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Sodium and Rubidium as Possible Nutrients for Sugar Beet Plants

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Summary. This study concerned the degree to which Na or Rb could substitute for K in the growth of sugar beet plants when K in the culture solution was low (1 meq/liter) or high (12 meq/liter).

Sodium at high concentrations increased the growth of plants in a basal nutrient medium when either deficient in K or when adequately supplied with K alone. Redistribution of K from petioles to blades could not fully explain these results. Therefore, the essentiality of Na per se for growth of sugar beet plants may be inferred.

Rubidium increased the growth of plants significantly when supplied in small doses to a nutrient medium deficient or adequately supplied with K. The amount of K added and the mode of Rb addition to solution cultures should be carefully considered when studying the effect of Rb on growth. High Rb concentrations were toxic, especially to the growth of fibrous roots.

Sodium or Rb have been shown to enhance the growth of sugar beet plants under either low or high K conditions. Essentiality of either Na and/or Rb per se for growth of sugar beets may be inferred, but other criteria should be fulfilled also for conclusive proof.

Potassium is the only univalent cation generally recognized to be indispensable for growth of all plants. Sodium appears to be essential for the growth of *Atriplex vesicaria* (3). With many other plant species beneficial effects of Na on growth have been noted in media high or low in K (10, 12, 14, 16, 17). The beneficial effect of Na has been explained as a sparing action on K through redistribution of K from places of abundance to those of deficiency (10, 15). This explanation is not complete when a large amount of Na, added to a low K medium, increases growth above that in a high K medium with no Na addition.

Rubidium, chemically very similar to K, might be expected to replace K, at least partially, as an essential element for plant growth. Plants cultured in solutions inadequately supplied with K, have increased in growth from the addition of small amounts of Rb (13). Maynard and Baker (11) reported that Rb did not substitute for K in the growth of tomato, and that solutions containing K and Rb in ratios below 5, expressed on an equivalence basis, reduced growth and resulted in a characteristic symptom of injury. Hurd-Karrer (7) demonstrated that Rb injury is an inverse function of the available K concentration in the nutrient solution; symptoms were reduced as the relative K concentration increased. Therefore, in studying K-Rb interactions in plant systems, results will also depend on the relative K and Rb concentrations in the nutrient solution as well as the absolute concentration of each.

The present investigations concerned the influence of Na, Rb and K on the growth of the sugar beet plant and their distribution among various organs, different in age.

Materials and Methods

Beta vulgaris seed, var. MS NB1 × NB4, was treated with 1 % Phygon and cultured in vermiculite, watered with a basal nutrient solution lacking K. The composition of the basal nutrient solution, in mmoles per liter, was: 0.5 $MgSO_4$, 0.25 $Ca(H_2PO_4)_2$, 1.875 $Ca(NO_3)_2$, and 0.125 $CaCl_2$. Micro-elements were added in ppm as follows: 2.5 Fe, 0.25 B, 0.25 Mn, 0.05 Zn, 0.01 Cu, and 0.005 Mo. Iron was supplied as the ferric-ammonium ethylenediamine tetra-acetate complex (8). When the seedlings were in the early 2-leaf stage, they were removed and the roots washed nearly free of vermiculite. Seedlings were supported individually in a cork ring with non-absorbent cotton and transferred at random, 3 per 20 liter aerated culture solution tank.

Three greenhouse experiments were conducted: the first, a Na series; the second, a Rb series; and

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the third, containing both a Na and a Rb series. Each of the 3 cations was added as the sulfate salt. Five replicates were used for the first 2 experiments and 4 for the last.

