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EFFECTS OF CYTOKININ-CONTAINING PRODUCTS ON THE GROWTH AND PHYSIOLOGY OF LETTUCE

The University of Arizona M.S. 1986

EFFECTS OF CYTOKININ-CONTAINING PRODUCTS ON THE GROWTH AND PHYSIOLOGY OF LETTUCE

by

Jose Gabriel Vitoria Levy

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For the Degree of

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In the Graduate College

THE UNIVERSITY OF ARIZONA

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Finally, I would like to dedicate this work to my father and my deceased mother for the interest and support they always gave to me.

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ABSTRACT

Field and greenhouse trials were designed with varieties of crisphead and butterhead lettuce (Lactuca sativa L.) to evaluate the performance of benzyladenine and Burst (trademark name for a chemical purported to contain cytokinin-like properties).

In the field, application of Burst to crisphead lettuce at a rate of 1.18 ℓ/ha produced no significant differences in fresh and dry weights, leaf area, head size, and number of leaves, when compared to controls. Maturity in treated plants was not affected either.

In the greenhouse, experiments were performed with butterhead lettuce grown in pot or hydroponically. Foliar applications of Burst at the rate of 1.18 ℓ/ha (adjusted to a per pot basis), and soil applications at the rate of 1 Burst: 500 water (v/v) to pot grown plants had no significant effects on growth parameters or on transpiration, stomatal resistance and photosynthesis when compared to controls.

In hydroponic experiments in the greenhouse, application of benzyladenine at a concentration of 5×10^{-7}M to the nutrient solution produced a significant decrease in fresh leaf and root weights, dry leaf and root weights, and leaf area of treated plants. Photosynthesis was significantly increased in treated plants.

At the recommended rates and timing of applications, Burst had no effect on increasing maturity and yields.

CHAPTER 1

INTRODUCTION

Plant growth substances play a very important role in plant growth and development. Although the naturally occurring growth substances regulate several plant growth processes, application of exogenous growth substances may modify plant growth for the benefit of man.

Cytokinins have been used extensively in the past to attempt to modify some of the metabolic processes occurring in the plant. The term cytokinin is universally accepted as a generic name for substances which promote cell dividion and exert certain growth regulatory functions.

In 1961, Miller isolated a naturally occurring cytokinin from immature maize kernels, which he called zeatin. Zeatin is an N6 substituted adenine found in RNA. The t-RNA fraction of RNA is especially rich in zeatin. Barnes (1980) reported on the production of cytokinins in potato (Solanum tuberosum) cells, mainly zeatin riboside. He showed that up to 40% of the free cytokinins are due to breakdown of t-RNA. In the years following the discovery of zeatin, several other cytokinins were isolated from various sources. All the naturally occurring cytokinins are considered to be isopentyl adenine derivatives.

Cytokinin containing extracts have been isolated from several hundred species of higher plants and it is confidently assumed now that

cytokinins are present throughout the plant kingdom and in the t-RNA fraction of numerous animals and microorganisms.

Currently, the number of synthetic cytokinins with biological activity has increased to several hundred. Numerous derivatives of adenine have been synthesized, and many are as active as cytokinins.

Several urea type cytokinins have also been tested and are active in cytokinin assays. Though these urea type cytokinins seem to be less effective than the adenine type cytokinins, they showed a similar range of biological activities, including cell division stimulation in tobacco tissue culture, lettuce seed germination, axillary bud growth, and delay of senescence in detached leaves.

Many studies have been conducted on the effects of synthetic cytokinins on horticultural crops, including vegetables. Benzyladenine (BA) and kinetin have been the subjects of extensive studies. Seaweed extracts containing natural cytokinins have been used broadly in the formulation of commercial products such as Burst, Cytex, Seaman 600, and Kelpac 66. Burst increased yields in watermelons, cantaloupes and bell peppers, and is being tested on several other vegetable crops including lettuce (unpublished data). Burst is manufactured by Burst Agritech, Inc., of Overland Park, Kansas.

To further evaluate the capability of Burst to act as a plant growth regulator, we performed a series of experiments whose objectives were: (a) to determine the effects of foliar applications of Burst on fresh and dry weights, leaf area, head size, and number of leaves of

crisphead lettuce plants under field conditions; (b) to determine the effects of foliar and soil applications of Burst on fresh and dry weights, leaf area, number of leaves, net photosynthesis, transpiration, and diffusive resistance of butterhead lettuce grown in pots in a greenhouse; (c) to determine the effects of root applications of benzyladenine on the above-mentioned parameters in butterhead lettuce grown hydroponically in a greenhouse.

CHAPTER 2

LITERATURE REVIEW

Cytokinin Isolation and Activities

Cytokinins are a major class of plant growth regulating substances. Their definite discovery occurred in 1955, due mainly to the works of Miller, Skoog, von Saltza and Strong. They discovered a cytokinin which they called kinetin because of its specific ability to bring about cytokinesis in cells of tobacco pith. Later, in 1963, the first natural cytokinin was isolated from corn (Zea mays) and was termed zeatin.

Free cytokinins are found in higher plants and are excreted by a number of microorganisms, mainly bacteria and fungi. They have specific biological effects in living tissues. In tissue culture, kinetin plays a major role in plant differentiation. Skoog and Miller (1957) discovered that with a particular combination of concentrations of kinetin and indoleacetic acid, the pith of tobacco tissues could give rise to buds or to roots. Thus, morphogenesis can be controlled to a high degree by varying the amounts of the two types of growth hormones in the culture medium. Cytokinins are also an important factor in the regulation of cell division, especially mitosis. Nishinari and Syono (1980) showed a relationship between cytokinin levels and mitotic index. They

found that the highest peaks in cytokinin levels of cultured tobacco cells corresponded to the highest mitotic index. They concluded that cytokinin control comes at the G2 phase or in the transition from G2 to mitosis.

Senesence of detached mature leaves of certain plants can be delayed by the application of cytokinins such as kinetin or benzyladenine. Richmond and Lang (1957) discovered that kinetin could delay senescence in detached leaves of cocklebur (Xanthium). This delay is probably due to the ability of kinetin to reduce or prevent the accelerated protein loss typical of detached leaves, and at the same time, to delay the loss of chlorophyll and extend the life span of the leaf. These studies were further investigated by Mothes and Englebrecht (1961). They sprayed kinetin directly to excised leaves and found that only those areas where kinetin was sprayed remained green. Thus, the effect was quite localized. Also, the treated areas of yellowing leaves became greener. Fuller, Kuhnle, Corse and Mackey (1977) were able to increase broccoli storage life at 13 C by 2 to 3 days by making single treatments with 100 ppm aqueous solutions of two natural cytokinins, zeatin and dihydrozeatin. Usually, broccoli without cytokinin treatment remains salable for only two days at that temperature. The anti-senescence effects of cytokinins are further supported by studies with excised carnation flowers (Eisinger, 1977). By applying kinetin to cut carnation flowers, he was able to expand their life span. He suggested that kinetin might be replacing the natural cytokinins which are normally supplied to the flower by the parent plant.

Through a series of studies using radioactive amino acids and non-radioactive kinetin, Mothes and Engelbrecht (1961) found that the amino acids migrated to and accumulated in the areas of the leaves treated with kinetin. Thus, by causing mobilization of metabolites to the sites of application, cytokinins are able to create new source-sink relationships in the plant.

Further research on growth substances has revealed the hormonal regulation mechanisms of plant growth and development. These experiments have led to the development and use of synthetic growth substances in agriculture, where they have the potential to play a role almost equal to that of fertilizers and pesticides. At the present time, plant growth regulators are used to control fruit set and development, abcission, senescence, rate of growth, onset and termination of dormancy and rest, and several other metabolic processes.

Crop Responses to Cytokinins

Production costs have spiralled in recent years as fertilizer and other costs have increased; and thus, supplements or alternatives to fertilizers have been sought. Several hundred synthetic substances containing cytokinin-like activity have been manufactured and tested with various degrees of success in different plant species.

Cytex, one of these manufactured substances, has been tested in several crops including peanuts (Arachis hypogaea L.) and potatoes. Cytex is a water soluble seaweed extract, containing a cytokinin activity equivalent to 100 ppm kinetin as calibrated using a bioassay.

Ketring and Schubert (1981) applied four rates of Cytex to several peanut cultivars at different growth stages. Some increases in yield were obtained but they were unable to obtain consistent and significant effects on reproduction of peanuts with foliar Cytex sprays. Foliar application of Cytex to 'Russet Burbank' potatoes in Idaho (Dwelle and Hurley, 1984) produced no measurable response. They may be due to manufacture of sufficient natural cytokinins by this cultivar under conditions in Idaho. Van Staden and Brown (1979) had reported earlier that potato tubers synthesize and supply cytokinins for initial bud growth. Lang and Langille (1984) reported an increase in total yield of 'Kennebec' when Cytex was applied at a concentration of 15 ml/liter during the initial stages of tuberization.

