Emerging knowledge of the organelle outer membranes – research snapshots and an updated list of the chloroplast outer envelope proteins

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Keywords: Arabidopsis, chloroplast, membrane proteins, mitochondria, outer membrane

Mitochondria and chloroplasts are two distinct organelles essential for plant viability. They evolved from prokaryotic endosymbionts and share a common ancestor with extant Gram-negative bacteria (Gray et al., 1999; Gould et al., 2008). Successful conversion of the free-living prokaryotes to the cytoplasmic organelles via endosymbiosis required conservation and adaptation of the outer membranes to the dramatic change of surroundings. In prokaryotes, the outer membrane serves as a physical barrier that protects cells from the extracellular environment and allows import of necessary nutrients, and also directly participates in interaction with other organisms (Nikaido, 2003). As part of the semi-autonomous organelles, by contrast, the outer membranes of mitochondria and chloroplasts have gained ability to participate in intracellular communication and organelle biogenesis, i.e., import and export of various ions and metabolites, import of nuclear-encoded proteins, various metabolic processes including the biosynthesis of membrane lipids, and division and movement of the organelles that require physical interaction with cytoplasmic components (Breuers et al., 2011; Inoue, 2011; Duncan et al., 2013). Our understanding of the organelle outer membranes have been advanced greatly in the last decade or so, and the last eight years have seen about a three-fold increase in the number of proteins identified or predicted to be in the chloroplast outer envelope of Arabidopsis thaliana (Arabidopsis) [total 117 proteins listed in Table 1; compare 34 proteins in Inoue (2007)]. This Research Topic is intended to provide snapshots of recent research on the organelle outer membranes. It collects seven original research, three review and two method articles, which can be divided into four groups according to the subjects – (1) outer membrane protein targeting, (2) functions, targeting and evolution of protein import components, (3) lipid metabolism, and (4) method development.

1. Protein Targeting to the Organelle Outer Membranes

All proteins identified so far in the organelle outer membranes are encoded in the nucleus (e.g., Table 1), and most of them use internal signals for targeting. This is distinct from the case for most nuclear-encoded proteins found inside the organelles: they are synthesized with N-terminal extensions, which are necessary and sufficient for proper targeting via the general pathway and cleaved upon import in the matrix (mitochondria) or stroma (chloroplasts). Lee et al. (2014) review the current knowledge of pathways and signals needed for targeting of three types of outer membrane proteins – signal-anchored (SA), tail-anchored (TA), and β-barrel proteins. SA and TA proteins are anchored to the membrane via a single transmembrane (TM) α-helix with either N_intermembrane space-C_cytosol (for SA) or N_cytosol-C_intermembrane space (for TA) orientation. β-Barrel proteins are integrated into the membrane via a single transmembrane β-strands, whose formation appears to require evolutionarily conserved machinery in the membrane. Marty et al. (2014) have used a transient expression system with Nicotiana tabacum Bright Yellow-2 suspension cells to identify two types of
TABLE 1 | One hundred and seventeen proteins identified or predicted to be in the outer membrane of the Arabidopsis chloroplast envelope.3

