REVIEW

30-year progress of membrane transport in plants

Rainer Hedrich · Irene Marten

Abstract   In the past 30 years enormous progress was made in plant membrane biology and transport physiology, a fact reflected in the appearance of textbooks. The first book dedicated to 'Membrane Transport in Plants' was published on the occasion of the 'International Workshop on Membrane Transport in Plants' held at the Nuclear Research Center, Jülich, Germany [Zimmermann and Dainty (eds) 1974] and was followed in 1976 by a related volume 'Transport in plants II' in the 'Encyclopedia of plant physiology' [Lüttge and Pitman (eds) 1976]. A broad spectrum of topics including thermodynamics of transport processes, water relations, primary reactions of photosynthesis, as well as more conventional aspects of membrane transport was presented. The aim of the editors of the first book was to bring advanced thermodynamical concepts to the attention of biologists and to show physical chemists and biophysicist what the more complex biological systems were like. To bundle known data on membrane transport in plants and relevant fields for mutual understanding, interdisciplinary research and clarification of problems were considered highly important for further progress in this scientific area of plant physiology. The present review will critically evaluate the progress in research in membrane transport in plants that was achieved during the past. How did 'Membrane Transport in Plants' progress within the 30 years between the publication of the first book about this topic (Zimmermann and Dainty 1974), a recent one with the same title (Blatt 2004), and today?

Abbreviations

ABA	Abscisic acid
a_{K^+}	K^+ activity in the xylem sap
CCCP	Carbonyl cyanide m-chlorophenylhydrazone
D-arab	D-arabinose
E_m	Membrane potential
GFP	Green fluorescent protein
glc	Glucose
L-arab	L-arabinose
L-rham	L-rhamnose
$MgPP_i$	Inorganic pyrophosphate
P_i	Inorganic phosphate
P_x	Xylem pressure
QTL	Quantitative trait loci
TPP^+	Triphenylphosphate
TRP	Trans-root potential

Thermodynamics and electrochemistry of membrane transport

In 1974, the selective permeability of biological membranes was compared to synthetic ion-exchange resins which have been developed and studied because of their technological value in electrically driven membrane separation processes such as electro-dialysis. As a result theoretical flux equations have been formulated and used to describe the functioning of membranes in general. These equations describing the

R. Hedrich (✉) · I. Marten
Molecular Plant Physiology and Biophysics,
Julius-von-Sachs Institute for Bioscience,
University of Wuerzburg, Julius-von-Sachs-Platz 2,
97082 Wuerzburg, Germany
e-mail: hedrich@botanik.uni-wuerzburg.de

membrane potential, Donnan potential, ionic mobilities, transmembrane fluxes, flux coupling, active transport, osmotic effects, streaming potentials and unstirred layers can now be found in basic physical–chemical literature and some physiology textbooks.

Water transport and osmotic processes

The theory of water transport across plant membranes and coupling between solute and water flow based on non-equilibrium thermodynamics was applied to describe swelling and shrinking of *Chara* cells (Dainty et al. 1974). Osmoregulation-dependent carbohydrate metabolism or glycerol content at that time was studied with the flagellates *Ochromonas* and *Dunaliella* (Kauss 1974; Ben-Amotz 1974). A topic which is still hot, since tolerance to heat-, cold-, and salt stress of higher plants also depends on the ability to synthesize compatible solutes (Grallath et al. 2005). To directly measure the cell pressure (turgor) of giant algae and higher plant cells, the turgor pressure probe was developed (Zimmermann et al. 1969). Data recorded with the turgor pressure probe and its derivative, the xylem pressure probe (Balling et al. 1988), in relation to those obtained with the Schollander pressure bomb (Schollander et al. 1965) keep alive controversial discussions about the mechanism of water transport in trees already for decades (Wei et al. 2000; Zimmermann et al. 2000, 2004; Angeles et al. 2004; see http://www.biozentrum.uni-wuerzburg.de/physikomedica/aktuelles/streitgespraeche.html). Meanwhile, the nature of the water pores in biological membranes was demystified by the identification of water-conducting membrane proteins and encoding genes (see Nobel price 2003 to Peter Agre; Maurel et al. 1993; Kammerloher et al. 1994; Schäffner 1998; Maurel and Chrispeels 2001; King et al. 2004; Tornroth-Horsefield et al. 2006). Furthermore, new inventions were developed such as coupled pressure potential- and ion activity measurements that allows the continuous and simultaneous monitoring of changes in ion activity, pressure and potential in, e.g., individual xylem vessels (Fig. 1; Wegner and Zimmermann 2002, 2004).

Electrical properties of membranes

On the basis of their discovery of the reversible breakdown in 1973, Zimmermann et al. (1974) developed a method to inject foreign materials into living cells without deterioration of cellular functions and membrane. This patented method is nowadays well known as
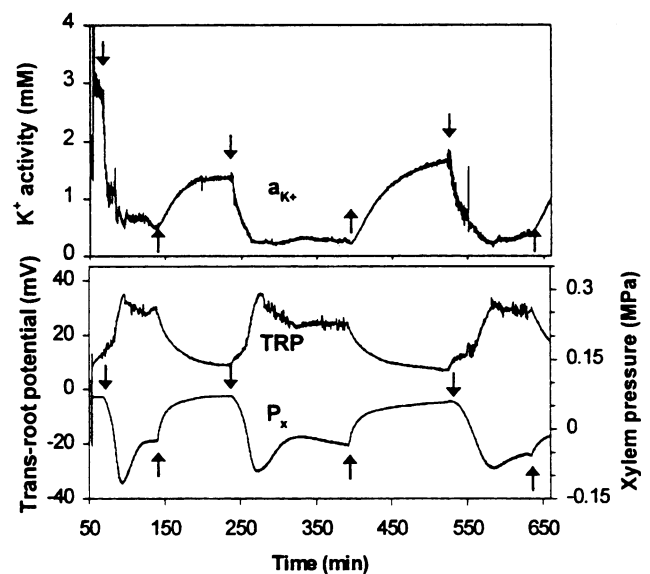

