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Aluminum and Temperature Alteration of Cell Membrane Permeability of *Quercus rubra*[1]

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ABSTRACT

This report extends research on Al-induced changes in membrane behavior of intact root cortex cells of Northern red oak (*Quercus rubra*). Membrane permeability was determined by the plasmometric method for individual intact cells at temperatures from 2 or 4 to 35°C. Al (0.37 millimolar) significantly increased membrane permeability to urea and monoethyl urea and decreased permeability to water. Al significantly altered the activation energy required to transport water (+32%), urea (+9%), and monoethyl urea (−7%) across cell membranes. Above 9°C, Al increased the lipid partiality of the cell membranes; below 7°C, Al decreased it. Al narrowed by 6°C the temperature range over which plasmolysis occurred without membrane damage. These changes in membrane behavior are explainable if Al reduces membrane lipid fluidity and kink frequency and increases packing density and the occurrence of straight lipid chains.

Al^3 toxicity is the major factor limiting plant growth in acid soils. Concentrations in soil solution as low as 0.12 mM Al significantly reduced growth of *Quercus rubra* L. (6). Micromolar concentrations of one or more Al monomers (Al^{3+}, $Al(OH)^{2+}$, $Al(OH)_2^+$) (10, 15) and polynuclear-hydroxy Al complexes (19) can disturb many physiological processes in plant cells and are considered as bioactive forms of Al. Cell membranes may be a primary injury site in the Al toxicity syndrome (10). Vierstra and Haug (29) using electron paramagnetic resonance spectroscopy showed that Al decreased membrane lipid fluidity and increased the temperature for the phase change to the gel state in isolated and intact cell membranes of *Thermoplasma acidophilum*. Reduction of membrane lipid mobility by Al was also observed in root plasma membrane-enriched microsomal fractions of *Zea mays* (27). Pettersson *et al.* (20) reported that enhanced degradation of the thylakoid was the most pronounced ultrastructural change induced by Al in *Anabaena cylindrica*. Al, 10 μM, caused severe injuries to chloroplast membranes of *Spinacea oleracea* (9).

Interactions of Al with membrane proteins may also be important in Al toxicity. Because Al can remove Tb^{3+} from membrane proteins, Caldwell (4) deduced that Ca^{2+} can also be displaced by Al from wheat root plasma membrane protein sites. This displacement is one of the primary steps in Al toxicity. Al bound to calmodulin and reduced calmodulin-related transmembrane potential in plasma membrane-enriched barley root vesicles (24). Al produced calmodulin conformational changes in the plasma membrane-enriched microsomal fraction of *Zea mays* root (27). Al, 10 to 50 μM, induced a decrease in Mg^{2+}-ATPase activity (23).

Information, however, concerning the effects of Al toxicity on intact plant cell membranes is scarce, and the mechanisms need additional clarification. The effects of Al on proton efflux and membrane potential were examined in the intact cells of wheat roots (14, 18). Zhao *et al.* (30) reported that Al decreased water and increased nonelectrolyte permeation across cell membranes in intact *Q. rubra* root cortex cells at room temperature (23°C). The present study further describes how Al changes the cell membrane properties of intact cells of Northern red oak root cortex. The study examines how Al alters permeation of water, urea, and EU across cell membranes at temperatures from 2 or 4 to 35°C. Associated objectives were to determine how Al affects the Ea of permeation, the phase status, and the lipid partiality of cell membranes.

MATERIALS AND METHODS

Plant Materials

Acorns of Northern red oak (*Quercus rubra* L.) were germinated on moist filter paper and grown for 7 to 10 d at 25°C in one-tenth strength Ingestad's nutrient solution (in μM: 179 NH_4^+, 179 NO_3^-, 65 $H_2PO_4^-$, 63 Mg^{2+}, 96 K^+, 63 SO_4^{2-}, 100 Ca^{2+}, 247 Cl^-, 2 Fe^{3+}, and essential micronutrients). The pH was maintained between 4.0 and 4.2 with HCl or NaOH.

