Predicting Cation Ratios in Corn from Saline Solution Composition

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ABSTRACT

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The response of *Zea mays* (L.) cv. Pioneer 3906 to nutrient cultures that varied in Na/Ca ratios was studied at 5 different salinity levels; 0, -0.1, -0.2, -0.3 and -0.4 MPa. Principles of ion exchange theory were used to relate the cation composition (Ca, Mg and Na) in the shoots to activity ratios in the root media. The data are expressed using the Gapon convention where the selectivity coefficient is related to the equivalent fraction of the exchange ions. Plots of the cation ratios of Ca/Na, Ca/Mg and Mg/Na can be represented by a single line regardless of salinity level. This information supports the concept derived from physiological studies that the uptake of Ca, Mg and Na by salt-stressed plants is passive. The data suggest that the ratios of these cations in corn shoots can be predicted for various salinities from solution composition of the root media and shoot ion concentrations at a single salinity level.

Key words—Gapon equation, ion exchange, selectivity, cation uptake.

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INTRODUCTION

The importance of the adsorption and exchange processes that occur on charged plant surfaces for the acquisition of cations from the root media has long been recognized. Cation uptake initially occurs via the root apoplast. Cations diffuse directly from the external solution and are rapidly exchangeable with those in the free space of the root cortex (Heintze, 1961; Haynes, 1980; Macklon and Sim, 1981). The properties of the root–shoot apoplastic system are modified by the ionic charges of the cell wall matrix substances (Läuchli, 1976) and by the concentration of cations bound in exchangeable form on the walls and the exterior surfaces of the plasmalemma (Haynes, 1980; Kirkby and Pilbeam, 1984). Classical ion exchange laws have been used to explain the transport of ^{45}Ca through plant stems. This pattern of movement has been characterized as a reversible exchange phase and an irreversible adsorption phase (Biddulph, Nakayama, and Cory, 1961). The xylem cylinder has thus been visualized as an ion exchange column that regulates the upward movement of ions through a series of exchange reactions on the negatively-charged wall surfaces (Knight, Crooke, and Inkson, 1961; Bell and Biddulph, 1963; van de Geijn and Petit, 1979; Demarty, Morvan, and Thellier, 1984).

The Ca-nutritional status of the plant is strongly influenced by the ionic composition of the external medium. Calcium deficiency in plants can be induced when the percentage of

external Ca falls below a critical value. Geraldson (1957) observed that blossom-end rot in tomatoes occurred when the Ca level (in parts 10^{-6}) was less than 16% to 20% of the total soluble salts in the soil solution. The critical Ca requirement for the optimum growth of cotton roots has been related to the molar ratio of Ca to total cations (Ca/TC) in solution (Howard and Adams, 1965). In a study of the factors in Solonetzic soils that reduce crop performance, Carter, Webster, and Cairns (1979) reported that Ca deficiency in barley occurred when the Mg/Ca ratio in solution exceeded 1 or when the Ca/TC ratio was lower than 0·15. Adams and co-workers reported that the Ca/TC ratio, expressed in terms of ion activity, was a more accurate measure of Ca availability (Bennett and Adams, 1970; Adams, 1974; Wolt and Adams, 1979). These principles have recently been applied to the study of Ca nutrition in plants under a constant level of salinity stress. The Na–Ca interactions at the plasmalemma were related to the activities of Ca and Na in the external solution (Cramer, Läuchli, and Polito, 1985; Cramer and Läuchli, 1986; Cramer, Läuchli, and Epstein, 1986). Since they did not obtain the same exchange constant for the two Ca concentrations used in their experiments, they proposed that Ca-displacement by Na takes place at two different types of Ca^{2+}-binding sites.

Exchange adsorption is a mechanism for regulation of the transport and distribution of cations within the shoot (Marschner, 1986). In particular, Ca in the xylem can be controlled to a considerable extent by charge density, concentration of cations other than Ca and the removal of Ca from the exchange sites by adjacent cells along the conducting vessels (Marschner 1983). Even if specific ion carriers exist, cation uptake can be treated as the result of a selectivity process. In this instance the ion carrier still manifests an ion selectivity that can be represented by exchange theory. The objective of this study is to use ion exchange theory to describe cation uptake as well as transport of cations by plants under saline conditions.