Fig. 1 Effect of light irradiation on the K^+ activity in the xylem sap (a_{K_+}), xylem pressure (P_x) and trans-root potential (TRP) recorded in a vessel of a 29.7-cm-long root of a 20-day-old intact maize plant. The root was impaled 28.6 cm above the root tip at laboratory light irradiation (about 10 μmol m^{-2} s^{-1}; relative humidity = 51%, $T = 22°C$). About 20 min after the impalement, the plant was subjected repeatedly to light irradiations of 300 μmol m^{-2} s^{-1} (*down arrow*) with intermittent periods of low light irradiations (*up arrow*). From Wegner and Zimmermann with copyright permission of Blackwell Publishing (2002)

"electroporation" and used for the transfer of solutes and DNA for transfection of cells.

In 1974, membrane transport was mainly studied with electrophysiological techniques and flux studies on the basis of radioisotopes on intact plants, tissues, plant cell or algae cultures and single giant algae. In addition, membrane vesicles isolated from plant organs served as a model to elucidate membrane ion and metabolite transport. The electrical properties of membranes such as of root membranes were determined by microelectrode impalement under current clamp conditions. The membrane potential, reflecting the assembled behaviour of all electrogenic transporters, was recorded in response to the environment. Upon changes in the ionic composition of the nutrient solution and addition of the inhibitors, the membrane potential altered in a characteristic manner. From these changes the contribution and properties of individual transporter classes were deduced. Thereby the presence of H^+ pumps, SO_4^{2-}, PO_4^{3-}, Cl^- transporters, etc., and in some cases even their stoichiometry was predicted. With giant algae like *Chara* and *Nitella*, the water net alga *Hydrodictyon*, filamentous fungi like *Neurospora crassa* or rhizoids of liverwort *Riccia fluitans* voltage-clamp was applied and the membrane

current studied directly. Thereby the charge carriers could be identified. Furthermore the kinetics of current activation, de-, and inactivation was determined and associated with distinct transporter types.

Jaffe et al. (1974) studied "Transcellular currents and ion fluxes through developing fucoid eggs" using the common seaweed *Pelvetia fastigiata* as a model. Membrane potential- and osmotic changes were recorded together with K^+ and Cl^- uptake and plasma membrane permeability changes. Later similar pioneering studies of Brownlee's lab (Brownlee et al. 1998) recorded fertilization currents and identified various ion channel types including membrane stretch-induced ones. Thereby a Ca^{2+} gradient was found in the tip of polarized growing *Fucus* eggs (Taylor et al. 1996; Brownlee et al. 1998). Similar relations and several molecular aspects have been identified in polar growing root hairs (for review see Bibikova et al. 2004). One should also mention the use of vibrating microelectrodes to monitor the extracellular current fields of polar growing cells (Kühtreiber and Jaffe 1990; Pierson et al. 1994; Tegg et al. 2005).

Coster and Smith (1974) performed high-resolution membrane capacitance measurements on *Chara corallina* with focus on pH effects. As a result they predicted "In biological membranes such fixed charges could arise from the ionization of $-NH_2$ and $-COOH$ groups of basic and acidic amino acids in the membrane proteins, and the fixed charge concentration would thus be pH dependent." In the 1980s the first plant K^+ channels were identified in the plasma membrane of guard cell protoplasts (Fig. 2a; Schroeder et al. 1984) while in the 1990s plant K^+ channels localized in the plasma membrane and sensitive to pH changes have been cloned and their protonatable domains and residues identified (Fig. 2b; Anderson et al. 1992; Schachtman et al. 1992; Sentenac et al. 1992; Hoshi 1995; Ketchum and Slayman 1996; Marten et al. 1999; Hoth et al. 1997, 2001; Lacombe et al. 2000; Geiger et al. 2002). Recent capacitance measurements (gating charge movement) associated with the opening and closing of the *Arabidopsis* guard cell K^+ channel KAT1 provided new insights into the gating of plant inward rectifiers (Fig. 2c; Latorre et al. 2003).

