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Review article

Physiology of L-carnitine in plants in light of the knowledge in animals and microorganisms

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ABSTRACT

L-carnitine is present in all living kingdoms where it acts in diverse physiological processes. It is involved in lipid metabolism in animals and yeasts, notably as an essential cofactor of fatty acid intracellular trafficking. Its physiological significance is poorly understood in plants, but L-carnitine may be linked to fatty acid metabolism among other roles. Indeed, carnitine transferases activities and acylcarnitines are measured in plant tissues. Current knowledge of fatty acid trafficking in plants rules out acylcarnitines as intermediates of the peroxisomal and mitochondrial fatty acid metabolism, unlike in animals and yeasts. Instead, acylcarnitines could be involved in plastidial exportation of *de novo* fatty acid, or importation of fatty acids into the ER, for synthesis of specific glycerolipids. L-carnitine also contributes to cellular maintenance though antioxidant and osmolyte properties in animals and microbes. Recent data indicate similar features in plants, together with modulation of signaling pathways. The biosynthesis of L-carnitine in the plant cell shares similar precursors as in the animal and yeast cells. The elucidation of the biosynthesis pathway of L-carnitine, and the identification of the enzymes involved, is today essential to progress further in the comprehension of its biological significance in plants.

1. Introduction

The presence of L-carnitine in plant is known since several decades [1]. Its central role in animal and microbial physiology motivates past and current studies about its role in plant physiology. L-carnitine is essential in the metabolism of lipids in animals, especially for the exchange of fatty acids between organelles. The processes of fatty acid trafficking in the plant cell are not fully understood, and L-carnitine could be a cofactor in specific pathways. Similarly, L-carnitine is involved in different aspects of cell maintenance in animals, yeasts and bacteria, while some recent findings suggest a similar role in plants. In this review, we examine the data about L-carnitine in the context of plant physiology in comparison to animal and microbial physiology. Putative implications of L-carnitine in the plant kingdom are discussed bringing to light possible directions for further studies.

2. Summary data on L-carnitine in the microbial and animal kingdoms

L-carnitine, L-3-hydroxy-4-*N*-*N*-*N*-trimethylaminobutyrate, also denominated vitamin B_T, belongs to the group of quaternary ammonium compounds. Since its discovery in 1905 by two groups of scientists [2,3], L-carnitine has been found in all living kingdoms. For instance, the L-carnitine content reaches 39 μg g^{-1} in the liver, 64 μg g^{-1} in the kidney and 113 μg g^{-1} in the heart of rodent [4], and up to 35 μg g^{-1} in the yeast *Saccharomyces cerevisiae* [1] (Table S1).

L-carnitine has a fundamental role in animal and fungal energy metabolism by esterifying fatty acids (FA) and acetate [5]. The esterification of FA or acetate on L-carnitine leads to acyl(acetyl)carnitines. Carnitine esterification requires carnitine transferase activities that catalyze the exchange between coenzyme A (CoASH) and L-carnitine on acyl or acetyl moieties [6]. Depending on their specificity for acetate, medium chain FA (MCFA) or long chain FA (LCFA) they are classified as carnitine acetyltransferase (CAT; EC 2.3.1.7), carnitine octanoyltransferase (COT; EC 2.3.1.137) and carnitine palmitoyltransferase (CPT; EC 2.3.1.21), respectively.

In animals, CAT is present in all tissues. It is detected in the peroxisome, the endoplasmic reticulum (ER), and the mitochondrion (Fig. 1A) [7]. COT has been identified in the mitochondrion [8], in the peroxisome [9–11] and in the ER [7]. Concerning CPT, two isoforms exist: CPT1 present on the mitochondrial outer membrane and CPT2 on the mitochondrial inner membrane. The plasma membrane [12], the peroxisome [13], and the ER [14] also display a CPT activity. In the yeast *Saccharomyces cerevisiae* (Fig. 1B), a single gene encodes a CAT

