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Sorting of nuclear-encoded chloroplast membrane proteins

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Among the many organelles in eukaryotic cells, chloroplasts have the most complex structure, with multiple suborganellar membranes, making protein targeting to chloroplasts, particularly to various suborganellar membranes, highly challenging. Multiple mechanisms function in the biogenesis of chloroplast membrane proteins. Nuclear-encoded nascent proteins can be targeted to the outer envelope membrane directly from the cytosol after translation, but their targeting to the inner envelope and thylakoid membranes requires multiple steps, including cytosolic sorting, translocation across the envelope membranes, sorting in the stroma, and insertion into their target membranes. In this review, we discuss the current knowledge about the sorting mechanisms of proteins to the two envelope membranes and the thylakoid membrane, along with perspectives for future research.

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Introduction

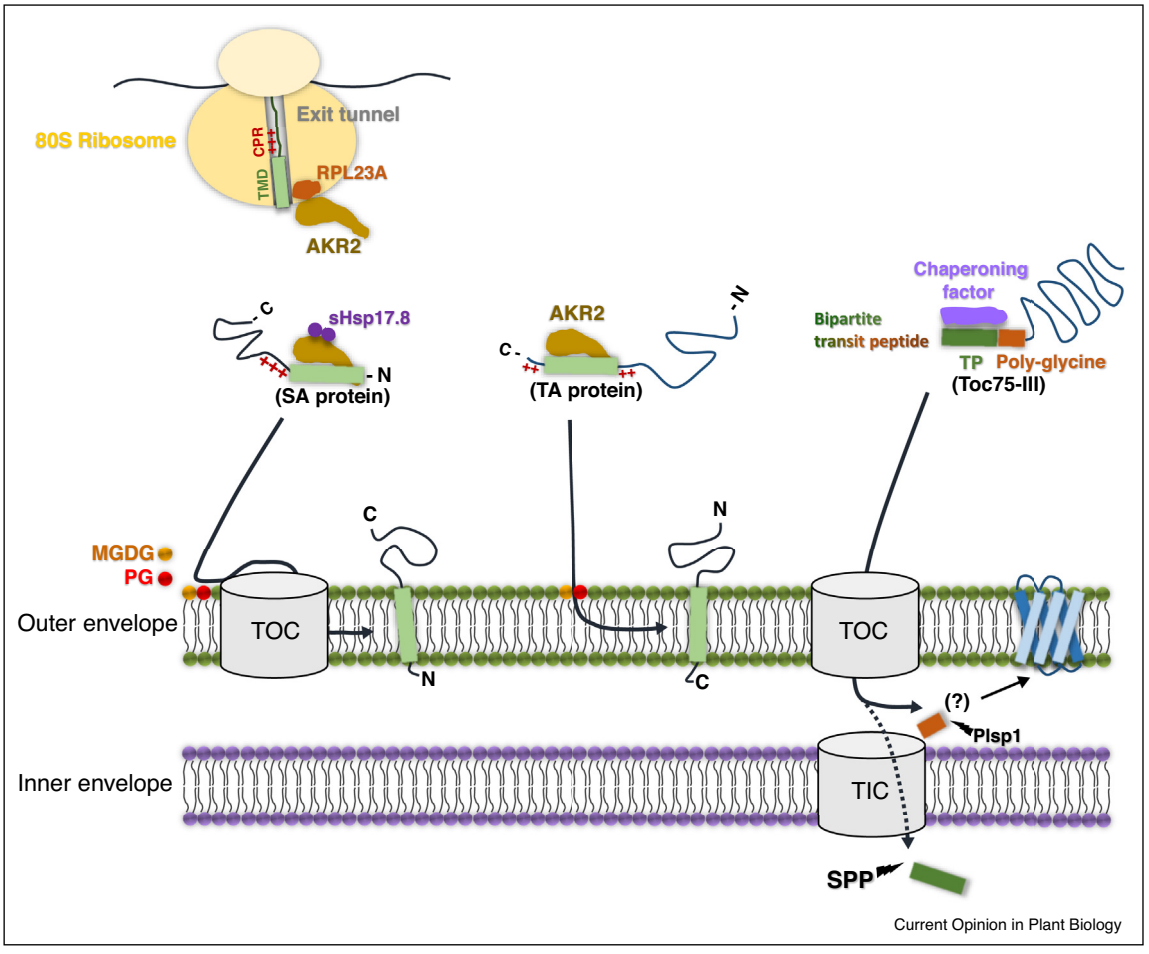
Of the large number of organelles in eukaryotic cells, chloroplasts have the most complex structure, with three types of membranes, including the outer envelope membrane (OEM), inner envelope membrane (IEM), and thylakoid membrane [1]. These membranes not only serve as barriers that divide the cellular or suborganellar spaces, but they also play critical roles in anchoring the proteins that carry out key chloroplast functions [1]. Thus, proper biogenesis of these suborganellar membrane proteins is of primary importance for the functioning of chloroplasts. Numerous studies on the targeting of chloroplast proteins have focused on stromal proteins with transit peptides (TPs); various factors and their action mechanisms have been elucidated at the molecular level, and the nature of TPs has been extensively studied [2–8]. Recently, significant progress has also been made in uncovering the mechanisms of protein targeting to the OEM, IEM, and thylakoid membrane at the molecular level [1,9,10]. However, much less is known about membrane proteins compared with soluble stromal proteins. The targeting of membrane proteins is much more complex due to the presence of hydrophobic transmembrane domains (TMDs), and additional steps are required for the sorting and insertion of these proteins into suborganellar membranes [10]. In this review, we summarize recent findings on the sorting and targeting mechanisms of proteins to the three membranes of the chloroplast and highlight some unanswered questions about the sorting of proteins between these membranes.

