NUTRITIONAL ASPECTS OF THE PHYSIOLOGY OF TIPBURN DISORDER IN HEAD LETTUCE

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTERS OF SCIENCE

IN HORTICULTURE

DECEMBER 1980

By

Ann Aya Yanagi

Thesis Committee:

Richard M. Bullock, Chairman
John J. Cho
Charles L. Murdoch

We certify that we have read this thesis and that in our opinion it is satisfactory in scope and quality as a thesis for the degree of Master of Science in Horticulture.

THESIS COMMITTEE

Ron Bullock
Chairman

J C Cho

Charles L. Murdoch

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Introduction

Of the vegetable crops grown in Hawaii, lettuce was second in production value for 1979 (33). Of all diversified agricultural crops, lettuce ranks ninth behind the more extensively grown crops as sugarcane, pineapple, macadamia nuts, papayas, anthuriums, potted foliage plants, coffee, and tomatoes. Lettuce is grown on 650 acres with major production areas being in Kamuela, Hawaii and Kula, Maui. Despite an increase in acreage, Hawaii's lettuce farmers can only supply 43 percent of our people's consumtive needs. Therefore, any disease or disorder can affect the supply and price of lettuce at our local markets.

Tipburn, a physiological disorder which causes a browning and drying of the leaf margins on the growing, inner leaves surrounding the heart of the plant, limits the production of saleable heads wherever lettuce is grown. This occurs not only in Hawaii, but also in the major lettuce producing areas of the nation, as Arizona and California.

On Maui, the incidence of tipburn during the year can range from 0 to 100 percent depending on the weather conditions, (mainly high temperatures), at that time of year. Often, with high incidence rates, the plants are not harvested and are rogued over instead. The farmer takes great losses in not being able to get any crop yield from the land, and the consumer pays higher prices because of the shortage. Incidence rates of 40 percent or more usually occur during the summer months of production (see Figures 4 and 5).

The occurence of tipburn in the inner leaves of the head sets up ideal conditions for secondary infections by bacterial or fungal rotting micro-organisms (40). Pathogen populations tend to be fairly high in fields on Maui. This accounts for further limitations on production and is especially important in the storage and shipping of lettuce throughout the islands.

Because tipburn is a major problem of head lettuce growers in our state, a thesis study was conducted to study the nutritional relationships of nitrogen, calcium, and boron fertilizers with any consequent changes or influences these might have on the development of tipburn.

Literature Review

Tipburn was recognized as early as 1892, as a physiological disorder, yet it is still a major problem for head lettuce growers in the state of Hawaii (40). The search for the causes and control of tipburn continues. Research results have been variable, and while the cause of tipburn seems simple, many factors influence the development of this complicated disorder.

Tipburn is characterized by the browning and necrosis of the leaf margins on the inner leaves surrounding the heart of the plant (75). Boron deficiency causes symptoms in lettuce similar to those of tipburn. Boron deficiency symptoms include a malformation of the younger leaves with the appearance and coalesence of dark spots in the leaf margins. This injury does not affect the outer leaves of the plant, but is confined to the younger leaves including the growing point. This is similar to tipburn symptoms described by Termohlen and van den Hoeven (75). McHargue and Calfee (51) showed that normal leaves were produced by supplying boron to the deficient plants. Lettuce has a definite boron requirement for normal plant growth and development (50,51). This requirement may be accentuated during the heading period, when nutrient demand in the plant is high (89). In more recent work, Crisp, Collier, and Thomas (17) induced tipburn symptoms by growing lettuce under boron deficient nutrient solution conditions.

Struckmeyer and Tibbitts (73) compared calcium and boron deficiency symptoms in lettuce with tipburned leaves. Their study indicated that boron deficiency symptoms were more similar, anatomically, to tipburn symptoms than calcium deficiency symptoms. They suggested that a boron deficiency interferes with the proper functioning of laticifers in latex bearing plants, such as lettuce, thus inducing tipburn symptoms. Latex tipburn is one of the types mentioned by Termohlen and van den Hoeven (75).

In the plant, boron forms complexes with polyhydroxyl compounds of which one type interacts with chains of cellulose or other long chain polyhydroxyl compounds (24, 29). Calcium's major role in plants is in the maintenance of cell membrane integrity, which other cell functions depend upon (2, 9, 24). Both elements are involved in cell wall structures, and a lack of calcium and boron in the plant can lead to cell wall breakdown and necrosis, which are typical symptoms of tipburn injury. Ashkar and Ries (1) found that all parts (midrib, leaf margins, and leaf blades) of tipburned leaves are low in calcium, magnesium, manganese, and boron in comparison to normal leaves.

A lack of available calcium and boron in the soil can limit the growth and development of a normal root system of a lettuce plant. Roots grown with a low supply of these nutrients are short, stubby, and brown; and nutrient uptake can be limited (24, 34).

The transport of calcium and boron from roots to shoots occurs passively in the transpiration stream of the plant (7, 8, 45). Thus, the nutrient levels of calcium and boron in the plant can be influenced by environmental factors, mainly humidity and temperature conditions, that increase the transpiration rate of the plant (57, 78). However, this does not happen in the marginal leaf tip tissues in the head of a lettuce plant that are susceptible to tipburn injury. The plant's structure in head formation sets up a microenvironment in the interior of the head of a relatively higher humidity than the rest of the plant. The leaf tips have a very low transpiration rate, and for this reason, may not get adequate levels of calcium and boron for normal leaf development, although apparently adequate levels of calcium and boron exist in the soil (38, 76, 78).

Calcium and boron are immobile elements (13, 19, 32, 58); once xylem uptake and translocation for deposition in the leaves occurs, these elements will not move to areas where they may be of greater need. The younger leaves of a plant must get a continuous supply of calcium and boron from the transpiration stream for normal leaf development as little movement of calcium and boron occurs in the phloem, and translocation from leaf to leaf does not occur (19, 20, 24).

Deficiency, as well as toxicity levels of boron in the substrate result in subnormal levels of calcium in the tissues (52). This may account for the discrepancies in the literature regarding calcium and boron nurtition. Liming has been shown to induce a boron deficiency, as boron becomes unavailable to plants due to its insolubility at high pHs (41, 63). This is reflected in a high calcium/boron ratio. Calcium/boron ratios of leaf tissue have been considered indicators of the boron status in certain crops, i.e. a high calcium/boron ratio is an indicator of boron deficiency in rutabagas (18, 30). However, the addition of calcium fertilizers to the soil increased the boron content in plant tissues of groundnuts (65). In other cases, it has been shown that foliar sprays of boron increase the levels of calcium in the leaf tissues of apple seedlings (70). It is believed that boron promotes the absorption and utilization of calcium by keeping it in a soluble form, and symptoms of a calcium deficiency may well be a manifestation of a boron deficiency (48). Boron apparently increases the permeability of the plant roots to the movement of calcium (10). Marsh (48) found that soluble calcium levels in the plant depend on the total calcium as well as the boron content in the substrate. Crisp, Collier, and Thomas (17) found no evidence that the calcium content of lettuce plants is affected by the boron content in the substrate, but they believe that tipburn is the result of an interrelationship between a calcium and boron deficiency, which in part, may be influenced by auxin levels during some stage of the plant's development.

Tipburn in head lettuce has generally been accepted as the consequence of a localized calcium deficiency (46, 54, 76). The results of experiments done with calcium nutrition are so varied that it is hard to determine what exactly is occuring within the plant and between the plant and its environment. Control can be achieved with calcium treatments under greenhouse conditions (1, 46, 54, 76), but field experiments usually fail (15, 39, 68). The method of culture; soil versus nutrient solutions, as well as the use of foliar sprays and a variety's susceptibility to tipburn can account for some of the variability in response. Soil applications of calcium do not always provide for the calcium needs of the plant (15, 39, 68), while foliar sprays and nutrient solutions prevent tipburn in some cases (1, 46, 54, 76), and in other cases, have no control over tipburn (14, 39, 46, 68, 71). Other environmental factors, such as high temperature and soil moisture can override the main cause of tipburn (a calcium deficiency), in that tipburn still occurs although soil calcium levels are not limiting to uptake (15). The mechanisms by which a calcium deficiency occurs are still unknown. It is believed that it may be due to:

1. a depression in calcium absorption, uptake, or translocation.
2. an immobilization or chelation of calcium before it can be utilized by young, developing tissues.
3. an increase in plant growth rate so that the calcium requirement of the plant cannot be met.
4. a combination of any of the above.

Calcium absorption and uptake are influenced by soil and root properties; translocation and mobility of calcium is related to the immobility of calcium within the plant; chelation of calcium by respiratory byproducts is related to increased respiration rates of the plant; and plant growth rates are enhanced by different environmental factors (19, 53, 54, 55, 66, 76). The mechanisms by which a deficiency can occur basically fall into two groups -- factors that influence or limit nutrient uptake and rate of movement, and factors that influence the growth rate of the plant.

A localized calcium deficiency as the result of an increased growth rate of the plant is generally accepted as the cause of this calcium deficiency in lettuce called tipburn (54). The growth rate of plants is influenced by many uncontrollable environmental factors, but controllable factors that affect root development and nutrient uptake can play an important role in the appearance and severity of calcium deficiency symptoms (66). The lettuce plant does not have a growth rate of a linear pattern, but undergoes a rapid change, (increase in growth rate), during the period of head formation (89). Nutrient demand is also high during this period. It has been shown that seventy percent of the total nutrient uptake of the lettuce plant occurs during this period (23, 88, 89), therefore, any factor limiting nutrient uptake during this period can accelerate the appearence of deficiency symptoms and the occurrence of tipburn.

Many factors in the soil environment can limit the uptake of nutrients; factors that affect the availability of calcium and boron to the plant and factors which antagonize calcium and boron uptake (ion competition).

The availability of calcium and boron to the plant is affected by many different factors in the soil environment. Boron availability is affected by the plant species, soil organic matter, soil calcium, soil pH, clay content, type of clay, soil texture, and soil moisture levels. But due to potential errors in soil analysis, and because so many factors affect boron availability, a soil analysis can only be a rough estimate of what is available for the plant. Boron fixation in Hawaiian soils tend to be fairly high, depending on the soil's origin and extent of weathering (59, 74).

Calcium availability is affected by plant species, ratio of calcium/magnesium in the soil, soil pH, type of clay, soil moisture and aeration, and soil texture (13, 21, 29, 38, 83).

Nutrients are absorbed by the plant root in ionic form as anions or cations. The ionic form of the nurtient greatly affects the metabolism and absorption of other nutrients. Cation-cation interactions generally affect transport across cell membranes and tend to be inhibitory interactions of a competitive nature. Calcium becomes available to plants when the degree of saturation in the exchange complex is high. This availability is reduced if 50 percent or more of the base sites on the soil colloids are filled with Na^+ or K^+ (24). The cations: Al^{+++}, Mg^{++}, K^+, Na^+, NH_4^+, Mn^+, and H^+, directly and indirectly, depress calcium uptake. Increased root temperatures increased the uptake of K^+, which in turn, depressed calcium uptake (12). High levels of Mg^{++}, K^+, H^+, Na^+, and NH_4^+ in the nutrient media aggravates calcium uptake, and enhance the appearance of deficiency symptoms (42, 86, 87). Magnesium was found to increase the occurrence of tipburn (1). Increasing the magnesium supply from a deficient to adequate level can increase calcium uptake, but a further increase in magnesium will reduce calcium uptake by the plant (69).

When plant calcium levels are low, phytotoxicities from trace elements and even Mg^{++} and Na^+ can occur (87). Aluminum toxicities tend to be more prevalent at pHs below 5.0-5.5 The ameliorating effects of calcium on toxic trace elements is well known, and calcium may be tied up this way, thus preventing an aluminum toxicity, but enhancing a calcium deficiency (22, 27, 86, 87).

Cation-cation and anion-anion interactions also occur with boron. High fertilization rates of nitrogen enhance tipburn development in head lettuce (1). They also decrease the uptake of boron by the plant (29, 84). Boron levels in the plant decreased with increasing nitrogen rates, inducing a boron deficiency. Additions of nitrogen decreased the severity of boron toxicity symptoms. Turner (84) showed increases in boron content in plant tissues with increasing nitrogen rates, and that high nitrogen rates like high calcium or potassium rates may induce a boron deficiency. With high boron levels in the substrate, increasing potassium levels increased the severity of boron toxicity symptoms. At low boron levels, increasing potassium levels intensified the severity of boron deficiency symptoms (29, 63).

