



## Potassium in plants – Still a hot topic

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In 2014 the Journal of Plant Physiology published the special issue “Potassium Effect in Plants” (Dreyer, 2014). Ten articles, meanwhile cited more than 1300 times (source Scopus, April 2021), provided contemporary views on the role of  $K^+$  in plants from different perspectives (Ahmad and Maathuis, 2014; Anschutz et al., 2014; Benito et al., 2014; Demidchik, 2014; Hamamoto and Uozumi, 2014; Nieves-Cordones et al., 2014; Pottosin and Dobrovinskaya, 2014; Véry et al., 2014; Zörb et al., 2014). Now, about seven and a half years later, Dev T. Britto, Devrim Coskun, and Herbert J. Kronzucker revisited this theme and provide in their Humboldt review “Potassium physiology from Archean to Holocene: A higher-plant perspective” an unprecedentedly wholistic view on potassium in the biosphere (Britto et al., 2021). Even if the title suggests otherwise, the authors do not limit themselves to plants, but very clearly and memorably compare the role of potassium in plants with that in animal organisms. Of course, as the authors note, full coverage of this topic would require many volumes forcing them to make a selection. The result is a well-done up-to-date outline of the fascinating and utilitarian subject of  $K^+$  transport physiology in plants, showing that  $K^+$  in plants is not old hat but still a hot topic.

Britto et al. (2021) pick up on new developments in the field and thus provide important stimuli for new thinking. For example, they devote an entire subchapter to the affinity concept, which has been the fixed point for  $K^+$  research in plants for more than 50 years and has become generally established in the studies of nutrient transport. However, recent approaches point to inconsistencies in this concept and question its validity (Dreyer and Michard, 2020). The affinity concept dates back to the ground-breaking studies of Emanuel Epstein and co-workers (Epstein et al., 1963; Epstein and Hagen, 1952) who could distinguish between two different types of  $K^+$  transport systems in plants using an empiric data analysis approach. The measured transport rates could be described mathematically very well by a special type of hyperbolic functions, also called Michaelis-Menten functions that have their theoretical basis in enzyme kinetics. Such a mathematical description is not yet to be criticized. It was quite suitable, in times without molecular knowledge, to pinpoint mechanistic differences between one transporter type that apparently saturated at low concentrations (= “high affinity”) and another that did so only at higher concentrations (= “low affinity”).

Only more than 30 years later at the dawn of the genomic era it could be clarified that  $K^+$  channels contribute predominantly to the originally described “low affinity” component while proton-coupled  $K^+$  transporters could be assigned to the “high affinity” component. Therefore, Britto et al. (2021) are correct that it would be premature to throw out, with the proverbial bathwater, the entire legacy of Michaelis-Menten modeling. However, latest theoretical insight into membrane transport in plants clearly demonstrate that the interpretation from these models that “high affinity” transporters are active at low concentrations, while “low affinity” transporters take over at higher concentrations, has largely misled our thinking in the last decades. The core of truth of Epstein’s concept got buried in unjustified misinterpretations.

To better explain this heretical statement, it may be useful to think outside the box. Besides membrane transport, many processes in nature can be described by hyperbolic functions. One of the most prominent might be the dependence of the growth rate of bacterial cultures on the nutrient concentration in the medium (Monod, 1949). Although the same mathematics as that of Michaelis-Menten modeling serves very well to describe the experimental data, bacterial growth has nothing to do with this type of kinetics, but can be derived from a different theoretical approach (Scott et al., 2010). Thus, the simple mathematical coincidence that transport data might apparently be described by hyperbolic functions is no proof of the correctness of the underlying theoretical concept of Michaelis-Menten kinetics. Britto et al. (2021) present the inconsistencies that may occur when taking the Michaelis-Menten approach for granted and conclude that new concepts need to emerge that help to quantify and to categorize the experimental data of nutrient transport in plants. This conclusion could be taken even further: There is an urgent need for a solid theoretical foundation that not only describes the observed phenomena, but can also clearly explain them based on first principles.

Actually, we are not too far away from this vision. The physico-chemical fundamentals of transport processes are well understood. One obstacle that remains to be overcome is the complexity of the biological systems under study. Britto et al. (2021) mention in their review “innovative computational cell biology” approaches that allow to

