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MEASUREMENT OF ALUMINUM TOXICITY. I. EFFECTS OF ALUMINUM IN SOIL SOLUTION OF ROOT GROWTH

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Studies found in the literature of root growth inhibition by such cations as H^+, Al^{+3}, Mg^{+2} and K^+ could all be related to the ratios $(Ca)^{1/2}/H$, $(Ca)^{1/2}/(Al)^{1/3}$, $(Ca)^{1/2}/(Mg)^{1/2}$ or $(Ca)^{1/2}/(K)$. The data is consistent with the hypothesis that all of these ions may induce a calcium deficiency in the meristematic section of the growing root tip and thereby have an important influence on growth of the whole plant.

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MEASUREMENT OF AL TOXICITY:

I. EFFECTS OF AL IN SOIL SOLUTION ON ROOT GROWTH[1/]

H. G. Zandstra and D. R. Bouldin[2/]

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SOIL BRIEF

The concentration of Al in soil suspensions was varied by additions of $Ca(OH)_2$ and concentrations of $CaCl_2$. Root growth in the suspensions was measured using corn and sorghum seedlings. The root growth was not a single-valued function of pH or Al^{+3} activity in solution but it was a single-valued function of the solution parameters pH - 1/2pCa or 1/3pAl - 1/2pCa. The latter parameters appear to be the best means of estimating soil acidity effects on seedling root growth of corn and sorghum.

ABSTRACT

The concentration of Al in soil suspensions was varied by additions of $Ca(OH)_2$ and concentrations of $CaCl_2$. Root growth in the suspensions was measured over a 60 hour period using corn and sorghum seedlings. The observed root growth was not a single-valued function of pH or Al, but it was a single-valued function of the solution parameters pH - 1/2pCa or 1/3pAl - 1/2pCa.

Studies found in the literature of root growth inhibition by such cations as H^+, Al^{+3}, Mg^{+2} and K^+ could all be related to the ratios $(Ca)^{1/2}/H$, $(Ca)^{1/2}/(Al)^{1/3}$, $(Ca)^{1/2}/(Mg)^{1/2} + K)$. The data is consistent with the hypothesis that all of these ions may induce a calcium deficiency in the meristematic section of the growing root tip and thereby have an important influence on growth of the whole plant.

Additional Index Words: Calcium deficiency, cation activity ratios, corn, sorghum, seedlings.

Short Title: Al toxicity: I. Effects on root growth

The degree of correlation between root growth and exchangeable aluminum or percent aluminum saturation of the exchange complex has varied considerably among experiments, particularly when different soil types were considered (Adams and Pearson, 1967). Adams and Lund (1966) found a reasonably consistent relation between the activity of Al in the displaced soil solution and root growth. The relation, although a great improvement over that with exchangeable Al, varied among soil types. These differences were in some cases considerable; an activity of 10^{-5} M Al in the Bladen subsoil reduced relative root length by about 70%, but in the Dickson subsoil, reduction in relative root length at the same Al activity was approximately 35%.

Recently, Soileau et al. (1969) considered Al toxicity and Ca deficiency to be closely related. They used the term "Al induced Ca deficiency" in the discussion of their results. Lund (1970) studied the effects of Ca on root growth of soybeans and found that reductions in root growth from high solution Al activities were lessened by increasing the Ca activity in solution. To interpret his results, Lund (op. cit.) used the ratios $^{a}Ca/^{a}H$ for the effects of ph, $^{a}Ca/\Sigma^{a}$ cations for the effects of Mg and K, and $^{a}Ca/^{a}Al$ for the effects of Al on root growth.

The experiments discussed in this paper were designed to evaluate the hypothesis that the toxic effect of Al on root growth is directly related to the activity of Al in the soil solution. In considering this hypothesis other possible Al toxicity indices are discussed.

MATERIALS AND METHODS

The basic experimental technique in this study involved measuring growth rates of seedling roots in well mixed, dilute suspensions of soil. The soil suspensions have the advantage over solutions that the composition is buffered and stabilized by the soil.

Soil Preparation

The soil used in the root growth studies was collected at the Carimagua Research Station in the Eastern Plains of Colombia, S. A. The surrounding vegetation was predominantly savannah (*Trachypogon vestitus*) and the yearly precipitation is approximately 1700 mm. The soils of the Eastern Plains are highly weathered with medium to heavy textures. They are very acid, highly Al saturated and low in P. The Carimagua silty clay loam was classified by Guerrero as a Kaolonitic, isohyperthermic, Typic Haplustox and is representative of the soils in the region (Table 1).

Samples of 150 g air dried and ground Carimagua topsoil were each combined with 300 ml of 10^{-3} M, 5 x 10^{-3} M or 10^{-2} M $CaCl_2$. Various amounts of $Ca(OH)_2$ were added and thoroughly mixed. These treatments are listed in Table 2 for experiment 1 and in Table 3 for experiment 2. The mixtures were continuously aerated with acid washed air and stirred twice daily for 10 days. After 10 days, the mixtures were allowed to settle overnight. The pH was determined by placing the glass electrode in the soil suspension and the reference electrode in the supernatant solution.

Supernatant solutions were centrifuged, and they were analysed for Al by the aluminon procedure (Mclean, 1965, pp. 988-989), and for Ca

and Mg by atomic adsorption in solutions containing 0.5% La. The activities of Al^{+3}, Ca^{+2} and Mg^{+2} were calculated assuming the monomeric hydrolysis mechanism for Al^{+3} (Lindsay et al, 1959) using pK=5.02 and the Debye-Huckel equation with distance-of-closest-approach constants reported by Kielland (1937). Approximations were repeated until the difference between successive estimates of the activity coefficient was less than 0.002. No correction for ion pair formation was made.