Much of the work done from the 1920s to the present deals with environmental factors, and the calcium and boron status in the plant in relationship to tipburn incidence and severity. Some have been successful, while others have not, in controlling tipburn with calcium nutrient solutions. This discrepancy may be due to the relationship between the calcium concentration and total salt concentration in the substrate that affects the development of tipburn (25). Calcium uptake and utilization depend not only on the presence of Ca^{++} in the soil solution, but on the presence of other cations, accompanying anions, and the general constitution of the plant. Calcium uptake decreased, in the presence of Li^{++}, Na^{+}, or K^{+} and in that order. In the presence of NO_3, uptake increased; but uptake decreased with Cl^{-}, Br^{-}, or SO_4^{-} and in that order (8). Sonneveld and van den Ende (71) with the use of various salts--(Na^{+}, K^{+}, Ca^{++}, and Mg^{++}) chloride, and sodium (NO_3^{-}, Cl^{-}, SO_4^{-}, and HCO_3^{-}) showed increased severity of tipburn with most of the salts, especially sodium bicarbonate. Only calcium chloride gave a significant reduction in severity. They believe that because lettuce shows such wide response to the type of salts applied, tipburn can occur with just a slight imbalance among the ions in the soil solution. Gerard (76) found that plants need more soil calcium for maximum root elongation when total salt concentration in the soil solution is high, otherwise root elongation can be inhibited and the uptake of calcium and boron minimized.

Borkowski and Ostrzycka (5) also found evidence for this ion imbalance theory. Through the use of various calcium fertilizers and calcium sprays, they showed the least tipburn with 3 and 6 percent Lena (a flotation sediment from the copper mines which contain 186 ppm K, 18 percent Ca, 2.8 percent Mg, Cu and Mn) as opposed to calcium carbonate soil applications and calcium foliar sprays. With the addition of 3 and 6 percent Lena, various amounts of these nutrients may create a more favorable ionic environment in the soil for ion uptake. Geraldson (25) showed that calcium deficiencies in tomatoes and celery can be enhanced depending on the amount and type of ions in the nutrient solution. This is best illustrated in the following table for tomatoes and blossom end rot:

Table 1.*

Effects of partially replacing calcium with potassium, sodium, ammonium, or magnesium (on an equivalent basis) in the hydroponic solution on the yields and quality of tomatoes.

Ca(ppm)/total salt (ppm)	% BER (fruit)	%Calcium (leaves)
150/1000	0	1.35
50/1000-Na	16	.95
50/1000-Mg	22	.67
50/1000-K	40	.80
50/1000-NH_4	75	.47

* Taken from Geraldson 1971.

The ratio of 150 ppm calcium to 1000 ppm total salts ($CaNO_3$, K NO_3, $MgSO_4$, NH_4PO_3, and micronutrients) under hydroponic nutrient culture, gave complete control of blossom end rot, a calcium deficiency in tomatoes. The replacement of 2/3 of the calcium nitrate with (Mg^{++}, K^+, Na^+, NH_4^+) nitrate shows the various effects of the different ions in enhancing blossom end rot and decreasing the calcium levels in the leaves. This also points out the competition for uptake between the ions in solution, and its effect on the resulting calcium levels in the plant leaf tissues.

The growth rate of the plant has a major role in the appearance of tipburn in head lettuce. From the earliest observations the growth rate or the succulence of the plant and the effect of different environmental factors has been noted in relation to the development of tipburn. Tipburn has been associated with the vigor and growth rate of the plant enhancing a calcium deficiency (11, 54, 62, 68, 72, 77).

Different environmental factors influence the growth rate of the plant. Factors such as high humidity (6, 11, 49, 77, 79), high temperatures (16, 53, 54, 55, 77), high light intensities and durations (1, 80), high nitrogen fertilization (1, 11, 56, 68, 69), and high soil moisture levels, (4, 15, 62), all contribute to an enhancement of the growth rate of the lettuce plant, and play an important role in the occurrence and severity of tipburn in the field.

Cox, McKee, and Dearman (16) confirmed previous work regarding the rapid growth theory when they correlated the incidence of tipburn with the relative growth rate of six cultivars, grown under controlled environments. Tipburn development within cultivars was correlated to relative growth rates during the exponential growth phase period (head formation). Many interacting factors are involved in the growth rate of the plant. Retardation of the growth rate can result in partial control of tipburn (14, 16, 39, 56, 77, 79) and in other cases, complete control can be achieved, but the quality of lettuce suffers (5, 85).

From the previous work, one can see that the environment plays a major role in the development of tipburn. The morphology of the lettuce plant during the heading period creates a microenvironment within the plant of an entirely different nature than the outside prevailing conditions (78). High humidity and high temperatures with low light conditions exist within the lettuce head, which enhances the development of tipburn. High humidity results in low transpiration rates; reducing calcium movement into these tissues (76, 78). High temperatures increase the respiration rates of the plant, and the chelation of calcium may occur (1, 53, 54, 55, 77). Low light or dark conditions may play an important role, as the onset of tipburn occurs only in the dark (11, 77).

Controlling environmental factors that influence the growth rate of the plant as a means of controlling tipburn can be impractical. Controlling the factors that exist within the head can drastically alter the plant's morphology. Therefore, other means of control must be looked at. Cation-cation and cation-anion relationships exist between calcium and the various forms of nitrogen fertilizers. The form and quantitiy of nitrogen applied to plants can greatly affect the levels of calcium within the plant. Under high nitrogen and high calcium conditions, calcium uptake is decreased (1). With high nitrogen fertilization, vegetative growth is promoted and requires more calcium than can be absorbed and moved to the rapidly growing tissues (69).

The form of nitrogen supplied to plants plays a major role in affecting levels of calcium in the plant. Generally ammonium fertilizers tend to be detrimental because:

1. The acidifying effects of ammonium salts in the soil initiate a more rapid leaching of calcium due to the replacement of the calcium ion by ammonium on the soil colloid. A reduced availability of the remaining calcium occurs due to the pH effect on nutrient availability (26, 63). When the pH is highly acid,

(pH 5.0), aluminum toxicity can appear as an induced calcium deficiency (22, 27, 87).

2. The ammonium ion competes with calcium in the soil for plant uptake (24), and an ammonium toxicity can appear as an induced intracellular calcium deficiency (36).
3. Ammonium fertilizers decrease the uptake of water by the plant (61). This can reduce the amount of calcium taken up by the plant as calcium moves in the transpiration stream.
4. Ammonium fertilizers decrease total cation uptake (42, 43, 44).
5. Ammonium fertilizers result in higher amino acid content in the roots as compared to the shoots (36), which Ashkar and Ries (1) feel plays an important role in the development of tipburn, since amino acids can chelate calcium and make it unavailable to the plant.

Nitrate fertilizers tend to be a better choice in supplying the nitrogen fertilization needs of the lettuce plant, since they enhance water uptake by the plant (8), and also enhance total cation uptake (8, 43, 44). This can affect the levels of calcium in the plant tissues (8). Leh (47) found less tipburn in plants given nitrate rather than ammonium fertilizers.

Nitrate translocation from the roots to the shoots is accompanied by an equivalent amount of cations. If nitrate is reduced in the roots and translocated as amino acids, a low cation content can occur in the shoot (3, 43). In a comparison of various nitrogen fertilizers for head lettuce, Gardner and Pew (23) found that nitrate nitrogen fertilizers resulted in higher nitrate levels in the plant. Kirkby and Mengel (43) showed that cation levels doubled in plants given nitrate fertilizers rather than ammonium fertilizers. Inorganic anion levels were unaffected by the nitrogen source, but electroneutrality in the plant was maintained by the production of more organic acid anions.

Changes in organic ion composition induced by ion uptake and ion metabolism influence the accumulation of inorganic cations and anions in the plant tissue. Inorganic cation accumulation is influenced by factors that induce changes in the levels of organic acid anions in the tissue and by the nutrient composition and nutrient levels in the media (36).

Materials and Methods

The soil used in all experiments was a Keahua cobbly silty clay, with a pH of 5.8-6.2. The Keahua series belongs to the Torroxic Haplustoll soil subgroup consisting of well drained soils derived from weathered basic igneous rock.

A nonionic surfactant, (Tween-20)^{R}, was added to all foliar sprays at .001 percent v/v.

Soil analysis for potassium, calcium, phosphorous, magnesium, soil pH and salinity levels were obtained from colorometric tests done by the University of Hawaii's Tissue and Soil Analysis Lab. Calcium was also determined by ammonium acetate extraction at ph 7.0.

Soil sampling was before and after each experiment and consisted of a composite of samples taken from each pot (greenhouse studies) or from different areas of the field plots at 0-3 and 6-9 inch depths. Initial field sampling consisted of a composite of samples from four different areas at 0-3 and 6-9 inch depths.

Tissue analysis was by the University of Hawaii's Tissue and Soil Analysis Lab. Boron analysis was by the dry ash method, nitrogen analysis by the Kjehldal method, and the other nutrients by a vaccum x-ray fluorescent quantometer.

Tipburn incidence rates were based on the percent of total harvested heads affected by tipburn. Tipburn severity ratings were on a 1-6 scale, where 1 is no injury and 6 is severe injury and unsaleable. Head weights were determined on total number of heads harvested. Overall visual head quality was based on a 1-9 scale with anything less than 5 being unsaleable.

Monthly tipburn incidence rates were based on 20 or 25 heads taken from plots given the basic fertilization programs. Incidence rates were reported for December 1979 up until September 1980, except for January, when bad weather destroyed the crop.

Greenhouse Experiments. The following experiments, 1-4, were conducted in Pope Laboratory Greenhouses, University of Hawaii, Manoa Campus. These experiments used 8 inch diameter plastic pots. A tipburn resistant head lettuce variety, Mesa 659, was used in the first three experiments, and a susceptible leaf lettuce variety, Green Mignonette, (Manoa lettuce), was used in the fourth experiment.

Lettuce (Lactuca Sativa) was seeded in Supersoil[R] in styrofoam speedling trays[R] or plastic cells. The trays were kept under mist for one week and seedlings were transplanted three weeks later. Plants were watered every Monday, Wednesday, and Friday, and soil moisture levels were brought up to field capacity as indicated by soil irrometers.

The main plots for soil treatments in the four experiments included the use of calcium sulfate at 400 lb. calcium/acre with the addition of 800 lb./acre of 10-30-10 fertilizer. Subplot treatments included factorial combinations of succinic acid 2,2-dimethylhydrazide (Alar[R]) at 5000 ppm, benzyladenine at 25 ppm, and Solubor[R] (20.5% boron) at 0.08 ppm as foliar sprays in one experiment; and calcium sulfate at 105 ppm, Solubor[R] at 2 ppm, calcium sulfate and Solubor[R], and distilled water as foliar sprays in a second experiment. No foliar sprays were used in a third experiment. In addition, main plots in experiment 4 included a 1:1 mix of perlite and calcium sulfate treated soil, calcium hydroxide at 811.5 lb. calcium/acre, calcium magnesium carbonate at 454 lb. calcium/acre, and calcium carbonate at 800 lb./acre. Subplot treatments included foliar sprays of 0.04M calcium nitrate, Solubor[R] at 1 ppm, calcium nitrate and Solubor[R], and distilled water.

The soil was watered after soil treatments were made, and tilled before the seedlings were transplanted.

The first two experiments were split plot experimental designs with main plots in a randomized complete block, and replicated four times. Experiments 3 and 4 were completely randomized designs with 24 and 5 replications, respectively.

Tissue analysis done on four and six week old seedlings; mature head leaf sections of a composite of five heads consisting of the outer two leaves, the middle sixth and seventh leaves, inner leaves, and core pieces, and of mature roots.

