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Electrogenic Membrane Transport in Plants

A Review*

F.-W. Bentrup

Abteilung Biophysik der Pflanzen, Institut für Biologie I der Universität Tübingen, D-7400 Tübingen, Federal Republic of Germany

Abstract. This review treats some examples of electrogenic transport across the outer plasmamembrane (plasmalemma) of plant cells. The selection includes primary active uniport by membrane ATPases (e.g., the proton pump), secondary active transport of hexoses by proton-dependent cotransport, and passive uniport of amines. Primacy is given to the presentation of electrophysiological data and to the discussion of voltage-dependence of the transport mechanisms.

Key words: Current-voltage relationship – Electrogenic membrane transport – Membrane ATPases – Plasmalemma.

Introduction

The purpose of this presentation is to outline electrogenic transport across the outer plasmamembrane (plasmalemma) of plant cells using few examples currently under study. This selection excludes transport across the tonoplast membrane which separates the cytoplasm from the cell vacuole, as well as across organellar membranes. The reader is referred to recent reviews dealing with general plant cell electrophysiology and membrane transport (Bentrup 1978; Poole 1978), and with membrane potentials in photosynthesis (Junge 1977).

A transmembrane electrogenic pathway both contributes and responds to the transmembrane electrical potential difference, ψ_m. In order to detect and characterize a putatively electrogenic pathway, it seems indispensible to work out a complete equivalent circuit for ψ_m; current-voltage (I–V) relationships are particularly useful to identify pathways through their voltage-dependence. It will be shown that such I–V data may specify the mechanism by which a transported molecule and its membrane channel interact during translocation. Unfortu-

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nately, the I–V analysis is restricted to cells which may be subjected to linear cable theory, thus excluding, for instance, pertinent experiments on the higher plant cell in situ. Clearly, it is essential – and feasible through Cole's theorem (Cole 1968) – to obtain current densities so that electrical conductance and radiotracer flux data may be compared.

Examples of electrogenic transport have been selected from different transport categories according to the terminology of Mitchell (1967):
(1) Primary active uniport by an ion-translocating membrane ATPase ("electrogenic pump"),
(2) Secondary active symport (cotransport) of hexoses with H^+, and
(3) Passive uniport of ammonia.

Electrogenic Ion Pumps

Ion-translocating ATPases have been postulated to operate in the plasmalemma of numerous plants throughout the plant kingdom, the most wide-spread case being the proton pump. Two other pumps carry presumably HCO_3^- and Cl^-, respectively. The bicarbonate pump is considered in the final paragraph. Electrogenic chloride pumping occurs in the marine giant green algae *Acetabularia* and *Halicystis (Derbesia)*. The former alga requires Cl^- in the external medium for the electrogenic voltage to develop (Gradmann 1970). In perfused cells of the latter, closely related species the short-circuit current at $\psi_m = 0$ is fully (> 99%) accounted for by influx of $^{36}Cl^-$ (Graves and Gutknecht 1976).

The proton pump has been assumed to be the principal electrogenic pump in the thallophytes and higher plants. For obvious reasons, in this case cogent evidence for the identity of the transportee is lacking. Evidence for an ATP-dependent hyperpolarizing mechanisms comes from experiments with inhibitors of oxidative and photophosphorylation. Immediate depolarization upon addition of azide or cyanide, for instance, may be correlated with the cellular level of ATP. In *Neurospora,* the kinetics of depolarization and ATP-decay after addition of KCN strikingly match (Fig. 1). The fit yields a modified Michaelis-Menten equation given in the graph. The k_m which is 2 mM ATP at 25° C has been interpreted to reflect the affinity of the membrane ATPase for ATP (Slayman et al. 1973).

In fact, a *Neurospora* plasmamembrane ATPase has been isolated and characterized by Scarborough (1977) and by C. W. Slayman and coworkers (Bowman and Slayman 1977; Bowman et al. 1978). This ATPase differs clearly from the mitochondrial ATPase by the pH optimum of 6.8 vs. 8.25, by its insensitivity toward oligomycin and its high affinity for ATP (its activity in the presence of other mucleotides is less than 6% of the ATP value). Most interestingly, its k_m of 1.8 mM ATP is fairly close to the above quoted value of 2 mM ATP for half-saturation of the putative ATP-fueled proton pump. From the need of detergents during purification, Bowman et al. (1978) conclude that, by contrast to bacterial and organellar ATPases, the *Neurospora* plasmamembrane ATPases is an integral membrane protein resembling more the (Na^+, K^+)

