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ABSTRACT

The electrophysiology of root cells of the marine halophyte, *Salicornia bigelovii* Torr., has been investigated. Cellular concentrations of K⁺, Cl⁻, and Na⁺ and resulting cell membrane potentials were determined as functions of time and exposure to dilutions of artificial seawater. Treatment of these data by the Nernst criterion suggests that Cl⁻ is actively transported into these root cells, but that active transport need not be invoked to explain the accumulation of Na⁺ at all salinities investigated nor for K⁺ at moderate to high salinities. In low environmental salinity, the cell electropotential of *Salicornia* root cells was found to respond to inhibitors in a fashion similar to that observed in glycophytes; in high environmental salinity, root cell membrane potential appears to be insensitive to bathing salinity and m-chlorocarbonylcyanide phenylhydrazide induces membrane hyperpolarization, in contrast to the response of glycophytes to such treatments. The fact that measured membrane potentials exceed diffusion potentials for Na⁺, K⁺, and Cl⁻ and the observation of a rapid depolarization by CO in the dark suggests an electrogenic component in *Salicornia* root cell membrane potentials.

MATERIALS AND METHODS

Plant Material. Plants containing mature seeds were collected from homogeneous stands along the beach and surrounding marsh land near Galveston, Texas. Seeds were removed from these field-dried plants by scraping and were stored at 4°C until needed. Seeds were germinated upon cheesecloth placed in illuminated shallow enamel trays for 7 days (or more, in some instances) at 23°C, the cheesecloth was watered with distilled H₂O to start germination and the tray covered with transparent plastic to retard evaporation. At the end of this period, seedlings were transferred to Vermiculite and thenceforth watered with a given concentration of ASW. ASW was prepared by dissolving 1.47 kg of Instant Ocean salts mixture (Aquarium Systems, Inc.) in distilled H₂O to give a final volume of 37.85 liters; 15.9 ml of liquid trace elements were added after dissolution of the salt (23). The major components of this solution (designated 100% ASW), in mm, are: 519 Cl⁻, 444 Na⁺, 6.0 SO₄²⁻, 49.4 Mg²⁺, 9.5 K⁺, 9.2 Ca²⁺, 2.3 HCO₃⁻, 0.4 H₂BO₃, 0.25 Br⁻, and 0.09 Sr²⁺. For a complete listing of the components of this solution, see reference 23. Dilutions of ASW were prepared by diluting 100% ASW with distilled H₂O. The pH of 100% ASW and its dilutions was found to be approximately 7.6.

Seedlings were grown under light banks consisting of a mixture of General Electric F48PG 17 CW, Sylvania F48T 12-VHO GRO WS, and Duro-Test 48T12 HO 800 vamp Vita-Lite fluorescent bulbs (10.5 μW cm⁻² nm⁻¹ at 655 nm) timed to give a 14-h daylight/10-h night regime. A diminished light, created by doubling the distance between the seedlings and the bulbs, was utilized during the first 7 days of plant growth to retard evaporation.

Electrical Measurements. Root tips approximately 1.0 cm long were removed from plants 7–30 days old with a razor blade and inserted into a micro flow chamber placed upon a microscope stage (6, 20). Before impalement, excised root tips were held in aerated ASW of the same composition as that used for electrical measurement. The microchamber was perfused with varying dilutions of ASW by gravity flow. Drastic changes in ASW concentration during electrode impalement led to poor electrical measurements, possibly due to the alterations induced by such changes in cell turgor pressure; therefore, tissue was allowed to equilibrate for 10–15 min to any change in perfusate before electrical measurements were recorded. Contrary to observations on glycophyte cell PD (20, 21), the measured PD in *Salicornia* root cells did not appear to change with time during the first 5–6 h following excision. Tissue was discarded if, under microscopic examination, it appeared damaged or had been excised for more than 3 h.

Cell potentials were recorded using Ling-Gerard glass capillary micro salt bridges and silver/silver chloride electrodes, as detailed elsewhere (20, 21). Glass salt bridges were pulled from capillary tubing containing glass fibers (Omega Dot capillary tubing, Frederick Haer Co., Ann Arbor). Electrodes used had resistances of less than 10 meqhm in 100% ASW, and were changed frequently during recording sessions. Cells used for electrical measurements were chosen from cortical cells in the same region of the root tip.
approximately 100–200 μm above the root cap, since PD values have been found to vary between different regions of plant roots (20). The potential difference between an agar-filled reference electrode placed in the bathing medium and an electrode placed within a cell by micromanipulation was amplified by a Winston Electronics model 1090 microelectrode preamplifier and recorded with a strip chart recorder.

