MINERAL NUTRITION OF THE GENUS <u>BRASSICA</u> WITH PARTICULAR REFERENCE TO BORON

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V

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Since 1910 many investigators from countries in various parts of the world have reported the necessity of small quantities of boron for the growth of plants. Studies have been made on at least fifty different plants which include monocotyledons and dicotyledons. These contributions have built up our knowledge of the importance of boron in plants. However, the function of boron in the plant has not been definitely established and it is hoped that the research reported on the following pages will give further information which will ultimately assist in establishing the role of boron in plants.

The genus Brassica was chosen for these studies as some of the plants in this group show boron deficiency under field conditions. Members of this genus are rapidly growing plants which may be conveniently used in nutrition studies. This group of plants is of further interest because man has selected for edible purposes types with storage roots, others with an abundance of foliage, two with many flowers, and a fourth type with an edible stem.

The investigations reported here aim to give some information on how long plants will survive with the boron stored in their seeds and the optimum quantity for the development of these plants. The data also give some light upon the importance of boron in different stages of development of the plants of the genus Brassica. It is hoped that the description of boron deficiency in those plants where it has not been described will be of practical use to the vegetable grower.

Some information is also given upon the anatomical abnormalities resulting from a deficiency of boron.

LITERATURE REVIEW

The influence of boron on plant growth was first studied by Peligot (66) in 1876. His experiments showed that the toxic effect of boron caused the leaves to turn yellow and die. For many years research workers studied the quantity of boron in sea water, soil and plants but it was not proved to be an essential element until 1910 when Agulhon (1) grew wheat in sand cultures with varying levels of boron. From 1910 to 1923 very little study of boron nutrition was made. At the latter date Warington (80) reported "The Effect of Boric Acid and Borax on the Broad Bean and Certain Other Plants." The number of investigators has increased continuously since Warington published her paper and particularly since 1930. Recently a number of investigators have published literature reviews covering the general field of boron nutrition (7, 8, 17, 19, 27, 55, and 70). Two comprehensive bibliographies have also been published; the first by Willis (84) was published in 1935 with a second edition in 1936. The second was prepared by Harding and Schmidt (31) and includes the literature from Willis's second edition to June 1938.

Brown heart of rutabagas and heart rot and dry rot of sugar beets were observed many years ago. Woods (86) described the symptoms of boron deficiency in rutabagas in 1915, naming the condition "Black Heart." However, the cause of the disease was not known until 1933 when MacLeod and Howatt (51) showed that it was controlled in rutabaga by applications of borax to the soil. Jamalainen (39) published extensively on the investigations in Finland in 1935 on the same plant. Dearborn and Raleigh (16) were the first to publish that browning of cauliflower was controlled by the addition of boron to the soil. In 1936 Snyder, Grant and Donaldson (74) described deficient turnips as pithy or punky instead of the watery center found in rutabagas. Little or no investigation has been carried out on other members of the genus Brassica. Boron deficiency has occurred in several other vegetables, particularly celery in which it is expressed as a cracking of the petiole (67). Boron deficiency has also been observed in tree fruits. In this group of plants internal cork of apples has received the most attention, the major part of the work being done in New Zealand under the direction of Askew (2, 3, 4, and 5).

The leaves of many plants are chlorotic when boron is deficient. Hill and Grant (34) have shown that the margins of rutabaga leaves are the first part of this plant to be affected. Hurst and MacLeod (38) have found that these leaves later become red on the under side and fall early. Chlorotic areas are found between the veins of tobacco leaves according to van Schreven (78). The same author in a later paper reported the curling upward of leaves of deficient plants in water cultures and the curling downward in sand cultures when boron was inadequate (79).

The skin of rutabagas grown without an adequate supply of boron has a rough surface (10, 74, and 13). On the other hand, several investigators have stated that there were no external symptoms (65, 20, 74, 61, and 39).

Most of the investigators reporting on the apical meristem have stated that the first symptom of boron deficiency was death of this tissue (9, 41, 42, 48, 52, 57, 59, and possibly others). McMurtrey in 1929 was in agreement with the above view yet in 1935 (54) he reported that death of the apical meristem was the last symptom of boron deficiency in tobacco. With rutabagas Jamalainen (39) found this meristem was killed only in cases of severe deficiency. Coulson and Raymond (13) have said the apical meristem of rutabagas was not killed.

Warington in her studies of <u>Vicia</u> <u>faba</u> (80) found that the pith and ground parenchyma near the xylem of the stem became disintegrated and discolored in plants not adequately supplied with boron. The phloem has been found to be distorted in tomatoes (42), in potatoes (41) and in tobacco (78). The phloem of tomato and tobacco was found to be enlarged due to cell elongation and to cell division, particularly in a radial direction (78 and 79).

In experiments with <u>Pisum</u> <u>sativum</u> Sommer and Sorokin (76) observed that the root caps were deformed or entirely lacking on plants grown without boron while Warington (81) found a black sheath over the root tips which had stopped growing. Sommer and Sorokin (76) found many more secondary roots which were much nearer the tip on plants grown without boron than on plants grown with boron.

The total sugar and starch content of the leaves is higher in boron deficient plants than in healthy ones (22, 29, 30, and 42). The roots of such plants are low in sugar (19, 36, 61, and 64). Shive (72) found more soluble nitrogen and less protein in cotton suffering from boron deficiency than in healthy plants. On the other hand, Holland and Jones (36) found an increase in the protein in rutabagas associated with boron deficiency.

Eaton (21) has shown that the boron content of cotton plants is greatest in the leaves and that it increases with increasing applications of boron. The boron content of plants has been published by Bertrand and de Wall (6) and Löhnis (37). The former shows that four of the Brassica contain from 21.9 to 53.3 milligrams of boron per kilogram of dry matter. Löhnis found less boron in seeds than in other parts of the plant. The boron is apparently fixed and cannot be translocated as in magnesium deficiency.

The variability among varieties of rutabagas in susceptibility to boron deficiency has been shown by Dennis and O'Brien (19). In their experiment the variety Picton was taken as a standard with a susceptibility of 100 per cent and the other varieties studied varied from 0 to 226 per cent. Coulson and Raymond (13) found a variety difference of 73 per cent in rutabagas. O'Brien and Dennis (62) and Riggs, Askew and Chittenden (67) have shown that turnips are not as severely affected by boron deficiency as rutabagas.

Rigg (68) found that an acre of rutabagas required 60 grams of boron and that healthy roots contained 18 to 19 ppm of boron, on a dry weight basis, while those with brown heart contained 4 to 6. The most extensive soil analyses dealing with boron deficiency have been made on apple soils in which Askew (4) found that the top six inches of soil producing healthy apples had 0.35 to 1.10 ppm of boric acid while the soil producing apples with internal cork had only 0.2 to 0.3 ppm. Askew working with other investigators (5) found the greatest amount of boron in the top soil. Howatt[1] found only 0.4 to 0.8 ppm of boron present in New Brunswick soils and other workers in Canada had shown that over 1.0 ppm of boron was required to produce healthy rutabagas (34 and 13). Many investigators in the United States (23, 35, 41, 42, 43, 72, 75, 76, and others) working with various crops have found that 0.5 ppm of boron is sufficient to prevent the disorder.

The effect of soil pH on boron deficiency has not been definitely established. Some investigators believe the symptoms increase with increasing alkalinity (8 and 13) while others believe the deficiency is more severe in acid soils (32) and still a third group believes that pH has no effect (37).

The seasonal effect has caused the amount of brown heart of rutabagas to vary from 38 to 80 per cent (13),

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[1]Information obtained by the author in conversation with Dr. J. L. Howatt of Experimental Farm, Fredericton, N.B.

and several investigators have found boron deficiency to be more severe in dry seasons than in wet ones (8, 11, 17, 18, 26, 58, 63, 68, and 86).

Warington (82) stated "The boron deficiency symptoms were less pronounced under short day than under full day conditions." Likewise Willis and Piland (85) have not observed boron deficiency on alfalfa in North Carolina in the winter and therefore believe there is a photoperiodic effect. Hoagland and Snyder (35) found that 0.1 ppm of boron was enough to prevent deficiency during the winter months but this amount was not sufficient in the summer.

McMurtrey (53) has studied the effect of removing boron at different times and found that the increase in height of tobacco plants was directly proportional to the time of removal. The recovery of boron deficient plants was slow when boron was supplied after four weeks of starvation. McMurtrey (52) also observed that aeration of water cultures in which tobacco plants were growing hastened the development of boron deficiency.

The function of boron has not been established but Young (87) and Shive (36) believe that boron is concerned in metabolism. Without this element the translocation of carbohydrates is retarded or prevented (43). Boron has an intimate relation with calcium metabolism (9 and 83). It has also been expressed that boron exerted some control over the swelling of the plasma colloids (71 and 16).

MATERIALS AND METHODS

The seeds used in the first experiment were germinated on waxed cheesecloth as described by Johnston (40). In the other experiments the seeds were germinated in quartz sand. The seedlings were transplanted to their permanent cultures before the leaves were evident. The water culture studies were made in two types of containers; in one experiment two-quart fruit jars covered with heavy brown paper were used while in the other experiments tall liter pyrex beakers were used. The latter were cleaned with cleaning solution and painted with a coat of black paint which was later covered with white paint. The sand cultures were conducted at the University of Maryland in two-gallon coffee urns while at the University of Maine some experiments were conducted in one-gallon crocks, while others were conducted in two-gallon crocks, both glazed inside and out and provided with a three-fourths inch drainage hole in the side flush with the bottom. Ottawa silica sand was used in the first experiments and a gray river sand was used for the later experiments. The gray sand was tested before it was used and was found to be equally as good as white sand for boron deficiency studies. In the early experiments the sand was washed with a 5 per cent solution of hydrochloric acid and then washed free of chlorine.

The treatments were assigned from Latin Squares taken at random except in two experiments in which the jars were paired and one in which the factorial design of experiment (25) was used. The data were analyzed by the analysis of variance (24) in all cases where it was possible. Odds of 19 to 1 have been considered significant.

In all but a few of the last experiments the plants were supplied with a type I three salt nutrient solution by the continuous flow method as described by Shive and Stahl (73). In these experiments the salts and the quantity used were the same as those used by Johnston and Dore (43), Johnston and Fisher (44) and Fisher (23). The pH of the nutrient solution was 4.8 and its osmotic pressure was 0.61 atmospheres. Other data on the nutrient solution will be found in Table I. When the plants were young they received three-fourths of a liter of nutrient solution daily while for the larger plants the amount was increased to two liters per day.

Some of the experiments were conducted with no boron added to the nutrient solution while others had various levels of boron. Other experiments were conducted in which the plants were supplied with a moderate amount of boron for a period and then the sand was flushed with a nutrient solution containing no boron, following this the plants were grown for the remainder of the test without boron. In these experiments plants were also grown with an inadequate supply of boron for a period followed by an adequate supply. Boron was always supplied as boric acid usually in a solution such that one cubic centimeter added to a liter of nutrient solution gave 0.1 ppm of boron.

TABLE I

The Basic Nutrient Solution Used for Most Experiments

Salt	Grams of salt per liter of nutrient solution	Partial molecular concen-tration	Element or ion	Parts per million	Milli-equiva-lents
$Ca(NO_3)_2$	.82044	.005	Ca	200.000	10.0
			NO_3	620.000	10.0
			N	140.064	
$MgSO_4$	.24076	.002	Mg	48.640	4.0
			SO_4*	194.000	4.0
			S*	64.753	
KH_2PO_4	.27228	.002	K	78.190	2.0
			PO_4	190.000	6.0
			P	62.036	
$MnSO_4$	.00269	.00002	Mn	.970	.035
$ZnSO_4 \cdot 7H_2O$	.00099	.000003	Zn	.225	.007
$CuSO_4 \cdot 5H_2O$	.00010	.0000004	Cu	.089	.003
Iron (ic) tartrate	.00500	.000009	Fe	.973	.052
Total	1.34226	.00903			

*These also include the sulfate or sulfur in the manganese, zinc and copper salts.

Root boxes were used to study the development of roots supplied with nutrient solutions with and without boron. Root studies were also made in water cultures.

At frequent intervals during the experiments one or more of the following measurements were made: the number of leaves, the length of the longest leaf, the width of the widest leaf, the height of the plant and occasionally other measurements were made. At harvest the same data were obtained and the fresh weight of stem, leaves, head or edible part and in a number of cases the fresh weight of roots was recorded. In a few of the experiments dry weights were also obtained.

Histological studies were made on both field and greenhouse material. The specimens were embedded in paraffin by the N-butyl method, and sections about 10 microns thick were cut with a rotary microtome. They were stained with safranin for photomicrographs but for observation under the microscope several stains were used.

EXPERIMENTAL RESULTS

Plant Growth without Boron

The first experiment was conducted to determine whether or not the salts, sand and jars were sufficiently free from boron to conduct the investigations, and to determine how long plants would grow without boron. The data from this experiment are presented in Table II. Using increase in dry weight as a criterion of growth it is evident that the quantity of boron in the materials was not

TABLE II

Average Dry Weight in Milligrams of Seeds and Tops of Seedling Plants of Different Ages Supplied with Nutrient Solutions Containing Different Amounts of Boron

Kind of plant	Parts per million of boron	Dry seeds	Time in days from soaking the seeds for germination						
			8	14	17	28	37	64	94
			Germinated seeds	Seedlings ready to transplant	Seedlings ready to transplant	Young seedlings	Young seedlings	Old seedlings	Old seedlings
Rutabaga	0	2.22	1.81	2.46	2.33	22.12	25.34	194.86	2.62
	.001				2.37	29.62			
	.01				2.41	29.50		731.35	
	.1				2.20	30.74	503.12		
Cauliflower	0		3.39			25.84	46.77	20.92	
	.001							106.89	
	.01					28.55		600.06	
	.1				3.03	28.88			

enough to support normal growth. These data also show that the boron present in the seed will only maintain normal growth for a very short time. Without the addition of boron the cotyledons were not normal in size or shape. Without boron the first true leaves fail to develop or develop abnormally (Fig. 1). The true leaves normally develop between the 17th and 28th day from germination and the data

Fig. 1. Cauliflower plants grown with no boron, 0.001 and 0.01 ppm of boron.

show that during this period the plants supplied with boron increased in dry weight at a greater rate than those not supplied with this element. Table III presents the percentage of moisture of plants grown in this experiment and while the data are somewhat variable they indicate that plants suffering from boron deficiency have a smaller percentage of moisture than healthy plants from the 28th day on. This point will be presented more convincingly in a later experiment.

TABLE III

Percentage Moisture in Seeds and Seedlings of Rutabaga of Different Ages Supplied with Nutrient Solutions Containing Different Amounts of Boron

Parts per million of boron	Dry seeds	Time in days from soaking the seeds for germination						
		8	14	17	28	37	64	94
		Germinated seeds	Seedlings ready to transplant		Young seedlings		Old seedlings	
0	4.72	97.44	94.50	89.21	90.73	83.57	88.79	89.20
.001				88.02	90.10			
.01					90.83		91.75	
.1					90.68	91.60		

Each new lot of sand and containers was tested with plants to see if they were satisfactory for boron deficiency studies. In one experiment the variability of different lots of seed was studied.

The results of this experiment which lasted 30 days from the time the seeds were soaked for germination are presented in Table IV; and Figure 2 illustrates the growth of some of the seedlings. When the 10 seedlings in the jar were not uniform they were divided into two groups, one in which the true leaves did not develop and one in which they did. Figure 2 shows that the cauliflower was most uniform but less than 7 per cent of the seeds contained enough boron to develop true leaves on the plants. The seedlings which did not show boron deficiency symptoms averaged two to six times as heavy on the fresh weight basis as those which did

TABLE IV

Fresh Weight, Dry Weight and Per Cent Moisture in Thirty-day-old Seedlings Grown from Six Different Lots of Rutabaga and Cauliflower seeds. Each Figure Represents an Average of 10 Plants

Kind of plant	Measurements		
	Fresh weight	Dry weight	Per cent moisture
	mgm.	mgm.	
Rutabaga	100.8	14.0	85.04
	119.8	14.2	85.60
Cauliflower	142.8	18.2	81.96
	100.2	16.4	83.63
	92.3	16.9	81.69
	107.2	19.5	82.74

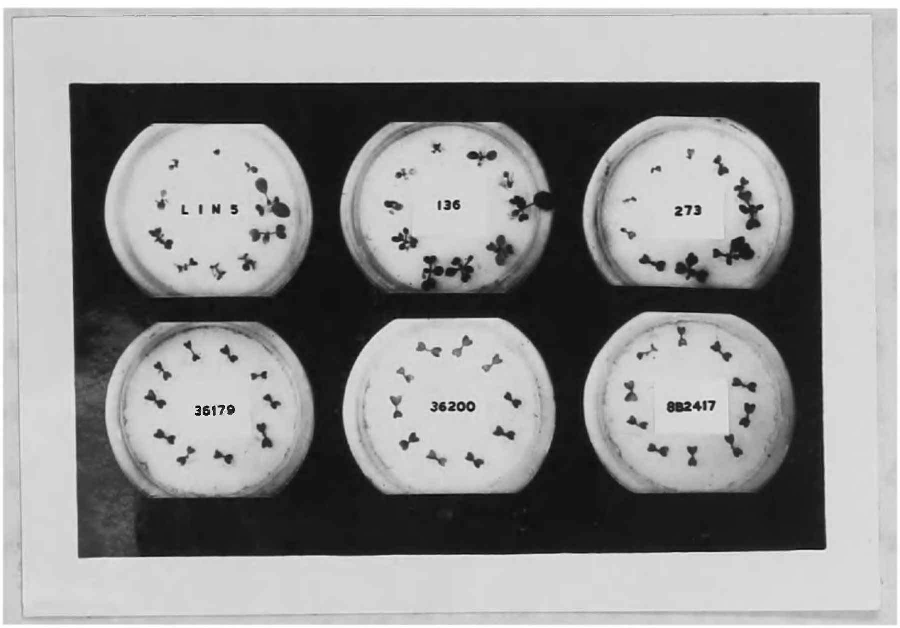

Fig. 2. Plants grown without boron for 30 days. Top left and center rutabagas, others cauliflower.

show boron deficiency. The dry weight shows less variation, the more deficient seedlings having from a little less than one half the weight of the healthy ones to a little more than one third of the weight of healthy ones. Without exception the more deficient plants have a smaller percentage of moisture.

The Effect of Different Quantities of Boron on Plant Development

The second experiment was conducted to study the effect of different levels of boron on the growth of rutabagas.[2] The levels of boron were established from the results of three investigators. The results of experiments conducted by Johnston and Dore (43) showed that the two varieties of tomatoes studied grew best in the solution with 0.55 ppm of boron. Newell presented evidence which Johnston and Fisher (44) published showing an increase in growth of tomatoes with increasing concentrations up to 0.55 ppm and a decrease from this concentration up to 2.75 ppm. On the other hand, Hoagland and Snyder (35) had found that 0.1 ppm of boron was sufficient to grow strawberries during the winter months. From this evidence the boron levels were taken as 0.1, 0.3 and 0.5 ppm. The plants were grown for 17½ weeks from October 6th to February 2nd.

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[2]This experiment was conducted at the University of Maryland from October 1936 to January 1937.

The width of the widest rutabaga leaf was measured at intervals and these data are presented in Table V and plotted in Figure 3. These data show that the

TABLE V

Width of the Widest Leaf of Rutabaga at Different Periods of Development

Parts per million of boron	Age of plants in days							
	31	38	56	63	69	76	84	122
	Inches	Inches	Inches	Inches	Inches	Inches	Inches	Inches
.1	4.53	5.43	8.19	8.70	9.04	9.53	9.93	11.49
.3	4.57	5.64	8.14	9.02	9.72	10.13	10.55	11.69
.5	4.45	5.63	7.82	8.33	8.83	9.18	9.50	11.11

leaves of the plants supplied with 0.1 ppm and 0.3 ppm are wider than the leaves of plants grown with 0.5 ppm in all cases, the difference at any one date is not significant. However, when all of the data are considered as a whole the leaves of plants grown in 0.1 ppm are found to be significantly wider than those grown in 0.5 ppm and the data associate high significance with the wider leaves of the plants receiving 0.3 ppm in comparison to those receiving 0.5 ppm. The table and graph both show that the difference in leaf width was greatest in the latter part of the growth period. This shows that 0.3 ppm extended the period of most rapid growth or lengthened the nearly straight part of the growth curve. The diameter of the storage root of rutabagas was also measured and the data which are similar to those for leaf width are

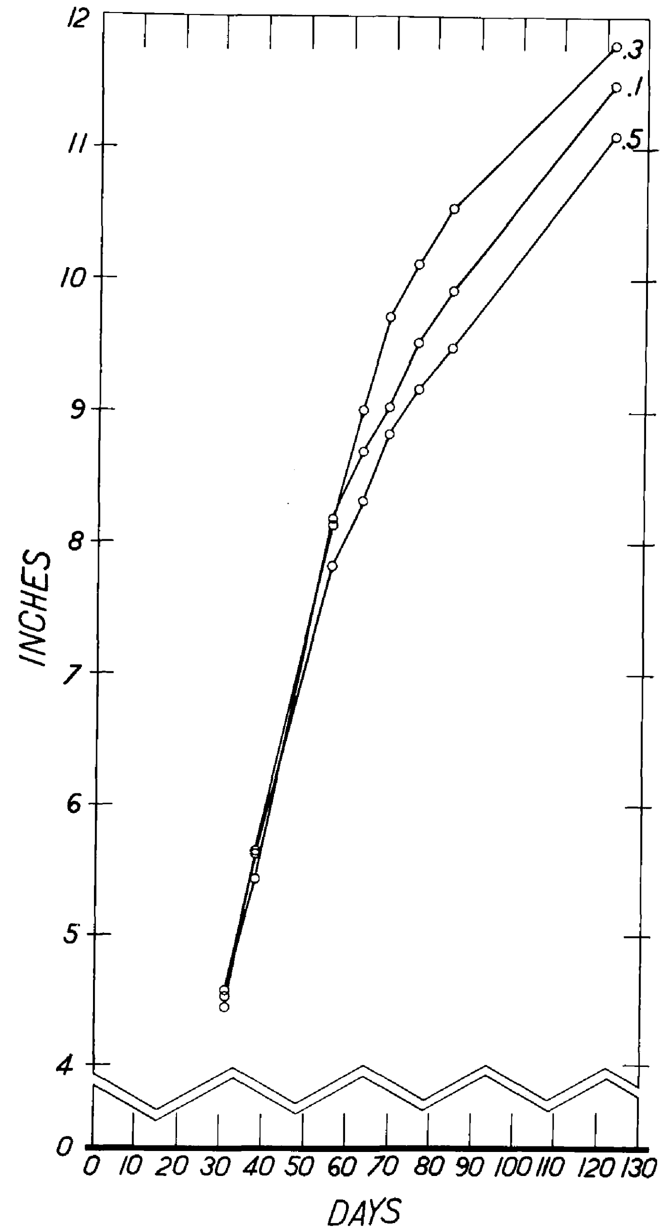

Fig. 3. Curves showing the average width in inches of the widest rutabaga leaf of plants grown with 0.1, 0.3 and 0.5 ppm of boron measured at different ages.

presented in Table VI.

