GROWTH AND METABOLIC EFFECTS OF BORON DEFICIENCY IN SOME PLANT SPECIES OF ECONOMIC IMPORTANCE

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ABSTRACT

Ten species of economic importance, representing eight different taxonomic groups were grown in refined sand culture at normal and deficient levels of boron. Boron deficient plants of all the species showed visual symptoms, depression in growth and decrease in boron concentration. On the basis of visual symptoms and depression in growth at 55 days, lettuce, sugarbeet and radish were found to be very sensitive to boron deficiency and can be used as indicator plants for recognizing the deficiency under field conditions. Barley was found to be comparatively resistant to boron deficiency. Boron deficiency resulted in marked metabolic disturbance in plants. It stimulated the specific activity of catalase, peroxidase and acid phosphatase in leaves and decreased the total dehydrogenase activity of roots. Boron deficiency caused an accumulation of non protein nitrogen and a decrease in protein nitrogen. Except in french bean, the concentration of total and reducing sugars was also decreased by boron deficiency. French bean showed a reverse trend. Boron deficiency also caused a decrease in the ascorbic acid content of plants. On the basis of growth and metabolic effects of boron deficiency, radish was found very suitable for investigating the metabolic role of boron in plants.

INTRODUCTION

The present investigation was taken up to find out suitable indicator plants which would help in diagnosing boron deficiency under field conditions in U.P., many areas of which are reported to be marginally deficient in the available quantity of this element (Kanwar & Randhawa, 1974). Ten common plant species—cauliflower, cabbage, radish, flax, sugarbeet, lettuce, carrot, tobacco, french bean and barley—about which there is some information on boron deficiency from outside India (Berger, 1949; Wallace, 1951; Stiles, 1961; Hewitt, 1963; Purvis & Carolus, 1964), were chosen as the test plants. Some of these species were also assayed for some biochemical parameters in order to select a plant suitable for studying the role of boron in plant metabolism.

MATERIAL AND METHODS

Ten species of crop and vegetable plants of economic importance—cauliflower (*Brassica oleracea* L. var. *botrytis*), cabbage (*Brassica oleracea* L. var. *capitata*), radish (*Raphanus sativus* L.), sugar beet (*Beta vulgaris* L.), lettuce (*Lactuca sativa* L.), carrot (*Daucus carota* L. var. *sativa*), tobacco (*Nicotiana tabacum* L. var. white burly), french bean (*Phaseolus vulgaris* L.), barley (*Hordeum vulgare* L. var. K. 12) representing eight different taxonomic groups were grown in refined sand culture at normal and deficient levels of boron. The composition of the nutrient solution and the details of the culture technique used in the study have been described earlier (Agarwala & Sharma, 1976). Normal boron plants were supplied 0.37ppm. boron. In plants raised for boron deficiency, no boron was added to the nutrient medium. There were six pots for each treatment.

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Study was made of the visual effects of boron deficiency, dry matter yield and tissue concentration of boron in each of the ten species. The leaves of normal and boron deficient plants of six species—cauliflower, cabbage, lettuce, french bean, radish and flax were estimated for protein and non-protein nitrogen and for reducing and total sugars. Four of these species—cauliflower, radish, lettuce and french bean—were investigated for the effect of boron deficiency on ascorbic acid content and the specific activity of catalase, peroxidase and acid phosphatase in leaf tissue extracts and for total dehydrogenase activity in roots.

The dry matter yield of plants was determined by drying the plants in a forced draught oven at 70°C for 24 hours. Tissue concentration of boron was estimated by the method of HATCHER AND WILCOX (1950).

For the estimation of nitrogen and sugars, plant material was fixed in boiling 80% ethanol and macerated in a top drive homogeniser. The proportion of fresh mateiial to alcohol was kept as 1:10. The alcohol soluble and insoluble fractions were separated by centrifuging at 800×g. The alcohol soluble portion and the subsequent washings from the residue were pooled and made to volume and aliquots from this were drawn for the determination of non-protein nitrogen and sugar. The alcohol insoluble material was used for the estimation of protein nitrogen.

