THE EFFECT OF GIBBERELLIN ON THE GROSS MORPHOLOGY, FLOWERING, AND FRUITING OF CERTAIN HORTICULTURAL CROPS

By

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AN ABSTRACT

Submitted to the School for Advanced Graduate Studies of Michigan
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JEROME HULL, JR. ABSTRACT

Studies were initiated to determine the effect of applications of gibberellin on fruit set, rate of fruit development, ultimate fruit size and rate of vegetative development of the apple, cherry, peach and strawberry. Robinson strawberry plants grown in the greenhouse and treated with 10 to 1,000 micrograms of gibberellin produced elongated petioles, peduncles, pedicels and crowns. Treatments resulted in formation of some abnormal fruit. Achenes did not develop on such fruit. Receptacular development of abnormal fruit occurred not in the area of the pistils, but in the toral tissue acropetal to the calyx and basipetal to the area of the pistils. Plants treated with 100 micrograms of gibberellin in November and December produced more flowers than non-treated plants. Response of strawberry plants grown in the field and treated with 100 ppm gibberellin were similar to greenhouse investigations.

One percent lanolin paste applications of gibberellin or indolebutyric acid applied to the pistils of non-developing flowers on gibberellin-treated strawberry plants produced a slight swelling of the receptacle. The indolebutyric acid treatment produced the greater amount of swelling. The longer the application of the lanolin paste mixture was delayed following bloom, the less the amount of receptacular development.

The gibberellin stimulus did not appear to be translocated basipetally

in the strawberry crown. When 500 micrograms of gibberellin was applied directly to the stolon, the stimulus appeared to be translocated in both directions.

Shoot length and diameter of rooted East Malling IX, XII and XVI cuttings were not increased through foliar application of 100 ppm gibberellin. Foliar applications of gibberellin applied to mature bearing apple trees during full bloom or three weeks later did not influence fruit set or development. All treated trees flowered and fruited normally the following season.

Shoot growth of one-year-old Mahaleb seedlings was not increased through foliar applications of 10 to 100 micrograms of gibberellin applied when shoot elongation began. One-year-old Montmorency cherry trees sprayed with 100, 500 or 1,000 ppm gibberellin after formation of terminal buds produced a second flush of growth. Shoots of treated trees had greater fresh and dry weights than the controls.

Fruit set and development of mature bearing Montmorency cherry trees sprayed with gibberellin during full bloom, or 26 days later, were not affected. Trees treated while in full bloom flowered normally the following season, while the post-bloom application resulted in a partial inhibition of flowering the following season.

Applications of 100 micrograms of gibberellin did not result in

increased shoot elongation of seedling Elberta peach trees. Fruit set and rate of development of mature peach trees was not affected by applications of 100 ppm gibberellin during full bloom, 26 days later, or two and one-half months later. While trees treated during full bloom flowered normally the following season, the trees receiving post-bloom applications produced no flowers the following spring.

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To My

Parents

Jerome and Doris Hull

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TABLE OF CONTENTS

TABLE OF CONTENTS CONT'D

TABLE OF CONTENTS CONT'D

INTRODUCTION

The last century has been marked by startling changes in the agricultural industry. This revolution has been brought about mainly by a vast accumulation of agricultural technology. It is true that farm mechanization has played an important role, but mechanization alone could not account for the rapid advancements so recently achieved by the American farmer.

Successful farming is no longer the livelihood of an uneducated peasant, but is performed by the agricultural specialist employing many scientific principles. It has truly become an art of applied biology.

One of the more recent fields of study to have a wide range of application in agriculture is that of plant growth regulators. By employing these compounds, scientists have found it possible to control or regulate the growth, development, and function of many different plants and specialized plant parts. Compounds such as naphthaleneacetic acid and 2, 4-dichlorophenoxyacetic acid serve as a stimulus to many plant scientists to continue investigations of new chemical compounds. Such compounds are tested for possible biological activity and subsequent practical applications.

A recent group of metabolic compounds exhibiting potent biological activity are the gibberellins. While gibberellin was first isolated in 1938 by Japanese chemists (Stowe and Yamaki, 1957), it was not made

available to research workers in America until isolation in 1954 by a group of United States Department of Agriculture scientists (Stodola et al., 1955).

It has since capitvated the imaginative minds and skills of scientists throughout the nation. Experiments were designed to determine its biological capabilities and limitations. However, most of this work involved studies with vegetable plants with very little reported on the response of pomological crops to the use of gibberellins.

Fruit thinning, fruit set, rate of fruit development, and ultimate fruit size, are important criteria to pomologists. They are also interested in the relationship of shoot and spur development in new orchard plantings to bring trees into bearing condition as early as possible, and to obtain as much fruiting as possible on mature fruit trees. Studies were initiated to determine if gibberellin might exert an influence on any of these phenomena.

Strawberries are grown commercially in Michigan under the matted row system (Shoemaker, 1948). Experiments were performed to ascertain if gibberellin would result in acceleration of runner development and produce a matted row earlier in the season in new plantings. Commercial strawberry producers and home gardeners are continually seeking means of producing larger strawberries and obtaining greater yields. Gibberellin was evaluated as a possible material for achieving these goals.

Agriculturists are continually requesting information about new

chemical compounds. It was felt that these investigations would provide some information to enable agricultural scientists to render accurate judgment and recommendations.

REVIEW OF LITERATURE

Floral Initiation in Deciduous Tree Fruits

In order to determine the influence of a plant regulator on floral initiation in tree fruits, one must first know when floral initiation normally occurs. Flowers in deciduous fruit trees are generally initiated the previous season in the developing buds (Gourley and Howlett, 1941). Their rate of development varies, but they usually are not completely formed until just prior to anthesis the following spring.

Floral Initiation in the Apple: Floral differentiation was observed in the Gravenstein apple June 11 in California (Tufts and Morrow, 1925), while in Wisconsin the first clear evidence of flower parts in the Hoadley was observed on June 30 (Goff, 1899). Drinkard (1909-1910) observed that the Oldenburg started initial flower bud development about June 20. He also noted a prolonged period of flower bud formation and found little difference in time of formation and subsequent development of flower buds of early, medium, and late blooming apple varieties.

Rasmussen (1929) observed blossom bud differentiation by August 7, 1928, and July 19, 1929, in the Baldwin, while floral differentiation in the McIntosh was evident July 29, 1928 and July 17, 1929. The year 1928 was a rainy year, while 1929 was dry and sunny, with a prolonged drought during part of June and July.

Floral Initiation in the Cherry: The first evidence of transition from a vegetative to floral apex in Prunus Mahaleb at Glen Dale, Maryland, was observed on July 29 (Tillson, 1947). Goff (1899) reported the earliest indications of flower development in King's Amarelle cherry to be July 11 in Wisconsin. In California, Tufts and Morrow (1925) observed floral differentiation in the Early Richmond cherry on July 12.

Floral Initiation in the Peach: Goff (1900) observed the first microscopic evidence of floral formation in the Bokara peach in Wisconsin on September 14. Quaintance (1900) found initiation of floral differentiation on July 23 in Demming's September peach in Georgia. Drinkard (1909-1910) reported indications of the initial steps of flower bud development in the Luster peach variety in Virginia on July 7. At Iowa Park, Texas, the Dr. Burton and Early Rose Cling peaches began initiation of floral parts August 10, while Frank started September 3, and four other peach varieties first produced floral parts by September 13 (Pickett, 1942). Tufts and Morrow (1925) in California observed the first evidence of floral differentiation in the Elberta peach in late July.

Dorsey (1935), studying the development of the peach shoot in Illinois, observed flower buds to be present in June. He made no microscopic investigations, but reached his conclusion on the basis of axillary bud formation and position.

Factors Observed to Influence Floral Initiation: Factors which influence the number of floral buds initiated have been more thoroughly investigated in the apple than in the stone fruits. This was probably due to the biennial bearing habit of many of the older fruit varieties. That these conditions would be applicable to the stone fruits is not necessarily true, but would give an indication of some factors which have influenced the time and number of floral buds initiated.

The leaf area of mature fruit trees and its relationship to developing fruit has been investigated to determine its influence on floral initiation. Magness (1917) defoliated several apple varieties in Oregon on June 26-28. He observed that floral initiation would not occur and flower buds develop in most varieties in the absence of a fair amount of leaf area. Harley, Masure and Magness (1941) found that 58 square centimeters of healthy leaf surface were required to form a blossom bud on girdled branches, while 110 to 180 square centimeters were required on ungirdled Yellow Newton branches. They reported that floral initiation depends upon time of apical bud formation. Investigations by Struckmeyer and Roberts (1942) on Wealthy apple trees on the effects of defloration and defoliation indicated that floral induction occurred at least three weeks prior to the appearance of blossom primordia.

Roberts removed alternate leaves from new branches of American plum species over a period of time from July 13 to August 24. He found

blossom bud formation to be entirely inhibited at the nodes where leaves were removed on July 13. The inhibiting effect of defoliation decreased as the period of defoliation became later in the season, until on August 24, the foliation merely resulted in a decrease of the final size of buds at the defoliated nodes.

Drinkard (1913-1914) subjected five-year-old Kings of Pippins on Paradise stocks to various treatments throughout the growing season. He found that while spring pruning tended to discourage flower bud formation, summer pruning the last of June stimulated this formation, and fall pruning had no effect. Root pruning April 23 did not result in much flower bud formation, but if done when floral bud differentiation began, it had marked stimulation. Ringing trees on April 23 had no effect on floral bud formation, but when done May 31, it resulted in a stimulation of flower bud formation.

To evaluate the effect of shading on floral initiation, Auchter et al. (1926) covered half of Staymen and Grimes Golden apple trees with muslin cloth just before blossoming. The trees remained covered until May 15. They found that shading prevented practically all blossom bud formation. Paddock and Charles (1928) enclosed limbs of Rome apple trees in muslin for periods of seven to 61 days. Enclosing limbs after bloom had no effect on blossom formation. Limbs enclosed before bloom for one week only were not affected, but when such treatment was extended two to seven weeks, no blossoms were produced the next season.

Moisture has been observed to influence floral initiation. Gourley (1915) observed that Baldwin apple trees produced the largest number of blossom buds under conditions where the moisture was lowest during the period of flower bud formation. Degman et al. (1932) found that the percentage of growing points flowering was lower in irrigated than in non-irrigated plots for both Oldenburg and Rome Beauty. Kirby (1918) observed that Jonathan and Grimes Golden trees produced the largest proportion of flower buds when grown in sod. He also noted that flower buds were differentiated earlier on sod plots than on plots receiving some cultivation each year.

Applications of plant growth regulators during the growing season have resulted in fewer flowers the following season. In an experiment performed at Beltsville, Maryland by Magness, Batjer and Baynes (1943), Winesap spurs, bearing one apple and having a secondary or new spur growth, were treated with naphthaleneacetic acid and naphthaleneacetamide on May 26. Treatment with a lanolin paste of either chemical reduced the number of flowers initiated, but lanolin alone also reduced floral initiation. None of the treatments increased the number of flowers initiated.

A reduction in the number of flower buds formed on mature bearing Elberta and Halehaven peach trees was found to have occurred as a result of spraying the trees the previous season with naphthaleneacetic acid, naphthylacetamide, or 3-chloroisopropyl-N-phenylcarbamate, at all stages of fruit

development from "shuck-off" to four weeks later (Kelley, 1955). The greatest reduction in number of flower buds was observed for trees sprayed four weeks after "shuck-off". Lombard (1958) observed that Redhaven peach trees sprayed with 30 ppm naphthaleneacetic acid 42 days after bloom in 1957 had significantly smaller number of flower buds on their terminal growth in 1958.

Factors Affecting Strawberry Morphology

The strawberry plant in the vegetative condition is a monopodium. Under a 14-hour day and 10-hour night, the plant remains vegetative and produces runners. A 10-hour photoperiod and 14-hour dark period result in the initiation of flowers.

Effect of Plant Growth Regulators on Runnder Development: Carlson and Moulton (1951) observed a 46 and 91 percent reduction in the number of runners and retardation of growth of Premier strawberry plants through application of 2, 4-D and one-half and two pounds per acre respectively. Except for runner reduction, the plants appeared normal at the end of the growing season. While isopropyl-N-phenylcarbamate at 5, 10 and 15 pounds per acre also reduced the number of runners formed with no apparent injury to the plants, dichloral urea, nine pounds per acre, greatly reduced runner production.

Factors Affecting Leaf Development: Darrow (1930) observed that leaf size increased in succeeding leaves developing from April to June in Howard 17 plants, and that leaf size dropped off then in plants producing runners,

but not in plants which had their runners removed. He found the limiting factor of plant growth to be generally temperature. The highest rate of leaf production occurred between 68 and 79°F.

Went (1957) observed that increasing the temperature from 10 to 20°C, and the photoperiod from 8 to 16 hours, increased the size of leaflets and length of petioles. He found the reverse to be true in peduncle elongation. Longer petioles were observed during periods of runner formation than during periods of flower initiation.

Dormancy in the Strawberry: Darrow and Waldo (1933) reported that ordinary varieties go into a rest period under very short daily light periods and low temperatures in the fall. When the light period was lengthened in the greenhouse the first of September, all varieties tested made vigorous vegetative growth throughout the entire winter and required no rest period.

Flower Development in the Strawberry: Schilletter and Rickey (1929) observed that the first five runner plants produced, all formed approximately the same number of flowers. The third runner plant produced slightly more flowers than any of the other runner plants; otherwise, there was a general decrease from the first to the tenth runner plant, falling rapidly after the fifth runner plant.

Lack of pollination is not the only reason that some flowers fail to produce fruit. Wray (1861) reported three types of strawberry seedlings:

staminates, pistillates, and hermaphrodites. According to Darrow (1925), a great variation in the setting of fruit was found in the perfect flowered varieties, resulting chiefly from sterile pistils. He concluded that, under most conditions, pistil sterility seems to be determined in the fall (Darrow, 1927). Five hermaphrodite varieties were rooted at intervals from July 15 to September 9. In every variety an increase in the percentage of flowers not setting fruit was evident in the later rooted plants. He observed some varieties to vary in amount of sterility when planted in different soil types, and thought this may have been one factor of sterility. However, the soil types were obtained by planting in different locations, and therefore the cause of sterility might have been due to location or nutrition.

It is possible that pistil sterility may be responsible for failure of most strawberry flowers to form fruit. Valleau (1918) theorized that hermaphrodite strawberry varieties may have been derived from staminate forms rather than pistillate. Therefore, the pistil of the flower would probably be more likely to be influenced by adverse environmental conditions. He noticed that varieties with a high percentage of aborted pollen grains still produced a portion of functional grains.

Development of the Strawberry Fruit: The strawberry fruit is an aggregate fruit in which the individual fruitlets are the achenes and the edible portion is composed largely of receptacle or torus tissue. The principal tissues

concerned in the development of the fleshy receptacle are the cortex and pith.

Havis (1943) observed that the cortex developed more rapidly than the pith. While some cell division occurred in the pith during the entire period of development of the fruit, most of the cell division in the cortex ceased shortly before anthesis.

Effect of Plant Growth Regulators on Strawberry Fruit Development: Gardner and Marth (1937) sprayed a pistillate strawberry selection during a portion of its blooming period with 0.1, 0.05, 0.025, 0.01 and 0.005 percent concentrations, respectively, of indoleacetic acid. All concentrations resulted in many of the blossoms producing apparently normal achenes, which proved to be devoid of embryos. With concentrations of 0.05 and 0.1 percent indoleacetic acid, a number of the receptacles developed and ripened into apparently normal fruits. However, never more than one fruit of an inflorescence developed completely. At the lower concentrations, the receptacles made only a slight initial growth, which soon ceased, although the achenes usually developed. They planted several hundred achenes and obtained only one rather weak seedling.

Hunter (1941) sprayed individual blossoms of three pistillate varieties, Louise, Portia and Simcoe, with 1.0, 0.5 and 0.25 percent indoleburyric acid, 1-naphthylacetic acid and colchicine. Parthenocarpic fruits were

produced in abundance from all concentrations of indolebutyric acid and the lower concentrations of the other two chemicals. The one percent 1-naphthylacetic acid application initiated fruit development, but injured the pedicels so severely that most fruits did not reach maturity. An application of one percent colchicine caused no damage, but it did not stimulate the development of the fruits. Unlike Gardner and Martin (1937), Hunter was able to obtain more than one fruit per inflorescence. The "seeds" were sown as soon as the fruit was ripe, but only one plant was obtained.

Removing the achenes from the strawberry receptacle has been reported to arrest the enlargement of the receptacle (Nitsch, 1949). When the achenes of the Marshall strawberry were removed nine days after pollination and the "berry" coated with lanolin paste containing 100 ppm of beta-naphthoxyacetic acid, the treated strawberry developed and ripened in the same manner as the non-treated fruit (Nitsch, 1950). A 0.3 percent beta-indolebutyric lanolin paste was very effective also.

The Effect of Gibberellin on Plant Development

Effect of Gibberellin on Shoot Development: A wide variety of plants respond to applications of gibberellin by an increase in growth. Marth, Audia and Mitchell (1956) made a survey of the response of plants of various genera and species of gibberellin, and observed marked differences in the responsiveness of the different plants. The most obvious effect was an increase in

stem elongation with longer internodes. The greatest amount of elongation was obtained when plants were treated just at the beginning of stem elongation.

Brian and Hemming (1955) applied gibberellin to the foliage of pea seedling varieties at concentrations ranging from 0.3 to 10.2 micrograms per plant. They observed differences not only due to treatments and varieties, but to interactions of both. The slower growing varieties exhibited a greater response to the material. The distinction between tall and dwarf varieties was virtually eliminated by applications of gibberellin.

Kemp et al. (1957) reported that gibberellin dosages below one microgram per plant would produce visible effects, while dosages of 100 micrograms or more had essentially the same initial effects, but the effects persisted over a longer span of time. They reported gibberellin to be readily absorbed by intact plants through their roots, epidermis of stems, and leaves. It was found to be highly mobile in intact plants and to promote elongation of stems, petioles, and to a lesser degree, leaf blades.

Gray (1957) also observed alteration of leaf shape and size following treatment with gibberellin. The leaf margin of the tomato became smooth rather than indented. African violet leaves were longer and narrower, while the Pinto bean retained its normal shape, but developed larger leaves. These plants also had longer leaf petioles.

Effect of Gibberellin on Plant Fresh Weight and Dry Weight: While the references to shoot elongation as affected by gibberellin applications usually have been consistent, the published investigations on fresh weights and dry weights have not always been in agreement. Brian et al. (1954) grew peas and wheat in solution culture and added gibberellin to the solution. They obtained an increase in fresh and dry weights of the shoots, but a reduction of both fresh and dry weights in the roots.

Leben and Barton (1956) reported an increase in both fresh and dry weights of Kentucky Bluegrass when treated with gibberellin at 28, 56 or 112 grams per acre. Grassland in Australia treated with two ounces of gibberellin per acre, yielded an increase in dry weight in the first cutting. However, there was a decrease in the dry weight of the treated plots in the second cutting. This would seem to indicate that either the effect of the gibberellin application had disappeared or that the plants had exhausted their reserve food supply in producing the increased yield in the first cutting.

