# STUDIES ON ANTAGONISTIC PHENOMENA AND CATION ABSORPTION IN TOBACCO IN THE PRESENCE AND ABSENCE OF MANGANESE AND BORON

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(WITH TEN FIGURES)

## Introduction

Tobacco is very sensitive to slight variations in cultural or nutritional conditions, and is thus particularly suitable for physiological studies. Most tobacco is ultimately to be burned (smoked), and as a result great interest centers in the burning qualities of the leaf and the relation of these to the ash resulting and to factors governing ash composition. All of the above items in turn are reflected in the growth of the plant. The object of the present investigation was to study, by means of water cultures, the absorption of mineral nutrients. The bases, and factors governing their translocation within the plant, were studied specifically.

## Methods

In beginning experiments, a cultural method described by LUNDEGÅRDH (6) was employed. Tobacco plants of Havana seed type about four weeks old, were grown in sterile quartz sand with added weak nutrient solution. These were transferred to glass tubes about 45 mm. in diameter, of 200 to 250 ml. capacity, and filled with a measured quantity of a nutrient solution. The plants, one for each vessel, were fastened in a cork stopper 40 mm. in diameter,

## TABLE I

Composition of nutrient solutions in the potassium series. Concentrations given in grams per liter

	CON-			A (LOV	V K CON	ITENT)		
SALTS	CENTRA-			Con	CENTRAT	ION	##	
	TION	N	Р	К	CA	MG	Mn	в
	<i>gm</i> .	gm.	gm.	gm.	. gm.	gm.	gm.	gm.
$Ca(NO_3)_2 \cdot 4H_2O$	0.847	0.100			0.143			
$NaH_2PO_4 \cdot H_2O$	0.156		0.017					
Variable								
A B C				0.026				
$K_2SO_4$ .06; .185; .6	0.308			0.020		0.030		
$MgSO_4 \cdot 7H_2O$ $MnCl_2 \cdot 4H_2O$	0.001		]			0.030	0.0003	
$H_3BO_3$	0.001						0.0000	0.0008
Fe-citrate	0.01							
Total		0.100	0.017	0.026	0.143	0.030	0.0003	0.0008

#### PLANT PHYSIOLOGY

# TABLE I—(Continued)

Cor		E	G (MEDI	UMKO	ONTENT	)	
CENTRA-			Con	CENTRAT	ION		
TION	N	Р	К	CA	MG	Mn	В
gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.
0.847	0.100	0.017		0.143			
0.100		0.017					
			0.082				
					0.030	0.0003	
0.005						0.0000	0.0008
0.01	0 100	0.017	0.000	0 1 4 2	0.020	0 0002	0.0008
	TION gm. 0.847 0.156 0.308 0.001	CENTRA- TION N   gm. gm.   0.847 0.100   0.156 0.308   0.001 0.005	CON- CENTRA- TION M P   gm. gm. gm.   0.847 0.100 0.017   0.308 0.001 0.005   0.01 0 0	CON- CENTRA- TION CON- CENTRA- N CON- CENTRA- N   gm.	CON- CENTRA- TION CONCENTRAT   0.156 0.100 gm. gm. gm. gm. 0.143   0.308 0.001 0.005 0.01 0.082 0.182	CON- CENTRA- TION CONCENTRATION   0.100 0.100   0.156 0.017   0.308 0.082   0.001 0.005	$\begin{array}{c c c c c c c c c c c c c c c c c c c $

#### COMPOSITION OF NUTRIENT SOLUTIONS IN THE POTASSIUM SERIES. CONCENTRATIONS GIVEN IN GRAMS PER LITER

# TABLE I—(Concluded)

COMPOSITION OF NUTRIENT SOLUTIONS IN THE POTASSIUM SERIES. CONCENTRATIONS GIVEN IN GRAMS PER LITER

	Con-			С (ню	нК со	NTENT)		
SALTS	CENTRA-			Con	CENTRAT	NON		
	TION	N	Р	K	CA	MG	Mn	в
	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.
$Ca(NO_3)_2 \cdot 4H_2O$	0.847	0.100	0.015		0.143			
$NaH_2PO_4 \cdot H_2O$ Variable	0.156		0.017					
A B C								
K <sub>2</sub> SO <sub>4</sub> .06; .185; .6	0.000			0.26		0.000		
$MgSO_4 \cdot 7H_2O$	$\begin{array}{c} 0.308\\ 0.001 \end{array}$					0.030	0.0003	
$MnCl_2 \cdot 4H_2O$	0.001						0.0003	0.0008
Fe-citrate	0.000							0.0000
Total		0.100	0.017	0.26	0.143	0.030	0.0003	0.0008

which was supported by a wire folded over the edge of the tube. Blackened cardboard folded around the tubes excluded light from the roots. The tubes, in triplicate for each treatment, were placed in a rack and transferred to a photothermostat (6). The nutrient solutions are given in tables I and II and the cultural variations in tables III, IV, and VII.

In all of the solutions purest Kahlbaum salts were used. In order to obtain a true, clear solution where it was necessary to employ calcium sulphate, a saturated solution of this salt was used (solubility in water of room temperature about 0.23 per cent.). The solution was analyzed as to Ca content and a quantity was added sufficient to meet the Ca requirements of the different nutrient solutions. The reaction of solutions was equalized as nearly as possible at the beginning of the experiment. It varied slightly from a pH of 5.2 to 5.4. The solutions were changed weekly and plants were harvested after 45 days.

In later experiments, seedlings were grown in a soil flat. After six weeks they were transferred to one-liter Jena glass beakers each containing a measured quantity of nutrient solution. The beakers had been treated for about a month with a weak HCl solution. They were then thoroughly rinsed

SALTS	CON- CENTRA-			A (LO	W CA CO	NTENT)		
	TION	N	Р	K	CA	MG	MN	в
	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.
$Ca(NO_3)_2 \cdot 4H_2O$	0.25	0.03			0.042		:	-
$NaH_2PO_4 \cdot H_2O$	0.156		0.017					
KNO3	0.214	0.03		0.082				
$\operatorname{NaNO}_3$	0.037	0.006						
$Mg(NO_3)_2 \cdot 6H_2O$	0.32	0.034				0.03		
MgSO₄ · 7H₂O								
MnCl <sub>2</sub> ·4H <sub>2</sub> O	0.001						0.0003	
$H_3BO_3$	0.005							0.0008
K <sub>2</sub> SO <sub>4</sub>								
Fe-citrate	0.01							
$Na_2SO_4 \cdot 10H_2O$	0.32							
$CaSO_4 \cdot 2H_2O^{}$								
Total		0.100	0.017	0.082	0.042	0.03	0.0003	0.0008

