BORON NUTRITION OF THE GRAPE

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INTRODUCTION

Although Agulhon's (1) experiments as early as 1910 demonstrated a beneficial response from boron in the nutrition of certain higher plants, practical interest in boron as a fertilizer element did not develop until after the recognition, twenty years later, by Brandenburg (5) of a boron deficiency of the beet under field conditions. In fact, in the United States during this twenty-year interval, attention was directed rather toward toxicity from excess boron. In domestic potash, which was utilized by the fertilizer industry due to the curtailment of foreign sources during World War I, considerable boron was found as an impurity. Another instance of toxicity to plants resulted from the use of irrigation waters of the West which contained boron in excessive amounts. It is unfortunate that none of this work on toxicity uncovered any instance of beneficial response from boron application. This was not because boron deficiencies did not exist, for Atwater (3) recently has pointed out that the symptoms of abnormality in many plants which we now know are correctible by the addition of boron, were recognized and described years before the role of boron in plant nutrition was suspected. "Black-heart" of beets, "internal cork" of apples, and "cracked-stem" of celery are examples of such abnormalities.

Since Brandenburg's discovery of the relation of boron to "black-heart" of beets, there has been an ever-increasing number of reports of boron deficiencies with other plants found under field conditions. At the present time this list includes representatives of perhaps twenty or more species. In the light of our present knowledge of the boron relationships in the soil and plant, there is reason to assume that under certain conditions boron may be found to be a limiting factor in the growth of any of our economic plants. The comparatively narrow range between deficient, optimum, and toxic levels of boron in the soil, and the widely different response of species to a certain level of boron nutrition, necessitate the accurate definition of the plant and soil conditions at given levels.

In the spring of 1939 there was observed in a vineyard growing on light sandy soil in South Carolina, foliar symptoms which resembled symptoms of boron deficiency as they have been described for other plants. Since there had been at that time no report in the literature of boron deficiency in the grape under field conditions, and since it was early apparent that the observed symptoms varied widely with season and with varieties, it was considered necessary to definitely ascribe the nature and cause thereof through experimental procedure. Such procedure has involved studies of the response of the grape to boron both in the vineyard and under controlled greenhouse conditions. The vineyard studies were conducted at the Sandhill Experiment Station, Columbia, South Carolina, and the greenhouse and laboratory studies at the Horticultural Department of the University of Maryland.

REVIEW OF LITERATURE

It is the intent to review in this section only that literature which is concerned with the boron nutrition of the grape. Excellent and up-to-date bibliographies (18) and (43) and reviews (11) of the general field of boron soil-plant relationships are available. To adequately cover this entire field in the present review would be impractical and to generalize would be misleading. However, findings in the work with other plants, which are pertinent to the results of these experiments, will be discussed with the results.

Maier (21) in 1937 showed that boron is necessary for the normal development of grape seedlings grown in water culture nutrient solution. Oinoue (28) reporting in the following year on the setting of fruit in the Muscat of Alexandria variety of grape, found that the application of boron in concentration of .01 percent as the aqueous solution of sodium borate to ten year old vines twenty days before flowering, resulted in better germination of pollen grains from the treated vines and in more than twice the set of fruit. He also found that application of a .001 percent solution to the stigmas at blossoming time greatly increased the set of berries.

The above are the only references found in the literature dealing specifically with the effect of boron on the grape. There seems to have been no instance of the trial of boron as a fertilizing element in vineyard soils, and, with the exception of Maier's work, the grape has not been used in controlled nutrient culture experiments involving boron deficiency.

OBJECTIVES OF EXPERIMENTS

The objectives of the experiments herein reported were as follows: (1) to study the effects of boron applications to a vineyard soil upon the growth and fruiting of the vines; (2) to study the development and control of boron deficiency in vines in nutrient culture; and (3) to determine the levels of boron in the current seasons growth of the vine under various conditions of boron nutrition. These objectives were approached by: (a) the use of a vineyard which was found to respond to borax fertilization; (b) the growth of vines in sand culture with and without boron in the nutrient substrate; and (c) boron analysis of leaves and other parts of normal and deficient vines.

PART I

EFFECT OF BORON FERTILIZATION OF THE GRAPE UNDER VINEYARD CONDITIONS

MATERIALS AND METHODS

<u>The Vineyard.</u> The experimental vineyard is located in the Sandhill area near Columbia, South Carolina, on a deep phase of Norfolk sand. This soil is very low in organic matter and natural fertility, giving crop response to applications of many of the plant food elements. The vineyard had received annual applications at the rate of 600 to 800 pounds per acre of a mixed fertilizer, analyzing 8 percent nitrogen, 4 percent phosphorus, and 8 percent potassium. In addition, 1500 pounds per acre of dolomitic limestone was applied in 1932, and 1000 pounds per acre of basic slag in 1938. The pH of the surface soil was about 5.8 in 1939. The vineyard consisted of a varietal block of forty or fifty varieties and a stock-cion test block. Vines were spaced eight feet apart with ten feet between rows. At the time of inception of the field experiments in 1939 the vines were from five to nine years of age and each variety included five to ten vines.

In June, 1939, two or three vines of each of the ten varieties, Delaware, Lenoir, Herbert, Herbemont, Barnes, Extra, Portland, Ontario, Concord, and Catawba were treated with borax at the rate of ten pounds per acre applied to the surface of the soil in bands on either side of the vine. In May, 1940, half of the vines of the remaining varieties in the varietal block and half of each stock-cion combination were treated in like manner. In September, 1942, another application of borax was given to all vines previously treated. All borax applications were made by mixing the borax with sand to insure more even distribution and the material was incorporated in the soil by cultivation. All other fertilization and cultural treatments were the same for all vines.

Yield records were obtained from the individual vines and observations were made periodically on the growth and condition of the treated and untreated vines.

Sampling and Analytical Methods. Leaf samples from borax treated and untreated vines of fourteen varieties were analyzed for boron content. Samples were taken on May 1, May 29, August 9, and September 10, 1941, and on June 17 and September 11, 1942. Normally the fourth leaf from the shoot tip was taken. On actively growing vines the leaves at this point were young and about three-fourths mature size; however, leaves of different samples were not comparable in this respect, due to boron deficiency, crop load, and seasonal conditions. Ten to fifteen leaves composed a sample. One treated and one untreated vine of each variety were sampled, and the same vines were used throughout the test. Also samples of shoot growth were obtained for a study of boron distribution in the current seasons growth.

Boron determinations were made by the quinalizarin method, following the procedure of Maunsell (24) and using a Coleman spectrophotometer in obtaining colorimetric readings.

RESULTS

Boron Deficiency Symptoms and Remedial Effect of Borax. Foliar symptoms were noted in June, 1939, which suggested the possibility of boron deficiency. These symptoms included a well-developed pattern of chlorotic areas toward the leaf margin and between the leaf veins (figure 1). These chlorotic areas remained intact even in severe cases with little or no development of necrotic areas or burning of the leaf margins. The surface of affected leaves was abnormally roughened with raised areas between the veins, resulting in a cupping of the leaf toward the under side (figure 2). Premature defoliation did not occur.

The new leaves produced after treatment with borax showed no evidence of abnormality, although the older leaves remained chlorotic. However, the late season growth on untreated vines also showed little evidence of abnormal symptoms.

Shortly after the start of growth in early May of 1940, the shoots on a number of vines that were not treated with borax the previous year were developing abnormally with pronounced stunting of growth and a frequent tendency toward the production of several lateral shoots from a single node, especially from the nodes most distant from the trunk of the vine (figures 3, 4, 5, and 6). The internodes were very short and the leaves small and often misshapen. Flower clusters were developed but were twisted, malformed, and failed to set fruit. The weak, stunted vegetative growth in some instances made the flower clusters appear unusually prominent (figure 4). Untreated vines of some varieties showed less extreme symptoms, involving only slight chlorosis or cupping of the younger leaves, similar to those observed the previous year.

The borax-treated vines of the ten varieties receiving the application in 1939 showed no indications of the symptoms in the spring of 1940 and were developing normally in every respect. Borax treatment in May, 1940, of abnormal vines resulted in normal development of the new growth observed in July of that season. Again, as in 1939, it was noticed that the later growth on the untreated vines was not as badly affected as the early season growth.

Figure 1. Chlorotic pattern of boron deficiency on foliage of Lenoir observed in the vineyard. Note small curled leaves in lower portion of photograph.

Figure 2. Boron deficiency symptoms on the variety, Carman, under vineyard conditions.
Upper: Normal development.
Lower: Chlorosis, cupping, and malformation of the young leaves.

In the following season of 1941, the occurrence of the symptoms was comparable to that observed previously with the exception that possibly certain varieties were affected less severely. Of the 100 or more vines of the several varieties showing definite symptoms of boron deficiency before receiving borax treatment in May, 1940, only two individual treated vines failed to show complete recovery and normal growth in 1941.

In 1942 and 1943 boron deficiency symptoms again appeared on untreated vines, but in not as extreme form as on the two previous seasons. In general, differences in growth and fruitfulness between treated and untreated vines were less than formerly. Several factors may account for this: (1) the effect of the borax treatments in 1939 and 1940 may have been largely dissipated, although treated vines in no instance showed boron deficiency symptoms; (2) over-cropping of boron-treated vines in 1942 (figure 12) accompanied by very dry weather in the late summer and autumn weakened these vines; and (3) crop failure on the untreated vines for the several years previously may have resulted in a more favorable plant-soil boron relationship.

Varietal Differences under Boron Deficiency Conditions. Great differences in varietal response to the deficiency existed. Table 1 gives a rating of the varieties in this respect. Ontario, Carman, Armalaga, Seneca, and Geneva are representative of varieties which were severely affected, showing extreme foliar symptoms, stunting of growth in the spring and practically complete crop failure. Catawba, Bailey, Lenoir, Concord, Extra, Herbert, and Niagara were among those moderately affected, showing some foliar symptoms, especially at the time of blossoming, and more or less affect of yield. Champion, Portland, Fredonia, R. W. Munson, and Isabella showed little or no evidence of foliar symptoms although fruit

Figure 3. Effect of borax treatment on the Delaware variety under vineyard conditions.
Upper: Normal growth at time of blossoming in 1940 after borax application in 1939.
Lower: No borax. Note chlorosis and stunting of growth.

Figure 4. Effect of boron deficiency on Herbemont.
Upper: Severe symptoms before borax treatment in June, 1939. Photographed May, 1940. Vine still not entirely normal. Note slow development on right side of vine.
Lower: Untreated vine showing very extreme boron deficiency symptoms. Note stunting of shoot growth and prominence of blossom clusters on shoots. Note also that upper arms are more affected than lower arms.

Figure 5. Effect of boron deficiency on shoot development of Extra at time of blossoming.
Upper: Normal growth in May, 1940, of vine treated with borax in June, 1939. In May, 1939, this vine showed extreme symptoms of boron deficiency.
Lower: Stunted growth of untreated vine.

Figure 6. Boron deficiency in Ontario in the vineyard.
Upper: Grafted vine which showed severe symptoms in 1939 before borax treatment. Developing normally when photographed May, 1940.
Lower: Vine on own roots showing severe symptoms, including stunting of developing shoots and "Witch's Broom" effect.

production may have been affected in some instances. It may be pointed out that extreme differences in yield and vigor of the various varieties were existant from time of planting in the vineyard. However, the severity of the symptoms was apparently not correlated with inherent vigor of the variety. Thus, while the weakly growing Delaware, Headlight, and Ontario were severely affected, the equally weak Portland and Moore's Early showed little evidence of the deficiency. Similarly, the rankly growing Carman, Bailey, and Extra showed symptoms of deficiency while the vigorous vines of R. W. Munson, Cloeta, and Champion remained normal. From the list of varieties given in table 1, there is indication that varieties of labrusca parentage were less affected by boron deficiency.