Nitrogen was estimated by the semi-micro-kjeldahl method. For the estimation of non-protein nitrogen, a suitable aliquot of the alcohol soluble material was freed of alcohol by heating on a water bath and then treated for 2 hours with 5% salicylic acid in sulphuric acid at room temperature. The salicylic acid was removed by treating with powdered sodium thiosulphate.The sample was then digested by the mehtod of CHIBNALL, REES AND WILLIAMS, (1943). For estimation of protein nitrogen a portion of alcohol insoluble material was dried and digested as in case of alcohol soluble material. The clear digests were made to volume and estimated for ammonia. Ammonia was distilled in a MARKHAM's appraratus into a boric acid buffer and estimated by titration against 0.002 NH_2S0_4 containing CONWAY AND O'MALLEY indicator (CONWAY & O'MALLEY, 1942).

Aliquot for sugar determination was treated with neutral lead acetate and filtered. Lead was removed by precipitating with disodium hydrogen phosphate added in slight excess. The filtrate was made to volume and reducing sugars were estimated by the mtehod of NELSON (1944). Total sugars were estimated as reducing sugars after hydrolysis of the non-reducing sugars by invertase. Values for non-reducing sugars have been obtained as the difference between reducing and total sugars.

Ascorbic acid was estimated in fresh leaf tissue after extraction with 6% metaphosphoric acid by rapid titration with 2, 6—dichlorophenol indophenol according to the procedure described by HARRIS AND RAY (1933). Catalase, peroxidase and acid phosphatase were assayed in crude tissue extracts of comparable young leaves, as described earlier (AGARWALA, SHARMA & FAROOQ, 1965).Total dehydrogenase activity of roots was measured by the triphenyl tetrazolium chloride (TTC) reduction method developed by SRIKANTAN AND KRISHNAMURTI (1955).

All estimations were made in triplicate and the mean values are presented in the text.

RESULTS AND DISCUSSION

GROWTH AND VISUAL SYMPTOMS OF BORON DEFICIENCY

Boron deficiency caused growth depression in each of the ten plant species examined. In flax, lettuce and tobacco, growth depression appeared considerably early, at 15 to 20 days of sowing of seeds. In tobacco, when boron supply was withheld, a large percentage

Tabie 1—Visual symptoms of boron deficiency in ten plant species grown in sand culture under boron deficiency

Visual symptoms	Plant species									
	Cauliflower	Cabbage	Radish	Flax	Sugarbeet	Lettuce	Carrot	Tobacco	French bean	Barley
1. Bluish green tints on foliage	30 (O) +	30 (Y)			30 (Y)(U) +					
2. Cupping of leaves	35(Y) +++	45 (Y) ++	35-40 (Y) +++		35 (Y) +	60 +++				
3. Rolling of leaf margins downwards (D), upwards (U).			30 (Y)(DU) +++		30 (Y)(U) ++	60 (DU) +++		40 (Y)(D) ++		
4. Lamina, thick and brittle	40 (Y) +++	50 (Y) ++	50 (Y) ++						40 +++	
5. Distortion of mid-rib	40-45 (Y) +++	50-55 (Y) ++	50 (Y) ++							
6. Chlorosis	70 (O) +++	75 (O) +	50 (O) ++	40 (Y) +++		30-35 +++	60 (O) ++			
7. Death of the growing point	70 ++			50 +++	55 +++	70 +++	80 +	75 ++	30-35 ++++	
8. Purple or violet pigmentation of the chlorotic leaf areas.	75 (O) +++	75 (O) ++								
9. Translucent areas on lamina		45 (Y) +++								
10. Raised water-soaked areas				30 ++						
11. Brown necrotic spots on the leaves.						30-35 (Y) +++				70(O) ++
12. Wilting of leaf margins	45-50 ++				40 +	75 +				
13. Scorching of leaf apex (A), margins (M) and base (B).		75 (M) +	60 (M) +	+	45(O)(B) +++	55 (Y)(A) ++		40 (O)(B) +++	20(Y) +++	70(A) +