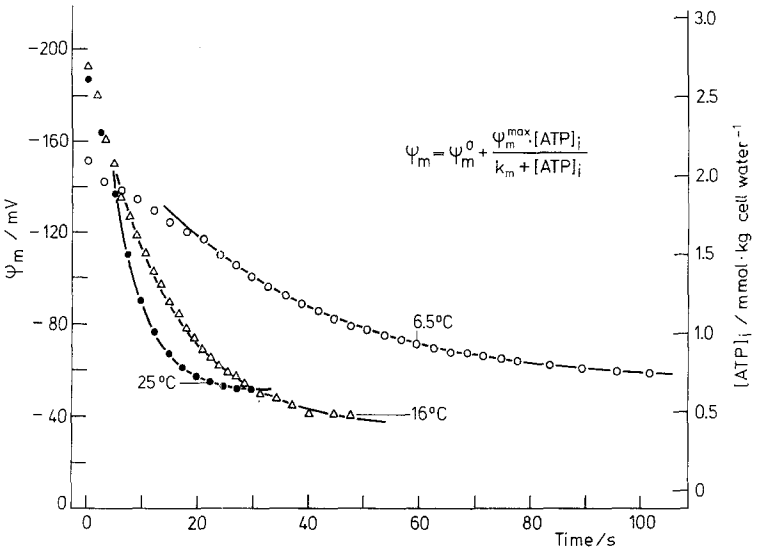

Fig. 1. Time course of membrane potential, ψ_m, and cellular ATP concentration, $[ATP]_i$, after addition of cyanide at time zero to hyphae of *Neurospora crassa*. The solid curves have been obtained from ATP-assay (10 mM KCN, right ordinate) and fitted to the given points of voltage recordings (25 mM KCN, left ordinate) by means of the modified Michaelis-Menten equation. ψ_m^0 is the membrane potential when the electrogenic pump is inoperative; ψ_m^{max} is the maximal voltage contributed by the pump, and k_m indicates the ATP concentration for $\psi_m^{max}/2$. After Slayman et al. (1973)

ATPase of animal cells and the Ca^{2+}-ATPases of sarcoplasmic reticulum. It possesses a single major polypeptide subunit of about 96,000 daltons. Evidence for a Mg^{2+}-activated plasmalemma ATPase, presumably the proton pump, was presented by Shimmen and Tazawa (1977) who perfused internodal cells of the giant green alga *Chara corallina* with various concentrations of Mg^{2+} and ATP and measured membrane potential and conductance across the plasmalemma.

I–V analysis, first of all, must sever a putative electrogenic pump from the other membrane channels shunting it, as a rule. Since a specific inhibitor of the proton pump, comparable to ouabain inhibition of the (Na^+, K^+) ATPase, has been found only recently, investigators hitherto relied upon inhibition of ATP-synthesis (as in Fig. 1) or a decrease of temperature, in order to abolish any contribution of the electrogenic pump to ψ_m. (Vanadate has been found recently to interact specifically with cell membrane ATPases including the *Neurospora* ATPase; Bowman et al. 1978.)

Apparent pump inhibition via a temperature decrease occurs at values below 10° C in *Acetabularia* (Gradmann 1970) and 8° C in *Riccia* (Felle unpublished data). Figure 2 shows I–V curves of the aquatic liverwort *Riccia fluitans* at 20 and 5° C. Whereas the I–V curve at 20° C features a fairly linear (ohmic) conductance range at membrane currents smaller than $\pm 1\ A\ m^{-2}$, the presumably passive channels remaining operative at 5° C show the diode-like behaviour known from other cell membranes (comp. Cole 1968). The graphically obtained difference is attributed to the electrogenic pump. A similar

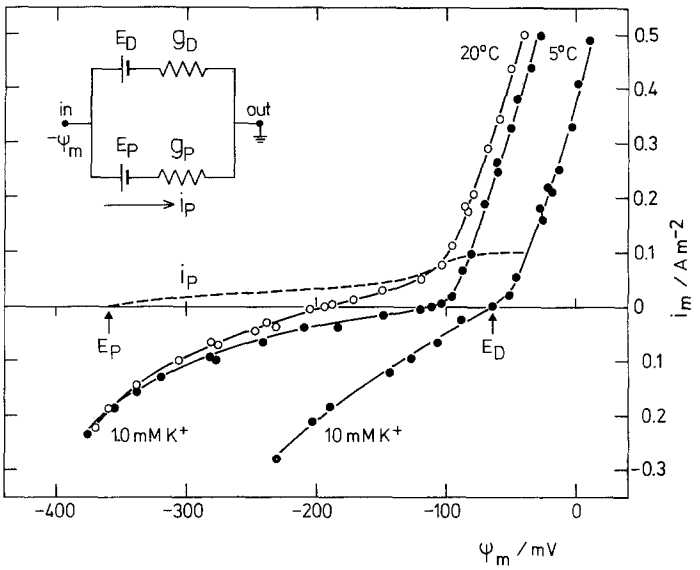

Fig. 2. Current-voltage curves from rhizoid cells of *Riccia fluitans* at 20° C (○) and 5° C (●), respectively, at different external K^+ concentrations as indicated; pH 5.6, 1 W m^{-2} white light. The dashed curve has been obtained by subtracting, at 1.0 mM K^+, the 5° C-curve from the 20° C-curve. See text for description of the equivalent circuit. From Felle (unpublished data)

procedure has been used in *Acetabularia* (Gradmann 1975) and *Neurospora* (Slayman and Gradmann 1975; Gradmann et al. 1978).