<u>Field Experiments</u>. The following experiments, 5-8, were conducted at the Pulehu field on Maui. Experiment 5 was done in the field greenhouse with tipburn resistant head lettuce variety, Calmar. Another tipburn resistant head lettuce variety, Mesa 659, was used in Experiments 6-8. A tipburn susceptible head lettuce variety, Monterery, was planted with soil treatments 1 and 2 only, but with 0, 3, or 6 foliar spray applications in Experiment 8. Only tipburn incidence and severity rates were reported for this variety.

Lettuce was seeded in Promix ^{R} in styrofoam speedling ^{R} trays. Trays were kept under mist for one week and the seedlings were transplanted three weeks later. Foliar 60^{R} (1-2 tsp./gal.) was sprayed on seedlings, once every weeek before transplanting in the field.

At the end of experiment 6, a composite of soil samples taken from field plots was analyzed by the Soil Analysis Lab at Oregon State University in Corvallis, Oregon for calcium levels with ammonium acetate extraction at pH 7.0 and boron levels with hot water extraction.

Tissue analysis was on mature head sections consisting of a composite sampling from 5 heads, where the outer two leaves, middle sixth and seventh leaves, inner leaves, and core pieces were taken.

Experiments 5, 6, and 8 were split plot experimental designs, with soil treatments as main plots and in a randomized complete block, while experiment 7 was a strip plot design. All treatments were replicated four times, except in Experiment 5, treatments were replicated three times.

In Experiment 5, regular preplant fertilizer applications of treble superphosphate at 700 lb./acre, muriate of potash at 170 lb./acre, magnesium sulfate at 125 lb./acre, and borax at 10 lb/acre were made.

Drip irrigation was installed to regulate the watering, and plants were watered forty minutes every Monday and Wednesday and sixty minutes every Friday. Irrigation rates were maintained at 0.28-0.56 inch/week, 0.89-1.12 inch/week, and 1.40-1.60 inch/week. Nitrogen was applied as calcium nitrate in solutions of 0, 50, 100, 200, 400, and 800 ppm (total nitrogen) to the plants at transplanting and four weeks later.

Subplot treatments included foliar spray applications of 6 percent calcium chelate (This ^{R} liquid calcium) at 0.03 ppm, Solubor ^{R} at 1 ppm, calcium chelate and Solubor ^{R}, and distilled water, applied to plants receiving 200 ppm nitrogen and 0.84-1.12 inch/week irrigation. Sprays were applied three times a week (every Monday, Wednesday, and Friday) for two weeks, starting one month after transplanting.

In tissue sampling, the heads were cut in four sections; the apex and basal inner, and the apex and basal outer; pieces were taken from each section.

In Experiment 6, calcium sulfate at rates of 100, 200, and 400 lb. calcium/acre, with and without boron at 2.85 lb./acre was mixed into the soil two weeks before transplanting. Fertilizer, 10-30-10, at 800 lb./ acre was added. A second postplant side dress application of 16-16-16 at 300 lb./acre was applied two and a half weeks after transplanting. A foliar application of succinic acid, 2,2-dimethylhydrazide (Alar [R]) at 5000 ppm was applied three weeks after transplanting. Only tipburn incidence rates were reported here.

Tissue sampling was only on plants which received varying rates of calcium plus or minus boron.

In Experiments 7 and 8, main plot fertilizer treatments include:

1. 10-30-10 at 1000 lb./acre.
2. 10-30-10 at 1000 lb./acre and 150 lb. calcium/acre as calcium hydroxide.
3. Ammonium nitrate at 100 lb. nitrogen/acre and 150 lb. calcium/acre as calcium hydroxide.
4. Ammonium nitrate at 100 lb. nitrogen/acre.
5. Calcium nitrate at 100 lb. nitrogen/acre.

Soil treatments 3, 4, and 5 recieved P as phosphoric acid and K as potassium chloride in equivalent amounts given in treatments 1 and 2. Treatment 5 received additional calcium hydroxide to bring the calcium level to an amount equivalent to that in the other treatments.

In Experiment 7, half of the fertilizer treatments were applied two days before transplanting, and the other half was side dressed three weeks later. In Experiment 8, all the fertilizer treatments were preplant applications to the same field plots used in Experiment 7.

Subplot treatments were foliar sprays which consisted of a combination of 0.04 M calcium nitrate and 0.50 ppm boron applied to the plants in increasing frequencies of 0, 3, or 6 applications, with the last spray application 1½ weeks before harvest. In experiment 8, chelated calcium (This [R] liquid calcium) was substituted for calcium nitrate.

Plants were watered Monday, Wednesday, and Friday, so that total irrigation levels were 1.50-1.70 inch/week.

Fifteen heads per treatment in Experiment 7 and twenty heads per treatment in Experiment 8 were examined for tipburn incidence and severity and head weight and quality.

Results

Greenhouse Experiments

In the first experiment, foliar sprays of Alar [R], benzyladenine, Solubor [R], and factorial combinations of the preceeding had little effect, as tipburn symptoms were seen three days after the first spray application. Incidence rates were 62 and 50 percent for calcium treated and untreated soils. Incidence rates increased to 88 and 96 percent, just after the second spray application. Greenhouse temperatures were high and problems with bolting occured.

In the second experiment, foliar sprays of calcium sulfate, boron, calcium and boron, and distilled water gave complete control of tipburn in calcium treated and untreated soils, but this was nonsignificant and lettuce heads were small. Tissue analysis data are given in Table 1.

Table 1. Effect of foliar sprays and calcium soil treatments on calcium and boron levels in mature leaf tissues, var. Mesa 659. Tissue analysis based on composite of five heads, no replications.

Head Section	Foliar Sprays			
	Water	Calcium	Boron	Caleivant Boron
	With No Soil Calcium			
Boron (ppm) Outer	39	31	49	38
Calcium (%) Outer	1.89	1.93	2.71	2.09
Calcium (%) Middle	1.25	0.94	1.29	1.20
Calcium (%) Inner	0.43	0.46	0.38	0.27
	With Soil Calcium			
Boron (ppm) Outer	34	36	39	40
Calcium (%) Outer	1.75	(0.96)	2.39	2.51
Calcium (%) Middle	1.01	1.06	0.87	1.46
Calcium (%) Inner	0.38	0.19	0.33	0.48

In the third experiment, incidence rates were 71 percent for plants grown in untreated soil and 42 percent for plants in calcium treated soils. This was not significant, however, because of high variation. Incidence rates differ, but this was not reflected in changes in levels of calcium and boron in the tissue analysis data (Table 2).

Table 2. Calcium and boron levels in mature leaf sections and in mature roots of plants grown in calcium treated and untreated soils. Tissue analysis based on a composite of five heads with no replications.

Section	Calcium (%)		Boron (ppm)	
	Treated Soil	Untreated Soil	Treated Soil	Untreated Soil
Outer leaves	0.99	1.12	23	28
Middle leaves	0.54	0.40	16	17
Inner leaves	0.28	0.28	11	13
Core	0.51	0.38	15	13
Roots	0.45	0.49	36	32
Total	2.78	2.67	101	103

In the fourth experiment, different sources of soil calcium and subsequent effects on soil pH had little effect on tipburn incidence. The addition of perlite to soil calcium sulfate fertilizer increased tipburn severity and the use of foliar sprays were significant at the 0.01 percent level in reducing the severity of tipburn, however, no observable calcium or boron increases were seen in the tissue analysis data (Tables 3 and 4).

Table 3. Effect of foliar sprays and calcium soil treatments on the severity of tipburn in var. Green Mignonette.

Soil Treatments	Foliar Sprays: Water	Calcium	Boron	Calcium & Boron	$\bar{X}$
	Severity*				
Control	2.60	2.00	3.20	3.20	2.75b**
Calcium hydroxide	3.00	2.00	2.60	1.60	2.30b
Calcium sulfate	3.40	1.80	3.00	2.00	2.55b
Calcium sulfate perlite	3.60	3.40	4.00	3.20	3.55a
Calcium carbonate	2.00	1.40	2.20	2.40	2.00b
Calcium mangnesium carbonate	3.00	1.00	3.00	1.40	2.10b
$\bar{X}$	2.93a	1.93b	3.00a	2.30b	

* Severity based on 1-5 scale, where 1 = no injury, 3 = moderate, 5 = severe.
** Mean separation by Duncan's Multiple Range Test at 0.05% level.

Table 4. Effect of foliar and soil treatments for var. Green Mignonette on calcium and boron levels in mature leaf tissues. Tissue analysis based on composite of five heads with no replications.

Treatment		Calcium %	Boron ppm
FOLIAR	Control	0.75	44
	Calcium	0.67	41
	Boron	0.74	36
	Calcium and Boron	0.71	48
SOIL	Calcium Sulfate & Perlite	0.95	37
	Calcium Sulfate	0.86	37
	Calcium Magnesium Carbonate	0.76	38
	Calcium Magnesium Carbonate and foliar calcium spray	0.67	29
	Calcium Magnesium Carbonate and foliar boron spray	0.69	38

Field Experiments. In experiment 5, head quality, head weight, tipburn incidence, and severity were not affected by treatments. Tipburn incidence was quite variable and ranged from 25 to 100 percent. The total number of heads harvested per treatment was small. Tissue analysis showed that higher nitrate nitrogen rates (N_{400} and N_{800}) resulted in higher levels of calcium, boron, and nitrogen in plant tissues (Table 5). The position of sample also influences the levels of calcium, boron, and nitrogen in the plant tissue. The inner leaves have less calcium and boron than the outer leaves (Table 6).

Table 5. Effect of Nitrogen rates on calcium, boron, and nitrogen in mature leaf plant tissues.

Nitrogen Rates (ppm)	Calcium (%)	Boron (ppm)	Nitrogen (%)
N_0	0.49b*	19a	1.93d
N_{50}	0.46b	19a	1.87d
N_{100}	0.44b	19a	2.32c
N_{200}	0.48b	19a	2.49c
N_{400}	0.55a	21b	2.79b
N_{800}	0.57a	22b	3.18a

* Mean Separation by Duncan's Multiple Range Test at 0.05% level.

Table 6. Calcium, boron and nitrogen levels in different head sections.

Head Section	Calcium (%)	Boron (ppm)	Nitrogen (%)
Apex-Inner	0.34c*	15b	2.19b
Apex- Outer	0.72a	23a	2.44b
Basal-Inner	0.33c	17b	2.58a
Basal-Outer	0.60b	23a	2.15a

* Mean Separation by Duncan's Multiple Range Test at 0.05% level.

Foliar sprays of 1.8M calcium chelate and 1.8M calcium chelate plus 1 ppm boron resulted in a highly significant increase in boron levels in the plant tissue. Boron levels in inner leaves were lower than in the outer leaves (Table 7). Calcium and nitrate levels in the plants were not affected by foliar sprays. Calcium, boron, and nitrogen levels in the plants were unaffected by irrigantion levels.

Table 7. Effect of foliar sprays and position of head (outer vs. inner) and leaf (apex vs. basal) cut on boron levels in plant tissues.

Foliar spray	Apex-Inner	Apex-Outer	Basal-Inner	Basal-Outer	$\bar{X}$
Calcium	14.5	23	17	24	20c
Boron	16.5	36.5	22	35.5	28b
Calcium & Boron	22.5	52	22.5	52	37a
Water	16	24.5	18	24	21c
$\bar{X}$	17b	34a	20b	34a	

* Mean separation by Duncan's Multiple Range Test at 0.05% level.

In experiment 6, the different rates of soil calcium with and without boron had no effect on tipburn incidence and severity rates. Succinic acid 2,2-dimethylhydrazide (Alar ^{R}), reduced the growth rate as treated plants were harvested one week later than untreated plants, and some reduction in tipburn incidence was achieved (Table 8). Alar ^{R} in combination with soil applications of calcium and boron give the best reduction in tipburn incidence.

Table 8. Effect of soil treatments and foliar application of Alar on tipburn incidence. Means of four replications given.

Treatment	Incidence
Control	50%
Alar	57%
Alar and Boron (soil)	57%
Boron (soil)	62%
Alar and Calcium (soil)	47%
Calcium (soil)	57%
Alar and Calcium and Boron (soil)	42%
Calcium and Boron (soil)	64%

In Experiment 7, ammonium nitrate and calcium soil applications, with three foliar spray applications significantly reduced tipburn incidence at the 0.01% confidence level (Figure 1). However, all treatments had little effect on head weights, tipburn severity, and head quality.

