

Membrane-Transport Systems for Sucrose in Relation to Whole-Plant Carbon Partitioning

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ABSTRACT Sucrose is the principal product of photosynthesis used for the distribution of assimilated carbon in plants. Transport mechanisms and efficiency influence photosynthetic productivity by relieving product inhibition and contribute to plant vigor by controlling source/sink relationships and biomass partitioning. Sucrose is synthesized in the cytoplasm and may move cell to cell through plasmodesmata or may cross membranes to be compartmentalized or exported to the apoplast for uptake into adjacent cells. As a relatively large polar compound, sucrose requires proteins to facilitate efficient membrane transport. Transport across the tonoplast by facilitated diffusion, antiport with protons, and symport with protons have been proposed; for transport across plasma membranes, symport with protons and a mechanism resembling facilitated diffusion are evident. Despite decades of research, only symport with protons is well established at the molecular level. This review aims to integrate recent and older studies on sucrose flux across membranes with principles of whole-plant carbon partitioning.

Key words: Carbohydrate metabolism; molecular transport; membrane proteins; phloem physiology; gene expression.

INTRODUCTION

Sucrose (Suc) is the principal product of photosynthesis used for the distribution of assimilated carbon in plants. Suc is produced in the cytoplasm, directly from the products of photosynthesis or from the utilization of storage reserves, and may follow several fates. A prominent transport fate is to move cell to cell via plasmodesmata through the collective cytoplasm of plant cells called the symplasm (*-plasm* terminology is used here in preference to *-plast*, following the arguments of Erickson (1986)). Alternatively, Suc may cross an endomembrane to enter an organelle—principally the vacuole for storage—or it may cross the plasma membrane to enter the collective cell-wall space (apoplast) for subsequent uptake into adjacent cells. As a relatively large, polar solute, Suc requires proteins to facilitate efficient movement across membranes. Physiological studies support active transport energized by the proton motive force and facilitated diffusion across both the tonoplast and the plasma membrane. For energized transport, Suc/H⁺ antiport to move Suc into vacuoles is supported by physiological studies and Suc/H⁺ symport to move Suc out of vacuoles is supported by molecular evidence. Suc/H⁺ symport across the plasma membrane is well established while a mechanism with characteristics of facilitated diffusion remains enigmatic. Genes and proteins catalyzing Suc/H⁺ symport have been called Suc transporters (SUT) or Suc carriers (SUC), and those participating in passive transport have been called Suc facilitators (SUF). No genes or proteins catalyzing Suc/H⁺

antiport are identified. In this document, SUT will be used when referring to proteins mediating Suc membrane transport in general and gene/protein names will be used when referring to specific SUTs.

Research progress on the central role of SUTs in whole-plant carbon partitioning is reflected in the history of excellent reviews. Robert Giaquinta (1983) and Daniel Bush (1993) published extensive reviews on physiological and biochemical considerations of Suc membrane transport, respectively, before molecular cloning techniques were widely applied. Sylvie Lalonde and colleagues (2004) and Norbert Sauer (2007) subsequently published extensive surveys on the *SUT* genes that were rapidly being characterized. More recently, reviews emphasizing monocot SUTs (Braun and Slewinski, 2009), the regulation of SUT activity (Kuhn and Grof, 2010), and SUT activity in relation to photosynthetic primary productivity (Ainsworth and Bush, 2011) have appeared. This review aims to integrate earlier research with more recent findings in the context of whole-plant Suc partitioning.

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BIOCHEMICAL SUMMARY OF Suc MEMBRANE TRANSPORT

Michaelis-Menton plots showing biphasic kinetics for uptake of Suc across membranes into developing cotyledons and isolated leaf disks have been available for decades (Figure 1) (Sovonick et al., 1974; Lichtner and Spanswick, 1981; Maynard and Lucas, 1982a). The first phase, evident at low concentrations, is saturable and requires a proton gradient (Giaquinta, 1977) and the second phase is linear with Suc concentration and unsaturable. The first phase is described as being mediated by a high-affinity/low-capacity mechanism and the second phase has been referred to as a low-affinity/high-capacity mechanism. The development of isolated membrane vesicles as experimental tools was fundamental to elucidating the biochemical characteristics of Suc transport across plant membranes, including $K_{0.5}$ for both H^+ and Suc, pH and membrane potential dependence, stoichiometry, electrogenicity, and specificity (Bush, 1990; see Bush (1993) for detailed review and discussion). It is clear now that the saturable phase represents thermodynamically unfavorable uptake of Suc energized by the proton-motive force and catalyzed by Suc/ H^+ symporters. All SUTs isolated to date are characterized as Suc/ H^+ symporters with the exception of several SUFs identified in legumes (discussed below). Despite the identification of SUFs, the linear phase is not defined at the molecular level.