In *Acetabularia* the analysis is complicated by the fact that the pump pathway is modulated by green light (Gradmann 1978) and undergoes "metabolic" action potentials during which the electric current through the pump reverses and hence might transiently switch it from ATP-consumption to ATP-synthesis (Gradmann 1976).

The I–V curves for the electrogenic pump of the quoted plants have been entered in Fig. 3. Each of the curves may be viewed as a fragment of a sigmoid I–V curve. Such a curve has been predicted by Finkelstein (1964). Recently Läuger (1979) has worked out a sigmoid pump curve on the grounds of a rate theory approach to a channel-type electrogenic ion pump. A sigmoid pump curve is plausible when a finite number of ATPase ("pump") molecules per unit area of membrane undergo two coupled chemical reactions: ATP-hydrolysis driving a saturable positive outward current, i.e., proton efflux (*Neurospora, Riccia*) or Cl^- influx (*Acetabularia*), respectively. At zero current the molar free energy of ATP-hydrolysis, $\Delta G_{ATP}/n$, is just balanced by the electrochemical potential gradient created by the pump for the ion *j;* then

$$-\Delta G_{ATP}/n = \Delta\tilde{\mu}_j \,. \tag{1}$$

The coefficient n denotes the stoichiometry of the two coupled reactions. Eq. (1) holds only, if the reactions are strictly coupled, that is, if the membrane ATPase converts the free energy of ATP completely into ion translocation. The

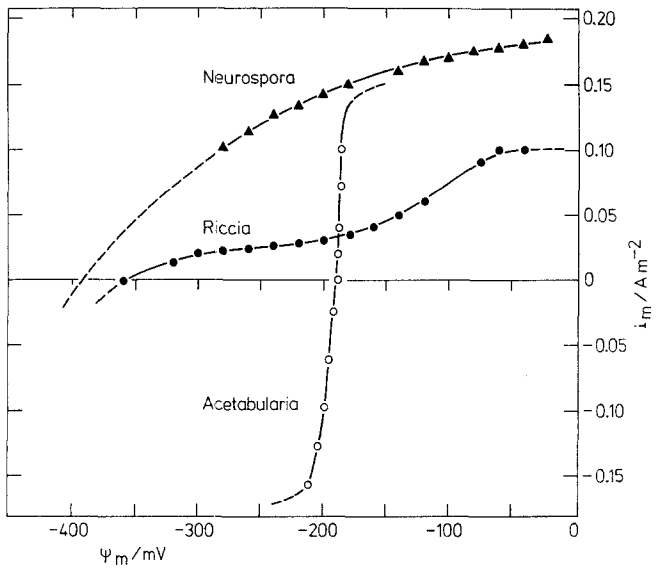

Fig. 3. Current-voltage curve of electrogenic ion pumps of the plasmalemma of *Riccia* (from Fig. 2), *Neurospora* (after Gradmann et al. 1978) and *Acetabularia* (after Gradmann 1975)

equilibrium or reversal potential of the pump, E_p, is the electrical term of $\Delta\tilde{\mu}_j$ (correctly, of $\Delta\tilde{\mu}_j/F$). In fact, E_p accounts for most of $\Delta\tilde{\mu}_j$ in the given cases so that, roughly, at ψ_m values more negative than E_p synthesis of ATP by reversal of the pump mechanism may be anticipated. Membrane punch-through prevents that the membranes of *Neurospora* and *Riccia* be hyperpolarized beyond their E_p value of -400 and -360 mV, respectively. In *Acetabularia,* where the reversal potential is only -190 mV (see Fig. 3), pump reversal and associated ATP-synthesis seems possible as already mentioned above.

In any case, the pump pathway is obviously shunted by the other transmembrane ion pathways represented by E_D and g_D in Fig. 2. The resulting membrane potential is around -220 mV in *Riccia,* -200 mV in *Neurospora,* and -170 mV in *Acetabularia.* At these voltages the pump work at more than half-saturation, that is, like a high-resistance current source. The stoichiometry n [Eq. (1)] still is a matter of debate. From various sets of data for ψ_m, external and internal pH from *Chara, Neurospora* and *Phaeoceros,* Walker and Smith (1977) calculated a remarkably constant value for $\Delta\tilde{\mu}_{H+}$ of about -26 kJ mol^{-1}. Assay of the ATP turnover in *Chara* and *Neurospora,* on the other hand, gave ΔG_{ATP} values of -50 to -55 kJ mol^{-1}. Thus, according to Eq. (1), a two-proton per ATP pump operating near equilibrium ($\psi_m = E_p$) seems conceivable; in fact, it was postulated for *Chara* by Spanswick (1972) and supported by resistance measurements (Keifer and Spanswick 1978). Similarly, in *Acetabularia* a two-Cl^- ATPase is compatible with Eq. (1) (Gradmann 1975). However, the strongly negative E_p values derived for *Neurospora* and *Riccia* (Fig. 3) require a one-proton per ATP pump. This pump mode would deliver up to -500 mV, whereas 2 H^+/ATP would correspond to about -200 mV. A variable stoichiometry has also been considered (Gradmann et al. 1978).

