CellPress

Opinion

Mannitol in Plants, Fungi, and Plant–Fungal Interactions

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Although the presence of mannitol in organisms as diverse as plants and fungi clearly suggests that this compound has important roles, our understanding of fungal mannitol metabolism and its interaction with mannitol metabolism in plants is far from complete. Despite recent inroads into understanding the importance of mannitol and its metabolic roles in salt, osmotic, and oxidative stress tolerance in plants and fungi, our current understanding of exactly how mannitol protects against reactive oxygen is also still incomplete. In this opinion, we propose a new model of the interface between mannitol metabolism in plants and fungi and how it impacts plant–pathogen interactions.

Trends

Mannitol is proposed to have a role(s) in protecting cells and cellular structures against damage by reactive oxygen that is unrelated to previous models of radical scavenging.

The application of newer techniques, such as targeted gene disruption, now allows for new interpretations of the nature and role of mannitol metabolism in fungi.

Mannitol: The Versatile Carbohydrate

Polyols or sugar alcohols are chemically reduced forms of aldose or ketose sugars where the aldehyde or keto group has been reduced to an alcohol. Mannitol, the polyol structurally related to the aldohexose mannose, is perhaps the most widely distributed soluble carbohydrate in biological systems. In addition to being found in more than 100 higher plant species, mannitol is also present in algae, fungi, and lichens [1]. Mannitol metabolism has been relatively well characterized, and several comprehensive reviews on the basic biochemistry and physiological roles of mannitol in plants have been published [2–6]. A brief summary of mannitol metabolism and transport is presented in Figure I in Box 1.

While the role of mannitol and, by extension, the mannitol catabolic enzyme mannitol dehydrogenase (MTD) in resistance to both biotic and abiotic stresses is well established, the precise mechanism whereby mannitol provides this protection is far from settled. In fact, with growing interest over the past decade in the interface between plant and fungal mannitol metabolism during plant–pathogen interactions, several unexpected insights into the role of antioxidants and protein trafficking and secretion have emerged.

How Does Mannitol Act as both an Osmoprotectant and Buffer against Oxidative Stress?

While mannitol clearly has important roles in oxidative and osmotic stress protection and regulation in plants and fungi, our understanding of the precise mechanisms involved remains incomplete. Although mannitol is sometimes mistakenly assumed to be a simple osmolyte *in vivo*, perhaps because of its high concentrations in salt-tolerant plants, such as celery (*Apium graveolens*), measured mannitol concentrations *in vivo*, as well as water and osmotic potentials in mannitol-producing, transgenic plants and calli, are far too low for mannitol to function solely as an osmolyte [7,8]. Two mechanisms are commonly proposed to explain how mannitol can be an osmoprotectant without being an osmolyte. One is that it functions as a 'compatible' solute; the other is that it acts as an antioxidant. Organisms under stress sometimes accumulate specific compounds to high cellular concentrations that are still 'compatible' with normal physiological processes; these include sugars, polyols, amino acids, and amino acid derivatives. The role of compatible solutes in osmotolerant organisms, such as yeast and algae, was well

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Box 1. Mannitol Metabolism and Transport in Celery.

Mannitol accumulation and localization in plants is balanced by regulated synthesis, transport storage, and utilization in response to salt and drought stress. Unlike typical non-mannitol plants, where stomatal closure results in decreased CO_2 exchange and a consequent decrease in carbon fixation, celery grown under high salinity maintains total photoassimilate levels. This correlates with an increase in the relative concentration of mannitol versus sucrose [77,90,91], which, in turn, is associated with an increase in total activity of the mannitol biosynthetic enzyme M6PR in young leaves (a sink tissue) [90]. However, under these same conditions, there is little change in M6PR activity in mature (source) leaves, suggesting that they are already at maximum biosynthetic capacity. Coincident with this increase in mannitol synthesis, plants such as celery also decrease mannitol usage in sink tissues (e.g., roots) by downregulating production of the catabolic enzyme MTD. Salt-induced downregulation of *Mtd* RNA accumulation and *Mtd* gene expression is seen in cultured celery and olive cells [74,77,92,93]. Together with the salt-induced increase in synthesis, this results in significantly increased mannitol content in leaves and roots under salt and drought stress. Finally, olive cells and celery plants grown under salt or osmotic stress also increase expression of the mannitol transporters AgMaT3 and OeMaT1, respectively [91,93]. Although mannitol transport in the leaf mesophyll is thought to be symplastic (through the **plasmodesmata**), long-distance transport via the phloem is thought to involve apoplastic loading and unloading mediated by mannitol transporters, such as the *AgMat* proteins [66,91,94]. Once it reaches a sink tissue such as storage parenchyma cells, mannitol can be localized in vacuoles until metabolized [95]. Together, these features suggest that total mannitol content and localization in mannitol-metabolizing plants, such as celery and olive, are determined by balancing mannitol synthesis, use, storage, and transport in different tissues in response to stress (Figure I).

