⊹ POTASSIUM DEFICIENCY AND EXCESS IN GUAYULE
I. GROWTH RESPONSES AND MINERAL CONTENT[1] ✗

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(WITH TWO FIGURES)

The extensive literature dealing with the role of potassium in plant metabolism has been reviewed by HOFFER (20), by various authors (47) in a recent symposium and in several reviews on mineral nutrition of plants (11, 17, 18, 28, 39, 46). Very recently SIDERIS and YOUNG (42, 43, 44) have dealt with several aspects of the problem. HOAGLAND (19) has pointed out that at one time or another a role in almost every important physiological process in the plant has been ascribed to potassium. Yet, the mechanism of its role in any specific process has not been elucidated.

In several respects the guayule plant, *Parthenium argentatum* A. Gray, differs from most of the plants which have been subjected to detailed nutritional study. For example, incidence of the reproductive phase in guayule is not attended by cessation of vegetative growth nor by curtailed nutrient absorption. This behavior is contrasted with that of many annual plants, for which a period of rapid growth and mineral absorption is terminated by the reproductive phase. NIGHTINGALE *et al.* (31) found that a deficiency of potassium in tomato plants induced premature fruiting. The result was withdrawal of a large portion of the potassium from the vegetative parts to the fruits. RICHARDS and TEMPLEMAN (40) found that for the barley plant potassium deficiency resulted in continued tillering and failure of plants to head. The sodium content of the nutrient solutions appears to be a factor associated with the latter result (39). No effects analogous to the premature fruiting of tomato plants or to the retarded heading of barley plants are evident for guayule moderately deficient in potassium. The use of guayule plants in a study of potassium nutrition, therefore, has the advantage of permitting comparison between plants which are in different nutritional states, without complications of premature or delayed incidence of the reproductive phase.

When plants are grown in solutions containing insufficient potassium, the absorption of certain other nutrients is increased. Most considerably altered is the tissue content of other cations (3, 16, 30, 36, 39, 42), although the contents of anions, particularly phosphorus, may also be effected (24, 38, 39). In these circumstances it is difficult to distinguish between effects of potassium deficiency in the tissue and effects arising from accumulation

of other ions. An approach to this problem is the use of more than one series of treatments varying in proportions of cations other than potassium (**3, 11, 38**), or use of series differing in the form in which nitrogen is supplied (**38, 42, 49**). In any case it seems essential to know the tissue contents of each of the principal nutrients under the specific conditions of the experiment.

In this paper are reported growth responses and mineral contents of guayule plants supplied with low, intermediate and high levels of potassium. Two series of treatments differing in supply of calcium and sodium were employed in an attempt to distinguish between effects immediately associated with the potassium content of the tissues and effects resulting from accumulation or deficiency of other nutrients.

Methods

CULTURE TECHNIQUE

One thousand plants seventeen months of age of strain #593 were selected for uniformity at the Alisal Nursery of the Emergency Rubber Project at Salinas, California, on November 20, 1944. These plants ranged between 6.0 mm. and 9.0 mm. in crown diameter. Tops of all plants were pruned to three inches, thus removing all the leaves. Roots were pruned to four inches. The average dry weight of the pruned material was 3.2 ± 0.06 grams per plant. On November 21, these plants were planted at the rate of four per crock in washed fine gravel in three-gallon glazed crocks provided with drainage. Initial samples were selected at random for control analysis. Tap water was applied until December 23, when approximately 95 per cent of the plants had formed new shoots.

At this time the plants in each crock were thinned to three per crock. One hundred and eighty crocks were selected and arranged in three equal blocks. The sixty crocks within each block constituted six treatment plots of ten crocks each in random arrangement. The compositions of the nutrient solutions supplied are shown in table I. These solutions were prepared from 0.5 M stock solutions of C.P. salts and distilled water. The reactions of the solutions were between pH 5.6 and pH 5.8. The solutions were supplied manually at the rate of 200 ml. twice daily from December 23 until January 25. At this time the rate was increased to three daily applications of 250 ml. each.

The potassium concentrations were selected on the basis of a preliminary experiment which included treatments at five concentrations distributed over a wide range. Treatments K_1 and NaK_1 were expected to result in potassium deficiency, K_2 and NaK_2 to result in optimal growth, K_3 and NaK_3 to provide excessive potassium. The treatments comprised two series, series 1 being characterized by a moderate calcium concentration. In series 2, sodium was partially substituted for calcium to result in the same total ion-equivalent concentration as in series 1 for any given potassium level. Magnesium and phosphorus were supplied at uniform levels

throughout all treatments. Sulphate was the form in which variables of potassium were supplied.

The plants were removed in two harvests. The first harvest was on February 6 and 7, and the second on March 15, 16, and 17. For simplicity these harvests hereafter are referred to as those of February 6 and March 16. Plants from given blocks, representing all treatments, were removed on each date. All plants were harvested between 8:00 a.m. and 11:00 a.m. except in the case of the second block at the first harvest. This block was harvested between 1:00 p.m. and 3:00 p.m. on February 6. At each harvest the plants from one half the crocks in each plot were removed, (i.e., 45 plants per treatment) so the randomized arrangement was maintained. The greenhouse temperature was above 60° F. at all times. The average daily minimum temperature for the period was 68° F., average daily maximum temperature 80° F.

TABLE I

COMPOSITION OF THE NUTRIENT SOLUTIONS*

SERIES	TREATMENT DESIGNATION	EQUIVALENTS PER LITER				
		$Ca(NO_3)_2$	$NaNO_3$	K_2SO_4	$MgSO_4$	KH_2PO_4
1	K_1	0.0100	....	....	0.0020	0.0005
	K_2	0.0100	....	0.0025	0.0020	0.0005
	K_3	0.0100	....	0.0115	0.0020	0.0005
2	NaK_1	0.0040	0.0060	....	0.0020	0.0005
	NaK_2	0.0040	0.0060	0.0025	0.0020	0.0005
	NaK_3	0.0040	0.0060	0.0115	0.0020	0.0005

* In addition each solution contained: 1.0 p.p.m. Fe as ferric citrate, 0.5 p.p.m. B as H_3BO_3, 0.5 p.p.m. Mn as $MnCl_2$, 0.05 p.p.m. Zn as $ZnSO_4$, 0.02 p.p.m. Cu as $CuSO_4$, 0.01 p.p.m. Mo as H_2MoO_4.