Tissue analysis of mature inner leaf sections show little increase of calcium and boron levels, even after three and six spray applications were made (Table 9).

Table 9. Calcium and boron levels in mature, inner leaf sections of plants grown in five soil treatments with foliar applications of calcium nitrate and Solubor, in increasing frequencies. Tissue analysis based on composite of five heads, with four replications. Treatment means are given.

Soil Treatment	0 sprays		3 sprays		6 sprays	
	Calcium (%)	Boron (ppm)	Calcium (%)	Boron (ppm)	Calcium (%)	Boron (ppm)
1*	0.40	11	0.39	11	0.40	12
2*+	0.40	12	0.43	12	0.39	13
3*+	0.41	13	0.40	13	0.42	15
4*	0.38	16	0.37	13	0.37	13
5*+	0.38	13	0.40	13	0.41	14

* Soil treatments include (1) and (2) 10-30-10 fertilizer, (3) and (4), Ammonium nitrate, and (5) Calcium nitrate.

+ Soil treatments receiving calcium hydroxide.

Tissue analysis of the inner head sections indicates that the addition of soil boron at the 100 bl. calcium/acre level, increases plant calcium and boron levels. With higher rates of soil calcium, levels of calcium and boron in the plant tissues slowly dropped off (Table 10).

Table 10. Tissue analysis of mature leaf tissues in plants grown under varying calcium rates with boron fertilization. Data based on composite of five heads with no replications.

Calcium (%)

Section	Control	Control & Boron	100 lb/acre Calcium	100 lb/acre Ca & Boron	200 lb/acre Calcium	200 lb/acre Ca & Boron	400 lb/acre Calcium	400 lb/acre Ca & Boron
Outer	0.74	0.85	0.86	0.86	0.71	0.93	0.82	0.97
Middle	0.70	0.63	0.69	0.67	0.56	0.57	0.57	0.60
Inner	0.63	0.62	0.55	0.72	0.62	0.61	0.69	0.56
Core	0.92	0.84	1.18	0.95	0.83	0.82	0.82	0.85

Boron (ppm)

Section	Control	Control & Boron	100 lb/acre Calcium	100 lb/acre Ca & Boron	200 lb/acre Calcium	200 lb/acre Ca & Boron	400 lb/acre Calcium	400 lb/acre Ca & Boron
Outer	32	41	31	34	24	35	29	29
Middle	23	24	20	24	24	22	22	21
Inner	16	19	15	19	20	17	18	17
Core	26	26	26	23	30	25	22	23

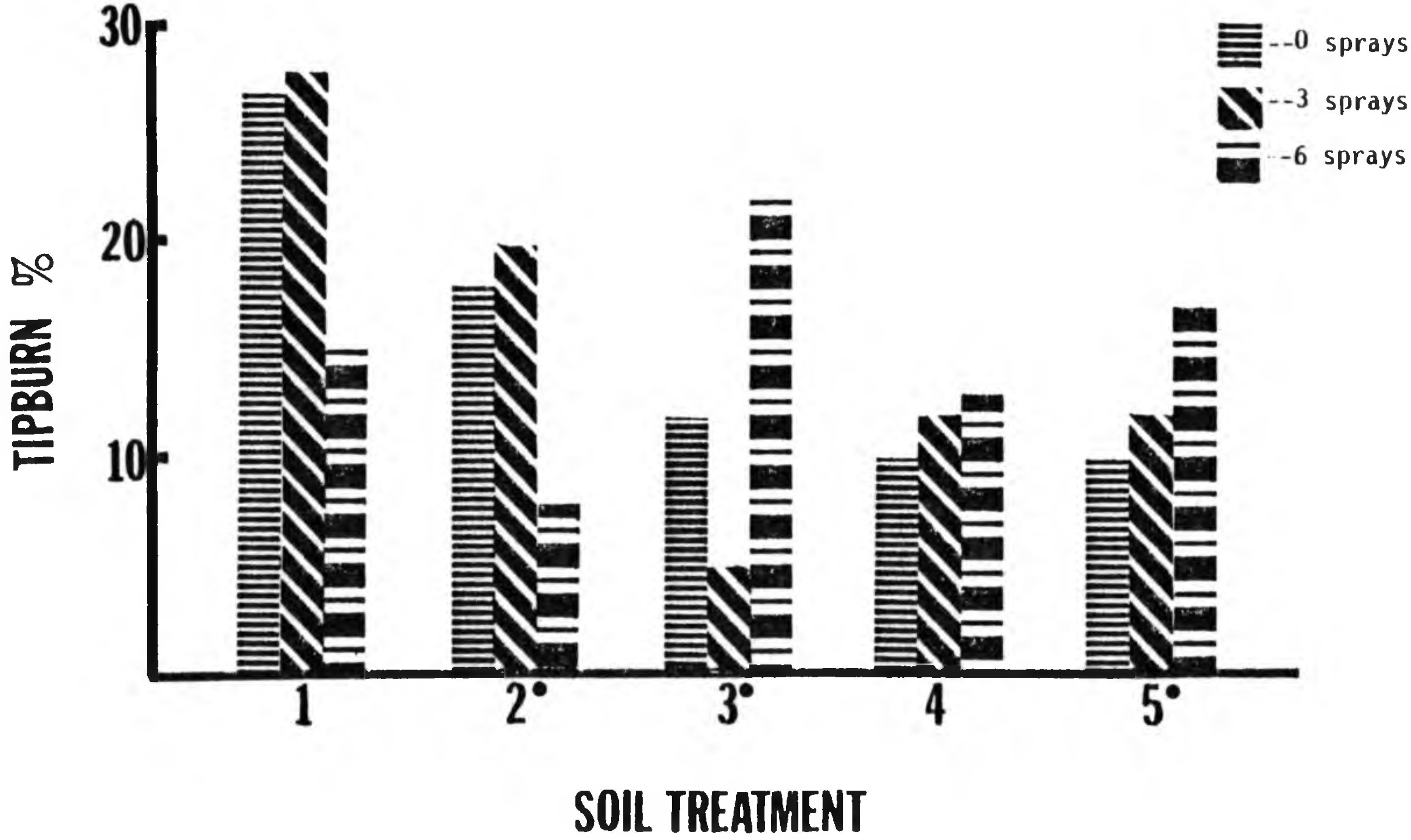

Figure 1. Effect of 0, 3, or 6 foliar sprays and five soil treatments on the incidence of tipburn. Mean separation by Duncan's multiple range test indicate a 1.13% difference between adjacent means to be significant at the 0.05% level. Soil treatments include: 1) and 2) 10-30-10 fertilizer, 3) and 4) Ammonium nitrate, and 5) Calcium nitrate. ● Received calcium hydroxide.

In experiment 8, tipburn incidence in var. Mesa 659 ranged from 45 to 95 percent. Tipburn incidence increased with increasing frequency of spraying. Increasing frequency of spray applications of chelated calcium and Solubor [R] increased the severity of tipburn (Table 11). Tipburn incidence and severity rates are given in Figures 2 and 3.

Table 11. Effect of spray frequency on the severity and incidence of tipburn.

Spray Frequency	Severity*	Incidence
0	2.41b**	67%c
3	2.72b	76%b
6	3.06a	83%a

* Severity based on 1-6 scale
** Mean Separation by Duncan's Multiple Range Test at 0.05% level.

Although there was a high incidence of bacterial rot in the field plots, and the quality of lettuce suffered, all heads were saleable.

Tipburn incidence in var. Monterey varied very little between 90 and 100 percent. Average severity index, regardless of treatments, was 4.50.

No tissue analysis data was available at this time.

Monthly Incidence Rates. Monthly incidence rates of tipburn were taken from December 1979 to August 1980. The incidence rates, calcium and boron levels in the inner and middle leaves, mean monthly minimum and maximum temperature are given in Figures 4, 5, 6, and 7. Coefficient of linear correlation values for tipburn incidence with temperatures and calcium and boron levels are given in Table 12.

Table 12. Correlation values for tipburn incidence with other parameters.

	Correlation Values	Significant at 0.01%	0.05%
Tipburn Incidence with:			
Monthly mean maximum temperature	.95	*	*
Monthly mean mimimum temperature	.80		*
Monthly mean maximum and mimimum temperature	.89	*	*
Calcium (%) in inner leaves	-.75		.754
Calcium (%) in middle leaves	-.52		.754
Boron (ppm) in inner leaves	-.75		.754
Boron (ppm) in middle leaves	-.78		*

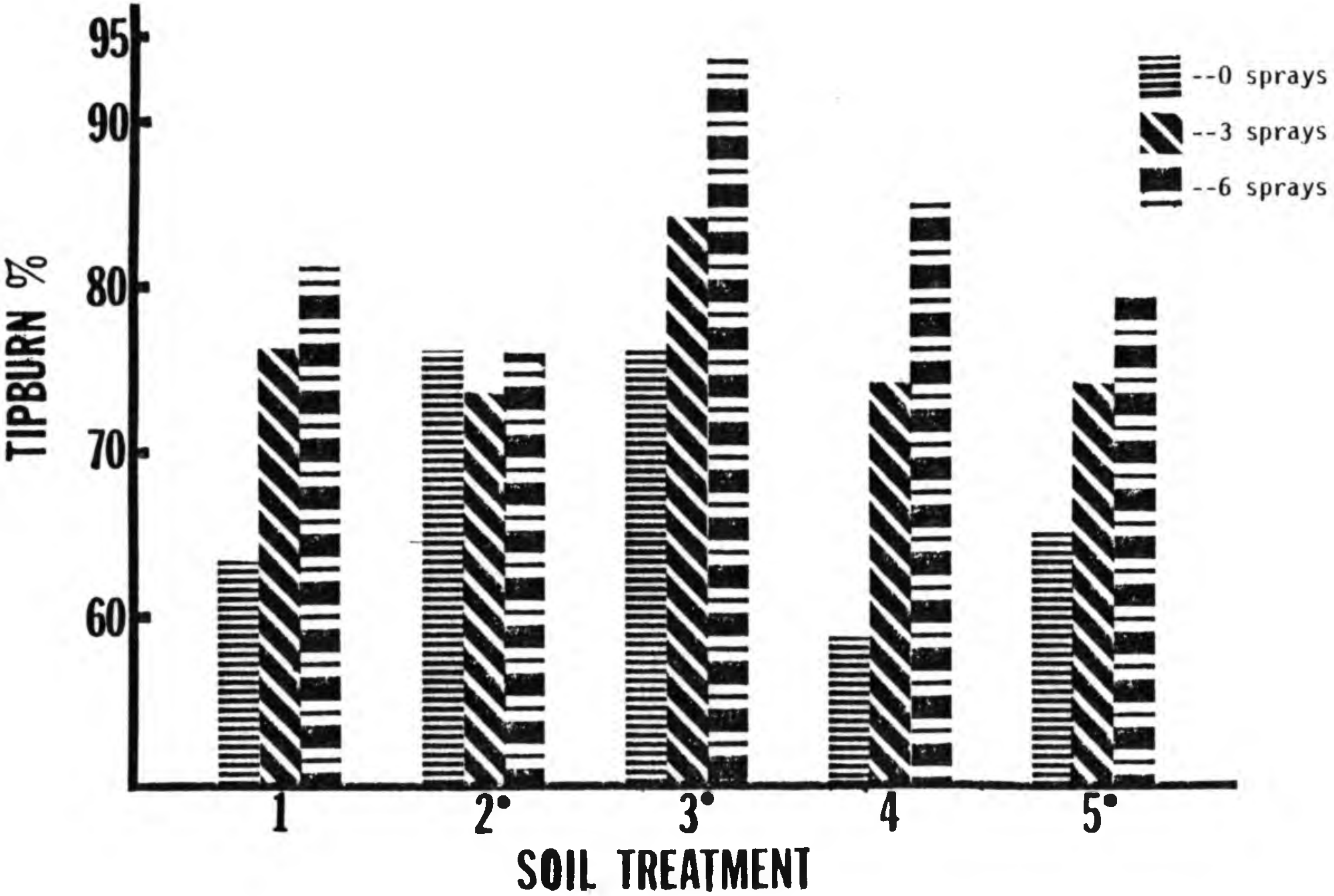

Figure 2. Effect of 0, 3, or 6 foliar sprays and fives soil treatments on the incidence of tipburn. Soil treatments include: 1) and 2) 10-30-10 fertilizer, 3) and 4) Ammonium nitrate, and 5) Calcium nitrate. ●Received calcium hydroxide.