# TABLE II

Composition of nutrient solutions in the calcium series. Concentrations in grams per liter

# TABLE II (Continued)

Composition of nutrient solutions in the calcium series. Concentrations in grams per liter

SALTS	CON- CENTRA-		]	B (MEDI	UM CA	CONTENI	?)	
GALIS	TION	N	Р	ĸ	CA	MG	Mn	в
	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.
$Ca(NO_3)_2 \cdot 4H_2O$	0.847	0.100			0.143			
$NaH_2PO_4 \cdot H_2O$	0.156		0.017					
KNO3								
$NaNO_3$								
$Mg(NO_3)_2 \cdot 6H_2O$								
MgSO <sub>4</sub> · 7H <sub>2</sub> O	0.308					0.03		
MnCl <sub>2</sub> ·4H <sub>2</sub> O	0.001						0.0003	
H <sub>3</sub> BO <sub>3</sub>	0.005							0.0008
K <sub>2</sub> SO <sub>4</sub>	0.185			0.082				
Fe-citrate	0.01							
$Na_2SO_4 \cdot 10H_2O$								
$CaSO_4 \cdot 2H_2O$								
Total		0.100	0.017	0.082	0.143	0.03	0.0003	0.0008

#### PLANT PHYSIOLOGY

## TABLE II (Concluded)

SALTS	CON-			С (ніс	н Са со	ONTENT	)	
SALTS	CENTRA- TION	N	Р	K	CA	MG	Mn	В
	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.
$Ca(NO_3)_2 \cdot 4H_2O$	0.847	0.100			0.143			
$NaH_2PO_4 \cdot H_2O$	0.156		0.017					
KNO <sub>3</sub>								
NaNO <sub>3</sub>								
$Mg(NO_3)_2 \cdot 6H_2O$								
$MgSO_4 \cdot 7H_2O$	0.308					0.03	1	
$MnCl_2 \cdot 4H_2O$	0.001					1	0.0003	
H <sub>3</sub> BO <sub>3</sub>	0.005				· ·			0.0008
K <sub>2</sub> SO <sub>4</sub>	0.185			0.082				
Fe-citrate	0.01							
$Na_2SO_4 \cdot 10H_2O$								
$CaSO_4 \cdot 2H_2O$	1.13				0.26		· ·	
Total		0.100	0.017	0.082	0.403	0.03	0.0003	0.0008

#### Composition of nutrient solutions in the calcium series. Concentrations in grams per liter

with distilled water to eliminate, as far as possible, contamination from the glass. The beakers were covered with blackened cardboard and on top of each was placed a sheet of black-varnished galvanized iron, in the center of which was a hole fitted with a 5-cm. cork stopper for holding the plant. Before transfer from the soil flat, each plant was thoroughly rinsed in distilled water and placed in a beaker. Non-absorptive cotton was packed around the stem of each plant. Each nutrient variant was set up in quadruplicate. The beakers were placed in artificially illuminated photothermostatically controlled chambers, described by LUNDEGÅRDH (6). The plants were allowed to grow for 60 days. Nutrient solutions were changed in the middle of the growth period. At this time a slight precipitation was evident in high-calcium solutions.

Nitrate nitrogen was determined in the solutions by the disulphonic acid method, and phosphorus by the phosphoceruleomolybdic acid method. Solutions, salts, and plant materials were analyzed for cations by the quantitative spectrographical methods described by LUNDEGÅRDH (6).

### Experimental results

THE EFFECT OF VARYING QUANTITIES OF CA ON GROWTH AND ON THE ABSORPTION OF POTASSIUM, CALCIUM, AND MAGNESIUM

Data for plant growth and cation absorption are given in tables III and IV; the first represents results from an experiment set up under the first procedure outlined under "Methods"; the second, under the revised procedure.

The data in table III show a marked response in growth as measured by

# TABLE III

DRY WEIGHTS AND ASH ANALYSES OF TOBACCO PLANTS GROWN IN NUTRIENT SOLUTIONS WITH VARYING AMOUNTS OF CALCIUM,\* EXPERIMENT 1

	D				ASH AN	ALYSIS		
TREATMENT AND	Dry w	EIGHT		ĸ	0	JA.	N	lg
PLANT PARTS	Plant	RELA- TIVE	Per gram	Per Plant Part	Per gram	Per plant part	Per gram	PER PLANT PART
	gm.		m. mol	m. mol	m. mol	m. mol	m. mol	m. mol
Low Ca								
Stems, leaves	0.416		1.240	0.516	0.259	0.108	0.330	0.137
Roots	0.110		1.030	0.113	0.052	0.016	0.285	0.031
Total plant	0.526	46		0.629		0.124		0.168
Medium Ca								
Stems, leaves	0.845		0.810	0.684	0.472	0.399	0.135	0.114
Roots	0.300		0.690	0.207	0.085	0.026	0.180	0.054
Total plant	1.145	100		0.891		0.425		0.168
High Ca								
Stems, leaves	1.010		0.760	0.768	0.426	0.430	0.086	0.087
Roots	0.370		0.720	0.266	0.089	0.033	0.202	0.075
Total plant	1.380	120	···· <b>··</b> ·	1.034		0.463		0.162

# TABLE IV

DRY WEIGHTS AND ASH ANALYSES OF TOBACCO PLANTS GROWN IN NUTRIENT SOLUTIONS WITH VARYING AMOUNTS OF CALCIUM,\* EXPERIMENT 1

	DDT T	DIGIT			ASH AN	ALYSIS		
TREATMENT AND	Dry w	FIGHL	] ]	ĸ	0	CA	N	ſĠ
PLANT PARTS	Plant	RELA- TIVE	Per gram	Per plant part	Per gram	PER PLANT PART	Per gram	Per plant part
<u>.</u>	gm.	1	m. mol	m. mol	m. mol	m. mol	m. mol	m. mol
Low Ca								
Leaves	1.26		1.47	1.85	0.68	0.86	0.55	0.69
Stems	0.31		0.82	0.43	0.12	0.62	0.08	0.04
Roots	0.21							
Total plant	1.87	40		2.28		1.48		0.73
Medium Ca								
Leaves	2.47		1.73	4.27	1.06	2.62	0.27	0.67
Stems	1.35		1.34	1.81	0.12	1.62	0.08	0.11
Roots	0.45		0.68	0.31	0.21	0.10	0.20	0.09
Total plant	4.27	100		6.39		4.34		0.87
High Ca		1						
Leaves	7.28		1.27	9.25	0.93	6.77	0.20	1.46
Stems	6.39		0.59	3.77	0.14	0.89	0.02	0.13
Roots	1.71		0.38	0.65	0.14	0.24	0.20	0.34
Total plant	15.38	360		13.67		7.90		1.93