GROWTH MEASUREMENTS AND TISSUE PREPARATION

Several measurements of growth were employed. In addition to determination of total fresh weights and dry weights, it was desired to have indexes of relative activity of stem tip and cambial meristems. For this purpose the longest shoot on each plant was selected for measurement. The "length of shoot" was taken as the distance from the point this shoot branched from the original stock to the highest leaf apex when flattened vertically. Trials showed that this measurement could be reproduced within about 1 cm. The "diameter of shoot" measurement was the average of two caliper readings taken at right angles to each other 1 cm. above the point of branching of the shoot from the original stock. Because the difference in these measurements resulting from nutrient treatments would not be large in any case, as large a number of observations as possible was desired. To this end measurements of length and diameter were obtained from each plant. With the same considerations with regard to number of observations, the fresh weight of the three plants from each crock was determined.

The procedure for obtaining weights and measurements and preparing the plant parts for analysis was as follows: The roots were washed free of gravel and rinsed in distilled water. After draining for a few seconds, remaining free water was blotted from them with toweling. Fresh weights were determined, and measurements of length and diameter of shoots made. The plants were then separated into the following parts: (1) mature leaves, all leaves below the eighth leaf on each branch; (2) expanding leaves, the eight youngest leaves on each branch. This actually included all expanding leaves and one or two fully expanded leaves; (3) young stem, all the stem growth resulting from the shoots produced since transplanting; (4) old stems; and (5) roots from the original stock separated at the crown; (6) flowers and fruit including the floral stalk; and (7) dead leaves, including all that had fallen during the treatment interval. After these separations the corresponding parts from all plants of the same plot were combined. Fresh weights were determined. Woody portions were chopped into small pieces. Samples were thoroughly mixed and portions dried to constant weight of 65° C. in a forced draft oven. The total dry weight of each plant part was determined. Composite samples were made by thoroughly mixing portions of dried samples from all plant parts other than the leaves. In these composite samples, each plant part was represented in the same proportion as originally present in the whole plants.

At the March 16 harvest 100-gram portions of the fresh leaf samples were frozen for sap expression. Details of the methods employed in freezing and thawing as well as the results obtained from the frozen samples are reported in another paper of this series (5).

METHODS OF ANALYSIS

Total calcium and magnesium contents of the leaves were determined by analysis of sap and press cakes from frozen samples (5). For the analysis of other constituents of the leaves and for all constituents of the composite samples, dried material was employed. Five-hundred-milligram portions of dried, finely ground material from the composite or leaf samples were weighed into porcelain capsules, moistened with sulphuric acid (1–10), dried at 105° C. and ashed at 600° C. for 16 hours. The ash was dissolved in dilute HCl, taken to dryness to dehydrate any silica, and redissolved in HCl. Calcium, magnesium, and sodium in the ash were determined by the official methods (1). Potassium was determined by the method of HIBBARD and STOUT (14). Sulphur and phosphorus were determined in ash prepared by the magnesium nitrate method (1). Sulphur was determined by the official method (1). A separate aliquot of the ash solution was used for determination of phosphorus by the method of FISKE and SUBBAROW (8). Total nitrogen including nitrate was determined by the modification of the procedure of PEPKOWITZ and SHIVE (32) described by KELLEY et al. (25).

Samples from each of the eighteen plots (i.e., three replicates of each treatment) were analyzed separately. Analysis of variance (45) was

applied to the analytical data as well as to the growth data.   Coefficients of correlation and indexes of correlation were determined as described by EZEKIEL (7).

Results

LEAF SYMPTOMS

At the time of the first harvest (February 6) symptoms of potassium deficiency in treatments K_1 and NaK_1 were beginning to appear.   Yellow-green circular areas on the older leaves could be observed by transmitted light.   No difference in degree of these symptoms could be observed between these two treatments.   On February 24, premature death of the oldest leaves of plants of these two treatments could be noted.   Drying of these leaves frequently progressed basipetally from the apex.   In other cases, the original chlorotic spots became brown and dried first.   At this time, it was noted that the entire foliage of plants receiving the K_3 and NaK_3 treatments was more yellow-green in color than the foliage of plants receiving the other treatments.   These symptoms were still evident at the time of final harvest (March 16).

Throughout the experiment a few extra crocks of plants had been supplied with the same six treatments as those of the main experiment.   These plants were maintained by continued application of these solutions for two additional months, so further development of the symptoms could be observed.   The plants receiving the K_1 and NaK_1 treatments eventually lost nearly all their mature leaves, but continued to grow, continually forming young leaves.   The foliage of plants receiving the K_3 and NaK_3 treatments became more yellow, and the older leaves showed a purple coloring suggestive of phosphorus deficiency.

GROWTH

As measures of total growth the total fresh weight per plant and total dry weight per plant are used.   These results as well as those for percentage dry matter for the whole plants are shown in table II.   At the time of the first harvest (February 6) the K_3 treatment had resulted in greater fresh weight than any other treatment, whereas, NaK_3 had resulted in the least amount of fresh weight and dry weight.   These comparisons are statistically significant for fresh weights.   Among the other four treatments, differences in fresh weight or dry weight were not significant at this time.   Percentage dry matter was significantly lower in K_3 than in K_1 or NaK_3.

On March 16, total fresh weight was less in series 2 than in series 1 at any given level of potassium supply.   Within each series total fresh weight and dry weight were significantly reduced by the low potassium treatment (i.e., K_1 was less than K_2 and NaK_1 less than NaK_2).   High potassium treatment resulted in reduction in growth only in series 2.   Percentage dry matter for the whole plants did not differ significantly among treatments.

TABLE II

TOTAL FRESH WEIGHT, DRY WEIGHT AND PERCENTAGE DRY WEIGHT

TREATMENT	TOTAL FRESH WEIGHT GRAMS PER PLANT		TOTAL DRY WEIGHT GRAMS PER PLANT		PERCENTAGE DRY MATTER	
	FEB. 6	MAR. 16	FEB. 6	MAR. 16	FEB. 6	MAR. 16
K_1	28.8	68.6	5.64	15.2	19.6	22.2
K_2	30.4	80.0	5.64	18.8	18.6	23.5
K_3	34.2	82.2	6.09	18.2	17.8	22.2
NaK_1	28.1	62.6	5.34	14.3	19.0	22.9
NaK_2	28.2	70.6	5.33	16.0	18.9	22.7
NaK_3	23.7	65.9	4.69	14.0	19.8	21.2
Difference required for significance						
0.05	3.17	5.96	0.558	1.45	1.40	n.s.
0.01	4.22	7.93	0.793	2.06	1.98	....