Featonby-Smith and Van Staden (1984) detected several significant differences on the growth and cytokinin content of Phaseolus vulgaris L. plants when Kelpac 66 was applied to the leaves. The levels of endogenous cytokinins were higher in treated than in control plants.

Seamac 600 had no significant effects on onion yield, bulb size or maturity (McGeary and Birkenhead, 1984), but in trials conducted by the manufacturer Seamac 600 significantly increased the yield of onion bulbs by 9.2 and 13.6%. The poor response of onion plants may be due to the plant's small leaf area and poor penetration through the thick waxy cuticle by foliar sprays.

Cytozome, a chemical purported to have cytokinin-like activities, was evaluated in a greenhouse (Ryan, Saghir, Shafyuddin, and Barsumian,

1982). Under the conditions of the trials, no significant effects were found on leaf weight, number of leaves, root length, weight, yield, or sucrose content of sugar beet, corn, and tomato plants.

Laibi (1985) showed that Burst had no statistically significant effects on growth parameters and yield of bell peppers (Capsicum annum L.). Very little literature has been published on studies with Burst, except for some local extension service reports. William Sims (1986) from the Cooperative Extension Service at the University of California, Davis, reported no significant effects of Burst on yield, earliness, or fruit quality of two tomato cultivars. Also, Tim Hartz, an Extension Vegetable Specialist at Texas A&M University, Weslaco, found no benefits of application of Burst to production of cantaloupes (Cucumis melo) or watermelon (Citrullus lanatus) (unpublished data). On the other hand, experiments conducted by the company manufacturer of Burst showed significant increases in yield of several vegetable crops such as broccoli, cantaloupe, squash, tomato, sweet corn, potato and pepper. It is also being recommended for application on several other vegetable and grain crops. Most of the trial work with Burst has been conducted by the manufacturer and very few results have been published.

Kinetin, benzyladenine and other cytokinins have been widely tested on vegetable and cereal crops though they have not been cleared for commercial use. Arteca (1982) found that kinetin increased the relative growth rates, total leaf area and total dry weight in two tomato (Lycopersicon esculentum Mill.) cultivars. This product was applied to the roots of plants grown in hydroponics. Barley (Hordeum

vulgare L.) yields were increased up to 57% following benzyladenine treatment at the preheading stage (Williams and Cartwright, 1980). This increase was attributed to increased weights of the individual kernels. Benzyladenine applications to leaves of bean plants showed that it can stimulate the growth of a treated whole leaf and at the same time bring about the inhibition of growth in other untreated leaves on the same plant (Leopold and Kawase, 1964). This observation is consistent with the apparent mobilizing action of cytokinins.

Sharma and Gupta (1972) reported an increase in flower numbers following foliar application of cytokinin to tomato plants. Grayburn, Green and Steucek (1982) conducted several tests with benzyladenine, kinetin and 6-(y,y-dimethylallylamino) purine (DMAAP) to evaluate the effects of these cytokinins on bud induction of detached leaves of Graptopetalum paraquayense E. Walther. They found that DMAAP was the most effective in stimulating bud induction and the higher the concentration, the sooner the appearance of leaf primordia and the higher the ultimate yield of buds. Mulgrew and Williams (1985) found that application of benzyladenine (Picea pungens Englm. trees at the time of bud break caused an increase in bud development, but these buds failed to elongate the following growing season and did not increase branching.

As can be seen, cytokinins produce a wide range of effects on crops, and when tested and used properly, the benefits can be enormous.

Cytokinins and Stress Interactions

The roots of unstressed plants produce cytokinins which are translocated to the upper part of the plant through the xylem. Itai,

Richmond and Vaadia (1968) exposed roots of sunflower (Helianthus annus), bean and tobacco plants to increased osmotic values in the nutrient medium, which resulted in decreased translocation of cytokinins from the roots. This decrease was reversible and upon termination of the stress, the cytokinin activity of the root exudate increased. They also observed a decline in the protein synthesis potential of the leaves brought about by the root stress, confirming the idea of influence of cytokinins on protein synthesis.

It is not known exactly whether the hormonal modifications that occur under certain circumstances in a plant exposed to osmotic root stress result directly from a modification of the plant water balance or from a decrease in root water potential. Mizrahi and Richmond (1971) studied the effects of application of kinetin to stressed tobacco plants grown in a nutrient solution. They reported an increase in the water potential of the leaves, which may be due to the effects of cytokinins on stomatal opening and transpiration. They further suggested that addition of cytokinins to cytokinin-deficient, stressed plants does not alleviate the symptoms of water stress, but rather intensifies them. In another similar study, Mizrahi, Blumenfeld, Bittner and Richmond (1971) found no change in the amount of extractable cytokinins when tobacco plants were placed under osmotic stress. Prisco and O'Leary (1973) studied the effects of BA application on salt stressed plants grown under high and low relative humidity. At low humidity, BA had no effect on plant growth. However, at high humidity, BA either had no effect or inhibited the growth of the plants by increasing stomatal resistance. Kinetin applied simultaneously with NaCl to seeds of

tomato, barley and cotton, was able to reduce the stress response to a certain extent and cause the breakage of osmotically induced dormancy (Bozcuk, 1981). This was probably due to an increase in the rate of protein synthesis, which was reduced under salt stress conditions. In an earlier study, Katz, Dehan and Itai (1978) were able to reverse either partially or completely the inhibitory effects of NaCl by applying kinetin to leaf discs of tobacco.

Cytokinins and Gas Exchange

Increases in rates of transpiration after application of cytokinins have been reported in several studies. Kirkham, Gardner and Gerloff (1973) observed an increase in transpiration rates of plants sprayed with kinetin. Apparently, kinetin causes the stomata to remain open, causing an increase in both stomatal conductance and water loss. Since stomata are involved in the regulation of gas exchange between plant leaves and the environment, stomata will affect both transpiration and photosynthesis. Livne and Vaadia (1965) observed stimulation by kinetin of transpiration rates and stomatal opening in barley leaves. Similar results were reported by Meidner (1969). Recently, Laibi (1985) reported inconsistent and nonsignificant effects on the rate of transpiration when Burst was applied to the roots of hydroponically grown green pepper plants. Similar results were obtained when kinetin was used.

Very few studies have been performed on the effects of cytokinins on photosynthesis. Laibi (1985) reported no significant differences in rates of photosynthesis when Burst was applied to the roots

of green pepper plants. In a similar experiment by Laibi, kinetin failed to produce any significant differences. Dong and Arteca (1981) showed that application of kinetin to roots of tomato plants was able to stimulate photosynthesis for two days, but after that, this parameter decreased. Later, the same authors (1982) confirmed that kinetin was able to stimulate photosynthesis and growth when applied to roots of tomato plants grown under hydroponics.

CHAPTER 3

MATERIALS AND METHODS

Three different sets of experiments were conducted to evaluate the effects of Burst (a commercial cytokinin) and benzyladenine (a non-commercial cytokinin) on several growth and physiological parameters of lettuce (Lactuca sativa L.) plants.

The field experiments with Burst were located in the three main lettuce growing regions of Arizona: Cochise, Yuma and Pinal Counties. In these areas, the trials were made in farmers' fields using different cultivars of lettuce for each experiment.

Two experiments were performed in the University of Arizona greenhouses. Butterhead lettuce cultivars were chosen for their speed in reaching maturity and relative ease of growth compared to crisphead lettuce.

In the following pages, each experiment will be discussed individually.

Experiment 1

Three field trials were made separately in Cochise, Yuma and Pinal Counties, using different cultivars of crisphead lettuce. In Cochise, the trials were started in the spring of 1985 and the cultivar used was 'Vanguard.' In the fall of 1985, trials were started in Yuma

and Pinal with the cultivars 'Viva' and 'Desert Queen' respectively. The plants were grown according to commercial practices with planting in Cochise during January and in Pinal and Yuma during September. The lettuce was grown in raised beds with two rows of lettuce per bed. The plants were furrow irrigated.

When approximately 50% of the plants had five leaves emerged (March 18 in Cochise, October 8 in Yuma, and October 12 in Pinal), the first foliar application of Burst was conducted. A second application was made two weeks after the first, and a third was made to weeks after the second. The application rate was 1.18 l/ha each time and the plants were sprayed to saturation. This rate is recommended by the company. To each treated plot was applied a one-liter solution containing 0.54 ml of Burst diluted in water (equivalent of 1.18 l/ha). Some plants were sprayed with water alone to serve as a check or control for comparison to the Burst treatment. All spraying was performed with a hand-held sprayer. Each trial was a randomized complete block design with five replications. Plot size for individual treatments was 1 meter by 4.6 meters (or one bed 4.6 meters long).

