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Minireview

The diverse members of the mitochondrial carrier family in plants

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Abstract Sequencing of plant genomes allowed the identification of various members of the mitochondrial carrier family (MCF). In plants, these structurally related proteins are involved in the transport of solutes like nucleotides, phosphate, di- and tricarboxylates across the mitochondrial membrane and therefore exhibit physiological functions similar to known isoforms from animal or yeast mitochondria. Interestingly, various studies led to the recognition of MCF proteins which mediate the transport of different substrates like folates, *S*-adenosylmethionine, ADP-glucose or ATP, ADP and AMP in plastids.

Keywords: Mitochondrial carrier family; Arabidopsis; Plant; Transport; Mitochondrion; Plastid

1. Introduction

Mitochondria, as the site of electron transport and ATP synthesis play a dominant role in the energy metabolism of almost every eukaryotic cell. The mitochondrion is surrounded by two membranes. The mitochondrial outer membrane shows a very high phospholipid to protein ratio, contains pores and channels allowing the influx of solutes and smaller molecules up to 5000 Da [1], while the inner membrane is tightly packed not only with protein complexes of the electron transport chain and ATP synthases, but also with a wide number of carrier proteins at a surprisingly high density [2].

Apart from ATP and ADP, various intermediates of the Krebs cycle and several other solutes are transferred across the mitochondrial inner membrane via structurally related hydrophobic proteins, representing the mitochondrial carrier family (MCF) [2–5]. Characteristic features of MCF proteins are (i) a molecular mass of about 30 kDa, (ii) three repeated domains each of about 100 amino acids in length consisting of two transmembrane spanning α-helices and (iii) the presence of one to three highly conserved sequence motifs, named the mitochondrial energy signature [6,7]. In 2003, Millar and Heazlewood reported 45 genes encoding MCF proteins in Arabidopsis [5], and an extended *in silico* screening allowed the identification of 13 additional members [3].

Several subgroups of MCF proteins were classified on basis of biochemical characteristics, phylogenetic relationships, amino acid similarities and ortholog/paralog analyses between corresponding carriers of yeast, animals and plants [3–5]. Assigning functions to unknown carriers often relies on their affiliation to a subgroup containing functionally related members. However, annotation of the function without experimental evidence is never decisive and maybe misleading.

Interestingly, not all members of the MCF are located in mitochondria since recent findings document that MCF carriers are also present in peroxisomes, glyoxysomes or plastids [8–13]. Therefore, computer based prediction of the localisation of MCF proteins is only one step towards a subcellular localisation and is sometimes ambiguous [3,5].

Furthermore, various mitochondrial located MCF proteins from mammals or plants possess cleavable N-terminal extensions, while others lack comparable targeting sequences but also enter this cellular domain. Several studies indicate that these extensions are not essential for correct targeting into mitochondria but probably enhance import specificity and efficiency [14–16].

Accordingly, the determination of the physiological role of a so far uncharacterised carrier not only requires the analysis of its biochemical properties and expression pattern but also the establishment of its exact cellular localisation. Furthermore, to investigate the physiological impact of carriers detailed analyses of transgenic plants with reduced amounts of the corresponding proteins are necessary.

This review summarises important characteristics of different mitochondrial and plastidic MCF proteins in plants.

1.1. ADP/ATP carriers and phosphate carriers

ADP/ATP carriers (AAC) mediate the export of ATP generated in the mitochondrion in counter exchange with cytosolic ADP. Their substrate affinities are regulated by the membrane potential and transport is inhibited by bongkrekic acid, atractyloside and carboxyatractyloside [2,17–19]. Due to the general importance of mitochondrial ATP production it is not surprising that in potato, a slight reduction of *aac* transcripts by antisense-technique resulted in a strong decrease of the tuber yield (Haferkamp, Tjaden unpublished data).