**CCCP and CO Solutions.** CCCP solutions were prepared by dissolving CCCP in absolute ethanol and diluting this stock immediately before use (18) to 1 × 10⁻³ M with ASW by direct injection of a small amount of the ethanol stock into the perfusion chamber. For control purposes, ASW containing an equivalent amount of ethanol was perfused through the chamber; ethanol itself, at this dilution (1%, v/v), had no effect on cell PD. CO solutions were prepared by saturation of ASW dilutions with C.P. grade CO by vigorous bubbling (10). These CO-saturated ASW solutions were injected into the microchamber after stopping the influx of nonpoisoned ASW.

**Tissue Ion Content.** Seedlings were separated into roots and shoots by cutting with a razor blade, the tissue thoroughly rinsed in distilled H₂O to remove adhering Vermiculite and salt, weighed after blotting with filter paper, and extracted with boiling water. K⁺ and Na⁺ in the water extracts were then determined by flame emission spectroscopy and Cl⁻ determined by amperometric titration.

### RESULTS

The PD of *Salicornia* root cells changes over a 2 week period following the transfer of 1-week old seedlings from distilled H₂O to varying dilutions of ASW (Fig. 1). The root cell potential of seedlings exposed to 10% ASW falls strongly and the internal ionic concentration increases with time (Table I); however, this drop in membrane potential does not appear to be a simple function of increasing internal salinity since the PD of root cells exposed to 100% ASW exhibit a slight but significant increase (F₁,₃ = 11.9, P < 0.05) even though these cells' ionic content also increases to levels higher than that in seedling roots at the start of the ASW exposure period (Table I). The intermediate salinities tested exhibit a gradual transition between these two responses. The change in root cell membrane potential at all salinities appears to be most pronounced during the first 2 weeks following transfer from distilled H₂O (Fig. 1). We investigated this period more closely as a possible time of adjustment of the plants to the stress of high environmental salinity.

A determination of the ionic content of plant roots 7 days after transfer to Vermiculite and the start of the ASW exposure indicated that the Na⁺ and K⁺ content of these seedlings is relatively constant despite the wide range of environmental salinity to which they were exposed (Table I). The Cl⁻ content of these roots shows an apparent increase with environmental salinity, the correlation between environmental and internal chloride having an r value of 0.916.

**Table I. Ionic Content of *Salicornia* Seedlings, 14 Days from Germination**

<table>
<thead>
<tr>
<th>ASW %</th>
<th>Root/ Shoot</th>
<th>Na⁺</th>
<th>Na⁺</th>
<th>K⁺</th>
<th>K⁺</th>
<th>Cl⁻</th>
<th>Cl⁻</th>
<th>Eₜ</th>
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<td></td>
<td></td>
<td>mm</td>
<td>μmol/g fresh wt</td>
<td>mV</td>
<td>mm</td>
<td>μmol/g fresh wt</td>
<td>mV</td>
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<td>μmol/g fresh wt</td>
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<td>μmol/g fresh wt</td>
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<tr>
<td>0</td>
<td>R</td>
<td>96</td>
<td>147 ± 3.6</td>
<td>-129</td>
<td>170 ± 3.6</td>
<td>30.3</td>
<td>-159</td>
<td></td>
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<tr>
<td>S</td>
<td>94</td>
<td></td>
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<tr>
<td>10</td>
<td>R</td>
<td>164 ± 2.5</td>
<td>-33.3</td>
<td>0.95</td>
<td>147 ± 3.6</td>
<td>-129</td>
<td>170 ± 3.6</td>
<td>30.3</td>
<td>-159</td>
<td></td>
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<td>S</td>
<td>96 ± 3.1</td>
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<td>20</td>
<td>R</td>
<td>220 ± 4.0</td>
<td>-23.4</td>
<td>1.90</td>
<td>130 ± 4.0</td>
<td>-108</td>
<td>104</td>
<td></td>
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<tr>
<td>S</td>
<td>140 ± 3.5</td>
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<tr>
<td>30</td>
<td>R</td>
<td>230 ± 4.7</td>
<td>-14.0</td>
<td>2.85</td>
<td>150 ± 4.2</td>
<td>-101</td>
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<td>S</td>
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<tr>
<td>50</td>
<td>R</td>
<td>240 ± 3.0</td>
<td>-0.2</td>
<td>4.75</td>
<td>142 ± 1.4</td>
<td>-86</td>
<td>260</td>
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<td>S</td>
<td>217</td>
<td>60 ± 3.1</td>
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<tr>
<td>80</td>
<td>R</td>
<td>183 ± 4.5</td>
<td>16.9</td>
<td>7.60</td>
<td>135 ± 3.6</td>
<td>-73</td>
<td>415</td>
<td>285 ± 4.7</td>
<td>9.6</td>
<td>-133</td>
<td></td>
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<tr>
<td>S</td>
<td>298 ± 2.0</td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>100</td>
<td>R</td>
<td>270 ± 4.1</td>
<td>12.7</td>
<td>9.50</td>
<td>115 ± 0.7</td>
<td>-64</td>
<td>519</td>
<td>310 ± 2.8</td>
<td>13.1</td>
<td>-133</td>
<td></td>
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<tr>
<td>S</td>
<td>364 ± 4.5</td>
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FIG. 1. Change in the PD of *Salicornia* root cells with time of exposure to various dilutions of ASW; percentages refer to dilution of Instant Ocean. Seedlings were germinated on cheesecloth watered with distilled H₂O for 1 week prior to time of transfer to ASW dilutions and Vermiculite culture; day zero of figure represents day of transfer to Vermiculite watered with appropriate ASW solution. Bars represent ±SD, points represent means of three to nine replicates.
The K⁺ content of the shoot is relatively constant over the range of ASW dilutions tested and noticeably lower than that of the roots; shoot Na⁺ and Cl⁻ content, however, increases strongly with increasing salinity (Table I). In fact, there is a strong positive correlation between both the Na⁺ content of the shoot and environmental Na⁺ (r = 0.966) and the Cl⁻ in these cells versus external Cl⁻ (r = 0.988). High shoot Na⁺ appears to be characteristic of halophytes in general (9).

