THE INFLUENCE OF BORON ON THE CHEMICAL COMPOSITION AND GROWTH OF THE TOMATO PLANT

EARL S. JOHNSTON AND W. H. DORE

(WITH NINE FIGURES)

Introduction

An investigation was undertaken by one of the writers for the purpose of determining the minimum potassium requirements of the tomato plant. It was planned to use water cultures in these studies. Although the solutions contained the so-called essential elements for normal plant growth it was soon discovered that the plants failed to grow. Since attention had been recently called to the importance of boron and manganese it was thought that a possible solution to the problem lay in adding these elements to the culture medium and a special experiment was conducted to test their effects on the growth of the tomato. Manganese (1.0 ppm.) was added to the nutrient solution as manganese sulphate and boron (0.55 ppm.) as boric acid. The four groups noted in table I consisted of nine cultures, each containing a single plant in a two-quart Mason jar.

TABLE I

DATA SHOWING AVERAGE HEIGHT AND DRY WEIGHT OF TOMATO PLANTS GROWN IN BORON DEFICIENT SOLUTIONS AND IN SOLUTIONS WITH 0.55 PPM. BORON AND WITH 1.0 PPM. MANGANESE

GROUP	SOLUTION	HEIGHT	DRY WEIGHT		
			TOPS	ROOTS	TOTAL
		cm.	*gm.*	*gm.*	*gm.*
A	No B and Mn	24.4	3.0	0.3	3.3
B	B and Mn added	55.2	6.4	1.5	7.9
C	Mn added	24.3	3.0	0.3	3.3
D	B added	55.2	5.4	1.2	6.6

An inspection of this table at once shows that the plants of cultures containing boron are far more normal than the others. It cannot, however, be concluded that manganese is not essential. Although chemicals of a good grade were used in these experiments there is no assurance that they were completely free from manganese and boron. Nevertheless, the experiment does show that the tomato plant requires an appreciable amount of boron over and above that present as impurities in the solutions used. Figure 1 shows very clearly the differences in growth of two representative

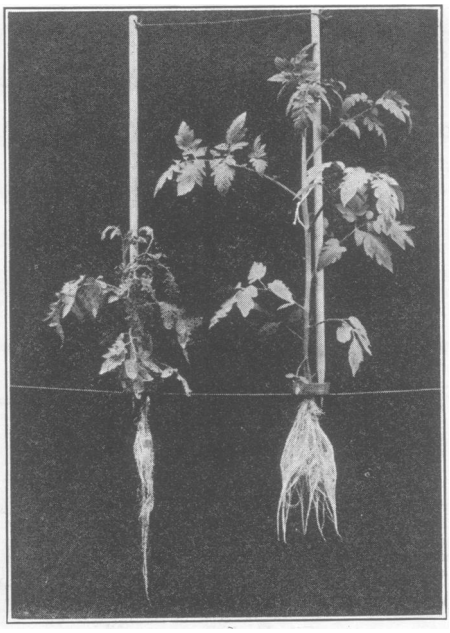

FIG. 1. Photograph showing boron deficient tomato plant (left) and one grown in a similar solution to which 0.55 ppm. boron as boric acid had been added (right).

plants of this experiment, one (left) from a culture deficient in boron, the other (right) from a similar solution to which boron (0.55 ppm.) as boric acid had been added.

The growth responses of the tomato to boron were so marked and interesting that a more detailed study was undertaken. The necessity of boron to the growth of other plants has been pointed out by other investigators within the last few years. The earlier workers with boron concerned themselves with detecting its presence in various plants. The amounts found as boric acid varied considerably, sometimes running as high as one per cent. or slightly above. The presence of boron *per se* in the plant is, however, no indication that it is essential for growth. The natural supposition would be that its presence is a detriment rather than an asset, since very small amounts are known to be exceedingly toxic. For reviews of the literature and descriptions of experiments indicating the necessity of boron for normal plant growth and development the reader is referred to BRENCHLEY (**2**), BRENCHLEY and WARINGTON (**3**), SOMMER and LIPMAN (**14**), SWANBACK (**15**), and WARINGTON (**16**). In a preliminary paper JOHNSTON and DORE (**8**) called attention to the necessity of boron for growth of the tomato plant.

Experimentation

The experiments described in this paper were carried out in the Division of Plant Nutrition at the University of California and in the Department of Plant Physiology at the University of Maryland. The variety of tomato used at California was the Santa Clara Canner, and at Maryland this same variety and Marglobe were used. The seeds were germinated between layers of moist filter-paper. When the roots were 2 to 10 mm. long the young plants were transferred to a germination net similar to that described by JOHNSTON (7). After the seedlings had reached approximately 2 to 3 cm. in length they were transferred to the culture solutions. Each culture consisted of a single plant supported by means of a little cotton in a paraffined flat cork stopper which fitted into a two-quart Mason jar containing the nutrient solution. The jars were wrapped with heavy paper to exclude most of the light from the roots.

The general nutrient solutions used in the California experiments were made up from the following salts: calcium nitrate, magnesium sulphate, magnesium phosphate (primary and secondary), potassium sulphate, manganese sulphate and ferric tartrate. The approximate calculated concentrations of the usual ions in this general nutrient solution expressed as parts per million and milliequivalents were:

	ppm.	milliequivalents		ppm.	milliequivalents
Ca	200	10.0	NO_3	620	10.0
Mg	60	4.9	SO_4	290	6.0
K	78	2.0	PO_4	74	2.3
Fe (enough to keep plants green)			Mn	1	0.0364

In the Maryland experiments the general nutrient solution was made up from salts specially prepared by J. T. Baker Chemical Co. for the Committee on Salt Requirements of the National Research Council, the manganese sulphate and ferric tartrate were of equally high grade but obtained from other sources. The Maryland solutions of slightly different composition had the following partial volume molecular concentrations:

$Ca(NO_3)_2$	0.005
$MgSO_4$	0.002
KH_2PO_4	0.002
$MnSO_4$	0.0000178

To these general nutrient solutions ferric tartrate (0.5 per cent. solution) was added at the rate of a cubic centimeter per liter per day while the plants were young. After the roots were well developed iron was added less frequently. Boron was added as boric acid to the cultures so designated. Expressed as parts per million and milli-equivalents the ions of the

basic solution used in the Maryland experiments had the following approximate values:

	ppm.	milliequivalents		ppm.	milliequivalents
Ca	200	10.0	NO_3	620	10.0
Mg	49	4.0	SO_4	194	4.0
K	78	2.0	PO_4	190	6.0
Fe (enough to keep plants green)			Mn	1	0.0364

A second preliminary experiment was conducted to determine an approximate range of tolerance of the tomato plant toward boron. Four sets of cultures were set up on October 29, 1926. Each set consisted of 10 two-quart culture jars with a single plant per jar. To the general nutrient solutions boron was added at the following rates:

Group A	0.000 ppm.
Group B	0.055 ppm.
Group C	0.550 ppm.
Group D	5.500 ppm.

The plants were harvested on December 10. The average length of stem and dry weight per plant as well as the approximate total transpiration are given in table II.

TABLE II

DATA SHOWING AVERAGE HEIGHT AND DRY WEIGHT OF TOMATO PLANTS, TOGETHER WITH THEIR APPROXIMATE TOTAL TRANSPIRATION WHEN GROWN IN SOLUTIONS CONTAINING DIFFERENT AMOUNTS OF BORON

Group	Boron	Stem height	Dry weight			Transpiration
			Tops	Roots	Total	
	ppm.	*cm.*	*gm.*	*gm.*	*gm.*	*cc.*
A	0.000	35.1	2.66	0.22	2.88	952
B	0.055	53.4	3.69	0.62	4.31	1584
C	0.550	54.3	3.63	0.63	4.26	1562
D	5.500	45.8	2.75	0.40	3.15	1152

Weekly measurements of stem height were made, but only the final average for each group is included in the table. While making the height measurements on December 2 it was observed that the stems and petioles of the plants in group *A* were exceedingly brittle. In later experiments it was found that this brittleness was characteristic of tomato plants grown in boron deficient solutions. In fact, the brittleness usually occurred before any visible manifestation of boron deficiency appeared. The brittleness of stems and petioles associated with boron deficiency is best described as similar to the breaking of a piece of cheese and not that characteristic of

turgid tissues, which usually break with a snap. The data in table II bring out quite clearly an approximate range of boron concentration, below and above which growth is inhibited. Plants of group A, to which no boron was added, showed a decided retardation of growth and distinct injuries. Another marked symptom of boron deficiency is the dying of the growing point of the stem. In a short time this tissue becomes blackened and dried, thus terminating stem elongation. The stem height measurements of table II bring this out as well as figure 1. Plants of group D, to which 5.5 ppm. of boron were added likewise showed a retardation of growth. These plants also showed distinct injury which, however, was unlike that occurring in the boron deficient plants. With this amount of boron the leaves died at the margins. A representative leaf from a plant of this group together with a leaf from a healthy plant is shown in figure 2. No marked differ-