Heads were evaluated for maturity prior to harvest by feeling the heads and rating them as mature, almost mature, immature or no head. See Appendix A for explanation of terms. Total plants per plot were also counted so that percentages could be calculated. Plants which did not form heads were not harvested, although the number of these per plot was noted. Outer leaves on heads were removed down to the cap leaves when harvesting.

Head size, fresh weight, leaf number, leaf area, and dry weight were measured. Dimensions of each head were recorded using a device which compresses the head slightly with even pressure. This device gives a more reliable estimate of dimensions because it reduces air space between leaves. Head width, length and height were multiplied to give a rough estimate of head size. Whole heads were weighed to determine fresh weights prior to taking leaf numbers. The number of leaves was recorded for each head with the first counted being the outer cap leaf and the last counted being 1.5 cm long. Leaf area was measured on 20% of heads selected randomly. Leaves were placed side by side on a grid marked in square centimeters, and total area covered by the leaves was recorded. After taking leaf number and area, the leaves were dried in paper bags at 45 C for three days. After drying, the leaves were reweighed to determine dry weights. For heads from Pinal, only head size and fresh weight were measured due to a bacterial rot problem which prevented storage of heads long enough to take leaf number and leaf area.

Data were analyzed via t-tests.

Experiment 2

This experiment was conducted in a greenhouse during early spring of 1986. The purpose was to study the effects of soil and foliar application of Burst on the growth and physiology of butterhead lettuce grown in pots. The variety 'Ostinata' was chosen because it is often used commercially in greenhouse lettuce production.

Two treatments and two controls were used: (a) foliar application of Burst at the recommended rate (1.18 l/ha) adjusted to a per plant basis; (b) soil application of Burst at the rate of 1 Burst: 500 water (v/v); (c) application of water to the foliage; (d) no application of water to the foliage. Since no recommendations were available for soil application of Burst, preliminary studies were made in order to determine a suitable concentration. Ten different concentrations ranging from 1:1000 (v/v) to 1:50 (v/v) were tried, and 1:500 was the one that was able to stimulate growth to the largest extent.

Three seeds were planted in 60 15.2 cm pots containing a soil mixture of 2 peat: 1 perlite: 1 vermiculite (v/v/v). Adequate moisture was applied to the pots for germination. Osmocote, a controlled release fertilizer (19-6-12) was applied at the rate of 8 g/pot (about 1300 cm^3 of soil mixture in a 15.2 cm pot).

The pots were divided in 3 groups of 20. The reason is that after each Burst application the plants were harvested so that fresh and dry weights and leaf area could be measured. Since two applications and one final harvest had to be made, 3 groups of pots were needed.

The plants were arranged in a randomized complete block design with five replications. The first Burst application was made when approximately 50% of the plants were at the fifth leaf stage, and two weeks later the second application was made. Since butterhead lettuce grown under greenhouse conditions grows very rapidly, it was decided that a third application, as recommended for crisphead lettuce grown in the field, would not be necessary.

During the course of this greenhouse study, temperatures ranged from a daytime maximum of 29 C to a nighttime minimum of 12 C. Relative humidity ranged from 12% to 91%.

The following parameters were measured 24 hours before and 24 hours after each Burst application: net photosynthesis, transpiration and stomatal resistance. Fresh and dry weights, number of leaves and leaf area were measured 24 hours after each Burst application.

For measurements of transpiration and stomatal resistance, an LI-1600 Steady State Porometer was used. Readings were taken from the middle lighter green and partly unfolded leaves. For photosynthesis, the amount of carbon dioxide consumed by an enclosed plant over a certain period of time was measured. Elapsed times were 90 seconds for young plants and 120 seconds for older plants. A plexiglass chamber of a known volume was used to obtain gas samples to be analyzed by an infra red gas analyzer. Two syringes were inserted into the chamber through a port and about 6 cm^3 of gas were drawn. The chamber was tightly sealed around the plant so that no other sources of CO_2 would interfere. This sealing was done by cutting in half a circular piece of styrofoam and placing it on top of the pot soil. A small hole was cut in the middle so the stem could pass through. The chamber was then placed on top of the foam and sealed with a caulking material. As soon as the plant was in place, the first syringe was pulled. After the alloted time elapsed, the second syringe was pulled. The difference in carbon dioxide levels between the two syringes was the amount consumed by the plant in photosynthesis. Net photosynthesis was calculated by integrating this value

with other data such as volume of the chamber, ambient temperature, atmospheric pressure, plant leaf area and time elapsed between sample drawings. See Appendix B for calculation method used. Fresh and dry weights, leaf number and leaf area were determined as explained in Experiment 1.

Data were analyzed via F-tests. Treatment means were compared using the least significance difference (LSD) test.

Experiment 3

This experiment was conducted in a greenhouse at the University of Arizona during late spring 1986. The purpose was to study the effects of application of benzyladenine (Sigma Chemical Company, St. Louis, Missouri) on the growth and physiology of butterhead lettuce var. 'Ostinata' grown hydroponically.

Seeds of lettuce were planted in a Speedling tray containing vermiculite. Adequate moisture was applied for germination. At approximately the third leaf stage, the plants were removed from the Speedling trays, the soil washed off the roots and placed in a hydroponic solution. The nutrient medium is described in Appendix C. The temperature in the nutrient solution was maintained at approximately 27 C. pH ranged from 6.8 to 7.0.

Benzyladenine was applied to the nutrient solution at a concentration of 5×10^{-7}M. Preliminary studies were made to determine a suitable concentration of benzyladenine. Five concentrations ranging from 5×10^{-6} to 5×10^{-8}M were tested, and 5×10^{-7}M produced the best

response. These are the concentrations usually used for plant applications (Pietraface and Blaydes, 1981; Mizrahi, Dostal, McGlasson and Cherry, 1975). Higher concentrations do not dilute readily in water. No concentrations were found toxic though 5×10^{-6}M caused some wilting at certain periods.

One benzyladenine treatment and one control were used. As a control, autoclaved water was applied because benzyladenine was dissolved by autoclaving. The first application of benzyladenine was made when approximately 50% of the plants were at the fifth leaf stage, and two weeks later the second application was made. The plants were previously divided in two groups of 12. One of the groups was treated once and harvested after the second treatment, and the other group was treated twice and harvested after the second treatment.

Net photosynthesis was measured 24 hours before and 24 hours after each treatment. Fresh and dry weights and leaf area were measured 24 hours after each treatment.

The plants were arranged in a randomized complete block design with six replications. There were 6 tubs for each treatment, with 2 plants per tub.

The methods used in the measurements were the same as those described in the previous experiments.

Data were analyzed via t-tests.

CHAPTER 4

RESULTS AND DISCUSSION

Experiment 1

Table 1 shows the effect of Burst on size of crisphead lettuce in Cochise County. Burst had no statistically significant effect on fresh weight, head size, leaf number, leaf area or dry weight. However, for each of the size parameters shown, means were slightly higher for plants treated with Burst compared to control plants. Perhaps, the variability between plants and small sample size was responsible for the lack of significance.

Table 2 shows the effect of Burst on maturity of crisphead lettuce prior to harvest in Cochise County. Nine days before the first harvest no differences in maturity were observed between Burst and control plants. Five days before the first harvest there were slightly more mature and almost mature heads in control plots than in Burst plots. However, these differences were not statistically significant.

Table 3 shows the effect of Burst on the percentage of heads harvested from a given area on two dates in Cochise County. On May 18, the first harvest, a slightly higher percentage of heads were harvested from control plots than Burst plots. These data are in agreement with the fact that control plots had slightly more heads, almost mature, and mature heads at five days prior to harvest. On May 25, the second

Table 1. Effect of Burst on Size of Crisphead Lettuce in Cochise County

Treatment[Z]	Fresh Weight (g)	Head Size (cm^3)	Leaf Number	Leaf Area (cm^2)	Dry Weight (g)
Control	416 a[Y]	1723 a	15.9 a	2983 a	19.8 a
Burst	418 a	1740 a	16.4 a	3110 a	20.2 a

Z Control sprayed with water
Burst applied foliarly at 1.18 ℓ/ha

Y Values in columns followed by same letter are not significantly different based on t-test at 5% level.

Table 2. Effect of Burst on Maturity of Crisphead Lettuce Prior to Harvest in Cochise County.