Analyses on basis of *aac*-promoter–reporter genes revealed ubiquitous expression of *aac1* (At3g08580) and *aac2* (At5g13490) with highest rates for *aac1* and moderate rates for *aac2* (Haferkamp, unpublished data). Expression of *aac3* (At4g28390) was solely detectable within actively growing tissues. These data are consistent with the relative occurrence of the individual AAC proteins in the mitochondrial membrane

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proteome from Arabidopsis [5]. Therefore, it can be postulated that the highly abundant carrier AAC1 fulfils the main function in energy transfer of Arabidopsis mitochondria.

During oxidative phosphorylation in mitochondria ATP is regenerated from ADP and Pi. The latter is provided by mitochondrial phosphate carriers (PiC) which catalyse a Pi/OH^- antiport [20] or a Pi/H^+ symport [16]. The two phosphate carriers PiC1 (At5g14040) and PiC2 (At3g4880) from Arabidopsis were shown to complement a yeast mutant lacking the endogenous carrier [21]. Interestingly, a third putative PiC from Arabidopsis (At2g17270) did not restore phosphate transport into mitochondria of the deletion mutant.

The high abundance of PiC1 and AAC1 in the mitochondrial proteome supports the idea of a metabolic interaction of these two proteins during ATP regeneration in Arabidopsis [5] (Fig. 1).

1.2. Uncoupling proteins

Uncoupling proteins (UCP) catalyse a nucleotide-sensitive, fatty-acid-mediated proton transport across the inner

