GROWTH RESPONSES OF TOMATO TO NUTRIENT IONS ADSORBED ON A PUMICE SUBSTRATE

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(WITH FIVE FIGURES)

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Introduction

Preliminary research with natural pumice (18, 23) has indicated that it might be a useful and inexpensive substrate in experiments on the mineral nutrition of plants. Appreciable surface activity appears to be associated with the high porosity of pumice. An experiment was undertaken to determine the availability to roots of specific elements held on different lots of pumice each of which had been immersed in a single salt solution. This investigation was designed to trace plant growth during the progressive diminution of an individual nutrient element in the substrate, the entire quantity of which was initially supplied in an adsorbed state on the pumice, in the presence of a nutrient solution containing all other essential ions in a soluble form and supplied at a uniform rate.

Methods

The pumice used in this experiment was first leached of its readily soluble components and different lots thereof then soaked in single salt solutions, each containing a different nutrient element as described below. A single lot of natural pumice (table I) consisting of pieces one inch or less in dia-

TABLE I

CHEMICAL ANALYSIS OF PUMICE*

Silica Alumina Iron oxide Titanium oxide Calcium oxide	72.90% 11.28 0.86 0.06 0.80	Soda Potash	3.64% 4.38 0.03 5.20 0.022 0.12
Magnesium oxide	0.36	Water soluble content	0.13

* Analysis furnished by Pumice Corporation of America.

meter was first leached of readily soluble material by submersion for 24 hours in a large volume of 0.04N hydrochloric acid solution containing acid in considerable excess of that required to neutralize the alkalinity of the pumice itself (21). The pumice was then washed in distilled water until no evidence of chlorine or shift in pH of the eluate could be detected. Three different sublots of this leached pumice were then immersed for 48 hours in 0.1M single salt solutions containing $CaCl_2$, $MgSO_4$ or KCl respectively. Analyses of these salt solutions containing pumice indicated considerable cation adsorption. Equilibrium in distribution of calcium, magnesium and potassium ions was attained between the salt solution and pumice during a 48-hour period of soaking. After soaking, these three sublots of pumice were again transferred to distilled water, thoroughly rinsed and then air dried.

A fourth or phosphate series was similarly prepared except that the natural pumice was initially leached in a 0.1N solution of NaOH and then soaked in an excess of 0.5N solution of H_3PO_4 . Four experimental series of 10 jars each of pumice were arranged as follows: the first containing the pumice previously soaked in CaCl₂, the second pumice soaked in MgSO₄, the third pumice soaked in KCl and the fourth pumice soaked in H₃PO₄. Uniform amounts, 3900 grams dry weight, of treated pumice were placed in three gallon glazed jars and again leached for one week in three liters of distilled water. At the end of this time the final amounts of the various ions still retained in adsorbed form on the pumice were determined (table II). Each pumice-adsorption complex constituted one experimental culture.

TABLE II

TOTAL QUANTITIES OF THE VARIOUS ELEMENTS IN MILLIEQUIVALENTS ADSORBED ON THE PUMICE PER JAR

Series	Element	QUANTITY INITIALLY ADSORBED	QUANTITY PRESENT AFTER PLANTS GROWN ON THE SUBSTRATE
		m.e.	<i>m.e.</i>
–Ca	Ca	77.85	122.82
-K	K	60.06	4.23
-Mg	Mg	47.34	2.49
-P	P	84.57	18.09

A nutrient solution (table III) containing all essential elements except one was added to each of the foregoing series. The only available source of

TABLE III

MILLIMOLAR CONCENTRATION OF SALTS IN ORIGINAL NUTRIENT SOLUTION ADDED TO VARIOUS SERIES*

		First to fourth week	3	
Control (gravel)	0.703 KNO ₃	0.522 KH,PO	0.591 MgSO4	$1.726 Ca(NO_3)_2$
-K (pumice)	0.699 NaNŎ,	0.741 NaĤ₅PÒ₄	0.591 MgSO	$1.726 \operatorname{Ca}(NO_3)_2$
-Mg (pumice)	0.703 KNO3	0.522 KH2PO	$0.598 \operatorname{Na_2SO_4}$	$1.726 \operatorname{Ca}(\mathrm{NO}_3)_2$
-Ca (pumice)	0.703 KNO ₃	$0.522 \text{ KH}_2 PO_4$	0.591 MgSO ₄	3.496 NaNO ₃
-P (pumice)	0.703 KNO ₃		0.591 MgSO4	$1.726 \operatorname{Ca}(\mathrm{NO}_{3})_{2}$
		Fifth to twelfth wee	ks	
Control (gravel)	1.406 KNO_3	$1.044 \text{ KH}_2 PO_4$	1.182 MgSO_{4}	$3.452 \text{ Ca}(\text{NO}_3)_2$
-K (pumice)	1.398 NaNŎ₃	1.482 NaH ₂ PO₄	1.182 MgSO_4	$3.452 \text{ Ca}(\text{NO}_3)_2$
-Mg (pumice)	1.406 KNO_3	$1.044 \text{ KH}_2 \text{PO}_4$	$1.196 \operatorname{Na_2SO_4}$	$3.452 Ca(NO_3)_2$
-Ca (pumice)	1.406 KNO_3	1.044 KH₂PO₄	1.182 MgSO₄	6.992 NaNO ₃
-P (pumice)	1.406 KNO_3		1.182 MgSO_{4}	$3.452 \mathrm{Ca(NO_3)_2}$

* All series received traces of microelement boron, copper, iron, manganese and zinc in nutrient solution.

this missing element was that adsorbed on the pumice. The series depending upon the pumice for their supply of the specific element are designated as -Mg, -K, -Ca and -P respectively. A fifth separate series comprising an inert quartz gravel substrate in which all essential elements were supplied in the nutrient solution in soluble form was also run and designated as the control series. The solutions were all drained weekly and immediately renewed at the ion concentrations indicated (table III). All culture solutions were brought to an initial pH of 6.4 with sodium hydroxide before addition to the jars. During growth of plants, chemical analyses for magnesium, potassium, calcium, nitrogen and phosphorus were made of the residual solutions drained from the jars at the end of each week (table IV).

