SELECTIVE ABSORPTION OF CATIONS BY HIGHER PLANTS

RUNAR COLLANDER

(WITH THREE FIGURES)

Introduction

For about a hundred years it has been known that plants do not absorb the different constituents of a nutrient solution in the same proportions as they occur in the solution; some salts or ions are taken up in relatively greater amounts than others. The mechanism of this salt selection exerted by the roots is, however, still quite obscure. It seems that one of the first steps towards an understanding of this important process should be a careful study of its results. A close examination of the proportions in which several kinds of ions are absorbed from nutrient solutions of known composition by different plant species should serve as a starting point for attempts to elucidate this process. This information, however, is still lacking. We have known, until now, very little about the proportions in which different ions are absorbed from nutrient solutions, of easily determinable composition, which contain the ions to be investigated in equivalent amounts.

It is the purpose of the present investigation to present such experimental data in suitable form to serve as the basis for a discussion of the nature of the selective activity of the roots of higher plants. To this end plants of a number of species have been cultivated in nutrient solutions containing several cations in equivalent amounts, after which the cation composition of the plants was determined by the method of quantitative spectral analysis. The study was thus limited to cations. Since they are less engaged in the metabolism of the plants the cations seem, in fact, more suitable for such studies than most anions.

A preliminary account of some results of this investigation has already been published (**7**).

Materials and methods

In order to get a satisfactory idea of the range of variation exhibited by different types of plants in their cation selectivity it was found necessary to extend this investigation to some twenty plant species among the phanerogams representing different ecological types and several taxonomical groups. The following species were studied: *Aster tripolium, Atriplex hortense, A. litorale, Avena sativa, Chenopodium bonus Henricus, Fagopyrum esculentum, Helianthus annuus, Lactuca sativa, Melilotus albus, Nicotiana tabacum, Papaver somniferum, Pisum sativum, Plantago lanceolata, P. maritima, Salicornia herbacea, Salsola kali, Sinapis alba, Solanum lycopersicum, Spinacia oleracea, Vicia sativa,* and *Zea mays.*

The plants were mostly cultivated in large enamel vessels, each containing 50 liters of nutrient solution. The vessels were covered with loosely fitting covers of plywood thoroughly impregnated with paraffin. The covers were perforated with numerous holes in which the seedlings were fixed with cotton-wool. It was thus possible to cultivate about 10 to 20 species in the same vessel under almost exactly identical conditions. The seedlings were obtained by germinating seeds in pure silica sand moistened with tap water of very low salt content. Analyses of the seedlings showed that their salt content, when they were planted in the culture vessel, was negligible as compared with the quantities of salt absorbed during their subsequent growth. The plants were cultivated in a greenhouse, the temperature of which fluctuated between about 18° and 25° C. The air in this greenhouse was pronouncedly dry; the transpiration of the plants must have been considerable. In most cases the seeds were sown at the end of March and the plants harvested about two months later when some of the plants (Pisum) were in bloom. Most of the species, moreover, did not develop flowers. Culture solutions were artificially aerated only in experiments with the solutions IV and V; in these cases the air was forced through filters of sintered glass. A distinct effect of the aeration on the development of the plants could not be detected.

As far as possible the culture solutions contained the cations to be compared in equivalent amounts and also those other ions necessary for the normal development of the plants. The solutions were prepared with glass-distilled water; only for solution I was tap water used. In the following list the salt concentrations are indicated as milligram equivalents per liter of solution.

Solution I: 4 $NaNO_3$ + 4 KH_2PO_4 + 4 $MgSO_4$ + 4 $CaCl_2$ (+ about 0.001 Sr as impurity).

Solution II: 2 $NaNO_3$ + 2 KH_2PO_4 + 2 RbCl + 2 $MgSO_4$ + 2 $Ca(NO_3)_2$ + 0.01 LiCl + 0.01 $MnCl_2$ + an unknown amount of Sr.[1]

Solution III: 4 KH_2PO_4 + 4 $MgSO_4$ + 4 $Ca(NO_3)_2$ + 0.01 LiCl + 0.01 NaCl + 0.01 $SrCl_2$ + 0.01 $MnCl_2$.

Solution IV: 2 KNO_3 + 2 KH_2PO_4 + 0.4 LiCl + 0.4 NaCl + 0.4 $MgSO_4$ + 0.4 $CaCl_2$.

Solution V: 2 $NaNO_3$ + 2 KH_2PO_4 + 0.2 $MgSO_4$ + 0.2 $CaCl_2$ + 0.2 $SrCl_2$ + 0.1 RbCl + 0.1 CsCl.

Solution VI: 2 KH_2PO_4 + 2 Ca $(NO_3)_2$ + 2 $MgSO_4$ + 0.05 NaCl + 0.05 $SrCl_2$ + 0.05 $MnCl_2$ + 0.05 $CuSO_4$.

[1] In preparing solution II, 0.0005 milligram equivalents $SrCl_2$ per liter of solution was intentionally added; the Ca salt used probably contained some Sr, thus the final Sr concentration of the solution is not known with certainty. A spectrographic determination of it was regrettably neglected.

To each solution was added some ferro-ammonium sulphate or ferro-tartrate and also a little of the "A–Z" salt solution of HOAGLAND, as quoted by SCHROPP and SCHARRER (**20**). The solutions were changed only once during the course of each experiment; distilled water was added when necessary and also some iron salt. At the end of most experiments the nutrient solutions were analyzed spectroscopically and also samples of the initial solution. A marked decrease of the concentrations of the cations most strongly absorbed (K, Rb, Mg, Ca, Sr) was sometimes observed. It is doubtful, however, if this factor greatly influenced the results obtained. At any rate, it must have affected all of the plants in a similar fashion, and it would only tend to diminish somewhat the observed difference between the abundantly and scantily absorbed cations.

Solution I was used in order to compare, in a preliminary way, the absorption of Na, K, Mg, and Ca; solution II for comparisons of Na, K, Rb, Mg, and Ca; solution III served to compare, on the one hand, K, Mg, and Ca with each other and, on the other, Na, Sr, and Mn. The amounts of Li taken up from this and also from the other solutions referred to were too small for reliable determination. Solution IV was used for comparisons between Li, Na, Mg, and Ca. The main purpose of solution V was to compare the accumulation of Cs with that of Rb, and of Sr with that of Ca, though the same solution makes possible also comparisons between Na and K, or Mg and Ca. Solution VI served only to compare the absorption of Cu with that of Sr and Mn. Besides the solutions mentioned above, some other culture solutions were used for special purposes.

An investigation of this type is made possible only by the use of quick analytical methods by which the amounts of several cations absorbed by the experimental plants may be determined quantitatively within a reasonable time. In this respect the methods of quantitative spectral analysis are clearly superior to the methods of ordinary chemical analysis. In this investigation only the technique of flame spectrography developed by LUNDEGÅRDH (**15**) was used. It permitted the determination, without difficulty, of ten different cations: Li, Na, K, Rb, Cs, Mg, Ca, Sr, Mn, and Cu.

When harvested, the plants were first weighed and then dried at about 105° C. and weighed again. They were then ashed with concentrated nitric acid and perhydrol in small Kjeldahl flasks (capacity 50 ml.) of Jena glassware or quartz. (Control experiments showed that the amounts of Na, K, Ca, etc., given off by the glass of the Kjeldahl flasks are practically negligible.) The resulting acid ash solution was diluted with distilled water in a volumetric flask of 10- or 25-ml. capacity after which the insoluble SiO_2 was filtered off. The filtered solutions were stored in small flasks of Jena glassware until used for spectroscopic analysis.

The magnitude of the analytical errors depends on several factors, which in our determinations were not always constant. The accuracy of the analyses therefore, cannot be generally stated by exact figures. It is, however, possible to get an approximate idea of the joint effect of the analytical errors and of the individual variability of the plants by comparing the analytical results from several specimens of the same plant species simultaneously cultivated in the same solution. Two such cases are reported in tables I and II. From them it is clear that a high degree of accuracy cannot be claimed. All conclusions from the analytical data obtained must thus be drawn with due allowance for the variability of the plant material as well as considerable analytical errors. Nevertheless, as will be seen from the following sections, several distinct rules concerning cation absorption by the plants studied can certainly be established.