When the radicle was 10 to 15 cm in length, a segment 0.5 to 1.0 cm from the tip was excised and longitudinally cut into 60- to 65-μm thick sections with a vibrating microtome (Lancer, model No. 12). The sections were floated on the background solution and immediately infiltrated by vacuum for about 1 min. Sections were then placed in fresh background solution for 1 h before treatment.

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[3] Abbreviations: Al, aluminum; Ea, activation energy; EU, monoethyl urea; K, permeability constants of water, urea, and EU; K_s, permeability constant of urea or EU; K_w, permeability constant of water; P_c, partition coefficient.

Solutions

A background solution (25 mM KCl and 3.7 mM $CaCl_2$) was prepared with distilled water and adjusted to pH 4.0 with HCl. All sucrose, urea, and EU solutions were prepared with this background solution. For treatment, all solutions additionally contained 0.37 mM $AlCl_3$ adjusted to pH 4.0.

Permeability Measurements

The solute permeability (K_s in cm s^{-1}) and water permeability (K_w in cm s^{-1}) of the plasma membrane and tonoplast in series were measured according to the methods described by Zhao *et al.* (30) and Stadelmann and Lee-Stadelmann (26). Each section was placed in a series of sucrose solutions (0.1, 0.2, 0.3, 0.4, 0.5, and 0.6 M) for stepwise plasmolysis. One or two sections were transferred into a perfusion chamber with a droplet of 0.6 M sucrose solution (equivalent to 0.74 osmoles) for the final plasmolysis. This solution was replaced in the perfusion chamber with 0.4 M sucrose (K_w measurement) or with iso-osmolal (0.74 osmoles) urea or EU solution (K_s measurement). One to six cells were evaluated on each tissue section. For each temperature one or two roots were sampled with a total of five to 15 cells observed. Deplasmolysis occurs with entry of the permeator and water into the cell, and deplasmolysis rate was used to calculate K_s or K_w for each individual cell.

The temperature effect on the response of K_s and K_w to Al was examined from 35 to 2 or 4°C. After the sections were cut, they were kept at the desired temperature throughout the experiment. During measurement the perfusion chamber was placed on a temperature-controlled microscope stage. Temperatures measured with a thermocouple inserted into the perfusion chamber next to the section were within ±0.6°C of the desired temperature. For treatments below 12°C, all the experiments were performed in a cold temperature-controlled room.

The experimental method we used to determine permeability changes *in vivo* does not differentiate between the permeability of cell membranes and tonoplast. Exploratory experiments conducted in this laboratory on epidermal cells of *Allium cepa* bulb scales indicate that most of the permeation resistance is located in the plasmalemma. Therefore, the permeability determined here for the intact root parenchymal cell of Northern red oak may be close to the permeability of the plasma membrane alone.

Lipid Partiality

Lipid partiality is a membrane property. Membranes with high lipid partiality are very permeable to lipid-soluble permeators. Lipid partiality equals the slope of the resistance to permeation ($1/K_s$) plotted against the inverse of P_c ($1/P_c$) (30, 31). The P_c equals the equilibrium concentration of the permeator (*e.g.* urea) in octanol divided by its equilibrium concentration in water. The value of P_c is 7.76×10^{-3} for urea and 214×10^{-3} for EU (30). A steep slope means that permeation resistance across the membrane changes greatly with the lipid solubility of the permeator. A zero slope means that the membrane has no lipid partiality and permeation resistance does not increase with the lipid solubility of the permeator.