| AGI no.\(^b\) | Name | References\(^c\) | Envelope\(^d\) | MitoOM\(^e\) |
|--------------|------|-----------------|---------------|-------------|
| **SOLUTE/ION TRANSPORT** | | | | |
| At1g20816 | OEP21-1 | (i)(ii)(iii) | YES | |
| At1g45170 | OEP24-1 | (i)(ii)(iv) | YES | |
| At1g78405 | OEP21-2 | (i)(ii) | YES | |
| At2g01320 | WBC7 | (i)(ii)(iii) | YES | |
| At2g17695 | OEP23/DUF1990 | (vii) | YES | |
| At2g28900 | OEP16-1 | (i)(ii)(iv) | YES | |
| At2g43950 | OEP37 | (i)(ii)(iii)(iv) | YES | |
| At3g51870 | PAPST1 homolog | (viii) | YES | |
| At3g62880 | OEP16-4 | (i)(ii) | | |
| At4g19860 | HXXK2 | (i) | | |
| At4g29130 | HXXK1 | (ii)(iii)(iv) | YES | |
| **PROTEIN IMPORT COMPONENTS AND THEIR HOMOLOGS** | | | | |
| At1g02280 | Toc33 | (i)(ii) | YES | |
| At2g16640 | Toc132 | (i)(ii)(iii)(iv) | YES | |
| At2g17390 | AKR2B | (i) | | |
| At3g16220 | Toc120 | (i)(ii) | YES | |
| At3g17970 | Toc64-III | (i)(ii)(iii)(iv) | YES | |
| At3g41410 | P39/OEP80tr1 | (i) | YES | |
| At3g46740 | Toc75-III | (i)(ii)(iv)(vi) | | |
| At3g48620 | P36/OEP80tr2 | (i) | YES | |
| At4g02510 | Toc159 | (i)(ii)(iv) | YES | |
| At4g09080 | Toc75-IV | (i)(ii)(viii) | YES | |
| At5g05600 | Toc34 | (i)(ii)(iv) | YES | |
| At5g19620 | OEP80/Toc75-V | (i)(ii)(iv) | YES | |
| At5g20300 | Toc90 | (i)(ii)(iv) | YES | |
| **PROTEIN TURNOVER AND MODIFICATION** | | | | |
| At1g02560 | ClpP5 (proteolysis) | (iv) | YES | |
| At1g07930 | E-Tu (protein synthesis) | (iii) | YES | |
| At1g09340 | HIP1.3/Rap38/CSP41B | (iv) | YES | |
| At1g63900 | SP1 (proteolysis) | (vi) | YES | |
| At2g11810 | MGD3 | (i) | YES | |
| At2g38670 | PECT1 | (i) | YES | |
| At3g06510 | SFR2/GGGT | (ii)(iv) | YES | |
| At3g25860 | P36/OEP80tr2 | (i)(ii)(iv) | YES | |
| **CARBOHYDRATE METABOLISM AND REGULATION** | | | | |
| At1g34430 | PDC E2 | (i)(ii)(iv) | YES | |
| At1g44170 | ALDH3H1 | (i) | YES | |
| At2g34590 | PDC E1beta | (i)(ii)(iv) | YES | |
| At2g47770 | TSPO | (i) | YES | |
| At3g01500 | beta CA1 | (i)(ii)(iv) | YES | |
| At3g16950 | PDC E3 | (i)(ii)(iv) | YES | |
| At3g25860 | PDC E2 | (i)(ii)(iv) | YES | |
| At3g27820 | MDAR4 | (i)(ii)(iv)(vii) | YES | |
| At5g17770 | CBR | (i)(iii)(iv) | YES | |
| At5g23190 | CYPD68B1 | (i)(ii)(iv)(vii) | YES | |
| At5g25900 | KO1/GA3 | (i)(ii)(iv) | YES | |
| **LIPID METABOLISM** | | | | |
| At1g77590 | LACS9 | (i)(ii)(iv)(vi) | YES | |
| At2g11810 | MGD3 | (i) | YES | |
| At2g27490 | ATCOAE | (i)(ii)(iv) | YES | |
| At3g06510 | SFR2/GGGT | (i)(ii)(iv) | YES | |
| At3g06960 | TGD4 | (i)(ii)(iv) | YES | |
| **FUNCTIONS/LOCATIONS DEFINED IN COMPARTMENTS OTHER THAN THE CHLOROPLAST OUTER ENVELOPE** | | | | |
| At3g63170 | FAP1 | (i)(ii)(iii) | YES | |
| At4g00550 | DGD2 | (i)(ii)(iv) | YES | |
| At4g15440 | HXXK2 | (i)(ii)(iv) | YES | |
| At4g29130 | HXXK1 | (ii)(iii)(iv) | YES | |
| **INTRACELLULAR COMMUNICATION** | | | | |
| At1g12230 | transaldolase | (i) | YES | |
| At1g13900 | PAP2 | (i)(ii) | YES | |
| At2g19860 | HXXK2 | (i)(ii)(iv) | YES | |
| At3g46740 | pTAC16 | (i)(ii)(iv) | YES | |
| At3g48620 | P36/OEP80tr2 | (i)(ii)(iv) | YES | |
| At4g02510 | Toc159 | (i)(ii)(iv) | YES | |
| At4g09080 | Toc75-IV | (i)(ii)(iv) | YES | |
| At5g05600 | Toc34 | (i)(ii)(iv) | YES | |
| At5g19620 | OEP80/Toc75-V | (i)(ii)(iv) | YES | |
| At5g20300 | Toc90 | (i)(ii)(iv) | YES | |
| **FUNCTIONS/LOCATIONS DEFINED IN COMPARTMENTS OTHER THAN THE CHLOROPLAST OUTER ENVELOPE** | | | | |
| At1g27390 | Tom20-2 (mito) | (i)(ii)(iii) | (ii)(iii) | |
| At3g01280 | VDAC1 (mito) | (i)(ii)(iii) | (ii)(iii) | |
| At3g12580 | Hsp70-4 (cytosol) | (i)(ii)(iii) | (ii)(iii) | |
| At3g21865 | PEX22 (peroxisome) | (i)(ii)(iii) | (ii)(iii) | |
| At3g46030 | histone H2B (nucleus) | (i)(ii)(iii) | (ii)(iii) | |
| At3g63150 | MIO2 (mito) | (i)(ii)(iii) | (ii)(iii) | |
| At4g14430 | enoyl-CoA isomerase | (i)(ii)(iii) | (ii)(iii) | |
| At4g16440 | Complex I subunit | (i)(ii)(iii) | (ii)(iii) | |
| At4g31780 | MGD1 (IEM) | (i)(ii)(iii) | (ii)(iii) | |
| At4g35000 | APX3 (peroxisome) | (i)(ii)(iii) | (ii)(iii) | |
| At4g38920 | vacuolar ATPase sub | (i)(ii)(iii) | (ii)(iii) | |
| At5g02500 | HSC70-1 | (i)(ii)(iii) | (ii)(iii) | |
| At5g06960 | Prx B (stroma) | (i)(ii)(iii) | (ii)(iii) | |
| At5g15090 | VDAC3 (mito) | (i)(ii)(iii) | (ii)(iii) | |