After these plants had been treated 122 days they were harvested and the measurements taken at this time are presented in Tables VII and VIII. This table shows that the plants receiving 0.3 ppm of boron weighed more and had larger

TABLE VI

Diameter of the Storage Root of Rutabaga at Different Periods of Development

Parts per million of boron	Age of plants in days					
	56	63	69	76	84	122
	Inches	Inches	Inches	Inches	Inches	Inches
.1	1.51	1.95	2.33	2.69	3.39	3.91
.3	1.57	1.97	2.34	2.66	3.31	4.04
.5	1.46	1.95	2.36	2.72	3.26	3.74

TABLE VII

Average Weight, and Per Cent Moisture of Rutabaga Plants Grown with Different Levels of Boron

Part of plant	Treatment	Measurements		
		Fresh weight	Dry weight	Moisture
	ppm.	gms.	gms.	%
Storage root	0.1	432.0	40.695	90.58
	0.3	454.8	41.251	90.70
	0.5	389.5	40.85	89.77
Feeding roots	0.1	41.5	9.800	76.38
	0.3	43.5	12.591	71.06
	0.5	41.8	11.846	71.66
Leaves	0.1	554.4	48.946	91.17
	0.3	622.2	56.729	90.88
	0.5	559.0	50.000	91.06
Total	0.1	1027.9	99.441	90.23
	0.3	1120.5	110.571	90.13
	0.5	990.3	102.696	89.73

TABLE VIII

Measurements of Rutabaga Leaves from Plants Grown with Different Levels of Boron. Each Measurement Represents the Average of Five Plants

ppm of boron	Number of leaves	Measurements of leaves		
		Greatest length Inches	Greatest width Inches	Length/Width Ratio
0.1	21.4	25.99	11.48	2.26
0.3	27.5	27.00	11.69	2.31
0.5	24.3	26.11	11.11	2.35

leaves than either the 0.1 or 0.5 ppm of boron. Significance can only be attached to the difference in weight of the plants grown with 0.5 and 0.3 ppm of boron and the difference in width of the leaves between the low and the high boron plants. None of the plants had external symptoms of boron deficiency but some of the storage roots were affected internally (Fig. 4).

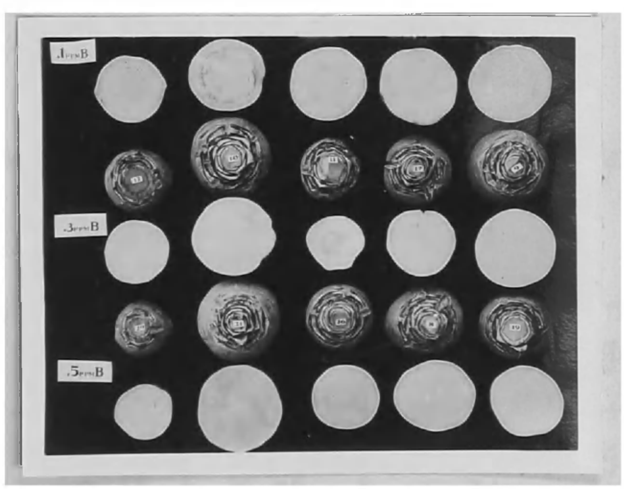

Fig. 4. Storage roots of rutabagas grown with 0.1, 0.3 and 0.5 ppm of boron.

One of the roots from the plants receiving 0.1 ppm had a brown ring while the others were of poor texture. The storage roots receiving 0.3 ppm were of much better quality except plant number 11 which had root nematodes. This plant had a poorly developed root with a brown ring which appeared like boron deficiency symptom. The roots of plants receiving 0.5 ppm of boron were of excellent quality and the color was a deeper yellow than that of roots of plants receiving other treatments.

Cauliflower was used as a test plant in another experiment[3] in which the levels of boron were the same as in the rutabaga experiment just described. The width of the widest leaf of each plant was again used as a measurement of growth. The average measurement of leaves of six cauliflower plants does not show a significant difference between treatments at any one date but the measurements tend to become significant on the 54th and 67th days. The widths of the widest leaves are recorded in Table IX and plotted in Figure 5.

TABLE IX

Widths in Inches of the Widest Leaves of Cauliflower Plants Grown with Different Levels of Boron and Measured at Different Ages of the Plants

ppm of boron	Age of plants in days				
	35	43	54	67	82
0.1	1.87	2.80	4.11	5.28	6.55
0.3	2.04	3.26	5.01	6.25	7.05
0.5	2.12	3.34	5.12	6.53	7.65

[3]This experiment was carried on at the University of Maine from May 2nd to July 25, 1937.

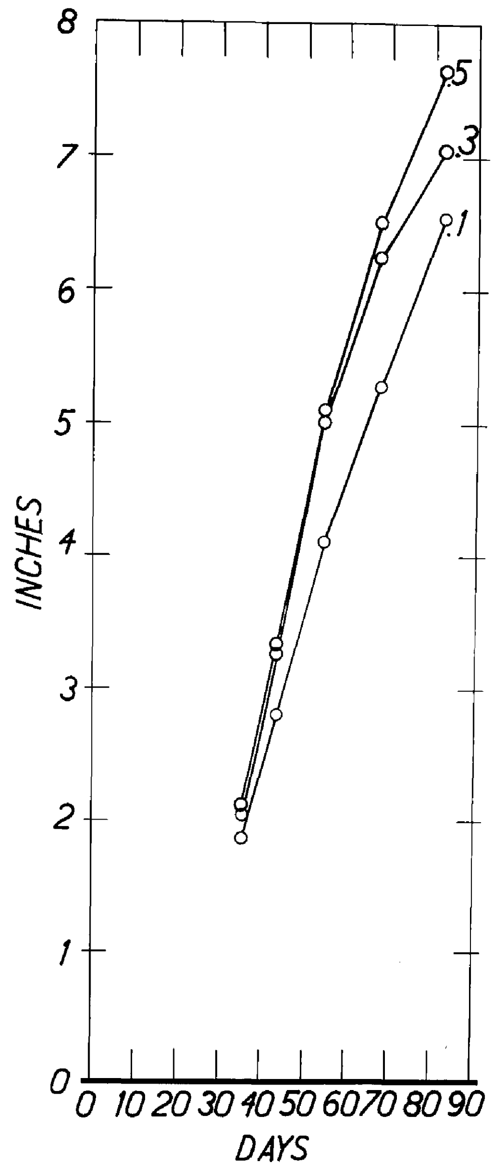

Fig. 5. Curves showing the average widths of the widest leaf in inches of cauliflower plants grown with 0.1, 0.3 and 0.5 ppm of boron.

These data like those for rutabagas show that 0.1 ppm of boron is below optimum for growth but unlike rutabaga the best growth was made with the highest concentration, 0.5 ppm. All plants were harvested on the eighty-second day after transplanting. At this time all of the heads receiving 0.5 ppm were marketable and only half of those receiving 0.3 ppm. The variability of plants receiving 0.1 ppm was greater than those receiving 0.3 or 0.5 ppm in that the 0.1 ppm group varied from plants with normal mature heads to plants without heads. Typical heads from plants grown with the low and high concentrations are shown in Figure 6. The data obtained at harvest are presented in Tables X and XI.

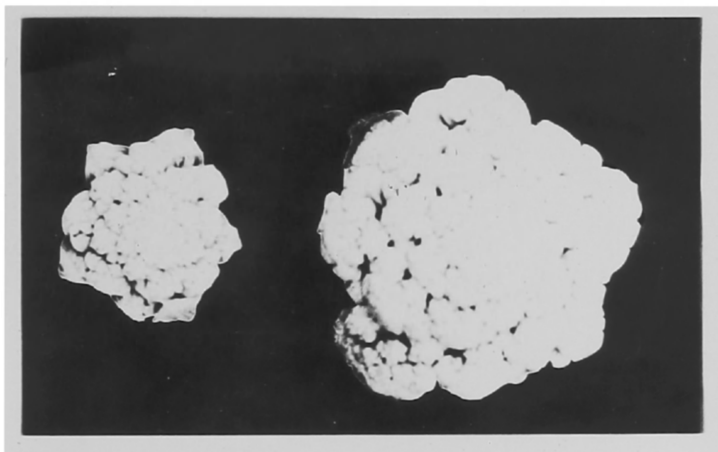

Fig. 6. Cauliflower heads at harvest. Left from plant receiving 0.1 ppm of boron and right from a plant receiving 0.5 ppm of boron.

TABLE X

Average Fresh Weight of Cauliflower Plants Grown with Different Levels of Boron

ppm of boron	Part of plant weighed				
	Head	Feeding roots	Stem	Leaves	Total
0.1	56.62	57.33	47.12	278.70	436.93
0.3	100.59	80.90	96.04	417.67	693.52
0.5	131.95	80.53	88.45	376.07	677.00

TABLE XI

Number of leaves, Leaf Measurements and Length/Width Ratio of Cauliflower Leaves from Plants Grown with Different Levels of Boron. Each Measurement Represents the Average of Six Plants

ppm of boron	Number of leaves	Measurements of leaves						
		Total length	Greatest length	Average length	Total width	Greatest width	Average width	Length* / Width
		Inches	Inches	Inches	Inches	Inches	Inches	Ratio
0.1	22.16	228.90	14.77	10.30	95.92	6.55	4.30	2.25
0.3	25.00	286.52	17.23	11.51	123.53	7.05	4.46	2.44
0.5	25.16	270.02	15.74	11.49	119.01	7.65	5.12	2.06

*Ratio of longest to widest leaves.

Both experiments show the same trend although the data in either experiment are significant in only a few cases. The medium level of boron, 0.3 ppm, produced a greater total weight of feeding roots, leaves and stem. The edible part was greatest in the rutabaga from the 0.3 ppm treatment and from the 0.5 ppm treatment in cauliflower. This would indicate that relatively larger amounts of boron were beneficial for head formation yet none of the plants grown with 0.1 ppm of boron showed boron deficiency in cauliflower. There was a distinct difference in maturity associated with the amount of boron. On the other hand, with rutabaga the amount of boron had less effect on the root weight and maturity but had more effect on the boron deficiency symptoms and on quality of the root.

The general results of experiments conducted specifically for histological studies may be mentioned here.

Cabbage plants were grown in nutrient solutions which contained 0.05 and 0.3 ppm of boron. In the experiment with green cabbage the higher concentration of boron produced larger heads, a greater leaf weight and a greater total weight than was produced with the lower concentration. The leaves below the head were retained longer on the plants with high boron concentration than on those with the low concentration. In the experiment with red cabbage, which is a slower growing plant, the low level of boron produced plants which were slightly better than those produced with 0.3 ppm.

In summarizing the results of the effect of different levels of boron on plant growth 0.3 ppm of boron produced the greatest total weight of rutabaga, cauliflower and green cabbage. The results with red cabbage indicate that this plant may have a slightly lower optimum which may be a varietal difference or may be caused by the difference in growth rate. Since these experiments were conducted Löhnis (49) has shown that 5 mg. of boric acid (0.87 ppm of boron) will prevent brown heart of rutabaga but 0.125 mg. of boric acid (0.02 ppm of boron) was not enough to prevent this disorder.

The Effect of Removal of Boron at Different Ages of Plants

Experiments were started August 23, 1937 to study the effect of the removal of boron at the end of 24, 46 and 67 days after transplanting. The test plants in this experiment were Brussels sprouts, broccoli, green cabbage, and red cabbage. Each treatment was replicated five times with each kind of plant. The plants in this experiment received 0.3 ppm of boron at the outset but after 24 days six plants were flushed with 2 quarts of nutrient solution containing 0.05 ppm of boron which remained the nutrient solution for 22 days. The original plan was to grow the plants with 0.3 ppm of boron for a period and then change them to 0.05 ppm of boron for the remainder of the experiment. However, when these plants had grown for 22 days with 0.05 ppm no external symptoms of deficiency were evident, therefore they were changed to a solution without boron. Another group of six plants of each kind in this experiment were flushed and changed to a solution without boron on the same day, i.e., 46 days from transplanting. Six other plants of each kind were changed from 0.3 ppm of boron to no boron when they were 67 days old. In another experiment to be described later the boron was removed from rutabaga at different ages of the plant. The data which pertain to the removal of boron are presented here with that for Brussels sprouts, broccoli, green cabbage and red cabbage. The width of the widest leaf of each plant was measured several times during the experiment and the average for each treatment is presented in Table XII and plotted in Figure 7. The plotted data show that the measurements were made at the end of the period of maximum growth and that all of the plants were growing at harvest or 88 days after they were transplanted. Those which had not received boron since they were 46 days old and those which had most of the boron removed from the solution when they were 24 days old were also growing on the 88th day.

TABLE XII

Average Widths of the Widest Leaves of Five Kinds of Plants of the Genus *Brassica* which had the Boron Removed from the Nutrient Solution at Different Ages of the Plant

Kind of plant	Age when boron was removed	Age of plant in days when measurements were made					
		56	66	73	80	88	108
	Days	Inches	Inches	Inches	Inches	Inches	Inches
Brussels sprouts	24	6.49	6.87	6.94	7.04	7.35	
	46	7.18	7.47	7.49	7.53	7.53	
	67	6.74	7.07	7.16	7.18	7.22	7.14
Broccoli	24	6.68	7.26	7.39	7.54		
	46	7.01	7.42	7.50	7.68		
	67	7.54	7.92	8.13	8.13		
Green Cabbage	24	7.83	8.35	8.51	8.70	8.74	
	46	7.88	8.48	8.64	8.74	8.82	9.02
	67	8.29	8.83	9.01	9.04	9.19	
Red Cabbage	24	6.91	7.38	7.86	8.13	8.30	
	46	6.89	7.68	7.97	8.39	8.68	
	67	7.11	8.25	8.71	9.18	9.61	10.05
		Age of plant in days when measurements were made					
		35	43	54	65	73	
		Inches	Inches	Inches	Inches	Inches	
Rutabaga	18	4.38	6.65	6.43	6.55	6.99	
	41	5.15	6.35	6.97	7.58	7.66	
	58	5.04	6.61	7.63	8.68	9.22	

The ratio of the average width of the widest leaf for any treatment to the width of the widest leaf for any other treatment is nearly constant for each kind of plant but varies from one kind of plant to another, Table XIII. Table XIII shows that the difference in rate of increase over the time of

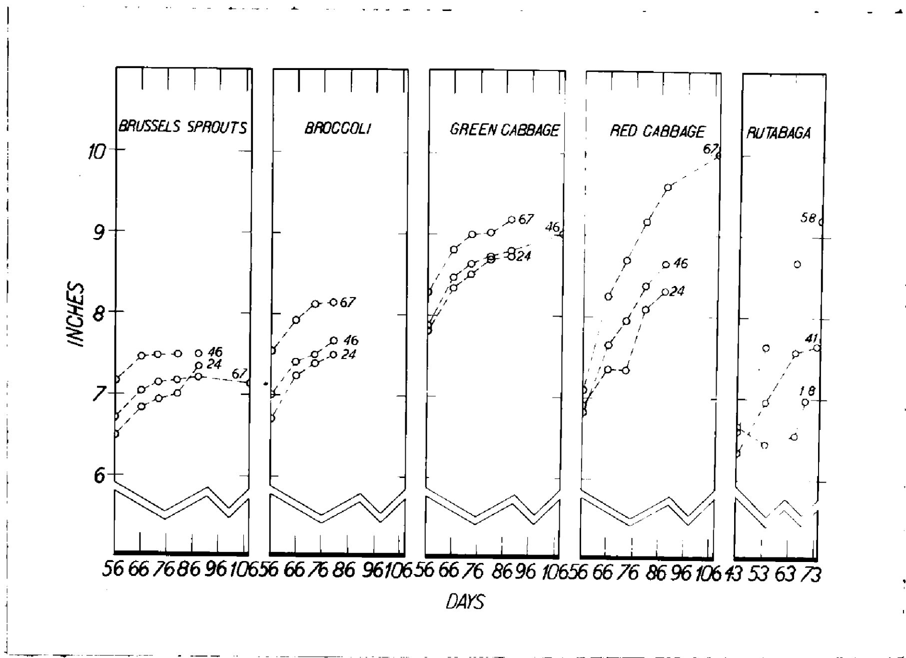

Fig. 7. Curves showing the average widths in inches of the widest leaves of Brussels sprouts, broccoli, green cabbage and red cabbage which had the boron removed when they were 24, 46 and 67 days old and rutabaga plants which had the boron removed when they were 18, 41 and 58 days old.

these observations was nearly constant. It will be noticed in this table and in Figure 7 that the rate of increase in growth was greater, at the time of the last measurements, for plants which had the boron removed early. This is shown in Brussels sprouts which had the boron removed when they were 24 days old. The rate of growth between the 80th and 88th days was greater than in either of the other treatments. This is shown to a lesser extent with broccoli and red cabbage and to a greater extent with rutabaga. Preceding this increase in rate of growth the older leaves turn yellow followed by death and abscission. In the case of rutabaga, data are presented under the next experiment to show that the older leaves die. The increase in the growth of each leaf and the

TABLE XIII

Ratios of the Widths of the Widest Leaves of Five Kinds of *Brassica* Plants. The Ratios were Obtained by Dividing the Width of the Widest Leaf of a Plant from which Boron was Removed at One Time by the Width of the Widest Leaf of a Plant from which Boron was Removed at Another Time

Kind of plant	Treatments constituting ratio	Age of plants in days when measurements were made				
		56	66	73	80	88
		Ratio	Ratio	Ratio	Ratio	Ratio
Brussels Sprouts	46/24	1.10	1.10	1.10	1.10	1.03
	67/24	1.04	1.03	1.03	1.02	0.98
	67/46	0.93	0.95	0.96	0.95	0.96
Broccoli	46/24	1.05	1.02	1.06	1.03	
	67/24	1.13	1.09	1.10	1.05	
	67/46	1.08	1.07	1.04	1.02	
Green Cabbage	46/24	1.01	1.01	1.01	1.00	1.01
	67/24	1.06	1.06	1.06	1.06	1.05
	67/46	1.05	1.04	1.04	1.03	1.04
Red Cabbage	46/24	1.00	1.04	1.01	1.03	0.96
	67/24	1.03	1.12	1.11	1.13	1.17
	67/46	1.03	1.07	1.09	1.09	1.22
		Age of plants in days when measurements were made				
		35	43	54	65	73
		Ratio	Ratio	Ratio	Ratio	Ratio
Rutabaga	41/18	1.18	0.95	1.08	1.16	1.10
	58/18	1.15	0.99	1.19	1.32	1.32
	58/41	0.98	1.04	1.09	1.15	1.20

growth rate together with facts which were not measured, such as development of new leaves after boron was removed, suggest that boron must have been translocated from the older leaves to the younger ones. A number of investigators in the past have said that boron was fixed and could not be used again (8, 42, 44, 56, 79, 80 and several others). However, in all of the experiments which the author has conducted the older leaves of deficient plants have turned yellow and died and the top of the plant has continued to grow, in the same way that plants deficient in calcium and magnesium maintain growth after the first appearance of deficiency symptoms.