Bukovac and Wittwer (1956) obtained a 50 percent increase in both the fresh and dry weights of celery in 30 days using gibberellin at 250 or 500 ppm. They did not achieve this with pea, bean, tomato, sweet corn, cucumber, lettuce or cabbage. Gray (1957) reported increased fresh and dry weights in the Pinto bean within one week from foliar applications of 10 and 100 ppm of gibberellin. Marth, Audia and Mitchell (1956) found that one ppm of gibberellin

as a foliar spray increased the fresh and dry weights of the soybean in one week. However, there were no differences after two weeks.

The differences or lack of differences reported for fresh and dry weights of plants treated with gibberellin might be the result of time of sampling. Since the effect of gibberellin, especially at low concentrations, is of short duration, weights may not differ at the final harvest, yet may vary considerably for a short period of time after treatment. Failure to obtain an increase in weight may also be partially related to the nature of plant response.

Effect of Gibberellin on Dormant Plants: Plants have been induced through applications of gibberellin into active growth under conditions not usually conducive for such active growth. Intact seeds of Malus Arnoldiana Sarg. require pretreatment in a moist medium at 5°C for at least four weeks--a pretreatment referred to as after-ripening. Barton (1956), using both aqueous solutions and lanolin paste applications of gibberellin, overcame the physiological dwarf condition of the non-afterripened embryos. She reported that the extension of the internodes of the treated seedlings was evident within 14 days after treatment. However, the internodes of non-treated seedlings began to elongate with increasing age and approximated the length of the treated seedlings after 50 days.

Epicotyl dormancy of tree peony seedlings was broken by applications of 1, 10, or 100 micrograms gibberellin to the hypocotyl of the germinated

seed, replacing the need of after-ripening usually accomplished by low temperature treatments (Barton and Chandler, 1957). Lippert et al. (1958) stated that a condition of physiological rest prevails in potatoes from time of tuber initiation until six to twelve weeks after harvest, depending on varietal characteristics. Foliar applications of 100 and 500 ppm gibberellin applied to the plants two and four weeks before harvest resulted in sprouting and secondary tuber formation on the main tubers.

Donoho and Walker (1957) stated that the Elberta peach tree needs an exposure time of 950 hours at air temperatures below 45°F to break its rest period and resume active vegetative growth in trees that had received less than 20 percent of their chilling requirement by two foliar applications of 1, 000 and 4, 000 ppm gibberellin. Furthermore, trees which had received 50 percent of the necessary hours of chilling temperatures made active vegetative growth following four foliar applications of 200 ppm gibberellin made at 10-day intervals.

Cooper (1957) applied a 100 ppm spray of gibberellin December 15 to young grapefruit trees with dormant buds. This resulted in a flush of new growth in all the lateral buds on the terminal shoot within 15 days (December 30), while buds on non-treated trees showed no sign of growth until 25 days later (January 25).

Slash pine (Pinus elliottii) trees, growing under 16-hour day length,

were induced into a dormant condition when grown under an eight-hour photoperiod for two to four weeks. This dormancy was broken subsequently by a 0.1 percent gibberellin application (Bourdeau, 1958). Dormancy, induced and maintained in the Camellia by short day conditions, was broken by periodic applications of gibberellin (Lockhart and Bonner, 1957).

The response of certain woody ornamental plants to gibberellin has been reported by McVey and Wittwer (1958). They found that single foliar applications of 1,000 ppm or weekly treatments of 100 ppm resulted in a second flush of growth in Enonymus fortunei vegetus. Magnolia soulageana in turn produced an additional flush of growth from weekly applications of 100 ppm gibberellin and from single applications of both 100 and 1,000 ppm. Increases in terminal growth of woody ornamentals, they stated, was accomplished by the development of longer internodes and an increased number of nodes.

The Effect of Gibberellin on Flower Initiation: The use of the gibberellins has created startling effects on the flowering of biennial and long day photoperiodic plants. Lang (1956) obtained flowering of the biennial Hyoscyamus niger without subjecting the plant to a cold period, when he applied five daily applications of gibberellin of two micrograms each, applied to the center of the plant rosette.

Bukovac and Wittwer (1957) produced flowering in carrots, cabbage,

kale, turnips, collards, and beets with two to ten treatments of gibberellin, applied to the foliage or plant apex. Except for carrots, they did not obtain complete induction of flowering unless the plants were grown at temperatures approaching those commonly required for flower induction.

Harrington, Rappaport and Hood (1957) obtained flowering in non-vernalized endive following weekly applications of 50 micrograms of gibberellin per plant. They found that the treated plants produced longer seed stalks, long peduncles, and smaller flowers. Carr et al. (1957), in Australia, were able to replace the requirement for vernalization in Centaurium minus Moench with 15 daily applications of gibberellin applied to the plant rosette.

Burk and Tso (1958), in Maryland, observed that flowering of the non-rosette Nicotiana species (short-day plant) was not affected by gibberellin, while the rosette-type species (long-day plants), flowered earlier as a result of the gibberellin treatments. Wittwer and Bukovac (1957) obtained flowering in lettuce, endive, radish, mustard, spinach, and dill, growing under non-inductive short photoperiods, by treating them with gibberellin. When these vegetables were treated with gibberellin and grown under long photoperiods, all but spinach and dill flowered earlier than the control plants.

While gibberellin has not promoted flowering of short day plants when grown under long day photoperiods, it has sometimes enhanced flowering of short day plants that have been under some limiting environmental conditions.

Lincoln and Hamner (1958) observed that the flowering response of intact Xanthium plants (short-day plants) with a full complement of young leaves and actively growing buds was not altered by foliar applications of gibberellin. The flowering response was increased, however, when gibberellin was applied to plants under conditions in which the flowering response would be restricted by the slow growth activity of the epicotyl. Greulach and Haesloop (1958) found that gibberellin could not be substituted for any short day requirement of Xanthium necessary for the initiation of reproductive development. However, it could substitute for additional photoinductive cycles when coupled with one short day.

Cathey and Stuart (1958) investigated the response of Chrysanthemum varieties to applications of gibberellin used at different times during the nine to ten week period of short photoperiods required for flowering. They obtained the greatest amount of stem elongation from plants treated during the third week. Rapid stem elongation was related to a decreased number of lateral inflorescences. Peduncle elongation was most pronounced when applications of gibberellin were made in the fourth week and earlier flower development resulted from applications made in the seventh week.

Bukovac, Wittwer and Teubner (1957) studied the flowering response of tomatoes to applications of gibberellin, and observed that the use of gibberellin resulted in an increase in the number of nodes to the flowering stage,

but as a result of accelerated growth, the treated plants flowered earlier. The number of flowers in the first cluster of the treated plants was reduced.

Effect of Gibberellin on Pollen Development: Chandler (1957) germinated pollen on agar containing 31 to 1, 000 grams of gibberellin per liter of medium. Nine plants gave no germination on either the control or gibberellin media. Germination of Lilium pollen was stimulated on the gibberellin medium over the control. Pollen germination from 10 plants was inhibited by all concentrations of gibberellin, but the pollen responded by coiling, enlarging of the tips of the tubes, and even exuding of the cytoplasm. Pollen from seven plants showed an increase in percentage of germination and a marked increase in tube length, when germinated on agar media containing gibberellin.

Vasil (1957), in India, excised the anthers of Allium cepa at leptotene-zygotene or even at leptotene and grew them satisfactorily in media containing gibberellin. The excised anthers produced tetrads and one-celled microspores. In all other plants investigated, the anthers excised at the leptotene-zygotene stage failed to develop.

Harrington, Rappaport and Hood (1957) observed that endive treated with gibberellin produced small flowers with brownish stamens and very little pollen. Pollen stained with acetocarmine was pink, indicating that it should be viable, but no seed developed. Nelson and Rossman (1958) induced various degrees of

male sterility in maize by foliar applications of gibberellin at 500 to 2, 500 ppm. They thought the critical stage of plant development for most effective chemical induction of male sterility to be when the immature male inflorescence was approximately one inch in length. Silks of treated plants were functional.

Effect of Gibberellin on Fruit Set: Persson and Rappaport (1958) pruned the main stem on a male-sterile tomato to force two shoots from the cotyledonary axils, and then compared treatments of 100 micrograms of gibberellin to the stem apex, the peduncle of single inflorescence, and the first or second fully expanded leaf above the second open flower cluster of one of the laterals. They observed an increase in the set of parthenocarpic fruit on both the treated and non-treated laterals when gibberellin was applied to the foliage. Treating the peduncles was not observed to result in an increase in the set of parthenocarpic fruit. An application of 100 milligrams of gibberellin to the soil resulted in the greatest amount of fruit set. Rappaport (1957) reported increased fruit set, both normal and parthenocarpic, for the Earlypak tomato following foliar treatments of gibberellin. Spraying the fruit did not increase its size.

Thompson Seedless grapes sprayed after fruit set with 20 and 50 ppm of gibberellin produced very large berries and berry clusters (Weaver, 1958). Flowering clusters of Black Corinth grapes were dipped into solutions ranging from one to 500 ppm of gibberellin. Concentrations of 5 to 500 ppm gibberellin resulted in an excellent set of enlarged berries. A fairly good set was reported also from the use of one ppm dip, but the clusters were straggly, due to a large number of small underdeveloped berries.

METHODS AND MATERIALS

Introduction: A series of studies was conducted during 1957 and 1958 to determine the effects of gibberellin on the strawberry, apple, peach and cherry, and any practical applications that might be derived from the use of gibberellin. All experiments were performed at East Lansing, Michigan, between January, 1957 and October, 1958. Greenhouse investigations were conducted in the Michigan State University plant science greenhouses. Field studies were made on the Michigan State University horticultural farm. All plants were grown under the naturally occurring photoperiods.

The term gibberellin does not distinguish between the four known chemically different gibberellin compounds. These gibberellins are more accurately referred to as gibberellin A_1, A_2, A_3 and A_4. Gibberellin A_3 has also been referred to as gibberellin X, and gibberellic acid, with the last term appearing most often in the literature.

Two gibberellin materials were used in these investigations. Potassium gibberellate, the potassium salt of gibberellic acid, was supplied by Merck and Company, Incorporated, Rahway, New Jersey. This compound is often abbreviated GA and this abbreviation has been used in certain tables in this thesis. The other gibberellin compound was a mixture of gibberellin A_1 and A_3, furnished by the Charles Pfizer Company, Brooklyn, New York. Biological

activity of both gibberellins appeared to be similar.

Foliar applications of a known concentration of gibberellin were employed in the field investigations. In the greenhouse studies, aqueous gibberellin solutions were applied to the apex or young expanding leaf of a plant with a micropipette. This made it possible to apply a measured amount of gibberellin to each individual plant.

Whenever possible data were subjected to an analysis of variance. A comparison of treatment means at the 5 percent level was performed using the multiple range test as advocated by Duncan (1955), and the results expressed accordingly. When one and two values were missing in a randomized block design, the missing values were calculated according to methods described by Snedecor (1957). Formulae derived by Baten (1939) were used to calculate three missing numbers.

Effect of Gibberellin on the Strawberry (Fragaria spp.): Robinson strawberry plants were potted in 6-inch clay pots and placed on a bench in the greenhouse on February 8 and 12, 1957. Plants were treated on February 17 with 10, 50 or 100 micrograms of gibberellin per plant, applied with a micropipette to the shoot apex to determine if strawberry plants would exhibit any response to applications of gibberellin. Each treatment included 18 replications of three plants per replication, and 54 non-treated plants served as controls.

The length of the petioles of the new leaves was measured March 5, 1957. The number of visible scapes was counted and measured, and the number of opened flowers were recorded on March 7. The length of the elongated crown was measured on April 4. The number and weight of all fruit produced was recorded at periodic intervals from April 5 to April 22, 1957.

The potted plants were placed on a three-tiered bench on April 22, 1957. Runners were allowed to hang over the side of the pots and develop accordingly. The length of the runner between the mother plant and first runner plant, and between subsequent runner plants was measured on June 8, 1957, to determine the effect of the applications of gibberellin on runner elongation.

A study was conducted in the greenhouse in the fall of 1957 to determine if Robinson strawberry plants, which had not been subjected to an extended period of freezing temperatures, could be stimulated to develop more rapidly through applications of gibberellin. Runner plants, which had developed during the summer, were dug, potted in 6-inch clay pots and placed on a bench in the greenhouse on October 14, 1957. These plants were removed from non-treated plots and plots that had received one to four applications of gibberellin in the field between April 28 and July 7, 1957, and were maintained in separate groups according to their previous treatments. All the leaves and a portion of the root system were pruned from each plant prior to

potting. Ten plants in each group were treated with 100 micrograms of gibberellin on October 20, and ten plants in each group kept for controls.

Periodic records were kept on the number of leaves per plant developing from October 29 to December 30, 1957 to determine if the treatments hastened the vegetative development of the plant. Data were also taken on the visible appearance of the peduncle, the number of flowers that developed, and the percent fruit set. The percent fruit set was calculated on the basis of the number of normally developed fruit, and did not include any distorted fruit.

There is a relationship between the time of rooting of the strawberry runner plant and the number of flowers that it will produce (Schilletter and Rickey, 1929). An investigation was performed in the greenhouse during the fall and winter of 1957-58 using the first five runner plants to develop on the stolon, to determine if the flower and fruit development for the different series of runner plants would be affected differently by gibberellin. Robinson strawberry runner plants were dug in the field November 23, 1957 and separated according to their sequence of development on the runners. The plants used were the first, second, third and fourth runner plants to develop on the runner. These plants were potted in 6-inch clay pots and placed on a bench in the greenhouse November 24 in a randomized block design. The following treatments were used:

(a) Control.

(b) 100 micrograms of gibberellin applied to the crowns November 27, 1957.

(c) 100 micrograms of gibberellin applied to the crowns December 16, 1957.

(d) 100 micrograms of gibberellin applied to the crowns January 11, 1958.

(e) 100 micrograms of gibberellin applied to the crowns December 16, 1957, and again on January 11, 1958.

Each treatment included ten replicated plants for each group of runner plants.

A number of the flowers in both the treated and non-treated plants were emasculated on January 9 and 10, 1958, so that pollen viability might be evaluated. Pollen from flowers on the treated plants was placed on the stigmas of emasculated flowers of non-treated plants, and pollen from flowers on the control plants was placed on the emasculated flowers of the plants treated with gibberellin. Other flowers of both treated and non-treated plants were brushed with a camel's hair brush to insure self-pollination. Pollen from several primary flowers of the various treatments was stained with acetocarmine solution to determine viability.

The total number of flowers produced per plant was recorded February 19, 1958, and the number of fruit, both normal and abnormal, was counted March 4.

The effect of a lower concentration of gibberellin was also evaluated in the greenhouse. Robinson strawberry plants, dug in the field in November, were potted in 6-inch clay pots and placed on a bench in the greenhouse on November 27, 1957. All the mature leaves and a portion of the roots were pruned off each plant and the plants treated November 27 with 1, 10, 50 or 100 micrograms gibberellin applied to the crown. A randomized block design was used and included 12 replicated plants for each treatment and 12 replicated non-treated plants.

The length of two petioles per plant and the peduncle was measured February 14, 1958. Pollen from some of the primary flowers of both the non-treated and the treated strawberry plants was stained with acetocarmine February 15. The number of flowers per plant was recorded February 19, and the number of fruit counted on February 28, 1958.

An investigation to evaluate the effect of applications of higher concentrations of gibberellin was conducted in the greenhouse in 1958. Robinson strawberry plants that had been dug in the field in November, 1957, and kept in cold storage at 0° C, were potted in 6-inch clay pots and placed on a bench in the greenhouse on February 12, 1958. A randomized block design was employed with eight plants per treatment. Treatments included a control and applications of 100, 500 or 1, 000 micrograms gibberellin per plant, which were applied to a young developing leaf on March 14, 1958.

Records of petiole length, peduncle length, flower number, and crown elongation were taken April 27, 1958. The number of runners, length of runners, and distance between runner plants were recorded on May 18. The crown diameter at the base of the crown was measured May 24, using a vernier caliper.

Robinson strawberry plants were obtained from a commercial nursery on March 14, 1958. Some of these plants were placed in cold storage at 0°C for later investigations, and others were potted in 6-inch clay pots and placed on a bench in the greenhouse on March 15. The plants were treated with 1, 10, 100, 500 or 1,000 micrograms of gibberellin on March 27. The aqueous gibberellin solution was applied to a young expanding leaf. A randomized block design was used, with eight replicated plants per treatment, and eight non-treated plants.

Flowers were brushed with a camel's hair brush to provide pollination. Petiole length, peduncle length and length of crown elongation were measured May 16. The number of runners, flowers, and fruits was also counted. On May 24, 1958, the length of the pedicel of the primary flower was measured, the number of runners counted, and the diameter of the crown measured. The length of runners, number of runner plants, and distance between runner plants was also recorded.

The previous experiment was repeated and in addition, a modification

of the procedure described by Nitsch (1950), using lanolin paste applications of plant growth regulators on strawberry fruits, was employed to observe the effects on fruit development on the plants treated with gibberellin. Plants which had been kept in cold storage since March 14, 1958 were potted in 6-inch clay pots and placed in the greenhouse on April 2, 1958, and treated with gibberellin on April 9. Data were taken on the rate of flower opening from April 23 to May 12, 1958. Flowers were brushed with a camel's hair brush at periodic intervals to facilitate pollination. Certain flowers on the treated plants were coated with a lanolin paste containing one percent indole-butyric acid on May 10. Certain other flowers were treated likewise with a one percent lanolin paste mixture of gibberellin on May 11, 1958.

Measurements of crown diameter, crown elongation, and petiole length were made on June 3. The number of runners and flowers was also recorded. Peduncle and pedicel lengths were measured June 5, 1958, when an evaluation was made of the effect of all treatments on fruit set and development.

The above experiment was repeated using plants started in the greenhouse on April 9, 1958. The initial gibberellin treatments were applied April 15 to a young expanding leaf on each plant. Records were taken on rate of flower opening from May 1 to May 23. The flowers were coated with a lanolin paste containing either one percent indolebutyric acid or gibberellin on May 11, approximately six days after they had bloomed. Data on the

plant development, as affected by applications of gibberellin, were taken June 4 and 5, 1958.

The translocation of the gibberellin stimulus in the strawberry stolon was investigated. Robinson plants were started in the greenhouse on February 8, 1957, and one runner was permitted to develop on each plant and to form runner plants. In 18 plants the first and second runner plants were potted in 3-inch clay pots, and the remainder of each runner and subsequent runner plants hung over the side of the bench. The runner plants of the other 18 plants were not potted to prevent rooting. One June 24, 1957, 100 micrograms of gibberellin were applied to a mature leaf of each of the first runner plants of six rooted and six non-rooted runner plants. Six of the second runner plants in each group were treated similarly. The runner plants of six plants in each group were not treated. The length of the petioles of the mother plant and first two runner plants on each runner were measured July 28 and August 10, 1957.