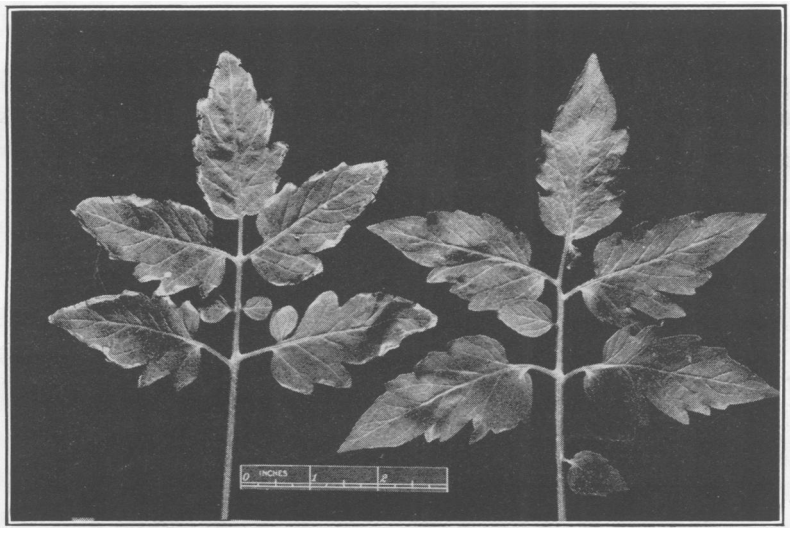

FIG. 2. Photograph showing boron injury to the leaf of a tomato plant (left) when grown in a nutrient solution containing 5.5 ppm. boron as boric acid. Normal leaf (right) does not show the dried and dead margins.

ences in growth were noted between the plants of groups B and C so that it might be concluded tentatively that boron in these particular culture solutions was equally good for growth of the tomato plant at concentrations of 0.055 and 0.55 ppm. It must be remembered that while 0.055 ppm. of boron may be sufficient for normal growth under one set of conditions it may be insufficient under others.

Immediately following the second experiment an investigation was started with the object of determining the chemical differences between

normal tomato plants and those grown in boron deficient media. Tomato seeds (Santa Clara Canner) were germinated in a manner already described and on December 15, 1926, the seedlings were set out in the culture jars. Two sets of cultures were used in this experiment, one, group A, without boron, except for traces that might have been present as impurities in the culture solutions, and another, group B, to which boron (0.55 ppm.) was added as boric acid. This experiment, as well as the two preliminary ones, was carried out at Berkeley, California. Each group contained 40 plants, four of which were used in preliminary microscopical tests; the remaining 36 plants of each group were harvested on February 7, 1927. The nutrient solutions were not renewed during the entire growing period. In these experiments the amount of mineral elements contained in the solutions was sufficient for good vegetative growth over the periods studied. During certain seasons in other experiments when transpiration rates were higher it was necessary to add distilled water to replace that lost, but this was not necessary in the present case.

Because of the changes in the various constituents (particularly in the amount and kind of carbohydrates) that are taking place in plant tissues during the day, special care was exercised in harvesting the plants in order that the two groups might be as comparable as possible. Six plants from each group were alternately harvested. Considerable time was consumed in this operation and without a doubt plants harvested in the morning differed considerably from those harvested in late afternoon. For this reason it seems advisable to include a table showing the time of day as well as the character of the sky when each set of six plants from the two groups was harvested. These data are presented in table III.

TABLE III

DATA SHOWING ORDER AND CONDITIONS OF HARVESTING TOMATO PLANTS

GROUP	CULTURE NUMBERS	TIME OF HARVEST		CHARACTER OF SKY
		BEGINNING	ENDING	
A and B	1– 6	9:53 a.m.	10:37 a.m.	Bright and dull
A and B	7–12	11:42 "	12:18 p.m.	Bright
A and B	13–18	2:22 p.m.	2:51 "	Bright
A and B	19–24	3:50 "	4:20 "	Bright
A and B	25–30	5:14 "	5:36 "	Clear sunset
A and B	31–36	7:30 "	7:54 "	Dark

Plants (7 to 30) of group B, which were harvested during the warmest and brightest part of the day, were in a wilted condition. The other plants

of group B were turgid when harvested. None of the plants in group A (those deficient in boron) were severely wilted at any time of the day. Plants numbered 10 and 27 in group A, and 3 and 14 in group B differed somewhat in their forms of growth from the other plants. Such variations are to be expected with a variety like the Santa Clara Canner which is highly heterogenous as noted by LESLEY and ROSA (9). Despite these variations in growth, injuries were apparent in all of the boron deficient plants.

Analytical methods

PRELIMINARY PREPARATIONS

Preparation of samples.—The harvesting operations consisted of dissecting the plants into leaves, stems and roots. An attempt was made to pull the expanded leaf tissue from the mid-rib. The petiole and often a small portion of the mid-rib were thus included with the stem tissue. The roots were severed in a plane just above the position where they branched out freely from the base of the stem. Without removing the plants from their culture jars the leaves were severed, weighed and dropped into boiling 95 per cent. alcohol. The stems were then cut from the roots and treated similarly, and finally the roots received the same treatment. The boiling process was continued for approximately 15 minutes after the plant tissues had been introduced. The flasks containing the plants and alcohol were then stoppered with paraffined cork stoppers. On cooling, the softened paraffin hardened, automatically sealing the flasks. The material was thus effectively preserved for analysis.

Separation of the sample into alcohol-soluble and alcohol-insoluble matter.—The contents of each flask were filtered and each filtrate was collected in a 1-liter graduated flask. The undissolved portion was placed in Soxhlet extraction tubes and extracted with 85 per cent. alcohol until colorless. The green solution resulting from the extraction was concentrated and added to the original filtrate. The combined alcoholic solution was then made up to volume.

Determination of the alcohol-insoluble dry matter.—The colorless insoluble residue was placed in tared weighing bottles, dried in an oven at 100° C. and weighed. The difference in weight was recorded as *alcohol-insoluble matter.* The material so obtained was used for the determination of *starch, hemicelluloses, galacturonic acid, lignin-suberin* and *cellulose.*

Determination of alcohol-soluble dry matter.—A 25-cc. aliquot portion was taken from each of the liter flasks and total solids were determined by weighing after exaporating in a tared porcelain dish and drying in an oven at 100° C. From the weight of solids thus obtained, the weight of *alcohol-soluble dry matter* in the liter of solution was calculated by multiplying by 40.

Determination of total dry matter.—The value representing the total dry matter was obtained by adding together the values of the *alcohol-soluble* and *alcohol-insoluble dry matter.* Water was determined by subtracting this sum from the corresponding green weight of the tissue.

Analysis of the alcohol-soluble portion

Preparation for the determination of sugars.—100-cc. portions of the alcoholic solutions were placed in Erlenmeyer flasks and evaporated to dryness on the steam bath with the steam turned low so as to avoid undue heating of the sugars. To remove chlorophyll and other substances preparatory to determining the sugars, the dried residue was digested three times with benzene on the steam bath, the benzene solution being poured through a folded filter. The combined benzene filtrates were evaporated in a tared beaker, dried, weighed and recorded as *benzene-soluble matter.*

One portion of the benzene-insoluble residue was in the original flask and another on the folded filter. Both were heated over the radiator to expel adhering benzene. 15 cc. of hot water were next added to the flask and, after a few minutes, when the sugars had dissolved, the solution was poured through the filter-paper dissolving the rest of the residue. Flask and filter were washed with a few cubic centimeters of hot water collecting the solution in a 110-cc. flask.

The filtrate was cooled to room temperature and basic lead acetate added drop by drop until no further precipitation occurred. The excess lead was removed by adding saturated sodium oxalate solution in slight excess. The solution was then made up to 110 cc. and unless the analysis was to be completed at once about 1 cc. of toluol was added to the solution as a preservative.

Reducing sugars.—Reducing sugars were determined on 25-cc. aliquot portions of the prepared solution by a slight modification of the Munson and Walker method, (C. A. Browne, Handbook of Sugar Analysis, p. 426, New York, John Wiley and Sons, 1912.) The precipitated cuprous oxide was collected on tared asbestos Gooch crucibles and washed with water in the usual manner, but instead of drying and weighing as cuprous oxide, the precipitates were ignited in a muffle furnace to cupric oxide and weighed as such. The weight of cupric oxide was multiplied by the factor 0.9 to give the weight of cuprous oxide and the corresponding weight of glucose was then obtained from Munson and Walker's tables.

Reducing sugars after inversion.—55 cc. of the prepared solution were placed in a 110-cc. flask, and 5.5 gm. of solid citric acid added. The mixture was then boiled for 10 minutes. After cooling to room temperature the solution was made alkaline to phenolphthalein by adding NaOH solution

and thereafter dilute acetic acid was added until the red color disappeared. The solution was made up to 110 cc. and reducing sugars determined on 50-cc. portions in the same manner as before.

Sucrose.—Sucrose is obtained by difference between reducing sugars before and after inversion.

