Journal of Plant Biochemistry & Physiology
ISSN: 2329-9029

Sansebastiano and Piro, J Plant Biochem Physiol 2014, 2:2
DOI: 10.4172/2329-9029.1000e122

Editorial Open Access

The SNARE Proteins (In Plants) Beyond the Nobel Prize

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SNAREs (N-ethylmaleimide-sensitive factor adaptor protein receptors) are small polypeptides characterized by a specific domain called SNARE motif. This can form a coiled-coil structure and interacts with other SNARE motifs via hetero-oligomeric interactions to form highly stable protein-protein interactions. The derived complex is called SNARE-complex and allows membrane fusion. SNAREs also interact with several proteins acting as regulators of this complex formation. Their indubitable importance was certified by the Nobel Prize 2013 for Medicine, awarded to the scientist who clarified the way they interact, James E. Rothman. Nobel Prize was shared with the other two scientists contributing to the description of vesicle traffic, Randy W. Schekman, and Thomas C. Südhof, but SNAREs certainly have central role in the determination of traffic specificity. Recently the model that won the Nobel was enormously enriched by further discoveries, about SNAREs in particular. In fact SNAREs stoichiometry reveals that they are more abundant than required for membrane traffic.

The regulation of vesicle traffic certainly remains the most important role of these proteins but in doing so, SNAREs have a clear influence on several signalling pathways. SNAREs take part to receptors turnover through endocytosis and exocytosis but they can also directly gate channels and interact with membrane proteins potentially involved in signalling processes. Phosphorylation of SNAREs upon elicitation and hormonal control are known. I will try here to briefly review these diversified functions to have a complete overview of SNAREs importance.

Certainly membrane fusion is mediated by interactions between complementary SNAREs distributed on the vesicles and the target membrane. This complex is formed by three or four types of distinctive SNAREs contributing to the formation of a four-helix bundle [1]. On the base of their localization (Functional classification) SNAREs have been classified into vesicle-associated (v-SNAREs) and target membrane–associated SNAREs (t-SNAREs) [2]. This classification does not take into account the role of SNAREs in the context of homotypic fusion events or progressive anterograde traffic.

A different classification based on the presence of specific amino acids in the center of the SNARE motif (Structural classification) was developed to resist the pressure of new puzzling discoveries. So SNAREs have been indicated as Q-SNARE with a conserved glutamine residue in the middle of the SNARE domain and R-SNAREs with a conserved arginine instead [3]. Functionally classified t-SNAREs generally are Q-SNAREs, and v-SNAREs generally are R-SNAREs. Q-SNAREs are of three types: Qa-, Qb-, and Qc-SNAREs. The SNAP-25-like proteins of Q-SNAREs constitute a special class with both Qb- and Qc-SNARE motif. The R-SNAREs can either have a short or a long N-terminal regulatory region, gaining the designation of brevins (lat. *brevis*, short) and longins (lat. *longus*, long). Plants only have longins [4].

The SNARE proteins are able to drive, alone, vesicle fusions *in vitro;* however, *in vivo,* these SNAREs interact with many proteins, which act as regulators [5,6]. Regulation of SNAREs action is probably at the base of some of their interesting roles in signalling processes.

Gravitropism is controlled by complex molecular mechanisms that involve signalling and growth adjustments. Many gravitropic responsive genes have been isolated in *Arabidopsis thaliana* and the Qa-SNARE AtVAM3/SYP22 (*SGR3)* and the Qb-SNARE AtVTI11 (*ZIG*/*SGR4*) have been found to play an important role in shoot gravitropism [7].

Tip growth in pollen tubes can be taken as an example of growth processes. It was recently shown that the localization of pollen specific syntaxin SYP125 was asymmetrically localized behind the apex at the plasma membrane, while another pollen-specific syntaxin, SYP124, was differently distributed [8,9] suggesting for these SNAREs a role in the definition of exocytic sub-domains.

Also the transport capacity of selected ion and solute transporters is regulated by SNAREs. Well known is the trafficking of GLUT4 (Na^+-coupled Glc transporter). The SNARE complexes involved in fusion of GLUT4 vesicles include mammalian Syntaxin 4, SNAP-23 and VAMP2 within the lipid rafts of plasma membrane. GLUT4 transporters from the apical plasma membrane are recycled by endocytosis and the sequestering in specialized GLUT4 vesicles [10]. Another interesting example is the traffic of the KAT1 (Kv-like K^+ channel) of epidermal cells whose turnover at the plasma membrane is tightly controlled through a mechanism evoked by ABA [11].

In particular Grefen and co-workers [12,13] provided direct evidence that SYP121 is part of a scaffold of proteins associated, by direct interaction, with channel KAT1 for the transport of K^+. In fact, few SNARE proteins are known to interact with ion channels, notably mammalian Syntaxin 1A, which binds several different Ca^{2+} and K^+ channels in nerves.

In addition to these diversified roles that may, anyhow, be reconducted to the functioning of fusogenic SNARE complexes, some SNAREs have been found to interfere with membrane fusion. If a specific SNARE concentration become inversely proportional to the expected fusogenic activity, such SNARE can be defined as interfering (i-SNARE; 13). Probably i-SNAREs inhibit fusion by substituting for or binding to a subunit of a fusogenic SNARE pin to form a nonfusogenic complex, as it was observed for Golgi-localized SNAREs [14].

Mammalian and yeast i-SNAREs (syntaxin 6/Tlg1, GS15/Sft1, and rBet1/Bet1) were found functionally conserved but i-SNARE characterization in plants is still poor. The recent investigation of SYP5s i-SNARE effect gave just a little contribution to this topic [15]. An alternative mechanism for the i-SNARE effect can be found in yeast where the endosomal (Tlg1 and Syn8) and vacuolar form (Vam7) of the Qc-SNAREs, interact with V-ATPase subunits influencing membrane potential and, consequently, fusion [16]. More proteins potentially able to interact with SNAREs can have a direct influence on membrane

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Received June 06, 2014; **Accepted** June 07, 2014; **Published** June 09, 2014

Citation: Sansebastiano GD, Piro G (2014) The SNARE Proteins (In Plants) Beyond the Nobel Prize. J Plant Biochem Physiol 2: e122. doi:10.4172/2329-9029.1000e122

potential such as ion channels, as shown in the case of SYP121, able to interact and control the K(+) channel KC1 [12].

There is a higher number of SNAREs in plants as compared to fungi and animals [17]. This is due to the expansion of number of members in conserved SNARE subfamilies and not due to the evolution of new isoforms. There are 60 SNAREs in dicotyledonous *Arabidopsis thaliana* (The Arabidopsis Genome Initiative 2000), 57 SNAREs in monocotyledonous *Oryza sativa* (International Rice Genome Sequencing Project 2005), and 69 SNAREs in the *Populus trichocarpa* (Tree black cottonwood [18]. In contrast the yeast *Saccharomyces cerevisiae* encode for 21-25 SNAREs and *Homo sapiens* encodes 35-36 SNAREs [1,19]. This variety certainly contributes to define many compositionally distinct compartments. These can be sorted into subsets of different size and shape. The distribution of the mass of an organelle among different compartments depends on the relationship between the budding and fusion exponents. It is possible to switch between multiple small compartments and a single large compartment as it was seen in organelles such as the Golgi or late endosomes under a variety of perturbations [20]. SNARE genes duplication could be the driving force for the emergence of new organelles.

In conclusion SNAREs and the other components of membrane traffic machinery have just started to show their real importance for eukaryote cell life and evolution.

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