The soil was rinsed until the conductivity of the wash solution was less than 0.05 millimohs. The soil was then dried at 45°C until moist, broken up with a spatula, further dried at 45°C and ground by mortar and pestle. Subsamples of this soil were used in the root growth experiments.

Germination of seedlings

Seeds were germinated between sheets of filter paper placed on a glass plate and moistened with a solution of 10^{-3} M $CaCl_2$. The entire assembly was wrapped in black plastic, except at the base, which was placed in a tray with distilled water. The glass plate was set at an angle of about 20° from the vertical during germination of the seeds. After germination, seedlings were rinsed by floating them in a tray with distilled water. At the initiation of the experiment, the length of primary roots of corn seedlings varied from 3.5 to 4.5 cm and of sorghum seedlings from 2.5 to 3.5 cm. The varieties used were Pioneer X-306 for corn and DeKalb R. S. 610 for sorghum.

Measurement of root growth

Polyethylene drying tubes, 20 cm long and with an inner diameter of 1.4 cm, were fitted with a device designed to aerate and stir the

solution, and at the same time circulate the solution through a layer of soil as illustrated in figure 1. This device consisted of a hypodermic needle stuck through a rubber stopper. A slot was cut in the stopper and a glass tube was fitted into the slot and over the needle in a manner that allowed free entrance of liquid at the base of the glass tube. In each polyethylene drying tube 27 ml of prepared equilibrium solution was recombined with 5 g of the dried soil (see soil preparation). The composition of the equilibrium solutions remained virtually constant during the experimental period and is described in Table 2 (Expt. 1) and Table 3 (Expt. 2).

During the addition of solution and soil, air under pressure of a 40 cm water column was passed through the hypodermic needles. The rapid flow of air created sufficient suction at the base of the glass tube to carry with it lenses of liquid, which were released into the bulk solution at the top of the glass tube. The amount of solution passing upward through the glass tubes, estimated by observations of the size and frequency of the liquid lenses, varied from 4 to 10 ml/min. This insured frequent percolation of the entire solution through the soil during the experiment. After the soil suspension had cleared, pregerminated seeds were placed in the inverted caps of the drying tubes on top of each tube. Experiments were continued for 60 hours during which several measurements of root length were made. This period allowed substantial differentiation of root growth between treatments.

In experiment 1, the initial length of the seedling roots varied considerably and this resulted in difficulty in interpretation of the final root length. Inspection of the roots at the end of the experiment

indicated that the proximity of swollen lateral root primordia to the root apex provided a useful index of root growth inhibition, as initiation of the lateral primordia progresses from the seed downward and is a function of the inhibition of the apical meristem. This measure was therefore chosen to evaluate treatment effects in experiment 1. In experiment 2, more care was taken in the selection of seedlings so that additional root growth during a 60-hour period could be used to measure treatment effects.

RESULTS

In the experiments reported here, the more severely damaged roots (i.e. those which grew least) were swollen and crooked. The root tip was blunt, often compound and the root cap was often split and partially sloughed off. The epidermis and cortex showed deep, lengthwise cracks and because of their transparent, glossy appearance, the stele could be easily distinguished. In some cases, swollen root primordia could be found all along the root, often causing cracking of the cortex without emerging from it. Root elongation ceased after as few as 24 hours in sorghum seedlings and 36 hours in corn seedlings and was sometimes so small that most of it could be accounted for by cell elongation alone.

Experiment 1

The proximity of swollen lateral root primordia to the root apex was substantially altered by $Ca(OH)_2$ treatments, but showed only minor and statistically non-significant effects of $CaCl_2$ concentrations (Table 2). Because increases in $CaCl_2$ levels decreased pH and substantially increased Al activity in solution (Table 2), $CaCl_2$ treatments should have inhibited root growth under the hypothesis that the activity of Al regulates toxicity effects on root growth. The lack of effect of $CaCl_2$ was therefore considered evidence for rejection of this hypothesis.

Experiment 2

To further evaluate the primary hypothesis, a second experiment was designed which included more $Ca(OH)_2$ levels than experiment 1. In this experiment, increases in $CaCl_2$ concentration of the equilibrium solution decreased solution pH and increased Ca^{+2} and Al^{+3} activities as expected. The effects of these changes in solution composition on root

growth were, however, minor (Table 3) and statistically non-significant, thus confirming the results of experiment 1.

Plotting solution pH and Al^{+3} activity against root growth (Fig. 2A) and 2B) illustrates that root growth was not a single-valued function of pH or Al^{+3} activity, but depended as well on the concentration of $CaCl_2$. In both figures, root growth showed greater tolerance to low solution pH and high Al^{+3} activity at the higher $CaCl_2$ level. The hypothesis that root growth reductions in acid soils are single-valued functions of pH or the activity of Al^{+3} in the soil solution must therefore be rejected or modified.

As illustrated in Fig. 2A and 2B, root growth was closely related to pH or Al^{+3} activity for a fixed level of $CaCl_2$, but this relationship differed among $CaCl_2$ concentrations. Thus a soil solution parameter is needed which accounts for these observations. Cation activity ratios have been formulated (Schofield, 1947), which are independent of soil solution ratio and variations in salt concentration, so long as no extensive changes are made in the suite of exchangeable cations. These ratios have been used extensively to describe the dependence of ions in the soil solution on the exchangeable ions (Turner and Clark, 1965; Frink and Peech, 1963). These ratios are of the general category:

$$\frac{(M_1^{v+})^{1/v}}{(M_2^{w+})^{1/w}},$$ where M_1 and M_2 are cations with valences v and w, respectively.

or in logarithmic form:

$$1/w\ pM_2^{w+} - 1/v\ pM_1^{v+}.$$

Such ratios, calculated for pH as pH - 1/2pCa and for the Al^{+3} activity as 1/3pAl - 1/2pCa, when plotted against root growth, showed a unique relation to root growth independent of the $CaCl_2$ concentration of the matrix solution as illustrated in figures 3A and 3B.

