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SHORT COMMUNICATION

Differential distributions of trafficking and signaling proteins of the maize ER-Golgi apparatus

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ABSTRACT

The Endoplasmic Reticulum (ER)-Golgi apparatus of plants is the site of synthesis of non-cellulosic polysaccharides that then traffic to the cell wall. A two-step protocol of flotation centrifugation followed by free-flow electrophoresis (FFE) resolved ER and Golgi proteins into three profiles: an ER-rich fraction, two Golgi-rich fractions, and an intermediate fraction enriched in cellulose synthases. Nearly three dozen Rab-like proteins of eight different subgroups were distributed differentially in ER- vs. Golgi-rich fractions, whereas seven 14-3-3 proteins co-fractionated with cellulose synthases in the intermediate fraction. FFE offers a powerful means to classify resident and transient proteins in cell-free assays of cellular location.

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The Endoplasmic Reticulum (ER)-Golgi apparatus of all eukaryotic cells is the site of synthesis and packaging of glycoproteins and proteoglycans to be trafficked to the cell surface. In plants, the Golgi is also the site of synthesis of non-cellulosic polysaccharides of the cell wall. We combined flotation centrifugation with subsequent free-flow electrophoresis (FFE) to provide highly enriched ER-Golgi membranes from etiolated maize coleoptiles for glycome and proteome analysis.[1] Of more than 2,000 proteins identified in the Golgi membranes, over 200 were associated with nucleotide-sugar synthesis and transport, polysaccharide synthesis, and a host of enzymes associated with downstream cell wall metabolic processes. FFE resolved the ER-Golgi membranes by flotation centrifugation into four fractions that comprise two fractions of Golgi membranes enriched in glycosyl transferases and non-cellulosic polysaccharide synthases, an ER fraction, and an intervening fraction uniquely rich in cellulose synthase (CesA) proteins.[1] Consistent with role of the Golgi apparatus as the secretory organelle of the cell, we report here that, in addition to the protein machinery for cell-wall polysaccharide synthesis, numerous proteins that function in trafficking of vesicles to the cell surface and in cell signaling were identified. Using the MapMan functional annotations in the Plant Proteome Database,[2] 62 Golgi-associated proteins were classified as trafficking and signaling-related, including small GTPases, including several homologs of Rat Sarcoma (Ras) and Ras-binding (Rab) proteins, 14-3-3-like proteins, calcium-binding and calcium-dependent proteins, and several other proteins associated with vesicle fusion and trafficking (Table 1). FFE separation of ER and Golgi membranes revealed that many proteins of same class were distributed differentially across the four fractions of ER-Golgi based on the electrophoretic mobility of their membranes of residence or transport.

Small GTPases of the maize ER-Golgi

Small GTPases related to heterotrimeric G proteins are established components of signal transduction in eukaryotes and comprise a superfamily of proteins of diverse and non-redundant function.[9] Small GTPases form five subfamilies in human and yeast genomes, including the Ras- and Rab-proteins that serve as regulators of vesicle budding, motility and fusion, the ADP-ribosylation factor (ARF) GTPases that function as regulators in vesicle trafficking, the Rho GTPases involved in actin dynamics, and Ran GTPases involved in nuclear trafficking.[3] The Arabidopsis genome contains 93 of these proteins in four of the subgroups, with true Ras proteins absent from plant genomes.[3] We identified 32 small GTPases in the ER-Golgi of elongating maize coleoptiles, including a Rho1, a Ran and Ran-activating protein (RANGAP1), three ARF and ARF-like (ARL) proteins (Table 1). Rab proteins form eight subgroups based on homology,[4] and at least one member of all eight was identified. Arabidopsis RabA1,

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Table 1. Maize signaling and trafficking proteins identified in ER- and Golgi membranes from etiolated maize coleoptiles.

