Protein transport within the plant cell endomembrane system: an update
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The secretory pathway plays a central role in plant development and morphogenesis. Storage protein deposition, plant cell division and the expansion of the plasma membrane and extracellular matrix all require the synthesis and trafficking of membranes, proteins and polysaccharides through this network of organelles. Increasing evidence demonstrates that the plant secretory pathway is more complex than previously appreciated and that its formation and maintenance are guided/regulated by many different mechanisms.

Introduction

The basic secretory pathway is comprised of several discrete organelles, including the endoplasmic reticulum (ER) and the Golgi apparatus, that are involved in the assembly, post-translational modification, trafficking and correct localization of newly synthesized proteins to the plasma membrane and vacuole. Trafficking between the various subcompartments of these organelles is thought to be primarily mediated by small carrier vesicles. In the past 10 years or so many of the basic molecular components involved in the formation and consumption of these vesicles have been identified in yeast and mammalian cells and related components have been identified in plants. This conservation is not surprising given that the basic organization of the plant secretory system is morphologically similar to that of other eukaryotes. There are a number of features, however, that distinguish the plant secretory pathway from other eukaryotes. One cannot simply infer how a plant process is regulated/controlled/guided/regulated by many different mechanisms.

Sorting of storage protein mRNA to different ER subdomains in cereal seeds

In cereals, two major classes of storage proteins accumulate in the cells of maturing seeds: prolams are retained within protein bodies (PBs) that are delimited by the ER membrane, whereas globulins are transported through the Golgi apparatus and deposited in vacuoles (see Figure 1). In cereals, two major classes of storage proteins accumulate in the cells of maturing seeds: prolams are retained within protein bodies (PBs) that are delimited by the ER membrane, whereas globulins are transported through the Golgi apparatus and deposited in vacuoles (see Figure 1). The different fates of these storage proteins may be linked to the differential distribution of mRNAs encoding these proteins and their translocation into distinct subdomains of the ER [2]. Interestingly, prolamin mRNA charged polysomes are not directly anchored to the PB membrane, rather they are found to be associated with the cytoskeleton [5*]. Similarly, elongation factor-1, which is required for synthesis of the protein, binds to the cytoskeleton surrounding PBs in maize seeds [6]. These observations suggest that the cytoskeleton plays a direct role in the segregation and localization of PB-ER-specific mRNAs from messages that are translated on other ER domains.

Storage protein deposition in the ER

The four structurally distinct prolamin-type storage proteins of maize, the zeins (α, β, δ, γ), are deposited and arranged in an orderly fashion within ER-derived PBs. Inter- and intramolecular interactions between these subunits are necessary for proper PB formation. Indeed, coexpression studies have recently shown that γ-zein and β-zein are necessary for the efficient deposition of α-zein and δ-zein in ER-PBs, respectively [7,8*]. These interactions, however, must be properly organized within the ER as demonstrated when a gene encoding a mutant α-zein that is defective in signal sequence cleavage was expressed, causing the aberrant PB morphology associated with the floury2 phenotype [9,10].

Deposition of wheat storage protein aggregates is also dependent on a retention/aggregation mechanism between different storage protein subunits in the ER. Expression in tobacco of only a single gliadin subtype, γ-gliadin, resulted in its degradation in a post-ER compartment [11]. In contrast to the maize and rice prolams, however, the dense gliadin/glutenin deposits are transported via a novel Golgi-independent mechanism from the ER to the protein-storage vacuole (PSV) [12]. Similarly, the globulin storage proteins in developing pumpkin cotyledons initially
aggregate in the ER and are subsequently transported via electron-dense precursor-accumulating vesicles (PACV) to PSV [13•]. Little is known about how these protein aggregates are distinguished from other secretory proteins and packaged into ER-to-PSV vesicles. The formation of ER-to-Golgi transport vesicles in yeast and mammalian cells is driven by the COPII (coat protein II) vesicle coat protein complex [14]. Arabidopsis homologs of COPII components have been identified and localized to the ER, indicating that COPII also mediates ER-to-Golgi transport in plant cells [15]. The mechanisms involved in PACV and COPII-vesicle formation are likely to differ because PACVs are