14. Thickening of the stem				30 +			40-45 ++
15. Cracks in the cortical region							40-45 +
16. Development of accessory buds		55 +	60 +	55 +++			
17. Browning of roots	+	+	+	+	+	+	+
18. Necrosis of root tips	+	+	+		+	++	++

*—Observations refer to 55 days growth
O—refers to older leaves
Y—refers to younger leaves
The number of the plus (+) signs denote the severity.

of seeds failed to germinate and seedlings showed a high mortality soon after emergence. In cauliflower, french bean and sugarbeet, growth depression also became manifest early, at 20 to 25 days growth. In french bean, appreciable depression in growth was observed even before the first set of compound leaves emerged. Under conditions of boron deficiency growth almost ceased in sugarbeet after 30 to 35 days, and in french bean after 50 to 60 days. The boron deficient plants of both the species died between 60 and 75 days. Growth depression due to boron deficiency appeared last, at about 60 days growth, in barley.

Under conditions of boron deficiency each of the ten species examined developed specific symptoms of boron deficiency. In all, about eighteen different types of visual symptoms were observed. Some of them were common to many species, while some others were confined only to a few species (Table 1, Plates 1, 2). Symptoms which were most common were (a)death of the growing point, (b) rolling or cupping of the leaf margins, and (c) chlorosis and scorching of the leaf lamina. Symptoms which were less common were (a) purple or violet pigmentation of the chlorotic leaf margins, an effect confined to cabbage and cauliflower, (b) short, somewhat thickened, stem with longitudinal cracks, observed in flax and french bean, (c) development of accessory buds, observed in cabbage, radish and flax, and (d) translucent areas all over the leaves and stem as in flax.

While some of the visual symptoms of boron deficiency observed here have been describede arlier (McMurtrey, 1929; McHargue & Calfe, 1932, 1933; Lohnis, 1937; Chandler, 1940; Walker, McLean & Jolivette, 1941; Wirrington, 1940; Skok, 1941; Woodman, 1941; Wallace, 1951; Odhnoff, 1957; Bussler, 1964), many symptoms observed here are new to literature. These include the apperance of (*a*) water soaked areas on the leaves and stem of flax, (*b*) inhibition of germination in tobacco grown in boron deficient medium, (c) small brown necrotic spots all over the foliage of boron deficient barley, and (d) minute dull green water soaked spots turning into translucent areas in cabbage. It was observed here that the death of the growing point was not always the first external symptom of boron deficiency. In cauliflower, flax, sugarbeet, lettuce, carrot and tobacco, death of the growing point was preceded by other visual symptoms. In cabbage and barley, death of the growing point did not take place at all. This is not in agreement with the observations made by Stiles (1961) that the first external symptom of boron deficiency is generally the death of the growing point.

Dry Matter Yield

In each of the plant species investigated, the dry matter yield of plants was depressed by boron deficiency (Table 2). At 55 days growth, the order of depression in dry matter production of the different plant species was in the decreasing order : tobacco>lettuce>sugarbeet>radish>cauliflower>french bean>cabbage.

At 85 days growth, the extent of the depression in dry matter yield due to boron deficiency was almost equally marked in cauliflower, cabbage, radish, flax, lettuce and tobacco, but the effect on barley was considerably less than in any of the other plant species examined. In cauliflower, cabbage, carrot and french bean, the depression in the dry matter yield of roots was more marked than in tops but the reverse was true for radish, barley, lettuce, flax and sugarbeet. In tobacco, the depression in yield due to boron deficiency was almost equally marked in tops and roots.