DISCUSSION

The relation between the measures pH and pH - 1/2pCa can be presented by:

$$pH = (pH - 1/2pCa) + 1/2pCa,$$

so that the difference between the two relations of root growth versus pH in figure 2A, can be accounted for by the differences in pCa in solution. Thus, plotting root growth against pH will give rise to a series of parallel curves, one for each particular Ca activity in solution, and the lateral displacement between the curves will be related to the difference in Ca activity. A similar argument applies to pAl, as:

$$pAl = 3(1/3pAl - 1/2pCa) + 3/2pCa,$$

which accounts for the shift in the curves in figure 2B.

Lund (1970), in his experiments 2 and 3, studied the effects of pH and Ca concentration on root growth. The measure pH - 1/2pCa calculated from these experiments explains the observed rates of root growth very well (Table 4 and Fig. 4A). (Treatment 5 is an exception, but this value appears to be erroneous, as indicated by comparison with treatment 7). The measure used by Lund, $^{a}H/^{a}Ca$, may be inverted and transformed to the negative logarithm to give pH - 1/2pCa as follows,

$$pH - pCa = 2(pH - 1/2pCa) - pH.$$

The relation between root growth and pH - 1/2pCa (Fig. 4A) may then be replaced by a series of relations with pH - pCa, each relation representing a selected pH value. Except for treatment 5 (not plotted), the rates of root growth fit the curve representing the appropriate pH quite well (Fig. 4B).

In experiments 4 and 5, Lund (Table 5, 1970) studied the interaction of Ca and Mg and of Ca and Mg + K. He plotted root growth against $Ca/\Sigma(M_i)$, and obtained a separate curve for each interaction (Fig. 5A). As the availability of Ca may be affected by the introduction of another dominant ion, the ratio

$$\frac{(Ca)^{1/2}}{(Mg)^{1/2} + (K)}$$

was calculated and plotted against the rate of root growth (Fig. 5B). The good agreement obtained between the calculated activity ratio and root growth demonstrates the importance of ionic valence in the effects of interfering ions on root growth. The resulting fit may be regarded as fortuitous because no allowance was made for the difference in exchange behaviour between Mg and K ions. To do this the activity ratio should be:

$$\frac{(Ca)^{1/2}}{(Mg)^{1/2} + c(K)} .$$

It appears from these results that c may be close to 1.0.

The results discussed show that effects of Al toxicity, low Ca : Mg ratios, low pH and Ca deficiency on root growth can all be related to the same type of soil solution function:

$$\frac{(Ca)^{1/2}}{\Sigma c_i (M_i)^{1/v_i}} ,$$

where M_i is any cation, v_i its charge and c_i a constant related to differences in exchange behaviour of the cations in the denominator. This indicates that all these effects are either induced Ca deficiencies at the growing root tip, or a series of cation toxicities which can be minimized by the presence of Ca. Because of the specificity of Ca in

these relations, they could reasonably be called induced Ca deficiencies.

The variables pH - 1/2pCa and 1/3pAl - 1/2pCa are, in effect, activity ratios and their correlation with root growth suggests that perhaps root growth is reduced by a deficiency of Ca induced by exchange reactions with an excess of another cation. This may account for the ameliorating effect of increasing Ca activity on reductions in root growth induced by low pH (Arnon and Johnson, 1942) and for the observations of Clarkson (1965) that symptoms typical of Al toxicity could be obtained using indium, gallium and lanthanum salts.

Comparison of the effects of Mg and K on root growth (Table 5) shows that a given activity of K inhibits root growth much less than the same activity of Mg in solution. Similarly, inhibition of root growth requires much higher Mg activities than Al activities. Activities of Mg which strongly interfered with root growth at a Ca activity of approximatley 0.8×10^{-3} M were approximately 16×10^{-3} M (Table 5). Substantially lower Al activities of 6×10^{-5} M to 10^{-4} M showed similar root growth inhibition at similar Ca activities (Table 3, treatments 5 and 7). The activity ratio employed by Lund (1970) and extensively discussed by Khasawneh (1971), $(Ca)/\Sigma(M_i)$, does not take into account the substantial effects of ionic valence evident in the above mentioned results, and is therefore not applicable to soil solutions in which the relative dominance of mono, di- or tri- valent ions varies.

Because mono- and di- valent ions are much less effective than Al in reducing root growth, precipitation of Al by $Mg(OH)_2$, KOH or NaOH may lead to complicated effects on plant growth. In case the original Ca content of the soil or solution is high enough, low levels of these bases may improve root growth, primarily by precipitating Al, but as the

amount of added base is increased, the concentration of the added ion may become high enough to induce a Ca deficiency. At this point the simple ratio 1/3pAl - 1/2pCa becomes inadequate and more complicated function of Al plus the associated cations must be used in the denominator. In most field situations, however, Al toxicity can be adequately defined by 1/3pAl - 1/2pCa since in general the denominator of the general function $(Ca)^{1/2}/\Sigma c_i(M_i)^{1/v_i}$ is largely dependent on the concentration of trivalent Al.