Yield Response to Borax. The effect of the borax application upon fruit production has been even more striking than its effect upon vegetative growth. Yield records of 1940 of six varieties treated with borax in 1939 are given in table 2 and the 1941 yield records of 33 varieties treated with borax in 1940 are given in table 3. All of the varieties in 1940 and 28 of the 33 varieties in 1941 produced more fruit from the borax-treated vines. With 18 varieties the treated vines yielded more than double the untreated vines and a number of the untreated vines were practically barren. The responses in yield were not necessarily closely related to the vegetative responses. With several varieties borax greatly increased yields even though foliar symptoms were not pronounced on the untreated vines of the same variety. This is illustrated by the performance of Lenoir, a very vigorously growing variety under Sandhill conditions. Foliar symptoms of the deficiency in this variety were never acute, seldom more than a slight chlorosis and cupping of the leaves, yet untreated vines produced very little fruit (2.2 pounds per vine) whereas the yields of borax-treated vines were extremely heavy (22.5 pounds per vine). The

TABLE 1. Relative susceptibility of certain grape varieties to boron deficiency as indicated by foliar symptoms developing in 1939, '40, '41, and '42 on untreated vines.

Severely affected*	Moderately affected**	Slight or no observable symptoms***
Armalaga	Bailey	Champion
Carman	Barry	Cloeta
Delaware	Caco	Fredonia
Empire State	Captivator	Golden Muscat
Gaertner	Catawba	Hanover
Geneva	Champagne	Isabella
Hartford	Concord	Portland
Headlight	Diamond	R. W. Munson
Herbemont	Dutchess	
Ives	Elvira	
Lomanto	Extra	
Ontario	Herbert	
Seneca	Last Rose	
Sheridan	Lenoir	
Triumph	Lucile	
Wyoming	Lutie	
	Minnie	
	Niagara	
	President	
	Worden	

* Early season stunting of growth. Extreme deficiency symptoms. Little or no fruit production.

** Chlorotic pattern of foliage but no stunting in early season. Fruit production more or less affected.

*** No foliar symptoms, possibly fruit production affected.

difference in the crop on the Lenoir vines is shown in figure 7. The effect of boron on fruiting of other varieties is shown in figures 8, 9, and 10.

TABLE 2. Effect of borax treatment in 1939 on the yield of fruit in 1940.

Variety	Yield in pounds per vine (2 to 5 vines in each treatment)	
	Borax-treated vines	Untreated vines
Catawba	15.0	1.4
Delaware	2.8	0
Extra	9.4	5.2
Lenoir	41.8	2.5
Concord	5.0	1.3
Ontario	6.0	3.7

Another instance of the pronounced effect of boron upon fruitfulness was illustrated in the yield records of the reflex-stamen or self-unfruitful varieties. All of the five varieties of this type in the vineyard showed greatly increased yields from borax treatment (table 4). Fruit clusters of borax-treated vines of Herbert and Last Rose were well-filled and equal in appearance to those of self-fruitful varieties (figure 11). Treated and untreated vines were adjacent in the row and should have been equally favored for cross-pollination. Treatment did not affect the time of blossoming. The stamens of both treated and untreated vines were reflexed in the normal manner for varieties of this type and a number of clusters bagged in 1942 failed completely to set fruit either on treated or untreated vines.

TABLE 3. Effect of application of borax in 1940 upon yields of grape varieties in 1941.

Variety	Treated with borax		Untreated	
	Number of vines	Yield per vine (lbs)	Number of vines	Yield per vine (lbs)
America	1	1.0	2	1.1
Armalaga	5	7.4	5	0.4
Bailey	2	22.8	3	0.9
*Barry	2	5.6	3	0.2
*Brighton	1	4.7	1	0.2
Brocton	2	0.8	1	0.1
Caco	1	5.4	3	3.6
Carman	3	13.0	3	3.2
Catawba	4	3.2	3	0.6
Champagne	2	9.3	1	10.9
Champion	2	12.1	3	12.6
Cloeta	2	3.8	3	3.0
Delaware	6	3.4	3	2.0
Diamond	2	3.8	3	0.1
Edna	2	5.2	3	9.8
Extra	3	18.2	2	7.5
Fern	2	10.9	2	8.0
Fredonia	2	9.9	2	5.0
Hanover	2	6.2	1	0.8
*Herbert	4	8.9	3	0.1
Isabella	2	11.5	4	5.2
*Last Rose	1	14.5	1	0.0
Lenoir	5	22.5	6	2.2
*Lukfata	9	11.3	9	6.5
Lucile	2	3.9	4	1.3
Lutie	2	2.4	4	1.6
R. W. Munson	2	8.3	3	7.7
Niagara	2	4.1	4	1.5
Ontario	2	5.5	2	0.2
Portland	4	3.8	5	2.7
President	1	3.4	1	0.4
Vergennes	2	4.4	1	4.9
Worden	1	1.2	1	1.0
Average for all varieties		7.6		3.2

* Reflex-stamen varieties.

TABLE 4. Effect of borax upon 1941 yield of varieties of grapes having reflex-stamens.

Variety	Treated with borax		Untreated	
	Number of vines	Yield per vine (lbs)	Number of vines	Yield per vine (lbs)
Barry	2	5.6	3	0.2
Brighton	1	4.7	1	0.2
Herbert	4	8.9	3	0.1
Lukfata	9	11.3	9	6.5
Last Rose	1	14.5	1	0.0

Effect of Root-stock on Boron Deficiency. In 1940 there was little or no indication of boron deficiency in any of the varieties grafted on root-stocks in the stock-cion test block, although many of these same varieties, on their own roots, in the same block showed extreme symptoms. After borax treatment in 1940 to half of the vines in each stock-cion combination, it was evident in 1941 that there was a deficiency existant in the grafted vines, since the treated vines showed a greatly increased yield and in this season foliar symptoms were apparent on certain of the untreated vines. Apparently the deeper, more widely feeding root systems of the stock vines had delayed the development of boron deficiency in the cion variety grafted thereon.

Boron Content of Vines. The analyses of the series of leaf samples obtained periodically from vines of fourteen varieties in 1940 and 1941 are given in detail and in summary in table 5. The boron content of the leaves ranged from a low of 7.4 p.p.m. in the untreated Concord sample of September, 1941, to 106.8 p.p.m. in the borax-treated Portland sample of September, 1942. Variance analysis of the data (table 6) showed significant differences for all three of the main effects; treatments,

Figure 7. Effect of borax treatment on fruit yield of Lenoir.
Upper: 1940 crop on vine receiving borax in 1939.
Lower: No grapes produced by untreated vine but vine is growing vigorously showing no evidence of foliar symptoms of boron deficiency at this time of season.

Figure 8. Effect of borax treatment on fruit yield of Bailey.
Upper: Heavy crop on vine receiving borax in 1940.
Lower: The few clusters produced on the untreated vine are ragged. Growth is heavier on the untreated vine because of the lack of crop. Both vines photographed July, 1941.

Figure 9. Effect of borax on the fruit yield of Catawba.
Upper: 1940 crop on vine receiving borax in 1939.
Lower: 1940 crop on untreated vines. Catawba developed some seedless berries on untreated vines.

Figure 10. Effect of borax treatment on fruit yield of the reflex-stamen variety, Herbert.
Upper: 1941 crop on vine receiving borax in 1940.
Lower: Complete crop failure on untreated vine.
Both vines blossomed freely and were subject to similar pollination conditions.

Figure 11. Fruit clusters of the reflex-stamen variety, Herbert, on vine receiving borax treatment.

Table 5. Boron content of leaf samples from borax-treated and untreated vines

In p.p.m. of dry material

VARIETY	TREATMENT*	MAY 1, 1941	MAY 29, 1941	AUG. 9, 1941	SEPT. 10 1941	JUNE 17, 1942	SEPT. 11 1942	VARIETY MEANS BY TREATMENTS	VARIETY MEANS
Armalaga	Treated	19.9	68.9	37.9	29.0	25.0	62.8	40.6	31.2
	Untreated	12.0	39.6	20.4	26.4	18.1	13.8	21.7	
Bailey	Treated	19.9	41.1	38.0	41.1	16.8	38.5	32.6	32.7
	Untreated	7.8	46.4	25.0	24.3	19.4	73.6	32.8	
Carman	Treated	22.0	28.7	34.5	41.8	27.6	68.8	38.9	36.1
	Untreated	14.6	24.0	39.1	36.0	34.0	51.9	33.3	
Catawba	Treated	14.2	47.7	33.7	34.4	13.7	93.6	39.6	36.4
	Untreated	14.0	57.6	42.0	34.6	17.8	33.2	33.2	
Concord	Treated	13.3	32.7	38.6	19.7	11.8	30.9	24.5	21.3
	Untreated	13.4	18.8	38.5	7.4	8.4	22.0	18.1	
Delaware	Treated	25.0	64.3	25.5	36.0	13.6	77.0	60.2	46.6
	Untreated	12.6	85.1	40.8	19.4	13.5	25.9	32.9	
Edna	Treated	17.8	23.2	46.7	28.8	20.5	14.3	25.7	26.5
	Untreated	23.6	24.2	40.4	24.0	18.8	33.0	27.3	
Ellen Scott	Treated	20.3	74.3	53.0	40.8	35.2	68.4	48.7	41.6
	Untreated	20.8	58.4	35.5	25.7	30.4	36.4	34.5	
Extra	Treated	38.5	55.9	36.8	28.2	17.3	41.1	36.7	36.6
	Untreated	34.2	59.1	32.0	38.2	16.8	38.3	36.4	
Fern	Treated	39.0	22.8	37.9	26.0	22.9	34.5	30.5	27.5
	Untreated	22.2	18.0	31.6	20.0	19.1	35.5	24.4	
Lenoir	Treated	36.2	46.4	45.7	29.3	17.1	50.8	37.6	32.4
	Untreated	21.2	38.1	30.4	29.0	12.2	32.5	27.2	
Lucile	Treated	30.5	40.3	45.3	55.1	26.0	55.8	42.1	37.8
	Untreated	30.8	41.6	36.8	35.4	12.2	44.1	33.5	
Portland	Treated	22.2	40.5	52.4	61.5	30.3	106.8	52.3	40.4
	Untreated	17.0	39.9	26.8	29.0	22.6	35.0	28.4	
R. W. Munson	Treated	38.1	51.6	37.3	44.7	46.0	54.5	45.4	44.7
	Untreated	34.0	47.0	35.7	44.7	49.7	52.4	43.9	
Means of sampling dates by treatments	Treated	25.5	45.9	40.4	36.9	23.1	57.0		
	Untreated	19.9	42.7	33.9	28.2	20.9	37.7		
Means of sampling dates...		22.7	44.3	37.2	32.5	22.0	47.3		

Mean of all treated samples.. 38.1
Mean of all untreated samples.. 30.5

Difference between means necessary for significance (5 per cent level)
(a) Between varieties.. 8.7
(b) Between sampling dates.. 5.6
(c) Between treatments.. 3.2
(d) Between variety-treatments.. 13.4
(e) Between sampling date-treatments.. 8.0

* Borax applied to treated vines at rate of 10 pounds per acre in May, 1940.

sampling dates, and varieties. Borax-treated vines had a higher boron content of the leaves than untreated vines. The boron content of the leaves was lowest in the early part of the growing season. The varieties Delaware, R. W. Munson, Ellen Scott, and Portland had the highest boron concentration with averages above 40 p.p.m.; while Fern, Edna, and Concord had concentrations below 30 p.p.m. It was evident that leaf boron content of the varieties was not necessarily in accord with varietal susceptibility to boron deficiency. Significant interactions between treatments and sampling dates and varieties showed that the effect of the treatment upon boron content of the leaves was not the same throughout the season and that varietal differences also varied with time of sampling.

TABLE 6. Variance analysis of data on the boron content of leaves from borax-treated and untreated vines.