Schematic representation of the different routes involved in the intracellular trafficking of vacuolar and storage proteins and some of their unique features that have been observed in various plant cells. (a) Golgi-mediated transport of soluble proteins to the central vacuole in vegetative tissues and suspension-cultured cells. It is unknown if this step is mediated by one or more than one distinct vesicle class. The recently characterized prevacuolar compartment(s) (PVC) may exist in other plant cell types as well. (b) Transport of storage proteins in developing pea cotyledon. Storage protein aggregates form at the trans-side of the Golgi and are transported via dense vesicles (DV) to protein-storage vacuole (PSV). Hydrolases are transported from the Golgi apparatus to the lytic vacuole (LV), possibly by clathrin-coated vesicles. (c) Transport of proteins to the vacuoles in developing pumpkin cotyledons. The storage proteins that aggregate in the ER are packaged and exported from the ER to the PSV in precursor-accumulating vesicles (PACV). Precursor processing proteases are transported through the Golgi apparatus and maybe directed to the PACV, which is consistent with the appearance of complex glycans in these vesicles [13•]. (d) Storage protein sorting in developing rice endosperm. Prolamins accumulate in the ER and remain in ER-membrane delimited protein bodies (PB-ER), whereas glutelin is transported to the vacuole via the Golgi apparatus. Glutelin mRNA is localized to the rER, whereas prolamin mRNA is segregated to the protein body forming region of the ER (PB-ER). (e) Deposition of storage proteins in developing maize endosperm. Zeins are deposited in ER-PB. (f) Storage protein transport in developing wheat endosperm. The majority of wheat endosperm storage proteins are initially deposited into the ER. These deposits are then directly transported to the vacuole, and possibly taken up by an autophagic-like mechanism. A minor portion of the soluble storage proteins in these cells is transported to the vacuole via the Golgi apparatus.
significantly larger (200–400 nm in diameter) than ER-to-Golgi vesicles (60–80 nm) and contain significant amounts of the ER resident molecular chaperone, binding protein (BiP) [13*].

ER chaperones and protein folding

BiP, a member of the Hsp70 family, has been strongly implicated in the assembly of storage protein deposits in the ER [8*,13*,16,17]. Analysis of the assembly of phaseolin, the homotrimeric vacuolar storage glycoprotein from common bean, has also demonstrated that BiP associates with the monomeric protein before it trimerizes [18,19*] and with misfolded protein subunits in the ER [20*]. In addition to BiP, the folding and oligomerization of newly synthesized membrane and soluble secretory protein requires the coordinate action of the ER-resident molecular chaperones, protein disulfide isomerase (PDI), calreticulin, and the type-I membrane protein, calnexin. Mutations that disrupt proper disulfide bond formation have been shown to affect the synthesis of 11S globulins, a class of seed storage proteins [21*] and the deposition of gladin monomers into PB [22,23]. This process is sensitive to the redox state of the ER [21*] and is likely to be facilitated by PDI. In tobacco, a large fraction of BiP is associated with calreticulin [24*]. This interaction maybe important for the regulation of the level of free BiP in the ER and/or for the ER-retention of BiP. Calnexin and BiP have also recently been shown to interact with the vacuolar type-proton pump (V-ATPase) from oat seedlings [25*]. Binding of these molecular chaperones to the V-ATPase may facilitate the assembly of this large multimeric complex. Another possible function for these two chaperones could be to inhibit the activity of the V-ATPase in the ER by gating the opening of the proton-conducting channel. Indeed BiP has been shown to bind in vitro to the lumenal side of the Sec61p protein-translocation channel (translocon), that transports nascent polypeptides across the ER membrane, thereby preventing the free movement of small molecules out of the ER [26]. Thus, it will be interesting to determine if the proton pump–chaperone complexes are active.

