Boron in Relation to Water Balance in Plants

Genevieve Lukman Leaf

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Introduction

Several recent investigators have suggested that boron may affect the water balance of plants (22). Schmucker (16) stated that the main role of boron is to control the structure of the protoplasm. The data of Dennis (6) indicated that boron regulates the water relations of the plasma colloids. Schropp and Arenz (17) found that boron prevented unusual swelling of the plasma colloids which would interfere with the ascent of water in the stem. Reports by Bobko (2) indicate that wilting of cotton was decreased with the application of boron and related date by Willis and Piland (21) for Romaine lettuce grown without the addition of borax to the soil disclosed that this crop was subject to severe wilting during the day. The present investigation was undertaken to determine the effect of various levels of boron in the nutrient solution on the moisture content of the leaves, stems, and roots of *Nicotiana tabacum* var. Little Turkish at different stages of development. Attention was also given to boron levels in relation to the water content of tissues during periods of water shortage and wilting.

Experimental Procedure

Pure quartz gravel was washed free of soluble phosphates in distilled water to which hydrochloric acid had been added. Equal quantities of gravel were placed in 78 two-gallon jars which were fitted with a pyrex glass vertical feeding tube. A side-arm level gauge and a ¼ inch boron-free glass aeration tube were stoppered into each jar. Withrow's medium light nutrient solution containing micro-nutrients other than boron was added to the gravel. Chemically pure salts known to be free of traces of boron were used.

Seeds of *Nicotiana tabacum* var. Little Turkish were planted (February 21) in flats containing one part loam to two parts sand. Seeds germinated in about ten days (March 2). Three weeks after germination (March 23) three seedlings were transplanted to each of 75 jars. Three jars were used as controls to measure the rate of water evaporation directly from the gravel. A record of the amount of water and solution added to each jar was maintained throughout the experiment. Solutions at first were changed completely every ten days, later every five to seven days as the plants enlarged.

Three weeks after transplanting (April 15), the plants were thinned to one per jar. Before the plants were separated into series, those from three jars were removed for analysis of fresh and dry weights. Each plant was sectioned into leaves and roots. The jar contents were transferred to a pan in which the roots were washed free of the gravel. After determination of fresh weights, the plant parts were immediately dried in an oven at 100-105 C. to prevent enzymatic activity and then dried to constant dry weight. They were comminuted in a Wiley mill and triplicate samples transferred to tared weighing bottles for weighing. From these weights the absolute dry weight of the sample was computed. Composite samples were used for calculations given below.

Four weeks after transplanting to jars, plants were divided into four series with 12 jars each. Series A contained no boron; B—1 p.p.m. boron (as borax); C—4 p.p.m.; and D—20 p.p.m. The remaining 24 plants were retained on Withrow's solution (without boron) to be used later in series E. Several days later these minus boron plants showed a slight necrosis at the terminal bud, and one feeding of 0.1 p.p.m. boron was added to prevent abnormal development.

The pH of the nutrient solutions of all the series maintained at 5.4-5.6 throughout the experiment. Within a week differences in form and appearance became apparent in plants of the various series. The nutrient solution was changed to Withrow's cloudy weather solution to reduce the succulence of the plants. The diurnal range of temperature in the plant house was maintained at 78-84 F. during this time.

Fourteen days after the first boron feeding, three plants from each of the four series were removed and carefully sectioned for fresh and dry weight analysis. The remaining 24 plants were divided into series E with 40 p.p.m. boron. Two weeks after beginning boron feedings in these series, fresh and dry weights were taken of a total of six plants, three plants from each series being merged as composite samples (A, table I).

Three weeks after beginning boron feedings in the one, four and 20 p.p.m. boron series, the water supply was gradually reduced to induce temporary wilting in three jars of each series. Differences in the onset and degree of wilting were observed and recorded. Three plants from each of these low-moisture sets were analysed for fresh and dry weights four weeks after feeding boron while wilting was manifest (B, table I). The remaining plants of these sets were then watered again to restore turgor.

When flower buds became evident six to eight weeks after beginning boron applications, the liquid was again gradually reduced to induce wilting. The 18 low-liquid plants were harvested in the late blossoming stage and their fresh and dry weights recorded (C, table I).