TABLE IV

SOLUBLE IONS IN PARTS PER MILLION IN RESIDUAL NUTRIENT SOLUTIONS AS DRAINED FROM JARS AT WEEKLY INTERVALS DURING GROWTH OF PLANTS IN EACH SERIES

1	Weeks	1	2	3	4	5*	6	7	8	9	10	11	12
	Series		Calciun	n in res	idual n	utrient	soluti	on, p.	р. m .				
Contr	rol (gravel)		37.6	62.8	58.0	103.2	85.2	65.6	60.0	36.4	16.4	28.6	40.0
-Mg	(pumice)		70.4	88.4	54.0	97.6	74.0	15.2	12.8	6.4	5.8	0.0	6.4
-K ँ	(pumice)	138.0	100.0	80.0	62.8	60.0	72.8	0.0	12.0	5.8	0.0	10.0	22.0
–Ca	(pumice)	636.0	184.0	176.8	56.6	50.4	13.6	11.0	6.4	4.7	4.0	13.4	5.3
-P	(pumice)	40.0	27.2	22.0	18.8	40.0	80.0	17.6	19.2	27.0	9.6	12.6	32.0
		P	otassiu	m in re	sidual	nutrier	ıt solu	tion,	p.p.m.				
Cont	rol (gravel)		40.0	24.8	9.6	24.2	0.0	5.4	0.0	0.0	0.0	0.0	2.0
-Mg	(pumice)		55.6	22.8	35.8	45.2	5.0	5.0	0.0	5.0	0.0	0.0	0.0
-K °	(pumice)	500.0	320.0	169.8	102.4	68.8	25.6	2.4	Tt	0.0	2.2	0.0	0.0
-Ca	(pumice)	80.0	28.2	45.8	32.6	45.6	40.6	9.6	17.7	41.2	35.2	64.0	27.2
-P	(pumice)	12.4	7.6	7.0	6.0	9.0	5.0	0.0	0.0	3.0	0.0	0.0	0.0
		M	agnesiu	ım in r	esidual	nutrie	nt solu	tion,	p. p.m				
Cont	rol (gravel)		15.0	21.0	18.0	21.3	9.9	2.1	7.8	9.0	8.4	9.9	11.1
-Mø	(pumice)		48.0	61.5	10.2	30.0	13.5	3.0	1.2	1.5	T	Т	T
- K	(pumice)	14.2	22.8	14.4	12.0	8.1	13.8	1.5	1.2	Т	Ť	2.4	4.8
-Ca	(pumice)	15.2	22.5	19.2	14.4	15.3	2.4	1.8	1.8	2.1	3.9	12.3	1.8
-P	(pumice)	10.8	12.0	12.0	11.1	14.1	15.0	4.8	2.4	2.4	2.1	3.0	6.9
		N	litroge	n in re	sidual	nutrien	t solut	ion, r	.p.m.				
Cont	rol (gravel)		64.8	61 5	54 5	71.5	31.0	13 6	48	16	18	47	51
-Ma	(numice)		84.0	75.0	72.0	80.5	56.0	43.0	5.9	11	14	2.5	46
-K	(pumice)	83.5	89.0	72.5	66.0	77.5	59.5	37.0	3.1	13	23	42	72
-Ca	(numice)	74.0	77.5	76.0	75.0	79.0	71.5	41.5	32.2	80.0	79.0	84 0	72.0
-P	(pumice)	56.0	62.0	63.5	61.0	78.5	70.0	48.5	7.8	1.1	1.4	1.7	2.0
		Pł	osphor	us in r	esidual	nutrie	nt solu	ition,	p.p.m				
Cont	rol (gravel)		15.0	13.0	22.5	25.0	10.5	1.1	Т	1.3	т	1.4	17
-Mo	(numice)		19.0	18.8	17.5	21.8	19.5	4.3	$\hat{\mathbf{T}}$	0.0	$\hat{\mathbf{T}}$	Ť	1.4
- K	(pumice)	22.5	22.5	23.5	46.0	21.8	20.0	1.0	1.2	0.0	$\hat{\mathbf{T}}$	3.2	1.6
-Ca	(numice)	17.5	16.5	16.8	13.3	23.3	24.3	17.6	23.0	36.5	16.0	27.5	17.5
-P	(pumice)	185.3	180.2	107.1	68.0		16.0	3.0	Т	1.6	0.0	0.0	0.0

* Concentration of salts in original nutrient solution (Table III) doubled at fifth week and so maintained thereafter.

† T indicates a trace present.

Seeds of tomato, variety Pan America, were germinated in sand at a temperature of approximately 27° C. The sand was kept moist with distilled water, and an occasional application of dilute complete nutrient solution was made to prevent the appearance of deficiency symptoms. On February 9, 24 days after the seeds were sown, plants which had attained a uniform height of 45 millimeters were transferred to the jars of all series. Throughout the period of the experiment, these plants were pruned to one main axis for convenience of handling and measurement. Mean diurnal and nocturnal temperatures were maintained at 29° C and 19° C respectively. A mean relative humidity of 50% was maintained over the period of the experiment. Mean intensity of normal daylight for the months during which the plants were grown was 1250 foot-candles. On overcast days, natural daylight was supplemented with 40-watt fluorescent "daylight" lamps.