Days Before First Harvest	Treatment[Z]	% of Heads[Y]		
		Immature	Almost Mature	Mature
9	Control	99.3	0.0	0.7
9	Burst	99.3	0.0	0.7
5	Control	81.4	15.0	3.6
5	Burst	84.3	12.9	2.8

Z Control sprayed with water
Burst applied foliarly at 1.18 ℓ/ha

Y Total number of heads for Burst and Control plots was 140 each

Table 3. Percentage of Mature Heads at Two Harvesting Dates in Cochise County.

Harvest Date	Treatment[Z]	% of Mature Heads
May 18	Control	76
	Burst	73
May 25	Control	91
	Burst	91

Z Control sprayed with water
Burst applied foliarly at 1.18 ℓ/ha

harvest, both control and Burst plots had similar percentage of heads harvested.

Figures 1 and 2 show fresh weight and head volume when broken down as percentage in various increments. All of these figures show no trend for control or Burst to have heavier or larger heads.

Tables 4 and 5 show effects of Burst on size of crisphead lettuce in Pinal and Yuma, respectively. Plants treated with Burst only were not significantly different from control plants for fresh weight, head size, leaf number, leaf area or dry weight, except for head size at Pinal and dry weight at Yuma, where controls were significantly higher than Burst.

Tables 6 and 7 show effects of Burst on maturity of crisphead lettuce at harvest in Pinal and Yuma, respectively. No major differences in percentages of mature or almost mature heads were observed at either location. At Pinal, but not Yuma, a higher percentage of immature heads were found in Burst plots. Percentages of plants forming no heads tended to be higher in control plots, although this difference was very small.

Figures 3, 4, 5 and 6 show fresh weight and head volume when broken down as percentage in various increments. All of these figures, as for Cochise, show no trend for control or Burst to have larger or heavier heads.

Based on these data, Burst had no overall positive or negative effect on size or maturity of lettuce heads. We would not advise using

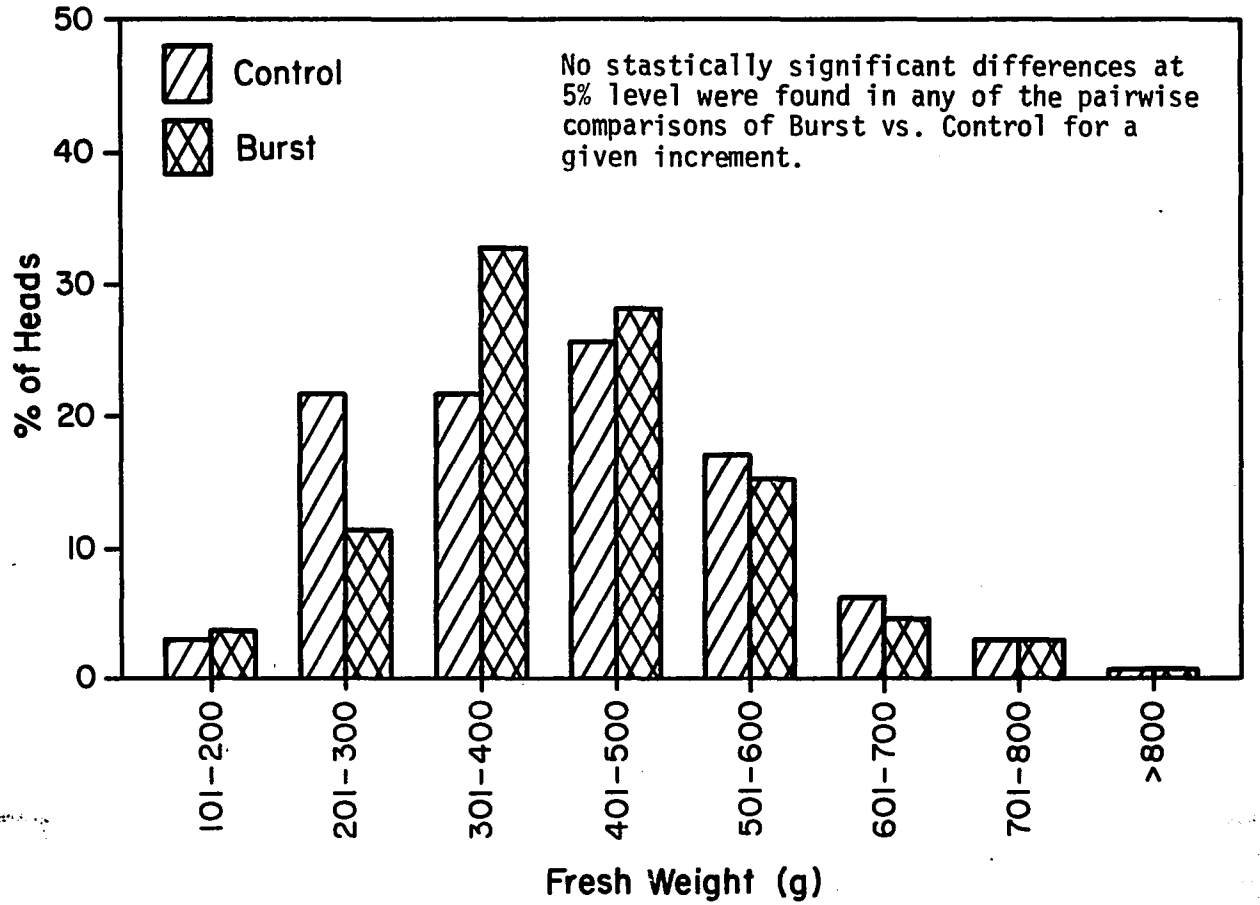

Figure 1. Percentage of Heads Per 100 g Increments in Fresh Weight (Cochise County)

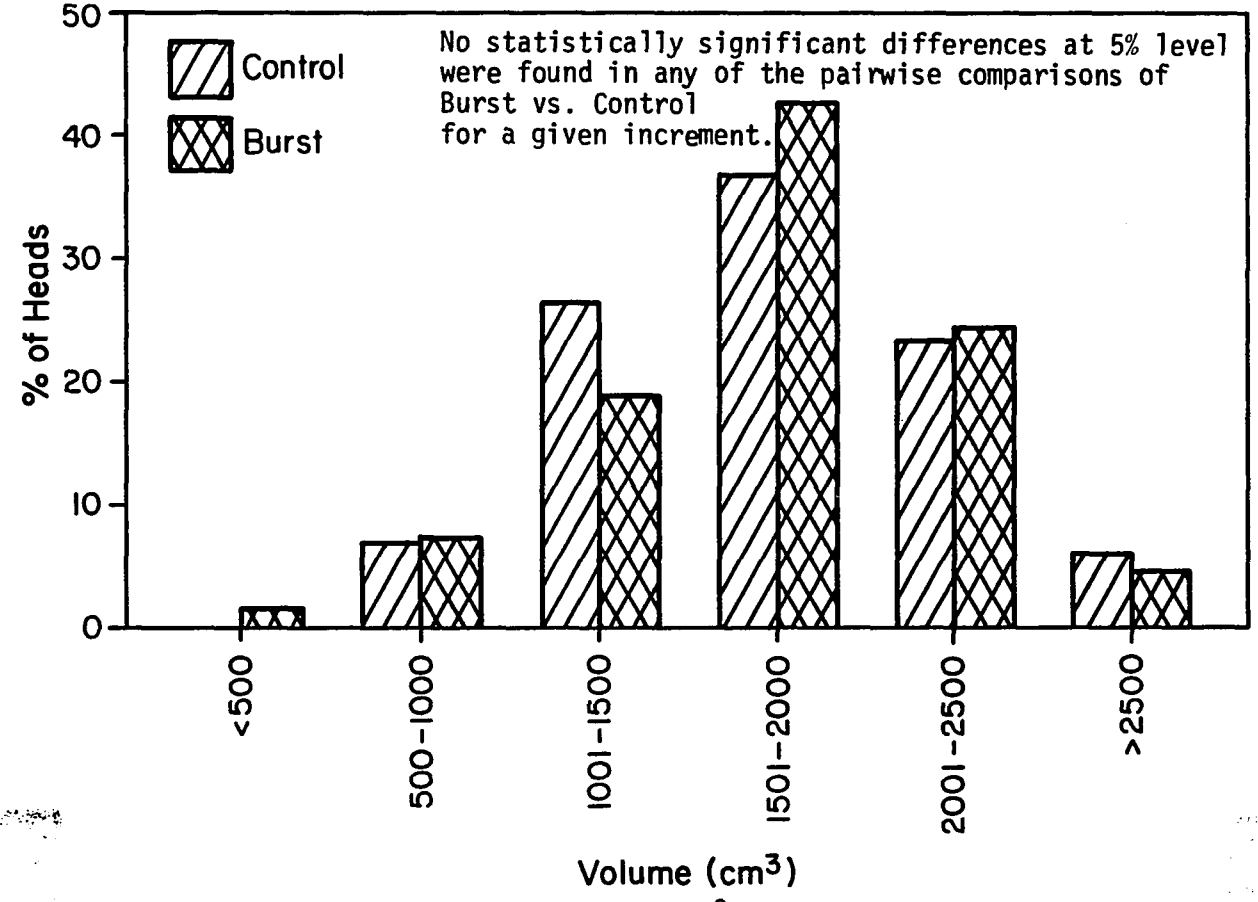

Figure 2. Percentage of Heads per 500 cm^3 Increments in Volume (Cochise County)

Table 4. Effect of Burst on Size of Crisphead Lettuce in Pinal County

Treatment[Z]	Fresh Weight (g)	Head Size (cm^3)
Control	425 a[Y]	1976 a
Burst	485 a	1856 b

Z Control sprayed with water
Burst foliarly applied at 1.18 ℓ/ha

Y Values in columns followed by same letter are not significantly different based on t-test at 5% level.