The data obtained at harvest are presented in Tables XIV and XV which show that in 83 per cent of the cases an increase in the duration of boron treatment resulted in an increased growth. The increase in fresh weight was greatest to least, in the edible part of the plant, stem, leaves, and feeding roots, respectively. McMurtrey (53) working with tobacco found that the height of plant was directly proportional to the length of time boron was supplied. In this experiment only one of the plants, rutabaga, approached a direct proportion of the time of boron removal to weight of the plant parts. The other weight measurements are far from being directly proportional to the length of time boron was supplied, Figure 8. The stem length is not plotted but approaches the curve for leaf weight. These curves show that the edible part of the plant does not grow at the same rate as the other plant parts. Also, the edible part of the different kinds of plants does not grow at the same rate. From the results of this experiment it does not seem possible to make a definite statement about the relation of the length of time boron is supplied to the fresh weight of the plant produced. In McMurtrey's experiment

TABLE XIV

Average Fresh Weight in Grams at Harvest of Plants from which Boron was Removed at Different Ages. Each Measurement is the Average for Six Plants

Kind of plant	Age when boron was removed	Part of plant				Total
		Edible part*	Feeding roots	Leaves	Stem	
	Days	Grams	Grams	Grams	Grams	Grams
Brussels Sprouts	24	6.58	50.26	202.42	42.50	301.75
	46	28.37	68.25	271.42	54.50	427.54
	67	29.00	79.91	559.25	130.93	799.08
Broccoli	24	2.03	58.38	318.75	108.41	487.87
	46	4.53	63.51	347.63	133.73	549.40
	67	48.85	106.40	445.83	224.05	825.13
Green Cabbage	24	47.16	36.47	388.25	53.41	525.29
	46	258.42	39.58	431.67	63.66	793.33
	67	483.50	39.41	368.16	54.25	945.12
Red Cabbage	24	0.00	31.59	309.00	47.95	388.54
	46	0.50	38.50	374.13	53.47	466.60
	67	110.08	57.87	537.91	123.33	829.19

*The edible part is the sprouts of Brussels sprouts, and the head of broccoli and cabbage.

the boron was removed over a shorter period of time, 29 days, while in this experiment the removal was over a longer period, up to 67 days. In this experiment the boron was not completely removed on the 24th day, which suggests that the slight amount of boron supplied from the 24th to the 46th day increased the growth over the theoretical, based on the growth of plants which had the boron removed on the 46th and 67th days. The increase in growth over that expected for the 24-day study distorts the straightline tendency ihto a curve, Figure 8. However,

TABLE XV

Measurements, and Length/Width Ratio, of Leaves from Plants from which Boron was Removed at Different Ages

Kind of plant	Age when boron was removed	Measurements of leaves				
		Total leaf length	Greatest leaf length	Total leaf width	Greatest leaf width	Length/Width
	Days	Inches	Inches	Inches	Inches	Ratio
Brussels Sprouts	24	140.14	12.55	86.25	6.95	1.81
	46	194.80	12.20	120.85	6.70	1.82
	67	482.79	14.15	282.45	6.75	2.10
Broccoli	24	181.08	18.69	73.81	7.44	2.51
	46	197.29	17.59	83.90	7.96	2.21
	67	305.08	19.91	122.66	8.38	2.14
Green Cabbage	24	135.86	12.78	103.10	8.98	1.42
	46	132.31	13.03	108.17	8.25	1.58
	67	135.03	13.20	98.89	9.09	1.45
Red Cabbage	24	152.36	13.58	97.86	8.50	1.59
	46	185.16	13.99	122.58	8.89	1.57
	67	164.41	13.64	134.29	10.30	1.32

when the fresh weight is plotted against the amount of boron supplied the curves for each plant are almost exactly the same, Figure 9. From the curves shown in Figures 8 and 9 it does not appear that there is a straight-line function between the fresh weight of plant parts and the length of time boron is supplied, or the amount of boron supplied.

The best measurable index of boron deficiency appears to be the fresh weight of the edible part, Table XIV and Figures 8 and 9. The total fresh weight is a very good measure of the behavior of the plant as a whole but does not express the development of the edible part. On a fresh weight basis

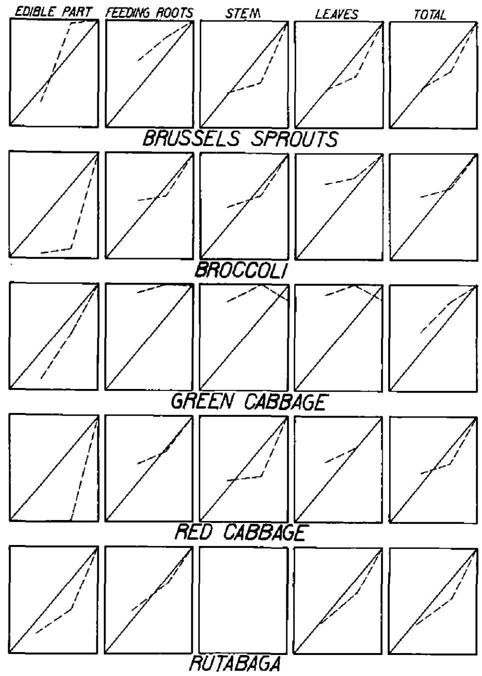

Fig. 8. The relation of the fresh weight of plant parts, which had the boron removed at different ages, to the time boron was supplied. Each graph is drawn so that the diagonal represents direct proportion. The abscissa represents 0 to the maximum number of days boron was supplied and the ordinate represents 0 to the maximum weight of the plant part considered for the particular kind of plant.

the feeding roots, stems and leaves all develop at approximately the same rate.

From the results of this experiment it would appear that the best method of producing boron deficiency symptoms would be to supply plants with an adequate supply of boron for a short period, about 18 to 24 days, and follow with nutrient solution containing no boron. This was done for certain species of the genus Brassica not studied in this experiment.

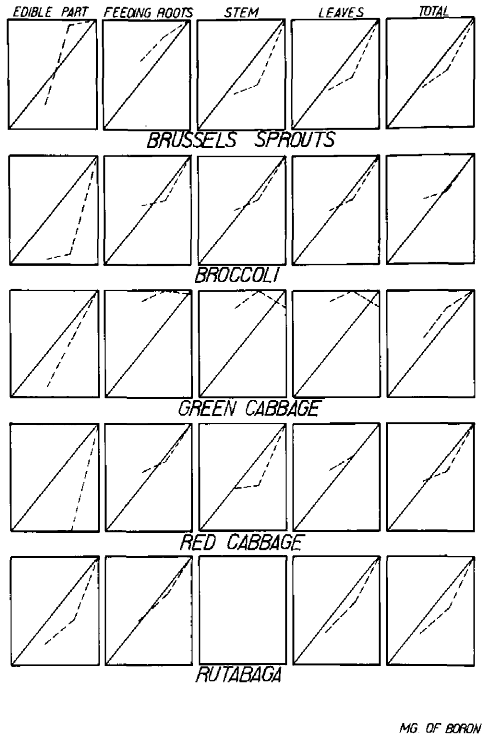

Fig. 9. The relation of the fresh weight of plant parts of plants, which had the boron removed at different ages, to the amount of boron supplied. Each graph is drawn so that the diagonal represents direct proportion. The abscissa represents 0 to the maximum milligrams of boron supplied and the ordinate represents 0 to the maximum weight of the plant part considered for the particular kind of plant.

To prevent any question about the meaning of terms used in the description of boron deficiency symptoms, certain words are described briefly. Brown heart is a name given to an area of dead cells found in the roots of rutabagas and turnips and in the stem of kohlrabi. In the early stages of deficiency this appears watery and in very severe cases it produces a cavity. In the severe cases it is sometimes called hollow heart. The words cork, corky and corky appearance refer to a rough, light brown area on the surface of plant parts. It will be shown in the section on histology that in the majority of cases this is not a true cork. Cracks are longitudinal splits in the petioles, stems and roots of plants except in Chinese Cabbage where they are transverse. Curling is an abnormal bending downward of the midrib. Dwarfing is a reduction in size of plant parts usually without a reduction in the number of parts. Rolling is a marginal bending upward or downward of the leaf from the midrib. In rugose leaves the veins and veinlets are sunken and the spaces between them are elevated. Swellings are protuberances composed of much elongated thin walled cells. Wrinkled veins follow a very irregular path in the plane of the leaf blade.

As there are a few symptoms which are common to almost all *Brassica* plants grown without an adequate supply of boron, they will be stated here. The leaves of plants developing after boron deficiency occurs are shorter and narrower than the leaves of healthy plants. However, the length-width ratio is seldom significantly changed. The entire plant is dwarfed and the apical meristem of diseased plants dies prematurely. Usually all other symptoms appear before this meristem is destroyed.

The following descriptions of boron deficiency are arranged alphabetically by the horticultural name of the plant. The sequence of boron deficiency symptoms may vary with the age of the plant at the time boron becomes the limiting factor.

Broccoli, *Brassica oleracea*, var. *italica*. Horticultural variety, Italian green sprouting. In the greenhouse this plant shows boron deficiency earlier than the other plants studied. In the field, however, it does not show symptoms as early as cauliflower or rutabaga. The first external symptom of boron deficiency is a curling and rolling of the leaves followed by an abscission of the older leaves, Figures 10 and 11. Soon small swellings appear on the stem

Fig. 10. Broccoli leaves showing curling and rolling.

and under side of the petiole, which later have a corky appearance, Figure 12. About the same time longitudinal cracks of various lengths appear on the petiole, most frequently on the under side, Figure 13. The leaves are very brittle. If the plant is not in bud or flower the stem stops growing quickly, resulting in a flat top, and lateral shoots develop more rapidly than usual. When the plant is in bud the

Fig. 11. Broccoli grown with 0.05 ppm of boron for 22 days and then with no boron. This plant had curled and rolled leaves and abscission of the older leaves occurred.

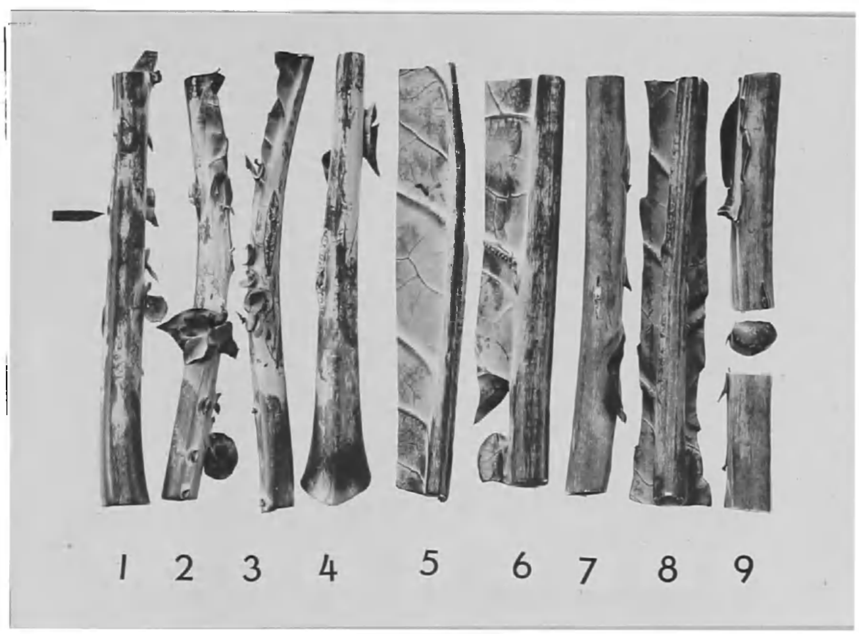

Fig. 12. Petioles and midribs of broccoli showing the development of swelling and cork. In number 1 the swelling is just starting. In number 2 it is somewhat larger and is transparent with a light green color. In the remaining petioles and midribs the swellings have the appearance of small shallow cracks with a corky surface. In number 6 the swellings are just beginning to appear on the secondary veins.

Fig. 13. Petioles from broccoli plants which had received boron but not enough for healthy growth. The most severe crack split the petiole. The second petiole from the left has two swellings on it.

individual buds turn brown and abscission of the buds takes place before the head is marketable. This causes the head to be irregular in shape and of poor quality, Figure 14. When the plant is in blossom abscission of the seed pods occurs before seed is developed. In the field plants have been observed with curled leaves, cracked petioles, cork on the stem and petiole, and abscission of buds.

Fig. 14. All of the buds on one of the clusters of the head on the left have fallen off and part of the buds on other clusters. The head on the right has brown buds scattered over it.

Brussels sprouts, Brassica oleracea var. gemmifera, DC. Horticultural variety Special Italian. Brussels sprouts do not show the symptoms of boron deficiency as quickly as do broccoli nor do the symptoms progress as rapidly after they appear. The first external symptom is the appearance of swellings which later have a corky appearance. These may appear on the petioles or stem. The swellings which appear on the stem occur just above the axillary bud and spread vertically and laterally, Figure 15. The veins of the leaves of plants which do not receive sufficient boron are wrinkled, Figure 16. The leaves at the base of plants showing deficiency fall off before the basal leaves of healthy plants. Chlorosis is very common, occurring at the margin first and progressing toward the midrib, Figure 17. Later a red pigment develops on the under side of the leaf. The death of the tip of the plant is usually the last external symptom, Figure 18. When the defi-

Fig. 15. Swellings on the stem of Brussels sprouts.

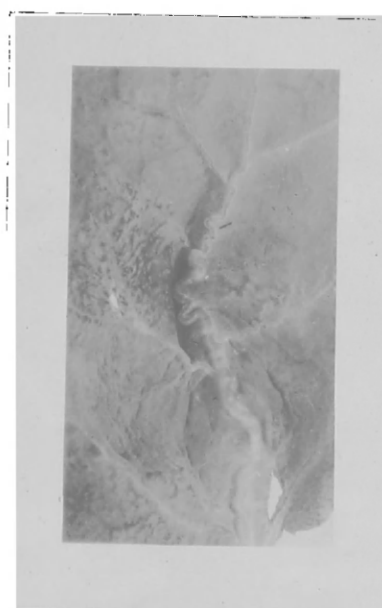

Fig. 16. Leaf showing wrinkled veins.

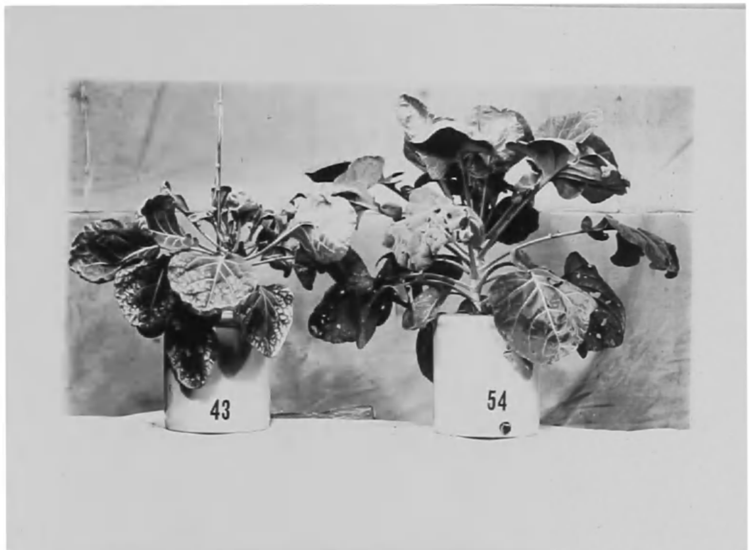

Fig. 17. The plant on the left did not receive an adequate quantity of boron and shows rugose, chlorotic leaves. The plant on the right is healthy.

Fig. 18. Brussels sprouts showing the premature death of the apical meristem.

ciency occurs before the sprouts begin to develop, no sprouts are produced or they are very small. If the deficiency occurs after the sprouts have started to develop, the sprouts are smaller than usual and the outside leaves are distorted and curled outward forming very loose, sprouts, Figure 19.

Fig. 19. Brussels sprouts produce very loose sprouts when boron is deficient.

Cabbage, Brassica oleracea var. capitata, Linn. Horticultural varieties Early Jersey, Wakefield and Mammoth Red Rock. The leaves of boron deficient cabbage plants droop and have a wilted appearance yet feel very thick and stiff. The leaves which develop when the plant is not adequately supplied with boron are curled, due to a difference in growth rate of the different parts of the leaf. Some of the leaves may be broken by the strain resulting from the difference in growth rate, Figure 20. Such leaves are very brittle and break easily when touched. Like the preceding plants, cabbage, particularly the red cabbage, has swellings which later cork over. In cabbage these gradually develop up the petiole, on the under side, on to the midrib and occasionally are found on the secondary and tertiary veins, Figure 21. When the deficiency occurs before the head starts

Fig. 20. Plant number 10 shows the wilted appearance of a plant receiving too little boron. Plant number 2 has leaves broken by the mechanical stresses set up when boron is not supplied. Plant number 11 produced no head. Plant number 15 is healthy.

Fig. 21. A red cabbage leaf which shows swellings on the under side of the petiole and midrib. The interior of the stem of the plant has brown spots especially near the top.

to form, no head is produced, Figure 22. However, if the head is fairly well developed when the deficiency occurs, abscission of the outside leaves of the head occurs, causing the head to appear yellow, Figure 23. Almost all of the midribs of the outer leaves of the head may have cork at the time of harvest, Figure 24. The stem of cabbage plants which have not been adequately supplied with boron have brown areas similar to those found in cauliflower suffering from this deficiency. In the field, plants have been observed in which abscission of the outer leaves of the head has occurred and with brown areas in the stem.

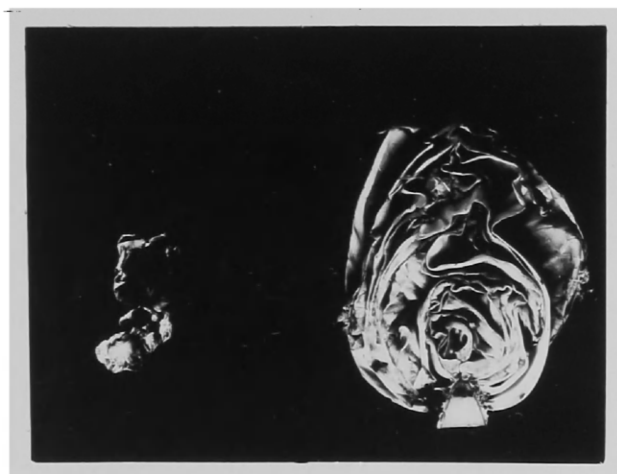

Fig. 22. Cabbage plants produce no head if deficiency occurs before head formation begins (left). However, if head formation has started a small loose head is produced with a brown area in the top of the stem (right).

Kimbrough (45) in reporting on the effect of sources of nitrogen found that nitrate of soda was superior to calcium nitrate for the growth of cabbage. The description and pictures indicate that his cabbage plants were suffering from boron deficiency even when supplied with Chilean nitrate of soda.

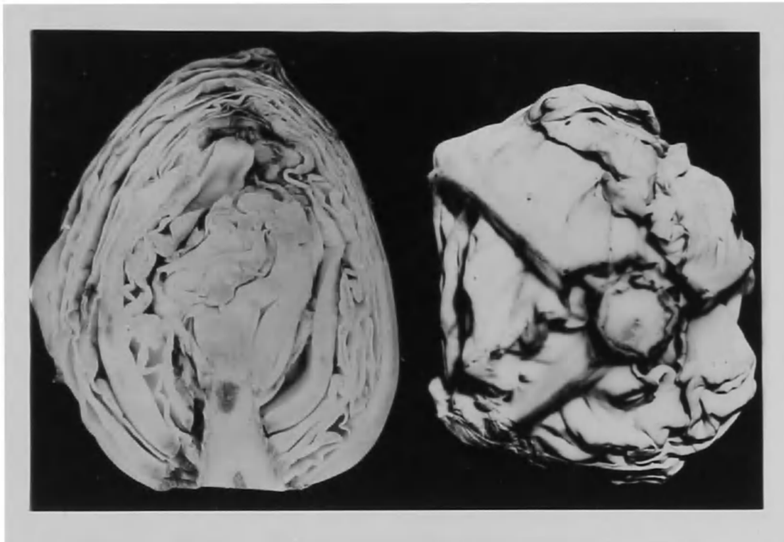

Fig. 23. When boron deficiency occurs after the head is formed abscission causes the leaves to separate from the stem. The picture on the left is of a plant grown in the greenhouse while that on the right is from a field-grown plant.

Fig. 24. The outer leaves of a cabbage head suffering from severe boron deficiency. Note the corky appearance of the midrib and veins.

Cauliflower, Brassica oleracea var. botrytis, Linn. Horticultural variety Super Snowball, several strains. Brown rot of cauliflower has been known for twenty-five or thirty years and has caused serious damage to cauliflower, particularly in New York in some seasons. Chupp and Horsfall (12) published a description of the disease in 1933 and stated the disease was most severe in seasons with low rainfall during June and July. These investigators and others could not isolate any organism and Chupp and Horsfall thought the trouble might be related to water heart in rutabaga. In 1935 Dearborn and Raleigh (14) controlled this disease, also called internal browning, with applications of borax of 1.25 to 5 pounds per acre. The latter investigators with Thompson (15) published the results of greenhouse and field experiments a year later showing the trouble was controlled with 6 pounds of borax per acre.

The first symptom of boron deficiency in cauliflower is a rolling of the leaves, usually downward. At this time the leaves are very brittle, breaking easily when touched and occasionally breaking without being touched, Figure 25. Later the younger leaves are very badly rolled and curled and the intermediate leaves may be rugose. In severe cases the young leaves have an enlarged midrib, with no leaf blade, Figure 26. Severely affected leaves frequently have cork on the midrib. Plants suffering from this deficiency are always dwarfed. When boron deficiency is not severe a head is developed which has watery or brown areas and the stems of

Fig. 25. The plant on the left received boron for only 18 days. The leaves are curled, rolled and cracked and the head is very small and brown. The plant on the right was supplied with boron continually.

Fig. 26. The two leaves on the left are from healthy plants and the four in the center are from boron deficient plants. The heads on the right are from healthy plants while the others are from deficient plants.

such heads have transparent or brown areas, Figure 27. No head is produced on extremely deficient plants. Some workers

Fig. 27. Field-grown plants with varying degrees of boron deficiency. The two heads on the right and part of the second one from the left are severely affected with boron deficiency. Note the watery and brown areas in the stem.

have claimed that boron deficient cauliflower has hollow stems but in a field experiment in 1937 no relation could be found between boron deficiency symptoms and hollow stem or between the amount of borax applied, up to 50 pounds per acre, and the number of plants with hollow stems. In plants showing boron deficiency the tissue around the cavity is always watery or brown. The same is also true for broccoli. Hartman (32) working at the same time at Purdue University and Long Island observed hollow stems with one of his boron treatments and stated "This was the only case in this experiment, or in any others, where hollow stem was produced in the greenhouse without known boron deficiency." The author has observed all of the symptoms of boron deficiency in cauliflower under field conditions.