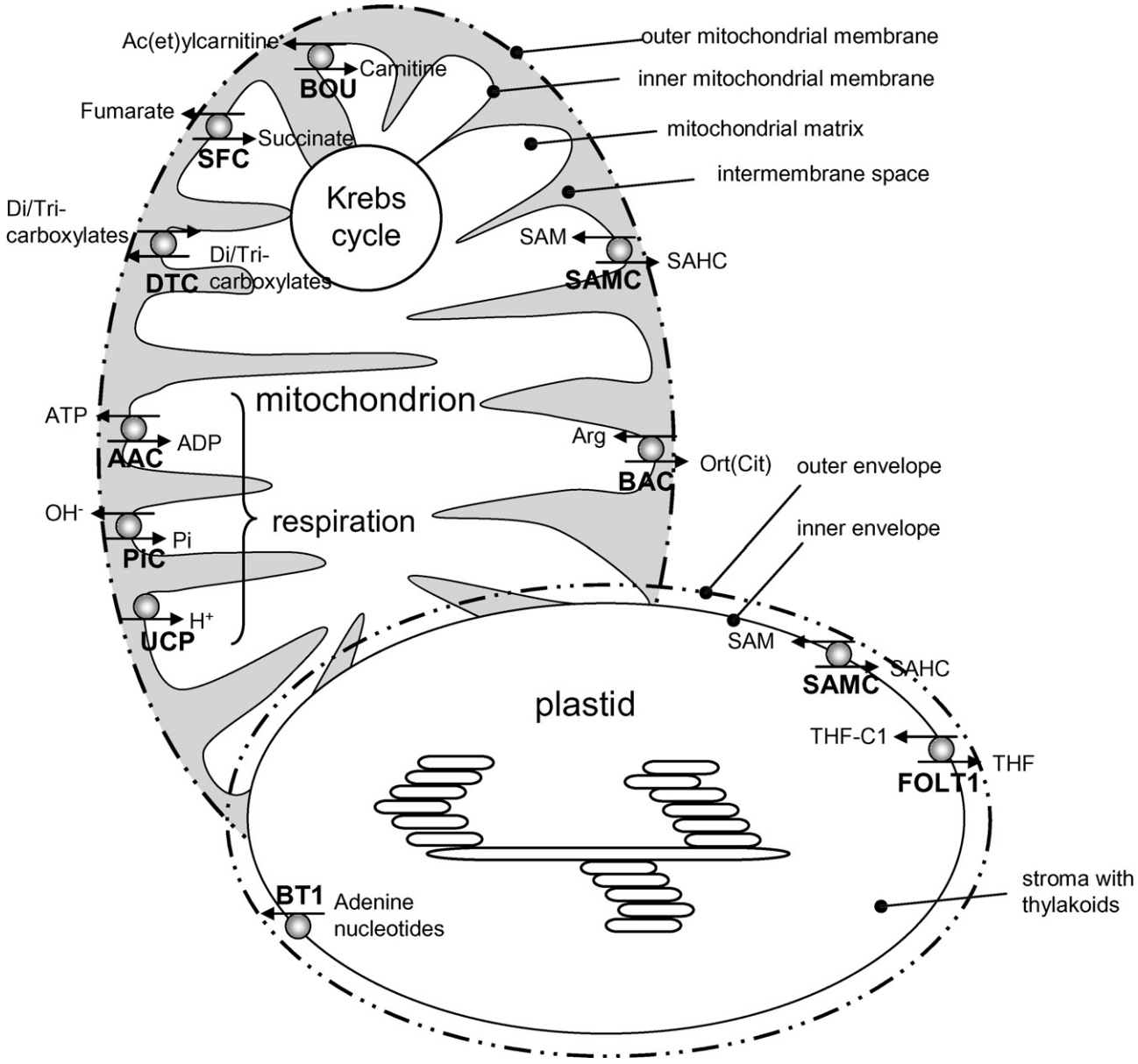

Fig. 1. Simplified model of the localisation and function of characterised MCF members from *Arabidopsis thaliana*. Intermediates of the Krebs cycle are the substrates of the SFC (succinate/fumarate carrier) and of the DTC (dicarboxylate/tricarboxylate carrier). Therefore, these carriers connect the Krebs cycle with various metabolic processes outside the mitochondrion. The AAC (ADP/ATP carrier) and the PiC (phosphate carrier) provide the substrates for ATP synthesis. The proton export mediated by the UCP (uncoupling protein) reduces the electrochemical gradient across the inner mitochondrial membrane. Arginine (Arg) is converted by mitochondrial localised enzymes to ornithine (Ort) or citrulline (Cit). BAC (basic amino acid carriers) mediate the required Arg/Ort or Arg/Cit exchange. With respect to the provision or removal of one-carbon units the substrates of the carriers SAMC (*S*-adenosylmethionine carrier) and FOLT1 (folate transporter) play an important role in different metabolic processes. The carrier BT1 exports adenine nucleotides which are exclusively synthesised in the plastids. BOU1 is assumed to mediate acylcarnitine/carnitine exchange which links fatty acid mobilisation with the Krebs cycle.

mitochondrial membrane, which results in the reduction of the proton gradient and in the generation of heat. The transport of protons is explained by two different models. The first one describes the transport of fatty acids by which protons are indirectly transferred across the mitochondrial membrane [22]. In a second model protons are the real substrate of the UCP and fatty acids serve as proton donors and acceptors [23]. As a consequence of UCP function ATP synthesis is bypassed. In this respect the inhibitory influence of nucleotides like ATP or GTP on UCP activity is unexpected and seems to be contra-productive.

UCPs were thought to play an exclusive role in thermogenesis of newborn, cold-acclimated, and hibernating animals. Therefore, the identification of corresponding proteins in plants was very surprising [24,25]. Recent analyses suggest that Arabidopsis possesses 6 potential UCP coding sequences (At3g54110; At5g58970; At1g14140; At4g24570; At2g22500; At5g09470) which are widely expressed in several organs and tissues [26]. However, the biochemical properties of only two of the UCPs from Arabidopsis are known [27,28]. It is necessary to mention that in other studies UCP4-6 were proposed to be potential dicarbonic acid transporters [3,5].

The activation of UCPs by reactive oxygen species and their occurrence in thermogenic as well as non-thermogenic plants indicates that the primary role of these proteins is not the organ specific production of heat but most likely the balance of cellular energy level in response to stress [25,26,29–31].