ΤА	В	\mathbf{LE}	V
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ELEMENTAL COMPOSITION OF VARIOUS PLANT PORTIONS AS PERCENTAGE OF DRY WEIGHT AND TOTAL QUANTITY IN MILLIGRAMS AT THE STEM ELONGATION STAGE

Element	Roo	TS	LEA	VES	STE	Stems		
	%	mg.	%	mg.	%	mg.		
			Control Serie	8				
Ca	1.40	0.70	4.24	14.42	3.24	2.27		
K	5.08	2.54	4.90	16.66	10.74	7.52		
Mg	0.60	0.30	0.76	2.58	0.83	0.58		
N	2.78	1.39	5.48	18.63	2.33	1.63		
Р	0.71	0.36	1.06	3.60	0.63	0.44		
			-Mg Series	1				
Ca	0.64	0.38	2.77	8.03	0.89	0.62		
ĸ	4.56	2.74	4.26	12.35	10.48	7.34		
Μø	1.00	0.60	1.28	3.71	1.13	0.79		
N	2.88	1.73	5.80	16.82	2.30	1.61		
P	0.72	0.43	1.08	3.13	0.61	0.43		
			-K Series	o ¹				
Ca	1.06	1.06	3.65	11.68	2.03	1.83		
ĸ	5.22	5.22	5.20	16.64	11.46	10.31		
Mo	0.62	0.62	0.73	2.34	0.68	0.61		
N	2.95	2.95	5.29	16.93	2.16	1.94		
P	0.93	0.93	1.05	3.36	0.74	0.67		
			-Ca Series	I				
Ca	1.53	1.38	4.15	13.28	3.02	2.42		
ĸ	3.60	3.24	4.52	14.46	10.24	8.19		
Mo	0.59	0.53	0.50	1.60	0.66	0.53		
N	2.78	2.50	5.36	17.15	2.50	2.00		
P	0.89	0.80	1.00	3.20	0.66	0.53		
			-P Series					
Ca	0.89	0.62	4.18	9.20	2.56	1.28		
ĸ	2.66	1.86	2.12	4.66	6.40	3.20		
ñø	0.66	0.46	0.71	1.56	0.78	0.39		
N	2.84	1.99	4.85	10.67	2.33	1.17		
P	2.54	1.78	1.15	2.53	0.99	0.50		
Р	2.54	1.78	1.15	2.00	0.33	0.00		

Samples for chemical analysis were taken in the late afternoon at five stages in the developmental cycle, as follows: at (1) stem elongation (table V), (2) flower bud primordia development (table VI), (3) anthesis (table VII), (4) early fruit enlargement (table VIII), and (5) the mid-fruiting

TABLE V	ΛI
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ELEMENTAL COMPOSITION OF VARIOUS PLANT PORTIONS AS PERCENTAGE OF DRY WEIGHT AND TOTAL QUANTITY IN MILLIGRAMS AT THE FLOWER BUD PRIMORDIA STAGE

LIEMENT	Roots		LEA	AVES	Stems		
	%	mg.	%	mg.	%	mg.	
			Control Serie	es			
Ca	1.47	2.94	4.14	49.68	3.24	8.10	
K	5.52	11.04	5.78	69.36	10.24	25.60	
Mg	0.69	1.38	0.77	9.24	0.87	2.18	
N	3.28	6.56	6.74	80.88	2.64	6.60	
P	0.85	1.70	1.07	12.84	0.78	1.95	
			-Mg Series	l	, e		
Ca	0.75	4.65	3.12	34.32	1.47	3.23	
ĸ	3.44	21.33	4.36	47.96	10.48	23.06	
Mø	0.87	5.39	1.25	13.75	1.09	2.40	
N	2.50	15.50	5.20	57.20	2.26	4.97	
P	0.93	5.77	1.06	11.66	0.64	1.41	
			-K Series				
Ca	1 32	4 36	3.93	40.48	2.62	5.24	
ĸ	4 70	15.51	5.80	59.74	10.54	21.08	
Ma	0.76	2.51	0.74	7.62	0.82	1.64	
N	2.46	8.12	5.15	53.05	1.95	3.90	
P	1.04	3.43	1.06	10.92	0.66	1.32	
			-Ca Series				
Ca	1 16	5.22	4.40	35.20	3.49	5.93	
Va K	2.98	13 41	4.64	37.12	9.10	15.47	
Ma	0.66	2.97	0.76	6.08	0.88	1.50	
N	2.60	11 70	6.68	53.44	2.20	3.74	
P	0.59	2.66	1.04	8.32	0.55	0.94	
			-P Series				
Co	1 57	11 78	3.77	62.21	2.76	9.11	
Ua T	2.00	15.00	2.20	36.30	5.68	18.74	
n Ma	0.62	4 65	0.74	12.21	0.92	3.04	
Mg	3.20	24 00	4,55	75.08	1.95	6.44	
P	109	8.18	1.01	16.67	0.78	2.57	
N P Ca K Mg N P Ca K Mg N P Ca K Mg N P Ca K Mg N P Ca K Mg N P	$\begin{array}{c} 0.05\\ 3.28\\ 0.85\\ \end{array}$	$\begin{array}{c} 4.65\\ 6.56\\ 1.70\\ \hline \\ 4.65\\ 21.33\\ 5.39\\ 15.50\\ 5.77\\ \hline \\ 4.36\\ 15.51\\ 2.51\\ 8.12\\ 3.43\\ \hline \\ 5.22\\ 13.41\\ 2.97\\ 11.70\\ 2.66\\ \hline \\ 11.78\\ 15.00\\ 4.65\\ 24.00\\ 8.18\\ \end{array}$	6.74 1.07 -Mg Series 3.12 4.36 1.25 5.20 1.06 -K Series 3.93 5.80 0.74 5.15 1.06 -Ca Series 4.40 4.64 0.76 6.68 1.04 -P Series 3.77 2.20 0.74 4.55 1.01	$\begin{array}{c} \textbf{3.24}\\ \textbf{80.88}\\ \textbf{12.84}\\ \textbf{34.32}\\ \textbf{47.96}\\ \textbf{13.75}\\ \textbf{57.20}\\ \textbf{11.66}\\ \textbf{40.48}\\ \textbf{59.74}\\ \textbf{7.62}\\ \textbf{53.05}\\ \textbf{10.92}\\ \textbf{35.20}\\ \textbf{37.12}\\ \textbf{6.08}\\ \textbf{53.44}\\ \textbf{8.32}\\ \textbf{62.21}\\ \textbf{36.30}\\ \textbf{12.21}\\ \textbf{75.08}\\ \textbf{16.67}\\ \textbf{16.67}\\ \end{array}$	$\begin{array}{c} 0.64\\ 2.64\\ 0.78\\ \end{array}$	$\begin{array}{c} 3.23\\ 3.23\\ 23.06\\ 2.40\\ 4.97\\ 1.41\\ 5.24\\ 21.08\\ 1.64\\ 3.90\\ 1.32\\ 5.93\\ 15.47\\ 1.50\\ 3.74\\ 0.94\\ 9.11\\ 18.74\\ 3.04\\ 6.44\\ 2.57\\ \end{array}$	

stage (table IX). At the first sampling the plants were in a period of rapid vegetative growth while at the second sampling flower buds had become visible to the eye. The flowering (anthesis) samples were taken after several flowers at the lowest inflorescence had reached anthesis, early fruit enlargement samples when the ovaries of these flowers had begun to enlarge and the mid-fruiting samples when fruits of the first inflorescence were fully enlarged and had just turned red.