#### PLANT PHYSIOLOGY

dry weight with increment of Ca in the nutrient solution. Dry matter production with the medium supply is more than double that of the low supply, although the high supply produced only 20 per cent. more dry matter than the medium. Stems and leaves increased in about the same proportion as the roots. In figure 1 a graphical presentation of the relation between growth, Ca supply, and Ca absorption is given.

Of greater interest, however, is the absorption of certain elements as reflected by the ash analyses. Absorbed Ca increased 45.3 per cent. per unit of dry matter above that for "low Ca" with the addition of about three times as much Ca as in the low solution. Further addition of calcium, however, lowered the Ca content per unit dry matter in the stems and leaves, although the total per plant increased but not in proportion to added Ca.

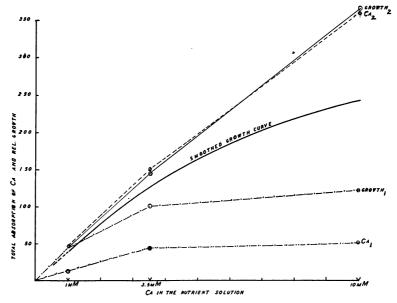


FIG. 1. Graphs showing the relation of growth to calcium supplied in the nutrient solution. The smoothed growth curve shows the general trend of experiments 1 and 2.

Considering the percentage content of Ca in the stems and leaves only, with "medium" as 100, the relationship of the low, medium, and high cultures was about 55, 100, and 90 respectively. The corresponding figures for K were about 153, 100, and 94 respectively, and for Mg, 244, 100, and 64. A low Ca supply in the nutrient medium causes a variation in the absorption of the three bases which occur in the plant in the order Mg > K > Ca, while at a high Ca supply the variation is slight and the order of occurrence is K > Ca > Mg. Since the order of Mg is directly reversed and the only

variable to account for this change is Ca, the antagonism Ca: Mg is plainly established.

A slight K: Ca antagonism is suggested which is emphasized, however, in following experiments where K is the variable. No Ca: K antagonism is indicated in figure 2 where the K content shows a considerable drop at medium Ca supply. With low Ca supply (1 millimol), and with K at 2.1 millimols, any antagonism that Ca may have possessed for K was entirely obscured by the differences in concentration of the two elements.

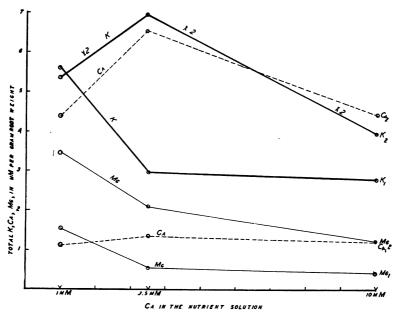


FIG. 2. Graphs showing the relation of total potassium, calcium, and magnesium absorbed per gram of root weight to varying supply of calcium in the nutrient solutions (experiments 1 and 2).

In the second experiment, table IV, with a growing period of 60 instead of 45 days, the high Ca supply produced a considerably higher yield of dry matter than shown in table III. The resulting growth was approximately proportional to Ca supplied in the nutrient solution as evident from relative weights and from figure 1. The data show that stem production was most influenced by Ca, followed by roots, with leaves least influenced by this element. These data also show that Ca noticeably affected the absorption of Mg, with no antagonistic effect on K. A slight pseudo-antagonism Ca: K is suggested at the highest Ca level, more plainly shown in figure 2.

The interrelationship of the three bases, K, Ca, and Mg, is similar to that in the first experiment; for K the relative figures for a low, medium, and high Ca supply is 78, 100, and 60; for Ca, 64, 100, and 57; and for Mg, 275, 100, and 44 respectively. The order for the three bases at the low Ca supply is Mg > K > Ca, and at the high Ca supply, K > Ca > Mg, which is identical with the results noted above.

The total absorption of the three bases at a low, medium, and high Ca supply, expressed by ratios with low Ca as 1, was: K, 1, 2.8, and 6.0; Ca, 1, 2.9, and 5.3; and Mg, 1, 1.2, and 2.6. With one exception, the absorption of the three bases progressively increased with increased Ca supply and, incidentally, dry matter production increased. The growth curve shown in figure 1 runs almost parallel to the curve of total Ca absorption. A smoothed growth curve shows the general trend of response to Ca as a growth factor.

# THE EFFECT OF VARYING QUANTITIES OF POTASSIUM ON GROWTH AND ON ABSORPTION OF POTASSIUM, CALCIUM, AND MAGNESIUM

In the second series of experiments K was varied and the resulting data are given in tables V and VI. A set of cultures containing no K was also included; these plants lived through the growing period but showed no progress in growth. In a trial without Ca, the plants soon died. In this comparison it is evident that the plants grown without K were able through transfer of K to progressively younger parts to maintain life, while the

	Darr				ASH AN	ALYSIS		
TREATMENT AND	Dry w	EIGHT	F	c	C	¦A	N	ſĠ
PLANT PARTS	Plant	RELA- TIVE	Per gram	Per plant part	Per gram	Per plant part	Per gram	Per plant part
	gm.		m.mol	m.mol	m.mol	m.mol	m.mol	m.mol
No K	0.060	5.2	Trace		0.770		0.390	
Low K Stems, leaves Roots Total plant	0.720 0.280 1.000	87.3	0.480 0.460	0.346 0.129 0.475	0.644 0.069	0.464 0.193 0.657	0.152 0.240	0.109 0.067 0.176
Medium K Stems, leaves Roots Total plant	0.845 0.300 1.145	100.0	0.810 0.690	0.684 0.207 0.891	0.472 0.085	0.399 0.026 0.425	0.135 0.180	0.114 0.054 0.168
High K Stems, leaves Roots Total plant	0.940 0.250 1.190	104.0	$1.530 \\ 1.250$	1.438 0.313 1.751	0.086 0.090	0.081 0.023 0.104	0.088 0.103	0.083 0.025 0.108

TABLE V

# Dry weights and ash analyses of tobacco plants grown in nutrient solutions with varying amounts of potassium,\* experiment $\mathbf{1}$

\* Low K = 0.66 millimols per liter.

no-Ca plants succumbed from failure to replenish the Ca. As seen in table V, only a trace of K was found in the plant material when this element was lacking in the solution, while Ca and Mg contents were the highest in this group of cultures.

