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THE INFLUENCE OF CALCIUM ION ACTIVITY IN WATER CULTURES ON THE INTAKE OF CATIONS BY BEAN PLANTS[1]

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It is becoming increasingly evident that the adverse effect of "alkali soils" (**14**) on plant growth is due in part to the decreasing availability of calcium associated with increasing proportions of sodium upon the exchange complex of the soil. RATNER (**12**) presents data to show that a given level of adsorbed Ca is less exchangeable in the presence of adsorbed Na than when H, Mg, and K are the complementary cations adsorbed. His evidence indicates (**11, 13**) that the energy of retention of Ca by soil colloids is sufficiently high in the presence of a relatively high level of adsorbed Na to prevent not only the intake of Ca by the plant but to actually remove Ca from the plant with the resultant death of the plant tissues from Ca starvation. He observed (**12**) that wheat seedlings failed to take in calcium from soil with an exchangeable-sodium percentage of 40. VAN ITALLIE (**16**) found that growth of Italian rye grass was impaired by an exchangeable-sodium-percentage in the soil of 26 and prevented by one of 50. THORNE (**15**) observed that the ability of tomatoes to take in calcium was reduced when the exchangeable-sodium-percentage was 40 or higher.

BOWER and WADLEIGH (**3**) employed cultures with nutrients adsorbed on ion-exchange resins (**1**) to ascertain the nutritional effects of varying exchangeable-sodium-percentages on growth and cation accumulation by four species of plants. They found that different species varied widely in their response to increasing proportions of adsorbed sodium on the cation exchange complex. Dwarf red kidney beans were especially sensitive to this condition. Increasing exchangeable-sodium-percentages, with concomitantly decreasing exchangeable calcium and magnesium percentages, were effective in inducing marked decreases in the accumulation of Ca and Mg in tops and increases in sodium accumulation. However, the most striking effect of the substrates upon cation accumulation was found in the roots. The content of Ca and Mg per unit weight of root tissue was constant for

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all treatments. On the other hand, even though exchangeable-potassium-percentage was constant for all treatments, there was a marked decrease in potassium accumulation in the roots with increasing exchangeable-sodium-percentage. The trend of potassium content of the roots was more closely related to growth than that of any other component studied. This relationship was regarded as a response to the phenomenon pointed out by JENNY and AYERS (**10**) to the effect that potassium adsorbed on soil colloids becomes less exchangeable as the adsorbed complementary ions are shifted from predominantly Ca to Na. Furthermore, potassium moves readily into the tops of bean plants whereas sodium tends to be restricted to the roots (**7**). BOWER and WADLEIGH (**3**) found very high accumulations of Na in the roots of plants at the higher exchangeable-sodium-percentages indicating a certain degree of cationic replacement in the roots. Thus, there was evidence that the very poor condition of the plants at the higher exchangeable-sodium-percentages was related to serious potassium deficiency in the roots, as well as Ca deficiency in the tops.

As a result of the aforementioned study, the question immediately arose as to what extent the plant responses observed in the presence of an ion exchange medium could be duplicated by plants grown in solution cultures varying as to calcium availability in the absence of ion adsorbents. This paper presents the results of a study of the problem.

Experimental procedure

Previously unreported data from the work of BOWER and WADLEIGH (**3**) are set forth in table I and provide the basis for the nutrient solutions used in the present study.

