

Review

The Plant Mitochondrial Transportome: Balancing Metabolic Demands with Energetic Constraints

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In plants, mitochondrial function is associated with hundreds of metabolic reactions. To facilitate these reactions, charged substrates and cofactors move across the charge-impermeable inner mitochondrial membrane via specialized transporters and must work cooperatively with the electrochemical gradient which is essential for mitochondrial function. The regulatory framework for mitochondrial metabolite transport is expected to be more complex in plants than in mammals owing to the close metabolic association between mitochondrial, plastids, and peroxisome metabolism, as well as to the major diurnal fluctuations in plant metabolic function. We propose here how recent advances can be integrated towards defining the mitochondrial transportome in plants. We also discuss what this reveals about sustaining cooperativity between bioenergetics, metabolism, and transport in typical and challenging environments.

Understanding Plant Mitochondrial Transport

The plasticity of **mitochondrial** (see [Glossary](#)) metabolism in plants requires flexibility in **inner mitochondrial membrane** (IMM) transport kinetics and direction. The primary thermodynamic factor driving the catalytic transport activity across the IMM is the **electrochemical gradient** or proton motive force comprising a **proton gradient** (ΔpH) and a **membrane potential** ($\Delta\Psi$) generated by the proton pumps of the electron transport chain. The direction of movement of charged species between the cytosol and mitochondria is determined by the electrochemical potentials across membranes, the transport mode by **carrier proteins** (active transport) and **ion channels** (passive transport) and the biochemical properties of these transporters. The molecular machineries responsible for metabolite translocation across the IMM are still being unraveled. In addition, the metabolic and **bioenergetic** interactions between these transporters and the electron transport chain have so far received little attention. In this review we propose a regulatory framework for understanding plant mitochondrial transport – the transportome – by combining recent work from metabolic, bioenergetic, biophysical, bioinformatic, and proteomic research.

Expanding the Plant Mitochondrial Transportome

The **mitochondrial carrier family** (MCF; mitochondria-localized carriers from this protein family are abbreviated to MCs) has been historically viewed as the principal set of membrane proteins that catalyze metabolite transport across the IMM. The release of the first model plant genome from *Arabidopsis* (*A. thaliana*) led to the identification of 58 MCF proteins [1,2]. They

Trends

An increasing number of specialized inner mitochondrial membrane transporters have been identified but their kinetic properties and biochemical characteristics remain poorly understood.

Flux balance analysis is an emerging tool for predicting the direction of metabolite movement across the mitochondrial membranes.

Inner mitochondrial membrane transporters function cooperatively with the electron transport chain to optimize metabolite transport necessary for sustaining mitochondrial metabolism without compromising ATP synthesis.

The mitochondrial 'transportome' is not only regulated collectively by the electrochemical gradient, but also by transcriptional coregulation to meet the dynamic metabolic requirements under different developmental and environmental conditions.

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each have a conserved tripartite motif of two transmembrane α -helices separated by hydrophilic loops in each repeat. However, at least 12 MCF members have since been localized to non-mitochondrial compartments (Box 1) [2,3]. In total, 28 MCF members have been experimentally confirmed by proteomic analysis and localization studies to be present in plant mitochondria, while another three are predicted to be mitochondrial based on *in silico* localization prediction and/or studies from other organisms (Table S1 in the supplemental information online).

Recently, the characterization of a set of non-MC type transporters in mammalian mitochondria [4–7] has extended the group of yeast and mammalian mitochondrial IMM transporters [8–10]. Interestingly these carriers are more complicated than the MCs in both structure and regulation. The pyruvate carrier MPC is a heterocomplex and is regulated by acetylation in animals and yeast [5,7,11,12], and the calcium uniporter MCU is reported to have a complex dependence on regulatory subunits [4,6,13,14]. This has initiated a new challenge to similarly identify novel and functional non-MC class of transporters in plant mitochondria. Some non-MC type transporters in plant mitochondria have been identified by discovery of novel transport proteins in organelle proteomes, by analysis of targeting prediction of plant transport proteins, or by similarity of plant proteins to non-MC type transporters found in animals or yeast. One study has selectively examined the membrane-spanning proteome of plant mitochondria in detail [15], while others

Glossary

Alternative electron transport pathways:

composed of non-classical electron donors or acceptors of the ETC (i.e., not complexes I–IV). The components responsible do not pump protons across the inner membrane. Plant mitochondria-specific components include the alternative NADH dehydrogenases and the alternative oxidase.