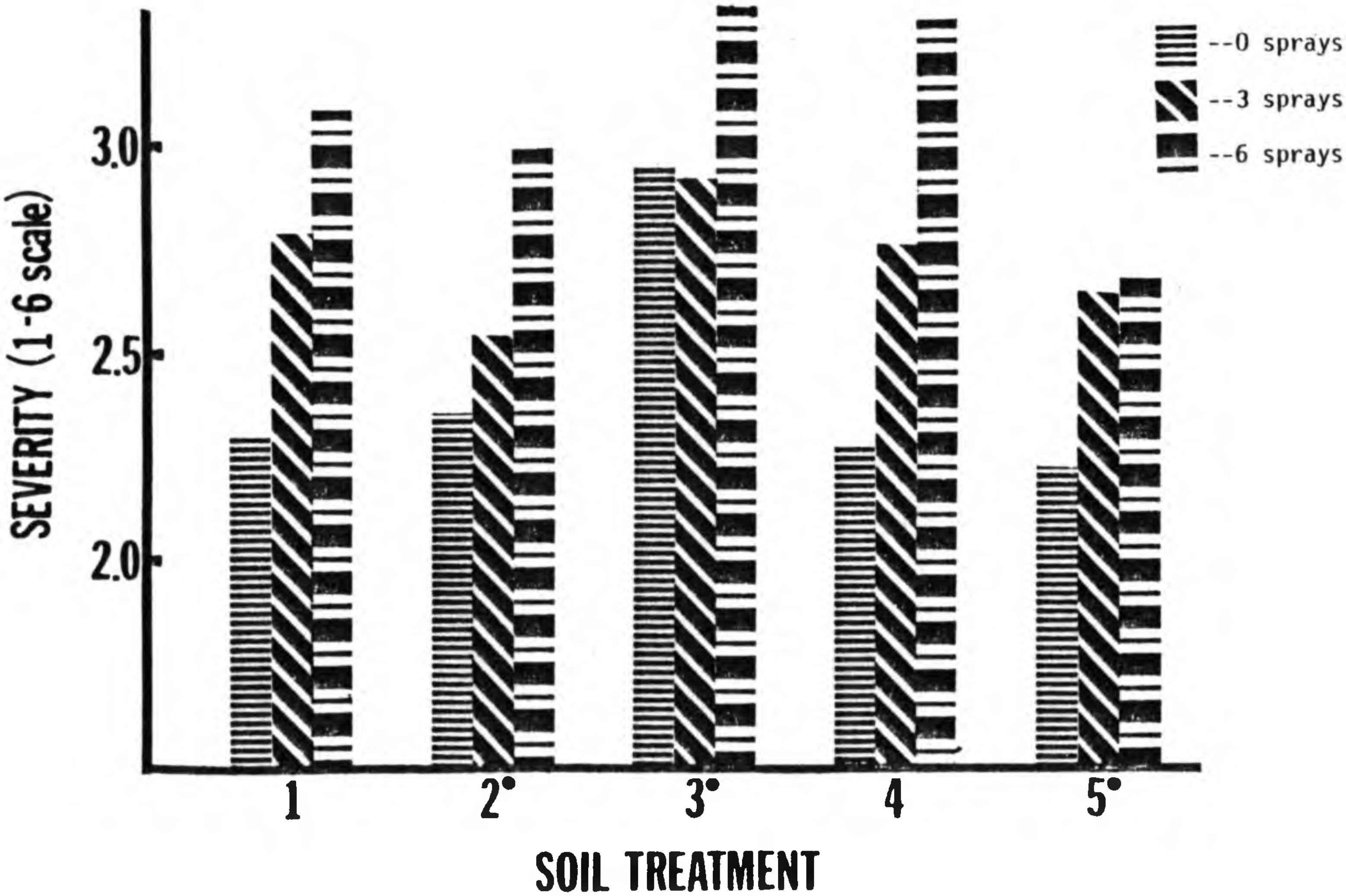

Figure 3. Effect of 0, 3, or 6 foliar sprays and five soil treatments on the severity of tipburn. Soil treatments include: 1) and 2) 10-30-10 fertilizer, 3) and 4) Ammonium nitrate, and 5) Calcium nitrate. ● Received calcium hydroxide.

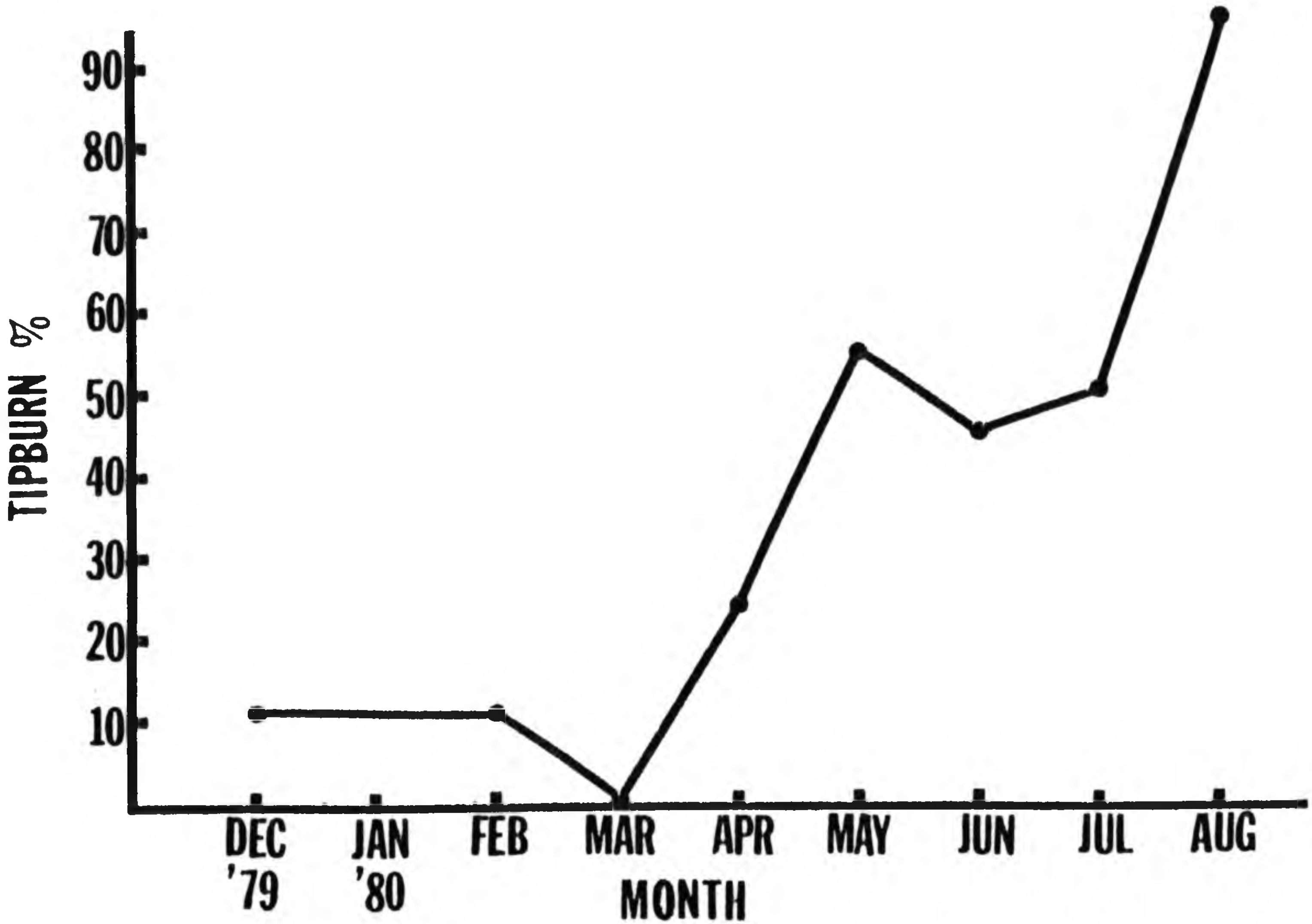

Figure 4. Monthly incidence rates of tipburn (%).

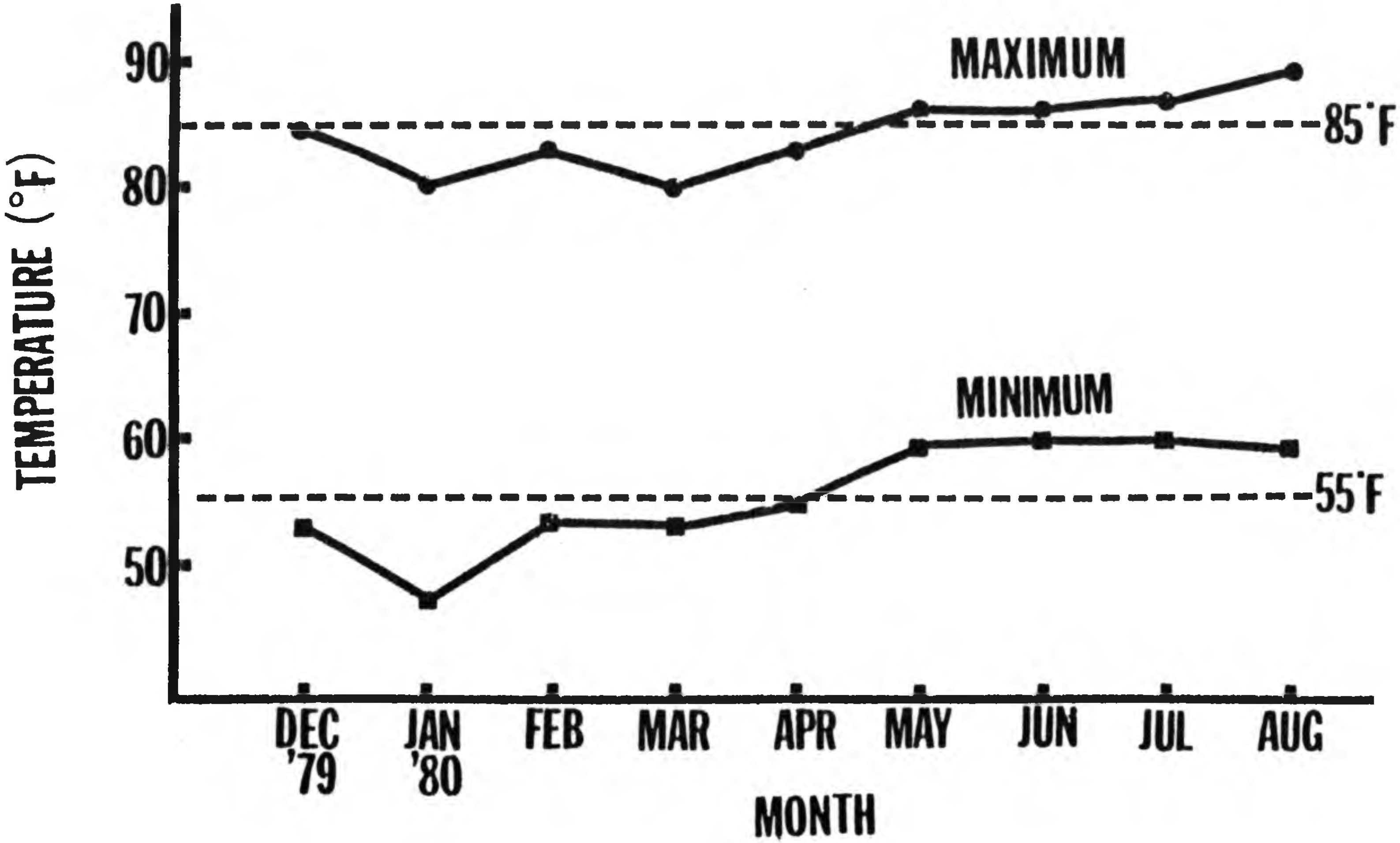

Figure 5. Monthly mean minimum and maximum temperatures for different months of the year.

