MASTER'S REPORT

BORON DEFICIENCY PROBLEM

OF

CELERY PRODUCTION IN HAWAII

submitted by

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LIST OF TABLES

BORON DEFICIENCY PROBLEM OF CELERY PRODUCTION IN HAWAII

I. INTRODUCTION

A. Importance of the boron problem in celery production in Hawaii.

The total volume of celery (Apium graveolens L. var dulce Pers.) consumed by the state of Hawaii has been increasing steadily during the last decade. Most of the celery used in the state has been imported from California, but in 1961, the island production of celery exceeded the importation. In 1960, according to the Crop Livestock Survey, Hawaii's production of celery was 1,775,000 pounds, compared to 1,814,000 pounds imported, and in 1961, Hawaii produced 2,035,000 pounds, and imported 1,566,000 pounds (87). Almost the entire production of celery for the state is concentrated in the South Kohala district on the island of Hawaii.

Because of the year round mild climate with temperatures averaging 59° F. in January, and 68° F. in September the warmest month, and the minimum hardly dropping below 40° F., and the maximum very seldom exceeding 84° F., celery and other vegetable crops are grown throughout the year (38). Most growers plant on the average about two to three crops per acre per year. Under such intensive cultivation, boron deficiency problem has become widespread and significantly important. At the present time, celery cannot be grown satisfactorily without the addition of boron to the crop or soil. Despite the addition of about 50 pounds of borax per acre per crop of celery, a boron deficiency problem still exists. Losses from boron deficiency have averaged about 5 per cent, but occasionally losses have been as high as 90 per cent. Since the markets require a steady supply of celery the year round, farmers normally plant from .05 acre to 0.5 acre every 7 to 14 days. Consequently, the annual loss to the farmers may not be too great, although losses for some crops may be very high.

II. PURPOSE OF REPORT

The problem of boron deficiency of celery in Hawaii is complex. The purpose of this report is to find answers to the important questions listed below by observing the cultural practices of the celery growers, and reviewing the literature on boron.

1. How important is boron in crop production?
2. The source of boron and the amount of boron applied by growers vary markedly.
   What are the sources of boron and how much boron does celery require?
3. In what different ways are boron deficiency symptoms manifested in celery?
4. Some celery varieties have been observed to develop boron symptoms more readily than others.
   Is there a genetic basis for this difference?
5. Under certain conditions even heavy applications of this micronutrient do not correct the cracked stem condition.
   What are the factors that influence boron availability?
6. Do the different soils in Hawaii differ markedly in boron content? How do they compare with continental United States?

III. IMPORTANCE OF BORON IN CROP PRODUCTION

A. The extent of boron problem.

1. History.

Boron has been used as fertilizer in Europe for about 400 years (72), but the essentiality of this element for plants was not established until the 20th century. H. Agulhon, is generally regarded as the first person who investigated the essential nature of boron on growth of plants. His work was published in 1910 in Paris. Other early workers, include Haselhoff (1913) who reported that very low concentrations of boron are required by plants. W. E. Brenchly (1914) worked on boron nutrition of peas (*Pisum sativum* L.) in London, P. Maze (1915) of France showed the boron requirement of corn (*Zea mays* L.), and Katherine Warington (1923) at Rothamsted Experimental Station in England, showed that boron was an essential element in beans (*Phaseolus vulgaris* L.) and other plants (72, 78, 88).

The earlier investigators found long ago that the range between toxicity and deficiency is very narrow. Some plants are injured by the presence of 0.5 p.p.m. in the soil solution, while others may need at least 0.1 p.p.m. for optimum growth. The optimum condition for one crop may be toxic to another (46, 55, 25, 88).

The cracked-stem of celery reported by A. C. Foster and G. F. Weber (30) in Florida in 1924 as a non parasitic disease was proved by Purvis and Ruprecht in 1937 that it was caused by a deficiency of boron, and could be controlled by application of borax to the soil (70). E. Brandenburg in Germany in

1931 showed that heart rot of sugar beets was caused by a deficiency of boron. Numerous reports of crops affected by deficiency or toxicity of boron have been published throughout the world since these discoveries were made. The Chilean Nitrate Education Bureau Inc. has published three volumes on the bibliography of boron (33).

2. Conditions under which boron deficiency is found.

Boron deficiencies are found generally in humid regions where fairly high rainfall tend to leach out the boron, and where soils are generally acid. Intensive cropping of alfalfa (*Medicago sativa* L.) and other crops have depleted some soils of boron. In calcareous soils, boron may be fixed in the soil and become unavailable to plants. In the United States, all the states east of the Mississippi River, the first two rows of states west of the Mississippi, and the Pacific States, which total 41 states have a boron problem (72).

3. Different crops affected by boron deficiency.

In many parts of the United States, the application of borax is necessary to obtain satisfactory yield of alfalfa (89). Apples (*Malus sylvestris* Mill.) must be supplied with boron to avoid corky fruits in the Pacific northwest and the eastern states (25). Other crops which are frequently affected by boron deficiency problems are sugar beets (*Beta vulgaris* L.), radish (*Raphanus sativus* L.), turnip (*Brassica rapa* L.), sweet potato (*Ipomoea batatas* (L.) Lam.) and olive (*Olea europaea* L.) (85). D. A. Russel in the 1957 USDA Yearbook of Agriculture (72) reports that boron deficiency has been reported in 90 crops, but the number of crops and the number of states are expected to increase as soils become depleted of boron. Recently, brown spots on leaves, corky petioles, and death of growing points of tea plant (*Thea sinensis* L.) due to boron deficiency have been reported from Uganda (14). In India, the black tip disease of mangoes (*Mangifera indica* L.) which causes break down of the distal end of the fruit has been traced to deficiency of boron (19). Small crops of avocados (*Persea americana* Mill.) in Florida during certain years seem to be correlated with low boron content of plants (36).

IV. BORON REQUIREMENT OF CELERY AND OTHER CROPS

Plants differ greatly in the amount of boron they contain, in their requirements and in their abilities to obtain boron from the soil. Generally, the grasses with a few exceptions do not require as much boron as other plants. The following Tables I and II taken from K. C. Berger (10) show the boron content of tops of plants grown in humid region soils, and the boron requirement of some crop plants.

TABLE I

AMOUNTS OF BORON FOUND IN TOPS OF PLANTS
GROWN IN SOILS

Kind of plant	B content of dry matter (p.p.m.)	Kind of plant	B content of dry matter (p.p.m.)
Barley*	2.3	Tobacco	25.0
Rye	3.1	Sainfain	36.2
Leek	3.1	Cabbage	37.1
Wheat	3.3	Soybean	37.2
Corn	5.0	Lentil	41.4
Spinach	10.4	Kidney bean	43.0
Black night shade	11.0	Turnip	49.2
Endive	13.1	Black mustard	53.3
Pea	21.7	Radish	64.5
White mustard	22.2	Beet	75.6
Platain	22.5	Dandelion	80.0
Carrot	25.0	Spurage	93.0
Meadow grass**	3.2	Poppy	94.7
Onion	4.3	Potato	13.9
Flax	7.1	Broad bean	15.4
Celery	11.9	Tomato	15.0
Mallow	13.7	Alfalfa	25.0

*Data from barley to poppy obtained from Bertrand and De Walle (1936).

**Data from meadow grass to alfalfa obtained from Bertrand and Silbeistein (1937).

TABLE II

BORON REQUIREMENT OF SOME COMMON FIELD AND VEGETABLE CROP PLANTS

Plants with high requirement (> 0.5 p.p.m.)	Plants with medium requirement (0.1 to 0.5 p.p.m.)	Plants with low requirement (< 0.1 p.p.m.)
Apple	Tobacco	Wheat
Alfalfa	Tomato	Oats
Red clover	Lettuce	Rye
Crimson clover	Peach	Barley
Sweet clover	Cherry	Buckwheat
Red beets	Olive	Corn
Mangolds	Pecan	Soybeans
Turnip	Cotton	Peas
Cabbage	Sweet potato	Green beans
Broccoli	Peanut	Lima beans
Cauliflower	Carrot	Strawberry
Asparagus	Walnut	White potato
Sunflower	Filbert	Blue grass
Radish	Onion	Brome grass
Brussel-sprouts	Pear	Other grasses
Celery		Flax
Rutabaga		
Burr clover		

Generally crops with low boron content have low boron requirement, and those with high boron content have high boron requirement (10). The range between sufficiency and deficiency is very narrow. In celery, plants containing less than 20 p.p.m. boron in most instances show boron deficiency, while those that contain more than this amount generally do not develop deficiency symptoms, provided the calcium content of the plant is not above normal (99). There is difference between celery varieties in their ability to take up boron when grown under the same condition with no apparent differences in root penetration (99). However, K. C. Berger reports that red beets (Beta vulgaris L.) require more available boron in the soil than sugar beets (Beta vulgaris L.) because of smaller root system of the red beets (10). For alfalfa (Medicago sativa L.) the critical boron content may be 10 p.p.m. (10).

