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Minireview

Component interactions, regulation and mechanisms of chloroplast signal recognition particle-dependent protein transport

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ABSTRACT

The chloroplast proteome comprises nuclear- and plastome-encoded proteins. In order to function correctly these proteins must be transported, either cotranslationally or posttranslationally, to their final destination in the chloroplast. Here the chloroplast signal recognition particle (cpSRP) which is present in two different stromal pools plays an essential role. On the one hand, the conserved 54 kDa subunit (cpSRP54) is associated with 70S ribosomes to function in the cotranslational transport of the plastid-encoded thylakoid membrane protein D1. On the other hand, the cpSRP consists of cpSRP54 and a unique 43 kDa subunit (cpSRP43) and facilitates the transport of nuclear-encoded light-harvesting chlorophyll-binding proteins (LHCPs), the most abundant membrane proteins of the thylakoids. In addition to cpSRP, the cpSRP receptor cpFtsY and the thylakoid membrane protein Alb3 are required for posttranslational LHCP integration in a GTP-dependent manner. In contrast to the universally conserved cytosolic SRP, the chloroplast SRP of higher plants lacks an SRP-RNA component. Interestingly, cpSRP-RNA genes have been identified in the plastome of lower plants, indicating that their cpSRP structure resembles the cytosolic SRP.

Introduction

Chloroplasts are complex organelles with a highly organized internal membrane system known as the thylakoids. Experimental analysis of chloroplast proteins and theoretical predictions of the chloroplast proteome led to the enumeration of approximately 3000 proteins, only half of which have already been identified and characterized (Ferro et al., 2010). The thylakoid membrane contains ~350 integral membrane proteins and the peripheral thylakoid proteins include ~170 proteins located on the stromal and ~130 proteins on the lumenal side (Sun et al., 2009). The thylakoid membrane of chloroplasts contains the four major photosynthetic complexes, photosystem I (PSI), photosystem II (PSII), the cytochrome b_6f complex and the ATP synthase. The proteins of these complexes are encoded either in the nucleus or in the chloroplast genome. Therefore, the biogenesis of the multi-subunit complexes requires coordinated protein synthesis, targeting and assembly of both the nuclear-encoded and chloroplast-encoded proteins. The vast majority of thylakoid membrane proteins is encoded in the nucleus and has to be transported posttranslationally into the chloroplast. The coordinated delivery of proteins to their final destination is a crucial issue for the function of thylakoid membrane protein complexes. Therefore, a sophisticated protein targeting and transport machinery has evolved.

Nuclear-encoded thylakoid proteins are synthesized as precursors in the cytoplasm and translocated into the chloroplast stroma by the general import pathway at the outer and inner envelope membranes, a process mediated by the Toc/Tic translocon (reviewed in Jarvis, 2008; Agne and Kessler, 2009; Benz et al., 2009a; Sommer and Schleiff, 2009). After import the targeting signals of these precursor proteins are proteolytically removed by a stromal processing peptidase (SPP), and the thylakoid proteins engage one of four independent thylakoid transport pathways (reviewed in Schünemann, 2007; Aldridge et al., 2009). Lumenal proteins are translocated across the thylakoid membrane by either the cpSec-pathway or the cpTat-pathway. Most integral thylakoid membrane proteins that have been analyzed are either inserted spontaneously without the assistance of other protein components and energy requirements or reach the membrane by the signal recognition particle (SRP) transport machinery.

Like all of these four transport mechanisms, the chloroplast SRP pathway evolved from a prokaryotic transport system. In bacteria, most inner membrane proteins are targeted cotranslationally by the signal recognition particle, and typical SRP-systems can be found in the cytosol of prokaryotes and eukaryotes (reviewed in Pool, 2005). The SRP minimally consists of a conserved 54 kDa subunit (SRP54) and a conserved SRP-RNA. It recognizes its substrate early in translation and via an interaction with the SRP receptor, the complex of SRP, ribosome and nascent chain is directed to the membrane. After transfer to the Sec translocon, SRP and the SRP receptor are released in a GTP-dependent reaction (reviewed in Cross et al., 2009). A homologous SRP54 protein has been identi-