	Degrees of freedom	Sums of squares	Variance	F
Treatments	1	2408	2407.7	22.65*
Varieties	13	6201	477.0	4.49*
Sampling dates	5	15840	3168.0	29.80*
Interaction:				
Treat. x var.	13	2104	161.9	1.52
Treat. x dates	5	1347	269.3	2.53*
Varieties x dates	65	12374	190.4	1.79*
Treat. x var. x dates	65	6911	106.3	
Total	167	22736		

*Significant at the 5% level.

Although by virtue of sufficient sampling dates, significant differences are found in the analytical data, it is quite apparent that individual variety analyses during the season gave seemingly inconsistent results. A basis for this inconsistency may be found if both sampling technique and growth and yield performance of the individual vines are considered. The inability to secure leaf samples of comparable ages from the various vines has been stated. Borax-treated vines producing heavy fruit crops quite often ceased terminal growth in midsummer while untreated vines without a crop continued in growth. The difference in fruiting which was quite pronounced in most varieties very conceivably has affected the boron level in the terminal leaves.

The variable boron content of various parts of the shoot given in the following discussion shows clearly the necessity for more adequate sampling and consideration of the fruiting status of the vine if inconsistencies are to be avoided or interpreted.

Distribution of Boron in the Current Season's Growth. Representative shoots of the current season's growth of treated and untreated vines were sampled in an effort to determine the distribution of boron in the several parts of the shoot. Vines of the Extra variety were sampled August 9, 1941; Carman vines, June 17, 1942; and Lenoir vines, May 5, 1943. The analyses of these samples are given in table 7.

The treated Extra vines had a slightly higher boron concentration than untreated vines with the greatest difference found in the mature leaves about midway the shoot. The old leaves of the shoots adjacent to the fruit clusters had the lowest boron content. The vines of both treatments were in active growth when sampled, but the treated vines had a much heavier crop of fruit.

The Carman vines, sampled in June when the fruit was developing, showed the lowest boron level in the leaves adjacent to the fruit clusters. The leaves on the basal half of the shoots from the borax-treated vines were higher in boron than the comparable leaves from the untreated vines, but the reverse was true of the leaves on the terminal half of the shoots.

TABLE 7. The distribution of boron in the current season's shoots of the grape.

Variety and time of sampling	Portion of shoot analyzed	Boron (p.p.m. dry wt.)	
		Borax-treated vines	Untreated vines
Extra - sampled Aug. 9, 1941. Light crop on untreated vines. Heavy crop on treated vines.	Old leaves adjacent to fruit clusters.	26.0	24.8
	Mature leaves mid-way on cane.	43.8	29.6
	Young leaves in active growth.	33.7	30.0
Carman - sampled June 17, 1942. No crop and boron deficiency symptoms on untreated vines in May. Normal growth at sampling. Heavy crop on treated vines.	Basal leaves below clusters.	55.6	38.1
	Leaves adjacent to clusters.	32.4	21.2
	Leaves above clusters.	34.7	46.8
	Young terminal leaves.	39.9	47.7
Lenoir - sampled at full bloom, May 5, 1943. No deficiency symptoms on untreated vines.	Leaves below cluster.	53.0	40.3
	Leaves adjacent to cluster.	47.3	36.0
	Leaves above cluster.	39.0	30.0
	Blossom cluster.	38.6	34.6
	Stem below cluster.	31.9	25.2
	Stem adjacent to cluster.	27.6	17.5
	Stem above cluster.	33.5	32.0

At the time of sampling, the untreated vines were in active growth with normal terminal leaves, but the leaves in the central portions of the cane showed boron deficiency symptoms. Again, the treated vines were carrying a much heavier crop.

A more complete sampling was made of the treated and untreated Lenoir vines in May, 1943, at the time of full bloom. On these vines the shoots were divided into three sections; the part below the blossom clusters, the part subtending the blossom clusters, and the part above the blossom clusters; with the stem and leaves and flower clusters analyzed separately. There was a progressive decrease in boron content of the leaves toward the tip of the shoot; the boron content of the three portions in the treated and untreated vines was 53.0, 47.3, 39.0, and 40.3, 36.0, 30.0 p.p.m. respectively. No symptoms of boron deficiency were observable at the time of sampling. The stem analyses also showed a higher boron content for the treated vines but positional differences were in different order than for the leaves with the highest boron level in the terminal portion and the lowest in the portion subtending the flower clusters. The content of boron in p.p.m. for the three stem portions of treated and untreated vines was 31.9, 27.6, 33.5, and 25.2, 17.5, 32.0 respectively. The boron content of the flower clusters of the treated vines was 38.6 p.p.m. and that of those of the untreated vines 34.6 p.p.m.

DISCUSSION

It was apparent throughout the experiment that the boron deficiency symptoms developed early in the growing season but failed to appear in the later growth of the shoot. With severely affected vines the deficiency resulted in a marked stunting of the new shoots shortly after growth commenced in the spring. With less severely affected varieties growth continued normally until after blossoming or set of fruit and then symptoms suddenly appeared on the young leaves at the growing shoot tips. After failure to set fruit, the shoot resumed normal growth. As a result, shoots examined in the latter part of the growing season often showed normal leaves at the base, then four or five leaves with deficiency symptoms, then a continued growth of normal leaves.

It is possible that during this later period of growth the relationship between the demand for boron by the actively growing tissues and the ability of the soil and root system to supply boron is more favorable than that existing in the early part of the season when growth is extremely rapid over all parts of the vine. The lower boron content of both treated and untreated vines in the early season is perhaps significant, indicating a higher rate of boron utilization and suggesting that the vines are at a boron level more near the critical deficiency point in the early part of the season. If we consider boron as especially essential in meristematic tissues, then the tendency toward exhibition of symptoms in the period of rapid growth expansion is quite logical. However, then it must also be assumed that the vine is unable to store sufficient boron in the trunk and (or) transfer it to the growing points at an adequately rapid rate for the early season growth.

The most important practical value of a series of plant analyses of a particular mineral nutrient is the establishment of optimum and critical levels of that nutrient in relation to deficiency symptoms and plant growth. In the present work, although borax application to the soil resulted in consistent and positive correction of abnormal fruiting and growth conditions and, in so doing, generally increased the boron content of terminal leaves on the shoots, the data obtained do not afford accurate definition of deficiency levels of boron for the grape. Several factors must be considered. In the first place, the analyses obtained, corroborated later by the results of sand culture experiments, make it questionable whether the terminal leaves of the shoot give the best indication of the boron status of the vine as a whole. Secondly and unfortunately, with the exception of the samples of May 1, 1941, no series of samples were taken at a time when the vines were actually developing symptoms of boron deficiency in the terminal leaves. The critical period for development of symptoms was found to be shortly after growth inception in the spring and at the time of fruit setting; thereafter, all vines, both treated and untreated, generally failed to show deficiency symptoms in the later growth. Since it seems that the symptoms of boron deficiency can only become apparent if the deficiency occurs when the leaves are in active meristematic condition, it is possible that such mature leaves may exhibit a very low boron level but no outward symptoms of deficiency, or likewise the converse may be true.

The effect of boron upon reproduction has been noted by a number of investigators but until recently emphasis has been placed rather upon the effect of the deficiency of the element upon vegetative parts of the plant. This is an obvious result of the economic importance of the deficiency in vegetative organs as, for instance, in "black-heart" of beets. It is possible that the effects of boron nutrition upon the reproductive processes of the plant, although more obscure, may be equally important.

The relationship found in the experimental vineyard between time of fruit set and the appearance of the deficiency symptoms in the meristematic areas, accompanied with the failure of boron deficient vines to set fruit, strongly suggests a very close association between boron nutrition and fruit setting of the grape. Moreover the effect upon the set of fruit was exhibited in instances where foliar effects were minor, if present at all, indicating a possible specificity of the function of boron in fruit setting.

Whether the boron effect is direct as an essential quantitative plant nutrient required in definite amounts or if the action is that of a catalyst upon organic metabolism is not known. Likewise, it would be of interest to know if the abscission of the flower is a direct result of the effect of boron deficiency on the cells in the pedicel or whether abscission results from failure of a satisfactory gametic union caused by lack of boron. Armalaga, Catawba, and certain other varieties set parthenocarpic fruits on the boron-deficient vines. This phenomena is quite often observed with many varieties under conditions unfavorable for fruit setting, especially with vinifera varieties where it is termed millerandage. Usually, however, only a few seedless berries to a cluster are developed. Boron-deficient vines of Armalaga exhibited complete millerandage, developing full clusters of very small, seedless berries (figure 13). In this connection, attention must be called to the work of Oinoue (28) who obtained greatly increased fruit set on the variety, Muscat of Alexandria, by spraying with a boron solution. This variety is quite subject to millerandage according to Winkler (44), who obtained an increased percentage of normal berries by reducing the crop in relation to leaf area. Muscat of Alexandria vines were at one time in the test block used in the present experiments, but were removed before 1939 when the foliar symptoms of boron deficiency were first recognised. These vines bore ragged clusters of fruit with a great many small, seedless berries. It is unfortunate that there was not opportunity to test the effect of borax fertilization on this variety.

Millerandage has been regarded for a long time as possibly a nutritional trouble as suggested by Hilgard (15) in California in 1887.

Figure 12. 1941 crop on Armalaga vine receiving borax in 1940. Vine is overbearing and weak vegetatively.

Figure 13. Parthenocarpic or seedless berries on clusters of Armalaga vine not receiving borax. Clusters and berries are about one-fourth normal size.

However, effective control by fertilizers has not been obtained. Snyder and Harmon (36) recently have reported a remarkable improvement in fruit setting of Muscat of Alexandria by application of commercial zinc sulfate to the pruning cuts of vines not showing foliar symptoms of "little-leaf" zinc deficiency. In this connection it is interesting to note that Schuster, et al (32) found commercial zinc sulfate to contain 15 p.p.m. of boron and suggest that this boron may be a beneficial factor in zinc sulfate treatment for "little-leaf".

Is it possible that millerandage of grapes and the related physiological trouble, coulure, should be included in Atwater's (3) "Ancient History" of boron symptoms?

The performance of the reflex-stamen or self-unfruitful varieties likewise shows a close relationship between boron nutrition and setting of fruit in the grape. Since both treated and untreated vines of the reflex-stamen varieties failed to set fruit on clusters which were bagged to prevent cross-pollination, it would seem that the beneficial effects of boron on these varieties was exerted in some manner on the function of the female organs of the flower rather than on the viability or potency of the pollen. Oinoue (28), however, found that boron application increased the germination of pollen of the Muscat of Alexandria grape.

Physiological or nutritional factors have been recognized as probably partly responsible for self-unfruitfulness in many horticultural species. Fruiting of the self-unfruitful (reflex-stamen) varieties of grapes is quite variable even under apparent comparable conditions for cross-pollination, differing widely with seasons, locations, and soils. Certain vineyards have been known to produce good crops of Brighton and Herbert regularly. The experiments reported suggest that the boron nutrition of the vine may be a strongly determinative factor in the fruiting of these varieties.

