

SOME EFFECTS OF CERTAIN GROWTH-REGULATING
SUBSTANCES UPON PREMATURE SEEDING
IN CABBAGE

By

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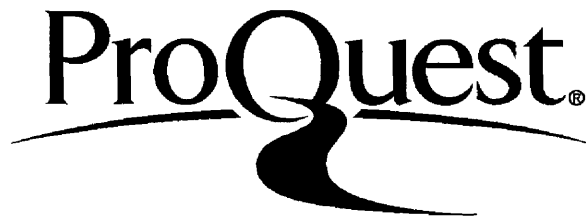
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ABSTRACT

Separate or interacting effects of growth-regulating substances, plant size, and cold-induction on flowering in Golden Acre and Round Dutch cabbage were studied in 1948 at Michigan State College and in 1949, 1950 and 1951 at Mississippi State College. Large (stem diameter 9 mm.) medium (6 mm.), and small (4 mm.) plants were sprayed either before, during or after cold-induction of 38° F. for 42 days. Medium size plants were sprayed before cold weather. Responses to chemicals were evaluated by determining histologically the time of flower initiation, seed stalk and flower appearance. The rate of flower development, plant height, head-core ratios, and an arbitrarily numbered growth phase index were also used in evaluating responses.

Only cold-induced plants flowered. Large plants flowered more readily than medium or small ones. Applying 15 ppm 2,4-dichlorophenoxyacetic acid (2,4-D) to medium size plants during cold-induction delayed flowering, inhibited seed stalk development, increased head-core ratios, and promoted vegetative growth. Vegetative growth was stimulated, head-core ratios and head firmness increased in noncold-induced plants sprayed with 20 ppm 2,4-D and 500 ppm alpha, ortho-chlorophenoxypropionic acid (ClPP). Sprays of 250 ppm ClPP applied to medium size Golden Acre plants before and after cold-induction hastened flowering three and two weeks respectively, and increased seed pod production. Plants sprayed during

induction remained vegetative. All large plants flowered but those sprayed during induction were two weeks later than controls. Essentially all small plants remained vegetative.

Medium size Round Dutch plants sprayed with 250 ppm maleic hydrazide (MH) before partial induction produced open heads in contrast to firm heads in controls. Most plants sprayed with MH during partial induction produced seed stalks but no flowers. Terminal buds were killed and growth inhibited generally by MH applied after partial induction. In limited tests alpha naphthaleneacetic acid (NA) stimulated vegetative growth, and 2,3,5-triiodobenzoic acid (TIBA) caused no appreciable effect.

Shoot apices did not become dome-shaped in the transition from vegetative to reproductive development, but remained morphologically unchanged. The most reliable morphological changes associated with reproductive growth were formation of longitudinal rows of cells in the rib meristem region, growth of lateral buds, and dwarfing of young leaves. These changes occurred about February 24 in large and medium plants. Morphologically flower initiation occurred first in medium size plants sprayed with 250 ppm ClPP before cold-induction; next in those sprayed after; then in the control and did not occur in plants sprayed during induction. With large plants initiation occurred first in plants sprayed before; second, in plants sprayed after; third, in the control; and last, in those sprayed during induction. Small plants remained vegetative.

Leaf and flower initials arose from periclinal cell division in the third and fourth cell layers of the flanking meristem just below the shoot apices. Flowers were produced laterally as leaves and did not terminate the seedstalk. The irregular appearance of flower parts were sepals, stamens, pistil and lastly petals.

The findings in this study were discussed on the basis of synthesis, level, economy, and distribution of phytohormones. A method was presented for numerically evaluating reproductive growth.

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Stallwattner

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INTRODUCTION

Cabbage, Brassica oleracea capitata, Linn., is a biennial. Growth and development of this crop may be divided in two phases: (1) the vegetative phase and (2) the reproductive phase.

The vegetative phase, as in all plants, consists of the development of the root system, and the shoot and leaf system. The reproductive phase consists of the development of flower buds, flowers, fruits and seeds. Before these reproductive structures develop in cabbage the central axis elongates, and forms a structure referred to as a seed stalk. Development of a seed stalk is, in this sense, a part of the reproductive phase.

When cabbage are seeded in the spring the plants form compact vegetative heads during late summer or early fall. If mature plants are wintered-over intact under mild weather conditions, the heads burst when growth starts the following spring. The terminal and several axillary buds elongate into seed stalks producing flowers and seed the following summer. Cabbage seeded late in the summer may not form heads before cold weather. If these plants are allowed to winter-over in cool weather they do not form heads, but shoot to seed when growth starts in the spring. This latter phenomenon of

shooting to seed without first forming a head is known as premature seeding, commonly referred to as "bolting".

Control of the vegetative and reproductive phases of growth is of great economic importance to two types of farmers. One type is interested in producing cabbage for the fresh market or for processing, and the other is interested in seed production. With the former the plants must be kept vegetative for market acceptance. The formation of seed stalks renders the crop worthless. The latter type has the opposite objective in view. Interests are directed toward seed stalk formation, seed production, and a high state of reproductiveness is desired.

In addition, plant breeders are interested in seed stalk formation. Only by inducing the reproductive response can plant breeders make crosses to develop new varieties with desired characteristics such as resistance to bolting or to diseases. Often breeders have difficulty in producing flowers for use in crossing desired varieties and species. This is especially true where cold storage facilities are lacking or inadequate. This necessitates resorting to naturally cool weather of long duration. As a result flowering occurs during early spring when the vegetable research worker is involved in many other duties.

Present methods employed commercially for controlling the vegetative and reproductive responses in cabbage, as well as many other crops, center around the knowledge of the effects that

certain environmental factors have upon the crop. First the crop for market is confined to the season of the year which is least conducive to bolting, yet conducive to good growth in that geographical locality. Second, the adjustment of seeding dates so the plants will not be easily induced to bolt when adverse weather occurs, and by supplying some protection, such as coldframes, for the seedlings during adverse weather. Third, the use of varieties which have some degree of resistance to bolting.

Neither of the above methods of control are entirely satisfactory. Weather conditions are difficult to predict and impractical to control under field conditions. In many localities they fluctuate from year to year. By choosing a seeding date which avoids temperatures conducive to seed stalk formation one year may not avoid these adverse conditions another year. Varieties which are "resistant" to bolting may be inferior in other respects. Resistance to bolting also accentuates the problem for the seed producer of inducing the variety to produce seed.

In Mississippi cabbage has been an important vegetable crop for about 60 years. The harvest period occurs in the early spring when the market is good. In order to harvest cabbage at this peak market season the plants are started in the fall and are wintered-over mainly in the field. Frequently the plants are subjected to prolonged periods of cool weather. If such conditions are extensive many of the plants bolt.

Loss due to bolting in commercial production is difficult to estimate. Most growers pull up and throw away all "possible-bolters" early in the season. With such a practice an accurate count of the plants which would actually bolt is hard to obtain. Loss also varies from year to year and among farms. It has been noted that as high as seventy-five percent of the plants on some farms will bolt during certain seasons, while in others bolting is negligible. In most instances bolting is estimated at five to fifteen percent.

Much work has been done and a vast repertory of information exists on the affects environmental factors have upon the responses of many plants. Even so, there is still too little concrete knowledge of the mechanism(s) involved in the plant when it is transformed from the vegetative to the reproductive phase of growth.

During the past decade effort has been directed toward the effect of growth substances upon growth responses. If a substance could be discovered that will inhibit seed stalk development, its application would be of great value to the fresh market grower. Conversely, if a substance were discovered that would induce or accelerate seed stalk formation it too would be valuable to plant breeders and seed producers. With such a material it might be that cabbage could be chemically induced to flower during any season of the year. These considerations were in mind when this study was undertaken.

LITERATURE REVIEW

Theories regarding the cause of flowering in plants have varied considerably among research workers during the past century. According to Caliachjan (9) Sachs advanced the theory about 1860 that vegetative and reproductive development in plants was hormonal in nature. Almost simultaneously Klebs introduced the theory that flowering depended upon the carbohydrate-nitrogen relationship. Klebs' theory was readily accepted and became popular. This theory was later upheld and caused to gain in popularity by Kraus and Kraybill's (50) work with tomatoes. The work of Garner and Allard (32) on photoperiodism in reality reopened and supported Sach's theory.

During the early 1920's other theories were advanced. Detjen (23) concluded that bolting was hereditary and behaved as a simple dominate factor. Sutton (85) suggested bolting in cabbage was a recessive factor. Similar conclusions were reached by Van Heel (91) while working with beets.

After Knott (46) failed to induce the reproductive phase by chilling Brassica seeds for several weeks during germination, he suggested that some environmental factor which occurred during the later stages of plant growth might be responsible for inducing the reproductive phase.

Plant research during the past few decades has provided much information with respect to the influence which various environmental factors have upon floral initiation and development.

Knowledge concerning the internal mechanisms involved is still meager.

Miller (59) and Boswell (7) studied several environmental factors associated with precocious seeding in cabbage. Miller's work showed temperature was the most important single factor associated with bolting in cabbage. Most of his work dealt with mature plants. He showed that 60 days of low temperatures (below 45° F.) were required to induce the reproductive phase.

Boswell's work conclusively demonstrated that plant size at the time of cold induction was a decisive factor. The larger the plants when the cold induction treatment was initiated the greater the number of plants which subsequently bolted. Plants with average stem diameters of 6 mm. or larger readily bolted when subjected to temperatures below 45° F. for two months. Two weeks of such low temperature changed the character of growth of large plants. Plants with stem diameters less than 6 mm. at the time of induction treatment did not bolt as readily as larger plants.

Based on the findings of Miller and Boswell with respect to temperature and size of plants, Knott (48) was able to control bolting very satisfactorily in California by manipulating the planting dates. Seven varieties were tested. There were variations among varieties, but in general, plants from the seedings made during August, September and early October produced heads in about four months. Plants from seedings made after October 15 were small when cool weather

occurred and produced heads the following spring.

Chroboczek (12) working with beets; Thompson and Knott (86) with lettuce; Knott (47) with spinach; Platenius (66) and Thompson (87, 88) with celery associated bolting in many vegetable crops with adverse weather conditions. A symposium recently published by Murneek, Whyte et al (62) and a book by Whyte (101) contain comprehensive reviews of experiments involving the effects of environmental factors upon developmental growth in plants.

During the past few years chemicals have been discovered to affect many of the phases of developmental growth in plants. Current attention is being directed by many scientists to the use of growth-regulating substances as a possible means of controlling floral initiation and floral development in a variety of plants. A complete review of the literature on this subject does not seem to be justified since several reviews which are both comprehensive and rather complete have been recently compiled (51, 62, 80, 97, 100, 107, 108). This review shall, however, embody several phases of research concerning information especially pertinent to this study.

Although the theory that the control of plant responses by chemical substances in which flowering is but one case was advanced a century ago (9) or even earlier (100), it was Went (99) who first extracted a substance with growth-regulating properties.

Hitchcock and Zimmerman (38) were among the first to report that growth-regulating substances have a pronounced effect upon

flowering in plants. They applied indolebutyric, indolepropionic, phenylactic and phenylproprionic acids to the soil in which Turkish tobacco plants were growing and observed that flowering was hastened when either of these substances were applied about one month before the normal flowering date. These findings, however, were not confirmed in studies made by Murneek (61) with tomatoes, tobacco, and soybeans.

The most spectacular example of chemically controlling vegetative and reproductive responses in plants is with the pineapple. Clark and Kerns (15) reported that the pineapple could be made to flower earlier than the normal by applying low concentrations of naphthaleneacetic acid. In sharp contrast, flowering could be delayed or even suppressed by applying high concentrations of the same substance. A solution containing 0.01 percent of naphthaleneacetic acid applied 30 days before the normal date for floral differentiation delayed flowering 90 days in Hawaii.