Ea and Phase Change

For each permeator, with and without Al, ln K_s and ln K_w were plotted against the inverse of the absolute temperature (Arrhenius plot). Arrhenius plots were used to calculate Ea values (kJ mol^{-1}) for permeation of water, urea, or EU across cell membranes. The Ea was calculated according to the formula of Johnson *et al.* (13): $Ea = -bR$, where b is the slope, as determined by regression, of the Arrhenius plot between 29 and 12°C, and R is the gas constant (8.31 J $°K^{-1}$ mol^{-1}). Temperatures above 29°C were not used because they appeared to indicate the beginning of a phase change. The contribution of the membrane to Ea was calculated by subtracting published Ea values for the diffusion of water in water or urea in water from the observed Ea. The published Ea values are 19.2 and 18.8 kJ mol^{-1} for water and urea in water, respectively (17). The Ea value for urea in water was also used to evaluate for the Ea of EU diffusion in water.

RESULTS

The means and variations of the data used to determine the relationships discussed in this paper are presented in Table I. As expected, permeabilities (K_s, K_w) decreased as temperatures were lowered from 35 to 4 or 2°C (Figs. 1 and 2). The lipid partiality of the membrane to urea and EU was increased by low temperature (Fig. 3). The Arrhenius plots (Figs. 1 and 2) indicate that the membrane was in the gel state at lower temperatures, but we could not determine the exact critical temperatures of the phase changes. The Ea values for permeation of water, urea, and EU across the membrane were 23.9, 48.2, and 61.3 kJ mol^{-1}, respectively (Table II) determined over the temperature range of 12 to 29°C. The contributions of the membrane to Ea were 4.7, 29.4, and 42.5 kJ mol^{-1} (Table II). Membrane contribution was estimated by subtracting the Ea of diffusion in water from the total Ea of diffusion into the cell. This assumes that the Ea for the transport into the cell depends on the Ea for diffusion in water and the Ea for diffusion across the membrane. According to the Zwolinski *et al.* (31) diagrams in the article by Zhao *et al.* (30), the permeators encounter minimal transport resistance at membrane interfaces in red oak root cortex cells.

The many effects of Al treatment (0.37 mM Al) on membrane behavior are summarized in Table III. Al decreased permeability to water throughout the temperature range of 35 to 2°C and increased the K_s from 35 to 9°C (Table I, Fig. 4). Below 7°C, K_s was decreased by Al. The Al-induced changes in membrane permeability (12 to 29°C) to water, urea, and EU were significant ($P = 0.001$). Below 12°C, Al changed permeability less (Fig. 4). Al decreased lipid partiality at temperatures above 9°C and increased it below 7°C (Fig. 3). The response is opposite to that of K_s. From visual estimates, Al treatment raised the temperature of phase change to the gel state by 1 to 3°C (Figs. 1 and 2).

Al increased the Ea values by 31.8% for the K_w and 9.1% for K_s across cell membranes (Table II). Al decreased by 6.7% the Ea for the permeation of monoethyl urea (Table II).

Table I. *Effects of 0.37 mM Al and temperature on permeability constants for permeation of water, urea, and EU into oak root cortex cells*

Each *K* is expressed as mean ± SD of 5 to 15 cells.