Active transport I: ion pumps

Slayman (1974) wrote "Over the past 10 years our understanding of the nature of biological membrane potentials and the relation of those potentials to metabolism, to transport of ionic substances, and to the transport of uncharged substrates has undergone a major revolution". Stimulated by Mitchell's prediction (1961), membrane processes in mitochondria, chloroplasts and halobacteria were studied and confirmed the chemiosmotic hypothesis. Furthermore, Slayman (1974) postulated "It is now clear that the animal-type Na^+/K^+ transport system is very rare among non-animal cells and tissues, if it exists there at all." Indeed in the past two decades the molecular structure of H^+ pumps rather than that of Na^+/K^+ pumps was identified in plants subdivided into gene families and associated with different membrane types such as plasma membrane P-type-, vacuolar V-type and F_1/F_o-type ATPases/synthases. When the mitochondrial F_1/F_o-ATPase was crystallized (Abrahams et al. 1993, 1994), the structural basis for understanding the conversion between chemical and metabolic energy was laid (see Nobel price 1997 to Sir John Ernest Walker). Since 1985 different groups succeeded in monitoring pump currents generated by the animal Na^+/K^+ ATPase (Gadsby et al. 1985; Fendler et al. 1985; Lafaire and Schwarz 1986; Nakao and Gadsby 1986). The first direct recordings of ATP-driven H^+ currents were performed in plants when the patch clamp technique was applied to isolated vacuoles (Hedrich et al. 1986). Later it was shown by similar recordings that H^+-ATPases and H^+-PP_iases co-reside in the same vacuole (Fig. 3a; Hedrich et al. 1989; for analysis of PP_iases see also Davies et al. 1992; Obermeyer et al. 1996). The prediction of Nelson (1992) that V-type ATPases cannot operate in the inverse proton-driven ATP synthesis mode was challenged by recordings on vacuoles where via patch pipettes the vacuolar lumen was clamped to pH 4.5. At 0 mV, pH 7.5 in the bath ("cytosol") and presence of ATP, protons were pumped into the vacuole while ATP replacement by ADP and P_i triggered outward H^+ pump currents (Fig. 3b; Gambale et al. 1994). Thus H^+ fluxes through the V-type ATPase can drive ATP synthesis and vice versa. Under most physiological conditions, however, ATP drives protons through the V-type ATPase into the vacuole lumen.

Balke et al. (1974) as well as Leigh et al. (1974) reported about the cation sensitivity of the plasma membrane ATPase of oat and maize roots, respectively. In their studies on membrane vesicles the authors attempted to identify why monovalent cations and anions can stimulate ATP-driven H^+ pumping. Since vesicles represent a thermodynamically ill-defined system, H^+ pumping results in pH change of the vesicle lumen and charging of the membrane. The latter could be balanced by potassium uptake or anions slipping through leaks or anion channels. Owing to cytoplasmic K^+ concentrations in the 100 mM range, K^+-dependent stimulation of the H^+
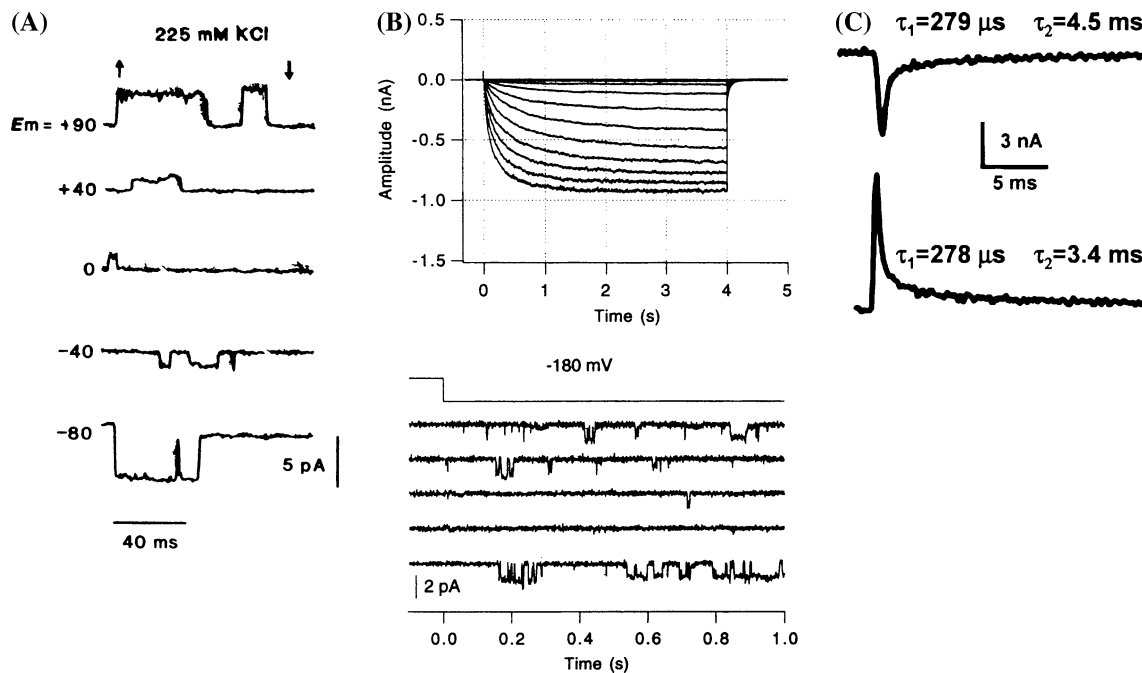
Fig. 2 First recording of a plant K^+ channel in the plasma membrane (**a**) and characterization of KAT1 (**b, c**), one of the first cloned plant K^+ channel, heterologously expressed in *Xenopus laevis* oocytes. **a** Recordings of K^+-selective channel currents in an inside-out membrane patch from *Vicia faba* guard cell protoplasts. The membrane potential E_m was held at + 40 mV and stepped by 100-ms-lasting voltage pulses to potentials in the range from + 90 to −80 mV. In all records the pulse starts at the upward-pointing *arrow* and stops at the downward-pointing *arrow*. The experiments were performed in the presence of symmetrical high K^+ solutions (225 mM). From Schroeder et al. (1984) with copyright permission by Nature Publishing Group's (http://www.nature.com/). **b** Properties of the KAT1 currents. Upper traces: representative KAT1 macroscopic currents recorded in the cell-attached configuration on *Xenopus* oocytes in response to 4-s voltage pulses to −80 to −180 mV in 10-mV increments and then to −50 mV. Lower traces: representative KAT1 single-channel openings elicited in response to voltage pulses from 0 to −180 mV in the inside-out configuration. Reproduced from Hoshi (1995) with copyright permission by The Rockefeller University Press. **c** Gating currents induced by KAT1 channels. Upper trace represents ON gating currents measured at −180 mV. Lower trace gives the OFF gating currents recorded at 0 mV after a −180 mV pulse. *Grey lines* are biexponential fits with the indicated fast and slow time constants. Reproduced and modified from Latorre et al. (2003) with copyright permission by The Rockefeller University Press