CONCLUSIONS

The results of the experiments reported here demonstrate that the soil solution parameters pH - 1/2pCa and 1/3pAl - 1/2pCa are superior to either pH or pAl in explaining variation in growth of sorghum and corn seedling roots in 60 hours. Data in the literature together with the experimental data reported here demonstrate that root growth is best related to cation ratios in solution such as pH - 1/2pCa, 1/3pAl - 1/2pCa and $(Ca)^{1/2}/(Mg^{1/2} + K)$. The results of the data reviewed are consistent with a non-specific competition between interfering ions and Ca.

The effect of interfering cations on root growth is highly dependent on their valence and the frequently employed activity ratio $(Ca)/\Sigma(M_i)$ does not appear to be as useful as the ratios listed above and presumably the general function $(Ca)^{1/2}/\Sigma C_i(M_i)^{1/v_i}$ is more useful.

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Figure 1. Assembly for root growth studies used in Experiments 1 and 2.

Figure 2. The increase in root length of corn and sorghum seedlings in 60 hours (ΔL) plotted against the pH and pAl of the solutions. Circles represent the results with 10^{-3} M $CaCl_2$ solutions, squares represent the results with 10^{-2} M $CaCl_2$ and the lines are drawn in visually for reference purposes.

Figure 3: The increase in root length of corn and sorghum seedlings in 60 hours (ΔL) plotted against the relations (pH - 1/2pCa) and (1/3pAl - 1/2pCa) of solutions. Circles represent results with 10^{-3} M $CaCl_2$ solutions, squares represent results with 10^{-2} M $CaCl_2$ solutions and the lines are drawn in visually for reference purposes.

Figure 4: Taproot elongation rate of soybean ($\Delta L/\Delta t$) plotted against pH - 1/2pCa and pH - pCa. In figure B, calculated curves are at pH 5.6 (a), pH 4.75 (b), pH 4.5(c) and pH 4.0 (d). Points are experimental observations, lines are drawn in visually for reference purposes (data from Lund, 1970).

Figure 5: The rate of soybean taproot elongation rate ($\Delta L/\Delta t$) plotted against two ion activity ratios in solution. Points are experimental observations, lines are drawn in visually for reference purposes.

Table 1: Chemical analyses of samples of the soil profile from Carimagua. (Guerrero, R. 1971. Soils of the Colombian Llanos Orientales. Composition and Classification of selected soil profiles. Ph. D. Thesis. North Carolina State University, Raleigh, N. C.)

Table 2: The pH, activity of Al in solution and proximity of swollen root primordia to the root tip for different additions of $ca(OH)_2$ and concentrations of $CaCl_2$, experiment 1.

Table 3: Solution parameters and root growth of corn and sorghum seedlings in 60 hours for different additions of $Ca(OH)_2$ and concentrations of $CaCl_2$, experiment 2.

Table 4: Soybean taproot elongation in nutrient solutions at different concentrations of Ca and pH (from Lund, 1970).

Table 5: Soybean taproot elongation in nutrient solutions with different concentrations of Ca, Mg and K (from Lund, 1970).

Table 1. Chemical analyses of samples of the soil profile from Carimagua. (Guerrero, R. 1971. Soils of the Colombian Llanos Orientales. Composition and classification of selected soil profiles, Ph. D. Thesis. North Carolina State University, Raleigh, N. C.)

Depth cm.	pH H_2O 1:1	pH KCl 1:1	Organic carbon %	CEC*	Exchangeable Ca	Exchangeable Mg	Exchangeable K	Exchangeable Na	Exchangeable Al	Sum of Cations†	Base Saturation‡ %
				meq/100 g							
0- 8	4.8	3.6	3.1	13.0	0.4	0.1	0.1	0.2	3.4	4.2	23.5
8- 22	4.7	3.6	1.7	10.1	0.2	0.1	0.1	0.2	3.2	3.8	15.8
22- 46	4.4	3.8	1.1	8.8	0.2	0.1	0.1	0.1	1.9	2.4	20.8
46-132	4.9	4.1	0.6	6.0	0.1	0.1	0.1	0.1	0.6	1.0	40.0
132-140	5.4	4.3	-	7.0	0.2	0.1	0.1	0.2	0.3	0.9	67.0

* By ammonium acetate at pH 7

† Not including H

‡ Relative to sum of cations

Table 2. The pH, activity of Al in solution and proximity of swollen root primordia to the root tip for different additions of $Ca(OH)_2$ and concentrations of $CaCl_2$, experiment 1.

No.	Treatment $Ca(OH)_2$ † meq/100g	$CaCl_2$ ‡ M/1x10^3	pH	aAl M/1x10^5	D* cm
1	0.0	1	4.02	10.7	4.4
	0.0	5	3.98	14.2	3.4
3	0.0	10	4.02	15.7	4.5
4	1.75	1	4.83	0.2	10.4
5	1.75	5	4.65	0.7	10.6
6	1.75	10	4.46	1.8	9.5
7	3.50	1	5.71	0.1	12.9
8	3.50	5	5.41	0.3	11.2
9	3.50	10	5.14	0.5	10.5

* Distance of swollen root primordium closest to the root tip.

† Effects on D were significant at 1% probability level.

‡ Effects on D were non-significant or 5% probability level.

Table 3. Solution parameters and root growth of corn and sorghum seedlings in 60 hours for different additions of $Ca(OH)_2$ and concentrations of $CaCl_2$, experiment 2.

