fruit but also in retaining high photosynthetic ability in source leaves (Cheng et al., 2008). Sorbitol also facilitates phloem boron transport by the formation of boron-sorbitol complexes in rosaceous fruit trees (Brown and Hu, 1996; Hu et al., 1997). A role for sorbitol in boron mobility has been reported in tobacco plants transformed with S6PDH (Brown et al., 1999a).

1) Sorbitol 6-phosphate dehydrogenase (S6PDH)

S6PDH has been purified and characterized from apple seedlings (Kanayama and Yamaki, 1993). ATP is a potent inhibitor of S6PDH activity, that is, there is competitive inhibition against NADPH in the direction of sorbitol 6-phosphate synthesis. Zhou et al. (2003) showed the regulation of S6PDH activity by divalent cations and inorganic phosphate. Several effectors of sucrose-related enzymes regulate carbon flow into sucrose. Regulation of S6PDH activity might also be important in regulating sorbitol biosynthesis in leaves.

Kanayama et al. (1992) first cloned cDNA encoding S6PDH from plants. In phylogenetic analysis, S6PDH is included in the plant aldose phosphate reductase group, which is separate from the bacterial sorbitol 6-phosphate metabolizing enzyme (Fig. 1). S6PDH mRNA, protein, and activity are high in source leaves and cotyledons of apple seedlings (Kanayama et al., 1995). Furthermore, the concentration of S6PDH mRNA is higher in mature than immature leaves, which are sink organs on developing shoots of peach and pear trees (Sakanishi et al., 1998; Suzue et al., 2006). S6PDH may therefore be controlled by sink-source conversion in leaves of developing shoots. Suzue et al. (2006) further reported in ‘La France’ pear that S6PDH activity is more than ten-fold higher than sucrose phosphate synthase activity in mature leaves, and that sucrose phosphate synthase activity remains at an almost constant level throughout developmental stages of leaves. This suggests that S6PDH, rather than sucrose phosphate synthase, is the main source enzyme in rosaceous fruit trees.

Using transgenic tobacco plants, Tao et al. (1995) showed that apple S6PDH plays a role in sorbitol biosynthesis. Kanamaru et al. (2004) demonstrated that S6PDH is essential in sorbitol biosynthesis by transgenic apple plants. They showed that sorbitol content is markedly decreased and sucrose content is increased in transgenic apple plants in which the expression of S6PDH is suppressed. This finding indicates that sucrose production can compensate for a decrease in sorbitol production and that the expression of S6PDH regulates the distribution of carbon flow into sorbitol or sucrose. Cheng et al. (2005) further showed that starch is also increased in transgenic apple plants with suppressed expression of S6PDH. Fruit from apples transformed

![Phylogenetic tree of amino acid sequences of polyol-related enzymes](image-url)

**Fig. 1.** Phylogenetic tree of amino acid sequences of polyol-related enzymes. Unrooted neighbor-joining phylogenetic tree was constructed using the ClustalW multiple sequence alignment. Accession numbers are X97606 (Medicago sativa, alfalfa), AF133841 (Xerophyta viscosa), X57526 (Hordeum vulgare, barley), AB016256 (Malus pumila, apple, SDH), AB025969 (Prunus persica, peach, SDH), AB183015 (Lycopersicon esculentum, tomato), U83687 (Apium graveolens, celery), AF055910 (Orobanche ramosa, broomrape), BT001243 (Arabidopsis thaliana), BT025872 (Arabidopsis thaliana), AK104885 (Oryza sativa, rice), EF576940 (Prunus persica, peach, S6PDH), D11080 (Malus pumila, apple, S6PDH), AF415012 (Sorbus aucuparia, European rowan), AJ002527 (Clostridium beijerinckii), AF132127 (Streptococcus mutans), AF396831 (Lactobacillus casei), and Y14603 (Erwinia amylovora).
with S6PDH cDNA was analyzed by Teo et al. (2006), who found that although fruit weight and firmness did not change, there was an increase in glucose and a decrease in malate content after suppression of S6PDH expression. This increase in Brix value and decrease in acidity favor high fruit quality. Kanamaru et al. (2004) and Teo et al. (2006) examined apple vegetative growth and found some inhibition after suppression of S6PDH expression and promotion after overexpression of S6PDH, suggesting that sorbitol is a favorable photosynthate for apple vegetative growth.