At each sampling, plants were divided into roots, stems and leaves including petioles. In the final harvest, fruits were also sampled separately. Percentage dry weight of these portions was determined in a Brabender Moisture Tester at a temperature of 100° C. Leaf areas were determined at each sampling by tracing the leaf outlines on paper and computing areas with a planimeter. Plant material for chemical analysis was killed at a temperature of 100° C, dried rapidly at 80° C in a forced draft oven and ground to 40 mesh in a Wiley mill. Chemical analyses for magnesium, po-

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ELEMENTAL COMPOSITION OF VARIOUS PLANT PORTIONS AS PERCENTAGE OF DRY WEIGHT AND TOTAL QUANTITY IN MILLIGRAMS AT THE FLOWERING STAGE (ANTHESIS)

Element	R	DOTS	Le	AVES	S	TEMS	
	%	mg.	%	mg.	%	mg.	
			Control Ser	ries			
Ca	1.69	74.36	3.43	459.62	1.65	59.40	
K	2.12	93.28	3.28	439.52	3.76	135.36	
Mg	0.50	22.00	0.53	71.02	0.45	16.20	
N	3.56	156.64	5.73	767.82	3.55	127.80	
Р	0.98	43.12	0.63	84.42	0.59	21.24	
			-Mg Serie	8			
Ca	0.89	54.29	3,49	471.15	2.12	72.08	
ĸ	2.20	134.20	4.26	575.10	5.20	176.80	
Mg	0.47	28.67	0.49	66.15	0.50	17.00	
N	3.24	197.64	6.30	850.50	3.83	130.22	
P	0.81	49.41	1.03	139.05	0.78	26.52	
			-K Serie	8			
Ca	0.97	83.42	3.87	634.68	2.21	101.66	
ĸ	1.42	122.12	2.98	488.72	5.01	230.46	
Mø	0.47	40.42	0.44	72.16	0.41	18.86	
N	1.88	161.68	4.19	687.16	2.36	108.56	
P	0.55	47.30	0.96	157.44	0.64	29.44	
			Ca Serie	s			
Ca	0.46	15.18	3.05	341.40	1.48	74.00	
ĸ	2.68	84.44	3.20	358.40	3.60	180.00	
Mo	0.47	15.51	0.57	63.84	0.55	27.50	
N	4.44	146.52	5.58	624.96	4.19	209.50	
P	0.81	26.73	0.93	104.16	0.84	42.00	
			-P Series	8			
Ca	1.19	86.87	4.37	638.02	2.65	87.45	
ж Ж	1 60	91.98	2.42	353.32	2.88	95.04	
Mo	0.66	48.18	0.59	86.14	0.59	19.47	
N	5.08	370.84	6.60	96.36	4.55	150.15	
P	0.78	56.94	0.91	132.86	0.69	22.77	
Ca K Mg N P	$1.19\\1.60\\0.66\\5.08\\0.78$	86.87 91.98 48.18 370.84 56.94	-P Serie: 4.37 2.42 0.59 6.60 0.91	s 638.02 353.32 86.14 96.36 132.86	$2.65 \\ 2.88 \\ 0.59 \\ 4.55 \\ 0.69$	$\begin{array}{c} 87.45\\ 95.04\\ 19.47\\ 150.15\\ 22.77\end{array}$	

tassium, calcium and phosphorus were made by modification of the methods of WOLF and ICHISAKA (27) and for nitrogen by modification of the method of KOCH and MCMEEKIN (13).

Data and discussion

NUTRIENT SOLUTION RESIDUES

Transplanted seedlings immediately began rapid growth. There soon were definite indications from the analyses of the jar residues (table IV)

that ions previously adsorbed on the pumice had been released to the nutrient solution (11, 12). This was particularly evident in the -K, -Ca and -P series in which large quantities of the adsorbed ions were found in the first solution residues. The uniformly healthy appearance of the plants confirmed this observation as none of them developed nutrient deficiencies during the first several weeks of growth. During the first six weeks it also

TABLE VIII

ELEMENTAL COMPOSITION OF VARIOUS PLANT PORTIONS AS PERCENTAGE OF DRY WEIGHT AND TOTAL QUANTITY IN GRAMS AT THE EARLY FRUIT ENLARGEMENT STAGE

ELEMENT	Roots		Lea	VES	Stems		
	%	gm.	%	gm.	%	gm.	
			Control Series				
Ca	1.91	0.149	3.12	1.030	1 69	0 198	
K	2.20	0.172	2.53	0.832	2.20	0.257	
Mg	0.71	0.154	0.53	0.175	0.34	0.040	
N	2.21	0.172	2.13	0.703	1.29	0.151	
Р	1.08	0.084	0.59	0.195	0.55	0.064	
			-Mg Series				
Ca	1.06	0.144	3.30	1.109	1.47	0.162	
К	1.62	0.220	3.28	1.102	2.92	0.321	
Mg	0.36	0.049	0.53	0.178	0.42	0.046	
N	1.86	0.253	2.25	0.756	1.78	0.196	
Ρ	0.56	0.076	0.78	0.262	0.59	0.065	
			-K Series				
Ca	0.93	0.099	3.93	1.152	1.89	0.178	
K	0.94	0.100	2.10	0.615	1.94	0.182	
Mg	0.63	0.068	0.66	0.193	0.56	0.053	
N	2.46	0.261	2.68	0.785	1.50	0.141	
Р	0.61	0.065	0.61	0.179	0.50	0.047	
			-Ca Series				
Ca	0.35	0.026	2.40	0.538	0.57	0.051	
K	3.52	0.264	3.36	0.753	2.20	0.196	
Mg	0.49	0.037	0.76	0.170	0.55	0.049	
N	3.08	0.231	3.25	0.728	2.48	0.221	
Р	1.08	0.081	0.85	0.190	0.72	0.064	
			-P Series				
Ca	0.63	0.081	3.62	1.104	1.43	0.109	
K	1.24	0.159	2.20	0.671	1.82	0.138	
Mg	0.77	0.099	0.77	0.235	0.49	0.037	
N	2.51	0.321	2.68	0.817	2.25	0.171	
Р	0.36	0.046	. 0.37	0.113	0.42	0.032	