Table 5. Effect of Burst on Size of Crisphead Lettuce in Yuma County

Treatment[Z]	Fresh Weight (g)	Head Size (cm^3)	Leaf Number	Leaf Area (cm^2)	Dry Weight (g)
Control	442 a[Y]	1963 a	13.9 a	2827 a	17.0 a
Burst	441 a	2008 a	13.9 a	2673 a	14.6 b

Z Control sprayed with water
Burst applied foliarly at 1.18 ℓ/ha

Y Values in columns followed by same letter are not significantly different based on t-test at 5% level.

Table 6. Effect of Burst on Maturity of Crisphead Lettuce in Pinal County

Treatment[Z]	Number of Heads	% of Heads[Y]		
		Immature	Almost Mature	Mature
Control	3.5	13.9	13.0	69.6
Burst	0.8	20.5	12.3	66.4

Z Control sprayed with water
Burst foliarly applied at 1.18 ℓ/ha

Y Total number of heads in Burst treated plots was 124
Total number of heads in control plots was 117

Table 7. Effect of Burst on Maturity of Crisphead Lettuce in Yuma County

Treatment[Z]	Number of Heads	% of Heads[Y]		
		Immature	Almost Mature	Mature
Control	2.5	1.9	24.4	71.2
Burst	0.6	0	26.3	73.1

Z Control sprayed with water
Burst foliarly applied at 1.18 ℓ/ha

Y Total number of heads in Burst treated plots was 159
Total number of heads in control plots was 156

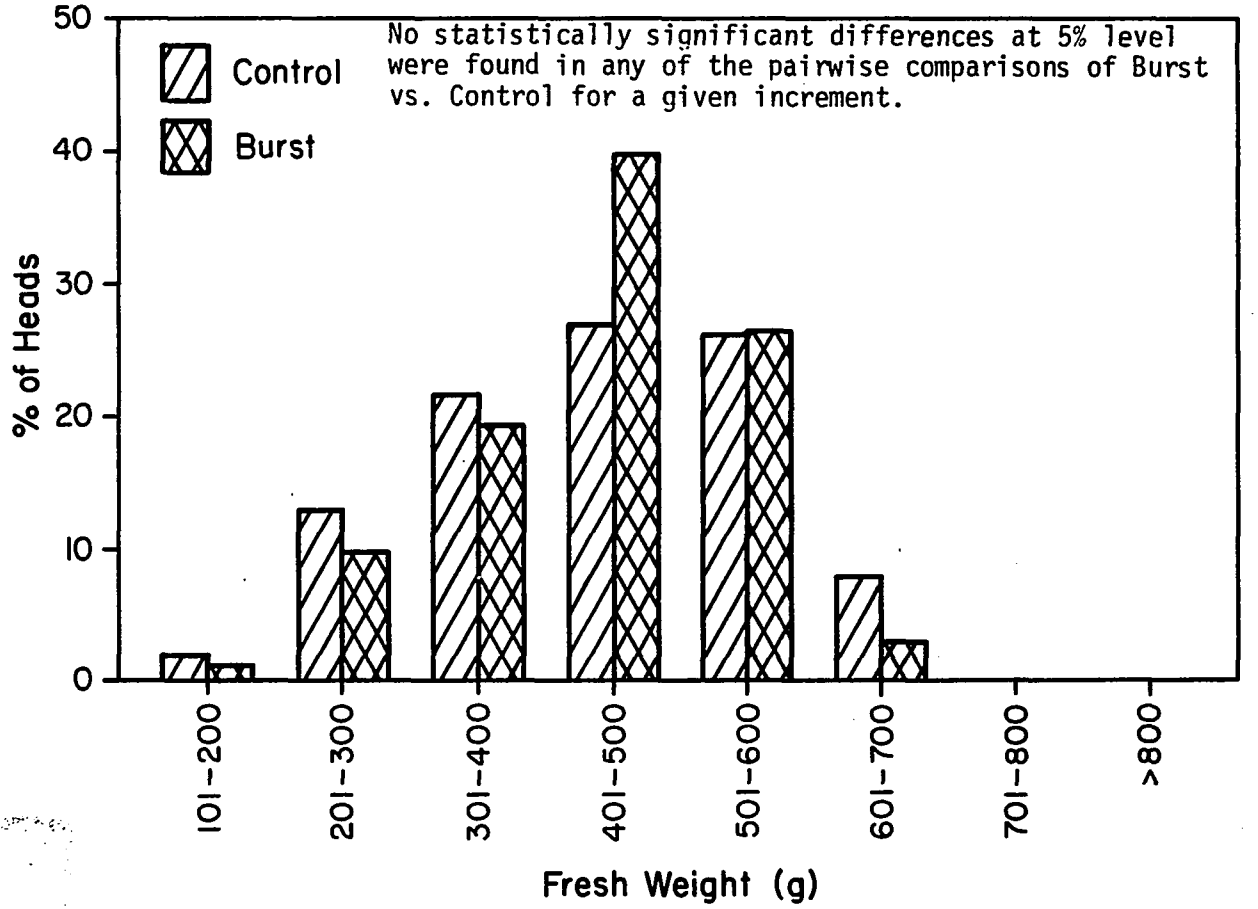

Figure 3. Percentage of Heads per 100 g Increments in Fresh Weight (Yuma County).