The remaining 18 jars (three jars per series A to E) were maintained at adequate nutrient levels until fruit-capsule stage. These plants were employed in an experiment to determine what effects, if any, the various boron levels had upon the ability of tissues to retain moisture during sustained periods of wilting and desiccation. One plant from each series was wilted by withholding water, removed from the jar, and first weighed intact. It was then divided into leaves, stem and roots, and these samples were dried to constant weight (A, table II). The two remaining plants of each series were allowed to wilt by withholding nutrient solution. At wilting they were harvested, and fresh weights for the wilted but intact plants were determined. One plant from each series, A to E, was sectioned as above and the fresh weight of each of these wilted parts was determined. After comminution, triplicate samples were taken of parts of this plant, dried to constant weight and data recorded (B, table II).

One plant was left on the greenhouse table to dry intact and was weighed as a unit every 3-4 days until thorough desiccation had occurred. It was then divided as above, and triplicate samples were dried to constant weight (C, table II). The data for plants

Figure 1. General habit of tobacco plants two weeks after beginning boron treatments. Left, Series A: 1 p.p.m. boron; Center, Series B: 1 p.p.m. boron; Right, Series D: [illegible] p.p.m. boron.

in this drying process were used to determine how differences in degrees of desiccation might be correlated with the various levels of boron supply.

Data and Discussion

Gross Morphology

Series A: No Boron

As early as five days after segregation, plants in this series showed uneven leaf growth and terminal buds showed the characteristic browning due to boron deficiency. A week later the deficiency signs became more pronounced in contrast to the large, slightly succulent plants of the B and C series. Slight chlorosis was visible around the margins of the leaves, and shortened internodes were evident. Two weeks after the first boron feeding a record was taken of the general characteristics of the plants in the series (Fig. 1).

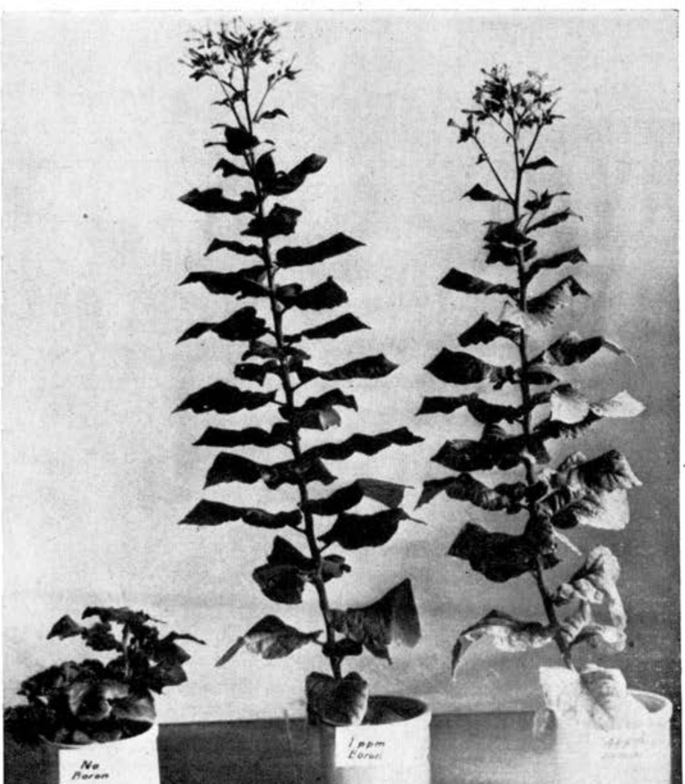

Figure 2. General habit of tobacco plants at full bloom. Plants are same as those shown in Figure 1.

The plants had an average height of 20 cm., with internodes averaging 2.5-3cms. Chlorosis became general, progressing inwardly from the margins of younger leaves. The older leaves became thickened and distorted, whereas the youngest leaves remained very small with necrosis at the terminal meristem. After necrosis of the terminal bud, axillary buds became abundant, giving a semi-rosette appearance to the plants. Several weeks later, boron-deficient leaves were puckered, thick, glabrous, and sticky to the touch. The browned areas extended basipetally from the terminal bud through the midribs and secondary veins of the leaves. Some of the leaves developing from the lateral buds were present. On the whole, the plants displayed a stunted growth.