We did not find drastic changes in root salt content to occur between 15 and 24 days from germination (Tables I and II), a period which corresponded to significant PD changes in root cells. A slight increase in root cell content during these 10 days is accompanied by a drop in Cl⁻ content and an accompanying slight decrease in Na⁺ in most ASW concentrations tested; the converse being true for the cellular concentrations of these ions in the shoot (Tables I and II). Since this pattern of cell ion content change is roughly the same across all salinity values investigated, it does not seem that root cell electropotential changes can be explained by changes in internal salt concentration alone. Also note that during this time period, growth of both the shoot and roots of this plant was very slight.

To further explore *Salicornia* root cell PD behavior, we employed metabolic inhibitors to estimate the active contributions to cell PD and the Nernst criterion to arrive at the diffusion potentials of these three monovalent ions. The Nernst equation is represented by:

\[ E_N = \frac{RT}{xF} \ln \left( \frac{[K^+]_o}{[K^+]_s} \right) = \frac{RT}{xF} \ln \left( \frac{[Na^+]_o}{[Na^+]_s} \right) = \frac{RT}{xF} \ln \left( \frac{[Cl^-]_o}{[Cl^-]_s} \right) \]

where \( E_N \) = Nernst potential in volts; \( R \) = universal gas constant; \( T \) = absolute temperature; \( F \) = Faraday; \( x \) = ionic valence, and superscripts, i and o, refer to activities (concentrations) of ions inside and outside the cell, respectively. This relationship can be used to estimate a diffusion potential between the cell interior and the bathing medium for each of the ions considered under conditions of independent, passive ion movement and flux equilibrium between root cells and the root environment (13, 14). Predicted PD values for each ion can then be compared to measured electrical potentials (Tables I and II). Such comparisons in non-photosynthetic glycophyte cells usually show the PD of such cells to be close to a diffusion potential for K⁺; i.e. for most non-photosynthetic glycophyte systems, a 10-fold increase in the ratio of K⁺ outside the cell to that inside causes a -58 mV change in PD (12, 21). This is clearly not the case in *Salicornia* root cells for any of the three ions tested (Tables I, II, and IV).

Using a converse approach, one may compare the actual ion content of the tissue with that predicted by the Nernst relation. In both 14- and 24-day old seedling roots exposed to ASW for 7-17 days, respectively, predicted values for K⁺ are usually higher than those measured, values for Na⁺ always much higher and values for Cl⁻ are also far higher than those predicted by the Nernst equation (Table III). In low ASW concentrations, K⁺ approaches its predicted concentration, but the strong increase in cell K⁺ content predicted by the Nernst relation for increasing ASW concentrations does not occur. These data suggest that Cl⁻ is accumulated by *Salicornia* roots at the expense of metabolic energy in all dilutions of ASW investigated; however, metabolic energy need not be invoked to explain the accumulation of Na⁺ or for K⁺, except for the lowest ASW concentrations investigated (Table III).