Temp	K_w		*K* Urea		*K* EU	
	0Al	+Al	0Al	+Al	0Al	+Al
°C	10^{-3} cm/s		10^{-8} cm/s		10^{-7} cm/s	
35	5.6 ± 0.8	3.8 ± 0.2	8.2 ± 0.2	15.4 ± 1.1	11.7 ± 1.2	20.3 ± 1.7
33	4.7 ± 0.4	3.4 ± 0.2	6.5 ± 0.2	12.1 ± 1.1		
32					9.6 ± 0.6	15.6 ± 1.0
31	4.5 ± 0.1	3.1 ± 0.1	5.8 ± 0.2	10.3 ± 0.7		
29			5.2 ± 0.2	8.2 ± 0.3	7.5 ± 0.5	13.4 ± 0.1
27	3.5 ± 0.1	2.7 ± 0.1	4.3 ± 0.2	7.1 ± 0.0		
26			4.0 ± 0.2	6.5 ± 0.3		
25					6.6 ± 0.4	11.7 ± 0.2
24			3.8 ± 0.1	5.7 ± 0.3		
23	3.1 ± 0.1	2.3 ± 0.1			5.7 ± 0.4	9.9 ± 0.2
22			3.1 ± 0.2	5.1 ± 0.2		
21			2.8 ± 0.2	4.5 ± 0.3	4.4 ± 0.5	8.2 ± 0.3
20	2.7 ± 0.1	2.0 ± 0.2			4.0 ± 0.1	7.4 ± 0.2
19			2.7 ± 0.2	3.8 ± 0.3		
18	2.6 ± 0.2	1.8 ± 0.0			3.6 ± 0.2	6.7 ± 0.4
17			2.3 ± 0.2	3.6 ± 0.3		
15	2.4 ± 0.1	1.7 ± 0.1	2.0 ± 0.2	3.1 ± 0.4	3.1 ± 0.2	4.7 ± 0.2
14			1.7 ± 0.2	2.8 ± 0.2		
12	2.2 ± 0.1	1.2 ± 0.1	1.6 ± 0.2	2.4 ± 0.3	2.1 ± 0.2	3.5 ± 0.4
10			1.5 ± 0.2	1.8 ± 0.2	2.1 ± 0.2	2.7 ± 0.2
9	2.0 ± 0.1	1.2 ± 0.1	1.1 ± 0.1	1.3 ± 0.1	1.7 ± 0.1	2.2 ± 0.1
7	1.8 ± 0.1	1.0 ± 0.0	1.0 ± 0.1	0.82 ± 0.10	1.4 ± 0.2	1.2 ± 0.2
6	1.6 ± 0.1	0.87 ± 0.05	0.82 ± 0.08	0.63 ± 0.07	1.1 ± 0.0	0.88 ± 0.07
4	1.4 ± 0.1	0.73 ± 0.05	0.69 ± 0.08	0.41 ± 0.09	0.14 ± 0.01	0.08 ± 0.01
3	1.2 ± 0.1					
2	1.0 ± 0.1	0.59 ± 0.05				

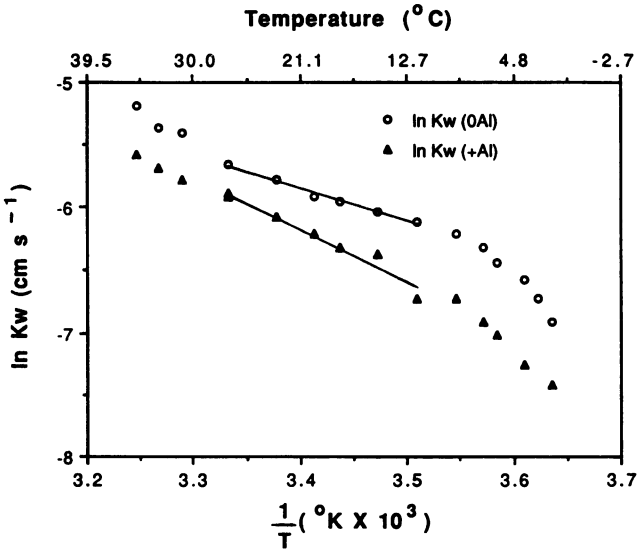

Figure 1. Arrhenius plot (ln K_w *versus* the inverse of the absolute temperature [1/T]) for control cells (0Al) and cells treated with 0.37 mM Al (+Al), Northern red oak root cortex. The slope is the best fit regression for temperatures from 12 through 27°C.

