Available online at www.sciencedirect.com
SCIENCE DIRECT
Gene 354 (2005) 99 – 109
GENE
SECTION
FUNCTIONAL GENOMICS
www.elsevier.com/locate/gene

Review

Chloroplast membrane transport: Interplay of prokaryotic and eukaryotic traits

Ute C. Vothknecht*, Jürgen Soll

Department of Biology I, Botanisches Institut der LMU München, Menzinger Street 67, München D-80638, Germany

Received 16 January 2005; received in revised form 15 February 2005; accepted 15 April 2005
Available online 23 June 2005
Received by D. Leister

Abstract

Chloroplasts are specific plant organelles of prokaryotic origin. They are separated from the surrounding cell by a double membrane, which represents an effective barrier for the transport of metabolites and proteins. Specific transporters in the inner envelope membrane have been described, which facilitate the exchange of metabolites. In contrast, the outer envelope has been viewed for a long time as a molecular sieve that offers a mere size constriction to the passage of molecules. This view has been challenged lately, and a number of specific and regulated pore proteins of the outer envelope (OEPs) have been identified. These pores seem to have originated by adaptation of outer membrane proteins of the cyanobacterial ancestor of the chloroplast. In a similar fashion, the transport of proteins across the two envelope membranes is achieved by two hetero-oligomeric protein complexes called Toc (translocon in the outer envelope of chloroplasts) and Tic (translocon in the inner envelope of chloroplasts). The phylogenetic provenance of the translocon components is less clear, but at least the channel protein of the Toc translocon is of cyanobacterial origin. Characteristic of cyanobacteria and chloroplasts is furthermore a specialized internal membrane system, the thylakoids, on which the components of the photosynthetic machinery are located. Despite the importance of this membrane, very little is known about its phylogenetic origin or the manner of its synthesis. Vipp1 appears to be a ubiquitous component of thylakoid formation, while in chloroplasts of land plants, additionally a vesicle transport system of eukaryotic origin might be involved in this process.

Keywords: Thylakoid formation; Metabolite transport; Tic and Toc; Vesicle transport

1. Introduction

1.1. The endosymbiotic origin of chloroplasts

Chloroplasts are the characteristic organelles of photosynthetic algae and plants. An endosymbiotic event between an ancestor of today's cyanobacteria and a mitochondria-containing host cell resulted in the formation of this organelle (Mereschkowsky, 1905; Margulis, 1970). It is believed that this primary endosymbiosis occurred only once in the history of plant evolution and gave rise to all plastids (Palmer, 2000). Thus, all present-day chloroplasts share a common ancestry, even though they are found in organisms as varied as glaucocystophytes, green and red algae, or land plants. They are also found, rather unexpectedly, in the Apicomplexa, a group of parasitic living organisms that include the malaria agent *Plasmodium falciparum* and other human and livestock pathogens (Foth and McFadden, 2003).

Well before the endosymbiotic creation of chloroplasts, the cyanobacteria had developed the capacity for oxygenic photosynthesis. Therefore, the endosymbiont was in possession of two photosystems as well as the oxygen-evolving complex and had also evolved a specialized internal

Abbreviations: FNR, ferredoxin-NADP(H)oxidoreductase; OEP, outer envelope protein; Tic, translocon in the inner envelope of chloroplasts; Toc, translocon in the outer envelope of chloroplasts; TPR, tetratricopeptide repeat; VDAC, voltage-gated anion-selective channel; Vipp1, vesicle-inducing protein in plastids 1.

* Corresponding author. Tel.: +49 89 17861 273; fax: +49 89 17861 185.
E-mail address: vothknecht@lrz.uni-muenchen.de (U.C. Vothknecht).

0378-1119/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.gene.2005.04.021

membrane system, the thylakoids, on which the photosynthetic machinery is located (Xiong and Bauer, 2002). An important aspect of the endosymbiotic creation of chloroplasts was the introduction of oxygenic photosynthesis into the eukaryotic kingdom. Nonetheless, this was not the only feature of the cyanobacterium that was retained during chloroplast evolution. Many of the metabolic capacities of the plant cell rely, at least in part, on processes taking place inside the chloroplast (i.e., fatty acid biosynthesis, nitrite and sulfate reduction, and amino acid biosynthesis).

Chloroplasts still contain multiple copies of their own circular genome and they encode about 50–150 of the estimated 2000–5000 proteins that make up the plastidal proteome (Leister, 2003). To synthesize these proteins, chloroplasts have retained the competence for DNA replication, transcription, and translation. However, the majority of genes from the original endosymbiont were either lost or transferred to the nucleus of the host cell (Martin and Herrmann, 1998). For almost all of their functions, chloroplasts depend on proteins that are encoded in the nucleus and which have to be transferred into the organelle.