What is the fate of misfolded secretory proteins in the ER? Recent studies in yeast and mammalian cells have indicated that the ER has a protein-degradation pathway that can recognize and selectively remove polypeptides from the secretory pathway. Misfolded proteins are retrotranslocated through the Sec61p-translocon from the ER to the cytosol and degraded by the ubiquitin/proteasome system [27]. The existence of this pathway in plant cells can be inferred from a recent experiment showing that ER-targeted ricin A-chain, which hydrolyzes a phosphodiester band of rRNA and destroys ribosome activity, can inactivate protein synthesis in the cytosol [28]. It remains to be determined, however, whether this pathway is part of the general ‘quality control’ mechanism in plants for removing unfolded or misfolded secretory proteins such as assembly-defective phaseolin which was found to be slowly degraded in a brefeldin A (BFA)-insensitive (i.e. Golgi-independent) manner [20*]. Alternatively, some misfolded proteins may be exported from the ER and directly targeted to the vacuole for degradation through the BFA-insensitive direct pathway(s) used to deliver pumpkin globulins and wheat gliadins to the PSV.

Golgi-mediated sorting to the different types of plant vacuoles

Soluble vacuolar proteins that are not directly targeted from the ER to the vacuole are sorted away from secreted proteins within the trans-Golgi apparatus. Several independent vacuole sorting mechanisms have been identified in plants including sequence-specific vacuolar targeting signal (ssVTS) mediated targeting, carboxy-terminal propeptide signal (CTPP)-mediated transport, and aggregation-mediated targeting [29]. Interestingly, the ER retention signal HDEL has recently also been shown to function as a vacuolar targeting signal [30*] and some peptide sorting sequences may behave as both ssVTS and CTPP [31]. Cargo proteins containing these different signals are not sorted to the vacuole by the same machinery. First, wortmannin blocks the sorting of CTPP-containing proteins but does not affect ssVTS-mediated sorting [32]. Second, some plant cells, such as the parenchyma cells of developing seed cotyledons, root tip cells and barley aleurone cells, contain at least two distinct vacuolar compartments [33,34,35*]. In barely root tip cells, a CTPP-containing protein, barley lectin, and a ssVTS-containing protease, aleurain, are localized in separate functionally distinct vacuoles [33]. In addition, sorting proteins that accumulate in PSV of developing pea cotyledons are not packaged into trans-Golgi derived clathrin coated vesicles (CCVs), rather they appear to be transported in smooth dense vesicles (DV) that are distinct from the ER-derived PACVs of pumpkin cotyledons [36].

Recognition and packaging of proteins containing vacuolar sorting signals into Golgi-derived transport vesicles is likely to be mediated by their interaction with specific transmembrane cargo receptors. The saturable nature of phaseolin targeting to the vacuole in transgenic tobacco cells supports this idea [37*]. A putative plant vacuolar sorting receptor, BP-80, that binds specifically to ssVTS in vitro, was isolated from CCVs [38,39] and cloned [40*]. Related proteins have also been detected in Arabidopsis (AtELP, [41]) and pumpkin (PV72/82, [42**]). These ~80 kDa type I transmembrane proteins share common structural features with the mammalian epidermal growth factor receptor and the yeast vacuolar sorting receptor, Vps10p. These proteins have a large luminal domain containing cysteine-rich repeats thought to be involved in ligand binding, a single transmembrane spanning domain and a short cytosolic tail. Within the cytosolic tail are a Tyr-containing binding motif [43] and a di-acidic motif (DXE) that functions as an export signal from the ER [44]. Consistent with their putative roles as cargo receptors, BP-80 and AtELP have been localized to the trans-Golgi,
CCVs and post-Golgi membranes (prevacuolar compartment; PVC) [38,39,41,45**]. Binding studies have suggested that the Tyr-containing motif of the cytosolic tail of AtELP interacts with the Golgi-localized clathrin AP-1 adaptor complex [45**]. AtELP and BP-80 are, therefore, likely to mediate the transport of cargo from the trans-Golgi to the prevacuolar compartment via CCVs, although the natural cargo for these receptors remains to be determined. Interestingly, PV72/82 was isolated from ER-derived PACVs [13*,42**]. This protein has been shown to recognize the NLPS amino acid sequence of 2S albumin in PACVs suggesting that PV72/82 is indeed a bona fide sorting receptor for 2S albumin [42**]. Many questions about the role of PV72/82 and the formation of PACVs remain to be resolved, however, including why a protein that is packaged into ER-to-PSV vesicles has both a putative AP-1 binding motif and a di-acidic ER-export motif in its cytosolic tail.