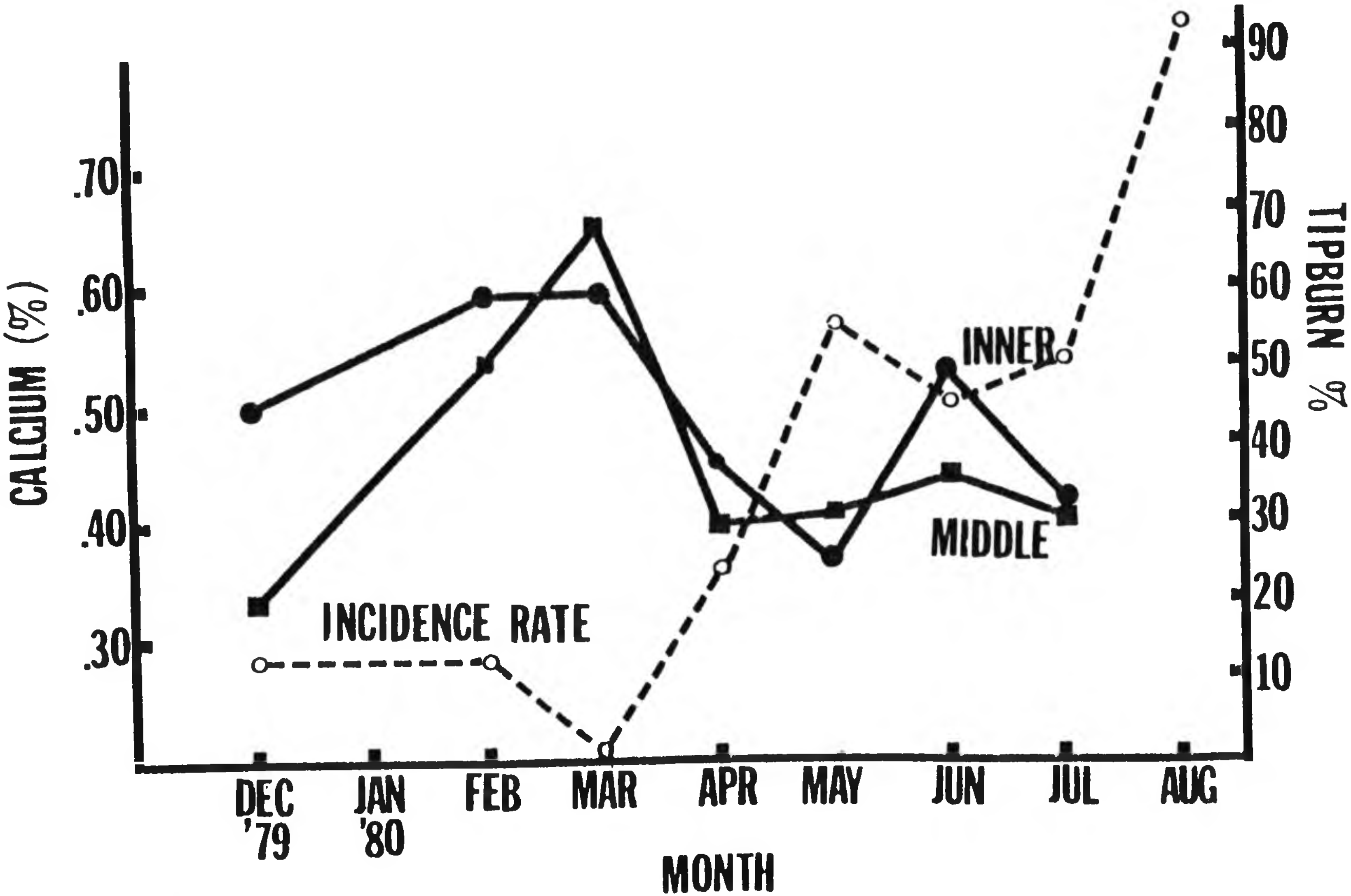

Figure 6. Calcium (%) levels in inner and middle head sections for different months of the year in relation to monthly tipburn incidence rates.

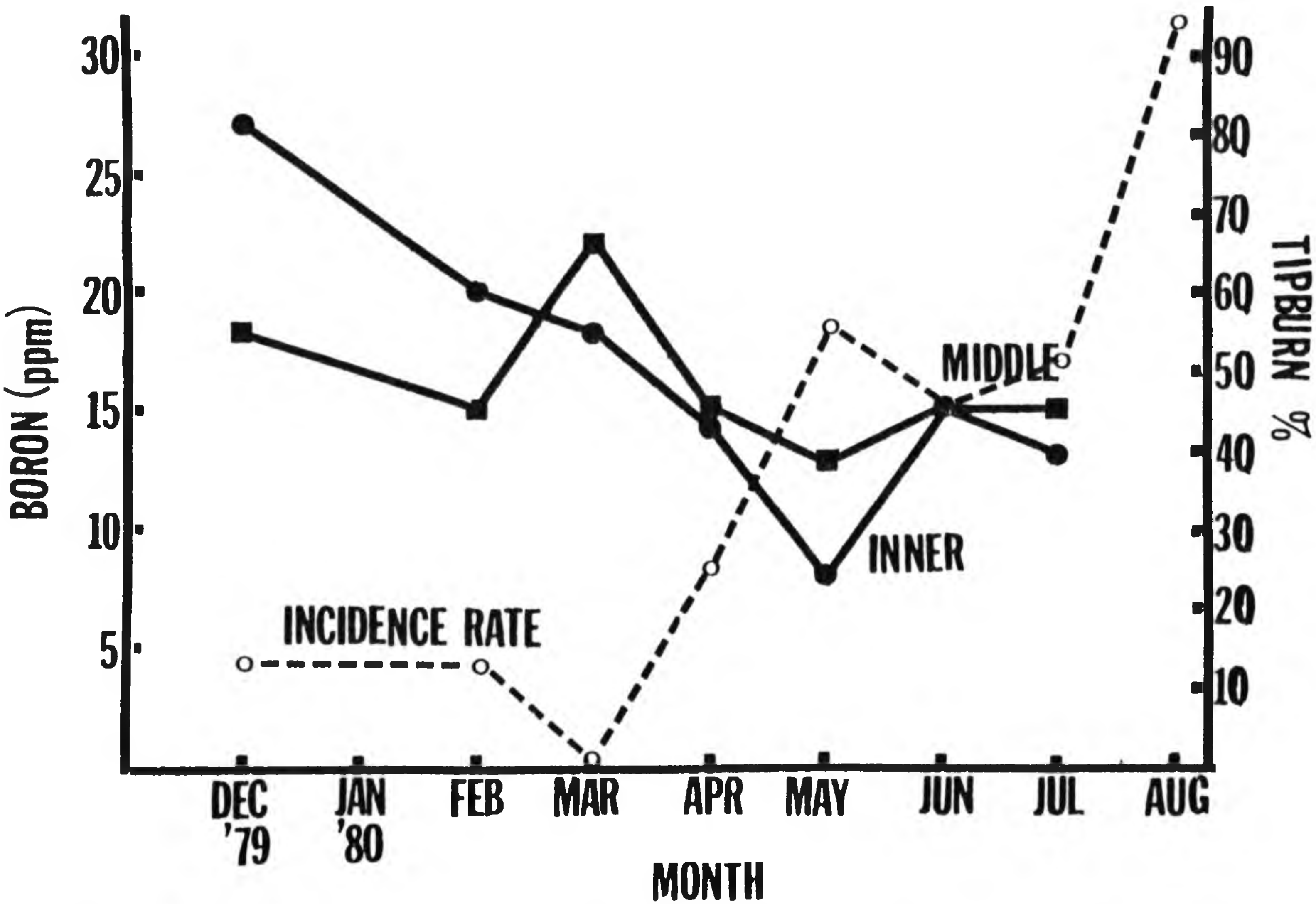

Figure 7. Boron (ppm) levels in inner and middle head sections for different months of the year in relation to monthly tipburn incidence rates.

Discussion

Complete control of tipburn in head lettuce was not achieved under greenhouse or field conditions (Figures 1 and 2). It is felt that there are too many uncontrollable, independent, and interacting factors affecting the calcium nutrition of the plant. Tipburn in head lettuce is recognized as a localized calcium deficiency that affects leaves that are in a phase of rapid growth. The mechanisms by which a calcium deficiency occurs are still unknown, and a localized calcium deficiency can occur even though soil calcium levels are not limiting to calcium uptake (Table 10).

The above conditions are not unique as Ashkar and Ries (1), Kruger (46), Misaghi and Grogan (54), and Thibodeau and Minotti (76) found that under controlled laboratory conditions, they could control tipburn, while Jenkins (39) failed under field conditions. Soil applications of calcium under either field or greenhouse conditions do not always meet the needs of the plant and tipburn can still occur (15, 39, 67).

It is felt from this work that a calcium deficiency is actually a manifestation of another nutrient deficiency, i.e. boron, as boron helps promote the absorption and utilization of calcium by keeping it in a soluble form (48). Boron, apparently increases the permeability of the plant roots to the movement of calcium (10). In addition, deficiency as well as toxicity levels of boron in a substrate may result in subnormal levels of calcium in the tissue (52). There is a fine line between concentration levels that constitute a deficient as compared to a toxic boron condition in the plant, and these levels differ for different plants species (29, 31). It is believed that symptoms of a boron deficiency may be accompanied by those of a calcium deficiency and because of the similarities between the two deficiencies, may be masked as a calcium deficiency, or be mistaken as such (31).

There is some suggestion in the literature that a boron deficiency in latex bearing plants, such as lettuce, interferes with the proper functioning of laticifers so that the laticifers swell and burst with the release of latex, producing tipburn symptoms (73, 81, 82). Latex tipburn is one of the types mentioned by Termohlem and van den Hoeven (75).

Levels of calcium and boron, as determined by tissue analysis, in tipburn susceptible tissues of a lettuce plant are consistently low, (Tables 1, 9, and 10), and never reach standard levels of 1.07-2.15 percent calcium and 25-40 ppm boron in normal, mature leaf tissues (64). Growth restrictions of the plant, with no deficiency symptoms appearing, occur at 0.93-1.29 percent calcium and 20-23 ppm boron (64). Younger, developing tissues may have higher requirements for normal leaf development (29), and levels for field grown lettuce tend to be lower (64). Boron levels in mature leaf tissues were sometimes in the toxic range (Table 4), and this may account for low calcium levels in the tissue.

It is not always easy to detect crop abnormalities with plant tissue analysis alone, especially with calcium and boron deficiencies, where just a small difference in concentration levels can result in either a normal or deficient reaction by the plant (37). Ammonium acetate extraction analysis of soil calcium is a fairly accurate assessment of the available calcium in the soil (38), and analysis show 5000-6000 pounds of available calcium per acre (data not shown). Boron soil analysis is more difficult and less reliable as methods of analysis vary between laboratories.

Outer leaves and core pieces have higher levels of calcium and boron than inner leaves and middle leaves (Tables 6 and 10). Ashkar and Ries (1), Misaghi and Grogan (54), and Thibodeau and Minotti (76) also found evidence to support this. Although calcium and boron levels may be higher in the outer leaves and core pieces, they can be unavailable from these plant tissues to other plant parts, due to a chelation by other metabolites before being incorporated into new cell walls (1, 54, 55). Once deposited in the leaves, these elements will not remobilize to other areas, where they may be of greater need (19, 20, 24). The fact that calcium and boron are immobilized in older plant tissues and are resistant to redistribution creates the biggest problem for the control of tipburn in head lettuce. A large portion of what makes up the edible part of the lettuce plant consists of tissue susceptible to the development of tipburn. These younger, developing tissues are entirely dependent on either the transpiration stream for a continuous supply of calcium and boron or on the older plant parts for a share of their calcium and boron. As redistribution does not occur, the plants must get their calcium and boron through the transpiration stream. Due to head formation, high humidity conditions prevail within the head, and transpiration and the movement of calcium and boron to those leaves in the head are inadequate to meet the tissues' needs when the plant is pushed into a faster growth rate than is normal. Head formation also prevents the accessibility of those leaves to foliar spray applications for corrective measures.