was noted that solution residues from all pumice series had a lower pH than that of the original solution. Stout working with hemp observed a similar pH shift in the jar residues (23). This response was in contrast to the controls in gravel which exhibited a rise in pH (fig. 1). Correlated with the rise in pH after the sixth week was extreme diminution in the amount of the various elements originally adsorbed on the pumice which were recovered in the nutrient solution residues (table IV). A large fraction of the calcium found in the first week's residues of most of the pumice series was undoubtedly due to the soluble calcium derived from the pumice itself. This was indicated not only by leaching data, but also indirectly by the fact that at the end of the second week the concentration of calcium in these residues for most of the series had dropped by 50%. An additional fact pointing in this direction was that in some series, particu-

TABLE IX

ELEMENTAL COMPOSITION OF VARIOUS PLANT PORTIONS AS PERCENTAGE OF DRY WEIGHT AND TOTAL COMPOSITION IN GRAMS AT THE MID-FRUITING STAGE

Element	Ro	OTS	LE	AVES	ST	EMS	FR	UIT
	%	gm.	%	gm.	%	gm.	%	gm.
			Co	ntrol Seri	es			
Ca	2.77	0.255	4.15	1.926	1.76	0.308	0.40	0.167
ĸ	1.38	0.127	1.82	0.845	1.30	0.228	4.00	1.672
Mg	0.48	0.044	0.62	0.288	0.40	0.070	0.08	0.033
N	1.88	0.173	1.71	0.793	0.96	0.168	2.68	1.120
Р	1.18	0.109	0.46	0.218	0.43	0.075	0.74	0.309
			_	Mg Series	1			
Ca	2.36	0.236	3.82	1.627	2.03	0.371	0.43	0.186
ĸ	0.90	0.090	2.12	0.903	1.14	0.208	4.18	1.810
Mg	0.07	0.007	0.42	0.179	0.26	0.048	0.10	0.043
N	1.65	0.165	1.88	0.801	0.83	0.152	1.85	0.801
Р	0.78	0.078	0.59	0.251	0.47	0.086	0.71	0.307
				-K Series				
Ca	1.88	0.328	4.41	3.136	1.66	0.305	0.35	0.142
ĸ	1.90	0.157	0.98	0.697	0.74	0.136	2.30	0.934
Mg	0.44	0.077	0.75	0.533	0.40	0.073	0.05	0.020
N	2.05	0.357	2.05	1.458	1.15	0.211	1.78	0.723
Р	0.59	0.103	0.51	0.363	0.38	0.070	0.48	0.195
			-	-Ca Series				
Ca	0.71	0.105	1.77	0.660	0.60	0.100	0.38	0.078
а Я	1 34	0.199	2.18	0.813	0.88	0.147	3.12	0.644
Ma	0.23	0.034	0.86	0.321	0.52	0.087	0.11	0.023
N	2.50	0.371	3.01	1.123	2.01	0.335	1.88	0.388
P	0.62	0.092	0.91	0.339	0.72	0.120	0.67	0.138
				-P Series				
Ca	1 40	0 192	4.07	1.679	1.30	0.266	0.28	0.077
Ua K	0.72	0.099	1.20	0.495	0.76	0.155	2.02	0.553
Ma	0.12	0.079	0.58	0.239	0.29	0.059	0.05	0.014
N	1 99	0.273	2.50	1.031	1.19	0.243	1.99	0.544
P	0.31	0.043	0.31	0.128	0.28	0.057	0.45	0.123
T	0.01		_					

larly -K, the quantity of calcium in the jar residues during the first four weeks was double that added in the original solution as shown by comparisons between tables III and IV. In comparing data on the composition of the nutrient solutions and that of plant tissue at the stem elongation phase (tables IV and V), it is interesting to note that high concentrations of potassium in the substrate are correlated with low calcium content in the tissues. This phenomenon of diminution in absorption of one element in the presence of an abundance of another (antagonism) has been observed by numerous workers (5, 8, 9, 15).

The amount of soluble calcium in the substrate is extremely variable, as shown by analyses for this ion in the -Ca series in which the original nutrient solution was lacking in calcium (table III). The total quantity of calcium present in the substrate at the end of the growing period was greater than the quantity determined as initially present (table II). Since analyses made before and after plant growth were determined for different samples of pumice, the variable leachability of calcium from the natural



FIG. 1. Shifts in pH of the nutrient solutions. Determinations made with a LaMotte Roulette Comparator.

pumice became distinctly evident. After the seventh week, the quantity of originally adsorbed elements found in the nutrient solution was very limited, indicating almost complete cessation of release of these ions by the pumice to the nutrient solution.

During the flower bud initiation phase, larger quantities of nitrogen and phosphorus were found in the residues than were contained in the nutrient solution supply of the current week, suggesting some elimination of these elements from the plants (tables III and IV). Other investigators have also reported the apparent loss of ions by the plants to the soil solution during this developmental phase (7, 10, 14, 19).