In Florida, Cooper and Reese (18) induced pineapple to flower during the fall with ethylene, acetylene, and naphthaleneacetic acid. Normally the pineapple does not flower until January under Florida conditions. Indole compounds were not effective. Cooper (17) inhibited flowering in pineapple by applying large amounts of naphthaleneacetic acid, and promoted flowering with small amounts. When this substance was applied during certain season of the year plant response was different. When applied in July flowering was

inhibited and when applied in October flowering was hastened. The results obtained in Florida are not in complete agreement with those obtained in Hawaii.

A more recent report by Van Overbeek (96) indicates that many of the "drawbacks" to the chemical control of flowering in the pineapple have been overcome. Pineapple plants begin to flower after being exposed to cool night temperatures in the fall and continue to flower during the winter months. Under normal culture most varieties begin to flower and produce fruit at the age of eighteen months. Some varieties, such as the Puerto Rican Cabezona, take as long as five years to flower. Applying 0.25 to 0.50 mg. of naphthaleneacetic acid per plant gives almost complete control of flowering in the Red Spanish variety in Puerto Rico. Plants receiving this treatment bear their fruit on a slender or restricted peduncle. Such fruit falls over easily. This hazard can be overcome by treating chemically induced plants with Beta naphthoxyacetic acid after fruit development is underway. To control premature flowering large amounts of naphthaleneacetic acid are necessary. Thus, according to Van Overbeek the chemical control of developmental growth in the pineapple is a reality. This practice, under commercial usage, enables growers to make a single harvest of an entire planting. Whereas, several harvests are required, due to irregularities of maturity among plants, where flowering is not chemically controlled. With the proper use of naphthaleneacetic acid pineapple plants can be

made to flower during any month of the year (96). Auxin is involved in controlling the floral process in this plant (97). Small amounts of growth-regulating substances will promote flowering (95).

Reports of work with other crops have yielded varied results. Dostal and Hosek (25) were the first (1937) to show that flowering could be inhibited by auxin. They successfully reverted "flower ready" Cercaea intermedia to the vegetative habit with indoleacetic acid in lanolin paste. The possibility that high levels of auxin may be harmful to floral initiation was also suggested by Galston (30). Considerable evidence exists to support this postulation. Zimmerman and Hitchcock (106) promoted flowering in tomatoes with triiodobenzoic acid. The number of flowers per cluster were increased, and seedlings were induced to flower before the normal flowering time by spraying the plants with 25 to 500 mg/l of triiodobenzoic acid. Similar results were obtained by Waard and Roodenburg (98) with a solution containing 200 mg. of triiodobenzoic acid per liter of water. Galston (31) found triiodobenzoic acid to augment the flowering response of Peking and Biloxi soybeans, to inhibit apical dominance, internodal elongation and the activity of indoleacetic acid. This chemical failed to induce vegetative soybean plants to flower but greatly increased the flowering response to photoperiodically induced plants. Galston suggested that triiodobenzoic acid had "florigenic" properties which promote flowering. In this connection he considers the two growth phases to oppose

each other. Florigen tends to promote floral differentiation and auxin (the growth hormone) antagonizes florigen by favoring vegetative growth. Photoperiodically induced Xanthium, a short day plant, sprayed with 500 ppm indoleacetic acid and naphthaleneacetic acid by Thurlow and Bonner (90) formed no floral primordia. These authors conclude that auxin content decreases under short day conditions which promoted floral development. The application of auxin-like chemicals tend to augment the auxin content in the plant and nullify the induction treatment. Green and Fuller (33) delayed floral initiation in petunia and soybean plants, by applying indoleacetic acid to the roots. Flower development was also delayed on plants initiating flowers at the time for treatment.

Leopold and Thimann (52) applied low (1 mg/l or less) concentrations of indoleacetic acid and alpha naphthaleneacetic acid to Wintex barley, a long day plant, and increased the number of floral primordia over that of the control. In contrast, flowering was inhibited when high concentrations (1 to 400 mg/l) of these auxin-like chemicals were applied. Teosinte, a short day plant, showed no such response to the chemical treatments. Dosages of naphthaleneacetic acid up to 400 mg/l caused inhibition of flowering in every case. These authors considered that with barley, as with the pineapple, auxin concentration exerted an effect on flowering. It appeared that floral and vegetative growth were promoted by low and inhibited by high auxin concentration. Leopold and Thimann did not

consider auxin to be necessarily antagonistic to the production of a floral hormone. This concept is not in complete agreement with that of Galston (31), and Hamner (37).

Bonner (4) and Bonner and Thurlow (6) inhibited flowering in photo-induced Xanthium with naphthaleneacetic acid and indoleacetic acid (auxins), and promoted flowering under short photoperiod with 2,4-dichloranisole and 2,3,5-triiodobenzoic acid (anti-auxins or auxin antagonists). The most suitable concentrations were 10 mg/l of naphthaleneacetic and 2,4-dichloranisole, and 30 mg/l of triiodobenzoic acid. When triiodobenzoic and naphthaleneacetic acids were combined into one treatment the plants showed no response to either chemical. Rice (70) applied various growth-regulators to several crop plants and concluded that auxin and auxin-like chemicals delay flowering in most plants. Leopold and Guernsey (55) have recently reported the role of auxin in flower initiation of the Alaska pea. The object of their study was to develop a simple method for measuring the effects of added substances upon flowering. Pea seedlings germinated in paper towels were soaked for four hours in the desired substance. The node at which flowers occurred was used as a criterion for measuring plant response. Environmental factors were found to influence the node where flowers first appeared, and a control was run with each treatment under several environmental conditions. Under the condition of their control treatment the first flowers occurred, in general, at the seventh node.

Naphthaleneacetic acid caused a quantitative inhibition of flowering at temperatures of 18-20° C. However, the auxin treatment promoted flowering in plants held at 10° C. Plant constituents as sucrose, arginine and malic acid were tested and found to inhibit flowering. Auxin applied in combination with such substances or under low temperature conditions nullified their inhibiting effect and promoted flowering.

Flowering was delayed in stocks by Johnson (43) and inhibited in mustard by spraying the plants tri-weekly with beta-naphthoxyacetic acid. Alpha-naphthoxyacetic acid was less effective. Hitchcock and Zimmerman (39) delayed flowering in dandelions by spraying the plants with 2,4,6-trichlorophenoxyacetic acid.

Wittwer, Coulter and Carolus (102) controlled bolting experimentally in celery by spraying the plants with ortho-chlorophenoxypropionic acid. Clark and Wittwer (14) obtained interesting results with lettuce and celery plants that were sprayed with growth-regulating substances. Several experiments were conducted with lettuce involving several chemicals, concentrations, and times of application. Elongation of the seed stalk was apparent first in plants treated with alpha ortho-chlorophenoxypropionic acid in concentrations of 25 ppm and with 2,4-dichlorophenoxyacetic acid in concentrations of 10 ppm. Treating small plants with 2,4-dichlorophenoxyacetic acid appeared to dwarf subsequent growth. Seed stalk elongation was hastened in plants treated at eight to twelve weeks of age, and

when repeated applications were made. Progeny of the treated plants exhibited a stimulative response similar but of lower magnitude than the treated parent. This stimulative response persisted even in the second generation. In each instance, stimulation in seed stalk elongation was accomplished early in the season, and Grand Rapids the variety most susceptible to bolting showed the greatest response. From this series of experiments chemical concentrations and time of application were found to have a pronounced influence on the effect growth-regulating substances have upon developmental growth.

Their data from the celery experiments suggest that floral primordia differentiated at the slowest rate in 2,4-D treated plants, and that a fluctuation of phytohormone content in the meristem region was associated with rate of developmental growth. Plants of Cornell 19, the variety that readily bolted, and plants receiving a cold treatment which induced bolting exhibited higher concentrations of phytohormones than non-bolting plants. A low level of phytohormones existed in the meristems at or just preceding seed stalk differentiation.

Since Schoene and Hoffman (78) reported maleic hydrazide to have unique growth regulating properties many papers on the responses of plants to this chemical have been published. A very complete compilation of these investigations has been made by Zukel (108, 109). Much of the work with maleic hydrazide has been directed toward temporary or permanent growth inhibition of grasses

and weeds. Considerable work, however, toward the control of sprouting in storage, and the vegetative and reproductive responses in a number of crop plants has been published.

Preharvest foliar sprays of maleic hydrazide have controlled storage sprouting and spoilage of onions (103), carrots and onions (104), potatoes (44), onions, potatoes, sugar beets and a number of root crops (65, 105).

The inhibition of stem growth, bolting and flowering by maleic hydrazide has been reported. Erickson and Price (27) sprayed cold-induced sugar beets, variety U.S. 56 with 0.1 and 0.5 percent maleic hydrazide. Stem tips in many plants were killed by both concentrations. The newly developed leaves of plants treated with 0.1% maleic hydrazide showed formative effects. Bolting plants became vegetative, and the elongated stems produced terminal rosettes of leaves; but root growth was not retarded by the treatment. Naylor and Davis (64) applied maleic hydrazide in concentrations up to 0.8 percent to 11 plant species from 5 families. The responses were remarkably similar. Sensitivity to maleic hydrazide appeared to dissipate with plant age, and plants treated in the seedling stage produced no flowers. Flowering was prevented in tobacco and photo-induced Xanthium by high concentrations. Xanthium treated with low concentrations required a 30 minute longer dark period for induction. Naylor (63) sprayed the upper and lower sides of Turkish tobacco leaves with 0.05 to 0.8 percent maleic hydrazide when the plants were beginning

to flower. Plants sprayed with concentrations greater than 0.2 percent ceased to flower; lower concentrations suppressed terminal growth and development of inflorescences. Maleic hydrazide stopped flower bud development on photo-induced Xanthium plants. Inhibition of flowering in Virginia bright leaf tobacco (Ciferri) and Havana seed tobacco (Peterson) sprayed with maleic hydrazide has been reported.

Naylor (63) and Moore (60) obtained striking effects with maleic hydrazide on flower development in corn. Plants sprayed with concentrations as low as 0.025 percent produced sterile staminate inflorescences.

Maleic hydrazide has delayed flowering in mustard (20), radish (40), and prevented bolting in onions (13) and suppressed flowering in Croft Easter lilies (83).

Crafts, et.al. (21) studied the response of 13 crop species to maleic hydrazide. Although different species varied in behavior, the age of the plant at time of treatment was a primary factor in determining plant response. Young plants were more responsive than old plants. In contrast to papers cited above in which maleic hydrazide inhibited reproductive development Crafts (19) found that bolting was stimulated in lettuce when 0.1 percent maleic hydrazide was applied to 20-day old seedlings.

Barnard and Warden (1) applied 0.1 and 0.5 percent maleic hydrazide to New York 12 lettuce seedlings one week old and observed that treated plants had greater bolting tendencies than

controls. Kosar and Thompson (49) promoted bolting in young lettuce and prevented bolting in old lettuce with 0.1-1.0 percent maleic hydrazide sprays.