MATERIALS AND METHODS
Seeds of *Zea mays* L. (cultivar Pioneer 3906) were soaked for 30 h in a continuously aerated solution of 0·5 mol m^{-3} $CaSO_4$, then spread on moist paper and germinated in the dark. Three-day-old seedlings were placed on cheesecloth supported between 2 plastic grids with 1·7 cm^2 openings. The seedlings, separated by the grid partitions, were covered with moist vermiculite during the early stages of growth. The grid assemblies were transferred to the glasshouse and supported over plastic pots containing 28 dm^3 of continuously aerated nutrient solution. The composition of the nutrient solution in mol m^{-3} was: 2·50 $Ca(NO_3)_2$, 3·00 KNO_3, 1·50 $MgSO_4$, $1·67 \times 10^{-1}$ KH_2PO_4, $5·00 \times 10^{-2}$ Fe (as sodium ferric diethylenetriamine pentaacetate), $2·31 \times 10^{-2}$ H_3BO_3, $4·80 \times 10^{-3}$ $MnSO_4$, $4·00 \times 10^{-4}$ $ZnSO_4$, $2·00 \times 10^{-4}$ $CuSO_4$ and $1·00 \times 10^{-4}$ H_2MoO_4.

Four days after germination the plants were thinned to 20 seedlings per pot and salination was initiated with mixtures of NaCl and $CaCl_2$. Salts were added once a day in equal increments over a 4-d period to decrease the osmotic potentials (*OP*) of four saline treatments ($-0·1$, $-0·2$, $-0·3$ and $-0·4$ MPa) each with 5 different Na/Ca ratios (Table 1). Pots were arranged in a randomized block with 3 replications. The experiments included 3 pots of non-salinized plants (*OP* $= -0·04$). The pH of the solutions was measured daily and was maintained between 5·0 and 6·0 with KOH and H_2SO_4. The solutions were completely renewed on days 10, 15 and 19 following germination. The experiment was conducted in July 1985 when the average daily maximum and minimum temperatures in the glasshouse were 36 °C and 23 °C, respectively. A second experiment at *OP* $= -0·04$ and $-0·1$ MPa with Na/Ca ratios ranging from 17·8 to 0·23 (molar basis) was conducted during August 1985. The average daily maximum and minimum temperatures in the glasshouse were 32 °C and 22 °C, respectively.

The shoots were harvested 21 d after germination. The shoots were examined for injury and symptoms of nutrient stress, then weighed. The shoots were oven-dried at 70–75 °C, reweighed and ground in a blender. Sodium, calcium, magnesium and potassium were determined on nitric-perchloric acid digests of the dry shoot samples by atomic absorption spectrophotometry.

Cation exchange capacity of 21-d-old roots was determined using a modification of the procedure described by Helmy and Elgabaly (1958). After saturation of the roots with H^+ at pH 2·0, the roots were

rinsed with distilled water, then placed in a 1·0 kmol m^{-3} KCl solution for H$^+$-K$^+$ exchange. The resultant acidity in the KCl was titrated with standard base. The reported values were corrected by subtracting blank titrations.

Activities of the major cations in each of the nutrient solutions were calculated from the concentrations of the salts by use of an ion speciation model with the constants given by Suarez (1977). The cation composition of the shoot sample was treated as if it were the product of an ion exchange process. The data are expressed using the Gapon selectivity constant (K_g), which relates the equivalent fractions of the exchange ions to the activities of the ions in solution (Sposito, 1981). For Na–Ca exchange the constant is expressed as follows

$$K_g = E_{Ca} \cdot a_{Na^+}/(E_{Na} \cdot (a_{Ca^{2+}})^{0·5}) \tag{1}$$

where E denotes equivalent fraction of a given cation on the exchanger phase and a denotes activities of the ions in solution. It is initially assumed that the activities of ions on the exchanger phase are equal to the equivalent fraction and that the adsorption occurs on one set of sites.

RESULTS AND DISCUSSION

Table 1 shows the effect of various Na/Ca ratios in the external media on the shoot weight and shoot-cation concentrations in the corn cultivar, Pioneer 3906, stressed at different osmotic potentials. Increased salinity decreased shoot weight but at any given salinity level, the external Na/Ca ratio had no significant effect on dry matter production. This cultivar

TABLE 1. *Dry weight, fresh weight and ion concentrations in shoots of* Zea *mays (L.) cv. Pioneer 3906 grown in a range of Na/Ca ratios at five levels of added salinity*

Gapon selectivity coefficients are given for saline treatments.