Under greenhouse conditions, foliar sprays of calcium and of calcium and boron reduce the severity of tipburn, but the levels of these elements were not changed significantly as measured by tissue analysis (Tables 3 and 4). The reasons for this are not clearly understood.

Fluctuations in the soil moisture regime from the addition of Perlite[R] to the soil increased the severity of tipburn (Table 3). Previous work on the effect of soil moisture on tipburn support this (56, 77).

The addition of mangesium in soil applications of Dolomite in combination with foliar sprays of calcium and of calcium and boron show the lowest severity ratings (Table 3). Magnesium may be deficient in Hawaiian soils, wherever the high and constant use of ammonium fertilizers occurs, as this initiates a more rapid leaching of soil calcium and magnesium (28). This also suggests that tipburn development may be related to an ion imbalance in the soil (25). Foliar sprays of calcium and of calcium and boron provide evidence for their role in tipburn development.

The nutritional status in lettuce plants can be changed with calcium, boron, or nitrogen fertilizers with almost no effect on tipburn incidence or severity. Calcium soil treatments can help get calcium into the plants (Tables 4, 5, and 10). Soil applications of boron can help put calcium into tipburn susceptible tissues, i.e. inner head sections, (Table 10), but this depends on calcium levels in the substrate, as high levels of liming have been shown to induce a boron deficiency (41, 63).

Foliar sprays of calcium and boron increased boron levels in the plant (Table 7), showing again that calcium and boron together are more effective than either by itself.

Nutrient foliar sprays tend to be variable in their effectiveness, as seen in Table 1, where levels of calcium in different head sections increased or decreased depending on the type of foliar spray applied. In another experiment, however, (Table 4), foliar sprays had little or no effect on calcium and boron levels in the plant. Both experiments were conducted in greenhouses. In a field experiment, foliar sprays had no effect on increasing calcium and boron levels even after three or six foliar sprays of calcium and boron were applied (Table 9). It is not quite understood why foliar sprays work in some instances and fail in others. It may be related to the immobility of calcium and boron in the plant and the inaccessibility of leaves to foliar sprays once head formation starts.

Calcium concentration levels may be important in influencing levels in the tissues, as soil application of calcium in combination with foliar applications of calcium and boron increased levels in plant tissues more than soil applications of calcium or boron alone (Tables 1 and 10). Furthermore, this combination also significantly reduced tipburn incidence, but depended on the soil nitrogen source and the frequency of spraying (Figure 1).

Although the calcium needs of the plant were always supplied, exogenously, plant uptake and translocation did not always prevent the development of tipburn. Through a series of experiments, it was found that soil applications of boron had no effect on tipburn incidence (Table 8). However, these levels may have been too low to have any effect on calcium uptake. Because Hawaiian soils tend to have fairly high retention capacities for boron (59, 74), it is proposed that further studies be conducted to determine how high soil applications have to be, to get saturation levels of calcium and boron in lettuce plants, and how levels of these two elements affect each other in the plant tissues. Such a study may help to solve this tipburn mystery.

The form of nitrogen fertilizers did not always affect the levels of calcium and boron in the plant. Under controlled field greenhouse conditions, higher nitrate nitrogen rates increased boron, calcium and nitrogen levels in the plant tissues (Table 5). Under the influence of nitrate levels, inner leaves have less calcium and boron than the outer leaves (Table 6). This did not happen in field experiment seven, in a comparison of various nitrogen fertilizers and their effects on calcium uptake. Furthermore, boron uptake appeared not to be affected as the tissue levels of both calcium and boron were found to be consistently low (Table 9). Nitrogen rates may have been too low, as 100 pounds of nitrogen per acre was used in the field experiment, and 200 and 400 pounds of nitrogen per acre in the field greenhouse experiment. Also, in the field greenhouse experiment, a preplant soil application of boron may have promoted calcium and nitrogen uptake, as no boron was applied to the soil in the field experiment. This has been reported by Turner (83) and Sankaran, Sennaian, and Morachan (65). Calicum levels could not be a limiting factor to calcium uptake, as calcium was added with the nitrate, and soil tests reveal high amounts of available calcium (data not shown).

The response of head lettuce to different forms of nitrogen depends on the plant species. Differences among species are partly due to the ability of the plants to assimilate nitrogen in the roots, and to the form in which nitrogen is translocated. If nitrogen is translocated from the roots as amino acids, a low cation level can occur in the shoots (3). Hoff, Wilcox, and Jones (36) found higher levels of amino acids in the roots of tomato plants, but Kirkby and Mengel (43) were able to get higher cation levels into tomato plants with nitrate fertilizers. This may be related to concentration effects, and the same thing may have happened in the lettuce plant.

The nitrification process in soils is a dynamic situation, with ongoing conversions between the nitrogen forms going on, and leaching losses occurring. Thus, the plant roots may not have equal access to the different ions and differences in uptake can occur (82).

The occurrence of tipburn may also be related to the presence and balance among the other ions in the soil media (25) or be a matter of ion competition between calcium and ammonium ions (23, 36).

Monthly incidence rates were high (93%) during experiment eight's harvest. In experiment 7, monthly incidence rates were 45% and a soil treatment X spray frequency interaction was highly significant in reducing tipburn incidence. In experiment 8, tipburn severity and incidence rates increased with an increase in spray applications, regardless of soil treatments (Figures 1, 2, 3, and 4). The two experiments did not produce the same results, even though the same soil treatments and same concentrations of calcium and boron were used and given in the same frequencies. This may be attributed to the use of calcium chelate (This [R] Liquid Ca), and the byproducts in that spray. It is a low dosage product, and by using the same calcium level used in experiment 7, the lettuce may have developed toxicity symptoms from the phenolic acids and other byproducts in the solution (23). The frequency of foliar spraying was significant in reducing head weights, (data not shown), and this may have been an expression of toxicity effects.

The main problem with boron availability is not associated with reactivity problems of soluble boron with fertilizer byproducts, but more to problems with uniform dispersal and distribution (67). This may have accounted for such high tipburn incidence and severity rates (Figures 2 and 3).

Monthly incidence rates have a fairly high negative correlation with calcium and boron levels in the inner and middle leaf sections of a head. This provides further evidence that calcium and boron are involved in the development of tipburn. There is a high correlation of tipburn incidence with temperatures, especially mean monthly maximum temperatures. Misaghi and Grogan (54) feel that temperature is the major factor initiating the development of tipburn, as temperatures within the head can be up to 6^{o}C higher than the outside air temperatures. Mean monthly maximum and minimum temperature also have a high correlation with tipburn incidence. There seems to be an increase in tipburn incidence with monthly mean minimum temperatures above 55^{o}F and with monthly mean maximum temperatures above 85^{o}F (Figure 5). This temperature effect may be to increase plant growth rates, even at night, so that calcium and boron uptake cannot match tissue needs and deficiency symptoms appear.

In the greenhouse, succinic acid 2,2-dimethylhydrazide (Alar ^{R}), benzyladenine, and boron sprays in factorial combinations had no effect on tipburn. This may be attributed to greenhouse cultural conditions as high temperatures prevailed, and getting the plants to head properly was a problem. In the field, some reduction in tipburn incidence was achieved, (Table 8), as Alar in combinations with soil applications of calcium and boron show the least tipburn incidence. It is suggested that Alar sprays probably reduced the plant's growth rate, so higher uptake rates and movement of calcium and boron could occur. Boron must have a definite role in influencing the calcuim nutrition of the plant as Alar with soil calcium alone gave a higher incidence rate if boron was not added.

Although Alar reduced the incidence of tipburn, complete control was not attained. Ashkar and Ries (1) also show a reduction in tipburn severity. Growth control is an important factor in controlling tipburn, but the use of Alar sprays commercially, may be impractical in that head weights were reduced, and this may not be acceptable by the lettuce growers. Since Alar affects the growth rate of the plant, perhaps other plant growth regulators which affect the translocation of adsorbed calcium, as seen with an application of ethephon spray (14) can be utilized. Ethephon, alone had no effect on tipburn, but in combination with calcium chloride gave significant reduction in tipburn severity.

A tipburn deficiency in lettuce affects the indoleacetic acid oxidase system and high levels of IAA can occur in the plant (17). It is believed that this affects the growth rate of the plant, but it is unknown whether nutrient adsorption and translocation are affected.

References Cited

1. Ashkar, S.A. and S.K. Ries (1971). Lettuce Tipburn as Related to Nutrient Imbalance and Nitrogen Composition. J. Amer. Soc. Hort. Sci. 96:448-452.

2. Bangerth, F. (1979). Calcium Related Physiological Disorders of Plants. Ann. Rev. Phytopathol. 17:97-122.

3. Barker, A.V. and D.N. Maynard (1972). Cation and Nitrate Accumulation in Pea and Cucumber Plants as Influenced by Nitrogen Nutrition. J. Amer. Soc. Hort. Sci. 97:27-30.

4. Bert, J.S., Jr. and S. Honma (1975). Effect of Soil Moisture and Irrigation Method on Tipburn and Edgeburn Severity in Greenhouse Lettuce. J. Amer. Soc. Hort. Sci. 100:278-282.

5. Borkowski, J. and J. Ostrzycka (1973). The Control of Blossom-end Rot of Tomato and Tipburn in Lettuce by Using the Proper Fertilization. Acta Horticulturae 29:327-339.

6. Bottenburg, G. and T.W. Tibbitts (1968). Lettuce Growth and Tipburn Incidence Under Controlled Humidity. Hort. Sci. 3:124.

7. Bowen, J.E. (1972). Effect of Environmental Factors on Water Utilization and Boron Accumulation and Translocation in Sugarcane. Plant and Cell Physiol. 131:703-714.

8. Buneman, G. and P. Ludders (1970). Calcium Uptake and "Calcium Deficiency Disorders" of Plants Under the Influence of Other Nutrients. J. Aust. Institute of Ag. Sci. 36:285-291.

9. Burstrom, H.G.(1968). Calcium and Plant Growth. Biol. Rev 43:287-316.

10. Carolus, R. (1975). Calcium Relationships in Vegetable Nutrition and Quality. Comm. in Soil Sci. and Plant Analysis 6:285-298.

11. Carsner, E. (1947), Studies on Tipburn of Sugar Beet and Lettuce. Phtyopath. 37:360.

12. Chang, S.Y., R.H. Lowe, and A.J. Hiatt (1968). Relationship of Temperature to the Development of Calcium Deficiency Symptoms in <u>Nicotiana tabacum</u>. Agronomy J. 60:430-435.

13. Chapman, H.D. (1966). <u>Diagnostic Criteria for Plants and Soils</u>. Univ. of Calif. Press, Berkeley. pp33-92.

14. Corgan, J.N. and D.J. Cotter (1971). The Effect of Several Chemical Treatments on Tipburn of Head Lettuce. Hort. Sci. 6:19-20.

15. Cox, E.F. and A.S. Dearman (1976). Effect of Water and Calcium on Lettuce Tipburn. 27th Ann. Rept. U.K. Natn. Veg. Res. Stn. 1976:59-60.

16. --------, J.M.T. McKee, and A.S. Dearman (1976). The Effect of Growth Rate on Tipburn Occurrence in Lettuce. J. Hort. Sci. 51:297-309.

17. Crisp, P., E.F. Collier, and T.H. Thomas (1976). The Effect of Boron on Tipburn and Auxin Activity in Lettuce. Sci. Hort. 5:215-226.

18. Drake, M., D.H. Sieling, and G.D. Scarseth (1941). Calcium-Boron Ratio as an Important Factor in Controlling the Boron Starvation of Plants. J.Amer. Soc. Agron. 33:454-462.

19. Epstein, E. (1972). Flow in the Phloem and the Immobility of Calcium and Boron: A New Hypothesis in Support of an Old One. Experientiae 29:133-134.

20. -----------(1972). Mineral Nutrition of Plants: Principles and Perspectives. John Wiley & Sons, Inc., N.Y. 412 pp.