Maize Accession number[1]	Description	Mascot Spectral Counts	MaxQuant MS/MS Counts	Arabidopsis Putative Orthologs[2]
Small GTPases[3]				
GRMZM2G071071	Rho GTPase1	nd	11	At5g27540 (MIRO1)
GRMZM2G079817	Ran GTPase-activating protein	5	nd	At3g63130 (RANGAP1)
GRMZM2G157334	Ran GTP binding protein	6	nd	At5g55190 (RAN3)
GRMZM2G127648	Rab RIC2-like (RabA1b)	46	5	At1g16920 (RabA1b)
GRMZM2G101938	Rab 11B-like (RabA1d-1)	64	48	At4g18800 (RabA1d)
GRMZM2G018619	Rab RIC2-like (RabA1d-2)	62	5	At4g18800 (RabA1d)
GRMZM2G020661	Rab 11B-like (RabA1f)	45	nd	At5g60860 (RabA1f)
GRMZM2G029486	Rab 11A-like (RabA2a-1)	30	nd	At1g09630 (RabA2a)
GRMZM2G020544	Rab11C-like (RabA2a-2)	19	6	At1g09630 (RabA2a)
GRMZM2G144008	Rab11A-like (RabA2b-1)	39	5	At1g07410 (RabA2b)
GRMZM2G154960	Rab11C-like (RabA2b-2)	42	nd	At1g07410 (RabA2b)
GRMZM2G061912	Rab RGP2-like (RabA2b-3)	25	nd	At1g07410 (RabA2b)
GRMZM2G093186	Rab RGP2 11A-like (RabA2b-4)	27	9	At1g07410 (RabA2b)
GRMZM2G164527	Rab A4A-like (RabA4a-1)	nd	19	At5g65270 (RabA4a)
GRMZM2G061280	Rab11D-like (RabA4a-2)	47	nd	At5g65270 (RabA4a)
GRMZM2G122805	Rab11D-like(RabA4a-3)	43	nd	At5g65270 (RabA4a) At4g39990 (RabA4b)
GRMZM2G335738	Rab ARA4-like (RabA5a)	14	2	At5g47520 (RabA5a)
GRMZM2G173878	Rab 2B-like (RabB1c-1)	9	nd	At4g17170 (RabB1c)
GRMZM2G330430	Rab B1C-like (RabB1c-2)	nd	6	At4g17170 (RabB1c)
GRMZM5G836471	Rab 18-like (RabC1)	nd	4	At1g43890 (RabC1)
GRMZM2G097728	GTP-binding protein YPTM2 (RabD2a-1)	36	nd	At1g02130 (RabD2a)
GRMZM2G097746	Rab 1A-like (RabD2a-2)	nd	12	At1g02130 (RabD2a)
GRMZM2G106960	Rab 1B-like (RabD2c)	40	19	At4g17530 (RabD2c)
GRMZM2G061900	Rab ARA-3-like (RabE1c)	48	nd	At3g46060 (RabE1c)
GRMZM2G362088	Rab RHN1(RABF1-like) (RabF1)	17	2	At3g54840 (RabF1)
GRMZM2G158887	Rab G3F (RAB7B-like) (RabG3f)	nd	49	At3g18820 (RabG3f)
GRMZM2G169694	Rab 6A-like (RabH1b)	24	35	At2g44610 (RabH1b)
AC166636.1_FGP008	Rab-6A-like (RabH1a)	17	nd	At5g64990 (RabH1a) At4g39890 (RabH1c) At2g22290 (RabH1d) At5g10260 (RabH1e)
AC197246.3_FGP001	Rab ARA4-like	12	nd	
GRMZM2G357399	ADP-ribosylation factor (ARFA1e)	nd	4	At3g62290 (ARFA1e)
GRMZM2G081622	ADP-ribosylation factor (ARLA1b-1)	nd	6	At3g49860 (ARLA1b) At3g49870 (ARLA1c) At5g67560 (ARLA1d)
GRMZM2G007188	ADP-ribosylation factor 8B (ARLA1b-2)	9	nd	At3g49860 (ARLA1b) At3g49870 (ARLA1c) At5g67560 (ARLA1d)
Rab protein regulators[4]				
GRMZM2G050890	Prenylated Rab acceptorF2	49	33	At1g55190 (PRA1F2)
GRMZM2G432662	Prenylated Rab receptorB4-1	14	12	At2g38360 (PRA1B4)
GRMZM5G831519	Prenylated Rab receptorB4-2	24	nd	
GRMZM2G089783	Prenylated Rab receptorB4-3	3	3	At2g38360 (PRA1B4)
ER-Golgi Protein Trafficking[5]				
GRMZM2G178618	Coatomer γ-subunit2	nd	3	At2g16200
GRMZM2G042089	Coatomer δ-subunit delta	8	2	At5g05010
GRMZM2G036034	Coatomer γ-subunit gamma	5	nd	At2g16200
GRMZM2G141587	Coatomer β-subunit-2C	nd	2	
GRMZM2G115775	SNARE domain Syntaxin51(SYP51)	28	13	At1g16225, At1g16230 At1g16240, At1g79590
GRMZM5G838961	Golgi SNAP receptor complex1-2	nd	3	At2g45200
GRMZM2G063420	SNARE coiled-coil Bet1-like	nd	2	At1g29060 At4g14600
GRMZM2G064268	Protein YIF1A-1(HRF1-like)	6	4	At1g30890, At3g59500
GRMZM2G135599	Protein YIF1A-2 (HRF1-like)	3	nd	At1g30890, At3g59500
Molecular Chaperones				
AC217050.4_FGP006	14-3-3c	16	nd	
GRMZM2G091155	14-3-3m	8	2	At3g02520 (GF14η)
GRMZM2G106424	14-3-3q	8	nd	
GRMZM2G140545	14-3-3p	7	nd	At1g78300 (GF14ω)
GRMZM2G078641	14-3-3z	15	nd	At3g02520 (GF14η)
GRMZM2G102499	14-3-3f	51	19	At3g02520 (GF14η)
GRMZM5G866082	14-3-3o	8	nd	At3g02520 (GF14η)
Calcium Binding				
GRMZM2G010093	Calcineurin B-like 3	3	nd	At4g26570 (CBL3)
GRMZM2G025387	Calcium-dependent protein kinase3	8	6	At4g23650 (CPK3)
GRMZM2G430600	Calmodulin5	nd	4	At2g27030 (CAM5)
GRMZM2G391364	Calmodulin13a	5	nd	At1g12310 (CML13)
GRMZM2G324643	Calmodulin13b	2	3	At1g12310 (CML13) At1g62820 (CML13)
GRMZM2G115628	Calmodulin7	2	nd	
GRMZM2G004703	Calmodulin7	2	nd	

