Nonosmotic Effects of Polyethylene Glycols upon Sodium Transport and Sodium-Potassium Selectivity by Rice Roots

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ABSTRACT

Addition of polyethylene glycol (PEG) as an osmotic agent (at ~230 kilopascals and less) had no effect upon transpiration rate but reduced sodium uptake (from 10–50 moles per cubic meter NaCl) by up to 80%. PEG (at ~33 kilopascals) also reduced chloride uptake but had no effect upon the uptake of potassium from low (0.5–2.0 moles per cubic meter) external concentrations. However, the increased uptake of potassium occurring between 2 and 10 moles per cubic meter external concentration was abolished by PEG. Similar concentrations of mannitol had no effect upon sodium uptake in rice. PEG, in similar conditions, had much less effect upon sodium uptake by the more salt-resistant species, barley.

20Na studies showed that PEG reduced the transport of sodium from root to shoot, but had a long half time for maximal effect (several days).

14C-labeled PEG was shown to bind to microsomal membranes isolated from rice roots; it is suggested that this is due to multipoint attachment of the complex ions of PEG which exist in aqueous solutions. It is argued that this reduces passive membrane permeability, which accounts for the large effect of PEG on sodium influx in rice and the different effects on sodium influx and (carrier-dependent) potassium influx.

Polyethylene glycols were first used in plant physiological studies some 40 years ago when they were employed as carriers for growth substances, although in more recent years, the primary use of these compounds has been as osmotics. This use of PEGs as osmotic agents stems from the work of Dean and Moore (5) and McClendon and Blinks (12) and has continued since although beset with a number of difficulties.

Central to the use of PEG as an osmotic agent is a knowledge of the osmotic potentials of aqueous solutions. These potentials were initially determined from measurements of freezing point depression (4) but, more recently, vapor pressure osmometry and thermocouple psychrometry have been favored although controversy still exists over the best methods to use (11, 20). All the measurements have, however, clearly indicated that the solute potentials of PEG solutions are much lower than an ideal solution at an equivalent concentration. The unusual osmotic properties of aqueous solutions may be a consequence of hydrogen bonding to the ether oxygen (17), the presence of ordered cages of water around the PEG molecules in solution (see 13), or to the existence of the solution of polyoxonium cations (2, 17). Steuter et al. (20) speculate that the existence of the polyoxonium ions may affect the availability of nutrients and, certainly, interactions between PEG and nutrient solutions have been hinted at if not rigorously quantified (13).

The most common problem with PEG in physiological work has been toxicities. This was noted for commercial products (7, 10) but the toxic elements, which are presumably residues of the catalysts (such as aluminum) used in polymerization, can be effectively removed by either dialysis or passage through ion-exchange columns (7, 10, 16). Formaldehyde which appears on heating (18) and possibly on standing in sunlight at room temperature may also be an important contaminant. With suitable precautions, however, the use of PEGs as inert osmotics has attained general acceptance. Some other observations, however, which may relate to the peculiar properties of aqueous PEG solutions, are not easy to explain. Most notable are their ability to clump red-blood cells (19) to precipitate soluble enzymes (21) and to promote fusion of isolated plant protoplasts (9).

In the studies reported in this paper we initially employed PEG, in its conventional role as an inert osmoticum, to separate osmotic and ionic aspects of salinity damage to rice seedlings. However, we found effects upon ion transport and selectivity which could not be accounted for by known influences of PEG upon the water potential of the medium. The effect of PEG upon ion selectivity by the root, at concentrations below the threshold for reducing transpiration, are described, and a possible mode of action proposed.

MATERIALS AND METHODS

Growth of Plants. Seeds of Oryza sativa L. were obtained from the International Rice Research Institute, Manila, and the elite breeding line IR 2153-26-3-5-2 used unless otherwise stated. Seeds were imbibed for 24 h in aerated deionized water and then transferred to grids over the surface of a culture solution containing (in mol m⁻³) K (2.1), Ca (0.75), Mg (1.6), P (1.0), SO₄ (2.2), NH₄ (1.4), NO₃ (1.4) and micronutrients, as described by Yoshida et al. (26). Rice was grown under a 12-h photoperiod at 70 w m⁻² PAR at 30°C and 70% RH. The dark period was 25°C and 80 to 90% RH. Solutions were not aerated and there was a continuous vertical airflow of 0.25 ms⁻¹ (model E15, Conenviron). Hordeum vulgare L. cv 'Igri' was similarly germinated but grown under a 16-h photoperiod with day/night temperatures of 22°C/17°C.