Analysis of the alcohol-insoluble portion

Starch.—To 1 gram of the alcohol-insoluble material 100 cc. of water were added, after which the mixture was boiled for 15 minutes to gelatinize the starch. After cooling to room temperature, 0.1 gram of takadiastase and 10 drops of toluol were added. The mixture was placed in the incubator room at 28° C. and left over night. After removing the solution from the incubator room it was boiled for 15 minutes to inactivate the enzyme and then filtered through a Gooch crucible containing a disk of mercerized cotton cloth as the filtering medium. The undissolved residue was saved for the *hemicellulose* determination. The filtrate was transferred to a 200-cc. volumetric flask, clarified with basic lead acetate, deleaded with sodium oxalate solution and made up to volume. The mixture was filtered through a dry filter and 50 cc. of the filtrate were mixed with 5 cc. of concentrated hydrochloric acid and boiled for 2.5 hours under a reflux condenser. After cooling to room temperature the solution was made alkaline with sodium hydroxide solution, then slightly acid with dilute acetic acid. It was then made up to volume and reducing sugars expressed as glucose. Starch was calculated by multiplying by the factor 0.9.

Hemicelluloses.—The residue remaining after the takadiastase digestion was transferred to an Erlenmeyer flask with a measured volume of water. To this were added 8 cc. of 12 per cent. hydrochloric acid and water to make a total volume of 100 cc. The mixture was heated on the hot plate under a reflux condenser for 2.5 hours. The insoluble residue was then filtered off and washed and the filtrate transferred to a 200-cc. volumetric flask. After cooling to room temperature the solution was made alkaline with NaOH, then slightly acid with acetic acid. It was clarified by adding basic lead acetate in slight excess followed by sodium oxalate solution to remove the excess lead. The solution was made up to 200 cc., mixed, filtered through a dry filter, and reducing sugars determined in 50-cc. portions. The results were calculated to the hexosan formula by multiplying the glucose value by 0.9.

Residue after hemicelluloses.—The insoluble residue remaining after the hydrolysis of the hemicelluloses was collected on a Gooch crucible containing a filtering disk of mercerized cotton cloth, dried in the oven at 100° C. and weighed.

Lignin-suberin.—The dried residue after hydrolysis of hemicelluloses was digested for 24 hours in 20 cc. of 72 per cent. sulphuric acid. The mixture was then diluted with 300 cc. of water, heated to boiling, filtered on a Gooch crucible with a cloth filter disk, washed, dried and weighed.

Cellulose by loss.—The material soluble in the 72 per cent. sulphuric acid was regarded as cellulose. The value was obtained by subtracting the *lignin-suberin* value from the *residue after hemicelluloses.*

Galacturonic acid.—Galacturonic acid was determined by DORE'S (5) modification of the Lefevre method. One gram of the alcohol-insoluble dry material was placed in a liter flask with 100 cc. of 12 per cent. hydrochloric acid. The flask was placed in a carbon dioxide absorption train and, after sweeping out the carbon dioxide due to inorganic carbonates and that previously present in the flask by a current of carbon-dioxide-free air, the decarboxylation reaction was carried out by heating the flask in an oil bath at 130° C. The carbon dioxide produced by this reaction was swept out of the flask and absorbed in a weighed Geissler potash bulb, suitable precautions being taken to prevent other reaction products from passing over. The reaction was continued until the Geissler bulb showed constant weight, which usually required 4.5 hours. The weight of carbon dioxide multiplied by 4 gives the weight of hexuronic acid present in the plant tissue. Since the galacturonic acid of pectic substances is the only hexuronic acid definitely known to occur extensively in plant tissues, it is assumed that the hexuronic acid value is identical with the galacturonic acid content. This in turn is a measure of the pectic substances, but since the factor is variable, no attempt has been made to express the results in terms of pectic substance.

Chemical data

The data presented in table IV give in detail the green weights of leaves, stems and roots of individual plants. As is to be expected, considerable variation in growth occurs, but in general the plants in each group were fairly uniform. The average total green weights of the subgroups of group A fluctuate with the time of day at which the samples were obtained. Reference to table III will show this. These average values drop from 41.6 in the first period to 36.9 in the third, then rise to 40.1 in the last. Such variations in green weight are to be expected as the water content of the plants varies with a change in atmospheric conditions throughout the day. The low value of 36.9 in the third period is, however, due to the low value of the leaves of plant numbered 18. Several leaves from this plant had been removed several days previous to the date of harvest and their weights are not included in the table. If the other five values are averaged then 36.9 becomes 38.4. The third, fourth and fifth

subgroups then become practically equal with reference to their total green weights. The subgroup values of group B do not show any regular decrease or increase in the total green weight. With the exception of the fourth period the values are quite uniform. These general observations suggest the possibility that plants of group B are slightly better able to maintain a constant moisture content in spite of the fluctuating condition of their environment which tends to bring about a water deficit of the tissues, while plants of group A seem to lack this ability. Such a general inspection of the data would indicate a somewhat greater state of saturation deficit occurring in the boron deficient plants during the middle of the day than was the case under like conditions in the normal plants grown under similar environmental conditions. This, however, is not the case as will be seen from the discussion of table VI.

The amounts of alcohol-insoluble and alcohol-soluble dry matter in plants grown in boron deficient solutions and in solutions to which boron was added are presented in table V. For convenience this table is divided into three sections, l, s, and r, representing respectively data from leaves, stems and roots. In part V—l it will be noted that no significant difference was found between the average total dry weight per plant in group A and that in group B, the latter being slightly greater, 0.27 gram, or about 14 per cent. In each group the percentage of alcohol-insoluble dry matter is approximately twice that of the alcohol-soluble material. The alcohol-insoluble matter is 7 per cent. less in the boron deficient plants than in the normal plants while the alcohol-soluble dry matter is correspondingly increased. A survey of these values for the plant stems in part V—s shows an increase of approximately 60 per cent. in dry matter of the normal plants over the boron deficient ones, these values being 2.83 and 1.76 grams respectively. While the actual difference between the two groups is significant, the percentage of alcohol-insoluble and alcohol-soluble matter of the total dry weight is the same. Part V—r clearly shows the greater average total dry matter in the roots of group B plants. Here the increase is over 200 per cent., by far the greatest of measurable quantities noted in these experiments. The relative proportion of alcohol insoluble and soluble matter in the two groups is practically the same.

So far as the data of table V go, it appears that no marked difference in chemical composition of roots and stems is to be expected between plants of the boron deficient group and those grown in a medium containing boron. There is, however, indication of a difference in chemical composition of the leaves from plants in these two groups. The leaves of the boron deficient plants contain a higher percentage of alcohol-soluble matter than do the normal leaves. Since many of the metabolically important constituents

TABLE IV

DATA SHOWING GREEN WEIGHTS OF LEAVES, STEMS, ROOTS AND THE TOTAL WEIGHT OF INDIVIDUAL PLANTS GROWN IN BORON DEFICIENT SOLUTIONS AND IN SOLUTIONS TO WHICH BORON (0.55 PPM.) WAS ADDED