Osmotic potential (MPa)	Growth media Na	Ca (mol m^{-3})	Plant shoot[a] Fresh weight (g shoots^{-1})	Dry weight	Na	Ca (mmol kg^{-1} dry wt.)	Mg	K	K_g Ca-Na	Mg-Ca
Control[b]	0·0	2·5	41·4±1·2	2·72±0·38	0·30±0·06	94·4±3·8	90·6±2·7	2090±43		
−0·1[b]	19·6	3·6	45·4±1·6	2·85±0·10	67·8±3·7	81·9±9·8	78·5±6·6	2070±107	0·93	2·18
	16·3	6·0	40·5±2·3	2·63±0·12	21·9±3·4	107±2	73·8±5·4	2126±65	2·38	2·62
	12·5	8·7	46·4±2·2	3·13±0·10	11·3±2·3	119±8	68·5±6·5	1967±42	3·21	3·21
	8·0	11·9	40·7±3·8	2·92±0·24	2·9±0·5	124±8	63·0±2·7	1872±109	9·64	3·79
	3·0	15·5	37·8±5·5	2·75±0·40	0·87±0·12	154±2	68·5±3·2	1903±72	9·39	3·49
−0·2[b]	39·5	4·7	34·1±2·3	2·53±0·21	126±27	86·8±3·1	78·9±3·0	1875±19	0·97	2·65
	32·8	9·6	32·8±2·8	2·52±0·23	55±14	106±5	72·1±5·7	1888±110	1·56	4·04
	25·2	14·6	34·2±2·0	2·70±0·20	24·9±5·6	126±5	66·3±3·5	1911±61	2·37	4·84
	16·2	21·6	29·8±2·8	2·25±0·27	7·5±0·8	173±12	72·6±6·8	1967±42	6·30	5·52
	5·9	29·0	35·7±1·2	2·84±0·16	1·9±0·2	170±5	54·9±1·4	1869±8	6·22	5·65
−0·3[b]	59·6	5·8	27·5±2·7	2·20±0·19	216±33	83·3±2·1	74·4±3·9	1798±47	0·73	3·21
	49·5	13·2	29·0±0·9	2·52±0·07	113±21	116±3	65·0±1·9	1738±43	1·09	4·47
	38·0	21·5	24·7±3·4	2·21±0·28	36·1±6·9	144±12	66·9±2·7	1763±108	2·59	5·94
	24·6	31·7	20·7±3·2	1·84±0·24	14·1±1·6	183±16	63·5±3·2	1723±52	3·54	6·46
	9·0	42·4	25·4±2·0	2·60±0·13	2·1±0·2	204±18	51·5±0·4	1657±118	10·66	6·35
−0·4[b]	79·5	6·9	19·8±1·2	1·94±0·02	199±21	70·1±1·4	64·8±2·0	1566±42	0·83	3·86
	65·7	16·6	23·3±1·7	2·23±0·14	128±21	123±9	61·6±3·1	1624±16	1·22	4·96
	50·0	27·5	15·6±1·0	1·58±0·14	43±5	131±8	65·1±1·2	1547±33	2·76	8·11
	32·2	40·0	16·2±1·3	1·62±0·12	31±12	202±25	59·8±2·7	1457±107	2·69	6·99
	11·5	54·5	18·2±2·0	1·84±0·20	3·5±0·4	221±17	53·9±1·9	1552±14	6·51	7·67
Control[c]	0·0	2·5	34·4±1·8	2·62±0·20	0·08±0·08	105±1	94·8±3·2	1596±57		
−0·1[c]	19·6	1·1	36·1±4·4	2·42±0·20	84±11	75·5±1·2	125±2	1745±58	1·26	1·17
	16·3	3·5	38·3±0·7	2·90±0·05	29·6±4·0	108±6	112±10	1435±143	2·39	2·32
	12·5	6·2	38·9±3·3	2·63±0·24	9·9±0·3	122±3	87·5±9·4	1778±98	4·68	2·79
	8·0	9·5	28·4±2·7	1·93±0·20	3·4±0·1	140±5	76·2±3·3	1798±86	8·13	3·23
	3·0	13·0	27·9±2·7	1·90±0·20	1·2±0·1	159±1	71·4±1·4	1887±89	8·35	3·67