With varying amounts of K in the nutrient solution (table V and fig. 3) the production of dry matter varies much less than in the case of Ca. From data in table V it is calculated that K increased 40.7 per cent. per unit of dry

-	Dry w				ASHAN	ALYSIS		
TREATMENT AND	DRIW	FIGHT	ŀ	X		A	N	ĺĢ
PLANT PARTS	Plant	Rela- TIVE	Per gram	PER PLANT PART	Per gram	Per Plant Part	Per gram	PER PLANT PART
<u> </u>	gm.		m.mol	m.mol	m.mol	m.mol	m.mol	m.mol
Low K	Ū							
Leaves	8.70		0.50	4.35	1.39	12.09	0.39	3.39
Stems	6.65		0.26	1.73	0.24	1.60	0.13	0.86
Roots	1.97		0.13	0.26	0.11	0.22	0.44	0.87
Total plant	17.31	320		6.34		13.91		5.12
Medium K								
Leaves	2.47		1.73	4.27	1.06	2.62	0.27	0.67
Stems	1.35		1.34	1.81	0.12	1.62	0.08	0.11
Roots	0.45		0.68	0.31	0.21	0.10	0.20	0.09
Total plant	4.27	100		6.39		4.34		0.87
High K								
Leaves	4.89		2.10	10.27	0.80	3.91	0.33	1.61
Stems	3.59		1.38	04.95	0.09	0.32	0.05	0.18
Roots	0.93		1.28	01.19	0.17	0.16	0.17	0.16
Total plant	9.41	220		16.41		4.39		1.95

#### TABLE VI

Dry weights and ash analyses of tobacco plants grown in nutrient solutions with varying amounts of potassium," experiment  $2\,$ 

\* Low K = 0.66 millimols per liter. Medium K = 2.10 '' '' '' High K = 6.66 '' '' ''

matter when about three times as much K was added for "medium K" as for "low K." Although further additions of K increased K per unit of dry weight, this latter did not respond to further additions, notwithstanding excessive absorption of this element. The relative content of the three bases in stems and leaves at a low, medium, and high K supply was for K: 60, 100, and 190; for Ca: 140, 100, and 18; and for Mg: 113, 100, and 65. Thus, at the low K supply the order in which the bases were absorbed was: Ca > Mg > K; and for the high K supply, K > Mg > Ca. Since Mg kept its place in the rank and since K was the only variable, the antagonism K: Ca is suggested.

There is an apparent pseudo-antagonism, Ca: K at the low K supply (0.66

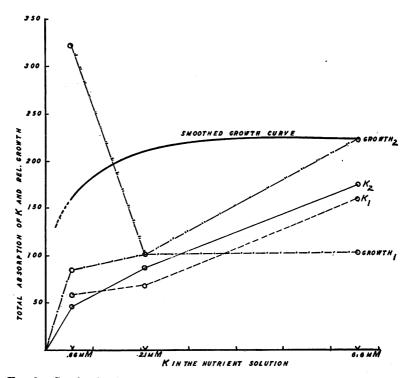


FIG. 3. Graphs showing the relation of total potassium to growth affected by varying the potassium in the nutrient solutions.

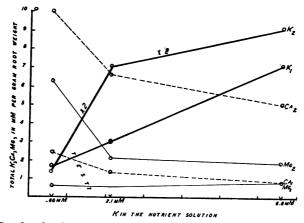


FIG. 4. Graphs showing the relation of total potassium, calcium, and magnesium absorbed per gram of root weight to varying supply of potassium in the nutrient solutions.

millimols per liter), while Ca was present at a concentration of 3.5 (fig. 4). Obviously, a true antagonism did not occur if this instance is compared with the one of medium K supply (2.1 millimols), with Ca constant as above. This K concentration caused a considerable drop in the Ca absorption. Therefore, Ca cannot be considered antagonistic to K although pseudo-antagonism is suggested when the concentration of Ca is vastly higher than that of K.

In the revised experimental procedure, the results of which are given in table VI, K had no direct influence on dry matter production at the concentrations used. In fact, the highest relative weight was produced with the lowest addition of K. It appears that a somewhat lower concentration of K would have been sufficient to produce normal growth.

With the increasing K supply in the nutrient solution, K progressively increased and Ca decreased, while Mg was only slightly affected. The interrelationship of the bases as previously computed is for K:24, 100, and 109; for Ca:154, 100, and 69; and for Mg:130, 100, and 95. At a low K supply the order of base absorption is Ca > Mg > K; at a high K supply, K > Mg > Ca. This ranking coincides with results of the previous experiment.

# EFFECT OF MANGANESE ON GROWTH AND ON THE ABSORPTION OF POTASSIUM AND CALCIUM

In the absence of Mn in the nutrient solution, deficiency symptoms of this element were pronounced at "high Ca," less at medium, and not noticeable at a "low Ca" supply. The symptoms first occur on the younger leaves (not

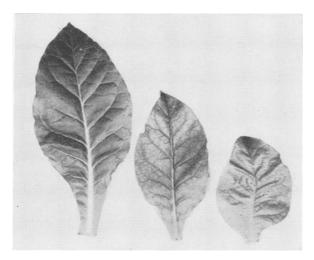


FIG. 5. Leaves from tobacco plants grown (to the left) with manganese and (the two to the right) without manganese.

the youngest) in the form of a chlorosis between the veins and resembles Mn toxicity (6) which, however, appears first at the growing point. The checkered appearance is not as firmly manifested as in the case of the toxicity. In some cases the leaves were crinkled and the size reduced (fig. 5). The roots at "high Ca" without Mn were like those described by McMURTREY (9), *i.e.*, "They did not show many branches but those they had were relatively long." The roots of these cultures were the only ones to reach the bottom of the 1000-ml. containers.