It would seem well worth while to investigate the possibility of a relationship existing between the boron nutrition and fruit set of other horticultural species exhibiting peculiar sterility problems. Evidence pointing to such a relationship is found in boron studies with other plants, although the work has not been specifically directed toward that end. Powers (30) found that "yellow-top" of alfalfa in Oregon was cured and hay yields greatly increased by boron fertilization. Shortly afterward Piland and Ireland (29), Hutcheson and Cocke (17), and Grizzard and Matthews (14) showed that boron not only controlled "yellow-top" of alfalfa, but also greatly stimulated seed production in the southeastern states. Heretofore, failure of alfalfa to set seed pods in the Southeast had been vaguely attributed to climatic factors or length of day. Reports of the effect of boron on set of fruit with several other plants have been made. Ark and Thomas (2) state that morning glory plants growing in an apple orchard suffering from "die-back" (a condition caused by boron deficiency) were found to have undue numbers of abscissed blossoms. Johnston (19) found fewer fruits set on boron deficient tomato plants. McMurtrey (25) found that flower buds of tobacco were shed and no seed pods set in absence of boron. Wester and Magruder (42) obtained an increased yield of lima beans on borax-fertilized field plots although there was no other evidence of boron deficiency. Purvis and Hanna (31) illustrated a decided response in the fruiting of lima beans grown in pot culture on a Keyport fine sandy loam. Holley and Dulin (16) found that cotton plants growing in boron deficient nutrient solution abscissed all blossoms. In view of the fact that cotton often sheds blossoms and young fruits under field conditions, it would seem interesting to investigate the effect of borax fertilization in the field.

The effect of blossoming, fruit set, and fruit development upon the boron level in the vine and its relation to the occurrence of deficiency symptoms is not clear. The flower clusters of Lenoir had a boron content comparable to that of the accompanying leaves. On the other hand, leaves subtending the fruit clusters on both treated and untreated vines of Carman and Extra showed less boron content than leaves on other portions of the cane. Does this indicate mobilization and a utilization by the fruit cluster of the boron in the adjacent leaves? As possible further evidence of the demand of fruit development on the boron supply is the lower level of boron found in the terminal portions of the heavily fruiting plus-boron Carman shoots, than found in comparable portions of low-yielding untreated shoots.

A detailed, quantitative study of the boron level in all parts of the vine with reference to fruiting is greatly needed to further clarify the problem of the effect of boron nutrition upon the reproductive processes of the grape.

PART II

EFFECT OF BORON ON VINES GROWN IN NUTRIENT SAND CULTURE

METHODS

The varieties selected for the greenhouse experiments included two self-fruitful and two self-unfruitful (reflex-stamen) varieties, in the hope that the flowering and fruiting of these two types could be observed under controlled conditions of boron nutrition, since the reflex-stamen varieties in the vineyard tests had responded so markedly to borax fertilization. In an attempt to obtain blossom cluster development, two-year vines were used and the canes were cut back to four buds instead of the usual one or two buds. However, the vines failed to blossom, having only two blossom clusters on the entire group of 48 vines.

Cultural Methods. The vines were grown in sand culture, using twenty-mesh, white quartz sand in glazed 2.5 gallon crocks provided with a hole in the bottom for drainage. Two-year old vines of the varieties Catawba, Herbert, Golden Muscat, and Lindley were obtained from a commercial nursery. Twelve vines of each variety were planted, one to a crock. Before planting the vines were pruned back to two canes of approximately four buds, and the roots trimmed to a length of six to eight inches. The vines of each varietal group were exceptionally uniform in appearance, and Catawba, Herbert, and Lindley were apparently of about equal vigor. The Golden Muscat vines were much smaller. The vines were planted March 23, 1943. Four buds were permitted to grow on each vine, other buds were broken off as they started to grow.

Two nutrient treatments, hereafter designated as "plus boron" and "minus boron," were used. The plus-boron solution contained: 170 p.p.m. of mono-potassium phosphate; 590 p.p.m. of calcium nitrate; 148 p.p.m. of magnesium sulfate; 172 p.p.m. of ammonium sulfate; 5 p.p.m. of iron citrate; 0.91 p.p.m. of manganese chloride; 0.11 p.p.m. of zinc sulfate; 0.04 p.p.m. of copper sulfate; 0.045 p.p.m. of molybdic acid; and 0.5 p.p.m. of boron from boric acid. The minus-boron solution was the same except for the omission of boron. Distilled water was used for all solutions. The pH of the solution was adjusted to approximately 6.0 by the addition of 0.1 normal sodium hydroxide. Each crock was flushed with 500 ml. of a nutrient solution three times a week. On other days the plants were given distilled water.

No disease or insect infestation occurred, and spraying was not necessary. During the latter part of the experiment some of the vines wilted slightly due to excessively high temperatures in the greenhouse, but no permanent damage resulted. The test was discontinued after three months' growth.

Linear growth of all canes was measured at weekly intervals throughout the experiment. Fresh and dry weights of all vines were obtained at the conclusion of the test and samples were taken for chemical analysis at that time.

The crocks were arranged on a ground plot in the greenhouse in four varietal blocks of twelve vines each. The plus-boron and minus-boron treatments were applied to alternate vines in each block. Seven weeks after planting, three of the plus-boron Golden Muscat vines were changed to minus-boron treatment and three minus-boron vines were changed to plus-boron treatment. A week later a similar change was made with the Catawba and Herbert vines.

The nutrient sand culture seemed well adapted for grapes since the plus-boron vines exhibited well-developed, normal foliage and each vine made a total shoot growth of ten to fifteen feet in the three-month period. This is comparable to good field growth in the first season after planting.

Sampling and Analytical Methods: Estimation of boron was by the quinalizarin method (24). Four classes of material were sampled for analysis: (a) lower leaves, consisting of mature leaves toward the base of the cane usually including the second to fourth leaves; (b) upper leaves, consisting of the four or five young, smaller leaves at the end of the shoot; (c) lower stem, the portion of the shoot subtending the lower leaves; and (d) upper stem, that portion subtending the upper leaves. The upper leaves of class (b) were in actively growing condition in all normal plus-boron vines but were much older and apparently had ceased growth in the boron deficient vines. All leaf samples included the petiole. The stem samples included tendrils. Material from the three vines constituting a treatment were generally composited to form a sample. A few Golden Muscat vines were sampled individually. All samples were taken at the conclusion of the experiment with the exception of a series taken from the Catawba and Herbert vines at the time of institution of the minus-plus and plus-minus boron treatments.

Calcium was determined by a modification of the rapid method proposed by Carolus (8). The calcium oxalate precipitate was suspended in a glycerol-water mixture and the degree of turbidity, estimated by the use of a Coleman spectrophotometer, used as a measure of the calcium present by comparing with the turbidity of known standards.

RESULTS

Deficiency Symptoms. The Catawba and Golden Muscat vines started into growth within a week after planting. Herbert and Lindley were about ten days later. Growth inception within each varietal group was remarkably uniform. The first observable symptoms of boron deficiency appeared on Catawba and Golden Muscat April 27, or about one month after growth commenced. Lindley and Herbert showed the first symptoms on May 9 or in a comparable period with the other varieties from the time of growth inception. At the time of the first observable boron deficiency, the plus-boron Catawba vines had made about 120 cm. of shoot growth, the Golden Muscat vines 70 cm., the Herbert vines 110 cm., and the Lindley vines 155 cm.

The boron deficiency symptoms in the early stages were exhibited as (1) a diffuse yellowing or chlorosis of the younger leaves, (2) brownish, watersoaked areas developing in the terminal tendrils, and (3) cupping of the third or fourth leaf from the shoot tip. The exact order of the appearance of these symptoms was difficult to determine and seemed to vary with the variety. On the Golden Muscat vines chlorosis seemed to be the first evidence of deficiency while with Catawba and Herbert the water-soaked areas on the young tendrils were first in appearance. The cupping of the young leaves was generally downward or toward the ventral side, but not always so. A further early indication of the deficiency which will be discussed later was shown in the growth rate of the vines.

Later stages of the deficiency consisted largely of a progressive worsening of the earlier symptoms shown on leaves and tendrils. The leaves became more cupped and rugose, the chlorosis developed between the veins and in extreme cases, entire areas of the leaf became necrotic. The tendrils developed transverse cracks and later died back from the tips. Normal and boron deficient leaves of Herbert and Lindley are shown in figures 14 and 15. The appearance of the deficiency in a mature leaf of Golden Muscat is shown in figure 16.

Figure 14. Boron deficiency symptoms on leaves of Herbert grown in sand culture.

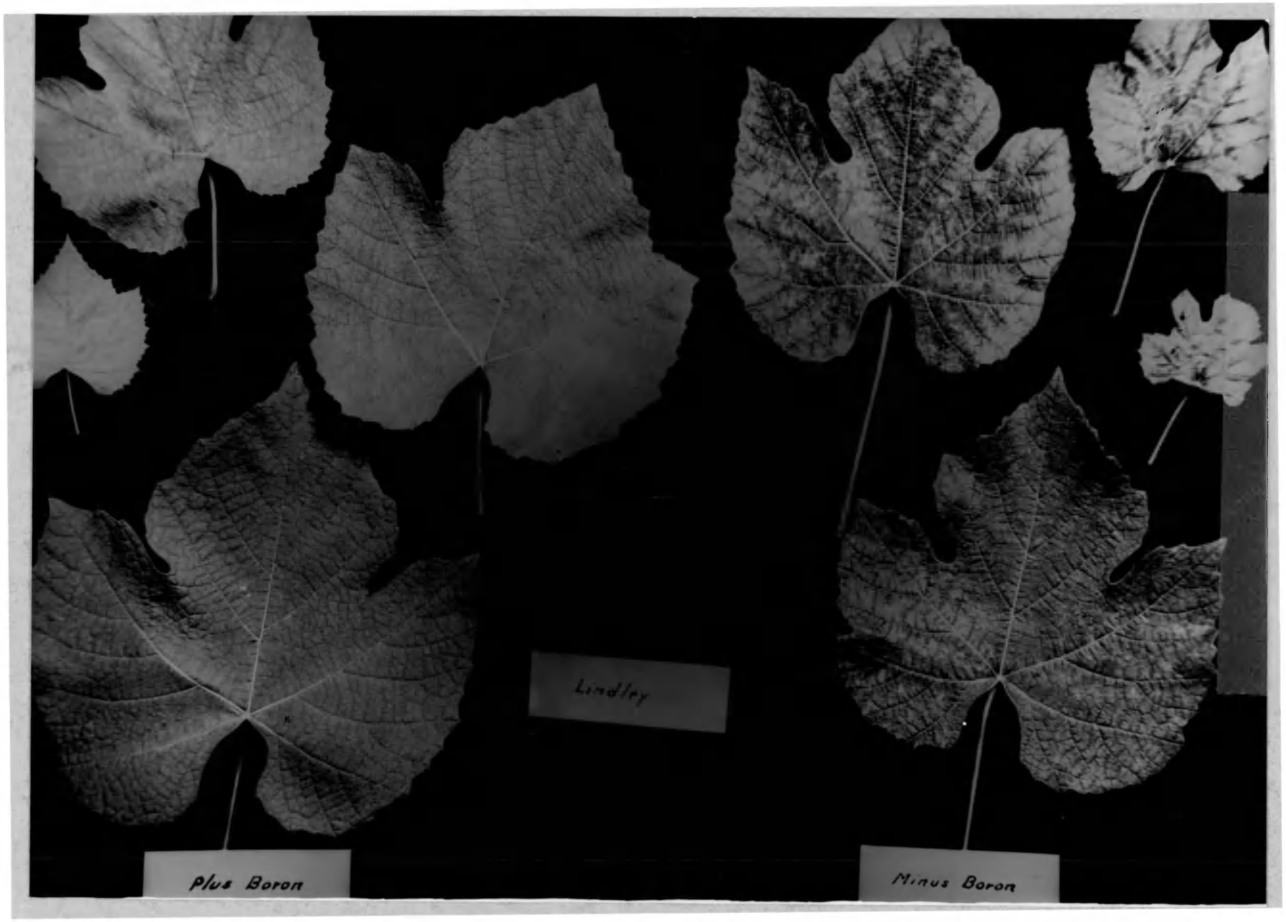

Figure 15. Boron deficiency symptoms on leaves of Lindley grown in sand culture.

Figure 16. Appearance of boron deficiency symptoms on a mature leaf of Golden Muscat. Note the rugose condition and the interveinal and marginal chlorosis.

