SEEDSTALK DEVELOPMENT IN CELERY AS INFLUENCED BY CERTAIN GROWTH REGULATORS

Thesis for the Degree of M. S.

MICHIGAN STATE COLLEGE

Llewellyn LeGrande Coulter

1948

This is to certify that the

thesis entitled

Seedstalk Development in Celery
as Influenced by Certain Growth Regulators

presented by

Llewellyn LeGrande Coulter

has been accepted towards fulfillment
of the requirements for

M. S. degree in Horticulture

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Date March 10, 1948

M-795

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By

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A THESIS

Submitted to the School of Graduate Studies of Michigan State College of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Horticulture

March 1948

THESIS

4/1/48
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ACKNOWLEDGMENTS

The writer wishes to acknowledge his indebtedness to Dr. S. H. Wittwer for his wholehearted assistance throughout the course of the experiment and in the preparation of the manuscript. Appreciation is also extended to Dr. R. L. Carolus for his encouragement and valuable suggestions.

SEEDSTALK DEVELOPMENT IN CELERY AS INFLUENCED BY CERTAIN GROWTH REGULATORS

INTRODUCTION

Premature seeding, frequently referred to as "bolting", is one of the most serious problems in production of the early crop of celery. The plants, normally biennial, develop as annuals and produce seedstalks the first year. Development of a full and tender heart is replaced by the growth of a massive seedstalk. When this happens a crop having a potential value of at least $400 per acre, becomes worthless. Thompson (17) has investigated this premature seeding and has demonstrated that its inception is primarily a result of the exposure of early spring plantings to low temperatures. Initiation of primordia and subsequent development of seedstalks occurs when plants are exposed to a temperature of 40-50 degrees for a period of two weeks or more. These conditions are frequently associated with the climatic areas where the highest quality celery is grown and for this reason the problem applies particularly to Michigan, New York, and California.

In general, the varieties which normally produce the earlier, higher quality celery are the ones most likely to develop seedstalks prematurely. Control of this untimely flowering would eliminate the risk of loss and permit the production of an early high quality crop. The production of superior varieties which is now limited to the more tem-

perate areas and to late plantings in northern climates, might be expanded to any celery producing locality. The crop could be started in the field earlier and the grower would be able to take advantage of the higher prices offered by an early market for a high quality celery.

A number of methods have been tried to prevent seeding with varying degrees of success. Growers have adopted the practice of hardening their plants by withholding water rather than by exposing them to low temperatures. This procedure has somewhat reduced the amount of seedbed induction of flowering but does not influence the amount of floral initiation, which may afterward occur in the field. Portable covers have been devised for protection of plants in the field. These covers are suitable for protection against freezing temperatures of short duration but their use is expensive and they do not protect plants from continued low temperatures which promote premature seeding. Varieties, having non-bolting tendencies, have been introduced. They are very resistant to bolting but unfortunately do not provide the grower with a high quality celery for the early market. The above procedures, including protective plant covers, late plantings and varieties resistant to bolting, have not yet provided a practical control of premature seeding. On the assumption that some chemicals of the plant growth regulator type might have the faculty

to affect the initiation of flowering and subsequent seedstalk development in celery, a number of experiments were designed to test the hypothesis.

REVIEW OF LITERATURE

Recent investigations concerned with the control of reproductive and vegetative development in plants have revealed many intricate relationships which the carbohydrate-nitrogen ratio hypothesis (14) does not adequately explain. The role of photoperiodism established by Garner and Allard (9) and of vernalization, as reviewed by Whyte (24), inaugurated a new line of research to determine the mechanisms controlling plant development. Cajlachjan (1) conducted a number of experiments with two species, Chrysanthemum undicum and Perilla nankinensis, which are particularly sensitive to photoperiod. He concluded that flowering in these two species is induced by a material, ("florigen") which is synthesized in the leaves and translocated to the buds. This material functions independently of the carbohydrate-nitrogen balance or the concentration of auxin. Similar results have been obtained by Stout (16), who observed flowering in biennial sugar beets to which reproductive annual scions had been grafted. Additional evidence of this nature has been secured by Hamner and Bonner (10) in grafting experiments with Xanthium pennsylvanicum and Melchers (15), who made experimental grafts with a number of species.