This experiment was repeated in 1958 with a few modifications. Robinson strawberry plants were started in the greenhouse on March 15, 1958, and one runner was permitted to develop on each plant. The plants were divided into two groups in June, and the first two runner plants in the first group were potted in 6-inch clay plots. The runner plants in the second group were not potted to prevent rooting. The plants received the following treat-

ments on July 9, 1958:

(a) Control.

(b) 500 micrograms of gibberellin applied to a mature leaf of the first runner plant.

(c) 500 micrograms of gibberellin applied to a mature leaf of the second runner plant.

(d) 500 micrograms of gibberellin applied to the node on the runner between the first and second runner plants.

(e) 500 micrograms of gibberellin applied directly to the runner between the first runner plant and the next distant node.

Each treatment contained eight replicated plants for the non-potted runner plant group, and eight replicated plants for the potted runner plants. The length of two petioles on the mother plants and first and second runner plants was measured August 20, 1958.

Catskill strawberry plants were dug on April 19, 1958, and potted in 8-inch clay pots. They were placed on a bench in the greenhouse and divided into two groups in July. The runner plants were handled in the same manner as described above for the Robinson runner plants. The plants were treated similarly also with 500 micrograms of gibberellin on August 1. Petiole measurements were taken August 21, 1958 on the mother plants and first and second runner plants. Two petioles on each plant were measured, and

measurements subjected to an analysis of variance to determine if differences existed between treatments for the individual mother plants and the runner plants.

Portions of rows of year old strawberry plants growing in the Michigan State University Horticultural Department variety testing plots were sprayed with a foliar application of 100 ppm gibberellin on April 29, 1957 to determine if different strawberry varieties would respond similarly to applications of gibberellin. Varieties treated included Robinson, Catskill, Premier, Tennessee Beauty, Red Crop, Crimson Flame, M 1322 and Pocahontas. The scapes were visible, but the plants were not in full bloom at this time. The distance from the base of the peduncle to the calyx of the primary flower was measured on May 26. Fifty peduncles were measured for each variety in both the treated and non-treated portions of the rows.

The treated row portions of Robinson, Catskill and Premier measured 20 feet. The yield of fruit for both the treated and non-treated plants was obtained from June 15 to June 29, 1957.

The effect of applications of gibberellin on strawberry plants was also investigated under field conditions. On April 23, 1957 one row each of Catskill and Premier strawberry plants were planted on the Michigan State University horticultural farm. The rows were 90 feet long and three feet apart, and the plants were set approximately 18 inches apart in the row. Two rows of

Robinson and an additional row of both Catskill and Premier were planted on April 28. The planting was divided into ten equal plots. Each plot contained two rows of each of the varieties with six plants in each row.

Treated plots received foliar applications of gibberellin at 100 ppm on the dates specified in Table I. All blossom buds were removed on May 14 and as they appeared thereafter during the growing season.

The runners on all the plants were counted on June 25 or June 29, 1957. Two average plants in each row in each plot were selected on June 30, and measurements made of all their runners. The number of runners on these selected plants was counted August 17, 1957, and any elongation of the crown on these plants was recorded.

On May 4, 1958, three entire rows, one of each variety, were sprayed with 100 ppm of gibberellin. This application was made irrespective of the previous season's treatments. The material was applied before any inflorescences were visible, and two weeks before full bloom occurred. Fruit was harvested from all plots between June 12 and July 14, 1958.

Effect of Gibberellin on the Apple (Pyrus Malus L.)

The effect of applications of gibberellin on the shoot growth of rooted East Malling cuttings was investigated in the greenhouse in 1957. Rooted Malling IX and XVI cuttings were potted in 6-inch clay pots on January 28, 1957 and the potted plants randomized on a bench in the greenhouse. The Malling IX

TABLE I

Plot Design for Field Study of Effects of Foliar Applications of Gibberellin on Robinson, Premier and Catskill Strawberry Plants, Showing Plots Which Received the Applications of Gibberellin and the Dates of the Applications in 1957.

Plot	GA (ppm)	Date of Application
I	100	April 28, May 30, June 8, July 7
II	0	
III	100	July 7
IV	100	April 28
V	100	April 28, May 30, July 7
VI	0	
VII	100	April 28, May 30, July 7
VIII	0	
IX	100	April 28, May 30
X	0	

cuttings were treated with 10, 50 and 100 micrograms of gibberellin per plant on February 2, 1957. Each treatment included three replicated plants, and three non-treated plants were used as controls. The Malling XVI cuttings were treated similarly on February 14.

Shoot growth on all cuttings was measured March 18. The applications of gibberellin were repeated March 20, and subsequent shoot measurements made April 1, 9 and 19, 1957.

An investigation was made of the number of applications of gibberellin and the time interval between applications on the vegetative growth of rooted Malling cuttings. Rooted Malling IX and XII cuttings were potted in 8-inch clay pots and placed on a greenhouse bench on May 20, 1957. These cuttings were pruned on June 1 to one shoot per plant, and the diameter of the cuttings measured immediately below this shoot. Plants were then subjected to the following treatments:

(a) control.

(b) 100 ppm gibberellin weekly.

(c) 100 ppm gibberellin at two week intervals.

(d) 100 ppm gibberellin every four weeks.

Each treatment consisted of three replications of four plants per replication for each Malling selection. The gibberellin was applied as a foliar application, and contained a very small amount of Tide* as a wetting agent.

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*Trade mark of detergent manufactured by Proctor and Gamble Company.

Shoot length was measured June 23, August 16 and September 28, 1957. Diameter measurements were also taken September 28, at which time the investigation was discontinued.

Individual mature bearing apple trees of Jonathan, Delicious, McIntosh, Grimes Golden and Wealthy varieties were treated in the spring of 1957 to evaluate the effect of gibberellin on fruit set and development. Two branches were selected on each tree to which foliar applications of 10 and 100 ppm of gibberellin were applied May 9. A third branch of each tree was selected as a control. The trees were in full bloom when treated. The number of fruit persisting on the respective branches was counted on August 17, 1957.

One-half of individual mature bearing Jonathan, McIntosh, Northern Spy and Wealthy apple trees received foliar applications of gibberellin at 100 ppm on May 28, 1957. This application was made approximately 20 days after full bloom to observe the influence of gibberellin on fruit and shoot development.

Effect of Gibberellin on the Cherry (Prunus Cerasus L. and Prunus Mahaleb L.)

Shoot Growth: Seedling Mahaleb cherry trees, which had been dug in the field in the fall of 1956 and stored in a cold storage at 0°C, were potted in 6-inch clay pots on January 17, 1957, and placed on a greenhouse bench. All trees were pruned to eight inches in height. Applications of 10, 50 or

100 micrograms of gibberellin per plant were applied to the terminal bud on February 2. Each treatment included nine replications of three trees per replication. Twenty-seven trees were left as controls. The length of all developing shoots was measured April 6 and 27, 1957.

In a second investigation, 28 one-year-old Montmorency cherry trees were obtained from a commercial nursery in March, 1958. They were potted in silica sand in 12-inch clay pots and placed in the greenhouse on March 29, 1958. Fresh weight determinations were made prior to potting so that the effect of gibberellin on any increase in plant weight could be calculated. The nutritional level of the trees was maintained with three applications per week of a standard Hoagland solution. The sand was flushed with tap water about once every two weeks to prevent localization of salts.

By May 21, all but three of the trees had set terminal buds. At this time all trees were randomized as four groups of seven trees each. Three groups received foliar applications of 100, 500 or 1,000 ppm gibberellin, respectively, and a non-treated fourth group was used as a control. The trees were pruned to three lateral branches. Trunk diameter was measured six inches above the graft union.

Periodic measurements of all shoot elongation were made from May 21 to July 3, 1958, when it was noted that all the trees had again formed terminal buds. On July 11, 1958 the trees were again sprayed with the same

concentrations of gibberellin that they had received on May 21. A final record of all shoot growth and of trunk diameter was taken on August 20, 1958. Six trees from each treatment were then harvested to determine the fresh and dry weights of the tops and the roots. The graft union was used as a dividing line between the top and the root. Top and root dry weights were obtained by drying the tops and roots to a constant weight in an oven at 72° C.

Flowering and Fruiting: Single branches on six individual mature Montmorency cherry trees were selected to be used in an evaluation of the effect of applications of gibberellin on fruit set of sour cherries. Branches received foliar applications of 10 and 100 ppm gibberellin on May 2, 1957. The trees were in full bloom at this time. Fruit persisting on the branches was counted July 6, 1957.

A foliar application of gibberellin at 100 ppm was applied to two mature bearing Montmorency cherry trees on May 28, 1957, to ascertain whether the material might have an effect on the size of developing fruits. This was slightly more than three weeks after full bloom and both trees were bearing a crop of fruit.

Effect of Gibberellin on the Peach (Prunus Persica Batsch.)

Stimulation of Seedling Growth: Elberta peach seeds, which had previously been subjected to stratification, were potted in 4-inch clay pots and placed on a bench in the greenhouse on February 5, 1957. Following ger-

mination, they were treated on February 16, with 10, 50 and 100 micrograms of gibberellin per plant. Each treatment included ten replicated plants in a randomized block design, and ten non-treated plants were used as a control.

Plant height was measured March 18, 1957, and on March 20, the plants were again treated with gibberellin at the same concentrations as initially applied. Measurements of shoot elongation were made on April 2, 9 and 19, 1957.

Flowering and Fruiting: Three branches of each of six individual mature Halehaven peach trees were selected to be used in an evaluation of the effect of gibberellin on fruit set of peaches. Two branches received foliar applications of 10 or 100 ppm of gibberellin on May 2, 1957, the third branch being used as a control. Sprays were applied when trees were in full bloom. The number of fruits persisting on the trees was counted on July 13, 1957.

One-half portions of two mature bearing Redhaven peach trees received a foliar application of gibberellin at 100 ppm on May 28, 1957 to determine if such an application would enhance fruit size and rate of development. This was three and one-half weeks after full bloom, and the trees were bearing a full crop of fruit.

Half-tree portions of six mature Halehaven trees received a foliar application of 1, 000 ppm gibberellin on July 20, 1957 to determine if shoot growth could be stimulated, and fruit size increased. This was two and one-half months after full bloom, and approximately one month before fruit ripening. These trees had been used earlier in the season for investigating the effect of gibberellin on fruit set. The selection of the half-trees to be treated was made irrespective of their previous treatments.

RESULTS

Strawberry Response to Applications of Gibberellin

Robinson strawberry plants started in the greenhouse on February 8 and treated with gibberellin February 17 produced visible response to the gibberellin treatments within two weeks. Data presented in Table II indicate the effect of gibberellin on petiole length, peduncle length, crown elongation, and flower and fruit development. A statistical analysis indicated that plants in all the gibberellin treatments produced petioles that were significantly longer than petioles on the control plants. While peduncles were not produced in all plants, the peduncles produced by the treated plants were markedly taller than peduncles on the non-treated plants.

The number of flowers in bloom on March 14 was greater in the treated plants (Table II). This was interpreted as an indication of earlier flowering following treatment with gibberellin. The number of fruit harvested, expressed on a percent basis, was slightly less for the treated plants (Table II). However, the weight per fruit was markedly lighter in the treated plants; the berry weight decreasing as the concentration of gibberellin applied increased (Table II).

Treatments of 50 and 100 micrograms of gibberellin per plant resulted in an internodal elongation between the petioles. This caused the

TABLE II

The Effect of Gibberellin on the Petiole Length, Peduncle Length, Crown Elongation, Flowers per Peduncle, and Fruit of Robinson Strawberry Plants. Plants Treated February 17, 1957.

Observation	Date	Micrograms GA per Plant			
		0	10	50	100
Petiole length (cm)	March 5	5.3	7.7	10.2	10.2*
Peduncle length (cm)	March 7	1.4	5.8	12.6	10.2
Crown elongation (cm)	April 4	--	0.1	5.6	9.3
Flowers per Peduncle	March 14	2.5	2.9	4.2	3.9
Fruit per Plant	April 5-22	1.2	0.8	1.0	0.9
Weight per Fruit (gm)		4.8	3.9	2.0	1.0

*Observation analyzed statistically. The various gibberellin treatments not underscored by a common line differ significantly at the 5 percent level.

crowns of treated plants to erupt from their normal rosette pattern of growth and extend vertically as a stem (Table II, and Figures 1 and 2). The extended crown lacked sufficient strength to remain erect and grew in a horizontal plane as it continued to elongate.

As the effect of the applications of gibberellin was dissipated, the crown resumed its normal rosette-type of growth with shorter leaf petioles. This rosette-type crown formed roots when it established contact with the soil.

Plants treated with 50 and 100 micrograms of gibberellin are compared with a non-treated plant in Figure 3. It can be observed that while treated plants produced longer petioles and peduncles than the control plants, there was essentially little difference between the 50 and 100 microgram treatments. Peduncle elongation was increased more than petiole elongation, which resulted in the peduncles extending above the leaves.

The normal pattern of fruit development was not observed on all plants treated with 50 and 100 micrograms of gibberellin. The achenes on many of the fruits did not develop. Receptacular tissue of these flowers in the area supporting the pistils did not swell, and the non-functioning achenes remained appressed on the non-expanded receptacles. The torus of these flowers, just above the calyx and beneath the area of appressed achenes, expanded slightly two to three weeks after anthesis and colored at the

Figure 1

Crown elongation of Robinson strawberry plant treated with 50 micrograms gibberellin on February 17, and photographed on April 18, 1957.

Figure 2

Crown elongation of plant receiving 100 micrograms gibberellin on February 17, and photographed on April 18, 1957.

Note how distant portion of crown has started to resume a rosette appearance with shortened petioles.

corresponding time when the fruit of non-treated plants ripened. Fruit from treated plants is compared with fruit from non-treated plants in Figure 4.

Data do not accurately illustrate the effect of gibberellin on runner development. This was complicated because not all plants produced an inflorescence and fruit. Flowering and fruiting tend to delay runner formation so that plants not fruiting probably would initiate runners earlier and produce them more abundantly. Photoperiod probably exerted an influence also, since runner formation has been reported to occur under 14 hours of light in a 24 hour cycle (Hartmann, 1947). Figure 5 shows the pattern of runner formation in treated and non-treated plants. Runner formation at the nodes of the treated plants appeared to be retarded while the crown was elongating.

Data presented in Table III indicate that treatment with gibberellin appeared to have an effect on the length of runner development between runner plants. The distance between the mother plant and the first runner plant was greater in all treatments, as compared to non-treated plants. However, the distance between subsequently measured runner plants was greater in the controls. The only exception occurred between the second and third runner plants in the 100 microgram per plant treatment.

Robinson strawberry plants, which were dug in the field before

Figure 3

Comparison of Robinson strawberry plants receiving 0, 50 and 100 micrograms gibberellin on February 17, and photographed on March 14, 1957.

Left to right: 0, 100 and 50 micrograms gibberellin per plant. Note elongation of petioles and peduncles of treated plants and slight difference in degree of response between the 50 and 100 microgram applications.

Figure 4

Comparison of fruit from non-treated plants (above) and plants treated with 100 micrograms of gibberellin on February 17, 1957. Photographed April 18. Treatment resulted in longer pedicels and abnormal fruit.

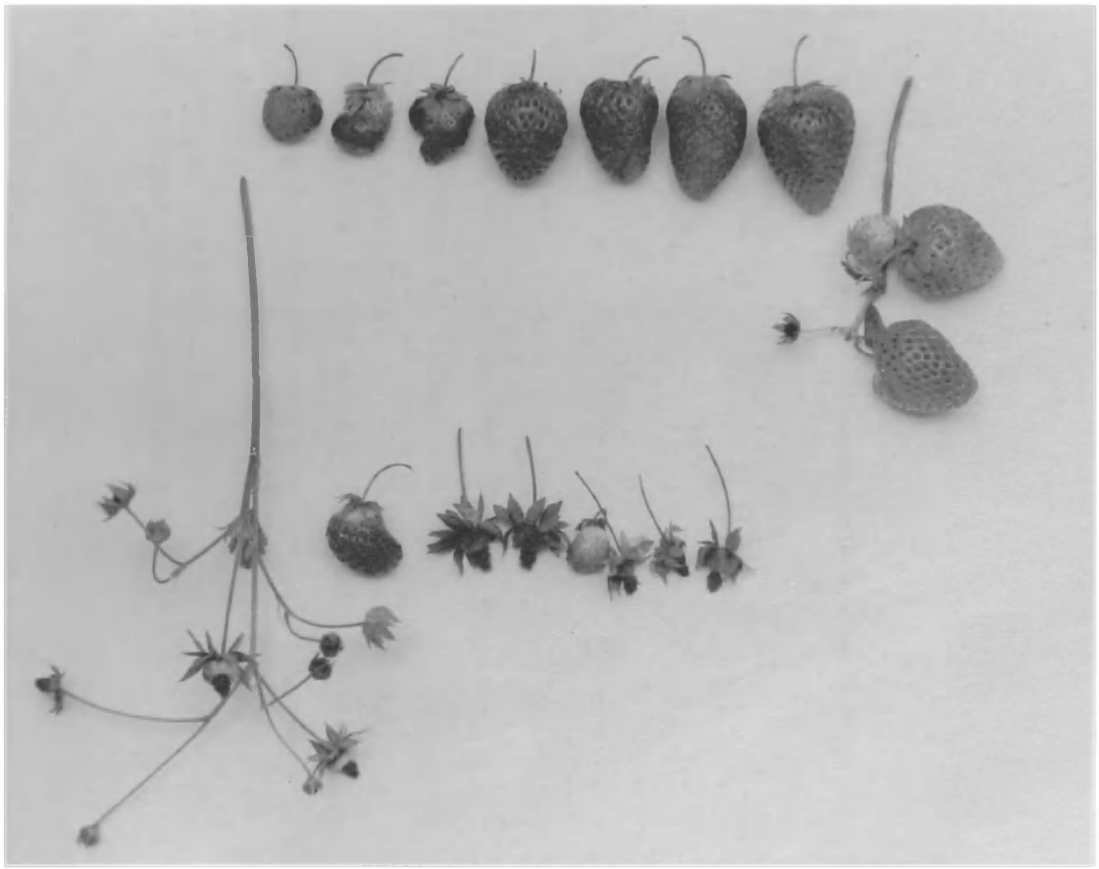


TABLE III

The Effect of Gibberellin on the Runner Length Between the Mother Plant and First Runner Plant and Between Runner Plants of Robinson Strawberry Plants Treated February 17, 1957, and Measured June 8, 1957.