Since the PD in these roots does not seem, in general, to respond in a fashion suggesting a relation to the passive distribution of Na⁺, K⁺, or Cl⁻, and because the root PD responds so differently with time at high and low ASW dilutions, we decided to investigate the active components of cell PD from plants grown in 10 and 100% ASW by means of metabolic inhibitors. Cell PD, measured in either young (Fig. 2, A and B) or older (Fig. 2, C and D) seedling roots, responds in a similar fashion to the uncoupling agent CCCP; at low external salt concentrations, a depolarization of root cell PD results, but at high salt concentrations, a hyperpolarization results. A much different result has been found for the respiration blocking agent, CO (Fig. 3); blocking electron transport by infusing the tissue with CO and forming the light reversible iron carbonyl complex (and supposedly stopping respiration) by turning off the microscope illuminator (2, 10), causes a depolarization of cell PD in either high or low ASW concentrations.

The response of *Salicornia* root cell PD over a short time period to changes in external salinity is quite different from that found for glycophytes. Changing the salinity of the solution bathing roots taken from plants grown in 100% ASW causes a rise in measured electropotential values, when the bathing salinity increases from 20 to approximately 50% ASW; at higher salinity, measured values remain relatively constant (Table IV).

**DISCUSSION**

In low salinity, the PD of *Salicornia bigelovii* root cells appears to behave in a manner similar to that of glycophyte cells (1, 2, 8, 10, 13, 20), and markedly different from the behavior of glycophyte cells in increasing salinity. The membrane PD of pea stem cells, for example, is depolarized both by 10 μM CCCP and saturated aqueous CO in the dark (2, 10) in much the same way that the PD of *Salicornia* roots behaves in 10% ASW. The hyperpolarization of *Salicornia* cell PD by 10 μM CCCP in high external salinity, however, appears to be a departure from glycophyte behavior (Fig. 2). It is not known whether this hyperpolarization

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**Table II. Ionic Content of *Salicornia* Seedlings, 24 Days from Germination**

<table>
<thead>
<tr>
<th>ASW</th>
<th>Root/ Shoot</th>
<th>Na⁺</th>
<th>Na⁺</th>
<th>E₅</th>
<th>K⁺</th>
<th>K⁺</th>
<th>E₅</th>
<th>Cl⁺</th>
<th>Cl⁻</th>
<th>E₅</th>
<th>E₅</th>
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</thead>
<tbody>
<tr>
<td>%</td>
<td></td>
<td>mv</td>
<td>μmol/g fresh wt</td>
<td>mv</td>
<td>μmol/g fresh wt</td>
<td>mv</td>
<td>51.9</td>
<td>140 ± 4.9</td>
<td>25.3</td>
<td>-118</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10 R</td>
<td>S</td>
<td>44.4</td>
<td>101 ± 2.1</td>
<td>-20.1</td>
<td>0.95</td>
<td>157 ± 8.1</td>
<td>-130</td>
<td>191 ± 6.6</td>
<td>14.1</td>
<td>-140</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20 R</td>
<td>S</td>
<td>88.8</td>
<td>190 ± 2.1</td>
<td>-19.4</td>
<td>1.90</td>
<td>92 ± 4.9</td>
<td>-99</td>
<td>192 ± 3.5</td>
<td>229 ± 4.2</td>
<td>-145</td>
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<td></td>
</tr>
<tr>
<td>30 R</td>
<td>S</td>
<td>133</td>
<td>180 ± 9.1</td>
<td>-7.7</td>
<td>2.85</td>
<td>160 ± 5.0</td>
<td>-103</td>
<td>199 ± 11.8</td>
<td>6.2</td>
<td>-145</td>
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<tr>
<td>50 R</td>
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<td>222</td>
<td>189 ± 4.2</td>
<td>4.1</td>
<td>4.75</td>
<td>163 ± 3.5</td>
<td>-90.2</td>
<td>248 ± 6.6</td>
<td>-1.2</td>
<td>-142</td>
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<tr>
<td>80 R</td>
<td>S</td>
<td>355</td>
<td>189 ± 4.2</td>
<td>4.0</td>
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<td>-17.1</td>
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</tr>
<tr>
<td>100 R</td>
<td>S</td>
<td>444</td>
<td>140 ± 9.8</td>
<td>29.4</td>
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<td>167 ± 5.4</td>
<td>-73.2</td>
<td>265 ± 4.2</td>
<td>-17.1</td>
<td>-149</td>
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</tr>
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</table>

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is a phenomenon peculiar to *Salicornia*, to halophytes, or to high external salinity, but it is apparently not related to the age of the tissue (Fig. 2).