TABLE I

AVERAGE CATIONIC COMPOSITION OF EFFLUENT OF CULTURES USED BY BOWER AND WADLEIGH (3)

EXCHANGEABLE NA IN SUBSTRATE	CATIONS IN EFFLUENT			
	Ca	Mg	K	Na
%	*m.e./l.*	*m.e./l.*	*m.e./l.*	*m.e./l.*
0	5.4	2.6	3.1	2.5
15	3.9	1.7	2.8	11.6
30	3.1	1.3	2.5	15.9
45	3.0	1.0	2.5	24.3
60	2.9	0.9	2.6	29.4
75	2.6	0.8	2.5	28.8

It is evident that the concentrations of the cations K, Ca, and Mg in the effluent were ample for normal plant growth if a solution of comparable composition had been used in a solution culture study. Furthermore, the highest amount of sodium present should not have been specifically toxic to bean plants (**7**). Thus, in order that the above mentioned plant responses could have taken place, the cationic exchange medium must have affected the distribution and activity of the cations in the diffuse double layer about this adsorbent, consequently affecting the relative activities of these cations and their qualitative distribution on the absorbing surface of the roots. Hence, nutrient solutions were prepared for the present study having a wide variation in calcium activity in the absence of added sodium chloride and in the presence of an addition of 24 m.e./l. NaCl. All nutrient solutions contained the following components:

5 m.e./l.	KNO_3
0.5 "	KH_2PO_4
2 "	$MgSO_4$
1.0 p.p.m.	Fe as FeCitrate
0.5 "	Mn as $MnSO_4$
0.5 "	B as HBO_3

The variation in calcium additions is shown in table II. The calculation of the activity coefficients for Ca was by means of the formulation of Debye and Hückel as given by GLASSTONE (**9**, p. 940–943).

Four 8-day-old dwarf red kidney bean seedlings were transferred to each 5-gallon crock of adjusted culture solution on April 30, 1948. Each of the

TABLE II

CONCENTRATION OF $CaCl_2$ AND NaCl IN NUTRIENT SOLUTIONS TOGETHER WITH THEIR IONIC STRENGTH AND THE ACTIVITY OF THE CALCIUM ION

SOLUTION DESIGNATION	$CaCl_2$ ADDED *m.e./l.*	NaCl ADDED *m.e./l.*	IONIC STRENGTH	ACTIVITY CO-EFFICIENT FOR Ca, α_{Ca} @ 25° C.	ACTIVITY OF Ca $\alpha_{Ca} \times 10^3$ @ 25° C.
4	4		.0155	.559	1.22
1	1		.0110	.611	.31
1/4	0.25		.0099	.628	.079
1/8	0.125		.0097	.631	.039
S4	4	24	.0395	.394	.79
S2	2	24	.0365	.408	.41
S1	1	24	.0350	.416	.21
S1/2	0.5	24	.0342	.420	.11
S1/4	0.25	24	.0339	.422	.053
S1/8	0.125	24	.0339	.424	.027

10 nutritional treatments was replicated three times. Each culture was vigorously aerated by means of a carbon-tube aerator. The cultures were equipped with constant level devices so that when fresh solution was added each morning, any excess would flow off from the bottom of the culture jar. Four quarts of fresh nutrient solution were added to each culture each morning except during the last week of the experiment when six quarts were added daily. This was done to prevent extreme depletion of the prescribed levels of calcium. The extent of depletion which did take place is illustrated by the data in table III. Consequently, the Ca concentrations shown in table III should be taken as more nearly indicative of the conditions affecting

plant growth than those given in table II. The rapid rate of replenishment helped to maintain the pH of the solutions at 5.6–6.0.

The plants were harvested on May 19, 1948, weighed, and separated into leaves, stems, and roots. The roots were thoroughly washed in distilled water. The dried tissue was ground in a Wiley mill and wet-ashed by the method of GIESEKING *et al.* (**8**). The cationic composition of the dry tissue was determined by methods given in reference (**14**) with a modification (**5**) of the uranyl zinc acetate method for Na in plant material.

