

SOME EFFECTS OF BORON SUPPLY ON THE CHEMICAL COMPOSITION OF TOMATO LEAFLETS

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(WITH THREE FIGURES)

Introduction

Recent reports in the literature dealing with the effects of boron supply on plant growth have considered associated effects on the mineral composition of plants. Reports that boron supply may influence the accumulation or utilization of other elements have led certain investigators to postulate a regulatory rôle for boron in this respect (10, 39, 52). There is, however, a noteworthy lack of agreement among investigators as to the specific effect of boron on the accumulation of any given element. Some of this lack of agreement may be due to the use of a wide variety of crops by different workers and to the use of sand or solution cultures in some studies and various soils in others. There still remains, however, considerable disagreement in this respect among investigators who have worked with plants grown in soils, or among those who have used sand or solution culture techniques.

It has been reported that as the supply of boron to plants was increased either by fertilization of soils or by additions to nutrient cultures: the calcium content of plants or of various tissues was increased (27, 28), decreased (14, 22, 27, 29) or remained constant (9, 26, 33); the potassium content was increased, (14, 21) or decreased (20); the magnesium content was increased (9, 41), decreased (20), or remained constant (9, 28); the phosphorus content was decreased (10, 11, 21, 53), or unchanged (33); and the iron content was increased (5), decreased (9, 29), or remained constant (28).

Several investigators have pointed out that boron may be concerned with nitrogen and protein metabolism of plants (32, 45, 46, 54). Other results indicate that the protein or total nitrogen content of plant tissues increased (8, 21, 28, 31, 36, 42), decreased (4, 11, 29, 44), or was unchanged (6, 34, 43, 50) when boron supply to the plant was increased.

Several miscellaneous effects of boron supply have been noted which are pertinent to this discussion. An increased boron supply has been found to alleviate the deleterious effect of high potassium concentrations (17). An increased potassium supply, however, has alleviated (40) or accentuated (38) boron deficiency. It has also resulted in an increased (38) or decreased (7) boron content in the plants. Other workers (23, 25, 47, 55) have noted the existence of a boron-calcium relationship in the nutrition of plants, and the suggestion has been made that boron is involved in the regulation of a calcium-potassium interaction (40). Also, the effects of increased iron supply in alleviating boron toxicity (14) and of increased boron supply in alleviating iron toxicity (24) have been pointed out. Studies of the ash con-

tent of plants have shown that an increased boron supply is associated with a decreased ash content (4, 11, 15), an increased ash content (25), or unchanged ash content (27). Increased (27) and decreased (12) percentage dry matter has been reported with an increased boron supply to the plant.

The literature, therefore, shows striking disagreement concerning the effects of boron supply on the mineral content of plants. Many of the effects noted are of a sufficiently great order of magnitude to be of importance both from the standpoint of the nutritive value of food crops and from the standpoint of plant nutrition. The present study was undertaken in an attempt to determine, under carefully controlled conditions, the effects of wide variations in boron supply on the chemical composition of tomato leaflets. The treatments were designed to include rates of boron supply which would produce plants exhibiting symptoms of a severe boron deficiency, plants with symptoms of severe boron toxicity, and plants of apparently normal boron nutrition. In this investigation, the contents of fourteen of the essential nutrient elements have been used as criteria of chemical composition.

Materials and methods

Two experiments were conducted at Ithaca, New York, during the summer of 1943. In experiment 1, seeds of an inbred strain of Bonny Best tomatoes were planted in the greenhouse May 1. The seeds were germinated in small crocks filled with pure quartz sand and supplied with a nutrient solution of the following composition (p.p.m.): Ca, 285; K, 223; Mg, 69; N, 168; S, 144; P, 70; Fe, 5.0; Mo, 0.05; Mn, 0.5; Zn, 0.05; Cu, 0.02. This solution will hereafter be referred to as basal nutrient. Eighteen seedlings were transplanted into two-gallon glazed crocks with one seedling per crock on May 20, and all plants were placed outdoors. Nine plants were supplied with the basal nutrient throughout their life span; the remaining nine plants were supplied with the same nutrient solution containing in addition 0.5 p.p.m. of B. Three plants of each treatment were randomized as to position in each of three rows. A total of nine plants was used in each treatment.