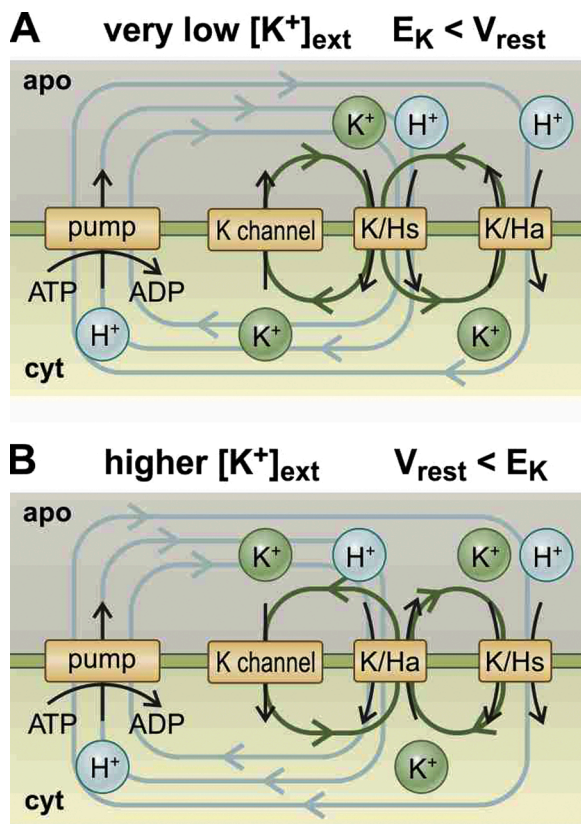
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**Fig. 1.** K<sup>+</sup> homeostasis at the plasma membrane. Due to thermodynamic constraints, homeostatic conditions at the plasma membrane are inextricably linked to K<sup>+</sup> and H<sup>+</sup> cycles. Only then can  $E_K$  be adjusted by regulating the various transporter activities (Dreyer, 2021). Control of K<sup>+</sup> homeostasis involves, besides the H<sup>+</sup>-ATPase, three K<sup>+</sup> transporter types (i) K<sup>+</sup> channels, (ii) H<sup>+</sup>-coupled K<sup>+</sup> symporters (K/Hs) and (iii) H<sup>+</sup>-coupled K<sup>+</sup> antiporters (K/Ha). (A) When  $[K^+]_{ext}$  is very low, the K/H-symporter takes up K<sup>+</sup> that is released either by K<sup>+</sup> channels, which are active at the resting membrane voltage  $V_{rest}$ , or by K/H-antiporters. (B) When  $[K^+]_{ext}$  is higher (i.e.,  $V_{rest} < E_K$ ), K<sup>+</sup> channels and K/H-symporters reabsorb K<sup>+</sup> that is released by K/H-antiporters. In both cases, the proton-fluxes via the K/H symporters and antiporters are compensated by protons pumped out of the cell with ATP consumption.

simulate idealized situations, which then can be compared with the complex real world. Such an approach is not uncommon and very successful in physics and chemistry and could also add important perspectives to our view in plant sciences. Just recently, the long-standing dogma of “low and high affinity” transporters was further challenged in another computational cell biology approach (Dreyer, 2021). Surprisingly, the computational simulations could provide mechanistic explanations for several enigmatic observations outlined by Britto et al. (2021). Most strikingly is the long-term-steady-state K<sup>+</sup> efflux from root cells to the external medium that was detected in compartmental analysis by tracer efflux (CATE) studies. Britto et al. state that “this baseline flux occurs simultaneously with the opposing [...] unidirectional influx of K<sup>+</sup>”. This efflux could be quite pronounced even when  $[K^+]_{ext}$  is very low, i.e., also at near-starvation conditions, raising the question why such a shunt pathway has not yet been evolutionarily eradicated. Computational cell biology experiments unmasked these apparently futile K<sup>+</sup> cycles (Britto and Kronzucker, 2006) as an essential mechanism to adjust cellular K<sup>+</sup> homeostasis (Dreyer, 2021). Universal thermodynamic laws require that a cell adapt  $E_K$  ( $=RT/F \cdot \ln\{[K^+]_{ext}/[K^+]_{cyt}\}$ ) flexibly to maintain a constant  $[K^+]_{cyt}$  under variable  $[K^+]_{ext}$ . This can only be achieved by an interplay of different transporters (Fig. 1). Thus, channels (= “low affinity”) and proton-coupled K<sup>+</sup> transporters (= “high affinity”) in the old dogma) operate always jointly in the same

concentration range. Together, they accomplish a task that they cannot do on their own. Important for this successful interaction is the different energization of the K<sup>+</sup> transporters. While at very low  $[K^+]_{ext}$  only the K/H symport has sufficient energy for K<sup>+</sup> uptake (Fig. 1A), at higher  $[K^+]_{ext}$  also channels can contribute (Fig. 1B). The new vision on K<sup>+</sup> homeostasis thus reconciles Epstein’s finding of at least two different K<sup>+</sup> transporter systems with the observation of significant K<sup>+</sup> efflux to the external medium even in steady state conditions. Remarkably, the “energetics concept” is properly based on accepted thermodynamic rules, while the “affinity” of a K<sup>+</sup> transporter towards the transported ion plays no role in this concept. Such new insights provoked Britto et al. (2021) to state that the term “affinity” well may fall into disuse when describing transporter systems.

The Humboldt review of Britto et al. (2021) impressively illustrates that research on K<sup>+</sup> transport in plants has been a steady driving force in the past, influencing research on nutrient transport in general. Recent new developments have also predominantly been established initially for K<sup>+</sup> transport processes, which shows that potassium in plants is not old hat but still a hot topic.

### Declaration of Competing Interest

The author reports no declaration of interest.

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