The initial concentrations from the K, Na and Rb additions, applied at transplanting, are given in tables I and II. Two K treatments were applied as sulfates, 1 meq/liter ("low K" treatment, to produce K deficiency symptoms 3–4 wks after transplanting) and 12 meq/liter ("high K" treatment, to support favorable growth during the whole experimental period, i.e., 55 days). The high K treatments were applied in 2 increments, 8 meq/liter at the time of transplanting; 4 meq/liter, 6 weeks later. The basal solutions, exclusive of K, Na or Rb, were added 3 times to all pots without changing the culture solution; once at the time of transplanting, the other 2 times at 2 to 3 week intervals depending on rate of growth. In the first experiment, for the high Na concentrations, (16 and 32 meq/liter) the salt was added in partial doses at intervals, to avoid undesirable osmotic effects. To achieve a medium low in K, the K supply concentration was reduced; concomitantly, the absolute amount of Ca, and to a lesser extent Mg, constituted a larger proportion of the cations supplied.

The pH of the solutions was adjusted when necessary, within the range of 5.5 to 6.0 with either 1.0 N H_2SO_4 or 1.0 N NH_4OH. Culture solutions were analyzed for ionic composition during the experiment, results of which have been reported elsewhere (4).

Leaves were separated at harvest into young, mature, mature with K deficiency symptoms, and old leaves. Each group was subsequently divided into blades and petioles. Fibrous roots were removed from the storage root and rinsed 3 times with distilled water, then centrifuged for 5 minutes at 43 × g to give a consistent moisture content for fresh weight determination. Plant parts were weighed, dried in a forced-draft oven at 80°, and reweighed. Dried tissues were ground to pass a 40 mesh screen.

Storage roots from individual pots were pulped and mechanically mixed. Samples (frozen on dry ice for subsequent analysis) were assayed in duplicate for sucrose content by the method of Browne and Zerban (2). Other samples were dried, weighed, ground, and analyzed for cations.

For cation determination, the plant material was dry ashed, as described by Johnson and Ulrich (9). Calcium and Mg were measured by the atomic absorption technique (1), using a Perkin-Elmer instrument model 290. In the Na series, K and Na were determined by the flame emission technique (9), using a Beckman model D.U. spectrophotometer with flame attachment in conjunction with a Photovolt model 520 photomultiplier unit. For tissues containing Rb, K was determined by atomic absorption using a Perkin-Elmer model 303 since there was no spectral interference by Rb when Rb concentration was low, as in the usual flame emission technique.

Chemical interference by K in the Rb determination by atomic absorption was avoided by the addition of a high K concentration (50 meq/liter) to the aliquots used for Rb determination. This completely masked any effect due to differences in K concentration in plant tissues. Another advantage of applying high K concentrations during these determinations was the ability to measure low Rb concentrations.

Results

Mature and old leaf blades of plants grown in a medium low in K showed typical K deficiency symptoms. They began as a browning of the blade (especially the lower surface thereof), progressing from the margins inward between the veins to the brown scorch that was intensified in bright sunlight. midrib and basal areas. The blade then showed a Meanwhile, young leaves remained healthy with no sign of deficiency.

Data on growth, sucrose concentration of the storage root, and nutrient content of the different

Table I. *Effects of Sodium and Potassium on Growth of Sugar Beet Plants*
The data are the means of 5 replicates for experiment 1, and 4 for experiment 3.

Treatments				Shoots		Fibrous roots			Storage roots			
Expt. no.	No.	K (meq/liter)	Na (meq/liter)	Fresh g	Dry g	Fresh g	Dry g	Ratio* Shoots/Roots	Fresh g	Dry g	Sucrose %	Sucrose g
1	1	1.0	0.0	304	27.5a**	33.3	3.3a	8.2	58	7.4a	8.0g	4.8
	2	1.0	1.0	408	38.9b	50.6	5.5c	7.1	95	11.7b	7.8fg	7.4
	3	1.0	2.0	506	46.4c	59.7	5.9c	7.8	119	13.9c	7.3ef	8.6
	4	1.0	4.0	726	55.0d	63.0	6.6d	8.4	154	17.1d	6.7d	10.2
	5	1.0	8.0	1096	70.0e	65.3	6.5d	10.8	213	23.1e	5.5c	11.8
	6	1.0	16.0	1607	87.5g	69.6	5.7c	15.4	323	27.8f	3.2b	10.3
	7	1.0	32.0	1719	97.2h	81.5	5.6c	17.5	357	28.9f	3.0a	10.5
	8	12.0	1.0	1170	79.8f	69.0	4.9b	16.2	402	42.0g	5.6c	22.4
3	1	12.0	0.0	1050	76.3a	70.8	5.0a	15.4	351	40.5a	5.9a	20.7
	2	12.0	1.0	1120	84.1b	84.0	5.6ba	15.0	416	48.1b	6.2a	25.8
	3	12.0	8.0	1250	91.1c	101.0	6.7cb	13.5	429	50.8cb	6.6a	28.3