There is also a maximum amount of boron which plants can tolerate, and should the maximum be exceeded toxicity symptoms will develop. J. I. Wear (89) who has worked with crops in Alabama clays, clay loam, sandy loam and fine sand soils with pH generally ranging between 5.3 to 5.6 with base exchange capacity of 2.6 to 9.9 m.e. per 100 gm. soil, has classified some crop plants according to borax requirement as follows:

Very sensitive crops - Not more than 5 pounds of borax per acre broadcast - cotton (Gossypium hirsutum L.), cucumbers (Cucumis sativus L.), peas (Pisum sativum L.), snapbeans (Phaseolus vulgaris L.), soybeans (Glycine max (L.) Merr.), and strawberries (Fragaria chiloensis Duchesne var. ananassa Bailey).

Sensitive crops - 10 pounds borax per acre broadcast or 5 pounds per acre drill - barley (*Hordeum vulgare* L.), celery (*Apium graveolens* L. var. *dulce* Pers.), clover (*Trifolium* spp.), oats (*Avena sativa* L.), potatoes (*Solanum tuberosum* L.), squash (*Cucurbita maxima* Dene.), and wheat (*Triticum aestivum* L.).

Tolerant crops - 20 pounds of borax per acre broadcast or 10 pounds per acre in drill - cabbage (*Brassica oleracea* var. *capitata* L.), carrots (*Daucus carota* L. var. *sativa* DC.), corn (*Zea mays* L.), lettuce (*Lactuca sativa* L.), lima beans (*Phaseolus limensis* Macf.) onions (*Allium cepa* L.), peppers (*Capsicum frutescens* L.), radish (*Raphanus sativus* L.), rye (*Secale cereale* L.), and spinach (*Spinacia oleracea* L.).

Very tolerant - not more than 30 pounds of borax per acre broadcast or 15 pounds per acre drill - apples (*Malus sylvestris* Mill.), alfalfa (*Medicago sativa* L.), beets (*Beta vulgaris* L.), cauliflower (*Brassica oleracea* L. var *botrytis* L.), tomatoes (*Lycopersicon esculentum* Mill.), and turnips (*Brassica rapa* L.).

F. M. Eaton (25) has prepared similar list of plants under sensitive, semitolerant, and tolerant in which many fruit tree crops are included. Since Eaton did the work in California, it is not unusual that some disagreements are evident. In Hawaii, some farmers have applied as much as 150 pounds of borax per acre without any noticeable toxicity symptoms. M. Yamaguchi (98) report that 50 pounds per acre application has caused damage to celery crop in California. J. J. Oertli and H. C. Kohl (65) in studying tolerance of various plants to excessive supplies of boron, suggest that the tolerant species must accumulate boron at a slower rate.

V. SYMPTOMS OF BORON DEFICIENCY

A. General symptoms on crops.

Each crop has its characteristic boron deficiency symptoms but all crops more or less follow these steps in development of symptoms. Generally, the meristem is affected first, resulting in termination of growth and death of the growing points of roots and shoots. Lateral branching from the side of the main shoot starts developing abnormally, giving the plant a rosette appearance. Internodes are shortened and leaves may thicken, curl, become chlorotic or develop anthocyanin pigment. Petioles and leaves become brittle. Flowers and fruits may not form (88, 25, 84, 89).

Histologically boron deficiency of plants results in increased cell division in the cambium, less cell differentiation, cell walls remain thin, and parenchyma tissue increase with reduction in development of conductive tissue and death of phloem (84).

B. Effect of photoperiodism in symptom development.

R. MacVicar and B. E. Struckmeyer (54) grew soybean plants under the influence of long daylight (17-18 hours), normal daylight, and short daylight (9 hours) with and without boron. The plants grown under long daylight developed boron deficiency symptoms much more severely than those under short days. Under short day condition, the soybean (Glycine max (L.) Merr.) plants did not develop normally, and required less boron since the plants only developed to one-fourth the size of the long day plants. The boron content of the plants showing severe boron deficiency symptoms under long photoperiod and plants not showing evidence of deficiency under short photoperiod was about the same.

C. Celery boron deficiency symptoms.

Boron deficiency on celery is exhibited by brown checking, cracked-stem, atrophy of the heart and split hearts. In Hawaii, the most common sympton is brown checking; however, atrophy of the heart and cracked-stem symptoms are also frequently encountered.

1. Brown checking.

The term brown checking has been used by A. R. Spurr (82) and by M. Yamaguchi and P. A. Minges (99) to describe the brown corky development on the inner curved portion or adaxial surface of the petiole. Usually on the brown lesions are many small cracks or checks. Brown checking is also referred to as adaxial cracked-stem.

It starts off first as a water-soaked oblong spot on the inner surface of several newly formed petioles. These spots turn gray to brown and develop transverse crack at maturity of plant. The affected area may be 0.4 to 0.9 cm. wide, and 3.6 to 11.0 cm. long, and involve the upper one-half to two-thirds of the petioles (80).

Under more severe condition of deficiency of boron, cracked-stems on the abaxial outer surface of the petiole developed as well as on the adaxial surface.

2. Cracked-stem.

Cracked-stem of celery was first described by A. C. Foster and G. F. Weber in 1924 in Florida (30). They described it as "the appearance of cracks or breaks in the epidermis of the stalk, extending often along the entire area.

These breaks or cracks appear immediately over the ribs or vascular bundles. The epidermis curls back, appearing much like the teeth of saw." These tears or cracks appear on the upper rachis and secondary petioles, and turn brown in color.

Generally, boron deficiency symptoms on celery develop when the plants are making the most rapid growth, and there is a big demand for nutrients and moisture. M. Yamaguchi, et. al., (100) concluded that the vigorously growing celery plants in California were more susceptible to boron deficiency. Celery plants that have been fertilized with nitrogen or complete fertilizer and were growing faster than the unfertilized, developed boron deficiency symptoms more frequently than the checks or unfertilized (100).

In Hawaii, celery growers report that boron deficiency symptoms become evident about six weeks after transplanting, but the highest percentage occur just about the eleventh or twelfth week when the plants are just about ready to be harvested.

3. Split heart and atrophy.

Roy Bardin (8) has described another condition usually associated with cracked-stem or brown checking and that is a split heart or double. Split heart or double may arise from "an early failure of the main shoot apex" according to Bardin, and lateral or adventitious buds develop taking the place of the single main stem.

A complete disappearance of the heart, or heart atrophy, which is reported to be the most severe symptom of boron deficiency on celery, was reported in 1942 in Canada by R. O. Lachance, et. al., (52). They report that stem-cracking, dwarfing and heart atrophy appear in this order of severity.

In Hawaii, atrophy of the heart has been observed usually on the largest, healthy looking plants. The center or the heart of the celery is completely gone. The surface where the heart should be is smooth as if someone had cut it off with a knife. There is generally brown checking on a few petioles of celery plants having the heartless condition, but dwarfing has not been noticed.

4. Internal morphologic changes.

The collenchyma tissue is considered the primary site for the development of cracked-stem. When boron is lacking the collenchyma cells do not develop normally, and the walls remain thin. A. R. Spurr (81) believes that most of the carbohydrate materials which usually build up the collenchyma tissue are condensed into wall material of the phloem parenchyma and the ground parenchyma. These cells develop thicken walls under boron deficient condition. Apparently, boron affects the rate and process of carbohydrate transformation into wall material. The corners of the collenchyma cells do not develop the typical corner thickening.

5. Fluorescence.

A. R. Spurr (80) examined the stalks of Utah 10-B showing both brown checking and cracked-stem symptoms under AH4-100W mercury lamp with corning filter 5860, which provided peak ultraviolet radiation at the 365 mμ line. The brown check petioles exhibited bright light blue fluorescence around the tissue and extended about 3 mm. beyond the margin of the lesions. The area of the necrotic cells gave the most intense blue color and diminished in intensity with distance away from them (80).

There was a second fluorescent phenomenon associated with the brown checking and cracked-stem displayed bright-yellow or gold color on the surfaces of most of these lesions. These fluorescences occurred as small scattered spots or flecks in greater abundance in older leaves than on younger leaves (80).