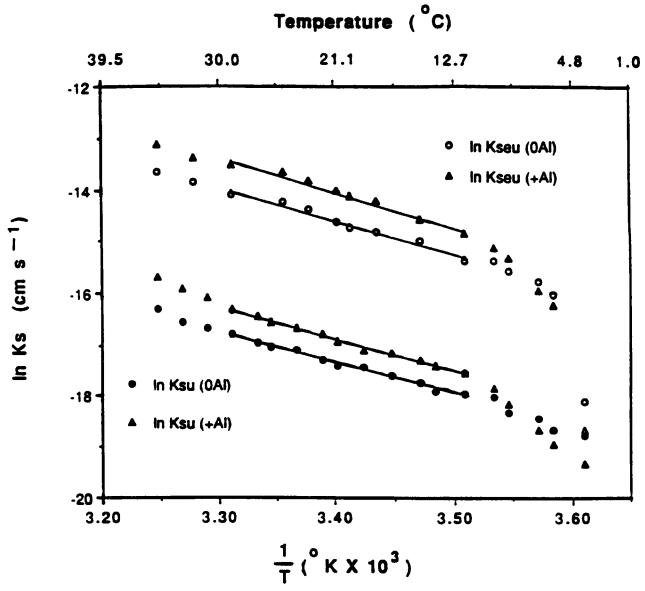

Figure 2. Arrhenius plot for urea and EU permeation across cell membranes in control cells (0Al) and cells treated with 0.37 mM Al (+Al), Northern red oak root cortex. The slope is the best fit regression for temperatures from 12 through 29°C.

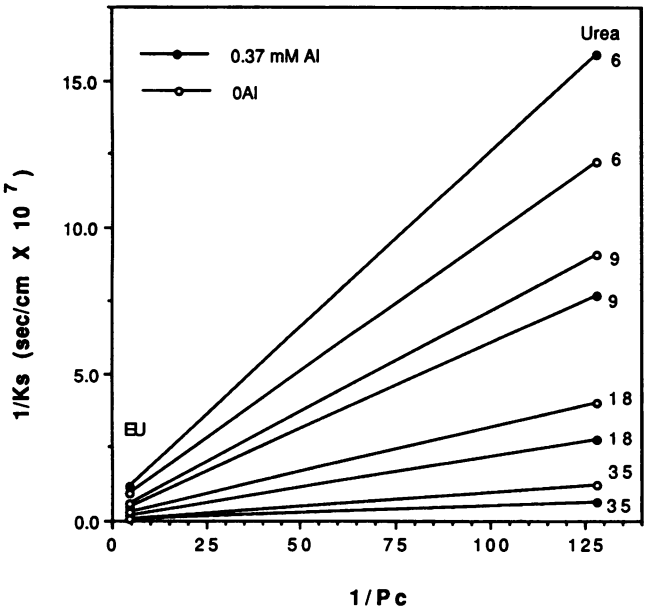

Figure 3. Permeation resistance (1/*K*) of urea and EU as a function of 1/Pc, where Pc is the partition coefficient of urea or EU in octanol/water at 20°C. A steep slope means that permeation resistance across the membrane changes greatly with the lipid solubility of the permeator. A flatter slope means the membrane has a lower lipid partiality, and permeation resistance increases only slightly with the lipid solubility of the permeator.

Although all of the Al effects on Ea were statistically significant ($P = 0.001$), the authors are most confident about the Al-induced changes in the Ea of water. Aluminum altered the membrane contribution to Ea by +162% for water but only +15% for urea and −10% for EU (Table II).

Al increased cell damage at both high and low temperatures. With EU as the permeator during deplasmolysis, cells began to burst at 29°C in the Al-treatment and at 32°C in the control. At 32 to 35°C, the frequency of damage was higher in Al-treated sections. Although most cells appeared normal at low temperatures, some cells did not plasmolyze, whereas other protoplasts burst during deplasmolysis. This cell damage first occurred at a higher temperature in Al-treated cells (8°C) than in control cells (4 to 6°C).

The shape of the plasmolyzed protoplast was influenced by both Al and temperature. Above 10°C almost all plasmolyzed protoplasts were convex, whereas below 10°C the frequency of concave plasmolysis increased with decreasing temperature. Al further increased the frequency of concave plasmolysis.

DISCUSSION

The observed effects of Al (Table III) confirm that cell membranes can be important sites for Al action in plant cells and provide further details about the mechanism of the Al action.