In reporting the results of a series of elaborate experiments involving temperature ranges, nitrogen levels and several concentrations of maleic hydrazide applied to celery plants at different stages of plant development, Jackson (41) showed complete experimental control of the vegetative and reproductive responses in this crop. Each factor studied, maleic hydrazide, nitrogen and temperature, separately or in combination influenced seed stalk development in Cornell 19 celery. Low temperature, low chemical concentrations and a medium level of nitrate were found to be most conducive to seed stalk development. Young plants sprayed with 50 to 250 ppm maleic hydrazide following a low temperature treatment of 40° F. and grown at a nitrate level of 20 ppm flowered earlier and more profusely than the controls. High temperature, high chemical concentrations and a low or high nitrate level favored vegetative development. Jackson obtained chemical induction of the reproductive phase in young celery plants which were held at a temperature above 65° F. Timing of the application and the concentration employed were very important. Plants 10 to 14 weeks of age when treated with 100 ppm of the chemical showed the most reproductive response. Concentrations below 75 ppm were not effective except with cold-induced plants.

In comparison to stimulating the reproductive response with low concentrations of maleic hydrazide on young celery plants, bolting was suppressed with high concentrations applied during the later stages of plant development. All concentrations above 500 ppm applied during the later stages of growth inhibited seed stalk development in cold-induced and non-cold induced plants. A single application of 1000 ppm of maleic hydrazide to older plants gave almost complete control of seed stalk development without any apparent injury to the marketable portion of the plant.

Lang (51) has recently made a rather complete review of the literature concerning the physiology of flowering and the effects of growth-regulating substances on flowering.

Morphological Studies

Several theories have been employed in describing the organization of the meristematic tissues in the terminal growing point of plants. Eames and MacDaniels (26) mention two theories which are the histogen theory and the tunica-corpus theory. In the former theory the three major regions of the stem are considered to arise from separate histogens. The outer region is called the dermatogen, the central region or core the plerome, and the region between the dermatogen and the plerome, the periblem. The dermatogen forms the epidermis, the periblem forms the cortex and the plerome forms the pith.

The tunica-carpus theory, formulated by Schmidt (77) in 1924, has become the more widely accepted theory among anatomists. Two regions unlike in structure develop in the stem apex due to different rates and planes of cell division. The outer region is called tunica and the inner region corpus. The cells in the tunica are small and divide primarily in anticlinal planes. The growth in area is primarily in the tunica. Cells of the corpus, which account principally for growth in volume, divide in many planes. The principal disadvantage to this method of describing the architecture of the apex is that the tunica and corpus regions are not clearly defined in many plants. For this reason Foster (28) working with Cycas, Boke (3) with Trichocereus and Opuntia, and Satina and Blakeslee (76) with Datura modified the tunica-carpus theory. The shoot apices were divided into three or more zones or groups of initials. Foster has made an adequate review of the literature on the structure and growth of the shoot apex.

Griffith (35) studying the terminal and lateral growing points of four species of Araucaria divided them in four descriptive zones. The tunica was referred to as zone 1, corpus initials as zone 2, peripheral zone or flanking meristem as zone 3, and zone of rib meristem as zone 4. Shoushan (79) working with Lilium favored numbering the cell layers and referred to them as first layer, second layer, and so on from the outer layer inward. This method eliminates confusion of the various zones as there is no distinct line of demarcation in many

plants between the tunica and corpus but rather a gradual transition from one to the other.

Various morphological changes have been reported to occur in many plants with or even before the switch to reproductive from vegetative development. Changes such as a greater stem diameter associated with reproductive growth were observed in sour cherry (71), plum (72), and apple (73, 74). It was later found (82) with apple that the marked secondary thickening of the fruit spur occur after flower bud initiation. Roberts and Ocra (75) and Struckmeyer and Roberts (84) examined stem tips at the fourth node of several species of flowering and non-flowering plants. They found certain anatomical characteristics associated with flowering. Flowering plants, in contrast to non-flowering plants, had less active cambium, thick walled cells in the pericycle, perimedullary zone and phloem, and thin walled cells in the parenchymatous tissues.

Boswell (7) studied the terminal growing points of cabbage from late fall to early spring. The first evidence of seed stalk primordia differentiation was noticed in samples collected February 4. Primordia developed irrespective of plant size in all reproductive plants at about the same time. He did not find a significant correlation between plant size and size of stem apex, but noted an increase in size of the apices of potentially reproductive plants. Differences in size of apices were detectable by the time growth ceased in the fall or even earlier. Great enlargement of the apices of potential

seeders occurred during the winter and early spring, whereas the apices of vegetative plants remained unchanged through their development. Boswell reported that flowers did not necessarily accompany an elongating axis and destruction of the terminal bud did not prevent floral development. He found that seed stalk primordia developed rapidly forming branches with many well developed flowers which emerged from the head about April 1.

Thompson (89) conducted a microscopical study of cabbage from fall seeding until the plants reach maturity. His study was directed mainly at the development of the flower. Floral primordia were first observed during late February and early March. The order of floral organ appearance was found not to follow the usual acropetalic succession. The sepals were the first organs to appear followed by the stamens, carpels, and lastly the petals.

MATERIALS AND METHODS

The experiments herein described were conducted in the greenhouse at Michigan State College during the 1948-49 season, and in the field and greenhouse at Mississippi State College during the 1949-50 and 1951-52 seasons. Two cabbage varieties, Golden Acre and Round Dutch which are widely grown in commercial production, were selected for the study. Golden Acre is susceptible and Round Dutch resistant to bolting. Seeds for planting were obtained from the Ferry-Morse Seed Company and the same or comparable stocks were used in all experiments.

The growth-regulating substances used were 2,4-dichlorophenoxyacetic; alpha, ortho-chlorophenoxypropionic; 2,3,5 tri-iodobenzoic; alpha naphthaleneacetic; and maleic hydrazide, hereinafter referred to as 2,4-D, ClPP, TlBA, NA, and MH, respectively. The first four chemicals were used in the form of true acids. The fifth, MH, was a water soluble diethanolamine salt formulation prepared by the Naugatuck Chemical Division of United States Rubber Company, containing 30 percent by weight of the active ingredient.

Fresh stock solutions of these substances were prepared at the beginning of each experiment by dissolving one gram of the crystals in 100 millileters (ml.) or 95 percent ethyl alcohol, except for MH. It was found that when MH, which is prepared in solution form by the manufacturers, was diluted with alcohol to make standard stock solutions a white precipitate formed after a few weeks

in storage. Therefore, standard stock solutions of MH were prepared in distilled water. The stock solutions were diluted to the desired concentration at the time of treatment with tap water. All concentrations are expressed in parts per million (ppm) of the growth substance.

The experimental design in each instance consisted of a randomized complete block. Whenever applicable, the data contained in these investigations were analyzed for statistical significance. Least differences required for significance (L.S.D.) among treatments were calculated by analysis of variance (81).

Materials and methods which are specific to an experiment are outlined in detail and precede the presentation of results for each experiment.

TERMINOLOGY

The term head-core ratio is the length of a cabbage head divided by its core length.

The term growth phase index is a numerical value applied to cabbage plants denoting the degree of vegetativeness and/or reproductiveness. A zero value denotes complete vegetativeness, whereas a value of eight denotes complete reproductiveness.

The term shoot as used in this paper refers to the entity of the terminal and lateral growing points and the differentiated tissues.

The term growing point as used in this paper refers to the differentiating tissues in its entity in and about the shoot tip.

The term apex as used in this paper refers only to the non-differentiated tissue located in the extremity of the shoot tip.

EXPERIMENT 1, 1948-49

The first experiment was designed to obtain preliminary information. Information was desired as to whether certain growth substances influence seed stalk development in cabbage; which chemical had the greatest inhibitive and which chemical had the greatest promotive influence on growth; and the relative tolerance of cabbage to various concentrations of a number of growth substances.

MATERIALS AND METHODS

Seeds were planted February 24, 1948 in the horticultural greenhouse at Michigan State College. The seeding media used in the flats consisted of a mixture of equal parts of field soil and sand. Four hundred and fifty uniform seedlings of each variety were transplanted March 19 to 3-inch clay pots and again on April 14 to 4-inch clay pots. The purpose of first transplanting to 3-inch pots was to conserve greenhouse space.

The potted plants in each variety were arranged into seventeen groups of twenty-five plants each in such a way that the plants in one group were as nearly as possible the same size as the plants in each of the other groups. The plants in each group were then numbered from one through twenty-five. Each of seventeen groups of plants for each variety received one of the following treatments on April 18.

Treatment Number	Chemical	Concentration (PPM)
1	2,4-D	5
2	2,4-D	10
3	2,4-D	15
4	2,4-D	20
5	ClPP	50
6	ClPP	100
7	ClPP	250
8	ClPP	500
9	TlBA	50
10	TlBA	100
11	TlBA	250
12	TlBA	500
13	NA	100
14	NA	250
15	NA	500
16	NA	1000
17	Water	Control

After the stock solutions were diluted with tap water 5 grams of Drest were added to each gallon of solution. The Drest was used to improve the spreading of the solution on the surfaces of the waxy leaves.

In order to prevent contamination among chemicals, different pipettes and containers were used for each chemical. Solutions for

treatments were prepared in deep enameled pans and each plant was dipped in the desired solution for ten seconds. The pots in which the plants were growing were inverted and only the above-ground part of the plant was emersed into the solution. Plants at the time of treatment had four and five well developed leaves and the stem diameters averaged six millimeters.

The first ten plants in each treatment were kept in the greenhouse where the temperature was maintained above 55 degrees Fahrenheit ($^{\circ}\text{F}$) by means of a thermostatically controlled steam heating system. These plants are referred to as noncold-induced plants. Treatments were arranged in random order in each of two replicates. The plants remaining in each group were placed in coldframes for a cold-induction treatment which induces bolting. They are referred to as the cold-induced plants. The treatments were arranged in three randomized complete blocks of five plants each.

Outside night temperatures exceeded 45°F . after May 25, and the plants were moved May 28 to a cold storage room located in the horticultural building. The temperature in the storage room was controlled by a thermostat and held constant $\underline{-2^{\circ}}$ at 38°F . Lighting was inadequate for plant growth, therefore, the plants were carted out of the building and placed in the sunlight every other morning at seven o'clock and returned to the storage room that evening at five o'clock.

After fifty-nine days of induction treatment where the night

temperatures were below 45° F. these plants were returned to the greenhouse where the temperature was maintained above 55° F.

All plants were transplanted to eight-inch pots June 17 and 18. The potting media consisted of a mixture of two-thirds field soil and one-third muck. In order to keep the plants well supplied with nutrients 200 ml. of a nutrient solution was applied bimonthly to each pot. The solution consisted of one ounce of 10-52-17 soluble fertilizer and two ounces of ammonium nitrate dissolved in three and one-half gallons of water. Rotonone dust was used to control cabbage worms and sulfur to control soft rots.

Aerial elongation of the plants was measured in centimeters (cm) each week beginning April 23 and ending November 20. Morphological modifications produced by the chemicals were noted periodically. Notations of the general character of growth, firmness of heads and number of probable seeders were also made. In collecting the data on the heading characteristics a score of 1 was assigned to firm; 2 to loose; and 3 to open heads.

Results: Noncold-induced plants

Pronounced modifications of the foliage were apparent in certain treatments a few hours after they were applied. These modifications were characterized by twisting and cupping of the mature leaves. In some instances the leaves were twisted to the extent that the abaxial side of the leaf was in the adaxial position. Twisting and

cupping occurred among all plants treated with 2,4-D in concentrations greater than 5 ppm, and with 250 and 500 ppm of ClPP. These modifications were temporary because all plants recovered within 36 hours after treatment.

Five days after treatment there was general epinasty, widening and thickening of the petioles and main stems and cupping of the leaves of plants treated with 2,4-D and ClPP. Plants treated with 2,4-D were most affected and Golden Acre appeared to be more affected than Round Dutch.