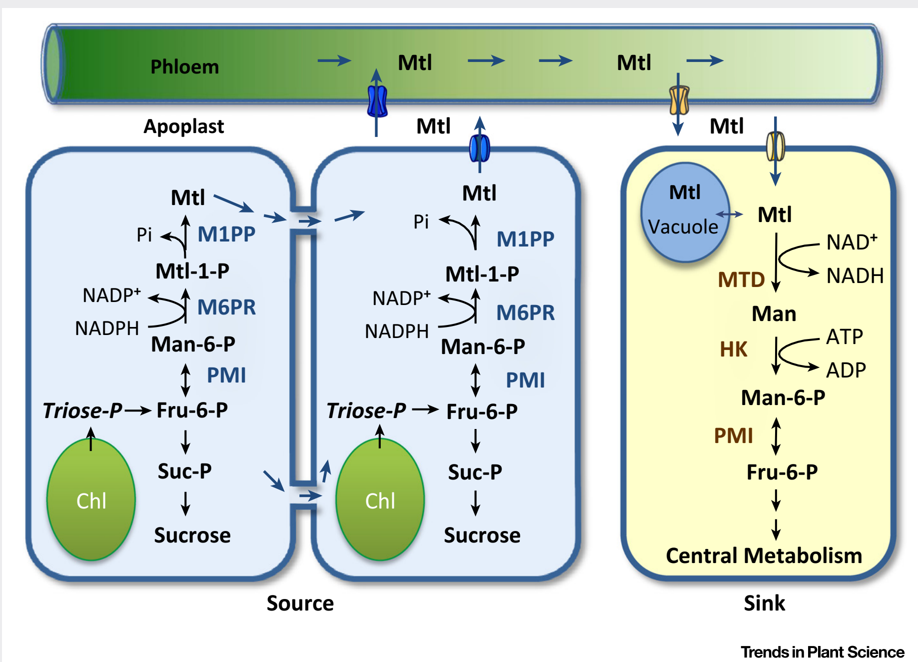

Figure I. Mannitol Synthesis, Transport and Catabolism in Celery. Abbreviations: Chl, chloroplast; Fru-6-P, fructose 6-phosphate; HK, hexokinase; M1PP, mannitol-1-phosphate phosphatase; M6PR, mannose-6-phosphate reductase; Man, mannose; Man-6-P, mannose 6-phosphate; Mtl, mannitol; Mtl-1-P, mannitol 1-phosphate; MTD, mannitol dehydrogenase; PMI, phosphomannose isomerase; Suc-P, sucrose phosphate. AgMat transporters are indicated by: , , , .

Glossary

Apoplast: everything outside the cell plasma membrane; also referred to as the extracellular space.
Plasmodesmata: pores connecting the cytosol of adjacent cells, bridging the apoplast to form a semicontinuous symplastic space throughout the plant.
Symplast: everything in a plant cell inside the plasma membrane.

established by the 1980s [9–11]. These compatible solutes are thought to act as osmoprotectants because they can interact with the hydration shell around proteins and cellular structures to protect and stabilize them under conditions of low osmotic potential [12,13].

Another widely accepted hypothesis is that mannitol protects against osmotic stress by acting as an antioxidant. Decreased water potential can result in the formation of potentially damaging reactive oxygen species (ROS) [5,14–16]. The idea that mannitol ameliorates these effects in plants by quenching ROS arises from several studies. An early study by Smirnoff and Cumbes