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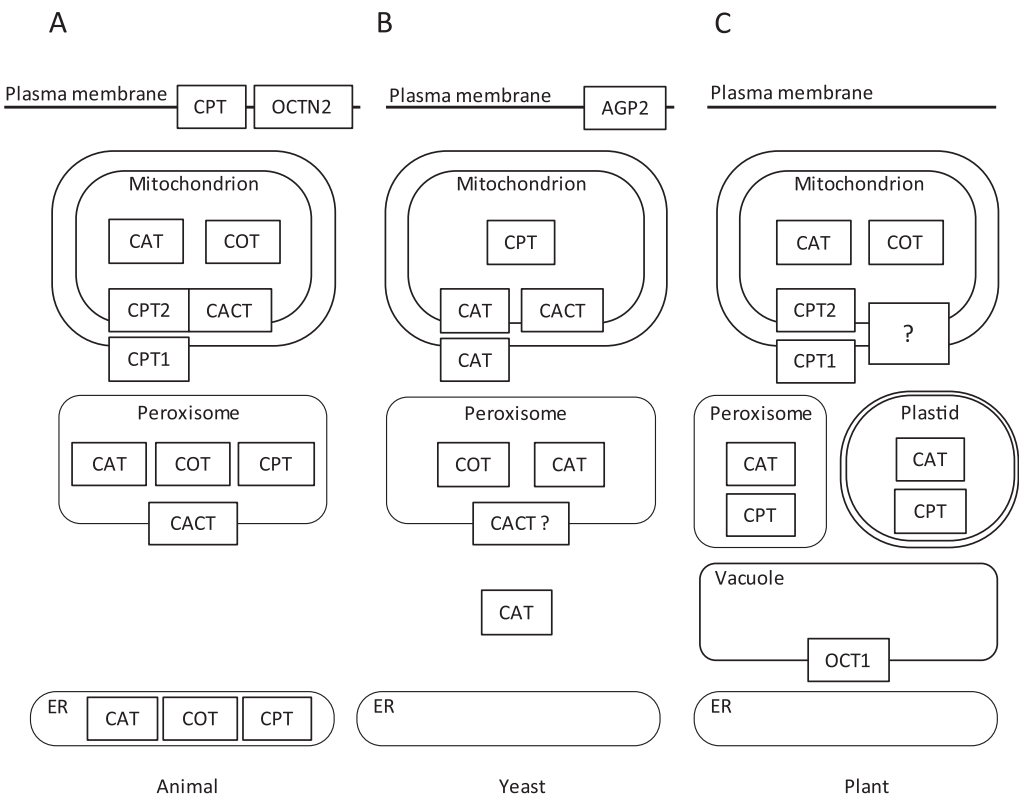

Fig. 1. Subcellular localizations of enzymatic activity linked to carnitine system in animal (A), yeast (B) and plant cells (C). ER: endoplasmic reticulum, CAT: carnitine acetyltransferase, COT: carnitine octanoyltransferase, CPT: carnitine palmitoyltransferase, CACT: carnitine acylcarnitine translocase, OCT1: organic cation/carnitine transporter 1, OCTN2: organic cation/carnitine transporter novel type 2, AGP2: general aminoacid permease 2.

which can be targeted either to the peroxisome or to the mitochondrial inner membrane [15]. The mitochondrial outer membrane appears to possess another CAT, encoded by a different gene, facing the cytosol [16]. It seems to be homologous to the cytosolic CAT identified in the fungus *Aspergillus nidulans* [17]. Yeast peroxisome and mitochondrion display a COT and CPT activity, respectively [18].

Carnitine acyl(acetyl)transferase enzymes are involved in the intracellular trafficking of FA and acetate in yeasts and animals. In animals, the best-characterized function of L-carnitine is the transport of long chain acyl-CoA through the mitochondrial membranes to feed the β-oxidation pathway [6]. This system, known as the carnitine shuttle (Fig. 2), requires the two CPT enzymes and a carnitine acylcarnitine translocase (CACT). Firstly, CPT1 converts the acyl-CoA into an acylcarnitine ester and releases the CoASH. Then, the CACT transports the acylcarnitine into the mitochondrial matrix. Finally, CPT2 releases L-carnitine and regenerates acyl-CoA inside the matrix. CPT2 and CACT form a complex, suggesting carnitine and acylcarnitine channeling between the two enzymes [19]. L-carnitine is re-exported to the cytoplasm and the acyl-CoA enters the β-oxidation pathway. In animal tissues, another β-oxidation takes place in the peroxisome. It concerns the partial oxidation of very long chain FA (VLCFA) into MCFA. The MCFA are subsequently converted into medium-chain acylcarnitines by the peroxisomal COT activity [20]. The acylcarnitines are then transported to the mitochondrion to complete β-oxidation [21,22]. The detection of a peroxisomal CACT [23] indicates that acylcarnitine exportation from the peroxisome is carried out by a carnitine shuttle system.

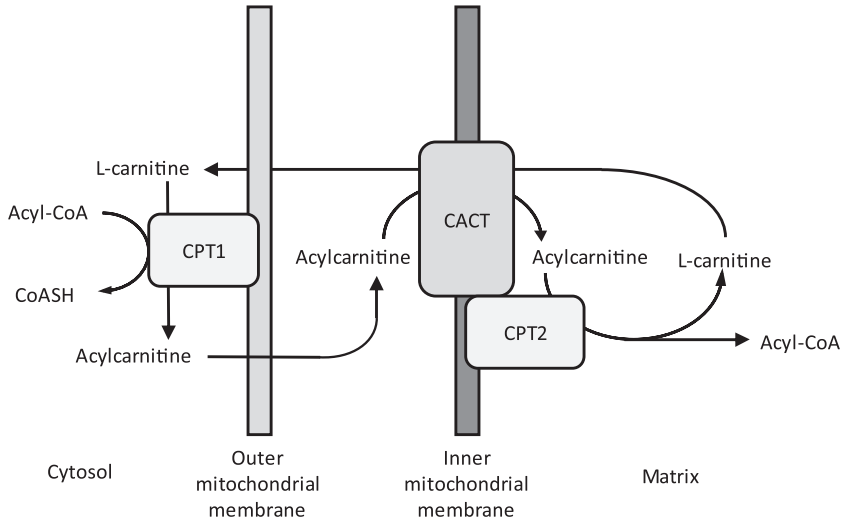

Fig. 2. Schematic diagram of the carnitine shuttle system in the animal mitochondrion. CACT: carnitine acylcarnitine translocase, CPT: carnitine palmitoyltransferase.