GROSS MORPHOLOGY

STEMS.—Until the 12th week of plant growth, the stem height of the -Mg and -K plants exceeded the controls (table X). During the 12th week

MCILRATH: PUMICE SUBSTRATE

	SERIES	VAES DAES OL DES DABER OL
T WEEKLY INTERVALS	-H	ЕМ НЕ ІӨНТ С М.
	CA SERIES	VAES C.V.BEF OL DES C.V.BEF OL
L SERIES A	I	тем неіднт Сем.
TEM HEIGHT, NUMBER OF NODES AND LEAVES FOR EXPERIMENTAL	-K SERIES	NAES
		ODES Amber Of
		тем неіент См.
	S	NAES CIMBEE OL
	-MG SERIF	ODES Ambey Ol
		гем неієнт См.
	RIES	EVAES AMBER OL
MEAN S'	TROL SE	о ле я "О м век оь
	- S	A CM [.]

TABLE X

SERIES	LEAVES NUMBER OF	v.		œ) =	13	15	17	10	21	23	24
	NODES Nowber of		• •	- 6	,1	12	18	21	24	28	31	33
A SERIES -P	ЗТЕМ НЕІЄНТ ІN СМ.	82	10.3	12.5	20.1	28.3	36.5	47.2	57.4	69.0	80.3	89.3
	LEAVES NUMBER OF	9	-	. 6	12	14	16	17	20	21	21	22
	NUMBER OF	ۍ ا	œ	10	13	16	19	22	25	29	32	33
SERIES –C	Sten неіднт Втем неіднт ім см.	7.2	11.5	15.3	24.9	35.8	44.2	52.0	58.0	69.5	77.3	83.5
	геулез Иллев об	5	7	10	12	15	17	19	22	23	23	23
	NODES Nodes of	4	×	11	14	18	20	23	28	29	29	30
F SERIES -K	Зтем неіент іи см.	7.0	13.6	18.4	28.4	40.8	51.6	62.4	73.8	78.8	83.0	86.3
	LEAVES NUMBER OF	5	7	6	12	14	16	18	21	22	23	23
	NODES N AMBEK OL	4	2	10	13	17	20	24	27	29	32	34
-W	Зтем неіент іи см.	7.7	12.4	16.6	26.3	37.9	48.2	56.6	67.3	75.5	82.3	90.0
CONTROL SERIES	UUMBER OF	9	œ	10	13	15	16	18	21	22	23	25
	NODES Nodes of	4	6	11	14	18	20	24	26	29	31	33
	ЗТЕМ НЕІЄНТ ІN СМ.	7.0	12.7	16.8	26.9	37.2	47.5	57.2	69.0	75.3	81.0	87.3
,	WEEKS	5	ო	4	£	9	7	×	6	10	11	12

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the rate of stem elongation of the -K series showed a considerable decline. Correlated with this reduction in rate of stem elongation was a diminished quantity of potassium in the stem (table IX). The stem elongation rate of the -Ca series of plants was slightly less than that of the controls throughout the growth period. In the -P series the stem elongation rate was below that of the controls in early developmental stages but finally surpassed the controls during the 12th week.

Control, -Mg, -K, -Ca and -P series of plants all maintained about the same rate of node initiation (table X). The mean internodal length in -K and -P series was slightly greater than the control at the 12th week, though not significantly so. The -Ca series exhibited a slightly shorter internodal length.

LEAVES.—Taking into account the number of leaves that abscised, the total number of leaves initiated in all series was about the same (table X). The leaf area of the control plants exceeded that of all plants of the pumice series at the first sampling (elongation), but by the flower bud primordial stage the leaf area of the plants of the –Mg series was in excess of the controls (fig. 2). At the final fruit phase the leaf area of the –Mg series far exceeded that of the control plants. Leaf areas of the –K and –P series were slightly less than that of controls.

FLOWERS.—There was no significant difference in the number of flowers in comparable inflorescences of the various series. Flower abscission in the -Mg and -Ca series, however, was 9% greater than in the control, while in the -K series of plants it was about 1% greater. The -P series had 1% less flower abscission than the control.

DEFICIENCY SYMPTOMS.-In the seventh week some of the plants of the -Ca series began to show such signs of typical calcium deficiency as retarded vegetative growth and yellowing of the leaves of the upper part of the plant (1). By the ninth week these symptoms had become very severe in some of the plants of the -Ca series but were not evident in others of the same series. This fact points to the irregular availability to plants of the calcium from pumice. Other investigators have noted a similar irregular release of calcium from synthetic ion-exchange resins employed in mineral nutrition ex-On the basis of improved plant growth and composition, a reperiments. duction in the pH of the substrate evidently improved uptake of calcium. Thus plants were apparently taking up little or no calcium from the substrate at pH 7.0, as shown by deficiency symptoms and low calcium content of tissues. Upon reduction of hydrion concentration of the nutrient solution to pH 4.5 by addition of small amounts of acid, however, some of the plants previously manifesting deficiency symptoms showed indications of early recovery. New leaves were produced, but often they were abnormally thick and showed a tendency to curl downward at the margins. Some plants did not respond favorably to acidification of the nutrient solution. Analyses indicated that this pH shift caused greater leaching of calcium from pumice in some of the jars than in others. Reasons for this irregular

response were not clear. The appearance of blossom-end rot in the -Ca series during the tenth week may also be regarded as an indication of calcium deficiency (16, 22, 26).

ROOTS.—As a general rule roots of plants grown on pumice were larger and more uniformly distributed throughout the substrate. The roots of the control plants in gravel were comparatively short and more abundant at the upper levels of the substrate. The roots of the plants of the –Ca series developed several thick laterals and displayed extensive browning with some decay, typical symptoms of calcium deficiency (1).



FIG. 2. Mean leaf areas of plants of the various experimental series.