(*Continued*)

Table 1. (Continued).

Maize Accession number[1]	Description	Mascot Spectral Counts	MaxQuant MS/MS Counts	Arabidopsis Putative Orthologs[2]
GRMZM2G134668	Calnexin	156	19	
GRMZM2G358059	Calreticulin1	47	32	At1g56340 (CRT1)
GRMZM2G028516	Calreticulin3	2	nd	At1g08450 (CRT3)
GRMZM2G058305	Calcium-dependent protein kinase3′	7	nd	At4g23650 (CPK3)
GRMZM2G058870	Guanine-nucleotide-exchange factor (GEF)	8	5	At3g60860 (BIG2)
Signal Cleavage				
GRMZM2G112366	Signal peptidase complex1 (SPC1)	7	nd	At2g22425 (SPS1)
GRMZM2G131321	Signal peptidase complex2(SPC2)	nd	3	
GRMZM2G077463	Signal peptidase complex3(SPC3)	3	3	
Protein Sorting				
GRMZM2G068489	Vacuolar protein sorting29 (VPS29)	3	nd	At3g47810 (VPS29)
GRMZM5G825524	Vacuolar protein sorting35 (VPS35)	2	nd	At1g75850 (VPS35B)
GRMZM2G389362	Vacuolar sorting receptor1 (VSR1)	nd	6	At3g52850 (VSR1)

[a]Maize accession numbers as in MaizeGDB v.2/v.3 (https://www.maizegdb.org/)
[b]Arabidopsis nomenclature as in UniProtKB (https://www.uniprot.org/)
[c]Nomenclature defined in Vernoud et al.[3] following Periera-Leal and Seabra.[4]
[d]Nomenclature as in Kamei et al.[5]
[e]Nomenclature as in by Brandizzi and Barlowe,[6] and Barozzi et al.[7]
[f]Maize nomenclature defined by Kumar et al.[8]

RabA2 and RabA4 are thought to be involved in the regulation of cargo content in Golgi vesicles trafficked to the wall,[10] with RabA1 specifically regulating TGN-plasma membrane transport.[11]

Bidirectional transport between ER and Golgi is mediated by COPI and COPII carrier protein complexes.[6] COPI retrograde transport involves ARF/ARL ribosylation factors and several different coatomer proteins, for which we identified a β-, a δ-, and two γ-subunits (Table 1). RabA6 has been shown to function as a regulator of COPI-independent retrograde transport from the Golgi to the ER.[12]