Cholodny (2) postulated that chemicals endowed with the properties of growth substances might be introduced into a plant at different stages of growth and affect its development. The major emphasis of subsequent studies having to do

with testing the effects of introducing synthetic growth substances into plants, were directed at the control of the three phases of reproductive development referred to by Thompson (18) as a) initiation of the flower, b) development of the flower, and c) development of the seed. The observations reported by a number of investigators have given support to the concept that plant development can be controlled by growth regulating chemicals. Hitchcock and Zimmerman (11) were able to stimulate flowering of Turkish tobacco by applying phenylpropionic, indolepropionic, and indolebutryic acids to the soil. This acceleration of flowering was due to the hastening of terminal growth after flower buds were formed. Stimulation has also been observed by Galston (8), who applied 2,3,5-triiodobenzoic acid to soy beans. The treatment augmented the flowering response due to photoperiodic induction but failed to initiate flowers independently. However, Dostal and Hosek (7) were successful in reverting "flower ready" stem tips of Circaea intermedia to the vegetative habit by applying to them a .25 percent paste of heteroauxin. Similar results were obtained by Zimmerman and Hitchcock (25), who modified the development of tomato buds. Axillary shoots and terminal buds were induced to terminate in flower clusters by soil treatments of foliage spray applications of 2,3,5-triiodobenzoic acid. Using Mathiola incana annua (annual stock) as a test plant, Johnson (13) reported that

86% of the plants treated with alpha-naphthoxyacetic acid remained in a vegetative condition while only 6% of the control plants failed to reproduce. The effect of growth substances on flowering, the generation following treatment, has been recently demonstrated by Hitchcock and Zimmerman (12). Dandelion plants were sprayed with solutions of 1000 ppm 2,4,6-trichlorophenoxyacetic acid and it was found that seed from these plants were significantly reduced in germination, and plants, in turn, grown from the seed were delayed in flowering. Thurlow and Bonner (19), in a recent report, noted a complete inhibition of the photoperiodic response of Xanthium by spraying the plants with 500 ppm naphthaleneacetic acid or indoleacetic acid. Initiation of flower primordia in pineapples with ethylene gas was accomplished by Traub (20). In this type of induction there was no change in the amount of auxin and it was concluded that ethylene itself is a hormone.

The commercial use of growth substances, for the control of reproductive development in plants, has been successful in the pineapple industry. Clark and Kerns (3) and also Cooper (5) have found that naphthaleneacetic acid can be used to induce differentiation of the pineapple inflorescence. According to Van Overbeek (21), 2,4-dichlorophenoxyacetic acid also hastens flowering but possibly due to the retarding of leaf development, the stimulation by

this substance is not as rapid as that of naphthaleneacetic acid. His investigations further disclosed that, by the single application of naphthaleneacetic acid, the Cabezona variety of pineapple can be made to flower at any time during the year, irrespective of the photoperiod, even under conditions where long days would normally prevent development of primordia. However, Van Overbeek (22) further states that continuous treatment with either ethylene or auxins may delay flowering indefinitely. Clark and Kerns (4) and later Cooper (5) have shown that flower induction by ethylene may be completely prevented by subsequent application of auxin. Continued experimental work by Van Overbeek (23) has indicated that the flower inducing free auxin of the axis evolves from the bound auxin of the juvenile leaf bases. Origin of the reproductive response from similar plant parts of celery was determined by Curtis and Chang (6) when they found that the initiation of the floral primordia occurs as a result of the exposure of the young inner heart leaves to cool temperatures.

PRELIMINARY TEST WITH NON-BOLTING GOLDEN PLUME

Materials and Methods

A preliminary test with celery to determine the vegetative responses and limits of tolerance to growth substances was started in the greenhouse during the fall of 1946. Seed of Non-Bolting Golden Plume (Ferry-Morse, Stock no. 2352) was planted in flats of sand, October 28. A minimum temperature of 65 degrees was maintained in the greenhouse during germination and the following period of growth. A total of 55 seedlings were transplanted to individual five inch clay pots filled with compost soil, November 25. Two weeks later all pots were fertilized with a solution containing one half ounce of ammonium-nitrate and one half ounce of an all soluble fertilizer having an analysis of 12-54-18* per gallon of water. On January 15, the 55 potted plants were separated into 11 groups of five plants each. The five plants in each group were sprayed with one of the following:**

a) 5 ppm - 2,4-dichlorophenoxyacetic acid (2,4-D)

b) 25 ppm - " " "

c) 50 ppm - " " "

d) 5 ppm - triiodobenzoic acid (TIBA)

e) 200 ppm - " "

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*Obtained from the Victor Chemical Company, Chicago.