Chinese Cabbage, Brassica pekinensis. Horticultural variety Chihili (Celery Cabbage). Boron deficiency in Chinese cabbage is first expressed as curling and rolling of the leaves, particularly at the tips. Later the deficient plants have rugose leaves much like the leaves of savoy cabbage, Figure 28. When the deficiency extends for a period

Fig. 28. The two Chinese cabbage plants on the left show boron deficiency as curled rugose leaves. The plant on the right received boron.

of time the midrib becomes cracked inside transversely and the leaf becomes chlorotic, Figure 29. This is the only plant in the Brassica group which has transverse cracks and is unlike celery which has the cracks on the outside of the petiole (67). Deficient Chinese cabbage plants do not produce a marketable head as the top of the stem is killed very early, Figure 30. No symptoms of boron deficiency in this plant have been observed in the field.

Fig. 29. The leaf on the left shows transverse cracking of Chinese cabbage due to insufficient boron. The leaf on the right is healthy.

Fig. 30. Without boron Chinese cabbage do not produce a marketable head. The heads on the left and right are from plants well supplied with boron, while those in the middle are deficient.

Kale, Brassica oleracea var. acephala, DC. Horticultural variety Dwarf Blue Scotch. Like Chinese cabbage this rapid growing plant has fewer symptoms than some of the slow growing plants. When boron is withheld from the nutrient solution the leaves of kale are more curled and rolled than the leaves of deficient plants already described, Figure 31.

Fig. 31. The kale plant on the left received boron only during its early stage of growth, the one on the right received boron continually.

Chlorosis is distributed over the entire leaf, Figure 32. The leaves of deficient plants are frequently rugose. Like other plants in this genus, brown dead areas appear inside the stem before the tip dies, Figure 33. The tip does not die until the internal breakdown has extended to the outer part of the stem, cutting off the supply of nutrients from the root. Lateral shoots frequently develop below the dead tip.

Fig. 32. Healthy kale leaves have a dark green color (left) while boron deficient leaves are chlorotic.

Fig. 33. Longitudinal section through the stem of kale plants. The stem in the top row left is from a healthy plant. The other stems show varying amounts of boron deficiency.

Kohlrabi, Brassica oleracea var. Caulo-Rapa, DC. Horticultural variety White Vienna. Unlike most of this group kohlrabi plants with boron deficiency grow more erect than those plants which do receive boron, Figure 34. The

Fig. 34. The two kohlrabi plants on the left show boron deficiency. The one on the right is healthy.

curling and rugosity of the leaves is not quite as noticeable and the swelling on the stems in deficient plants is less common than in other members of the genus Brassica. If the plant is deprived of boron before the edible part of the stem starts to develop, little or no development takes place. However, when boron is removed from the plant after the edible part has begun to enlarge, further development is slightly retarded and the surface becomes more or less covered with cork, Figure 35. Such stems are often abnormal in shape and develop watery or brown areas and in some cases become hollow, Figure 36. These symptoms have been observed only in the greenhouse.

Fig. 35. The outer surface of kohlrabi becomes rough when boron is insufficient (two on left).

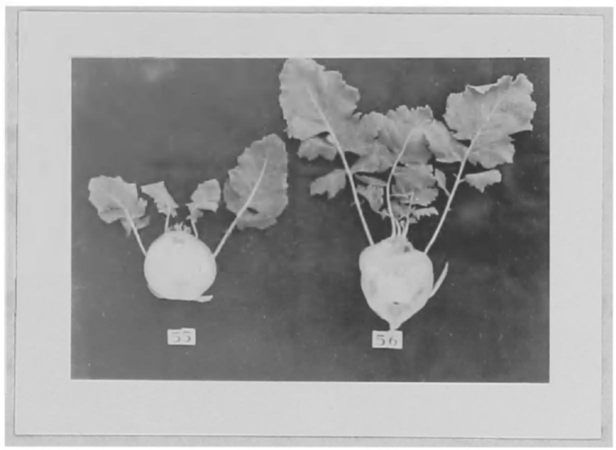

Fig. 36. The inside of kohlrabi stems become watery, brown or hollow when the plants are deprived of boron.

White Mustard, Brassica alba, Boiss. Horticultural variety White London. White mustard supplied with boron for 18 days has no deficiency symptoms when grown for greens. However, plants grown for seed fail to flower when boron deficiency occurs before flower formation and fails to fruit when the deficiency occurs just after flower formation. Deficient plants are dwarfed, have curled leaves which frequently roll down, and show rugosity, Figure 37. Deficient plants have fewer seed stalks and the ones produced are short with malformed blossoms and leaves.

Fig. 37. The two white mustard plants on the left did not receive enough boron. The one on the right is healthy.

Rape, Brassica Napus, Linn. The symptoms of boron deficiency in rape are almost exactly the same as those for kale. Rape plants are dwarfed with rugose, chlorotic, rolled leaves. Frequently the petioles are cracked and the stem usually has brown dead areas.

Rutabaga, Brassica Napo-brassica, DC. Horticultural variety American Purple Top. Brown heart of rutabaga has been observed for twenty-five years or more. In 1915 Woods (86) described the disease and presented the results of the previous season's work which showed that the condition was not caused by an organism and could be partially controlled by the use of manure. Hurst (37) came to similar conclusions in 1930. In 1934 MacLeod and Howatt (50) found that brown heart could be controlled by applying 10 pounds of borax per acre in the row.

Since 1934 investigators all over the world have studied browning of rutabaga and the amount of boron necessary to control it.

In the summer of 1934 experiments were conducted in the field in the rutabaga section of Maine. Since that time many experiments have been conducted with rutabaga in the field and in the greenhouse. The field experiments have shown that 5 and 8 pound applications were not sufficient but the 10 pound applications prevented brown heart in all of the trials in the rutabaga section. In one experiment in 1937 in which the rate of borax varied from 5 to 50 pounds per acre the highest application produced much better rutabagas than the lower ones but none of the applications produced rutabagas entirely free from brown heart. Cauliflower were grown in the same field as the rutabaga and only a small percentage of these plants showed boron deficiency. Probably a small part of this difference was due to species variation but most of the difference was due to seasonal effect. The soil was wet when the cauliflower was planted followed by a heavy rainfall. Later, when the rutabaga was planted there was very little rain and a dry growing season followed. Other investigators have found a seasonal effect for rutabagas (11, 26 and 86), for apples (68), for sugar beets (8, 46 and 58), for potatoes (63) and for crops in general (17 and 18). Because of the great difference in results obtained in this field, from almost no boron deficiency in cauliflower to almost 100 per cent in rutabaga, apparently due to seasonal conditions, very little emphasis is being placed on the numerous field experiments conducted in various parts of the State.

When rutabaga is not adequately supplied with boron in either greenhouse or field, the plants are dwarfed, and have curled leaves which are rugose, Figure 38. The older leaves are more brittle and more horizontal in plants

Fig. 38. The rutabaga plant on the left has boron deficiency. The one on the right is healthy.

not supplied with boron than in healthy plants. In severe cases of deficiency the leaf margins are chlorotic (51), a reddish purple pigment develops on the under side of the leaves and the leaves fall prematurely (38), Figure 39.

Fig. 39. A rutabaga plant severely affected with boron deficiency. This plant had chlorotic leaf margins with pigment on the under side. (This is an enlargement from a color film).

In 1935 the author with others (10) stated that rutabagas affected with boron deficiency often had rough skins and the roots were cracked, Figure 40. However, it has been the opinion of some investigators (20, 61, 65 and 74) that there were no external symptoms. The severity of the deficiency varies the amount and the type of the injury inside

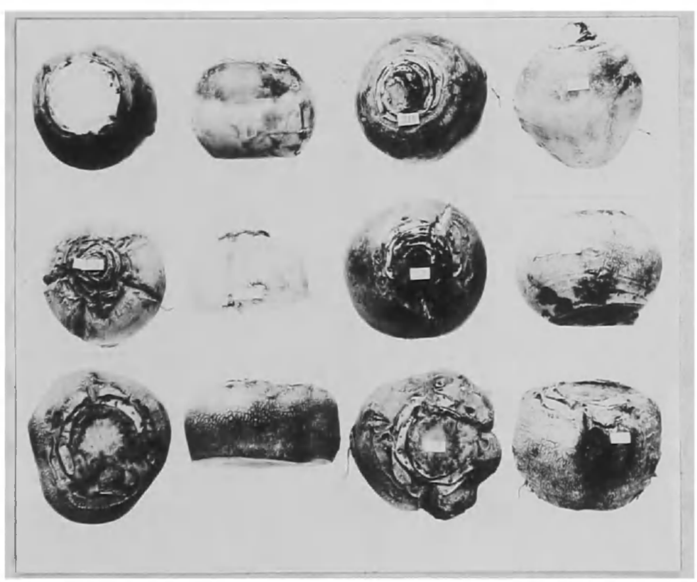

Fig. 40. This picture shows the top and side view of the same rutabaga. Top row healthy, bottom two rows have brown heart.

the storage root. In some cases the injury has a watery appearance, in others brown spots and in most severe cases it may be hollow, Figure 41. The brown heart in roots has various designs. The affected areas may be small and scattered or they may have a tendency to be grouped or they may be in rings, Figure 42. Brenchley (8), Donaldson (20) and O'Brien and Dennis (61) have stated that brown heart did

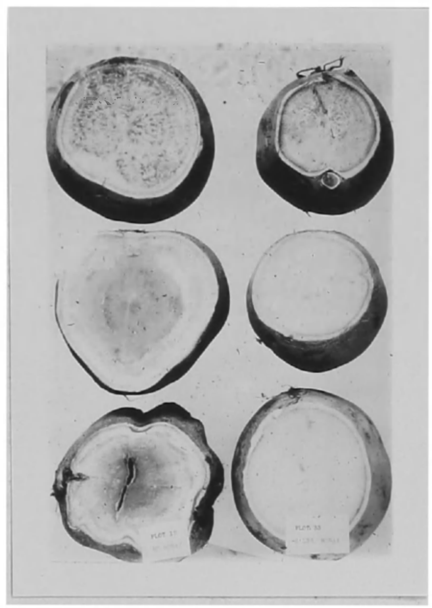

Fig. 41. Rutabagas with no borax, and with 5 pounds per acre. Without borax the roots were watery, brown or hollow hearted. With 5 pounds of borax per acre some of the roots were normal and some had brown heart.

not extend to the top of the rutabaga and Rigg, Askew and Chittenden (69) have stated that brown heart did not extend to the bottom. However, the author has observed rutabagas in the field which were affected at the top and down to the bottom of the storage root. In the greenhouse boron deficient rutabagas are smaller than healthy ones but in the field there is little or no difference in size.

Fig. 42. The rutabaga in the top left hand corner is healthy. The others show varying degrees of brown heart.

Turnip Brassica Rapa, Linn. Horticultural variety Purple Top White Globe. The boron deficiency symptoms are almost exactly the same for turnips as those for rutabagas, Figure 43.

Fig. 43. Turnips have a rough surface when grown without boron (two on left), while healthy roots have a smooth surface (right).

The Growth of Plants Supplied with Boron at Different Periods Compared with Plants which had the Boron Removed at Corresponding Periods

Eighteen rutabaga plants were transplanted into individual jars and supplied with nutrient solution containing 0.05 ppm of boron. At the same time another group of eighteen plants was transplanted which received 0.3 ppm of boron in the nutrient solution. When the plants had grown for 18 days six of the plants receiving the low concentration of boron were flushed with two quarts of nutrient solution containing 0.3 ppm of boron and were supplied with this solution to the end of the experiment. At the same time six of the plants receiving 0.3 ppm of boron were changed to 0.05 ppm as in the preceding experiment (page 26). Forty-one days after transplanting, the six plants just mentioned were changed to a no boron solution and six plants which had received 0.3 ppm of boron from the beginning of the experiment were changed to no boron. On the same day six plants which had received 0.05 ppm of boron from the beginning of the experiment were changed to 0.3 ppm of boron. The last change was made when the plants were 58 days old at which time the last six plants receiving high boron were changed to no boron and the last six receiving low boron were changed to high boron.

The widest leaf on each plant was measured and tagged 35 days after transplanting. The widest leaf and the tagged leaf were measured several times before harvest. The data obtained from these measurements are presented in Table XVI and plotted in Figure 44.

TABLE XVI

Widths in Inches of the Widest Leaves and of the Tagged Leaves of Rutabaga Plants Grown with an Inadequate Supply of Boron Followed by an Adequate Supply Compared with Plants Grown with an Adequate Supply Followed by a Solution without Boron

Days from transplanting	0.3 ppm of boron changed to no boron			0.05 ppm of boron changed to 0.3 ppm		
	18 days	41 days	58 days	18 days	41 days	58 days
	Inches	Inches	Inches	Inches	Inches	Inches
			Width of Widest Leaf			
35	4.38	5.15	5.04	5.08	5.05	4.99
43	6.65	6.35	6.61	6.50	6.35	6.44
54	6.43	6.97	7.63	7.18	7.25	7.25
65	6.55	7.58	8.68	8.29	8.29	8.17
69-75	6.99	7.66	9.22	9.45	9.50	9.54
			Width of Tagged Leaf			
35	4.38	5.15	5.04	5.08	5.05	4.99
43	6.38	6.35	6.08	6.30	5.90	6.00
54	6.44	6.44	6.23	6.25	5.92	6.19
65	6.16	6.63	6.75	6.48	6.29	6.35
69-75	4.55	6.55	6.22	6.75	6.24	6.51

The width of the widest living leaf is a measure of plant growth while the width of the tagged leaf is only a measure of the growth of that leaf. The decrease in width of the tagged leaf indicates approximately the time that death occurred. These data show that death occurs first on those plants which received 0.3 ppm of boron for 18 days followed by 0.05 ppm for 23 days. The tagged leaf on these plants died when the plants were 54 days old or 13 days after

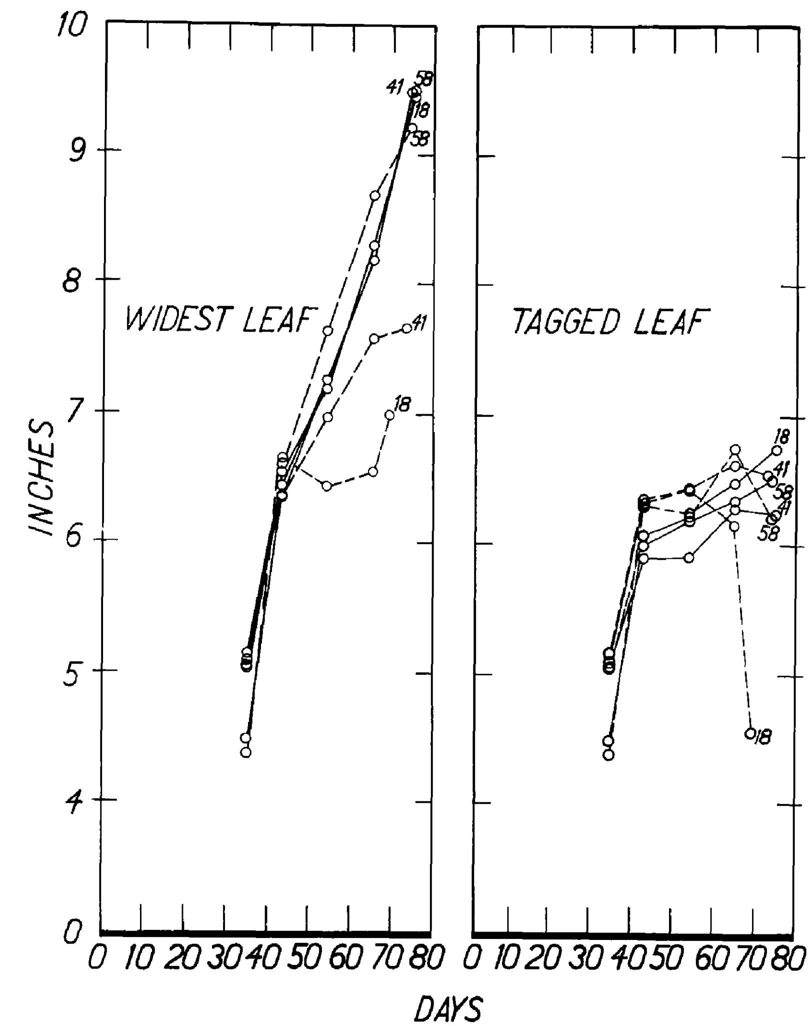

Fig. 44. Curves showing the average widths in inches of the widest leaves and of the tagged leaves (widest when the plants were 35 days old) of rutabaga plants grown with an inadequate supply of boron followed by an adequate supply (solid line) and grown with an adequate supply followed by a solution without boron (dotted line).

the boron was removed. The tagged leaf lived 24 days after the removal of boron in the 41 day treatment and 7 days after the removal of boron in the 58 day treatment. This indicates a slight storage or a translocation of boron. From the discussion presented in the previous experiment, pages 28 to 31, the theory of translocation is preferred. A study of Table XVI and Figure 44 shows that all of the tagged leaves of plants changed from 0.3 to no boron decreased in width before the end of the experiment. The greatest decrease in width of the tagged leaf is with the early removal of boron and this is associated with an increase in rate of growth of the widest leaf which is not shown for any other treatment. In many plants severely affected with boron deficiency the plants appeared to be in such poor condition that death was expected very soon, yet before death the lower leaves withered and fell off which enabled the plant to survive until more leaves fell, supplying more boron to the plant. The lateral shoots may fall off for a short time supplying enough boron to keep the plant alive for several days.

At harvest the plants grown with 0.05 ppm of boron and changed to 0.3 ppm of boron were much better than the group started with 0.3 ppm of boron and changed to no boron. The storage root which was the nearest to the mean for each treatment is shown in Figure 45. The storage root had a smaller diameter than the stem when the plants received the 0.3 ppm of boron for only 18 days. These roots were very rough on the outside and some parts of them had decayed. Some plants had leaves with yellow margins on the upper surface and reddish purple margins on the under surface, Figure 39. The plants with this treatment were harvested 69 days after transplanting because one plant was so severely affected with boron deficiency that it appeared to be dying. Plants of this treatment as well

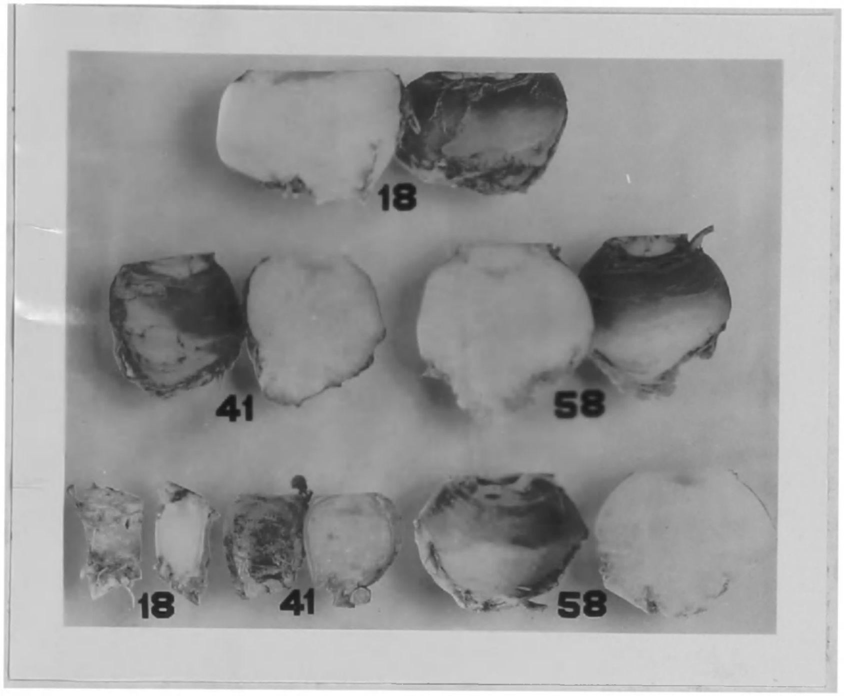

Fig. 45. The top and center rows show rutabagas from the group of plants changed from 0.05 ppm of boron to 0.3 ppm, the change being made at 18, 41 and 58 days respectively. The bottom row shows rutabagas started with 0.3 ppm of boron and changed to a solution of 0.05 ppm of boron at 18 days, then to no boron at 41 days, and 0.3 ppm to no boron at 41 and 58 days respectively.

as some of those which were changed from 0.3 ppm to no boron 41 days after transplanting had lost their apical dominance. The change from 0.3 ppm to no boron made at 58 days had much less effect upon the plants than other changes from 0.3 ppm to no boron, but the average weight of these plants was less than the average weight of the plants from any of the 0.05 to 0.3 ppm of boron treatments. None of the plants started with 0.05 ppm and changed to 0.3 ppm of boron showed external symptoms of boron deficiency and the internal symptoms were not severe although some of the plants had a trace of brown heart. The data obtained at harvest are presented in Tables XVII and XVIII which show that the plants

TABLE XVII

Average Fresh Weight in Grams at Harvest of Plants from Which Boron was Removed at Different Ages Compared with Plants Which had an Inadequate Supply of Boron Changed to an Adequate Supply at the Same Time

Treatment	Fresh Weight			
	Roots			
	Storage	Feeding	Leaves	Total
	grams	grams	grams	grams
0.3 to no boron				
18 days	69.77	30.58	217.83	318.18
41 "	155.95	50.67	381.36	587.98
58 "	370.11	79.45	644.50	1094.06
0.05 to 0.3 boron				
58 days	361.13	96.82	733.22	1191.17
41 "	361.28	105.10	810.03	1276.41
18 "	408.12	102.23	728.28	1238.63

TABLE XVIII

Measurement, and Length/Width Ratio, of Leaves from Plants from which Boron was Removed Compared with Leaves from Plants which had an Inadequate Supply of Boron Changed to an Adequate Supply

Treatment	Number of leaves	Measurement of Leaves		
		Greatest length	Greatest width	Length/Width
		Inches	Inches	Ratio
0.3 to no boron				
18 days	13.17	19.07	6.99	2.73
41 "	15.50	21.75	7.66	2.84
58 "	18.83	25.75	9.22	2.79
0.05 to 0.3 boron				
58 days	19.17	26.02	9.54	2.73
41 "	20.33	25.85	9.50	2.72
18 "	19.33	25.10	9.45	2.66

started on the low amount of boron which was later increased grew much better than those plants started with a high amount of boron which was later removed. The average weight of each plant part of plants changed from 0.3 ppm to no boron at 18 days and 41 days was significantly smaller than the plant parts of plants of all other treatments in this experiment. The data for the other treatments were not significantly different. The results of this experiment, like the last, show that the growth of plants is not directly associated with the time or the amount of boron supplied. From the fresh weight of the entire plant or of the storage root it is evident that 0.05 to 0.3 ppm of boron treatments produced plants of about the same size regardless of time of change. However, the quality was improved with early change from 0.05 to 0.3 ppm of boron.