The first *SUT* genes identified and sequenced were isolated from spinach (*SoSUT1*; *Spinacia oleracea*) and potato (*StSUT1*; *Solanum tuberosum*) cDNA-expression libraries that were

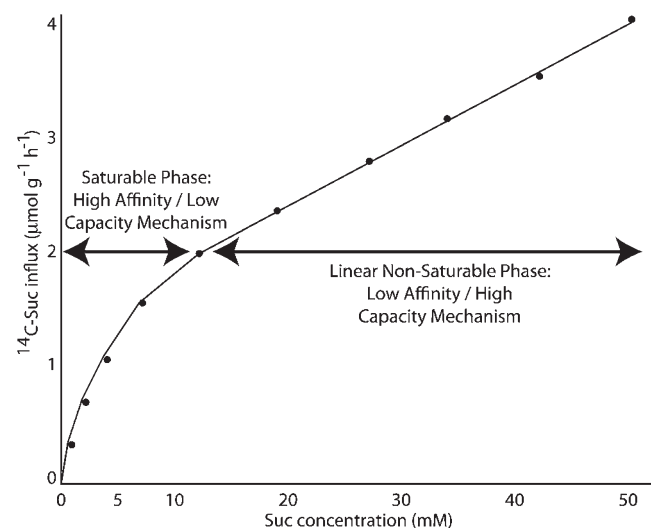


Figure 1. A Representative Plot of [^{14}C]Suc Influx into Leaf Disks Relative to External Suc Concentration.

The graph shows the saturable phase ascribed to a high-affinity/low-capacity mechanism, now known to be catalyzed by Suc/ H^+ symporters, and the linear, non-saturable phase, ascribed to a low-affinity/high-capacity mechanism. Although described as having characteristic of facilitated diffusion, the mechanism remains unknown. The plot is drawn based on Maynard and Lucas (1982a).

screened in yeast. The yeast strain used was engineered to grow on Suc as the sole carbon source only if Suc were internalized via a cDNA-encoded transporter (Riesmeier et al., 1992, 1993). Subsequently, *SUT* genes were isolated from numerous species by sequence homology (Gahrtz et al., 1994; Sauer and Stolz, 1994; Burkle et al., 1998; Aoki et al., 1999) and more recently by analysis of sequenced genomes and EST libraries (Meyer et al., 2000; Aoki et al., 2003; Sauer et al., 2004; Baud et al., 2005). It is now apparent that all plants have a small family of *SUT* genes that are members of the major facilitator superfamily, with 12 membrane spanning domains and the N- and C-termini on the cytoplasmic side of the membrane.

Members of the SUT family cluster into distinct clades and these are useful in forming hypotheses on function. Aoki and colleagues identified three distinct branches (Type I, II, and III) in one of the earliest comprehensive trees (Aoki et al., 2003), as did Lalonde and colleagues (Clade I, II, and III) (Lalonde et al., 2004). As expected, these trees have the same basic structure, but the Type/Clade naming is not consistent, with Aoki's Type II and III branches corresponding to Lalonde's Clade III and II, respectively. As more sequences were identified, the number of major branches has increased from three to four (Sauer, 2007), to the current five (Braun and Slewinski, 2009; Kuhn and Grof, 2010), as the Type II (Clade III) branch has undergone further subdivision. However, inconsistency in nomenclature remains, with various authors using different conventions. Furthermore, individual genes were initially named in the order they were identified and then on homology to existing genes, such that gene names do not provide an intuitive indicator of sub-family membership. The Groups 1 through 5 convention (Braun and Slewinski, 2009) will be used in this document. Table 1 summarizes the characteristics of the five groups and provides representative members of each.

Group 1 comprises monocot-specific SUTs involved in phloem transport, Suc uptake into sink tissues including grain filling, and general retrieval from the apoplasm (Aoki et al., 1999, 2003, 2004; Scofield et al., 2007; Braun and Slewinski, 2009; Slewinski et al., 2009). All appear to localize to the plasma membrane and have moderate affinity for Suc, with $K_{0.5}$ values ranging from 3.7 mM for ZmSUT1 from maize (*Zea mays*) (Carpaneto et al., 2005) to 10.6 mM for HvSUT1 from barley (*Hordeum vulgare*) when tested in *Xenopus* oocytes by electrophysiology (Sivitz et al., 2005). Group 1 SUTs are thought to contribute to the saturable uptake kinetics in monocots and have the highest specificity for Suc among the SUT groups (Sun et al., 2010).

Group 2 comprises dicot-specific SUTs that are also involved in phloem loading, uptake of Suc into various sink tissues, and general retrieval from the apoplasm. This group has received the greatest attention because they were the first SUTs identified, are active in species amenable to manipulation with genetic and molecular techniques, and because members have a clear function in phloem loading and carbon partitioning. They localize to plasma membranes and mediate high-affinity saturable uptake with $K_{0.5}$ for Suc ranging from 0.066 mM for

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