**Grateful acknowledgment is extended to the Dow Chemical Co., Midland, Michigan for providing some of the chemicals used in these tests.

f) 500 ppm - triiodobenzoic acid

g) 50 ppm - naphthaleneacetic acid (NA)

h) 200 ppm - " "

i) 500 ppm - " "

j) 200 ppm - alpha-orthochlorophenoxypropionic acid (CLPP)

k) control (water spray only).

The chemicals were applied in aqueous solutions by means of small household sprayers. Particular care was taken to thoroughly wet all of the aerial plant parts. For each chemical, a different sprayer was used, which was free from contamination of other growth substances and was carefully cleaned between each change in concentration of the material applied. All plants were transplanted to 8 inch clay pots containing compost soil, February 17 and moved to the cold frame April 17. Minimum night temperatures in the cold frame averaged 41 ± 2 degrees Fahrenheit through May 26.

Results

2,4-D exhibited a striking differential response, depending upon the concentration used. Fifty ppm of 2,4-D produced severe epinasty of the leaves within 24 hours following treatment. At this time petioles and edges of the leaflets were curled downward. Ten days after treatment these structures had regained their normal appearance.

However, the developing leaves emerging from the terminal cluster began to show formative effects. Many of them developed deeply indented margins which gave them an appearance similar to carrot leaves and the stem plate region was surrounded by a tumorous growth. Seedstalks were first observed on plants treated with 50 ppm of 2,4-D on May 18. Seeding was rapid and the stalks averaged eight inches in height at the time seedstalks began to appear on plants treated with 25 ppm. On August 26 (Figure 1), plants which had received the higher concentration (50 ppm), were completely mature and the seed had ripened. In contrast, those sprayed with 25 ppm were only beginning to flower. The lowest concentration, 5 ppm, produced seed stalks on a date, May 29, equivalent to that of the control plants.

Celery seedlings sprayed with triiodobenzoic acid (TIBA) responded in an entirely different manner from those treated with 2,4-D. Plants did not exhibit any epinastic or formative effects. However, in the group which had been sprayed with 500 ppm of this substance, one plant began developing a seedstalk May 12. The remaining four had become reproductive by May 18. The other concentrations of TIBA produced seedstalks on an average date of May 29, comparable to the time of bolting in the control plants.

Naphthaleneacetic acid (NA), in the concentrations used did not significantly influence growth or development of treated plants. Some activity was observed where a solu-

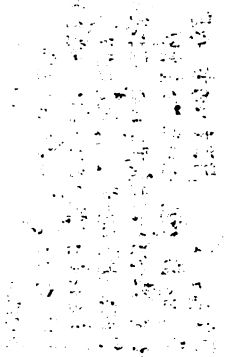

Fig. 1. Effect of 2,4-D on maturity of Non-Bolting Golden Plume. Right, plants sprayed with 50 ppm; left, 25 ppm.

tion of 500 ppm caused a definite upward curvature of petioles in such a manner that they partly enfolded the heart of the plant. This curvature was very temporary and within 72 hours normal growth was resumed. All concentrations of NA produced seedstalks at a time comparable to the controls which began to bolt May 29.

Only one concentration (200 ppm) of alpha-orthochlorophenoxypropionic acid (CLPP) was used. It had no observable effect upon vegetative or reproductive development of the celery plants under the conditions of this experiment.

FIELD EXPERIMENTS

General Methods

Plants were started by sowing the celery seed in flats of sand and the young seedlings transplanted, when the first true leaves appeared, to three inch clay pots filled with compost soil. Supplementary feeding with a nutrient solution, containing one half ounce of ammonium-nitrate and one half ounce 12-54-18 (100% soluble) per gallon of water, was given all plants March 18. Plants designated to receive reproductive induction were exposed to low temperatures in the cold frame, while plants which were to receive no induction were retained in the greenhouse.