Electrogenic Sugar Transport

Secondary active transport of sugar by chemical coupling to a transmembrane electrochemical gradient through a charged carrier seems to occur not only in bacteria, algae and fungi, but also in higher plants (Bentrup 1978). It is puzzling that the studied examples include electrogenic transport of hexoses by photoautotrophic plants which do not depend upon uptake of organic carbon compounds, namely, *Chlorella* (Komor and Tanner 1974, 1976), *Lemna* (Ullrich-Eberius et al. 1978), and *Riccia* (Felle and Bentrup 1980). Prima facie plausible, however, appears that movements of the principal sugar transportee in the higher plant, saccharose, occurs via proton-dependent cotransport, as has been postulated on the grounds of circumstantial evidence for phloem loading by Giaquinta (1977) and for uptake by cotyledons by Komor (1977) and Hutchings (1978).

Essential criteria for a carrier-mediated electrogenic sugar transport are specificity and voltage-dependence; furthermore, identification and stoichiometry of the charged cosubstrate (driver ion) is required. Figure 4 illustrates that the *Riccia* membrane well discriminates between the different hexoses, measured as membrane depolarization $\Delta\psi_m$. Application of the Michaelis-Menten formalism, to be discussed below, implies that the sugar S binds to a hexose-specific saturable site on the membrane, presumably the carrier X. This notion is suggested by the maximal depolarization of 60 mV common to all hexoses tested, and by the observation that joint addition of different hexoses

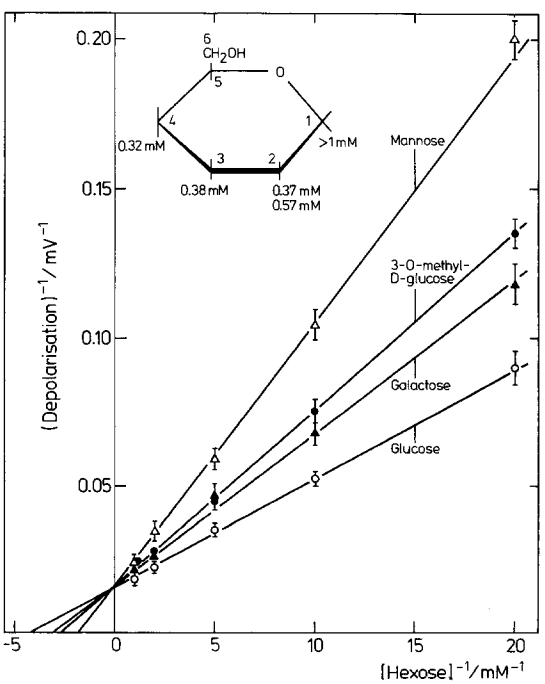

Fig. 4. Lineweaver-Burk plot of the hexose-induced membrane depolarization, $\Delta\psi_m$ after 30–60 s upon addition of the indicated hexose to thalli of *Riccia fluitans*. According to $\Delta\psi_m = \Delta\psi_m^{max}/(1 + k_m/C_{hexose})$, the maximal depolarization $\Delta\psi_m^{max}$ is 62 mV, and the k_m values are 0.24 mM glucose, 0.32 mM galactose, 0.38 mM 3-0-methyl glucose, 0.57 mM mannose. Not shown: 0.37 mM 2-deoxy glucose and 34 mM fructose. The k_m values have been placed at the particular C-atom of the hexose backbone where the given hexose differs from glucose. From Felle and Bentrup (1980)

indicate competition for the same binding site. If one assigns the derived k_m values to the binding reaction,

$$X + S \rightleftharpoons XS ,$$

the data suggest that the C1 and C2 atoms of the hexose backbone are crucially important for the binding reaction. In fact, 1-(α)- and 1-(β)-O-methyl glucose did not significantly depolarize the *Riccia* membrane. Protonation of the complex,

$$XS + H^+ \rightleftharpoons SXH^+ ,$$

then is generally assumed to create the electrogenicity of the transport mechanism. It is consistent with the finding of a pH-dependent saturable uptake of ^{14}C-3-O-methyl glucose showing a similar k_m (0.2 mM) as the electric experiment of Fig. 4 (Felle and Bentrup 1980). Yet these conclusions are not cogent.