FRESH AND DRY WEIGHTS.—Analyses based on fresh and dry weights of the various parts of plants indicated that the weights of roots of plants grown on pumice were consistently higher than for the controls in gravel (table XI). The weights of the shoots of all pumice series, with the exception of -Ca, were quite comparable to the controls. The shoots of the -Ca series of plants were consistently lower in weight. In all cases the top-root ratios of the plants grown on pumice were lower than the controls, because of the more extensive root systems of the pumice-grown plants (table XI). TABLE XI

FRESH AND DRY WEIGHT IN GRAMS, PERCENTAGE DRY WEIGHT AND TOP-ROOT RATIO AT VARIOUS DEVELOPMENTAL STAGES OF THE EXPERIMENTAL SERIES

5	оітаЯ Я\Т	11.49	10.42	7.47	5.02	6.49		
MID-FRUITING	.тw тяЦ %	$\begin{array}{c} 9.1\\ 14.2\\ 16.8\\ 6.2\\ 6.2\end{array}$	14.7 11.4 16.6 6.0	12.6 13.6 16.9 6.6	12.2 12.2 15.4 7.3	11.6 14.1 10.2 5.8		
	лч тя.	$\begin{array}{c} 9.2 \\ 46.4 \\ 17.5 \\ 41.8 \end{array}$	10.0 42.6 18.3 43.3	17.4 71.1 18.4 40.6	14.9 37.3 16.7 20.6	13.7 41.3 20.5 27.4		
	тw нгаяч.	$\begin{array}{c} 101.1\\ 326.7\\ 104.2\\ 672.3\end{array}$	68.0 373.6 109.9 721.8	138.3 530.8 108.5 615.2	$\begin{array}{c} 121.7\\ 305.8\\ 108.1\\ 282.8\end{array}$	$118.3 \\ 292.5 \\ 101.2 \\ 471.8 $		
EARLY FRUIT ENLARGEMENT	оітаЯ Я\Т	5.73	3.28	3.65	4.17	2.98		
	.тw тяС %	8.8 12.5 13.4	11.2 11.8 13.4	11.0 12.1 12.0	10.6 11.9 14.5	12.6 13.2 12.2		
	.тw тяП	7.8 33.0 11.7	13.6 33.6 11.0	10.6 29.3 9.4	7.5 22.4 8.9	12.8 30.5 7.6		
	.тw нгаяч	89.2 263.7 87.2	121.3 258.0 81.8	96.1 242.4 78.4	70.6 188.0 61.3	101.2 230.7 62.7		
FLOWERING	отая я\т	3.86	2.77	2.44	2.90	2.45		
	.тw тяЦ %	10.6 10.8 10.0	11.4 10.5 8.2	10.7 10.2 9.6	9.9 9.8 9.2	10.6 9.8 9.2		
	.тw тяЦ	4.4 13.4 3.6	6.1 13.5 3.4	8.6 16.4 4.6	5.0 11.2 3.3	7.3 14.6 3.3		
	тw нгэяЧ.	41.9 124.2 36.1	53.8 128.7 42.0	80.0 161.1 47.4	50.4 114.6 36.4	68.3 148.5 35.6		
FLOWER BUD PRIMORDIA	огтая я\т	7.25	2.13	3.73	2.16	2.64		
	.тw тяС %	7.6 9.0 5.2	8.4 9.0	6.7 8.5 5.0	9.7 7.9 4.6	8.8 11.9 6.4		
	.тw тяЦ	$\begin{array}{c} 0.20\\ 1.20\\ 0.25\end{array}$	0.62 1.10 0.22	0.33 1.03 0.20	0.45 0.80 0.17	0.75 1.65 0.33		
	.тw нгаяЧ	1.60 13.20 4.90	5.20 11.90 4.60	4.70 12.10 4.70	4.70 10.10 3.60	8.50 13.90 5.00		
* STEM ELONGATION	tortan N\T	8.20	6.00	4.10	4.44	3.86		
	.тw тяС %	5.9 7.5 	6.8 7.3 4.2	7.4 7.3 4.1	8.4 8.1 4.4	9.4 9.3		
	.тw тяС	0.05 0.34 0.07	0.06 0.29 0.07	0.10 0.32 0.09	0.09 0.32 0.08	0.07 0.22 0.05		
	Рі.Аит роктіс .тw нгая 1	R 0.83 L 4.58 S 1.75 F	R 0.90 L 3.68 S 1.65 F	R 1.36 L 4.37 S 2.10 F	R 1.03 L 4.00 S 1.70 F	R 0.73 L 2.40 S 0.99 F		
SERLES		Cont.	-Mg	-K	-Ca	<u>4</u>		

* R-roots, L-leaves, S-stems and F-fruit. + Based on dry weights.

Fruit produced by the first and second inflorescences of plants of the gravel control, -Mg, -K and -P series were all comparable in size. Fruits of the -Ca plants were much smaller than those of any other series (fig. 3). The mean fresh weight of fruits on plants in the gravel controls was greater than that for all pumice series except -Mg (table XI). The percentage dry



FIG. 3. Representative fruit at the mid-fruiting stage (82 days). First inflorescence bottom row, 28 day old fruit; second inflorescence center, 21 day old fruit in control, -Mg, -K and -Ca series, 14 day old fruit in -P series; third inflorescence top row, 14 day old fruit in control, -Mg and -K series, seven day old fruit in -Ca series, and four day old fruit in -P series.

weight of the fruits of the pumice series was about equal to that of the control except for the -Ca culture in which it was much higher.

TISSUE ANALYSIS

In the samples taken during the stage of rapid stem elongation it was found that the percentage of magnesium, potassium and phosphorus in the plants grown on pumice and which had been supplied these elements in the adsorbed form exceeded the corresponding values of the control series (table V). In these cases the total quantity of the elements present in the plant tissue was also greater (fig. 4). The percentage and total amount of calcium in the plants of the -Ca series was about the same as in the controls.

At the flower bud primordial stage the percentages and total quantities of magnesium and phosphorus were present in the plants of the adsorbedion series in equal or higher amounts than in the corresponding gravel controls (table VI). Although the percentage of potassium in the -K series and calcium in the -Ca series was higher in the leaves and stems, the total quantity thereof was less (fig. 4).