Even during the warmer portions of the day, only very slight wilting was apparent in this series and was confined to the youngest leaves near the terminal buds. In one plant which had a dominant lateral shoot, wilting occurred only at the leaves near the terminal bud. When leaves failed to recover their turgor they showed yellowing and browning after prolonged wilting. Towards the termina-

Table 1

Fresh and Dry Weights of Leaves, Stems and Roots.

p.p.m.	fresh weight*			dry weight			moisture content		
boron	leaves	stems	roots	leaves	stems	roots	l.	s.	r.
	gms.	gms.	gms.	gms.	gms.	gms.	%	%	%
	A. Two weeks after boron application								
0.0	46.10	11.46	9.10	4.05	1.11	0.69	91.3	90.3	92.5
1	70.13	35.00	18.90	6.98	2.34	1.41	90.1	94.4	92.6
4	64.80	29.35	18.50	4.40	1.93	1.14	93.3	93.5	93.9
20	43.07	20.50	12.03	3.64	1.58	1.04	91.6	92.3	91.4
40	91.15	32.60	57.56	6.98	2.83	5.94	92.4	91.3	89.7
	B. Four weeks after boron application								
0.0	26.76	22.37	10.65	6.10	3.23	2.91	77.3	85.6	72.7
1	95.90	106.75	31.35	16.03	13.55	8.15	83.4	88.3	74.1
4	75.45	111.95	24.50	13.61	14.99	7.57	82.0	86.7	69.1
20	36.95	83.05	17.13	10.16	12.64	4.71	72.6	84.8	72.5
40	43.90	69.33	30.10	10.35	7.10	3.10	76.5	89.8	89.7
	C. Six to eight weeks after boron application								
0.0	132.77	41.67	39.36	11.87	2.61	2.28	91.1	93.8	94.2
1	215.06	194.30	111.36	18.21	23.44	11.87	91.6	88.0	89.4
4	160.73	155.32	68.53	17.28	21.32	11.38	89.3	86.3	83.4
20	115.45	124.35	56.05	12.28	11.12	5.16	89.4	91.1	90.8
40	93.67	85.17	43.40	13.29	10.94	2.84	85.9	87.2	93.5

*All "fresh weight" data in table is for plants whose leaves begun to show visible symptoms of wilting.

tion of the experiment, the older leaves which had remained brittle during the entire experiment showed a slight paling of their green color along laminar margins in cultures from which nutrient solution had been withheld for several days.

Series B: 1 p.p.m. Boron

This group began vigorous growth several days after boron was administered. Two weeks later, plants averaged 36 cms. in height with an average internodal length of 5 cms. Leaves were large and succulent, had a normal green color, and gave the appearance of being healthy in every respect. The leaves above the third and fourth internodes began to show a uniform twist at one side of the base of the blade. Several weeks later it was noted that under high insolation (during the brightest part of the day, 12 noon to 2 p. m.) small, clear, watery "dew spots" were evident on lower leaves. These seemed to be incipient chlorotic areas which developed first in the lower leaves but were not evident above the eighth node. Above this level the blades were both twisted and puckered. The general texture of the leaves was not affected. This condition of plants with 1 p.p.m. of boron was essentially similar to that of plants receiving 4 p.p.m. (Fig. 2) but took longer to develop. At maturity the plants had attained a height of 86 cms. and were sturdy with a large surface of individual leaves.

Wilting occurred readily in all series receiving boron. Plants of series B and C exhibited the greatest degree of wilting when the water supply was reduced. The plants in series B, however, recovered turgidity less rapidly than did those of the 4 p.p.m. series. The severest wilting occurred in older leaves and extended to the upper six nodes. After six days of continuous wilting the lower leaves assumed a yellowish cast. During periods of low water supply in the prefloral stage, the youngest leaves remained turgid until harvest. However, after the plants had formed fruit, low water supply caused wilting; and it extended progressively upward. After nutrient solution had been withheld for three days, even the youngest leaves wilted, in contrast to those plants which were maintained at a normal water level whose upper leaves remained turgid and whose lower leaves at this stage exhibited some tip necrosis.