TABLE III

CONTENT OF Ca IN CULTURE SOLUTIONS JUST BEFORE BEING REPLENISHED WITH FRESH SOLUTION ON MAY 12, 1948

CA IN ORIGINAL SOLUTION	CA IN SOLUTIONS JUST BEFORE REPLENISHMENT	
	WITHOUT NaCl	NaCl ADDED
m.e./l.	*m.e./l.*	*m.e./l.*
4	4.08	4.14
2		2.23
1	.98	1.18
0.5		.59
0.25	.19	.20
0.125	.06	.06

Observations

The growth responses of the plants are shown in figure 1. It appears that maintenance of the Ca level at 0.5 m.e./l. was adequate for these bean plants both in the presence and absence of added NaCl. Addition of NaCl to the cultures did not vary relative growth response at the different levels of Ca nutrition. Tops of plants with added NaCl were only 58% as heavy as those without this salt. This decrease in growth was undoubtedly the result of decreased water availability from the increase in osmotic pressure of the nutrient solution since addition of 24 m.e./l. of NaCl increased osmotic pressure of these solutions by one atmosphere. The observed growth depression accompanying the addition of 24 m.e./l. NaCl to the substrate is much greater than that reported by GAUCH and WADLEIGH (**7**) for dwarf red kidney beans grown in comparable nutrient solutions. This latter study was carried on in December under relatively low light intensity. GAUCH[3] found that the relative growth depression with beans on saline substrates was much greater during the spring months with higher light intensities than during the winter when visible radiation was low.

The only plants which showed symptoms of malnutrition at the conclusion of the growth period were those subjected to the lowest level of calcium supply. The symptoms consisted largely of a slight chlorosis near the margins of the older leaves. These plants had also showed some of the symptoms of moisture stress during the heat of the day.

[3] Gauch, H. G. Unpublished data, U. S. Regional Salinity Laboratory.

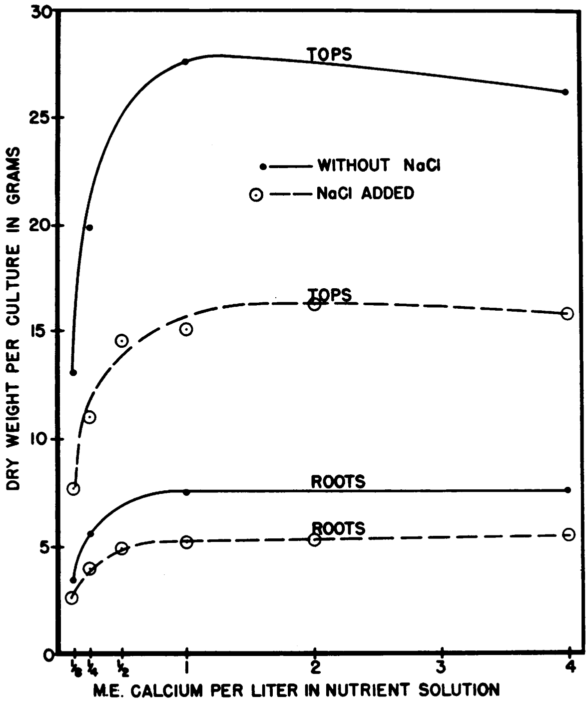

FIG. 1. Growth response of plants.

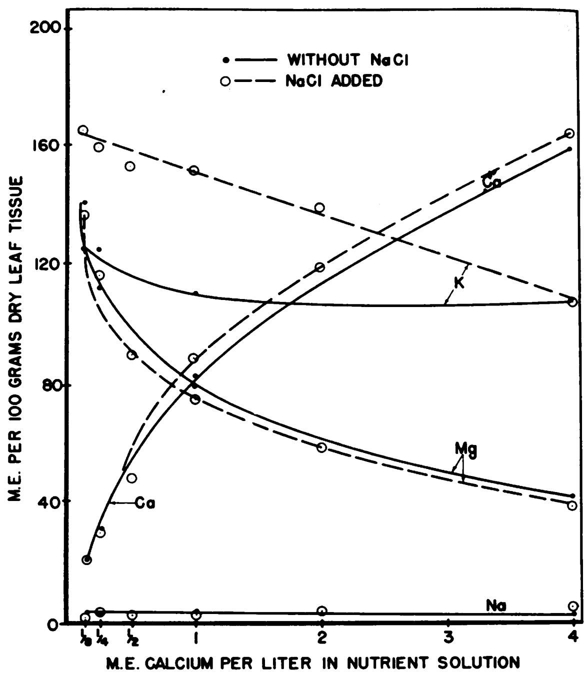

FIG. 2. Cation accumulation in leaf tissue.