The hyperpolarization by CCCP but depolarization by CO at high salinity (Figs. 2 and 3) suggests a different mode of action for these two inhibitors. The common assumption is that plant cell membrane potentials are a composite of a diffusion potential, due to the passive distribution of ions, and an active electrogenic potential due to the metabolic pumping of ions across the cells' limiting membranes (13, 15). The electrogenic pump is usually thought to be driven by ATP breakdown (13, 15) and conditions which decrease the ATP pool in cells should eliminate this voltage component. Both CCCP and CO (in the dark) have been suggested to lower cytoplasmic ATP levels in other organisms. If they do so and the electrogenic pump depends upon ATP, then one should expect a similar effect on membrane potential, and, in fact, they do have a similar effect upon cell PD in halophyte tissues (2, 11). However, CCCP is also known to increase in membrane permeability, especially with respect to H⁺ (18) and Cl⁻ (17). Therefore, the hyperpolarization caused by CCCP at high salinity values could involve an increase in cell membrane permeability. For example, if CCCP increased the membrane permeability to H⁺, the resulting PD changes observed in Figure 2 could be explained by an internal pH of approximately 6.5 in 10% ASW and 4.5 in 100% ASW. In fact, acidification of plant cell cytoplasm in response to salinity has been observed (9).

Another possibility might entail a low concentration of Cl⁻ in the cytoplasm that would present a low E₉ for this ion in low salinity and a high E₉ in response to high salinity. If CCCP were to increase the plasma membrane permeability to Cl⁻, this could
lead to a membrane hyperpolarization if external Cl\(^-\) was high and a depolarization of external Cl\(^-\) was low.

In both of these models, the sustained nature of the hyperpolarization is difficult to account for, i.e. why does the cell remain hyperpolarized for up to 20 min (Fig. 2) when (supposedly) only diffusion is operating? Why is the hyperpolarization not transient, as is sometimes experienced with CN\(^-\) inhibition (2)? Under CO poisoning (Fig. 3) the potential reached most closely approaches that of a K\(^+\) diffusion potential, of those considered (Fig. 3 and Table I), as if, under CO poisoning, E\(_m\) depends largely upon K\(^+\). The fact that Cl\(^-\) and Na\(^+\) do not appear to be near passive equilibrium (i.e. that predicted by the Nernst equation) between these cells and the bathing medium should not be surprising, since these ions are usually found to be removed from equilibrium in glycophytes as well (14). On the other hand, the glycophyte literature suggests that K\(^+\) is usually closer to equilibrium values than we have found for Salicornia roots. These discrepancies between actual and equilibrium values could be due to a number of factors, including active pumping of the ions in question and compartmentation of salt within the tissue; thus, the ionic content of the component in which the electrical measurements were performed may differ from those estimated here. The tip of the electrode, for instance, might be in the vacuole whose ionic content and, therefore, the PD measured, might differ from measurements resulting from an electrode tip placed within the cytoplasm. In glycophytes, at least, this possibility does not seem to be a problem, since the potential difference across the tonoplast is usually found to be slight and vacuolar PD measurements thus closely reflect cytoplasmic values (7 and refs. therein). It is not possible to determine the contribution of cytoplasm/vacuolar ion content differences from the present data.

Some ions besides the three investigated could also be involved in determining the membrane PD in Salicornia root cells. The uncoupler data discussed above would suggest H\(^+\) as a distinct possibility.

Root cells of the halophyte S. bigelovii exhibit cell PD values which differ in several respects from equivalent measurements on glycophytic species. Some of the deviation from glycophytic behavior, such as hyperpolarization by CCCP, appears to be found in the presence of high external salinity. Another deviation is the lack of decrease of cell PD with increasing environmental salinity. Whether these differences from glycophyte behavior are related to the adaptation of this plant to its environment must await further experimentation.

Finally, Cl\(^-\) is apparently accumulated at the expense of metabolic energy by Salicornia roots in all environmental salinities; Na\(^+\) accumulation at all salinities and K\(^+\) accumulation at all but the lowest salinities investigated does not appear to require metabolic energy. The fact that E\(_m\) exceeds E\(_K\) for Na\(^+\), K\(^+\), and Cl\(^-\) and the rapid depolarization induced by CO in the dark suggests that Salicornia root cell PD contains an organic component as has been suggested for glycophyte cells (1, 12, 13).

Acknowledgments—We wish to thank Drs. N. Higinbotham, C. B. Osmond, B. Etherton, U. Lütge, R. M. Spanswick, and W. S. Fierce for helpful suggestions during the preparation of this paper.

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