No.	GROUP A (BORON DEFICIENT)				GROUP B (BORON—0.55 PPM.)			
	Leaves	Stems	Roots	Total	Leaves	Stems	Roots	Total
1	15.0	24.0	4.3	43.3	15.6	32.5	10.9	59.0
2	12.9	22.4	2.8	38.1	16.2	33.9	14.2	64.3
3	14.6	22.6	3.7	40.9	16.8	31.0	15.2	63.0
4	16.2	20.8	3.0	40.0	13.9	30.3	11.1	55.3
5	15.5	22.6	3.4	41.5	15.3	35.8	11.5	62.6
6	17.8	24.8	3.1	45.7	16.2	32.7	13.6	62.5
Total	92.0	137.2	20.3	249.5	94.0	196.2	76.5	366.7
Average	15.3	22.9	3.4	41.6	15.7	32.7	12.8	61.1
7	14.6	22.6	3.1	40.3	15.3	33.7	12.9	61.9
8	14.9	22.9	3.4	41.2	16.5	31.7	14.2	62.4
9	16.7	22.0	2.9	41.6	16.1	33.0	17.3	66.4
10	14.1	19.9	3.2	37.2	15.4	34.2	12.3	61.9
11	14.1	21.2	2.8	38.1	14.3	31.2	11.9	57.4
12	12.6	21.1	3.4	37.1	13.6	30.6	12.9	57.1
Total	87.0	129.7	18.8	235.5	91.2	194.4	81.5	367.1
Average	14.5	21.6	3.1	39.3	15.2	32.4	13.6	61.2
13	14.5	20.7	3.4	38.6	16.2	34.7	17.1	68.0
14	15.8	18.4	2.8	37.0	18.1	32.4	16.8	67.3
15	14.6	20.6	3.8	39.0	15.2	31.6	13.0	59.8
16	12.4	21.7	3.5	37.6	15.2	30.3	12.7	58.2
17	13.9	22.5	3.4	39.8	16.6	28.8	16.3	61.7
18	6.4	20.0	3.2	29.6	13.3	30.5	10.2	54.0
Total	77.6	123.9	20.1	221.6	94.6	188.3	86.1	369.0
Average	12.9	20.7	3.4	36.9	15.8	31.4	14.4	61.5
19	15.6	23.1	2.8	41.5	16.7	35.0	12.6	64.3
20	12.9	20.6	3.5	37.0	15.9	35.4	13.3	64.6
21	12.6	21.0	3.2	36.8	17.4	41.7	14.1	73.2
22	13.0	19.3	3.3	35.6	15.8	34.3	14.4	64.5
23	14.3	22.7	3.6	40.6	17.3	35.3	14.6	67.2
24	17.4	20.6	3.1	41.1	16.9	36.7	14.8	68.4
Total	85.8	127.3	19.5	232.6	100.0	218.4	83.8	402.2
Average	14.3	21.2	3.3	38.8	16.7	36.4	14.0	67.0
25	15.3	20.3	3.7	39.3	13.8	28.4	9.0	51.2
26	12.6	21.9	3.0	37.5	16.8	34.6	14.1	65.5
27	12.5	21.6	3.1	37.2	16.6	34.1	13.5	64.2
28	15.6	21.6	2.4	39.6	16.9	35.5	14.8	67.2
29	13.4	21.1	3.0	37.5	17.2	35.8	13.7	66.7
30	13.8	21.6	3.7	39.1	16.0	32.3	12.0	60.3
Total	83.2	128.1	18.9	230.2	97.3	200.7	77.1	375.1
Average	13.9	21.4	3.2	38.4	16.2	33.5	12.9	62.5
31	13.6	22.5	3.6	39.7	15.7	39.4	11.6	66.7
32	15.0	22.8	3.8	41.6	15.0	33.7	11.8	60.5
33	11.3	19.8	3.2	34.3	16.9	35.6	12.3	64.8
34	15.4	20.5	3.6	39.5	17.1	33.5	11.4	62.0
35	16.6	23.5	3.3	43.4	14.2	35.0	9.3	58.5
36	16.0	23.2	2.9	42.1	16.3	30.2	9.9	56.4
Total	87.9	132.3	20.4	240.6	95.2	207.4	66.3	368.9
Average	14.7	22.1	3.4	40.1	15.9	34.6	11.1	61.5
Grand total	513.5	778.5	118.0	1410.0	572.3	1205.4	471.3	2249.0
Grand average per plant	14.3	21.6	3.3	39.2	15.9	33.5	13.1	62.5

TABLE V—l

DATA SHOWING AMOUNT OF DRY MATTER IN *leaves* OF PLANTS GROWN IN BORON-DEFICIENT SOLUTIONS AND IN SOLUTIONS TO WHICH BORON WAS ADDED

GROUP A (BORON DEFICIENT)	ALCOHOL INSOLUBLE		ALCOHOL SOLUBLE		TOTAL
	gm.	*per cent.*	*gm.*	*per cent.*	*gm.*
1– 6	7.62	64	4.32	36	11.94
7–12	7.22	62	4.41	38	11.63
13–18	6.72	*	*	*	*
19–24	6.96	61	4.39	39	11.35
25–30	6.68	61	4.27	39	10.95
31–36	7.06	61	4.57	39	11.63
Average per plant.....	1.17	62	0.73	38	1.91
Group B (boron 0.55 ppm.)					
1– 6	8.40	69	3.72	31	12.12
7–12	8.93	70	3.74	30	12.67
13–18	9.11	69	4.12	31	13.23
19–24	9.84	69	4.49	31	14.34
25–30	9.41	70	3.96	30	13.37
31–36	8.82	69	3.96	31	12.78
Average per plant.....	1.51	69	0.67	31	2.18

* Results not determined because alcohol-soluble material of these leaves was lost from a broken flask.

TABLE V—s

DATA SHOWING AMOUNT OF DRY MATTER IN *stems* OF PLANTS GROWN IN BORON-DEFICIENT SOLUTIONS AND IN SOLUTIONS TO WHICH BORON WAS ADDED

GROUP A (BORON DEFICIENT)	ALCOHOL INSOLUBLE		ALCOHOL SOLUBLE		ORIGINALLY ALCOHOL SOLUBLE BUT SUBSEQUENTLY PRECIPITATED		TOTAL
	gm.	*per cent.*	*gm.*	*per cent.*	*gm.*	*per cent.*	*gm.*
1–18	21.32	65.0	11.26	34.4	0.21	0.6	32.79
19–36	19.99	65.7	10.34	34.0	0.08	0.3	30.41
Average per plant	1.15	65.35	0.60	34.2	0.01	0.45	1.76
Group B (boron 0.55 ppm.)							
1–18	32.18	66.4	15.84	32.7	0.45	0.9	48.47
19–36	34.61	64.7	18.41	34.4	0.45	0.8	53.47
Average per plant	1.86	65.5	0.95	33.6	0.02	0.9	2.83

TABLE V—r

DATA SHOWING AMOUNT OF DRY MATTER IN *roots* OF PLANTS GROWN IN BORON-DEFICIENT SOLUTIONS AND IN SOLUTIONS TO WHICH BORON WAS ADDED

GROUP A (BORON DEFICIENT)	ALCOHOL INSOLUBLE		ALCOHOL SOLUBLE		TOTAL
	gm.	*per cent.*	*gm.*	*per cent.*	*gm.*
1–18	3.96	81.5	0.90	18.5	4.86
19–36	4.17	81.9	0.92	18.1	5.09
Average per plant	0.23	81.7	0.05	18.3	0.28
Group B (boron 0.55 ppm.)					
1–18	13.29	84.2	2.50	15.8	15.79
19–36	13.41	83.3	2.68	16.7	16.09
Average per plant	0.74	83.8	0.14	16.3	0.88

of plant sap are soluble in alcohol, these results immediately suggest that there are significant differences in the active mobile constituents of the two groups of plants; while the insoluble constituents, which include the framework constituents of the plant, are much alike in the two groups. As will be shown later, this is the situation which actually exists.

In table VI data are presented which show the water content of leaves, stems and roots as related to the green and dry weights of plants grown in boron deficient solutions and in solutions containing boron. The weight measurements are expressed in grams and represent the total weight from 6 plants in the case of leaves and from 18 plants in case of stems and roots. In the discussion of table IV attention was called to an apparent decrease in water content in plants of group A. In table VI such a decrease is apparent for leaves of plants in group A harvested during the warm part of the day namely, plants numbered, 7–12, 19–24 and 25–30. However, if the water content of the leaves of each group is compared with the dry weight values, the ratio of water per unit of dry matter is found to be fairly constant throughout the day. On the other hand, these ratio values for leaves of plants in group B fluctuate quite regularly with the periods of the day during which they were harvested. It must be concluded from the data in this table that leaves of the normal tomato plants (group B) showed a tendency to lose water toward midday, while those in the boron deficient group maintained practically the same water-dry weight ratio values throughout the day. Actual observation of the plants as they were harvested bears this out. The leaves of plants 7 to 30 of group B that were collected during the middle of the day were wilted. Leaves of the other plants of this group, 1 to 6 and 31 to 36, which were collected in early

TABLE VI

DATA SHOWING THE WATER CONTENT OF LEAVES, STEMS AND ROOTS OF PLANTS GROWN IN BORON DEFICIENT SOLUTIONS AND IN SOLUTIONS TO WHICH BORON WAS ADDED

CULTURES	GROUP A (BORON DEFICIENT)				GROUP B (BORON–0.55 PPM.)			
	GREEN WEIGHT	DRY WEIGHT	WATER	WATER PER UNIT DRY WEIGHT	GREEN WEIGHT	DRY WEIGHT	WATER	WATER PER UNIT DRY WEIGHT
	gm.	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Leaves 1–6	92.0	11.94	80.06	6.71	94.0	12.12	81.88	6.76
7–12	87.0	11.63	75.37	6.48	91.2	12.67	78.53	6.20
13–18	*	*	*	*	94.6	13.23	81.37	6.15
19–24	85.8	11.35	74.45	6.56	100.0	14.34	85.66	5.97
25–30	83.2	10.95	72.25	6.60	97.3	13.37	83.93	6.20
31–36	87.9	11.61	76.29	6.57	95.2	12.78	82.42	6.45
Average per plant	14.5	1.91	12.61	6.57	15.9	2.18	13.72	6.29
Stems 1–18	390.8	32.79	358.01	10.92	578.9	48.47	530.43	10.94
19–36	387.7	30.41	357.29	11.75	626.5	53.47	573.03	10.72
Average per plant	21.6	1.76	19.87	11.33	33.5	2.83	30.65	10.83
Roots 1–18	59.2	4.86	54.34	11.2	244.1	15.79	228.31	14.5
19–36	58.8	5.09	53.71	10.6	227.2	16.09	211.11	13.1
Average per plant	3.28	0.28	3.00	10.9	13.09	0.88	12.21	13.8

* Results not determined because alcohol soluble material of these leaves was lost from a broken flask.

morning and late evening were not wilted. From the work of RENNER (**12**), LIVINGSTON and BROWN (**11**), LIVINGSTON (**10**), JOHNSTON (**6**) and others, such a diminution in water content is to be expected during the day in normal healthy plants. An interesting point to be mentioned is that none of the leaves from plants in group A was severely wilted at any time. On *a priori* reasoning alone it might be concluded that either the water absorbing and conducting tissues of the boron deficient plants were entirely adequate to supply water to the leaves as fast as lost by transpiration, or that the structure of the leaves was such as to greatly retard water loss.