Electrogenic sugar transport has frequently been proposed in terms of a cyclic carrier model. Examples are, except for the already mentioned cases, glucose transport in the fungi *Saccharomyces* (Van Steveninck and Rothstein 1965) and *Neurospora* (Slayman and Slayman 1974). Figure 5A shows this type of carrier model for the *Riccia* membrane. In no case, however, experimental evidence has been advanced for the formation of the ternary complex SXH^+. Also, does X first bind S and is then protonated or vice versa? Assumed that the sugar is charged and transported through SXH^+, this complex must show up in an equivalent circuit for the depolarized state of the membrane.

The circuit of Fig. 5B includes the hexose-induced current pathway with an e.m.f., namely, E_{sc}, and a conductance, g_{sc}. The hexose-induced inward current i_{sc} is given by

$$i_{sc} = g_{sc}(E_{sc} - \psi'_m), \tag{2}$$

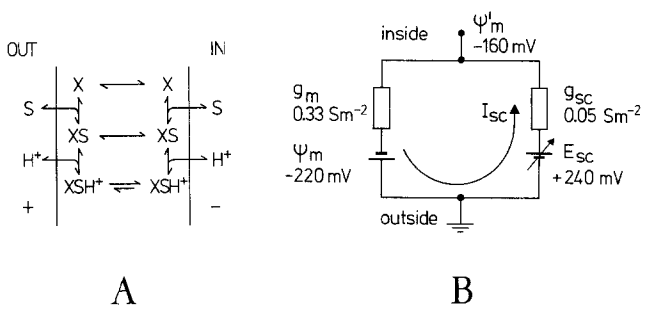

Fig. 5. A Cyclic carrier model for electrogenic cotransport of H^+ with an uncharged substrate S by means of a carrier X which is protonated at the outside and deprotonated at the inside (cytoplasm) of the membrane under the influence of the protonmotive force. **B** Equivalent circuit for the membrane potential of *Riccia fluitans* thallus cells in the hexose-induced, maximally depolarized state ($\psi'_m = \psi_m + \Delta\psi_m^{max}$) at pH 5.6. The left limb represents the regular active and passive pathways adding up to ψ_m and g_m (comp. the circuit of Fig. 2). The right limb represents the sugar-induced electrogenic current pathway. After Felle and Bentrup (1980)

where $E_{sc}-\psi'_m$ is the electrogenic sugar-driving force of about 400 mV at the onset of hexose uptake. g_{sc} is obtained from the sugar-dependent increase of the membrane conductance g_m; then E_{sc} can be calculated and may be assumed to reflect the equilibrium potential of the ternary complex, E_{SXH^+}. This e.m.f. becomes increasingly negative, as the intracellular sugar concentration rises, and satisfactorily accounts for the observed repolarization during prolonged uptake periods (Felle and Bentrup 1980).

Any interpretation of apparent k_m values from electrical data must realize that these values are a priori illusive if g_m is nonlinear over the range of ψ_m covered by the depolarization $\Delta\psi_m$. The equivalent circuit yields that i_{sc} is equal to and opposite in sign to the outward current i_m it causes to return through the regular membrane pathways (left limb in Fig. 5B):

$$-i_{sc} = i_m = g_m \cdot \Delta\psi_m \,. \tag{3}$$

Hence, as i_{sc} increases as a function of, for instance, sugar concentration, $\Delta\psi_m$ will correctly indicate i_{sc} only as far as g_m is constant. In *Riccia*, g_m increases by a factor of about 12 as ψ_m approaches -100 mV, in fact, E_D at 1.0 mM K^+ (Fig. 2), whereas the hexose-induced voltage saturates already at -160 mV (Fig. 4). Clearly, if ψ_m would approach E_D, it would simulate saturation of i_{sc} and hence too low k_m values.

Provided this difficulty can be settled by I–V analysis, the question of the significance of i_{sc} and k_m values is to be raised. Undoubtedly, the assumptions about the hypothesized carrier mechanism of Fig. 5A must be specified. Geck and Heinz (1976) have worked out specific cotransport models and considered the effect of ψ_m on k_m and J_{max} (i.e. i_{sc}) of the overall transport process. From their paper it is evident, that any type of cotransport model requires that the overall transport rate is limited by the transmembrane translocation step rather than binding and releasing reactions, respectively, at the membrane surfaces. In fact, the k_m values of Fig. 4 could be assigned to the binding reaction of a cotransport system also, if the binding site were located within the membrane and thus were part of the voltage-sensitive translocation step. Obviously, hexose-dependent I–V relationships are needed.