Symptoms of Mn deficiency were very pronounced in "low K" plants, less in "medium," and not noticeable in "high K" plants. The effects with K were thus in reverse order from those with Ca which suggests that Ca is antagonistic to Mn, while K is indifferent.

The data given in table VII show that the presence and absence of Mn (0.0054 millimol per liter) produced vast differences in dry matter in certain instances. With a low Ca supply dry matter in the absence of Mn was six times that obtained where Mn was present. At high Ca supply conditions were reversed so that about 3.5 times as much dry matter was produced in the presence of Mn as in its absence. These results suggest that at a low Ca supply without Mn, there being no antagonism of Mn toward Ca, the Ca could be utilized to the limit. At the high Ca supply the antagonistic action of Mn on Ca was not sufficient to prevent absorption of Ca.

The data of table VII show similar results for "high Ca" and "low K." The latter without Mn resembles "high Ca" with Mn. The presence or absence of Mn at high supply had little influence on growth, suggesting that the antagonism K: Ca obscured the effects of the absence of the essential Mn. The slightly larger weight where Mn was absent might suggest that an antagonism Mn: K was responsible.

The result of these experiments on the absorption of bases in the absence of Mn cannot be considered conclusive since the normal functions of the plant were obviously disturbed. The data of table VIII suggest, however, that Ca is antagonistic to Mn and that Mn is antagonistic to K.

The antagonistic phenomena in relation to Mn are more clearly shown from the standpoint of Mn absorption and translocation by varying the supply of Ca and K in the nutrient solution. Data from such an experiment are given in table VIII. The mobility of Mn, or its relative translocation from the roots to other parts of the plant, may be expressed by a ratio of the Mn content found in stems<sup>1</sup> and leaves and that found in roots. This

<sup>1</sup> No Mn was detected in the stems, when analyzed separately, irrespective of presence of Mn in the nutrient solution. This may be explained on the basis that there would not at any one time be a measurable amount present in the stem where Mn apparently is not stored. It suggests, moreover, that Mn is not a part of compounds formed in the leaf and later translocated into the stems. This is in line with the viewpoint that Mn acts as a catalytic agent. TABLE VII

DRY WEIGHTS AND ASH ANALYSES OF TOBACCO PLANTS GROWN IN NUTRIENT SOLUTIONS WITH VARYING QUANTITIES OF POTASSIUM AND CALCIUM; AND WITH AND WITHOUT MANGANESE\*

		DRV WEIGHT	втант				ASH A	ASH ANALYSIS		
			TUDIA	_		Ū	ONCENTRAT	CONCENTRATION PER GRAM	R	
TREATMENT AND PLANT PARTS	PI	Ріант	REL	RELATIVE		К	0	CA	<b>P</b> <sup>24</sup>	Mœ
	r.	MN	F	MN		Mn	Ā	Mn		Mn
	WITH	WITHOUT	WITH	WITHOUT	WITH	WITHOUT	WITH	WITHOUT	WITH	WITHOUT
5	gm.	gm.			m.mol	m.mol	m.mol	m.mol	m.mol	m.mol
Low Ca Lower leaves	$\left\{ \begin{array}{c} 1.26 \end{array} \right.$	} 5.55			1 47	0.98	0.72	0.99 0.36	0.55	0.65
Stems	0.31	3.33				1.11		0.06		0.09
Koots Total plant	1.78	1.42 10.30	40	240	0.82 2.28	0.49 10.45	0.14 1.48	0.08 4.20	0.73	0.31 3.96
High Ca Lower leaves Medium ''	7.28	2.85			1.57 1.10	2.31	1.54 0.88 0.98	) 1.71 0.66	0.19	} 0.34
1 op Stems Roots	) 6.39 1.71	) 2.75 0.79			0.38	1.95 1.95 0.43	0.14 0.13 0.13	0.39	0.02	0.10
plant	15.38	6.39	368	150	13.67	11.20	7.90	4.67	1.93	1.59
Low K Lower leaves Top '' Stems	} 8.70 6.65	$\left.\begin{array}{c}3.45\\2.04\end{array}\right.$			$\begin{array}{c} 0.37\\ 0.53\\ 0.26\end{array}$	$\begin{array}{c} 0.63 \\ 1.25 \\ 0.65 \end{array}$	$1.77 \\ 0.41 \\ 0.24$	1.87 0.61 0.29	$0.44 \\ 0.19 \\ 0.13$	0.51 0.41 0.21
Roots Total plant	1.97 17.31	0.57 6.06	405	142	$0.13 \\ 6.34$	0.17 4.67	0.11 13.91	0.30 5.05	0.44 5.12	0.72 2.42
es		6 L J			2.20	2.95	1.22	0.96	0.28	0.19
Top ", Top					1.75	2.27	0.28	0.51	0.36	0.23
8	3.59	2.45			1.38	2.03	0.09	0.29	0.05	0.10
Koots Total plant	0.93	9.70	220	227	1.28	24.38	0.17 4.39	0.22	0.17	0.18

SWANBACK: ANTAGONISM AND CATION ABSORPTION

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### TABLE VIII

MANGANESE CONTENT IN MILLIMOLS PER GRAM DRY WEIGHT OF TOBACCO PLANTS GROWN IN NUTRIENT SOLUTIONS WITH VARYING AMOUNTS OF CALCIUM AND POTASSIUM; AND TRANSLOCATION QUOTIENTS FOR MANGANESE

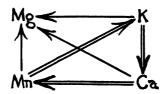
		Growth	I PERIODS	
TREATMENT AND PLANT PARTS		SE X 0.001 GRAM		RANSLOCATION
	45 days	60 days	45 days	60 days
	m.mol	m.mol		
Low Ca				
Leaves, stems	0.74	0.75	0.91	1.95
Roots	0.82	0.60	0.91	1.25
Medium Ca				
Leaves, stems	0.25	0.36		
Roots	0.36	5.00	0.70	0.07
High Ca				
Leaves, stems	0.16	0.33		
Roots	0.10	5.60	0.61	0.06
10005	0.20	0.00		
Low K				
Leaves, stems	0.22	0.20	0.40	0.10
Roots	0.51	2.10	0.43	0.10
Medium K				
Leaves, stems	0.25	0.36		
Roots	0.36	5.00	0.70	0.07
	0.00	0.00		
High K	0.90	0.00		
Leaves, stems	0.30	0.28	0.61	0.09
Roots	0.49	3.20		1

ratio is designated the translocation quotient (Tq). Data from translocation quotients in table VIII show that the least resistance to Mn absorption is offered by "low Ca" and the highest by "high Ca." Since "medium Ca" is intermediate a rather definite antagonism Ca: Mn is suggested.

