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Sucrose Transporters Regulate Sugar Partitioning in Plants

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ABSTRACT

Sugar partitioning is general definition of assimilate allocation from source to sink organs while sucrose is distributed over the long distance through phloem sieve tubes towards heterotrophic organs. Sucrose transporters regulating the efflux of sucrose into the apoplast of the source and sink cells. They belong to integral cell membrane proteins encoded by numerous genes in plants. Recent insights on molecular aspects of transporters underscore the crucial role of sucrose transporters in different plant biological phenomena. Some investigations with regard to potential role of sucrose transporters on sugar partitioning and consequent stimulated responses of plants are discussed in current review article.

Keywords: Acclimation, Antisense, Gene, Photosynthesis, Sink, Source, Symporter

INTRODUCTION

Sucrose is the end product of photosynthetic process and, in most plants; it is the predominant form of carbon transported to the heterotrophic tissues [1-3]. Sugar partitioning or in a more meaningful definition, sucrose allocation between sink-source tissues is a fundamental process in all plants. More than 80% of the photosynthetic carbon product is transported via the plant's phloem vascular system to heterotrophic organs of plants [4]. This transport system comprises three steps: (i) loading of photosynthates into the sieve element companion cell complex (se-cc complex) of minor veins in exporting leaves, (ii) translocation from source to sink, and (iii) unloading in growing or storing sinks [5]. The movements of most solutes through the membrane are mediated by membrane transport proteins which are specialized to varying degrees in the transport of specific molecules. Sucrose transporters (SUT) are structurally integral proteins in the cell membrane mediating sucrose movement in or out of the cell. The transport is active and has been described as a sucrose-proton co-transport with a 1:1 stoichiometry [6]. Sucrose transporter function in vacuole have been characterised as sucrose/H+ symporters and efflux of sucrose into source or sink apoplast is supported by sucrose/H+ anti-porters [7]. From a structural point of view, transporters are highly hydrophobic proteins and belong to the class of metabolite transporters consisting of two sets of six membrane spanning regions, separated by a central cytoplasmic loop [8].

SUCROSE TRANSPORTERS GENE FAMILIES

Over the last decade, genes encoding SUT proteins have been isolated from a wide range of both monocot and dicot plant species [9,10]. Lemoine [11] and Williams et al. [12] have reported that two or more SUT genes for many of these species are known to exist. In Arabidopsis, five SUT genes have been functionally characterized [13-17]. In addition, four further putative SUT sequences can be found in public databases. In potato and tomato, three SUT genes with different sucrose transport characteristics have been detected [16,18,19]. Through a study using a yeast heterologous expression system, the first SUT gene in monocots was found in rice (OsSUT1) [20]. Aoki et al. [21] in an extensive study using the published draft sequence of the rice genome, identified, cloned and analysed the expression of four putative sucrose transporters in rice: OsSUT2, 3, 4 and 5 **(Figure 1)**.

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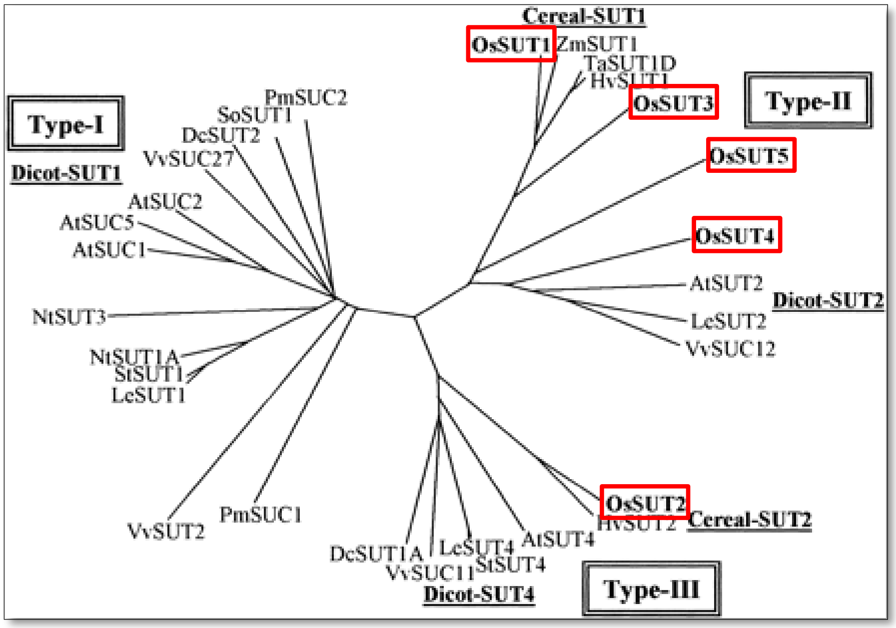