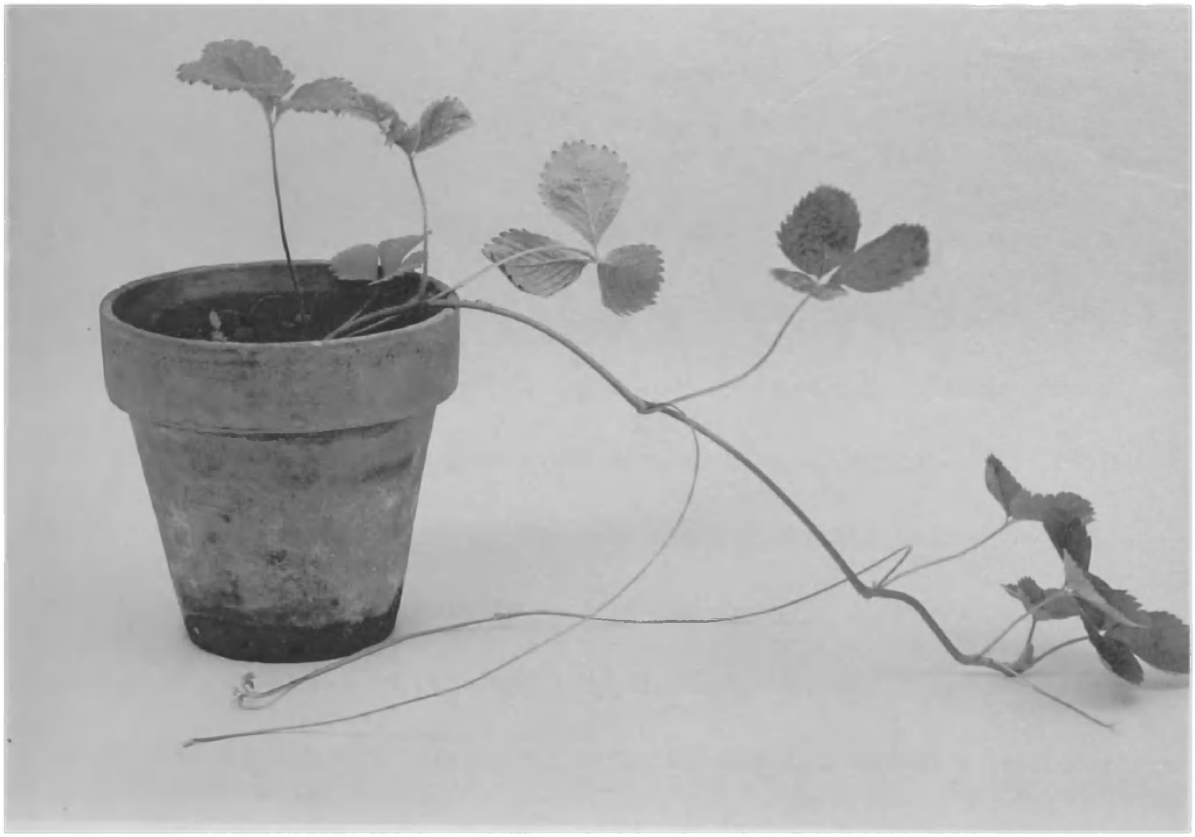
Micrograms GA per Plant	Runner Length to First Runner Plant		Runner Length First to Second Runner Plant		Runner Length Second to Third Runner Plant	
	No. Plants	Distance (cm)	No. Runners	Distance (cm)	No. Runners	Distance (cm)
0	89	35.1	63	42.8	36	41.3
10	93	40.5	66	40.3	25	35.5
50	137	44.9	98	38.7	38	37.2
100	137	43.1	90	39.3	22	42.1

Figure 5

Comparison of strawberry runner development of non-treated plant and plant receiving 100 micrograms gibberellin on February 17. Photographed April 18, 1957.

Top: Plant treated with 100 micrograms gibberellin showing elongated crown and a runner developing from each node. Note retarded stage of development of runners and runner plants.

Bottom: Non-treated plant exhibiting normal pattern of plant and runner development. Note presence of runner plants.



they had been exposed to an extended period of freezing temperatures, were placed in the greenhouse October 14 and treated with 100 micrograms of gibberellin on October 29, 1957. The plants were segregated into groups according to previous summer treatments of gibberellin. The number of leaves per plant, developing between October 29 and December 30, 1957 were counted and indicated that the gibberellin treatment had essentially no effect on leaf number nor rate of leaf appearance. However, the applications of gibberellin on October 20 applied to the plants in the greenhouse resulted in a marked difference in flower number and rate of development.

The total number of flowers produced by the treated and control plants during December and January is illustrated in Figure 6. The percent of the flowers in bloom at weekly intervals in December is illustrated in Figure 7. Thus, it is shown that not only were more flowers in bloom on a certain date in the treated plants, but that the percent of the total number in bloom on a specific date was also greater for the treated plants. This would indicate that plants treated with gibberellin both flowered earlier and produced more flowers per plant.

The number of flowers per peduncle is illustrated in Figure 8 and presented in Table IV. Observations on all dates revealed more flowers per peduncle for treated plants. While the summer applications of gibberellin did not appear to have any effect on flower number, the plots varied

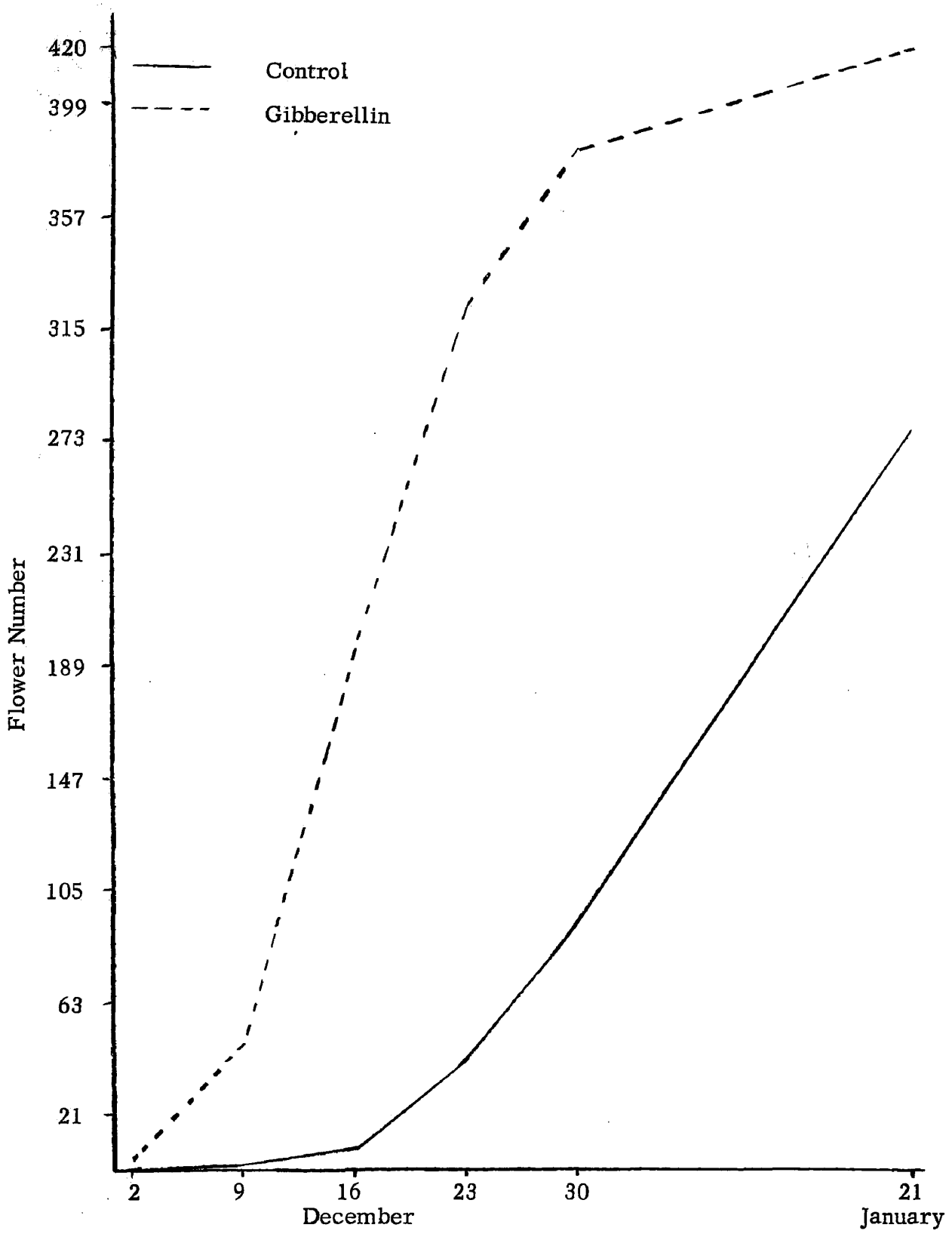


Figure 6. Total number of flowers produced by Robinson strawberry plants treated with 100 micrograms GA per plant on October 20, 1957.

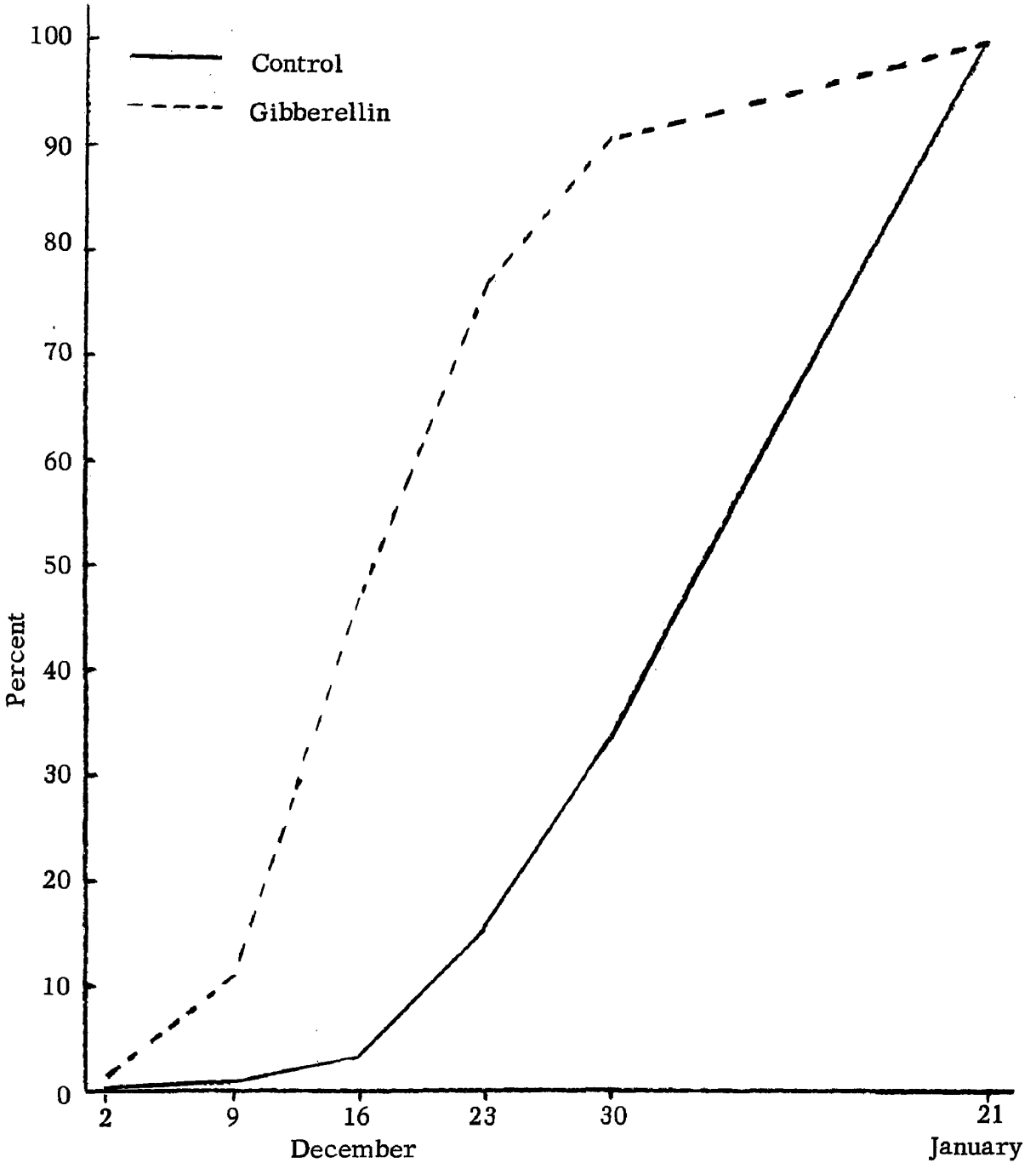


Figure 7. Percent flowers in bloom on respective dates of Robinson strawberry plants treated with 100 micrograms GA per plant on October 20, 1957.

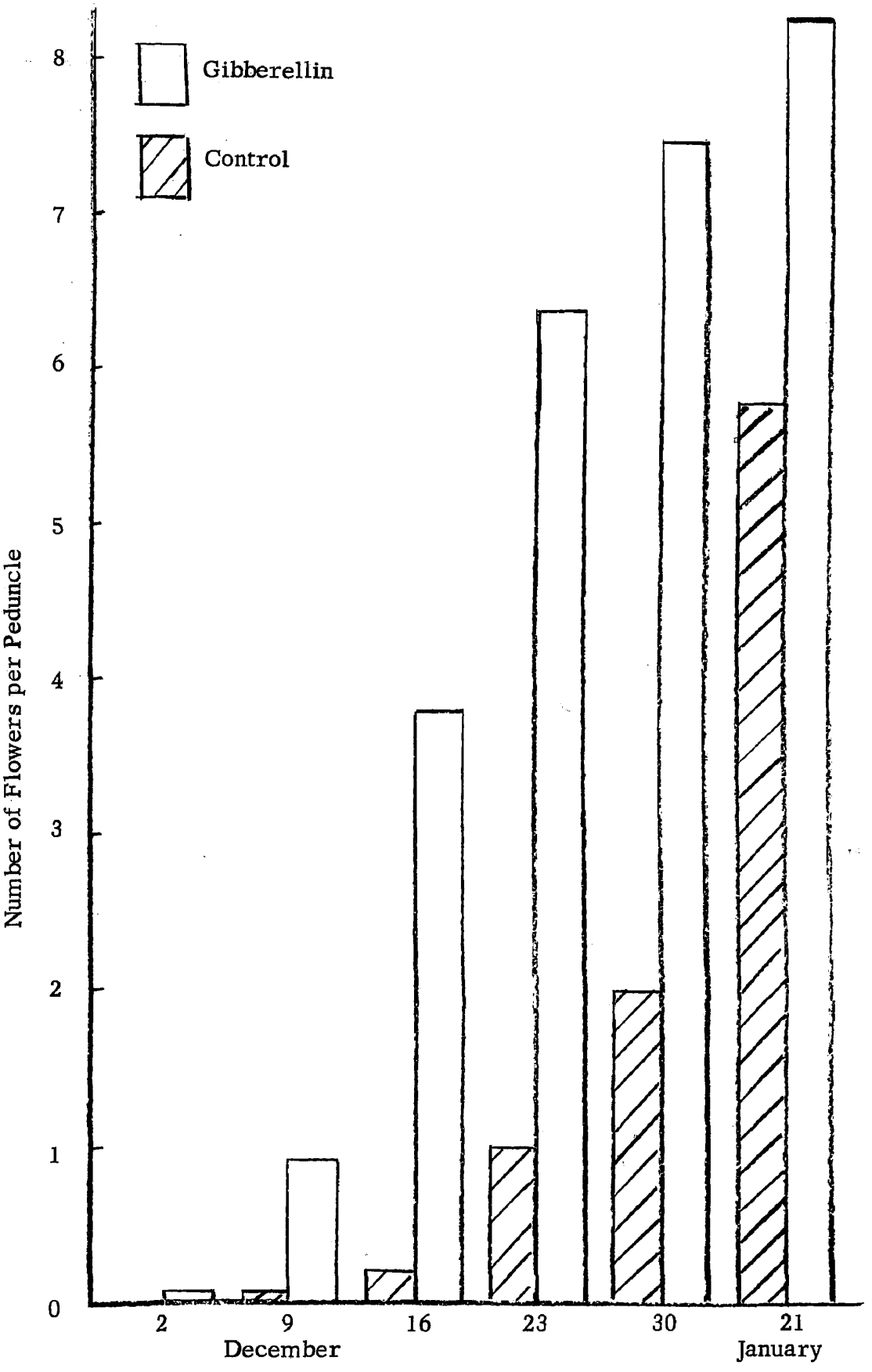


Figure 8. Effect of 100 micrograms GA per plant on number of flowers per peduncle of Robinson strawberry. Plants treated October 20, 1957.

TABLE IV

Number of Flowers and Fruit per Peduncle and Percent Fruit Set of Robinson Strawberry Plants Treated with 100 Micrograms Gibberellin on October 20, 1957. Plants Placed in Greenhouse Ocrober 14 and Fruit Counted February 5, 1958.

Field Plot Number*	No. Summer Applications 100 ppm GA	Micrograms GA October 20	Flowers per Peduncle	Fruit per Peduncle	Percent Fruit Set
II	0	0	6.0	2.3	38
		100	7.7	1.2	16
III	1	0	6.4	2.3	36
		100	9.7	1.3	13
IV	1	0	5.4	2.0	37
		100	8.9	1.4	16
V	3	0	5.8	3.2	55
		100	8.7	2.7	31
IX	2	0	5.5	1.4	25
		100	6.8	0.7	10
Average of all plots		0	5.8	2.2	38
		100	8.3	1.4	17

*Plot numbers correspond to field plot numbers in Table I.

slightly in number of fruit produced per flower stalk and percent fruit set (Table IV). Yields were greatest for the plants in plot V and smallest for plants in plot IX. In all plots, however, the number of fruit per peduncle and percent fruit set was greatest in plants not treated with gibberellin on October 20, 1957. An average of the data for all plots indicates the percent set was twice as great in the non-treated plants. This is slightly misleading, however, since treated plants produced more flowers. This increase in flower number and less fruit per plant would tend to give a much lower percent fruit set. Some abnormal fruits were observed somewhat similar to abnormalities observed for treated plants in the previous greenhouse investigation.

A few plants from each plot were observed to have developed several runners. This phenomena, however, occurred only on plants treated with gibberellin after being transferred into the greenhouse.

Runner plants transferred from the field to the greenhouse November 24, 1957 were treated with 100 micrograms of gibberellin either November 27, December 16, January 11, or both December 16 and January 11. Pollen from treated plants was stained with acetocarmine and the majority of the pollen stained light pink, indicating viability. However, some pollen grains were collapsed and failed to stain. Non-treated flowers were emasculated and pollinated with pollen from treated flowers, and generally produced

normal fruit. Treated flowers emasculated and pollinated with pollen from non-treated flowers generally did not form fruit. However, a few of such treated flowers did yield normal fruit.

The number of flowers and fruit per plant, percent fruit set and percent of flowers yielding abnormal fruit for treated and non-treated plants for each group of runner plants are presented in Table V. The number of flowers per plant may or may not have been affected by treatment with gibberellin. Since a number of flowers were removed for pollen viability evaluation experiments before flower numbers were recorded, a comparison would probably not be valid because, of necessity, more non-treated flowers were removed. In general, all treatments resulted in less fruit per plant and a decreased percent fruit set. The treatment of January 11, applied when the plants were in bloom, had less effect on fruit set than any other treatment. Plants treated both December 16 and January 11 yielded the smallest amount of fruit and the greatest percentage of abnormal fruit, in which the receptacle supporting the pistils failed to develop. While plants treated on November 27 yielded a high percent of abnormal fruit, they also produced a considerable yield of normal fruit.