The plants were transplanted on May 26 to a well drained and fertilized muck soil, having a pH of 6.8. They were later sidedressed with sixty pounds per acre of ammonium-nitrate June 4 and with eighty pounds per acre of 6-12-12, July 7. The experimental design of the plots is indicated in Figure 2. The two experiments were laid out adjacently, with the ten plants in each treatment being separated into two sections, each section containing five plants of one treatment. One of these sections was planted in such a manner as to constitute one replicate for all treatments while the other section was planted in the same sequence and represented the second replicate. For a given chemical treatment, two additional replicates making a total of four, were in each case provided since

2ca2 2ca1 1ga2 1ia1 2bb2 2db1 1fb2 1hb1 1aa1
2da2 2fa1 1ha2 1ab1 2cb2 2eb1 1gb2 1ib1 1ba1
2ea2 2ga1 1ia2 1bb1 2db2 2fb1 1hb2 1aa2 1ca1
2fa2 2ha1 1ab2 1cb1 2eb2 2gb1 1ib2 1ba2 1da1
2ga2 2ia1 1bb2 1db1 2fb2 2hb1 2aa1 1ca2 1ea1
2ha2 2ab1 1cb2 1eb1 2gb2 2ib1 2ba1 1da2 1fa1
2ia2 2bb1 1db2 1fb1 2hb2 2aa2 2ca1 1ea2 1ga1
2ab2 2cb1 1eb2 1gb1 2ib2 2ba2 2da1 1fa2 1ha1
2bb2 2db1 1fb2 1hb1 1ea1 2ca2 2ea1 1ga2 1ia1
2cb2 2eb1 1gb2 1ib1 1ba1 2da2 2fa1 1ha2 1ab1
2db2 2fb1 1hb2 1aa2 1ca1 2ea2 2ga1 1ia2 1bb1
2eb2 2gb1 1ib2 1ba2 1da1 2fa2 2ha1 1ab2 1cb1
2fb2 2hb1 2aa1 1ca2 1ea1 2ga2 2ia1 1bb2 1db1
2gb2 2ib1 2ba1 1da2 1fa1 2ha2 2ab1 1cb2 1eb1
2hb2 2aa2 2ca1 1ea2 1ga1 2ia2 2bb1 1db2 1fb1
2ib2 2ba2 2da1 1fa2 1ha1 2ab2 2cb1 1eb2 1gb1

---------- Experiment I ----------

First item of a group indicates variety:
1. Non-Bolting Golden Plume
2. Cornell 19
3. C&L Non-Bolting Pascal

Second item of a group indicates treatment:
1. As listed on page 15

Third item of a group indicates the temperature:
a. Coldframe
b. Greenhouse

Fourth item indicates time of treatment:
1. First treatment
2. Second treatment

3g1 2d2 2a1 3g1 2d2 2a1
3h1 2e2 2b1 3h1 2e2 2b1
3i1 2f2 2c1 3i1 2f2 2c1
3a2 2g2 2d1 3a2 2g2 2d1
3b2 2h2 2e1 3b2 2h2 2e1
3c2 2i2 2f1 3c2 2i2 2f1
3d2 3a1 2g1 3d2 3a1 2g1
3e2 3b1 2h1 3e2 3b1 2h1
3f2 3c1 2i1 3f2 3c1 2i1
3g2 3d1 2a2 3g2 3d1 2a2
3h2 3e1 2b2 3h2 3e1 2b2
3i2 3f1 2c2 3i2 3f1 2c2

--- Experiment II ---

NOTE: Temperature in Experiment II is not indicated.

Figure 2. Planting plan of field experiments.

equal numbers of plants (10) were given cold induction (cold frame) and warm temperature exposure (greenhouse), respectively. Plants were set eight inches apart in rows which were spaced at a distance of forty-two inches.

Growth substances were applied in the same manner as was used in the preliminary experiment. The following series of chemicals with their respective concentrations were applied at various times in the field experiments:

a) 5 ppm - 2,4-D
b) 50 ppm - "
c) 50 ppm - TIBA
d) 500 ppm - "
e) 50 ppm - NA
f) 500 ppm - "
g) 100 ppm - CLPP
h) 500 ppm - "
i) control (water spray only)

The first treatment was made with plants which had three true leaves and were 4 inches in height (Figure 3). When spraying in the field, a rectangular wooden frame, twenty inches high, was placed around each plot to eliminate drift to plants of other plots.

Fig. 3 (left). Size of plants at time of first application.
Fig. 4 (right). Tumorous growth and carrot-like leaves of seedling treated with 50 ppm 2,4-D.