With the low, medium, and high K supply there is no regularity in Mn translocation quotient relations. At the "low K" level, however, the translocation quotient even lower than that at "high Ca" suggests that increased Ca absorption incident to "low K" is responsible for reduced Mn translocation. In this connection it should be recalled that the relative absorption of Ca was greater at "low K" than at "high Ca."

Although no special Mg test similar to those with Ca and K was undertaken, the analytical data in table VI and VII indicate that the absorption of this element is depressed under low Ca and low K supplies in the presence of Mn. It appears, however, that the antagonism Ca: Mn is stronger than that of Ca: Mg. Therefore, it may be concluded that the rank of absorption may be Mn > Mg; K > Ca.

Graphically this may be visualized in the following way:



The arrows point in the direction of the antagonism, the heavy lines suggesting a strong antagonism, the lighter lines a weaker antagonism. Potassium is thus antagonized only by Mn which is in line with the excessive absorption of this latter element, when other elements do not provide a counter antagonism. According to this concept Mg is antagonized by all three of the other elements. Its absorption must be controlled and is possible only because of the counter antagonistic effects of the other elements on one another.

# The effect of boron on growth and on the absorption of calcium and potassium

In a previous paper (17) the writer has shown that boron is essential for normal growth of tobacco plants. In the present work these findings have been confirmed. Deficiency symptoms (arrested top growth, crinkled and brittle leaves) occurred (fig. 6) soon after the experiment was begun



FIG. 6. Boron deficiency ("high Ca").

at low-Ca and -K and high-K supplies. At a high Ca supply the symptoms did not appear until the middle of the growing period. The reason for this may be that minute traces of B (too small to detect by any known analytical method) adhered to the Ca salt used to obtain the high Ca supply. Boron content was apparently sufficient to sustain growth for a certain length of time.

IX	
TABLE	

DRY WEIGHTS AND ASH ANALYSES OF TOBACCO PLANT GROWN IN NUTRIENT SOLUTIONS WITH VARYING QUANTITIES OF POTASSIUM AND CALCIUM; AND WITH AND WITHOUT BORON

							ASH	ASH ANALYSIS		
		TRY WEIGHT	Тны	- <u>-</u>			CONCENTR.	CONCENTRATION PER GRAM	МA	
TREATMENT AND PLANT PARTS	Å	Plant	RE	RELATIVE		K		CA		MG
		В		В		В		в		В
	WITH	WITHOUT	WITH	WITHOUT	WITH	WITHOUT	WITH	WITHOUT	WITH	WITHOUT
T 7.	gm.	gm.			m. mol	m. mol	m. mol	m. mol	m. mol	m. mol
Low Ca Lower leaves	1.26	0.71			1.47	1.23	0.72	0.68	0.55	0.78
Stems Roots	0.31	0.23			0.82	0.50	0.14	0.12	0.08	0.14
Total plant		0.94	40	20	2.28	0.99	1.48	0.51	0.73	0.58
High Ca Lower leaves Madium ''	7 98	3.31			1.57	1.30	1.54 0.88	1.35	0.19 0.23	0.17
Top "' munam		1.95			1.15	1.69	0.38	16.0	0.18	0.23
Stems Roots	6.39 1.71	1.35 0.77			0.59 0.38	$1.13 \\ 0.74$	$0.14 \\ 0.13$	$0.52 \\ 0.29$	$0.02 \\ 0.20$	0.07 0.03
Total plant		7.38	368	170	13.67	9.70	7.90	7.15	1.93	1.12
Low K Lower leaves Ton ''	8.70	0.84			0.37 0.53	1.05	$1.77 \\ 0.41$	1.05	$0.44 \\ 0.19$	0.47
Stems Roots	6.65 1 97	0.20			0.26	0.38	0.24	0.42	0.13	0.23
Total plant	17.31	1.04	405	20	6.34	0.96	13.91	0.97	5.12	0.44
High K Lower leaves	00 1	1.94			2.20 9.95	2.22	1.22	1.49	0.28	96 U
,, uou		0.62			1.75	1.77	0.28	0.37	0.36	0000
Stems		0.84			1.38	1.77	0.09	0.15	0.05	0.09
Roots	0.93	0.25	000	0	1.28	0.53	0.17	0.22	0.17	0.44
Total plant		3.65	220	80	16.41	6.92	4.39	3.31	1.95	1.11

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Data from the boron experiment are found in table IX. In studying the ash analyses it is found that the presence or absence of B in the nutrient solution had a consistent effect on the absorption of the bases; in some instances, the plants without B accumulating more bases per unit of dry weight than those with B supplied. When this occurred it apparently was caused by retarded growth since normal plants were not obtained in the absence of B.

From the difference between the amounts applied and the amounts found at renewal of solutions and at the termination of the experiment, the amount of nitrate nitrogen absorbed by the plants was estimated. The absorption relationship only between treatments that showed great differences are considered. The data are given in table X. Invariably, more nitrates were

TREATMENT	NITRATE-NITROGEN		
	m. mol.		
Low Ca with B	12.8		
'' Ca without B	25.8		
High Ca with B	3.3		
"Ca without B	7.6		
Low K with B	3.9		
<b>''</b> K without B	21.4		
High K with B	4.0		
"K without B	11.0		

TABLE X

NITRATE NITROGEN ABSORBED IN MILLIMOLS PER GRAM DRY MATTER

absorbed in the absence of B. The smallest difference appears in "high Ca." This is reflected in the small differences in cation absorption of the high-Ca treatments with and without B (table IX).

# THE EFFECT OF VARYING QUANTITIES OF POTASSIUM AND CALCIUM ON THE ABSORPTION OF IRON, SODIUM, AND PHOSPHORUS

From the data in table XI it is suggested that the absorption of Fe is retarded by Ca. The approximate "Tq" for Fe is 1.0 at "low Ca," where in the cultures with larger amounts of Ca, the quotient is lowered to 0.20 or less. The accumulation of Fe in the roots in the presence of larger quantities of Ca might be due to a diminution of the pores in the cell walls which Ca is known to produce. It is possible also that insoluble Fe-compounds are formed and, therefore, not translocated away from the roots.