In an experiment designed to evaluate the effect of a lower concentration of gibberellin, strawberry plants were transferred from a field planting to the greenhouse on November 25, 1957, and treated with 1, 10, 50 or

TABLE V

Effect of Gibberellin on Number of Flowers and Fruit per Plant, Percent Fruit Set, and Percent of Flowers Yielding Abnormal Fruit of Robinson Strawberry Plants. Plants Started in Greenhouse November 24, 1957 and Treated with 100 Micrograms of Gibberellin on November 27, December 16, January 11, and both December 16 and January 11.

Date Treated	Runner Plant	Flowers per Plant	Fruit per Plant	Fruit Set (Percent)	Flowers Producing Abnormal Fruit (Percent)
Control	1st	6.9	2.6	37.8	0.0
	2nd	6.1	2.4	40.0	0.0
	3rd	8.5	2.9	34.1	0.0
	4th	7.1	3.3	45.6	0.0
Average for Treatment		7.2	2.8	38.7	0.0
November 27	1st	11.0	2.4	21.8	20.9
	2nd	8.4	2.2	26.2	17.9
	3rd	8.2	1.4	17.1	12.2
	4th	6.8	1.2	17.6	16.2
Average for Treatment		8.6	1.8	20.9	17.2
December 16	1st	17.1	1.3	7.6	1.2
	2nd	12.1	1.0	8.3	14.1
	3rd	9.6	1.8	18.8	10.4
	4th	7.9	1.0	12.7	6.4
Average for Treatment		11.9	1.3	10.9	7.3
January 11	1st	7.6	1.0	14.7	4.4
	2nd	8.1	1.8	22.2	6.2
	3rd	9.1	3.0	33.0	7.7
	4th	5.0	0.5	10.0	0.0
Average for Treatment		7.9	1.8	23.1	5.8
December 16 and January 11	1st	11.4	0.2	1.8	29.8
	2nd	11.9	0.9	7.6	20.2
	3rd	9.6	1.3	13.5	25.0
	4th	9.6	1.3	13.5	26.0
Average for Treatments		10.6	0.9	8.7	25.2

100 micrograms of gibberellin per plant on November 27. Plant responses to these applications are presented in Table VI. Plants which received only one microgram of gibberellin did not differ from the controls in any observations. Petioles and peduncles were significantly longer on plants treated with 10, 50 or 100 micrograms of gibberellin. Plants receiving applications of 10 and 50 micrograms of gibberellin per plant appear to have produced more flowers than the control plants. This may not be a valid analysis, since some blossoms were removed from the control plants and plants treated with 50 and 100 micrograms of gibberellin for pollination studies. The percent fruit set of normal berries was relatively the same for all treatments, except plants treated with 100 micrograms of gibberellin, which yielded a considerable lower percent of normal fruit. Abnormal fruits were also produced on plants treated with 50 or 100 micrograms of gibberellin. Figure 9 compares a representative plant from each treatment.

The elongation response of the petioles and peduncles to the gibberellin concentrations is plotted in Figure 10. One can observe that the response of the peduncles to applications of gibberellin is accentuated over a wider range of concentrations than occurred in the petioles. There was only a slight increase in the petiole elongation at the concentrations of gibberellin greater than 10 micrograms, while the peduncles continued to exhibit a marked response to the 50 and 100 microgram applications.

TABLE VI

Effect of Applications of Gibberellin on Petiole Length, Peduncle Length, Number of Flowers per Plant, and Fruit Development of Robinson Strawberry Plants. Plants Potted in Greenhouse November 25, 1957 and Treated November 27.

Observation	Date	Micrograms GA per Plant				
		0	1	10	50	100
Petiole length (cm)	February 14	4.1	4.8	7.3	8.5	9.7*
Peduncle length (cm)	February 14	5.3	5.5	12.1	17.3	19.9*
Fruit set (percent)	February 28	29.9	34.8	37.6	26.7	17.5
Abnormal fruit (percent)	February 28	--	--	0.7	5.3	30.9
		0	1	100	50	10
Flowers per plant	February 19	6.8	8.3	8.8	10.9	11.8*

*Observations analyzed statistically. The various gibberellin treatments not underscored by a common line differ significantly at the 5 percent level.

Figure 9

Comparison of Robinson strawberry plants receiving different amounts of gibberellin. Plants started in the greenhouse November 25 and treated with gibberellin on November 27, 1957. Photographed January 12, 1958.

Left to right: Plants receiving 0, 1, 10, 50 and 100 micrograms gibberellin.

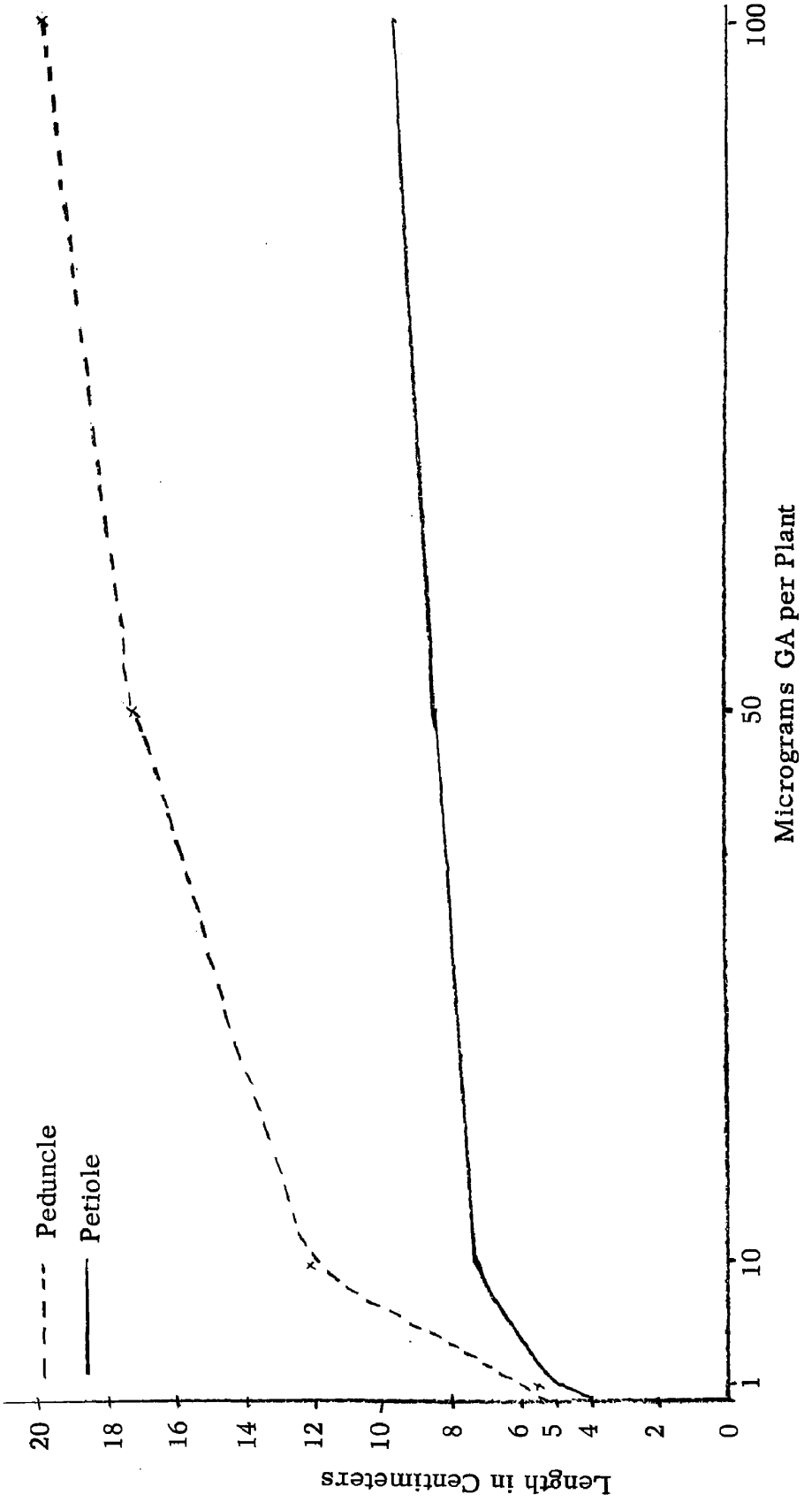


Figure 10. The effect of various concentrations of gibberellin on petiole and peduncle length of Robinson strawberry plants. Plants started in greenhouse November 25 and treated November 27, 1957. Measurements recorded February 17, 1958.

Certain flowers in each treatment were emasculated and treated with pollen from non-treated plants, or plants that had received 50 or 100 micrograms of gibberellin. Emasculated flowers on the non-treated plants produced fruit irrespective of their pollen source. All emasculated flowers on plants treated with one and 100 micrograms of gibberellin that received pollen from non-treated plants failed to set fruit. The majority of emasculated flowers on plants treated with 10 micrograms of gibberellin and pollinated with non-treated pollen produced normal berries. Similarly treated flowers on plants treated with 50 micrograms of gibberellin and pollinated with pollen from non-treated plants generally did not yield fruit. Pollen stained with acetocarmine appeared to be viable.

Robinson strawberry plants held in cold storage at 0°C from November 24 to February 12, and then potted and placed on a greenhouse bench, were treated with 100, 500 and 1, 000 micrograms of gibberellin per plant on March 14, 1958. Data presented in Table VII indicates the response of the plants to these treatments. Both petiole and peduncle length were increased by all applications, the lengths becoming increasingly greater with increasing concentrations of gibberellin. Flower number appeared to be reduced on treated plants and the percent fruit set reduced to nil for plants treated with 500 and 1, 000 micrograms of gibberellin. While plants treated with 500 and 1, 000 micrograms of gibberellin yielded no fruit, over 60 percent of the flowers produced abnormal fruit.

TABLE VII

Effect of Applications of Gibberellin on the Petiole and Peduncle Length, Crown Elongation and Diameter, Flower Number and Development, and Runners per Plant of Robinson Strawberry Plants Started in Greenhouse February 12, and Treated March 14, 1958.

Observation	Date	Micrograms GA per Plant			
		0	100	500	1, 000
Petiole length (cm)	April 27	8.0	9.9	15.0	16.9*
Peduncle length (cm)	April 27	7.0	9.1	14.0	18.4
Flowers per plant	April 27	7.4	5.0	4.0	5.6
Fruit set (percent)		44.0	10.0	0.0	0.0
Abnormal fruit (percent)	April 27	0.0	43.3	66.7	61.5
Crown elongation	April 27	--	3.6	29.6	38.1
Crown diameter	May 24	10.8	9.6	5.7	6.6*
Runners per plant	May 18	4.3	4.3	3.0	4.0
Average runner length (cm)	May 18	29.6	60.5	41.2	40.9
Runner plants per mother plant	May 18	1.3	3.4	1.3	2.0

*Observations analyzed statistically. The various gibberellin treatments not underscored by a common line differ significantly at the 5 percent level.

Crown elongation was markedly increased through the 500 and 1, 000 microgram applications of gibberellin. A significant reduction in crown diameter was also observed with these two treatments. While the runner number per plant did not appear to be affected by treatment with gibberellin, the average runner length was longer on treated plants. The distance between the mother plant and first runner plant was 37. 8, 42. 2 and 40. 5 centimeters, respectively, for the 100, 500 and 1, 000 gibberellin-treated plants, as compared to 31. 1 centimeters for the non-treated plants.

Robinson strawberry plants which were started in the greenhouse March 15, 1958, were treated with gibberellin at 1, 10, 100, 500 and 1, 000 micrograms per plant on March 27. Observations on plant development as affected by various treatments are presented in Table VIII. Significant increases in petiole length were obtained with applications of 500 and 1, 000 micrograms gibberellin only. While all treatments except the one microgram application resulted in longer peduncles, only 10, 500 and 1, 000 micrograms gibberellin-treated plants produced longer pedicels on the primary flower. Flowers were brushed with a camel's hair brush when in bloom to insure transfer of pollen to the stigma. The number of flowers per plant was similar for all treatments, but the percent fruit set was markedly reduced or inhibited by the 100, 500 and 1, 000 microgram applications. Abnormal fruit were formed in all gibberellin treatments, the percentage increasing greatly at the higher concentrations.

TABLE VIII

Effect of Foliar Applications of Gibberellin on the Vegetative and Floral Development of Robinson Strawberry Plants. Plants Started in Greenhouse March 15, 1958, and Treated with Gibberellin March 27.

Observation	Date	Micrograms Gibberellin per Plant					
		0	1	10	100	500	1,000
Petiole length	May 16	9.8	10.0	11.5	11.4	13.7	12.9*
Flowers per plant	May 16	8.1	9.6	9.0	8.0	7.5	8.0*
Abnormal fruit (percent)	May 16	0.0	0.3	13.2	23.4	44.2	57.8
Fruit set (percent)**		27.7	33.7	37.7	9.4	0.0	0.0
Crown elongation (cm)	May 16	0.0	0.0	0.0	2.0	43.0	45.6
Crown diameter (mm)	May 24	12.3	12.5	12.4	11.2	8.2	6.8*
Runners per plant	May 24	3.0	3.3	3.5	3.5	3.6	2.3
Runner length	May 24	42.0	42.5	56.1	54.9	34.2	28.5
Runner plants (ave.)	May 24	2.1	1.9	3.4	2.6	0.3	0.5
Runner length mother plant to 1st runner plant	May 24	36.8	36.8	41.8	43.2	39.5	36.8
		0	1	10	100	1000	500
Peduncle length (cm)	May 16	7.8	8.8	13.4	16.3	18.3	22.3*
		0	1	100	10	1000	500
Pedicel length (cm)	May 24	2.9	3.4	3.5	4.0	3.9	4.3*

*Observations analyzed statistically. Values of various gibberellin treatments not underscored by a common line differ significantly at the 5 percent level.

**Fruit normal in appearance possessing enlarged achenes and receptacular tissue with no distortion in calyx region.

Crown elongation was produced by plants treated with 100, 500 and 1, 000 micrograms of gibberellin, and crown diameter was significantly reduced on plants receiving 500 and 1, 000 micrograms of gibberellin. The number of runners per plant was relatively consistent in all treatments. The runner length and number of runner plants per mother plant were greatest for the 10 and 100 microgram treatments, and least for the 500 and 1, 000 microgram applications.

A repetition of the previous experiment, with plants started in the greenhouse April 12 and treated April 19, produced similar results (Table IX). The lower gibberellin concentrations, one and 10 micrograms, produced slightly longer peduncles and a greater percentage of abnormal fruit than in the previous study. All treatments except the one microgram application of gibberellin appeared to have hastened flowering slightly.

The elongation response of the petioles and peduncles was plotted free-hand against the gibberellin concentrations (Figure 11). The response of both plant parts diminished beyond the 500 microgram concentration. However, the intensity of the response between one and 500 micrograms was much greater for the peduncle. The rate of elongation for the petioles was less with all concentrations of gibberellin applied, although the decrease in response to the 1, 000 microgram application was less than for the peduncle.

Certain flowers that were not developing on gibberellin treated plants

TABLE IX

Effect of Foliar Applications of Gibberellin on the Vegetative and Floral Development of Robinson Strawberry Plants. Plants Started in Greenhouse April 1 and Treated with Gibberellin April 9, 1958.

Observation	Date	Micrograms Gibberellin per Plant					
		0	1	10	100	500	1,000
Petiole length (cm)	June 3	9.2	10.8	9.7	10.4	13.6	12.9*
Peduncle length (cm)	June 5	8.7	11.8	15.3	18.8	24.8	22.9*
Pedicel length (cm)	June 5	3.0	3.1	3.7	3.8	4.5	5.1*
Flowers per Plant	May 12	6.4	7.6	7.8	7.7	8.6	8.1*
Fruit set (percent)**	June 3	47.1	31.1	15.9	12.9	0.0	0.0
Abnormal fruit (percent)	June 3	0.0	18.0	41.9	48.3	85.3	93.7
Crown elongation (cm)	June 3	0.0	0.0	0.0	4.1	35.3	39.0
Runners per plant	June 3	2.3	3.4	3.8	3.3	2.6	2.8
		1	0	10	100	1000	500
Crown diameter (mm)	June 3	12.3	11.1	10.8	9.9	8.0	7.5*

*Observations analyzed statistically. Values of various gibberellin treatments not underscored by a common line differ significantly at the 5 percent level.

**Fruit normal in appearance possessing enlarged achenes and receptacular tissue with no distortion in calyx region.

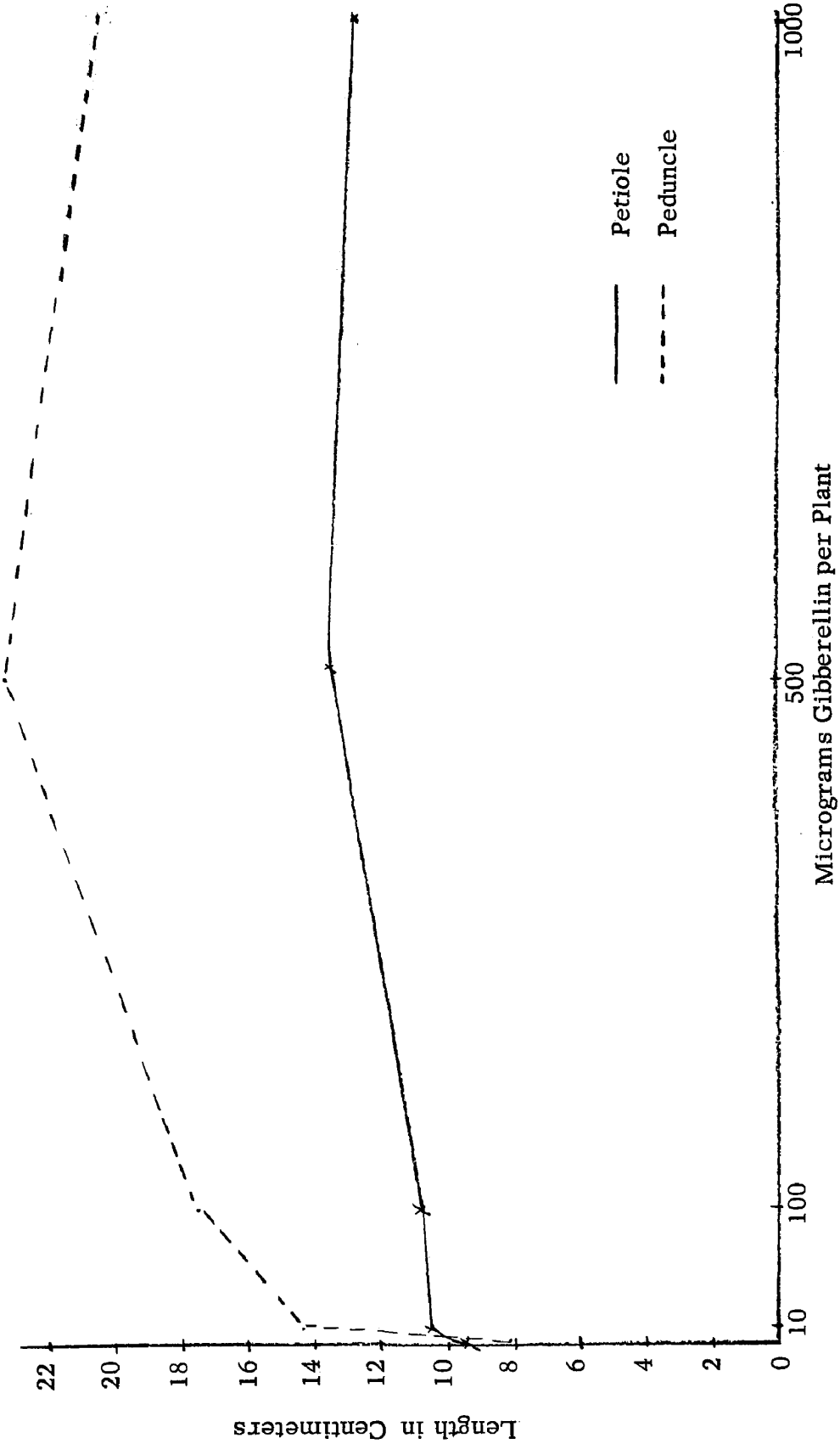


Figure 11. Petiole and peduncle response of Robinson strawberry plants treated with various concentrations of gibberellin. Values are averages of two experiments. Plants in first experiment started February 12, treated February 14, and measured April 27, 1958. Plants in second experiment started March 15, treated March 27, and measured May 16, 1958.

were coated with either a one percent gibberellin-lanolin paste, or a one percent indolebutyric acid-lanolin paste May 10 and 11, which was 12 to 13 days after flowering. The second and third flowers on the inflorescence to flower were treated. Forty percent of the flowers treated with the one percent gibberellin-lanolin paste produced a slight swelling of the receptacle. Eighty-three percent of the indolebutyric acid-lanolin paste treated flowers produced some enlargement of the receptacle.