2) NAD-dependent sorbitol dehydrogenase (SDH)

Oura et al. (2000) purified SDH from Japanese pear fruit and used kinetic analysis to show how it favors the conversion of sorbitol to fructose. Yamada et al. (1998) first isolated cDNA encoding SDH from apple fruit, and expression analyses have been carried out in apples and other rosaceous fruit trees (Bantog et al., 2000; Yamada et al., 1999, 2001, 2006c). These reports indicate the importance of SDH in sugar accumulation into fruit. Kanayama et al. (2005) used divergent peach cultivars to show that SDH activity is likely responsible for fructose concentration in fruit. Recently, four to nine members of the SDH gene family and the physiological roles of some of these in sink organs have been reported in apple and Japanese pear trees (Ito et al., 2005; Nosarzewski and Archbold, 2007; Nosarzewski et al., 2004; Park et al., 2002). Nosarzewski et al. (2004) demonstrated the importance of SDH in early fruit development by finding that SDH protein comprises 7–8% of the total extractable protein in young fruit 1–3 weeks after flowering.

Interesting studies have reported the regulation of sorbitol metabolism by soluble carbohydrates and plant hormones. Sorbitol increases SDH protein concentration and activity in apple fruit tissue while fructose decreases them (Iida et al., 2004). Sorbitol may function as a signal molecule in the utilization of soluble carbohydrates. This hypothesis is supported by the finding that stem girdling and suppression of S6PDH expression decrease the supply of sorbitol into sink tissues and affect SDH activity (Berüter and Feusi, 1997; Zhou et al., 2006). Roles for gibberellins in increasing sink strength and SDH activity have also been reported in Japanese pear fruit (Zhang et al., 2007).

3) Sorbitol transporters

Isolation and expression analysis of sorbitol transporters recently provided useful information on loading and unloading systems, which are important in sorbitol translocation in rosaceous fruit trees. These transporters likely act as proton/sorbitol cotransporters for active uptake across the plasma membrane with the proton pump. Watari et al. (2004) found sorbitol transporters expressed in phloem tissues in apple source leaves, suggesting apoplastic phloem loading. Nadwodnik and Lohaus (2008) also suggested a mixture of apoplastic and symplastic phloem loading in peach plants by measuring subcellular concentrations of sorbitol.

Apoplastic unloading could also be important in fruit. Gao et al. (2003) isolated cDNAs encoding sorbitol transporters from sour cherry and suggested their role in sink activity in fruit and young leaves. Zhang et al. (2004) provided evidence of the spatial localization of a functional monosaccharide transporter for apoplastic phloem unloading in developing apple fruit. For future studies, noninvasive analysis using a positron-emitting tracer imaging system will be useful for real-time observations of photoassimilate translocation (Kikuchi et al., 2008).

2. Physiological studies of mannitol metabolism and transport in horticultural crops

Mannitol is widely found in plants and microorganisms. In some horticultural crops (e.g., celery, olive, delphinium), it is a major soluble carbohydrate.

Mannitol is a primary photosynthate and translocatable carbohydrate in celery. It is synthesized through mannose 6-phosphate reductase (M6PR) from mannose 6-phosphate, which is formed from fructose 6-phosphate by phosphomannose isomerase. In celery, M6PR, the key enzyme in mannitol biosynthesis, has been purified and characterized (Loescher et al., 1992), and M6PR cDNA has been isolated and its role in source organs shown (Everard et al., 1997). The physiological role and amino acid sequence of celery M6PR are similar to those of S6PDH in rosaceous fruit trees. Celery and broomrape (Orobanche, a parasitic herbaceous plant) M6PR are phylogenetically separated from S6PDH, although both are included in the plant aldose phosphatase reductase group (Fig. 1). Aldose phosphate reductase homologs from rice and Arabidopsis are also included in the M6PR group rather than the S6PDH group.

Mannitol is oxidized to mannose by mannitol dehydrogenase (MDT), and the resultant mannose is used through subsequent hexokinase and isomerase reactions. Celery MTD has been purified and its cDNA cloned (Stoop et al., 1995; Williamson et al., 1995). Mannitol transporters have also been isolated and characterized from celery, and play a role in mannitol transport in phloem tissues through the proton symport mechanism (Juchaux-Cachau et al., 2007; Noiraud et al., 2001).