* Dry weight basis.
** Letters in common within a column and experiment and series of treatments indicate no significant differences at the 1 % level.

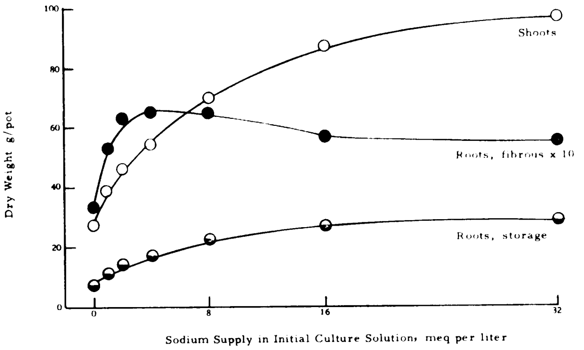

FIG. 1 Effects of sodium supply concentrations on growth of sugar beet plants under low K conditions.

plant parts at various levels of Na or Rb supply are presented in tables I and II, and figures 1 and 2. The fresh and dry weight data include leaves that senesced as a result of either K deficiency or Rb toxicity.

Plant Growth. A) Sodium. Symptoms of K deficiency decreased and then failed to appear as the Na supply was increased. At a high Na addition, growth of shoots and fibrous roots was significantly increased over that attained with a high K medium alone. The growth curves for shoots under low K conditions (figs 1, 2) indicate that a plateau was nearly reached at the 32 meq/liter Na supply level, suggesting that only a slight increase in growth might have been expected with higher Na additions. Data of table I likewise reveal that Na addition to a medium adequately supplied with K significantly increased growth.

B) Rubidium. High Rb concentrations supplied to a medium low or high in K were toxic to growth (table II). The leaves showed symptoms of toxicity, which increased as the Rb concentration increased. Affected leaves tended to be oval rather than lanceolate in shape, and had a certain degree of crinkling. The petioles were weak, tending to twist.

The same pattern of growth occurred when a low Rb level (1 meq/liter) was added to a low K medium. However, when the Rb was applied in doses of 0.1 meq/liter at intervals depending on the rate of growth, plants were without toxicity symptoms (table II, expt. 3, treat. 3). Growth was significantly increased over treatment 1, where Rb was not added; likewise over treatment 2, where 1 meq Rb/liter was added as a single dose at transplanting.

Storage-Root Weights and Sucrose Content. A)

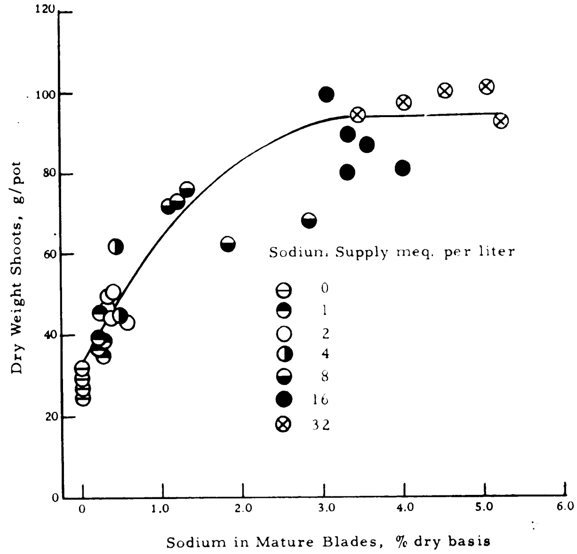

FIG. 2. Calibration curve of growth, under low K conditions (1 meq K/liter).

