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Mini-Review

Heteromerization of Arabidopsis Kv channel α-subunits

Data and prospects

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Potassium translocation in plants is accomplished by a large variety of transport systems. Most of the available molecular information on these proteins concerns voltage-gated potassium channels (Kv channels). The Arabidopsis genome comprises nine genes encoding α-subunits of Kv channels. Based on knowledge of their animal homologues, and on biochemical investigations, it is broadly admitted that four such polypeptides must assemble to yield a functional Kv channel. The intrinsic functional properties of Kv channel α-subunits have been described by expressing them in suitable heterologous contexts where homo-tetrameric channels could be characterized. However, due to the high similarity of both the polypeptidic sequence and the structural scheme of Kv channel α-subunits, formation of heteromeric Kv channels by at least two types of α-subunits is conceivable. Several examples of such heteromeric plant Kv channels have been studied in heterologous expression systems and evidence that heteromerization actually occurs *in planta* has now been published. It is therefore challenging to uncover the physiological role of this heteromerization. Fine tuning of Kv channels by heteromerisation could be relevant not only to potassium transport but also to electrical signaling within the plant.

Arabidopsis Kv Channel α-Subunits Sorted into Four Functional Groups

A variety of transport systems are used by plants to translocate potassium: the model plant *Arabidopsis thaliana* has more than 30 different genes encoding K^+ transporter proteins.[1-5] Most of the molecular information on these proteins is available for the family of voltage-gated potassium channels (Kv channels). The Arabidopsis genome contains a total of nine genes that encode α-subunits of Kv channels:[6] *GORK*, *SKOR*, *KAT1*, *KAT2*, *AKT1*, *SPIK*, *AKT5*, *AKT2* and *AtKC1*. Based on knowledge of their animal homologues, and on biochemical investigations,[7,8] it is broadly admitted that four such polypeptides must assemble to yield a functional Kv channel. From studies of the K^+ currents resulting from the expression of single genes from Arabidopsis and other plants in heterologous contexts (e.g., Xenopus oocytes, *Sf*9, yeast or COS cells, plant protoplasts), Kv channel α-subunits have been sorted into four functional groups.

GORK[9,10] and SKOR[11] form depolarization-activated channels. Such channels are generally referred to as outward-rectifying K^+ channels (K_{out} channels) because they are open only at voltage values where the driving force for K^+ is, in general, directed towards the extracellular medium. Noteworthy is the unique sensory mechanism of GORK and SKOR channels that adjusts their activity to the external K^+ concentration and guarantees that these channels mediate only potassium efflux.[12]

In contrast, the seven other Arabidopsis Kv channel α-subunits (KAT1,[13,14] KAT2,[15] AKT1,[16,17] SPIK,[18] AKT5 (Koziolek, unpublished data), AKT2[19,20] and AtKC1[21,22]) form hyperpolarization-activated Kv channels. Due to functional disparities they can be sorted into three groups. KAT1, KAT2, AKT1, SPIK and AKT5 are inward-rectifying Kv channel α-subunits (K_{in}) because the homomeric channels they form are active below a voltage threshold (E_{act}) that is, in general, negative to the K^+ equilibrium potential (E_K). As a consequence they open only at voltages values where, under standard physiological conditions, the driving force for K^+ diffusion is directed towards the cell interior. At very low extracellular K^+ concentrations, however, E_K would be negative relative to E_{act} and these channels would drive K^+ efflux in the E_K to E_{act} voltage range, as has been shown for KAT1 expressed in Xenopus oocytes.[23]

With respect to voltage-dependence of activity, AKT2 is remarkable because post-translational modifications (phosphorylation of serine residues at positions 210 and 329) induce a shift of the activation potential of the AKT2 channel to very positive values. As a

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consequence AKT2 channels behave as K^+ selective open-leaks, i.e., they are open at all physiological voltages.[24-29] Both phosphorylated open-leak and dephosphorylated inward-rectifying AKT2 channels contribute to the cellular K^+ current. Therefore the inward-rectification of the K^+ current is weak. Based on this criterion the AKT2 polypeptide, together with orthologs from other plant species, forms a third functional group of plant Kv channel α-subunits (K_{weak}).

Finally AtKC1 has been proposed to belong to a fourth group of "silent" Kv channel α-subunits (K_{silent})[22] because it is reported not to form functional channels when expressed alone in heterologous expression systems.[21] Actually, due to its participation to heteromeric Kv channels, AtKC1 is likely to contribute to the membrane K^+ conductance and should rather be regarded as a regulatory α-subunit,[30] as outlined below.

Heteromerization of Kv Channel α-Subunits does Occur in Arabidopsis

Data published in the last eleven years, obtained after co-expression experiments in heterologous expression systems, such as Xenopus oocytes, yeast cells or in plant expression systems,[15,21,30-39] have provided evidence that plant Kv channel α-subunits are in principle endowed with the potential to form not only homomeric but also heteromeric channels. It has been shown, for instance, that heteromerization is possible among different K_{in} channel α-subunits (e.g., KAT1 and KAT2)[15,21,34] and between different K_{out} channel α-subunits (e.g., GORK and SKOR), but not between K_{out} and K_{in} channel α-subunits (e.g., SKOR and KAT1).[32] The molecular basis for this discrimination was shown to be located within the cytoplasmic C-terminal regions of the α-subunits.[32] In contrast, functional heteromeric channels were reported for combinations of different hyperpolarization activated Kv α-subunits (between K_{in} and K_{weak} α-subunits[31,33,38] and between K_{in} and K_{silent} α-subunits[21,30,35-37,39]). The potential of heteromeric assembly was not limited to subunits originating from the same species. Also subunits from different species were shown to form functional heteromeric channels[21,31,36,37,39] although this is merely a biophysical tool devoid of physiological meaning. For the aggregation process it was proposed that compatible plant Kv α-subunits assemble—similar to their animal counterparts[40]—first into dimers; and then, two dimers form a functional tetrameric Kv channel.[30,32]