In olives, mannitol is also a major soluble carbohydrate, and mannitol transporters and MDT play a role in mannitol metabolism and transport (Conde et al., 2007). Transcripts for the olive mannitol transporter increase throughout the maturation of olive fruit, suggesting that the transporter is involved in mannitol accumulation during fruit maturation. Where boron is limited, increased mannitol maintains boron remobilization in olive plants (Liakopoulos et al., 2005). Hu et al. (1997) reported that boron is present in the phloem of...
celery as the boron-mannitol complex. In some ornamental plants, the occurrence of polyols determines boron toxicity symptoms (Brown et al., 1999b).

Delphinium contains a considerable amount of mannitol. Tanase et al. (2005) reported that decreases in mannitol and other sugars in flowers under low light likely facilitate ethylene evolution and flower abscission in potted delphinium. Flower abscission can be prevented by ethylene inhibition; however, flower quality is still reduced by the wilting of sepalas and the development of pistils. Kikuchi et al. (2003) suggested that MTD is related to pistil development and that sucrose-related enzymes are important in sepal wilting.

3. Physiological studies on various polyols

SDH-like sequences are widespread in the plant kingdom, as shown in genome projects on plant species that do not synthesize sorbitol as a major photosyntheate.
In spite of this, little information is available at the molecular level on SDH-like sequences in non-rosaceous plants. Ohta et al. (2005) first found molecular evidence of the presence of SDH in a non-rosaceous plant, tomato. They produced recombinant protein from a tomato SDH-like sequence and identified the protein as SDH by enzymatic characterization. In addition, the antisense transformation of tomato with the SDH-like sequence decreased SDH activity, indicating the contribution of the sequence to SDH activity in tomato. Cataldi et al. (1998) and Roessner-Tunali et al. (2003) detected a small amount of sorbitol in tomato. These findings suggest the presence of sorbitol metabolism in tomato. Furthermore, arabitol, a substrate for tomato SDH, accumulates in the leaves of tomato plants infected with a fungal pathogen (Clark et al., 2003). Because arabitol accumulation is important in pathogenicity, SDH possibly has antifungal activity by catabolizing arabitol. mRNAs for SDH-like proteins whose amino acid sequences are 80% or more identical to that of tomato SDH can be expressed in non-rosaceous plants of various families, including monocotyledons and gymnosperms, suggesting that functional SDH is widespread in the plant kingdom (Fig. 2).

SDH expression and activity are also observed in another fruit, strawberry, which is a sucrose-translocating plant and contains only a small amount of sorbitol (Duangsrisai et al., 2007, 2008). Strawberry SDH expression is high in the young and mature stages of fruit and is controlled by soluble carbohydrates and phytohormones, suggesting that SDH may play a role in development and response to the environment.

Plantain (Plantago major) is a non-rosaceous, sucrose- and sorbitol-translocating species that has been well studied at the molecular level. Polyol transporters have been cloned from plantain, and their expression is reportedly induced by salt stress (Pommerenig et al., 2007; Ramsperger-Gleixner et al., 2004). In contrast, the expression of SDH, which catabolizes sorbitol, is decreased by salt stress, resulting in an increase of sorbitol in plantain. Plantain is considered salt tolerant because of the above molecular mechanism.

D-mannoheptulose, a seven-carbon sugar, and perseitol, a seven-carbon polyol, are the dominant soluble carbohydrates in avocado (Liu et al., 1999a, 1999b). Liu et al. (2002) suggested that the seven-carbon sugar plays important roles in carbon allocation in avocado trees and inhibits fruit ripening.

Various polyols are found in ornamental plants of many species; for example, carnation and redbud contain pinitol (Griffin et al., 2004; Norikoshi et al., 2008). Redbud accumulates pinitol under environmental stress and pinitol is the methyl ester of chiro-inositol, a cyclitol (cyclic polyol). Interestingly, soybean contains pinitol, which reportedly improves health in conditions associated with insulin resistance, such as diabetes mellitus and obesity (Morinaga et al., 2006). Bornesitol, a methyl ester of another cyclitol, myo-inositol, is a dominant soluble carbohydrate in sweetpea (Ichimura et al., 1999).