Table II. *Effects of Rubidium and Potassium on Growth of Sugar Beet Plants*
The data are the means of 5 replicates for experiment 2, and 4 for experiment 3.

Expt. no.	No.	Treatments K (meq/liter)	Treatments Rb (meq/liter)	Shoots Fresh g	Shoots Dry g	Fibrous roots Fresh g	Fibrous roots Dry g	Ratio* Shoots/Roots	Storage roots Fresh g	Storage roots Dry g	Sucrose %	Sucrose g
2	1	1.0	0.0	331	26.5c**	32.0	3.1e	8.4	45	4.8c	6.3b	2.8
	2	1.0	1.0	530	39.1d	28.0	2.6d	14.8	49	6.3d	6.5b	3.2
	3	1.0	2.0	446	27.9c	22.0	1.7c	16.0	29	3.2b	3.6a	1.0
	4	1.0	4.0	211	13.9b	10.4	0.8b	16.7	8	1.0a	...***	...
	5	1.0	8.0	42	3.3a	2.3	0.1a	23.7	2	0.3e	...	...
	6	12.0	1.0	1323	80.1e	80.9	5.3f	15.1	308	27.1f	4.4a	13.6
3	1	1.0	0.0	331	31.2a	39.4	3.4a	9.2	69	7.5a	8.1a	5 6
	2	1.0	1.0	453	46.4b	32.3	3.5a	13.3	92	13.0b	7.9a	7.3
	3	1.0	0.1×10	678	65.4c	47.4	3.1b	12.8	166	24.4c	9.2a	15.3
	4	12.0	0.0	1050	76.3b	70.8	5.0b	15.4	350	40.5b	5.9a	20.7
	5	12.0	1.0	1318	93 2c	85.5	5.6c	16.6	380	42.7c	5.4a	20.5
	6	12.0	8.0	698	46.3a	38.2	2.6a	17.9	93	10.6a	5.8a	5.4

* Dry weight basis.
** Letters in common within a column, experiment, and series of treatments indicate no significant difference at the 1 % level; treatments 1–3 and 4–6 of experiment 3 have been analysed statistically separately.
*** Insufficient samples for analysis.

Sodium. Storage-root weights of plants low in K were significantly increased as the Na supply was increased, but did not exceed the weights of plants high in K (table I, treat. 3). The sucrose percentage decreased as the Na supply increased; however, total sucrose stored increased because of a proportionately large increase in storage-root weight. Storage-root weight of plants high in K increased significantly with an increase of Na supply, also leading to an increase in the total sucrose content.

B) Rubidium. High Rb concentrations in a low K medium (table II) decreased the growth of storage roots and the sucrose percentage therein. Low Rb supply added to a medium low or high in K significantly increased storage-root growth and generally, the sucrose percentage.

Chemical Analyses of Plant Tissues. A) Sodium. The K, Ca, and Mg concentrations in the different plant parts generally decreased with increase of the Na supply in the culture solution (table III). Redistribution of K (to a lesser extent Ca and Mg) from petioles to blades, influenced by the accretion of Na, is indicated by the comparatively larger reduction of the petiole K composition values compared with a much smaller reduction of K in the blades. Mature blade K percentages (without symptoms) remained fairly constant in spite of the large increase in the Na content of these tissues (fig 3).

B) Rubidium. Rubidium supply decreased the contents of Ca, Mg, and to a certain degree K in some plant parts (table IV). The increase in K composition of the mature and old blades was presumably due to displacement of K from the petioles to the blades, induced by Rb. Rubidium tended to accumulate to higher values in blades than petioles. This was in contrast to Na, which was generally higher in petioles (table III).

Table III. *Cation Concentrations (% Dry Basis) in Leaves of Sugar Beet Plants as Affected by Cation Treatments*
The data are the means of 5 replicates.