The previous experiment was repeated a third time to more fully evaluate the effect of gibberellin on the rate of flowering and the effect of lanolin paste applications of gibberellin or indolebutyric acid on fruit development of plants previously treated with gibberellin. The response of Robinson strawberry plants, started in the greenhouse April 9 and treated with 1, 10, 100, 500 or 1, 000 micrograms of gibberellin on April 15, 1958 are presented in Table X. Results obtained were similar to the previous experiments with two exceptions. No significant differences for petiole and pedicel lengths were obtained between any treatments. All treatments appeared to have resulted in slightly earlier flowering.

The second and third flowers of the inflorescence to bloom on the plants treated with 100, 500 and 1, 000 micrograms of gibberellin received an application of either one percent gibberellin-lanolin paste or one percent indolebutyric acid-lanolin paste May 11. This was five to six days after the flowers

TABLE X

Effect of Foliar Applications of Gibberellin on the Vegetative and Floral Development of Robinson Strawberry Plants. Plants Started in Greenhouse April 9,and Treated with Gibberellin April 15, 1958.

Observation	Date	Micrograms Gibberellin per Plant					
		0	1	10	100	500	1,000
Petiole length (cm)	June 4	8.5	8.4	8.5	9.4	10.1	10.8*
Peduncle length (cm)	June 5	6.0	7.1	11.8	12.6	14.2	14.4*
Pedicel length (cm)	June 5	2.2	2.2	2.9	3.2	3.6	3.3*
Flowers per plant	May 23	7.9	7.9	7.1	6.1	8.2	7.4*
Fruit set (percent)	June 4	33.4	71.4	19.3	16.3	0.0	0.0
Abnormal fruit (percent)	June 4	0.0	3.1	12.2	22.4	71.2	65.0
Crown elongation (cm)	June 4	0.0	0.0	0.9	4.3	32.8	49.8
Crown diameter (mm)	June 4	10.8	10.1	9.6	8.5	6.8	6.3*
Runners per plant	June 4	0.9	1.6	1.1	1.5	1.0	1.4

*Observations analyzed statistically. Values of various gibberellin treatments not underscored by a common line differ significantly at the 5 percent level.

had bloomed. Of the flowers treated with the gibberellin-lanolin paste, 88 percent produced a slight swelling of the receptacle. Ninety-three percent of the flowers coated with an indolebutyric acid-lanolin paste produced an enlargement of the receptacle. Figure 12 shows that the indolebutyric acid treated flowers attained a larger size than the gibberellin treated flowers. Fruit size in both treatments was inferior to the size of normally developing fruit. The lanolin paste treatments did not result in development of the achenes.

The petioles, peduncle, flowers and crown exhibited the most consistent responses to gibberellin investigations in the greenhouse. A chlorotic effect was also observed in the young leaves. This condition tended to disappear in the older leaves. Figure 13 shows a developing leaf exhibiting a light chlorotic margin on each of the leaflets.

Plants of a seedling strawberry (M 1156), transferred to the greenhouse in September and treated with 100 micrograms of gibberellin on October 24, 1957, did not exhibit the same morphological changes in the same pattern as observed for the Robinson variety. Figure 14 shows the elongation of the main crown and then extension of a crown shoot from the elongated main crown. Elongation of the branch crowns occurred on Robinson plants also, but the elongation of all the crowns for this variety had a common origin and did not elongate from an elongating crown.

Figure 12

Comparison of "fruit" from gibberellin treated plants coated with one percent lanolin paste of indolebutyric acid or gibberellin, with fruit from a non-treated plant which developed normally.

Left: Fruit developing from flower coated with one percent indolebutyric acid-lanolin paste mixture.

Center: Fruit developing from flower coated with one percent gibberellin-lanolin paste mixture.

Right: Fruit from non-treated plant.

Plants treated April 15 and flowers coated May 11, five to six days after blooming. Photographed June 10, 1958.


IBA
GA

Figure 13

Leaf of Robinson strawberry plant showing chlorotic margin of the leaflets developing following application of 100 micrograms of gibberellin. Plant treated December 16, 1957, and photographed January 12, 1958.

Figure 14

Strawberry seedling (M-1156) exhibiting crown elongation with extension of a crown shoot from the main crown which had previously elongated.

The crown of a M-1156 strawberry plant treated with 100 micrograms of gibberellin elongated, but the length of the petioles arising from the elongated crown did not differ from the non-treated plants (Figure 15). The peduncle of another M-1156 plant elongated greatly with elongation occurring between all the nodes of the primary axis, but not between the second and third nodes of the lateral branches of the primary axis (Figure 15).

Rooted and non-rooted runner plants were used in 1957 to study the translocation of the gibberellin stimulus in strawberry runners. Application of 100 micrograms of gibberellin per plant to either the mother plant, first runner or second runner plant resulted in longer leaf petioles and crown elongation in the treated plant only. This vegetative stimulation was not observed in the attached plants. It did not appear to be translocated either from the treated runner plant to the adjacent runner plants or the mother plant. Similar results were obtained with both the rooted and non-rooted runner plants. Occasionally, runner plants developing from runners arising from treated runner plants produced elongated crowns. Figure 16 shows plants treated with gibberellin and the attached non-treated plants.

In addition to treating the three individual plants as in 1957, the node between the first and second runner plants and the runner between the first runner plant and this node were also treated in the 1958 investigation. Applications of 500 micrograms of gibberellin per plant were applied. Both

Figure 15

Effect of gibberellin on the morphological development of strawberry seedling (M-1156) plants in the greenhouse. Plants treated with 100 micrograms of gibberellin on October 24, 1957, and photographed on January 12, 1958.

Top: Non-treated plant on left, and treated plant on the right. Petioles on elongated crown of treated plant did not elongate in response to gibberellin. Note elongated, weak, spindly peduncle and pedicels.

Bottom: Peduncle of treated plant showing elongation between all the internodes of the primary axis.

Figure 16

Comparison of Robinson strawberry plant and runner plants which had gibberellin applied to either the first runner plant or second runner plant to determine if the gibberellin stimulus moves through the runner.

Top: Control, no gibberellin applied.

Center: Gibberellin applied to first runner plant only. Note elongation of crown in treated runner plant only.

Bottom: Gibberellin applied to second runner plant only. Note crown elongation has been limited to this plant.

rooted and non-rooted runner plants were evaluated for both Robinson and Catskill varieties.

Applications of gibberellin to the mother plant resulted in a vegetative response limited to the treated mother plant only for both varieties with both rooted and non-rooted runner plants. Vegetative stimulation occurred in the non-rooted first runner plant of both varieties only when the first runner plant was treated. The first runner plants that were rooted responded to applications of gibberellin to the runner between the first runner plant and the next distant node also.

Applications of gibberellin to the rooted second runner plants of the Robinson variety was the only treatment to yield a vegetative response. However, in the non-rooted Robinson runner plants and rooted Catskill runner plants, vegetative stimulation in the second runner plant was obtained from applications of gibberellin which had been applied to the second runner plants, to the node between the first and second runner plants, and to the runner between the first runner plant and next distant node. The second runner plants, which had not been rooted for Catskill variety, responded to applications of gibberellin applied to the second runner plant and the runner between the first runner plant and next distant node.

The response of different strawberry varieties to foliar applications of gibberellin was investigated in 1957. Data presented in Table XI indicate

TABLE XI

Effect of Foliar Application of 100 ppm of Gibberellin on the Length in Centimeters of Flower Stalks of Certain Strawberry Varieties Treated April 29 and Measured May 26, 1957.

Variety	Petiole Length (cm)	
	Non-Treated Plants	Treated Plants
Robinson	6.2 ± 1.32*	13.1 ± 2.8
Premier	5.7 ± 1.8	11.2 ± 1.98
Catskill	12.2 ± 2.26	24.2 ± 4.35
Tennessee Beauty	14.3 ± 2.07	24.23 ± 2.87
Red Crop	8.8 ± 2.18	17.02 ± 2.30
M-1322	13.2 ± 2.57	19.7 ± 2.64
Pocahontas	12.5 ± 2.5	24.4 ± 3.67
Crimson Flame	14.0 ± 2.73	24.3 ± 3.9

*Standard deviation $= \sqrt{\frac{\Sigma X^2 - \frac{(\Sigma X)^2}{n}}{n-1}}$

that all varieties receiving an application of 100 ppm of gibberellin applied April 29, 1957, produced significantly longer peduncles than the non-treated plants. The treated Robinson, Premier and Catskill plants yielded 92, 87 and 120 percent respectively as much fruit as the non-treated plants. Fruit from treated plants was normal in appearance.

Plants set in the field in 1957 and treated with gibberellin exhibited responses similar to those obtained in the greenhouse. Peduncles elongated and made inflorescences more accessible, which made blossom removal during the first season easier and faster. Data presented in Table XII show the effect of applications of gibberellin on runner development. Observations on June 29 indicated that plants receiving two or more foliar applications of gibberellin had produced fewer runners than the control plants. This same pattern tended to prevail on August 17 for Premier and Catskill varieties. Except for plot I, which received four applications of gibberellin during the summer, the differences between the plots in number of runners for the Robinson variety on August 17 were small and inconsistent.

The effect of the applications of gibberellin on runner length and crown elongation is indicated in Table XIII. Average runner length for all varieties on June 30 was greater in plot I, which had received three applications prior to measuring. Measurements for the other plots varied considerably irrespective of treatment. Crown elongation was evident in all treated plots on

TABLE XII

The Effect of Foliar Applications of Gibberellin on Number of Developing Runners of Premier, Catskill and Robinson Strawberry Plants Planted in 1957 and Runners Counted June 29 and August 17, 1957.

Plot	Number of Gibberellin Applications	June 29, 1957			August 17, 1957		
		Premier	Catskill	Robinson	Premier	Catskill	Robinson
I	4	0.3	1.9	1.6	4.3	5.8	8.5
II	0	2.0	2.7	3.2	7.3	9.0	11.0
III	1	2.9	2.3	4.6	9.0	7.8	15.0
IV	1	1.9	2.7	3.9	8.3	5.0	9.3
V	3	0.3	1.8	1.1	7.5	6.5	12.0
VI	0	2.2	2.0	3.6	13.8	11.5	13.8
VII	3	0.3	0.9	0.7	7.5	7.0	11.3
VIII	0	1.3	2.8	3.0	11.5	10.8	14.5
IX	2	0.5	1.7	1.8	7.3	6.8	13.5
X	0	1.9	2.9	3.3	10.5	7.3	15.8

TABLE XIII

Effect of Foliar Applications of Gibberellin on Runner Length and Crown Elongation of Premier, Catskill and Robinson Strawberry Plants, Planted April 29, 1957, Runner Length Measured June 30 and Crown Elongation Measured August 17, 1957.

Plot	Number of Gibberellin Applications	Average Runner Length (cm)			Crown Elongation Length (cm)		
		Premier	Catskill	Robinson	Premier	Catskill	Robinson
I	4	45.9	51.9	60.8	19.1	12.5	31.3
II	0	20.3	50.9	31.1	--	--	--
III	1	25.1	42.3	35.3	--	--	--
IV	1	24.4	31.7	20.7	2.0	9.7	5.4
V	3	27.1	34.0	4.5	6.4	16.9	33.0
VI	0	23.2	18.7	31.9	--	--	--
VII	3	29.5	28.8	25.1	6.6	18.7	23.6
VIII	0	20.7	39.7	24.1	--	--	--
IX	2	21.0	36.5	26.8	4.8	4.2	36.1
X	0	16.4	34.0	30.1	--	--	--

August 17, except plot III, which was not sprayed with gibberellin until July 7. The amount of elongation of the individual crowns tended to be directly proportional to the number of applications of gibberellin applied. Figure 17 shows a plant in plot I that received four applications of gibberellin. The crown elongation resulted in a more distant location of the plant apex from the plant's original root system.

One-half the plants in each variety in each plot were sprayed with a 100 ppm foliar application of gibberellin on May 4, 1958. The peduncles and petioles produced following this treatment were elongated and more erect (Figure 18). Table XIV presents data on the fruit yield as affected by variety and applications of gibberellin in 1957 and 1958. Yields in all plots were reduced for plants sprayed with 100 ppm gibberellin on May 4, 1958. Many plants sprayed with gibberellin in 1958 failed to produce fruit or yielded abnormal fruit similar to abnormal fruits obtained in previous greenhouse studies.

The yield in plots I and II were reduced by factors other than the applications of gibberellin. A heavy rainstorm in July, 1957 washed away plants and covered others in plots I and II with eroded soil. In addition, plants in plot I had to compete with an infestation of quack grass (Agropyron repens). Plants in plot X were dug in the fall of 1957 and used for greenhouse studies during the fall and winter of 1957-58. In general, the yield of fruit in 1958

Figure 17

Strawberry plant receiving four foliar applications of 100 ppm gibberellin between April 28 and July 7, 1957. Photographed August 18, 1957. Elongation of main crown and two crown shoots has resulted in a more distant location of the crown apices from the plant's original root system.

Figure 18

Three rows of strawberry plants on right sprayed with 100 ppm gibberellin on May 4, 1958. Other rows not treated. Photographed May 31, 1958. Gibberellin resulted in elongated and more erect peduncles, and flowers that were very prominent.

TABLE XIV

Effect of Gibberellin on the 1958 Yield in Grams of Premier, Catskill and Robinson Strawberry Plants Set in the Field in the Spring, 1957. Certain Plots Received Foliar Applications of Gibberellin in 1957 and One-half of Plants in each Variety in each Plot were Sprayed with 100 ppm Gibberellin May 4, 1958.

Plot	Number of Gibberellin Applications (1957)	Premier		Catskill		Robinson	
		Treated 1958	Non-treated 1958	Treated 1958	Non-treated 1958	Treated 1958	Non-treated 1958
I	4	334	384	310	408	208	1128
II	0	1261	2238	1269	2948	515	3152
III	1	1822	6587	1490	5004	371	3646
IV	1	1717	7488	2207	4039	565	3111
V	3	1106	4188	2642	3894	486	3279
VI	0	1441	7018	2932	5643	874	3971
VII	3	813	5087	5761	4769	729	4202
VIII	0	1992	7497	8931	7898	1228	3596
IX	2	1262	6050	3221	6154	865	4397
Total		11748	46537	28763	40757	5841	30482
Percent*		25	100	71	100	19	100

$$^{*}\text{Percent} = \frac{\text{total variety yield treated plants 1958}}{\text{total variety yield non-treated plants 1958}} \times 100$$

did not appear to be increased in plots treated with gibberellin in 1957 compared with the control plots. Premier and Catskill plots treated with gibberellin in 1957 yielded slightly less fruit than control plots. Differences between the plot yields in the Robinson variety were inconsistent.

A severe late spring frost on May 23, 1958, killed many of the primary flowers which were in bloom. These flowers on plants sprayed with 100 ppm gibberellin on May 4, 1958 exhibited an unusual pattern of development. Figure 19 shows development in injured Premier blossoms compared to normally developing fruit. While the pistils had been killed by the freezing temperatures, the toral region above and adjacent to the calyx, expanded and colored red; yet the receptacular tissue supporting the pistils did not swell.