[a] Values are the means of five replications ±s.e.
[b] Experiment conducted during July–August 1985.
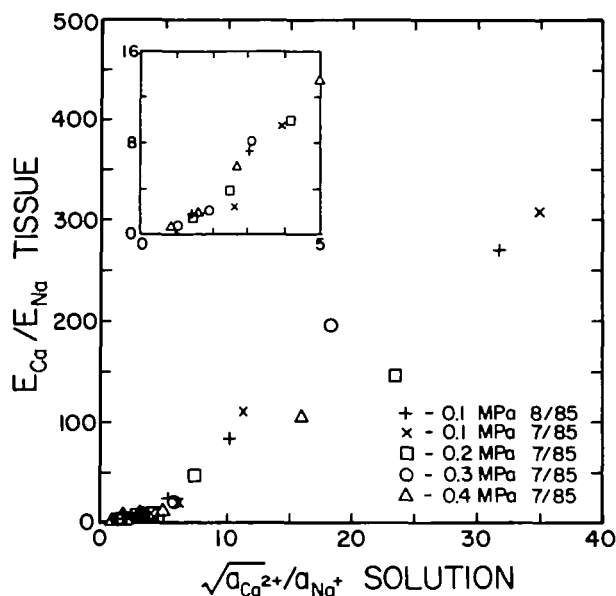[c] Experiment conducted during August 1985.

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FIG. 1. Relationship between E_{Ca}/E_{Na} in corn shoots and $(a_{Ca^{2+}})^{0.5}/a_{Na^+}$ in nutrient solution at -0.1, -0.2, -0.3 and -0.4 MPa osmotic potential.

exhibited foliar injury symptoms at the two highest substrate Na/Ca ratios at all salinity levels. Injury was evident on 20, 20, 47 and 16% of the shoots harvested from the highest Na/Ca ratio treatments at $OP = -0.1, -0.2, -0.3$ and -0.4 MPa, respectively. At the next highest Na/Ca ratio, 3–5% of the shoots were injured at all salinity levels. At $OP = -0.4$ MPa, the injury was characterized by severe wither-tip and deep blade serration; at $OP = -0.1$ MPa, by moderate wither-tip and shallowly-serrated blades. These symptoms were not observed on shoots from any other treatment. The type of injury we observed has been associated with Na-induced Ca deficiency in the corn cultivar Pioneer 3906 (Maas and Grieve, 1987) as well as in other cereals (Kawasaki and Moritsugu, 1979).

The relationship between the activities of Ca^{2+} and Na^+ in the nutrient solution and the Ca and Na composition of the corn shoots is shown in Fig. 1. Data from plants grown during both time intervals are included in Fig. 1. Apparently the differences in temperature during the growth period did not affect the results. The data at all salinity levels, with a wide range in Na/Ca ratios, can be represented by one line. This finding supports data obtained from physiological studies that indicate large fractions of Ca are held on adsorption sites on the cell wall and that Ca uptake is largely a passive process (Hanson, 1984; Kirkby and Pilbeam, 1984; Macklon, 1984; Clark, 1984). Active Ca uptake by a specific metabolic pathway would result in separate curves for each salinity level, with Na/Ca ratio in the plant shoot increasing with increasing salinity.