In table III are shown the dry weights of the several parts into which the plants were separated. There are a few points which could not have been seen from the weights of the whole plants. On March 16, the dry weights of expanding leaves from treatments K_1 and K_2 were nearly identical; whereas, the weights of mature leaves in common with the weights of other live portions were less in K_1 than in K_2. The lower weights of mature leaves in K_1 may be partially accounted for by the greater weight of dead leaves in this treatment. In series 2, analogous differences were not found,

TABLE III

DRY WEIGHT OF PLANT PARTS

PLANT PART	TREATMENTS					
	K_1	K_2	K_3	NaK_1	NaK_2	NaK_3
FEBRUARY 6						
	gm.	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Expanding leaves	0.79	0.67	0.77	0.70	0.67	0.45
Mature leaves	1.24	1.35	1.45	1.21	1.24	1.14
Flowers plus fruits	0.30	0.29	0.27	0.30	0.30	0.18
Young stems	0.55	0.57	0.57	0.54	0.50	0.35
Old stems	1.52	1.51	1.65	1.44	1.44	1.41
Roots	1.24	1.25	1.38	1.15	1.18	1.16
Total	5.64	5.64	6.09	5.34	5.33	4.69
Dead leaves	0.06	0.08	0.28	0.11	0.25	0.26
MARCH 16						
	gm.	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Expanding leaves	3.87	3.92	3.70	2.94	3.56	2.89
Mature leaves	2.49	3.69	4.12	2.98	3.22	2.86
Flowers plus fruit	1.43	1.79	1.59	1.23	1.39	1.07
Young stems	3.41	4.76	3.93	3.17	3.34	2.90
Old stems	1.87	2.16	2.25	2.03	2.13	2.11
Roots	2.14	2.49	2.66	1.99	2.39	2.16
Total	15.21	18.81	18.25	14.34	16.03	13.99
Dead leaves	1.93	1.47	1.38	1.20	1.28	1.62

rather the weight of both young and old leaves were lower in NaK_1 than in NaK_2. In comparing treatment K_2 with K_3, it is notable that on March 16 the weight of young stems was much higher in K_2. The weights of flowers plus fruits and of expanding leaves were slightly higher in K_2. However K_3 had the greater weight of mature leaves and slightly greater weights of old stem and roots. In series 2, NaK_3 had a lower weight of each live part and a greater weight of dead leaves relative to NaK_2.

Measurements of diameter and length of the longest shoot are shown in table IV. On February 6, shoot diameters in K_3 were significantly greater than in any other treatment except NaK_3. The only other comparison representing a significant difference is that between K_1 and NaK_3. On March 16, shoot diameters were significantly smaller in K_1 than in K_2, and significantly smaller in K_1 or NaK_1 than in K_3 or NaK_3. It is noteworthy that although certain individual comparisons did not show significant differences, a general trend of increasing diameter growth was asso-

TABLE IV

DIAMETER AND LENGTH OF THE LONGEST SHOOT

| | TREATMENTS | | | | | | DIFFERENCES REQUIRED FOR SIGNIFICANCE | |
	K_1	K_2	K_3	NaK_1	NaK_2	NaK_3	0.05	0.01
	FEBRUARY 6							
Diameter (mm.)	3.08	3.18	3.49	3.16	3.24	3.35	0.24	0.31
Length (cm.)	24.1	23.8	24.1	24.5	22.2	19.4	1.38	1.82
	MARCH 16							
Diameter (mm.)	4.73	5.12	5.36	4.83	5.03	5.36	0.37	0.48
Length (cm.)	30.6	30.1	27.1	30.3	27.6	25.7	1.21	1.60

ciated with increasing potassium supply in each series at each harvest. On February 6, lengths of shoots were less in NaK_2 and NaK_3 than in other treatments, and less in NaK_3 than in NaK_2. Among the other four treatments differences were not significant. At the final harvest, K_3 may be classed with NaK_2 and NaK_3 as less than the other three treatments. At this harvest as at the first, lengths of shoots were less in NaK_3 than in any other treatment.

It is evident from the data presented that the growth response to the treatments employed was rather complex. Thus, although the low potassium treatment had reduced the fresh weights and dry weights of plants in each series at final harvest, the high potassium treatment resulted in reduction in growth only in series 2. A general difference in growth response to the two series of nutrient treatments was indicated. Variations in diameter and length of shoot were not correlated, and indicated alteration in the form of the plants by the various treatments. Before interpretation of these results is attempted, however, the mineral contents of the plants will be considered.

MINERAL CONTENT

The percentage composition of leaf tissues and of composite samples at the February 6 and March 16 harvests are recorded in tables V and VI respectively. In interpreting these results it is, of course, evident that a higher concentration in leaf tissues than in the composite samples does not necessarily mean that the concentration in the leaves is higher than in any other plant part, but rather the composition of the composite sample repre-

TABLE V

CONCENTRATION OF ELEMENTS IN LEAF TISSUES AND IN COMPOSITE SAMPLES
AND PROPORTIONS OF TOTAL QUANTITIES PRESENT
IN THE LEAVES ON FEBRUARY 6

TREAT-MENT	TISSUE	PERCENTAGE OF THE DRY WEIGHT						
		K	Na	Ca	Mg	N	P	S
K_1	Expanding leaves	2.66	0.26	4.63	0.75	5.98	0.471	1.22
	Mature leaves	1.84	0.28	6.27	1.40	4.20	0.415	1.52
	Composite*	1.76	0.20	0.60	0.15	1.27	0.412	0.23
K_2	Expanding leaves	5.63	0.11	3.71	0.78	5.40	0.446	1.33
	Mature leaves	4.50	0.11	5.05	1.05	4.38	0.359	1.49
	Composite	2.85	0.13	0.58	0.10	1.33	0.440	0.23
K_3	Expanding leaves	7.62	0.06	3.07	0.69	4.80	0.440	1.17
	Mature leaves	7.66	0.05	3.65	0.85	4.77	0.325	1.62
	Composite	4.46	0.08	0.52	0.08	1.32	0.418	0.30
NaK_1	Expanding leaves	4.03	0.70	3.45	1.19	5.49	0.471	1.17
	Mature leaves	3.48	0.59	4.29	1.75	4.31	0.359	1.38
	Composite	1.60	0.74	0.50	0.15	1.34	0.434	0.24
NaK_2	Expanding leaves	5.36	0.44	3.09	1.00	5.17	0.443	1.15
	Mature leaves	4.89	0.44	3.23	1.35	4.37	0.304	1.46
	Composite	2.78	0.48	0.50	0.11	1.25	0.428	0.23
NaK_3	Expanding leaves	7.27	0.23	2.14	0.83	4.58	0.459	1.23
	Mature leaves	6.72	0.23	2.42	1.05	4.20	0.297	1.65
	Composite	3.99	0.26	0.44	0.09	1.16	0.462	0.22