TABLE I

ANALYSES OF FOUR SPECIMENS (A, B, C, D) OF NICOTIANA CULTIVATED IN SOLUTION IV. MILLIGRAM EQUIVALENTS PER KILOGRAM OF DRIED PLANT SUBSTANCE

SPECIMEN	LI	NA	K	MG	CA	MN
A	101	20	......	475	800	......
B	95	20	1700	510	605	5.0
C	109	34	1960	590	660	5.2
D	100	27	1800	530	635	6.1
Mean	101	25	1820	540	700	5.4

TABLE II

ANALYSES OF FOUR SPECIMENS (A, B, C, D) OF SINAPIS CULTIVATED IN SOLUTION V. MILLIGRAM EQUIVALENTS PER KILOGRAM OF DRIED PLANT SUBSTANCE

SPECIMEN	NA	K	RB	CS	MG	CA	SR
A	430	1700	77	92	500	540	340
B	590	1420	88	91	440	640	540
C	850	1340	77	86	610	700	505
D	590	1560	91	96	560	660	550
Mean	615	1510	83	91	520	640	480

In many cases the roots of the plants grown in the same culture vessel were found to be so interwoven with each other that it would have been very difficult to disentangle them. In such cases one had to analyze the plants without roots. It may thus be questioned whether the data obtained in this manner are at all representative of the total cation content of the plant and hence of its cation selectivity. In order to answer this question some analyses of detached roots and shoots were made. These showed, in agreement with the corresponding results of BURSTRÖM (**5**), that: the equivalent percentages of K, Rb, and Cs were roughly the same in the roots as in the shoots; that the percentages of Li, Ca, and Sr were lower in the roots than in the shoots; and finally that the percentages of Mg, and especially those of Na, Mn, and Cu, were higher in the roots than in the shoots. Of the total cation content of the plant on the average only about $\frac{1}{10}$ was found in the roots. From a closer examination of these data, which are not given here in detail, one may infer that analyses of the shoots alone give a rather satisfactory picture of the cation content of the entire plants except that the Na content is perhaps sometimes found to be slightly too small and that the Mn and Cu contents may possibly be far too small. It seems possible, however, that the major part of the last two mentioned cations has been in some way precipitated on the root surface or in the cell walls of the roots without being truly absorbed by the living parts of the plant.

The culture experiments with solution I were performed in 1935; with solution II, partly in 1936 and partly in 1938; with solutions III, IV, and V in 1937. Temperature, light, and other conditions were uncontrolled and, therefore, different in the different years.

Analytical results

The main body of analytical data is presented in tables III to VII. Some of the figures given represent the average of 2 to 4 samples analyzed.

The analytical results were originally calculated so as to indicate the cation content in milligram equivalents per kilogram dry weight of plant material. The figures calculated in this way are, of course, influenced by the varying accumulation of starch, cellulose, and other organic substances in the plant. In order to avoid this, most analytical data are here given in another form: the sum of equivalents of all cations found in one kilogram dry weight was calculated and the amount of each cation expressed as percentage of this sum. In tables III to V, VII, and VIII all values for cations are expressed in this way. In tables VI and X this was not possible and the cation contents in these tables are therefore given as milligram equivalents per kilogram dry weight. In all tables under the head "total" the sum of the milligram equivalents found in one kilogram dry plant material is given. In each series the values for two plants with maximum cation content are printed with heavy faced type and those for two plants with minimum cation content are in italics.

Specific differences concerning the cation selection

THE MAGNITUDE AND SPECIFIC CHARACTER OF THE DIFFERENCES

An inspection of tables III to VII reveals that the different species vary in their capacity for selective accumulation of cations; but it is also seen that the amplitude of the specific variations is very different in regard to the different cations.

The greatest variations were met in the case of sodium. Thus, of the plants cultivated in solution I (table III) the one richest in Na had a relative Na content (percentage of total cations) 32 times greater than that of the plant poorest in Na. With solution II (table IV) an even greater difference was encountered. The maximum Na percentage was 56 times greater than the minimum one. The corresponding ratios $Na_{max.} : Na_{min.}$ were in the case of the plants cultivated in solution III, 29 (table V); solution IV, 86 (table VI); and solution V, 19 (table VII). It is easy to convince oneself of the truly specific character of these variations. In spite of the fact that the culture experiment analyses were performed in different years, we see that certain plant species (*Atriplex hortense, A. litorale, Plantago maritima,* Salicornia, Sinapis) are invariably characterized by a high Na content; certain other species (Fagopyrum, Zea, Helianthus) are as constantly distinguished by a remarkably low Na content. These specific differences in the absorption of Na remain essentially unaltered irrespective of the fact that the Na content of the culture solution was in some experiments rather high (25 per cent. of the sum of all cation equivalents in solution I) and in others very low (only 0.08 per cent. for solution III).

TABLE III

ANALYSES OF ENTIRE PLANTS CULTIVATED IN SOLUTION I

SPECIES	EQUIVALENT PERCENTAGES†					
	NA	K	MG	CA	SR	TOTAL‡
Atriplex hortense	**19.7**§	*39*§	**31**	*10*	*0.0037*	**4790**
A. litorale	10.7	56	23	*10*	0.0058	4340
Avena	3.7	**73**	14	*8*	*0.0037*	*2040*
Fagopyrum	*0.9*	*39*	27	**33**	**0.0107**	3230
Helianthus	*2.3*	54	17	27	0.0083	3020
Nicotiana	4.0	51	24	21	0.0056	4440
Pisum	6.0	62	*12*	20	0.0080	*2140*
*Plantago lanceolata**	12.2	45	18	24	0.0101	3690
*P. maritima**	**28.5**	*39*	*11*	21	....	4370
Solanum	4.1	44	25	27	0.0104	4290
Spinacia	4.5	52	31	13	0.0061	**6520**
Vicia	10.6	44	19	26	**0.0105**	2470
Zea	2.9	70	16	11	0.0052	2420
Culture solution	25.0	25	25	25	0.0062	....

* Both species of Plantago were cultivated in pure silica sand irrigated with solution I. Tops were used for analyses.

† The sum of equivalents of all cations found in one kilogram dry weight was calculated and the amount of each cation expressed as percentage of this sum.

‡ In all tables under the head "Total" the sum of the milligram-equivalents found in one kilogram dry plant material is given.

§ In each series, the values for two plants with maximum cation content are printed with heavy faced type and those for two plants with minimum cation content are printed in italics.

Towards the other alkali cations the different species behave much more uniformly. Thus, the highest relative potassium content of the plants

TABLE IV

ANALYSES OF PLANTS (WITHOUT ROOTS) CULTIVATED IN SOLUTION II

Species	Equivalent percentage							
	Na	K	Rb	Mg	Ca	Sr	Mn	Total
Aster	5.2	27	30	*14*	23	....	0.22	3060
Atriplex hortense	**27.9**	12	14	32	15	*0.014*	0.36	4900
A. litorale	10.3	*11*	20	31	28	0.018	0.36	**5160**
Avena	4.7	25	**41**	15	*14*	*0.013*	0.44	2620
Chenopodium	0.9	23	27	28	21	0.016	0.18	4390
Fagopyrum	0.5	19	18	39	23	0.019	0.53	3320
Helianthus	*0.7*	24	29	21	25	0.021	0.39	3770
Lactuca	5.7	24	34	*13*	22	0.015	**1.19**	3620
Melilotus	8.4	22	25	19	25	....	0.22	2270
Nicotiana	3.5	**28**	28	22	19	0.024	*0.07*	3550
Papaver	5.4	25	**37**	18	16	*0.014*	0.15	2970
Pisum	1.4	23	27	18	32	0.024	0.49	2150
Plantago lanceolata	6.9	22	30	19	22	0.025	0.12	3460
P. maritima	**16.3**	12	*12*	23	37	**0.030**	0.23	3130
Salicornia	12.5	*11*	*13*	**50**	*14*	0.016	*0.04*	**8230**
Salsola	1.3	16	15	**40**	27	....	0.18	3540
Sinapis	10.9	18	26	18	30	**0.035**	0.26	3650
Solanum	3.5	15	22	25	33	0.022	0.51	3360
Spinacia	4.6	23	24	33	15	0.016	0.41	4860
Vicia	8.6	22	28	16	25	0.021	**0.57**	2060
Zea	*0.7*	**31**	28	29	*13*	....	0.29	*2220*
Culture solution	20	20	20	20	20	?	0.10	....

cultivated in solution I was only 1.9 times greater than the lowest one. In the plants cultivated in the other solutions the corresponding ratios ($K_{max.} : K_{min.}$) were, respectively, 2.8 (solution II), 2.3 (solution III), and 1.8 (solution V), *i.e.*, always of a quite different order of magnitude than in the case of Na. It could now perhaps be supposed that the relative constancy of the K content would be connected in some way with the fact that

TABLE V

ANALYSES OF PLANTS (WITHOUT ROOTS) CULTIVATED IN SOLUTION III

Species	Equivalent percentage						
	Na	K	Mg	Ca	Sr	Mn	Total
Atriplex hortense	**2.31**	47	**32**	18	0.054	0.37	**4450**
Avena	0.32	**75**	16	*8*	*0.025*	0.58	2320
Fagopyrum	*0.08*	*32*	**42**	24	0.073	0.46	3480
Helianthus	*0.09*	45	25	29	0.083	0.68	4070
Lactuca	0.38	**69**	*13*	16	0.040	**0.89**	2820
Pisum	0.25	55	13	31	0.054	**1.62**	*1540*
Plantago maritima	**0.66**	*35*	24	39	**0.103**	*0.30*	3690
Solanum	0.21	45	26	29	**0.070**	*0.11*	4010
Spinacia	0.14	55	**32**	*13*	*0.026*	0.37	**5090**
Vicia	....	61	*13*	25	0.052	0.33	*2120*
Culture solution	0.08	33	33	33	0.08	0.08	....