Experiment I

This experiment was designed to determine the influence of various concentrations of growth substances applied at different dates to varieties differing in their susceptibility to premature seeding. By growing some plants continuously at a relatively high temperature, the author hoped to determine if some of these substances would stimulate flowering. Cornell 19 (Ferry-Morse, Stock no. C6313) was selected to represent the early high quality types which most often produce seedstalks prematurely. Non-Bolting Golden Plume (Ferry-Morse, Stock no. 2352) was also selected because it is particularly resistant to premature seeding. Seed of these varieties was sown in the greenhouse, January 28. The young seedlings were transplanted March 5 and held in the greenhouse at a minimum night temperature of 60 ± 1 degree Fahrenheit. On April 4, the potted seedlings were selected at random and arranged in nine groups of twenty plants each. The spray treatments were then applied according to the plan already outlined for chemicals and concentrations. Thirty-six hours following treatment, half of each group were removed to a cold frame where the plants were exposed to minimum night temperatures of 41 ± 2 degrees Fahrenheit. The other half remained in the greenhouse at the night temperature of 60 ± 1 degree Fahrenheit. On May 26, both lots were transplanted to the field. At the same time ninety

plants from the greenhouse and ninety plants from the cold frame reserved for field treatment, were also planted in the experimental plot.

Experiment II

The plan for this experiment was essentially the same as that in Experiment I. However, C&L Non-Bolting Pascal (Angler and Musser, Stock no. 69511) was substituted for Non-Bolting Golden Plume and only plants which had been exposed to low temperatures were used. Seeds were sown in the greenhouse February 16 and the young seedlings were transplanted to 3 inch pots, April 6. These were held at an average night temperature of 60 ± 1 degree Fahrenheit. All of the plants were moved to the cold frame April 14, where the minimum night temperatures were 43 ± 2 degrees Fahrenheit. The potted seedlings, selected at random, were arranged in nine groups of twenty plants each and sprayed May 2, as previously described. Field planting of these seedlings and ninety other seedlings as yet untreated was completed June 1. These ninety seedlings were sprayed June 6, according to the plan of treatment outlined under general methods.

Results with Cornell 19

In all treatments of Cornell 19, with one noteworthy exception, seedstalks developed freely within a short time after field planting. On July 1, bolting was clearly evident on control plants from the group of treatments exposed to low cold frame temperatures. In Experiment I, these plots which had not received any chemical treatment were bolting 100% by August 21 (Figure 5). In sharp contrast to this prolific bearing of seedstalks on the controls, plants sprayed with 100 ppm of CLPP and subsequently exposed to the same low temperatures as the control plants, remained in a completely vegetative condition throughout the season (Figure 6). The chemically treated plants developed full hearts and possessed all the desirable qualities of a marketable celery. Similarly, seeding on the control plants grown in the continuously warm environment of the greenhouse, before field planting, began August 20. When plots were noted September 30, 80% of this group had bolted. Again, without exception, those plants which had received the spray of 100 ppm CLPP; yet otherwise identically treated showed no evidence of a transition to the reproductive stage of development. Companion treatments of plants grown in the cold frame and sprayed with 500 ppm CLPP produced seedstalks in 80% of the plants. This concentration of CLPP sprayed on plants grown under warm

conditions did not effect the number of plants which became reproductive. Furthermore, applications of CLPP (Experiment II), after plants had been exposed to low temperatures favorable for induction of seedstalks, did not influence the number of plants which bolted, regardless of the concentration employed.

The growth of seedstalks was clearly influenced by 2,4-D, when this chemical was applied in a concentration of 50 ppm. In Experiment I, where this treatment was applied before the low temperature induction (Figure 7) or in the field afterward, weekly measurements revealed that the growth increments reach a maximum one week before those of control plants. The formative effects of this concentration of 2,4-D were essentially the same as those observed in Non-Bolting Golden Plume.

Results With Non-Bolting Golden Plume

Plants of this variety failed to produce seedstalks irrespective of the chemical treatment or temperatures of early growth. However, the leaves of plants sprayed with 50 ppm of 2,4-D showed epinastic responses similar to those observed in corresponding treatments of the preliminary experiment. This higher concentration of 2,4-D again promoted the development of carrot-like leaves and tumorous growths in the region of the stem plate (Figure 4). Such tumors were associated with a greater enlargement of the stem

(Photo taken August 24)

Fig. 5. Control plants of Cornell 19 which had received thermal induction of seedstalks.