QUANTITY IN THE LEAVES
PERCENTAGE OF QUANTITY PRESENT IN THE WHOLE PLANTS

	K	Na	Ca	Mg	N	P	S
Average of all treatments	48.4	33.4	80.0	84.3	52.8	33.1	77.7

* Composite samples of all tissues other than leaves. Each tissue is represented in the same proportion as found at harvest.

sents an average composition of all other parts. With the exceptions of sodium and phosphorus the concentrations were generally higher in the leaves than in the composite samples. With respect to potassium, a notable exception was the K_1 treatment on March 16. Also shown in tables V and VI are the amounts of nutrients in the leaves expressed as percentage of the amounts present in the whole plants. These values are, of course, based on the proportion of the whole plant represented by leaf tissue, as well as the concentrations in the tissues. These figures illustrate the relatively very high proportions of calcium, magnesium, and sulphur present in the leaves.

The low proportion of sodium in the leaves on March 16 is of interest. Although the proportion was somewhat higher in NaK_3 than in other treatments, the distribution of this element was quite different from that of potassium. These results do not show in what plant part the sodium was concentrated, but they recall the higher percentage of sodium in trunks and roots than in other parts of the orange trees studied by REED and HAAS (36), the higher concentrations in roots than in tops of a number of plants

TABLE VI

CONCENTRATION OF ELEMENTS IN LEAF TISSUES AND IN COMPOSITE SAMPLES
AND PROPORTIONS OF TOTAL QUANTITIES PRESENT
IN THE LEAVES ON MARCH 16

TREAT-MENT	TISSUE	PERCENTAGE OF THE DRY WEIGHT						
		K	Na	Ca	Mg	N	P	S
K_1	Expanding leaves ...	1.49	0.02	5.79	1.02	5.15	0.307	1.92
	Mature leaves	1.41	0.05	7.19	1.17	4.12	0.276	2.12
	Composite*	1.60	0.23	0.92	0.21	1.89	0.390	0.28
K_2	Expanding leaves ...	4.14	0.02	4.61	0.84	5.04	0.270	1.84
	Mature leaves	5.40	0.02	5.79	0.89	4.05	0.220	2.40
	Composite	2.70	0.11	0.80	0.13	1.89	0.412	0.27
K_3	Expanding leaves ...	8.99	0.05	2.44	0.54	4.45	0.254	2.29
	Mature leaves	10.01	0.00	3.25	0.51	3.68	0.183	2.82
	Composite	3.91	0.07	0.60	0.13	1.74	0.452	0.44
NaK_1	Expanding leaves ...	2.70	0.23	3.75	1.37	5.14	0.307	1.90
	Mature leaves	2.54	0.37	5.29	1.69	4.06	0.297	2.40
	Composite	1.25	0.87	0.52	0.19	1.75	0.434	0.34
NaK_2	Expanding leaves ...	4.73	0.30	3.47	1.02	4.86	0.285	1.99
	Mature leaves	6.33	0.39	4.27	1.20	3.96	0.288	2.61
	Composite	2.35	0.53	0.62	0.15	1.76	0.459	0.39
NaK_3	Expanding leaves ...	8.89	0.20	2.00	0.62	4.27	0.248	2.13
	Mature leaves	10.67	0.22	2.32	0.66	3.78	0.220	2.83
	Composite	3.83	0.19	0.54	0.13	1.72	0.489	0.38

QUANTITY IN THE LEAVES
PERCENTAGE OF QUANTITY PRESENT IN THE WHOLE PLANTS

	K	Na	Ca	Mg	N	P	S
Average of all treatments	57.4	20.3	81.9	80.4	63.9	29.9	82.3

* Composite samples of all tissues other than leaves. Each tissue is represented in the same proportion as found at harvest.

studied by COLLANDER (4), and similar results obtained by HAYWARD et al. (13) for peach trees.

To evaluate the absorption of individual and total cations and anions under the conditions of this experiment, the total mineral contents of the plants have been calculated in terms of milliequivalents. Each element is expressed in the ionic form supplied in the nutrient solutions (e.g., total nitrogen as NO_3^-, total phosphorus as $H_2PO_4^-$ and total sulphur as $SO_4^=$). These are the forms in which these elements are assumed to have been absorbed, notwithstanding subsequent assimilation within the plants. In table VII cation and anion contents, before and after applying the nutrient treatments, are expressed as milliequivalents per plant. From the growth

data it is evident (table II) that among the treatments K_1, K_2, NaK_1, and NaK_2 there were no significant differences in total dry weights or fresh weights on February 6. Direct.comparisons of absorption of nutrients by plants of these treatments are possible. For comparisons involving the other two treatments at this date and all treatments on March 16, differences in growth must be considered.

Differences in potassium concentration in the nutrient solutions resulted in large differences in potassium absorption. Only relatively small differences in potassium contents were evident between K_1 and NaK_1, or between

TABLE VII

MINERAL CONTENT OF WHOLE PLANT

TREATMENT	MILLIEQUIVALENTS PER PLANT						
	K	Na	Ca	Mg	N	S	P
	INITIAL ANALYSIS						
	1.36	0.035	0.50	0.18	1.12	0.38	0.31
	FEBRUARY 6						
K_1	2.7	0.55	6.8	2.4	10.4	2.3	0.76
K_2	5.1	0.30	5.6	1.9	10.3	2.3	0.79
K_3	8.8	0.18	4.8	1.7	10.7	2.8	0.79
NaK_1	3.2	1.62	4.6	2.9	9.8	2.2	0.73
NaK_2	5.2	1.09	3.9	2.2	9.4	2.3	0.68
NaK_3	5.9	0.53	2.5	1.6	7.5	2.4	0.64
DRFS* 0.05	0.89	0.24	0.56	0.26	1.13	n.s.	0.084
0.01	1.27	0.38	0.80	0.37	1.61		0.119
	MARCH 16						
K_1	6.0	0.95	24.2	7.1	33.4	9.5	1.8
K_2	17.0	0.55	24.1	6.6	38.4	12.0	2.1
K_3	28.4	0.33	14.3	4.5	35.5	15.4	2.1
NaK_1	6.7	4.0	15.3	8.8	29.9	9.7	1.8
NaK_2	15.1	3.1	15.8	7.3	33.1	11.9	1.9
NaK_3	22.3	1.2	8.4	3.9	26.6	11.1	1.7
DRFS* 0.05	1.96	0.07	1.98	0.77	3.10	1.16	0.28
0.01	2.78	0.12	2.81	1.09	4.41	1.64	0.39

* Difference required for significance.