VI. BORON MOVEMENT IN PLANTS

A. Movement through transpiration stream.

In studying the accumulation of boron in corn leaf, J. D. Sayre (73) noticed that the boron moved into the margins of the leaves very rapidly. Three days after the addition of boron to the gravel culture, the boron content of the margins of the corn leaves increased 15 times, and in 6 days it increased to about 20 to 30 times what it had been before the addition of borax to the culture. The boron content of the margins of the leaves was found to be 3 to 11 times more than the remainder of the blade.

Harry C. Kohl, Jr. and J. J. Oertli (50) used flood lights to cause excessive transpiration, and even forced water through Easter and rubrum lily leaves (*Lilium longiflorum* Thund.) by means of compressed air to study the movement of boron in and out of the leaf. They concluded that the movement of boron is a passive process, and follows the transpiration stream under adequate to excessive supply of boron in substrate.

The boron content increased hyperbolicly from the leaf base to the leaf tip. The lack of movement of boron from leaves may be due to lack of transport by phloem. The injury to leaf by excess boron is local, and the loss of boron through guttation may be a protective mechanism against boron toxicity (50).

Transpiration rate of boron deficient plants has been found to be decreased. This decrease in transpiration rate is due to (1) less water uptake in boron deficient plants; (2) higher sugar and colloid concentration in leaves; and (3) reduced number of functional stomates (6).

B. Distribution of boron in plant tissues.

The lower leaves of corn plants contained less boron than the middle leaves, and the middle leaves contained less boron than the upper leaves. Similar results were obtained by K. C. Berger, et. al., (11) whether boron was added or not. Where boron was not added, the lower, middle and upper leaves contained 8.2 p.p.m., 9.2 p.p.m., and 17.6 p.p.m. boron respectively, and where boron was added at the rate of 15 pounds borax per acre, there were 25.2 p.p.m., 25.2 p.p.m. and 32.0 p.p.m. boron for the lower, middle, and upper leaves respectively. A. S. Baker and L. Cook (5) found that the boron content of the apical portion (top 1 to 2 inches) of boron deficient plants was considerably lower than that of more mature plant parts. However, the boron content of the apical portion of normal plants is higher than the lower portion. They state since boron is not translocated from the mature portions of the plant to the apical meristem, analysis of the apical portion should give a reliable measure of the uptake of boron by the plant.

J. J. Oertli and H. C. Kohl (65) in studying the tolerance of various plant species to excessive supplies of boron first grew plants in quartz sand supplied with regular Hoagland solution permitting normal growth of plants before subjecting them to 10 p.p.m. boron. They discovered that the distribution of boron in the leaves and the pattern of boron toxicity are related to the venation of the leaf. The boron in the plant is moved in the transpiration stream, and is concentrated in this stream by the transpiration process. In parallel veinal leaves such as the grasses, lilies and carnations (Dianthus caryophyllus L.), the toxicity patterns were in the form of tip burns and burning at end of veins; on plants with more or less circular leaf, such as geranium (Pelargonium spp.), marginal necrosis was found almost all around; on leaves with network veins, there was a tendency toward interveinal necrosis (65).

Different species varied in the time required to produce boron toxicity symptoms. Tomato (Lycopersicon esculentum Mill.) and perrennial rye-grass (Lolium perenne L.) developed toxicity symptoms in 8 days; gladiolus (Gladiolus hortulanus Bailey), stock (Matthiola bicornis (Sibth. & Sm) DC.), and chrysanthemum (Chrysantemum morifoltum (Ramat.) Hemsl.) in 12 days; rose (Rosa spp.), begonia (Begoniaceae) and carrots (Daucus carota L. var sativa DC.) in 20 days; carnation (Dianthus caryophyllus L.) in 57 days and azalea (Rhododendron spp.) in 77 days. The distribution of boron in leaves is very uneven. Analysis of the necrotic, chlorotic, and green areas were made on the various leaves. The necrotic spots had boron content, which varied from 770 p.p.m. to 8280 p.p.m., the chlorotic spots varied from 370 p.p.m. to 3130 p.p.m. boron, and the green areas had 40 p.p.m. to 1850 depending on species (65).

The intracellular fractions of sunflower (Helianthus annuus L.) and mung bean (Phaseolus aureus Roxb.) tissue were separated by differential centrifugation by Skok and McIlrath (78), and all fractions were found to contain boron. The mitochondria and microsomes contained less boron than the nuclei, plastid or the supernatant portion.

C. Utilization of boron.

With only a few exceptions, plants cannot survive for very long without a continuing source of boron. John Skok (78) found that sunflower plants provided with 50 µg. boron per plant in nutrient solution developed deficiency symptoms at about the 18th or 19th day, and the terminal regions gradually became necrotic. However, the leaves that were mature before available boron was depleted, remained green.

In an experiment with broccoli (Brassica oleracea L. var. botrytis L.), W. R. Benson, et. al., found that even if boron is withheld from half grown broccoli containing 50 p.p.m. boron it will continue to grow. The stem continued to increase in weight and accumulate boron for 44 days duration of the experiment. The lower leaves did not show any loss of boron. Leaves 7 to 22 above the older leaves showed decrease in total boron. The younger leaves accumulated boron even though the external supply was cut off indicating reuse of boron. (9).

VII. THE VARIOUS ROLES OF BORON IN CROP PRODUCTION

Hugh G. Gauch, and W. M. Dugger, Jr. (33) have made a review of the literature on the physiological action of boron in higher plants and have enumerated and discussed 16 roles.

1. Flowering and fruiting processes.

   Under boron deficient condition, plants may fail to produce flowers or seeds. Seed production in alfalfa was increased 600 per cent against 3 per cent increase in hay when boron was applied to the crop.

2. Pollen germination. (Related to flowering and fruiting.)

   Boron is required for proper germination and growth of pollen tube. Some bursting or malformation of pollen tube noted under condition of boron deficiency.

3. Cell division.

   Boron is required in nitrogen metabolism and formation of protein into protoplasm and is prerequisite to cell division. Without boron, bean and tomato stomata cells are modified and some non-functional and epidermal cells are malformed.

4. Nitrogen metabolism.

   Under boron deficiency, there is decrease in protein, but increase in amino acids. Nitrates may be increased or decreased, but ammonium nitrogen is increased.

5. Carbohydrate metabolism.

   Boron deficiency generally results in accumulation of carbohydrate in the leaves. Translocation of carbohydrate from leaves to other portions of the plant depend upon boron.

Necrosis of phloem under boron deficiency further affects translocation of carbohydrate.

6. Active salt absorption.

It is stated that active salt absorption is an energy-requiring process. Since boron is involved in translocation of sugars to roots, it would indirectly be necessary for active salt absorption. "Boron-deficient plants were unable to absorb calcium as readily as boron-sufficient plants".

7. Hormone movement and action.

Boron is involved in the production of plant hormones and their translocation. Boron-deficient broccoli placed horizontally to geotropic stimulus failed to respond. Growth and differentiation are growth-regulator-controlled responses. Sprays with boron prevent premature formation of abscission layer in apples and tomatoes. Suggestion is made that sugar movement affect hormone movement. Under boron-deficiency, vascular differentiation may be lacking or abnormal. Boron-deficient peas produced abnormal, stunted sprouts which could be corrected by boron application.

8. Constituent of membranes.

Experimental evidence lacking.

9. Pectin substances (metabolism).

The organisms Aspergillus and Penicillium which do not need boron, do not synthesise true pectic compounds. "The evidence on the relationship between boron and the pectin level of plants is currently in a contradictory state".

10. Maintenance of conducting tissues.

The conducting tissues, particularly the phloem, break down and become necrotic and non-functional. The rate of the development of the boron deficiency symptom generally follow the respiratory rate involving first the cambia, then the phloem and finally the xylem.

11. Water relations.

Without boron the pollen grains take up water rapidly without regulation and burst. Fruits of prunes (*Prunus domestica* L.) and big cherries (*Prunus avium* L.) have been prevented from cracking during rainy weather by boron sprays. The transpiration rate of a plant supplied with adequate boron, is higher than a plant with deficiency of boron, but under high moisture stress, the boron deficient plant transpired at higher rate than the boron sufficient plant. Also, boron deficient plants are more brittle and cracking of potato tubers in high lime soil can be prevented by boron application.

12. Fat metabolism.

Lack of boron interferes with the production of fat, and fat content of soybean can be increased by boron application.