Seedlings were transplanted aged 7 d into black plastic boxes (1 L capacity) or into individual black-painted Pyrex tubes. Treatments with NaCl and PEG were imposed 7 d later and, according to the experiment, harvests were generally made 7 to 10 d later. Control plants took up large quantities of NaCl during

1 Supported by the United Kingdom Overseas Development Administration.
this period and toxicity symptoms (such as rolling of young leaves and death of old leaves) became evident at 50 mol m$^{-3}$ NaCl. For survival experiments, the population of plants was maintained for 22 d after salinization. For K$^+$ uptake experiments, treatments were imposed at 7 d and harvests made at 21 d.

**Analysis of Plant Material.** Shoots were excised, dried under forced draught at 50°C and the dry weight recorded. Dried material was extracted in acetic acid (100 mol m$^{-3}$, 90°C, 2 h). Cations were determined in the extract by atomic absorption spectrophotometry (Pye Unicam SP 800) and chloride by an electrode (E.I.L.). Transpiration was measured by loss of weight from seedlings fitted into glass tubes with nonabsorbant cotton wool after correction for evaporation losses from the solution surface.

**PEG Binding to Microsomal Membranes.** Rice roots were homogenized in (sucrose (400 mol m$^{-3}$), Tes-NaOH (25 mol m$^{-3}$, pH 7.2), EDTA (3 mol m$^{-3}$)) at 3 ml/g tissue in a vortex-type blender (Kenwood) for 1 min at 4°C. The homogenate was filtered through terrylene cloth and centrifuged for 20 min at 17,500 g max (M.S.E.). The supernatant was recentrifuged for 27 min at 190,000 g max (M.S.E.) and the pellet kept as the microsomal fraction. Aliquots of the microsomal preparation were resuspended in a medium containing sucrose (400 mol m$^{-3}$), Tes-NaOH (1 mol m$^{-3}$, pH 7.2), CaCl$_2$ (1 mol m$^{-3}$), and MgSO$_4$ (1 mol m$^{-3}$). $[^{14}]$CPEG 4000 (99% 2500–6000 kDa, Amersham International) was added (final concentration, 2.88 mmol m$^{-3}$; 3.2 TBq mol$^{-1}$; reaction volume 2 ml) and the suspension placed in a shaking bath for 1 h. The reaction mixture was diluted with buffer to 45 ml and centrifuged at 190,000 g max for 27 min. The pellet was resuspended in 1 ml, diluted to 45 ml, and recentrifuged. The washing operation was then repeated. The final pellet was resuspended in 750 µl buffer and, together with samples of the supernatant, radioactivity was determined in 'Aquasol' (New England Nuclear) by liquid scintillation spectrometry (Beckmann). Protein was measured on subsamples by a standard Folin reagent assay.

**RESULTS AND DISCUSSION**

**Survival of Seedlings in Salinity.** Rice is very sensitive to salinity and 50 mol m$^{-3}$ NaCl affects even the more resistant varieties at the seedling stage (6). Seedlings (age, 14 d) were salinized with NaCl (-230 kPa, 50 mol m$^{-3}$) with or without the addition of PEG 1540 (-230 kPa, 70 g l$^{-1}$) and the survival of the plants followed. The addition of PEG dramatically reduced the rate of death of individuals compared with the treatment with NaCl alone (Fig. 1). At this concentration salinity damage is unlikely to be due to water deficits since the combined treatment (NaCl + PEG) had the lower water potential but permitted the better survival and is seen primarily as Na (and/or Cl) ion toxicity (6, 23, 24). The rate of net transport of Na from root to shoot in saline conditions can be 10 mmol g$^{-1}$ dry weight roots d$^{-1}$ (25) which is comparable with a halophyte and some 10 times typical saturation values for K$^+$ net transport in glycophytes (22). It is not, in our view, likely that rice has evolved a Na$^+$ carrier system of this enormous capacity and we consider that Na influx in rice must be mediated largely by carrier-independent membrane leakage. The beneficial effect of PEG could, then, have been due to its lowering the water potential of the medium, so reducing the transpirational volume flow and consequently the net flux of salt to the shoot.