K_2 and NaK_2. At the high potassium level the considerable difference in size of the plants precludes direct comparison.

Calcium absorption was significantly decreased with each increment of increase in potassium concentration in each series during the period preceding February 6. The difference in calcium concentrations of the nutrient solutions of series 1 and series 2 resulted in differences in calcium contents of the plants at each level of potassium supply. The magnesium concentration was identical in all solutions. Therefore, all differences in absorption of this nutrient were affected by variations of concentrations of the other nutrients. Absorption of magnesium as that of calcium decreased

with each increment of increase in potassium supply. At low and intermediate levels of potassium supply, magnesium absorption was higher in series 2 than in series 1.

Absorption of sodium decreased with each increment of increase in potassium concentration. Although relatively high concentrations of sodium were supplied (table I) absorption of this element was very low compared to that of the other cations. This is particularly evident when it is considered that the solution concentration of sodium in series 2 was higher

TABLE VIII

MINERAL CONTENT OF WHOLE PLANTS

TREATMENT	MILLIEQUIVALENTS PER 100 GRAMS OF DRY TISSUE								
	K	Na	Ca	Mg	TOTAL CATIONS	N*	S*	P*	TOTAL ANIONS
	INITIAL ANALYSIS								
	44	1.1	16	5.7	66.8	37.4	10.0	12.1	59.4
	FEBRUARY 6								
K_1	48	9.8	120	42	221	185	41	13.5	239
K_2	91	5.3	99	33	228	183	41	13.7	237
K_3	145	3.0	79	28	255	177	45	13.0	235
NaK_1	60	30.0	87	54	231	183	41	13.6	238
NaK_2	97	20.0	73	42	232	176	43	12.8	232
NaK_3	126	11.0	54	34	226	159	51	13.7	224
DRFS† 0.05	21	3.1‡	9.8	4.1	n.s.	8.4	5.5	n.s.	9.6
0.01	29	4.8	13.9	5.7	....	11.9	7.8	....	n.s.
	MARCH 16								
K_1	39	6	159	47	251	220	62	11.6	294
K_2	90	3	128	35	256	205	64	11.2	280
K_3	155	2	78	25	260	195	85	11.3	291
NaK_1	47	28	108	61	244	209	68	12.1	289
NaK_2	94	20	99	45	258	206	74	11.8	292
NaK_3	160	9	60	28	257	186	79	12.4	277
DRFS† 0.05	6.8	3.9‡	8.5	0.9	n.s.	14.8	5.8	n.s.	n.s.
0 01	9.7	6.5	12.0	1.2	....	21.1	8.3	....	....

* Anions are assumed to have been absorbed in the ionic forms supplied in the nutrient solution, i.e., NO_3^-, $SO_4^=$, and $H_2PO_4^-$.
† Difference required for significance.
‡ Variance analyses for sodium are based on treatments of series 2 only.

than that of magnesium in any treatment, of potassium at low and intermediate levels, and of calcium in series 2. A small but significant absorption resulted in series 1 where sodium was not deliberately supplied.

The absorption of nitrogen, sulphur and phosphorus was affected relatively little by differences in treatments employed. The bulk of the anion absorption was accounted for as nitrate. Absorption of this ion was slightly lower in series 2. However, individual comparisons are not significant except at the high potassium level. The low phosphorus absorption was related to a low solution concentration of this nutrient. Despite the rela-

tively wide range of sulphate concentration supplied, no significant difference in absorption of this nutrient had resulted at the time of the first harvest.

In the above comparisons mineral contents have been considered in terms of milliequivalents per plant. This is undoubtedly the most direct basis for comparison, but is strictly applicable only where treatments have not resulted in differences in growth. Where such differences have resulted, some information on relative absorption may be obtained by expressing the quantities in terms of concentration. McCALLA and WOODFORD (30) utilized this method in their study of effects of limiting one element in wheat. In the present experiment the number of comparisons can be increased to include the K_3 and NaK_3 treatments at the first harvest and all treatments at the second harvest. In table VIII, individual and total cation and anion contents of whole plants are expressed in terms of milliequivalents per 100 grams of dry tissue. It may be seen that differences in potassium concentration within the plant were compensated by reciprocal differences in concentrations of other cations, thus maintaining a nearly constant total cation concentration for a given age of plant. Similarly, decreased calcium concentration in plants from the series 2 treatments were compensated by increases in sodium, magnesium and in most cases, slight increases in potassium concentration.

The total equivalent concentration of anions was nearly constant among the various treatments. Relatively small decreases in nitrogen content of plants receiving the high potassium treatment were in several cases associated with small increases in sulphur content. It is evident, however, that although solution concentrations of sulphate varied considerably, relatively little difference in total absorption of this ion resulted.

Discussion

The difficulty of predicting the effect of a given concentration of an ion in the culture solution upon the amount of that ion found in the plant is well known (12, 33, 37). For example, PIERRE and BOWER (33) list six of the factors which may influence the effect of other cations upon the absorption of potassium: level of K, concentrations of cations in relation to K, kind of cation, presence of other cations, kind of plant, pH of solution. It might be noted that the absorption of each of the cations present in the solution may be influenced by each of these factors.