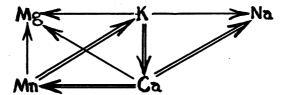
The absorption of Na was retarded more by Ca than by K. The "Tq" of Na would probably decrease rapidly with increasing supply of Ca, and increase with increasing K. It might be gathered that there is a stronger antagonism Ca: Na than K: Na.

## TABLE XI

TREATMENT	Fe	$TQ_{FE}$	NA	$\mathrm{Tq}_{\mathbf{NA}}$	Р	$TQ_{P}$
	m.mol		m.mol		m.mol	
Low Ca Stems, leaves Roots	$0.005 \\ 0.005$	1.0	0.29 0.69	0.42	$\begin{array}{c} 0.14\\ 0.46\end{array}$	0.30
Medium Ca Stems, leaves Roots	$\begin{array}{c} 0.005\\ 0.023\end{array}$	0.20	0.05 0.11	0.45	0.14 0.16	0.87
High Ca Stems, leaves Roots	0.003 0.020	0.15	trace 0.07		0.15 0.14	1.07
Low K Stems, leaves Roots	$\begin{array}{c} 0.005\\ 0.022\end{array}$	0.20	0.05 0.17	0.30	0.19 0.23	0.82
Medium K Stems, leaves Roots	$0.005 \\ 0.023$	0.20	$\begin{array}{c} 0.05\\ 0.11\end{array}$	0.45	0.14 0.16	0.87
High K Stems, leaves Roots	$0.005 \\ 0.024$	0.20	$\begin{array}{c} 0.05\\ 0.05\end{array}$	1.00	0.17 0.16	1.06

THE CONTENT OF IRON, SODIUM, AND PHOSPHORUS IN MILLIMOLS PER GRAM DRY WEIGHT OF PLANTS GROWN WITH VARYING QUANTITIES OF CALCIUM AND POTASSIUM

Adding Na to the graphic presentation of interrelated antagonisms given previously suggests the following relationship:



It is difficult to explain why the absorption of Na is dominated by Ca and K. It is possible that the greater hydrolization of Na salts plays a part. It is possible also that after Ca and K have entered the stems and leaves they may exercise their antagonistic action toward Na. It is doubtful that insoluble compounds of Na accumulate in the roots.

Phosphorus differs from the other elements discussed in that it is absorbed as an anion. The P content per unit of dry weight varies somewhat, yet its "Tq" appears to be much more significant, varying directly with Ca and to a lesser degree, with K. It appears that Ca facilitates the translocation of P. When K is present in greater abundance, it likewise aids somewhat in this function.

# Discussion

In figure 7 are given the smoothed curves of absorption of K, Ca, and Mg

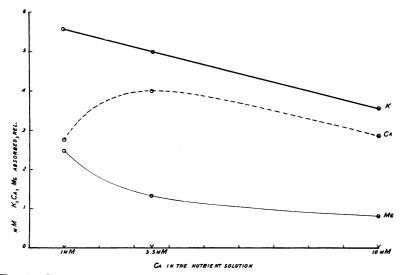


FIG. 7. Smoothed absorption curves of potassium, calcium, and magnesium with varying supply of calcium in the nutrient solution.

in the two experiments with varying Ca in the nutrient solution. With increasing Ca supply, K decreases per unit dry weight in a straight line curve. The curve for the variable Ca at first increases and later parallels the K curve. When it is recalled that total absorption of Ca parallels growth, it suggests that this element fills a function closely related to the growing processes, *e.g.*, cell division. Ca was stored in the tissues in proportion to

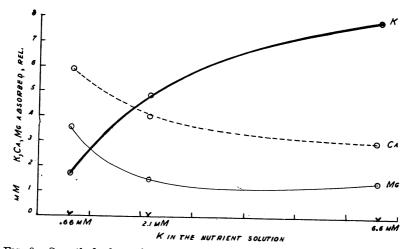


FIG. 8. Smoothed absorption curves of potassium, calcium, and magnesium with varying supply of potassium in the nutrient solution.

the tissues formed. In the absence or insufficient supply of Ca, cells at the heliotropic or geotropic growing points fail to develop.

Magnesium decreases in the plant as the Ca concentration is increased in the nutrient solution. The trend of the curve, however, seems to indicate that the greater the outer concentration of Ca, the less depressing is the effect on Mg; this is apparently a result of decreased inner concentration of Ca.

In figure 8 are shown the smoothed curves of absorption of K, Ca and Mg under varying concentrations of K in the nutrient solution. Potassium is absorbed somewhat in proportion to K present in the solution, while Ca and Mg are decreased.

Any study of base absorption and translocation in plants must consider antagonism. BURSTRÖM (2) in studying cation absorption in oats defines "antagonism" as the ability of one ion to retard the absorption of another. RUBINSTEIN (13) recognizes a "pseudo-antagonism" for cases of apparent antagonism due to difference in ion concentration. The writer believes that a true picture of antagonistic phenomena cannot be correctly estimated without considering both categories. It should also be considered what forces or conditions govern antagonism and pseudo-antagonism which must necessarily be operative in the root zone. In antagonism where the force or nature of one ion is matched with one of different character, it is evident that the permeability of the plasma membrane of the outer root cells is involved. LUNDEGÅRDH (6) has pointed out that this permeability to elements (ions) in solution stands in a direct relation to the diameter of the ions and to a certain extent to their specific mobility. Furthermore, the degree of hydrolization of inorganic ions is a factor, since they vary in their affinity to mole-This affinity increases with valence and decreases with size cules of water. of ions. Thus, K ions possess a greater mobility than Ca ions and the latter a greater mobility than Mg ions. It is concluded therefore that the cause of antagonism is due to variation in mobility and size of ions, and to a certain degree-hydrolization.

Pseudo-antagonism, evident in the end result in the same way as antagonism, operates through the force of mass action, and is not a matter of ion equivalence but of a difference in ion concentration. The operation of mass action thus produces an apparent antagonism, or more properly, a pseudoantagonism. It is clear that both these categories, due to different causes, warrant consideration in a discussion of ion absorption. The curves presented in figures 7 and 8 support the views given above.

In the present work the evidence confirms the findings of other investigators (9, 11) that Mn is essential for normal growth and development of plants. The absorption of K, Ca, and Mg in the presence and absence of Mn has been discussed under the individual experiments. It may be of interest, however, to view the relative absorptions of K and Ca, *i.e.*, in percentages of quantities supplied in the nutrient solutions with and without Mn. A graphical summary is given in figure 9.