The changes in Ea for permeation of water, urea, and EU across cell membranes were examined (Table II). Published values of Ea for water permeation across different liposomes range from 15.5 to 71.1 kJ mol^{-1} (5). For urea, published Ea values for permeation across biological membranes range from 44.3 to 57.7 kJ mol^{-1} (17). The Ea values in this study are within the ranges reported.

Al increased the Ea for water transport as well as the resistance to water transport across cell membranes. These concomitant changes may occur when Al bridges the phospholipid head groups of the membranes and neutralizes membrane surface charges. As a result, there is an increase in the packing density (10, 21) and rigidity of cell membrane lipids (1, 11, 12). Al ions can bind to phosphatidylserine at the phosphodiester group in synthetic membranes (1) and to negatively charged phospholipid head groups in maize root cell membranes (27). In phosphatidylcholine liposome model systems, one Al cation may bind to the phosphodiester group whereas linkage to either two or three phosphatidylcholine molecules is less probably (ref. 12; B. Etherton, personal communication). Al may also affect lipid fluidity by binding to proteins and changing lipid-protein interactions. Calmodulin is an example of a membrane protein whose conformation and associated partner enzyme activities were changed by Al (23, 24).

In the temperature range of 9 to 35°C Al decreases water permeability while increasing urea and EU permeability (Table III, Figs. 2 and 3). Zhao *et al.* (30) made similar findings at 23°C. These results suggest that water and urea family permeators do not cross the cell membranes in the same way. All three permeators cross the membrane by the diffusion-solution mechanism, but water also enters into the free volumes of kinks of the hydrocarbon chain and migrates across the membrane together with the kinks (28). Blok *et al.* (2) proposed that the Ea for permeation of water was associated with kink formation and the breaking of H bonds. The

Table II. *Effects of Al on Ea (kJ mol^{-1}) for water, urea, and EU permeation into red oak root cortex cells*

Permeator	Ea^{mo} [a]	Ea^{ma}	$\frac{Ea^{ma} - Ea^{mo}}{Ea^{mo}} \times 100$	Ea^{w}	$Ea^{mo} - Ea^{w}$	$\frac{Ea^{ma} - Ea^{w}}{Ea^{mo} - Ea^{w}}$
Water	23.9	31.5	31.8	19.2	4.7	2.62
Urea	48.2	52.6	9.1	18.8	29.4	1.15
EU	61.3	57.2	−6.7	18.8	42.5	0.90

[a] Abbreviations: Ea^{ma}, Ea of diffusion across membrane with 0.37 mM Al treatment; Ea^{mo}, Ea of diffusion across membrane without Al treatment; Ea^{w}, Ea of diffusion in water alone (values from ref. 17); $Ea^{mo} - Ea^{w}$, $Ea^{ma} - Ea^{w}$, Ea attributable to membrane.

Ea associated with kink formation depends on the physical state and the composition of the lipid bilayer (2). When Al increases the packing density and decreases the mobility of the hydrocarbon chain, the Ea for the kink formation increases, fewer kinks occur (7), and they are less dynamic relative to the membrane without Al. As a result, membranes exhibit a much higher resistance to water permeation. The increase in Ea, especially the 162% increase in the Ea attributed to the membrane (Table II), indicates that Al changed the nature of the average pathway for water.

On the other hand, nonelectrolyte permeation may be facilitated by straight hydrocarbon chains (25). The more than 50% increase in urea and EU permeation with Al treatment (Fig. 4) is consistent with this hypothesis. More permeation sites may become available because the Al-treated membrane has lower kink frequency and relatively higher packing density. That Al had little effect on the Ea for urea and EU permeation suggests that Al increased the number of pathways but did not change their nature.

The changes in the lipid partiality with temperature and with Al treatment are complex (Fig. 3). Above 9°C, lipid partiality increased as temperature decreased. Furthermore, the addition of the ethyl moiety to the urea molecule had less effect on absolute permeation resistance as the temperature increased. Similar temperature effects were found for the permeation of propionamide, butyramide, and valeramide across red blood cell membranes at 20, 25, and 30°C (8). Al decreased lipid partiality at all temperatures above 9°C but increased lipid partiality for the gel state (6°C in Fig. 3).