Bioenergetics: studies of the transformation of energy in living organisms.

Carrier proteins: membrane components often with high substrate specificity. They facilitate the movement of substrates against the electrochemical gradient by linking the transport of another substrate down the electrochemical gradient or by using energy generated from the hydrolysis of ATP.

Electrochemical gradient: usually established by an ion that can move across a membrane. The gradient consists of two parts, an electrical potential and a difference in the chemical concentration across a membrane.

Electrogenicity: the ability to produce a change in the electrical potential of a membrane.

Flux balance analysis: mathematical model for simulating metabolism in genome-scale reconstructions of metabolic networks.

Inner mitochondrial membrane

(IMM): consists of two main connected compartments: a cristal membrane (a series of membranous tubules) and the inner boundary membrane (which lies parallel to the outer membrane).

Ion channels: pore-forming membrane proteins that allow substrates to diffuse down the electrochemical gradient.

Membrane potential ($\Delta\Psi$): the voltage or 'potential' across a membrane; typically the inside of a plant cell is negative with respect to the outside (less than -100 mV), whereas the mitochondrial matrix is negative with respect to the intermembrane space and is dependent on the metabolic state of mitochondria (ca -150 to -250 mV).

Mitochondria: catabolic powerhouses of eukaryotic cells that use oxidation of organic acids to drive a membrane potential that is

Box 1. Why Are Some MCF Members Located in Non-Mitochondrial Membranes?

MCF 'not in mitochondria' may appear an oxymoron, but this 'MCF' annotation does not always reflect the location of transporters. By combining what has been reported about the extra-mitochondrial location of 12 MCF members in *Arabidopsis* (Table I), and experiments on their targeting, we can offer an explanation for their subcellular distribution. Three MCF proteins contain no N-terminal presequence and are found in the endoplasmic reticulum (ER-ANT [113]), plasma membrane (PM-ANT [114]), or Golgi (UCP2 [115]). An explanation for this may be the specific transmembrane domain lengths in these proteins that reflect the average for ER, Golgi, and PM retention [116]. In the case of the ER- and PM-targeted ANT's at least, the mitochondrial equivalents have cleavable N-terminal extensions that are required to enable their import into mitochondria [117]. Six transporters are found in plastids, and in four of six cases these proteins have cleavable N-terminal presequences. In the case of BT1, removal of the N-terminal extensive led to re-targeting of this plastid protein to the mitochondrion [118]. Three transporters are found exclusively in peroxisomes but none contained either classical PTS1 C-terminal sequence or the N-terminal presequences observed for plastid-targeted MCF proteins [119,120]. Visualization of GFP constructs shows that the N-terminus of PNC1/PNC2 needs to be exposed to ensure peroxisomal targeting [119], and this may suggest divergent PTSII targeting sequences in the N-terminal region of these proteins. Overall it appears that the transmembrane domain structure of MCF is sufficient and selective for entry into mitochondria in many cases, but that some sequence variants are more readily retained in other cell membranes. A subset of MCF has acquired N-terminal extensions that can override the transmembrane domain targeting to more directly specify subcellular location.

Table I. Localization of Non-Mitochondria Targeted MCF Proteins in *Arabidopsis*

AGI Accession	Aliases	C	P	O
At5g17400	ER-ANT			✓
At5g56450	PM-ANT			✓
At5g58970	UCP2			✓
At2g39970	PXN		✓	
At3g05290	PNC1		✓	
At2g35800	SAMTL	✓		
At2g47490	NDT1	✓		
At4g32400	BT1	✓		
At5g01500	PAPST1	✓		
At5g42130	MFL1	✓		
At5g66380	FOLT1	✓		

Abbreviations: C, chloroplast; O, other compartments; P, peroxisome.

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