	Treatment								
	$Ca(OH)_2$ †	$CaCl_2$ ‡				$pH - \frac{1}{2}pCa$	$\frac{1}{3}pAl - \frac{1}{2}pCa$	ΔL -corn*	ΔL -sorghum*
No.	meq/100g	$M/1x10^3$	pH	PCa	pAl	$(M/1)^{\frac{1}{2}}$	$(M/1)^{3/2}$	cm/60hr	cm/60hr
1	0.0	1	4.02	3.33	3.97	2.35	-0.34	2.3	0.5
2	0.0	10	4.02	2.38	3.80	2.83	0.07	3.7	0.5
3	0.22	1	4.07	3.12	3.80	2.51	-0.28	2.5	0.3
4	0.22	10	3.97	2.38	3.66	2.74	0.00	3.0	0.5
5	0.44	1	4.15	3.01	4.00	2.65	-0.17	3.1	0.3
6	0.44	10	4.00	2.38	3.72	2.81	0.05	3.0	0.4
7	0.87	1	4.34	2.93	4.47	2.87	0.02	5.5	0.7
8	0.87	10	4.11	2.36	3.98	2.93	0.13	5.1	0.9
9	1.75	1	4.83	2.88	5.79	3.40	0.50	10.2	2.6
10	1.75	10	4.46	2.31	4.76	3.29	0.40	9.0	2.3
11	3.50	1	5.71	2.91	6.90	4.26	0.85	12.0	8.0
12	3.50	10	5.14	2.26	6.07	4.01	0.89	11.6	8.0

* Additional root length 60 hours after placement of seedlings into solutions.

† Effects on L were significant at 1% probability level for both corn and sorghum.

‡ Effects on L were not significant at 5% probability level for both corn and sorghum.

Table 4. Soybean taproot elongation in nutrient solutions at different concentrations of Ca and pH (from Lund, 1970).

Treatment No.	pH	Ca ppm	pH - 1/2pCa†	pH - pCa†	ΔL/Δt* mm/hr
1	5.60	0.05	2.65	-0.30	2.66
2	5.60	0.50	3.15	0.70	2.87
3	5.60	2.50	3.50	1.40	2.70
4	4.75	0.05	1.80	-1.15	0.11
5	4.75	0.50	2.30	-0.15	0.91
6	4.50	0.05	1.55	-1.40	0.04
7	4.50	0.50	2.05	-0.40	1.36
8	4.50	2.50	2.40	0.30	2.38
9	4.00	2.50	1.90	-0.20	0.44
10	4.00	5.00	2.05	0.10	1.26

* Rate of elongation during 48 hours after placement of roots into solution.

† No activities were calculated.

Table 5. Soybean taproot elongation in nutrient solutions with different concentrations of Ca, Mg and K (from Lund, 1970).

	Treatment			$\frac{(Ca)^{\dagger}}{E(M_i)}$	$\frac{(Ca)^{1/2\dagger}}{(Mg)^{1/2}+(K)}$	$\Delta L/\Delta t^{*}$
	Ca	Mg	K			
No.	meq/l	meq/l	meq/l			
1	2	38	0	0.05	0.22	1.56
2	4	36	0	0.10	0.32	2.59
3	8	32	0	0.20	0.48	3.25
4	2	19	19	0.02	0.25	2.07
5	4	18	18	0.04	0.37	2.69
6	8	16	16	0.09	0.56	3.15

* Rate of elongation during 48 hours after placement of roots into solutions.

† Parentheses denote approximate activities.