13. Buffer action.

The borate and phosphate ions may function as essential juice buffers.

14. Precipitation of excess cations.

No evidence presented to show that excess cations might react with boron to form insoluble salts.

15. Regulatory effect on other elements.

"The total boron level in plants is decreased as the external concentration of calcium is increased". However, variation of boron in the substrate does not affect the percentage of calcium in plant tissues. Boron effects the level of soluble calcium in the plant. As the boron is increased, the active soluble calcium also increases. Generally, increasing potassium level of substrate accentuate boron-deficiency problem at low external levels of boron. Low supply of boron may result in accumulation of magnesium.

16. Role of boron on translocation of sugars.

In 1953, H. G. Gauch and W. M. Dugger, Jr. proposed another function of boron and that is translocation of sugar (32, 33). It is based on the hypothesis that boron combines with sugar to form a sugar-borate complex. They suggest that the ionizable sugar-borate can be more easily translocated across cell membrane than the non-ionized sugar molecules. Evidently, this idea was conceived when J. K. Khym and L. P. Zill separated sugars by ion exchange process using boron (32). Another hypothesis suggested is that "boron is a constituent of membranes, and that sugar forms a temporary union with borate at these loci". They favor this view over the first hypothesis. K. C. Berger (10) cites the work of M. E. Smith of Australia who states that in squash leaf 50 per cent of the boron is immobilized in the cell wall or intra-cellular substance.

To show that the movement of sucrose in plants is facilitated by application of boron, Gauch and Dugger (32) took excised lima bean and pea root tips and measured the respiratory utilization of sucrose with and without the addition of 0.5 p.p.m. boron. Increases of 50 to 85 per cent in respiration were observed after 10 hours in the boron treatment. Thus indirect evidence is presented that the increased "respiration is effected by an increase in the rate of entry and movement of the substrate (sucrose) to the respiring cells in the root tips."

There are evidences that leaves of boron deficient plants are generally abnormally high in sugar and other carbohydrates compared to other parts of the plant (46).

W. J. McIlrath and B. F. Palser (56) found only slight improvement by spraying 10 per cent sucrose to tomato, turnip, and cotton plants, which did not receive any boron in the sand culture. The leaves of boron deficient unsprayed turnip and cotton plants had lower percentage of total sugars and higher percentage of starch than the non-deficient unsprayed plants. Application of sugar to boron deficient plants resulted in increase of total carbohydrate in leaves of tomato and cotton, as compared to unsprayed plants, but did not increase in turnip. The roots of boron deficient tomato and turnip plants had lower percentage of carbohydrate than adequate boron plants primarily due to phloem necrosis which prevented translocation of carbohydrate from leaves to the roots. In cotton where there was no phloem necrosis, the roots of boron deficient plants contained about the same percentage of carbohydrate as the non-deficient plant roots (56).

In another experiment, Gauch and Dugger immersed single leaf of an intact plant into a solution of labeled sucrose, and measured the absorption and movement of the labeled sucrose within the plant. Where 10 p.p.m. boron was supplied with the sugar, the movement of radioactive sucrose was very rapid and widely distributed throughout the plant. The stem tip of plus boron had 550 per cent more radioactivity than the plant not receiving any boron. Without the boron, sucrose entered in small amounts and was more or less confined to stem portion near the point of entry. For this experiment, the plant was conditioned by 48 hour period of darkness to deplete carbohydrate and was kept at low level of nutrition (32).

Not all of the researchers who have worked with boron agree completely with the hypothesis that boron is essential for translocation of sugar and that sugar reacts with boron to form sugar-borate complexes, nor do they agree that boron is a constituent of cell membranes and facilitates passage of sugars by forming a temporary union with sugar. Those who disagree think that there is some relationship between boron and sugar translocation, but that it is not a direct one. They feel that the relationship is "indirect and related to cellular activity and growth rather than directly to the formation of a boron-sugar complex." (78).

John Skok (78) concludes that sugars and other materials move from leaves to growing tips because of a gradient. The metabolically active regions use carbohydrate faster because of high growth rate and high respiration rate. Conversely the metabolic rate of boron deficient plant is low and translocation of sugars to the meristematic region is reduced. By adding boron to deficient plants, the metabolic rate is raised and there will be increased movement of sugar into the area. Skok (78) cites the reduced rate of translocation of C^{14} sugar into top portions of boron sufficient plants where the terminal buds were removed 24 hours before the sugar application. Where the terminal buds were intact, the translocation rate was about 50 percent greater.

However, the reduction in translocation was even greater for the partially boron deficient plants.

T. F. Neales of Australia (62) grew excised roots of flax (Linum usitatissimum L.) in nutrient culture. He concluded that "growth inhibitory effect of deficiency of boron was unrelated to sugar translocation in flax roots". Both boron deficient and sufficient plants evidently took up C^{14} sucrose from the growth medium in a similar manner. He believes in the view that boron is essential for cell division and that "any apparent effects of boron in sugar translocation are unrelated to its function in growth" (62).

Bean leaves kept in dark to reduce carbohydrate before infiltration with 4 per cent glucose was found to synthesise more starch than comparable leaves infiltrated with 4 per cent glucose and various levels of boron (22). W. M. Dugger, Jr., et. al., proposed that boron decreases the enzymatic conversion of glucose 1-phosphate to starch. They conclude that since more glucose 1-phosphate is available under boron treatment for synthesis of sucrose or other hexose phosphate and an increase in these soluble carbohydrate in situ may therefore result in an increase in translocation from the site of synthesis to some other plant part". J. J. Dyer and K. L. Webb (24) persued the proposal made by Skok that the role of boron in translocation of sugar is indirect, and related to cellular activity and growth rather than directly to the formation of borate-sugar complex. They felt that in boron deficient plants prior to the breakdown of phloem, the capacity to translocate sugar must be present although at reduced rate. If boron is not directly essential for translocation of sugar, then translocation should increase by inducing metabolic activity or growth in boron deficient plants by the application of auxin.

They applied 5 p.p.m. naphthalene acetic acid solution directly on buds of bean plants growing in mineral nutrients, and also 0.01 p.p.m. N.A.A. to the roots at the time plants were showing incipient boron deficiency symptoms. N.A.A. was applied to both boron sufficient and boron deficient plants before $C^{14}O_2$ was supplied to leaves. The amount of C^{14} appearing in terminal region of boron deficient plants was significantly less than in boron sufficient plants. However, in boron deficient plants treated with N.A.A., the amount of ethanol soluble C^{14} translocated to the buds was not significantly different from the boron sufficient plants. Evidently, the meristems of boron sufficient plants contain an optimum concentration of auxin, and the addition of N.A.A. to it inhibited translocation of C^{14} when compared to the control boron sufficient plants because of excess auxin. The auxin concentration is below optimum in boron deficient plants, and application of N.A.A. increased translocation of C^{14}. Similar results were obtained for the roots treated with N.A.A. with the exception that no inhibition of translocation in boron sufficient plants treated with auxin was detected. N.A.A. applications increased translocation of C^{14} to the root system in both boron sufficient and boron deficient plants. It is reported that continued application of N.A.A. to either the buds or the roots resulted in improved shoot growth of the boron deficient plants (24).

They conclude that the function of boron in translocation of sugar is indirect and that boron is essential to auxin metabolism, possibly synthesis.

A. Additional roles or uses for boron.

1. Boron promotes nectar secretion.

When alsike clover (*Trifolium hybridum* L.) flowers failed to attract bees for pollination, F. O. Holmes (31) became concerned over this problem. He applied complete minor elements and 2 oz. of borax separately over two-100 square foot areas, and a few days after treatment, the bees started to visit the flowers again. It is believed that boron promoted nectar secretion.

Similar difficulty was experienced with raspberries (*Rubus* spp.) but it took two boron applications before bees responded to the boron treatment (41).

2. Effect of boron on rooting of cuttings and root elongation.

Although boron has been used to increase seed production in alfalfa, clover, and corn and in aiding insect pollination of alsike clover, its use in promoting rooting of cuttings has only recently been reported. C. J. Weiser (91) has been able to increase the rooting percentage of clements (*Clementis* spp.) cuttings by a 12 hour soaking of the bases of cuttings in a combination of 50 p.p.m. indole butyric acid and 50 p.p.m. boron before placing them in propagating benches under intermittent mist. At the end of a 56 day rooting period, he obtained 53.3 per cent rooting from water, 74.4 per cent from I.B.A., 53.3 per cent from boron, and 85.6 per cent from I.B.A. plus boron treatments. He felt that the boron did not increase or initiate rooting, but promoted root growth or elongation (91).