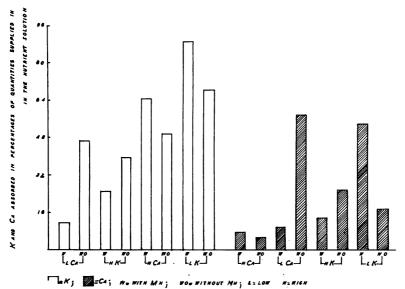


FIG. 9. Graphical summary of potassium and calcium absorption in percentages of quantities supplied in the nutrient solution, with and without addition of manganese.

The efficiency of K utilization was greater in absence of Mn at "low Ca" and "high K." The reverse is true at "high Ca" and "low K." Where Ca dominated, Mn facilitated the utilization of K, which was adversely affected when K dominated. The greatest relative utilization occurred at low-K supply in the presence of Mn.

In viewing Ca absorption, it is evident that where K is dominating ("low Ca," "high K"), utilization of Ca is improved in the absence of Mn. Where, however, Ca dominated ("high Ca," "low K") addition of Mn benefitted the utilization of Ca. The highest efficiency of Ca utilization was derived from a low-Ca supply without Mn. Therefore, it is concluded that Mn retards the absorption of Ca, when pseudo-antagonism is operative on the Ca ions.

From a practical viewpoint, Mn is of greater importance in soils where Ca dominates (a high-Ca level or a relatively low level of K) than where Ca is deficient. Applications of Ca (lime) should be guided by the actual content of active Mn in the soil (4). In Rhode Island (3) where soils are generally low in Mn, crops have shown symptoms of Mn deficiency through excessive liming.

On the other hand, in the tobacco growing district of Connecticut where soils are kept rather acid, the problem of excessive absorption of Mn is a serious one since a content of more than 0.03 per cent. Mn per unit dry weight of the leaf causes discoloration of the ash, known to the cigar trade as muddy or brick colored ash (1).

The diagram in figure 10 shows the absorption of Ca in percentages of Ca supplied in presence and absence of B. Most striking is the treatment "low K." The lowest efficiency obtained in the utilization of Ca occurred in the absence of B while the highest occurred with boron present. Here Ca was dominating as in "high Ca," where B had little effect on Ca utilization. This may mean that B produces a pseudo-antagonism to Ca. Where this is

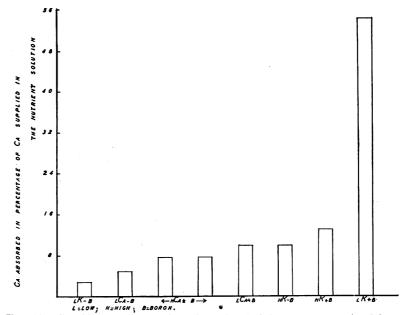


FIG. 10. Graphical summary of calcium absorbed in percentage of calcium added to the nutrient solution in the presence or absence of boron.

strong enough, addition of B does not improve the efficiency of Ca. This, however, should not be confused with the positive physiological need of B. Moreover, where Ca was physiologically deficient ("low Ca," "high K") the presence of B facilitated the utilization of Ca. It is concluded, therefore, that B aids the absorption of Ca. The practical aspect of this finding is the application of B to soils where Ca absorption needs to be improved, that is, where K, Mg, H, and  $NH_4$  (7) or other ions exert antagonism or pseudo-antagonism sufficiently to limit Ca absorption below growth requirements. In line with this are the observations of McMURTREY (10) on B deficiency symptoms of tobacco under field conditions.

There is some resemblance between Ca deficiency and B deficiency symptoms of tobacco in the injury to the terminal bud, although MCMURTREY (8)states that lack of boron affects the bases of the young leaves, while tops and margins are affected by lack of Ca. The writer has observed, however, that die-back of the mid-vein at the base also occurs on Ca deficient tobacco plants upon longer standing. WARINGTON (15) has shown that a close association exists between Ca and B in the absorption and utilization of Ca. It is likely that a close association also prevails within the plant. From the work by JOHNSTON and DORE (5) it may be inferred that the production of pectic substances may be related to the presence of B. They state that B is apparently essential to cell division, to which function the presence of Capectate is also related in the wall formation (12). Further studies are required to elucidate the definite relationship between Ca and B.

In this paper the expression "Translocation Quotient" (Tq) has been introduced. It expresses the ratio between ions present in stems and leaves (per unit dry weight) and identical ions found in the roots. It would appear that the use of a quotient or ratio might aid in any interpretation of data. The nearest approach to a "Tq" is BURSTRÖM'S (2) "total absorption per unit root weight," employed in the present work for computations involved in figures 2 and 4. While this latter calculation is useful to establish antagonism, simpler calculations shown in this paper have served a similar purpose and perhaps more convincingly. The "Tq" may be useful in studies of rate of growth where magnitude and variation in treatment are compared in order to observe cation as well as anion translocation.

#### Summary

In this paper work has been reported on absorption of bases (mainly the three cations K, Ca, Mg) studied by means of water cultures. Tobacco of a type commonly grown in the Connecticut Valley (Havana Seed) was used as a test plant. Moreover, the interrelated antagonistic effect of these ions were observed. A distinction between antagonism and pseudo-antagonism was made, and the reason for it outlined. It was shown that, while K is antagonistic to Ca, this ion under certain conditions may effect a pseudo-antagonism toward K. The same is true with Ca versus Mg.

The effect of varying quantities of K and Ca in the nutrient solution on the absorption of Fe, Na and P was also observed. Ca depresses the uptake and translocation of Fe and is antagonistic to Na. The translocation of P is aided by Ca.

The absorption of the three cations was also studied in the absence and presence of B and Mn in the nutrient solutions. In general it was found that B aids absorption and utilization of Ca.

Mn under certain conditions has a regulating influence on the absorption of Ca, while this ion *per se* is antagonistic to Mn.

A "translocation quotient" (Tq) has been suggested in this paper to be used in connection with absorption data in order to facilitate interpretation of translocation phenomena.

This work was conducted in the laboratories of Professor H. LUNDE-

GÅRDH, Centralanstalten, Stockholm, Sweden. The author is greatly indebted to Professor LUNDEGÅRDH and his associate, Dr. HANS BURSTRÖM, for use of laboratory and equipment as well as valuable suggestions pertaining to this study.

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