Tissue Concentration and Total Content of Boron

In each of the plant species examined, tissue concentration of boron in top parts was markedly depressed by boron deficiency (Table 3). The extent of the decrease in the tissue

Table 2—Mean values for the dry matter yield of ten plant species grown with and without boron in sand culture

Plant species	Plant part	55 days growth		85 days growth	
		with boron	without boron	with boron	without boron
		g dry matter/plant			
Cauliflower	tops	0.727	0.284	3.845	0.608
	roots	0.081	0.023	0.683	0.047
	total	0.808	0.307	4.528	0.655
Cabbage	tops	0.573	0.297	2.973	0.496
	roots	0.049	0.023	0.646	0.044
	total	0.232	0.320	3.619	0.540
Radish	tops	1.058	0.314	4.188	0.446
	roots	0.220	0.084	0.446	0.125
	total	1.278	0.398	4.634	0.571
Flax	tops	0.364	0.170	2.078	0.239
	roots	0.032	0.018	0.222	0.037
	total	0.369	0.188	2.300	0.276
Sugarbeet	tops	0.315	0.079		
	roots	0.063	0.016		
	total	0.378	0.095		
Lettuce	tops	0.728	0.121	3.073	0.420
	roots	0.088	0.018	0.601	0.140
	total	0.816	0.139	9.674	6.051
Carrot	tops			0.770	0.120
	roots			1.078	5.001
	total			1.848	0.171
Tobacco	tops			1.460	0.177
	roots			0.274	0.029
	total			1.734	02.06
French bean	tops	1.267	0.620		
	roots	0.255	0.070		
	total	1.572	0.690		
Barley	tops			12.130	9.470
	roots			0.632	0.622
	total			12.762	10.092

Table 3—Tissue concentration and total content of boron in top parts of ten plant species grown with and without boron in sand culture

Plant species	55 days growth		85 days growth	
	with boron	without boron	with boron	without boron
	μg boron/g dry matter			
Cauliflower	30.0	12.5	35.0	13.5
Cabbage	39.5	12.5	31.0	16.0
Radish	45.0	12.0	42.0	21.0
Flax	36.0	6.0	36.0	9.5
Sugarbeet	45.0	15.0	..	..
Lettuce	44.0	19.5	29.5	9.8
Carrot	..	..	37.5	9.8
Tobacco	..	..	41.3	18.5
French bean	26.5	11.0	..	..
Barley	..	..	13.0	0.88
	μg boron/plant			
Cauliflower	21.8	3.6	133.1	8.6
Cabbage	22.6	3.8	93.1	8.0
Radish	47.6	3.9	177.7	9.4
Flax	13.1	1.0	74.8	2.2
Sugarbeet	14.2	1.2	..	..
Lettuce	32.1	4.1	88.6	4.2
Carrot	..	..	28.3	9.2
Tobacco	..	..	68.6	3.3
French bean	37.0	6.8	..	..
Barley	...	..	157.7	8.4

concentration of boron due to boron deficiency varied in the different plant species examined. Maximum reduction in tissue concentration of boron was brought about by boron deficiency in barley and flax. Except in lettuce, where tissue boron at 85 days growth was lower than at 55 days growth, there was no appreciable difference in the boron content of plants at the two stages of growth—55 days and 85 days. The concentration of boron in barley plants was the least but, inspite of this, barley did not show so marked visual symptoms and decrease in dry matter production as in the other species thus indicating that boron requirement of barley was very low. This is in accord with the findings of Marsh (1942), Shkolnik and Makarov (1949) and Neales (1960) who noted that monocots have a low requirement of boron than dicots, and the observations of Hewitt (1952) that "cereals are difficult" subjects for boron deficiency.

It was observed that in lettuce plants subjected to boron deficiency, there was no increase, on the other hand there was a decrease in the boron content of plants during the period 55 to 85 days, but plants continued to grow during this period, presumably meeting the boron requirement by redistribution of boron within the tissues. These results are in agreement with the findings of THORNEBERRY (1961) who has shown that boron initially taken up by plants may be redistributed within the plant and utilized for continued growth when an external supply of the element is witheld. The obsrevations of JOHNSTON AND FISHER (1930) that in tomato, boron is apparently fixed in tissues and is not available for growth does not seem to apply to all plant species.