1.3. Di- and tricarboxylate carriers

Transport of di- and tricarboxylates across the mitochondrial membrane connects the Krebs cycle with diverse metabolic processes, for example gluconeogenesis, the glyoxylate cycle, and the synthesis of amino acids and nucleic acids. In Arabidopsis, tobacco and obviously also in several other plant species dicarboxylate/tricarboxylate carriers (DTC) catalyse an electroneutral transport of a broad spectrum of single protonated tricarboxylates (citrate, isocitrate and aconitate) in exchange with unprotonated dicarboxylates (2-oxoglutarate, oxaloacetate, malate, maleate, succinate and malonate) [32]. Transcripts of the *dtc* gene (At5g19760) from Arabidopsis were detectable in most tissues and the expression was influenced by the availability of nitrogen. The observed expression pattern supports the assumption that the DTC fulfils not only a housekeeping role in plant metabolism but also a specialised function during nitrogen assimilation [32].

A succinate/fumarate carrier from Arabidopsis (SFC1; At5g01340) was identified by complementation of a yeast mutant lacking the endogenous isoform *Sc*ACR1 [33]. Latter protein accepts a broad spectrum of di- and tricarboxylates with preference of succinate and fumarate [34]. The observed gene expression pattern suggests a possible role of SFC1 in gluconeogenesis during germination of seedlings and pollen as well as in ethanolic fermentation [33].

1.4. Basic amino acid and carnitine carriers

Basic amino acids serve as a nitrogen source, are mobilised from storage proteins during germination of seeds and are precursors of proline, polyamines and alkaloids. In plant mitochondria arginine is converted by arginase to urea and ornithine [35]. However, the role of mitochondria in NO production and the existence of a mitochondrial located arginine dependent nitric oxide synthase in plant were recently controversially discussed [36–39]. Transport of arginine across the inner mitochondrial membrane is mediated by basic amino acid carriers (BAC). Both characterised BACs from Arabidopsis operate in a counter exchange mode and exhibit partial overlapping specificities for basic amino acids with a high preference of arginine [40–42]. Due to its biochemical properties and the gene expression pattern BAC1 (At2g33820) may be involved in arginine/ornithine exchange during mobilisation of storage proteins in germinating seeds [40,41]. A different physiological function of BAC2 (At1g79900) was assumed as gene expression is low in germinating seeds but high in flowers. This carrier accepts arginine, ornithine and citrulline as substrates and therefore BAC2 could be involved in proline, polyamine and alkaloid synthesis or in the shuttling of ammonia between mitochondria and plastids [40,42,43].

During seedling germination in peroxisomes fatty acids are mobilised and undergo respiration in the mitochondrion. The MCF carrier BOU1 (“A BOUT DE SOUFFLE”; At5g46800) was hypothesised to mediate the required carbon import into mitochondria by ac(et)ylcarnitine/carnitine exchange [44]. Interestingly, recent analyses suggest that plant peroxisomes export the majority of carbons as citrate but not in form of ac(et)ylcarnitine and also an acyl-CoA carnitine acetyltransferase has not yet been identified in plants [45]. The investigation of the biochemical characteristics of BOU1 is mandatory to verify the physiological function of a carrier which is not only structurally related to acetylcarnitine/carnitine carriers from yeast but also to BAC from plant.

1.5. Brittle1 and related transporters

Starch synthesis is dependent on the provision of the nucleotide sugar ADPglucose which is synthesised by a plastidic ADPglucose pyrophosphorylase (AGPase) in dicotyledonous plants and mainly by a cytosolic isoform in cereals [46–48]. Several lines of evidence indicate that the MCF protein Brittle1 (BT1) mediates the required ADPglucose transport into cereal plastids. Firstly, endosperm tissues of a maize mutant with a defect in the *brittle1* locus show reduced starch levels and contain higher cytosolic ADPglucose levels in immature kernels [49]. Secondly, the BT1 protein is abundant in maize endosperm tissues and located in the inner envelope membrane of amyloplasts [49–51].