The thickened stems of plants treated with 2,4-D eventually became so enlarged that the epidermis split forming a slit parallel with the longitudinal axis of the plant, Figure 1. Within a few days these slits became filled with proliferated tissue of tumorous-like growth. From these affected areas arose adventitious tubular structures which later developed into lateral shoots with morphological characteristics identical with the main stem, Figure 2. Leaves developing on these adventitious shoots and on the main stems above the tumors were much dwarfed, cupped and the petioles were elongated. Growth in diameter of the main stem was restricted above the tumors. This restriction was especially pronounced on plants treated with 20 ppm of 2,4-D.

Less proliferation resulted from the ClPP concentrations, but some occurred on plants treated with 250 and 500 ppm. No pronounced modifications were observed in plants treated with TlBA or NA.



Figure 1. A cabbage plant treated with 20 ppm 2,4-D showing thickened stem and split epidermis.



Figure 2. A cabbage plant treated with 20 ppm 2,4-D showing proliferation of tissues, and an adventitious shoot arising from the area affected.

Plants kept continuously in the greenhouse made rapid growth early in the season. Growth in height of the Golden Acre variety is shown in Table 1. These data show the average height of the plants to the terminal bud for each treatment on the dates specified. Although the plants were measured each week only the measurements taken at approximately 2-month intervals are presented. It can readily be seen that most of the growth occurred by July 24 and in most instances little growth was made between July 24 and September 18. July and August temperatures were very high in the greenhouse and may account for the reduced growth rate during this period.

Increasing the 2,4-D concentration applied resulted in a gradual increase in plant height from time of treatment to May 21. The average height of the plants treated with 5 ppm was not statistically different from that of the control. Plants treated with 10, 15, and 20 ppm were significantly higher than the control.

Differences were small on May 21 among the plants treated with various concentrations of ClPP. Only plants treated with 100 ppm had an average height statistically greater than the control plants. Treatment with TlBA did not alter the average heights of the plants. Applications of 100, 250 and 500 ppm NA slightly increased the average height over that of the control.

By July 24 slight variations existed in average plant heights among the several treatments but were not great enough to be statistically significant. When this experiment was terminated

Table 1. Height of Cabbage Plants as Influenced by Growth-Regulating Substances (Variety Golden Acre, Noncold-Induced).

Growth Substances		Dates of Measurement		
Chemical Symbol	PPM	May 21	July 24	Sept. 18
(Centimeters)				
Control	-	7.1	26.0	32.0
2,4-D	5	9.6	23.8	27.4
	10	11.8	26.3	34.2
	15	13.8	27.8	30.9
	20	14.3	28.7	30.8
ClPP	50	8.4	22.3	28.7
	100	10.6	28.8	34.5
	250	9.7	23.1	26.2
	500	9.2	22.8	30.4
TIBA	50	9.8	22.7	27.2
	100	9.6	26.5	29.4
	250	9.5	23.9	29.1
	500	7.7	22.0	30.2
NA	100	10.2	27.5	34.2
	250	10.9	28.0	37.3
	500	10.1	27.8	33.0
	1000	9.3	21.1	32.5
L.S.D.	@ .05	3.0	4.5	N.S.
	@ .01	4.1	N.S.	

September 18, no treatment differed statistically from the control.

Application of 2,4-D to Round Dutch stimulated aerial growth during the first month following treatment and as can be seen in Table 2 average height increased with the increase in concentrations. In fact, the average height of the plants receiving each of the three higher concentrations was almost twice that of the control plants on May 21.

Plants receiving either of the ClPP concentrations had grown to greater heights by May 21, than the control. During the first month subsequent to treatment growth rates of these plants were significantly different from the control and from plants receiving 50, 100, and 250 ppm of TlBA. The above concentrations of TlBA appeared to stimulate growth in the Round Dutch variety. This response was in contrast to no stimulation with the Golden Acre variety. Only the 500 ppm concentration of NA significantly stimulated growth rate in the Round Dutch variety.

During the next 2-month period, May 21 to July 24, there was a trend indicating that the lower the concentration of 2,4-D the greater the rate of growth. This fact is demonstrated by the data in Table 2. These data show on July 24 no significant differences in average height of control plants and those in either of the 2,4-D treatments. Neither the growth-regulating substance nor its concentration altered the average height of plants to the extent that they sufficiently differed from the average height of the control plants at the end of the experiment.

Table 2. Height of Cabbage Plants as Influenced by Growth-Regulating Substances (Variety Round Dutch, Noncold-Induced).

Growth Substances		Dates of Measurement		
Chemical Symbol	PPM	May 21	July 24	Sept. 18
(Centimeters)				
Control	-	4.9	21.3	23.5
2,4-D	5	6.6	19.9	22.6
	10	9.5	22.8	25.4
	15	10.4	23.6	27.8
	20	11.1	24.9	27.7
ClPP	50	8.8	23.2	23.5
	100	7.6	23.9	27.7
	250	8.3	22.8	30.4
	500	9.2	23.2	28.8
TlBA	50	7.4	22.2	26.1
	100	6.4	21.3	27.6
	250	6.4	21.8	25.9
	500	6.0	23.4	25.4
NA	100	5.9	21.2	23.9
	250	5.8	21.8	26.6
	500	7.3	21.6	28.7
	1000	5.8	22.5	29.5
L.S.D.	@ .05	1.3	N.S.	N.S.
	@ .01	1.8	N.S.	N.S.

Based on the data presented above, with respect to growth of the Golden Acre and Round Dutch varieties as effected by growth-regulating substances, two main points stand out. (1) The application of 2,4-D, ClPP and NA in dilute solutions tend to stimulate aerial extension of the main axis of the plant soon after treatment. (2) Stimulation of growth is lost two to three months after treatment and the non-treated plants tend to reach approximately the same ultimate height as the treated plants.

Other points worthy of mention are: (1) In general the growth rate in Golden Acre was greater than in Round Dutch. (2) The response to the growth-regulating substances by the two varieties was, in general, somewhat similar.

Cold-Induced Plants

Foliar modifications, stem splitting and tissue proliferation occurred in about the same degree in cold-induced plants as described for the noncold-induced plants.

Growth in height of the Golden Acre plants and the values required for statistical significance are presented in Table 3. Plants treated with 2,4-D grew slightly faster than the control during the first month subsequent to treatment. Growth rate was increased, up to May 21, by 2,4-D. The difference in height between the control plants and those treated with 5 ppm was significant. Differences between the control plants and those treated with 10, 15 and 20 ppm were

Table 3. Height of Cabbage Plants as Affected by Growth-Regulating Substances (Variety Golden Acre, Cold-Induced).

Growth Substances		Dates of Measurement			
Chemical Symbol	PPM	May 21	July 24	Sept. 25	Nov. 20
(Centimeters)					
Control	-	5.5	15.2	24.3	32.5
2,4-D	5	6.3	16.5	27.0	37.5
	10	7.1	17.9	30.2	41.7
	15	7.1	17.4	29.2	40.2
	20	7.5	18.5	28.9	36.5
ClPP	50	5.8	15.9	26.8	36.2
	100	5.5	15.8	26.0	36.9
	250	5.3	14.8	26.5	32.5
	500	5.1	15.2	25.9	32.6
TlBA	50	5.9	15.0	27.6	37.3
	100	5.6	15.0	27.1	38.7
	250	6.0	15.1	27.1	36.5
	500	5.8	15.9	28.5	41.1
NA	100	7.0	15.7	26.7	36.5
	250	6.4	15.9	27.8	38.9
	500	6.0	15.7	27.1	38.5
	1000	4.7	14.3	25.9	34.7
L.S.D.	@.05	0.61	2.11	N.S.	N.S.
	@.01	0.82	N.S.		

highly significant. At no time during the growing season were any of the ClPP treated plants significantly higher than the controls. Plants treated with TlBA made growth almost identical with the controls throughout the experiment. A stimulation in growth was noted early in the season from 100 to 250 ppm NA, but did not prevail later in the season.

The data on growth in height of the Round Dutch variety are shown in Table 4. There was little difference in ultimate height of plants among the various treatments (except with 2,4-D at 20 ppm). The lower concentrations of 2,4-D and ClPP did not increase the ultimate height in this variety which was in contrast to the response shown by the Golden Acre variety. However, all concentrations of 2,4-D stimulated growth in both varieties early in the season as compared to the control. Plants treated with 50 and 250 ppm ClPP were also higher than the controls on May 21. On July 24 the differences between the heights of the control and plants treated with 15 and 20 ppm 2,4-D and 250 ppm ClPP were highly significant. There was little difference in the rate of growth for the 2,4-D treated plants and the controls between May 21 and July 24. Only those plants treated with 15 and 20 ppm were statistically higher than the controls. By September 25 the differences in heights among the 2,4-D treated and control plants were essentially the same.

Data concerning the effect of varying the concentrations of 2,4-D, ClPP, TlBA and NA on the heading characteristics and the

Table 4. Height of Cabbage Plants as Affected by Growth-Regulating Substances (Variety Round Dutch, Cold-Induced).

Growth Substances		Dates of Measurement			
Chemical Symbol	PPM	May 21	July 24	Sept. 25	Nov. 20
(Centimeters)					
Control	-	4.1	14.1	25.3	33.9
2,4-D	5	5.2	15.2	25.7	32.7
	10	5.0	14.7	26.2	34.0
	15	5.8	16.2	26.6	33.3
	20	5.1	16.7	29.4	39.3
ClPP	50	5.6	15.7	26.4	33.4
	100	4.7	14.7	26.4	32.2
	250	5.8	16.1	25.6	31.7
	500	4.6	14.5	24.7	30.3
TlBA	50	5.0	13.9	24.7	31.1
	100	3.9	13.9	25.6	32.0
	250	3.7	14.0	25.4	32.5
	500	4.7	13.8	24.7	31.1
NA	100	4.2	13.5	23.1	30.8
	250	4.9	14.8	27.1	33.6
	500	4.9	15.4	26.1	34.0
	1000	3.9	14.5	26.3	32.3
L.S.D.	@.05	0.84	1.45	N.S.	N.S.
	@.01	1.12	1.94		

number of probable seeders in Golden Acre are presented in Table 5. It appears that increasing the concentration of 2,4-D above 10 ppm resulted in a corresponding increase in the number of open heads. All of the plants treated with 20 ppm of 2,4-D produced open heads. Leaves and stems of these plants had many of the characteristics of reproductive plants, but none of them produced a true head nor flowers.

The heads tended to be less firm with the increase in concentration of each chemical except TlBA. This trend was very pronounced in plants treated with 2,4-D. Plants treated with 5 ppm received an average firmness score of 1.70 and as the concentration was increased to 20 ppm this score increased to 3.00. A larger number of probable seeders was noted in the plants treated with TlBA than with either of the other substances or the control.

These data are merely indications and should not be relied upon too strongly. The character of growth among the various treatments changed several times during the season. Early in the season, the stems and leaves of many plants were identical with those of reproductive plants. During July the temperatures in the greenhouse were above 90° F. most every day. After three weeks of these high temperatures the plants reverted from the reproductive to the vegetative phase of growth. Many plants, when they were about 30 cms tall began forming loose heads. Such a response suggests that the high temperatures during July nullified the cold-induction treatment resulting in a type of "devernalization".

Table 5. Head Characteristics and Number of Probable Seeders in Cabbage Plants as Influenced by Growth-Regulating Substances (Variety Golden Acre, Cold-Induced).

Growth Substances		Number Heads			Firmness	Probable
Chemical Symbol	PPM	Firm	Loose	Open ¹	Score ²	Seeders
Control		5	6	4	1.73	2
2,4-D	5	5	10		1.70	3
	10		15		2.00	9
	15		9	6	2.30	?
	20			15	3.00	?
ClPP	50	5	9	1	1.73	2
	100		14	1	2.07	6
	250	1	12	2	1.86	5
	500		12	3	2.13	6
TlBA	50		13	2	2.00	10
	100		15		2.00	5
	250		14	1	2.07	11
	500		14	1	2.07	9
NA	100	1	14		1.93	3
	250		15		2.00	6
	500		13	2	2.13	7
	1000		13	2	2.13	2

¹ Plants forming no true heads were referred to as "open heads".