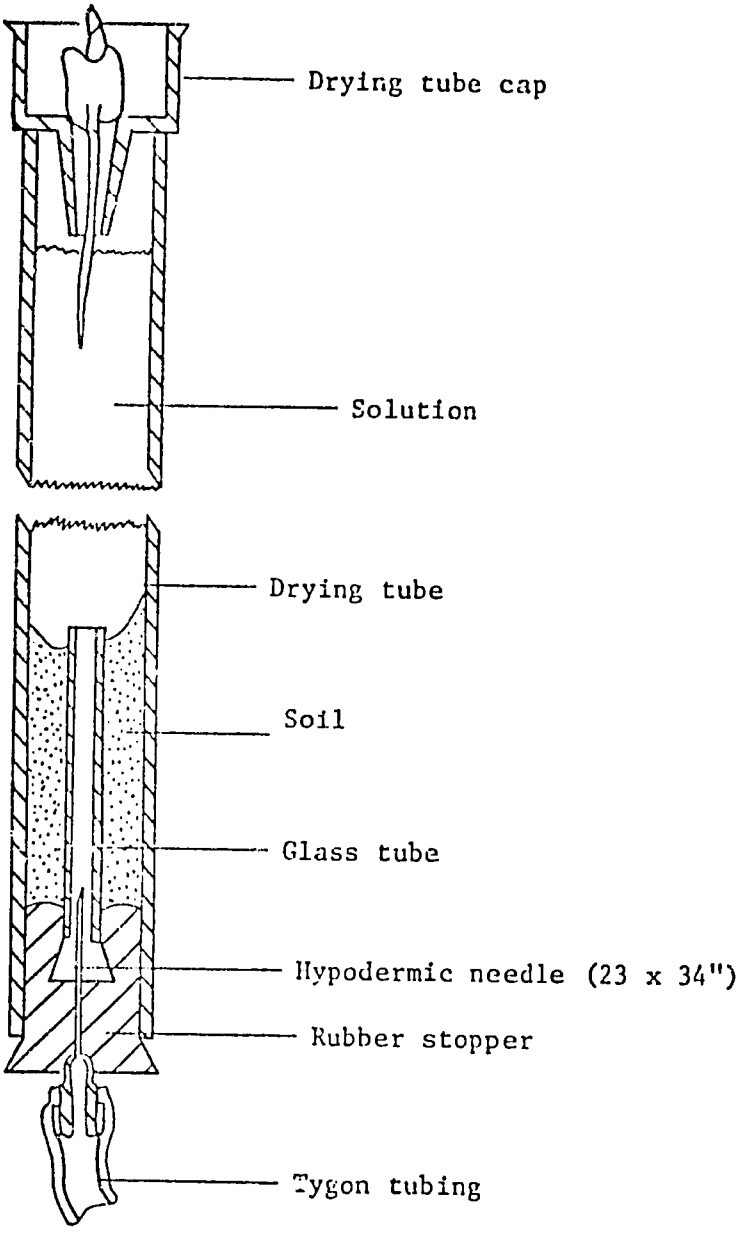

Figure 1: Assembly for root growth studies used in Experiments 1 and 2.

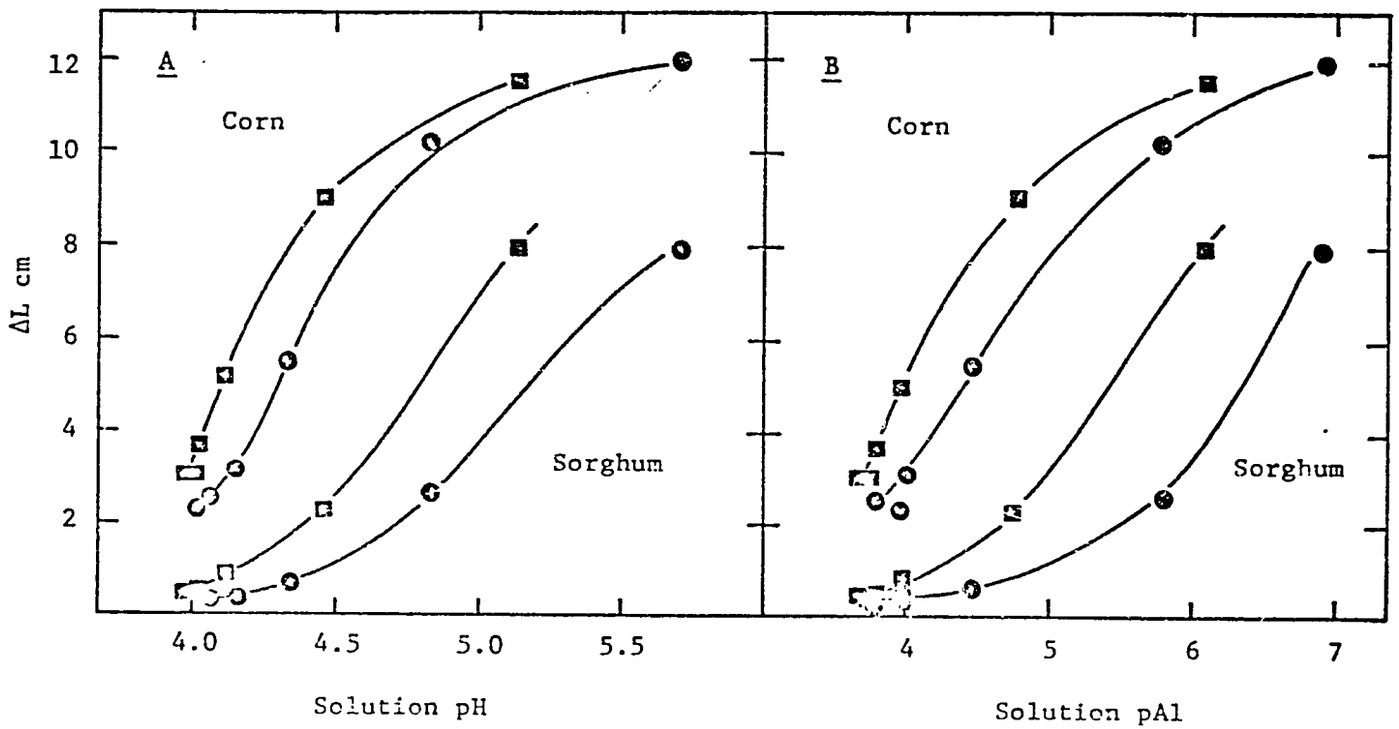

Figure 2: The increase in root length of corn and sorghum seedlings in 60 hours (ΔL) plotted against the pH and pAl of the solutions. Circles represent the results with 10^{-3} M $CaCl_2$ solutions, squares represent the results with 10^{-2}M $CaCl_2$ and the lines are drawn in visually for reference purposes.