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targeting signals for mitochondria TA proteins. They have then performed database search, increasing the number of mitochondria TA proteins from 20 to 54. Interestingly, 16 of the mitochondria outer membrane proteins identified by the previous work (Duncan et al., 2013) and Marty et al. (2014) are also found in the chloroplast outer envelope membrane (Table 1). This may suggest the presence of targeting mechanisms and functions shared between the outer membranes of the two organelles.

### 2. Functions, Targeting and Evolution of Protein Import Components

The most-studied chloroplast outer membrane proteins are subunits of the TOC (translocon at the outer-envelope-membrane of chloroplasts) machinery, which catalyzes the general pathway to import nuclear-encoded precursor proteins from the cytosol. Among the TOC components are homologous GTPases Toc159 and Toc34, which recognize the precursors and regulate their import, and Toc75, which forms a protein conducting channel. In Arabidopsis, there are four Toc159 isoforms which show substrate selectivity, two catalytically redundant Toc34 isoforms, and one functional Toc75 encoded on chromosome III (Table 1). Demarsy et al. (2014) review the current knowledge about how these subunits function and regulate protein import. Richardson et al. (2014) summarize available results and discuss functions, targeting and assembly of TOC subunits. Importantly, both review articles recognize outstanding questions about the TOC components, including the mechanisms of precursor recognition and their insertion into the membrane. By biochemical assays using chloroplasts isolated from pea seedlings, radiolabeled precursor proteins and recombinant proteins, Chang et al. (2014) demonstrate interaction of Toc159 isoforms called Toc132/Toc120 with a chloroplast superoxide dismutase (FSD1) that was predicted to comprise an exceptionally short import signal but has been shown otherwise, and also map the interaction domains beyond the N-terminus. The interaction of FSD1 with Toc132, but not with Toc159, was also demonstrated by a split-ubiquitin yeast two-hybrid assay (Dutta et al., 2014). Grimmer et al. (2014) have used an in vivo approach, transiently producing GFP-tagged proteins in protoplasts of various Arabidopsis mutants and determining their N-terminal sequences by mass spectrometry analyses, and demonstrate that a plastid RNA binding protein is a substrate of Toc159. The Arabidopsis protoplast transient expression assay has also been used to define sequences required for targeting and membrane integration of a Toc159 ortholog (Lung et al., 2014). A previous genetic screening had demonstrated that Toc132 and Toc75 enhance root gravitropism signal transduction (Stanga et al., 2009). Strohm et al. (2014) now provide evidence supporting the involvement of plastids, instead of direct participation of TOC subunits, in the gravitropism signal transduction. Finally, Day et al. (2014) report phylogenetic relationships and in vitro targeting of the Toc75 homologs including the truncated forms of OEP80/Toc75-V, which are also known as P39 (Hsueh et al., 2014) and P36 (Nicolaïsen et al., 2015) (Table 1).