Series C: 4 p.p.m. Boron

The leaves of these plants appeared uniform in form and size when deficiency symptoms were already evident in series A (no boron). A week later they showed some leaf distortion and a slight but very characteristic curvature on one side towards the under-

Table 2

Fresh and Dry Weights of Leaves, Stems and Roots at Senescence.

p.p.m. boron	fresh weight* leaves	fresh weight* stems	fresh weight* roots	dry weight leaves	dry weight stems	dry weight roots	moisture content entire plant
	gms.	gms.	gms.	gms.	gms.	gms.	%
A. Wilted by withholding water							
0.0	26.90	40.80	22.85	15.15	6.60	3.65	61.0
1	85.10	145.21	64.55	17.03	22.94	11.43	85.5
4	75.12	152.23	57.78	16.74	23.44	10.19	82.4
20	38.54	110.43	44.48	7.62	13.47	6.18	86.0
40	27.71	69.00	29.16	15.85	8.94	3.62	77.5
B. Wilted by withholding nutrient solution							
0.0	28.20	12.71	6.89	5.22	3.44	1.40	79.0
1	102.41	135.24	59.36	13.84	22.55	10.94	84.1
4	107.36	138.35	91.20	14.88	17.99	12.88	86.5
20	69.54	132.10	37.20	16.59	11.00	4.17	87.0
40	37.80	72.02	17.30	12.90	6.21	3.40	80.1
C. Desiccated at room temperature							
0.0		111.46**		16.09	5.12	2.66	78.5
1		346.00		15.51	23.53	9.98	85.6
4		312.50		16.70	23.64	9.46	84.1
20		205.63		14.40	12.86	6.93	83.5
40		133.77		13.87	10.09	3.72	79.0

*All "fresh weight" data in table is for plants whose leaves had begun to show visible symptoms of wilting.

**Fresh weights in this column are for entire plants.

side on the young leaves resulting from a differential growth rate on opposite sides of the leaf blade. A week later slight marginal browning indicated boron toxicity. The "dew-spots" described above appeared earlier, and chlorosis was more pronounced in this series. In general, the plants were morphologically similar to those receiving 1 p.p.m. of boron, except for their shorter height (fig. 2).

For the duration of periods of low water supply, plants in this series exhibited the most severe degree of wilting but also the quickest recovery. During the prefloral stage, wilting extended up to leaves of the terminal bud. Plants being maintained at a normal water level remained more turgid than those being similarly treated in series B at this time. Upon prolonged wilting (six days) the oldest leaves (lower three to five) became chlorotic.

Series D: 20 *p.p.m. Boron*

The plants of this series were fairly large, averaging 30 cms. in height with 2-3 cms. internodes. The leaves were smaller than those in the B and C series, exhibiting signs of leaf distortion and

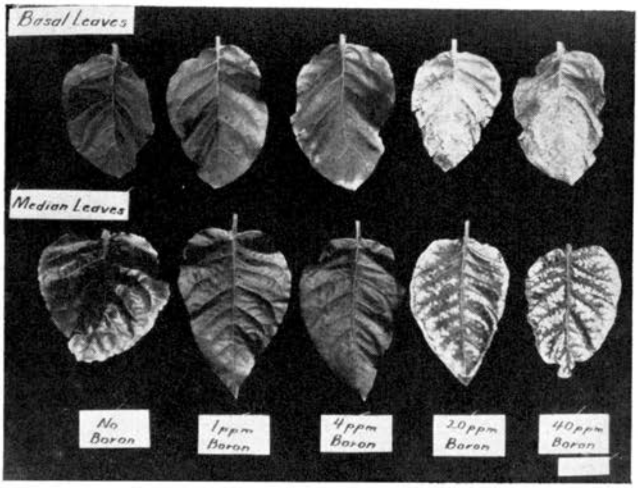

Figure 3. Chlorosis and leaf distortions associated with various boron dosages in mature tobacco.

brown necrotic areas on the lower ones. These spots first appeared as chlorotic areas which turned brown without falling out of the leaf. Obvious tip-burning progressed inwardly in the inter-veinal region. In general the leaves were lighter in color than those of series B and C. When water was withheld, lower leaves became yellow along the mid-rib in two days.

