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Review

Regulation of protein trafficking: Posttranslational mechanisms and the unexplored transcriptional control

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Endomembrane protein trafficking assures protein location through the endocytic and secretory routes. Trafficking pathways are diverse, depending on the proteins being trafficked, the final destination as well as their itinerary. Trafficking pathways are operated by machineries composed of a set of coordinately acting factors that transport proteins between compartments. Different machineries participate in each protein trafficking pathway, providing specificity and accuracy. Changes in the activity and abundance of trafficking proteins regulate protein flux. The preponderance of one pathway over another regulates protein location and relocation. Cellular requirements change during different processes and in response to stimuli; modulation of trafficking mechanisms must relocate proteins or alternatively increase/decrease the targeting rate of certain proteins. Conventionally, protein trafficking modulation has been explained as posttranslational modification of components of the relevant trafficking machinery. However, trafficking components are also transcriptionally regulated and several reports support that this regulation can modulate protein trafficking as well. This transcriptional modulation has an impact on plant physiology, and is a critical and fundamental mechanism. This scenario suggests a determinant mechanism that must be considered in the endomembrane protein trafficking research field.

Contents

Abbreviations: TGN/EE, trans-Golgi network/early endosomes; MVB/PVC, multi-vesicular body/prevacuolar compartment; SNARE, soluble N-ethylmaleimide-sensitive factor adaptor protein receptor proteins; PR, pathogen-related.

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1. Introduction

The physiology of a plant and its ability to respond to environment conditions depend on cellular functioning of the tissues. Since cellular processes occur in compartments within the cell, protein function depends on its suitable cell location. Once proteins are synthesized the proper destination has to be assured in order to maintain cell functioning and fulfill cell requirements. In some cases, proteins are relocated from the resident compartment to another as a constitutive behavior or as part of signaling pathways and regulation mechanisms.

The plant endomembrane system is composed of several membranous compartments that are physically and functionally interconnected through diverse and specific protein trafficking pathways [1,2]. These compartments are the plasma membrane, trans-Golgi network/early endosome (TGN/EE), multivesicular body/prevacuolar compartment (MVB/PVC), vacuole, Golgi apparatus and endoplasmic reticulum (Fig. 1A).

Protein trafficking among endomembrane compartments is diverse, depending on the type of protein being trafficked as well as the machinery involved in its journey. The trafficking pathways within the endomembrane system are broadly classified into secretory and endocytic routes according to the original location of the trafficked proteins (Fig. 1A). *De novo* synthesized proteins traffic to their resident compartment through the secretory route. Proteins previously located in their resident compartment traffic through the endocytic route to a different intracellular compartment. In the latter case the protein may recycle back to the original compartment or else to the vacuole for degradation through the endocytic pathway. The existence of endocytosis in plant was doubted for long time, however it is already probed that clathrin-mediated endocytosis is functional in Arabidopsis [3].

Within the endomembrane system, proteins traffic from a donor compartment to a target/acceptor compartment by means of vesicle/membrane flux as well as compartment maturation, which is driven by vesicle and tubule fusion, across specific and highly regulated pathways [1–5]. Endomembrane protein trafficking are driven by molecular machineries composed of proteins involved in packing the cargo protein into the vesicles, as well as the formation, recognition, tethering, and reception of the vesicle [5]. Active trafficking mechanisms are necessary to assure that newly synthesized proteins reach the resident compartment. Higher efficiency, likely more activity of the trafficking machinery, may be required if the level of synthesis of the delivered protein increases. Therefore the targeting pathways and thus trafficking proteins have to be flexible and efficient. Conversely, if the targeted protein level decreases, trafficking activity may decrease to levels sufficient to sustain cellular requirements.

It is important to consider that in many cases some trafficking proteins participate only in one particular trafficking pathway, giving specificity to the trafficking route. A typical plant cell has the trafficking machinery for the interconnected endomembrane system, allowing protein trafficking from the endoplasmic reticulum to the resident compartment and its relocation to a different compartment according to cell and plant physiological requirements. It is thus pertinent to understand protein trafficking as a dynamic process in which the machineries for a variety of trafficking pathways coexist. The direction of the cargo protein trafficking and location depend on the balance of all the different pathways affecting their movement. The equilibrium of different trafficking pathways will determine the amount of protein in each compartment. The capacity of changing the equilibrium may be useful when the presence or enrichment of certain protein changes in a particular compartment in response to a stimulus or perturbation. The protein level of trafficking machineries has been shown to be regulated at transcriptional under biotic and abiotic challenges. The equilibrium has to be reestablished to normality after plant recovery. Therefore transcriptional modulation of protein trafficking should be transitory and highly regulated.

Protein trafficking should be a highly regulated process allowing fine-tuned modulation according to plant cellular and physiological requirements. Trafficking coordination is more noticeable in the cases of a plasma membrane resident proteins that are internalized by endocytosis. The plasma membrane proteins are synthesized in the endoplasmic reticulum and then are trafficked to their resident compartment, the plasma membrane. These proteins are internalized to TGN/EE by endocytosis upon a particular stimulus. From the TGN/EE the proteins can either recycle back to plasma membrane

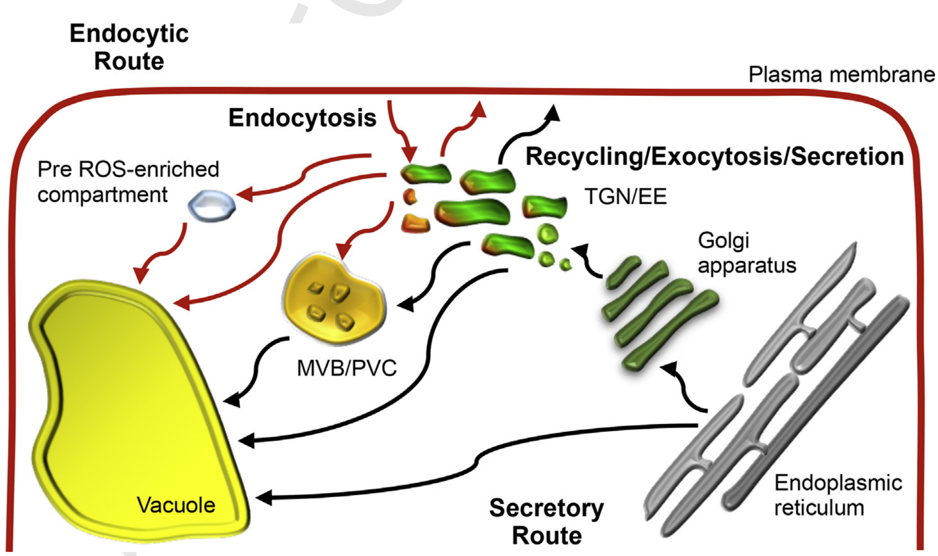

Fig. 1. Plant endomembrane protein trafficking pathways. Endomembrane system trafficking pathways transport proteins along its compartments; the plasma membrane, the Trans-Golgi/Early Endosome (TGN/EE), the Multivesicular Body/PreVacuolar Compartment (MVB/PVC), the vacuole, Golgi apparatus, endoplasmic reticulum and the putative Pre-ROS-enriched compartment. Endocytic and secretory trafficking pathways are represented by red and black lines, respectively. The endocytic route includes all protein trafficking pathways involved in protein relocation from the plasma membrane to intracellular compartments including TGN/EE, MVB/PVC and vacuole, which is defined as endocytosis, as well as, from those compartments back to the plasma membrane by recycling pathways. The secretory route includes the pathways involved in targeting *de novo* synthesized proteins from the endoplasmic reticulum to their resident compartments (black lines).