The crocks and plants were supported by stakes. All axillary growth of each plant was pruned off twice weekly. During the early growth stages, nutrient solution was supplied to the plants three times each week. As the summer progressed, nutrients were supplied every other day, and finally—when fruits were ripening—they were applied four times per week. The solutions were applied in 500-ml. quantities which were sufficient to insure an appreciable amount of drip, and each pot was watered with distilled water between nutrient applications. The first four fruits to ripen on each plant were picked on the morning of the day that complete color change had occurred and analyzed for vitamin content. All plants were harvested August 21 when they were 112 days old.

At the time of harvest the height of each vine and the number and total fresh weight of immature fruit on each plant were recorded. The leaflets of each plant were subsequently separated from the petioles and weighed.

The remaining parts of the vine were then harvested and the root systems washed free of sand. The leaflet, vine, and root materials of each plant were dried at 70° C. for 72 hours and dry weights recorded. The nine individual leaflet samples of each treatment were preserved for chemical analyses, the results of which are reported here.

In experiment 2, seeds of the same inbred strain of Bonny Best tomato were germinated in the greenhouse May 5, using the same equipment and base nutrient solution as in experiment 1. On May 25, fifty seedlings were transplanted into large crocks and placed outdoors. Five treatments with ten plants each were used which differed only in the amount of boron supplied to the plants in the basal nutrient solution. The boron concentrations (p.p.m.) were as follows: 0.5, 15.5, 30.5, 45.5, and 60.5. The respective treatments were started June 5 when the plants were 31 days old.

A randomized block design was used (13) with five replications (blocks). Each treatment consisted of a two-plant row in each block, and a total of ten plants was used in each treatment. The treatments were randomized as to position within a block by the use of TIPPETT's randomization tables (49).

The methods of supporting the plants, pruning, supplying nutrients, and harvesting ripe fruit for vitamin analyses were the same as for experiment 1. The plants were continued on their respective treatments until August 26 when they were 113 days old. Finally at harvest, the same procedure as in experiment 1 was used. The leaflets of the two plants in each block which received the same treatment were composited, and thus five leaflet samples or replications were available in each treatment for the purpose of this investigation.

Each leaflet sample was ground in a mortar and pestle to prevent mineral contamination (16), and duplicate analyses for K, Ca, Mg, S, Na, P, Mo, Cu, Mn, Zn, Fe, and Co were made by the method of PARKS *et al.* (35). Boron was determined by the method of NAFTEL (30); and organic-N (1), NO₃-N (51), and NH₃-N (1) were determined by the indicated methods. The mean of the duplicate analyses for any given element was used for each leaflet sample, the treatment means computed, and all differences between treatment means tested for statistical significance by the *t* test (48).

Results

Measurements of the growth and fruitfulness of the plants in both experiments are given in table I. In experiment 1, plants supplied with nutrient solution lacking boron were significantly smaller with less extensive root systems than those plants supplied with 0.5 p.p.m. boron in the nutrient medium. For convenience the former plants will be designated as boron-deficient and the latter as normal or control plants. Fruitfulness was also significantly less in boron-deficient plants. Mean differences in all characters except percentage dry matter of vines are highly significant statistically. In addition, severe deficiency symptoms similar to those obtained in other investigations were observed on vegetative parts of the plant (18, 19) and on fruits (19, 37) in the boron-deficient treatments.