With a gradual reduction in nutrient supply, wilting was very slight during the first three days, but was followed by a sudden transition to severe wilting. The lowest leaves were extremely dry and yellowed, exhibiting a skeleton of green veins so that it was difficult to observe the degree of wilting. The youngest leaves remained turgid throughout the wilting period, although more spotting was evident on them than on similar leaves of the plants maintained at normal water levels. During the wilting interval at the fruit-capsule stage, all but the youngest leaves appeared dry and yellow, only the mid-ribs remaining green in the younger leaves (fig. 3).

Series E 40 p.p.m. Boron

The plants grew to a height of 45 cms and showed pronounced spotting even on the youngest leaves. The newly developing leaves were distorted, and their margins curled downward, suggesting an uneven growth of the midrib. Chlorosis was clearly visible soon after boron application.

The leaves of this series were distorted and yellow similar to those of series D, but the symptoms appeared earlier in the plants' devel-

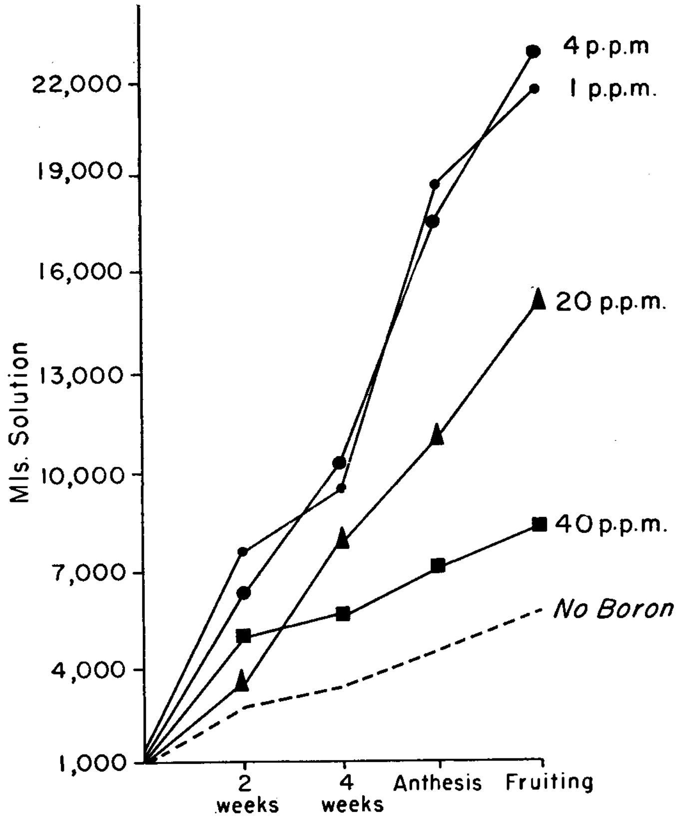

Figure 4. Amount of Liquid Absorbed During Growth of Tobacco Plants.

opment (fig. 3). Hence, it was difficult to detect the onset of wilting. All the leaves were dried and spotted. However, even when water had been withheld for four days from the plants in the prefloral stage, the vascular areas remained dark green.

Water Absorption

The amount of liquid absorbed by the plants in the various series until the time of harvesting was determined (fig. 4). The lowest actual liquid absorption was, at all times, associated with boron deficiency. Absorption curves indicate that greater water intake occurred during the first four weeks of application. In series A, when deficiency symptoms became pronounced, a gradual decrease in rate of absorption occurred. With the appearance of the deficiency symptoms there occurred reduction in growth (11, 12), death of the apical meristem (20), production of brittle leaves (8), shortened internodes (3) and failure to flower. Warington (20) in an investigation of *Vicia faba* noted that it was during the latter part of the growth period that lack of boron had its greatest effect and attributed this to the fact that boron probably depressed the uptake of calcium. Lowenhaupt (10) suggested that boron is probably necessary for the normal distribution of salts and sugars through the plants. Biebl (1) found that, with an optimum boron supply, transpiration was increased in *Pisum sativum*. Though plants of series B and C exhibited toxicity symptoms, they showed the greatest amount of water absorption and followed a normal course of development (fig. 2). Swanback (19) found 0.4 p.p.m. boron applied as boric acid to be the optimum dosage for tobacco plants, but McMurtrey (12), in testing the effects of boron in aerated and unaerated solutions for tobacco plants, concluded that the 0.5 p.p.m. boron produced the best growth.