There is but little difference to be noted in the average dry weight of leaves per plant of the two groups. A more striking difference is seen in the dry weights of the stems and roots of the plants of these groups. The average dry weight of stems of the normal plants was approximately 1.6 as great as the stems of the boron deficient plants. The most striking difference between the boron deficient plants and the normal ones occurs in the root development. Roots of the normal plants are practically three times

as great when dry weight is used as the criterion of measurement. Poor root development is apparently a definite characteristic of boron deficient plants since it has been observed in other plants by other investigators.

Table VII presents data showing the composition of alcohol-soluble matter in plants grown in boron deficient solutions and in solutions to which boron was added. These values are expressed as percentages of total dry matter in the leaves, stems and roots respectively. The leaves of the boron deficient plants have in every case a much higher content of reducing sugars and of total sugars than the corresponding normal plants. With but one exception the same relationship holds for their sucrose content. The total sugars in the leaves of the normal plants increase as the day advances to a maximum in the late afternoon. The total sugars in the leaves of the boron deficient plants likewise rise to a maximum in the late afternoon, but unlike the normal plants, the total sugars do not drop off in the early evening hours. In this respect the boron deficient plants show distinctly abnormal behavior, the significance of which will be discussed later.

The stems of the boron deficient plants have lower contents of reducing sugars and total sugars than the stems of the normal plants, the relationship being the reverse of that found in the leaves. The meaning of this will also be discussed later. The relationships in the roots are similar to those in the leaves; the boron deficient roots have much higher contents of reducing sugars, sucrose and total sugars.

Another very striking difference between the plants of the A and B groups exists in the percentages of benzene-soluble matter. This material occurs more abundantly in the leaves of the normal plants and in the stems of the boron-deficient plants. The values for the roots are practically the same. This benzene-soluble matter may include chlorophyll, fats, sterols and lipins. Unfortunately we have not found it practicable as yet to undertake a thorough study of this material.

The analytical data showing the composition of the alcohol-insoluble matter of these plants are given in table VIII. These data are likewise expressed as percentages of total dry matter for each of the plant tissues studied. Perhaps the most striking difference is the greater starch content of all the parts of the boron-deficient plants. The hemicellulose is likewise somewhat greater in the leaves of group A plants, but slightly less when the stems are compared. Galacturonic acid gives somewhat higher values for the leaves of group B plants. It is doubtful if the other values are significant. Cellulose is slightly higher in the leaves and stems of the normal plants.

The analytical data presented in tables VII and VIII have been summarized in table IX. For the leaves, the outstanding differences between

TABLE VII

DATA SHOWING COMPOSITION OF ALCOHOL-SOLUBLE MATTER IN LEAVES, STEMS AND ROOTS OF PLANTS GROWN IN BORON-DEFICIENT SOLUTIONS AND IN SOLUTIONS TO WHICH BORON WAS ADDED. THESE DATA ARE EXPRESSED AS PERCENTAGES OF TOTAL DRY MATTER OF LEAVES, STEMS AND ROOTS RESPECTIVELY

Cultures	Group A (boron-deficient)					Group B (boron—0.55 ppm.)				
	Alcohol-soluble matter	Reducing sugars (hexoses)	Sucrose	Total sugars	Benzene soluble matter	Alcohol-soluble matter	Reducing sugars (hexoses)	Sucrose	Total sugars	Benzene soluble matter
Leaves 1– 6	36	6.84	2.16	9.00	9.36	31	2.79	1.24	4.03	13.64
7–12	38	9.12	0.76	9.88	8.74	30	4.20	0.90	5.10	13.50
13–18	*	*	*	*	*	31	3.72	1.55	5.27	12.40
19–24	39	7.41	5.46	12.87	10.14	31	3.72	2.48	6.20	12.71
25–30	39	9.36	3.51	12.87	10.14	30	4.50	0.60	5.10	12.90
31–36	39	8.19	4.68	12.87	9.75	31	4.03	1.24	5.27	13.02
Average per plant	38	8.18	3.31	11.50	9.63	31	3.83	1.34	5.16	13.03
Stems 1–18	34.4	4.21	3.29	7.50	3.42	32.7	7.62	2.42	10.04	1.57
19–36	34.0	6.43	2.96	9.39	3.35	34.4	9.77	3.37	13.14	1.91
Average per plant	34.2	5.32	3.13	8.45	3.39	33.6	8.70	2.89	11.59	1.74
Roots 1–18	18.5	2.57	1.79	4.36	4.01	15.8	0.95	1.44	2.39	4.65
19–36	18.1	1.90	2.34	4.24	4.13	16.7	1.18	1.64	2.82	4.68
Average per plant	18.3	2.24	2.07	4.30	4.07	16.3	1.07	1.54	2.61	4.67

* Results not determined because alcohol-soluble material of these leaves was lost from a broken flask.

the two groups are their sugar, benzene-soluble matter and starch content. Somewhat similar differences appear in the stems, but the order is reversed for total sugars and benzene-soluble matter. Sugars formed in the leaves are, under normal conditions, transported to the stem. In the boron-

TABLE VIII

DATA SHOWING COMPOSITION OF ALCOHOL-INSOLUBLE MATTER IN LEAVES, STEMS AND ROOTS OF PLANTS GROWN IN BORON-DEFICIENT SOLUTIONS AND IN SOLUTIONS TO WHICH BORON WAS ADDED. THESE DATA ARE EXPRESSED AS PERCENTAGES OF TOTAL DRY MATTER OF LEAVES, STEMS AND ROOTS RESPECTIVELY

CULTURES	GROUP A (BORON-DEFICIENT)						GROUP B (BORON 0.55 PPM.)					
	ALCOHOL-INSOLUBLE MATTER	STARCH	HEMICELLULOSE	GALACTURONIC ACID	LIGNIN SUBERIN	CELLULOSE	ALCOHOL-INSOLUBLE MATTER	STARCH	HEMICELLULOSE	GALACTURONIC ACID	LIGNIN SUBERIN	CELLULOSE
Leaves												
1– 6	64	12.85	3.07	8.32	1.66	11.71	69	6.02	2.10	8.14	1.76	12.49
7–12	62	12.05	2.53	6.82	1.24	9.83	70	7.17	2.27	9.94	1.58	12.95
13–18	62*	11.61	2.38	8.56	1.67	11.93	69	7.67	2.18	10.35	1.45	10.94
19–24	61	11.61	2.44	7.44	1.49	10.52	69	8.89	1.38	10.07	1.38	12.11
25–30	61	11.61	2.39	9.27	1.31	9.30	70	10.81	1.99	7.98	1.96	10.26
31–36	61	12.44	2.51	9.88	1.37	9.18	69	9.88	1.38	10.49	2.07	12.59
Average per plant	62	12.03	2.55	8.38	1.46	10.41	69	8.41	1.88	9.50	1.70	11.89
Stems												
1–18	65.0	5.80	4.78	11.05	6.05	20.57	66.4	1.27	5.74	11.22	6.01	24.60
19–36	65.7	5.04	4.65	11.69	5.55	22.08	64.7	1.63	5.95	11.00	5.08	25.43
Average per plant	65.4	5.42	4.72	11.37	5.80	21.32	65.6	1.45	5.85	11.11	5.55	25.02
Roots												
1–18	81.5	0.65	7.04	12.06	14.30	18.58	84.2	0.34	6.60	9.43	12.71	19.07
19–36	81.9	1.31	6.35	10.97	14.66	18.14	83.3	0.13	6.76	11.00	12.91	18.45
Average per plant	81.7	0.98	6.70	11.52	14.48	18.36	83.8	0.24	6.68	10.22	12.81	18.76

* Results not determined because alcohol-soluble material of these leaves was lost from a broken flask. Average of other values.

deficient plants the sugars accumulated because of the apparent inability of the conducting tissues in these plants to translocate them. These data for the stems show that in the normal plants with uninjured phloem tissue the sugars pass into the stems and being able to continue further in these stems very little is condensed to starch. On the other hand in the stems of the boron-deficient plants with their injured conducting systems, the sugars cannot be moved so rapidly and are condensed to starch.