TABLE I
MEASUREMENTS OF GROWTH AND FRUITFULNESS, GIVING TREATMENT MEANS TOGETHER WITH THEIR STANDARD ERRORS

TREATMENT (BORON SUPPLY)	GROWTH						FRUITFULNESS					
	HEIGHT OF VINE	FRESH WEIGHT OF VINE	DRY WEIGHT OF VINE	PERCENT. AGE DRY MATTER	DRY WEIGHT OF ROOTS	TOTAL FRESH WEIGHT RIPE FRUIT	NO. OF FRUIT RIPENED PER VINE	SIZE OF RIPE FRUIT	NO. OF IMMATURE FRUIT	TOTAL FRESH WEIGHT IMMATURE FRUIT		
	cm.	gm.	gm.	%	gm.	gm.		gm./fruit		gm.		
A. Experiment 1												
0.0	67.7 ± 5.74	200.5 ± 23.10	37.1 ± 4.60	18.2 ± 0.75	4.7 ± 0.49	331.4 ± 106.71	4.9 ± 1.21	65.9 ± 14.77	0.2 ± 0.22	4.3 ± 4.30		
0.5	109.6 ± 4.39	356.0 ± 18.63	68.7 ± 3.18	19.4 ± 0.50	9.0 ± 0.70	831.7 ± 63.76	9.7 ± 0.81	88.5 ± 6.91	9.3 ± 1.38	499.1 ± 70.48		
B. Experiment 2												
0.5	101.5 ± 4.28	271.3 ± 21.69	47.9 ± 1.46	17.7 ± 0.28	8.4 ± 0.35	774.2 ± 49.51	6.9 ± 0.82	119.7 ± 9.59	10.4 ± 1.44	523.9 ± 52.24		
15.5	99.6 ± 5.21	176.6 ± 19.46	26.4 ± 1.75	15.1 ± 0.65	4.2 ± 0.23	621.8 ± 26.18	6.6 ± 0.45	97.3 ± 6.10	5.6 ± 1.19	143.1 ± 28.42		
30.5	88.7 ± 5.11	105.3 ± 13.73	14.7 ± 1.74	14.2 ± 0.44	3.3 ± 0.47	456.3 ± 30.86	6.1 ± 0.53	76.7 ± 3.85	1.0 ± 0.56	6.8 ± 2.45		
45.5	78.8 ± 6.10	66.3 ± 14.76	8.4 ± 1.34	13.7 ± 0.73	1.8 ± 0.20	354.7 ± 29.38	5.3 ± 0.52	69.7 ± 5.83	0.1 ± 0.10	2.4 ± 2.40		
60.5	55.3 ± 3.76	29.7 ± 2.35	4.0 ± 0.28	13.7 ± 0.47	1.2 ± 0.08	230.5 ± 26.19	3.7 ± 0.37	63.6 ± 7.51	0.4 ± 0.22	5.3 ± 3.80		

The data in table I show that significantly less growth and fruitfulness were associated with increased boron supply in experiment 2. Marked toxicity symptoms occurred on plants supplied with the four highest concentrations of boron, and the severity of the symptoms increased with increased boron supply. In this experiment the plants receiving 0.5 p.p.m. boron in the nutrient medium will be designated as control plants while those treatments using nutrients containing greater quantities of boron will be designated as toxic. The symptoms as well as the data concerned with growth and fruitfulness of the plants and results of vitamin analyses will be discussed in a subsequent paper.

The results of all chemical analyses are given in table II. Treatment means, together with their standard errors, are presented to aid in evaluating the statistical significance between treatments. In treatments where the amount of material available for analysis was limited, replicates were combined, and only the mean of duplicate analyses on a composite sample is available. It is not possible in these instances to use such values in a statistical test since no standard errors are presented. It is noteworthy that significant differences between treatments exist with respect to all elements except sodium.

The concentration of each element in leaflet material is presented graphically as a function of boron supply in figures 1, 2, and 3. In each graph the broken base line and the discontinuous nature of the curve indicates that results from two separate experiments differing in environmental variables other than nutrient supply were utilized. In noting the lack of coincidence of some analytical results of control plants in experiments 1 and 2, it should be recalled that differences in uncontrolled environmental factors also resulted in some differences in growth and fruitfulness (table I).

For convenience, boron supply is presented in different abscissal units for graphing results from experiments 1 and 2. In the curves the reliability of any point may be estimated from standard errors of means presented in table II. The unreliability of those points which represent results from composited samples is indicated by dotted portions of the curve.