Death of the terminal bud, a well-recognized symptom of boron deficiency with many plants, did not occur until the leaf and tendril symptoms were well advanced. However, finally the terminal bud died and abscissed. The terminal internodes of the deficient vines were much shorter than those of the normal vines. All of the affected parts exhibited abnormal rigidity and brittleness. Young leaves appearing after the onset of the deficiency were often misshapen and malformed. Deficiency symptoms did not develop on the lower leaves of the vine, even though the terminal parts were extremely affected. On rapidly growing shoots of the grape, the fifth or sixth leaf from the tip was the oldest leaf to show boron deficiency, and on these, symptoms were usually confined to marginal chlorosis only. This is illustrated in figure 17 which shows the entire growth produced by a minus-boron Lindley vine. The three lower leaves showed no evidence of deficiency symptoms even though the extreme symptoms at the tip had developed a month before the photograph was taken. Apparently, the symptoms are developed only in those parts which are in active meristematic condition at the time of occurrence of the deficiency. A possible exception to this occurred in the Golden Muscat vines which showed chlorosis on some of the basal leaves (figure 18). However, since the deficiency appeared on this variety before the canes had attained a length of 30 cm., it is possible that even these basal leaves were meristematic at the time of the inception of the deficiency.

Lateral buds in the leaf axils of affected canes were stimulated, but the shoot growth resulting was only a few centimeters in length.

Effect of Changing Nutrient Solution. Those vines changed from plus-boron to minus-boron culture and those changed from minus-boron to plus-boron will be referred to respectively as plus-minus and minus-plus boron vines. The Golden Muscat and Catawba vines showed extreme deficiency

Figure 17. A Lindley vine grown under minus-boron nutrition in sand culture. Note that the lower leaves show no evidence of deficiency even though growth had ceased and terminal symptoms were severe a month before the photograph was taken.

Figure 15. Basal portions of Golden Muscat vines grown in sand culture experiment. Left - minus-boron. Right - plus-boron.

Figure 19. The effect of boron on Golden Muscat vines in sand culture.
<u>Left</u> - Grown for three months under minus-boron nutrition.
<u>Right</u> - Grown for two months under minus-boron nutrition then for one month under plus-boron nutrition.

symptoms at the time of change. Ten days after boron application the minus-plus boron vines showed evidence of recovery and in fifteen to twenty days those vines were growing at a normal rate. Since the terminal bud had abscissed on the canes of these varieties, several lateral buds were forced, giving a bushy appearance to the canes when growth was resumed (figure 19). The Herbert vines showed only the first stages of deficiency at the time of changing from minus to plus boron. The terminal buds of these vines resumed growth. In all instances leaves on the minus-plus vines which showed deficiency symptoms at time of changing to the plus-boron nutrient solution retained all of those symptoms even though the new leaves were normal in growth and appearance. The occurrence of deficiency symptoms on the older leaves of a vine therefore does not necessarily indicate a boron deficiency existent in the vine at the time of observation.

The plus-minus boron vines were much slower in developing evidence of deficiency than the minus-plus vines were in recovering from the deficiency. The plus-minus Golden Muscat vines showed tendril necrosis twenty-five days after change of treatment. A week later the symptoms had progressed to an advanced stage of deficiency. The Catawba and Herbert plus-minus vines were even slower in exhibiting the deficiency, the first symptoms appearing in thirty days.

<u>Growth of Vines</u>. The periodic measurement of the canes of each vine throughout the course of the experiment gave an opportunity to correlate linear growth with development of the boron deficiency symptoms in the several treatments and varieties. Since a deficiency of boron affects primarily the apical meristematic areas, it is quite evident that the deficient vines should show a distinct curtailment of linear growth. The total growth produced by the vines during the course of the experiment is given in table 8. The average linear growth made in each weekly period by the

plus-boron and minus-boron vines of the four varieties is shown graphically in figures 20, 21, 22, and 23.

TABLE 8. Linear growth of shoots produced by two-year old grape vines during three months of sand culture in the greenhouse experiment.

	Total linear growth of shoots (in cm)			
	Herbert	Catawba	Golden Muscat	Lindley
Continuous plus boron March 23 - June 23	383	371	324	424
Continuous minus boron March 23 - June 23	201	171	125	140
Plus boron until May 21, minus boron thereafter	366	325	241	
Minus boron until May 21, plus boron thereafter	393	246	218	

Since it is of importance to recognize the earliest exhibition of a nutrient deficiency rather than the extreme symptoms, it is of interest to know if the growth rate of the canes of the vines was affected prior to the appearance of definite observable symptoms. With the Golden Muscat vines there was less growth in the minus-boron vines during the week of April 18-25, although the first deficiency symptoms in the leaf were not observed until April 27. The appearance of the symptoms and reduction in growth in the Catawba and Herbert vines occurred about the same time. With Lindley a very distinct curtailment in growth rate was evident two weeks or more before foliar symptoms of the deficiency were apparent.

The growth rate of the vines which were changed from plus to minus and from minus to plus boron nutrition is shown in figures 24 and 25. The minus-plus boron Herbert vines which were just starting to show deficiency at the time of changing the treatments, quickly recovered and during the last two weeks were growing much faster than the plus-minus

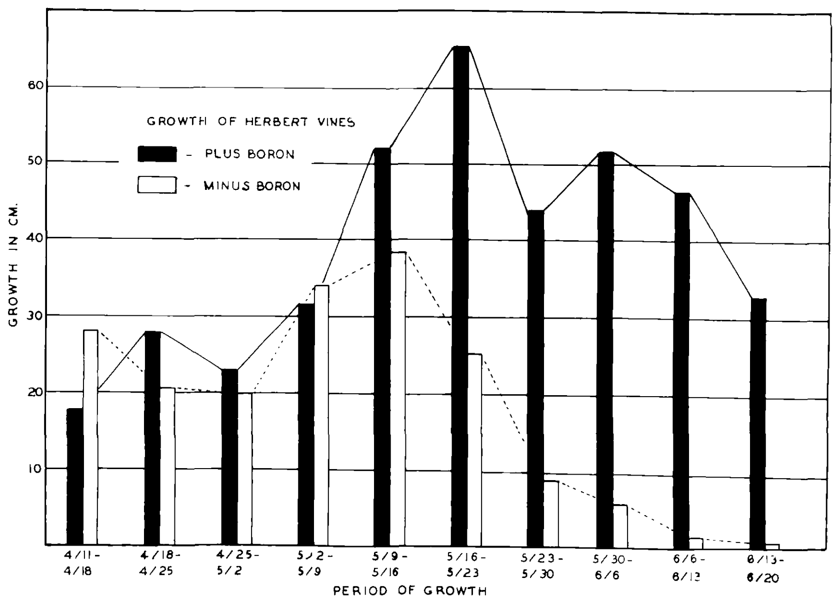

Figure 20. Growth of the Herbert vines in the sand culture experiment.

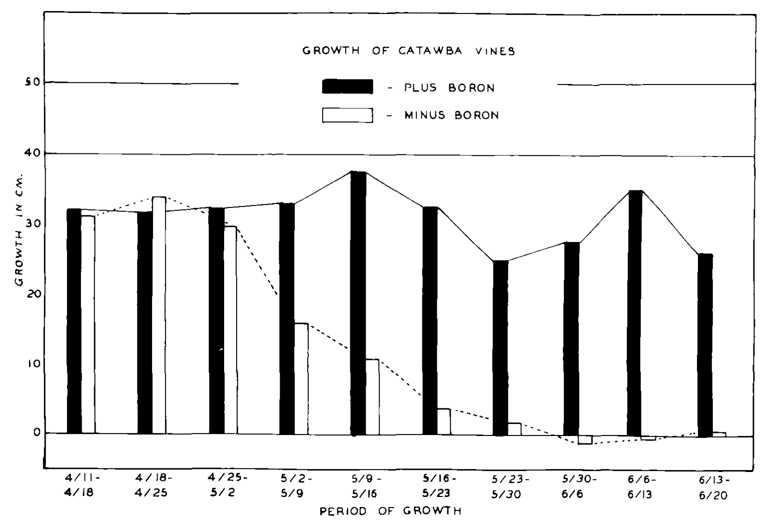

Figure 21. Growth of the Catawba vines in the sand culture experiment.

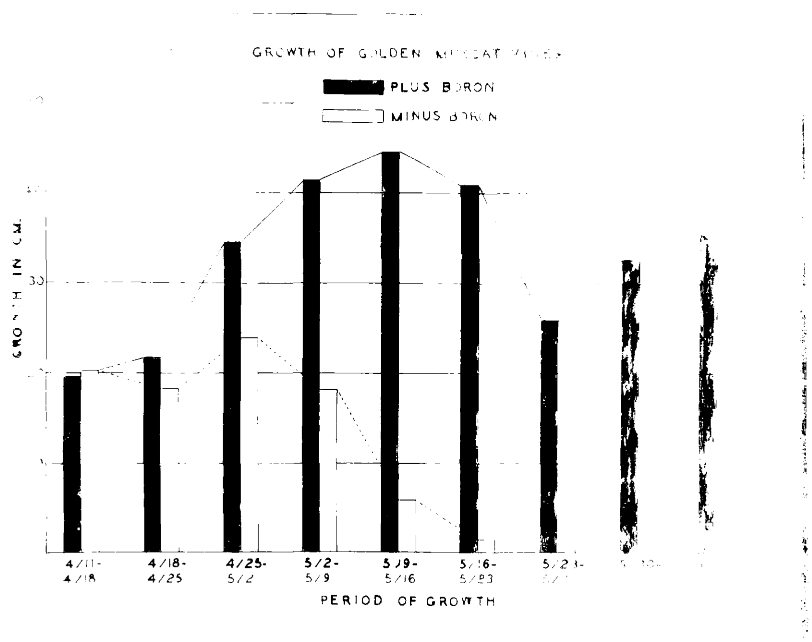

Figure 22. Growth of the Golden Muscat vines in the sand culture experiment.

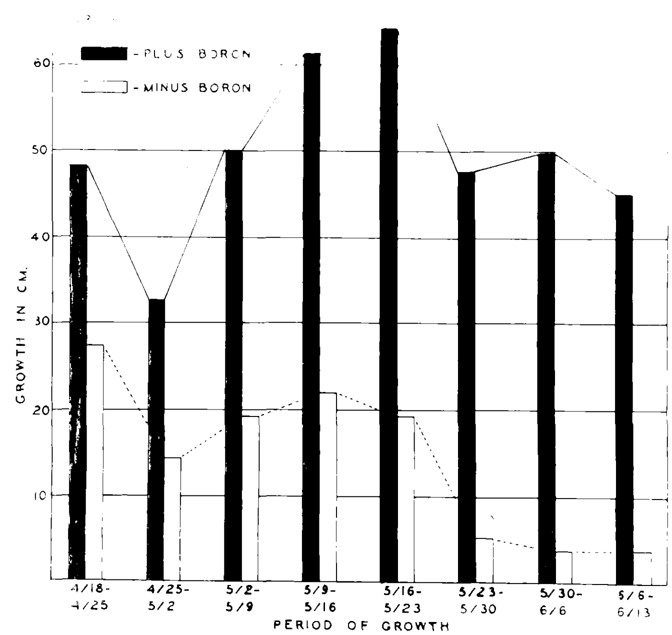

Figure 23. Growth of the Lindley vines in the sand culture experiment.