Volemitol, a seven-carbon polyol, is the major soluble carbohydrate in Primula (Hafliger et al., 1999), accounting for 25% of leaf dry weight and 24% of the phloem sap carbohydrate, suggesting its importance as a translocatable and storage carbohydrate. A key enzyme in volemitol biosynthesis is a novel ketose reductase, sedoheptulose reductase, which forms volemitol by the reduction of sedoheptulose, which is generally found in the form of its phosphate ester in the pentose phosphate cycle in plants.

Although the physiological roles of these various polyols are not always clear, they may be major carbohydrates in storage and translocation. Alternatively, they may be related to biotic and abiotic stress tolerance, which is a polyol-specific function. It is necessary to identify key enzymes for their biosynthesis, as found for sorbitol, mannnitol, and volemitol. The roles of polyols will be uncovered by suppressing key enzyme expressions or divergences in polyol biosynthesis.

4. Polyols in pathogenicity

High polyol concentrations accumulate in tomato after infection with a fungal pathogen (Clark et al., 2003). The role of this accumulated arabitol is likely osmoregulation by the pathogen, because water acquisition is important in pathogenicity. Polyol accumulation during infection has also been reported in cucumber and sunflower (Abood and Losel, 2003; Jobic et al., 2007).

Voegele et al. (2005) reported that mannitol accumulation in broad bean after fungal infection is due to fungal mannitol dehydrogenase, which could be related to carbon storage for the fungal pathogen and scavenging of reactive oxygen species (ROS), which are important in plant defense reactions. Because broad bean does not normally synthesize and use mannitol, this strategy of the fungal pathogen could be effective for pathogenicity. Arabitol is also accumulated after fungal infection of broad bean, possibly as a scavenger of ROS (Link et al., 2005). Using insertional mutagenesis of the fungal mannitol 1-phosphate dehydrogenase gene for mannitol synthesis, Solomon et al. (2005) showed that it is required for sporulation in planta of a wheat pathogen. These findings all indicate the importance of polyol accumulation by fungal pathogens in fungus-plant interactions.

Analysis of transgenic host plants in relation to plant mannitol catabolism and transport confirms the role of mannitol during infection and enhanced disease resistance. The overexpression of celery MTD, which plays a role in mannitol catabolism, in tobacco plants enhances disease resistance (Jennings et al., 2002). When the celery mannitol transporter is expressed in tobacco plants, sensitivity to mannitol-secreting pathogenic fungi is decreased, suggesting a role for polyol transporters in...
A pathogen is known to use a polyol synthesized by plants. Oh and Beer (2005) suggested that the capability of *Erwinia amylovora* to use sorbitol is an important factor affecting disease-causing activity in apple shoots. This is likely because *E. amylovora*, a bacterial plant pathogen, causes fire blight in rosaceous plants such as apple and pear.

5. Genetic engineering of polyol biosynthetic pathways

Sorbitol content is increased by drought stress in apple, peach, and loquat plants (Cui et al., 2003, 2004; Sircelj et al., 2005, 2007). Sorbitol is a reliable indicator of drought stress in apple trees, together with zeaxanthin, glutathione, and ascorbate (Sircelj et al., 2007). Since sorbitol accumulation under environmental stress is related to the induction of *S6PDH* expression, and *S6PDH* expression is also induced by abscisic acid, *S6PDH* is a multifunctional gene for the synthesis of translocatable carbohydrates and response to stress (Deguchi et al., 2002a, 2002b; Kanayama et al., 2006). The activity of celery MTD promoter is inhibited by salt stress, osmotic stress, and abscisic acid (Zamski et al., 2001); therefore, mannitol may accumulate under decreased MTD activity in celery as a response to abiotic stress. In a halophytic plant (*Mesembryanthemum crystallinum*), ononitol and pinitol are produced as a stress response through the action of inositol methyl transferase (Vernon and Bohmert, 1992). The inositol methyl transferase gene can be used for the production of pinitol and ononitol using transformation techniques (Chiera et al., 2006).

Since polyols are involved as compatible solutes, as mentioned above, there have been many efforts to engineer stress tolerance by accumulating polyols (Abebe et al., 2003; Deguchi et al., 2004; Karakas et al., 1997; Sheveleva et al., 1997, 1998; Sickler et al., 2007; Tarczynski et al., 1993). Such transformants often show growth inhibition (Abebe et al., 2003; Deguchi et al., 2004; Karakas et al., 1997; Sheveleva et al., 1998), which could be a serious problem for engineering stress tolerance although it can be useful for the production of pinitol and ononitol using transformation techniques (Chiera et al., 2006).