Due to its endosymbiotic origin, the chloroplast is surrounded by two membranes, which present a barrier that cannot be crossed unassisted by either proteins or metabolites. Consequently, the cell had to develop means to transport proteins into the chloroplast and to exchange metabolites between the stroma and the cytosol. The latter is enabled by a number of specific and regulated solute pores, ion channels, and metabolic transporters in both the outer and the inner envelope membranes (Neuhaus and Wagner, 2000; Bölter and Soll, 2001).

The former necessitated the development of a chloroplast targeting and import machinery for proteins (Fig. 1). Translocation across the envelope is promoted by the Toc (translocon on the outer envelope membrane of chloroplasts) and the Tic complex (translocon on the inner envelope of chloroplasts). They facilitate and control the protein import into the organelle and thereby present one of many regulation points of nucleus–organelle interaction. The protein import machinery was obviously not inherited en bloc from the cyanobacterial endosymbiont; it rather was constructed around a small number of pre-existing components that were recruited for this novel task. The newly

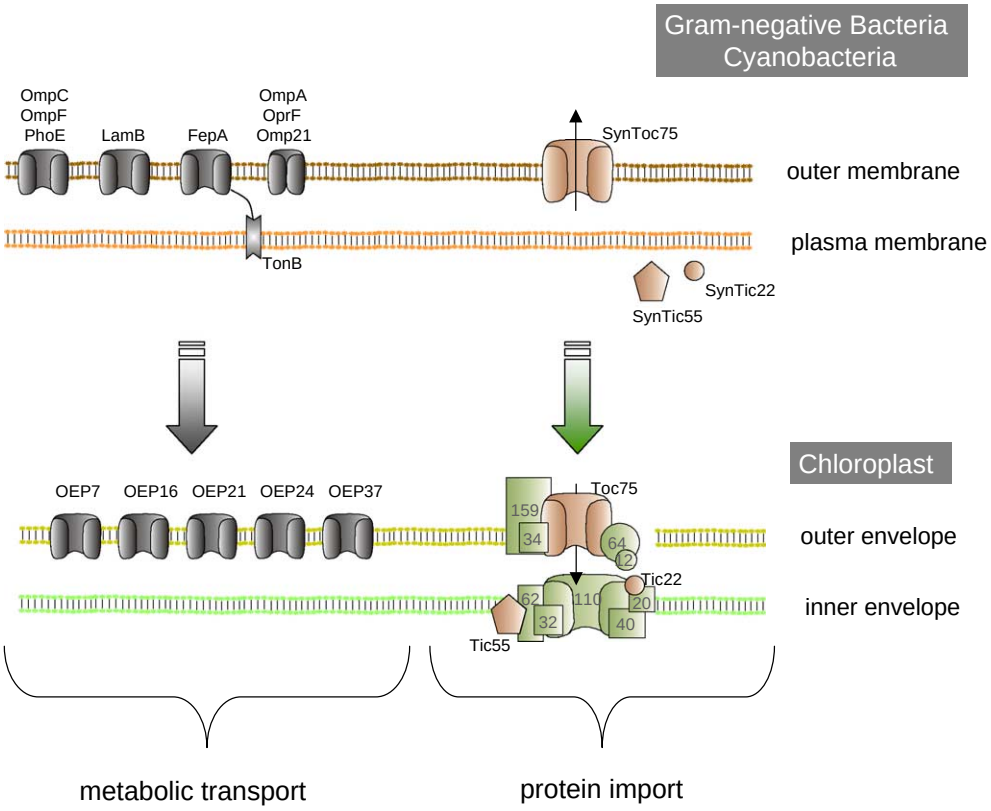

Fig. 1. Chloroplasts are plant organelles of prokaryotic origin. They are surrounded by a double membrane, the inner and outer envelopes. Import of proteins into the chloroplast and exchange of metabolite have to be achieved by passage through these membranes. To facilitate this exchange, chloroplast outer envelopes contain a number of specific and regulated pore proteins (OEPs), which are named by their respective molecular weights. These pores most likely originated from channel proteins of the outer membrane of the cyanobacterial ancestor that were adapted to their new function. In contrast, the transport of proteins across the two envelope membranes is achieved by two hetero-oligomeric protein complexes called Toc (translocon on the outer envelope of chloroplasts) and Tic (translocon on the inner envelope of chloroplasts). The phylogenetic origin of the Toc and Tic components is much less clear, but at least Toc75, Tic55, and Tic22 seem to have evolved from cyanobacterial proteins.