TABLE VI

Analyses of plants (without roots) cultivated in solution IV. Milligram equivalents per kilogram of dry weight

Species	Li	Na	Mg	Ca
Atriplex hortense	**103**	**475**	>475	398
Avena	55	20	280	*170*
Fagopyrum	*49*	*16*	>500	560
Helianthus	**108**	17	>475	**800**
Melilotus	75	21	450	625
Nicotiana	101	25	540	700
Pisum	50	29	250	245
Salsola	66	78	....	460
Sinapis	100	**140**	>475	**>875**
Vicia	79	83	315	365
Zea	*30*	*5.5*	430	*130*

TABLE VII

Analyses of plants (without roots) cultivated in solution V

Species	Equivalent percentage							
	Na	K	Rb	Cs	Mg	Ca	Sr	Total
Atriplex hortense	**24.1**	*37*	*1.6*	*1.0*	**27**	*5.7*	*3.9*	**5970**
Avena	3.4	**61**	**3.3**	1.7	14	10.9	5.4	2760
Fagopyrum	*0.4*	*37*	*1.6*	*1.0*	**24**	**21.2**	**13.7**	4660
Helianthus	1.6	49	2.5	1.5	20	14.8	10.5	3140
Melilotus	3.1	47	2.1	2.0	*13*	**19.2**	**13.3**	4050
Nicotiana	4.2	53	2.1	2.0	17	10.5	10.3	4280
Pisum	1.9	56	**3.3**	**2.5**	*12*	12.6	11.4	*1660*
Salsola	3.5	49	2.4	**2.3**	21	12.7	8.7	**5760**
Sinapis	15.6	38	2.1	**2.3**	13	15.7	12.2	3940
Vicia	**28.6**	*33*	2.3	2.2	17	8.6	7.3	2200
Zea	*1.3*	**67**	3.1	2.1	15	*6.4*	**5.0**	**2020**
Culture solution	42	42	2.1	2.1	4.2	4.2	4.2	....

TABLE VIII

Analyses of plants (without roots) cultivated in soil

Species	Equivalent percentage					
	Na	K	Mg	Ca	Sr	Total
Atriplex	28.0	35	24	13	0.019	3300
Helianthus	0.1	65	10	26	0.029	2930
Nicotiana	0.1	46	10	43	0.047	3030
Pisum	0.4	37	11	53	0.057	1730

K is an element essential for plant growth while Na is unessential. But that such an assumption would not be correct is shown by the fact that the elements Rb and Cs, though as unessential as Na, nevertheless show about the same range in this respect as does K. Thus, the ratio $Rb_{max.} : Rb_{min.}$ was, for the plants cultivated in solution II, 3.4, and in solution V, 2.1; whereas the ratio $Cs_{max.}:Cs_{min.}$ was found to be 2.5 in the case of the plants from solution V, which was the only solution containing this element. In spite of the fact that the differences in percentages of total base present as K, Rb, and Cs are relatively small it seems rather obvious that they are not merely due to analytical errors or accident; an inspection of the analytical data shows that there are some species (Avena, Helianthus, Pisum,[2] Spinacia, and Zea) which were always relatively rich in K, Rb, and Cs, while certain other species (*Atriplex hortense, Plantago maritima,* and Fagopyrum) were always found to be relatively poor in these elements. Such differences may therefore be designated as specific, at least for the most part.

In view of the old experience that there are certain "lithium plants" characterized by their great capacity to accumulate this element, one would perhaps expect a very large amplitude of variation in the absorption of this element, especially since the collection of plant species cultivated by us includes such a notorious lithium plant as Nicotiana. According to our experimental results, however, the variation of Li content is not excessive; the maximum relative Li content is only 3.6 times greater than the minimum. It should, however, be noted that we have not had opportunity to observe the most extreme cases of Li accumulation; according to TSCHERMAK (quoted by VON LINSTOW) there are plants (Cirsium) which accumulate Li to a distinctly greater degree than does Nicotiana.

The magnesium, calcium, and strontium contents also show a variability of moderate amplitude. Thus, the ratio $Mg_{max.}:Mg_{min.}$ was in the case of the plants cultivated in solution I, 2.8; in solution II, 3.8; in solution III, 3.2; and in solution V, 2.2. Though the Mg determinations, due to technical difficulties, were in general less accurate than perhaps any others, it is clear that these differences are, to a considerable extent, specific in their nature. Thus all Chenopodiacean plants (Atriplex, Spinacia, Salicornia, Salsola) and also Fagopyrum were always rich in this element; Pisum, Vicia, and Avena were, on the other hand, relatively poor in it.

The ratio $Ca_{max.}:Ca_{min.}$ was respectively, 4.1 (plants cultivated in solution I); 2.8 (solution II); 4.9 (solution III); 6.7 (solution IV); and 3.7 (solution V). The variations of relative Sr content were of about the same magnitude. The ratio $Sr_{max.}:Sr_{min.}$ was 2.9 in the plants of solution I; 2.7 in those of solution II; 4.0 in those of solution III; and 3.5 in the plants of solution V. The specific character of these differences is rather obvious. Avena, Zea, and Spinacia are constantly low in both Ca and Sr; Fagopyrum, *Plantago maritima,* Helianthus, and Sinapis absorb these elements relatively copiously.

[2] The total cation content of Pisum (per unit of dry matter) was always rather low. Its absolute K content is, therefore, not very high (7, fig. 1) even when the relative percentage of K is considerable.

It is thus evident that among the alkali and earth alkali cations Na is the cation which responds most to specific variations in the plants. This has, in fact, been observed already by VAN ITALLIE (**13**). In the cell sap of different species of Characeae, Na was also found to show a wider amplitude of specific variation than the other cations studied (**6**). It is not at all clear, however, why even Na should behave in such a peculiar fashion.

The manganese content of the plants also exhibits a high degree of variation. Thus the ratio $Mn_{max.} : Mn_{min.}$ amounts to 30 for plants cultivated in solution II and to 15 for plants in solution III; but contrary to all the elements so far discussed, the Mn content varies rather irregularly. The cause of these irregularities are not known with certainty. It seems conceivable, however, that it may be found in an occasional precipitation of some slightly soluble Mn compounds. It should also be noted that, due to the exceptionally high Mn content of many roots, the Mn absorption of the plants shows a very different aspect depending on whether the whole plant or only its aerial parts are analyzed.

The total sum of cation equivalents per unit of dry matter is also a distinctly specific character. Thus, for example, Atriplex, Salicornia, and Spinacia are invariably distinguished by an unusually great total of cation equivalents; Avena, Pisum, Vicia, and Zea, on the contrary, by a relatively small total. Since the first named plants are relatively high in water, however, their cation concentrations would appear lower if the fresh weight or the water content of the plants was chosen as a basis for the calculation instead of their dry matter.

THE SPECIFIC CATION SELECTION AS CORRELATED WITH THE ECOLOGICAL AND TAXONOMICAL CHARACTER OF THE PLANT

As already mentioned, *Salicornia herbacea, Plantago maritima, Atriplex hortense,* and *A. litorale* are among the species found to absorb the greatest amount of Na. This indicates that there exists a positive correlation between a strong absorption capacity for Na (or perhaps more correctly stated: a want of exclusion power against Na) on the one hand, and the halophytic character of the plant on the other. (*A. hortense,* though now a garden plant, was probably originally a halophyte). This rule is, however, not free from exceptions. *Aster tripolium,* though a typical halophyte, showed in our experiments a lower Na content than many non-halophytic plants; *e.g., Sinapis alba,* and *Vicia sativa.*[3] On the other hand, the low Na content of *Salsola kali* apparently makes an exception; the variety of Salsola cultivated by us turned out to be not the one which occurs on seashores but var. *tenui-*

---

[3] It should, however, be mentioned that Aster has been until now cultivated only once, in an experimental work; its cation selection has not been as thoroughly studied as that of most other species.

folia which is known to occur on landing places and rubbish heaps. It is thus no true halophyte.

It has been known for a long time that halophytes when growing on their natural saline substrates contain much more Na and Cl than do glycophytes growing on their natural non-saline substrates. In more recent years it has also been shown that halophytes absorb more Cl even from non-saline soils than do glycophytes from the same soil (**23**). As far as the present writer is aware, however, it has not been definitely established until now (**22**) that halophytes, when several alkali cations are equally available, nevertheless absorb relatively much more Na than do glycophytes under the same conditions. Probably this specific lack of power to exclude Na ions is a character which in some way enables the halophytes to thrive on saline substrates not suited to requirements of the glycophytes. The relations between salt selection and halophytic character is the subject of other investigations in this laboratory and the question will not now be discussed.

The data obtained in the present investigation are too incomplete to give a reliable picture of the correlation existing between the taxonomic position of a given plant species and the peculiarities of its cation selection. Only a few suggestions connected with this matter can be pointed out here.

Perhaps the most striking observation of this kind is the remarkably high Mg content found in all Chenopodiacean plants analyzed, *viz., Atriplex hortense, A. litorale,* Chenopodium, Salicornia, Salsola, and Spinacia. On the other hand the high Na content which is characteristic of the Chenopodiaceans (**4**) was lacking in the non-halophytic members of this family.

Further, it could be pointed out that both of the Graminae analyzed (Avena and Zea) are characterized by their low Ca and Sr content, a feature already known (**4**). Also, the three Leguminosae studied (Melilotus, Pisum, and Vicia) show a general resemblance in their cation absorption although the absence of marked peculiarities makes it difficult to state this resemblance more positively. Finally, the two species of Atriplex show an obvious similarity in their cation selection. On the other hand the two species of Plantago studied could—in spite of some character common to both of them—easily be distinguished on account of their different selection alone.