The results obtained by C. J. Weiser and L. T. Blaney (92) on English holly (Ilex aquifolium L.) using similar treatments were more spectacular. There was no rooting of cuttings with either water treatment or the boron treatment after 42 days. The 50 p.p.m. I.B.A. treatment gave 46.6 per cent rooting of cuttings with 5.1 average number of roots per cutting and 268 mm. average total root length. The combination of I.B.A. and boron gave 100 per cent rooting of cuttings with an average of 17.7 roots per cutting and 119.9 mm. average total root length per cutting. Thus with both I.B.A. and boron the rooting percentage was doubled, the average number of roots tripled, and the length of roots quardrupled over the I.B.A. treatment alone. When boron was not combined with I.B.A. but was delayed a week, the percentage of rooting dropped to 80 per cent, but did not markedly affect the number or length of roots. However, when boron application was made 2 weeks after the I.B.A. treatment, the percentage of rooted cuttings was decreased to 53 per cent, and the number and length of roots stayed the same as the I.B.A. treatment alone.

The I.B.A. plus boron on English holly have increased the percentage of rooting of cuttings, increased the number and length of roots and hastened rooting (92).

The effects of minus boron and plus boron in the development of field bean radicles for the first 96 hours were studied by W. J. Whittington (94). In the minus boron culture, no growth of the radicle took place after 30 hours, but the fresh and dry weights per radicle of the two treatments remained the same up to 96 hours, but in later harvest the minus boron plants had lower total root weight. The lateral roots of plus boron plants developed at a distance greater than 1 cm. from the apex, but in minus boron plants abortive lateral initials developed within 7-10 mm. from apex and some within the apex (94). L. S. Albert and C. M. Wilson (1) obtained similar results with tomato roots. In minus boron plants, the lateral roots appeared within 1 to 7 mm. from the root tip, where under normal condition, they would be found 5 to 7 cm. behind the tip. Some laterals developed sublaterals to give them a bushy appearance. In tomatoes withholding boron from the roots inhibited root elongation within 24 hours. Although 0.01 p.p.m. boron was adequate to sustain maximum rate of elongation for 24 hours, it was not sufficient to sustain maximum rate of elongation for 72 hours. The lateral roots in tomatoes that were emerging close to the injured tip were arising from the brown area where some cells were still alive. Root tips that are brown do not elongate when supplied with boron, but new laterals will elongate if given boron before they turn brown (1).

The bean roots of minus boron plants as compared to plus boron plants, had fewer number of cells per mm. section about 3 mm. from the apex because of swelling of the cells both longitudinally and radially. However, sections further away from the apex contained more cells than the normal roots due to formation of abortive lateral roots with many small cells. The frequency of cell division was 5 to 7 per cent for plus boron and only 0.5 per cent for minus boron after 48 hours (94). Considerable differentiation occurred in minus boron roots, and xylem elements were found in 2 mm. root apex, which normally contain only mirestematic cells (94). This indicates that balance in growth regulators within the plant has been disrupted.

3. Effect of boron on nitrogen fixation by Azotobacter.

The free living nitrogen fixing Azotobacter chroococcum does not seem to require boron as several croppings can be obtained from the same boron-free medium without diminuation in yield (4). If boron was required, it should have been picked up from the chance impurities in the medium by the first cropping, but each succeeding cropping gave similar yields. Nevertheless, by adding 1.5 p.p.m. and 10 p.p.m. boron to the medium, nitrogen fixed per gram of ethanol by Azotobacter was increased from 29.5 mg. to 36.9 mg. and 40.3 mg. respectively. More total nitrogen was fixed by the addition of 10 p.p.m. boron than by 1.5 p.p.m. boron; the additional boron to the medium also stimulated pigmentation by Azotobacter.

4. Others. Substitution of complexing substances for boron.

Attempts were made to use strontium, germanium, and aluminum in place of boron. $Sr\ Cl_2$ at 0.5 p.p.m. and 1.5 p.p.m. and 1.5 p.p.m. Sr, $Ge\ O_2$ at 5×10^{-5} M which is the same as 5 p.p.m. boron and $Al\ Cl_3$ at 5×10^{-5} were used. These gave about one week of temporary alleviation of boron deficiency symptoms. John Skok suggests that since boron is not re-utilized, the complexing reaction must be related to the formation of a structual unit or "building block" (77).

VIII. VARIETAL SUSCEPTIBILITY AND GENETIC FACTOR IN BORON DEFICIENCY PROBLEM

A. Varietal susceptibility of celery.

Ten varieties of celery were grown in three widely separated celery-growing areas of California by M. Yamaguchi and P. A. Minges (99) to test for susceptibility to brown checking. From 149 to 260 plants per variety were examined. Utah 10-B was the most susceptible, with 56.9 per cent of the plants showing brown checking. Utah 16-5, Utah Special, and Top-Ten had between 20 to 30 per cent brown checking, Utah had 14.6 per cent brown checking, Utah 16 (commercial strain), Utah 16 PC and Utah 16-8 each had 4.3 per cent brown checking, Utah 52-70 had 1.2 per cent brown checking (plants that showed brown checking were off-type plants), and Summer Pascal no brown checking. Both Summer Pascal and Utah 52-70 are reported to have the same degree of resistance.

Hawaiian celery growers have found Summer Pascal variety very resistant with no apparent cracked-stem or brown checking observed to date. PMD5 and Compact 2 are also resistant and no brown checking have been observed on them, but testing of these two varieties have been limited. Utah Jumbo and Utah 5270 are considered resistant too, but a few growers report about 2 per cent brown checking, and one grower reported 30 per cent brown checking in Utah 5270. Up to 25 to 40 per cent brown checking have been seen on Spartan and Slow Bolting No. 12. The other varieties, including Utah Special, Utah 15, Special tall Utah and Green Light have developed over 50 per cent cracked-stems on some plantings.

B. Inheritance of susceptibility to boron deficiency in celery.

The inheritance studies on susceptibility to low levels of boron in celery were done by D. T. Pope and H. M. Munger (69). The breeding line 548-54-1 which was derived from a cross between Cornell 19 and P.P.I. 120875 was used as the susceptible line. Summer Pascal, Easy Blanching, Cornell 619, Emerson Pascal and Utah 10-B, which did not show boron deficiency symptoms when grown in nutrient solution containing 0.01 p.p.m. boron, were used as the resistant lines. The F_1 progenies from 548-54-1 x Utah 10-B were all normal. The F_2 generation from crosses between 548-54-1 and the normal parents segregated in the ratio 3 normal to 1 susceptible. The F_1 backcrossed to 548-54-1 resulted in equal number of susceptible to normal and the F_1 backcrossed to normals all gave normal plants. These results indicated that susceptibility to boron deficiency is determined by a single recessive gene (69).

C. Inheritance studies on tomato.

In tomatoes, brittle stem, which is a symptom of boron deficiency, develops when the boron level of the substrate falls below 0.05 p.p.m. under long photoperiod (86). J. W. Wall and C. F. Andus (86) report that brittle stem sympton does not develop during the period of October through April, even on tomato line T3238, which has been found to be homozygous for brittle stem susceptibility. They used the T3238 line, derived from a cross between 2512A and STEP 68 and the variety Rutgers, as the normal variety for their inheritance studies. When T2328 was crossed with Rutgers and tested under 0.2 p.p.m. boron in substrate all F_1 progenies were normal. The F_2 generation segragated in ratio 3 normal to 1 brittle stem and the F_1 backcross to T3238 resulted in approximately 1 to 1 ratio for normal and brittle stem. Thus, susceptibility to boron deficiency in tomatoes is also conditioned by a single recessive gene. Under low boron condition, brittle stem is accentuated by any evironmental condition favoring growth and growth-deficiency relation is favored by this study on boron.

IX. EDAPHIC, CHEMICAL, AND ENVIRONMENTAL FACTORS INFLUENCING BORON AVAILABILITY OR FIXATION

A. Soil Texture.

The relationship between soil texture and available boron in soils was shown by J. J. Lehr in 1940, according to K. C. Berger (10). In Dutch soils, Lehr estimated the total amount of boron in different soils as follows: "Marine clays about 100 p.p.m. boron; river clays 20 p.p.m. boron; sandy soils averaged 5 to 25 p.p.m. boron in tourmaline and 1 to 2 p.p.m. in organic matter.

