

GROWTH AND DEVELOPMENT

Close relations of secretion and K⁺

Interaction of key regulators of exocytosis with potassium channels enhances both secretion and K⁺ uptake, making these processes intertwined and jointly coordinated.

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Cell growth implies an increase in both volume and surface area. Plant cells require vesicle traffic to deliver membrane and cell wall components to the plasma membrane to increase the cell surface. The cell volume expands by uptake of water through osmosis. To maintain turgor pressure, the increase in volume is compensated by uptake of solutes. Previous publications from the laboratory of Michael Blatt at the University of Glasgow, UK, showed¹ that the uptake of K⁺ — the most prominent osmotic agent in plant cells — is somehow linked to secretion by direct interaction of a plasma membrane SNARE protein, SYP121, with K⁺ channels KAT1 and KC1. Writing in *Nature Plants*, Grefen *et al.* demonstrate that the level of secretion controlled by SYP121 is enhanced by the interaction with active K⁺ channels². This, together with previous complementary studies, shows that the interaction of key regulators of secretion with K⁺ channels enhances both secretion and K⁺ uptake, by which

these processes become intertwined and jointly coordinated.

The fusion of vesicles with their target membrane is driven by complex formation of the SNARE proteins. A v-SNARE component present on vesicles forms a complex with two or three t-SNAREs on the appropriate target membrane, which provides the energy to fuse the membranes. To control vesicle fusion, t-SNAREs cycle between open and closed conformations. In the open conformation, the protein can form complexes with other SNAREs. In the closed conformation this is prevented by their N-terminal tail that folds back on the SNARE domain. Besides SNAREs, additional proteins are involved in regulating the timing, location, rate and specificity of vesicle fusion. One of these regulators, SEC11, binds and stabilizes t-SNAREs in the closed conformation³.

K⁺ transport into the cell by KAT1 and heterotetramers of KC1 and AKT1 ion channels depends on the membrane potential, as both are voltage-gated

channels. Inside-negative membrane potentials change the orientation of the voltage-sensing domains (VSDs) of KAT1 and KC1 from up to down, resulting in opening of the channel (Fig. 1). The mid-point voltage of KC1/AKT1 and KAT1 is around -210 mV, which means at that membrane potential half of the channels are open. Previously, it was shown that t-SNARE SYP121 binding shifts the mid-point voltage to -150 mV. Thus, SYP121 binding increases the channel sensitivity to voltage and facilitates K⁺ uptake. Grefen *et al.* show that SYP121 binds to the VSD of KC1 when it is in the down orientation. This provides an explanation for the shift in voltage sensitivity, as this binding likely stabilizes the open channel configuration. A surprising discovery made by Grefen *et al.* is that binding of SYP121 to the channel also enhances secretion². Previous studies have hinted at the underlying mechanisms, as KAT1/KC1 and SEC11 bind overlapping sites on SYP121. Thus, the activated VSD competes with SEC11