The total content of boron in the top parts of each of the ten plant species grown without boron was markedly less than in plants supplied normal boron (Table 3). The extent of the depression in the total content of boron in the top parts of the different plant species was not appreciably different. Maximum reduction in the total content of boron in the top parts of boron deficient plants was found in flax. Of the five plant species sampled at both 55 and 85 days growth, the total content of boron in top parts of four species—cauliflower, cabbage, radish and flax—was somewhat higher at 85 days than at 55 days growth. The total boron content of lettuce plants grown without boron at the two stages of growth, was not appreciably different.

NITROGEN AND SUGARS

In each of the six plant species examined, boron deficiency caused an accumulation of non-protein nitrogen; the effect being more pronounced in cauliflower, cabbage, flax and french bean than in lettuce and radish (Table 4). In each of these species, the accu-

Table 4—Concentration of nitrogen and sugars in six plant species grown with and without boron in sand culture

Plant species	Treatment	Nitrogen % fresh wt			Sugars % fresh wt		
		Pirotetn	Non-protein	Total	Reducing	Non-reducing	Total
Cauliflower	+ Boron	0.418	0.132	0.550	0.331	0.476	0.807
	— Boron	0.236	0.293	0.528	0.294	0.433	0.746
Cabbage	+ Boron	0.443	0.096	0.539	0.276	0.529	0.807
	— Boron	0.283	0.242	0.525	0.160	0.297	0.457
Radish	+ Boron	0.482	0.118	0.602	0.068	0.090	0.163
	— Boron	0.301	0.161	0.562	0.010	0.024	0.034
Flax	+ Boron	0.647	0.065	0.711	0.099	0.069	0.167
	— Boron	0.525	0.174	0.759	0.058	0.313	0.372
Lettuce	+ Boron	0.311	0.085	0.396	0.285	0.527	0.757
	— Boron	0.239	0.112	0.351	0.120	01337	0.452
French bean	+ Boron	0.561	0.069	0.630	0.009	0.093	0.102
	— Boron	0.531	0.189	0.720	0.048	0.395	0.434

mulation of non-protein nitrogen was accompanied by a decrease in protein nitrogen; the effect being most marked in cauliflower and the least in french bean. A decrease in protein nitrogen content of boron deficient plants has earlier been reported for spinach (SCRIPTURE & MCHARGUE, 1944), bean (BAUMEISTER, 1941) and nastrutium (BRIGGS, 1943).

In the six plant species in which sugars were estimated the effect of boron deficiency on sugars was not the same (Table 4). As a result of boron deficiency total sugars were depressed in cauliflower, cabbage, radish and lettuce and increased in flax and french bean. In boron deficient plants of cauliflower, cabbage, radish, lettuce and flax, reducing sugars were depressed, but in boron deficient french bean plants, there was marked accumulation of reducing sugars. A marked accumulation of non-reducing sugars was found in boron deficient flax and french bean but in cauliflower, cabbage, radish and lettuce, non-reducing sugars were depressed. While the increase in the concentration of sugars in the top parts of french bean observed here is in accord with the observations made for certain other plants in which it was attributed to a breakdown in the conducting system of the boron deficient plants (JOHNSTON & DORE, 1929; HAAS & KLOTZ, 1931; SCRIPTURE & MCHARGUE, 1943, 1945), the low levels of sugars in the leaves of boron deficient plants of other species examined here would suggest an involvement of boron in carbon assimilation.

ASCORBIC ACID

As in the case of tobacco leaves (STEINBERG, SPECHT & ROLLER, 1955), the ascorbic acid content in the leaves of each of the four species examined here—cauliflower, radish, lettuce and french bean—was found to be decreased by boron deficiency (Table 5). In lettuce, depression in ascorbic acid was accompanied by a decrease in sugars but in french bean the reverse was true indicating that depression in ascorbic acid could not be attributed to low concentration of sugars in boron deficient plants.

Table 5—Ascorbic acid content in leaf tissues of cauliflower, radish, lettuce and french bean plants grown with and without boron in sand culture.