ATPase does not represent a mechanism of regulation in vivo. At about ten times higher Ca^{2+} concentrations as in the cytoplasm, the H^+ ATPase was inhibited by 100% (Kinoshita et al. 1995). Nevertheless, the physiological relevance of this Ca^{2+}-dependent inhibition is still scant too. In the meanwhile, however, charge balancing K^+- and anion channels have been identified (for review see Amtmann et al. 2004; Dreyer et al. 2004a, b).

Besides pumping protons, in plant cells membrane-bound ATPases have been shown to transport other cations such as Ca^{2+}, Na^+ (in the moss *Physcomitrella patens*, Benito and Rodriguez-Navarro 2003) and heavy metals. The molecular mechanism of plant heavy metal transport is at its very beginning and thus basis for bioremediation even more so. A view on this open field is given by Rosser and Dominy (2004). In comparison more is known about plant Ca^{2+}-ATPases (for review see López-Marqués et al. 2004). The fact that *P. patens* harbours a bacteria-like Na^+ pump allowing the moss to survive even severe salt stress leads to the questions whether higher plants lost this pump, or mosses received it more recently (past million years) by horizontal gene transfer from bacteria. The answers to this question may come from genome analyses of algae, equisetae, ferns and other mosses than *P. patens*. A new class of ATPases named ABC transporters was even shown to transport substrates of diverse structure including herbicides, glutathionylated compounds, glucuronides and malonylated chlorophyll catabolites (Rea et al. 1998; for review see Martinoia et al. 2002). Gradmann and Klemke (1974) proposed a Cl^- pump to operate in giant cells of the marine alga *Acetabularia mediterranea*. So far, this hypothesis was not yet approved by isolating the gene and studying the Cl^- pump function of the gene product.
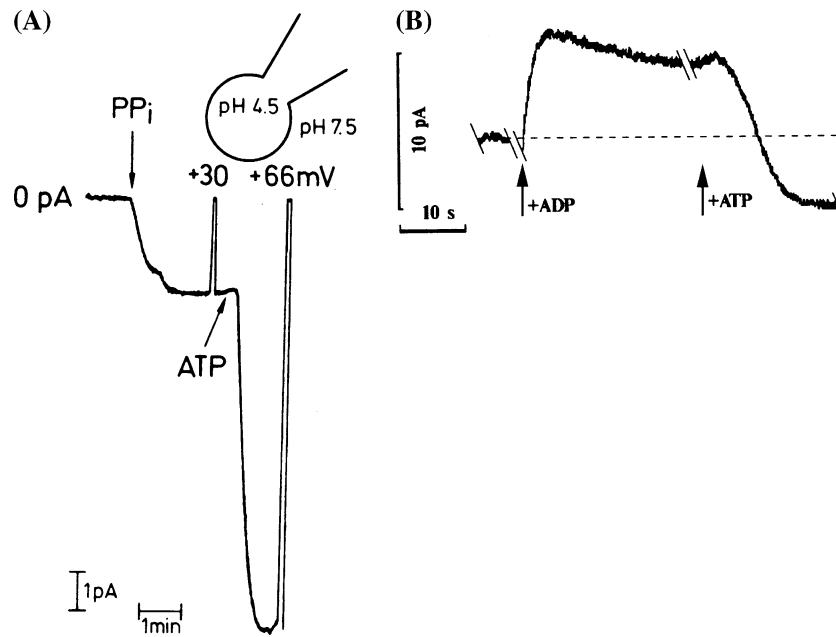
Fig. 3 a, **b** Proton-translocating pyrophosphatase and ATPase on the same vacuolar membrane. **a** Voltage-clamp recording of pump currents from a whole vacuole. The membrane was clamped to 0 mV. Application of 100 μM pyrophosphate (MgPP$_i$) to the extracellular solution generated ~2.5 pA which increased to 11.5 pA when 5 mM MgATP was present in addition. Reproduced from Hedrich et al. (1989). **b** Inward and outward H$^+$ currents through the vacuolar ATPase following application of "cytosolic" 5 mM MgADP and its replacement by 5 mM ATP in the presence of 10 mM KP$_i$ and a proton gradient across the vacuolar membrane (pH$_{bath}$ = 8, pH$_{vacuole}$ = 4). Reproduced and modified from Gambale et al. (1994) with kind permission of Springer Science and Business Media (1994). Note that in contrast to the present convention, the potentials given in **a** and **b** referred to the inner vacuolar membrane side rather than to the cytosolic membrane side resulting in current responses with opposite direction