Series B made the best growth in terms of yield and general vigor even though 1 p.p.m. of boron was definitely toxic. Eaton (7) observed similar results with toxicity symptoms in sunflower. He stated that " a concentration of boron of 1.0 p.p.m. was definitely toxic to the sunflower; the plants in this series, however, were decidedly larger than those grown at a concentration of 0.5 p.p.m.

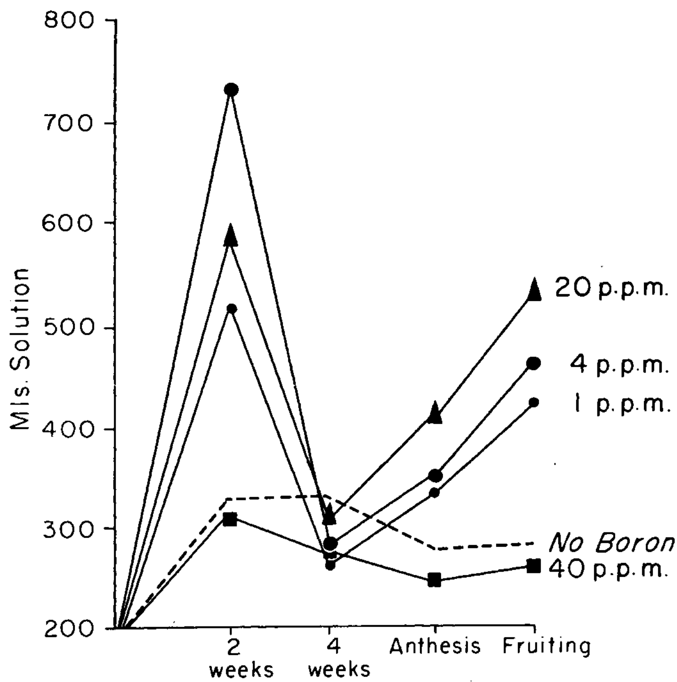

Figure 5. Liquid Absorbed by Tobacco Plants in Milliliters Per Unit of Dry Weight.

which was not toxic." Series D (20 p.p.m. of boron) was extremely toxic to plants. The amounts of water absorbed by series D paralleled series B and C during the various stages but at a lower level (table 1, figs. 4 and 5). A further increase in the concentration of boron as in series E (40 p.p.m.) produces an inverse condition such that the water absorption curve more nearly resembles that of the boron-deficient series. This decreased water absorption persisted although the plants grew to maturity and produced fruit. Flowering and fruiting occur in the toxic ranges. Swanback (19) found that while gradually increasing boric acid content of solutions for tobacco plants to 400 p.p.m., plants still grew normally and fruited at the higher concentrations although the toxicity symptoms were definitely visible. Also Cook (5) found in various plants grown in boron-treated soil that yellowing of the leaf indicated injury in toxic ranges, but the plants were not sufficiently injured to suffer a definite reduction in the yield. It thus appears that minus-boron treatment arrested growth, whereas slightly toxic boron dosages stimulated growth, and highly toxic boron decreased the rate although not inhibiting it completely.

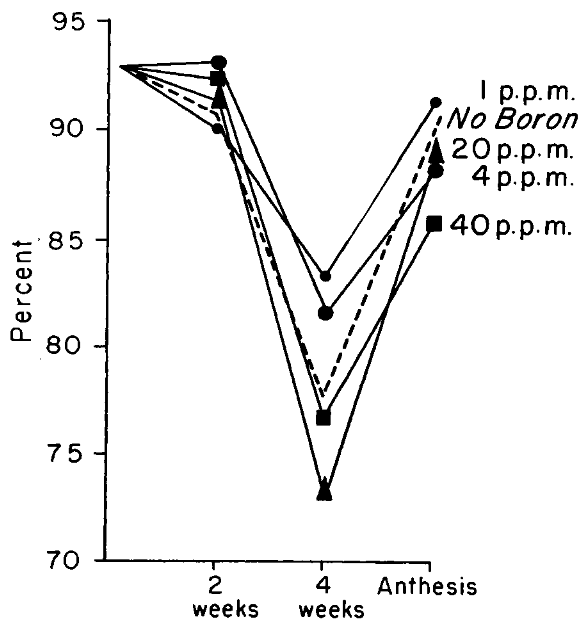

Figure 6. Moisture Content of Leaves of Tobacco Plants at Various Stages of Development.