The Development Expressed as Ratios of Some of the Plants in the Above Experiments, and Other Statistical Analysis of the Data

In order to determine whether or not all parts of a plant are equally affected by boron deficiency the results of the foregoing experiments are expressed as ratios in this section. Table XIX presents the length/width ratios of several kinds of Brassica plants with various boron treatments. These ratios show that the relative shape of leaves is not materially changed by the amount of boron supplied. The rutabaga data show that there is more difference between

TABLE XIX

Ratio of Leaf Length/Leaf Width of Different Kinds of Brassica Plants Grown with Different Amounts of Boron

Treatment	Amount of boron	Time of change	Kind of plant					
			Brussels sprouts	Broccoli	Green cabbage	Red cabbage	Rutabaga	Cauliflower
	ppm		ratio	ratio	ratio	ratio	ratio	ratio
Changed	0.3-0	Early	1.79	2.54	1.42	1.59	2.73	
"	.3-0	Medium	1.79	2.25	1.58	1.57	2.84	
"	.3-0	Late	2.09	2.38	1.45	1.32	2.79	
Continued	.1	None					2.26	2.25
"	.3	None					2.31	2.44
"	.5	None					2.35	2.06

experiments than between treatments in the same experiment. Table XX presents the fresh weight of leaves/fresh weight

TABLE XX

Ratio of Fresh Weight of Leaves/Root Weight of Different Kinds of Brassica plants Grown with Different amounts of Boron

Treatment	Amount of boron	Time of change	Kind of plant					
			Brussels sprouts	Broccoli	Green cabbage	Red cabbage	Rutabaga	Cauliflower
	ppm		ratio	ratio	ratio	ratio	ratio	ratio
Changed	0.3-0	Early	4.04	5.45	10.30	9.79	7.12	
"	.3-0	Medium	3.98	5.45	10.90	9.72	7.52	
"	.3-0	Late	7.01	4.18	9.45	9.32	8.11	
Continued	.1						13.36	4.87
"	.3						14.32	5.16
"	.5						13.39	4.68

of roots. These ratios are not as uniform as those for leaf length/leaf width, but with the exception of Brussels sprouts there is no significant difference between treatments. The ratios of the fresh weight of leaves/stem weight, Table XXI, shows significant differences with only one plant, red cabbage.

TABLE XXI

Ratio of Fresh Weight of Leaves/Stem Weight of Different Kinds of *Brassica* Plants Grown with Different Amounts of Boron

Treatment	Amount of boron	Time of change	Kind of plant: Brussels sprouts	Broccoli	Green cabbage	Red cabbage	Cauliflower
	ppm		ratio	ratio	ratio	ratio	ratio
Changed	0.3-0	Early	4.75	2.93	6.95	6.45	
"	.3-0	Medium	4.97	2.59	6.78	7.01	
"	.3-0	Late	4.27	1.97	6.77	4.35	
Continued	.1	None					5.92
"	.3	None					4.34
"	.5	None					4.25

On the other hand, fresh weight of leaves/fresh weight of the edible part, Table XXII, shows considerable change in the ratio except for rutabaga when the boron was removed from the nutrient solution. In this table the ratios for cauliflower did not change as much as the ratios for other plants but they changed more than the ratios for cauliflower in the other tables. From these tables it is evident that a deficiency of boron dwarfs the plant keeping all organs except the edible part in the same mass relationship. The ratio of total fresh weight/leaf weight, Table XXIII, shows an increase with duration

TABLE XXII

Ratios of Fresh Weight of Leaves/Edible Part of Plant of Different Kinds of *Brassica* Plants Grown with Different Amounts of Boron

Treatment	Amount of boron	Time of change	Kind of plant					
			Brussels sprouts	Broccoli	Green cabbage	Red cabbage	Rutabaga	Cauliflower
	ppm		ratio	ratio	ratio	ratio	ratio	ratio
Changed	0.3-0	Early	30.76	157.02	8.23		3.12	
"	.3-0	Medium	9.57	76.74	1.67	748.26	2.44	
"	.3-0	Late	19.28	9.12	.76	4.88	1.74	
Continued	.1	None					1.28	4.92
"	.3	None					1.37	4.15
"	.5	None					1.43	2.88

TABLE XXIII

Ratio of Fresh Weight of the Entire Plant/Leaf Width of Different Kinds of *Brassica* Plants Grown with Different Amounts of Boron

Treatment	Amount of boron	Time of change	Kind of plant					
			Brussels sprouts	Broccoli	Green cabbage	Red cabbage	Rutabaga	Cauliflower
	ppm		ratio	ratio	ratio	ratio	ratio	ratio
Changed	0.3-0	Early	43.4	65.6	58.5	45.7	45.5	
"	.3-0	Medium	63.8	69.0	96.2	52.5	76.76	
"	.3-0	Late	118.4	98.5	104.0	80.5	118.6	
Continued	.1	None					89.5	66.7
"	.3	None					95.9	98.4
"	.5	None					89.1	88.5

of the optimum amount of boron. The part of this table expressing the ratios for levels of boron shows a decrease in the ratio with the lowest and highest levels. As the length/width ratios of the plants grown with these treatments was not significantly changed the leaf width may be considered a good measure of leaf area. Therefore these ratios may be considered as expressions of efficiency of the leaf area to produce total fresh weight. The most efficient production is with 0.3 ppm of boron supplied continually. According to the data for rutabaga the efficiency varies with season of growth, being most efficient in the summer and least efficient in the fall.

The regression line of total fresh weight on leaf width for each treatment of each rutabaga and cauliflower experiment is plotted in Figure 46. In the rutabaga experiment in which boron was supplied at different periods of time in comparison with the removal of boron the lines have a more uniform slope than in the other experiments. These lines, with the exception of one, show a greater weight for a given increase in leaf width with plants well supplied with boron than with plants poorly supplied with boron. The experiment with rutabaga in which levels of boron were studied shows very little difference in the slope of the regression line. In the experiment with rutabaga in which the effect of removing the boron 31 days after transplanting was studied the plants all had about the same weight regardless of the leaf width, while the control plants (0.5 ppm continually) had narrower leaves

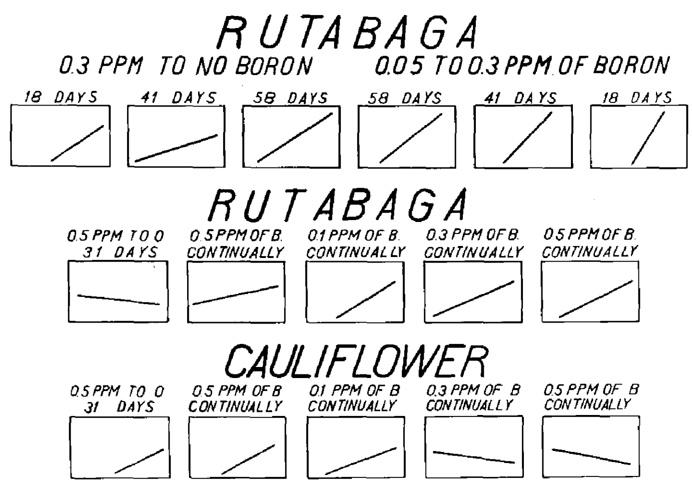

Fig. 46. Regression of fresh weight of plants on leaf width for each treatment of each rutabaga and cauliflower experiment (scatter diagrams with regression will be found in Appendix A).

on the heavy plants than on the light ones. The experiment on levels of boron and removal of boron was conducted at the same time and the lack of agreement of the two groups of plants receiving 0.5 ppm of boron may be explained by the variability which is expressed by the correlation coefficient, Table XXIV. With cauliflower the regression lines for the plants which had the boron removed and for the control (0.5 ppm) have approximately the same slope and nearly the same

TABLE XXIV

Regression Equation and Correlation Coefficient of Leaf Width to Fresh Weight of Plants of Rutabaga and Cauliflower Plants Grown with Different Treatments

Kind of plant	Treatment ppm of boron and days of treatment	Regression Equation* $E=\bar{y}+\frac{Sxy}{Sx^2}(X-\bar{x})$	Correlation Coefficient	Significance**
Rutabaga	0.3-no boron			
	18 days	70.12X-662.21	.9151	S
	" 41 days	31.73X+102.08	.3301	N
	" 58 days	62.60X-60.16	.4338	N
	All 0.3-no boron		.8943	HS
	0.05-.3 58 days	81.02X-353.78	.5576	N
	" " 41 days	107.57X-765.40	.6076	N
	" " 18 days	167.58X-1930.42	.6824	N
	All 0.05-.3		.5772	HS
	Total expt.		.88541	HS
	0.5-no boron	-11.48X+329.40	-.1340	N
	0.5	19.86X+513.23	.28809	N
	Total		.5771	S
	0.1	64.635X-457.41	.4640	N
	0.3	45.4636X+42.62	.7948	N
	0.5	51.1031X-123.46	.8206	S
	Total levels		.7764	HS
	Total of 0.5		.6178	S
	Total for expt.		.2985	N
	Total for all expts.		.5834	HS
Cauliflower	0.5-no boron	54.59X+590.12	.5978	N
	0.5	59.16X+511.145	.9228	HS
	Total	51.9461X+366.56	.6839	HS
	0.1	46.573X+236.74	.7936	N
	0.3	-13.4143X+786.76	-.1488	N
	0.5	-22.486X+929.14	-.9495	S
	Total	42.41X-87.05	.1865	N
	Total for 0.5	28.007X+68.18	.5215	N
	Total for all expts.	19.88X+162.08	.3739	S

*As the original data were obtained in half-inch units before substituting in this equation the inches will have to be multiplied by two to obtain the desired weight.

** N= not significant; S= 19 to 1; HS= 99 to 1.

points of origin. This experiment was conducted in the fall. The data for the experiment on levels of boron with cauliflower indicate that the heavy plants receiving 0.1 ppm of boron have wide leaves. On the other hand, the 0.3 ppm and 0.5 ppm treatments have narrower leaves on the heavy plants than on the light ones. This experiment was conducted in the summer. The correlation coefficient of both the 0.5 ppm are significantly high, one being positive and the other negative. This would indicate that there may be a seasonal effect on the correlation coefficient of leaf width and plant weight.

Root Development of Plants Grown With and Without Boron

To supplement the information on the fresh weight of roots presented in the previous experiments, plants were grown in root boxes and in water cultures to study the root development. Broccoli, Brussels sprouts and rutabaga were grown in water culture with pH 6.9 and Brussels sprouts and red cabbage were grown in solutions which had the pH varied from 4.0 to 8.5. In one experiment rutabaga plants were placed so that some of the plants had the roots divided, part being in a nutrient solution with boron and part in a nutrient solution without boron.

The development of roots in the root boxes, presents a very striking picture, Figure 47. These studies have shown that there is considerable difference in the growth rate of plants. The rutabaga roots grew the fastest, 20 inches in 17 days, and showed the greatest difference between no boron and 0.3 ppm of boron. With rutabaga, 3.0 ppm of boron did not

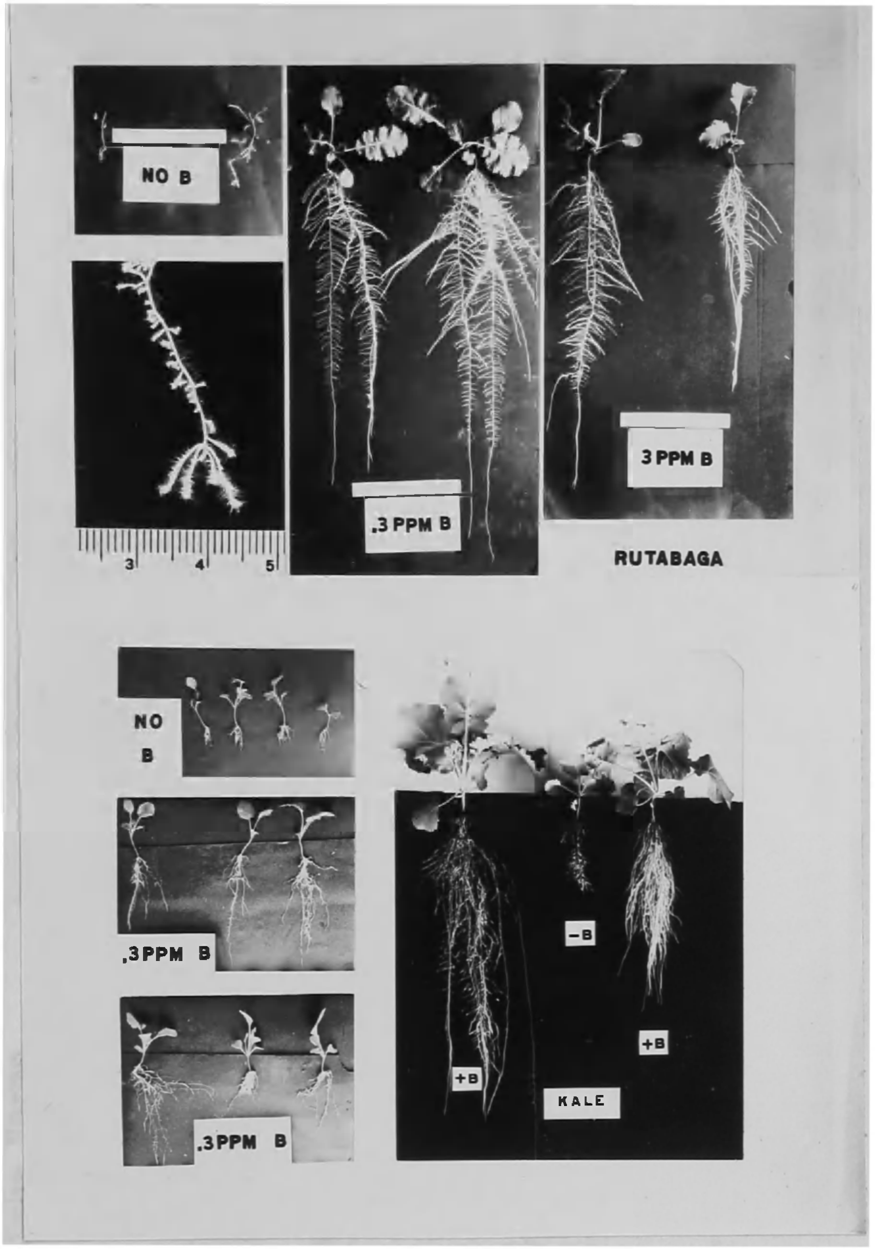

Fig. 47. Development of roots in root boxes. Top rutabaga x 1/10 with one root of the no boron treatment natural size. Lower left broccoli x 1/10. Lower right kale x 1/10.

appear to be very toxic. When boron was supplied more growth was obtained in all cases, although with other plants the results were not as striking as with rutabaga. The root lengths for some of the plants grown in the root boxes are presented in Tables XXV and XXVI. The average daily growth of each plant

TABLE XXV

Growth of the Longest Root of Plants Grown in Root Boxes Plus Boron (0.3 ppm) and Minus Boron

Days from setting plants	Kind of plant and treatment												
	Kale			Cauliflower				Rutabaga			Broccoli		
	Plus	Plus	Minus	Plus	Plus	Minus	Minus	Plus	Plus	Minus	Plus	Minus	Minus
	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.
0	14.0	8.5	8.5	4.6	2.1	6.5	4.6	4.1	6.1	5.1	6.9	3.9	3.8
1	16.7	8.9	8.5	4.8	2.2	7.0	4.7	4.3	7.1	5.4	7.7	4.0	4.1
2	19.1	9.4	8.5	4.9	2.8	7.6	5.2	6.5	8.2	5.7	7.9	4.1	5.2
3	21.7	10.5	8.5	5.7	3.3	8.4	5.7	8.3	9.1	6.4	8.3	4.2	6.4
4	24.0	11.6	8.5	7.8	4.4	9.9	6.9	9.9	11.3	7.2	10.0	4.5	9.5
5	26.4	12.9	8.5	8.8	4.7	10.4	7.3	9.9	12.0	7.9	10.7	4.7	11.6
6	29.0	14.3	8.5	10.5	4.9	11.5	8.4	10.2	13.0	8.4	11.8	5.0	13.3
7	32.0	15.3	8.5	--	5.1	12.5	9.2	11.3	13.7	9.3	12.8	5.3	--
8	37.0	17.5	8.5	--	--	12.8	10.2	12.6	13.7	10.9	13.1	5.8	--
9	41.1	19.2	8.5	--	--	12.9	10.5	15.5	13.7	13.2	13.7	6.4	--
10	43.5	19.5	8.5	--	--	12.9	10.6	18.6	13.7	15.4	14.2	6.9	--
11				18.5	12.5	13.2	10.8	19.4	13.8	16.9	15.6	7.3	22.7

receiving boron was 1.25 mm. whereas the average daily growth of each plant not receiving boron was 0.71 mm.

TABLE XXVI

Average Length of Longest Root, Average Weight, and Percentage Moisture of Rutabaga Plants Grown in Root Boxes and in Water Cultures with (0.3 ppm) and without Boron

Treatment	Longest root	Fresh weight		Dry weight		Moisture	
		Tops	Roots	Tops	Roots	Tops	Roots
	cm.	grams	grams	grams	grams	%	%
Root boxes plus boron	15.4	1.282	--	0.101	--	92.23	--
Root boxes minus boron	12.8	.460	--	.037	--	89.95	--
Water cultures plus boron	11.4	1.018	0.102	.078	0.033	92.30	91.92
Water cultures minus boron	10.6	.403	.043	.013	.009	87.17	79.92

The broccoli plants in Figure 47 were placed horizontally on a laboratory bench after the picture was taken. Several days later negative geotropism was shown by the plants which had received boron while the plants which did not receive boron did not respond, Figure 48.

The effect on root development of growing plants in water cultures with and without boron is shown in Figure 49. Without boron the number of secondary roots is greatly increased but the development of each root is greatly retarded. The secondary root may be only a millimeter in length. This had been previously observed in other crops by several investigators, Warington (81) in Vicia faba, Sommer and Soroknin, (76)

Fig. 48. The row of broccoli plants from lower left hand corner to the center did not receive boron and do not show negative geotropism. The other plants did receive boron and do show negative geotropism.

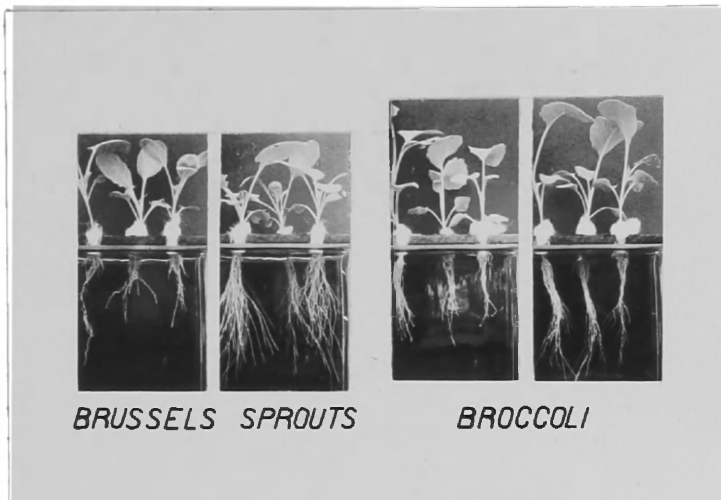

Fig. 49. The development of Brussels sprouts and broccoli roots without boron (left) and with boron (right).

in __Pisum sativum__ and van Schreven, (78) in __V. faba__ and flax. The roots in general are dark with a club-shaped enlargement near the end having a black tip. In these cultures the effect of boron deficiency was not noted until the third day after the plants were put in the no-boron solution. The fresh and dry weight, the percentage moisture and the length of the longest root for rutabaga plants grown for 36 days in water cultures are presented in Table XXVI. The figures show little difference in root length between plants grown with and without boron but do show a great difference in weight.