Active transport II: ion-dependent cotransport

At the end of the 1960s light-dependent glucose assimilation of *Chlorella vulgaris* was demonstrated (Tanner and Kandler 1967; Tanner 1969; Komor and Tanner 1971; Komor 1973; Komor and Tanner 1974a). It was observed that glucose uptake is active (H$^+$-gradient coupled) and glucose inducible. This sugar accumulation has been partly correlated to the large difference in the K_m values for glucose uptake and release (0.2 and 21 mM, respectively). The membrane potential measurements on the basis of the lipophilic cationic TPP$^+$ distribution (TPP$^+$: triphenylphosphate) were performed with *Chlorella* and further provided initial evidences for electrogenic sugar transport (Komor and Tanner 1976). The Chlorella glucose transporter has never been observed to function in vivo as a facilitator except in the presence of nystatin, a sterol-interacting polyene antibiotic (Komor et al. 1974). Therefore it was suggested that hexose/H$^+$ symporters do not only depend on the proton gradient and/or the membrane potential but possibly also on the lipid composition of the membrane. Thus Komor and Tanner laid the basis for understanding sugar transport coupled to primary energy sources and membrane lipid surrounding.

Among others Slayman (1974) predicted "It should be possible with cotransport systems of this type to hyperpolarize the membrane by driving H$^+$ ions outward along a large gradient of non-metabolizable sugars or amino acids." Studies on lower plants and bacteria already provided first evidences that such a process is possible in principle (Komor and Tanner 1974b; Bentaboulet et al. 1979). The proof of concept in higher plants, however, was still awaited. Recently, Carpaneto et al. (2005) tried to bite the bullet. Following expression of the H$^+$/sucrose carrier ZmSUT1 (Aoki et al. 1999) in *Xenopus* oocytes, Carpaneto et al. (2005) excised giant inside-out patches from the oocyte plasma membrane. Upon variation of the pH-gradient, magnitude and direction of sucrose-gradient and membrane potential, the authors could demonstrate the reversibility of the sucrose carrier under 'sink' conditions (Fig. 4a). Thereby it was shown that – as expected from a perfect thermodynamic machine – the sucrose gradient can drive H$^+$ flow. Like for H$^+$-coupled glucose transport in *Chlorella*, K_m values for sucrose uptake and release differed by factor of about 100. Following the basic studies of Tanner and Komor (see above), the *Chlorella* hexose uptake system HUP was cloned and *HUP* was functionally expressed in yeast
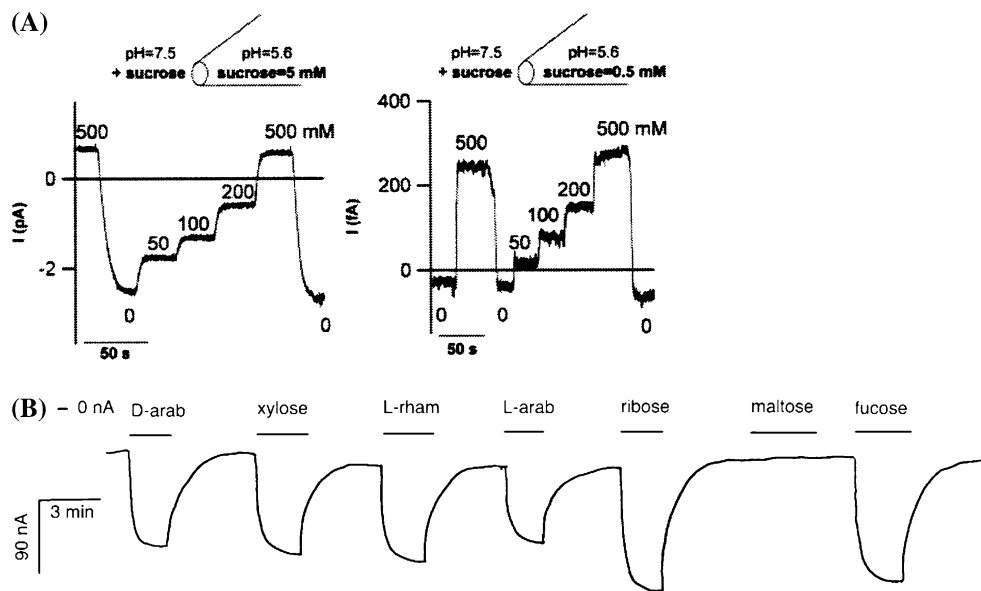
(A)

(B)

Fig. 4 a, b Ion-dependent cotransport. **a** Changes in cytosolic sucrose feedback on the magnitude and direction of ZmSUT1 currents. ZmSUT1 currents were recorded in inside-out giant patches derived from *Xenopus* oocytes in the presence of 5 mM (left graph) and 0.5 mM external sucrose (right graph). Schematic representations above each graph depict the proton and sucrose concentrations; cytosolic and external pH was 7.5 and 5.6, respectively, and sucrose concentrations were elevated from 0 to 50, 100, 200, and 500 mM as indicated. The membrane potential was clamped to 0 mV. From Carpaneto et al. (2005) with kind permission of ASBMB Journals. **b** *Arabidopsis* sugar alcohol permease homolog AtPLT5 transports a range of monosaccharides. *Xenopus laevis* oocytes, injected with AtPLT5 mRNA were clamped to −40 mV. Currents were recorded in the presence of different substrates as indicated by *bars* (D-arab: D-arabinose, L-rham: L-rhamnose, L-arab: L-arabinose, glc: glucose). Reproduced and modified from Reinders et al. (2004) with kind permission of ASBMB Journals