Moisture Content

The moisture content of the different organs varied in all series with the stage of development. Samples of leaves obtained two weeks after boron was introduced showed that the 4 p.p.m. plants contained the greatest percentage of water (table I, fig. 6). Series B (1 p.p.m.), which had shown the best development, contained the greatest percentage of dry weight in the leaves. Samples taken at the time that flower buds first appeared (table I) indicated that series B and C contained the most moisture. At this time plants showing effects of highly toxic dosages of boron contained the greatest percentages of dry weight, although the fresh weights were one half those exhibited by normal plants in series B (1 p.p. m.). At anthesis (table I), series B again had the highest fresh weight and highest moisture content. On the whole there is a progressive decrease in fresh weight and moisture content in leaves with increases in boron concentration.

During active vegetative growth the stems of B and C (1 and 4 p.p.m.) had the greatest percentages moisture with A and E (no boron and 40 p.p.m.) exhibiting the least (table I, fig. 7). When flower buds were evident, plants in series B and C still remained comparatively high in moisture. At anthesis, however, in spite of the high rate of water absorption by the entire plants, the stems in both of these series exhibited the lowest percentage of water. The minus-boron series showed the highest percentage of water. At all times stems of these series (B and C) had high fresh weights. Stem fresh weights were lowest in series A (without boron).

The roots of series C and B at two weeks had made the greatest

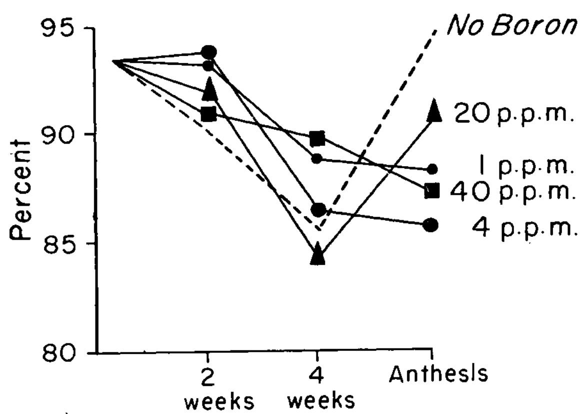

Figure 7. Moisture Content of Stems of Tobacco Plants at Various Stages of

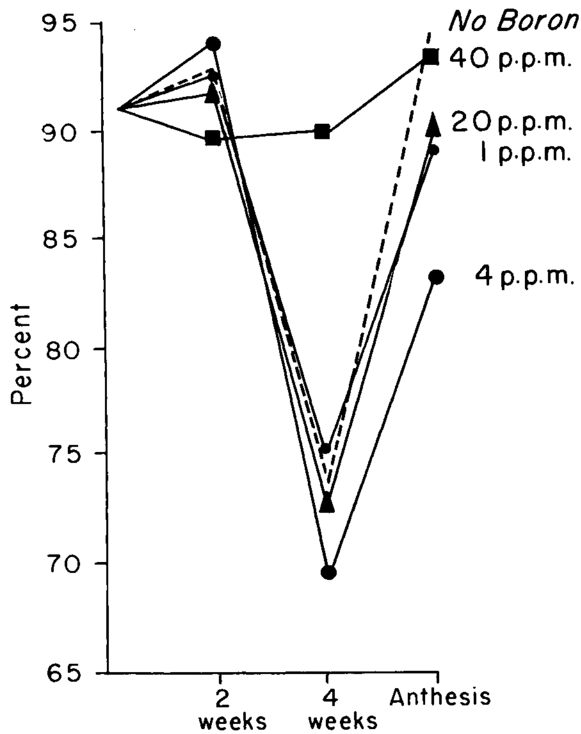

Figure 8. Moisture Content of Roots of Tobacco Plants at Various Stages of Development.

growth, having the highest fresh weights and moisture contents (table I, fig. 8). Plants in the toxic series of 20 and 40 p.p.m. boron had the lowest percentages of moisture. Several weeks later, however, plants in the highly toxic 40 p.p.m. series had the greatest percentage of moisture and contained the greatest percentage of moisture (table I). At anthesis both the boron-deficient and boron-toxic roots contained the greatest amounts of water.