² A score of 1 was assigned to firm, 2 to loose and 3 to open heads.

Table 6 shows the effect of varying the concentration of 2,4-D, ClPP, TlBA and NA on the heading characteristics and the number of probable seeders in cold-induced Round Dutch plants. Plants treated with 5 ppm 2,4-D produced more loose heads than the controls. When the concentration was increased to 10 ppm the number of plants producing firm heads was almost the same as in the control. Increasing 2,4-D concentrations to 15 and 20 ppm resulted in still greater increases in the numbers of firm heads produced and a corresponding decrease in the firmness score. Although more firm heads were produced by plants treated with 15 and 20 ppm of 2,4-D, these heads were only one-half as large as those produced by the control plants. This response of Round Dutch to 2,4-D appears to be opposite to that obtained with Golden Acre.

An increase in the firmness score was associated with an increase in concentration of ClPP, but no consistent relationship between the number of probable seeders and the concentration of ClPP was found. As the concentration of TlBA was increased, an increase in the number of firm heads and consequently a decrease in the firmness score was noted. A decrease in number of firm heads was associated with an increase in concentration of NA in concentrations up to 500 ppm. However, as the concentration of NA was increased to 1000 ppm there was an increase in number of firm heads produced.

Table 6. Head Characteristics and Number of Probable Seeders in Cabbage Plants as Influenced by Growth-Regulating Substances (Variety Round Dutch, Cold-Induced).

Growth Substances		Number Heads			Firmness	Probable
Chemical					Score ²	Seeders
Symbol	PPM	Firm	Loose	Open ¹		
Control		10	5	0	1.30	2
2,4-D	5	6	9	0	1.86	1
	10	9	4	2	1.53	0
	15	12	3	0	1.20	0
	20	14	1	0	1.07	0
ClPP	50	9	4	1	1.46	1
	100	7	8	0	1.53	3
	250	3	12	0	1.80	0
	500	2	13	0	1.86	2
TlBA	50	4	11	0	1.73	6
	100	5	10	0	1.70	0
	250	11	4	0	1.26	3
	500	13	2	0	1.13	2
NA	100	14	1	0	1.00	0
	250	10	5	0	1.33	1
	500	5	10	0	1.70	2
	1000	12	3	0	1.20	0

¹ Plants forming no true heads were referred to as "open heads".

² A score of 1 was assigned to firm, 2 to loose and 3 to open heads.

EXPERIMENT 2 - 1950

Information obtained from experiment 1 indicated that growth substances affected the character of growth of cabbage grown in the greenhouse. Experiment 2 was designed to obtain information on the effect growth substances might have upon the character of growth of cabbage grown in the field. Information was desired as to whether or not certain growth substances would induce or inhibit bolting and the relative tolerance of cabbage to various concentrations of these substances under field conditions.

MATERIALS AND METHODS

Seeds of the Golden Acre and Round Dutch varieties were planted October 10, 1949 in flats in the horticultural greenhouse at Mississippi State College. The seedlings were transplanted to cold-frames November 1 in treatment groups separated by eighteen-inch alleys. The purposes of the alleys were to facilitate the application of the growth substances and to allow space for placing water-repellant canvas shields to eliminate drift of spray from one plot to another.

Plants at the time of treatment had four and five well developed leaves and stem diameters which averaged about six millimeters. The growth substances and concentrations were as described in experiment 1. Application was made January 12, 1950 with a "Sure Shot" compressed air sprayer at 75 to 100 pounds pressure. Individual sprayers were used for each growth substance and the lower concentrations applied first. Immediately after use the sprayers were

washed by allowing tap water to run through them for at least two hours. The spray was applied to the entire plant with special emphasis placed on getting good coverage of the growing point. The spray was applied to the run-off.

Forty plants of each treatment were transplanted to the field February 20, ten in each of four randomized complete blocks. Plants were spaced fifteen inches apart in rows forty inches wide in plots located on soil classified as Kaufman clay loam. The soil was supplied with 1000 pounds per acre of 6-8-4 fertilizer applied in the drill before transplanting. An additional 200 pounds of nitrate of soda to the acre was applied as a side-dressing after the danger of cold weather had past.

Temperatures were ascertained by recording thermographs from the date of seeding until the completion of the experiment. Cultural practices were kept uniform for each treatment. Water for irrigation was applied as needed with a Perf-O-Rain sprinkler system attached to a domestic water line. Weeds were controlled with tractor drawn cultivators and by hand hoeing. Insects were controlled by dusting with D.D.T. and spraying with nicotine sulfate.

Plant heights were recorded semi-monthly in centimeters beginning March 9 and ending May 11, but only the bimonthly measurements are presented. The plants were harvested June 2 and June 6 and dissected for study with respect to their degree of development. The length of the central core and the total length of

the head was measured in all of the plants from each treatment. The point on the stem where the lower wrapper leaf was attached was used as a basal point for these measurements. From this basal point to the apex of the terminal bud constituted the central core. The distance from this same point to the uppermost point of the folded leaves which form the head constituted the total length of the head. The measurement for the total length of each head was then divided by its corresponding central core length. The resulting quotient is hereafter referred to in the thesis as the head-core ratio. The head-core ratio of each plant in a treatment was summed and the average determined. Ratio values ranged from one for reproductive to approximately two for vegetative plants with very firm heads. The head-core ratio was found to be a very effective method for scoring the plants with reference to the degree of reproductive and/or vegetative development except in plants that had progressed to more advanced degrees of reproductiveness.

There are several degrees of reproductiveness in cabbage. Plants produce firm, loose or no true heads. They may produce a poorly developed seed stalk with no flowers or well developed seed stalks with many flowers and fruits. For this reason it was found early in these studies that the head-core ratio did not present the entire picture. For instance, certain plants that had a head-core ratio of one produced a seed stalk and no flowers or fruits. Whereas others with a ratio of one produced several seed stalks and many

flowers and fruits. Therefore, a method was developed in which the varied degrees of vegetativeness and reproductiveness were placed on a numerical basis. The numerical values ranged from zero to eight as follows:

- 0-Vegetative plants producing very firm heads.
- 1-Vegetative plants producing firm heads.
- 2-Vegetative plants producing slightly loose heads.
- 3-Vegetative plants producing loose heads.
- 4-Vegetative-Reproductive plants producing very loose heads, and lateral buds that were slightly enlarged.
- 5-Reproductive plants with only a partial head, seed stalk emerged but poorly developed and producing no flowers.
- 6-Reproductive plants with no developed head, seed stalk present and no flowers or fruit present.
- 7-Reproductive plants with a well developed seed stalk and few to several flowers and fruit present.
- 8-Reproductive plants with several well developed seed stalks and many flowers and fruit present.

The above outlined numerical description was used in this and subsequent experiments reported in this paper. Such a method of evaluation is hereafter referred to as the "growth phase index".

RESULTS

The data on the effect of varying the concentration of the four growth-regulating substances upon the average heights of wintered-over Golden Acre and Round Dutch plants are shown in Tables 7 and 8, respectively.

Response of the Golden Acre Variety

The average heights of 2,4-D treated Golden Acre plants were not statistically different from the controls on March 9. Plants sprayed with 100 and 500 ppm ClPP, 50 and 250 ppm of TlBA, and 500 and 1000 ppm of NA were shorter than the controls. On April 13, plants sprayed with 15 ppm of 2,4-D were higher, and those sprayed with 50 ppm of TlBA were shorter than the plants of the control. The average height of the plants in the other treatments did not vary from the control. There were no significant differences on May 11 in the average heights of the plants among the various treatments.

Response of the Round Dutch Variety

The data with respect to Round Dutch (Table 8) were somewhat similar to that of Golden Acre. There were differences in heights among certain treatments March 9. Plants sprayed with 10 ppm of 2,4-D and 100 ppm of NA were higher than the controls. The effects of growth rate resulting from these growth-regulating substances occurred early in the season. This indicates that any increase or decrease in growth due to these substances occurs soon after treatment

Table 7. The Effect of Growth-Regulating Substances on the Height of Wintered-Over Golden Acre Cabbage.

Growth Substances		Dates of Measurement		
Chemical Symbol	PPM	March 9	April 13	May 11
(Centimeters)				
Control	-	4.5	7.1	16.2
2,4-D	5	5.4	8.2	15.2
	10	4.0	7.9	16.6
	15	5.4	8.8	14.8
	20	5.0	8.0	13.6
CIPP	50	3.6	6.4	15.0
	100	3.0	5.7	14.0
	250	3.6	5.8	13.0
	500	3.3	5.8	14.2
TIBA	50	2.8	5.4	12.6
	100	3.7	6.5	13.8
	250	2.6	5.7	14.4
	500	-	-	-
NA	100	3.8	6.4	15.7
	250	3.4	6.6	15.0
	500	3.0	7.4	16.2
	1000	3.3	6.2	15.9
L.S.D.	@ .05	1.2	1.7	N.S.
	@ .01	1.8	2.3	N.S.

Table 8. The Effect of Growth-Regulating Substances on the
Height of Wintered-Over Round Dutch Cabbage.

Growth Substances		Dates of Measurement		
Chemical Symbol	PPM	March 9	April 13	May 11
(Centimeters)				
Control	-	2.7	4.4	12.7
2,4-D	5	4.0	7.0	13.8
	10	4.8	7.2	13.7
	15	3.8	6.0	13.0
	20	4.4	8.4	14.8
ClPP	50	3.8	6.6	13.0
	100	3.6	5.8	13.0
	250	3.3	6.6	14.4
	500	3.2	5.1	11.7
TlBA	50	3.3	5.4	13.6
	100	3.1	5.4	13.8
	250	3.0	4.5	13.8
	500	3.8	6.6	14.2
NA	100	4.8	6.8	13.7
	250	3.2	5.2	13.6
	500	3.4	6.2	13.3
	1000	3.3	6.0	13.1
L.S.D.	@.05	2.0	N.S.	N.S.
	@.01	2.7		

if other environmental factors are favorable for growth. Later in the season these substances likely had been utilized or transformed into inactive materials.

Head-Core Ratio and Growth Phase Index

Application of 2,4-D, ClPP or TlBA had no effect on the head-core ratios of either variety, Table 9. However, application of NA at a concentration of 100 ppm to Golden Acre increased this ratio. The growth phase index was reduced in Golden Acre by 5 ppm of 2,4-D, 100 ppm of NA, and 50 and 500 ppm of ClPP. The differences in the indices of the control plants and those sprayed with 500 ppm of ClPP and 100 ppm NA were highly significant.

The indices for the Round Dutch variety resulting from the various treatments were not statistically different. Due to the lack of sufficiently cool or cold temperatures under the prevailing field conditions none of the plants produced seed stalks. The head-core ratio and the growth phase index were, under these conditions, not greatly changed by the growth-regulating substances.

Table 9. Head-Core Ratio and Growth Phase Index of Wintered-Over Cabbage as Influenced by 2,4-D, ClPP, TlBA, and NA Applied Before Cool Weather.

