Opinion

Cell PRESS

Transit peptide design and plastid import regulation

Hsou-min Li and Yi-Shan Teng

Institute of Molecular Biology, Academia Sinica, Taipei 11529, Taiwan

Import of most nuclear encoded proteins into plastids is directed by an N-terminal transit peptide. Early studies suggested that transit peptides are interchangeable between precursor proteins. However, emerging evidence shows that different transit peptides contain different motifs specifying their preference for certain plastid types or ages. In this opinion article, we propose a 'multi-selection and multi-order' (M&M) model for transit peptide design, describing each transit peptide as an assembly of motifs for interacting with selected translocon components. These interactions determine the preference of the precursor for a particular plastid type or age. Furthermore, the order of the motifs varies among transit peptides, explaining why no consensus sequences have been identified through linear sequence comparison of all transit peptides as one group.

Protein import into plastids is developmentally regulated

One of the most unique aspects of plastids in vascular plants is their development into different plastid types depending on the tissue and developmental stage. For example, in green photosynthetic tissues plastids develop into chloroplasts. In storage tissues such as potato tubers they develop into starch-grain filled amyloplasts. In seedlings germinated in the dark, plastids develop into etioplasts characterized by the presence of prolamellar bodies carrying chlorophyll precursors. In senescing leaves, chloroplasts develop into gerontoplasts containing catabolic enzymes for resource salvage. In addition, compared to chloroplasts in unicellular algae, land plants contain chloroplasts of different ages within a single individual.

Most plastid proteins are encoded by the nuclear genome and synthesized in the cytosol as higher molecular precursors with N-terminal targeting signals called transit peptides. Box 1 contains a brief summary of our current understanding of the import process (see also Figure 1 for central translocon components and [1–3] for reviews). Plastids of different types and ages contain many different proteins, as well as variable amounts of the same proteins. It has been assumed that plastid proteomes are controlled mostly by differential transcriptions of the protein-encoding genes. However, two very recent papers suggest that changes of plastid proteomes also require regulations at the protein import level [4,5]. The presence of a specific degradation system in the cytosol for chloroplast precursor proteins [6] also supports that plastid protein import is regulated. Accumulating evidence further suggests that import regulation is achieved through information contained within the transit peptide. However, sequences of transit peptides are extremely diverse. No consensus sequence motifs have been found even for the basic import mechanism. Here we combine all the results and propose a model of transit peptide design that can achieve regulation and also elucidate the enigma that transit peptides are heterogeneous and yet specific.

Transit peptide sequences are heterogeneous

Transit peptides are necessary and sufficient for directing protein import into plastids. However, the sequences and lengths of plastid transit peptides are the most diverse among organelle targeting signal peptides [7]. Only a few sequence features have been found. Consensus motifs and structures have been proposed but they were often later shown not to be conserved when a larger set of transit peptides was analyzed [8].

The average length of a plastid transit peptide is 50 amino acids [8], but varies from 13 to 146 amino acids [9], generally with very few acidic residues. It was thought that transit peptides were enriched with serine and threonine [9,10]. However, recent analyses of approximately 800 transit peptides from *Arabidopsis* (*Arabidopsis thaliana*) and rice (*Oryza sativa*) showed that the most abundant residue is indeed serine for *Arabidopsis* but alanine for rice. Threonine is enriched in neither species [8].

Recently two previously proposed transit peptide motifs [10–12] were reanalyzed using larger transit peptide databases, and the results seem to indicate that these motifs do exist and only need to be modified [13]. First, it was confirmed that the N terminus of transit peptides has a higher percentage of uncharged amino acids, suggesting that the N terminus of transit peptides may interact with Hsp70. Second, it was shown that a degenerate FGLK motif provides a very good prediction to discriminate transit peptides from signal peptides to other organelles. Based on further experimental analyses on transit peptides of precursors to the small subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (prRBCS) and ferredoxin (prFd), and two peptides representing their reverse sequences, a bimodal model of transit peptide design was presented [13]. The model proposed that chloroplast transit peptides have an uncharged amino terminus to interact with stromal Hsp70, followed by $\geq$22 residues to span the two membranes of the envelope, and then

Corresponding author: Li, H.-m. (mbhmli@gate.sinica.edu.tw)
Keywords: transit peptide; protein trafficking; plastid; developmental regulation.

1360-1385/$ – see front matter
© 2013 Elsevier Ltd. All rights reserved. http://dx.doi.org/10.1016/j.tplants.2013.04.003

CrossMark

Box 1. Protein import into young chloroplasts

Chloroplasts are the most abundant plastid type in green tissues. General interest in photosynthesis has also resulted in efforts to optimize chloroplast isolation protocols. Therefore, most of our knowledge about how proteins are imported into plastids has been obtained from studies using chloroplasts isolated from young leaves. The import process is mediated by the translocon apparatus with components located in and around the chloroplast outer and inner envelope membranes, namely the Toc and Tic (translocon at the outer and inner envelope membrane of chloroplasts) proteins (see [1–3] for more detailed reviews). The number following each acronym denotes the calculated molecular mass of the protein. Toc159, Toc75, and Toc34 are major components of the Toc complex (see Figure 1 in main text). Toc159 and Toc34 are GTPases functioning as receptors for precursors. Toc75 is the channel for translocation across the outer membrane. Three Tic proteins, Tic20, Tic21, and Tic110, have been suggested to function as channels across the inner membrane. For example, Tic20 has been shown to form a stable complex with the recently identified Tic56, Tic100, and Tic214, and these four proteins together form a preprotein sensitive channel when reconstituted into planar lipid bilayers [65]. Tic110 has also been suggested to function as the stromal side receptor for transit peptides, and also as a scaffold for recruiting/tethering stromal components involved in the translocation and folding of precursors. Three stromal ATPases, Hsp93, cpHsc70, and Hsp90C, have been shown to be critical for driving precursor translocation across the envelope membranes into the stroma [54,66–68]. Tic40 is a cochaperone that coordinates the actions of Tic110 and Hsp93. The function of Tic22 is less clear and may facilitate import at times when high import rates are required [69].

the degenerate FGLK motif to interact with the Toc receptors.