Figures 2, 3, and 4 show the cation accumulation in terms of m.e./100 gms. dry tissue for the leaves, stems, and roots of these plants.

The concentration of Ca in the various tissues increased directly as the concentration of this element in the culture solution was increased. The most pronounced increase in Ca content took place in the leaves; those from plants on cultures with 4 m.e./l. Ca contained eight times as much Ca in the tissue as those on cultures containing 1/8 m.e./l. The addition of 24

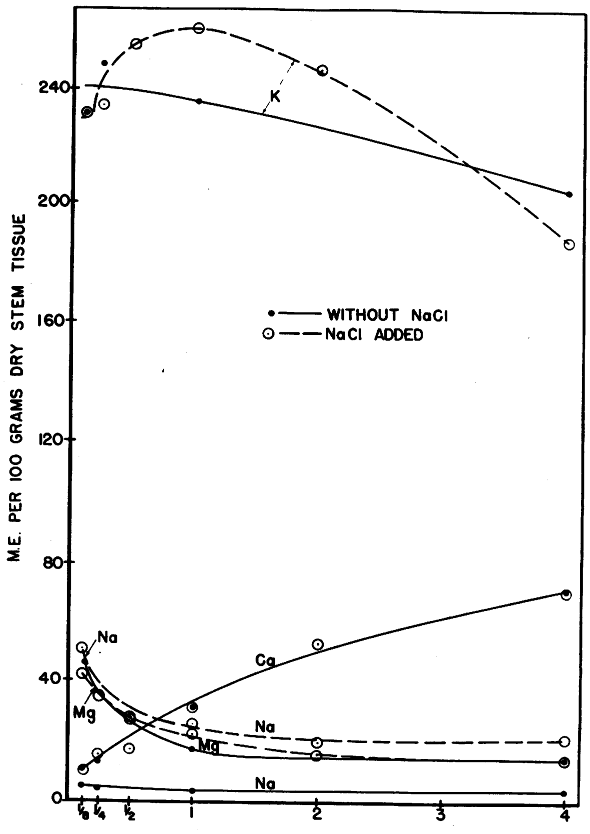

FIG. 3. Cation accumulation in stem tissue.

m.e./l. of NaCl had no effect on Ca concentration in the plant tissue at a given level of calcium supply, even though the resultant increase in ionic strength of these solutions caused a lowering of calcium ion activity at respective levels of Ca addition. (See table II.)

There was practically no variation in the Mg content of root tissue with variations in Ca supply in the absence of added NaCl; but when this salt was added, the general level of Mg in root tissue was lowered. The addition of NaCl to the substrate was not associated with any definite effect on the Mg content of tissue of the shoot. There was in the leaves and stems, however, an unusually high accumulation of Mg at the lower levels of Ca supply. This accumulation may have been sufficient to result in Mg toxicity in line with GAUCH's (**6**) observation that magnesium toxicity symptoms readily develop in bean plants on calcium deficient cultures.