By the time the plants had reached the flowering stage, the only plants of the adsorbed-ion series which had a percentage of elements equal to or greater than that found in control plants were the -Mg series, the stems of -K series, and the stems and leaves of the -P series (table VII). The total quantity of ions present when compared to control were higher in the -Mg, -K and -P series (fig. 4). In the fruit enlargement phase magnesium in the -Mg series was the only element supplied in an adsorbed form which occurred in the plants in equivalent or higher percentages and higher total quantities than in the gravel controls (fig. 4, table VIII). At this stage



FIG. 4. Mineral increment of the tomato plants at various stages of development. Series grouped by elements: C, control; -Mg designates that all magnesium was originally supplied in adsorbed form on pumice in this series; same for -K, -Ca and -P respectively. Data based on tables V to IX.

the percentage of calcium present in the -Ca plants was about one-half that found in the controls and the total quantity was only about one-third. During the stage of rapid fruit enlargement, visible signs of extreme calcium deficiency were correlated with the low calcium content of tissue of the -Ca series.

In all cases in which an element had been supplied in an adsorbed form, it was found in a smaller quantity in all tissues during the fruiting stage than in the corresponding control series (table IX), indicating that the total intake of the adsorbed element was less than from a nutrient solution containing all essential elements in the soluble form (20).

Certain striking transitions were observed in the composition of plants in the course of their development within a particular series. At the elongation phase in the -K series, there was a relatively high potassium concentration in the plant with a corresponding low calcium content (4, 5, 6, 8, 15), a condition reflecting the high concentration of available potassium ions (tables IV and V). This calcium deficiency (fig. 4) was also associated with an increased intake of magnesium and phosporus (24, 25). When plants in the -K series reached the fruiting stage, however, a potassium deficiency had developed and the intake of calcium had increased appreciably (tables VIII and IX) (2, 17, 25). This late increase in calcium intake was associated with a distinct gain in nitrogen content of the plants (3). In the -Ca series it was noted that with low intake of calcium there was a higher absorption rate of magnesium (17), but not of potassium.

Conclusions

On the basis of gross habit of the plants in the various series, it was found that growth in the -Mg, -K and -P pumice series was comparable to that in the gravel controls. The metabolic efficiency of tomato plants dependent upon the treated pumice for their supply of a given element was also comparable to that of the controls in gravel because the dry weight was essentially the same in both at maturity. Evidently sufficient quantities of magnesium, potassium and phosphorus were adsorbed on the pumice to satisfy the plant requirement for growth to maturity. On the other hand, the quantity of available calcium was inadequate for normal growth. In spite of the fact that plant growth was often comparable irrespective of whether an ion was originally supplied in an adsorbed or freely soluble form, the total quantity of an ion in the plant was less when supplied as a pumice-adsorption complex (20).

During the period that ions which had originally been adsorbed on the pumice were being rendered soluble, the plants were evidently wholly dependent upon this source of a given ion. After this time, however, due to weekly drainage and replacement of solutions, very small quantities or sometimes none of the originally adsorbed ions appeared in the nutrient solution. The plants nevertheless continued to absorb these elements in substantial amounts (fig. 5). To judge from increments of these ions in the plant tissues certain amounts of them were absorbed directly from the pumice-adsorption complex. An important factor in making adsorbed elements available to plants grown in pumice might well have been their more luxuriant root systems which were in extremely intimate contact with and ramified throughout the pumice to such a marked degree as to suggest a strong tropic stimulus. One consistent difference between the gravel and pumice-grown plants was a larger and more extensive root system in the cultures containing pumice shown by the uniformly smaller top-root ratio for the plants of all pumice series.

In contrast with previous investigations (18, 23) in which complete nutrient solutions were added to a pumice substrate, there was no indication in the present experiment that a pumice substrate as treated herein greatly accelerated plant development or materially improved plant growth as compared with ordinary gravel or soil cultures.



FIG. 5. Amounts of ions originally adsorbed on pumice which occur in nutrient solution residues and in entire tomato plants at various stages of development in the pumice series. Left, -K series shows potassium content of solution residues and of entire plants. Right, comparable data for magnesium and phosphorus in the -Mg and -P series.

Summary

1. This investigation employing the Pan America variety of tomato was undertaken to determine the availability for plant growth of ions of magnesium, potassium, calcium and phosphorus which had been adsorbed on a pumice substrate. Each of these ions was adsorbed on a separate lot of pumice and all the other essential elements were supplied in a nutrient solution. Four single ion pumice-adsorption complexes were employed and the series designated as -Mg, -K, -Ca and -P respectively. For comparison a control series with an inert quartz gravel substrate was also employed, to which all of the essential elements were supplied in nutrient solution.

2. Loss of appreciable amounts of previously absorbed nitrogen and phosphorus from tomato plants to the substrate was noted in all series at the flower initiation phase.

3. In the -K series, tissue content of calcium was low when the available potassium supply in the nutrient solution was high.

4. Compared with gravel, the pumice substrate as employed in this investigation did not enhance yield or accelerate maturation of tomato plants.

5. Plants in the -Ca series paralleled control plants grown in gravel in leaf and node number but plants of the -Ca series had a smaller total leaf area and were shorter than controls in stem height. Plants of the -Ca series exhibited symptoms of calcium deficiency.

6. Plants dependent upon magnesium, potassium and phosphorus adsorbed on pumice were comparable in stem height, total leaf area, number of leaves and number of nodes to those grown in gravel containing a complete nutrient solution. The total weight of fruit by plants in the -Mg and -K series produced in a 12-week growing period was comparable to gravel controls but slightly less than controls in the -P series.

7. Root systems of the plants grown in pumice substrates were much larger than those in the gravel controls. Roots of the pumice-grown plants ramified throughout the individual lumps of pumice and were in intimate contact with the pumice substrate as if responding to a strong tropic stimulus.

8. The total quantity of an element absorbed by the plants from a pumice-adsorption complex, treated as described, was less than when the ion was supplied in nutrient solution but plant growth was essentially comparable.

9. Pumice treated as described supplied sufficient amounts of available magnesium, potassium and phosphorus for normal growth but not enough of calcium. Calcium evidently is not held firmly by pumice, as indicated by the early leaching thereof into the nutrient solution. Pumice compares favorably with other artificial substrate used in nutritional studies. It is cheaper than most solid substrates, a fact which may permit use of pumice in large scale experimental and commercial operations.

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