Protein aggregation within the Golgi apparatus has been suggested to be another way in which proteins destined for the vacuole are segregated away from secreted proteins [36,46]. In developing legume seeds, electron-dense storage protein aggregates initially accumulate in the trans-Golgi and are present in DVs of about 130 nm in diameter that are thought bud from the Golgi [36]. As these DVs are similar in function and morphology to pumpkin PACVs (although their origin is different), it is possible that receptor-like molecules also function in the concentration and sorting of storage proteins into DVs. Following formation of the DVs these putative receptors may be released and removed from the vesicles by CCVs that have been observed to bud from the surface of immature DVs [36,47].

**Targeting and fusion of Golgi-derived CCVs to the prevacuolar compartment**

Transport of proteins from the trans-Golgi to the vacuole is likely to occur through the recently identified PVC which is analogous to the endosomal compartment in yeast and mammalian cells. Like other vesicular transport steps in the secretory pathway, the targeting and fusion of the Golgi-derived CCVs with the PVC is thought to be mediated through the pairing of compartment specific integral membrane proteins, known as SNAREs, that reside on the two fusing membrane species (i.e. vesicle v-SNAREs pair with target membrane t-SNAREs) [48]. Their interaction in vitro is modulated by a large host of regulatory factors (see Figure 2). In yeast, docking and fusion of Golgi-derived vesicles with the PVC is directed by the v-SNARE, Vti1p, and the t-SNARE, Pep12p, as well as the Sec1p-related protein, Vps45p. Another t-SNARE, Vam3p, is required for the transport step from the PVC to the vacuole [49] and for vacuole fusion [50]. Plant equivalents of these factors — AtELP12p, AtVPS45p, AtVAM3p and AtVTI1p — have been characterized [51•,52,53•]. The recent identification and localization of AtKnolle, a putative cell-plate t-SNARE [59], confers on Arabidopsis Research, Madison, 24–29 June 1998).

**Figure 2**

Schematic diagram of the critical components involved in NSF-dependent heterotypic or Cdc48p-dependent homotypic membrane fusion. (a) Targeting and fusion of Golgi-derived clathrin-coated vesicles (CCV) with the prevacuolar compartment. Heterotypic vesicle fusion at each step of the secretory pathway is mediated by the pairing of cognate compartment specific v- and t-SNAREs (e.g. AtVti1p and AtPep12p, respectively) and is modulated by a number of proteins including the general trafficking factors, the N-ethylmaleimide (NEM) sensitive factor (NSF), and soluble NSF-attachment proteins (SNAPs) including the general trafficking factors, the N-ethylmaleimide (NEM) sensitive factor (NSF), and soluble NSF-attachment proteins (SNAPs) [62] and specific members of the Rab/Ypt family of small GTP-binding proteins [63], the Sec1 protein family (including AtVPS45p) [64] and putative ‘velcro’ factors such as p115/Uso1p [65,66]. Following fusion, NSF and SNAPs catalytically disassemble the energetically stable SNARE complex. (b) Cell-plate membrane fusion. SNAREs are not only involved in the heterotypic fusion of secretory vesicles with their appropriate acceptor compartment but also function in the homotypic fusion of like-like membranes such as vacuoles [50] and ER-membranes [67]. The recent identification and localization of KNOLLE, a putative cell-plate t-SNARE [59••] and AtCDC48p [68], a fusion factor closely related to NSF, may lend some insight into the mechanisms of membrane fusion involved in cell-plate formation. CDC48p has been shown to be required for the homotypic fusion of ER membranes in yeast [67] and is localized at the cell-plate in dividing cells [68]. In contrast to NSF-dependent homotypic and heterotypic membrane fusion, however, which operate through the pairing of v- and t-SNAREs, Cdc48p-dependent homotypic fusion is mediated by direct t/t-SNARE interaction.
suggested that this compartment serves to recycle plant vacuolar cargo receptors back to the Golgi apparatus. Similarly, BP-80 resides both in the Golgi apparatus and PVCs in pea root tips [40•].