Addition of NaCl to the culture solution was accompanied by a high accumulation of Na in the root tissue. There was a definite trend for the Na content of root tissue to decrease with increasing concentration of Ca

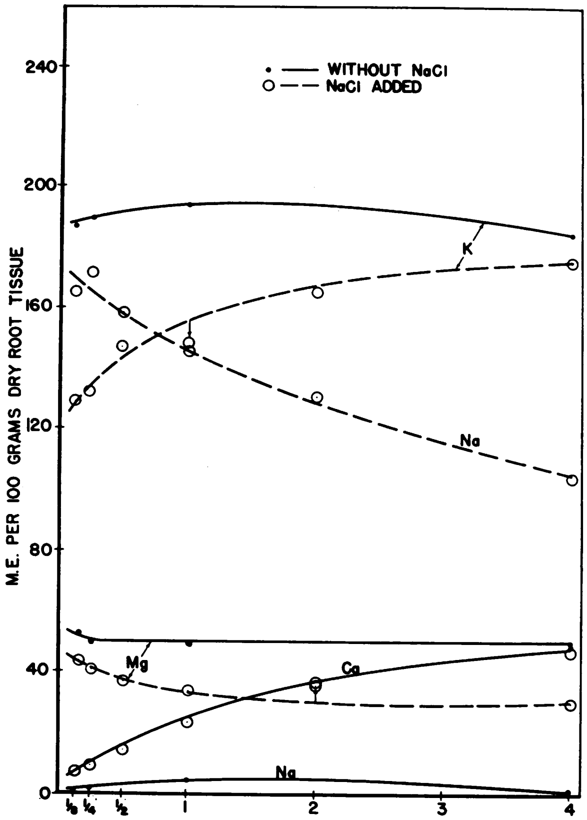

FIG. 4. Cation accumulation in root tissue.

in the culture solution. In the stems, there was a moderate tendency for Na to accumulate on addition of NaCl to the substrate. In confirmation of the observations of GAUCH and WADLEIGH (**7**), the addition of 24 m.e./l. to the water cultures had no effect on the Na content of leaf tissue of beans. This species exhibits a remarkable mechanism for accumulating Na in the roots while preventing its accumulation in the leaves.

The potassium content of all tissues in all treatments was unusually high. The concentration of this element in the root tissue showed little variation with varying levels of Ca supply in the absence of added NaCl. Addition of NaCl to the culture solution was accompanied by a decrease in the K content of root tissue; and there was a marked tendency in the latter series of plants for K content of roots to increase with increasing levels of Ca supply. In other words, there was evidence of a reciprocal relation between the contents of Na and K in the root tissue. This does not imply constancy of cation equivalence in unit weight of tissue, however, since the dry tissue of roots from plants receiving added NaCl contained an average of 90 m.e./100 gms. more cations than did that from plants without added NaCl.

The stem tissue of the plants grown in water cultures was phenomenally high in potassium, and there were only minor variations in the concentration of this element with wide variations in Ca supply. There was some tendency for the K content to be higher in stem tissue from plants subjected to added NaCl.

The average concentration of potassium in leaf tissue was considerably lower than that in stem tissue. Whereas, there was little variation in K content in leaf tissue from plants without added NaCl as a result of variation in Ca supply, the addition of NaCl to the culture solution was associated with appreciable higher concentrations of K in the leaf tissue together with a marked negative trend with level of Ca supply. Thus, it appears that the observed accumulation of Na in the root tissue was conducive to the partial displacement of K from this tissue with concomitant accumulation in the leaf tissue which was virtually devoid of Na. Correspondingly, the trend of potassium accumulation in leaf tissue with varying Ca supply in the NaCl series of plants was just the converse of the trend in potassium accumulation in root tissue in this series.

These data are supporting evidence for a reciprocal relationship in the accumulation of the four cations studied among three tissues of the bean plant on variations in calcium supply.

Discussion

In this experiment, a comparison is made between cation accumulation in bean plants grown in water cultures varying as to calcium activity and that of bean plants grown on cultures containing nutrients adsorbed on ion exchange resins with Ca activity theoretically varied by means of varying exchangeable-sodium-percentages. This is shown in figure 5. The solid lines show the levels of accumulation within the dry tissue of the tops (leaves and stems) of the four cations with varying levels of Ca supply. The comparable values for the plants grown on cultures with ion exchange resins are shown by the dotted lines. The arrows above the abscissa show the levels of Ca found in the effluent from cultures adjusted to various exchangeable-sodium-percentages indicated by the numbers adjacent to the arrows. The values for Ca are taken from table I.