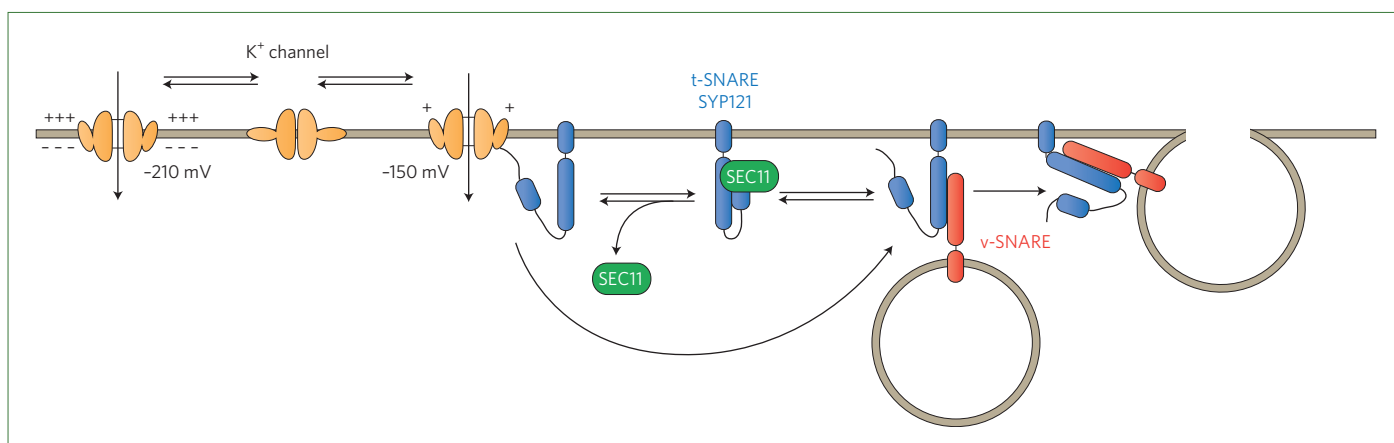


Figure 1 | Interaction between the voltage-sensing domains of K⁺ channels and t-SNARE SYP121 couples membrane potential and exocytosis. K⁺ uptake by inward rectifying potassium channels is dependent on hyperpolarization of the plasma membrane. An inward negative charge changes the voltage-sensing domain (VSD) orientation from up to down, resulting in opening of the channel. In the absence of SYP121, the mid-point voltage of the K⁺ channel KC1 is approximately -210 mV. Interaction of t-SNARE SYP121 with the down orientation of the VSD of KC1 shifts the mid-point voltage to approximately -150 mV, effectively enhancing the K⁺ uptake. SYP121 cycles between open and closed conformations. The SNARE in the open conformation allows complex formation with complementary v-SNAREs on vesicles, leading to vesicle fusion. The fusion-incompetent closed conformation is stabilized by binding of SEC11. Grefen and colleagues² demonstrate that the interaction between KC1 and SYP121 also enhances exocytosis. This is likely the result of competition of KC1 with SEC11, since both proteins interact with overlapping sites of SYP121.

and increases the pool of SYP121 in the open conformation. Consequently, binding of SYP121 to active VSDs makes secretion voltage dependent in addition to facilitating K⁺ uptake at a physiologically relevant membrane potential.

The coupling of K⁺ uptake to exocytosis may have an important role in maintaining turgor pressure in rapidly growing plant cells. However, some questions remain to be elucidated. For example, is this coupling restricted to SYP121-dependent exocytosis? Two extreme examples of rapidly expanding plant cells are root hairs and pollen tubes. The growth of these cells is indeed dependent on inward currents of K⁺ at the growing tip^{4,5}. However, the most prominent t-SNAREs involved in growth of root hairs and pollen tubes are likely SYP123 and SYP124/125, respectively^{6,7}. These SNAREs do not contain the SYP121 FxRF motif that binds KAT1 and KC1. This might imply that additional mechanisms control the coupling

of cell growth and K⁺ uptake. On the other hand, they do contain a similar FxKY motif at the same position, which is conserved in a wide range of plants. It would therefore be interesting to know whether these other members of the SYP12 family interact with the VSDs of KAT1 and KC1 or other K⁺ channels, as this could reveal whether this interaction is a generic mechanism by which secretion and potassium uptake are intertwined.

What is the biological significance of coupling secretion to membrane potential? This coupling increases secretion at a membrane potential at which SYP121 can also trigger K⁺ influx, which may be important for increasing the efficacy of coupling these two processes. Furthermore, the secretion-induced K⁺ influx results in membrane depolarization, which creates a shared negative feedback for membrane potential, K⁺ influx and secretion. Finally, the biological significance of linking

secretion and membrane potential may stretch beyond the coupling of cell growth and solute content. A wide range of cellular signalling processes, such as plant immune responses, are affected by membrane potential or local exocytosis^{8,9}. Therefore, coupling these processes could have implications that affect numerous fields of plant biology. □

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