Increasing boron supply resulted (fig. 1) in marked increases in the boron content of tomato leaflets. The standard errors and the number of degrees of freedom involved in each mean (table II) clearly show the differences in boron content from deficient to normal and from normal to toxic levels of boron supply are all highly significant. The boron contents of leaflets from plants grown in deficient and toxic treatments are in accord with other results (2) and with the observed deficiency and toxicity symptoms.

Protein content increased as the boron supply was increased (fig. 1). In experiment 1, the crude protein content of the plants receiving a normal (0.5 p.p.m.) supply of boron was significantly higher than that of the boron-deficient plants, and the plants receiving toxic (15.5 p.p.m. and higher) concentrations of boron (experiment 2) were significantly higher in organic

TABLE II
EFFECTS OF BORON SUPPLY ON THE CHEMICAL COMPOSITION OF TOMATO PLANTS

TREATMENT (BORON SUPPLY)	MILLIGRAMS PER GRAM DRY WEIGHT OF LEAFLETS									
	Ca	Mg	K	Na	P	S	Org.-N	NO ₃ -N	NH ₄ -N	
	mg./gm.	mg./gm.	mg./gm.	mg./gm.	mg./gm.	mg./gm.	mg./gm.	mg./gm.	mg./gm.	
A. Exp. 1										
0.0	39.4 ± 1.78 (7)	3.7 ± 0.23 (7)	24.3 ± 0.99 (7)	1.9 ± 0.45 (7)	8.2 ± 0.24 (7)	15.0 ± 1.49 (7)	25.2 ± 0.54 (7)	0.31 (2)	0.2 (2)	
0.5	55.3 ± 1.42 (9)	9.2 ± 0.56 (9)	18.3 ± 1.29 (9)	2.2 ± 0.16 (9)	7.2 ± 0.14 (9)	26.2 ± 1.36 (8)	29.0 ± 0.59 (9)	0.74 (2)	0.3 (2)	
B. Exp. 2										
0.5	62.7 ± 1.23 (5)	6.9 ± 0.05 (5)	14.0 ± 0.71 (5)	2.0 ± 0.34 (5)	8.8 ± 0.17 (5)	25.1 ± 1.12 (5)	27.4 ± 0.25 (5)	0.14 (1)	0.4 (2)	
15.5	48.7 ± 1.41 (5)	5.1 ± 0.21 (4)	21.3 ± 0.95 (4)	1.3 ± 0.24 (4)	11.6 ± 0.55 (5)	16.3 ± 1.05 (4)	38.9 ± 0.54 (5)	0.21 (2)	0.2 (2)	
30.5	41.2 ± 1.32 (5)	3.9 (1)	17.0 (1)	0.2 (1)	14.2 ± 0.50 (4)	10.0 (1)	45.2 ± 0.42 (5)	0.28 (2)	0.2 (2)	
45.5	38.4 ± 1.24 (3)				13.7 ± 1.88 (3)		49.0 ± 0.32 (3)		0.2 (1)	
60.5	39.6 (1)				15.2 (1)					

* The treatment means are reported together with their standard errors. Duplicate analyses were made on material from each replication and the number of replications are indicated in parentheses.

TABLE II (Continued)