McCALLA and WOODFORD (30) found that in wheat, limiting the supply of one nutrient resulted in an increased uptake of another nutrient absorbed as an ion of the same sign, or in a decreased total uptake of the nutrients as ions of the opposite sign. In the present experiment the absorption of individual and total anions was affected very little by the treatments. HOAGLAND (16) reported that in numerous water culture experiments decreasing percentages of potassium in the plant tissues were accompanied by increasing percentages of calcium and magnesium. Occasionally there was

found a nearly exact substitution of bases, but generally the total equivalents of bases absorbed by the plant was greater under high potassium conditions than under low. In several other cases it has been observed that where conditions of growth were similar, except for nutrient composition of the substrate, "ion substitution," or "mutual replacement" may take place to the extent that the total equivalent concentration of cations within the plant remains nearly constant, notwithstanding extreme variations in concentrations of individual cations (2, 21, 22). In the present experiment, the high potassium plants had slightly higher total cation concentrations in several cases, but these differences were not statistically significant (table VIII). In any case these differences were not great and the total cation content must be considered as nearly constant among the various treatments at either time of harvest. Under such conditions it is evident that an alteration in the absorption of any one of the cations results in an altered absorption of one or more of the other cations. Evidently the frequently observed accumulation of calcium or of calcium and magnesium in potassium deficient plants (3, 16, 30, 36, 39, 42) as well as the accumulation of potassium or of potassium and magnesium in calcium deficient plants (30, 35, 36) cannot be avoided, but only altered.

From these ionic substitution relationships arise the difficulty of distinguishing responses directly associated with deficiency of one cation from those which may be attributed to accumulation of other cations (9, 10, 15, 39). The tissue contents in this experiment with guayule present one advantage in this respect. There are three pairs of treatments comparable with respect to concentrations of potassium in the tissues, but differing in concentrations of calcium and magnesium. It is evident that a response which could be plotted as a continuous relationship to potassium content over the whole range of treatments could not be represented as a continuous relationship to calcium, or, for that matter, to magnesium or sodium.

At each harvest date a relationship between potassium content and shoot diameter was found. Correlation coefficients were + 0.616 and + 0.671 for plants harvested February 6 and March 16, respectively. Both coefficients were highly significant. Plots for the March 16 harvest are shown in figure 1. Individual points represent the separate plots. Treatment means are indicated by circles. A relationship between potassium and cambial activity has been indicated by other workers. With the aid of microchemical studies JANSSEN and BARTHOLOMEW (23) noted that in tomato plants grown in solutions lacking potassium, this element seems to be transferred to and localized in the meristematic and growing portions of the plant. NIGHTINGALE et al. (31) observed that when present in the plant in limited amounts, potassium is translocated freely from mature tissues to regions of active cell division. A condition in potassium deficient tomato plants was described where there was insufficient potassium to maintain cambial activity in the older portions of the stem, but enough potassium was present for active development of the meristematic stem tip.

The result was a considerable increase in length of the stems but very little increase in diameter. WALL (49) working with tomato plants observed that potassium deficiency had a greater effect on the weights of the plants than it had on the lengths of the tops. That the response in diameter growth to potassium is not confined to stem tissues is pointed out by NIGHT-INGALE et al. (31). Beets deficient in potassium increase mainly in length and little in diameter. In sweet potatoes (41) a similar response was observed.
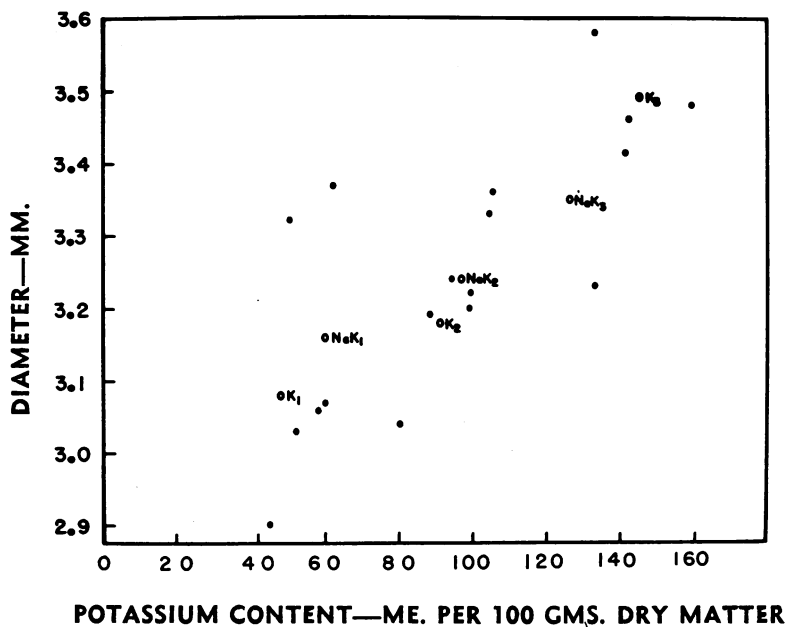
FIG. 1. Relationship between total potassium content and growth in diameter of the shoots for plants harvested March 16. Correlation coefficient = + 0.671. Correlation coefficient required for significance = 0.590 (n = 18, p = 0.01).

The results of the present experiment in contrast with those cited above indicate a response in diameter growth of the shoots over a wide range of potassium supply rather than only in the range where growth is limited by deficiency of this nutrient. In data recently reported by CULLINAN and BATJER (6) a similar trend is indicated in the peach tree. With increasing concentrations of potassium supply, the circumference of the trees appears to have increased beyond the range where the total weights of the plants increased.

When an attempt is made to relate the lengths of the shoots to the nutrient composition of the plants, it is noted that variations in calcium content (table VIII) parallel variations in shoot lengths (table IV), particularly in the range of low calcium contents. However, if one were to define the limiting tissue concentration of calcium in terms applicable to