Growth Substances Chemical		Head-Core Ratio		Growth Phase Index	
Symbol	PPM	G.A.*	R.D.*	G.A.*	R.D.*
Control		1.40	1.41	2.85	2.38
2,4-D	5	1.46	1.38	2.38	2.80
	10	1.45	1.43	2.68	2.49
	15	1.45	1.41	2.76	2.32
	20	1.45	1.49	2.82	2.34
ClPP	50	1.46	1.52	2.41	2.02
	100	1.49	1.48	2.68	2.28
	250	1.52	1.51	2.76	1.88
	500	1.52	1.42	2.31	2.41
TlBA	50	1.51	1.42	2.53	2.40
	100	1.53	1.45	2.56	2.33
	250	1.45	1.40	2.67	2.60
	500	-	1.46	-	2.27
NA	100	1.68	1.43	2.31	2.22
	250	1.40	1.41	3.04	2.31
	500	1.51	1.43	2.64	2.31
	1000	1.33	1.47	2.76	2.30
L.S.D.	@ .05	0.14	N.S.	0.40	N.S.
	@ .01	0.19		0.53	
General Variety Means		1.48	1.44	2.57	2.33

* G.A. - Golden Acre variety; R.D. - Round Dutch variety.

EXPERIMENT 3, 1950

Plant size when cold temperatures occur is known to be a factor which determines the extent of bolting in cabbage. Large plants bolt more readily than small plants. The purpose of experiment 3 was to determine the effects of growth substances on seed stalk development when applied to "large", "medium", and "small" plants at different times during a period of cool weather.

MATERIALS AND METHODS

To obtain "large", "medium", and "small" plants, seeds of Golden Acre were planted in the greenhouse September 17, October 10 and November 2, 1949. These seedlings were transplanted to cold-frames October 2, November 2 and November 23 for the first, second, and third seeding dates, respectively.

The plants of each size (large, medium and small) received one of the following treatments:

Treatment Number	Chemical	Concentration (ppm)	Time of Application
1	Control	-	-
2	C1PP	250	Dec.20, 1949
3	C1PP	250	Jan.23, 1950
4	C1PP	250	Feb.16, 1950
5	2,4-D	15	Dec.20, 1949
6	2,4-D	15	Jan.23, 1950
7	2,4-D	15	Feb.16, 1950

This made a total of twenty-one treatments. The diameters of the plant stems just below the first true leaf on December 20, 1949 averaged 9 mm. for the large, 6 mm. for the medium and 4 mm. for the small plants. The dates for time of application of the growth substances were selected because they were expected to more nearly cover the period of anticipated cool weather than any other two month period during the year. It was desired that the first spray date be before or at the beginning of cool weather; the second date during cool weather; and the third, after or near the end of cool weather. Temperatures in the coldframe were maintained above 50° F. until December 24 by means of a thermostatically controlled soil heating cable and by covering the coldframes with glass sash when temperatures lower than 50° F. were predicted. On December 24, the cables were disconnected and the sash removed from the coldframe. Unfortunately the winter of 1949-50 was mild. Low temperatures for periods of time sufficiently long to induce the reproductive phase did not prevail at Mississippi State College. The prevailing temperatures will be discussed in the section on results.

Large plants made rapid growth and became so crowded in the coldframe that they were transplanted to the field December 7, 1949. Therefore, the large plants were sprayed after they were transplanted to the field. Medium and small size plants were sprayed while in the coldframe and transplanted to the field February 17, 1950. In all instances precautionary measures to guard against contaminating

adjacent plots were employed as described in experiment 2.

The twenty-one treatments consisting of three plant sizes and seven chemical sprays were arranged in five randomized blocks in the field. Each of the first four blocks consisted of ten plants of each treatment from which data concerning growth and development were collected. The fifth block consisted of 50 plants reserved for making morphological studies of the terminal shoot.

This experiment was located adjacent to and received the same cultural treatment as described in experiment 2. Data were collected as described in experiment 2.

Heights of the plants were measured at approximately 2 week intervals from February 27 to May 11 inclusively, but only bimonthly measurements are presented. Large plants reach maturity and were harvested April 20. Therefore, they were not included at the later measuring dates (Tables 11 and 12). Medium and small plants were harvested May 12 and June 6, respectively. Consequently, the medium and small plants were measured twice after the large plants were harvested.

RESULTS

Temperature During Growing Season

Weekly average maximum and average minimum temperatures and weekly means during the period December 24, 1949 to June 30, 1950 are presented in Table 10. Average maximum temperatures for

Table 10. Average Weekly Maximum, Minimum and Mean Temperatures
from October 1, 1949, through June 30, 1950, State College,
Mississippi.

Date	Weekly Average Temperature*		
	Maximum	Minimum	Mean
Dec. 24 - Dec. 30	60.2	35.6	57.5
Dec. 31 - Jan. 6	67.1	49.0	58.0
Jan. 7 - Jan. 13	62.9	45.1	54.0
Jan. 14 - Jan. 20	68.4	44.6	56.5
Jan. 21 - Jan. 27	71.9	52.6	62.2
Jan. 28 - Feb. 3	65.3	47.3	56.3
Feb. 4 - Feb. 10	69.7	49.6	59.6
Feb. 11 - Feb. 17	63.0	40.4	51.7
Feb. 18 - Feb. 24	64.0	35.1	49.6
Feb. 25 - Mar. 3	61.9	36.6	49.2
Mar. 4 - Mar. 10	60.0	36.6	48.3
Mar. 11 - Mar. 17	65.4	40.7	53.0
Mar. 18 - Mar. 24	68.9	42.6	55.8
Mar. 25 - Mar. 31	71.7	46.7	59.2
Apr. 1 - Apr. 7	67.6	44.1	55.8
Apr. 8 - Apr. 14	71.4	43.5	57.4
Apr. 15 - Apr. 21	67.8	42.8	55.3
Apr. 22 - Apr. 28	81.0	56.0	68.5
Apr. 29 - May 5	78.1	61.6	69.8
May 6 - May 12	85.4	67.1	76.2
May 13 - May 19	82.9	60.0	71.4
May 20 - May 26	85.6	65.7	75.6
May 27 - June 2	86.4	79.0	82.7
June 3 - June 9	81.0	65.4	73.2
June 10 - June 16	89.6	66.7	78.2
June 17 - June 23	90.0	71.4	80.7
June 24 - June 30	90.7	67.6	79.2

* Seven daily temperature values included in each average.

each week were never below 60° F., and were well above 60° most of the period. Average minimum temperatures were 45° F. and below for only 12 weeks. Weekly mean temperatures were not as low as 45° F. for a single week during the period. The lowest weekly mean temperature reached was 48.3° F. and occurred during the seven day period March 4 - March 10, 1950. Temperatures were not low enough for sufficient time to induce reproductive development, however, they were sufficient to influence the character of head development in the large plants. These influences will be discussed later.

Data on seasonal growth in height of large, medium and small sizes of plants sprayed with ClPP and 2,4-D are presented to Tables 11 and 12, respectively. Large plants were much higher April 10, the final measurement date for the large plants, than the medium or small plants on each date of measurement. The final height reached by the medium size group was about the same as the large group, however.

ClPP Treatments

The effect of the time of applying ClPP on the rate of growth or ultimate height of large plants was not statistically significant. However, plants sprayed during cool weather were the highest of the group and those sprayed after cool weather were the lowest. There were significant differences in the rate of growth due to the time of applying ClPP in the plants of the medium group. Plants sprayed

Table 11. The Effect of Time of Application of 250 PPM ClPP On
the Average Height of Large, Medium and Small Wintered-
Over Cabbage (Variety Golden Acre).

Size of Plants	Time of Application*	Dates of Measurements				
		Feb. 27	Mar. 20	Apr. 10 (Centimeters)	Apr. 27	May 11
Large	Control	10.8	12.4	15.0	--	--
	Before	10.3	12.6	16.0	--	--
	During	11.2	13.3	16.9	--	--
	After	9.9	11.4	14.0	--	--
General Size Means		10.6	12.4	15.5		
Medium	Control	3.9	4.9	7.0	9.0	13.0
	Before	6.2	7.0	8.9	11.0	14.7
	During	7.0	8.8	10.9	12.8	16.2
	After	5.8	6.9	8.8	10.6	14.3
General Size Means		5.7	6.9	8.9	10.8	14.6
Small	Control	3.7	4.2	5.8	8.2	12.4
	Before	2.8	3.0	4.6	6.7	10.5
	During	3.8	4.0	6.1	7.8	12.1
	After	3.2	3.5	5.0	6.8	10.2
General Size Means		3.4	3.7	5.4	7.4	11.3
L.S.D.**	@ .05	2.9	3.7	3.2	--	--
	@ .01	4.0	4.9	4.3		

* Time of application in respect to cool weather.

** L.S.D. values apply to any time of application means within size groups, but not to general size means.

Table 12. The Effect of Time of Application of 15 PPM 2,4-D On
the Average Height of Large, Medium and Small Wintered-
Over Cabbage (Variety Golden Acre).

Size of Plants	Time of Application*	Dates of Measurements				
		Feb. 27	Mar. 20	Apr. 10	Apr. 27	May 11
		(Centimeters)				
Large	Control	10.8	12.4	15.0	--	--
	Before	11.6	13.2	16.1	--	--
	During	11.6	13.5	16.7	--	--
	After	9.7	12.5	15.0	--	--
General Size Means		10.9	12.9	15.7		
Medium	Control	3.9	4.9	7.0	9.0	13.0
	Before	7.6	9.0	11.0	12.8	16.8
	During	7.2	8.0	10.9	12.8	18.4
	After	7.3	9.4	11.8	13.9	17.8
General Size Means		6.5	7.2	10.2	12.1	16.5
Small	Control	3.7	4.2	5.8	8.2	12.4
	Before	3.6	4.1	6.2	7.8	11.6
	During	3.9	4.6	6.9	8.9	12.7
	After	3.4	4.2	6.7	9.2	12.8
General Size Means		3.6	4.3	6.4	8.5	12.4
L.S.D.**	@ .05	2.9	3.7	3.2	--	--
	@ .01	4.0	4.9	4.3	--	--

* Time of application in respect to cool weather.

** L.S.D. values apply to any time of application means within size groups, but not to general size means.

during cool weather were higher than the control plants. The rates of growth or the ultimate heights of the small plants were not materially altered by the treatments employed. It is of interest to note that plants sprayed with ClPP during cool weather were the highest in each size group.

2,4-D Treatments

The growth rates of large plants sprayed with 2,4-D at different times were statistically alike (Table 12). Medium size plants sprayed before, during, or after cool weather were higher than the controls on each measurement date. On April 10, plants sprayed after cool weather and plants in the control differed greatly in height. At no time during the growing season were the heights of the small treated plants different from the control plants. With 2,4-D, as with ClPP, the plants sprayed during cool weather were as high or higher than the plants among the other treatments.

Head-Core Ratio

An analysis of the head-core ratios of large, medium and small treated plants show no important differences resulting from the substances employed or the times of application. These data are presented in Table 13. There was a trend, however, for the average ratios of the small plants to be larger than those of the medium or large plants. Large plants were expected to have small ratios as these plants were sufficiently large at the beginning of cool weather

Table 13. The Influence of Time of Application of 250 PPM ClPP and 15 PPM 2,4-D On the Head-Core Ratio and the Growth Phase Index in Large, Medium and Small Wintered-Over Cabbage (Variety Golden Acre).

Growth Substances Chemical Symbol	Time of Application*	Head - Core Ratio Size of Plants			Growth Phase Index Size of Plants		
		Large	Medium	Small	Large	Medium	Small
Control		1.26	1.38	1.40	3.02	2.35	2.25
ClPP	Before	1.28	1.39	1.41	2.98	2.35	2.45
	During	1.20	1.34	1.32	2.98	2.60	2.65
	After	1.26	1.32	1.39	2.95	2.38	2.25
2,4-D	Before	1.28	1.36	1.42	2.52	2.15	2.38
	During	1.35	1.33	1.43	2.58	2.05	2.10
	After	1.28	1.29	1.33	3.42	3.00	2.70
L.S.D.	@ .05	N.S.	N.S.	N.S.	0.73	0.73	0.73
	@ .01				0.98	0.98	0.98
Size of Plant Means		1.27	1.34	1.39	2.92	2.41	2.40

* In respect to cool weather.

to produce seed stalks.