**Effects of PEG upon Na$^+$ Uptake and Transpiration.** PEG 1540 (at -230 kPa) did reduce transpiration in saline (50 mol m$^{-3}$ NaCl) conditions in most of the varieties examined but its effect upon Na$^+$ uptake by these varieties was more pronounced than the reduction in transpiration. Effects upon transpiration ranged from about 40% inhibition, to a stimulation in IR28 (Fig.
and 90% RH at 30°C aged 14 d and harvested 10 d later. [Na]xylem is apparent xylem concentration.

Table 1. Effect of Different Relative Humidities upon Growth, Transpiration, and Ion Uptake by Rice in Saline Conditions

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>70% RH</th>
<th>90% RH</th>
</tr>
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<tbody>
<tr>
<td>Dry wt</td>
<td>mg</td>
<td>254 ± 74</td>
<td>173 ± 29**</td>
</tr>
<tr>
<td>Transpiration</td>
<td>ml plant−1 (10 d)−1</td>
<td>120 ± 21</td>
<td>42.7 ± 8.3**</td>
</tr>
<tr>
<td>Shoot Na</td>
<td>mmol (g dry wt)−1</td>
<td>2.28 ± 0.62</td>
<td>0.822 ± 0.398**</td>
</tr>
<tr>
<td>Shoot Cl</td>
<td>mmol (g dry wt)−1</td>
<td>1.77 ± 0.47</td>
<td>0.830 ± 0.249**</td>
</tr>
<tr>
<td>Shoot K</td>
<td>mmol (g dry wt)−1</td>
<td>0.556 ± 0.056</td>
<td>0.691 ± 0.047**</td>
</tr>
<tr>
<td>[Na]xylem</td>
<td>mol m−3</td>
<td>4.84 ± 0.249</td>
<td>74 ± 19 NS</td>
</tr>
</tbody>
</table>

* Significance based on t tests: ** P = 0.01, * P = 0.05.

2 Abbreviations: Jn, transpirational volume flow; Jw, net transport of an ion (J) per unit of root weight and time.

Fig. 3. The effect of low concentrations of PEG upon seedlings of two varieties salinized with NaCl (50 mol m−3) when aged 14 d. Shoot dry weight (A), transpiration (O), and shoot sodium concentration (Q) as a % of controls without PEG but 50 mol m−3 NaCl alone (harvested after 7 d). Mean values, n = 10 at each treatment. Ten g CP = −33 kPa.

2. The reduction in shoot sodium concentration ranged from 30% to more than 80%. For instance, the apparent Na+ concentration in the xylem (calculated as Jn/Jw)2 was reduced from 6 to 3.5 mol m−3 in the salinity-resistant variety Bhura Rata and from 20 to 2 mol m−3 in the salinity-sensitive variety IR 2153-26-3-5-2 (Fig. 2), i.e. reductions of 40 to 90% (derived from data in Fig. 2). In contrast, a reduction in transpiration of 65% by increasing atmospheric humidity reduced the apparent xylem concentration of sodium by only 32% (Table I).

It seems, then, that PEG has effects upon Na+ uptake by rice varieties which are independent of its effects via changes in the water potential of the medium. This was examined further by considering effects of PEG at concentrations lower than those which would normally be used for osmotic stress (Fig. 3). Reductions in Na+ uptake of between 60 and 80% were produced at PEG concentrations which had no significant effect upon the transpiration rate (Fig. 3).