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Previous studies have shown that osmolytes, including polyols, have free radical scavenging properties (Shen et al., 1997; Smirnoff and Cumbes, 1989). Most of these results, however, were from *in vitro* experiments using relatively high concentrations of compatible solutes. Cuin and Shabala (2007) found evidence of an *in situ* mitigating effect of low concentrations of compatible solutes, such as mannitol, on ROS by monitoring ROS-induced ion fluxes across the plasma membrane. Recent studies have shown that polyols protect proteins against denaturation. Jaindl and Popp (2006) measured the activity and circular dichroism spectra of...
glutamine synthase and malate dehydrogenase and showed that cyclitols protect these enzymes from thermally induced denaturation and deactivation. Anderson (2007) determined structure-function relationships between polyols and the thermal stability of pepper leaf proteins, finding that the thermal stability of proteins increased with increasing numbers of OH groups and the polarity of polyols. Since mixtures of stabilizing and destabilizing compounds negate each other, the identification and removal of destabilizing compounds should have a similar effect to increasing stabilizers as a strategy for protecting protein conformation.

7. Concluding remarks

Polyols play a role not only in the translocation and storage of photosynthates, but also in biotic and abiotic responses in horticultural crops. Polyol metabolism might not be essential for plant development, as shown by the suppression of S6PDH expression, although it is possible that a very small amount of sorbitol is important or that less sorbitol decreases stress tolerance, and this cannot be ruled out until knockout plants are tested. Polyols are likely to be an alternative pathway and function specifically in stress responses.

The sorbitol/sucrose ratio diverges in the genus Prunus according to Moing et al. (1997b). Because sorbitol is a compatible solute, the ratio to sucrose could be related to environmental conditions. Some eucalypt species accumulate quercitol, a cyclitol derived from inositol, in drought stress conditions (Merchant et al., 2006). The presence and concentration of quercitol is segregated among eucalypt species according to taxonomy and geographic/environmental distribution (Merchant et al., 2007); therefore, the determinant of polyol levels could be related to evolutionary adaptation to environmental stress. Since a polyol molecule has multiple functions in relation to plant stress tolerance, engineering the polyol synthetic pathway will be a powerful tool if the side effects of growth inhibition can be avoided.

Nucleotide sequences of polyol-related enzymes have been found in various plant species that do not synthesize polyols as a major photosynthate as a result of recent progress in the genome project. Metabolome analysis also shows that polyols are synthesized as a minor component in various plant species, such as tomato and bean (Hernández et al., 2007; Roessner-Tunali et al., 2003); their physiological roles can be clarified by reverse genetic approaches. It is possible that a novel function for polyols will be found, because minor soluble carbohydrates can be important in plant growth, as described for trehalose (Schluempmann et al., 2003).

A cluster of the aldose reductase group in the phylogenetic tree of polyol-related enzymes is shown in Figure 1. Aldose reductases have been investigated in various non-rosaceous plants (Gavidia et al., 2002; Mundree et al., 2000), although their substrates are not always glucose and sorbitol. Aldose reductase homologs are also expressed in rosaceous fruit trees (data not shown). Although SDH is believed to be the main sorbitol-catabolizing enzyme, aldose reductase (NADP-dependent sorbitol dehydrogenase), which reduces glucose to sorbitol, has been partially purified from apple (Yamaki, 1984), and sorbitol can be converted to glucose in apple and pear fruits, as shown in tracer experiments using 

\[ ^{14}\text{C}-\text{sorbitol} \] (Ohkawa et al., 2008); therefore, further studies on aldose reductase will be necessary at the molecular level in rosaceous fruit trees. As for SDH, transgenic studies or other genetic approaches are necessary to confirm the physiological roles of the SDH gene family. The relationship between sorbitol catabolism and transport and watercore should also be investigated. Gao et al. (2005) suggested that decreased expression of a sorbitol transporter results in late watercore in apple fruit, while Yamada et al. (2006a, 2006b) found active metabolism and uptake of sorbitol in parenchyma cells of early watercored apple fruit.

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