TREATMENT (BORON SUPPLY)	MICROGRAMS PER GRAM DRY WEIGHT OF LEAFLETS							
	Mo	Fe	Mn	Co	Zn	Cu	B	
	$\mu\text{g./gm.}$	$\mu\text{g./gm.}$	$\mu\text{g./gm.}$	$\mu\text{g./gm.}$	$\mu\text{g./gm.}$	$\mu\text{g./gm.}$	$\mu\text{g./gm.}$	
A. Exp. 1								
0.0	7.0 \pm 0.38 (7)	460 \pm 31.7 (7)	146 \pm 7.4 (7)	0.26 \pm 0.008 (7)	31.6 \pm 2.38 (7)	18.6 \pm 0.86 (7)	7.6 \pm 1.19 (9)	
0.5	1.1 \pm 0.10 (9)	542 \pm 48.3 (9)	169 \pm 16.4 (9)	0.31 \pm 0.017 (8)	16.8 \pm 1.19 (8)	12.3 \pm 0.64 (8)	91.8 \pm 3.30 (9)	
B. Exp. 2								
0.5	1.2 \pm 0.03 (5)	277 \pm 7.4 (5)	123 \pm 3.4 (5)	0.18 \pm 0.014 (4)	21.8 \pm 1.51 (5)	11.8 \pm 0.55 (5)	147 \pm 18.5 (5)	
15.5	26.0 \pm 0.73 (5)	377 \pm 11.2 (5)	176 \pm 5.5 (5)	0.25 \pm 0.017 (4)	33.9 \pm 0.87 (4)	21.0 \pm 1.00 (4)	982 \pm 87.7 (5)	
30.5	4.9 \pm 0.34 (5)	438 \pm 19.7 (5)	184 \pm 7.4 (5)	0.35 (1)	51.9 (1)	22.0 (1)	1351 \pm 101.1 (5)	
45.5	3.6 \pm 0.25 (3)	447 \pm 35.2 (3)	203 \pm 15.2 (3)					
60.5	3.1 (1)	439 (1)	252 (1)					

nitrogen than the plants receiving a normal boron supply. The concentrations of ammonia and nitrate nitrogen present in these samples (table II) were very low and essentially constant for all treatments.

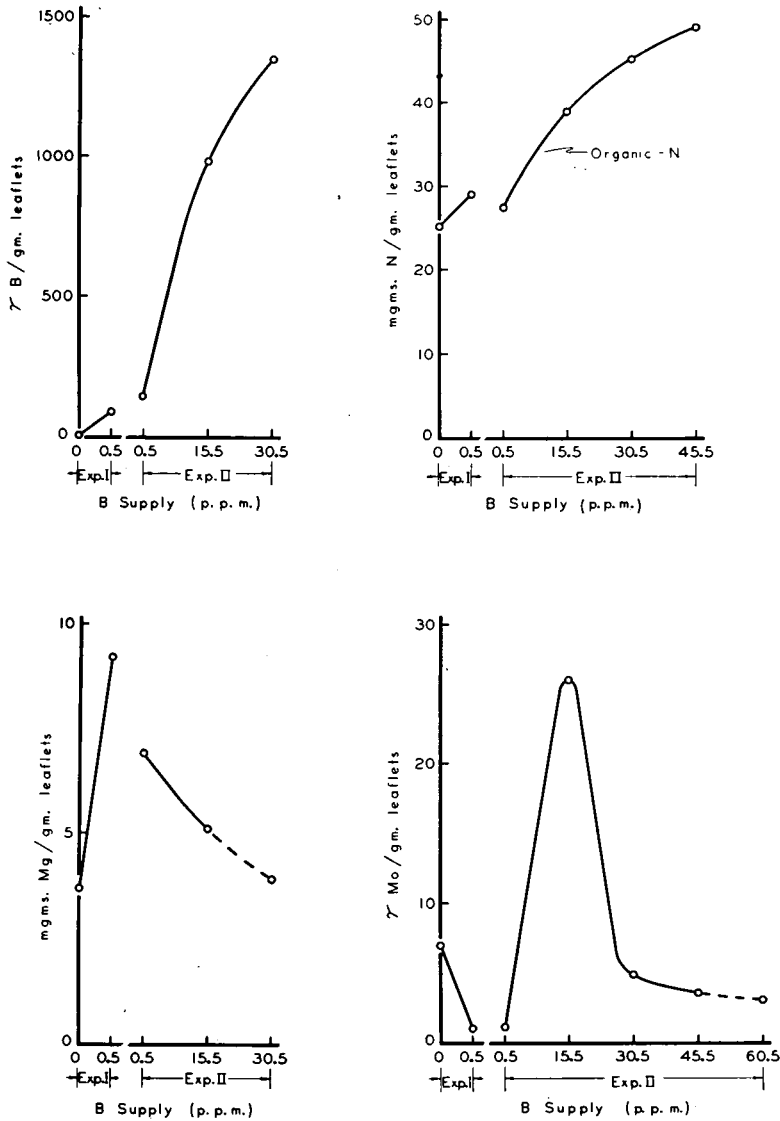


FIG. 1. The effects of boron supply on the boron, nitrogen, magnesium, and molybdenum concentrations in tomato leaflets.