various stages of development of the plant, selection of a plant part of a given physiological age would be necessary. In addition the concentration of soluble calcium is expected to be more closely related to the metabolic processes of the plant than is the total calcium which may include a considerable portion of insoluble, relatively inert salt. The calcium content of the sap expressed from frozen and thawed leaves of plants harvested March 16 has been determined, and from these determinations the "sap-soluble" fraction has been estimated. The details of these results are considered elsewhere (5) and only a portion of the results are employed for the immediate consideration. In figure 2 length of shoot is plotted against
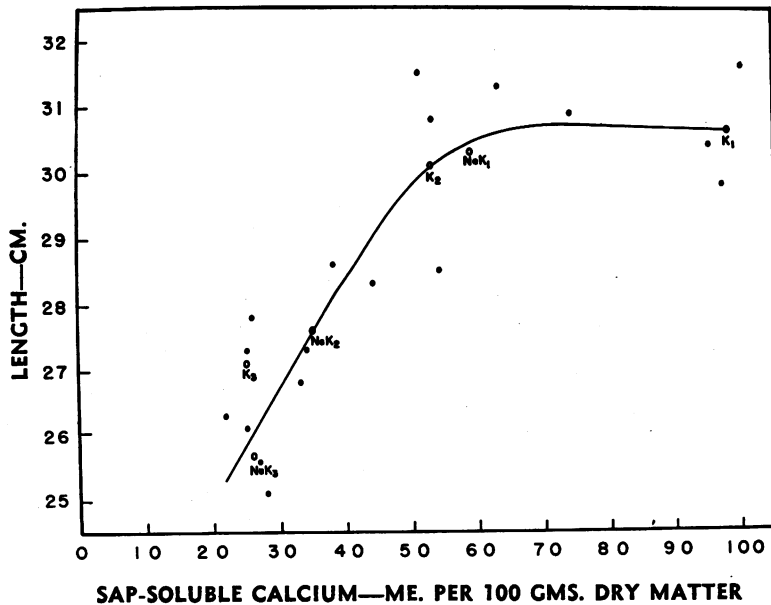
FIG. 2. Curvilinear relationship between sap soluble calcium content of the expanding leaves and growth in length of shoots. Plants harvested March 16. Small dots represent individual plots. Circles denote treatment means. Index of correlation = + 0.893.

the sap soluble calcium content of the expanding leaves. These plots appear to define a limiting relationship. A free hand curve has been fitted to these data as described by EZEKIEL (7). The index of correlation is + 0.893. Although here a highly significant relationship is shown, the range where calcium concentration limits growth in length of shoot cannot be defined on this basis with certainty, insofar as the length measurements represent the total growth during the whole period of nutrient treatment, whereas, the calcium contents are those at final harvest. In any case, it may be noted that the relationship between soluble calcium and length of shoot is essentially linear if the K_1 treatment is omitted. The plots may, then, be interpreted as indicating that growth in length of shoot was re-

lated to the soluble calcium concentration in the expanding leaves except where potassium content limited farther increase in length.

The relationship indicated between length of shoot and soluble calcium content of the expanding leaves is not at variance with frequent observations that the terminal meristems of root and stem tips are affected by calcium deficiency. For example HAAS and REED (12) found that in the roots of walnut seedlings the terminal meristems were the first tissues affected in solutions lacking calcium, although the terminal portions of the roots were actually higher in calcium content than were segments of the roots further removed from the meristems. GAUCH (10) found that the terminal stem meristems of bean plants growing in solutions lacking calcium, ceased growth before the axillary meristems, although the latter too eventually died.

Admittedly significant correlations do not of themselves demonstrate direct cause and effect relationships. In particular it should not be infered that growth in length of the shoots is related only to calcium and growth in diameter only to potassium. In fact REED (34) demonstrates that potassium and calcium are both necessary for completion of cell division. It was found that mitotic cell division did not take place without a suitable supply of potassium, although a certain amount of growth by stretching was possible. In the absence of calcium, cells of Spirogyra divided mitotically, but, new cell walls were formed imperfectly, if at all. The inability to form cellulose was also exhibited by the zygote of Spirogyra. Sections of the growing region of the root of corn plants which had grown in solution lacking calcium showed a number of cases in which the transverse septum had not formed after the process of nuclear division was complete.

Without specific reference to the mechanisms involved, aside from the proposition that adequate concentrations of both potassium and calcium are necessary for normal cell division, differential growth responses may be attributed to difference in mobility between potassium and calcium within the plant. As indicated above, potassium is highly mobile and when present in limiting amounts may be readily translocated from more mature tissue to terminal meristems with the result that little or no increase in diameter takes place although growth in length may continue. It is not, then, surprising that an increase in potassium content results in a relatively greater response in diameter growth than in growth in length of the guayule shoots. In contrast to potassium, calcium may be more slowly retranslocated from mature tissue to more terminal portions of the plant. For example, REED and HAAS (35) found that where calcium salts were withheld from young orange trees, the trunks and roots were the last to be depleted of calcium. MASON and MASKELL (29) presented evidence indicating that in the cotton plant potassium and phosphorus may be re-exported from the leaves via the phloem and transported downwards towards the roots or upwards into the growing bolls, while calcium is re-exported much more slowly, if at all.

In the present experiment it may be noted (tables V and VI) that the calcium content of the expanding leaves was invariably lower than that of the mature leaves, whereas the potassium content of expanding leaves equaled or exceeded that of the mature leaves in the low potassium treatments (K_1 and NaK_1). These observations may be taken as evidence of the different mobilities of these elements in the guayule plant. In this connection it should be noted that the potassium in the leaves is almost entirely soluble whereas a considerable portion of the calcium of the leaves is insoluble (5).

Another consideration involves the differential calcium requirements of various plant parts. If the plants of NaK_3 were actually deficient in calcium it is evident that the calcium requirement of the guayule leaves is relatively high, inasmuch as the expanding leaves of these plants had a calcium content of 2.00 per cent of the dry weight on March 16. The average content of parts other than leaves was much lower, as indicated by the composition of the composite samples. Samples of young and old stems from the plants harvested on February 6 were analyzed separately for calcium. Results of these analyses (table IX) show that the stems had lower calcium contents which were not subject to as great variation resulting from nutrient treatments as were those of the leaves (table V).

TABLE IX

CALCIUM CONTENT OF STEM SAMPLES OF PLANTS HARVESTED FEBRUARY 6

TREATMENT	YOUNG STEMS % OF DRY MATTER	OLD STEMS % OF DRY MATTER
K_1	1.00	0.63
K_2	0.81	0.61
K_3	0.76	0.59
NaK_1	0.78	0.54
NaK_2	0.77	0.45
NaK_3	0.67	0.45

The growth response in length of shoots may be explained on the basis that the meristematic tissues of the stem tips and expanding leaves must be supplied from calcium currently absorbed and not supplemented by retranslocation from mature tissues, with the consideration that the expanding leaves have a high requirement for calcium. The stem tissues have a lower calcium requirement, which was satisfied in plants of all treatments to the extent that growth in diameter was not limited by calcium.