VALIDITY OF THE ABOVE MENTIONED RULES UNDER OTHER GROWTH CONDITIONS

It has already been pointed out that in spite of the fact that culture experiments were performed during the course of several years and that the external conditions (temperature, etc.) were not constant, the specific differences in cation selection were essentially constant. Nevertheless, it seemed questionable if these specific characters would persist when the growth conditions were more profoundly changed; *e.g.,* when the plants were grown not in water culture, as in the experiments so far reported, but in ordinary soil. To test this question, four plant species (*Atriplex hortense,* Helianthus, Nicotiana, and Pisum) were cultivated in a pot filled with ordinary garden soil and watered with tap water. The results of the analyses are given in table VIII. It is easily seen that the four plant species, also when cultivated in soil, have maintained most of those cation selection peculiarities which we already know from the water culture experiments:

1. The Na content exhibits a much greater degree of variability than that of any other cation studied.
2. Atriplex is by far the richest in Na of the four species studied. The difference in this respect between Atriplex and the three other species is even markedly greater for plants cultivated in soil than for those grown in water culture. Atriplex contained about 200 to 300 times more Na than Helianthus and Nicotiana whereas corresponding difference in the water culture experiments was generally almost ten times smaller.
3. Among the four plants studied, Atriplex had the smallest percentage of K.
4. Atriplex had by far the highest Mg percentage.
5. Atriplex had distinctly the lowest Ca and Sr percentages.
6. The Ca and Sr contents of the four plants varied in a strictly parallel manner.
7. Atriplex had the highest, and Pisum the lowest, total equivalents of cations per unit of dry matter.

As compared with these concordances between the results of the soil and the water culture experiments the discordances are relatively slight; the K percentage of Pisum in the soil culture was found to be unusually low and, above all, the Ca and Sr content of Helianthus in the soil culture was decidedly too small as compared with that of the other plants. Discrepancies, especially as to elements like Ca and Sr, are in fact easily conceivable. These elements occur in the soil not only as constituents of the soil solution, but also in an adsorbed state and probably also as slightly soluble solid salts ($CaCO_3$, etc.); the absorption of these salts is dependent on the chemical disintegrating power of the roots which in water culture experiments plays no rôle at all.

In this connection, some experiments carried out by other investigators deserve mention. NEWTON (**16**) grew six crop plants in a nutrient solution containing 4.7 milligram equivalents per liter of K, 4.6 of Mg, and 8.0 of Ca. Among the plant species studied were *Helianthus annuus, Pisum sativum,* and *Zea mays.* The difference between the cation contents of these plants was slight with the exception of Zea. It was found to contain 3.0 times less Ca than Pisum and 4.3 times less Ca than Helianthus. Our own results are quite in accord with these observations.

Bertrand and Ghitescu (**2**) cultivated four plant species side by side in a garden. Among them were *Avena sativa* and *Fagopyrum esculentum.* It was found that Fagopyrum contained, per unit of dry matter, 1.5 times more K, 3.7 times more Mg, and 4.3 times more Ca (but 51 times less Na) than did Avena. For the sake of comparison it may be stated that of our plants cultivated in solution II, Fagopyrum contained almost as much K, 3.3 times more Mg, and 2.1 times more Ca (but 7.2 times less Na) than did Avena. The general trend of the results in both experiments is thus undoubtedly the same although the differences as to Na are decidedly more pronounced among the plants of Bertrand and Ghitescu than among ours.

Finally, van Itallie (**13**) cultivated eight species of phanerogams in pots filled with three kinds of soil: (a), a poor sandy soil; (b), the same soil with some Na_2SO_4 added; and (c), the first mentioned soil with Na_2SO_4 and K_2SO_4 added. Among the plants studied were *Avena sativa* and *Sinapis alba* (white mustard). From the data given by van Itallie it may be calculated that the plants contained approximately the relative cation percentages indicated in table IX. These figures show that Avena had absorbed about 2 to 3 times less Na and Ca, but in most cases about twice as much K, as had Sinapis; the Mg percentages were almost the same in both plants. On the other hand, in our own experiments with the solutions II and V (tables IV and VII), Avena had taken up 2 to 3 times less Na, about 2 times less Ca, about 1½ to 2 times more K, and about as much Mg, as did Sinapis. The agreement between the principal results of van Itallie and ours is thus very good.

TABLE IX

Approximate cation percentages of Avena and Sinapis cultivated by van Itallie in three different kinds of soil (A, B, C)

Plant	Na			K			Mg			Ca		
	A	B	C	A	B	C	A	B	C	A	B	C
Avena	5	17	11	68	61	66	11	10	10	16	12	13
Sinapis	14	26	19	32	28	41	14	14	11	40	34	29

Summing up the results of the above comparisons of plants cultivated under different conditions, we may conclude that the main differences in cation selection between our plant species grown in water culture are by no means restricted to the special conditions prevailing in our experiments. They are, at least to a considerable extent, of a general nature. On the other hand, it has been clearly demonstrated (**21**) that the external conditions do definitely affect the cation selection of higher plants.

Features common to the cation selectivity of all the plants studied

From emphasis upon the differences between various plant species, we now put the question: which features are common to the cation selectivity of all the plants?

CONSTANT RELATIONSHIPS BETWEEN CATIONS

As a first constant feature we may point out the striking fact that all of our experimental plants absorb rubidium very nearly with the same rapidity as potassium, from a solution containing equivalent amounts of these cations.

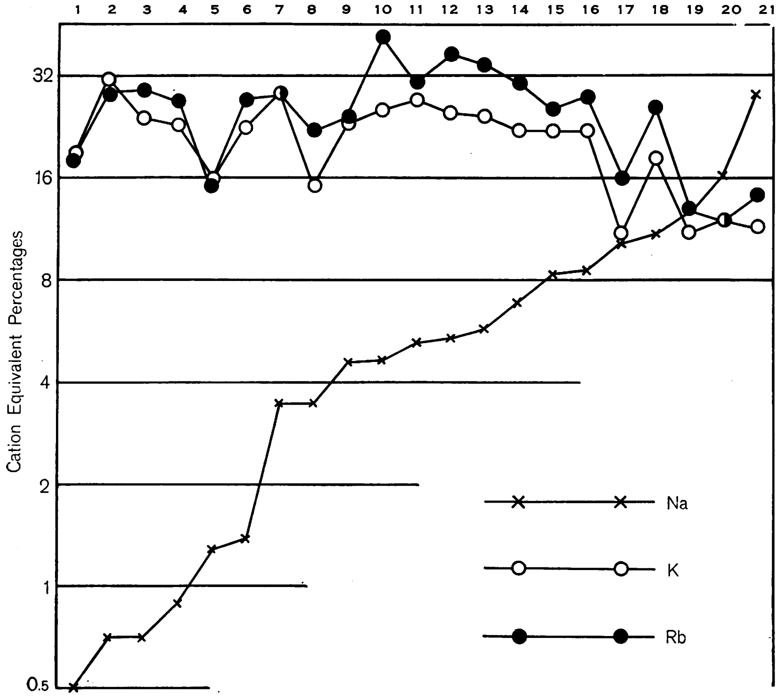

FIG. 1. Equivalent percentage of Na, K, and Rb in plants cultivated in solution II containing these cations in equivalent amounts. The plants are arranged according to increasing Na content.

1. Fagopyrum	12. Papaver
2. Zea	13. Lactuca
3. Helianthus	14. *Plantago lanceolata*
4. Chenopodium	15. Melilotus
5. Salsola	16. Vicia
6. Pisum	17. *Atriplex litorale*
7. Nicotiana	18. Sinapis
8. Solanum	19. Salicornia
9. Spinacia	20. *Plantago maritima*
10. Avena	21. *Atriplex hortense*
11. Aster	

This is clearly seen from table IV and figure 1. According to the results, the ratio $K_{absorbed}:Rb_{absorbed}$ varies only between the values 1.0: 1.88 (*Atriplex litorale*) on the one side and 1.1: 1.0 (Fagopyrum, Salsola, Zea) on the other. It is not possible to decide from the data of table IV, whether the apparent variations of this ratio are real or perhaps due only to analytical errors. That the ratio between K and Rb absorbed is at least approximately constant is remarkable.

In the experiment with solution V (table VII), which contained a 20 times lower concentration of Rb than of K, the amounts of Rb taken up by the plants were all about 20 times smaller than the corresponding amounts of K. At first sight this seems strange since ions are generally taken up relatively more abundantly from dilute solutions than from those more concentrated. An explanation of this result, however, will be given later in this paper.

A second characteristic common to all of the plants studied is that they absorb cesium nearly as rapidly as rubidium, and thus also as rapidly as potassium (table VII). According to the analytical results the ratio $Rb_{absorbed}:Cs_{absorbed}$ varies between 1.9: 1.0 (Avena) on the one side and 1.0: 1.1 (Sinapis) on the other; the average is about 1.3: 1.0. In this case it is questionable whether the ratio in reality varies slightly or is constant.

While the last three members of the alkali-metal series show such a close resemblance in their behavior towards the plants it is rather remarkable that between the first three members of this group (Li, Na, and K) no correlation can be detected; that is, apart from the fact that the plants richest in Na contain a slightly lower percentage of K than do most other species.

A third characteristic common to all of the plants studied is that they take up strontium at almost the same rate as calcium; the analytically determined ratio $Ca_{absorbed}:Sr_{absorbed}$ varies in the experiment with solution V (table VII) between 2.0: 1.0 and 1.0: 1.0. Again these variations do not exceed the limits of experimental error.