Fig. 6. Cornell 19 treated with 100 ppm of CLPP before the thermal induction of flowering. (Photo taken August 24)

plate and appeared to stimulate the development of additional leaf stalks (Figure 8).

Results With C&L Non-Bolting Pascal

Records of this pascal type were incomplete as a result of tip burn and black heart which made it impossible to secure adequate measurements. However, all normal plants produced seed stalks and there was no indication that one treatment affected plants in a manner different than any other.

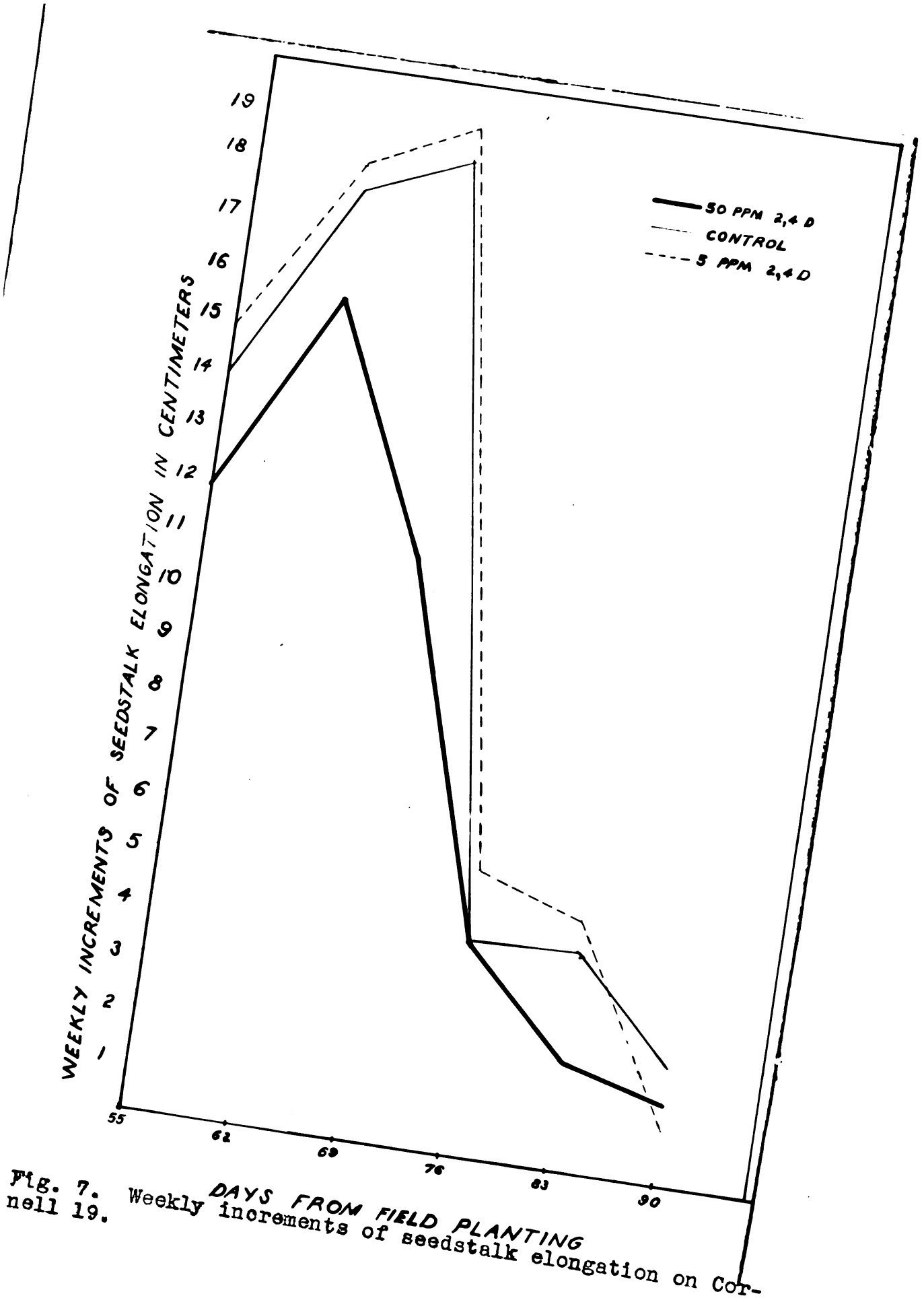

Fig. 7. Weekly increments of seedstalk elongation on Cornell 19.