**Exocytosis and cell-plate formation**

Plant cell growth and expansion is accomplished by the delivery and fusion of Golgi-derived exocytotic vesicles carrying membranes and cell wall components with the pre-existing plasma membrane. Similarly, the vesicles that fuse to form the cell-plate in dividing plant cells are thought to bud from the Golgi [54]. Very little is however known about the formation, trafficking and fusion of these vesicles. For example, it remains to be determined whether exocytosis and cell-plate formation are mediated by a single homogeneous vesicle population or whether multiple Golgi-derived vesicle populations exist, carrying distinct sets of cargo, that in the case of cell-plate formation would converge and fuse to form a new plasma membrane and cell wall **de novo**. Recent studies in plants, yeast and mammalian cells have suggested the existence of multiple parallel vesicular routes that transport distinct sets of cargo from the Golgi to the plasma membrane [55–57]. In expanding cells these vesicles are likely to be targeted to the growing regions of the cell cortex. During cell-plate formation, one or more of these pathways may become polarized toward the plane of division, as they appear to do during cell division in yeast [58]. In this way, the time at which plasma membrane and secreted proteins are synthesized may dictate their deposition at the cell surface or the cell-plate. Consistent with this hypothesis is the observation that the putative t-SNARE, Knolle, which is expressed during mitosis, is localized specifically to the cell-plate of dividing *Arabidopsis* cells [59••].

To identify components involved in exocytosis from the Golgi apparatus, Nakano and coworkers have screened for *Arabidopsis* cDNAs that would complement the yeast late secretory pathway mutant, *sec15* [60]. Sec15p is a component of the exocyst complex required for the Golgi-to-plasma membrane transport [61]. Interestingly, one gene that was identified, **RMA1**, does not encode a Sec15p homolog, rather it belongs to a new class of genes containing the RING-finger motif (a protein motif that binds two Zn\(^{2+}\) ions in a unique ‘cross-brace’ structure) that is conserved in all multicellular organisms. Whether RMA1p is actually involved in secretion in plant cells requires further study.

**Conclusions**

A notable strength of the work highlighted above has been the integration of ideas and observations from a number of systems and different plant cell types over the last several years. Nevertheless caution needs to be exercised when it comes to deciding whether a particular secretory process is a general one or if it is restricted to only a limited set of cells (i.e. those from a specific tissue or developmental stage). For instance, is the direct ER-to-vacuole transport pathway observed in developing wheat and pumpkin seeds utilized in other cell types? We would like to encourage frequent discussions of such ideas through formal and informal venues such as the recently formed Secretory Pathway Group listserver (SECPATWY@LIST.MSU.EDU). Morphological, biochemical and genetic studies of the plant secretory pathway are beginning to provide a detailed molecular description of how the elaborate endomembrane network of organelles in plant cells is established and how it functions in the growth and development of the whole organism.