If the nutrient solution contains Ca and Sr in different concentrations, each of these cations is taken up in amounts directly proportional to the concentration of that ion in the solution. The cation occurring in a lower concentration is thus in this case *not* absorbed relatively more abundantly. This is clearly seen from figure 2 which refers to the experiment carried out with solution III. This solution contained Sr in a concentration 400 times lower than the concentration of Ca and the graph shows that the amounts of Sr taken up by the plants are nearly exactly 400 times smaller than the amounts of Ca absorbed by the same plants. It is also striking to see how the Ca and Sr curves fluctuate in parallel. This indicates that the absorption power of a given plant species for Sr is always proportional to the absorption power of the same species for Ca. The data obtained with solu-

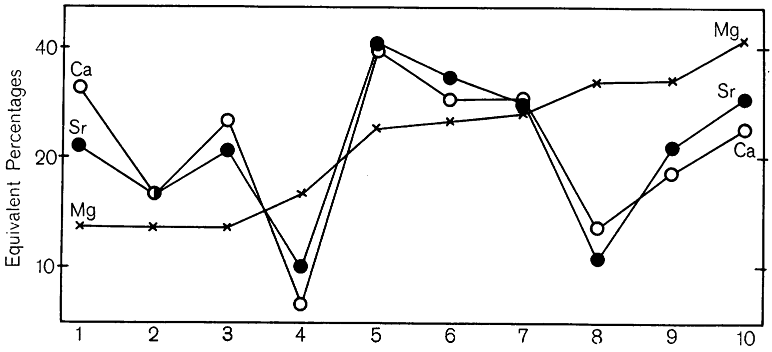

FIG. 2. Equivalent percentage of Mg, Ca, and Sr in plants cultivated in solution III containing, among other constituents, 4 milligram-equivalents of Mg and Ca and also 0.01 milligram-equivalents of Sr per liter. The Sr percentages are represented 400 times magnified. Plants are arranged according to increasing Mg content.

1. Pisum
2. Lactuca
3. Vicia
4. Avena
5. *Plantago maritima*
6. Helianthus
7. Solanum
8. Spinacia
9. *Atriplex hortense*
10. Fagopyrum

tions I, II, and IV would, if represented graphically, give very similar curves. In all cases the relative Mg content varies independently of the relative Ca and Sr content or at least nearly so.[4]

OTHER CATIONS

It might be conceivable that a given cation (A) would be absorbed by all plants in constant ratio to another—say five or ten times more slowly than another cation (B). Such a case would in itself not be more surprising than our finding that Rb and Cs are, in all plant species studied, absorbed with almost the same rapidity as K, or that Sr is taken up by all plants almost as rapidly as Ca. It is, therefore, a remarkable and rather unexpected fact that those ionic ratios, which are constant for different plants, are equal to, or at least approximate to, unity; *i.e.*, the above named ratios $K_{\text{absorbed}} : Rb_{\text{absorbed}} : Cs_{\text{absorbed}}$ and $Ca_{\text{absorbed}} : Sr_{\text{absorbed}}$, seem to be the only ones that are independent of the specific nature of the plant. All other ionic ratios which deviate from unity are also very variable from species to species. The explanation is not quite clear, but perhaps it may be found in the assumption that the plants are unable to "distinguish" between K, Rb, and Cs and also between Ca and Sr.

---

[4] In a preliminary account (7) it was claimed that there also exists a positive correlation between the Mg and Ca contents, although some exceptions were obvious. This statement was based on a comparison of the absolute Mg and Ca contents which show, in fact, a rough parallelism. This parallelism is, however, mainly attributable to the fact that there are some plants which are poor in salts and others that are rich in them.

The variation in most ionic absorption ratios from species to species is so great that it is impossible to arrange even the four cations most closely studied (Na, K, Mg, and Ca) in a constant series according to decreasing absorption. Thus in table III the series K $>$ Ca $>$ Mg $>$ Na, and K $>$ Mg $>$ Ca $>$ Na both occur in several plants; but also the series K $>$ Mg $>$ Na $>$ Ca (Atriplex), and K $>$ Na $>$ Ca $>$ Mg (*Plantago maritima* have been encountered. Table IV shows an even more complex situation: from solution II sometimes K or Rb, sometimes Mg, sometimes Ca, and sometimes even Na is taken up most copiously; in solution II, however, just as in solution I, the cations Na, K, Mg, Ca, and also Rb occur in equivalent amounts. This striking difference between the behavior of the plants in solution I and II seems to be due to a peculiar kind of mutual competition between K and Rb ions; this will be more closely examined later. These interactions between different cations make it still more difficult, of course, to put forth any series of general applicability for cation absorption.

In spite of these complications we shall now try to find from the analytical data contained in tables III to VII some more or less general rules concerning the absorption of the different cations. In doing this we restrict our comparisons to those cations which are present, in the same culture solution, in equivalent concentrations.

LITHIUM.—Earlier literature statements (**4, 14**) about "lithium plants" easily give the impression that this element would be accumulated to a very high degree by some plants. As far as I am aware there are, however, no previous culture experiments carried out with solutions of known Li concentrations which permit a quantitative estimation of the actual Li accumulation by any plant. The experimental results obtained in the present investigation show that, although different plant species behave differently towards Li ions, this element always belongs to those which are absorbed in relatively small amounts. Thus the eleven plant species cultivated in solution IV (table VI) which contained Li, Na, Mg, and Ca in equivalent amounts all absorbed much less Li than either Mg or Ca; and thus also much less K or Rb. Remarkably enough this is even true of such a typical (though not extreme) lithium plant as Nicotiana. On the other hand, the majority of the new plant species studied took up somewhat more Li than Na.

It is conceivable that Li would be accumulated to a relatively greater extent when present in very low concentration in the nutrient solution. Even in this case, however, the accumulation is apparently moderate since all of the plants cultivated in solution I were found to contain more Mn than Li, with the single exception of Nicotiana which had absorbed about twice as much Li as Mn. This solution contained about 0.005 milligram equivalents of Li and Mn per liter in addition to other ions.

SODIUM.—As previously pointed out, the extent to which this element is absorbed varies very much depending upon the specific nature of the plant in question. Nevertheless, Na seems to be the one least absorbed of all the cations studied or, in other words, the one most perfectly excluded. Perhaps the most striking example of the exclusion of Na is afforded by Fagopyrum cultivated in solution V (table VII). From this solution (containing in addition to other ions, 2 milligram equivalents of Na and K, and 0.2 milligram-equivalents Mg and Ca) Fagopyrum was found to have taken up about 90 times less Na than K, and about 5 to 6 times less Na than Mg or Ca.

Na is in most cases absorbed less, often much more, than K, Rb, Ca, Mg, Ca, and Sr.[5] In many cases the absorption of Na is even less than that of Li or Mn.

POTASSIUM AND RUBIDIUM.—These two cations are, in most cases, more easily absorbed than any others. Thus, if Rb is not present, K is nearly always[6] taken up in greater amounts than any other cation studied (tables III, V). Even when the absorption of K is suppressed by the presence of an equal amount of Rb (solution II), no other cations are accumulated much more than K and Rb.

CESIUM.—This cation seems to be absorbed almost as easily as Rb and thus about as easily as K.

MAGNESIUM, CALCIUM, AND STRONTIUM.—Sr is absorbed, by all of the plants studied, almost as readily as Ca. Mg, on the other hand, is absorbed to concentrations 5 times as great by some species and by others only to concentrations $\frac{1}{3}$ of those of Ca and Sr. Generally speaking the alkaline earths are accumulated in quantities which amount to about 1/9 to 1/1 of the simultaneously absorbed quantities of K (tables III, V) if the absorption of K is not suppressed by Rb. In the presence of an equivalent amount of Rb, however, the alkaline earths are often taken up to even a greater degree than is K.

MANGANESE.—The plants cultivated in solution III, which contained equivalent amounts of Mn and Sr, were always found to have absorbed distinctly more Mn than Sr; the amounts of Mn found in the shoots for the most part surpass their Sr content by about 10 to 20 times (table V). In spite of this, it seems very questionable whether it would be justifiable to conclude that Mn is in general more easily absorbed than Sr. It should be noted that in the above experiment the absorption of Sr has probably been strongly sup-

---

[5] From solution III (see table V) containing Na and Sr in equivalent amounts, Na was taken up as copiously or in most cases even more copiously than Sr, but this result is probably due to the "antagonistic" effect of Ca. This element occurs in the culture solution in a concentration 400 times higher than that of Sr and thus may be able to suppress the absorption of Sr very strongly.

[6] The only exception from this rule is Fagopyrum which, when cultivated in solution III, contains a little more Mg than K (table V). In view of the relatively low accuracy of the Mg determinations it is, however, questionable whether this single exception is a real one.

pressed by the Ca ions, the concentration of which in the culture solution III was 400 times higher than that of the Sr ions.

A comparison of the quantities of Mn and Na absorbed from solution III is probably more justifiable. The ratio $\mathrm{Mn}_{\mathrm{absorbed}} : \mathrm{Na}_{\mathrm{absorbed}}$ varies between about 8 : 1 (Helianthus) and 1 : 6 (Atriplex). This indicates that on the average Mn is taken up to about as small a degree as is Na.