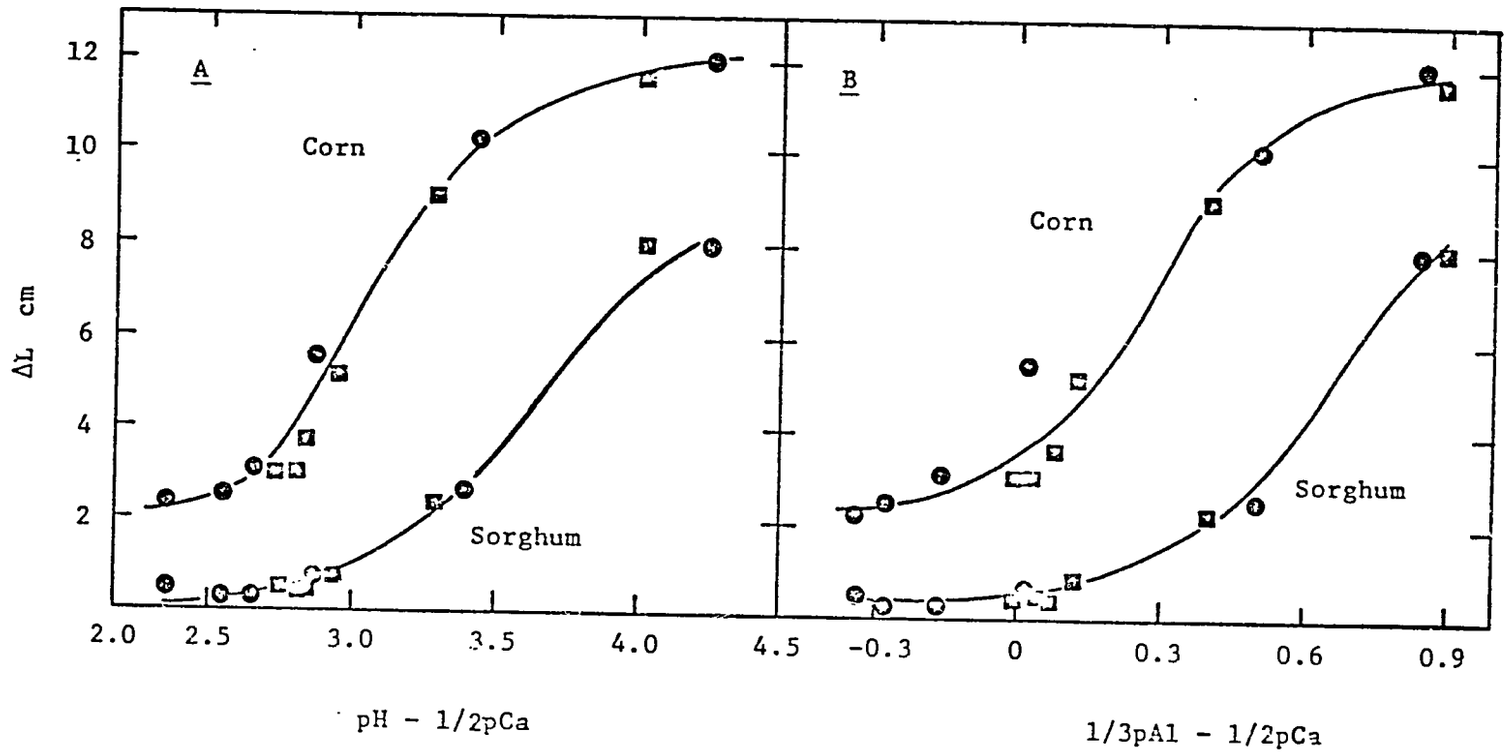

Figure 3: The increase in root length of corn and sorghum seedlings in 60 hours (ΔL) plotted against the relations (pH - 1/2pCa) and (1/3pAl - 1/2pCa) of solutions. Circles represent results with 10^{-3} M $CaCl_2$ solutions, squares represent results with 10^{-2} M $CaCl_2$ solutions and the lines are drawn in visually for reference purposes.