21. Foy, C.D. (1974). Effects of Soil Calcium Availability on Plant Growth in Plant Root and Its Environment. E.W. Carson (ed.), University Press of Virginia, Charlottesville. pp 565-600.

22. ---------, R.L. Chaney, and M.C. White (1978). The Physiology of Metal Toxicity in Plants. Ann. Rev. Plant Phys. 29:511-566.

23. Gardner, B.R. and W.D. Pew (1979). Comparison of Various Nitrogen Sources for the Fertilization of Winter-grown Head Lettuce. J. Amer. Soc. Hort. Sci. 104:534-536.

24. Gauch, H.G. (1972). Inorganic Plant Nutrition. Dowden, Hutchinson, & Ross, Inc., Stroudsburg, Pennsylvania. 488pp.

25. Geraldson, C.M. (1970). Intensity and Balance Concept as an Approach to Optimal Production in Recent Advances in Plant Nutrition Vol. 2, R.M. Samish (ed.), Gordon & Breach Science Publishers, N.Y. pp352-364.

26. Gerard, C.J. (1971). Influence of Osmotic Potential, Temperature, and Calcium on Growth of Plant Roots. Agronomy J. 63:555-558.

27. Green, R.E., R.L. Fox, and D.D.F. Williams (1965). Soil Properties Determine Water Availability to Crops. Hawaii Farm Science 14:6-9.

28. Green, R.E., M. Mori, and W.W. McCall (1962). Soil Acidification Under Flower Culture in the Kula Area. Hawaii Farm Science 11:4-7.

29. Gutpa, U.C. (1979). Boron Nutrition in Crops. Advances in Agronomy 31:273-307.

30. ----------- and J.A. Cutcliffe (1972). Effects of Lime and Boron on Brown-heart, Leaf Tissue Calcium/Boron Ratios, and Boron Concentrations of Rutabagas. Soil Sci. Amer. Proc. 36:936-939.

31. ---------- and --------------(1975). Boron Deficiency in Cole Crops Under Field and Greenhouse Conditions. Comm. in Soil Sci. and Plant Analysis 6:181-188.

32. Hanger, B.C. (1979). The Movement of Calcium in Plants. Comm. in Soil Sci. and Plant Analysis 10:171-193.

33. Hawaii Agricultural Reporting Service (1979). Statistics of Hawaiian Agriculture 1979. Hawaii Dept. of Ag. Marketing and Consumer Service Division and U.S.D.A. Economics, Statistics, & Cooperative Service. Honolulu. 96pp.

34. Haynes, J.L. and W.R. Robbins (1948). Calcium and Boron as Essential Factors in the Root Environment. J. Amer. Soc. Agron. 40:795-803.

35. Hiatt, A.J. and J.E. Legget (1974). Ionic Interactions and Antagonisms in Plants in Plant Root and Its Environment, E.W. Carson (ed.), University Press of Virginia, Charlottesville. pp101-134.

36. Hoff, J.E., G.E. Wilcox, and C.M. Jones (1974). The Effect of Nitrate and Ammonium Nitrogen on the Free Amino Acid Composition of Tomato Plants and Tomato Fruits. J. Amer. Soc. Hort. Sci. 99:127-130.

37. Ishizuka, Y. (1971). Nutrient Deficiencies of Crops. Food and Fertilizer Technology Center, Taiwan. pp 1-11.

38. Jackson, T.L. (1980). Personal Communication.

39. Jenkins, J.M., Jr. (1959). Brown Rib of Lettuce. Proc. Amer. Soc. Hort. Sci. 71:587-590.

40. Jones, L. (1892). Greenhouse Diseases. Vt. Agri. Expt. Stn. Rept.--5th Annual 84-85.

41. Kamprath, E.J. and C.D. Foy (1971). Lime-Fertilizer Plant Interactions in Acid Soils in Fertilizer Technology and Use, 2nd Edition. Soil Sci. Soc. of Amer. Inc., Madison. pp105-152.

42. Kirkby, E.K. (1979). Maximimzing Calcium Uptake. Comm. in Soil Sci. and Plant Analysis 10:89-113.

43. -------------and K. Mengel (1967). Ionic Balance in Different Tissues of the Tomato Plant in Relation to Nitrate, Urea, or Ammonium Nurtition. Plant Phys. 42:6-14.

44. --------------and A.H. Knight (1977). Influence of the Level of Nitrate Nutrition on Ion Uptake and Assimilation, Organic Acid Accumulation, and Cation-Anion Balance in Whole Tomato Plants. Plant Phys. 60:349-353.

45. Kohl, H.C., Jr. and J.J. Oertli (1960). Distribution of Boron in Leaves. Plant Phys. 35:420-424.

46. Kruger, N.S. (1966). Tipburn of Lettuce in Relation to Calcium Nutrition. Queensland J. Agri. and Ani. Sci. 23:379-385.

47. Leh, H.O. (1970). Investigation of Tipburn of Lettuce With Special Reference to Nutrient Uptake. AachrBl. dt. Pflschutzdients, Stuttg. 22:86-89.

48. Marsh, R.P. (1942). Comparative Study of the Calcium-Boron Metabolism of Representative Dicots and Monocots. Soil Sci. 53:75-78.

49. Mc.ginty, R.A. and R.C. Thompson (1925). Preliminary Notes on Tipburn of Lettuce. J. Amer. Soc. Hort. Sci. 22:341-346.

50. McHargue, J.S. and R.K. Calfee (1932). Effect of Boron on the Growth of Lettuce. Plant Phys. 7:161-164.

51. -----------and------------(1933). Further Evidence That Boron is Essential for the Growth of Lettuce. Plant Phys. 7:305-313.

52. Minarik, C.E. and J.W. Shive (1939). The Effect of Boron in the Substrate on Calcium Accumulation by Soybean Plants. Amer. J. Botany 25:827-831.

53. Misaghi, I.J. and R.G. Grogan (1978a). Effect of Temperature on Tipburn Development in Head Lettuce. Phytopath. 68:1738-1743.

54. ----------and----------(1978b). Physiologial basis for Tipburn Development in Head Lettuce. Phytopath. 68:1744-1753.

55. ----------and R.G. Grogan, and C.D. Day (1977). Comparison of Respiratory Metabolites in Healthy and Tipburn Lettuce Plants. Proc. Amer. Phyto. Soc. 4:102.

56. Newhall, A.G. (1925). Studies on the Tipburn Disease of Lettuce. Phtyopath. 15:727-728.

57. Oertli, J.J. (1963). The Influence of Certain Environmental Conditions on Water and Nutrient Uptake and Nutrient Distribution in Barley Seedlings With Special Reference to Boron. Advancing Frontiers of Plant Sci. 6:55-85.

58. ----------and W.F. Richardson (1970). The Mechanisms of Boron Immobility in Plants. Phys. Plant. 23:108-116.

59. Okazaki, E. and T.T. Chao (1968). Boron Adsorption and Desorption by Some Hawaiian Soils. Soil Sci. 105:255-259.

60. Pearson, R.W. (1975). Soil Acidity and Liming in the Tropics. Cornell Int. Ag. Bull. 30. 66pp.

61. Quebedeaus, B., Jr. and J.L. Ozbun (1973). Effects of Ammonium Nutrition on Water Stress, Water Uptake, and Root Pressure in Lycopersicon esculentum Mill. Plant Phys. 52:677-679.

62. Rawlins, T.E. and R.L. McClain (1925). Tipburn and "Slime" Diseases of Lettuce in California. Phytopath. 5:727-728.

63. Reeve, E. and J.W. Shive (1944). Potassium-Boron and Calcium-Boron Relationships in Plant Nutrition. Soil Sci. 57:1-14.

64. Roorda van Eysinga, J.P.N.L. and K.W. Smilde (1971). Nutritional Disorders in Glasshouse Lettuce. Centre for Agr. Publishing and Documentation, Wageningen. 56 pp.

65. Sankaran, N., p. Sennaian, and Y.B. Morachan (1977). Effects of Forms and Levels of Calcium and Levels of Boron on the Uptake of Nutrients and Quality of Groundnut. Madras Ag. J. 64:384-388.

66. Scaufem N.A. and D.T. Clarkson (1978). Calcium Related Disorders in Plants--A Possible Explanation for the Effect of Weather. Plant and Soil 50:723-725.

67. Sauchelli, V. (1969). <u>Trace Elements in Agriculture</u>. Van Nostrand Reinhold Company, N.Y. 247 pp.

68. Schmidt, R. (1930). Final Report of Field Plot Experiments and Observations on the Cause of Lettuce Tipburn. 53th Annual Report N.C. Agri. Expt. Stn. 53:127-133.

69. Shear, C.B. (1975). Calcium Related Disorders of Fruits and Vegetables. Hort. Sci. 10:361-365.

70. Shear C.B. and M Faust (1970). Calcium Transport in Apple Trees. Plant Phys. 45:670-674.

71. Sonneveld, C and J van den Ende (1975). The Effect of Some Salts on Head Weight and Tipburn of Lettuce and on Fruit Production and Blossom-end Rot of Tomatoes. Neth. J. Agri. Sci. 23:191-201.

72. Stone, G.E. and R.E. Smith (1900). The Rotting of Greenhouse Lettuce. Mass. Agri. Expt. Bull. 69. 40 pp.

73. Stuckmeyer, B.E. and T.W. Tibbitts (1965). Anatomy of Lettuce Leaves Grown With a Complete Nutrient Supply and Without Calcium or Boron. Proc. Amer. Soc. Hort. Sci. 87:324-329.

74. Tamimi, Y.N. and D.T. Matsuyama (1977). The Role of Fertilizers in Hawaiian Soils. 11th Annual Hawaii Fert. Conference 1977. 20 pp.

75. Termohlen, G.P. and A.P. van den Hoeven (1966). Tipburn Symptoms in Lettuce. Acta Hort. 4:105-108.

76. Thibodeau, P.O. and P.L. Minotti (1969). The Influence of Calcium on the Development of Lettuce Tipburn. J. Amer. Soc. Hort. Sci. 94:372-376.

77. Thompson, R.C. (1926). Tipburn of Lettuce. Colo. Agri. Extn. Bull. 311. 31 pp.

78. Tibbitts, T.W. (1979). Humidity and Plants. Bioscience 29:358-363.

79. ------------and G. Bottenburg (1976). Growth of Lettuce Under Controlled Humidity Levels. J. Amer. Soc. Hort. Sci. 10:70-73.

80. ------------and R. Rama Rao (1968). Light Intensity and Duration in the Development of Lettuce Tipburn. J. Amer. Soc. Hort. Sci. 93:454-461.

81. ------------and M. Read (1976). Rate of Metabolic Accumulation into Latex of Lettuce and Proposed Association With Tipburn Injury. J. Amer. Soc. Hort. Sci. 101:406-409.

82. ------------, B.E. Struckmeyer, and R. Rama Rao (1964). Tipburn of Lettuce as Related to Release of Latex. Proc. Amer. Soc. Hort. Soc. 86:462-467.

83. Tisdale, S.L. ans W.L. Nelson (1975). <u>Soil Fertility and Fertilizers, 3rd Edition</u>, Macmillan Publishing Co. Inc., N.Y. 694 pp.

84. Turner, J.K. (1970). Boron in Agriculture. U.S. Borax and Chemical Corporation, Los Angeles. 40 pp.

85. van den Ende, J., P. Koornneef, and C. Sonneveld (1975). Osmotic Pressure of the Soil Solution: Determination and Effects on Some Glasshouse Crops. Neth. J. Agri. Sci. 23:181-190.

86. Wallace, A. and R.T. Mueller (1980). Calcium Uptake and Distribution in Plants. J. Plant Nutrition 2:247-256.

87. ----------, E.M. Romney, R.T. Mueller, and G.V. Alexander (1980). Calcium-Trace Metal Interactions in Soybean Plants. J. Plant Nutrition 2:79-86.

88. Welch, N.C., K.B. Tyler, and D. Ririe (1979). Nitrogen Stabilization in the Pajaro Valley in Lettuce, Celery, and Strawberries. California Ag. 33:12-13.

89. Zink, F.W. and M. Yamaguchi (1962). Studies on the Growth Rate and Nutrient Absorption of Head Lettuce. Hilgardia 32:471-500.