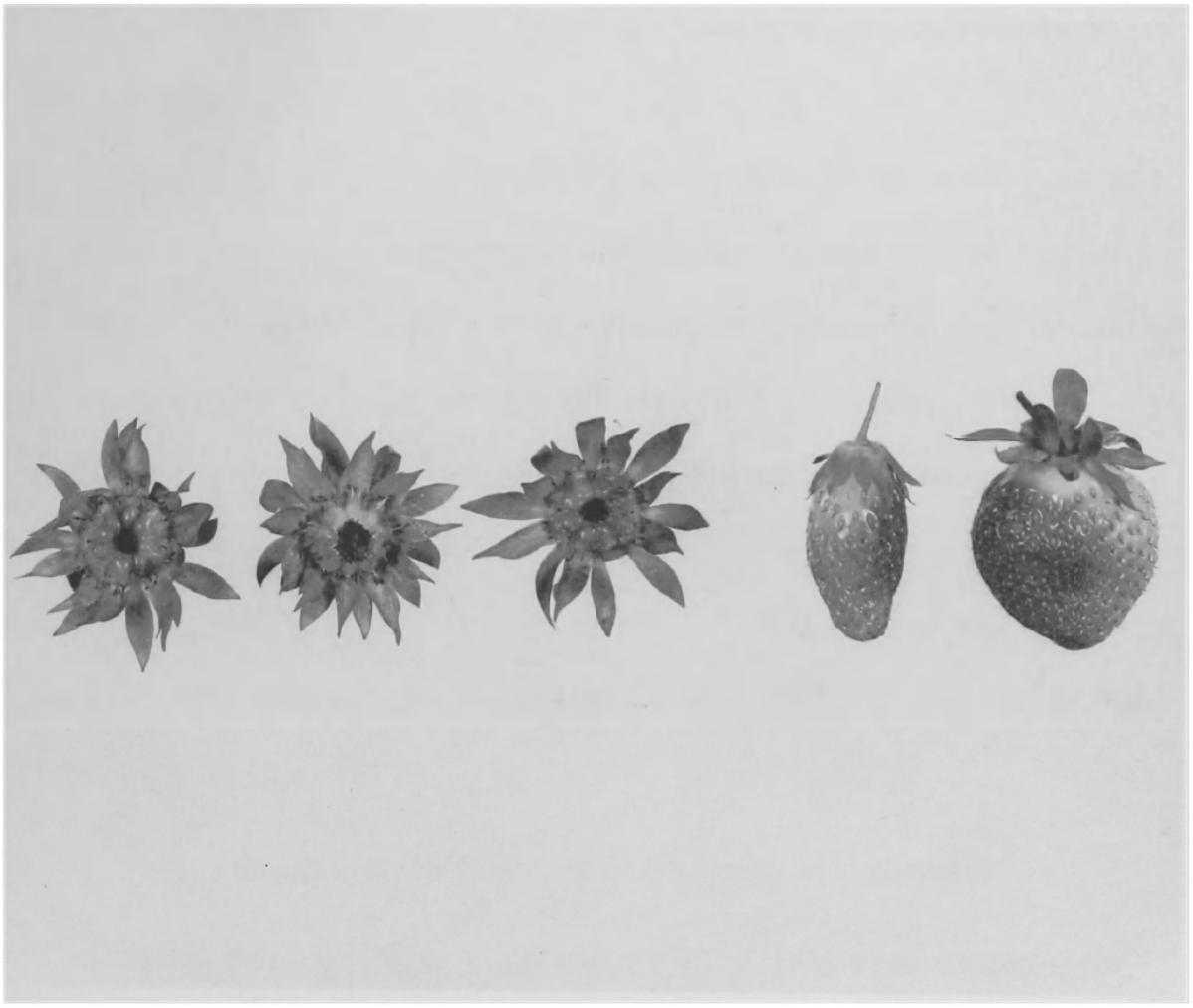
Response of the Apple to Applications of Gibberellin

Shoot growth of rooted Malling IX and XVI cuttings treated with 10, 50 and 100 micrograms of gibberellin in January and February, 1957 was comparable to shoot growth of the non-treated plants. There were no statistically significant differences in shoot length on any of the dates that measurements were taken.

Rooted Malling IX and XII cuttings sprayed with 100 ppm of gibberellin at one week, two week and four week intervals, exhibited little response to any of the treatments. No statistically significant differences were obtained in either trunk diameter or shoot elongation, from any of the treatments in either

Figure 19

Comparison of developing fruit from gibberellin treated plants that were injured by spring frost with normally developing fruit from non-treated plants. Three fruits on left from plants sprayed with 100 ppm gibberellin on May 4. Two fruits on right from control plants and not injured by frost. Photographed June 10, 1958. Fruits from treated plants, which had pistils killed by frost, show some receptacular development beneath the pistil area in the region of the stamens.



of the Malling IX or XII plants. A few of the Malling XII plants died one to two weeks after planting as a result of poor root systems. Plants died irrespective of the treatments, but death occurred three to four days earlier in the gibberellin treated plants.

Foliar applications of 10 and 100 ppm gibberellin applied to bearing apple trees in full bloom (May 9) appeared to have no effect on the fruit set or rate of fruit development in 1957. These phenomena were more influenced by the amount of bloom on the branches used in this investigation than by any application of gibberellin. Applications of gibberellin sprayed on the apple trees three weeks after full bloom (May 28) had no effect on shoot growth or fruit size. Bearing apple trees, sprayed in 1957 with 100 ppm of gibberellin either in full bloom or three weeks later, flowered and set fruit normally in 1958.

Response of the Cherry to Applications of Gibberellin

Shoot Growth: Year-old Mahaleb cherry trees were started in the greenhouse January 17, 1957, and treated with 10, 50 and 100 micrograms of gibberellin per plant on February 2, 1957. An analysis of variance of the total shoot elongation indicated that no significant differences existed between any of the treatments on either April 6 or 27, 1957. The length of the shoots developing from the terminal bud only of each tree to which the aqueous gibberellin solution had been applied was measured on April 6. A statistical analysis

of these measurements failed to indicate any significant differences between any of the treatments.

Year-old cherry trees, treated with gibberellin following formation of terminal buds in the greenhouse in 1958, produced a second flush of growth in the same season. The seasonal linear growth following applications of gibberellin is illustrated in Figure 20, and presented in Table XV. There were no differences in total linear shoot growth 13 days after the initial May 21 application of gibberellin. During the following 20-day period, however, each of the treated trees showed a visible increase in linear shoot growth of both terminal and lateral buds. A tree treated with 1, 000 ppm gibberellin compared with a non-treated tree is shown in Figure 21. The lateral buds induced to initiate shoot growth were in the distal region of the previous flush of growth. All shoot elongation had ceased and terminal buds had again formed by July 3, 1958.

A slight flush of growth was obtained following the second application of 500 and 1, 000 ppm of gibberellin on July 11, 1958. This growth was spindly, weak and poor in vigor, and most of it wilted and died back by the time the experiment was terminated on August 20.

Trunk diameter was significantly greater in all the gibberellin treatments (Table XV). Lateral branches on treated trees also exhibited an increase in diameter (Figure 21). There was an increase in fresh and dry

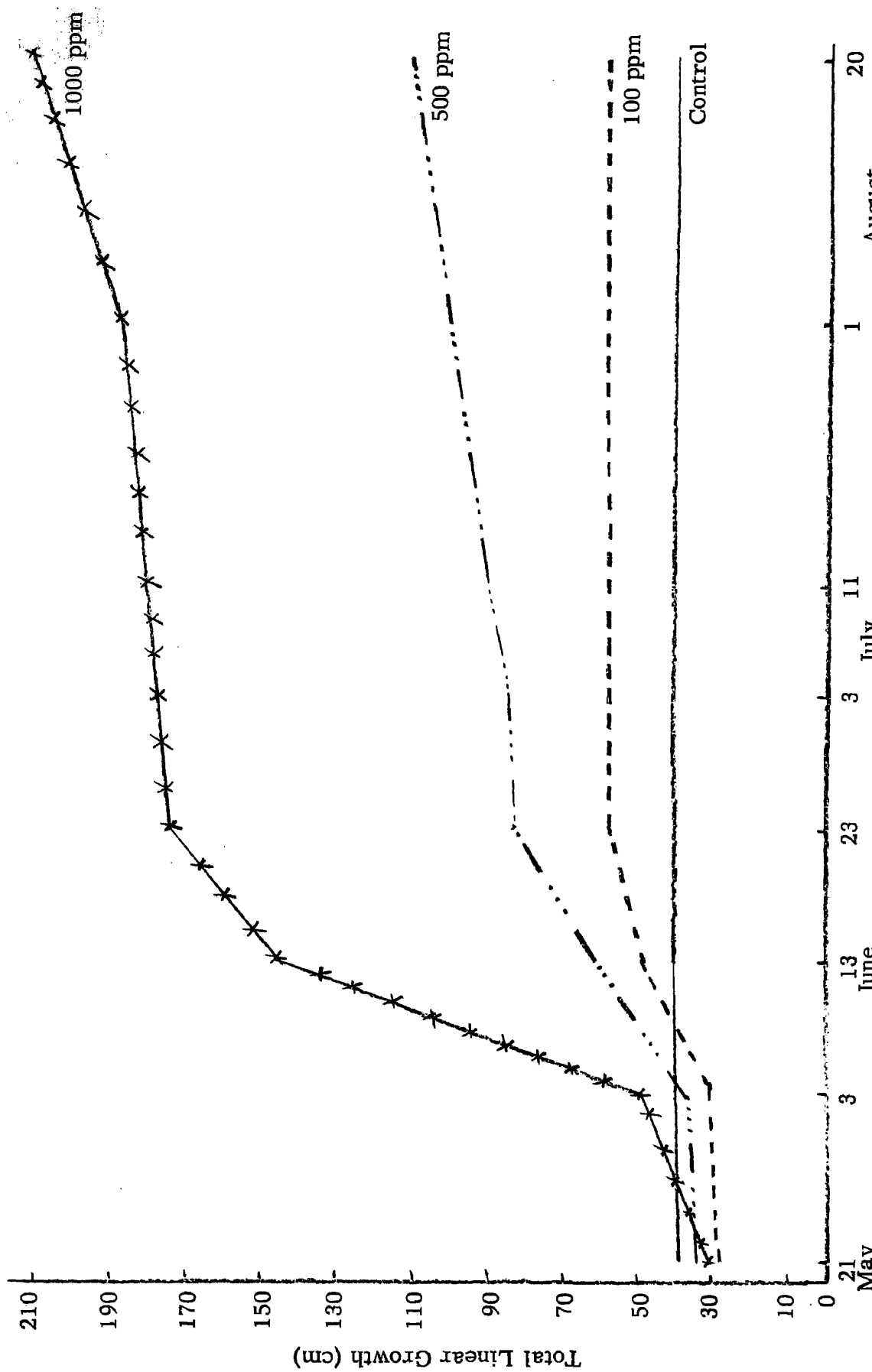


Figure 20. Effect of foliar applications of gibberellin on May 21 and July 11, 1958 on the total linear growth of Montmorency cherry trees.

TABLE XV

Effect of Two Foliar Applications of Gibberellin on the Total Linear Growth, Trunk Diameter, Fresh and Dry Weights, and Top/Root Ratio of Montmorency Cherry Trees. Trees Potted in Greenhouse March 29, 1958, and Treated with Gibberellin May 21 and July 11, 1958.[1/]

Measurement	Foliar Application (ppm) GA per Tree			
	0	100	500	1,000
Total linear growth (cm)	40.6	58.3	112.3	212.2*
Trunk diameter increase (mm)	.9	2.3	3.4	3.5*
Original fresh weight	105.8	97.7	97.5	104.7*
Final fresh weight	173.2	196.5	211.2	243.8*
Final dry weight	64.8	70.8	77.7	89.5*
Top dry weight	18.7	26.5	34.8	43.3*
Root dry weight	46.2	44.3	42.8	46.2*
Top/root ratio	.40	.60	.81	.94*

*Observations analyzed statistically. Values for various gibberellin treatments not underscored by a common line differ significantly at the 5 percent level.

[1/]All weights are expressed in grams.

Figure 21

Effect of foliar application of gibberellin on one-year-old Montmorency cherry trees.

Left: Tree on left sprayed with 1, 000 ppm gibberellin on May 21, and repeated on July 11. Non-treated tree on the right. Photographed September 22, 1958. Note stocky growth on treated tree.

Right: Tree on left sprayed with 1, 000 ppm gibberellin on May 21. Non-treated tree on the right. Photographed June 10, 1958.


CHECK
1000 PPM

weights in all the gibberellin treatments. Trees receiving foliar applications of 1, 000 ppm gibberellin were significantly heavier than the controls and the 100 ppm gibberellin treatment.

The final dry weight of the roots was essentially the same (Table XV and Figure 22). The dry weights of the tops increased with the increasing concentrations of gibberellin applied. Top dry weight in both the 500 and 1, 000 ppm gibberellin treatments was significantly heavier than the control. This increase in dry weight of the tops in the gibberellin treatments with no increase in the root dry weights resulted in an increase in the top to root ratio.

The flush of growth resulting from the 500 and 1, 000 ppm applications of gibberellin on May 21 exhibited an unusual pattern of development. The lateral appendages appearing in the proximal region of this flush of growth appeared to be bud scales arising from elongated internodes and modified stipules (Figure 23). These vegetative structures were light green and were restricted to the lower region of the shoots which developed following the initial applications of gibberellin. Occasionally a small bud developed in the axis of these modified appendages.

Effect on Flowering and Fruiting: Foliar applications of 10 and 100 ppm gibberellin applied to Montmorency cherry trees in full bloom (May 2, 1957) had no effect on fruit set, fruit development, or shoot growth. Applications three weeks after full bloom (May 28, 1957) had no effect on fruit size or shoot growth.

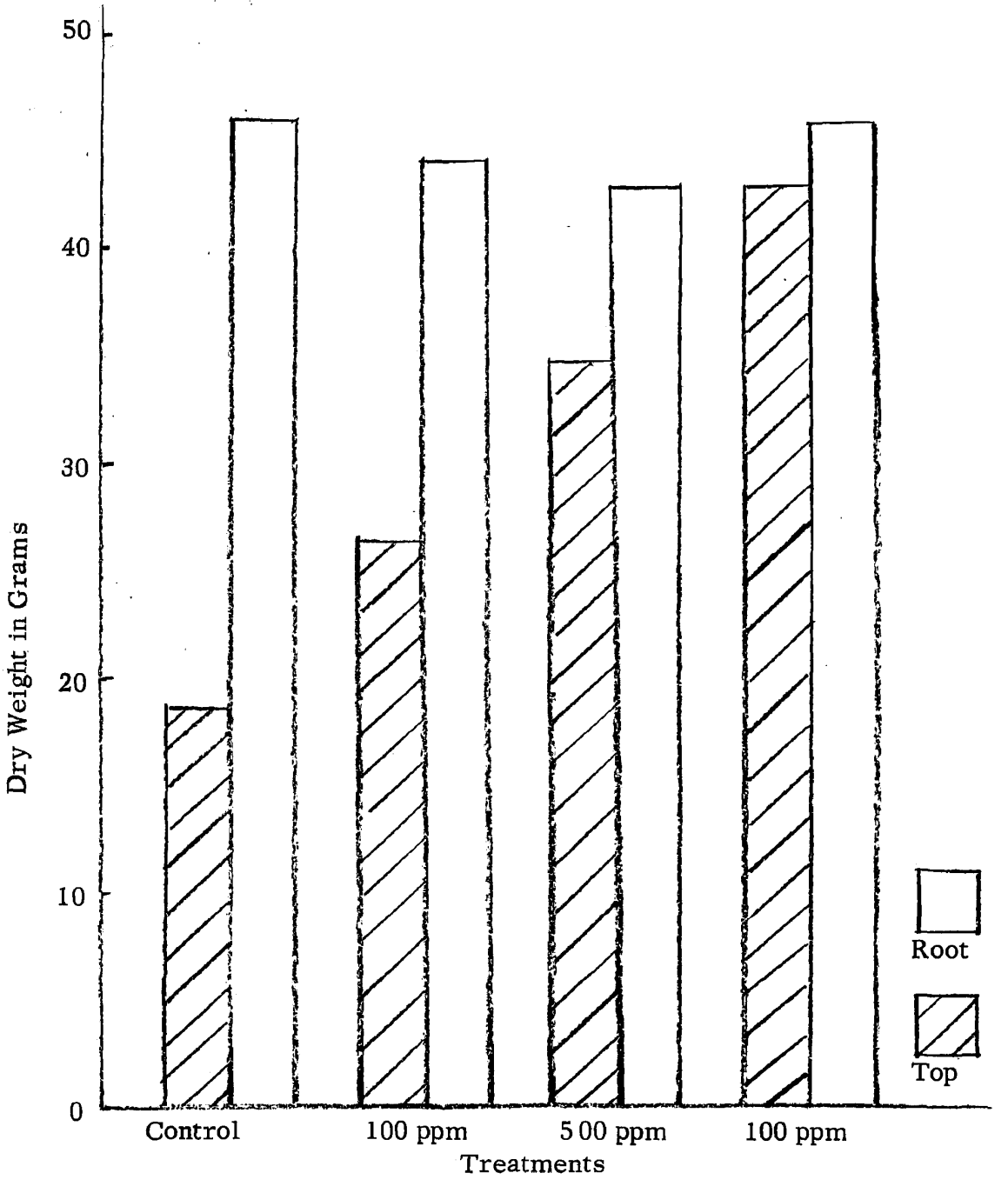


Figure 22. Effect of gibberellin on dry weight of tops and roots of Montmorency cherry trees (applied May 21 and July 11).

Figure 23

Modified shoot development occurring on the second flush of growth produced by year-old Montmorency cherry trees following a foliar application of 1, 000 ppm of gibberellin applied on May 21, 1958. Note elongation of internodes between bud scales and modification of the stipules and leaves which developed at the nodes immediately above bud scales. Similar effects were obtained on shoots developing from both terminal and lateral buds. Photographed June 10, 1958.

Differences in the pattern of flowering were observed in 1958 between non-treated mature bearing cherry trees and certain of the mature bearing cherry trees treated with gibberellin in 1957. Flowering in 1958 appeared normal on all branches sprayed with gibberellin while in full bloom in 1957. Trees sprayed with gibberellin three weeks after full bloom (May 28) in 1957, presented an altered flowering response in 1958 (Figure 24). There was some flowering in the distal portion of the shoots on the treated trees, but none on any of the spurs. Treated spurs were entirely vegetative, while non-treated trees contained many fruiting spurs. Flowering and fruiting occurred only at the first few nodes adjacent to the terminal bud.

Response of the Peach to Applications of Gibberellin

Effect on Seedling Growth: Shoot growth of seedling Elberta peach trees treated with 10, 50 and 100 micrograms of gibberellin in February and March, 1957, was comparable to the shoot growth of the non-treated seedling trees. A statistical analysis indicated that significant differences in shoot length did not exist between any of the treatments on any of the dates that plant height was measured.

Effect on Flowering and Fruiting: Foliar applications of 10 and 100 ppm gibberellin applied during full bloom (May 2, 1957) to Halehaven peach trees did not have any effect upon fruit set, and no observable effect upon subsequent shoot growth and fruit development.

Figure 24

Effect of gibberellin on the flowering and fruiting of Montmorency cherry trees in 1958.

Top: Tree in foreground received a spray of 100 ppm on May 28, 1957. Only a few flowers were produced in 1958 on the tree treated with gibberellin in 1957, while the non-treated trees flowered profusely. Photographed May 10, 1958.

Bottom: Shoots and spurs from above tree and non-treated tree. The two spurs and shoot on the left received 100 ppm gibberellin application on May 28, 1957. Non-treated spurs and shoot are on the right. Photographed June 10, 1958.

Fruit size and rate of shoot development of Redhaven peach trees was not affected when the trees were sprayed three and one-half weeks after full bloom (May 28, 1957) with 100 ppm of gibberellin. Foliar applications of 1,000 ppm of gibberellin two and one-half months after full bloom (July 20, 1957) did not affect the fruit size and rate of development of Halehaven peaches. This application did result in elongation of the shoot growth.

The post-bloom applications of gibberellin in 1957 resulted in complete absence of flowers in the treated portion of the peach trees for both varieties in 1958 (Figure 25). Shoots in the treated portion of the tree exhibited bare nodes throughout their central region. Similar shoots in the non-treated half of the tree flowered and produced fruit. Applications of gibberellin during full bloom in 1957 did not affect flowering and fruit set in 1958.

Figure 25

Effect of gibberellin on the flowering and fruiting of Halehaven and Redhaven peach trees in 1958.

Top: Shoots exhibiting the flowering response of Halehaven peach trees sprayed with 1, 000 ppm of gibberellin on July 20, 1957, and photographed May 8, 1958. Treated shoots (left) lack flowers.

Bottom: Shoots exhibiting the fruiting response of Redhaven peach trees sprayed with 100 ppm gibberellin on May 28, 1957, and photographed June 10, 1958. Treated shoots on left. Note absence of fruit or vegetative growth in central portion of treated shoots.