Electrogenic Uniport of Amines

The plasmalemma of *Riccia* is instantaneously and reversibly depolarized by micromolar concentrations of ammonia and methylamine (Felle 1980). This observation supports carrier-mediated electrogenic uniport of NH_4^+ and $CH_3NH_3^+$ rather than permeation of the free bases NH_3 and CH_3NH_2, respectively. Figure 6 presents I–V relationships in the presence of different ammonia concentrations. The main plot shows that, at zero current, ψ_m decreases with concentration and tends to saturate at E_D (Fig. 1). It also contains the information, after subtraction of each curve from the control curve, that at a given ψ_m between about -300 and -100 mV both the current and the slope of the curves, i.e., the amine-induced conductance, Δg_m, increase and saturate with

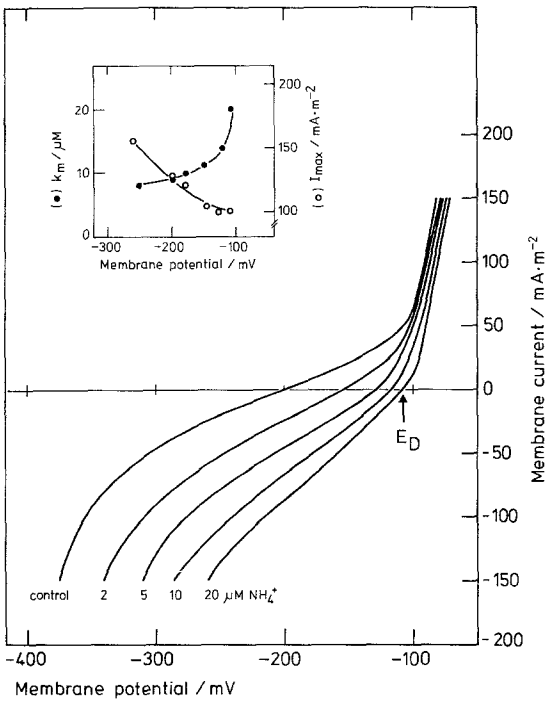

Fig. 6. Current-voltage curves of the plasmalemma of *Riccia fluitans* after addition of ammonia concentrations as indicated. *Inset:* From the I–V curves an ammonia-dependent saturation current, I_{max}, and the ammonia concentration for $I_{max}/2$, that is, k_m has been plotted vs membrane potential. After Felle (1980)

the ammonia concentration. Figure 7A shows Δg_m for both amines. The Lineweaver-Burk plot of Fig. 7B yields apparent k_m values of 12 µM NH_4^+ and 50 µM $CH_3NH_3^+$, and a common maximum Δg_m of about one S m^{-2}.

This maximum amine-induced conductance is larger than the regular g_m at ψ_m values more negative than E_D, namely, 0.3 to 0.4 S m^{-2}, but is smaller than $g_m = 8$ to 12 S m^{-2} at $\psi_m \lesssim E_D$. Consequently, using the rationale of the preceding paragraph, the ψ_m-dependent change of g_m sufficiently accounts for the observation that the amine-induced $\Delta\psi_m$ saturates at E_D. In terms of Eq. (3), the amine current would be underestimated by $\Delta\psi_m$. In fact, apparent k_m values from $\Delta\psi_m$ data are lower than those obtained from Fig. 7, namely, 2 µM NH_4^+ and 25 µM $CH_3NH_3^+$ (Felle 1980).

Returning to Fig. 6, its inset graph indicates that both the maximal amine-induced current I_{max} and the apparent k_m value for $I_{max}/2$ depend upon ψ_m. As for I_{max}, it seems plausible that a carrier-mediated passive electrogenic cation uniport increase with ψ_m. On the other hand, the voltage-dependence of k_m specifies that the rate-limiting step of the ammonia-uniport mechanism is under control of ψ_m. In a concurrent study of the amine transport by characean cells a quite similar voltage-dependence of both parameters have been found (Walker et al. 1979). According to these authors the voltage-sensitive k_m value indicates that the amine-binding site is located within the membrane.

Does this amine pathway also transport amino acids? In *Riccia,* a number of biogenic amino acids depolarize the plasmalemma. The apparent k_m values for $\Delta\psi_m^{max}/2$ are, for instance, 13 µM L-serine and 30 µM D-serine (Felle et al.