(Sauer and Tanner 1989; Sauer et al. 1990). Later metabolically engineered yeast was used by Frommer's group to identify the first sucrose carrier from higher plants (Riesmeier et al. 1992). The *Arabidopsis thaliana* genome harbours gene super families for hexose and sucrose uptake whose subfamily members often are expressed in a cell type- or organelle-specific manner (for review see Williams et al. 2000; Büttner and Sauer 2000; Lalonde et al. 2004). This, however, is only the tip of an iceberg, since recently the first members of sugar alcohol transporters have been identified, some of which transport sugars too (Fig. 4b; Noiraud et al. 2001; Gao et al. 2003; Ramsperger-Gleixner et al. 2004; Reinders et al. 2004; Klepek et al. 2005; for review see Bush 2004).

Light-dependent changes of membrane potential

For studying this topic, Felle and Bentrup (1974) used the aquatic liverwort *R. fluitans*, since it resembles the electrophysiological phenomena of higher plants. Its large cells facilitate microelectrode techniques, and its rhizoid cells protruding into the milieu lend themselves favourable to impedance measurements. Up to three electrodes were inserted into single rhizoid cells of intact liverwort (Felle and Bentrup 1974). Thereby it was shown that the membrane potential in the light is less responsive to K^+ changes than in the dark. In the light, however, the hyperpolarized membrane potential was sensitive to H^+. Hansen (1974) made the attempt to quantitatively describe the action of light on the membrane potential to separate different light effects and biochemical reactions involved. Using the patch clamp technique, Assmann et al. (1985) could show that blue light activates the H^+ pump of the guard cell plasma membrane (cf. Roelfsema et al. 2004 for studies with intact guard cells). This activation is mediated via blue light perception by the photoreceptors phot 1 and 2 and in turn binding of 14-3-3 protein to the phosphorylated H^+-ATPase (Kinoshita et al. 2001, 2003; Ueno et al. 2005; for review see López-Marqués et al. 2004).

Weisenseel and Haupt (1974) as well as Schäfer (1974) characterized the phytochrome system that along with other photoreceptors plays a role in photomorphogenesis. The red and blue light syndrome is now part of photobiology chapters in textbooks and developed into a field of its own. It became apparent that not only proton pumps but also the activity and transcription of ion channels can be indirectly

regulated upon blue light. A transient blue light-induced depolarization prior to inhibition of hypocotyl elongation seems to be partly caused by blue-light stimulated anion channels (Spalding and Cosgrove 1989; Cho and Spalding 1996). The initial, rapid growth inhibition was shown to depend on the blue light receptor phototropin (phot) which is responsible for Ca^{2+} transients (Baum et al. 1999; Folta and Spalding 2001). Light-controlled Cl^- channels were also observed in mesophyll cells of pea (Elzenga and Van Volkenburgh 1997). Stoelzle et al. (2003) demonstrated that Ca^{2+} channels are activated by blue light via the phot1/2-dependent signalling pathway while Fuchs et al. (2003) could show that blue light triggers the activity of a particular K^+ channel gene in the maize coleoptile. This process which finally leads to phototropic bending of this organ is mediated via the phytohormone auxin (Philippar et al. 1999). It should be mentioned, however, that only very recently directly blue or green light-activated ion channels have been identified in *Chlamydomonas* (Nagel et al. 2002, 2004). These channelrhodopsins (ChR) represent channels which harbour a rhodopsin molecule as a chromophore. Since vision of all mobile organisms seems to be based on rhodopsin, plants when becoming sessile may have lost rhodopsin-based signalling.

The effect of photosynthetic radiation on membrane potential responses of the giant chloroplast enclosing membranes in mesophyll cells was studied by applying microelectrodes on *Peperomica metallica* by Vredenberg (1974) as well as on the hornwort gametophytes from *Phaeoceros leavis* by Davis (1974). Schönknecht et al. (1988) applied the patch clamp technique to giant thylakoid blebs from *P. metallica* and identified depolarization-activated anion channels. Voltage-dependent anion channels were also found in the thylakoid membrane of the alga *Nitellopsis obtusa* (Pottosin and Schönknecht 1995). Whether or not these anion channels may account for light-dependent depolarization and represent a ClC gene product (see below) await future analysis. Flash spectroscopy, taking advantage of light-dependent thylakoid intrinsic electrochromic shifts, were used by Junge et al. (1974) to unravel photosynthetic electron transport and ATP synthesis. Though the photosynthesis research has a long-standing background holding its own 'International Congress of Photosynthesis' for already 40 years, transport of metabolites and ions (other than protons) across the inner and outer envelope, however, remained part of both fields 'Plant Membrane Transport' and 'Photosynthesis' (Kunze et al. 2002; Weber and Flügge 2002; Weber et al. 2005; Vothknecht and Soll 2005).