We identified four Prenylated Rab Acceptor (PRA) proteins in maize Golgi membranes (Table 1). PRAs are membrane-associated proteins that modulate vesicle trafficking as receptors of Rab GTPases and SNARE family Vesicle-Associated Membrane Protein2 (VAMP2), where they are thought to assist in release of Rab GTPases from the Rab-GDI protein.[5] Arabidopsis PRA1 is implicated in both secretory and endocytic intracellular trafficking in the endosomal/prevacuolar compartments of ER and Golgi apparatus, with PRA1 F2 and PRA1 B4 localized in vesicular structures with networks of ER strands.[5] PRA1 is implicated in the promotion of small GTPases trafficking through the endomembrane system by binding to the hydrophobic isoprenoid moieties of the small GTPases.[13]

Flotation density-gradient centrifugation alone provided a rich source of ER and Golgi membranes, and FFE resolved these proteins into four major fractions (Figure 1(a)). Established marker proteins indicated that the most electrophoretically mobile 'Fraction 28 (F28)' was enriched with ER-proteins, whereas F34 and F37, representing the bulk of the protein recovered, contained known Golgi markers and glycosyl transferases and non-cellulosic polysaccharide synthases.[1] A concentration of cellulose synthases (CesAs) was found in F31. We report here that signaling- and trafficking-related proteins were differentially distributed across the four fractions containing ER-Golgi membranes. Thirteen Rab proteins, representing the A, D, E and H classes were more highly enriched in the ER fraction F28 than in those of the Golgi (Figure 1(b)). By contrast, six other Rabs, three RabAs, a RabB1, and a RabF1, were more highly enriched in the Golgi fractions (Figure 1(c)). These findings underscore that substantial sub- and neofunctionalization might have occurred within in each subgroup, and, thus, membrane locations are not subgroup-specific.

Other diverse trafficking proteins enriched in the Golgi fractions included YIF1-like transport proteins, SNARE Syntaxin51 (SYP51) proteins, a PRA1, a guanine-nucleotide exchange protein, and two coatomer proteins (Figure 1(c)). Members of the SNARE family of proteins are typically associated with the ER or terminal locations of tonoplast and plasma membrane, and with retrograde Golgi to ER transport as components of COPI complexes.[6,7] We show here that they partition primarily with the bulk Golgi membranes rather than with the ER (Figure 1(c)). Conversely, many known ER markers that concentrate in F28 also show substantial abundance in the Golgi fraction, indicating the possibility that the ER specifically associates with the *cis*-Golgi face and remains tightly associated during FFE. This finding is consistent with laser-trapping studies that showed strong interactions of Golgi with ER tubules.[15] Also consistent with strong ER-Golgi interactions is the presence in the Golgi-rich fractions of the signal peptidase complex subunit1, YIF1, several Rab proteins, and two coatomer proteins associated with retrograde transport from Golgi to ER (Figure 1(b,c)).

Molecular chaperones in Golgi trafficking

We identified seven 14-3-3-like proteins in maize Golgi (Table 1). The 14-3-3 proteins are a family of cellular scaffolds with diverse regulatory functions in eukaryotes.[16] They are a major class of molecular chaperones linked to signal transduction pathways regulating cell cycle checkpoints, MAP kinase activation, apoptosis and programs of gene expression.[17] The 30 kDa proteins form homo- and heterodimers, which can aggregate further into homo- and heterotetramers.[18] All seven maize 14-3-3 proteins