TABLE IX

SUMMARY OF ANALYTICAL DATA OF TOMATO PLANTS EXPRESSED AS PERCENTAGES OF TOTAL DRY MATTER OF LEAVES, STEMS AND ROOTS RESPECTIVELY

AMOUNT OF BORON ADDED TO NUTRIENT SOLUTION (PPM.)	LEAVES		STEMS		ROOTS	
	A 0.00	B 0.55	A 0.00	B 0.55	A 0.00	B 0.55
Reducing sugars (hexoses)	8.18	3.83	5.32	8.70	2.24	1.07
Sucrose	3.31	1.34	3.13	2.89	2.07	1.54
Total sugars	11.50	5.16	8.45	11.59	4.30	2.61
Benzene soluble matter	9.63	13.03	3.39	1.74	4.07	4.67
Starch	12.03	8.41	5.42	1.45	0.98	0.24
Hemicellulose	2.55	1.88	4.72	5.85	6.70	6.68
Galacturonic acid	8.38	9.50	11.37	11.11	11.52	10.22
Lignin and suberin	1.46	1.70	5.80	5.55	14.48	12.81
Cellulose	10.41	11.89	21.32	25.02	18.36	18.76

A very striking characteristic of the boron-deficient tomato plants is the extreme brittleness of the petioles and mid-ribs. This brittleness is perhaps best described as similar to the breaking of a piece of cheese. It is entirely unlike the breaking of a turgid tissue or stem. Because of this peculiar characteristic, it was suspected that pectic substances were absent, or at least less abundant, in the middle lamella of the boron-deficient plants. Absence of a cementing substance between the cells might be the reason for such brittleness. At the suggestion of Prof. J. H. Priestley, microscopic examinations were made using the customary pectin stains but no distinct differences could be observed between sections from normal and from boron-deficient plants. The galacturonic acid determinations given in table VIII are not significantly different for the two groups, and when these figures are calculated to the basis of alcohol-insoluble dry matter (a more comparable basis, since the fluctuating soluble constituents are eliminated) the difference between the two groups is so slight as to fall within the experimental error of the determination. It is apparent that neither the microchemical observations nor the galacturonic acid determinations support the

theory that brittleness is due to a deficiency of pectic material. A special experiment was therefore carried out for the purpose of obtaining enough leaf material for pectic analysis.

This experiment was made at the University of Maryland. On November 1, 1927, young tomato seedlings were set out in two-quart culture jars. The cultures were divided into three groups, a single plant per culture. All the solutions were similar with the exception of their boron content. To group A no boron was added. Groups B and C contained 0.011 and 0.55 ppm. respectively of boron as boric acid. At the end of six weeks the leaves were cut from the plants at the base of the leaf blade. It is unfortunate that the petioles were not included in the samples, but since the mid-rib shows the same characteristic brittleness as the petioles, not a great deal of additional information would have been obtained by including the petioles. The pectic materials[1] were determined by the general methods described by CONRAD (**4**) and by APPLEMAN and CONRAD (**1**). The data are presented in table X.

TABLE X

DATA SHOWING RELATION OF BORON TO PECTIC MATERIALS IN TOMATO LEAVES EXPRESSED AS PERCENTAGE OF THEIR DRY WEIGHT

AMOUNT OF BORON ADDED TO NUTRIENT SOLUTION (PPM.)	0.00	0.011	0.55
Pectin	0.00	0.00	0.00
Pectic acid and pectates	0.00	0.00	0.00
Protopectin	6.98	6.54	5.85
Reducing sugar	5.42	4.51	4.11
Sucrose	0.22	0.31	0.50
Total sugar	5.64	4.82	4.61

So far as pectin, pectic acid and pectates are concerned no measurable quantities were found in any of the groups, even though the boron deficient plants were characteristically brittle. The leaves of plants supplied with 0.55 ppm. boron showed somewhat less protopectin than the leaves of group A. It must be concluded from the evidence here presented that the brittleness is due to something other than pectic materials. It is interesting to note that the total sugar analyses follow in general the results obtained in the California experiments.

Growth data

The first boron experiment conducted at Maryland was outlined for the purpose of comparing the growth of two different varieties of tomato plants

[1] The analyses in this experiment were made by Dr. C. M. Conrad.

in water cultures of three concentrations of boron, 0.0, 0.011 and 0.55 ppm. Each of the six groups was composed of 20 cultures of one plant each. The experiment covered the period from September 10 to October 22, 1927. The average data per plant of each group are presented in table XI.

TABLE XI

DATA SHOWING WEEKLY HEIGHT (CM.), TOTAL TRANSPIRATION (CC.) AND GREEN AND DRY WEIGHTS (GM.) EXPRESSED AS THE AVERAGE PER PLANT PER EACH GROUP

WEEK ENDING 1927	PLANT GROUPS					
	A	a	B	b	C	c
	cm.	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*
September 17	2.5	2.8	3.1	3.3	3.0	3.3
24	4.2	4.4	6.5	6.7	6.3	6.8
October 1	7.4	5.8	14.3	13.2	14.2	13.7
8	13.0	10.0	28.1	24.6	29.2	26.0
15	17.3	13.3	29.2	27.1	35.8	31.6
22	19.6	17.0	29.3	27.5	41.4	36.5
	cc.	*cc.*	*cc.*	*cc.*	*cc.*	*cc.*
Transpiration	380	253	1565	1389	2085	2033
Green weight	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Tops	15.6	11.6	43.8	40.5	50.9	48.6
Roots	2.7	2.3	10.7	10.6	18.9	19.4
Total	18.3	13.9	54.5	51.1	69.8	68.0
Dry weight						
Tops	1.32	0.95	4.20	3.89	4.79	4.29
Roots	0.14	0.11	0.69	0.67	1.35	1.31
Total	1.46	1.06	4.89	4.56	6.14	5.60

Note: A, B, C; Santa Clara Canner; a, b, c, Marglobe.
A, a, No boron added to solutions.
B, b, 0.011 ppm. boron added as boric acid.
C, c, 0.55 ppm. boron added as boric acid.

The first boron-deficiency signs were noted in groups A and a on September 19, only nine days after the seedlings were set out in the culture jars. Four days later the cotyledons and leaves were a distinct purple in color. In all probability this color was due to anthocyan, which is frequently associated with an excess sugar accumulation. Such an excess was found in the California experiments and later to a less degree at Maryland. The indications were that the conducting tissues were either destroyed or never properly developed in these plants.

The height measurements at the end of the first week indicate some injury to plants of groups A and a, and by the end of the second week little

doubt can be held as to the falling off in their rates of stem elongation. In groups A and a the terminal shoot soon died. This brought about a very peculiar form of growth. One, and often several lateral shoots developed in a manner illustrated in figures 3 and 4. The dead terminal shoot is clearly seen in figure 3. Attention is also directed to the swollen condition

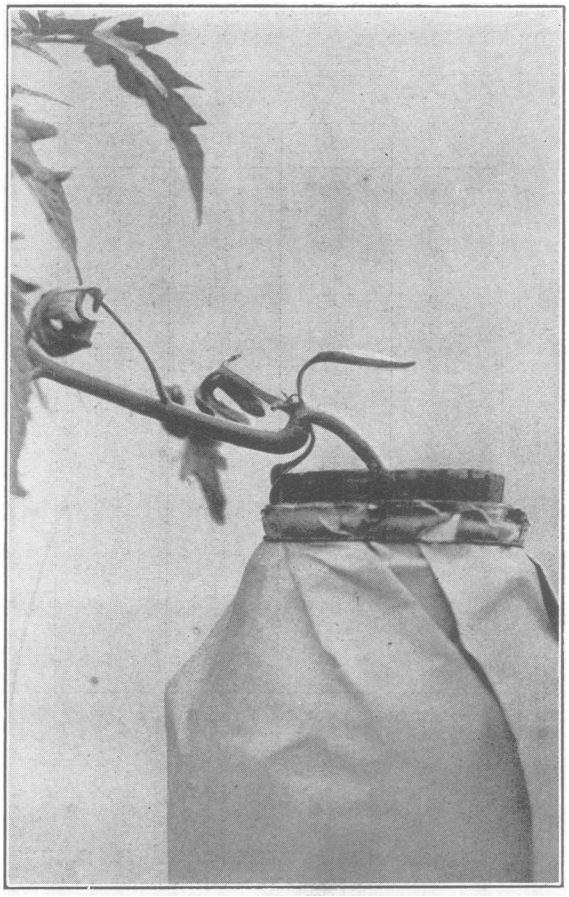

FIG. 3. Photograph showing a boron-deficient tomato plant, with dead terminal shoot and lateral shoot greatly thickened at its base.

of the new shoot at a point just above the place where it joins the main stem. It would appear as if reserve food materials were accumulating at this point because of the inability of the conducting systems to transport them down the main stem.

A comparison of the two varieties shows Santa Clara Canner somewhat superior to Marglobe when stem height, and green and dry weights are used as growth criteria. Each variety was equally susceptible to boron-deficiency injuries and for such studies either one may be used. The data

FIG. 4. Photograph showing a boron-deficient tomato plant in which a number of new shoots have arisen below the dead terminal shoot.

of table XI show another interesting point. The values for groups B and b at the end of the experiment are between those for groups A, a and C, c in every case. Indications are that boron has a quantitative effect. With 0.011 ppm. boron in the nutrient solution, growth could take place at a rate similar to that where 0.55 ppm. was used, but only up to a certain point. From this point the inadequate supply of boron became the limiting factor. This is quite clearly shown in the weekly height measurements. Practically no difference in height existed on October 1 between groups B and C, and b and c. One week later, B and b plants showed signs of retarded growth and by October 22 there was no question as to their inferiority when compared with the plants of groups C and c. This difference in stem heights is shown in figure 5. In a similar experiment carried out a little later in the year under slightly less favorable growing conditions practically the same results were found. Representative plants from the three groups in this experiment (boron added to solutions were 0.0, 0.011,

FIG. 5. Photograph showing tomato plants growing in similar solutions with the exception of the boron concentration. Left, without boron; center, 0.011 ppm. boron; right, 0.55 ppm. boron.