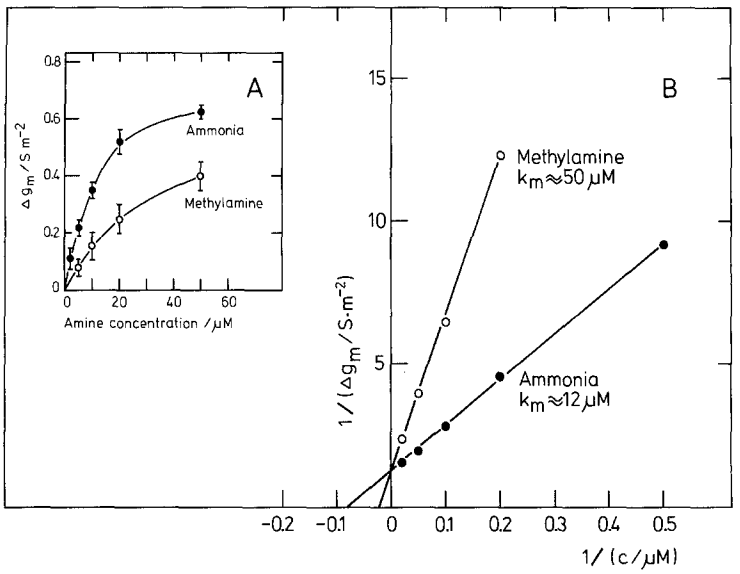

Fig. 7. Change in electrical slope conductance, Δg_m, of the plasmalemma of *Riccia fluitans* as a function of ammonia and methylamine concentration, respectively. After Felle (1980)

1979); by contrast, β- and γ-amino acids produced no significant depolarization (H. Felle and J. Tittor, unpublished data). These findings support the idea that ammonia and amino acids use separate pathways through the *Riccia* membrane.

Localized Membrane Transport

On a macroscopic, cellular scale an inhomogeneous distribution or activity of transmembrane electrogenic pathways will establish transcellular patterns of electric current density and electric fields. Transcellular electric fields across animal and plant cells and organs have been observed for decades, particularly, in association with cell growth and morphogenesis. For a recent review see Jaffe and Nuccitelli (1977). The studied examples include the above introduced giant alga *Acetabularia;* the activity of its electrogenic chloride import pump is highest at the developing apex of growing cell segments (Novák and Bentrup 1972).

Localized electrogenic transport is also associated with photosynthesis. Figure 8 shows that upon illumination the pH on the cell surface of the several centimeters long characean internodal cells develops into discrete alternating acid and alkaline regions. The alkaline bands have been long known from deposits on the cell wall of $CaCO_3$. Electric currents of about 75 mA m^{-2} density circulate between the acid and alkaline bands (Walker and Smith 1977). As outlined by the scheme of Fig. 8, an ATP-fueled electrogenic bicarbonate import pump is assumed to drive the observed current at the acid bands (A); the return

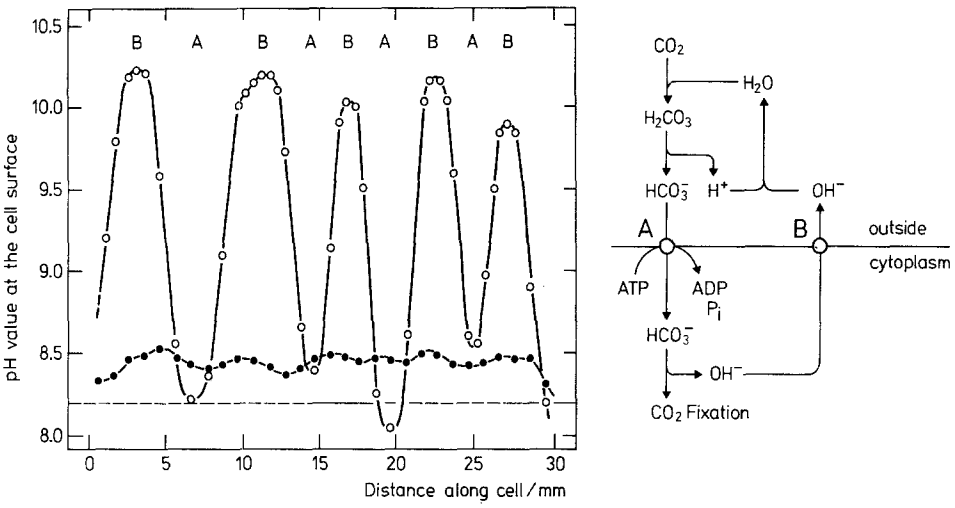

Fig. 8. Profile of extracellular pH at the surface of internodal cells of the giant alga *Chara corallina.* (○) In a solution containing 0. 2 mM KCl, 10 mM NaCl, 0.2 mM $CaSO_4$, and 1.0 mM $NaHCO_3$. The pH pattern developed after one hour of illumination (20 W m^{-2}). (●) The pH on the same cell was mapped after 30 min in the dark and subsequently 1 h of illumination in solution with 10 mM K^+ and 0.2 mM NaCl (other components as above). The dashed line indicates the background pH of the solution. After Lucas and Dainty (1977a). See text for explanation of the scheme

current is carried by passive electrogenic uniport of OH^- (H^+) at the alkaline bands (*B*).