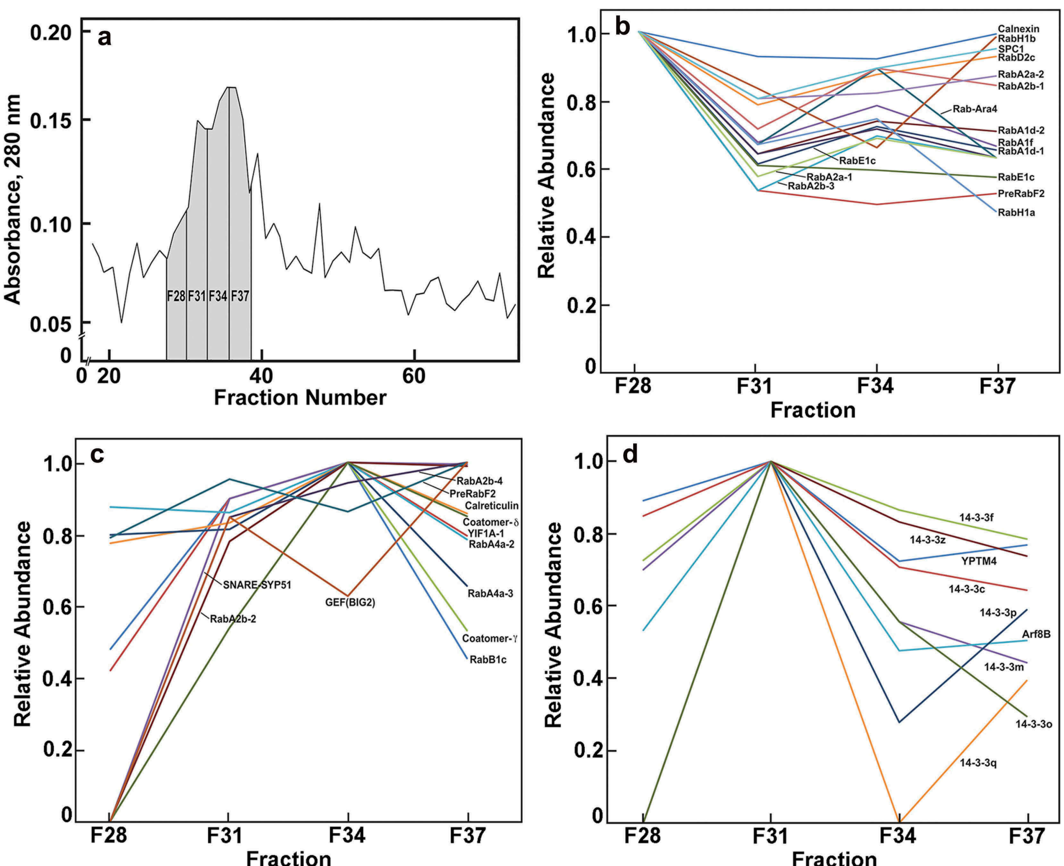

Figure 1. Relative distribution of ER-Golgi-associated proteins across four major fractions recovered after FFE. Three fractions from FFE were pooled; fractions 27–29 were pooled to give F28, and so forth. (a). Relative abundance of proteins estimated by Absorbance at 280 nm. (b). Relative abundance of proteins most abundant in F28. (c). Relative abundance of proteins most abundant in F34 or F37. (d). Relative abundance of proteins most abundant in F31. Nomenclature as in Table 1. Methods used for flotation centrifugation, FFE, and proteomics analysis are described in Reference 1. The MS proteomics data have been deposited to the ProteomeXchange Consortium via the partner repository,[20] with the data set identifier PXD007612 and null.

showed a distinct peak of proteins in F31 between the major ER and Golgi fractions (Figure 1(d)). The only two other proteins enriched in F31were an ARF8B and a YPT-type Rab protein. Fraction 31 is specifically associated with an enrichment of CesA proteins.[1] As the Golgi is the site of the formation of large multi-membered ‘particle rosette’ cellulose-synthase complexes, an intriguing possibility emerges that 14-3-3 proteins are not associated with non-cellulosic pectin- and hemicellulosic polysaccharide synthases of the Golgi, but uniquely involved in the assembly of rosette complexes for export to the PM. The 14-3-3 proteins function by binding to sites of phosphorylation to induce conformational changes and protein-protein interactions,[8,19] and it is known that phosphorylation of CesA1 at specific sites is required for normal cellulose synthesis and microtubule-dependent mobility of the rosette.[20]

Outlook

Flotation centrifugation in sucrose density gradient steps results in rapid enrichment of ER and Golgi membranes that are resolved electrophoretically into sub-fractions by FFE.[1] In reports to date, proteomic analyses of these fractions have given snapshots of resident and transiting components of the Golgi. The unexpected finding of an enrichment of Ras-like and Rab proteins in the ER might reflect the sites of insertion for subsequent transport to sites of residence. We have inferred that cohorts of associated proteins are co-fractionating by FFE, but this remains to be tested by flux measurements in pulse-chase experiments. FFE is also expected to be helpful in defining the full complements of proteins in post-Golgi processing compartments, such as the *trans*-Golgi network, endosomes, and other compartments involved in exo- and endocytosis.

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Author Contributions

I.O.O., J.L.H., and N.C.C. designed research; I.O.O., S.M.G.F-N., U.K.A., B.W.P., J.L., and N.C.C. performed experiments; I.O.O., U.K.A., B.W.P., J.L.H, M.C.M., and N.C.C. analyzed data; I.O.O., U.K.A., B.W.P., J.L. H., M.C.M., and N.C.C. wrote the article.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed

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