Figure 1. An un-rooted dendrogram of plant SUTs based on deduced amino acid sequences. The OsSUT genes are highlighted by red boxes.
Adopted from [21]

Using expression profiling, the role of OsSUT1 during germination and early growth of rice seedlings has been examined in detail. This gene was present in the companion cell's sieve elements of the scutellar vascular bundle, where it may play a role in phloem loading of sucrose for transport to developing shoot and roots. OsSUT1 was also present in the coleoptiles and the first and second leaf blades and phloem of primary roots [22]. In another study, twenty-six suppression lines were created using an antisense construct containing a portion of the 3'-coding and non-coding regions of OsSUT1 driven by the maize ubiquitin-1 promoter. The functional analysis of OsSUT1 antisense lines revealed the important role of this OsSUT1 gene on germination, growth and grain filling of rice plants [23]. With the aim of investigating the role of OsSUT1 in the transport of assimilates along the entire long-distance pathway, an experiment using a promoter::GUS (ß-glucuronidase) reporter gene and immunolocalization of OsSUT1 proteins was conducted in rice. The results revealed that the mature phloem of vegetative tissue is involved in long distance assimilate transport pathway during grain filling. It was proposed that OsSUT1 may play a primarily role in the phloem loading of sucrose retrieved from the apoplast along the transport pathway [24].

As previously explained, sucrose supply to terminal sink organs is crucial for the energy status and the control of flowering, seed setting and filling and final yield product [25,26]. Besides, tight regulation of sucrose allocation is required to modulate carbon allocation in response to changing environmental conditions. Sucrose transporters are tightly regulated at various levels, allowing adaptation to external stimuli such as temperature, light regime, photoperiod, pathogen attack or other stresses [7,27,28]. In a case study the effects of sugar partitioning on salinity tolerance of rice antisense lines was investigated [29] and an overview is presented in continuing.

SALINITY TOLERANCE OF SUCROSE TRANSPORTERS ANTISENSE LINES

Sugar is depleted in the roots of sensitive rice cultivars after exposure to salt stress. In order to investigate this phenomenon further, we took advantage of reverse genetics by using sucrose transporter antisense lines to modify sucrose allocation in rice plants. Studies were carried out with the hypothesis that the knock-down of an acclimatory response involving a key metabolite such as sucrose would decrease the performance of the plants. Surprisingly, morpho-physiological evaluation showed that the transgenic lines performed the same or better than the wild type under salt-stress. In addition, during salt stress, antisense lines demonstrated higher sucrose, glucose-6-phosphate and fructose-6-phosphate levels in the roots of transgenic plants as compared to WT plants. To examine why this might occur, we first measured the root starch contents of lines but could not see any reasonable trend. We then profiled the expression levels of genes in the sucrose transporter family in plants grown with or without salt, and detected a significant increase in the expression of *OsSUT2* and *OsSUT4* genes in antisense lines as compared to WT, which could explain higher maintenance of sugars in the roots of antisense lines under salt stress. All these observations support the hypothesis that the modification of sucrose allocation toward the root upon salt stress improves the salinity tolerance of rice cultivars [29].

To the best of our knowledge, the experiments that comparatively investigate the metabolic phenotype as regards sugars in rice cultivars under salt stress are rare. In this regard, the only study we know of was by Boriboonkaset et al. [30] who looked at the effect of exogenous sugar classes and concentrations on the salt-tolerance of indica rice (*Oryza sativa* L.) and concluded that exogenous sucrose and glucose in the root play a direct role as a carbon source, improving salinity tolerance and maintaining growth and development in rice cultivars. Therefore, not only is a higher indigenous supply of sugars (mainly sucrose) to the root – as discovered in current project – improve the salinity tolerance of rice cultivars, but also an exogenous supply of sugars helps significantly. These issues strongly support the hypothesis that sugar maintenance in the root of rice plants upon salt stress improves the salinity tolerance of lines. Based on the results a non-linear sugar accumulation in the root of plants in response to salt stress was monitored. In this regards, the cultivars showed an extreme sugar accumulation in intermediate salt-acclimation. This promising hypothesis has potential practical applications for plant breeders.

CONCLUSION

To sum up, overexpressing and silencing of sucrose transporters genes provide strong evidence of the importance of sucrose transporters role in the axial pathway and terminal sink organs of heterotrophic tissues in different plants. Sugar allocation to different organs is regulated by sucrose transporters. Therefore, sucrose transporters play a major role in response of plants to environmental stimuli, determining the seed setting and filling after flowering, influencing pollen tube growth, assigning the process of tuberisation and controlling some other developmental phenomena in plants. Recent insights on molecular aspects of sugar partitioning and future perspectives of that, motivates the scientist to modify targets involved in sucrose allocation in plants and test its potential application to improve the plant performance.

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