Fig. 8. Non-Bolting Golden Plume treated with 50 ppm 2,4-D. Center, control.

DISCUSSION

The variety of celery, Cornell 19, which is particularly susceptible to premature seeding, was prevented from seeding when the seedlings were sprayed with 100 ppm of CLPP thirty-six hours before exposure to cool temperatures. These seedlings produced normal marketable celery with no apparent reduction in growth or malformations of the plant structures. This indicated that general stunting and consequent delay in maturity was not responsible for the inhibition of the seedstalk development. Microscopic examination of the heart area at the end of the growing season revealed that no floral primordia had been developed. The same concentration of this chemical when applied after thermal induction had an opportunity to take place, failed to influence subsequent flowering. In view of the evidence presented above, it seems reasonable to conclude that the inhibition of the formation of floral primordia was due to the activity of CLPP in counteracting the effect of substances associated with thermal induction ("florigen"?), which normally would initiate the reproductive stage of development.

The differential response of reproductive structures to varying concentrations of 2,4-D and CLPP was rather consistent throughout the experiment. Since each plant in all treatments was completely covered with spray, it is probable that a certain amount of water would be required to wet a given plant. The amount of chemical that any one plant re-

ceived would then vary with the concentration of the solution and the area of the leaf surface. The two plants of Cornell 19 which failed to bolt when treated with 500 ppm of CLPP could have conceivably received an amount of chemical equivalent to the amount the plants treated with 100 ppm received. Van Overbeek (21) has demonstrated that the control of flowering in pineapple depends upon the total amount of chemical the plant absorbs and not directly upon the concentration of the spray solution. The stimulation of flowering by 2,4-D on one hand and the retarding of flowering by a different concentration of that material, on the other hand, has also occurred in pineapples (3), and has been observed by the writer in flax. The actual mechanism which is responsible for this differential response has not been explained. However, since seedstalks which may be stimulated by 50 ppm of 2,4-D arise at the same time as those of control plants, it is probable that the increased rate of growth is due, primarily, to an increased rate of elongation of the type reported by Hitchcock and Zimmerman (11).

SUMMARY

Premature seeding of celery is a major problem in such areas as Michigan, New York, and California where it is frequently exposed to cool temperatures when the plants are young. The crop, normally biennial, responds as an annual and produces seedstalks the first year. Celery, which responds in this manner, is of no commercial value. A successful method for controlling this early seeding is very desirable.

Growth regulating chemicals have been reported to influence reproduction in such crops as pineapple, and a series of experiments were set up to determine their effect upon the reproductive response in celery. The following chemicals were applied in aqueous solutions by means of small household sprayers, at the concentrations indicated:

a) 5 ppm - 2,4-dichlorophenoxyacetic acid (2,4-D)
b) 50 ppm - " "
c) 50 ppm - triiodobenzoic acid (TIBA)
d) 500 ppm - " "
e) 50 ppm - naphthaleneacetic acid (NA)
f) 500 ppm - " "
g) 100 ppm - alpha-orthochlorophenoxypropionic acid (CLPP)
h) 500 ppm - " "

Treatments were applied to Cornell 19, a variety which is

very susceptible to premature seeding, and to the more resistant varieties, Non-Bolting Golden Plume and C&L Non-Bolting Pascal. Applications were timed with reference to the period when plants were exposed to low temperatures, in such a manner that one group was sprayed 48 hours preceeding exposure to cool growing conditions. A second group received treatment two weeks after plants had been moved to the cold frame and a third group, two weeks after field planting. Simultaneous tests were made on plants which were not subjected to low temperatures.

Seedstalk development was completely inhibited in plants treated with 100 ppm of CLPP, forty-eight hours before these plants were exposed to low temperatures. This material did not influence reproductive growth when applied at any other time or at any other concentration. Fifty ppm of 2,4-D increased the rate of seedstalk elongation and some evidence was found that 25 ppm of 2,4-D retarded elongation.

Additional experiments are necessary to establish CLPP as a means of preventing premature seeding, and to obtain more information with respect to variety response, time of treatment, and concentrations required. However, the results obtained in this investigation indicate that CLPP at a concentration of 100 ppm may provide a practical method for control of bolting in celery.

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