It is evident that use of the Ca concentration of the effluent from the ion-exchange resin cultures as a basis for plotting the trends in accumulation of the four cations presents a misleading picture in the light of the results from the water culture study. That is, Ca concentration of the effluent was not a valid measure of calcium availability from the ion exchange resins if Ca accumulation from water cultures is taken as a standard.

The data show that addition of NaCl to the culture solution had no significant effect on Ca accumulation in bean tissue when various levels of Ca supply were maintained in water cultures even though the increased ionic strength of the solutions effects a decrease in calcium ion activity. Furthermore, the data on Ca accumulation by bean plants given by GAUCH and WADLEIGH (7) fit in very well with that here presented even though the

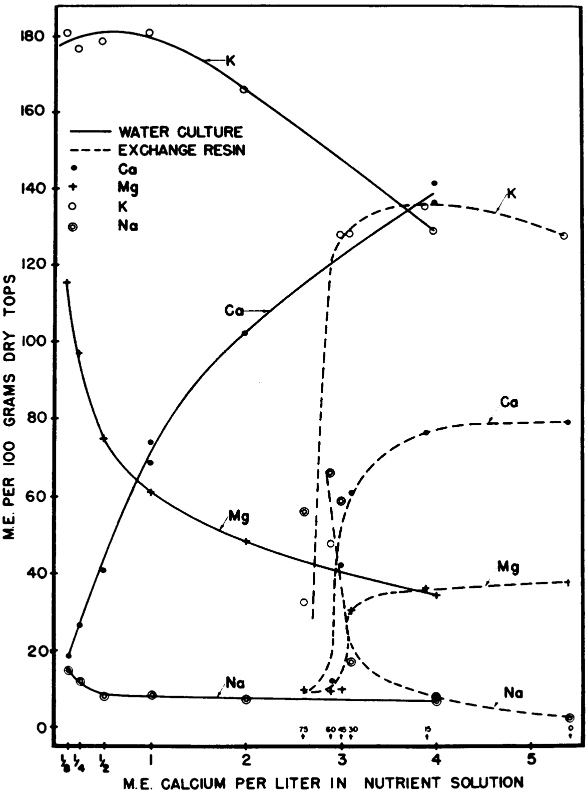

FIG. 5. Comparison of cation accumulations in tops of two groups of plants. Values for plants grown on exchange resins based on calcium concentration of effluent from these cultures.

respective groups of plants were grown during different seasons. It is reasonable, therefore, to take the curve showing Ca accumulation in the tops as an index of Ca availability in the substrate. This was done in figure 6. The arrows on the Ca curve designate the various levels of Ca accumulation in the tops of bean plants grown on cultures with ion exchange resins. The figures adjacent to the arrows show the exchangeable-sodium-percentage in the various cultures. By projecting these intercepts on the Ca-curve vertically to the abscissa, a set of values are derived which show the theoretical level of Ca that would need to be maintained in water cultures to effect the levels of Ca accumulation shown by the tissue from plants grown with ion-exchange resins. Correspondingly, the levels of accumulation of the other three elements in this latter group of plants are also shown as functions of this theoretical level of Ca supply. The derived trend in Mg accumulation is reasonable on the grounds that percentage of exchangeable Mg decreased with increase in exchangeable-sodium-percentages, thereby effecting an appreciable range in Mg availability. The values for Na accumulation may also be readily explained on the basis of percentage of exchangeable Na.