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**References and recommended reading**

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- outstanding interest


Large 200–400 nm diameter vesicles that accumulate storage protein precursors were purified from pumpkin seeds. These vesicles contain an electron-dense storage proteins surrounded by an electron-translucent layer. Numerous storage protein aggregates were also found to be present in the ER suggesting that these vesicles are ER-derived and that they mediate the transport of the insoluble storage protein aggregates to vacuole.


In the ER nascent secretory proteins containing N-glycans are modified by the action of an GlcNAcβ1,4Glcnac β1,6N-acetylglucosaminyld transferase. Subsequently, the three terminal glucose residues are removed by ER-resident glucosidases. In this paper, the role of glucose trimming on the folding and assembly of bean phaseolin was analyzed using an in vitro system. In the presence of specific inhibitors of glucose trimming, the assembly of phaseolin was found to be accelerated. In contrast, polypeptides bearing partially trimmed glycans were unable to properly trimerize. Glycan chains and their accessibility to glucosidases are, therefore, likely to modulate the assembly of phaseolin.


In this paper, the rate of an assembly-defective form of the trimERIC storage protein, phaseolin, was analyzed in the leaves of transgenic tobacco. Assembly defective phaseolin was bound to BIP in the ER and slowly degraded by a Brefeldin-A insensitive process, suggesting that its turnover does not require Golgi-mediated secretory protein transport. These results provide strong evidence for the presence of a 'quality control' mechanism in the ER of plant cells that eliminates malformed proteins.


Seed legumin contains two conserved disulfide bonds that are important for the initial formation of 9S trimers in the ER and their assembly into 11S hexamers in the PSV. In this paper mutant subunits were constructed in which the critical cysteine residues for the interchain bond (IE) connecting the acidic and basic chains and the intrachain bond (IA) were disrupted. Whereas oxidized glutathione stimulated the trimerization of the wild-type protein no stimulation was observed for the assembly of IE mutant subunits and it was diminished for the IA mutant. IE mutant trimers were not capable of assembly into hexamers unless they were in the presence of wild-type subunits.


In this paper a large fraction of BIP was found to be in a stable complex with another soluble ER-resident molecular chaperone, calreticulin. Formation of this complex was not affected by either the presence or absence of stress conditions that lead in an increase in the number of unfolded proteins in the ER. On the basis of antibody accessibility studies the binding of BIP to calreticulin and to unfolded proteins appears to be different. The BIP-calreticulin complex can be disrupted by low pH but not by divalent cation chelators and complex formation is independent of the ER retention signal on BIP.


The V-ATPase complex consists of a peripheral sector (V1) and a membrane integral sector (V0). A 64 kDa polypeptide that copurifies with oat V-ATPase subunits was positively identified as the ER-membrane chaperone, calnexin, and shown to interact directly with the V-ATPase complex in purified ER membrane fractions by coimmunoprecipitation. Monoclonal antibodies against the catalytic subunit of the V1 complex precipitated the entire V-ATPase complex as well as calnexin and BIP.


Light microscopy was used to study the structure and function of vacuoles in living protoplasts of barley (Hordeum vulgare cv Himalaya) aleurone. Aleurone protoplasts contain two distinct types of vacuole: the protein storage vacuole and a lysosome-like organelle. In contrast to the two vacuole compartments in barley root tip cells, both of the vacuole types of aleurone cells contain the tonoplast marker protein αTIP. The effects of the phytotoxins, ABA and GA, on the formation and morphological change of these two vacuoles are reported.


Phaseolin is a trimeric glycoprotein that accumulates in the vacuoles of common bean seeds and in transgenic tobacco leaf cells. Golgi-mediated transport of wild-type phaseolin to the vacuole was found to be saturable and to lead to the secretion of the overexpressed protein. Deletion of the four carboxy-terminal residues of phaseolin did not inhibit the trimerization but
required for Golgi-to-vacuole transport. In addition, AtELP is also present in the undefined compartment was shown to correspond to a post-Golgi pre-terminal targeting determinant. Plant Physiol 1996, 111:469-474.

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