R. V. Olson and K. C. Berger separated the Spencer and Carrington silt loam soils into sand, silt, and clay fractions and found that the boron content also varied with soil texture. In Spencer silt loam soil, the sand fraction which comprised 54.4 per cent of the soil, held only 13.7 per cent of the available boron; the silt fraction making up 36.0 per cent of the soil had 50.2 per cent of the available boron; the clays making up only 9.5 per cent of the soil contained 36 per cent available boron in total soil (66). J. I. Wear (89) determined the boron content of 253 samples of Alabama soils by soil textures and reported the following water soluble boron in these soil types, "clays .171 p.p.m., clay loams .152 p.p.m., silt loams .130 p.p.m., fine sandy loam

.091 p.p.m., sandy loams .068 p.p.m., loamy sand .062 p.p.m. and sands .032 p.p.m.". He also found that the coarse textured soil, such as the sands, did not accumulate much boron after the first year even with increasing boron application, while in the clays and clay loam soils, boron continued to increase with each application. J. W. Biggar and M. Fireman also found that the retention of boron was increased with fineness of soil texture.

J. Kubota, et. al., (51) in studying the movement of boron in two Wisconsin soils, found the available boron content of sand very low and silt loam high. When 40 pounds of boron per acre were applied to the surface of Plainfield sand, the boron moved beyond the 30 to 36 inch depth within six months, while the boron in the heavier superior silt loam similarly treated had moved to about a 6 inch depth in the same period. With Miami silt loam, the bulk of the boron was concentrated in the 6 to 12 inch depth, but some boron was found in the 12 to 18 inch depth (51). G. M. Wilson, et. al., (97) used 10, 20, and 40 pound rates of borax on clay and sandy loam soil, and obtained increasingly higher available boron with increasingly higher rate, and the bulk of the boron found in the first 8 inches in the clay soils after 18 months. In the sandy loam soil, most of the boron had concentrated in the 16 to 24 inch depth. Here again the available boron was highest with the highest treatment, but it was just about one-half of the boron content found in the clay soil.

B. <u>Soil moisture.</u>

One of the most severe case of cracked-stem of celery occurred during the drought period in the fall of 1961 in Kamuela, Hawaii.

Evidently, the capacity of the sprinkler system was insufficient to take care of the moisture requirement of the celery plants at the time of most rapid development. By installing larger pipes for sprinkler system and providing plants adequate moisture, the boron problem was partially corrected.

There are many reports that dry weather accelerates the appearance of boron deficiency symptoms on crops growing in soils low in available boron. F. M. Eaton and L. V. Wilcox found that part of the boron added to the soil becomes fixed upon drying (27). L. B. Latimer (53) found that drought in June and July in New Hampshire was the chief predisposing factor causing boron deficiency in apples.

A. B. Burrell (14) states that if two trees show the same mid-season leaf boron content, but if one suffers drought condition and the other does not, the one that was subjected to low moisture condition will have lower boron concentration in the fruit. G. H. Cannell, et. al., studied the effects of irrigation on nutrient uptake of celery, and found that the absorption of boron and molybdenum decreased with decreased soil moisture (15).

By using the split root technique on tomatoes, J. A. Hobbs and B. R. Bertramson proved adequately that even though the surface soil may have a high boron content, plants will not be able to take up sufficient boron for their needs if the soil is kept dry. Half of the root system of one plant was kept in dry surface soil, while the other half was kept in moist subsoil containing very low boron. (In most subsoils, the boron content is very low.) The plant did not develop normally as a result of inability to obtain sufficient boron from the soil (39).

In humid areas the soluble boron salts are leached out easily, consequently, most soils in high rainfall areas are low in available boron (10).

C. Soil organic matter.

Darrell A. Russel (72) cites the work of several Italian workers, who found that organic boron is the most soluble form of boron, but no further detail is given. R. V. Olson and K. C. Berger (66) investigated the effect of the destruction of organic matter with H_2O_2 upon the available boron present in the soil and its ability to fix boron. In the different silt loams and sands used in the experiment, the available boron in the soils was increased by destroying the organic matter, indicating that some of the boron held and fixed by the organic matter was released. They further found that the percentage of boron fixed after adding 20 p.p.m. boron was greater when the organic matter was present. When the organic matter was destroyed, the percentage boron fixed was generally decreased. In other words, the ability of soil to fix boron was reduced by the destruction of organic matter. K. C. Berger (10) reports that in acid soils, there is a correlation between available boron and organic matter of the soil, with higher amounts of available boron found with higher organic matter content of the soil. In alkaline soils, the pH and the available calcium have more influence on availability than organic matter.

D. Soil reaction.

When R. V. Olson and K. C. Berger (66) added 30 milliequivalent Ca as calcium chloride per 100 grams of soil, the pH of the soil was changed from 5.6 to 4.8, but fixation was unchanged. When 20 milli-equivalent Ca was added in the form of calcium hydroxide, it changed the pH of the soil suspension to 9.2, and resulted in increased fixation from 6.3 to 33.7 per cent. This experiment showed that the pH is an important factor in fixation of boron. In acid soils, they found no correlation between boron fixation and pH. The cations of the bases had little influence on boron fixation, but the increase in pH produced resulted in fixation. When calcium hydroxide was compared with sodium hydroxide at similar pH ranges, the per cent of available boron fixed was the same in one type of soil, but the fixation was slightly higher for calcium hydroxide in another soil. The boron that is fixed with the addition of calcium hydroxide can be released again by lowering the pH of the soil with hydrochloric acid (66). By applying sulfur to the soil, A. R. C. Haas was able to increase the available boron of the soil from 1.99 p.p.m. to 4.26 p.p.m. (34). N. R. Page found that by increasing the pH and phosphate of the soil, the uptake of boron by sunflower was decreased (67).

E. Liming and boron fixation.

In fields where heart rot of sugar beets was a problem, R. L. Cook and E. E. Miller (17) noted that the calcium content of the soils was invariably higher than normal. They suggested that boron was fixed in the form of insoluble borates of calcium and magnesium. J. I. Wear (89) found that excessive lime caused boron deficiency of legumes. M. A. Norland and R. W. Starostka report that boron application to acid soil increased the yield of alfalfa, but yield was not increased when borax was applied to calcareous soil (63). Varying amounts of lime from 0, 2, 4, 6, 8, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 per cent were used by A. R. Midley and D. E. Dunklee (80) to fix boric acid. The highest fixation - 94 per cent - was obtained by 20 per cent lime and further increase in percentage of lime decreased fixation. Calcium carbonate, CaO, $BaCO_3$ and $MgCO_3$ were about equally effective in fixing boric acid. R. Q. Parks and B. T. Shaw (68) found that boric acid formed an insoluble precipitate with calcium saturated bentonite, and also with calcium alumino-silicate.

The investigations by Olson and Berger (66) on the effect of $Ca(OH)_2$ and $CaCl_2$ in fixing boron was reported earlier under pH. They concluded that the change in soil reaction by the addition of $Ca(OH)_2$ and NaOH is the important factor, and that the cations of the bases had little influence on boron fixation. When the boron content of the substrate was kept constant, but the calcium content was progressively increased, the soluble boron content within the tomato plant tissue decreased with increase in calcium in the substrate. R. Reeve and J. W. Shive (71) also found that the boron accumulation in the plant is considerably modified by the calcium concentrations in the substrate, and is independent of boron. H. E. Jones and G. D. Scarseth (47) report that plants will make normal growth, only when a certain balance in the intake of calcium and boron exists. When this balance is upset by having high intake of calcium with low boron, the plant will suffer from insufficient boron. In strongly acid soils containing low available calcium, a small addition of borax may cause boron injury to plants. They found the ideal balance between Ca/B for tobacco (<u>Nicotiana tabacum</u> L.) to be about 1200:1, for soybeans 500:1 and for sugar beets about 100:1. About the same ratio for Turkish tobacco plant was reported by M. Drake, et. al., (21). R. L. Fox and W. A. Albrecht (31) studied the calcium boron interaction on _Lemna minor_ L. on clay suspension. Boron content of _Lemna_ increased with increasing calcium in substrate and the high calcium counteracted the toxic effect of boron. The Ca/B ratio was very low.

J. J. Oertli (64) doing water culture experiment with sunflower (_Helianthus_ spp.) and tomatoes concluded that the concentrations of calcium and or potassium had practically no effect on boron uptake by plants. He also reports that healthy leaves showed more than a hundred fold variations in the Ca/B ratio, suggesting that this ratio is not of great importance.