Solute transport in algae and cell suspension cultures

Raven (1974) and Wagner (1974) studied the energy- and pH dependence of $^{36}Cl^-$ influx and efflux in *Hydrodictyon africanum* and *Mougeotia*, respectively. In 1996, pH and ATP-dependent anion channels have been identified (Schulz-Lessdorf et al. 1996; for review see Barbier-Brygoo et al. 2000) and genes encoding for H^+-coupled NO_3^- symporters have now been cloned for a wide range of higher plant species including *Hordeum vulgare* (Trueman et al. 1996), *Nicotiana plumbaginifolia* (Quesada et al. 1997), *Glycine max* (Amarasinghe et al. 1998) and *A. thaliana* (Filleur and Daniel-Vedele 1999; Zhuo et al. 1999). Although the latter also transports chloride, the nature of the predicted H^+/Cl^- symporter (Sanders 1980) is still scant. In this context it should be mentioned that some ClCs can function as Cl^-/H^+ antiporters (Accardi and Miller 2004; Picollo and Pusch 2005). Findenegg (1974) focussed on Cl^- and HCO_3^- uptake by *Scenedesmus obliquus* and predicted as follows: "Carbonic anhydrase may act as a permease for these ions in the plasmalemma". This is clearly not the case. The genomes of blue-green algae have been sequenced. There is no evidence that the carbonic anhydrase represents a membrane protein (for review see Hewett-Emmett and Tashian 1996), but ClC-like anion channels have been found in cyanobacteria and in planta (Hechenberger et al. 1996; Lurin et al. 2000). ClC channels in mammals are permeable to both Cl^- and HCO_3^- (for review see Fahlke 2001).

Walker (1974) reviewed attempts to study "chloride transport to the charophyte vacuole" and Davis (1974) the H^+ activities in *Phaeoceros* vacuoles. Since then the vacuolar H^+-ATPase consisting of 11 subunits has been cloned and analysed (for review see López-Marqués et al. 2004). Martinoia et al. (1985) who is well experienced in the isolation of intact vacuoles assumed that the vacuole membrane needs to be energized to mediate Cl^- and malate uptake (for review see Martinoia et al. 2000). Recently, the first dicarboxylate transporter gene AttDT was identified (Emmerlich et al. 2003). AttDT is localized in the vacuolar membrane and transports malate. Alike the situation for the plasma membrane, we are still awaiting the identification of the first vacuolar Cl^- transporter. Possibly, ongoing plasma membrane- and vacuole proteome studies (Carter et al. 2004) will identify the respective candidates.

NH_4^+ transport was studied by Barr et al. (1974). The replacement of K^+ with NH_4^+ in the K^+ solution at pH 5.7 caused a 45-mV-depolarization while the application of NH_4^+ in the presence of K^+ had no effect. Meanwhile, it has been shown that inward-rectifying

K^+ channels mediate NH_4^+ flux (Schachtman et al. 1992; Dietrich et al. 1998; Becker et al. 1996 and references therein). Thus, in the presence of K^+, transport of NH_4^+ is suppressed and depolarization below the Nernst potential for K^+ prevented. Furthermore, genes have been cloned whose products facilitate the NH_4^+-selective transport (for review see Loque and von Wiren 2004). Ammonium uptake by the latter system appears to be membrane potential-driven rather than H^+-coupled (Ludewig et al. 2002). Thoiron et al. (1974) studied the sulphate permeability of *Acer pseudoplatanus* cell suspension culture. Simonis et al. (1974) and Jeanjean and Ducet (1974) examined phosphate uptake in *Anacystis nidulans* and *Chlorella pyrenoidosa*, respectively. The phosphate translocator protein located in the inner chloroplast envelope was biochemically characterized and the gene cloned by Flügge et al. (1989). In the meanwhile, several solute transporter types of the plasma- and organelle membranes have been cloned, localized and functionally characterized (for review see Hawkesford and Miller 2004; Weber et al. 2005).

Kinetics of transport

On the basis of the pioneering work of Epstein in the 1960s (Welch and Epstein 1968; Epstein 1972), Mertz and Higinbotham (1974), Vange et al. (1974) and Cram (1974) studied the kinetics of potassium-, sulphate- and chloride uptake in more detail. As reported by Epstein before, basically two phases could be separated: a high affinity and a low affinity system. In the following years it was argued that H^+-driven K^+ symporters mediate high-affinity transport and K^+ channels mediate low-affinity transport. However, thermodynamically this separation is not valid, since K^+ channels transport potassium ions driven by the electrochemical gradient of this ion. As a result even at micromolar K^+ concentrations K^+ channels are capable of mediating K^+ uptake at sufficient negative membrane potentials. The proof of concept in vivo was provided by the growth phenotype of the AKT1 channel mutant (Hirsch et al. 1998). *Arabidopsis* plants lacking the major root K^+ channel barely grow in micromolar K^+ solution. Thus, wild-type roots which under this conditions are characterized by membrane potential as negative as -240 mV can accumulate potassium up to 100 mM on the basis of channel-mediated transport. Additional unequivocal evidence for channels mediating high-affinity K^+ uptake was provided by Brüggemann et al. (1999). They showed by patch clamp studies on guard cell protoplasts that K^+ channels are active under these condi-

tions and transport this cation into the cell purely driven by the electrical gradient. Since the K^+ channel KAT1 is predominantly expressed in *Arabidopsis* guard cells, its gating behaviour was extensively characterized (cf. Fig. 2c; Marten and Hoshi 1997, 1998; Lacombe and Thibaud 1998; Tang and Hoshi 1999; Latorre et al. 2003; Lai et al. 2005). Recently, Hertel et al. (2005) observed KAT1 inactivation at sub-millimolar concentrations of extracellular K^+ when expressed in HEK cells. This result led to the conclusion that KAT1 cannot act at micromolar K^+ concentrations. In contrast, no evidences for KAT1 inactivation at extracellular nominal K^+-free solutions were obtained in *A. thaliana* guard cells (Brüggemann et al. 1999).