Plant species	With boron	Without boron
	mg ascorbic acid/100 g. fresh wt	
Cauliflower	126	63
Radish	122	72
Lettuce	19	8
French bean	92	36

ENZYMES

In each, cauliflower, radish, french bean and lettuce, which were assayed for enzyme activity, boron deficiency caused a stimulation in the specific activity of catalase, peroxidase and acid phosphatase in leaves and decreased the total dehydrogenase activity of roots (Table 6). The effect on each of the four enzymes was most marked in case of french bean and generally the least in lettuce. Similar observations have earlier been made for catalase activity in tomato (NASON, OLDEWURTEL & PROPST, 1952) and for acid phosphatase in tomato (HEWITT & TATHAM, 1960) and broad bean (HINDE & FINCH, 1966). Since

Table 6—Specific activity of catalese, peroxidase and acid phosphatase in leaves and total dehydrogenase activity in roots of cauliflower, radish, lettuce and french bean plants grown with and without boron in sand culture.

Treatment	Plant species			
	Cauliflower	Radish	Lettuce	French bean
	CATALASE (units)			
+ Boron	0.117	0.539	0.213	0.204
— Boron	0.548	0.628	0.365	0.403
	PEROXIDASE (mg, purpurogallin formed)			
+ Boron	6.86	3.67	2.64	4.02
— Boron	18.40	9.28	7.37	14.90
	ACID PHOSPHATASE (μg Pi liberated)			
+ Boron	262	229	207	274
— Boron	565	455	327	555
	Total Dehydrogenase activity (μg Triphenyl tetrazolium chloride reduced/g fresh wt.)			
+ Boron	134	100	266	149
— Boron	113	64	217	54

boron deficiency had caused a decrease in the total protein content of each of the four plant species in which it stimulated catalase, peroxidase and acid phosphatase, it would appaer that under boron stress either the different proteins are differentially synthesized or that it is involved in the activation of these eneymes.

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EXPLANATION OF PLATES

PLATE 1

1. Effect of boron deficiency in cabbage; compared to the normal plant (left) the growth of the boron deficient plant (right) is markedly stunted. The deficient plants also show interveinal chlorotic mottling of old leaves, development of axillary buds following the death of the growing point, and the collapse of the shoot.

2 & 3. Boron deficiency in cauliflower. Fig. 2 shows comparative growth of normal (left) and boron deficient (right) plants. The boron deficient plants exhibit foliar symptoms of the deficiency and fail to form root. Fig. 3 shows interveinal chlorosis with deep purple pigmentation along the margins and veins of the boron deficient plants. Cupping of leaves and collapse (breaking) of the petioles is also conspicuous.

4 & 8. Effect of boron deficiency on lettuce. Fig. 4 shows that compared to the normal plant (left) the growth of the boron deficient plant (right) is markedly reduced. Most plants collapse following the death of the apical point. Fig. 8 shows necrosis of the growing point and the young growths of a boron deficient plant. The foliage of these plants also show loss of turgor, necrosis, and distortion.