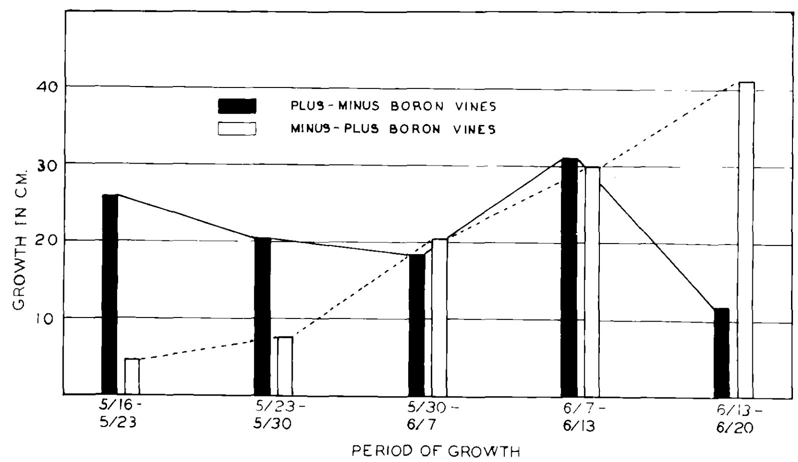

Figure 24. Growth of the plus-minus and minus-plus boron vi[illegible] the change of nutrient treatment.

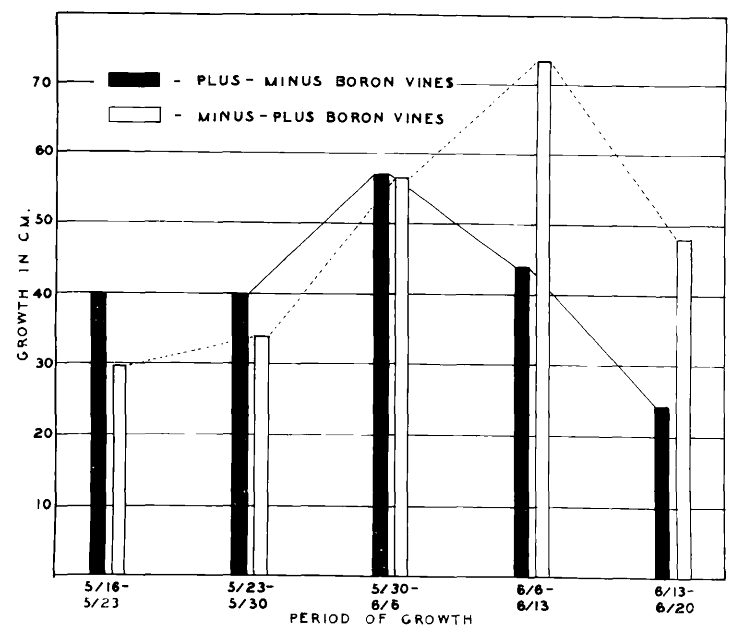

Figure 25. Growth of the plus-minus and minus-plus boron vines of the Herbert variety after the change of nutrient treatment.

boron vines. The minus-plus Catawba vines were extremely deficient at the time of change of treatment and required a somewhat longer period for recovery. The growth recovery of the vines which were changed from minus-boron to plus-boron nutrition in the greenhouse experiment was strikingly similar to the recovery from boron deficiency of vines in the vineyard, observed just after blossoming.

The data indicate that a slowing up in the linear growth of the grape may be the first evidence of boron nutrient deficiency, but the number of observations were too limited to afford strong proof. This possibility may be of great importance in interpreting field response to boron application, where it is conceivable that the plant may be on the borderline of boron deficiency for an extended period during which growth is seriously affected but definite symptoms are not apparent.

Weight of Vines. Green and dry weights of all new cane growth produced during the course of the experiment are given in table 9. Since composite samples of vines representing each of the treatments were taken for analysis, the dry weight percentages were calculated on a treatment sample rather than from individual vines. The effect of the boron treatment upon percentage dry matter is not consistent. With Herbert and Catawba there seems to be a definite increase in percentage dry matter, while with Golden Muscat and Lindley the converse is true. The total fresh and dry weights of the canes in all instances is greater in the plus-boron treatments, with the differences most accentuated in Golden Muscat and Lindley and least noticeable in Herbert. It had been noted that the growth rate of Golden Muscat and Lindley was affected earlier by the deficiency than the other varieties.

The vines which were changed from minus to plus boron nutrition in all instances showed increased weight over the continuous minus-boron vines.

TABLE 9. Weight of shoot growth made by two-year old grape vines during three months' sand culture in greenhouse experiment.
(All weights in grams.)

	Herbert			Catawba			Golden Muscat			Lindley		
	Green wt.	Dry wt.	Percent dry wt.	Green wt.	Dry wt.	Percent dry wt.	Green wt.	Dry wt.	Percent dry wt.	Green wt.	Dry wt.	Percent dry wt.
Continuous plus-boron March 23 - June 23	126.4	31.1	24.6	157.9	37.9	24.0	128.9	33.2	25.8	135.4	35.3	26.1
Continuous minus-boron March 23 - June 23	85.1	24.0	28.2	73.5	22.3	30.3	68.8	14.3	20.8	46.8	11.0	23.5
Plus-boron to May 21,* minus-boron thereafter	109.0	25.5	23.4	116.1	28.8	24.8	113.4	28.5	25.1			
Minus-boron to May 21,* plus-boron thereafter	120.8	26.0	21.5	108.5	24.4	22.5	107.4	19.8	18.4			

*Golden Muscat vines were changed in treatment on May 13.

Conversely those vines which were changed from plus to minus boron nutrition showed lower weights than the continuous plus-boron treatment. This is in agreement with the differences in growth rates previously noted.

<u>Boron Content of Continuously Plus-Boron and Minus-Boron Vines.</u> The boron content of all parts of all varieties receiving boron in the nutrient solution was higher than that of comparable parts of the vines from the minus-boron treatment (table 10). Varietal differences under each treatment were found. Herbert and Golden Muscat plus-boron vines were higher in boron than Catawba and Lindley. In the minus-boron series the leaves of Herbert and Catawba were higher in boron than those of Golden Muscat and Lindley. In the Lindley, Catawba, and Herbert plus-boron vines the upper leaves contained more boron than the lower leaves, but in Golden Muscat the reverse was true. In the minus-boron vines there was little difference in the boron content of upper and lower leaves, except in Lindley, where the lower leaves contained twice as much boron as the upper leaves. The boron content of the stems was less than half that of the subtended leaves in the plus-boron vines; however, in the minus-boron vines there was little or no difference in the boron content of leaf and stem material. Similarly, there was no difference in content of boron in the upper and lower stem of the minus-boron vines, whereas in the plus-boron vines the upper stem contained appreciably more boron.

It should be pointed out here that the boron content of the lower leaves of minus-boron Catawba and Herbert vines which were entirely normal in appearance as far as deficiency symptoms are concerned, was practically as low as that of the upper leaves which had exhibibited advanced stages of boron deficiency for a prolonged period previous to sampling.

Summarizing the evidence obtained from the continuous plus-boron and minus-boron series, it is found that the boron content in the deficient

TABLE 10. The boron content of grape vines after three months' growth in greenhouse sand culture.

Nutrient Treatment	Portion of vine analyzed	Boron in p.p.m. on oven-dry wt. basis			
		Catawba	Herbert	Golden Muscat	Lindley
Continuous plus-boron March 23 - June 23	Lower leaves	77.4	119.6	123.3	87.8
	Upper leaves	93.3	146.0	56.8	109.2
	Lower stem	29.3	29.0		
	Upper stem	41.1	41.4		
Continuous minus-boron March 23 - June 23	Lower leaves	27.0	24.4	12.7	21.6
	Upper leaves	23.4	23.6	15.8	10.8
	Lower stem	22.6	20.4		
	Upper stem	21.6	23.9		
Plus-boron until May 21, minus-boron thereafter*	Lower leaves	35.8	35.8	42.2	
	Upper leaves	26.3	31.7	16.9	
	Lower stem	39.0	25.0		
	Upper stem	44.1	25.2		
Minus-boron until May 21, plus-boron thereafter*	Lower leaves	152.4	90.9	46.3	
	Upper leaves	60.6	105.3	45.3	
	Lower stem	41.1	28.3		
	Upper stem	65.8	47.3		

*Golden Muscat vines changed in treatment May 13.

plants was more or less equalized in all parts at a level of 20 to 25 p.p.m. in Catawba and Herbert and somewhat lower in Lindley and Golden Muscat. The boron content of the plus-boron vines was much higher and more variable both within and between varieties. The leaves of the plus-boron vines built up a much higher boron content than the stems. Thus, while the stems of plus-boron vines contained from one and a half to two times the amount of boron in the minus-boron vines, comparable leaves contained four to six times as much.

<u>Boron Content of Plus-minus and Minus-plus Boron Vines</u>. The decided effect on the growth of the vine caused by alternation of the treatments on the Golden Muscat, Herbert, and Catawba vines has been stated. The severely deficient minus-boron vines showed complete recovery in the new growth while the normal plus-boron vines developed deficiency symptoms. A study of the boron content of these vines in comparison with the continuous plus-boron and minus-boron vines should be of value (table 10). The withdrawal of boron from the nutrient solution resulted in decreased boron content of both upper and lower leaves. In Herbert the upper stem also showed a marked lower boron content, but in Catawba both lower and upper stems of the plus-minus series were actually higher in boron than those of the continuous plus-boron vines. Here again, there is apparently a tendency toward equalization of boron content in the various plant parts under conditions of a low boron nutrition level. The upper leaves of the plus-minus vines are relatively lower in boron when compared to the continuous plus-boron vines than the lower leaves, but it must be kept in mind that these upper leaves of the plus-minus vines were formed after the change to a minus-boron nutrient solution.

Considering the minus-plus boron vines or those changed from a minus-boron to plus-boron nutrition, it has been stated that the recovery from deficiency symptoms and renewal of growth occurred shortly after the addition of boron or well before the end of the experiment when samples were taken for analysis. The boron content of these vines was found to closely approach or even exceed that of the continuous plus-boron vines. The upper leaves and stem of samples from the minus-plus boron vines were composed entirely of new growth made after the change of treatment. In the lower leaves and upper and lower stems of minus-plus vines of Catawba, the boron content was higher than that of the continuous plus-boron plants. With Herbert the leaf content was lower and the stem content about the same. With Golden Muscat the leaf content was considerably lower than that of the continuous plus-boron vines, especially in the lower leaves.

Thus far, comparative levels of the several treatments at the end of the experiment have been studied. Since, with Catawba and Herbert, canes were removed for sampling at the time of change of treatment from plus to minus boron nutrition and vice versa, there is opportunity to compare the boron content of these plants at the time of change and a month later when effects of the change of treatment were apparent. These data are given in table 11 and shown graphically in figures 26 and 27. In general, the previous data are substantiated. The change from a plus-boron to a minus-boron nutrient culture resulted in a much lower boron content of both lower and upper leaves, although the stems showed a gain in boron. The addition of boron to the nutrient solution caused a great increase in the boron level of vines grown previously in a minus-boron culture, with the highest content attained in the leaves.

For some reason the minus-boron vines sampled at the time of changing nutrient treatments May 21 showed a lower boron level than the continuous minus-boron vines when sampled a month later. Furthermore, the Herbert vines on May 21 had just developed definite evidence of boron deficiency, whereas the continuous minus-plus vines were in advanced stages of the deficiency when sampled a month later.

TABLE 11. The boron content of Herbert and Catawba grape vines before and after changing from plus to minus and minus to plus boron nutrient culture.