The higher fresh weights in the boron-treated series are in agreement with the results obtained by Briggs (4) on nasturtiums and Biebl (1) on *Pisum sativum*. Johnston and Fisher (9) found this true also of tomatoes. Briggs (4) further indicated that with increase in length of time of treatment there was a progressive decrease of moisture in the boron-deficient plants. The results of the present study do not indicate such a curve, since after 6-8 weeks without boron the moisture content appeared as high as that after two weeks. Although there was, during this interval, a slight gain in water absorption and a high increment in fresh weight, water retention in the plant at four weeks was poor. Comparisons of the deficient series with the other during the stage of anthesis are not feasible since series A did not flower or produce fruit.

The results reported here for tobacco conform with those of Johnston and Dore (8) for tomato plants. They found that both leaves and roots in plus boron series had higher green and dry weights than those grown in boron-deficient solutions. Lowenhaupt (10), experimenting with sunflowers, found that fresh weights were greater in the plus boron series, except for the leaves.

It is evident that the dry weight yields of all the plant parts increased with boron up to the 4 p.p.m. level and then decreased at higher boron levels (table I). McHargue and Calfee (11) noted similar results with lettuce grown with boric acid. Contrary to the observation of Willis and Piland (21) who noted that Romaine lettuce grown without additions of boron to the soil were subject to severe wilting during the hot days, the leaves of the minus-boron culture did not wilt appreciably but remained rather brittle. Johnston and Dore (8) describe a similar brittleness in tomato. This would suggest that boron in affecting the water balance has some influence on the cell colloidal complex so that tissues do not become flaccid during periods of high transpiration. In the present experiment plants with optimum concentration of boron responded normally to transpirational changes by wilting and subsequently regaining turgor; whereas in the highly toxic series, very little wilting was evident (22). Similar results have been reported by Moinat (14) and Johnston and Dore (8). Schropp and Scharrer (18) found that boron in soil cultures produced a favorable affect by increasing the yields in pots under drought conditions.

The percentages of moisture present in the intact plants at senescence confirm the results obtained at the other stages (table II). For the plants left to dry intact on the laboratory table, weighing every 3-4 days showed that the plus-boron series dried at comparable rates whereas the minus-boron plant took a week longer to dry to constant weight, indicating good moisture retention.

It may be concluded that boron at optimum and slightly toxic levels favors growth and increases yield, indicating normal absorption and transpiration. Moderate boron supply is coupled with a high degree of water retention in the leaves (22). Boron deficiency inhibits plant development, interferes with water absorption, and disturbs the water balance producing poorly developed, chlorotic leaves and a characteristically abnormal habit. A highly toxic dosage of boron interferes with the water content of leaves causing chlorotic areas to result.

Summary

Nicotiana tabacum var. Little Turkish, grown at boron levels of 0.0, 1, 4, 20, and 40 p.p.m., exhibited differences in amounts of water absorbed and moisture content of leaves, stems and roots at different developmental stages. From the results obtained it is indicated that:

1. Plants receiving no boron in the nutrient solution showed the least amount of liquid absorption at all times and these plants did not mature.

2. Dosages of 1 and 4 p.p.m. boron, although displaying toxicity symptoms, produced the largest dry weight yield and such plants showed the greatest amount of water absorption, with the maximum in the 1 p.p.m. boron series at anthesis.

3. Definitely toxic dosages of 20 and 40 p.p.m. boron caused a decline in vigor and in water absorbed without inhibiting maturation of plants. Water absorption in the 40 p.p.m. series approximated the amount absorbed by the minus-boron series.

4. In the leaves, there existed a progressive decrease in fresh weight and moisture content with increase in boron concentration at all stages of development.

5. In the stems, during vegetative growth, 1 and 4 p.p.m. dosages resulted in the highest moisture content, but during late anthesis a decline occurred.

6. In roots, during the first several weeks of boron application dosages of 1 and 4 p.p.m. produced the highest fresh weights and moisture contents. At anthesis, both the deficient and highly toxic dosages showed the greatest percentages of water present with dosages 1 and 4 p.p.m. containing the lowest, probably indicating interference with translocation of water in the deficient and toxic series since the aerial parts had a low percentage of moisture at this time.

7. Among plants left to dry intact, the minus-boron plant showed the slowest rate of desiccation.

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