Finally, it should be stressed once more that the roots contain relatively large quantities of Mn which have been left out of account in the above considerations. If the Mn content of the roots is included, the absorption of Mn appears considerably greater.

COPPER.—Cu is an example of a heavy metal which in very low concentrations can easily be determined in the flame spectrum. A culture experiment was started with solution VI containing besides other ions, Cu, Mn, and Sr in equivalent amounts (0.05 milligram-equivalents per liter). From the results given in table X it is clear that the amounts of Cu transferred from the roots to the upper parts of the plant are very small; in fact, considerably smaller than the corresponding amounts of Mn and Sr. In the roots, on the other hand, great amounts of Cu were found. It is questionable, however, whether these quantities were really absorbed by living cells or only precipitated on or in the cell walls of the roots.

TABLE X

Cu, Mn, AND Sr CONTENT OF (A) ROOTS AND (B) AERIAL PARTS OF PLANTS CULTIVATED IN SOLUTION VI. THE CATION CONTENTS ARE EXPRESSED AS MILLIGRAM EQUIVALENTS PER KILOGRAM DRY WEIGHT

SPECIES	Cu		Mn		Sr	
	A	B	A	B	A	B
Avena	100	<3.8	13	19	6	8
Helianthus	20	3.8	5	18	3	10
Pisum	190	<3.8	>175	15	14	8

CATION ABSORPTION SERIES

After this review of the absorption of single cations we may suitably return to the question of the arrangement of the cations studied in a series, according to decreasing absorption by the plants. It was pointed out that it is not possible to put forth such a single series valid for all of the plant species studied. If we, however, intentionally leave the less frequent types of cation selection out of account, it is possible to lay down a cation series roughly valid for some sort of average plant type. This series, which is here given only with explicit reservation for its limited validity, may be written as follows:

$$\mathrm{Rb,\ K,\ Cs} > \begin{matrix}\mathrm{Mg}\\ \mathrm{Ca,}\end{matrix}\ \mathrm{Sr} > \begin{matrix}\mathrm{Li}\\ \mathrm{Na}\\ \mathrm{Mn}\end{matrix}$$

Elements separated by a comma differ only slightly from each other as to their absorption. On the other hand, the symbols written above one another indicate elements the relative absorption of which is subject to variations so great that it would seem too arbitrary to give precedence to one of them.

The present writer knows no other experiments in which higher plants have been cultivated in solutions containing a considerable number of cations in equivalent concentrations and in which the amounts of different cations absorbed by the plants have been determined. It is, therefore, scarcely possible to compare the results arrived at in this investigation with the results of previous work by other investigators. Only in passing it may be pointed out that the above cation series agrees approximately, but not wholly, with that obtained in cultivating the alga *Tolypellopsis stelligera* in a nutrient solution, containing several cations in equivalent amounts (**8**). The cation series referring to Tolypellopsis is K $>$ Rb $>$ Ca $>$ Na, Li. The only difference is that the alga absorbs somewhat less Rb than K. Another Characean alga, *Nitella clavata,* studied by HOAGLAND AND DAVIS (**10**) yielded the series K $>$ Na $>$ Ca $>$ Mg. This cation series differs somewhat more from the series valid for the majority of phanerogams but coincides with that found in our experiments with *Plantago maritima.*

Some interactions between different cations in absorption

No attempt will be made here to discuss the intricate question regarding effects exerted by some cations on the absorption of others. Only a restricted but striking aspect of this problem will be considered.

It has already been shown that, in spite of the fact that the culture solutions I, II, and III all contained K, Ca, and Mg in equivalent amounts, all of the plants cultivated in solutions I and III absorbed distinctly more K than either Ca or Mg; the same plant species when cultivated in solution II were often found to contain more Mg or Ca than K. What is the cause of this apparent inconsistency? The most conspicuous difference between solutions I and III and solution II is that the first named solutions were free from Rb, while solution II contained as much Rb as K. It is possible, therefore, to explain the experimental results by assuming that Rb ions when present in the culture solution exert a specific depressing effect on the absorption of K ions.

If the above interpretation is correct it seems rather natural to expect that a similar effect would be obtainable with another pair of physicochemically allied cations (Ca and Sr). This is apparently the case, as may be concluded from the following chain of comparisons. From the analytical data presented in table VII it is obvious that Sr is absorbed almost as readily as Ca; from table IV it may be concluded that by almost all of the plant species represented Ca is absorbed distinctly more than Na. Hence, it seems logical to conclude that Sr should be taken up by most plant species at least as much as Na. Contrary to this view, however, table V shows that all of the plants cultivated in solution III (which contained Na and Sr in equivalent amounts) have taken up much less (about 10 times less) Sr than Na. This result is easily explained by the previous assumption that the Ca ions, being present in solution III in a concentration 400 times higher than the concentration of Sr, have strongly depressed the simultaneous absorption of Sr.

In order to prove, once more, the above assumptions, the following experiments were carried out: A series of seven culture solutions (A to G) was prepared so comparisons could be drawn between selected pairs of cultures in which, with reference to any one of the 6 cations investigated, the concentration of one cation was varied by a tenfold change. Besides constant concentrations of NH_4NO_3 (2 milligram equivalents), $MgSO_4$ (0.2 milligram equivalents), Fe-tartrate, and the components of the "A–Z" solution of HOAGLAND, the solutions had the following cation composition with their anion contents held as constant as possible:

SOLUTION	CONCENTRATIONS EXPRESSED AS MILLIGRAM EQUIVALENTS PER LITER					
	LI	NA	K	RB	CA	SR
A	0.2	2.0	2.0	0.2	0.2	......
B	*2.0*	2.0	2.0	0.2	0.2	......
C	0.2	*0.2*	2.0	0.2	0.2	......
D	0.2	2.0	*0.2*	0.2	0.2	......
E	......	2.0	2.0	*2.0*	0.2	0.2
F	......	2.0	2.0	0.2	*2.0*	0.2
G	......	2.0	2.0	0.2	0.2	*0.02*

Avena, Helianthus, and Pisum were cultivated in these solutions. Figure 3 shows graphically the amounts of K, Rb, and Sr absorbed by the plants. These amounts are expressed as milligram equivalents per kilogram dry matter. An inspection of the graphs reveals the following facts: The Rb content of the plants is not influenced to any degree by variations of the Li, Na, Ca, and Sr concentrations of the culture solution; but a decrease of its K concentration from 2.0 to 0.2 milligram equivalents (solution D) causes a very conspicuous increase in the Rb absorption of all plants. As to the absorption of K, the result is correspondingly, though somewhat less, uniform; the K content of the plants is also rather independent of the Li, Na, Ca, and Sr concentrations of the culture solution. When, however, the concentration of the Rb ions in the solution is raised from 0.2 to 2.0 milligram equivalents (solution E) it causes a distinct depression of the K absorption in both Avena and Helianthus. This depression is, however, for some unknown reason not evident in Pisum. With regard to the modification of the Sr absorption the three species studied again behave similarly: figure 3 shows that if the Ca concentration of the culture solution is raised from 0.2 to 2.0 milligram equivalents (and the Rb concentration simultaneously lowered from 2.0 to 0.2 milligram equivalents) the plants take up about 2 to 5 times less Sr.

It is thus evident that the absorption of Rb is more strongly depressed by K ions than by any other cation the concentration of which was varied in the above experiment. Correspondingly, the absorption of K is more strongly depressed by Rb ions than by any other cation studied. Finally, the absorption of Sr is suppressed more strongly by Ca ions than by any other cations tried. Whether Sr correspondingly suppresses the absorption of Ca has not been experimentally decided but seems, by analogy, very likely.

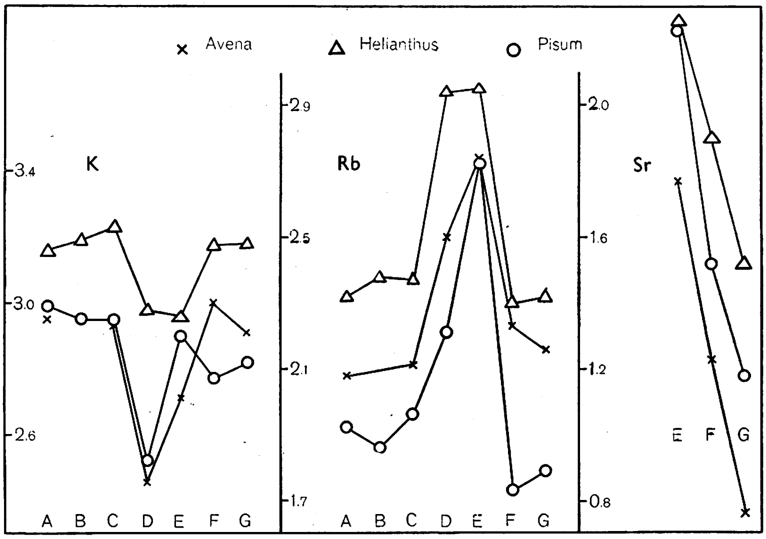

Fig. 3. K, Rb, and Sr content of Avena, Helianthus, and Pisum cultivated in the solutions A to G. The ordinates indicate logarithms of the cation contents expressed as milligram-equivalents per kilogram of dry matter.