	Treatments		Experiment 1					
No.	K meq/liter	Na meq/liter	Young blade	Young petiole	Mature blade	Mature petiole	MBs*	MPs*
				Potassium				
1	1.0	0.0	2.20	3.50	...**	...	0.52	2.55
2	1.0	1.0	2.06	3.06	...	...	0.50	2.10
3	1.0	2.0	1.89	2.70	...	...	0.52	1.73
4	1.0	4.0	1.77	2.09	0.78	1.66	0.52	1.38
5	1.0	8.0	1.73	1.86	0.74	1.13	0.44	0.66
6	1.0	16.0	1.71	0.81	0.73	0.62	0.30	0.18
7	1.0	32.0	1.78	0.73	0.79	0.53	...	...
8	12.0	1.0	3.08	5.19	3.83	11.40	...	...
				Sodium				
1	1.0	0.0	0.04	0.05	...	...	0.01	0.02
2	1.0	1.0	0.23	0.36	...	...	0.21	0.46
3	1.0	2.0	0.31	0.57	...	...	0.36	0.83
4	1.0	4.0	0.48	0.97	0.35	0.70	0.90	2.50
5	1.0	8.0	0.80	1.94	1.71	5.11	2.10	6.22
6	1.0	16.0	1.63	4.96	3.49	9.49	3.07	8.36
7	1.0	32.0	2.19	6.68	4.44	10.48	...	...
8	12.0	1.0	0.22	0.24	0.52	0.38	...	...
				Calcium				
1	1.0	0.0	1.43	1.41	...	...	2.46	2.45
2	1.0	1.0	1.39	1.45	...	...	2.10	2.45
3	1.0	2.0	1.24	1.37	...	...	2.14	2.17
4	1.0	4.0	1.10	1.19	1.66	1.17	1.98	1.50
5	1.0	8.0	0.95	0.81	1.52	0.75	1.73	0.77
6	1.0	16.0	0.65	0.39	1.18	0.35	1.43	0.73
7	1.0	32.0	0.39	0.17	0.77	0.21	...	...
8	12.0	1.0	1.10	0.52	1.65	0.46	...	...
				Magnesium				
1	1.0	0.0	0.64	0.70	...	...	1.16	1.51
2	1.0	1.0	0.75	0.64	...	...	1.02	1.26
3	1.0	2.0	0.56	0.61	...	...	0.91	1.09
4	1.0	4.0	0.49	0.50	0.64	0.61	0.99	0.97
5	1.0	8.0	0.45	0.40	0.92	0.65	1.14	0 65
6	1.0	16.0	0.47	0.27	1.06	0.28	1.06	0.35
7	1.0	32.0	0.49	0.15	0.99	0.16	...	...
8	12.0	1.0	0.61	0.45	1.35	0.50	...	...

* MBs or MPs represent blades or petioles with visual K deficiency symptoms.
** No plant parts in this category.

Table IV. *Cation Concentrations in Leaf and Root Tissues of Sugar Beet Plants as Affected by Cation Treatments*
The data are the means of 5 replicates. The concentrations are given on a % dry basis.