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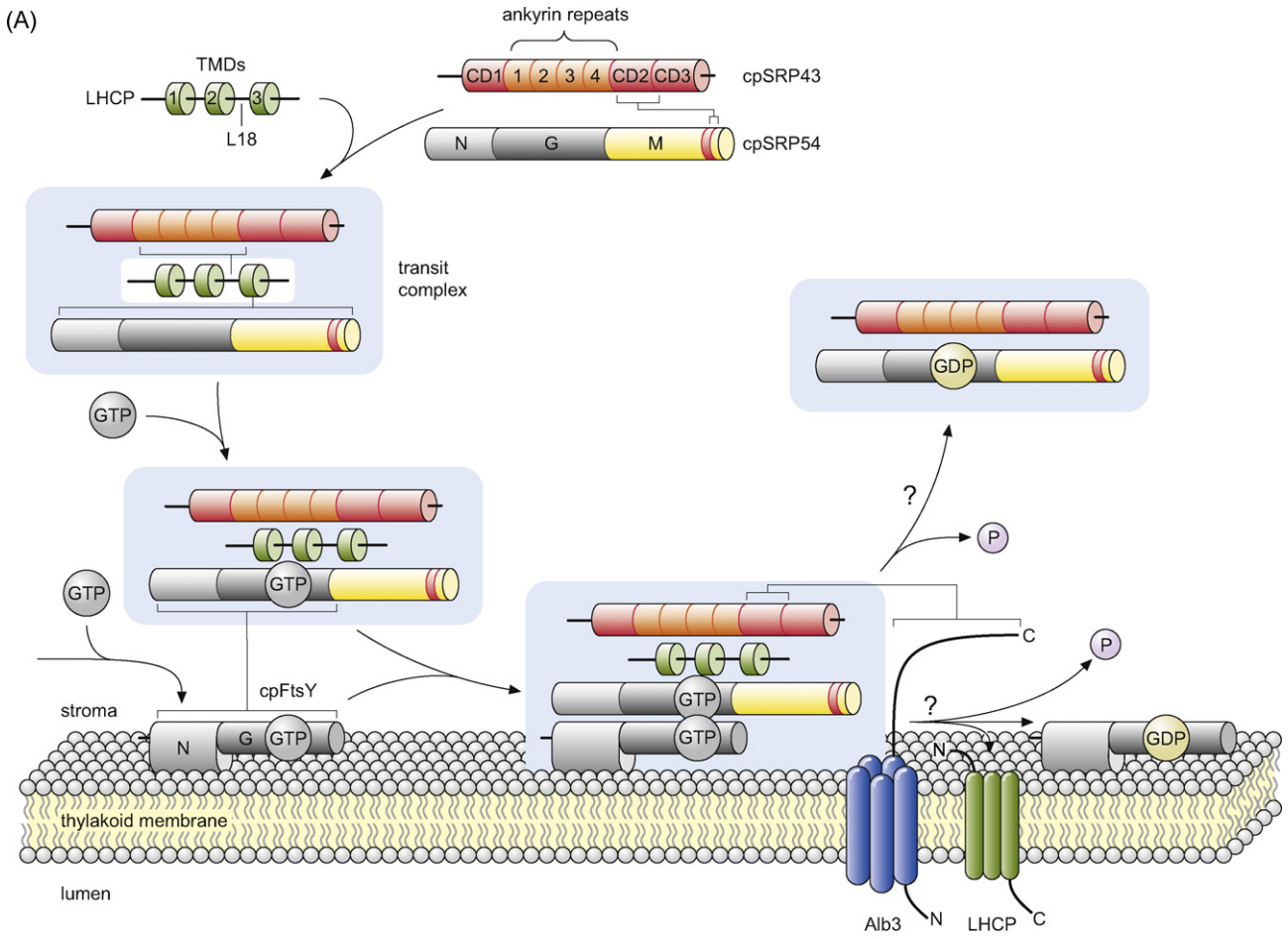
(A)
ankyrin repeats
TMDs
LHCP
1
2
3
L18
CD1
1
2
3
4
CD2
CD3
cpSRP43
N
G
M
cpSRP54
transit complex
GDP
GTP
?
P
GTP
GTP
C
P
cpFtsY
stroma
N
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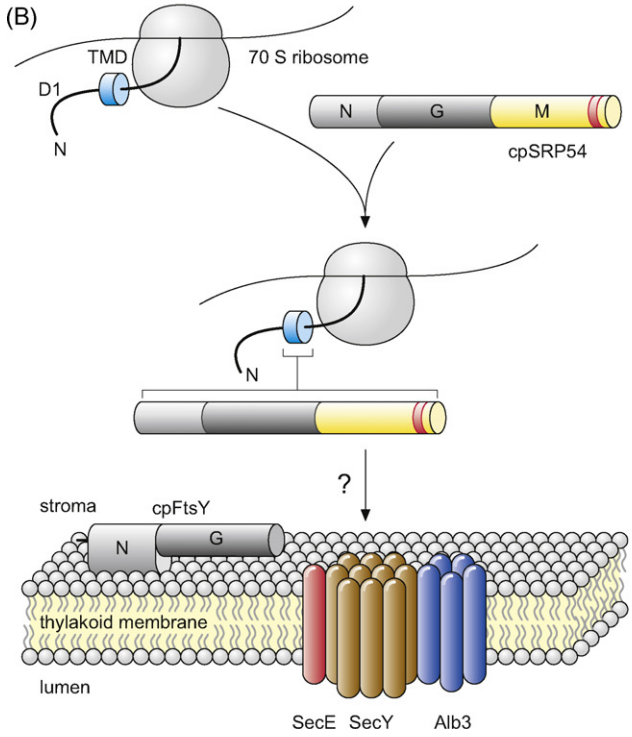
GTP
GTP
?
N
GDP
thylakoid membrane
lumen
Alb3
N
LHCP
C


(B)
TMD
70 S ribosome
D1
N
N
G
M
cpSRP54
N
?
stroma
cpFtsY
N
G
thylakoid membrane
lumen
SecE
SecY
Alb3