The pH study was to determine whether or not varying the pH with 0.3 ppm of boron in the nutrient solution would result in boron deficiency. In this experiment the test plants were broccoli, Brussels sprouts and red cabbage. The general appearance of the root system of plants grown at pH 4.0, 7.5 and 8.5 is the same as that of boron deficient plants, Figure 50. Close examination of these roots shows symptoms similar to but slightly different than symptoms of boron deficiency. With the low pH, the roots were only slightly thickened having a tendency to form a club on the end. Blackening of the tip was not as common as on roots growing without boron. The roots of plants grown in the higher pH solutions were more nearly normal than those grown in the low pH solution. The poor development of the roots in the low as compared to the high pH in this experiment were apparently

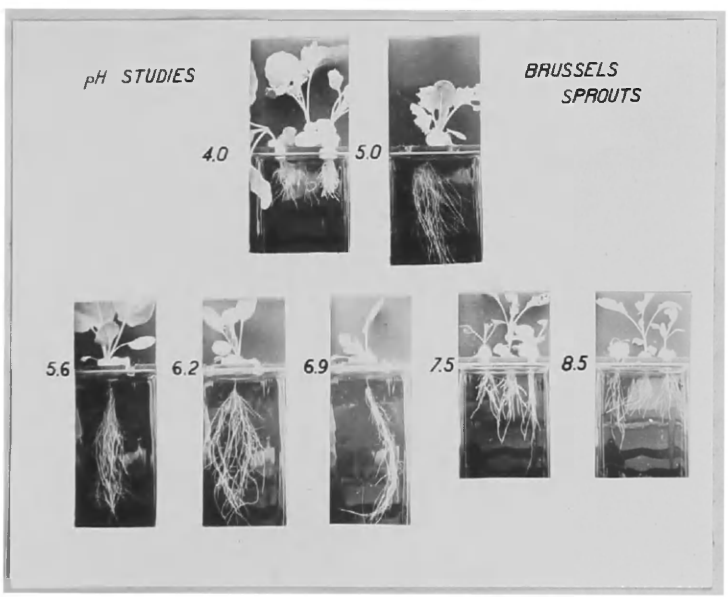

Fig. 50. The effect of pH on the development of Brussels sprouts roots.

caused by some factor other than fixation of boron. This is supported by Naftel's (60) recent work in which he shows lime directly affects the soil flora thereby indirectly affecting boron deficiency.

The experiment in which some of the rutabaga plants had the roots divided, part being in a nutrient solution without boron and part in a solution containing 0.3 ppm, presents very interesting information, Table XXVII. The condition

TABLE XXVII

Average Length of the Longest Root and Condition of the Roots and Tops of Rutabaga Plants Grown with Different Boron Treatments

Treatment	Length of longest root	Condition*	
		Roots	Tops
	cm.	relative	relative
All roots in no boron solution	10.35	2.0	1.2
Part of roots in no boron solution	12.94	2.2	3
and part in 0.3 ppm solution	17.95	3.2	
All roots in 0.3 ppm solution	14.78	2.3	2.0

*1 = poor, 2 = fair, 3 = good and 4 = excellent.

of the plants with the divided roots was good. All plants developed uniformly showing that the amount of boron necessary for growth is translocated laterally without difficulty. This is further shown by a greater development of the part of the roots of the divided plants in the no-boron solution than the roots of plants which were all in the no-boron solution.

The Effect of Supplying Boron Through the Leaves

This experiment was conducted to determine whether or not plants could receive enough boron through the leaves for normal development and whether or not plants showing boron deficiency could be restored with leaf applications of boron. Leaf applications were made with smears of boric acid in lanolin, glycerite of boroglycerine[4] alone and in lanolin and with hypodermic injections of boric acid. The boric acid in lanolin was the most satisfactory. The glycerite of boroglycerine alone killed the tissue to which it was applied but a large part of the boron was available to the plant. When this substance was applied in lanolin, little or no damage occurred. The hypodermic method of application was not satisfactory as the tissue around the needle dried out permitting the solution to pass by the needle and thereby reach the roots. All of the smear applications confined the boron to the leaves and permitted as vigorous growth in cauliflower and rutabaga as was obtained by applying boron in the nutrient solution to the roots. One rutabaga plant was grown without boron until nearly dead, after which lanolin containing boric acid was continually supplied to its cotyledons and leaves. This plant produced a root abnormal in shape and smaller than the roots of plants continually supplied with boron but there was no evidence of boron deficiency.

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[4]The method of preparing glycerite of boroglycerine can be found in the U. S. Pharmacopoeia. This mixture contains about 30% boron.

The Effect of Elements Other than Boron on Boron Nutrition

Two experiments were conducted to study the effect of elements other than boron on boron nutrition. In the first experiment broccoli was used while in the second kale was the test plant. The nutrient solutions for the first experiment were chosen from twenty-two which had been used in boron investigations. The nutrient solutions used had an osmotic pressure of approximately 0.6 of an atmosphere and a pH of approximately 5.0 but the solutions had considerable variation in the nitrogen, phosphorus and calcium content, Table XXVIII. All solutions were added to sand cultures by the

TABLE XXVIII

Physical Expressions of the Nutrient Solutions Used in the First Experiment on Effect of Elements Other than Boron on Boron Nutrition

Solution	Osmotic pressure		pH		Grams salt per L	Total ppm	Ratio of elements				
	Fresh	Used	Fresh	Used			N	P	K	Ca	Mg
Johnston and Dore	.61	.69	4.8	6.7	1.94	593	3	1	1.5	4	1
Hoagland and Snyder	.62	.63	4.8	8.0	2.31	787	4	.6	4.7	4	1
Shive	.48	.58	5.0	6.5	1.41	586	1	1*	1	1	1.4
Hill and Grant	.65	.92	5.3	6.9	1.65	590	6	.3	2.5	1	.1

*Phosphorus of this solution was taken as unity. Its absolute value is 49.6 ppm.

continuous flow method, therefore only one of the solutions was used as the original investigator used it (Shive 72). The nutrient solutions of Hoagland and Snyder (35) and Johnston and Dore (43) were used in the same concentration as that of the investigators. The solution of Hill and Grant (34) was changed to give the same weekly application of each element by the drip method as was furnished by their method of application.

In the first experiment the plants were grown with three levels of boron (0.05, 0.1 and 0.3 ppm of boron) employing three replicates at each level. The plants receiving one nutrient solution were very uniform regardless of the level of boron. Therefore, the data at harvest, except for boron deficiency symptoms, represent the average of twelve plants. The nutrient solution of Johnston and Dore produced the largest heads, the tallest plants and the greatest boron deficiency. With the 0.3 ppm of boron in this nutrient solution three of the plants showed no boron deficiency and the fourth had a large number of swellings and some cracks on the petioles and some cracked petioles. The plants supplied with the solution of Hoagland and Snyder had the greatest weight of suckers and next to the greatest amount of boron deficiency. The solution of Shive produced smaller plants than either of the solutions just mentioned and the plants had a very small amount of boron deficiency. Leaves of plants grown in this solution were covered with a large amount of bloom. Typical plants for each type of solution are shown in Figure 51, while the data obtained at harvest are presented in Table XXIX. The plants grown in the solutions of Hoagland and Snyder, and Shive had erect leaves making the plants appear taller than the plants grown in the other solutions.

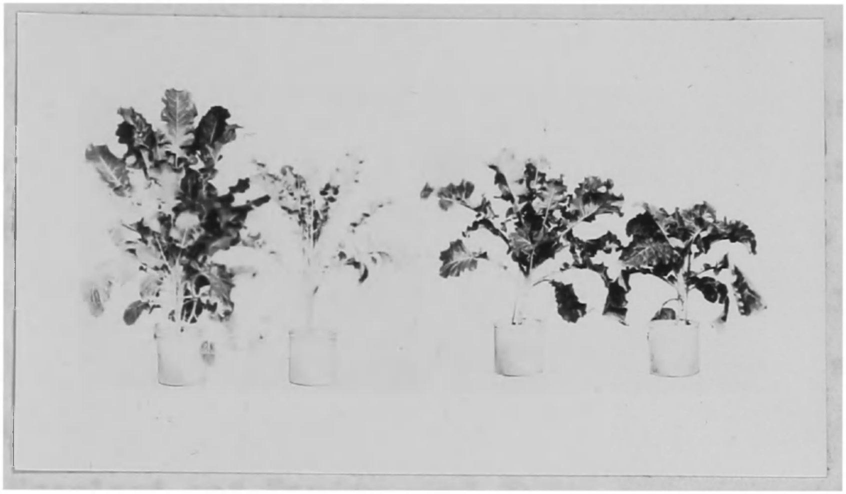


Fig. 51. Development of broccoli in different types of nutrient solutions. The formulas for the different types of nutrient solutions were obtained from (left to right) Hoagland and Snyder (35), Shive (72), Johnston and Dore (43), and Hill and Grant (34).

TABLE XXIX

Average Fresh Weight, Plant Height, Leaf Length, Leaf Length/ Leaf Width and Boron Deficiency Symptoms of Broccoli Plants Grown with Different Nutrient Solutions

Solution	Fresh Weight Head	Suckers	Total*	Height plant	Leaf length	Leaf Length /Width	Boron def.sym. by treatment 0.05	0.1	0.3
	grams	grams	grams	inches	inches	ratio	No.	No.	No.
Johnston and Dore	158	46	1020	25.2	22.4	2.6	8.0	3.25	8.25
Hoagland and Snyder	90	310	1655	23.3	26.0	2.7	4.25	3.0	2.5
Shive	40	25	673	21.2	21.2	2.9	1.25	.75	.5
Hill and Grant	24	42	571	17.1	18.3	2.2	1.0	.25	.5

*This includes stem, leaves, head and suckers.

The second experiment was planned so that each of four elements (N, K, Ca and Mg) were varied at three levels. The second experiment as far as possible had the same absolute amount of each element as the first. Nitrogen was used at the levels of the solutions of Johnston and Dore, Shive, and Hill and Grant and at a higher level. Potassium was used at the same levels as in the solutions of Shive, and Hill and Grant and at a higher level. Calcium and magnesium were supplied at the same concentrations as was used by Johnston and Dore, Hoagland and Snyder, and Shive and also with a higher concentration of each element. Phosphorus was furnished at the same concentration as that in the solution used by Shive. In selecting levels above the absolute amount used in the first experiment the ratio of two elements was given consideration. For example, the high potassium was set at 369.1 ppm because this would give approximately the same K/P ratio as that in the Hoagland and Snyder and in the Hill and Grant solutions. The ratios of different levels used in this experiment are given in Table XXX. All of the 81 possible combinations were studied, using 0.05 ppm of boron. The factorial design of experiment was used with hidden replicates.

In this experiment there was some difference in the development of boron deficiency for the different nutrient solutions. However, only ten of the eighty-one plants showed deficiency and it is not possible to associate this with any one element. Therefore the results of this experiment do not agree with those of the previous experiment in which there was an association of high calcium with boron deficiency.

TABLE XXX

Relative Composition of the Nutrient Solutions used in the Second Experiment on the Effect of Elements Other than Boron on Boron Nutrition. 1 = 49.6 ppm

Level	Relative Composition				
	N	P	K	Ca	Mg
Low	1.0	1.0	1.0	1.0	1.0
Medium	3.0	1.0	2.5	4.0	1.4
High	6.0	1.0	7.0	12.0	3.0

Histological Investigations

Warington (81) in 1926 studied extensively the effect of the absence of boron on the anatomy of Vicia faba. Similar studies were made on Pisum sativum by Sommer and Sorokin in 1928 (76). Following these investigations numerous investigators have reported anatomical symptoms in various plants, but as no studies had been published on members of the genus Brassica, detailed studies were planned principally with rutabaga. These studies were started in 1934 and many studies were made in 1935. After all the material was embedded and about one-half of the material on rutabaga had been studied and photographed, a publication by Jamalainen (39) on the anatomy of boron deficient rutabaga roots was released. He described and pictured, by drawing or photomicrograph, boron deficiency in xylem parenchyma, cell elongation (radially and tangentially), jammed cells and elongation of pith cells. Similar observations were made in this investigation (Fig. 52).

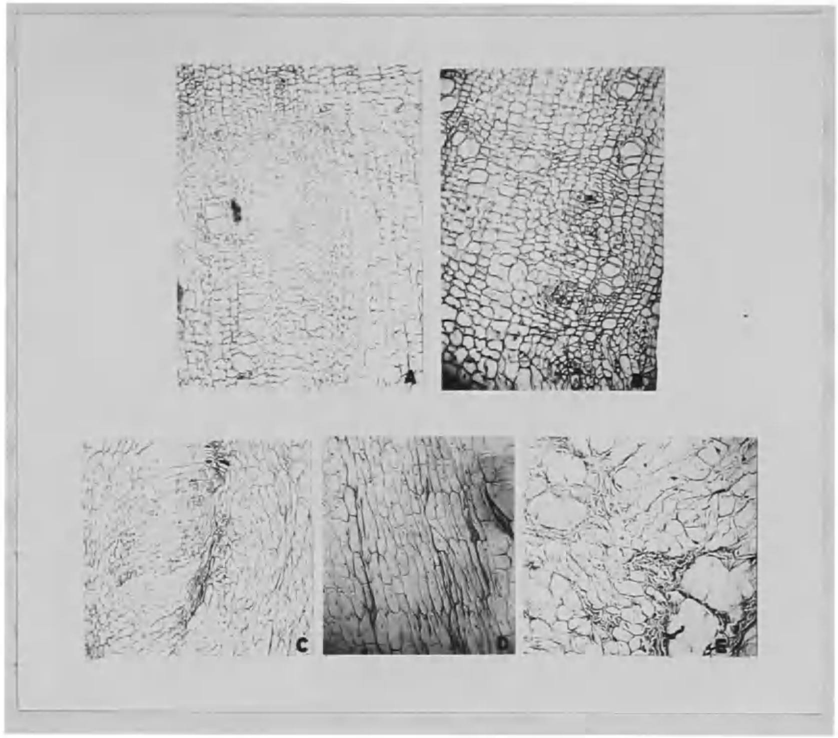


Fig. 52. Cross section of rutabaga storage root. A, normal cambium and xylem x50. B, slight enlargement and loss of some of the regularity x50. C, crushing of cells x50. D, cell elongation near the cambium x50, and E, crushed cells and elongation in various directions x80.

Most of the examples of the effect of boron deficiency on the anatomy of plants have been taken from rutabaga. However, sections of various parts of broccoli, Brussels sprouts, cabbage, cauliflower and kale have been examined. These studies have shown that boron deficiency causes the same type of internal breakdown in all of these plants as is shown in rutabaga. In Appendix B additional photomicrographs will be found which show the type of breakdown in other members of the genus Brassica which will be described here for rutabaga. Appendix B also includes a series of cross sections through a cork-like spot on a petiole.

Boron deficiency as it was concerned with the xylem parenchyma was associated with cell inclusions (Fig. 53 A and B). The number of cells showing these inclusions increases with an increase in the time that boron has been a limiting factor. When boron has been a limiting factor for only a short time the cork cambium functions normally or nearly so. On the other hand, if boron has been a limiting factor for some time the cork cambium produces cells irregularly. When boron has been a limiting factor for most of the life of the plant the cambium does not function. In the latter case the cells near the surface elongate considerably, Figure 53.

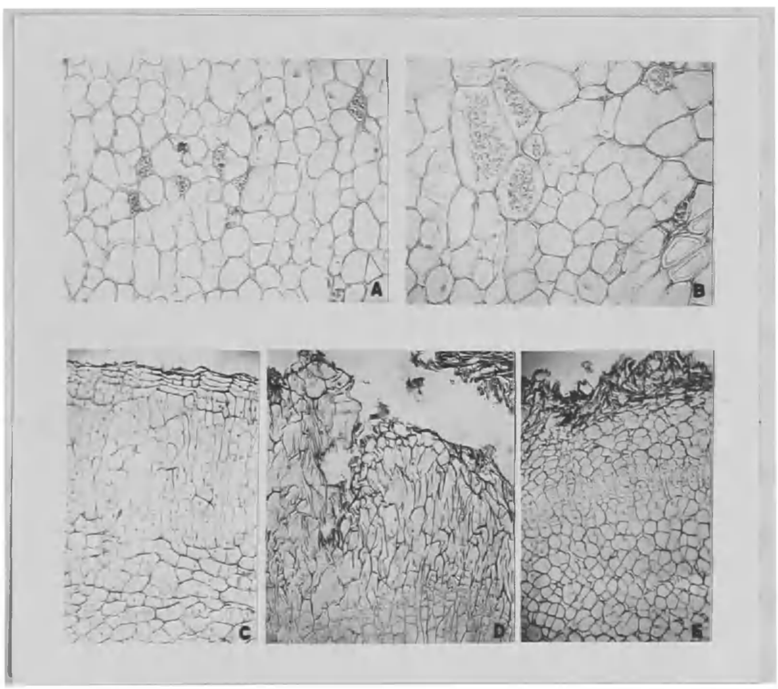


Fig. 53. Cross section of rutabaga storage root. A, cell inclusions x 120. B, cell inclusions x100. C, from a plant supplied with boron only a short time showing no cork cambium x 50. D, from a plant receiving boron for a longer time showing the function of the cork cambium where rough areas are produced on the surface x 50. E, from a plant with the same treatment as D but from an area where the surface was smooth.

Root tips from broccoli and Brussels sprouts were examined every other day after boron was removed. The root cap gradually disintegrates, similar to the disintegration in <u>Pisum</u> <u>sativum</u> reported by Sommer and Sorokin (76). Cell division at the apical meristem of the root ceases soon after boron is a limiting factor. This causes growth in length to stop. The cells near the tip enlarge radially more than usual causing the root to be club-shaped. Differentiation in the plerome progresses faster than in the dermatogen; thus secondary roots occur nearer the tip than the root hairs. Roots of deficient plants have many more secondary roots than normally but none of them attain any great length and many are only a millimeter in length. Figure 54 is typical of the roots examined.

The apical meristem of the stem is one of the last places to show injury, and death of this tissue is not evident until many of the cells below the meristem have been crushed. Typical rutabaga meristems are shown in Figures 55 and 56.

In the petioles some of the vascular bundles of deficient plants have crushed cells. The xylem and phloem are separated by dead or enlarged cells, Figure 57A. In the same petiole, bundles may be found which are normal or nearly so, Figure 57B. Cell enlargement in the bundles may cause the vessels to be twisted so that a longitudinal section of a vessel is seen in cross section of the tissue, Figure 57C. Parts of the vascular elements may be crushed or moved so that they are functionless, Figure 57D. The epidermal region of

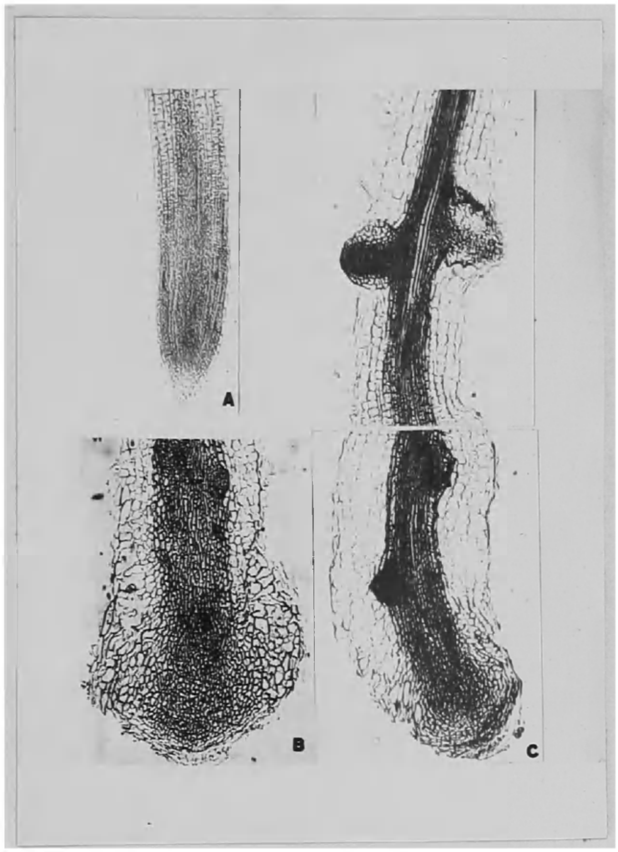


Fig. 54. Brussels sprout roots grown without boron. A, at the beginning of the experiment. B, three days later. C, after seven days without boron. Because of the curve in this root a pie shaped piece is omitted, the wide part being on the left.

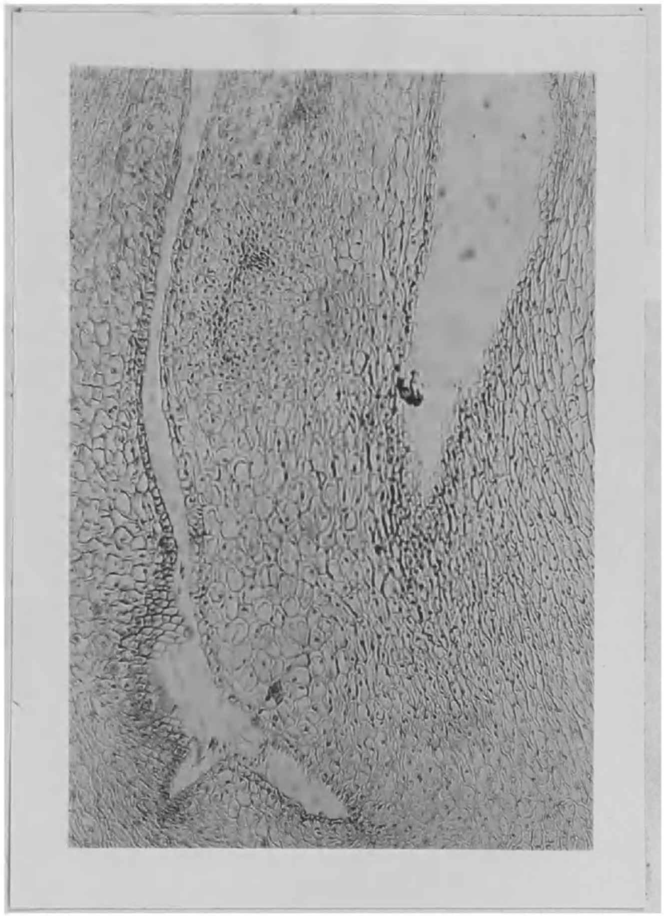


Fig. 55. Meristem of a rutabaga plant receiving boron for 58 days. This meristem contained no dead cells at the time of harvest, 72 days. x80.