Growth Phase Index

As might be expected, the large plants had high growth phase indices since they were the plants most likely to bolt. The average growth phase index of no treatment in any size group differed statistically from corresponding controls. However, the average index for the large and medium size plants sprayed with 2,4-D after cool weather was considerably greater than the indices for the plants sprayed with 2,4-D before or during cool weather. If the data from each size group are considered together they suggest that the time of application of 2,4-D had an effect upon the phase of growth. Apparently 2,4-D applied after sufficient cold for partial induction tended to stimulate the reproductive phase.

EXPERIMENT 4, 1950

The ultimate objectives of experiment 4 were identical with those of experiment 3. The cold treatment was different than that employed in experiment 3.

MATERIALS AND METHODS

Variety, seeding dates, size of plants at the beginning of the cold treatment, and the growth substances for this experiment were the same as described in experiment 3. One essential difference however was that the plants were subjected to a cold storage treatment, while in the preceding experiment they were exposed only to the cool weather which prevailed under natural field conditions.

Large, medium and small plants shown in Figure 3 were transplanted from the seedling flats to 4-inch clay pots October 3, 1949, November 2, 1949 and November 23, 1949, respectively. Seventy plants were potted for each of the twenty-one treatments. All plants were placed in a cold storage room on January 4, where the temperature was maintained at $38^{\circ} \pm 2^{\circ}$ F., and held for forty-two days.

The cold storage room measured 12 x 16 feet and was equipped with a 24-inch rotating fan which ran continuously giving a uniform temperature throughout the room. In order to supply adequate light for the plants, 40-watt Mazda bulbs wired in series were placed three feet apart and two feet above the plants. This lighting gave 25 to 30 foot-candles of light. Lights were turned on at seven o'clock each



Figure 3. Comparable sizes of cabbage plants at the beginning of cold-induction. 1. Large plants. 2. Medium plants. 3. Small plants.

morning and off at five o'clock each evening by means of an automatic timer. The above outlined cold storage treatment is hereafter referred to as the cold-induction treatment.

Plants receiving the growth substances before cold-induction treatment were sprayed December 20, 1949. Plants receiving the growth substances during cold-induction were sprayed January 23, 1950. The plants receiving the growth substances after the cold-induction treatment were sprayed February 15. Plants which received the application of growth substances during induction were moved to another room, sprayed, allowed to dry for two hours, and then returned to the cold storage room.

All plants were moved from the cold storage room February 14, and transplanted to the field February 21. Treatments were arranged in random order in each of five blocks. Each treatment in the first four blocks contained five plants which were used for the purpose of collecting data on plant growth and development. The fifth block contained fifty plants of each treatment and was reserved for morphological studies.

Cultural practices employed in this experiment were identical with experiments 2 and 3. In addition to collecting the data described for the preceding experiments, dates of seed stalk emergence, flowering, and pod maturity were recorded for each treatment. There was no need for a statistical evaluation of these data since plants in certain treatments produced seed stalks while others did not.

RESULTS

ClPP Treatments

Data with respect to the effect of the time of applying ClPP on the growth in height of the three sizes of plants are presented in Table 14. To show the extreme differences obtained among the treatments in this experiment, these data are also shown graphically in Figure 4. The points on the bar graph indicate the average height of the plants for each treatment on the dates specified in the legend. The vertical distance between the points indicate the increments in plant height between measuring dates. Large plants sprayed before cold-induction grew at essentially the same rate as those in the control throughout the experiment. The large plants which were sprayed during cold-induction grew at a slower rate than the control. The difference between their average heights on February 27 was significant. They were not significantly different on March 20 but were on April 10 and April 20. By April 27 the differences in the average heights of these two treatments were very apparent. The large plants in the control and those sprayed before and after cold induction were not measured after April 27. These plants, all possessing flowers and seed pods, had ceased to grow. Large plants sprayed during cold-induction were measured twice more, on May 4 and May 11. These plants produced flowers and seed pods much later than the plants in the control plot as will be discussed later.

Large plants sprayed with ClPP after cold-induction grew at

Table 14. The Influence of Time of Application of 250 PPM ClPP On
the Accumulative Average Height of Large, Medium and
Small Cabbage at Different Times During the Growing Season
(Variety Golden Acre, Cold-Induced).

Size of Plants	Time of Application*	Dates of Measurements					
		Feb.	Mar.	Apr.	Apr.	Apr.	May
		27	20	10	20	27	11
(Centimeters)							
Large	Control	11.0	12.7	16.8	23.2	37.0	-
	Before	11.3	13.1	17.7	24.4	36.9	-
	During	9.3	10.7	13.1	15.8	19.4	40.0
	After	10.0	10.5	14.6	19.5	26.6	-
General Size Means		10.3	11.8	15.6	20.7	30.0	
Medium	Control	3.9	4.8	10.7	13.5	17.4	46.9
	Before	3.9	4.9	11.8	19.6	35.0	50.0
	During	4.0	4.9	7.6	10.0	10.8	19.0
	After	3.8	4.4	9.3	13.5	20.7	42.6
General Size Means		3.9	4.8	9.8	14.2	21.0	39.6
Small	Control	2.9	3.4	7.7	9.4	11.2	18.2
	Before	2.8	3.4	7.4	9.5	11.9	18.0
	During	2.8	3.6	6.6	9.0	9.9	16.2
	After	2.6	3.5	7.4	9.1	10.6	18.9
General Size Means		2.8	3.5	7.5	9.2	10.9	17.8
L.S.D.** @ .05		1.4	2.3	3.1	5.6	8.0	-
@ .01		1.9	3.0	4.2	7.8	10.7	-

* Time of application in respect to cold-induction.

** L.S.D. values apply to any time of application means within size
groups, but not to general size means.

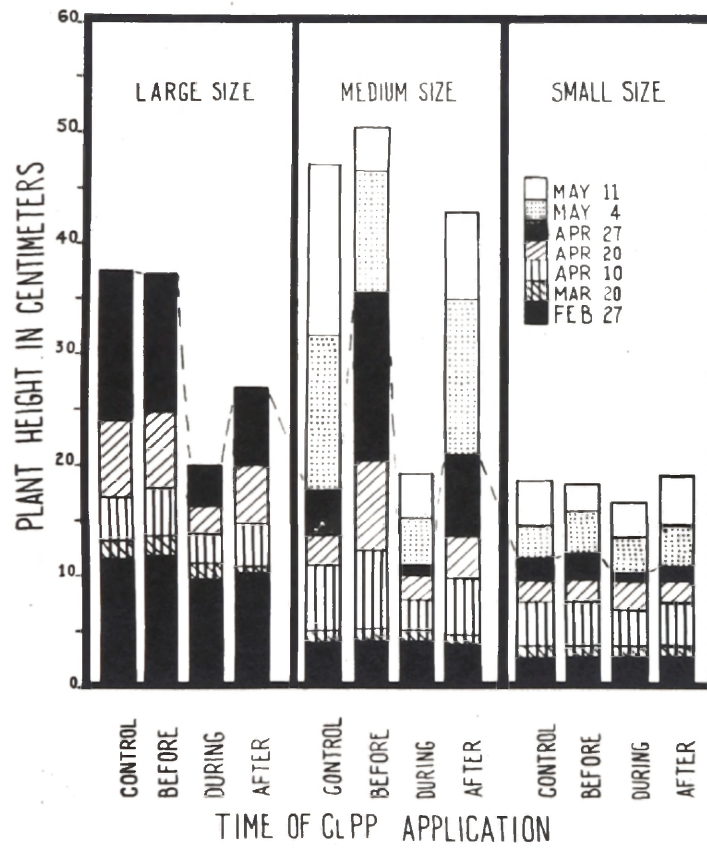


Figure 4. Comparative seasonal growth in height of large, medium and small Golden Acre cabbage plants sprayed with 250 ppm ClPP before, during and after cold induction.

a slower rate than the control plants. The difference in the average heights of the plants in these two treatments was noticable until April 27, the last date of measurement.

There were spectacular differences in the rate of growth of the plants in the medium size group as a result of the time of applying ClPP. Such differences did not occur however until late in the season. Treated plants did not differ in height from the controls until April 10. Plants sprayed before cold-induction were, on April 20, much higher than the plants in the control. Between April 20 and April 27, plants sprayed with ClPP before cold-induction made more rapid growth in height than any of the other plants in the medium size group. Plants sprayed during cold-induction made less rapid growth in height than the control plants. They were substantially lower in height on April 10 than the controls. The difference in average heights between this treatment and the control was not great enough for statistical significance on April 27. Although statistical analysis was not applied to the data for the two last dates of measurement because the plants in certain treatments had ceased to grow, the difference in average heights of the plants in the control and those sprayed during cold-induction was very apparent.

Plants in the same size group sprayed after the thermo-induction treatment made growth in height similar to the controls.

There were not outstanding differences in response to the time of applying ClPP exhibited by the plants in the small size group. Their

average heights showed no differences arising from treatment.

2,4-D Treatments

The data in Table 15 regarding the effect of time of applying 2,4-D on growth in height are presented in bar graph form in Figure 5. It can be seen at a glance that 2,4-D inhibited growth of cold-induced plants irrespective of the time of application and plant size.

The average height of large plants sprayed before cold-induction was not significantly less than that of the control plants until April 27. Plants in the large size group sprayed during or after cold-induction were not significantly different in height from those of the control at any time during the growing season.

Plants of medium size sprayed either before, during or after cold-induction were practically the same height as the controls up to April 27. As mentioned earlier, the plants in a few of the treatments in this experiment had reached their ultimate height by April 27. Therefore, the L.S.D. values were not calculated for the last date of measurement. It is apparent in Figure 5 that the plants which were sprayed with 2,4-D in general did not grow as rapidly or reach an ultimate height comparable to the controls. This is especially true with plants sprayed before or during cold-induction. Medium sized plants sprayed after cold-induction made the most rapid growth in height between April 27 and May 11 of any of the 2,4-D treatments.

The subsequent growth in height of the small plants was not altered by applying 2,4-D either before, during or after cold-induction.

Table 15. The Influence of Time of Application of 15 PPM 2,4-D On the Accumulative Average Height of Large, Medium and Small Cabbage at Different Times During the Growing Season (Variety Golden Acre, Cold-Induced).

Size of Plants	Time of Application*	Dates of Measurements					
		Feb. 27	Mar. 20	Apr. 10	Apr. 20	Apr. 27	May 11
		(Centimeters)					
Large	Control	11.0	12.7	16.8	23.2	37.0	-
	Before	10.2	12.0	14.4	18.5	26.2	48.1
	During	12.2	12.7	18.0	24.0	32.4	-
	After	9.4	10.8	15.4	21.5	32.4	-
General Size Means		10.7	12.0	16.2	21.8	32.0	-
Medium	Control	3.9	4.8	10.7	13.5	17.4	46.9
	Before	3.8	5.0	9.9	12.4	15.6	26.3
	During	4.6	4.5	9.4	11.8	13.6	24.7
	After	3.4	4.6	9.2	11.3	14.5	33.6
General Size Means		3.9	4.7	9.8	12.2	15.3	32.9
Small	Control	2.9	3.4	7.7	9.4	11.2	18.2
	Before	2.6	3.2	6.4	8.3	9.3	14.2
	During	2.8	3.8	6.3	9.2	9.5	15.3
	After	2.8	3.0	6.9	9.2	9.9	17.0
General Size Means		2.8	3.4	6.8	9.0	10.0	16.2
L.S.D.	@ .05	1.4	2.3	3.1	5.6	8.0	
	@ .01	1.9	3.0	4.2	7.8	10.7	

* Time of application in respect to cold-induction.