We suggest that Al may also bridge negative sites on the cell wall to the plasmalemma, thereby increasing cell wall adhesion of the protoplast. Such adhesion would explain the higher frequency of concave plasmolysis in Al-treated cells observed at temperatures below 10°C in this experiment and at warmer temperatures with higher Al concentrations by others (3).

Our results may have ecophysiological implications. Al might make roots more sensitive to chilling. Abnormal plasmolysis behavior began at warmer temperatures in Al-treated cells, 8°C, compared with 6 to 4°C in control cells; also, Al seemed to increase the temperature of the phase change to the gel state. The decrease in water permeability by lower temperatures could exacerbate those situations in which cold soils limit water transport to shoots that are in warm air. Whether Al reduces the permeability of entire root systems remains unclear. Although Kruger and Sucoff (16) found that Al in the medium reduced the water conductivity of entire root systems of Northern red oak seedlings, they interpreted this reduction in terms of Al effects on root to shoot ratios. No clear picture of Al effects on K_w in other species emerged from a review of the literature on this topic (22).

This study demonstrated that Al affects the behavior of membrane lipids in Northern red oak root cortex cells. Al increases the Ea of and the resistance to water transport across

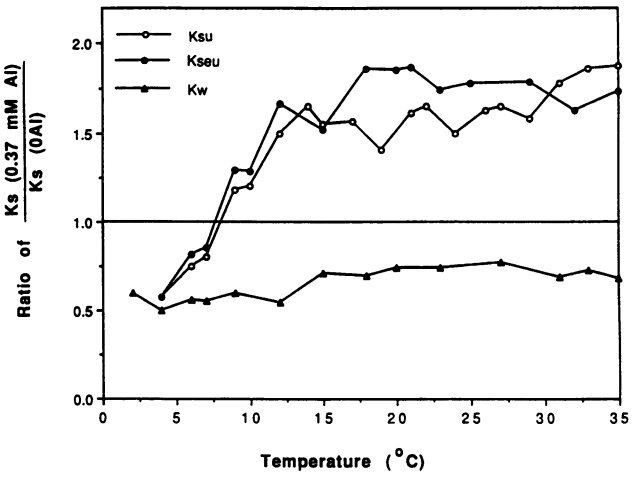

Figure 4. Ratio of *K* (with Al) to *K* (without Al) for water (K_w), urea (*K*su) and EU (*K*seu) at temperatures from 2 or 4 to 35°C. Ratios >1 mean Al increased permeability (*K*). Ratios <1 mean Al decreased *K*.

Table III. *Summary of the effects of 0.37 mM Al on cell membrane behavior, red oak root cortex cells*

Membrane Behavior	Al-Induced Change	Documentation
Permeability to water (35 to 2°C)	Decrease	Table 3; Figs. 1, 4
Permeability to urea and EU		Table 3; Figs. 2, 4
9–35°C	Increase	
4–7°C	Decrease	
Activation energy for water permeation	Increase	Table 2; Fig. 1
Activation energy for solute permeation		Table 2; Fig. 2
Urea	Increase	
EU	Decrease	
Lipid partiality of membrane		Fig. 3
9–35°C	Decrease	
4–7°C	Increase	
Temperature at which damage occurs during deplasmolysis		Not shown
>30°C	Lower by 3°C	
<8°C	Higher by 3°C	
Membrane adhesion to cell wall (concave plasmolysis form)	Increase	Not shown

cell membranes, possibly by reducing the kink frequency. Al increases nonelectrolyte permeability with minor but statistically significant changes in Ea, possibly by increasing the number of straight chain pathways. Al also narrows by 6°C the temperature span over which plasmolysis occurred without membrane damage.

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