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Sucrose accumulation in the sugarcane stem: pathways and control points for transport and compartmentation

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Abstract

The accumulation of high concentrations of sucrose in the stem of sugarcane has been the subject of many studies. Although models have been constructed from the available information, many steps in the transport and accumulation pathway remain unknown. Recent advances in molecular approaches may elucidate some of these processes. Genes encoding proteins associated with sugar synthesis and storage will provide valuable tools. In particular, the use of techniques to localize the sites of expression of sugar transporters and metabolic enzymes will assist in defining possible routes of sugar movement. When combined with an analysis of metabolite concentrations and enzyme activities in cellular and subcellular compartments, these novel approaches will contribute to an integrated picture of stem function. Control points identified will provide useful tools for selection of efficient genotypes and targets for molecular manipulations.

Keywords: Phloem; Sucrose metabolism; Sugarcane; Sugar transporters; Vacuole

1. Control points for sucrose storage

Mature sugarcane stems are capable of accumulating high concentrations of sucrose, approaching 650 mM in the storage tissues of some varieties (Welbaum and Meinzer, 1990). Although sucrose is commonly found in plant storage organs, it is generally at a low concentration, and starch is the predominant storage carbohydrate (Komor, 2000). Storage of assimilate as a small osmotically active molecule might be expected to create metabolic stresses in the cells of the storage tissue. Indeed, a study of the gene transcripts associated with the process of maturation in sugarcane internodes showed increased transcription of many genes involved in stress responses (Casu et al., 2004).

The partitioning of sugars into tissues, cells and subcellular compartments is determined by control points in transport pathways. Thus, knowledge of the location of these control elements in the tissue is crucial to an understanding of the sucrose storage process. In addition, these control points will be potential targets for manipulation in strategies to increase sucrose accumulation (Grof and Campbell, 2001). Recently, a number of genes which encode enzymes of sugar metabolism or sugar transport in

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sugarcane have been identified (Zhu et al., 2000; Carson and Botha, 2002; Carson et al., 2002; Grivet and Arruda, 2002; Casu et al., 2003). Together with a functional analysis of these enzymes, information on the localization of their expression and activity will enable us to build a model of the pathways and control points for sugar movement into the storage sink. This model will highlight where further investigation is required and will be used to develop strategies for increasing sucrose concentration.

2. Source to sink pathway

Sucrose is synthesized in the photosynthetic tissue of the leaf mesophyll. In some species, sucrose is able to move from the mesophyll cells to the conducting cells of the phloem via direct cell-to-cell connections known as plasmodesmata. Species with numerous plasmodesmata connecting the phloem cells to surrounding cells have been classified as symplastic phloem loaders (van Bel and Gamalei, 1992). However, there is good evidence that loading of sucrose into the phloem occurs from the apoplast in many species. Sucrose transporter proteins, which would permit the import of sucrose from the extracellular solution, have frequently been localized to the phloem cell membranes (Lalonde et al., 2003). Mutant plants with insertions in a gene encoding a sucrose transporter were unable to export sucrose normally (Gottwald et al., 2000). Further evidence that sucrose passes through the apoplast before entering the phloem was provided by transgenic tomato plants that were engineered to express invertase in the leaf apoplast (Dickinson et al., 1991). In the transgenic plants, starch accumulated abnormally in the leaf cells and growth was severely restricted, indicating that sucrose export from the leaf was impaired. The complete pathway of sucrose flow in apoplastic phloem loaders is not known but the vascular parenchyma is considered to be the most likely site for release of sucrose into the apoplast (Lalonde et al., 2003). In sugarcane, the conducting cells of the phloem are not connected to other cells of the leaf by plasmodesmata (Robinson-Beers and Evert, 1991). This suggests that phloem loading occurs from the apoplast in sugarcane leaves.

In the phloem, sucrose moves out of the leaf and towards sink tissues, including developing shoot and root apices and storage organs. The movement of sucrose through transport phloem is thought to be driven by concentration gradients (van Bel, 2003). In source tissues, loading of sucrose causes influx of water and the resulting high turgor promotes movement away from the source. Conversely, removal of the sucrose from phloem causes a reduction in osmotic pressure in sink phloem tissues (van Bel, 2003). Sucrose transporters continue to be expressed in transport phloem and may act in retrieval of sucrose lost to the apoplast by leakage (Lalonde et al., 2003). Although no direct measurements have been made in sugarcane, the $^{14}CO_2$ studies of Hartt et al. (1963) indicate that sucrose is the major carbohydrate transported in the phloem.

In the sink tissues, sucrose is unloaded from the phloem. Several pathways of unloading have been described (Patrick, 1997). At junctions between maternal and filial tissue and at interfaces between host and symbiont, the pathway of unloading always includes an apoplastic step. However, in vegetative tissues, movement may be either apoplastic or symplastic. In potato, the tubers are storage sinks that develop from shoot meristems. The movement of the carboxyfluorescein tracer dye, which is restricted to the symplast, showed that phloem unloading is predominantly apoplastic in stolons. However, the onset of tuber development and starch accumulation is accompanied by a switch to symplastic movement of solutes from phloem to storage parenchyma cells (Viola et al., 2001).

In storage tissues where soluble sugars are accumulated, the pathway of unloading includes an apoplastic step at the periphery of the phloem or in subsequent cell layers (Lalonde et al., 2003). For sugarcane, which accumulates soluble sugars into a tissue which is relatively mature, this type of pathway may be more relevant. Accumulation of soluble sugars in tomato fruits is an example of an unloading pathway that involves an apoplastic step. In developing fruits, the switch to soluble sugar accumulation is accompanied by a reduction in symplastic connectivity, shown by the movement of tracer dyes (Patrick, 1997). At this stage, invertase activity in the apoplast and hexose transport activity in the storage cells also develop. These observations suggest that sucrose is