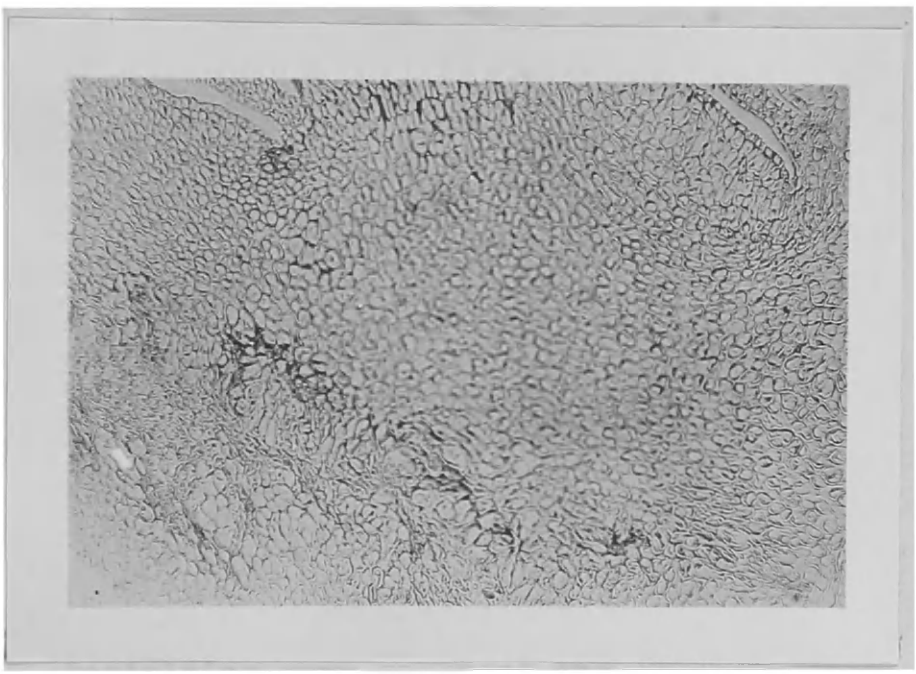


Fig. 56. Meristem of a rutabaga plant which received boron for 41 days. At harvest, 31 days later, the region of activity shows many dead cells. The tissue below this meristem had many collapsed dead cells. x80.

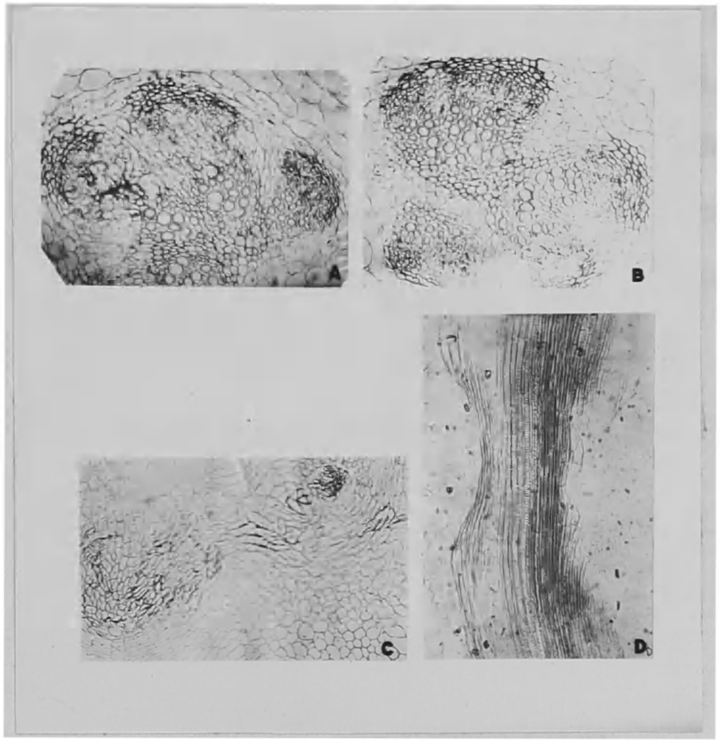


Fig. 57. Sections of petioles of rutabaga plants. A, cross section showing a vascular bundle containing many enlarged and crushed cells. B, a vascular bundle of the same petiole which is nearly normal, both x40. C, cell enlargement around a vascular bundle and vessel elements completely out of line due to abnormal cell enlargement, x32. D, longitudinal section showing the abnormal cell development, crushing and distorting a vascular bundle.

the petiole is abnormal when boron is lacking. The cells of the swelling which appear on the surface of the petiole are much enlarged parenchyma, Figure 58 A and B. The majority of these do not have a cork cambium, but occasionally one is present, Figure 58A. Micro-chemical tests show that only part of these swellings have suberized cell walls. Corky areas also appear on the surface of the petiole where the epidermis has been injured, Figure 58C. The normal epidermis is very regular, Figure 58D. Swellings like those on the

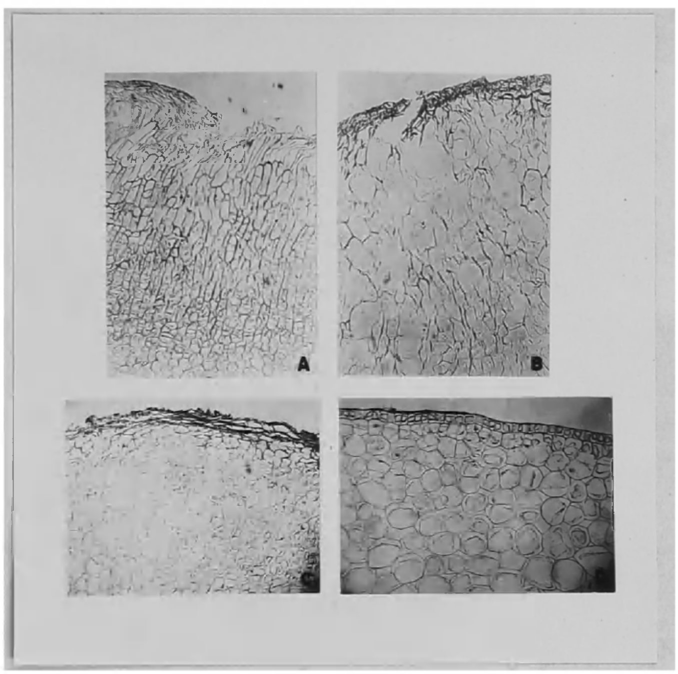
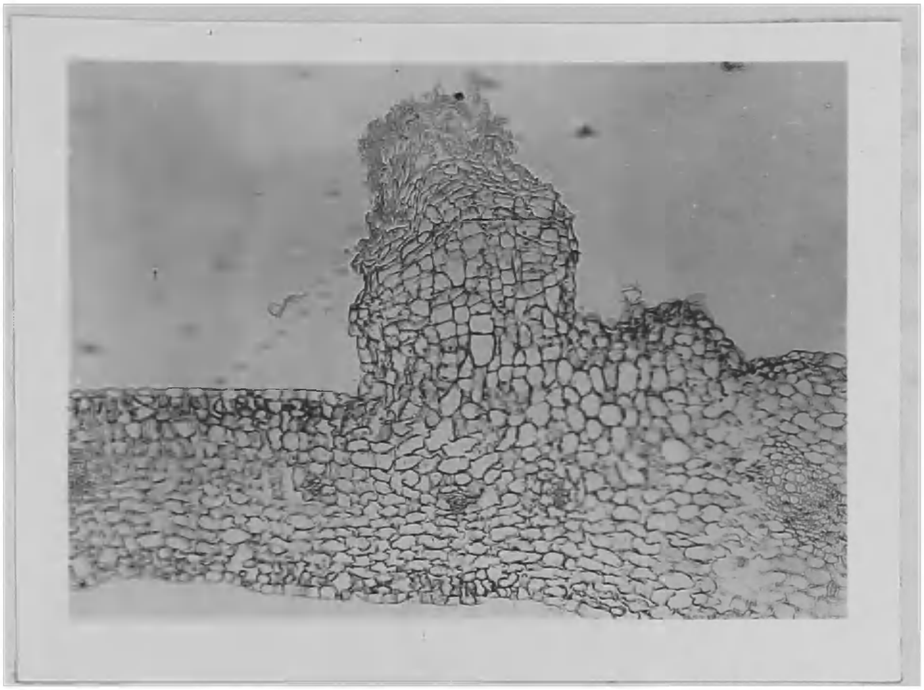


Fig. 58. Epidermal and cortical region of petioles of rutabaga plant. A, cell structure in a swelling with a cork cambium partially differentiated, x32. B, cell structure in a swelling without cork cambium cells, x32. C, dead cells on exterior of a petiole, x50. D, normal epidermis and cortex, x50.

petiole also occur on the leaf blade, Figure 59. Leaf blades of cabbage were cut to study the healing of wounds of plants



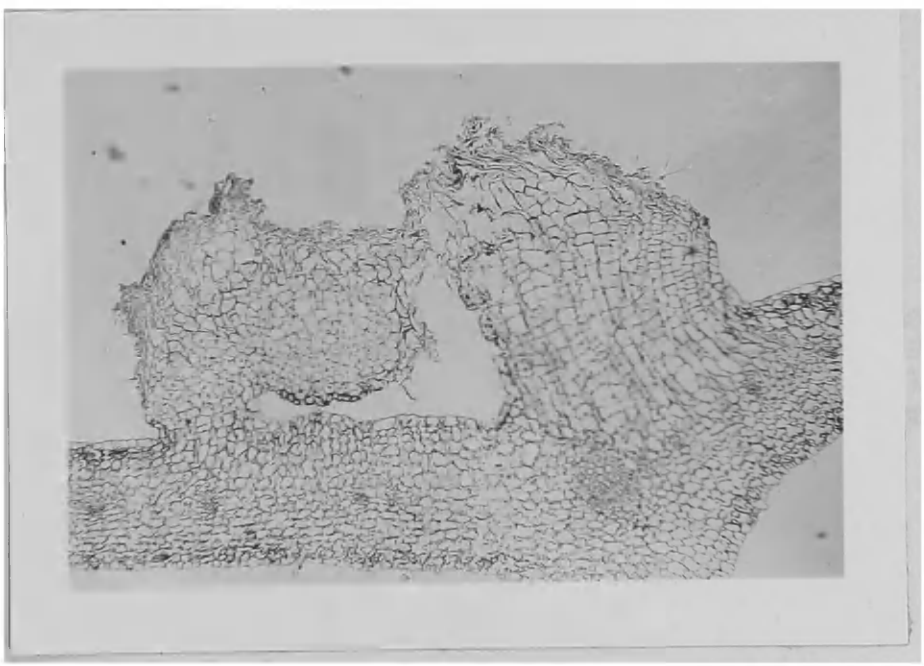


Fig. 59. Swellings on leaf blades, x80.

which received boron compared with plants which did not receive boron. Without boron no cork cambium is formed and the cells near the wound elongate. With a very small amount of boron (0.05 ppm) a cambium is formed and little or no elongation takes place. With a larger amount of boron (0.3 ppm) a very efficient healing occurs because of the development of a cork cambium which originates at or near a vein, Figure 60.

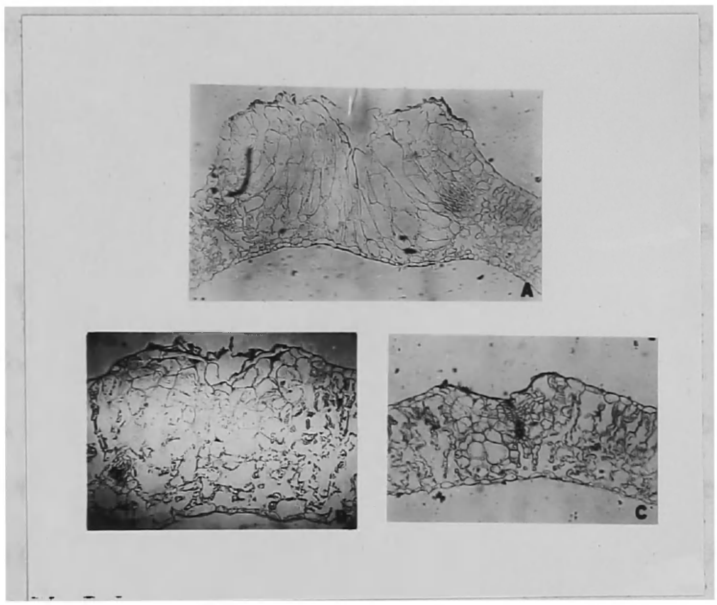


Fig. 60. Healing of cuts in cabbage leaves. A, without boron no cambium develops, x32. B, with 0.05 ppm of boron a rather inactive cambium develops, x40. C, with 0.3 ppm of boron an active cambium develops, x32.

GENERAL DISCUSSION

The amount of boron necessary for normal plant development within the genus Brassica is from 0.1 to over 0.5 ppm with the optimum approximately 0.3 ppm supplied continually. This places the low and high limits nearer together than Warington placed them from her investigations (80) which showed beneficial results between 0.004 and 4.54 ppm. The optimum concentration as determined by these experiments is lower than that reported by other investigators (4, 13, 33, 49 and 77). The optimum may vary slightly from season to season probably being related to growth rate of the plant. The seasonal effect in the field is probably a biological absorption of boron. The longer boron is supplied to the plant the greater will be the fresh weight produced, yet with these studies there seemed to be no straight line relationship between fresh weight of the plant and duration of boron application or between fresh weight of the plant and the amount of boron supplied. When boron is a limiting factor the edible part of the plant is dwarfed more than other parts. From this fact and the fact that there is not a straight line function one might postulate that a greater amount of boron may be necessary for the formation or development of the edible part of the plant. This postulation is strengthened by the failure of flowers to develop when boron is lacking. McMurtrey (52) obtained a falling off of the blossom buds before they opened with tobacco while with citrus Haas (28) obtained a reduction in flowering without boron. On the other hand, Warington (82) believed that boron was not associated with flowering.

The experiment in which rutabaga received an inadequate supply of boron (adequate for the young plant but not enough to mature it) followed by an adequate supply it was shown that there was no significant difference in total fresh weight or in weight of the storage root regardless of the time of change. However, the quality was greatly improved with the early change indicating that it is better to apply boron as a preventative measure rather than as a cure. As a cure a solution containing boron may be applied to the leaves. Experiments had been reported by a number of investigators of spraying the foliage of deficient plants and obtaining recovery, but the investigations reported here were conducted with substances confined on the leaf surface, indicating that plants are able to receive all of their boron through their leaves.

The failure of the boron deficient plants to show negative geotropism may be due to inability of the plant to produce growth substances, or may be caused by a lack of translocation of growth substances, or the tissues may be too old for cell elongation and division. Of these possible reasons the latter seems the most plausible as root studies show that the cells have become differentiated very near the tip.

Numerous investigators have believed that there was an increase in boron deficiency with increased application of lime. However, the experiments designed to study this effect show no significant difference in boron deficiency when the calcium content is varied from 64.0 to 602.0 ppm. The studies made so far do not show a relation with any single element. However, the writer believes that there is an association as there was a difference in the number of boron deficiency symptoms produced in the different kinds of nutrient solutions.

Parenchyma cells enlarge causing other cells to be crushed or causing swellings on the surface of petioles. Cell inclusions are often found in cells,particularly in the parenchyma. The crushing of cells and the presence of inclusions resemble in some respects death caused by freezing. The apical meristem of the root appears to be killed as a direct cause of boron deficiency while the apical meristem of the stem appears to be killed as an indirect cause of boron deficiency. The cork cambium of rutabaga roots produces cells irregularly and the cells produced enlarge irregularly when boron is withheld from the plant. In wounded tissue the cork cambium does not produce normal cells or the cambium may not develop.

The death and displacement of some of the phloem cells agrees with the results obtained by other investigators (41, 42 and 78) in tomatoes and potatoes. The same investigators (42 and 79) have shown that the translocation of carbohydrates from the leaf is impeded or prevented. The increase in the carbohydrate content of the leaves is probably responsible for the development of color in the boron deficient plants.

SUMMARY

The results of numerous experiments with several kinds of plants of the genus Brassica conducted in sand and water cultures may be summarized as follows:

1. Members of the genus Brassica do not contain enough boron in their seeds to normally develop the cotyledons and first leaves.

2. The greatest total weight of plants was obtained when 0.3 ppm of boron was supplied continually, yet 0.5 ppm produced larger heads on cauliflower.

3. The fresh weight of plants increased with duration of boron supply except for one kind of plant, red cabbage. The increase in weight was not a straight line function of the duration of boron application or the amount supplied.

4. In severe cases of boron deficiency there is a translocation of boron from the older leaves into the rest of the plant.

5. Boron deficiency symptoms vary with the kind and age of plant when boron is a limiting factor. The symptoms are curling and rolling of the leaves, rugosity of the leaves, chlorosis of the leaf margins, swellings of the stems and

petioles, brittleness of petioles, splitting of petioles and stems, a corky appearance of the petioles and stems, the development of brown areas in the stems, and a reduction in size and quality of the edible part.

6. Plants grown with an inadequate supply of boron followed by an adequate supply develop more nearly normal than plants adequately supplied at first and changed to a no-boron solution later.

7. The edible part of the plant develops very poorly when boron is a limiting factor but the other plant parts have the same mass relationship.

8. Plants supplied with the optimum amount of boron are the most efficient producers of mass.

9. Root development is retarded at pH 4.0, 7.5, and 8.5 but this is not due to fixation of boron.

10. Plants may receive all of their boron through the leaves.

11. No single element tried affects boron deficiency.

12. The undifferentiated cells of boron deficient tissue elongate in any direction, thereby crushing other internal cells, or causing the formation of swellings on the surface of petioles and stems.

13. The cork cambium of wounded tissue does not produce normal cells and in severe cases the cork cambium is not formed.

14. The effect of boron deficiency on the terminal meristem of the root and stem appears to be different.

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LITERATURE CITED

1. Agulhon, Henri
1910. Recherches sur la présence et la role du bore chez les végétaux. Thesis 155 pp. De L' Universitaté de Paris.

2. Askew, H. O.
1935. The boron status of fruit and leaf in relation to "Internal Cork" of apples in the Nelson district. New Zeal. Jour. Sci. and Tech. 17: 388-391.

3. ______________
1936. Internal cork of apples. Orchard, N.Z. 9: 185-188.

4. ______________, Chittenden, E. and Thomson, R.H.K.
1936. The use of borax in the control of "internal cork" of apples. New Zeal. Jour. Sci. and Tech. 18:365-380.

5. ______________, Thomson, R.H.K. and Kidson, E. B.
1937. The boron status of New Zealand fruit soils. New Zeal. Jour. Sci. and Tech. 18:789-796.

6. Bertrand, G. and de Wall, L.
1936. Recherches sur la teneur comparative en bore de plants cultivées sur le même sol. Annales Agronomiques 6:537-541.

7. Brenchley, Winifred E.
1936. The essential nature of certain minor elements for plant nutrition. Bot. Review 2:173-197.

8. ______________________
1937. Some deficiency diseases of crop plants. Jour. Min. Agr. 44:116-122.

9. ______________________ and Warington, K.
1927. The role of boron in the growth of plants. Ann. Bot. 41:167-187.

10. Chandler, F. B., Chucka, J. A. and Mason, I. C.
1935. Summary Report of Progress, 1935. Maine Agr. Expt. Sta. Bull. 380, pp. 229-230.

11. Chittenden, E. and Copp, L. G. L.
1937. The use of borax in the control of brown-heart of turnips. New Zeal. Jour. Sci. and Tech. 19: 372-376.

12. Chupp, Charles and Horsfall, James G.
1933. Brown rot of cauliflower. Plant Dis. Reptr. 17:157-159.

13. Coulson, John G. and Raymond, L. C.
1937. Progress report on the investigation of brown heart of swede turnips. Sci. Agr. 17:299-301.

14. Dearborn, C. H. and Raleigh, G. J.
1936. A preliminary note on the control of internal browning in cauliflower by the use of boron. Amer. Soc. Hort. Sci. Proc. 33:622-623.

15. _______________, Thomson, H. C. and Raleigh, G. J.
1936. Cauliflower browning resulting from a deficiency of boron. Amer. Soc. Hort. Sci. Proc. 34: 483-487.

16. Dennis, R. W. G.
1936. The relation of boron to plant growth. Sci. Prog. 32:58-69.

17. _______________
1937. A review of developments in the applications of boron in agriculture and horticulture. The Fertilizer, Feeding Stuffs and Farm Supplies Jour. 22, Nos. 19, 20 and 21.

18. _______________
1937. Boron and plant life. (Cont.) Fertilizer (London), 22:535-536.

19. _______________ and O'Brien, D. G.
1937. Boron in agriculture. West Scotland Agr. College Research Bull. No. 5. p.98.

20. Donaldson, Ralph W.
1937. Apply boron to prevent darkening of turnips. Better Crops with Plant Food 21: 20-22 and 36-37.

21. Eaton, F. M.
1932. Boron requirements of cotton. Soil Sci. 34: 301-305.

22. Eltinge, Ethel Taber
1936. Effect of boron deficiency upon the structure of Zea Mays. Plant Physiol. 11:765-778.

23. Fisher, Paul
1935. Responses of the tomato in solution cultures with deficiencies and excesses of certain essential elements. Md. Agr. Expt. Sta. Bull. 375, pp. 261-281.