Examination of the shape of the exchange curve and values for the exchange constants can provide information on ion uptake under saline or sodic conditions. For Ca/Na equivalent fraction ratios above 4·0 the relationship is represented by a straight line with a slope of 9·28 and an intercept of -23.8 ($r^2 = 0.96$). Since the intercept is not zero, K_g is not constant but rather ranges from values of 2·37 to 10·7 as E_{Ca}/E_{Na} increases from 4·0 to 310. These large K_g values indicate that the cation uptake process shows a strong preference for Ca. The Gapon equation for ion exchange was used because it produced plots with a more constant selectivity coefficient. This relationship has also been observed for Ca–Na exchange on clay
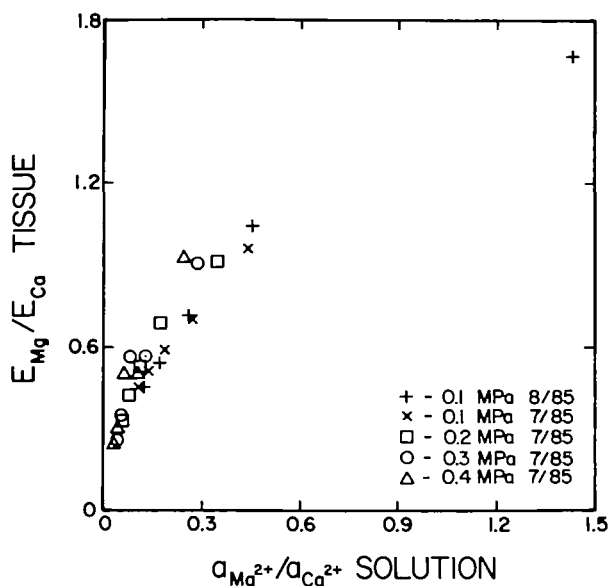
FIG. 2. Relationship between E_{Mg}/E_{Ca} in corn shoots and $a_{Mg^{2+}}/a_{Ca^{2+}}$ in nutrient solution at -0.1, -0.2, -0.3 and -0.4 MPa osmotic potential.

(Sposito, 1981), and accounts for the prevalent use of the Gapon equation over that of the Vanselow equation in soil exchange studies.

A prediction of the surface composition of an exchanger can be made by use of the diffuse double layer model which considers only electrostatic interactions. It is also assumed that the exchanger phase is an ideal solid solution (activity coefficients in the solid phase are equal to one and, therefore, activity can be represented by mole fraction). Bolt (1955) developed the following equation to relate the charge fraction of monovalent ions to total ions in the double layer.

$$\frac{\sigma}{\sigma_t} = \frac{a_{Na^+}}{\sigma(B \times 10^{-3} \cdot a_{Ca^{2+}})^{0.5}} \sinh^{-1}\left[\frac{\sigma(B \times 10^{-3})^{0.5}}{(a_{Na^+}/(a_{Ca^{2+}})^{0.5}) + 4v_c(a_{Ca^{2+}})^{0.5}}\right]$$

where σ/σ_t is the charge fraction satisfied by Na(E_{Na}), a_{Na^+} and $a_{Ca^{2+}}$ are the activities of Na$^+$ and Ca^{2+} in solution, B equals 1.06×10^{16} mmol^{-1} at 25 °C, σ is the surface charge density (mol m^{-2}), and v_c is related to the chemical potential midway between the two charged surfaces and taken as equal to 1. From the following assumptions and knowledge of the surface charge density σ, K_g can be calculated in a mono–divalent system as a function of the fraction of the charge neutralized by an ion.

Increased charge density, as well as increased concentration of the monovalent ion, results in a prediction of increased preference for the divalent ion. However, increased Na concentrations do not increase the selectivity of corn plants for Ca (Fig. 2) probably because of loss of membrane integrity. The selectivity values obtained at low exchangeable Na require relatively high surface charge densities, up to 2×10^{-5} mol m^{-2}. In contrast, at high plant Na concentrations the required surface charge density is as low as 7×10^{-7} mol m^{-2}. The surface area of the corn roots required to satisfy this calculation can be obtained by dividing the experimentally determined cation exchange capacity, 51 mmol(+) kg^{-1}, by the necessary surface charge density, 5×10^{-6} mol m^{-2}. The calculated surface areas range from 2 500 to 70 000 m^2 kg^{-1} and are about 25 to 700 times greater than those obtained by root

measurements under the microscope. These values are not unreasonable if we omit the data at very low Ca/Na equivalent fraction ratios since the cation exchange capacity includes not only the external surface but also surfaces surrounding the apoplastic free space.

The data from treatments with high a_{Na^+} in solution indicate that at Ca/Na equivalent fractions ratios less than 4·0, the plant has a relatively low affinity for Ca. This relationship can be more clearly seen in the expanded graph inset to Fig. 1. The data with a Ca/Na ratio of less than 4·0 can be represented by a straight line with a slope of 1·44 and an intercept of $-0·53$ ($r^2 = 0·79$) and a range of K_g values of 0·73 to 1·56 for E_{Ca}/E_{Na} ratios of 0·9–4·0. The K_g values obtained from this experiment are shown in Table 1. Values of K_g increase up to 10 for the high Ca treatments at all salinities. The data indicate that the selectivity for Ca is impaired (lower K_g) earlier (at a lower shoot Ca concentration) at high OP. This is consistent with the observation that at high salinity the plant root membranes lose their integrity and cease their regulatory function.