Nutrient Treatment	Portion of vine analyzed	Boron (in p.p.m. on dry wt. basis)			
		Herbert		Catawba	
		Before Changing	After Changing	Before Changing	After Changing
Plus-boron changed to minus-boron	Lower leaves	69.8	35.8	56.8	35.8
	Upper leaves	60.6	31.7	48.8	26.3
	Lower stem	19.4	25.0	26.1	39.0
	Upper stem	26.6	25.2	32.9	44.1
Minus-boron changed to plus-boron	Lower leaves	16.6	90.9	13.8	152.4
	Upper leaves	21.1	105.3	21.6	60.6
	Lower stem	14.4	28.3	12.5	41.1
	Upper stem	12.2	47.3	11.5	65.8

Boron and Calcium Content of the Vines. The boron and calcium contents of the vines of the several treatments are given in table 12. On the whole, no definite relationship between the boron and calcium levels in the tissues can be deduced from these data. The calcium content of the lower leaves of all treatments was much greater than that of the upper leaves and stems. There was no consistent difference between upper and lower stems. Some varietal differences were apparent, with Golden Muscat and Catawba showing greater calcium accumulation in the lower leaves than Lindley and Herbert. The only possible boron-calcium relationship that can be found is in the Catawba and Herbert vines, in which the upper leaves of the minus-boron vines have a higher calcium content than the plus boron vines. This holds true for both varieties and with both continuous and alternate boron nutrition series. However, this was not

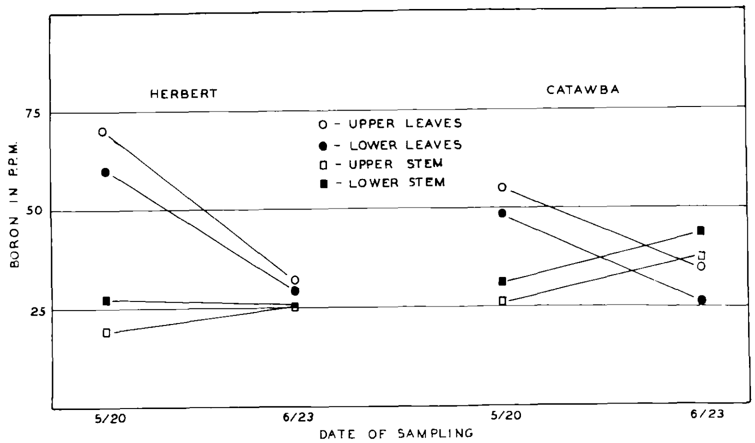

Figure 26. Effect of changing from plus-boron to minus-boron nutrition upon the boron content of the shoots. Treatments changed May 20.

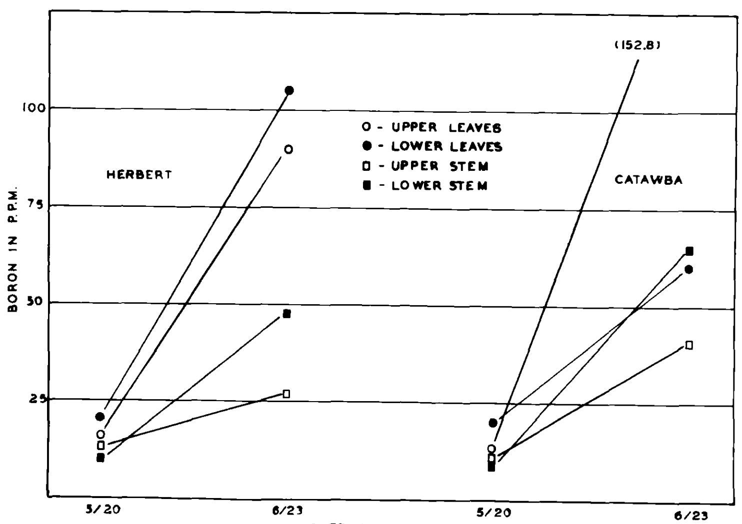

Figure 27. Effect of changing from minus-boron to plus-boron nutrition upon the boron content of the shoots. Treatments changed May 20.

TABLE 12. The boron and calcium contents of grape vines in greenhouse sand culture experiment.

Nutrient Treatment	Portion of vine analyzed	Catawba		Herbert		Golden Muscat		Lindley	
		B (p.p.m.)	Ca (mg/gr)	B (p.p.m.)	Ca (mg/gr)	B (p.p.m.)	Ca (mg/gr)	B (p.p.m.)	Ca (mg/gr)
Continuous plus-boron March 23 - June 23	Lower leaves	77.4	14.2	119.6	10.0	132.2 114.4	16.5 14.9	87.8	10.1
	Upper leaves	93.3	5.0	146.0	4.7	59.7 53.8	7.2 8.8	109.2	7.2
	Lower stem	29.3	5.3	29.0	4.1				
	Upper stem	41.1	4.7	41.4	4.4				
Continuous minus-boron March 23 - June 23	Lower leaves	27.0	11.8	24.4	11.0	12.7	8.1	21.6	10.1
	Upper leaves	23.4	7.4	23.6	6.9	15.8	7.0	10.8	7.6
	Lower stem	22.6	4.4	20.4	4.3				
	Upper stem	21.6	5.6	23.9	4.5				
Plus boron until May 21,* minus-boron thereafter	Lower leaves	35.8	14.1	35.8	9.8	39.4 44.9	10.9 17.9		
	Upper leaves	26.3	9.1	31.7	7.0	15.6 18.2	6.5 8.3		
	Lower stem	39.0	3.8	25.0	4.9				
	Upper stem	44.1	6.6	25.2	4.4				
Minus boron until May 21,* plus boron thereafter	Lower leaves	152.4	16.8	90.9	10.5	49.6	10.0		
	Upper leaves	60.6	5.9	105.3	5.5	47.0	6.8		
	Lower stem	41.1	4.7	28.3	3.7				
	Upper stem	65.8	3.6	47.3	4.2				

* Golden Muscat vines changed in treatment on May 13.

found in Lindley where the calcium contents of comparable leaves of plus-boron and minus-boron vines were almost identical, nor in Golden Muscat where the only difference was a relatively lower calcium content of the lower leaves of the continuous minus-boron treatment.

DISCUSSION

The data secured from the growth measurements and analysis of the vines grown in the sand culture experiments afford information on certain problems of boron nutrition concerning which there is found controversial or inconclusive statements in the literature. These problems involve, (1) the relationship between the boron content of the plant and deficiency symptoms, (2) consideration of the mobility or retranslocation of boron within the plant, and (3) the relationship between calcium and boron in plant nutrition.

Boron Content and Deficiency Symptoms. Batjer (4) has found that the difference in boron content between normal and boron deficient apple fruits may be very little. It has also been found that plants exhibit luxury consumption of boron in the presence of an adequate supply, building up a content far above the apparent critical level (33). These factors and perhaps others to be considered later present difficulties in an attempt to establish a definite relationship between boron content of the plant and apparent deficiency symptoms. It is clear that in a boron deficient vine the basal leaves, which are normal to all outward appearances, may be just as low or lower in boron than the upper leaves which may exhibit extreme symptoms. Thus the lower Catawba leaves on minus-boron vines on May 21 were normal in appearance but showed a boron content of 13.8 p.p.m., whereas the upper leaves which were in advanced stages of deficiency contained 21.6 p.p.m. of boron. Likewise, leaves with extreme boron symptoms may have a boron content equal to that of normal leaves if samples are analyzed following a period of adequate boron nutrition. This follows from the fact that only those leaves which are in actively meristematic condition can develop deficiency symptoms and from the corollary that mature leaves exhibiting boron deficiency symptoms do not become normal when subjected to boron nutrition. Confirmation of this is found in the analysis of the Golden Muscat vines (table 10) after changing from minus-boron to plus-boron culture. The lower leaves showed extreme deficiency symptoms, yet their boron content was equal to that of the young normal leaves.

In general all parts of vines which had been deficient for an extended period contained less than 25 p.p.m. of boron.

Mobility or Retranslocation of Boron within the Plant. There seems to be rather general agreement in the literature concerning the immobility of boron within the plant tissues and the consequent need of a constant supply furnished by the nutrient substrate for the maintenance of growth. Davidson (10) states, "This nutrient (boron) is not stored in plant tissues and transferred to regions of new growth as is the case with some other nutrients." McMurtrey (25) referring to boron nutrition of the tobacco plant says, "These symptoms could indicate that there is little or no transfer of boron from the older plant parts to the younger growing points." Dennis and Dennis (11) in reviewing the work on boron came to the conclusion that a constant supply of the element is necessary. Walker, et al., (38) with reference to the beet state, ".... it is apparent that boron rather readily becomes locked in an immobile form in the tissues of maturing organs, or regions within such organs, and once in that state is of little immediate use to the meristematic regions." Wolf (45) concludes that, "As boron enters the plant, the roots remove what they need for their development.

The remainder moves up into the stems and leaves of the plant where it is rapidly immobilized." This statement was apparently based upon the author's findings that the boron in plant tissues was insoluble in cold water and alcohol.

Although the above citations and many others support the contention that boron is present in an immobile form in the plant tissues, there is certain evidence to the contrary. Lowenhaupt (20) found that sunflowers grown for 23 days in a complete nutrient solution developed boron deficiency symptoms within 24 hours after transfer to a minus-boron nutrient solution. However, if the plants were changed to distilled water, the boron deficiency symptoms appeared much more slowly. Walker, et al (38) state, "When beet roots grown in the field with an adequate supply of boron were planted after a period of dormancy, in boron-free nutrient sand cultures, leaf and floral stem development was at first normal, but eventually the apical leaves showed symptoms of boron deficiency." If it is assumed that boron is necessary for the meristematic activity in this leaf and floral stem development, then the quantity of boron required must have been obtained, and hence transferred, from the beet root to the growing top since the nutrient substrate was boron-free. More direct evidence that boron exists in the plant in a mobile state is given by Shive (35) who found 28.7 percent of the boron in _Vicia faba_ and 78.4 percent of the boron in the corn plant, in the expressed sap of the plant tissues and therefore considered to be in a mobile, active state. In an earlier paper (34), Shive concluded that plants of tobacco and cotton cannot build up an available reserve of boron in their tissues to sustain normal development during subsequent deficiency of this element. The amount of growth and the time elapsed between removal of the plants from boron nutrition and the appearance of deficiency symptoms was not stated.

Eaton and Blair (13) suggest that boron is probably taken up by the plant as an inorganic radical in the transpiration stream and becomes immobile upon incorporation with a complex organic molecule.

In summarizing the findings and conclusions of the various workers on the problem of boron mobility and transfer in the plant, it would seem more accurate to interpret their results on a quantitative basis. It is undoubtedly true that a plant cannot store sufficient boron to maintain normal growth for an indefinite period, but this is equally true of other plant nutrients. The fact that boron deficiency may occur more rapidly upon removal of the element from the substrate than do deficiencies of other elements may indicate merely the inability of the plant to store reserve boron in as relatively adequate amounts as other elements, rather than absolute immobility of the boron present.

Certain of the results in the present experiment can be used as evidence concerning the mobility and transfer of boron in the current season's growth of the grape vine. The growth habit of the vine makes the grape peculiarly adaptable for such studies. In so far as the initial growth of the vines in the minus-boron treatments is concerned, it is impossible to definitely ascertain whether this growth utilized reserve boron in the roots and stem of the two-year old vine or whether boron was available in the sand culture media. However, it seems unlikely that the sand after being thoroughly washed and leached at the beginning of the experiment would provide available boron for the heavy initial growth. At any rate, growth occurred for about 30 days before symptoms of deficiency were observed. Other workers have apparently noted similar results. Weinberger and Cullinan (41) working with one-year old peach trees cut back to a single bud obtained normal growth for a period of about six weeks in a minus-boron sand culture. Similarly, Johnston and Fisher (19) found that tomato plants upon removal to a minus-boron nutrient water culture, continued in growth (stem elongation) for a period of about three weeks. During the first two weeks of this period the rates of growth in minus-boron and plus-boron cultures were not greatly different. It would seem that again we must assume that this growth necessitated the utilization of boron present in tissues laid down before the change in nutrient condition was effected. It is interesting to note that the authors use the concluding statement that, "Boron is ...... apparently fixed in plant tissues and cannot be used over and over again." This follows Warington's (40) earlier conclusions that "..... the supply of boron must be continual in order to be effective ..... and that it is in some way fixed by the plant and not in a state of circulation."