The plants grown with a normal boron supply had more than twice the magnesium content of the boron-deficient plants on a percentage or concentration basis. On a per plant basis, the difference would be even more striking owing to the increased yield at the normal level. There is a cor-

responding, though less marked, decrease in magnesium content with higher levels of boron supply. Trends in composition similar to that for magnesium would be accentuated if computed as content per plant, since trends in yield are similar to those shown for concentration.

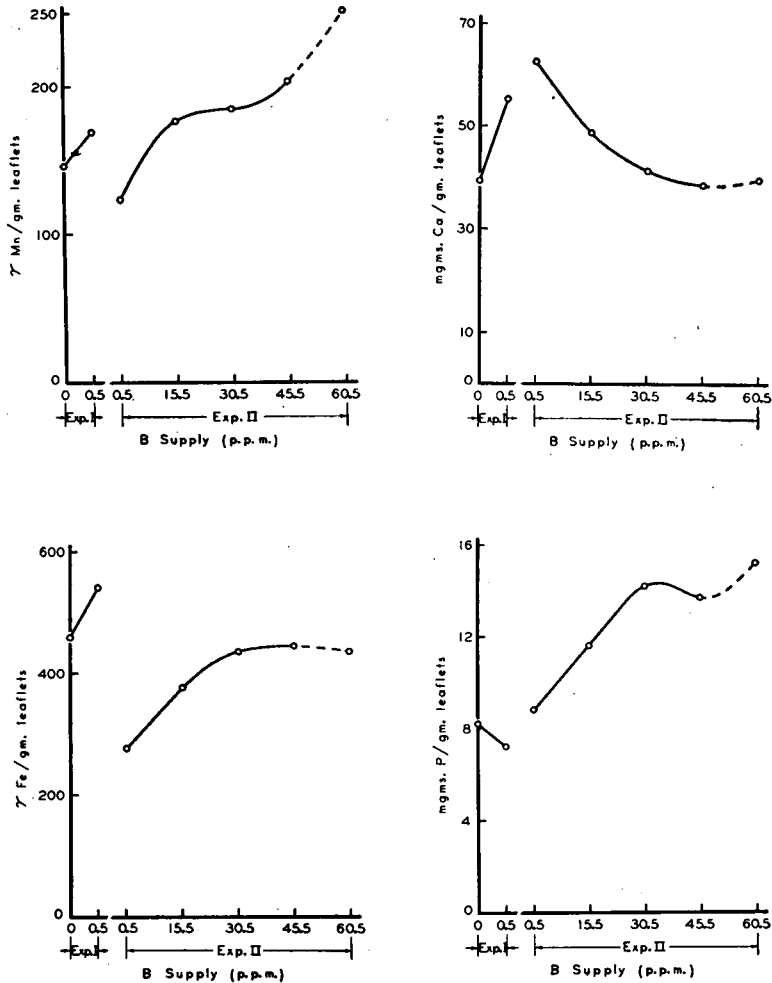


FIG. 2. The effects of boron supply on the manganese, calcium, iron, and phosphorus concentrations in tomato leaflets.

The concentration of molybdenum in these samples (fig. 1) was affected more strikingly by changes in boron supply than was that of any other element. Particularly noteworthy is the very high molybdenum content of plants grown in solutions containing 15.5 p.p.m. boron and the difference in molybdenum content between deficient and normal plants. A *t* test using the values and standard errors in table II shows these differences to be highly significant.