Comparisons were also made between PEGs of differing mean mol wt (up to 6000 D), and mannitol (a sugar alcohol which is commonly used as a low mol wt osmoticum). The different PEGs, all at 10 g l−1 (−33 kPa for PEG 1540, approximately −20 kPa for PEGs 4000 and 6000) all reduced the shoot sodium concentration after 7 d growth in 50 mol m−3 NaCl by 50 to 60% (Table II). Conversely, 10 g l−1 of mannitol (−145 kPa) had no effect whatsoever on sodium uptake (Table II). This provides confirmation that a specific effect of PEGs, independent of their osmotic effect, reduces Na+ uptake by rice.

Differential Effects of PEG on the Uptake of Ions. PEG 1540 at 10 g l−1 (−33 kPa) caused no significant change in the shoot K+ concentration, while the concentrations of Cl− and Na+ were depressed by 34% and 55%, respectively. PEG had no effect upon either shoot or root dry weights, nor upon the transpiration rate (Table III). Reduction of Na+ transport from 50 mol m−3 NaCl became apparent at only −3.4 kPa (1 g l−1) of PEG and increased progressively with PEG concentration; but K+ was unaffected (Fig. 4).

To examine this Na/K discrimination further, the effect of PEG on K+ transport was examined at a range of external K+ concentrations. Shoot K+ concentration was practically identical in plants grown at 0.5 and 2.0 mol m−3 K+ and at neither concentration was there any effect of PEG. At 10 mol m−3 K+, shoot K+ concentration increased by 60% in the absence of PEG but this increase was prevented in the +PEG treatment (Table IV). An additional component of K+ uptake, which can be distinguished by PEG, was evident at high (10 mol m−3) external concentrations of K+.

Time Course of the Effect of PEG on 22Na Uptake and Transport. Hitherto we have reported only long-term effects of PEG on ion transport and selectivity. 22Na uptake from 10 mol m−3 NaCl was followed plus and minus PEG 1540 (−33 kPa). A reduction in Na+ transport to the shoot was evident after 24 h and became proportionately greater with time (Fig. 5). There was no significant difference in the Na+ concentration in the roots: over 96 h, the net uptake of 22Na into the plant was...
Fig. 4. The effect of low concentrations of PEG 1540 (up to 10 g l⁻¹, −33 kPa) upon Na⁺, K⁺ and Cl⁻ concentrations in the shoots of IR 2153 salinized with NaCl (50 mol m⁻³), plus and minus the PEG treatments, when aged 14 d, and harvested 7 d later. Mean values, n = 10 at each treatment.

Table IV. Shoot K⁺ Concentration (mmol g⁻¹ dry wt) in Rice Plants Grown ± PEG 1540 (−33 kPa, 10 g l⁻¹) in a Full Culture Solution Containing K⁺ at 0.5, 2.0, and 10.0 mol m⁻³

<table>
<thead>
<tr>
<th>[K⁺] External mol m⁻³</th>
<th>Control Shoot [K⁺] mmol g⁻¹ dry wt</th>
<th>+PEG (−33 kPa) Shoot [K⁺] mmol g⁻¹ dry wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>0.810 ± 0.042</td>
<td>0.817 ± 0.077</td>
</tr>
<tr>
<td>2.0</td>
<td>0.859 ± 0.047</td>
<td>0.837 ± 0.043</td>
</tr>
<tr>
<td>10.0</td>
<td>1.411 ± 0.650</td>
<td>0.860 ± 0.055**</td>
</tr>
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</table>

reduced by 67%, whereas the root concentration itself remained unaffected (Fig. 5).

The effect of PEG was more pronounced if the roots were pretreated with PEG (Fig. 6). This indicates either that PEG takes some time to reach all its target sites or else that the effect itself depends at least partly on a characteristic of the roots with a long half time. Only in roots which had been pretreated with PEG was there any reduction in Na⁺ concentration in the root itself.

Mode of Action of PEG. Any proposed mechanism must be able to account for: (a) reduction in ion transport (Na⁺, K⁺, and Cl⁻) in the absence of effects upon either growth or transpiration; (b) differential effects upon Na⁺ and K⁺; and (c) a greater effect upon shoot Na⁺ concentration than upon root Na⁺ concentra-

Fig. 5. Time course of ²²Na uptake by seedlings of IR 2153 (aged 14 d at 4°C) from NaCl (10 mol m⁻³) minus (○) and plus (●) PEG 1540 (−33 kPa) over 96 h. Mean and SE, n = 20 at each point.