Interestingly, it has been shown in some cases that heteromerization is *preferred* to homomerization (KAT2/AKT2[38] and AtKC1/AKT1[30]), emphasizing the potential role of heteromerization in plant cell physiology. Obviously, some overlap of both time and spatial expression patterns is a prerequisite for subunits to assemble into heteromeric channels *in planta*. Regarding the K_{out} α-subunits SKOR and GORK, for instance, this condition appears not to be fulfilled. To our knowledge, no example of a native co-expression of both has been reported. By contrast, many cell types have been shown to express different hyperpolarization-activated Kv channel α-subunits. For example root epidermal/cortical cells express both AKT1 and AtKC1.[22] That both these subunits do contribute to heteromeric channels responsible for K^+ influx in roots was inferred by Reintanz et al.,[22] in their comparative study of wild-type versus *akt1-* and *atkc1-* knock-out plants. Likewise, guard cells are widely believed to express both KAT1 and KAT2, and it has been reported that they also express AKT2, AtKC1 and AKT1.[41] Until recently, only indirect indications had been provided of actual occurrence of in situ heteromerization of guard cell Kv channels.[42]

The ultimate proof that heteromeric channels exist in plants has recently been provided by Lebaudy et al.,[43] Using a set of specially designed transgenic plants, the assumption that plant K^+ channels would only be homomers could be confuted. Interestingly, an issue relative to the molecular scale ("do heteromeric K^+ channels exist *in planta*?") was solved after carrying out simple analyses of a macroscopic phenotype (plant transpiration rate).

Heteromerization Increases Functional Diversity

A priori, heteromeric channels are believed to display functional features inherited from their constitutive α-subunits. Hyperpolarization-activated Kv channel α-subunits characterized so far display fairly similar high selectivity for K^+, block by Cs^+ and activation by hyperpolarization. Regarding the latter property, however, they may significantly differ in their activation voltage-threshold and in their apparent gating charge. Besides, they also differ in other functional features such as their sensitivity to Ca^{2+} and pH[24,25,38,44] and susceptibility to post-translational modifications like (de-)phosphorylation.[5,45]

The recent characterization of AtKC1/AKT1 heteromeric channels by Duby et al.,[30] illustrates the impact of heteromerization. Being apparently unable to form functional homomeric channels, AtKC1 had often been called a non-functional or "silent" α-subunit. When expressed alone in tobacco[30] or Arabidopsis protoplasts (Alcon, unpublished), AtKC1 remains within the ER and apparently requires the co-expression of another α-subunit (AKT1 in Arabidopsis roots) in order to be targeted to the plasma membrane as part of heteromeric channels. Up to now, our efforts to uncover the molecular basis for this ER retention of AtKC1 have failed (Alcon and Jeanguenin, unpublished). With the current knowledge, the simplest hypothesis remains that AtKC1 is unable to assemble with itself, i.e., to form stable homo-dimers/tetramers, and that such multimeric assembly is a prerequisite for Kv α-subunits targeting to the membrane.[30] AtKC1 is thus functional as part of heteromeric channels only. Its obvious contribution to the channel features is a negative shift of the activation voltage threshold (E_{act}).[21,22,30] This appears to be physiologically significant, especially in conditions where the external K^+ concentration is very low (as is usually the case in the soil solution surrounding roots; i.e., plasma membrane E_K is very negative). By negatively shifting the activation threshold, the voltage gap from E_K to E_{act} can be closed and therefore shunt outward K^+ fluxes are minimized or even avoided. The counterpart of this fine-tuning is a reduction of the inward current at any given potential. In short, AtKC1 can be considered on the one hand as a modulator of the *AKT1* gene product that allows the adjustment of inward rectification to extreme conditions and on the other hand as its downregulator. More generally, AtKC1 will downregulate the activity of all heteromeric channels it participates in (with KAT1[21,30] and even with other Kv α-subunits, Jeanguenin unpublished).

Conclusion

Recent data has provided evidence that heteromeric channels exist in plants and that α-subunits show some kind of preference in choosing their assembly partner(s). Together with post-translational modifications, plant cells therefore possess additional degrees of

freedom to fine-tune the different functional features of their Kv channels according to their needs.

There is by now a large set of literature describing the role of plant Kv channels in the control of K^+ fluxes in relation with plant nutrition in a broad meaning of this term. This encompasses, e.g., roles in K^+ acquisition in roots (AKT1, AtKC1), translocation from roots to shoots (SKOR), circulation of K^+ from sources to sinks and back (AKT2, KAT2), and uptake/release from cells undergoing "rapid" volume changes like guard cells and other motor cells such as those found in *Samanea* pulvini.[46]

Less has been reported or discussed, on the other hand, regarding another likely function of Kv channels in plants: the control of cell membrane polarization at its steady-state as well as during fluctuations and thereby in the control of cell signaling (via voltage-gated calcium-permeable channels for instance). It can be expected that, like their animal cell homologues, plant Kv channels will participate in electrical signaling in the plant owing to their voltage dependence. Plants do show electrical signaling: electrical signals occur either locally, within a given cell (e.g., guard cells[47]), or propagate through symplasms at the organ or whole plant scale.[48] Considering that heteromerization will yield finely-tuned K^+ channels in terms of their voltage dependence, it will be worth further investigating the role of these channels in plant cell "excitability".

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