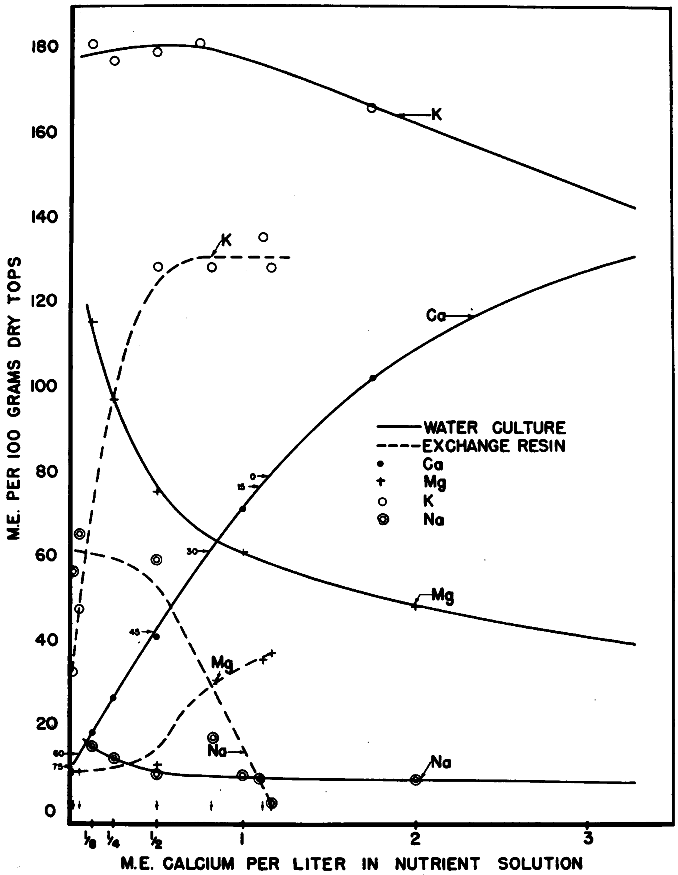

FIG. 6. Comparison of cation accumulations in tops of two groups of plants. Values for plants grown on exchange resins based on extrapolated calcium supply indicated by calcium content in tops.

On the other hand, even though potassium was supplied at constant levels for all treatments in the two respective types of culture, quite divergent trends were observed for potassium accumulation. Whereas, accumulation of potassium tended to approach a maximum at the lower levels of Ca supply in water culture, the opposite effect was very pronounced with the plants grown on ion exchange resins. This seemingly anomalous response as regards accumulation of potassium was not predictable from the results of the water culture study involving varying levels of Ca or from the composition of the effluent from the ion-exchange resin cultures.

ARNON and MEAGHER (**2**) have discussed the availability to plants of ions adsorbed on ion-exchange resins and have emphasized especially the relative unavailability of adsorbed Ca and Mg. BOWER and WADLEIGH (**3**) also noted this effect, and that it was enhanced by increasing proportions of adsorbed sodium. That is, the complementary ion effect is operative on exchange resins. A given proportion of potassium adsorbed on a soil colloid is more easily released if the complementary ion is calcium rather than sodium (**4, 10**). The ease of release of the various cations is Na > K > Mg > Ca. Consequently, increasing exchangeable-sodium-percentage theoretically decreases ease of release of K as well as Ca and Mg. Decreasing potassium availability did not take place in the water culture study. Therefore, a water culture study based on varying availability of calcium with the assumption that Ca availability was the principal factor involved in the study with ion-exchange resins was not successful in simulating the responses in the latter study. This consequence is interpreted as being due to the operation of the complementary ion effect, particularly in its action on the availability of potassium in the presence of relatively high proportions of adsorbed sodium.

Summary

Red kidney bean plants were grown in aerated water cultures varying as to calcium supply in the presence and absence of added NaCl. Accumulation of cations in the various parts of the plant was ascertained. This was compared with similar data from bean plants grown on substrates with nutrients supplied on ion exchange resins, with exchangeable sodium percentage being the primary variant but with exchangeable Ca and Mg percentage varying reciprocally. The operation of the complementary ion effect on the adsorptive surface induced a marked deviation from the response in water cultures particularly with reference to trends in accumulation of potassium.

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