0.55 ppm.) are shown in figure 6. The growth curves of groups A, B, C, for which data appear in table XI are presented in figure 7 and perhaps

FIG. 6. Photograph showing tomato plants growing in similar solutions with the exception of the boron concentration. Left, without boron; center, 0.011 ppm. boron; right, 0.55 ppm. boron.

show to a better advantage the quantitative effect of boron on stem elongation.

Another experiment was carried out with the purpose of growing plants for a period of 6 weeks in a solution supplied with boron, then changing to a boron-deficient solution, and also, to grow other plants in a boron-deficient solution and then change to a solution containing boron. This

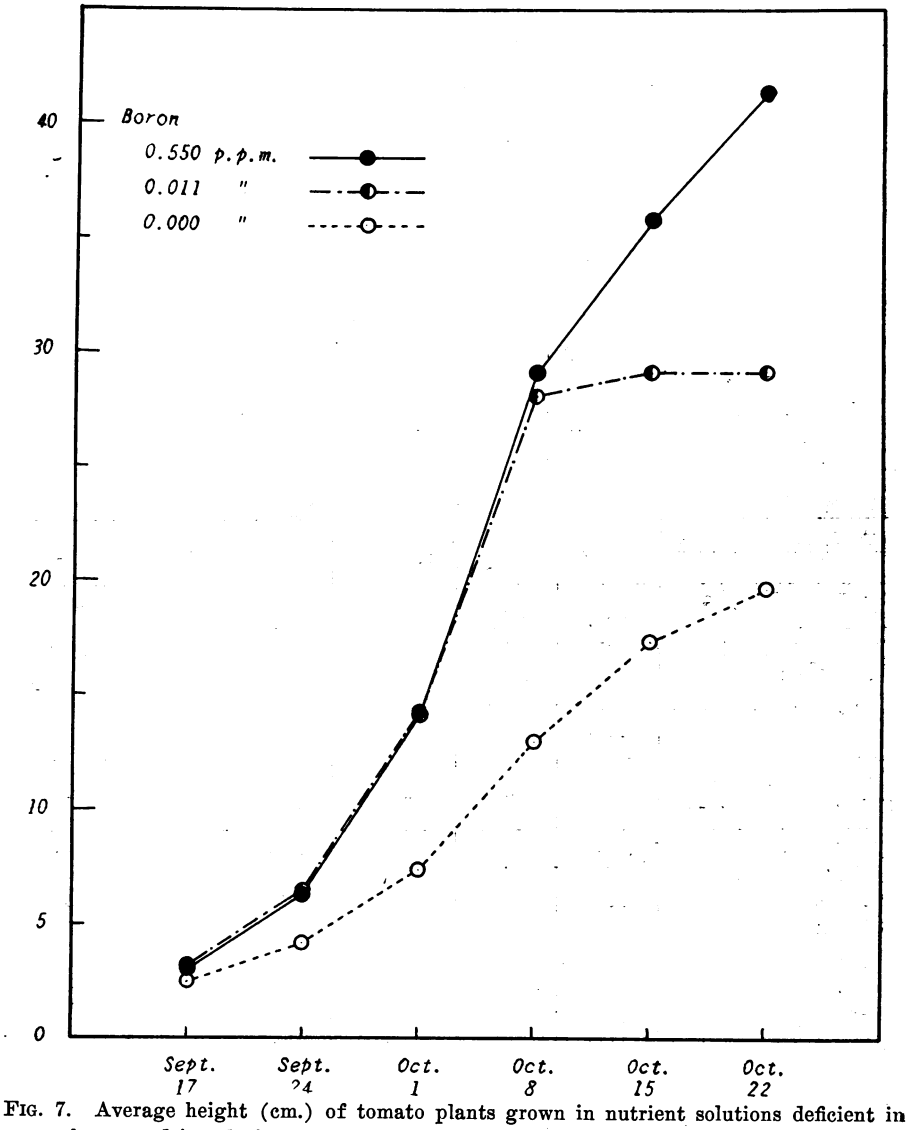

FIG. 7. Average height (cm.) of tomato plants grown in nutrient solutions deficient in boron and in solutions to which 0.011 and 0.55 ppm. boron had been added.

experiment was performed at Maryland with the Marglobe tomato. The plants were grown from November 1 to December 13 without changing the nutrient solutions. They were then grown for four more weeks after the proper changes had been made. The data of this experiment are presented in detail in table XII. At the end of 6 weeks distilled water was added to cultures whose solutions were not changed. All culture jars were of the two quart size with one plant per culture.

TABLE XII

DATA SHOWING AVERAGE HEIGHT (CM.) AND FINAL GREEN AND DRY WEIGHTS (GM.) OF TOMATO PLANTS GROWN IN NUTRIENT SOLUTIONS TO WHICH BORON HAD AND HAD NOT BEEN ADDED AT THE BEGINNING OF THE EXPERIMENT AND AFTER 6 WEEKS. AMOUNT OF BORON ADDED IS SHOWN IN PARENTHESIS AS PPM.

Period ending 1927	(0.55)		(0.55)	(0.0)		(0.0)
	cm.		*cm.*	*cm.*		*cm.*
November 8	2.5		2.4	2.1		2.4
15	4.7		4.4	4.4		4.6
22	7.5		7.0	7.3		7.5
29	13.6		12.4	13.2		13.4
December 6	17.8		16.1	17.5		17.9
13	24.9		22.9	20.3		21.0
Solutions renewed with	(0.0)	(0.55)	No renewal	(0.0)	(0.55)	No renewal
	cm.	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*
December 20	29.8	30.7	28.8	20.7	22.4	21.3
26	33.2	35.1	31.7	21.9	24.3	21.3
1928						
January 3	38.8	42.8	35.6	21.6	28.6	21.3
10	41.8	50.0	39.8	21.8	31.8	21.2
Number of plants in group	5	5	10	5	5	10
Green weight	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Tops	63	66	52	34	49	22
Roots	13	15	18	4	13	5
Total	76	81	70	38	62	27
Dry weight						
Tops	6.9	7.6	5.8	3.6	5.0	3.1
Roots	1.3	1.8	1.5	0.3	1.0	0.3
Total	8.2	9.4	7.3	3.9	6.0	3.4

The upper part of table XII shows the average height per plant in each group on the dates indicated in the first column. For the first six weeks

little variation can be seen between the plants of the first two groups each receiving 0.55 ppm. boron. Likewise little difference exists in the height of the plants of the two groups receiving no boron for this same time period. The plants of the latter two groups are slightly shorter on December 13 than those of the first two groups, but no significant differences can be detected on December 6, one week earlier. On December 13, the first and third groups were divided, thus making six groups. The treatments are indicated in the line between the dates December 13 and 20 of the table. As shown in the observation of January 10, four weeks after these changes were made, the effect of boron on stem elongation is very interesting. The average height of plants of group one, receiving no boron, is approixmately 8 cm. less than their controls. The original second group in which no solutions were renewed but which originally contained 0.55 ppm. boron has practically the same stem height value as the first half of group one. It thus appears as though a deficiency of boron were the limiting growth factor rather than a deficiency of any other element originally contained in the solution since all the elements of solutions in group one were renewed on

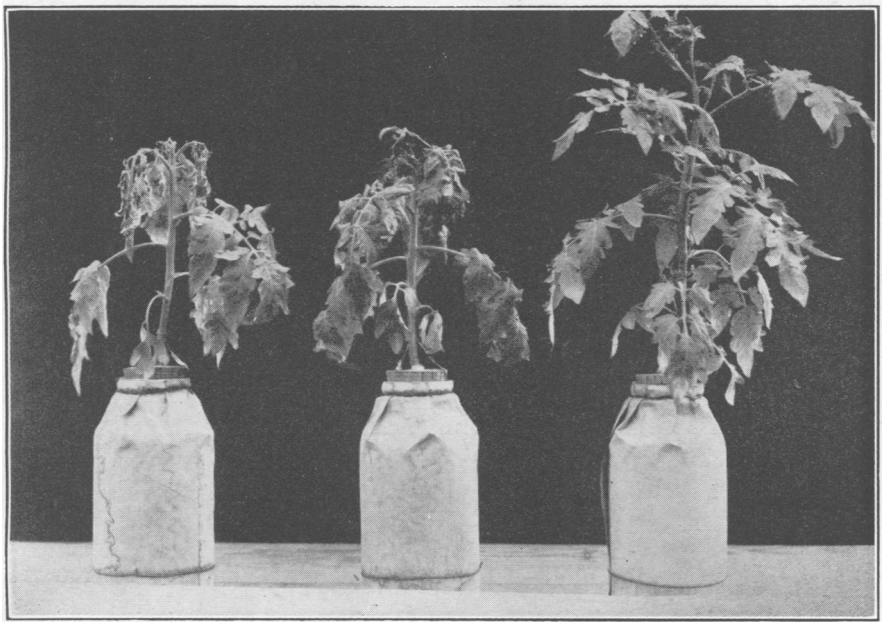

FIG. 8. Photograph showing tomato plants grown for six weeks in given concentrations of boron, then changed to other concentrations for a period of four weeks. The following treatments were used (reading from left to right): No boron and no renewal of solution; no boron, but solution renewed; no boron, then solution renewed plus 0.55 ppm. boron.

