

## Intracellular Metabolite Transporters in Plants

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### Abstract

Due to the presence of plastids, eukaryotic photosynthetic cells represent the most highly compartmentalized eukaryotic cells. This high degree of compartmentation requires the transport of solutes across intracellular membrane systems by specific membrane transporters. In this review, we summarize the recent progress on functionally characterized intracellular plant membrane transporters and we link transporter functions to Arabidopsis gene identifiers and to the transporter classification system. In addition, we outline challenges in further elucidating the plant membrane permeome and we provide an outline of novel approaches for the functional characterization of membrane transporters.

**Keywords:** Membrane; Biochemistry; Molecular transport; Transporters membrane proteins

### Introduction

Eukaryotic plant cells evolved a highly compartmentalized and complex metabolic network. The plastid and mitochondria organelles, and the vacuole [1], peroxisomes, Golgi, and ER compartments are embedded in the cytosol and each compartment contains a specific and often unique set of enzymes. Each sub-cellular reaction space is surrounded by at least one membrane, which forms a diffusion barrier that prevents the uncontrolled exchange of intermediates. Compartmentation allows for optimizing enzymatic reactions by providing various sub-cellular pH environments, it permits the simultaneous operation of pathways that compete for the same substrates, [2] it avoids futile cycles, and it confines toxic by product to defined sub-cellular reaction spaces. Frequently, however, metabolic pathways are interconnected across several compartments and depend on the supply of metabolic precursors from other parts of the cell [3]. Therefore, specific transport proteins are required to facilitate and to regulate the import and export of metabolites across compartmental boundaries. Metabolite transporters thus contribute to controlling the flux of solutes between compartments and are an integral and essential part of cellular metabolic networks. Given the large number of transported substrates, a wide spectrum of plant metabolite transporters has to be postulated [4]. Despite their importance for a functioning plant metabolism, our knowledge of intracellular transporters is still limited. In plants, as well as in other eukaryotic organisms, the majority of transport proteins have not yet been identified at the molecular level.

The recently established plant membrane protein database [5] ARAMEMNON offers a platform to easily predict putative transport proteins based on their protein sequences. Most of the intracellular metabolite transporters contain  $\alpha$ -helical transmembrane domains (TMDs) consisting of 16–23 amino acids. Several  $\alpha$ -helices form a selective 'pore' in the membrane that permits the controlled passage of hydrophilic solutes. To build such a pore, at least four or more transmembrane domains are required for a functional transport protein. It is estimated that the model plant [6] *Arabidopsis thaliana* contains 2705 proteins, with at least three predicted transmembrane domains, corresponding to 10% of the  $26^{200}$  proteins encoded by the *Arabidopsis* genome.

In recent years, significant progress has been made in elucidating the functions of many solute carriers in plants. This review will provide an overview of known intracellular transport proteins within the plant cell. Furthermore, it will outline the challenges and strategies for

functional analyses of the plant membrane permeome.

### Intracellular metabolite transporters

#### Metabolite transporters of the plastid inner envelope membrane

Plastids as the metabolic powerhouse of plant cells are involved in major pathways, such as photosynthetic carbon dioxide fixation, nitrogen and sulfur assimilation, and fatty acid, amino acid, as well as terpenoid biosynthesis [7]. These processes require numerous selective transport proteins for the controlled exchange of precursors, intermediates, and end products across the membranes. Plastids are surrounded by two membrane bilayers, the inner and outer plastid envelope membrane. The known metabolite carriers of the inner envelope exhibit high substrate specificity and are therefore considered to constitute a selectivity filter for metabolites [8]. Recent evidence indicates that the broad-specificity porin-like channel proteins of the outer membrane represent an additional layer of flux control across the plastid envelope. In this review, we focus on inner envelope membrane metabolite transporters, which have been intensively studied in recent years.

#### Plastidial transporters involved in inorganic phosphate homeostasis

Within plastids, Pi is an essential substrate for photosynthetic ATP biosynthesis as well as an exchange substrate for plastidic phosphate translocators, which are involved in carbon partitioning between starch and sucrose biosynthesis. It also participates in numerous enzymatic reactions and acts as an allosteric regulator of metabolic processes in plastids, such as starch synthesis. Thus, maintaining stromal Pi homeostasis is pivotal. A low plastidial Pi concentration impedes ATP synthesis and a net import of Pi into the stroma is required to prevent

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deleterious over-reduction of the photosystems. Especially slow conversion of triose-phosphate into sucrose in the cytosol sequesters the Pi in sugar-phosphates, [9] leading to inadequate Pi supply of the stroma via TPT. In contrast, the ATP import in exchange with ADP mediated by NTTs leads to a phosphate imbalance and thus necessitates export of Pi out of the stroma to prevent inhibition of starch synthesis by accumulated Pi. The identified Pi transporters are classified into four phosphate transporter (PHT) families and among them, proteins have been discovered poisoning plastidic Pi levels [10].

Within the PHT2 family in plants, only PHT2.1 has been functionally characterized so far. Localization studies using GFP as a reporter revealed that PHT2.1 is present in the chloroplast envelope. The transport activity was assayed in yeast cells lacking the plasma membrane Pi transporter. Recombinant PHT2.1 protein complemented the mutant and mediated a proton-coupled low-affinity Pi transporter [11]. The obtained Pi uptake into the yeast cells was dependent on an electrochemical gradient across the yeast plasma membrane. Given its transport properties, PHT2.1 might function as a Pi importer. The pH gradient across the envelope membrane established by the photosynthetic electron chain might be used to energize Pi transport into the stroma during the day. A mutation in the **PHT2.1** gene led to **Arabidopsis** plants with reduced leaf Pi content. Under Pi starvation, the redistribution of Pi from old towards young leaves was affected in the **pht2.1** mutant. PHT2.1 is preferentially expressed in the shoot, strongly up-regulated in leaves by light, and co-regulated with plastidic NADP-dependent malate dehydrogenase and thioredoxin, which implies a cross-talk of Pi homeostasis in the plastid with the redox status of the photosystem [12].

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