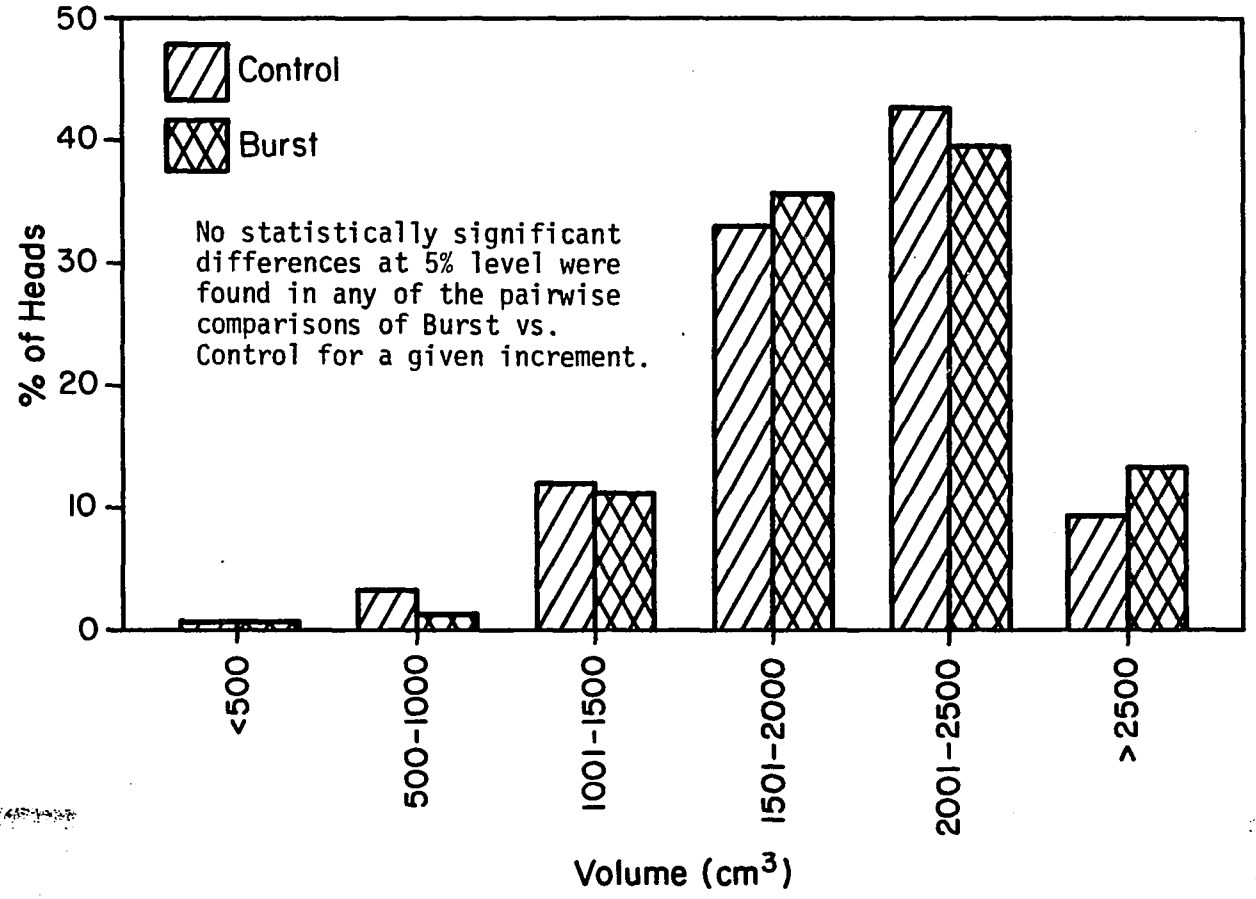

Figure 4. Percentage of Heads per 500 cm^3 Increments in Volume (Yuma County)

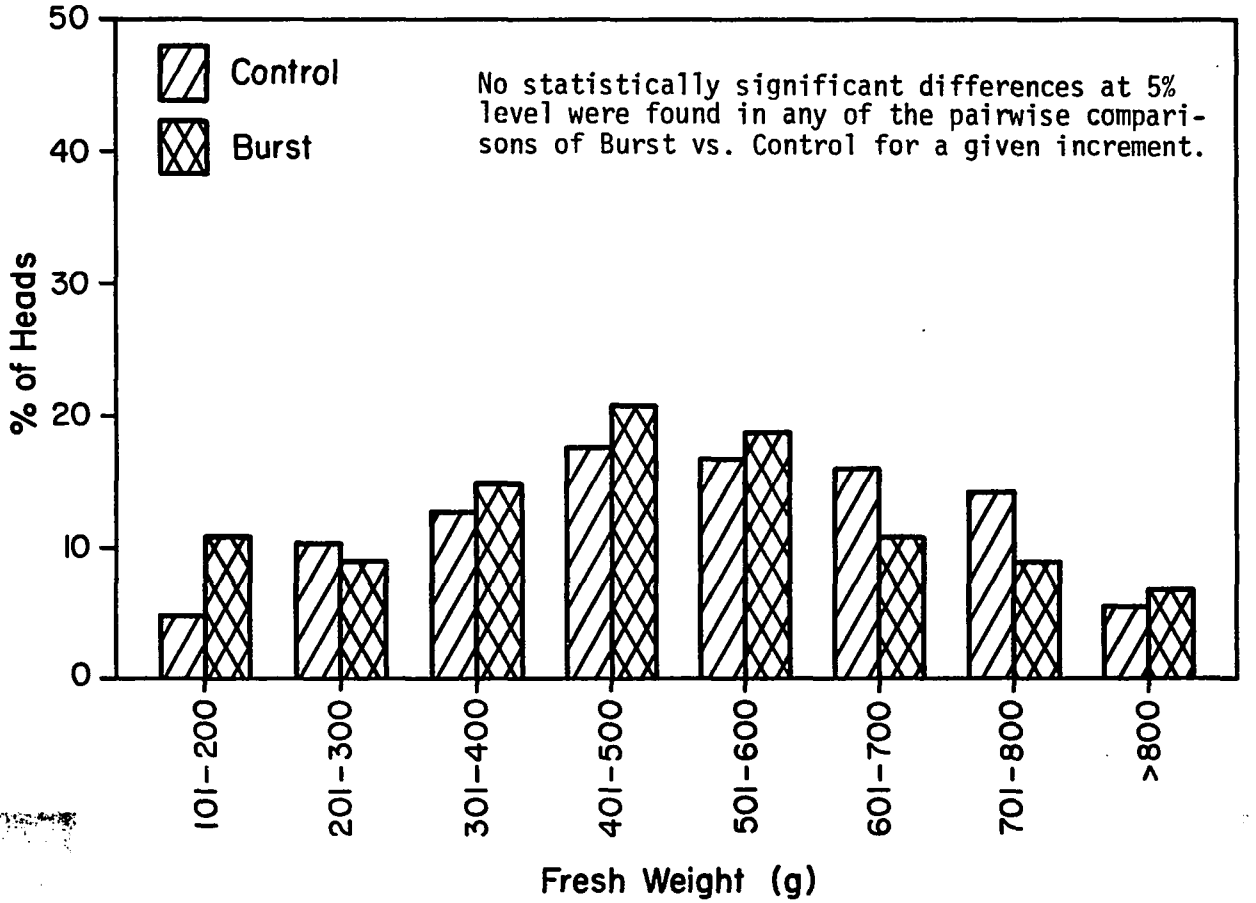

Figure 5. Percentage of Heads per 100 g Increments in Fresh Weight (Pinal County)

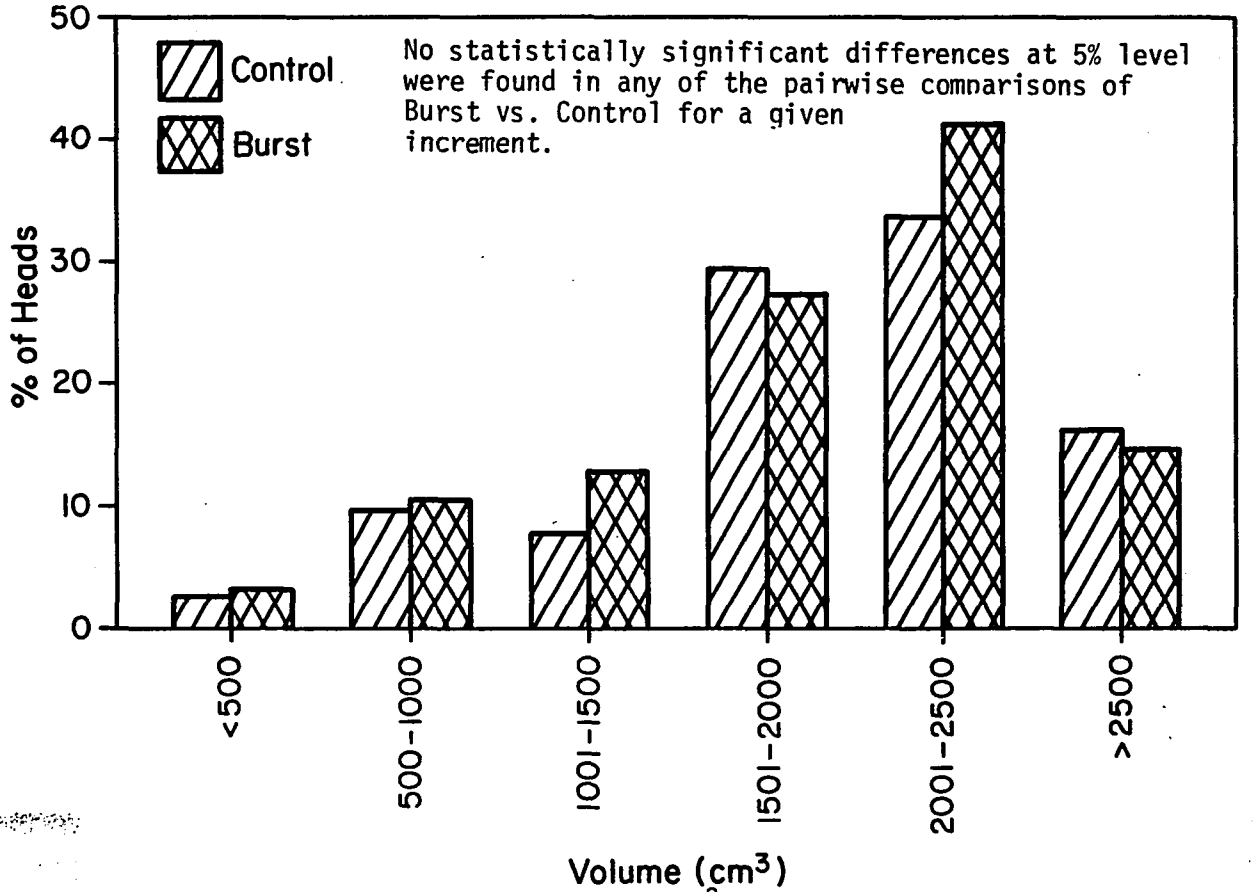

Figure 6. Percentage of Heads per 500 cm^3 Increments in Volume (Pinal County)

Burst at the recommended rate in lettuce. Laibi (1995) found that foliar application of Burst to field grown bell pepper plants had no significant effect on yield as measured by the number of fruits and their weights. In some instances, slight increase in size and yield were found, but these were often accompanied by a delay of maturity. Perhaps other rates or timing of applications would be more beneficial to lettuce than that used in this study.