5. Boron deficient french bean plant showing bleaching and distortion of the first formed trifoliate leaves.

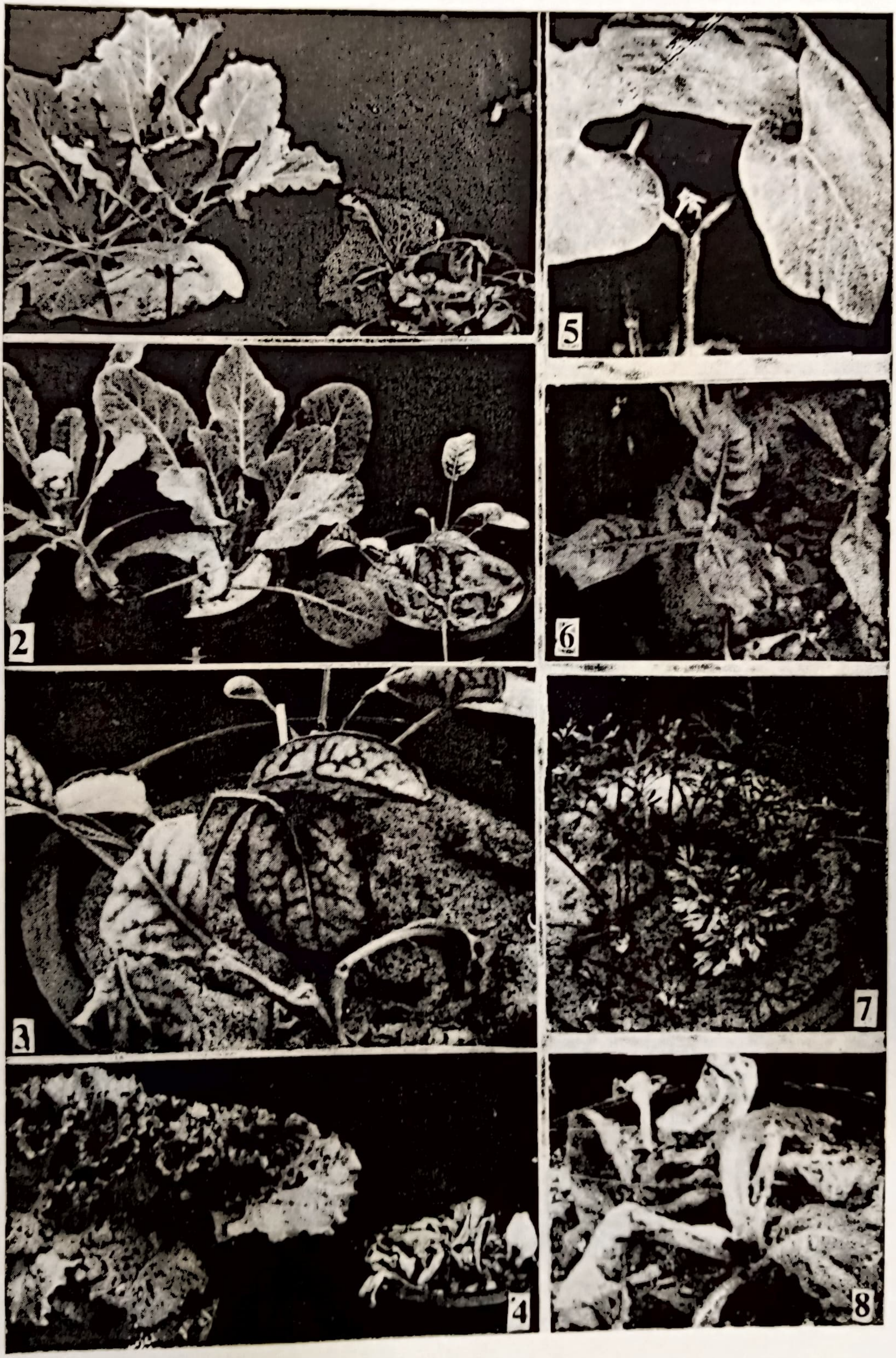
6. Boron deficient tobacco plants showing severely chlorotic leaves with scorched and ragged margins.

7. Boron deficient carrot plant showing chlorosis, bronzing and drying up of leaflets.

PLATE 2

9 to 11. Boron deficiency in radish. Fig. 9 shows comparative growth of normal (left) and boron deficient (right) plants. In the deficient plants, growth is severely arrested and plants fail to flower. In Fig. 10 the young leaves of boron deficient plants show severe distortion, incomplete development of lamina, bluish green pigmentation and coiling ('hooking') of the apical end of the mid rib. Fig. 11 shows severe chlorosis in an old leaf of a boron deficient plant.

12 & 13. Boron deficiency in flax. Fig. 12 shows comparative growth of normal (left) and boron deficient (right) plants. Plants raised in absence of boron develop severe symptoms of deficiency and fail to flower. In Fig. 13 boron deficient flax plant shows severe discoloration (bleaching) and distortion of the leaves and collapse of the apices of the main stem and branches.



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