It is found that the absorption of a certain kind of cation is most strongly depressed, not by cations of a pronouncedly different type (*e.g.*, the absorption of univalent ions by bivalent ions) but, on the contrary, by very closely allied cations. This might seem somewhat unexpected in view of some current conceptions of "ion antagonism." It was only in compiling this publication that the writer was made aware of the observations of Hurd-Karrer (**12**) according to which K salts are able to prevent the harmful effect of Rb salts, and Ca salts the toxic action of Sr salts. These observations were explained by Hurd-Karrer by assuming that Rb ions are replaced by K ions and Sr ions by Ca ions in the nutrition of the plants—an assumption which in view of the present investigation turns out to be entirely correct. BLANCK (**3**) has also observed that Rb may compete with K absorption (**24**). Moreover, HOAGLAND, DAVIS, and HIBBARD (**11**) made an analogous observation concerning the accumulation of anions in establishing that the absorption of Br ions by Nitella cells is depressed by Cl and I ions but not by SO_4 or NO_3 ions. These authors pointed out that it may be questioned whether the expression "ion antagonism" should be used to designate phenomena of this type. The following considerations seem to stress these doubts and also shed some light on the mechanism of the mutual hindrance observed.

It is a well-known fact that ions are in general absorbed to relatively greater extent from dilute than from concentrated solutions (**6, 8, 11, 25**). Using the terminology of STILES and KIDD (**25**) we may also express this by saying that the absorption ratio (the ratio $c_{\text{internal}} : c_{\text{external}}$) of a given ion increases when its concentration in the nutrient solution decreases. Also the results obtained in the present investigation offered several examples of this. It may suffice to quote one single typical example. The ratio $K_{\text{absorbed}} : Na_{\text{absorbed}}$ was in the case of Avena cultivated in solutions I and V which both contained K and Na in equivalent amounts, respectively $73 : 3.7 = 20$ and $61 : 3.4 = 18$; hence in both samples almost the same. Solution III, on the other hand, contained Na in a concentration 400 times lower than K. If the amounts of Na absorbed by the plants were directly proportional to the concentration of Na in the nutrient solution, one would expect to find in the Avena plants cultivated in solution III a Na percentage about $400 \times 19 = 7600$ times smaller than the corresponding K percentage. But in reality the Na percentage analytically found (0.32) was not 7600 but only 230 times smaller than the K percentage (75). In other words, when the concentration of Na in the culture solution was reduced 400 times (in relation to K) the amount of Na absorbed decreased only 33 times. Na was thus absorbed relatively much more from the dilute solution.

Strangely enough, however, Rb in the presence of K, and Sr in the presence of Ca, are conspicuous exceptions to this general rule. Thus Rb, when occurring in the culture solution in the same concentration as K (solution II), was accumulated roughly to the same extent as K and when occurring in a concentration 20 times lower than K (solution V) was accumulated in amounts roughly 20 times smaller than the simultaneously absorbed amounts of K. The behavior of Sr as compared with Ca is quite analogous. When both cations are present in equivalent concentrations (solution V) Sr is absorbed almost as readily as Ca; when Sr is given in a concentration 400 times lower than Ca (solution III) it is absorbed in roughly 400 times smaller amounts than Ca. Even when the concentration of Sr is only about 1/4000 of that of Ca (solution I) the proportionality in absorption is at least approximately maintained; the absorbed amounts of Sr are about

1/4000 to 1/2000 of those of Ca. Hence, the relative enhancement of absorption which in other cases is brought about by diluting the salt solution is not found in these cases. Why? One answer to this question is, of course, that K when present in a much higher concentration than Rb strongly depresses the accumulation of this ion and that Ca correspondingly depresses the absorption of Sr. But this answer, though in itself quite correct, does not explain the peculiar fact that this depression is exactly great enough to maintain the absorption ratio of Rb (as compared with that of K) and of Sr (as compared with that of Ca) constant in spite of the great variations to which the concentrations of these ions are subjected in the nutrient solutions used. The simplest explanation of this unexpected constancy of the absorption ratios seems to be that the plants are in a certain sense unable to "distinguish" between K and Rb and also between Ca and Sr in the same manner as they are unable to distinguish between two different isotopes of a given element. Just as the absorption ratio of the radioactive isotope remains about the same as that of the inactive isotope, (even when the two isotopes occur in extremely different concentrations in the external medium) so it is also easy to understand that the absorption ratio of Rb or Sr remains approximately the same as that of K or Ca when the proportions K : Rb and Ca : Sr are subjected to great variations in the culture solution. We must assume, however, that the absorption ratio depends, not upon the individual concentrations of K, Rb, Ca, and Sr, but upon the combined concentrations of K + Rb in the one case and of Ca + Sr in the other.

From the same point of view it is easy to explain some peculiarities in the results obtained with the culture solutions A to G. On first sight it might appear strange that, as the K concentration of the solutions was reduced 10 times, the amount of K absorbed decreased only about 2 to 3 times. As the concentrations of Rb and Sr were also 10 times reduced, however, the amounts of these cations in the plants decreased about 4 to 10 times. This result is understandable if we take into consideration the following facts. In solution E the joint concentration of Ca + Sr amounts to 0.4 milligram equivalents and in solution G to 0.22; the difference is thus moderate. Similarly, the combined concentration of K + Rb in solution E (4.0 milligram equivalents) differs only moderately from that in D (2.2 milligram equivalents). In these instances, therefore, the reduction of the concentrations of Sr or Rb must evidently cause a considerable decrease of the amounts of these elements absorbed. When, however, we compare solution A which contains 2.2 milligram equivalents K + Rb with solution D which contains only 0.4 milligram equivalents K + Rb we find that the total sum of these cations is much reduced in solution D. It thus seems only natural that the absorption ratio of K, just like that of Rb, should be considerably greater in D than in A.

It is then somewhat inappropriate, if the views presented above are correct, to use the term ''ion antagonism'' for the phenomena discussed; ''mutual competition'' or ''mutual replacement'' are expressions which would give a clearer picture of the actual situation.

Concluding remarks

In the present investigation stress has been laid on obtaining positive experimental facts concerning the selective cation absorption of plants. Hitherto such facts have rarely been available. While it would be highly important to give a theoretically satisfactory explanation of the selective absorption process in question on the basis of the facts thus established, the present writer, unfortunately, feels unable to do this as the problem is too intricate. Only a few general remarks may be ventured here.

There are at least two different processes which may account for the entrance of salts from the nutrient solution into the plant. The first is the transpiration stream which will carry the salts contained in the nutrient solution into the plant insofar as the salts are not hindered by some semipermeable or selectively permeable structures in the roots. Since the cell walls are generally much more permeable to both water and salts than are the protoplasts, it seems conceivable, and perhaps even probable, that the transpiration stream traverses the root cortex; flowing not only through the protoplasts but to a considerable extent also between them—*i.e.*, through the cell walls which probably exert only a relatively slight selective effect. It is probable, however, that there is at least one point in which the stream is forced to pass through living protoplasts. This point is the endodermis, the Casparian strips of which make its cell walls more or less impermeable to water and salts (**19**). Hence, the composition of the salt mixture entering the plant with the transpiration stream will, in any case, be controlled by the permeability of some living protoplasts. The same is true in regard to the salts which tend to enter the central cylinder of the root by diffusion from the nutrient solution. It seems advisable to consider whether or not it might be possible to explain the cation selection exerted by the plants in the light of current theories of protoplasmic permeability.

The ultra-filter hypothesis is evidently not able to explain our experimental results. From what we know about membranes acting as ultra-filters (*e.g.*, collodion and copper ferrocyanide membranes) the bivalent Mg, Ca, and Sr ions should permeate with considerably greater difficulty than the univalent Na ions. In reality, as we have seen, Na is taken up to a less degree by most of our experimental plants than are the alkaline earth cations. This finding also proves that, contrary to a wide-spread opinion, the diffusibility (or mobility) of the ions is not, or at least not alone, decisive for their absorption by the plants. In this connection it may be noted that from a purely physiological point of view the smallness of the Na absorption is perhaps somewhat surprising, since it is generally supposed that plant protoplasts are more permeable to Na than to Mg or Ca ions; plasmolytical experiments especially point in this direction. Either this supposition is wrong or the cation absorption of the plants is, to a considerable degree, determined by some factor other than protoplasmic permeability.

Turning then to the lipoid-solubility theory we note that at least in the system butyl alcohol/water, and thus probably in most systems of the type lipoid/water, the distribution coefficients of the cations decrease in the order: Li > Na > K > Rb > Mg > Ca > Sr [ALLEMANN, (1) and unpublished results]. This is, of course, not at all in harmony with the cation selection observed in the present investigation. However, according to OSTERHOUT, *et al.* (**17**) the relative solubilities in guaiacol increase in order Li < Na < K < Rb < Cs, which would be at least roughly in accordance with the behavior of the roots; but Mg and Ca are stated (**18**) to be much less soluble in this solvent than Na. This is again in contradiction to the selection exerted by most roots. We must bear in mind that the distribution of cations between lipoidal solvents and water is still very imperfectly known; it is thus possible that in the future lipoids may be found whose solvent capacity would better satisfy the theoretical demands now in question. At any rate it is so far quite uncertain that it will be possible to bring the cation selection of the plants even into purely formal agreement with the lipoid-solubility theory; not to speak of the possibility of explaining the cation selection in a truly plausible manner.