No.	Treatments K (meq/liter)	Treatments Rb (meq/liter)	Young blade	Young petiole	Mature blade	Mature petiole	Old blade	Old petiole	Roots Storage	Roots Fibrous
				Experiment 2						
				Potassium						
1	1.0	0.0	3.36	3.94	0.65*	2.95*	0.98	5.42	2.49	1.15
2	1.0	1.0	1.23	1.54	0.84	0.91	3.43	1.31	1.32	0.90
3	1.0	2.0	1.15	1.15	2.01	1.42	3.94	1.72	1.56	1.44
4	1.0	4.0	0.96	1.23	1.63	1.11	2.83	1.00	1.05	1.16
5	1.0	8.0	0.74	0.85	0.93	0.94	1.78	0.97	0.74	0.74
6	12.0	1.0	4.47	6.31	5.93	10.66	9.64	13.99	5.09	4.85
				Rubidium						
1	1.0	0.0	0.00	0.00	0.00*	0.00*	0.00	0.00	0.00	0.00
2	1.0	1.0	4.60	2.39	2.69	1.58	5.89	2.08	2.38	2.68
3	1.0	2.0	9.94	5.91	9.24	5.09	10.57	4.97	5.30	5.96
4	1.0	4.0	12.24	7.02	11.19	6.15	12.47	4.84	6.20	6.48
5	1.0	8.0	12.60	8.60	12.65	8.54	14.25	8.60	6.60	6.82
6	12.0	1.0	1.22	0.74	1.23	1.37	2.03	2.13	0.98	0.82
				Calcium						
1	1.0	0.0	1.10	1.43	2.52*	2.72*	3.81	2.18	0.30	3.95
2	1.0	1.0	1.22	1.53	2.59	2.00	2.82	2.74	0.28	1.67
3	1.0	2.0	0.85	1.10	1.86	1.34	2.26	2.18	0.28	0.68
4	1.0	4.0	1.00	1.23	1.82	1.58	2.54	2.72	0.33	0.78
5	1.0	8.0	1.00	1.46	1.30	2.10	2.50	3.40	0.69	0.85
6	12.0	1.0	0.85	0.80	1.70	0.92	2.20	0.72	0.26	1.03
				Magnesium						
1	1.0	0.0	0.42	0.58	1.12*	1.30*	2.17	2.19	0.24	0.46
2	1.0	1.0	0.38	0.59	1.07	1.25	1.85	3.01	0.23	0.69
3	1.0	2.0	0.44	1.07	0.90	1.75	1.57	3.30	0.47	0.51
4	1.0	4.0	0.46	1.13	0.73	1.79	1.63	3.73	0.50	0.56
5	1.0	8.0	0.31	1.30	0.54	1.54	1.17	2.67	0.85	0.57
6	12.0	1.0	0.34	0.28	0.69	0.51	1.45	0.76	0.19	0.31

* Represents leaves with visual K deficiency symptoms.

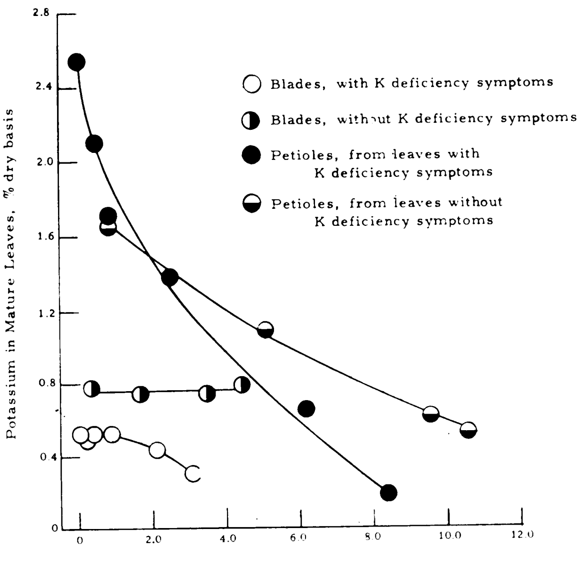

FIG. 3. Relation of K and Na in mature leaves of plants with and without K deficiency symptoms, in culture solutions low in K (1 meq/liter) with different Na concentrations.

Discussion

Sodium. This is probably the first instance reported for a non-saliniferous crop species where an increase of growth from addition of a high Na concentration to a medium low in K has exceeded that from a medium adequately supplied with K. Essentiality for growth may be inferred. The sparing action of Na on K, which induces the redistribution of K from places of relative abundance in petioles to those of deficiency in blades cannot explain this result since the blades, as well as petioles, in a medium high in K already contained K at an adequately high concentration. Therefore, a concept of metabolic cation balance is introduced to explain the results.