The responses shown with respect to the remaining nine elements might be grouped to show similarity in trends. Like boron and protein content (fig. 1) the concentration of manganese and iron (fig. 2), and cobalt (fig. 3) increase with increased boron supply in each experiment. A source of cobalt was not intentionally supplied in the nutrient medium. Analyses for cobalt in the samples were made since maladies have been associated with a lack

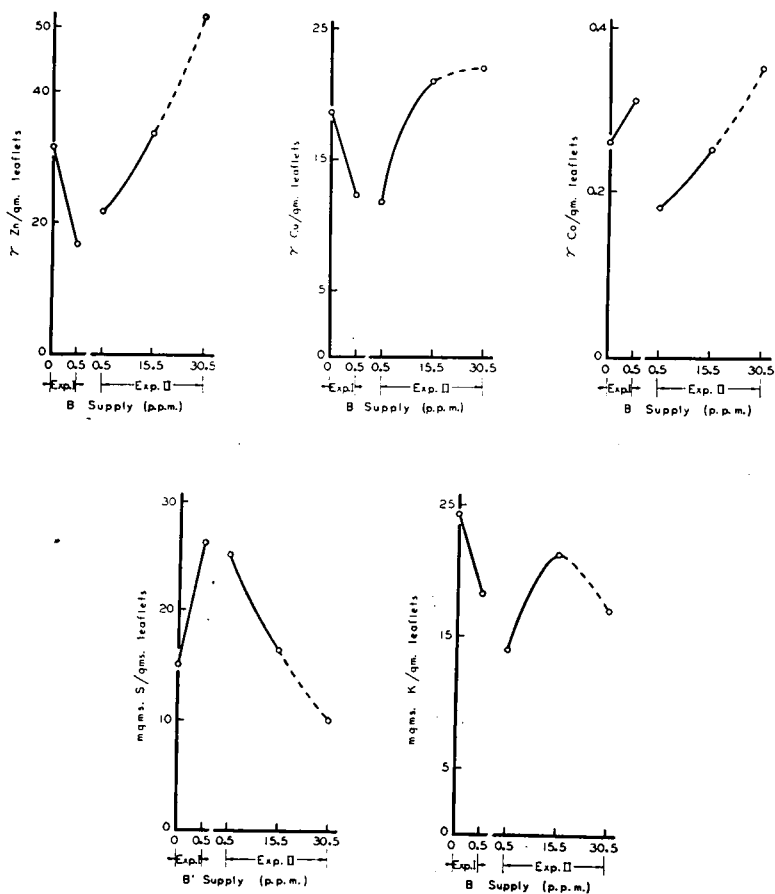


FIG. 3. The effects of boron supply on the cobalt, zinc, copper, sulfur, and potassium concentrations in tomato leaflets.

of cobalt in nutritional studies. The curve showing cobalt content of leaflets graphed as a function of boron supply is presented as a matter of theoretical interest and is based on the assumption of a constant cobalt supply as an impurity present in other salts or as an impurity contributed by the sand substrate. The validity of such an assumption is problematical. A similar assumption would be necessary for sodium. No statistically significant differences occurred, however, between treatments with respect to sodium content of the leaflets, and no graph is presented for this element.

Like magnesium (fig. 1), the maximum concentration of calcium (fig. 2) and sulfur (fig. 3) was found in control treatments of both experiments. Boron supplies of less than 0.5 p.p.m. or more than 0.5 p.p.m. were associated with a significantly lower concentration of these elements.

A minimum concentration of phosphorus (fig. 2), zinc, copper, and potassium (fig. 3) occurred in leaflets from control plants, and the trends shown are the reverse of those for the magnesium group. In boron deficient or toxic treatments the concentration of these elements was significantly greater.