See Gortner

There is, too, no clear evidence that the combined lipoid-filter theory, though making many different cation selection series theoretically conceivable, would be able to give a really credible explanation of the whole process.

It is in fact scarcely worth while to speculate very much upon the concordances and discrepancies between the current permeability theories and the cation selection exerted by the roots. From other investigations, especially of HOAGLAND and his collaborators (**9**) it is rather evident that this process is due principally to a complicated activity of the root cells. This is essentially independent of the transpiration stream and it cannot be deduced from our knowledge of the passive permeability of the protoplasts. This activity presents itself most obviously in the ability of the root cells to perform work in accumulating salts in high concentration from the very dilute solution surrounding them. The root cells probably actively secrete the salts taken up, releasing them to the xylem vessels in which they are conducted with the ascending sap to the shoot.

The problem of the salt selection of the higher plants is thus in the first place a question of the selectivity of the adenoid (active) salt transport of the root cells. There are, however, still other complications not yet mentioned. Thus, for example, some of the cations transported with the transpiration stream to the shoot are probably sent back along the sieve tubes to the roots where they are likely to impede, at least to some extent, the further absorption of cations of the same kind while other sorts of cations are retained in the shoot and thus exercise no repressing effect on the uptake of cations of their own kind.

It is evident that the problem of cation selection of the higher plants is an extremely intricate one.

Summary

Some 20 phanerogams representing different ecological types were cultivated in complete nutrient solutions containing several cations in equivalent amounts. After approximately two months of growth the cation composition of the plants was determined using LUNDEGÅRDH's method of quantitative spectral analysis. The cations most closely studied in this way were Na, K, Rb, Mg, Ca, Sr, and Mn. Li and Cs were also studied but less extensively; Cu only quite cursorily. The results obtained were as follows:

1. The differences between the plant species cultivated in a given solution are very unequal in regard to the different cations. They are very great in the case of Na and Mn contents; the maximum values are about 20 to 60 times greater than the minimum. They are considerable in the case of the Li, Mg, Ca, and Sr contents; the maximum values are about 3 to 5 times greater than the minimum. For K, Rb, and Cs, on the other hand, only moderate differences were observed; the maximum values were 2 to 3 times greater than the minimum. The cause of variation of different cations in such unequal magnitudes is not known.

2. The differences observed are, for the most part, truly specific in character. Single plant species are constantly (irrespective of the year of cultivation and composition of the culture solutions) found to be relatively rich in certain cations and other species as constantly relatively rich in other cations.

3. All halophytes cultivated (*Salicornia herbacea, Plantago maritima, Atriplex litorale, A. hortense*) were found to be very rich in Na, with the single exception of *Aster tripolium* which contained only moderate quantities of this element. *Fagopyrum esculentum, Zea mays,* and *Helianthus annuus* were, on the contrary, distinguished by their unusually large exclusion of Na. All Chenopodiacean plants, as well as Fagopyrum, were remarkably rich in Mg. Ca and Sr were absorbed in greatest amounts by Helianthus, Fagopyrum, and *Sinapis alba;* Avena, Zea, and Spinacia absorbed these two cations in the least amounts.

4. All plants studied absorb Rb and Cs with almost the same rapidity as K. They also take up Sr almost as readily as Ca. On the other hand

all the other cations studied show no distinct mutual correlation in their absorption rates by the plants.

5. The specific differences between the absorption characteristics of different plant species are so great that it is not possible to arrange the absorption of the cations studied in any certain order which would be valid for all plant species investigated. The following data are, however, valid for the majority of the species studied. K, Rb, and Cs are, in general, the cations most copiously accumulated. The next place is in most cases occupied either by Ca and Sr or, about as frequently, by Mg, Li, Na, and Mn; the latter were taken up by most plant species to a distinctly less extent than all of the six cations so far mentioned. The absorption of Na amounted generally to about 1/50 to 1/2 of the simultaneously absorbed K.

6. K and Rb ions and Ca and Sr ions depress the absorption of each other more than do any other cations studied in this respect. It is also remarkable that Rb or Sr, in the presence of an excess of K or Ca, respectively, do not obey the general rule that the absorption ratio of a given ion increases when the concentration of that ion in the medium decreases. On the contrary, the absorption ratios of Rb and Sr remain constant if only the total concentration of K + Rb, respective to Ca + Sr, is held constant. These findings are explained by assuming that the ions K and Rb, and Ca and Sr, behave in the salt absorption of plants somewhat as identical ions or as two isotopes of the same element.

7. The very complex nature of the selective salt absorption of higher plants is stressed.

The author is indebted to MR. ANTTI KYTÖNIEMI, MR. LEO LEHTORANTA, and MR. MAURI SIIVONEN for carrying out the spectral analyses on which this investigation is based. MR. KYTÖNIEMI also cultivated the plants grown in solution.

BOTANICAL INSTITUTE
UNIVERSITY OF HELSINGFORS
HELSINGFORS, FINLAND

LITERATURE CITED

1. ALLEMAN, ERNST. Bestimmung von Ionenteilungskoeffizienten. Zeitschr. Elektrochem. **34**: 373–387. 1928.
2. BERTRAND, GABRIEL, AND GHITESCU, VIRGIL. Sur la composition élèmentaire de quelques plantes cultivées. Compt. Rend. Acad. Sci. (Paris) **199**: 1269–1273. 1934.
3. BLANCK, E. J. Landw. **81**: 205. 1933. (Quoted from STEWARD (**24**)).
4. BORESCH, K. Die anorganischen Bestandteile. Handbuch der Pflanzenernährung und Düngerlehre. Herausgeg. von F. Honcamp. Vol. I. Berlin. 1931.

5. BURSTRÖM, HANS. Kemisk-fysiologisk analys av kalkningsoch gödslingsförsök på sur lerjord. (With German summary.) Meddel. no. 475 fr. Centralanst. för försöksväs. på jordbruksomr. Stockholm. 1937.
6. COLLANDER, RUNAR. Der Zellsaft der Characeen. Protoplasma **25**: 201–210. 1936.
7. ———. Über die Kationenelektion der höheren Pflanzen. Ber. d. bot. Ges. **55**: 74–81. 1937.
8. ———. Permeabilitätsstudien an Characeen. III. Die Aufnahme und Abgabe von Kationen. Protoplasma **33**: 215–257. 1939.
9. HOAGLAND, D. R., AND BROYER, T. C. General nature of the process of salt accumulation by roots with description of experimental methods. Plant Physiol. **11**: 471–507. 1936.
10. ———, AND DAVIS, A. R. The intake and accumulation of electrolytes by plant cells. Protoplasma **6**: 610–626. 1929.
11. ———, ———, AND HIBBARD, P. L. The influence of one ion on the accumulation of another by plant cells with special reference to experiments with Nitella. Plant Physiol. **3**: 473–486. 1928.
12. HURD-KARRER, ANNIE M. Rubidium and strontium toxicity to plants inhibited by potassium and calcium respectively. Jour. Washington Acad. Sci. **27**: 351–353. 1937.
13. VAN ITALLIE, TH. B. The rôle of sodium in the kation-balance of different plants. Trans. Third Internat. Congr. Soil Sci. **1**: 191–194. 1935.
14. VON LINSTOW, O. Die natürliche Anreicherung von Metallsalzen und anderen anorganischen Verbindungen in den Pflanzen. Repertor. specier. nov. reg. veget. Beihefte **31**. 1924.
15. LUNDEGÅRDH, H. Die quantitative Spektralanalyse der Elemente. Jena, 1929. 1934.
16. NEWTON, J. D. The selective absorption of inorganic elements by various crop plants. Soil Sci. **26**: 85–91. 1928.
17. OSTERHOUT, W. J. V., KAMERLING, S. E., AND STANLEY, W. M. The kinetics of penetration. VII. Molecular versus ionic transport. Jour. Gen. Physiol. **17**: 469–480. 1934.
18. ———, AND STANLEY, W. M. The accumulation of electrolytes. V. Models showing accumulation and a steady state. Jour. Gen. Physiol. **15**: 667–689. 1932.
19. DE RUFZ DE LAVISON, J. Du mode de pénétration de quelques sels dans la plante vivante. Rev. Gén. Bot. **22**: 225–241. 1910.
20. SCHROPP, W., AND SCHARRER, K. Wasserkulturversuche mit der "A–Z–

Lösung'' nach Hoagland. Jahrb. wiss. Bot. **78**: 544–563. 1933.

21. SCHMIDT, OSWALD. Die Mineralstoffaufnahme der höheren Pflanze als Funktion einer Wechselwirkung zwischen inneren und äusseren Faktoren. Zeitschr. Bot. **30**: 289–334. 1936.

22. STEINER, MAXIMILIAN. Zum histochemischen Nachweis des Natriums in der Pflanze. Ber. d. bot. Ges. **53**: 720–732. 1935.

23. ——————. Die Zusammensetzung des Zellsaftes bei höheren Pflanzen in ihrer ökologischen Bedeutung. Ergebn. Biol. **17**: 151–254. 1939.

24. STEWARD, F. C. Mineral nutrition of plants. Ann. Rev. Biochem. **4**: 519–544. 1935.

25. STILES, W., AND KIDD, F. The influence of external concentration on the position of the equilibrium attained in the intake of salts by plant cells. Proc. Roy. Soc. (London) B **90**: 448–470. 1919.