F. _Potassium-boron relationship._

E. Reeve and J. W. Shive (71) conducted water culture experiments with tomato plants to study the relationship between potassium and boron. They found that both boron toxicity at high boron levels and deficiency at low boron levels are progressively accentuated with increasing concentration of potassium in the substrate. The accumulation of potassium in the tissues of tomato plants is influenced by the potassium concentration of the substrate. They found that calcium and potassium had similar capacity to accentuate boron deficiency symptoms with increasing concentrations of these two cations in the substrate. However, at high levels of boron, increasing the calcium concentration of the substrate decrease boron toxicity, while increase potassium in the substrate tended to accentuate boron toxicity. K. C. Berger (10) suggests that the relationship between potassium and boron is of much less importance than that of calcium and boron, and he indicates that it is an indirect relationship, where adding potassium decreases uptake of calcium, thus upsetting the calcium - boron ratio.

H. Sinha (76) studied the effects of potassium - boron interactions upon the growth of soybean plants in soil low in boron. When above normal amounts of potassium was supplied without the addition of boron, the growth of soybean was adversely affected. However, when about 2 pounds per acre of boron was applied, normal growth took place even at the highest level of potassium, which was 20 per cent of the total exchange capacity of the soil. The boron contents of plants grown at high potassium level were considerably lower than those grown at normal level of potassium. He found that large amounts of potassium decrease the uptake of calcium and magnesium by the soybean plants, especially when the boron level of the soil is low.

J. B. Kendrick, et. al., (48) and M. Yamaguchi, et. al., (98) have found that high nitrogen and potassium increase incidence of brown checking in celery. Working with nutrient culture solutions, Yamaguchi et. al., (98) found that regardless of the boron level in the nutrient solution, the boron content of the petioles decreased with increasing potassium in the nutrient solution with normal level of nitrogen. Plants grown in 550 p.p.m. nitrogen and 234 p.p.m. potassium were lower in boron content than were those grown in 210 p.p.m. nitrogen at both 0.10 and 0.25 p.p.m. boron. They state that "the occurrance of brown checking in the field can be a result of low boron in the rapidly elongating portion of the petiole occasioned by high potassium accumulation. In some cases the boron content of the plant may be stretched thin due to fast growth following nitrogen application".

M. Yamaguchi and P. A. Minges (99) determined the potassium and boron contents of normal and brown checked celery plants in the field. They found that the plants showing brown checking are usually higher in potassium and lower in boron with higher K/B ratio. A 3000:1 K/B ratio is suggested as the borderline between normal and brown checking plants.

A. B. Burrell (14) compared (1) once a year spraying with sodium pentaborate (solubar) at 1 pound per 100 gallons, (2) 2 sprays with the same material at 7-10 days and 20-25 days after petal fall, and with (3) fertilizer borate in narrow ring on soil at 4 to 8 oz. per tree. He found that there was slight carry over of boron on sprayed plants but more carry over in the fertilizer borate treatment. However, one spraying each year gave highest boron especially in the fruits.

The combination of 100 to 150 p.p.m. boron, 30 to 40 p.p.m. beta naphthoxyacetic acid and 0.25 molar dextrose with Hidler nutrileaf or 20-20-20 gave the best yield and quickest and most pronounced response per unit of element used on tomatoes. They were applied on the yellow open blooms every week to 10 days (29).

G. <u>Magnesium - boron relationship</u>.

The relationship between magnesium and boron on the growth of tung trees (*Aleurites fordii* Hemsl.) was investigated by C. B. Shear, et. al., (75). The application of boron at 0.1 p.p.m. developed varying degrees of toxicity symptoms on tung leaves. They found that the severity of the symptoms was inversely correlated with the level of magnesium in the substrate. There was no correlation between the magnesium content of the leaf and severity of boron toxicity, and no correlation between boron content of the leaf and severity of symptoms. However, there was a close correlation between the severity of the toxicity symptom with the Mg/B ratio. With increase in Mg/B ratio, there is decrease in boron toxicity.

H. Fertilizer - boron relationship on celery.

Cannell, et. al., (15) applied 1, 2, and 4 tons of 10-10-10 fertilizer on celery and obtained correspondingly lower boron content of the leaves and petioles with increase in fertilizer rates. M. Yamaguchi, et. al., (98) found that high nitrogen and potassium tend to reduce boron absorption and increase incidence of boron deficiency. Even Summer Pascal which is suppose to be resistant to boron deficiency, showed slight brown checking and cracked-stem in high potassium and low boron medium.

Celery fertilizer practices in Hawaii. From 1½ to 3 tons of 10-10-5, 5-10-10, 14-14-14, 15-15-15, 11-48-0, or 7.6-6.7-12.5 are applied three to five times to a crop. On the bases of total plant nutrients, they range from 200 to 600 pounds N, 200 to 1000 pounds P, and 100 to 640 pounds K. Frequently, a light pre-planting application is made, but many make the first application 2 to 4 weeks after planting. The second application is made 2½ to 3 weeks later, and third application 4 to 5 weeks before harvesting, and last application 2 to 3 weeks before harvesting. Many omit the pre-planting application and apply most of the fertilizer between the 6th and 10th weeks. Borax is generally broadcasted over the field at the rate of 50 pounds per acre before planting, but some growers apply borax at the same rate about a month after transplanting, and a few use Sul-po-Mag at 50 to 100 pounds per acre rate before planting. Many incorporate boric acid in their regular weekly spray program for blight and insect control.

Because of the Sclerotinia sclerotiorum (Lib.) d By. problem on both lettuce and celery, many growers apply between 600 to 1000 pounds of calcium cyanamide for its control. The calcium cyanamide not only controls the fungus, but adds nitrogen and calcium to the soil. According to M. Alexander (2), calcium cyanamide is rapidly hydrolyzed in the soil to cyanamide and calcium hydroxide and a subsequent conversion of cyanamide to urea. The last microbial hydrolysis of urea to ammonia is enzymatic.

The use of calcium cyanamide may have fixed some boron in the soil and aggrevated the boron deficiency problem.

A few celery growers who mixed borax with complete commercial fertilizer suffered considerable damage from brown checking, despite heavy application of the borax-fertilizer mixture. Some of the low analysis complete fertilizers have lime as fillers, and this may have been the case with a few who have practiced mixing boron with other fertilizer ingredients on the farm.

IX. SOURCES OF BORON

A. Sources of boron in soils.

Much of the boron in soils occur as highly insoluble tourmaline and borosilicates (27, 72, 10, 68). According to F. M. Eaton and L. V. Wilson, traces of boron have been reported by J. W. Mellor in feldspar, pegmatite, Italian limestone, travertine basalt, sandstone, Chilean nitrate deposits, Commercial alkalies, iron ores, alumino-silicate minerals, etc. Free boric acid is found in craters of extinct volcanoes (27). The total boron content in the plow depth of an acre of most soil varies between 20 and 200 pounds (72). Most of the boron is insoluble and only less than 5 per cent of the total is available for plants.

Some of the naturally occurring borate minerals and compounds of boron are discussed by Eaton and Wilson (27) in U.S.D.A. Tech. Bul. No. 696. Some streams draining into the San Joaquin Valley from the coast ranges of California carry as much as 15 p.p.m. boron. Injury to citrus in Ventura County was traced to high boron content in irrigation water (27). The boron content of the sea water averages 4.50 p.p.m. (61).

The boron that is used in agriculture comes from mineral deposits in Death Valley, and the Mojave Desert, and from brine of Searles Lake in California (72). Yamaguchi and Minges (99) report that the boron content of soils in the celery problem area varied from 0.19 to a high of 2.1 p.p.m. and the irrigation water varied from 0.07 to 0.21 p.p.m. boron. Other crops in the area do not show boron deficiency.

Celery plants showing deficiency symptoms have high potassium and low boron in the leaves and petioles.

B. Boron content of Hawaiian soils.

L. A. Dean and T. Tanada (20) analyzed 20 representative surface soils in Hawaii, and found boron content ranging from 10 p.p.m. to 60 p.p.m. The available or hot water solution boron varied from 0.2 p.p.m. to 2.6 p.p.m. They also reported that only 3 soils fell in the deficiency range. The surface soils in all instances contained at least twice as much boron as corresponding sub-soils.