Fig. 6. The effect of PEG 1540 (−33 kPa) upon ²²Na uptake (from 10 mol m⁻³ NaCl), when supplied either simultaneously with the ²²Na or after 3 d preincubation of the roots with PEG. Seedlings of IR 2153 (aged 14 d at 4°C) were exposed to NaCl (10 mol m⁻³). PEG and ²²Na were supplied as per shaded regions in the figure. The sodium concentrations in root and shoot (mean and SE, n = 20) are shown.

PEG 1540 (at −33 kPa) produced only minimal reductions in the conductivity of NaCl and KCl solutions of 10 mol m⁻³ concentration (1.6 and 4.1%, respectively) and elicited no change in the activity of K⁺ as measured by a K⁺ ion electrode. PEG did not produce solution effects which could explain its large and differential effect upon Na⁺ and K⁺ uptake.

It follows that PEG must interact with the plant material and it is necessary to postulate, at least, that PEG travels substantial distances in the apoplast in quantities sufficient to affect membrane transport sites, carrier independent membrane permeability, or the membrane bypass flow. There are several reports that PEGs of substantial mean mol wt do in fact enter plant tissues. Carpita et al. (3) used a range of molecules of differing size, including PEG, to estimate the pore sizes of cell walls, observing the molecular size at which there was a transition from plasmolysis (collapse of the protoplast) to cytorrysis (collapse of the cell wall) in high external concentrations. Depending upon the plant tissue used, the range was from 3.5 to 5.2 nm. PEG 1540 has a mean diameter of 3.8 nm and the upper limit (5.2 nm) would
also include PEG 6000 (3). Even PEG 20,000 passed from root medium to leaves of beans unaltered (10). The rather long half time for full expression suggested by the pretreatment studies (Fig. 6) would be compatible with a rather slow permeation of PEG in the apoplastic continuity.

The data in Table IV are evidence that K⁺ transport at 10 mol m⁻³ K⁺ has a component which can be distinguished by PEG from the mechanism(s) responsible for K⁺ uptake at 2 mol m⁻³ K⁺. There are two possible explanations. (a) If all K⁺ uptake is carrier-mediated, then PEG must discriminate between different carrier molecules which would be responsible for K⁺ transport from different external concentrations. (b) There is some additional carrier-independent entry of K⁺ at high external K⁺ concentrations and it is this which is prevented by PEG. It is our opinion that the first postulate is not credible since it requires high molecular weight protein recognition by a PEG molecule of perhaps 6000 D. The Na⁺/K⁺ discrimination can be more reasonably explained by an effect of PEG on carrier-independent influx which is likely to be important in Na⁺ entry in saline conditions and is a plausible interpretation of the PEG-sensitive component of K⁺ uptake in Table IV.

Such carrier-independent pathways are membrane leakage, and the membrane bypass flow.

There is no direct evidence to dismiss a blockage of the bypass flow, other than implausibility. It would be necessary to suppose that PEG could distinguish between the bypass route (undifferentiated endodermis and endodermal rupture by lateral roots, etc.; cf. 14) and the rest of the water movement pathway. An explanation based solely on the bypass flow requires that this contributes at least 70% of the shoot Na⁺ at 10 mol m⁻³ NaCl and that -33 kPa of PEG blocks it specifically and effectively. We feel such a proposition to be untenable.

There are ways in which PEG could interact directly with the membrane. The action of PEG as a 'molecular bridge' was proposed by Kao and Michayluk (9) to account for its ability to promote protoplast fusion; it was envisaged as linking adjacent protoplasts together by multiple attachment. The enormous PEG concentrations (250–500 g l⁻¹ of PEG 1540) needed to achieve this, however, implicate the importance of other, probably osmotic, factors.