24. Fisher, R. A.
1925. Statistical methods for research workers. Oliver and Boyd, Edinburgh. p. 239.

25. ______________
1935. The design of experiments. Oliver and Boyd, Edinburgh. p. 252.

26. Gram, E.
1936. Bormangel og nogel andre mangelsygdomme. Tidsskr. Planteavl 41:401-449. (English summary, pp. 448-449.)

27. Green, Jesse R.
1938. Phosphate investigations on irrigated crops. Montana Agr. Expt. Sta. Bull. 356, pp. 2, 3, 5.

28. Haas, A. R. C.
1930. Boron as an essential element for healthy growth of citrus. Bot. Gaz. 89:410-413.

29. ______________ and Klotz, L. J.
1931. Further evidence on the necessity of boron for health in citrus. Bot. Gaz. 92:94-100.

30. ______________ and ______________
1931. Some anatomical and physiological changes in citrus produced by boron deficiency. Hilgardia 5:175-189.

31. Harding, Dorothy and Schmidt, Catherine M.
1938. Boron as a plant nutrient. Bibliography. Amer. Potash Institute Inc. p. 83.

32. Hartman, John D.
1937. Boron deficiency of cauliflower and spinach on Long Island. Amer. Soc. Hort. Sci. Proc. 35: 518-525.

33. Hill, H.
1936. Minor elements affecting horticultural crops. Sci. Agr. 17:148-153.

34. ________ and Grant, E. P.
1935. Growth of turnips in artificial cultures. Sci. Agr. 15:652-659.

35. Hoagland, D. R. and Snyder, W. C.
1933. Nutrition of strawberry plant under controlled conditions: (a) Effects of deficiencies of boron and certain other elements. Amer. Soc. Hort. Sci. Proc. 30:288-293.

36. Holland, E. B. and Jones, C. P.
1934. The relation of dark center to the composition of rutabagas. Jour. Agr. Res. 48:377-378.

37. Hurst, R. R.
1930. Diseases of forage crops. Rept. Dom. Bot. pp. 176-181.

38. __________ and MacLeod, D. J.
1936. Turnip brown heart. Sci. Agr. 17:209-214.

39. Jamalainen, E. A.
1935. Tutkimuksia Lantun Ruskotaudista. Valton Maatalouskoetoiminnan Julkaisuja 72:116.

40. Johnston, Earl S.
1921. The seasonal march of the climatic conditions of a greenhouse, as related to plant growth. Maryland Agr. Expt. Sta. Bull. 245, pp.41-98.

41. __________
1928. Potato growing in mineral nutrient media. Soil Sci. 26:173-177.

42. __________ and Dore, W. H.
1928. The relation of boron to the growth of the tomato plant. Science 67:324-325.

43. __________ and __________
1929. The influence of boron on the chemical composition and growth of the tomato plant. Plant Physiol. 4:31-62.

44. __________ and Fisher, P. L.
1930. The essential nature of boron to the growth and fruiting of the tomato. Plant Physiol. 3: 387.

45. Kimbrough, W. D.
1936. Effect of source of nitrate nitrogen and a mixture of minor plant nutrients on the growth of cabbage plants in pots. Amer. Soc. Hort. Sci. Proc. 34:488-494.

46. Ling, A. W.
1938. SUGAR BEET: Manuring and cultivation. Jour. Min. Agr. 14:806-811.

47. Löhnis, M. P.
1936. Boron requirement and boron content of crops. Chem. Weekblad 33:59-61. (Abstract, C.A.32: 6493.)

48 __________
1937. Injury to red currants resulting from malnutrition. Tÿdschrift Over Plantenziekten 43:33-56.

49. ______________
1938. Brown heart in swede, B. napus rapifera. Chronica Botanica IV:9.

50. MacLeod, D. J. and Howatt, J. L.
1934. Soil treatment in the control of certain soil-borne diseases of potatoes. Amer. Potato Jour. 11:60-61.

51. ______________ and ______________
1935. The control of brown heart in turnips. Sci. Agr. 15:435.

52. McMurtrey, J. E., Jr.
1929. The effect of boron deficiency on the growth of tobacco plants in aerated and unaerated solutions. Jour. Agr. Res. 38:371-380.

53. ______________
1933. Distinctive effects of the deficiency of certain essential elements on the growth of tobacco plants in solution cultures. U.S.D.A. Tech. Bull. 340.

54. ______________
1935. Boron deficiency in tobacco. Jour. Amer. Soc. Agron. 27:271-273.

55. ______________
1938. Distinctive plant symptoms caused by deficiency of any one of the chemical elements essential for normal development. Bot. Review 4:183-203.

56. ______________
1938. Symptoms of field-grown tobacco characteristic of the deficient supply of each of several essential chemical elements. U.S.D.A. Tech. Bull. 612.

57. Maier, W.
1936. Bormangelerscheinungen an Rebsämlengen in Wasserkulturversuchen. Gartenbauwiss 11:1-16.

58. Meyer, Hermann K.
1934. Neue Wege zur Bekämpfung der Herz-und Trockenfäule der Rübedurch Borax. Pflanzenbau 11:24-28.

59. Muckenhirn, R. J.
1936. Response of plants to boron, copper, and manganese. Jour. Amer. Soc. Agron. 28:824-842.

60. Naftel, James A.
1938. Recent studies on boron in soils. American Fertilizer 89:5-8, 24, 26.

61. O'Brien, D. G. and Dennis, R. W. G.
1935. Raan or boron deficiency in swedes. Scottish Jour. Agr. 18:326-334.

62. ______________ and ______________
1936. Further information relating to control of raan in swedes. Scottish Jour. Agr. 19:40-46.

63. ______________ and ______________
1936. The place of boron in potato cultivation. Scottish Fmr. and Farm. Wld. and Household, March 14, 364-365.

64. Osvald, Hugo and Peterson, Gunnar
1937. Experiments with boron against heart rot. Lantbrukshögskolans Annaler, 4:233-258.

65. Paterson, W. G. R.
1936. Raan in swedes. Scottish Fmr. and Farm. Wld. and Household. April 25. p. 4.

66. Peligot, E.
1876. De l'action que l'acide borique et les borates exercent sur les vegetaux. Compts. Rendus. Acad. Sci.83:686-688.

67. Purvis, E. R. and Ruprecht, R. W.
1937. Cracked stem of celery caused by a boron deficiency in the soil. Fla, Agr. Expt. Sta. Bull. 307, p. 16.

68. Rigg, Theodore
1937. Soil deficiencies in New Zealand. Rept. New Zeal. Assoc. Adv. Sci. 23:401-422.

69. ______________, Askew, H. O. and Chittenden, E.
1937. Brown heart of swedes and turnips in Nelson district: a boron deficiency ailment. New Zeal. Jour. Sci. Tech. 18:750-755.

70. Scharrer, K.
1936. Die Wirkung von Spurenelementen auf das Pflanzenwachstum. Ztschr. Pflanzenernähr., Düngung and Bodenkunde 44:223-247.

71. Schmucker, Theodor
1934. Über den Einfluss von Borsäure auf Pflanzen, insbesondere keimende Pollenkörner. Planta 23:264-283.

72. Shive, J. W.
1936. Adequacy of boron and manganese content of natural nitrate of soda to support plant growth in sand culture. N.J. Agr. Expt. Sta. Bull. 603, p. 36.

73. ____________ and Stahl, A. L.
1927. Constant rates of continuous solution renewal for plants in water cultures. Bot. Gaz. 84:317-323.

74. Snyder, G. B. and Donaldson, R. W.
1936. The use of borax in controlling dark center of turnips. Amer. Soc. Hort. Sci. Proc. 34: 480-482.

75. Sommer, A. L. and Lipman, C. B.
1926. Evidence on the indispensable nature of zinc and boron for higher green plants. Plant Physiol. 1:231-249.

76. ____________ and Sorokin, H.
1928. Effects of the absence of boron and of some other essential elements on the cell and tissue structure of the root tips of Pisum sativum. Plant Physiol. 3:237-260.

77. Swanback, T. R.
1928. The effect of boric acid on the growth of tobacco plants in nutrient solutions. Plant Physiol. 2:475-486.

78. Van Schreven, D. A.
1934. Uitwendige en inwendige symptomen van Boriumgebrek Bij Tabak. Tydschrift over Plantenziekten 40:122-125.

79. ____________
1935. Uitwandige en inwendige symptomen van Boriumgebrek Bij Tomaat. Tydschrift over Plantenziekten 41:22,23.

80. Warington, Katherine
1923. The effect of boric acid and borax on the broad bean and certain other plants. Ann. Bot. 37:629-672.

81. ____________
1926. The changes induced in the anatomical structure of Vicia faba by the absence of boron from the nutrient solution. Ann. Bot. 40:27-42.

82. ____________
1933. The influence of length of day on the response of plants to boron. Ann. Bot. 47:429-457.

83. ____________
1934. Studies in the absorption of calcium from nutrient solutions, with special reference to the presence or absence of boron. Ann. Bot. 48: 743-776.

84. Willis, L. G.
1936. Bibliography of references to the literature on the minor elements and their relation to the science of plant nutrition. Chilean Nitrate Educational Bureau, Inc. (Second Edition) p. 396.*

85. ______________ and Piland, J. R.
1937. Soil research. N. C. Agr. Expt. Sta. Ann. Rept. No. 60:17-18.

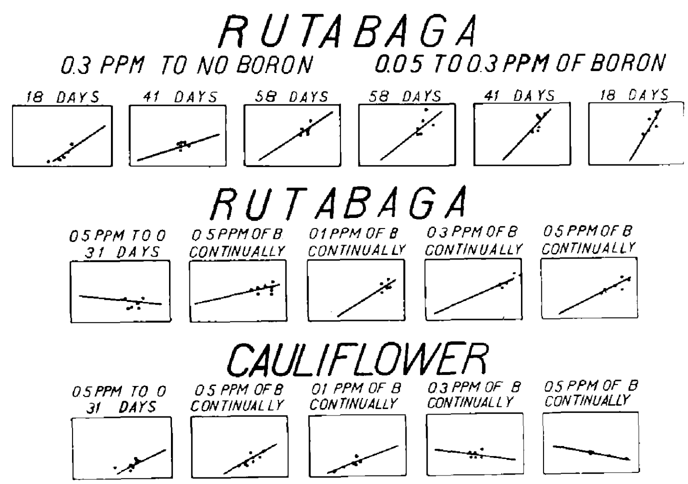
86. Woods, C. D.
1915. Field experiments in 1914. Maine Agr. Expt. Sta. Bull. 236, pp. 57-59.

87. Young, R. S.
1935. Certain rarer elements in soils and fertilizers and their role in plant growth. Cornell Agr. Expt. Sta. Mem. No. 174, p. 70.

* A third edition has been published since text was written. 1939, p. 488.

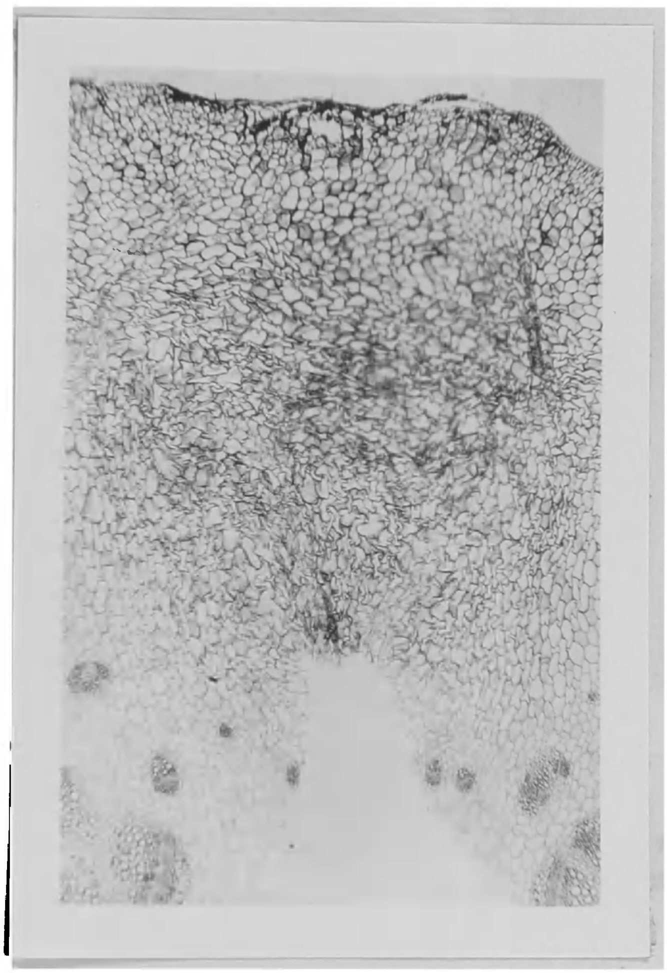
APPENDIX A

Scatter diagrams and regressions of total fresh weight on leaf width of rutabaga and cauliflower plants with different boron treatments.



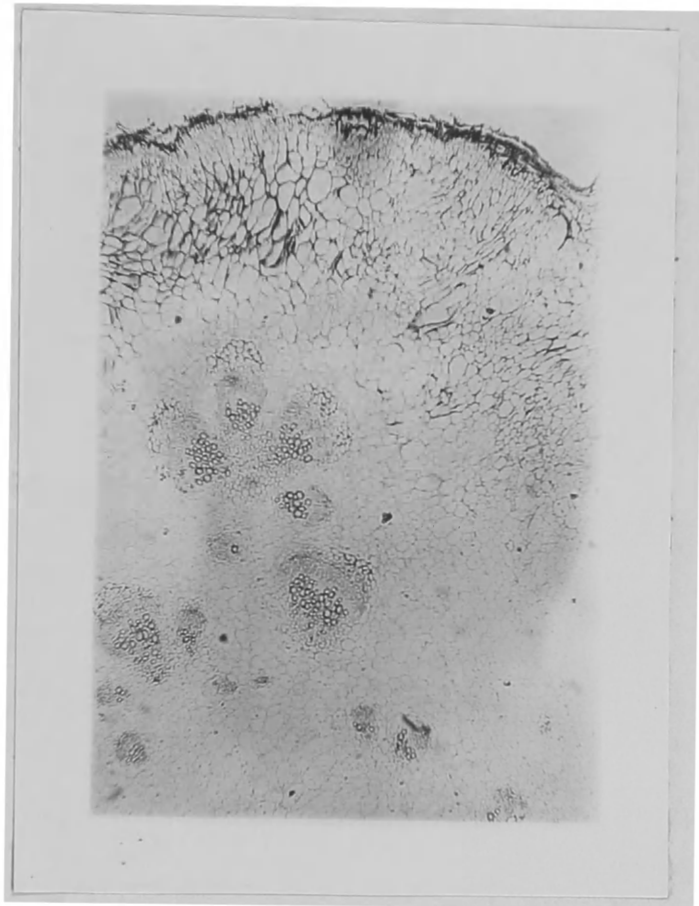
APPENDIX B

Photomicrographs of plants of the genus Brassica which received different boron treatments.



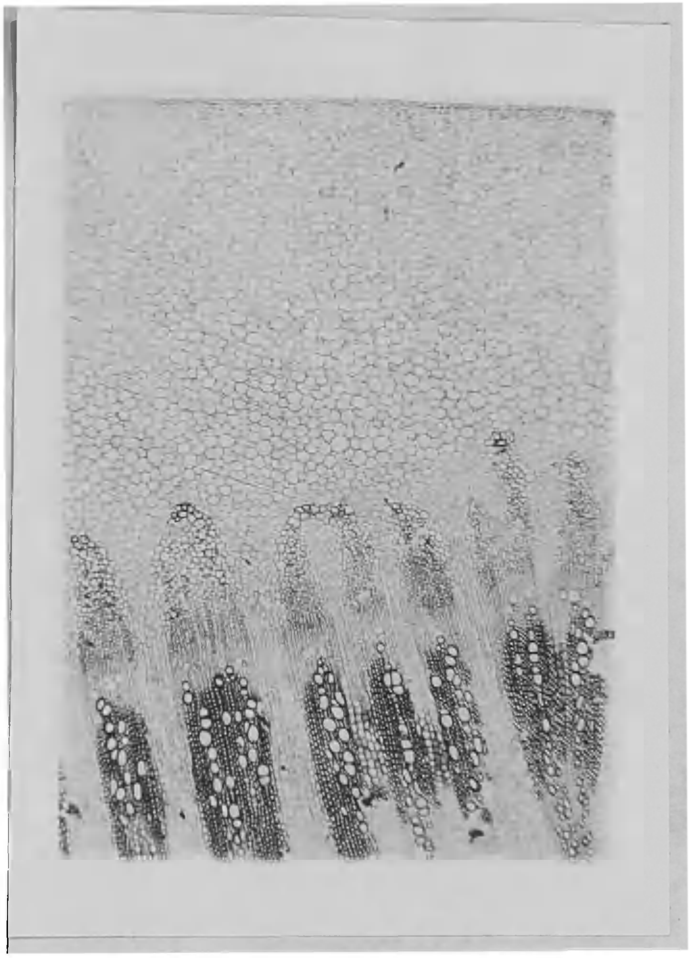
Cross section of the leaf pictured in figure 27. This petiole was cracked. x25.

Meristem of a cauliflower plant which received 0.3 ppm of boron continually. x25.



Cross section of a petiole of a red cabbage leaf showing a corky epidermis. This plant (No. 25) received boron for only a short period. x25.

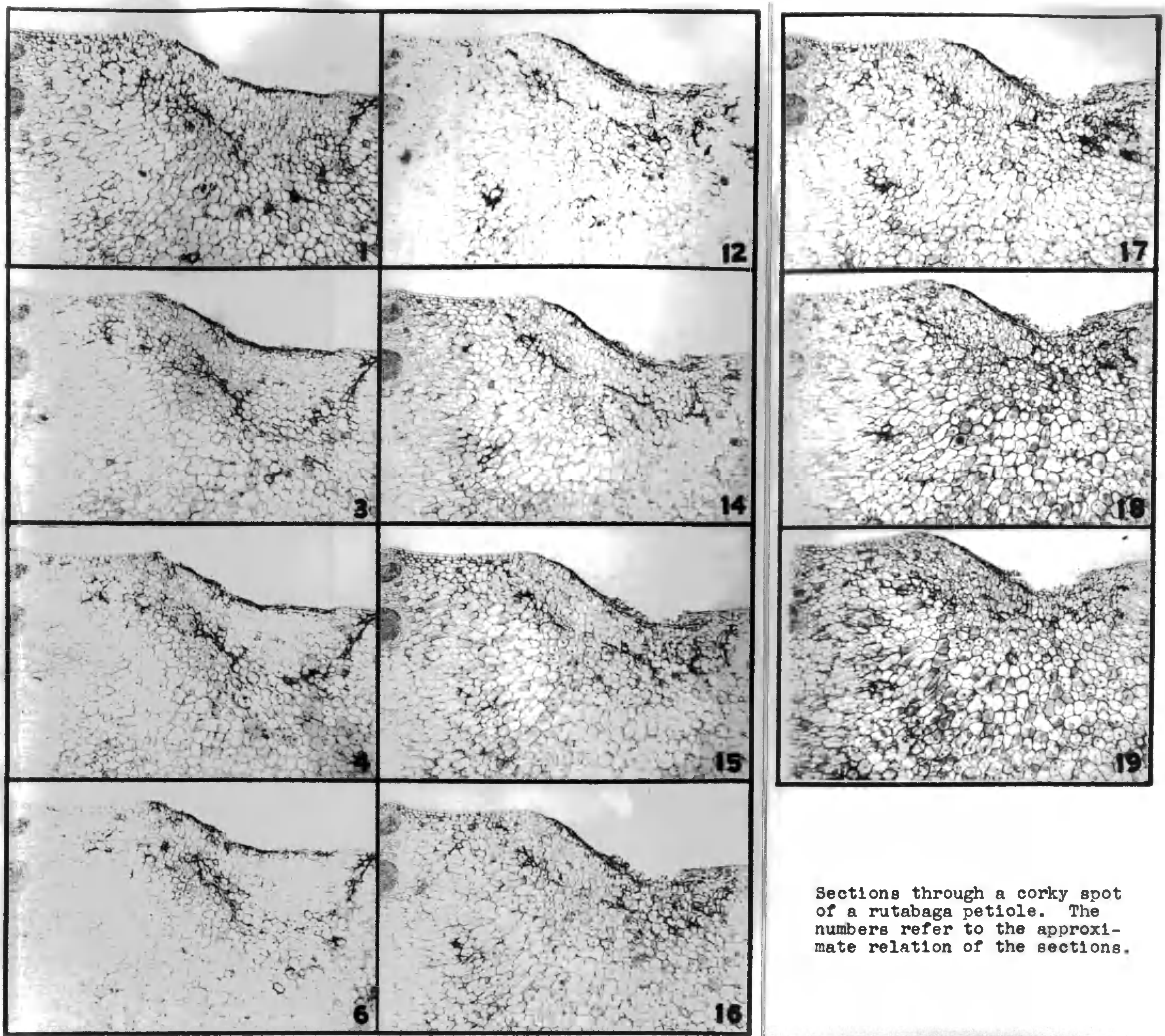
Cross section of a red cabbage stem showing crushed and elongated parenchyma. This plant (No. 25) received boron for only a short period. x25.



Cross section of a
red cabbage stem
showing normal
development. This
plant received 0.3
ppm of boron continually. x25

Cross section of a
green cabbage stem
showing crushed
cells in cortex.
This plant received
boron during only
part of its life.
x25.

Cross section of a kohlrabi stem
showing crushed cells in the cortex.
This plant received boron for only
a short time. x25.



Sections through a corky spot of a rutabaga petiole. The numbers refer to the approximate relation of the sections.