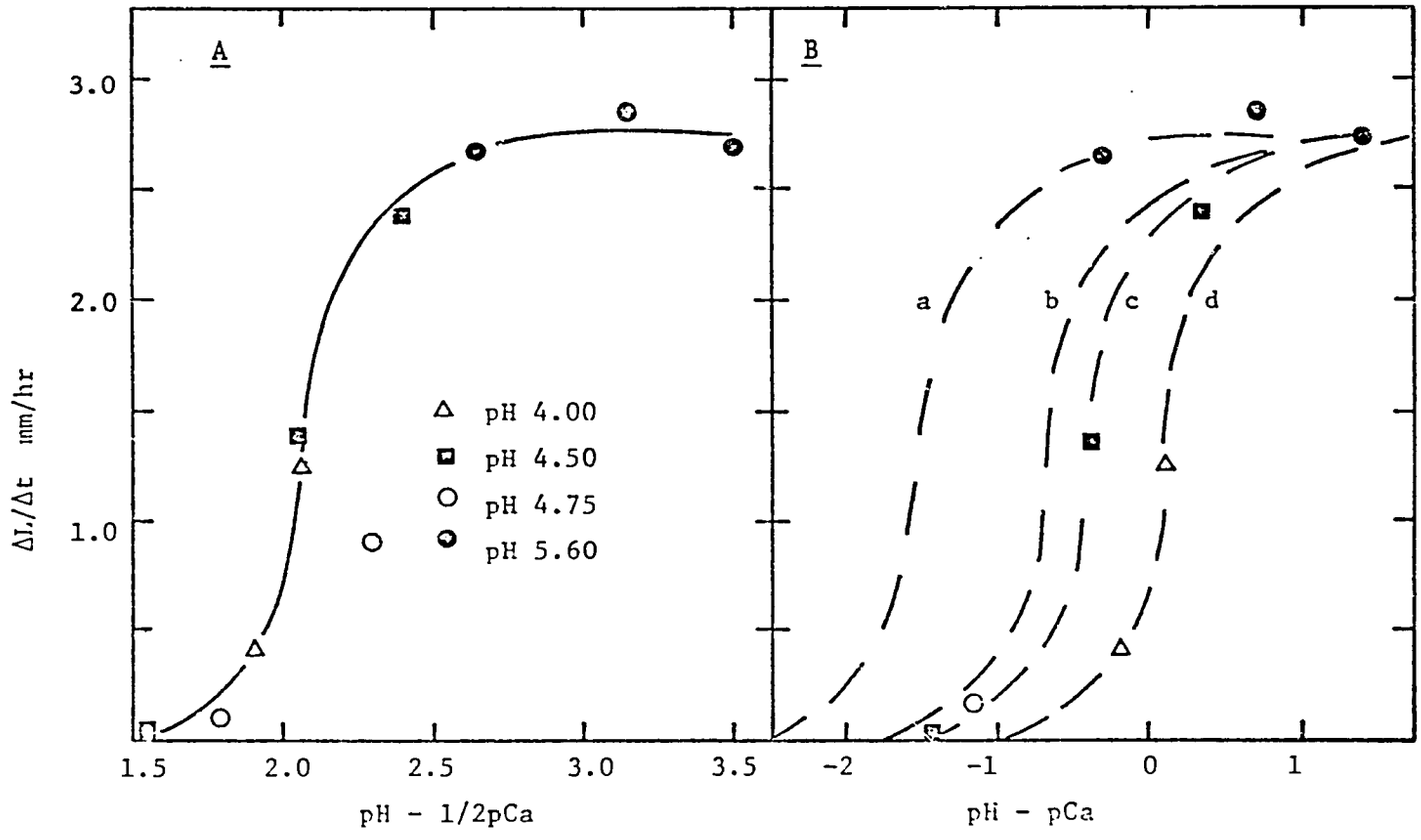

Figure 4: Taproot elongation rate of soybean (ΔL/Δt) plotted against pH - 1/2pCa and pH - pCa. In figure B, calculated curves are at pH 5.6 (a), pH 4.75 (b), pH 4.5 (c) and pH 4.0 (d). Points are experimental observations, lines are drawn in visually for reference purposes (data from Lund, 1970).

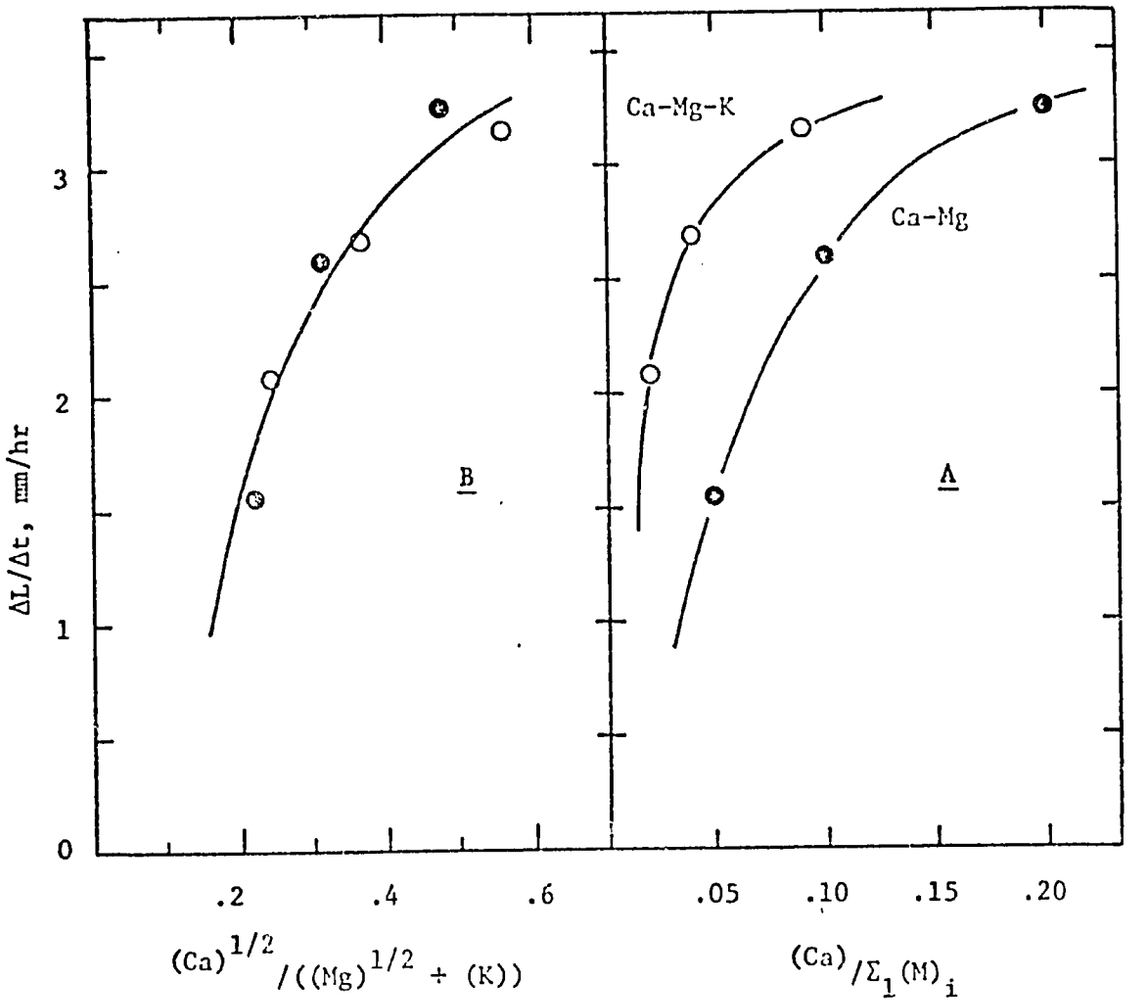

Figure 5: The rate of soybean taproot elongation rate ($\Delta L/\Delta t$) plotted against two ion activity ratios in solution. Points are experimental observations, lines are drawn in visually for reference purposes.