Several other possible reasons exist for why no conclusive results were found. Perhaps the Burst was not absorbed sufficiently. Use of a surfacant may be worthwhile in future studies to aid in absorption of the Burst. Another reason for no conclusive results may be that Burst is effective only when plants are growing under a slight stress. If plants in the present studies experienced no stress, they may have produced enough cytokinin on their own, and thus Burst would have no effect. When cytokinins are applied externally to plant tissues, they are metabolized to less active compounds. The biological activity of a particular cytokinin is thus dependent on the metabolism taking place in the plant. The cytokinins may be metabolized to form inactive compounds or conversely to other compounds which may have a different biological activity. Morris (1981) found that when $N^6(8\text{-}^{14}C)$ furfuryladenine was applied to the intact root of pea seedlings, it was almost completely metabolized to other compounds. Part of the ^{14}C was recovered in RNA, DNA and proteins. A last possible reason is that Burst may not be effective for lettuce. However, this last reason should not be concluded until other possibilities are considered further.

Experiment 2

The comparative effects of foliar and soil applications of Burst to butterhead lettuce cv. 'Ostinata' plants grown in a greenhouse are discussed in this section.

No significant effects of foliar or soil applied Burst were measured by fresh weight, dry weight, number of leaves or leaf area (Tables 8, 9, 10). In one instance, following the second application of Burst, we observed a significant decrease in the number of leaves in foliar treated plants relative to soil treated ones (Table 9). At the final harvest, fresh and dry weights in foliar treated plants were higher than in soil treated plants, but only dry weight was higher when compared to control plants (Table 10). However, these differences were not statistically significant. This seems to be in agreement with the findings of Muller and Leopold (1966) where metabolites accumulated in the areas of leaves treated with cytokinin. Soil treated plants seemed to be somehow inhibited as shown by the data, which are lower for treated than the controls in some cases. The application of Burst to the soil might create an osmotic effect that would inhibit uptake of water and cause some stress.

Tables 8, 9, and 10 show a steady increase with the second and third sampling for all measured parameters. This increase represents normal plant growth.

Data from the greenhouse pot experiments confirm findings of the field trials with respect to Burst. In only one case (when number of

Table 8. Effect of Burst on Size of Butterhead Lettuce 24 Hours After One Application.

Treatment	Fresh Weight (g)	Dry Weight (g)	Number of Leaves	Leaf Area (cm^2)
Burst[Z] Foliar	5.31 a[X]	0.27 a	9.8 a	158 a
Burst[Y] Soil	5.05 a	0.25 a	9.2 a	148 a
Control Water to Foliage	5.25 a	0.26 a	9.4 a	156 a
Control No Water to Foliage	6.61 a	0.35 a	10.6 a	182 a

Z Applied rate was 0.54 ml of Burst per liter of solution

Y Applied rate was 1 Burst:500 water (v/v)

X Values in columns followed by same letter are not significantly different based on F-test followed by LSD at 5% level. Values are means of 5 plants.

Table 9. Effect of Burst on Size of Butterhead Lettuce 24 Hours After Two Applications.

Treatment	Fresh Weight (g)	Dry Weight (g)	Number of Leaves	Leaf Area (cm^2)
Burst[Z] Foliar	67.20 a[X]	2.61 a	20.6 a	1270 a
Burst[Y] Soil	71.44 a	2.71 a	23.6 b	1360 a
Control Water To Foliage	68.77 a	2.62 a	23.0 ab	1370 a
Control No Water To Foliage	67.27 a	2.51 a	23.0 ab	1360 a

Z Applied rate was 0.54 ml of Burst per liter of solution

Y Applied rate was 1 Burst:500 water (v/v)

X Values in columns followed by same letter are not significantly different based on F-test followed by LSD at 5% level. Values are means of 5 plants.

Table 10. Effect of Burst on Size of Butterhead Lettuce at Final Harvest

Treatment	Fresh Weight (g)	Dry Weight (g)	Number of Leaves	Leaf Area (cm^2)
Burst[Z] Foliar	106.10 a[X]	8.83 a	30.2 a	1680 a
Burst[Y] Soil	96.23 a	8.64 a	28.8 a	1640 a
Control Water To Foliage	99.86 a	8.41 a	27.4 a	1740 a
Control No Water to Foliage	106.20 a	8.43 a	27.6 a	1640 a

Z Applied rate was 0.54 ml of Burst per liter of solution

Y Applied rate was 1 Burst:500 water (v/v)

X Values in columns followed by same letter are not significantly different based on F-test followed by LSD at 5% level. Values are means of 5 plants.

leaves were measured after two applications), did soil or foliar treatments have any effects compared with the untreated control.

In the same experiment, we found no significant differences in photosynthetic rates and stomatal resistance of treated and control plants (Tables 11 and 12). The transpiration rate in foliar treated plants was significantly higher than in soil treated plants and in other controls (Table 13). There was a trend for the treatments with lower stomatal resistance to have higher transpiration rates.

There are some possible reasons why no conclusive results were obtained. Both foliar and soil concentrations of Burst may have been too low for an effect to be seen. The timing of application could also have been a possible problem. It is possible that no uptake of Burst occurred, and if it did, no movement took place within the leaf. It has been confirmed that cytokinins applied to leaves do not move much, apparently because of the formation of conjugated compounds with components present in the leaf. Kemp, Knavel and Hamilton (1979) found through chromatographic procedures that the inner, developing leaves of lettuce plants contained most of the cytokinin activity. In such a case, foliar application of Burst to the outer leaves would have a stimulating effect, assuming that the chemical has cytokinin-like activity.

Overall, results are quite inconsistent and it seems that this chemical has no effect in stimulating soil or plant processes that would result in improved growth.

Table 11. Effect of Burst on Photosynthesis (mg CO_2 $dm^{-2}hr^{-1}$) of Butterhead Lettuce Measured on Four Different Days

Treatment	Dates of Measurement			
	3/11/86[Z]	3/13/86	3/25/86	3/27/86
Burst[Y] Foliar	37.77 a[W]	50.52 a	12.06 a	13.73 a
Burst[X] Soil	37.40 a	43.06 a	12.58 a	11.06 a
Control Water To Foliage	36.15 a	39.36 a	11.08 a	10.30 a
Control No Water To Foliage	43.36 a	39.36 a	11.73 a	12.30 a

Z 2/1/86 day seeds were planted
3/12/86 first Burst application
3/26/86 second Burst application

W Values in columns followed by same letter are not significantly different based on F-test followed by LSD at 5% level. Values are means of 5 plants.

Y Applied rate was 0.54 ml of Burst per liter of solution

X Applied rate was 1 Burst:500 water (v/v).

Table 12. Effect of Burst on Stomatal Resistance (scm^{-1}) of Butterhead Lettuce Measured at Four Different Dates

Treatment	Dates of Measurement			
	3/11/86[Z]	3/13/86	3/25/86	3/27/86
Burst[Y] Foliar	2.30 a[W]	1.98 a	3.26 a	4.76 a
Burst[X] Soil	2.43 a	2.53 a	3.61 a	4.51 a
Control Water To Foliage	2.56 a	2.46 a	3.63 a	5.35 a
Control No Water To Foliage	2.47 a	2.71 a	3.02 a	3.97 a

Z 2/01/86 day seeds were planted
3/12/86 first Burst application
3/26/86 second Burst application

W Values in columns followed by same letter are not significantly different based on F-test followed by LSD at 5% level. Values are means of 5 plants.

Y Applied rate was 0.54 ml of Burst per liter of solution

X Applied rate was 1 Burst:500 water (v/v)

Table 13. Effect of Burst on Transpiration ($\mu g\ cm^{-2}s^{-1}$) of Butterhead Lettuce Measured on Four Different Dates.

Treatment	Dates of Measurement			
	3/11/86[Z]	3/13/86	3/25/86	3/27/86
Burst[Y] Foliar	3.58 b[W]	4.61 B	3.60 a	2.66 a
Burst[X] Soil	3.46 ab	3.50 a	3.17 a	2.54 a
Control Water To Foliage	3.16 a	3.55 ab	3.33 a	2.32 a
Control No Water To Foliage	3.26 ab	2.97 a	3.70 a	3.03 a

Z 2/01/86 day seeds were planted
3/12/86 first Burst application
3/26/86 second Burst application

W Values in columns followed by same letter are not significantly different based on F-test followed by LSD at 5% level. Values are means of 5 plants.