This bimodal model is in good agreement with previous work on prRBCS transit peptides showing that the N terminus of the prRBCS transit peptide is important for translocation into the stroma, which may require binding to the stromal Hsp70. The central region of the prRBCS transit peptide is important for binding to the chloroplast surface [14], which involves interaction with the Toc complex. However, this model is not in agreement with previous work on the prFd transit peptide [11], which showed the opposite arrangement of the motifs: the N terminus of the prFd transit peptide is important for initial binding to chloroplasts, and a central region is required for translocation into the stroma.

In another example, using two algorithms to calculate affinities for DnaK as a representation for affinities to Hsp70, it was shown that with 115 transit peptides analyzed approximately 70% have a higher affinity for DnaK in their N-terminal third than in the rest of the transit peptide [15], in agreement with the bimodal model [13]. However, using one of the same algorithms and 727 transit peptides, it was calculated that the N-terminal 15 residues have a significantly lower DnaK-binding site frequency than other regions of transit peptides [16]. Nonetheless, interestingly, it has been shown that if transit peptides are first divided into multiple subgroups, conserved sequence motifs can be identified within each subgroup. Such division also greatly increases the accuracy of transit peptide prediction [17].

Transit peptides determine plastid-type preference

Many reports have shown that precursors for one type of plastids can be imported into another type of plastids [18–23], suggesting that the general import mechanism is similar in different types of plastids. However, it is also clear that different transit peptides have different plastid preferences. For example, in transgenic wheat (*Triticum aestivum*), both the non-photosynthetic ferredoxin III precursor (prFdIII) transit peptide and the prRBCS transit peptide can direct a GFP passenger protein to pollen amyloplasts, whereas only the prFdIII transit peptide

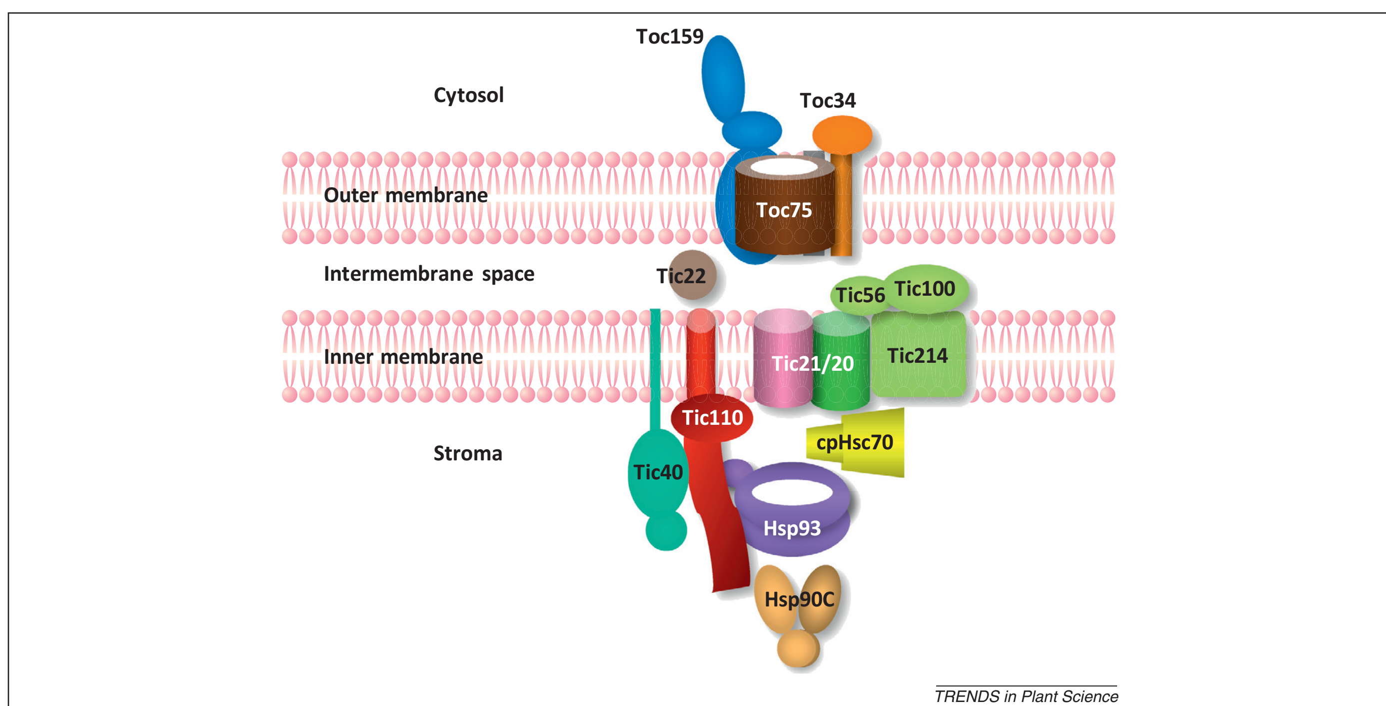

Figure 1. Schematic representation of central translocon components identified in young chloroplasts.

Download English Version:

https://daneshyari.com/en/article/2826255

Download Persian Version:

https://daneshyari.com/article/2826255

Daneshyari.com