December 13 and only distilled water added to cultures of the original second group. The green and dry weight data shown in the lower half of the table bring out this point but to a less extent. Turning now to the second part of the table, the groups originally receiving no boron, it will be noted that after six weeks of growth without boron the plants receiving boron for the last four weeks started to grow. By January 10, four weeks later, the plants in the second half of group four were 10 cm. taller than their controls. Both green and dry weight also indicate a remarkable

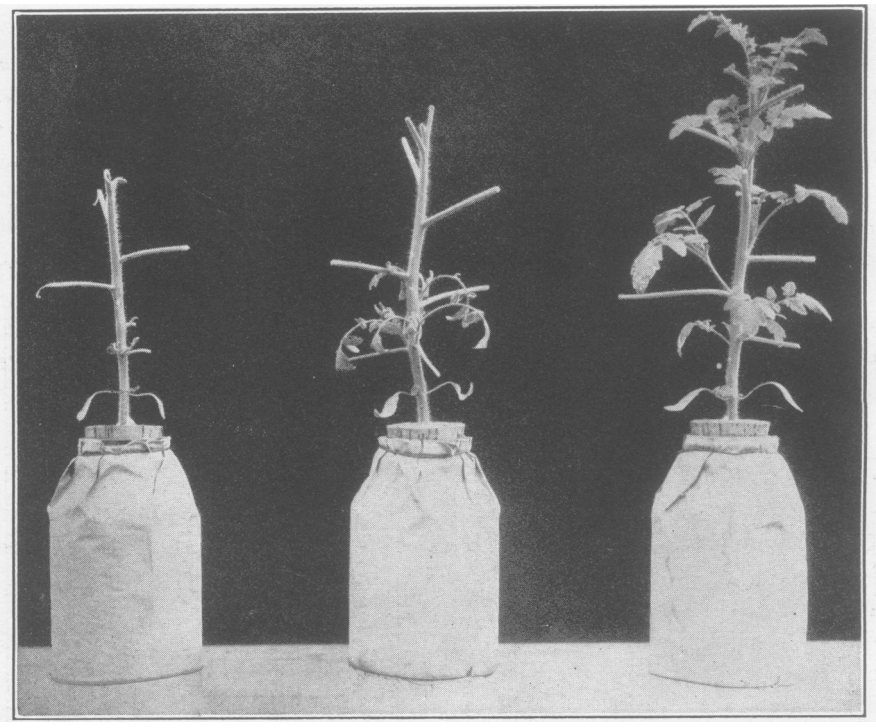

FIG. 9. Photograph showing new leaf growth in tomato plants after they had been defoliated. All solutions were similar with the exception of their boron content. Reading from left to right: No boron; 0.011 ppm.; 0.55 ppm.

increase in growth due to the action of the boron added to the nutrient solution.

This renewal of growth when the plants have not been deprived of boron for too long a period is shown in figure 8. The plants here shown are representative ones taken from groups receiving the last three treatments indicated in table XII. This remarkable influence exerted by boron on growth, especially on the formation of new cells in the growing points was observed in connection with the experiment from which data on the pectic materials

were obtained. After the leaves had been removed for analysis the defoliated plants were left standing in their respective culture media for four weeks. After this period it was observed that no new shoots had appeared on the plants of the boron-deficient solutions while new shoots and leaves were abundant on the plants in the group treated with 0.55 ppm. boron. The intermediate group of plants, those receiving 0.011 ppm. boron, contained a few new shoots and leaves. Figure 9 illustrates the appearance of representative plants from each of these three groups.

Discussion

The evidence presented by plant physiologists in recent years is such that boron must be regarded an essential element for the growth and normal development of many of the higher plants. As yet the exact function of this element is not known. To speak of it as stimulating in small concentrations and as toxic in larger concentrations means little as to its fundamental physiological relation to the plant. Toxicity is a matter of relative concentrations in the presence or absence of other substances. Even the "old" nutrient elements are toxic under certain conditions. The authors are in agreement with SOMMER AND LIPMAN (**14**) that to speak of the catalytic effect of an element merely expresses in other language ignorance in respect to its actual function.

BRENCHLEY (**2**) states, "The old 'nutrients' had certain definite characters in common, in that they were essential to plant growth, the growth being in a great degree proportional to the supply, a relatively large amount of the nutrients being not only tolerated but necessary. . . . Even those that cause increased growth or that may be essential for nutrition (boron) are not required in such quantities as potassium, phosphorus, nitrogen, etc., while there is no evidence that growth is proportional to supply." It is true that boron cannot be used in quantities nearly as great as potassium, phosphorus or nitrogen, yet in these experiments with the tomato there is evidence of a quantitative relationship between growth and the amount of boron supplied. Reference to table XI and to figures 5, 6 and 7 clearly show a difference in growth where 0.011 and 0.55 ppm. boron were used.

SOMMER (**13**) found in her work with monocotyledonous plants such as corn, abnormal tillering as well as withering of the growing points of the tops. This interesting growth formation is no doubt related in some way to the peculiar growth forms (see figure 4) produced in the tomato after the growing points of the stems died. Apical dominance enters the problem at this point. As soon as the influence of the terminal shoot on the development of lateral buds is removed, these lateral buds begin their growth. Such dominating influence can be eliminated by removing the terminal

growing point; it amounted to the same thing in the tomato when the terminal shoot died from a cause attributed to boron deficiency. On *a priori* reasoning the abnormal tillering of corn in SOMMER's experiments may in part be explained as a pruning effect; at least there is an interesting similarity in the behavior of these two widely different plants.

Although extremely small quantities of boron are essential to the tomato plant this element must be supplied constantly. There is apparently no reserve built up in the plant for future growth since plants grown for six weeks in solutions containing boron and then grown in boron-deficient solutions soon showed characteristic symptoms of boron-deficient injuries. This is apparent from the data given in table XII and is in agreement with WARINGTON's (**17**) statement, "The fact that boron can be detected in the stem, leaves, and pods of the broad bean implies that the element becomes distributed throughout the plant after absorption; and further, the need for the supply of boron to be maintained during the life of the plant indicates that the initial reserve of the element in the seed is insufficient for the needs of the plant, and that it is in some way fixed and not in a state of circulation."

A vital relationship exists between boron and the conducting tissues of the tomato. If boron is essential for cell division as seems to be the case in the meristematic tissue of growing points, its presence is just as much needed in the cambium cells where phloem and xylem tissues are forming. These are the tissues which together with the tip of the stem show greatest injury from a deficiency of boron. Both the chemical analyses and macroscopic observations indicated a failure on the part of the boron-deficient plants to remove sugar from their leaves. This is apparently related to the broken down condition of the conducting tissues. Microscopic examinations of the petioles and stems of boron-deficient plants showed phloem necrosis. These general observations are in agreement with the anatomical studies of WARINGTON (**17**) on *Vicia faba* grown in boron-deficient solutions.

At first it was thought the characteristic brittleness of stems and petioles of boron-deficient plants was in some way associated with pectic materials. The experimental data, however, fail to substantiate such a theory. The observation by BRENCHLEY (**2**) that boron occurs most abundantly in bark and lignified parts, suggests that brittleness may be related to a lack of proper lignification. No conclusions upon this point appear possible from the lignin-suberin values which we have obtained.

Conclusions

The conclusions drawn from a series of water culture experiments carried out at the Universities of California and Maryland with two varieties

of tomato, Santa Clara Canner and Marglobe, may be summarized as follows:

1. The element boron in a concentration of approximately 0.5 ppm. was found necessary for the normal growth and development of the tomato plants studied.

2. Tomato plants grown in boron-deficient solutions show four distinct types of injury; (a) death of the terminal growing point of stem; (b) breaking down of the conducting tissues in the stem; (c) a characteristic brittleness of stem and petiole; and (d) roots of extremely poor growth and of a brownish unhealthy color.

3. As a result of broken down conducting tissues the boron deficient plants differed markedly from normal plants in their chemical composition. Total sugars and starch were more abundant in the leaves and stems of the boron-deficient plants while a greater amount of benzene-soluble matter was found in the leaves of the normal plants and in the stems of the boron-deficient plants.

4. Evidence is presented which shows the possibility of a quantitative relationship existing between the amount of growth and the amount of boron present in the nutrient media.

5. A concentration of 5.5 ppm. boron in the nutrient solution was toxic to the tomato plants. Symptoms of boron toxicity are quite different from deficiency injuries.

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THE UNIVERSITY OF MARYLAND,
THE UNIVERSITY OF CALIFORNIA.

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