Discussion

It is clear from the results reported here that differences in boron supply have resulted in differences in the boron content of plant tissue. In the same plant tissue differences in the concentration of most of the elements considered in this investigation were obtained. Since the nutrient composition of the medium was constant with the exception of boron in all treatments, it seems clear that a differential rate of absorption must have occurred, unless differences in boron supply merely resulted in a redistribution of mineral elements among plant organs. Existing evidence would indicate the former situation to be the more likely. In either case, however, altered mineral content as a result of varied boron supply would be of fundamental importance in plant nutrition and in evaluations of the nutritive quality of food crops. If differential absorption occurred, the cause is not known. It obviously cannot be directly attributed to differences in total growth of the plants or to relative extent of root systems since, if such were the case, uniform trends in content of the different elements would have to exist. The data presented here do not support this contention. At least, similar trends with respect to any given element would have to be associated with growth differences in different experiments. Such a situation does not exist in these and other data. For instance, in this experiment maximum calcium content was associated with maximum growth, and in another experiment (3) maximum growth was associated with minimum calcium content.

The trends reported here do not seem to be associated with any particular type of ion. For instance, opposite trends can be found among cations (Ca and Cu) and among anions (P and S). In addition, opposite trends are evident among divalent ions (Ca and Zn), and no correlation of trends with the valence of ions was observed.

Although tomato leaflets are not consumed directly by animals, they represent the leafy portion of a vegetable crop. In the case of forages and many vegetables, the chemical composition of this leafy material is important nutritionally for herbivora and man. Thus, the trends shown in tomato leaflets may serve as a basis to examine effects which may be of value in other plants. For instance, in this experiment protein content of leaflets varied approximately 100 per cent. A decreased yield of dry matter, however, was also obtained in treatments supplied with toxic quantities of boron, and these treatments were high in protein. If somewhat greater protein content

resulted from an increased boron supply with little or no suppression of yield in a forage crop, it would have profound significance nutritionally. That such a situation might result in increased protein per plant in the case of tomatoes can be shown by an interpolation of yield and protein curves between the first two treatments of experiment 2.

It seems possible that some of the discrepancies to be found in published data might be explained by trends reported here. For instance, reports of increased magnesium content associated with increased boron supply are supported by these data if the levels of boron supply were in a low range. Reports of decreased magnesium content associated with an increased boron supply are supported by these data if the level of boron supply was in a relatively high range. Similarly, MINARIK and SHIVE (27) have noted that maximum calcium content is associated with optimum boron supply.

Results of investigations concerned with ionic interaction have been reported from this laboratory (3). In these studies calcium ion supply was significantly and positively correlated with calcium content of tomato leaflets. In the same treatments potassium ion supply was significantly and negatively correlated with calcium content of leaflets. Therefore, the net effect (calcium content of leaflets) was associated at least with both calcium and potassium ion supply. Similarly, a magnesium-calcium interaction was associated with magnesium content of leaflets, and a magnesium-phosphorus interaction was associated with phosphorus content of leaflets. The fact that differences in boron supply have resulted in differences in plant composition with respect to nearly all the elements examined suggests that boron may be a component of one or more interactions or that complex interactions involving more than two elements may exist.

Summary

1. The effects of boron supply, ranging from deficient to toxic concentrations, on the chemical composition of tomato leaflets were examined. Results from two experiments using plants grown in sand culture are reported. The concentrations of K, Ca, Mg, S, Na, P, N, Mo, Cu, Mn, Zn, Fe, Co, and B were used as criteria of chemical composition.

2. As boron supply was increased, the concentration of this element in leaflet material was significantly increased.

3. There were also significant and large differences between treatments with respect to the concentration of most of the other elements examined, as boron supply was increased. The concentration of some elements was altered as much as several hundred per cent.

4. The results reported offer a possible explanation for confusion which exists in the literature. For instance, reports of trends involving increased magnesium, calcium, or potassium concentrations, or decreased magnesium, calcium, or potassium concentrations associated with increased boron supply could all be supported by these data if one assumes different initial levels of boron supply.

5. It was evident that boron supply had specific effects with respect to different elements, since the trends shown in plant composition for varying boron supply were completely dissimilar for different elements.

6. Differences between trends shown for various elements could not be correlated with the type of ion (cation or anion), the valence of ions, or total growth of the plants.

7. The possible importance of these effects with respect to plant nutrition and to the nutritive value of food crops is discussed.

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