Y Applied rate was 0.54 ml of Burst per liter of solution

X Applied rate was 1 Burst:500 water (v/v)

Experiment 3

Table 14 shows the effects of benzyladenine on several growth parameters of butterhead lettuce after one application. Means were not significantly different except for root fresh weight in which control plants had significantly higher values. Interestingly, root dry weights were higher for benzyladenine treated plants than for control plants, but not significantly. All other growth parameters had slightly higher means for control plants.

A few hours after the benzyladenine application, the treated plants became slightly wilted and remained in this condition for about three days. It is possible that the concentration used, 5×10^{-7}M, may have been too high and have caused an osmotic stress in the plants which prevented uptake of water. An osmotic adjustment was probably reached three days later at which time the plants regained turgidity. Even so, the plants never reached the levels at which they were before treatment. The wilting may also have been due to an increase in transpiration rates. Benzyladenine and kinetin are known to cause the stomata to remain open long after the applications are made. After the second treatment the effects became more pronounced (Table 15). Means for control plants were significantly higher than for treated plants in every parameter measured.

Photosynthetic rates were not significantly different between treatments, except for one isolated case (Table 16). Overall, means were always higher for benzyladenine treated plants, although usually not statistically higher.

Table 14. Effect of Benzyladenine on Size of Butterhead Lettuce 24 Hours After One Application.

Growth Parameter	Treatment	
	Benzaladenine[Z]	Control
Leaf Fresh Weight (g)	32.53 a[Y]	39.21 a
Leaf Dry Weight (g)	1.56 a	1.92 a
Root Fresh Weight (g)	9.90 a	12.86 a
Root Dry Weight (g)	0.34 a	0.31 a
Leaf Area (cm^2)	618 a	688 2

Z Applied rate was 5×10^{-7}M

Y Values in rows followed by same letter are not significantly different based on t-test at 5% level. Values are means of 6 plants.

Table 15. Effect of Benzyladenine on Size of Butterhead Lettuce 24 Hours After Two Applications

Growth Parameter	Treatment	
	Benzyladenine[Z]	Control
Leaf Fresh Weight (g)	95.61 a[Y]	185.26 b
Leaf Dry Weight (g)	5.14 a	7.92 b
Root Fresh Weight (g)	33.99 a	45.07 b
Root Dry Weight (g)	1.64 a	2.14 b
Leaf Area (cm^2)	1525 a	1908 b

Z Applied rate was 5×10^{-7}M

Y Values in rows followed by same letter are not significantly different based on t-test at 5% level. Values are means of 6 plants.

Table 16. Effect of Benzyladenine on Photosynthesis (mg $CO_2 dm^{-2} hr^{-1}$) of Butterhead Lettuce Measured on Four Different Dates.

Treatment	Dates of Measurement			
	5/01/86[Z]	5/03/86	5/15/86	5/17/86
Benzyl[Y] Adenine	37.18 a[X]	34.81 a	16.71 b	13.13 a
Control	30.50 a	33.40 a	10.90 a	11.38 a

Z 3/18/86 day seeds were planted
5/02/86 first benzyladenine application
5/16/86 second benzyladenine application

Y Applied rate was $5 \times 10^{-7} M$

X Values in columns followed by same letter are not significantly different based on t-test at 5% level. Values are means of 6 plants.

The previous results are in agreement with the findings of several researchers who have observed inhibition by cytokinins in a variety of species (Smith and Thorpe, 1974; Kemp, Fuller and Davidson, 1957). Stenlid (1982) found that elongation of roots of wheat, flax and cucumber seedlings in the dark was strongly inhibited by kinetin, benzyladenine and several other native and synthetic cytokinins. These cytokinins proved to be strongly inhibitory even at very low concentrations. On the other hand, some cases have shown enhanced root growth with applications of kinetin. Wittwer and Dedolph (1963) found that some concentrations which suppressed top growth (height, dry weight) in peas and tomato plants, generally had lesser effects on root growth, and in some instances, enhanced it. Contradictory results were found by Bugbee and White (1984) who showed that application of kinetin to hydroponic solutions at concentrations ranging from 4.6 to 230 μM had no significant effects on fresh and dry weights of shoots and roots of tomato plants.

The data obtained from photosynthesis seem to be in agreement with the findings of Dong and Arteca (1982) who observed an increase in photosynthesis when kinetin was applied to the roots of tomato plants grown in a nutrient solution. The increase in photosynthetic rates suggests that there was an uptake of the cytokinin and a movement to the upper part of the plant. It would be interesting to determine or at least find evidence for the presence of benzyladenine in the leaves of both treated and untreated plants.

CHAPTER 5

CONCLUSIONS

Cytokinins are recognized as a class of plant hormones which, in addition to promoting cell division, also appear to regulate a wide range of other physiological processes. Most researchers agree that cytokinins are synthesized in the roots and translocated to the upper portions of the plants via the transpirational stream.

Free cytokinins in higher plants have been reported to occur in different organs: seeds, leaves, roots, seedlings and stems. In many cases, it is not known what the relationships are between endogenous and applied cytokinins, or the way they interact or inhibit each other. This is a concern for many researchers who have found no effects of applied cytokinins to plants and have suggested that endogenously occurring cytokinins may control the activity of exogenous cytokinins.

In these studies, we evaluated the capability of Burst and benzyladenine to improve size and quality and speed of maturity of lettuce plants. The results obtained were not positive and further studies on cytokinin activity will be needed before a conclusion is reached. The mode of action of cytokinins is still an unsolved puzzle. In many cases, it is not known whether or not endogenous cytokinins are involved in the regulation of physiological processes, or how they interact with externally applied cytokinins. Once some of these

questions are answered, it will be easier to evaluate the performance of plant hormones.

APPENDIX A

DEFINITION OF TERMS RELATED TO MATURITY STAGE

Rating	Relative Head Size	Firmness
Mature	Larger	Firm
Almost Mature	Large	Intermediate
Immature	Small	Soft

APPENDIX B

CALCULATION OF PHOTOSYNTHESIS

1. How to determine ppm CO_2 constant from the standard gases.

   Example:

Standards (ppm)	336	368
Readings from	328	363
Gas Analyzer (mVolts)	327	363
Mean	327.5	363

   Find the differences:

   368 - 336 = 32 ppm

   363 - 327.5 = 35.5 mVolts

   Divide 32 by 35.5 = 0.9014 This is the ppm constant

2. How to find ppm (change in ppm)

   Find the difference between the two syringe readings from one plant.

   Example: 395 - 302 = 93

   The difference (93) is multiplied times the ppm constant (0.9014). 93 x 0.9014 = 83.8302

   This represents the change in ppm

3. How to obtain net photosynthesis

$K = (\text{Time})\ (\text{Vol})\ (273/273 + {}^{o}C)\ (\text{Atm. Press.}/760\ \text{mm Hg})\ (44000/22.4)(10^{-6})$

K = Constant for a specific set of conditions

Time = 3600 sec/time in secs. that elapses between the syringes being pulled.

Vol = Volume of plexiglass chamber in liters

$273/273 + {}^{o}C$ = air temperature in degrees Kelvin

Atm. Press./760 mm Hg = Atm. press. in mm Hg where plant is located.

44000 = micro mole conversion

22.4 = Molar volume of gas at STP

$$\text{Net Photosynthesis} = \frac{K \times ppm}{L.A.} \quad (mg\ CO_2\ dm^{-2}\ hr^{-1})$$

K = Constant for the previous formula

ppm = Change in ppm found in Section 2

L. A. = Leaf area in square decimeters

APPENDIX C

NUTRIENT SOLUTION FOR HYDROPONICS

Flask I

(a)	$Ca(NO_3)_2.4H_2O$	268.8 g
(b)	Fe 330 Sequestrene	11.3 g

Add water to make a 1 liter solution

Flask 2

(a)	KNO_3	90.1 g
(b)	$MgSO_4$	112.4 g
(c)	KH_2PO_4	60.8 g
(d)	H_3BO_3	0.64 g
(e)	$MnCl_2.4H_2O$	0.54 g
(f)	$CuCl_2.2H_2O$	0.056 g
(g)	MoO_3	0.01 g
(h)	$ZnSO_4.7H_2O$	

Add water to make a 1 liter solution

Application: add 20 ml of solution in flask I per tank (8000 ml) the first day and 10 ml every week with mature plant. Then, add 50 ml of flask II per tank the first day.

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