The competition between Mg and Ca in plant shoots as related to the Ca and Mg ion activities in solution is shown in Fig. 2. The K_g values of 2·2–8·1 indicate a shoot preference for Mg over Ca. Although there is a slight effect of OP on Mg/Ca concentration in the shoot, Mg/Ca ratios in the shoot can be predicted from the activity ratio in solution. Since the external Mg concentration (1·5 mol m^{-3}) was constant in all treatments, the Mg^{2+} activity values are also relatively constant. The higher $a_{Mg^{2+}}/a_{Ca^{2+}}$ ratios, therefore, indicate a reduced $a_{Ca^{2+}}$. Decreased selectivity with increased $a_{Mg^{2+}}/a_{Ca^{2+}}$ ratios may be an indication of reduced membrane integrity because of insufficient Ca. The K_g values, given in Table 1, increase with decreasing $a_{Mg^{2+}}/a_{Ca^{2+}}$ ratio. The decrease in shoot-Mg concentration with increasing substrate Ca (Table 1) also supports the concept of passive Mg uptake (Macklon and Sim, 1976; Clark, 1984).

The Mg/Na cation ratios in plants grown at varying osmotic potential can be well predicted from the $(a_{Mg^+})^{0·5}/a_{Na^+}$ ratio in solution as shown in Fig. 3. Similar relations did not hold for K uptake. The poor relationship between the ratio of K to other cations in solution
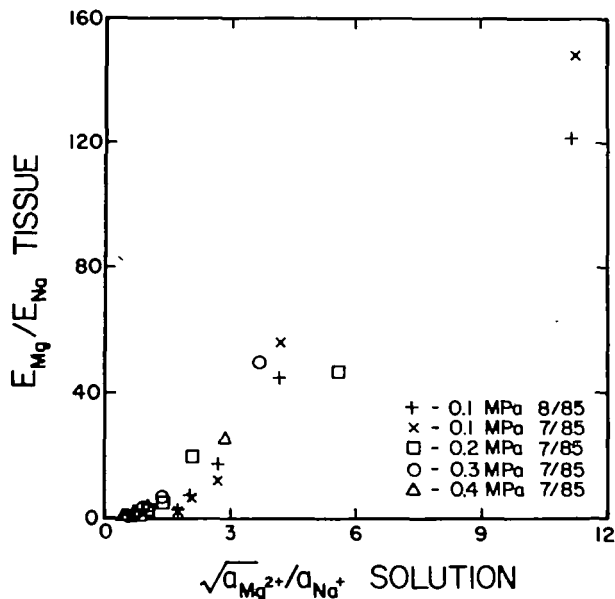

FIG. 3. Relationship between E_{Mg}/E_{Na} in corn shoots and $(a_{Mg^{2+}})^{0·5}/a_{Na^+}$ in nutrient solution at $-0·1$, $-0·2$, $-0·3$ and $-0·4$ MPa osmotic potential.

and the K/Σ cations in the shoots, supports the well-documented evidence that the uptake and transport of K is a metabolically-driven process (Marschner, 1986). Stassart, Neirinckx, and Dejaegere (1981) concluded that Ca and Na are adsorbed on the same sites in the cell wall of barley roots whereas K does not compete with Ca.

From the data presented above a reasonable prediction of Ca–Mg–Na ratios in corn shoots is obtained from their solution activities in combination with ion exchange theory. Analysis of the data by ion exchange procedures also allows for a more detailed treatment of the ion uptake process. Further work is necessary to determine the influence of environmental conditions on the constancy of the calculated selectivity values. Bernstein and Nieman (1960) proposed that increased ion uptake under high transpiration was due to an increase in the solute concentration in the apoplastic free space relative to that in the external solution. Similarly, the relative concentration of Na to $(Ca)^{0.5}$ would vary with changes in transpiration rate and thus alter the ion uptake relationships.

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