At *A,* operation of the ubiquituous proton pump instead of the bicarbonate pump is not excluded, although it is unlikely, because photosynthetic bicarbonate assimilation requires a rate of bicarbonate uptake which is comparable to the measured electric current density, i.e., around 300 nmol m^{-2} s^{-1} (Walker and Smith 1977). The postulated bicarbonate pump requires the presence in the external medium of Ca^{2+} which may be substituted by Mg^{2+} or Sr^{2+} but not by Mn^{2+}. Actually, Ca^{2+} controls the maximum rate but not the apparent k_m of HCO_3^- assimilation of about 0.45 mM HCO_3^-. Thus Ca^{2+} could allosterically affect the bicarbonate uptake mechanism (Lucas and Dainty 1977a).

At *B,* passive electrogenic efflux of OH^- instead of H^+ influx has been argued by Lucas (1979) on the grounds that insensitivity of the alkaline bands against the external pH is more consistent with substrate regulation at the inner, cytoplasmic membrane surface. Inhibition of the protoplasmic streaming by the microfilament-inactivating cytochalasin B reversibly changes the OH^- efflux pattern from the discrete bands into a network of numerous small but still localized efflux sites, indicating that localization in fact arises from localized activation of uniformly distributed efflux sites on the plasmalemma (Lucas and Dainty 1977b). Apparently the cytoplasmic streaming facilitates the transport of OH^- from the chloroplasts to the efflux sites. Possible modes of activation and deactivation of the OH^- uniport mechanism have been discussed by Lucas et al. (1977).

The plausible purpose of this spatial organization of electrogenic transport is to optimize bicarbonate uptake hence photosynthetic carbon fixation. In the steady state, the fractional areas of membrane surface occupied by bicarbonate pumping and efflux of photosynthetically generated OH^- is ruled by the inhibition of the HCO_3^- pump through CO_3^{2-} prevailing at the very alkaline pH of the OH^- efflux region. Similarly, aquatic higher plants take up bicarbonate at the lower surface and dispose of the evolving OH^- at the upper surface of their submersed leaves; the numerous accounts for this observation are available from the recent study of this phenomenon by Lucas et al. (1978). Obviously, the underlying modes of regulation of transport mechanisms are not restricted to the level of a single cell.

Concluding Remarks

Whereas only a minority of plants employ the transmembrane electrical potential gradient to develop excitability (Bentrup 1979), strongly electrogenic transport appears to be an ubiquituous mechanism throughout the plant kingdom: A big membrane potential – in fact, up to −300 mV (comp. Spanswick 1973) – is generated by an ATP-fueled electrogenic uniport ion pump and utilized by secondary transport systems accumulating mineral and organic nutritients from highly diluted environments like the soil or freshwater. Accumulation ratios easily exceed $1 : 10^3$. (The freshwater liverwort *Riccia fluitans* maintains an intracellular K^+ concentration of 80 mM compared to some 50 μM in its environment.) Such considerable concentration gradients, in turn, provide a strong osmotic driving force for water uptake and thus create the cell turgor. Both transmembrane gradients, of electrical potential and hydrostatic pressure, compress the membrane. Strong evidence, in particular from Zimmermann and coworkers, exist for the idea that the plasmalemma is a compressible structure which thereby acts as a pressure-sensor during regulation of turgor and turgor-linked processes like cell growth (Zimmermann 1978).

Analysis of plant cell membrane transport mechanisms is heavily impeded, both on the cellular and subcellular level, by the pronounced compartmentation of the plant cell. The cell wall, for instance, complicates the study of transport across the adjacent plasmalemma, because it is a cation exchanger with a fixed charge concentration in the 0.3 M range and, secondly, establishes an extra unstirred layer which shows up at low concentrations of well permeating substrates, as in the above mentioned amine transport of the giant characean cells which have about 10 μm thick cell walls.

Isolation and purification of plasmamembrane fractions is impeded by the presence of different intracellular lytic compartments including the cell vacuole which occupies 90 to 95% of the adult plant cell volume and may be as acid as pH 1; in *Acetabularia,* the vacuolar pH is about 2, the cytoplasmic pH about 8 (cf. Raven 1976). Current advances in the study of transport properties, mainly of ATPases, by means of plasmamembrane vesicles from different plants are available from the proceedings on plant membrane transport edited by Spanswick et al. (1980).

Promising, on the other hand, seems that electrogenic transport now is adopted by both irreversible thermodynamics and kinetic rate theory. Irreversible thermodynamics which already have proven adequate to describe the coupling of solute and water fluxes in plants (Zimmermann and Steudle 1978), is now extended to coupled reactions like ATP-dependent proton pumping or ion-linked cotransport (Heinz and Geck 1977; Westerhoff and Van Dam 1979). Using Eyring's rate theory, Läuger (1973) had worked out transport through membrane channels, and recently specified this molecular approach for active electrogenic ion pumping (Läuger 1979). On the grounds of this theory and pertinent spectroscopic data, Warshel (1979) has proposed different molecular models for the light-driven proton pumping activity of bacteriorhodopsin in *Halobacterium halobium.*

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