DISCUSSION

The generally observed effects of gibberellin on strawberry plants are in agreement with the only published reference to this plant (Wittwer and Bukovac, 1958). These vegetative overgrowths - elongation of petioles, peduncles, inflorescenes and crowns - paralleled those reported for many herbaceous plants.

An increased petiole length was generally obtained on plants receiving 10, 50, 100, 500 or 1,000 micrograms of gibberellin. That an increased petiole length was not obtained from any applications of gibberellin applied April 15, 1958, may have been the result of using a gibberellin A_1-A_3 mixture instead of gibberellic acid, time of treatment, or length of elapsed time between treatment and time of measuring. It is doubtful, however, that the lack of response resulted from using a gibberellin A_1-A_3 mixture rather than gibberellic acid. Applications of the mixture earlier had resulted in significant differences in petiole length, and a comparative study of the effect of different gibberellin compounds on vegetative growth indicated little difference between gibberellin A_1 and A_3 (Bukovac and Wittwer, 1958).

Darrow (1934) observed that strawberry plants grown in the greenhouse in winter months, and placed under additional lighting, produced longer petioles than plants grown under the natural day length. The lack of significant differences between the means of the April 15, 1958 treatments may

may have been the result of a longer photoperiod. However, since all treatment means were lower than the values for corresponding treatments in earlier investigations, it is probable that the measurements of petiole length were taken too soon - 19 days - after the application of gibberellin. The vegetative response may have appeared accentuated if the measurements of vegetative growth had been delayed the same length of time as in earlier studies.

The extensive crown elongation did not appear desirable. Elongated crowns lacked sufficient strength to remain erect and assumed horizontal positions as they continued to elongate. As the rosette-type growth was re-established, the rosetted crown rooted when it came in contact with the soil. Mann and Ball (1926) observed that plant vigor was often associated with the degree of contact between the crown and the soil. Plants treated with 100 to 1, 000 micrograms of gibberellin often had decidedly less contact between the crown and the soil than non-treated plants.

The slight inhibition of runners by applications of gibberellin appears to be a different phenomena than that reported by Carlson and Moulton (1951) and Carlson (1953). While they obtained runner inhibition with chemical treatments, the strawberry plants that they treated appeared normal at the end of the season. Applications of gibberellin generally resulted in modification of the pattern of the vegetative development. The runner development appeared to be inhibited, while the crown was elongating. As the crown begins to resume

the rosette-type of growth, the plants runner freely. This could be the result of disappearance of the gibberellin stimulus.

An investigation of many strawberry varieties at Glendale, Maryland by Waldo (1930) indicated that floral initiation begins in September or October, depending upon the variety, and that the primary flower was completely differentiated and ready to bloom in late November. Plants dug in the field in October and placed in the greenhouse immediately and treated with 100 micrograms of gibberellin per plant on October 29, did not flower until the first week in December. Thus, while treated plants flowered earlier than non-treated plants, gibberellin did not appear to hasten floral differentiation. These plants produced more flowers than the non-treated plants, however. Since floral initiation in the strawberry occurs under short days, and the flower bud is in a terminal position, it may be that applications of gibberellin under such conditions enhanced floral differentiation. If gibberellin promoted bud activity and environmental conditions favored floral initiation, it is possible that the applications of gibberellin might promote continued differentiation of floral primordia.

The failure of treated plants to produce normal fruit was probably caused by lack of developing achenes. Nitsch (1949) demonstrated a direct relationship between receptacular development and the presence of viable achenes. Since emasculated flowers of non-treated plants produced normal

fruit when pollinated with pollen from the gibberellin-treated plant, and pollen from the treated plants appeared viable when stained with acetocarmine, it would seem logical that non-functioning pollen was not responsible for abnormal fruit development in the plants treated with gibberellin. It is likely that the applications of gibberellin had an adverse effect on the sexual reproductive process of the strawberry plant during megasporogenesis, megagametogenesis, or embryological development. Since plants sprayed with 100 ppm of gibberellin, when in full bloom, produced normal fruit, it is doubtful if the embryological development was affected.

Rappaport (1957) observed that tomatoes treated with gibberellin yielded parthenocarpic fruit, and Wittwer et al. (1957) found gibberellin to be more effective than indoleacetic acid in induction of parthenocarpy in tomatoes. Nitsch (1952) states that "fruits developing parthenocarpically in nature are not seedless at the time the ovary development is definitely set in motion". However, the parthenocarpic fruit produced lacks embryos or endosperms. This would seem to indicate that tomatoes developing parthenocarpically on plants treated with gibberellin might have formed a megagamete. Since neither the achenes nor the receptacle of some flowers developed on the strawberry plants treated with gibberellin, it is probable that such flowers did not form megagametes. This would not indicate, however, whether megasporogenesis or megagametogenesis was affected by the application of gibberellin.

Flowers produced by gibberellin-treated plants, which were coated with either one percent gibberellin-lanolin or one percent indolebutyric acid-lanolin paste, did not produce as large a receptacle as the normally developing fruit on non-treated plants. When Nitsch (1950) removed achenes from developing fruit nine days after fertilization, and coated the "berry" with a one percent indolebutyric acid-lanolin paste, the "berries" attained a size comparable to normally developing fruit. "Berries" in his investigation had the advantage of developing under the influence of developing achenes during the first nine days, however. This could partially explain how he obtained larger receptacles in his investigation than were obtained in these studies from similarly treated flowers on the gibberellin-treated plants. Gardner and Marth (1937) and Hunter (1941), working with pistillate varieties, obtained parthenocarpic fruit by applying applications of indoleacetic acid, indolebutyric acid and naphthyl-acetic acid to the flowers of strawberry plants which had not been pollinated. While these plants had no source of pollen, it is probable that the flowers had formed a megagamete. The enlargement of the receptacles occurred, however, without any developing embryos.

Lack of receptacular swelling in the area of pistil attachment was not the only abnormality of the fruit development. No explanation is offered as to why the basal area of the receptacle would swell slightly, two to three weeks after the flowers bloomed, and take on a red color at the same time that comparable normally developing fruit ripened.

The effect of the gibberellin stimulus apparently was not translocated from the mother plant to any of the runner plants in the transport investigations as evaluated by vegetative stimulation. Nor was the stimulus observed to travel from any of the treated runner plants to another non-treated runner plant or the attached mother plant. The stimulus was observed to move from one node on a runner to the next distant node where a runner plant was developing. When the gibberellin was applied directly to the stolon between a runner plant and a node, the stimulus was observed to travel in both directions to runner plants. Hartman (1947) observed that the flowering stimulus would travel from a mother plant growing under a day length which was photo-inductive for flowering, to a runner plant growing under long day conditions and result in flowering in both plants. Runners that did not develop from treated strawberry plants until after the gibberellin had been applied, appeared to have sometimes translocated the stimulus as evidenced by the production of runner plants with elongated crowns. Apparently the gibberellin stimulus did not travel in a basipetal direction in the crown and, therefore, would not be translocated through runners which had developed prior to the application of the gibberellin.

Microscopic investigations by Goff (1899-1900) indicated that floral initiation occurred earlier in the growing season for the apple than for the peach and cherry, and that differentiation of floral parts occurred earlier in

the cherry than it did in the peach. It would be logical to assume that floral induction must precede floral differentiation and that the length of the induction period might vary among plant species.

Sensitivity to external stimuli during floral induction probably varies among plant species also. Results from investigations of summer sprays of potassium a-naphthaleneacetate to retard "bud-break" of fruit trees the following spring indicated that the apple was more resistant to the effects of such applications than the cherry and peach (Hitchcock and Zimmerman, 1943). The peach was most sensitive.

Defloration and defoliation experiments by Struckmeyer and Roberts (1942) indicated that induction occurred at least three weeks prior to the appearance of blossom primordia for the Wealthy apple. If floral differentiation in the apple varieties investigated occurred in June, it would appear from results obtained, that the applications of gibberellin had little or no effect on floral induction in the apple. If induction occurred prior to the applications of gibberellin, then the applications did not appear to destroy the induction effect.

Went (1957) reported that young, non-bearing peach trees would not initiate floral primordia until after a period of exposure to temperatures of 4 to 10 degrees C for two to three months. The cold period must be followed by a warm period for floral initiation, and then by another cold period to break the

dormant bud and enable it to flower. If this were true for mature bearing trees also, then the applications of gibberellin after bloom must have counteracted any induction effect of the preceding winter. Why did not the application during the period of full bloom inhibit flowering the following spring? This would seem to indicate that either induction must occur after the blooming period, or that the flowering stimulus was not as subjected to destruction by external factors at this time. Since floral differentiation in the peach varieties studied probably was initiated in August and September, it would appear that, for the peach, induction occurs after the period of full bloom in the previous season, and that the applications of gibberellin completely counteracted the induction stimulus. The peach may also be more sensitive to gibberellin.

That the cherry trees, receiving a post-bloom application of gibberellin produced some blossoms in the terminal region of the previous season's shoots, would seem to indicate that the gibberellin effect on floral initiation tended to dissipate or that blossom buds were differentiated over a longer period of time. It might also indicate that the sensitivity of the cherry tree to gibberellin is intermediate to that of the apple and peach in regards to floral initiation.

The mechanism whereby gibberellin overcame the dormant condition of the buds on the initial flush of growth of the year-old Montmorency cherry trees is difficult to interpret. Perhaps the cause of "rest" in the buds was photoperiodically induced. The effect of photoperiod on dormancy in the sour

cherry, Prunus cerasus L., is not known. Long days result in continuous growth in the peach, Prunus persica (L.) Batsch., yet long days do not prevent the onset of dormancy in the cherry, Cerasus avium L. (Nitsch, 1957b). It would appear that the young sour cherry trees studied in these investigations must fall in the latter group, since the trees formed terminal buds in May under the naturally occurring day lengths. It is probable that the phenomena responsible for the second flush of growth in the young Montmorency cherry trees following the initial applications of gibberellin are similar to the cause for growth of photoperiodically-induced dormant plants treated with gibberellin.

Exposure of plants to cold is the usual means of overcoming dormancy. Gibberellin has been able to fulfill this chilling requirement in the peach (Donoho and Walker, 1957). The review by Samish (1954) also indicates that the products of anaerobiosis are the active agents in breaking dormancy. Thornton (1945) subjected freshly harvested potato tubers to atmospheres containing only two to ten percent oxygen and broke both dormancy and apical dominance in the treated tubers.

The material used for the initial applications of gibberellin was an emulsifiable concentrate containing 0.5 percent potassium gibberellate. The oily base of this material may have resulted in an anaerobic condition in the dormant buds and thus overcome the dormant condition. The gibberellin then

could be acting as a stimulus to a non-dormant bud. The source of gibberellin in the second application, however, was a technical grade powder and contained no oily base. Yet a slight flush of growth was produced following the second gibberellin spray, which would tend to refute the value of the oily base of the original application. This weak, spindly growth following the second application, may have been the result, however, of only a partial breaking of the dormant buds.

It is possible that gibberellin may exert its influence on dormancy, genetically. Phinney (1956) overcame the inhibiting effect of a dwarfing gene in single-gene dwarf maize plants with gibberellin applications. If dormancy were genetically controlled, gibberellin might overcome the effect of the inhibiting gene or genes.

It is more probable that the response of the dormant buds to gibberellin involves a relationship with the auxin content of the plant. Application of auxin alone has been found to be insufficient to break "rest" of cambial cells (Samish, 1954). Nitsch (1957a) found that sumac plants treated with gibberellin contained a level of endogeneous auxin higher than non-treated plants. He also observed that short days resulted in a reduction in the level of endogeneous auxin and an increase in the level of endogeneous inhibitors.

The theory of auxin activity proposed by Muir and Hansch (1951) maintains that reaction of auxin with the plant substrate occurs at the ortho position

on the unsaturated ring of the auxin. Perhaps plants produce compounds which react at the ortho position of the auxin ring or make reaction between the auxin and substrate at this position impossible, thus resulting in inhibition or the formation of inhibitory compounds. Application of gibberellin then might block such an auxin inactivation process by reacting with the compounds produced in the plant before such compounds could inactivate the auxin. The application of gibberellin might exert its effect by reacting with the inactivated auxin complex to liberate the auxin. Either method of action would result in a higher auxin content in the plant, and might aid in breaking dormancy.

Explanation of the modification of stipule and leaf development in the basal portion of the second flush of growth produced by year-old Montmorency cherry trees treated with gibberellin is difficult, since no anatomical studies were made of representative buds. It is probable that the embryonic structures were very sensitive to the chemical and therefore the developmental pattern was altered. The second flush of growth probably resumed a normal growth habit, as the gibberellin effect diminished. With Liriodendron tulipifere L., the leaves for the first eight nodes of the shoot are formed in the developing bud during July to October of the previous season, and the other six to 12 leaves are formed the current year during the period of shoot expansion (Millington and Gunckel, 1950). If a similar pattern of development existed for the sour cherry, then the modified appendages of the second flush of growth

might correspond to the nodes developing in the bud at the time of treatment. The normal pattern of development would be observed where primordia developed after shoot elongation was initiated.

The third flush of growth produced following the second application of gibberellin to the young Montmorency cherry trees, was of poor vigor, and most of these weak shoots wilted and died back. Foster (1932) observed in Oklahoma that in the Black Hickory (Carya Buckleyi, var. Arkansana) organ formation ceased after the middle of May, and further development in the new terminal buds consisted in enlargement and specialization. Perhaps, since a second flush of growth was produced following the initial application of gibberellin, the subsequent buds were not so complete and fully developed as buds on the original shoots. It would appear that there is a limit to the amount of linear growth that a young Montmorency cherry tree can produce in one year in response to applications of gibberellin, or that the concentration of gibberellin in the second application may have been toxic to the new growth. Terminal buds formed on the second flush of growth were smaller and it is likely that the embryonic shoots were very sensitive to the gibberellin sprays.

Since a second flush of growth was produced by cherry trees sprayed with gibberellin, resulting in an increased number of leaves and increased foliage area, more photosynthetic products should have been produced.

This could account for the increased dry weight of the treated trees. The trees treated with gibberellin not only produced more growth, but were stocky and appeared very desirable commercially. This in contrast to the spindly growth reported for many herbaceous plants treated with gibberellin.

That the year-old Mahaleb seedling trees grown in the greenhouse and treated with gibberellin did not produce an increase in shoot growth was probably the result of timing of the application. While Marth et al. (1956) obtained the greatest amount of shoot elongation in treated plants when gibberellin was applied just as the stems began elongation, data from this investigation indicate that cherry trees are more responsive when treated after the terminal bud has set.

SUMMARY

An investigation was conducted during 1957 and 1958 to determine the response of the strawberry, apple, cherry and peach to applications of gibberellin.

Robinson strawberry plants grown both in the greenhouse and field plantings were treated with gibberellin. The plant responses to the applications of 10 to 1, 000 micrograms per plant, or 100 ppm sprays of gibberellin were generally characterized by marked increases in elongation of the petioles, peduncles, pedicels and crowns. Crown diameter was decreased with the resulting crown elongation. Runner formation appeared to be inhibited during the period of crown elongation. None of the applications of gibberellin increased fruit size or yield either in the greenhouse or field studies.

Applications of gibberellin prior to blooming resulted in failure of some of the strawberry fruit to develop normally. Treatments of 100 to 1, 000 micrograms of gibberellin resulted in the largest number of abnormal fruit. Fruit lacked developing achenes and the receptacular tissue in the area of the pistils failed to enlarge. Some flowers on treated plants produced a slight swelling of the toral tissue acropetal to the calyx and basipetal to the area of the pistils.

One percent lanolin paste applications of either indolebutyric acid or gibberellin applied to the pistils and the associated area of non-developing flowers on plants treated with gibberellin produced a slight swelling of the receptacle in the pistil area. The longer this application was delayed after bloom, the less the amount of swelling occurred. Receptacular development was greater on indolebutyric acid-treated fruit than for the fruit coated with a gibberellin-lanolin paste, especially when the application was delayed 12 to 13 days after blooming had occurred. Both treatments produced fruit of inferior size.

Robinson strawberry plants grown in the greenhouse and treated in November and December with 100 micrograms of gibberellin produced more flowers than control plants. Later gibberellin treatments (March and April), however, did not appear to result in increased flower number.

The gibberellin stimulus did not appear to move in a basipetal direction in the crowns. When 500 micrograms of gibberellin were applied to the stolon, the stimulus apparently moved laterally, in both directions, in the runner, but appeared to be more readily translocated distally.

Rooted East Malling IX, XII and XVI cuttings, grown in the greenhouse and treated either with 100 micrograms per plant or 100 ppm sprays of gibberellin, did not exhibit any increase in shoot length or diameter. Branches of mature bearing apple trees sprayed with either 10 or 100 ppm of gibberellin

during full bloom (May 9, 1957), or 100 ppm three weeks later (May 28, 1957), produced a crop similar to non-treated trees with no increase in fruit size. Treated trees flowered and fruited normally the following year.

Fruit yield of Montmorency cherry trees, sprayed with either 10 and 100 ppm gibberellin while in full bloom (May 2, 1957), or with 100 ppm 26 days later (May 28, 1957), did not appear to be affected in either fruit size or number. Flowering in the trees treated in full bloom was normal the following year, while the application 26 days after full bloom partially inhibited flowering the following spring. Some flowering occurred in the distal portion of the previous year's shoots only on treated trees.

One-year-old Mahaleb seedling cherry trees, grown in the greenhouse and treated with 100 micrograms gibberellin just as shoot elongation began, did not produce increased shoot growth. One-year-old Montmorency cherry trees, grown in the greenhouse and treated with 100, 500 or 1, 000 ppm gibberellin after the trees had formed terminal buds, produced a second flush of growth. Treated trees produced more linear growth, and when harvested 90 days after the initial treatment, had a greater dry weight. Root growth was not increased or decreased by these treatments.

Stipule development was modified in the basal region of the second flush of growth produced in the same season by trees receiving foliar applications of 500 and 1, 000 ppm gibberellin. This was accompanied by a sup-

pression of leaf development. There appeared to be elongation of the internodes between some bud scales also. A second application of gibberellin 61 days after the initial treatment resulted in a slight flush of growth which was undesirable in appearance and died back.

Seedling Elberta peach trees treated with 100 micrograms of gibberellin during shoot elongation did not develop more rapidly or over a more extended period of time than the control trees. Mature bearing Halehaven peach trees, sprayed with 10 and 100 ppm gibberellin in full bloom (May 2, 1957), or with 1, 000 ppm gibberellin two and one-half months later (July 20, 1957), did not vary from non-treated trees in fruit number, size, and time of ripening. Trees treated in full bloom flowered normally the following year, but trees treated two and one-half months later produced no flowers the following spring. Mature bearing Redhaven peach trees sprayed with 100 ppm gibberellin 20 days after full bloom (May 28, 1957) exhibited no response to gibberellin during the season treated, but failed to flower the succeeding year. Many nodes on the treated trees which failed to flower the following season, were also lacking in vegetative growth.

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