It is known that plant growth is the result of interrelated utilization of the different elements concerned in nutrition. Accordingly, the concept of cation balance presents a situation where the addition of an element (in this case Na) may cause positive or negative growth effects or, in some cases no effect, depending on the relative concentrations of other elements (in this case K). A certain cation balance could be beneficial to the activity of enzyme systems, since K and to a lesser extent Na have been reported in a recent review by Evans and Sorger (5) to activate many enzyme systems. Single salt solutions were used in most of those studies. It could be that enzyme activity would be equally great in a high K plant as in a low K high Na plant, in a way similar to the model suggested by Green and Taylor (6). They proposed that activation of adenosine triphosphatase (ATPase) is due to 2 binding sites, 1 for K and 1 for Na, and that maximum activation is obtained when both sites are appropriately occupied.

A minimum level of 0.8 % K in mature blades of sugar beet supports vigorous growth (fig 3). Sodium is responsible in mixed cation cultures for maintaining this level under low K supply, by displacing K already accumulated in the petioles (4). The constancy of the K level, accompanied by a range of nil to 4.0 % Na in blade tissues, resulted in a significant increase in growth (table I). This increase in growth, as well as that in a medium high in K when Na was supplied, support the proposed cation balance hypothesis.

The possibility also exists that sugar beet plants may require Na per se for growth and development but in such small amounts that their needs are generally satisfied from the traces of Na present in the non-sodium salts generally used under culture solution conditions. If this proves to be correct, then the following Na tissue contents will be necessary for maximum growth under the accompanying conditions:

Na_1 plus Na_2 in a medium low in K, or

Na_1 plus Na_3 in a medium high in K

where Na_1 = small amounts of Na essential per se for growth,

Na_2 = a sodium concentration needed for vigorous growth in a medium deficient in K,

Na_3 = a sodium concentration needed for vigorous growth in a medium high in K.

Rubidium. For Rb, 2 effects are of concern, beneficial and detrimental. The beneficial effect suggests essentiality for maximal growth. The significant increase in growth from the successive additions of small amounts of Rb (table II, expt. 3, treat. 3) may be due to increasing activity of some enzyme systems as a result of a proper cation balance between K and Rb. Rubidium at high concentration would adversely modify the balance resulting in limitation of the activity of such enzyme systems.

Present results indicate that the effects of Rb on growth depend on the Rb supply at a particular time as well as on the concomitant K concentration. The possibility of decreasing Rb toxicity by either increasing the K concentration or by avoiding the accumulation of excessive amounts of Rb at a particular time was examined and resulted not only in alleviating toxicity but even in increased growth (table II, expts. 2 and 3). Different enzymes may vary in their reaction toward the same Rb concentration. Thus 1 meq Rb/liter of external supply might inhibit some of the enzyme systems and enhance others, leading nevertheless to a slight increase in overall growth but with certain developmental abnormalities (table II, expt. 3, treat. 2). Rubidium at lower concentrations (treat. 3) could enhance the activity of most of the enzyme systems resulting in healthy plants with usual morphological characteristics and increased growth. High K concentrations induced more growth while decreasing Rb absorption, with a resultant decrease of the Rb concentration in the plant and therefore presumably a more effective cation balance than in plants supplied with high K only.

The severe reduction in growth that occurred from adding a high Rb concentration does not exclude the possibility that Rb might be favorable or even essential for plant growth if the Rb as well as the K concentrations were taken into consideration.

Shoot/Root Ratio. The increase in the shoot/root ratio as well as the absolute shoot and root growth when Na is supplied to a medium low in K, indicate a particularly favorable effect on the growth of the shoots. Presumably, with most of the assimilates produced being utilized for foliar vegetative growth, little may have remained for downward transport, resulting in a lower sucrose percentage in the storage root.

Additions of small amounts of Rb to a medium low in K were attended not only by an increase in growth, but also by an increase of the shoot/root ratio. This indicates that moderate Rb application increased the growth of the shoots to a larger extent than the fibrous roots. Rubidium then might be favorable for growth by increasing the photosynthetic area and effecting sucrose translocation to the storage roots. The possibility that Rb might also increase the photosynthetic activity of these leaves is not excluded. Increasing both leaf area and photosynthetic activity could provide more sugar translocation to the roots, thereby accounting in part at least for the increase in the sucrose percentage in the beet.

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