Although the relationships between these single nutrients and measurements of length and diameter of the shoots could not be expected to hold where one nutrient becomes severely limiting, and total growth is greatly affected, it is rather striking that they can be shown over as wide a range of tissue concentrations as presented by the plants of this experiment. For example, a comparison of weights of plants from treatments K_3 and NaK_3 (table II) shows a considerable difference in size of these plants at

final harvest, yet the diameters were essentially the same. Growth in NaK₃ appears to have been limited only in elongation of the shoots. On the other hand the limitation of growth in low potassium treatments was not associated with less growth in length of shoots, but with less growth in diameter. In fact most of the differences in total weight among the treatments can be explained by the differential growth responses of diameter and length of shoots. One exception is the significant difference in total fresh weight between treatments K₁ and NaK₁. This difference was not large, but a slightly greater reduction in growth in the NaK₁ treatment is indicated, although diameters and lengths of shoots were similar in the two treatments. There can be little doubt that the plants in each of these treatments were deficient in potassium, insofar as characteristic symptoms were indistinguishable between the two treatments and their time of incidence was the same. However, NaK₁ had a lower mortality of leaves (table III) and higher concentrations of potassium in its leaf tissues (tables V and VI). These observations indicate that NaK₁ was less deficient in potassium than K₁, despite the slightly lower yield of the former. This relatively small difference in growth perhaps does not warrant detailed consideration but it seems possible that some factor in addition to potassium deficiency was limiting growth in NaK₁. Although the sodium content of these plants was higher than that of plants from the other treatments, its concentration even in this case is not of a magnitude which would be expected to restrict growth. The effect might be ascribed to the relatively high magnesium content of tissues of this treatment. In this connection WADLEIGH and GAUCH (48) have shown guayule to be very sensitive to excesses of magnesium, although there are no data available which would indicate at what tissue concentration this element becomes toxic.

Within the limits of this experiment high concentrations of potassium *per se* did not result in decreased growth. At each harvest the K₃ treatment gave the highest yield, whereas NaK₃ gave much lower yield. The difference in growth between these two treatments seems related to the difference in calcium content. Further inspection of table II shows that in the interval between the two harvests, the plants of treatment K₂ made a greater increase in fresh weight than did those of K₃. From table III it may be seen that at final harvest K₃ exceeded K₂ in dry weight of mature leaves, old stems and roots, whereas K₂ excelled in weights of expanding leaves, young stems and flowers plus fruits. This evidence indicates that the higher total weight of plants in K₃ can be attributed to more rapid growth early in the experiment. However, associated with the apparent decline in rate of growth in this treatment, is the considerable decrease in calcium content of expanding leaves between the two harvests (compare tables V and VI). The calcium absorbed by these plants tended to be diluted by rapid growth. The total quantity of calcium absorbed in K₃ was comparable to quantities absorbed in NaK₁ or NaK₂ (table VII), but at final harvest the concentrations of calcium in tissues of K₃ were consid-

erably lower than were calcium concentrations in tissues of NaK_1 or NaK_2 (tables VI and VIII). Thus, in the early phases of the experiment sufficient calcium was available for maximum growth in K_3, but as the plants became larger a point was reached where the supply of calcium to the growing tissues was inadequate to maintain maximum growth rate.

Treatments K_3 and NaK_3 could not be distinguished by difference in time of incidence of the yellow-green appearance of the foliage (leaf symptoms). In this connection it is of interest that REED and HAAS (37) found walnut seedlings and young orange trees to be injured by high concentration of potassium only after considerable periods of growth. They reported that the foliage of the walnut seedlings eventually turned yellow, whereas the leaves of the orange trees developed characteristic yellow spots on which brown papillae appeared. WALSH and CLARKE (50) have reported a chlorosis of tomato associated with luxury consumption of K. Studies of lime induced chlorosis have shown in some cases a high potassium and low calcium content of chlorotic foliage (27).

The question of the function of sodium in plant metabolism has recently been revived and has been reviewed by RICHARDS (39), PIERRE and BOWER (33) and with particular reference to beet plants by LEHR (26). Beneficial results from application of sodium to plants deficient in potassium have often been reported. In this experiment little or no beneficial response to sodium was evident. As indicated above, of the two low potassium treatments, NaK_1 had a slightly lower yield of total fresh weight, although these plants had higher sodium contents than did those of other treatments. However direct comparison between the two low potassium treatments with respect to sodium response loses some force when it is considered that the calcium and magnesium contents of these plants differed.

The two series of treatments differed somewhat with respect to distribution of potassium at final harvest. Thus, the potassium concentration of leaf tissues of a given age group at a given level of potassium supply were generally higher in series 2, whereas, the concentrations of potassium in the composite samples were lower in this series (table VI). This may bear a relation to the fact that the sodium concentrations of the composite samples were higher than those of the leaf samples except in NaK_3. These observations might be taken as evidence for partial replacement of potassium by sodium in tissues other than the leaves, thereby increasing the supply of potassium to the leaves. But this is contrary to results for several crop plants where according to LEHR (26) it appeared that in the event of a potassium shortage most of the sodium went to the foliage, where it set free a certain quantity of potassium for use in other parts of the plant, such as the tuber of the potato, the grains of oats and barley, and the root of the beet.

Summary

1. Nursery produced guayule plants were grown in sand cultures. Two series of nutrient treatments were employed, each consisting of low, inter-

mediate and high potassium treatments. In series 1 calcium was supplied at a moderate level. Series 2 differed from series 1 in that part of the calcium was replaced by sodium in the nutrient solutions. The plants were harvested on two dates: when symptoms of potassium deficiency in the low potassium cultures were incipient, and after an additional period of growth during which effects of the treatments upon leaf symptoms and growth of the plants developed.

2. Large differences in the tissue contents of potassium were produced by variations in the potassium concentration of the nutrient solutions. Differences in potassium concentration within the plants were compensated by reciprocal differences in concentrations of other cations, thus maintaining nearly constant the total milliequivalents of cations per gram of dry matter.

3. Relatively little difference in individual or total anion contents of the plants was produced by the different treatments, although variations in the sulphate concentration of the nutrient solutions were considerable.

4. Although considerable concentrations of sodium were supplied in some of the treatments, relatively little of this element was absorbed. The concentration of sodium in the leaves was generally lower than the average concentration of this element in other parts of the plant.

5. A large proportion of the absorbed potassium, calcium, magnesium, nitrogen and sulphur was found in the leaves.

6. At given levels of potassium supply, plants from the two series of treatments contained comparable concentrations of potassium, but different concentrations of other cations. Hence a basis was provided for relating certain growth responses to concentrations of individual cations within the plants.

7. A relationship was shown between the potassium contents of the plants and growth in diameter of the shoots. Growth in length of the shoots was related to calcium contents of the plants. Rather complex effects of the treatments upon the total fresh weights of the plants could be explained largely by these two relationships.

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