Targeting of outer envelope membrane proteins

OEM proteins are classified into three groups: signal-anchored (SA), tail-anchored (TA), and β-barrel proteins. SA and TA proteins lack a TP. The targeting signal of SA proteins consists of the N-terminal TMD, with hydrophobicity values <0.4 on the Wimley–White hydrophobicity scale, and the C-terminal positive region (CPR) flanking the TMD [11–13]. These two features, which are necessary and sufficient for OEM targeting of SA proteins, are recognized by ankyrin repeat protein 2 (AKR2), a cytosolic factor for SA targeting [14]. AKR2A, one of the two AKR2 isoforms, interacts with ribosomes via RPL23A, which facilitates the recognition of the cargo during translation (Figure 1) [14,15••]. This interaction is enhanced when the targeting signal of SA proteins is placed in the exit tunnel of the ribosome. Thus, the sorting of post-translationally targeted OEM SA proteins also occurs during translation, as does SRP-mediated ER targeting. AKR2 also binds to chloroplasts via a coincidental interaction of its C-terminal ankyrin repeat domain (ARD) with two OEM lipids, monogalactosyldiacylglycerol and phosphatidylglycerol. The protein sHsp17.8, a member of the cytosolic small heat shock protein (sHsp) family, acts as a cofactor of AKR2 (Figure 1) [16,17]. In addition, TOC75 is also known to be involved in the insertion of SA proteins (Figure 1) [18]. Whether these two mechanisms are in the same pathway or independent from each other needs to be investigated.

The second group of OEM proteins is TA proteins with a C-terminal TMD. The TMD and its adjacent C-terminal sequence (CTS) function as the targeting signal for the

Figure 1



Sorting and insertion of chloroplast outer envelope membrane proteins. AKR2 functions as a targeting factor of chloroplast OEM SA proteins. AKR2 stably associates with translating ribosomes, which is enhanced when the targeting signal of CH SA proteins is placed in the exit tunnel of the ribosome. RPL23A serves as a binding site for AKR2. When the signal sequence of SA proteins emerges from the exit tunnel of the ribosome, AKR2 binds to both RPL23A and the targeting signal. After translation is complete, AKR2 may form a complex with the cargo protein and a cofactor, sHsp17.8, for targeting to the surface of the chloroplast. AKR2 recognizes the chloroplast by binding to two OEM lipids, MGDG and PG. AKR2 may function as a targeting factor of chloroplast OEM TA proteins. Chloroplast OEM β-barrel proteins such as TOC75 may use different pathway in a TP-dependent manner. *Abbreviations*: AKR2, ankyrin repeat protein 2; CPR, C-terminal positively charged region; MGDG, monogalactosyldiacylglycerol; PG, phosphatidylglycerol; Plsp1, plastidic type I signal peptidase 1; RPL23A, ribosomal protein L23A; SA, signal-anchored; sHsp17.8, small heat shock protein 17.8; TA, tail-anchored; SPP, stromal processing peptidases; TIC, translocon at the inner envelope membrane of chloroplasts; TOC, translocon at the outer envelope membrane of chloroplasts; TMD, transmembrane domain; TP, transit peptide; +++, positively charged amino acid residues.

OEM protein OEP9; this signal is sufficient for OEM targeting of other TA proteins [19]. However, TOC33 and TOC34 require the N-terminal GTPase domain in addition to the TMD and CTS for targeting and insertion to OEM [20,21]. Therefore, multiple targeting mechanisms exist for OEM targeting of TA proteins [19]. The targeting factor of TA proteins has not yet been identified. AKR2 may play a role in TA targeting, since it interacts with TA proteins such as TOC33, TOC34, and OEP9 (Figure 1) [19].

The third group of OEM proteins is β-barrel proteins. Of these proteins, the targeting of TOC75 has been the most extensively studied. TOC75-III has a cleavable bipartite signal peptide consisting of a typical TP and a polyglycine stretch, which are cleaved off by SPP (stromal processing peptidase) and Plsp1 (plastidic type I signal peptidase), respectively before insertion (Figure 1) [22,23]. Similarly, TOC75-V/OEP80, OEP24, and OEP37 are predicted to contain a TP, whereas OEP21 and TGD4 do not, raising the possibility that the composition of targeting signals varies depending on the type of protein, which suggests that multiple targeting mechanisms exist for OEM β-barrel proteins. In addition, it is not clear whether the function of TP in β-barrel proteins is similar to that of stromal proteins. Thus, how TP contributes to this

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