The relatively delayed appearance of deficiency symptoms after changing from a plus-boron to a minus-boron nutrition in the present experiment also suggests that there was utilization of reserve boron. It is interesting and perhaps suggestive that the period from the time of withholding boron from the nutrient solution until the appearance of deficiency symptoms, closely approximated the period from growth inception after planting until the initial symptoms of deficiency. Furthermore, the actual amount of cane growth made by the vines during these two periods was not greatly different.

More definite evidence of boron transfer within the vine is afforded by the analyses of the different parts of the vines of the several treatments. In all instances there was a definite reduction in boron content of the lower leaves on the canes of vines which were changed from plus-boron to minus-boron nutrition. Since these leaves were mature and inactive in growth at the time of change of treatment, their greatly lowered boron level can only be explained by assuming a transfer of boron to the upper and active meristematic regions. If the lower leaves were enlarging during this period, the lower boron percentage could conceivably result as a dilution of the boron present in the leaf. This possibility, however, definitely must be ruled out because of the mature condition of these lower leaves. Since the stems of the plus-minus vines were as high in boron as the stems of the continuous boron vines, it follows that the leaves serve largely for storage of reserve boron. This would be assumed from the fact that the leaves of the vines built up a much higher content of boron under plus-boron nutrient conditions than the stems. The apparent equalization of the boron level in various parts of boron-deficient plants may also be accounted for on the basis of transfer, since it was shown that a differential existed in these plants before the deficiency developed.

Quantitative estimation of the total extent of the retranslocation of boron within the vine is impossible to determine from the present data, since weights of plant parts involved were unobtainable and since no consideration was given to the boron present in the root system. However, in the Herbert vines there was found a reduction of approximately 35 p.p.m. of boron in the lower mature leaves. This amount, if transferred and made available to the actively growing parts could reasonably account for the growth made by these vines after the withholding of boron from the nutrient solution.

Although there is clear evidence that transfer of boron does occur, and that therefore it cannot be held that the boron in the vine is in an immobile state, it is likewise clear that transfer from the lower leaves can take place only above a certain level of boron content in these leaves. Thus leaves produced after changing to the minus-boron nutrient never exceeded the older leaves in boron content. In Herbert where the samples from the plus-minus boron vines were taken at the first indication of boron deficiency, the difference between the boron level in upper and lower leaves was very little. In Golden Muscat where the plus-minus vines had developed very definite boron deficiency symptoms at the time of sampling, the difference was quite pronounced with a much lower level exhibited by the upper leaves. This indicates a dilution of the boron by continued growth in the upper part of the cane following the inability of the lower leaves to supply boron when a certain level was attained. This level of boron in the lower leaves was not greatly different for the three varieties. Boron present in the leaves of the grape below this level presumably may be considered to exist in an immobile state, insofar as transfer adequate to maintain normal growth of the growing point is concerned. In the Herbert and Golden Muscat varieties this boron represents roughly one-third of the total boron in the leaves, and in the Catawba a somewhat larger fraction. This is greater than the estimation of the soluble or mobile boron in the dicot, Vicia faba, by Shive (35) attained by determination of the fraction of boron present in the expressed sap.

The method of attack on the problem of boron transfer within the plant by analysis of the plant parts was used by Brandenburg with the sugar beet. Brandenburg (6) found that when the source of boron supply was interrupted, the new leaves of the sugar beet were very low in boron content while the older leaves, formed while the supply of boron was plentiful, retained the normal amount of boron. This result is in apparent direct opposition to the present findings with the grape, i.e., the older leaves lose boron as the younger leaves are developed under minus-boron nutrition. It is quite conceivable, as suggested by Eaton and Blair (13) that the organic form of boron in the tissues of different species of plants may be greatly different, resulting in a widely varying percentage of the boron present in soluble or mobile form. Or is it possible that the anatomical structure of certain plants renders more difficult adequate transfer of materials from one part to another? The work of Walker, et al. (38) suggests, as has been stated, that with the beet there does exist some transfer of boron from root to leaves, but gives no evidence of transfer from older to younger leaves.

From the data presented herein on the analyses of the plant parts and on the growth of the vines in the several treatments, it seems logical to conclude that there was a definite transfer of boron from the lower mature leaves on the cane of the grape upward to the terminal actively growing parts, and that the amount thus transferred was sufficient to maintain normal growth of the cane for a limited period, or until the lower leaves were depleted of boron to a certain level. There is also indirect evidence that the roots and stem of the dormant vine may supply boron to the developing shoots. Thus while that part of the conclusion of Johnston and Fisher (19) to the effect that the boron in the plant tissue cannot be used over and over again, and, therefore, must not be considered in the nature of a catalytic agent in plant growth, must be accepted, their conclusion and that of many others that boron is fixed in an immobile state in the plant must certainly be modified.

Boron and Calcium Contents of the Vines. Brenchley and Warington (7) suggested that there is a definite association between boron and the absorption or utilization of calcium by the broad bean. This observation was confirmed by Swanback (37) working with tobacco seedlings. However, Marsh (22) found that the calcium absorption rate in the tobacco, faba bean, corn, and oats was not significantly influenced by boron content of the substrate within certain limits. Cook and Millar (9) found with beets that there was no apparent effect of boron in the nutrient media on the amount of calcium in the plant tissue, and Wallace and Jones (39) state that the status of calcium in the leaves and fruit of apples was not affected by boric acid injections although the boron content was thereby increased. Minarik and Shive (26) working with soybean plants found that both deficient and toxic amounts of boron in the substrate resulted in subnormal amounts of calcium in the plant tissue. Conversely, Muhr (27) found that calcium was usually higher in boron deficient plants. Recently, Marsh and Shive (23), Marsh (22), and Shive (35) working with corn found a very close correlation between the boron in the plant tissue and the active or soluble calcium present (that found in expressed plant sap), but found no correlation existing between the boron content and total calcium content. Shive (35) concludes that, "the proportional part of the total calcium in the plant which was maintained in the soluble, active state in which it could be translocated from points of supply to centers of metabolic activity, was determined not by the total calcium content of the plant but by the supply of available boron in the corresponding tissues, which in turn was determined by the boron concentration of the nutrient substrate."

Drake, et al. (13) suggest that the ratio of calcium to boron in the plant may determine whether or not the plant exhibits boron deficiency symptoms. With calcium-boron ratios in excess of 1340:1, boron deficiency appeared in tobacco plants. With lower ratios the plants remained normal although the boron content of the plants was the same at all ratios.

The data from the calcium and boron analyses of the vines in the sand culture experiments are in agreement with Shive's findings that there was no definite relation between total boron and total calcium in the plant. Since no attempt was made to determine the soluble calcium fraction, there is no evidence on the possible relationship between the soluble fractions of calcium and boron in the grape vine. The calcium-boron ratios (table 13) are higher in the boron deficient vines, but this is quite apparently a function of the boron level, rather than a cause contributing to development of the symptoms. In the calcium-boron ratios of the upper and lower leaves of the Catawba and Herbert vines of the continuous minus-boron and the plus-minus boron series, it is found that the lower leaves have the higher ratios, but, in contrast to the findings of Drake, et al. (12), these higher ratios are associated with less rather than more apparent deficiency symptoms. It must be remembered that the outward symptoms of deficiency on these vines did not necessarily reveal the actual state of deficiency. The ratios for the different parts of the same vine show the necessity for detailed sampling if calcium-boron relationships are to be studied. Leaves and stem portions had widely different ratios, and the ratios varied with respect to age of the leaf or stem.

It is clear that from the data obtained no conclusions can be drawn concerning possible boron-calcium associations in the grape vine.

SUMMARY

1. Application of borax to the soil at the rate of ten pounds per acre resulted in positive correction of abnormal growth and fruiting of a number of grape varieties in a vineyard on Norfolk sandy soil near Columbia, South Carolina.

2. Foliar symptoms of the boron deficiency were manifested by stunting of shoot growth in the early spring, by interveinal chlorosis of the developing terminal leaves, and by curling and malformation of the young leaves.

3. The deficiency of boron was most apparent in the early part of

TABLE 13. Calcium-boron ratios in leaves and stems of vines grown in plus and minus boron nutrient sand culture.

Nutrient Treatment	Portion of vine analyzed	Calcium/boron ratio	
		Catawba vines	Herbert vines
Continuous plus-boron March 23 - June 23	Lower leaves	184	84
	Upper leaves	54	32
	Lower stem	181	141
	Upper stem	114	106
Continuous minus-boron March 23 - June 23	Lower leaves	437	451
	Upper leaves	316	292
	Lower stem	195	211
	Upper stem	259	188
Plus-boron until May 21. Minus-boron thereafter	Lower leaves	394	274
	Upper leaves	346	221
	Lower stem	97	196
	Upper stem	150	175
Minus-boron until May 21. Plus-boron thereafter	Lower leaves	110	115
	Upper leaves	97	52
	Lower stem	114	131
	Upper stem	55	89

the growing season, the symptoms developing shortly after growth inception or, in less severely affected vines, just after development of the blossom clusters. Leaves produced by the vines in the latter part of the growing season seldom showed symptoms of the deficiency.

4. Vines showing boron deficiency formed blossom clusters but set very few fruits. Fruit yield was also affected on some vines which showed little evidence of deficiency in the foliage.

5. Certain varieties, in particular Armalaga, exhibited millerandage, i.e., set parthenocarpic fruits on boron deficient vines.

6. Borax greatly increased the set of fruit of the varieties with reflex stamens.

7. Varieties differed widely in their susceptibility to boron deficiency, but the degree of susceptibility was not necessarily correlated with the inherent vigor of the variety.

8. Varieties grafted on vigorous root-stocks developed the deficiency more slowly than the same varieties on their own roots, and to a lesser degree of severity, but no rootstock entirely prevented the occurrence of the deficiency.

9. Borax application to the vineyard soil increased the boron content of the grape leaves. Varieties varied in boron content, but boron content could not be correlated with severity of boron deficiency symptoms.

10. The boron content of the leaves was lowest in the early part of the growing season.

11. Boron deficiency in vines grown in sand culture developed in a similar manner to that observed in the field. In addition to the symptoms found under vineyard conditions, an early indication of boron deficiency in the vines in sand culture was the appearance of watersoaked, necrotic areas in the young terminal tendrils.

12. Two-year old vines planted in sand culture developed boron deficiency symptoms thirty days after inception of growth. The vines at this time had made from 70 to 155 cm. shoot growth.

13. Boron deficient vines resumed normal growth within ten days after changing to plus-boron nutrition. Normal vines changed to minus-boron nutrition continued to grow normally for 25 to 30 days before symptoms of deficiency were apparent.

14. Only those leaves that were in a meristematic condition at the time of development of the deficiency showed deficiency symptoms. The older, basal leaves on boron deficient vines remained normal in appearance even though the terminal leaves exhibited extreme symptoms.

15. In plus-boron vines the boron content of the leaves was much higher than that of the stems. There was no consistent difference between upper and lower leaves on the canes. Upper stems had a higher boron content than lower stems. The leaves of plus-boron vines had boron concentrations ranging from 57 to 146 p.p.m. and stems from 29 to 41 p.p.m.

16. In minus-boron vines the concentration of boron was more or less equalized in all parts of the vines at levels of approximately 20 to 25 p.p.m. in the Catawba and Herbert vines.

17. A boron content of approximately 30 p.p.m. constituted the minimum level of boron necessary for normal shoot growth of vines grown in sand culture.

18. Vines changed from plus-boron to minus-boron nutrition showed a definite lowering of the boron content in the lower mature leaves on the shoot to a point approaching the boron level of continuous minus-boron vines. Coincident with the decrease in boron in the lower leaves was the continued growth in length of the shoots for about 30 days after change of nutrition. From this, retranslocation of boron, at least in the

grape, seems rather definitely established.

19. Vines changed from minus-boron to plus-boron nutrition showed an increase in boron content of the mature lower leaves.

20. There was no definite correlation between the calcium and boron contents of the leaves or stems.

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