As non-cereal plants lack a cytosolic AGPase it was very surprising that proteins with high structural similarity to the BT1 protein are present in dicotyledonous plants. The characterisation of *St*BT1 (X98474) from potato revealed that this carrier is localised in the plastid envelope and catalyses the uniport of AMP, ADP and ATP [11]. The ubiquitous expression of the *St*BT1 and the retarded growth of Arabidopsis mutants lacking the corresponding *Atbt1* gene (At4g32400) indicate a housekeeping function of these proteins in metabolism [11] which is most likely the export of adenine nucleotides (Fig. 1). Since these molecules are exclusively synthesised in plastids [52] adenine nucleotide uniporters are also required in cereals. Latter postulation is supported by the observation that in monocotyledonous plants the ADPglucose carrier and a sequence similar to the purine nucleotide uniporters exist simultaneously [53].

1.6. Folic acid and S-adenosylmethionine carriers

Several cellular processes, for example, the synthesis of amino acids, of purines and of secondary metabolites as well as the

photorespiratory cycle depend upon the supply or removal of one-carbon units via tetrahydrofolate or via *S*-adenosylmethionine (SAM) [54].

The distribution of enzymes involved in the biosynthesis of folates necessitates a specific transport of tetrahydrofolate and its precursors between the cytosol, mitochondria and plastids [54]. Recently, the Arabidopsis protein FOLT1 (At5g66380) has been identified to be a homolog of the mitochondrial folate transporter of yeast or animals [10]. FOLT1 was shown to be localised in plastids (Fig. 1) and expression analyses revealed that *folt1* transcripts are detectable in all organs and tissues at all growth stages. Interestingly, plastidic FOLT1 was able to complement a yeast mutant deficient for the endogenous mitochondrial folic acid carrier and therefore is proposed to mediate transport of folic acid and of folate derivates. The existence of a second folate transporter in Arabidopsis was suggested as *folt1* knock out lines exhibited no phenotypical differences when compared with wild type plants [10].

SAM is exclusively synthesised in the plant cytosol and therefore has to be imported into plastids and mitochondria where it acts as a donor of methyl-groups. Consequently, the resulting *S*-adenosylhomocysteine (SAHC) has to be exported to undergo re-methylation in the cytosol. Recently, in the Arabidopsis genome two homologous (SAMC1: At4g39460 and SAMC2: At1g34065) of the yeast and mammalian SAM transporters were identified [12,13]. SAMC1 is believed to be the main SAM carrier in plants since it mediates a specific counter exchange of SAM and SAHC, exhibits a broad expression in various plant tissues, is up-regulated in response to wounding stress and is obviously more abundant than SAMC2 [12,13]. Furthermore, absence of SAMC1 has severe effects on prenyllipid metabolism and on plant growth [12]. Interestingly, SAMC1 is described to be localised in the plastid envelope but also a targeting into mitochondria was observed (Fig. 1). The GFP fusion construct containing the N-terminus of SAMC1 was exclusively targeted into the chloroplasts. Furthermore, SAMC1 was immuno-detected in chloroplasts, and to a lower extent probably in mitochondria [12]. Localisation of SAM1C in both chloroplasts and mitochondria is supported by analyses of the full-length SAMC1 fused to GFP which also revealed a dual targeting [13]. These observations led to the suggestion that the N-terminal extension is sufficient only for a plastidic targeting of SAMC1, whereas the complete sequence contains additional information for mitochondrial targeting. The biochemical properties, localisation and physiological function of SAMC2 are still unclear.

2. Conclusion

Analyses of several MCF members from plants have shed light on the physiological function of these carriers. Plant MCF proteins often exhibit biochemical characteristics similar to their counterparts from yeast or animals and therefore, a comparable role in the cellular context can be assumed. However, the function of the majority of 58 MCF proteins in the model plant Arabidopsis is still unknown. Interestingly, localisation studies revealed that at least three MCF members from Arabidopsis are located in plastids and therefore fulfil a specialised function in the plant cell. The lack of MCF protein function, like for example of the potential ADPglucose carrier from maize, of the *S*-adenosylmethionine carrier from Arabidopsis or of the ADP/ATP carriers in potato often has severe physiological effects on the metabolism which underlines the importance of the corresponding proteins in plants.

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