Salt stress

Jeschke (1974) focussed on the control of K^+ and Na^+ fluxes and K^+, Na^+ selectivity of roots. From experiments in the presence of the uncoupler CCCP he concludes that "the decrease of the Na^+ uptake in the presence of K^+ is consistent with the suggestion (Pitman and Saddler 1967) that the Na^+ efflux pump at the plasmalemma is involved not only in the selective K^+ and Na^+ transport but also in the selective accumulation of K^+ and Na^+ by barley roots." While screening salt-sensitive mutants SOS1, a plasma membrane H^+/Na^+ antiporter (Wu et al. 1996; Shi et al. 2000), and NHX1, a vacuolar H^+/Na^+ antiporter (Apse et al. 1999), were identified. When overexpressed, both antiporters increased the salt tolerance of plants. Wheat TaHKT1 primarily identified as a H^+/K^+ symporter (Schachtman and Schroeder 1994) finally turned out to transport K^+ on the expense of the Na^+ gradient (Rubio et al. 1995). In *A. thaliana* HKT1 was proposed to mediate Na^+-driven Na^+ uptake (Uozumi et al. 2000). Furthermore HKT1 was predicted to accomplish Na^+ loading into the phloem sap in leaves and Na^+ release in roots (Berthomieu et al. 2003). In rice several *HKT1* genes linked to Na^+ or K^+ transport exist (Horie et al. 2001; Maser et al. 2002; Garciadeblas et al. 2003), and a quantitative trait loci (QTL) seem to confirm a role of an HKT-type transporter in salt tolerance (Ren et al. 2005). Thus the picture about Na^+ recirculation in plants is getting clearer.

Salt stress in particular and environmental stress in general are transmitted in plants by changes in the ABA concentration (Jia et al. 2002; Sauter et al. 2002; Verslues and Zhu 2005). Pitman et al. (1974), Collins (1974) as well as Van Steveninck (1974) monitored the effect of abscisic acid on root ion transport. More

recent studies could demonstrate that ABA upregulates transcription of *GORK* (epidermis, cortex and stele; Ache et al. 2000; Becker et al. 2003) and downregulates *SKOR* (stele; Gaymard et al. 1998). Both K^{+} channels, GORK homomers and GORK/SKOR heteromers, have different properties (Dreyer et al. 2004a, b). Thus the K^{+} release channels GORK and SKOR are regulated in an opposite manner. GORK is activated in an ABI1-, ABI2- and calcium-dependent manner. Recently Levchenko et al. (2005) could show in intact *Vicia faba* plants that the guard cell anion channels are activated by cytosolic ABA ($K_m = 1–2$ µM) within 1 s. In earlier studies ABA-induced calcium oscillations have been reported in guard cells mechanically separated from their natural environment within the leaf (for review see Schroeder et al. 2001). On the basis of these studies models have been constructed (Leonhardt et al. 2004). The predictions of these models can now be tested in intact plants (for review see Roelfsema and Hedrich 2005).

Twenty years ago, at the botanical congress in Vienna 1984, the chairman of the plant transport session in his opening stated that in contrast to animals plants do not need channels. At the end of the session the first patch-clamp recordings of single K^{+} channels in the plasma membrane of guard cells were shown (Schroeder et al. 1984; Fig. 2a). Thereafter it was accepted that they exist, but this transporter class in the plant field was regarded to be not important. In the Annual Plant Reviews of 2004 (volume 15) almost 50% of the content deals with ion channels. Why? In the past 20 years, this field progressed very rapidly. Owing to the progress in molecular biology and genome sequencing projects, genes for different transporters often belonging to large gene families have been identified (Arabidopsis Genome Initiative 2000; Schwacke et al. 2003; Tuskan et al. 2004; International Rice Genome Sequencing Project 2005). Instead of 'the' expected sugar transporter or ion channel often several members of gene families together provide for the transport function. Thus the loss of a particular family member (e.g. AKT1, DND1, DND2; Hirsch et al. 1998; Yu et al. 1998, 2000) could but must not result in a strong phenotype (e.g. KAT1, AKT2/3; SPIK; Dennison et al. 2001; Szyroki et al. 2001; Deeken et al. 2002; Mouline et al. 2002). Following directed mutagenesis and using chimera between structural related but functional distinct transporters, the structure–function relationships have been unravelled. On the basis of the fusions of the transporters of interest with fluorescing proteins (GFP and chimera thereof) together with high-resolution microscopy, their cellular and subcellular localization was determined. Interaction screens in the following years will help to find regulator proteins and allow to position this class of membrane proteins in existing signalling networks. In the next decade besides channels, carriers and pumps membrane receptors will come into focus. With the latter it will be exciting to learn how ligand binding will trigger trans(membrane) protein signal transport.

The authors apologize for not having mentioned all important studies in the past and thus suggest reading Volume 15 of the Annual Plant Reviews (Blatt 2004) and other reviews from Assmann (2003), Talke et al. (2003), Véry and Sentenac (2003), Fehr et al. (2004), Pratelli et al. (2004) and Deutschle et al. (2005).

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