The potential for ionic interactions at the membrane surface to affect membrane permeability is considerable: for instance, PEG could form H-bonds with proteins and carbohydrates (cf. 9), and divalent Ca²⁺ ions could be involved in forming bridges between the membrane surface and the PEG molecule. Furthermore, the polyoxonium cation (2, 17) can presumably interact with fixed negative charges on the membrane surface. Ca²⁺ ions, which bind to phospholipid head groups in single and mixed phospholipid dispersions, cause both decreases in the fluidity of the hydrocarbon chains and selective aggregation of molecular species (cf. 15). If such effects occur in biological membranes in response to other ionic interactions, such as with the PEG molecule, then there are theoretical bases for understanding how PEG might reduce passive membrane permeability. Cation diffusion across artificial bilayer membranes is related to their fluidity, being lowest in the least fluid arrangements. Molecular movements in the plane of the membrane are inherent in the fluid mosaic model and would be important in passive leakage if this gave rise to transient pores (cf. 8). Multiple attachment between charged sites on the membrane and the PEG would reduce molecular movement in the membrane and/or stabilize it in a manner analogous to divalent metal ions.

PEG-membrane interaction was investigated by looking for evidence of binding of [¹⁴C]PEG to root microsomal membrane preparations. Microsomal membranes were incubated with [¹⁴C] PEG (in buffer with Ca⁴⁺ and Mg²⁺ ions). About 2 pmol PEG/mg protein remained associated with the membranes, after extensive washing, and presumably much more would have been more loosely associated. It was furthermore evident from the supernatant counts that this could not be explained by enclosure of the [¹⁴C] within the membrane vesicles (Table V).

It would be expected from this explanation that PEG should have much less effect upon a species with better control of Na⁺ uptake in the first place (i.e. a more salt resistant glycophyle—a better 'excluder' in that terminology). This was examined in barley, one of the more salt-resistant crop cereals. Sodium uptake to the leaves of barley was substantially lower than rice in the same conditions and was reduced by only 15% and 16% by PEG at -33 kPa and -230 kPa, respectively.

It is not necessary to postulate a role of PEG other than at the cortical plasma membranes if it is assumed only that the cortical vacuoles compete strongly for Na⁺ with flow to the xylem. In this event, restricted Na⁺ uptake at the plasmalemma would lead to transport to the shoot only once the cortical vacuoles had achieved their steady state. Consequently, shoot concentration could be affected more than root concentration (see Fig. 5) without postulating a need for a PEG effect inside the cortical plasmalemma.

The differential effect of PEG on Na⁺ and K⁺ uptake in rice emphasizes the different modes of entry of the saline and the nutrient ion. Moreover, the results emphasize the importance of uncontrolled Na⁺ entry in the sensitivity of rice to salinity and contrast it with the situation in the more resistant barley. The proposed explanation of the results reported here strongly implicates the passive ion permeability of the root membranes in salt sensitivity in rice. If this interpretation is correct, then quite minor changes in membrane properties can have profound effects upon salinity resistance of sensitive species. Rice has other physiological mechanisms to assist the resistance of the consequences of excessive NaCl uptake (23–25) as do many species. However, excessive uncontrolled salt entry is central to salinity damage.

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**Table V. Binding of [¹⁴C]PEG 4000 to Rice Root Microsomal Membranes**

The membrane preparations were incubated with [¹⁴C]PEG for 1 h, then separated by centrifugation from the labeling medium (supernatant 1) and washed twice by centrifugation and resuspension (supernatants 2 and 3). 1 and 2 are replicate experiments.

<table>
<thead>
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<th>Parameter</th>
<th>Units</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Supernatant 1</td>
<td>Bq ml⁻¹</td>
<td>391</td>
<td>362</td>
</tr>
<tr>
<td>Supernatant 2</td>
<td>Bq ml⁻¹</td>
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<td>0.38</td>
</tr>
<tr>
<td>Supernatant 3</td>
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<tr>
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<td>mg</td>
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<tr>
<td>PEG binding</td>
<td>pmol mg⁻¹ protein</td>
<td>1.96</td>
<td>1.62</td>
</tr>
</tbody>
</table>
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