C. Common boron amendments and uses.

1. Boric acid (H_3BO_3) contains 17.49 per cent boron (35) and 5.8 pounds provide one pound of boron.
2. Borax ($Na_2B_4O_7 \cdot 10H_2O$) contains 11.3 per cent B (89) and 8.8 pounds provide one pound of boron.
3. Fertilizer borate ($Na_2B_4O_7 \cdot 10H_2O$) commercial grade has 10.5 per cent B (89).
4. Fertilizer borate, high grade or tronabor ($Na_2B_4O_7 \cdot 5H_2O$) has 13.6 per cent B (89).
5. Polybor - 2 and - 3 (78% $Na_2B_8O_{13} \cdot 4H_2O$ and 20% $Na_2B_4O_7 \cdot 5H_2O$) has 20.5 per cent B (89). Same as solubor (14).
6. Colemanite ($Ca_2B_6O_{11} \cdot 5H_2O$) contains 10.1 per cent boron. This material is less soluble than borax and leach out slowly (89).
7. Howlight - borosilicate (89).
8. Ulexite - $NaCaB_5O_9 \cdot 8H_2O$ (35)

9. Boro-Spray - sodium pentaborate contains 18.1 per cent B or 5.5 pounds provide one pound of boron.

A. S. Baker and R. L. Cook (5) applied 40 pounds of borax per acre to alfalfa in 22 locations in Michigan, and obtained increase in yield of over 10 per cent in the second crop, but not the first crop. The application of borax did not always result in increased yields even though the boron content may be high. In other tests where 30 pounds of borax and 600 pounds per acre of 0-20-20 fertilizer were applied, there was no significance increase in yield in 9 out of the 10 plots selected. The boron content of the tops of the treated plants was much higher in every case. J. I. Wear report 15 to 30 pounds of borax applied to soils have increased yield, stand, and quality of alfalfa, and 10 to 15 pound per acre application on crimson clover increased seed production about 9 times (89).

Less soluble borosilicate glass was compared with soluble borax on Ranger alfalfa in sandy loam soil by E. R. Holden and A. J. Engel (40). Their results showed that increases in yields were obtained from 5 to 80 pounds borax, and from 12 to 360 pounds per acre of borosilicate glass.

Empty or black stalks of corn were corrected, and yield of corn improved by application of 15 pounds per acre of fertilizer borate ($Na_2B_4O_7 \cdot 10H_2O$) sidedressed in bands when corn was a foot high (11).

XI. SOIL IN WHICH BORON DEFICIENCY IS FOUND IN HAWAII

The soil in which boron deficiency is a problem is classified as Reddish Prairie (79). It is described as dark-colored soil of semi-arid and subhumid grasslands. There is no accumulation of carbonates as is found in the Reddish Brown soil located just below this area at lower elevations. The Reddish-Brown Pa soil has an accumulation of calcium carbonate at about 30 inch depth. It is believed that higher rainfall in this zone leached out the carbonates from the soil. The A horizon which is very dark is about 8 to 12 inches, and gradually turn lighter colored in the transitional B horizon that rests on parent material. The soil is moderately high in bases similar to the Reddish Prairie soils of the southcentral United States, but differ from them by having a friable character of Latasols. Precipitation ranges from 20 to 70 inches per year.

The chemical composition of the colloid fraction from typical Reddish Prairie soils of Hawaii reported by D. Sherman (79) is shown in Table III.

TABLE III

Chemical composition of colloid fraction from typical Reddish Prairie soil of Hawaii.

Depth (inches)	Colloid %	SiO_2	Fe_2O_3	Al_2O_3	TiO_2
0-6	56.9	15.2	23.2	29.0	3.4
6-12	43.9	17.0	21.8	41.0	4.6
12-24	42.2	17.2	29.4	32.6	4.8
24-30	24.0	17.7	20.8	30.8	4.8

Cation-exchange capacities are very high - 40 to 70 milliequivalents per 100 grams. No explanation for low silica - sesquioxide ratio and high cation-exchange capacity is given.

XII. MECHANISM OF BORON FIXATION IN SOILS

R. Q. Parks and B. T. Shaw (68) report that boron can be precipitated in combination with silicon and aluminum. The presence of calcium ions, high pH, and drying all tend to increase precipitation of boron. It may also substitute for aluminum in the calcium aluminosilicate. They feel that because of the greater ionic radii of aluminum, 0.50 Å vs. 0.20 Å for boron, the alumino-silicate would be more stable than the boro-silicate.

It is reported that boron fixation occurs in lateritic soils of the South, which have relatively high content of free alumina and iron. Ten per cent clay, similar to bentonite in the soil when overlimed, could fix in an insoluble form the boron contained in about 75 pounds of borax (68).

J. W. Biggar and M. Fireman (13) state that fixation of boron may take place by molecular adsorption, anion exchange, or chemical precipitation. Boron probably forms compounds with soluble aluminum, silicon, and iron. The borate ions may be also exchanged with the (OH) ions of the soil surface resulting in fixation of boron to other aluminum, silicon, and iron.

Since the percentage of soil colloids, iron, aluminum, and cation-exchange capacities of the Hawaiian soil are very high, it is very possible that boron can be readily precipitated chemically or be adsorbed by the colloid tightly so that plants can not get the boron. Fairly heavy application of borax in excess 50 pounds per acre has not caused toxicity, but in some cases have been insufficient for celery.

XIII. SUMMARY

The production of celery in Hawaii has become increasingly important. In 1961 for the first time, local production of celery exceeded the importation from the mainland.

Continuous intensive cultivation of vegetable crops has decreased the boron content of the soil to the point where application of boron to soil is necessary for success in crop production. Despite amendment of boron to the soil, losses from boron deficiency at times have been as high as 90 per cent.

Boron deficiency problem is found generally in humid and heavy rainfall areas, where soluble boron tend to be leached. It also occur under condition of heavy crop removal and in calcareous soils, or where overliming has fixed the boron in the soil.

The boron requirement of plants differ and the range between deficiency and toxicity is very narrow. Some crops require 0.5 p.p.m. of available boron, while this same amount would injure sensitive crops.

Boron is taken up by the transpiration stream and generally has the highest concentration in the leaves. The first symptom of boron injury appear as burning of the leaf tip and margins. Boron in plant tissues is not too mobile and must be provided continuously.

The order in which boron deficiency symptoms develop is similar in almost all plants. The meristematic regions of the shoots and roots are affected first when boron is lacking. Tissues of the meristematic regions are killed and there may be new buds developing below the meristematic region. Growth is stunted and in most plants, there is necrosis of the phloem. The leaves and stems become brittle. Any condition that favors growth such as long days, high nitrogen, or increase in temperature hastens symptom development.

On celery, the major symptoms are brown checking or small cracks on the adaxial or inner portion of the petioles, cracked-stem, and atrophy of the heart. Under ultra violet light, fluorescence can be observed from the cracked-stem and checks.

There are sixteen roles of boron which have been reviewed by Gauch and Dugger, including one which they proposed. Their proposed role of boron on translocation of sugars has not been entirely accepted by some investigators. They hypothesized the formation of sugar borate complex and movement through cellular membranes or the association of the borate ion with cellular membrane, which react chemically with the sugar molecule to facilitate passage. Those who disagree, feel that the role of boron in translocation of sugars is indirect and is associated with growth. Other roles include nectar production, rooting of cuttings, and promotion of increased nitrogen fixation by soil organisms.

Celery varieties vary in their ability to take up boron from the soil and susceptibility to boron deficiency has been found to be determined by a single recessive gene. Susceptibility to boron deficiency in tomatoes has also been attributed to a single recessive gene.

Generally, sandy soils do not contain as much boron as clays or silt loams, and the sandy soils lose boron faster than the finer textured soils. The organic matter in the soils also affects retention and fixation of boron.

Soil reaction has a great influence on availability of boron; as the pH of the soil is increased above neutrality the rate of boron fixation is also increased. Drying of the soil tend to influence fixation of boron and the occurrence of boron deficiency has been greater following drought periods.

The soil colloids, iron, aluminum, and cation exchange capacities of Hawaiian soils are high, which may account in part for the high boron fixation rate and the existence of boron deficiency problem.

The application of high rates of lime, nitrogen and potassium tend to accentuate boron deficiency sympton expression, but high rates of lime and magnesium have been shown to decrease boron toxicity. Some fertilizers used by celery growers contain lime as fillers, and unless the calcium content of the soil is low, their use is discouraged.

Boron deficiency symptoms in celery develop most frequently at the time plants are making the fastest growth and it is important that adequate levels of boron be maintained all the time. Celery plants given large amounts of fertilizers, especially those high in nitrogen and potassium, have been shown to reduce boron absorption. The rates of nitrogen and potassium used by many celery growers are high. Research should be conducted to find out the optimum levels of nitrogen and potassium necessary to maintain high yield of celery, and the level of nitrogen and potassium which will influence uptake of boron.

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