### Table 1 | Continued

| AGI no. | Name References | Envelope | MitoOM |
|---------|-----------------|----------|--------|
| At5g25740 | EM2473/MIRO1 (mito) | (iv) (vi) | (vii) |
| At5g35360 | CAC2/BC (IEM) | (v) | YES |
| At1g98920 | | (xx)(xi) | |
| At1g16000 | OEP6 | (iii) | |
| At1g27300 | | (iv)(v) | |
| At1g64850 | YES | (iv) | |
| At1g68860 | | (iv) | |
| At1g70480 | DUF220 | (v) (vi)(vii) | |
| At1g08990 | OEP9.2 | (iv) | |
| At2g06010 | | (xv) | |
| At2g34410 | | (xv) | |
| At2g32240 | DUF869 | (v) (vi) | |
| At2g32650 | PTAC18 like | (v) | |
| At2g44640 | | (iv) | |
| At3g26740 | CCL | (iv) | |
| At3g49350 | | (iv) | |
| At3g52230 | OMP24 homolog | (v) | |
| At3g52420 | OEP7 | (iv) | |
| At3g53560 | TPR protein | (iv) | |
| At3g63160 | OMP24 homolog (v) | (iv) | |
| At4g02482 | putative GTPase | (v) | |
| At4g15810 | NTPase | (iv) | |
| At4g17170 | RAB2 | (iv) | |
| At4g27680 | NTPase | (iv) | |
| At4g27990 | YGCT-B protein | (iv) | |
| At5g11560 | | (iv) | |
| At5g06250 | WAV2 | (iv) | |
| At5g21920 | YGCT-A | (iv) | |
| At5g21990 | OEP61-TPR | (iv) | |
| At5g27330 | | (iv) | |
| At5g42070 | | (iv) | |
| At5g43070 | WPP1 | (iv) | |
| At5g51020 | CRL | (vii) | |
| At5g59840 | RAB8A-like | (iv) | |
| At5g64816 | | (iv) | |

*Names and functional categories are based on literatures cited in this work and databases. See Supplementary Material Table 51 for the extended name (if any), the location curated by various databases, and other predicted properties based on the primary sequence for each protein.*

*Arabidopsis gene identifier (AGI) number, which represents the systematic designation given to each locus, gene, and its corresponding protein product by The Arabidopsis Information Resource (TAIR: https://www.arabidopsis.org/).*

*This list includes in total 117 proteins from two earlier review articles [32 from (i) Inoue (2007) and 44 from (ii) Breuer et al. (2011)], two recent chloroplast outer envelope proteomics studies [50 from (iii) Simm et al. (2018) and 58 from (iv) Guenimi-Carbone et al. (2019) and five reports on individual outer envelope proteins (v) PAP2 by Sun et al. (2012), (vi) SP1 by Ling et al. (2012), (vii) OEP23 by Goetz et al. (2015), (viii) PAPST1 by Xu et al. (2013), and (ix) pBP by Lagrange et al. (2003). Not. Note that Gigolashvili et al. (2012) predicts inner-envelope localization of PAPST1, and that the AGI number for pBP was updated from At4g06655.*

*Yes indicates that the given protein was found in the chloroplast envelope proteomic studies (Ferro et al., 2003, 2010; Föpplhich et al., 2003), which are listed in The Plant Proteome Database (PPDB: http://ppdb.tc.cornell.edu/) (Sun et al., 2009).*
3. Lipid Metabolism

Under phosphate starvation, phospholipids in the cell membranes, mainly those in extraplastidic compartments, are used as the source of free phosphates and substituted by galactolipids made in the chloroplast outer envelope. Murakawa et al. (2014) have used Arabidopsis mutants and feeding assays to show that the outer-envelope-dependent galactolipid synthesis is stimulated by sucrose supplementation and this stimulation in turn enhances utilization of the added sucrose for plant growth. This work nicely illustrates the physiological significance of the metabolic activity localized in the chloroplast outer envelope for plant growth and development.

4. Method Development

Hardre et al. (2014) report an attempt to apply biotin tagging and proteolysis to examine topology and membrane association of proteins in the spinach chloroplast. Although the work requires further refinement to achieve the desired specificity, the idea behind this approach is quite interesting. The toc159-null mutant is seedling-lethal thus has been examined as progenies of heterozygous parents. Tada et al. (2014) have established a method using Ziploc® container to grow the homozygous toc159 mutants on the sucrose-supplemented media to the point that viable seeds can be obtained. This cost-effective method should be useful to study not only the toc159-null plant but also other recessive lethal mutants of photosynthesis.

In summary, the collection highlights various questions about the organelle outer membranes and interdisciplinary approaches employed to address them. The future research should use these and other strategies to answer questions about the proteins of known functions, in particular those involved in protein homeostasis, as well as those of unknown functions (Table 1). The editor greatly acknowledges the excellent contributions of all the authors and constructive comments by expert reviewers to each of the articles.

Acknowledgments

This work was supported by the Division of Molecular and Cellular Biosciences at the US National Science Foundation (Grant No. 1050602).

Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpls.2015.00278/full

Table S1 | Extended names, curated locations and some other information of 117 proteins listed in Table 1.

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Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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