** L.S.D. values apply to any time of application means within size groups, but not to general size means.

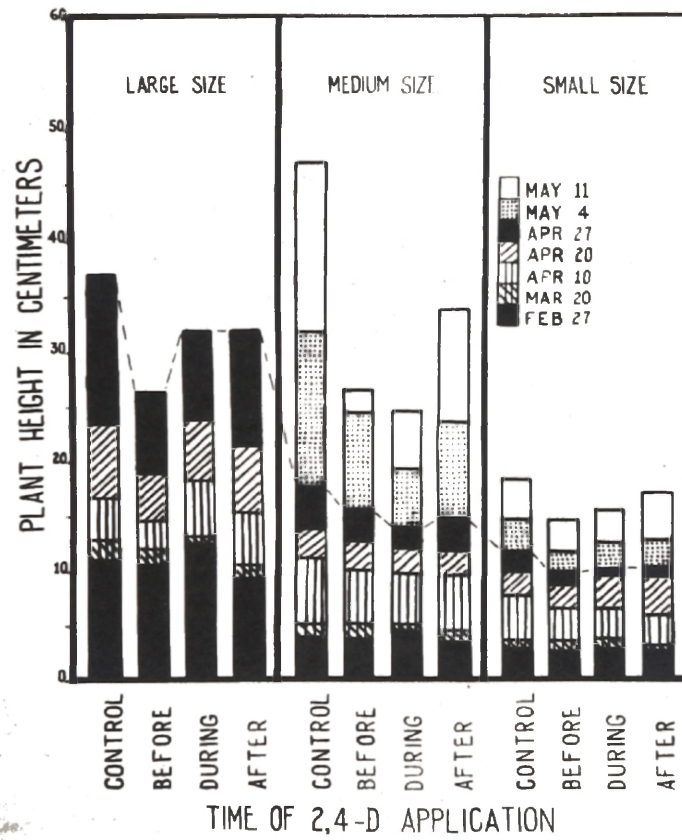


Figure 5. Comparative seasonal growth in height of large, medium and small Golden Acre cabbage plants sprayed with 15 ppm of 2,4-D before, during and after cold induction.

As shown in Figure 5, the controls were slightly higher on each date of measurement than plants in either of the other treatments, although these differences were not at any time significant.

Head-Core Ratio

It is of interest to compare the general size mean head-core ratios for large, medium and small plants, Table 16. This mean approached unity in large plants, was 1.16 for medium, and 1.46 for small plants. The time of application of ClPP and 2,4-D had no effect upon the head-core ratios within the group of large plants. All these plants became reproductive, produced seed stalks, flowers, and seed. Therefore, the average head-core ratio of each treatment approached unity.

Outstanding differences occurred in the head-core ratios among the various treatments in the medium size plants. A significantly larger head-core ratio resulted when plants were sprayed with ClPP during induction. Spraying before or after cold-induction resulted in head-core ratios comparable to the control. Plants receiving ClPP during induction had greater head-core ratios than those receiving 2,4-D during or after induction. Most plants sprayed during cold-induction with ClPP produced rather firm heads. In fact, all medium size plants were reproductive except those sprayed during induction with ClPP. Central cores in firm heads were shorter than in loose heads or in plants forming no true head. Consequently, plants sprayed with ClPP during cold-induction had larger ratios than the control.

Table 16. Head-Core Ratio of Growth Phase Index in Large, Medium and Small Cabbage Plants as Affected by Time of Application of 250 PPM ClPP and 15 PPM 2,4-D (Variety Golden Acre, Cold-Induced).

Growth Substances		Head - Core Ratio			Growth Phase Index		
Chemical Symbol	Time of Application*	Size of Plants			Size of Plants		
		Large	Medium	Small	Large	Medium	Small
Control		1.01	1.09	1.49	7.65	6.70	2.25
ClPP	Before	1.02	1.13	1.45	7.60	6.48	2.35
	During	1.06	1.32	1.46	6.70	3.42	1.48
	After	1.00	1.09	1.48	7.55	6.25	2.45
2,4-D	Before	1.02	1.20	1.49	7.35	4.80	1.55
	During	1.02	1.16	1.50	7.45	5.08	1.58
	After	1.01	1.14	1.36	7.55	5.20	1.98
L.S.D.	@ .05	0.12	0.12	0.12	1.16	1.16	1.16
	@ .01	0.16	0.16	0.16	1.55	1.55	1.55
General Size Means		1.02	1.16	1.46	7.41	5.42	1.95

* In respect to cold-induction.

Medium size plants sprayed with 2,4-D had rather large head-core ratios as compared to the control. Head-core ratios of plants sprayed before induction with 2,4-D were large but not large enough to be statistically different from the control.

The head-core ratios for the various treatments in the group of small plants were essentially the same except the small value for those sprayed with 2,4-D after cold-induction. This was, however, of no practical significance since essentially all of the small plants produced firm heads. Head-core ratios among the several treatments within the group of small plants were, in most instances, larger than the ratios of the medium size plants sprayed during cold-induction with ClPP. As will be shown later the heads of the plants receiving the latter treatments were less vegetative than those in the group of small plants.

Growth Phase Indices

The growth phase indices varied with the size of plants. The general size mean was high with large (7.41) and medium plants (5.42), but low with small plants (1.95). It is of interest also that the lowest growth phase index for each size group resulted when plants were sprayed with ClPP during cold-induction.

The indices among the treatments within large plants and among those within the group of small plants were not significantly different from their respective controls. As previously stated, all the large

plants were reproductive and most of all the small plants were vegetative. As a result, the response to the varied treatments within these two size groups was similar.

The growth phase indices of the medium plants varied appreciably with the treatments (Table 16). Plants sprayed with ClPP before induction scored almost the same index as the control. The index for plants sprayed during induction with ClPP was much smaller than for plants of any other treatment within the size grouping. Plants with an average index nearest these plants were those sprayed before induction with 2,4-D. These two indices were significantly less than the controls. The differences between the index of plants sprayed with ClPP during cold-induction and the indices among the remaining treatments were significant.

The only medium size plants to produce firm heads were those sprayed with ClPP during cold-induction. Some effects of time of application of ClPP upon phase of growth in medium size plants are shown in Figure 6. Plants on the left were sprayed before; those in the center, after; and those on the right, during cold-induction. The plants on the left produced flowers 11 days earlier than those in the center. Plants on the right were sprayed during induction and remained vegetative.

Plants sprayed before cold-induction with 2,4-D had the second smallest and those sprayed during induction had the third smallest growth phase index among the medium size plants. The index was



Figure 6. Some effects of the time of application of ClPP on the phase of growth in Golden Acre Cabbage. Left to right, spray applied before, after and during cold-induction. Photographed May 23, 1950.



Figure 7. Reproductive cabbage plants showing increased number of seed stalks resulting from ClPP treatment. No. 6. The control. No. 7. Sprayed before induction with 250 ppm of ClPP.

smaller for the plants sprayed after cold-induction than for the controls. Even though the indices are statistically smaller in 2,4-D treated than in control plants, the practical value with respect to inhibition of bolting in cabbage is questionable. All the medium size plants in each of the 2,4-D treatments were reproductive.

Seed Stalk Development

The effect of time of applying ClPP and 2,4-D on seed stalk development is shown in Table 17. The average number of days from the end of cold-induction to the appearance of seed stalks varied among treatments. Plants in certain treatments did not produce seed stalks. The absence of seed stalks was confined to the small plants.

ClPP Treatments

The time of application of ClPP affected the development of floral primordia in cabbage (Table 17). Applying this growth-regulating substance before induction to large plants had little effect upon the time the seed stalks emerged. When applied during induction seed stalk appearance was delayed 14 days in the large plants. Seed stalks appeared four days later on the large plants sprayed after induction than on the control plants.

Applying ClPP before induction hastened the appearance of seed stalks 17 days on medium size plants and 14 days on small plants. When applied during induction, this substance delayed and/or inhibited seed stalk and flower development in large, medium, and

Table 17. The Effect of Time of Application of 250 PPM of ClPP and 15 PPM of 2,4-D On the Average Number of Days from Completion of Cold-Induction to the Appearance of Seed Stalks and the Number of Plants Producing Flowers.

Growth Substances		Days to Seed Stalk Appearance			Number of Plants Producing Flowers		
Chemical Symbol	Time of Application*	Plant Size			Plant Size		
		Large	Medium	Small	Large	Medium	Small
Control		59	73	79	20	16	2
ClPP	Before	61	56	65	20	15	2
	During	73	82**	α	20	0**	0
	After	63	67	70	20	15	1
2,4-D	Before	67	70	α	20	10	0
	During	65	79	α	20	9	0
	After	59	76	α	20	12	0

* In respect to cold-induction treatment.

** Five plants produced seed stalks which barely burst through the outer leaves, but no flowers were produced by any of the plants in this treatment.

and small plants. Even though barely visible seed stalks were produced on five of the 20 medium size plants, they neither grew above the normal plant head nor produced flowers. The seed stalks that appeared were delayed as shown in Table 17. Seed stalks produced by medium and small plants sprayed after induction were visible in each size group six and nine days earlier, respectively, than in the corresponding controls.

Plants sprayed with ClPP before or after induction were more reproductive than the control. This increased reproductiveness was noted mainly in an increase in the number of seed stalk branches and seed pods. In Figure 7 are two representative plants. The plant sprayed before induction produced numerous seed stalk branches, whereas the control produced only five or six sparsely distributed branches.

The number of plants producing flowers in the medium and small sizes was the same for the control plants, those sprayed before and those sprayed after induction. None of the plants in these two size groups which were sprayed during induction produced flowers.

2,4-D Treatments

All large plants sprayed with 2,4-D bolted. Seed stalks appeared eight days later on those sprayed before and six days later on those sprayed during induction than on the controls. The number of days from the end of cold-induction to the appearance of seed stalks

on plants sprayed after induction with 2,4-D did not differ from the control.

Plants sprayed before induction were first to produce visible seed stalks in the medium size group. They were three days earlier than the controls. Plants sprayed during induction were six days later and those sprayed after induction were three days later than the control plants. A total of 16 out of 20 plants in the control produced flowers. Ten of the 20 plants sprayed before, nine sprayed during, and 12 plants sprayed after induction produced flowers.

Neither seed stalks nor flowers were produced on any of the small plants sprayed with 2,4-D. Based on these data it appears that 2,4-D had an inhibitory effect upon seed stalk development except with the treatments applied to large plants.

EXPERIMENT 5, 1951-52

It was desired to obtain additional information with respect to promoting the reproductive phase by the use of growth-regulating substances. In order to study this effect an attempt was made to partially induce the reproductive phase. Since Round Dutch is somewhat resistant to bolting it was employed in preference to the Golden Acre variety.

MATERIALS AND METHODS

Seeds of Round Dutch were planted August 22, 1951 in the greenhouse. The seedlings were transplanted to 4-inch clay pots October 1 and grown in the greenhouse until the stem diameters measured approximately 7 mm. These plants were then divided into eight groups of sixteen plants each in such a way that plants in one group were as nearly as possible the same size as plants in any other group. Each group was then divided into four replicates of four plants each. Each 16-plant group received one of the following treatments:

Treatment Number	Chemical	Concentration (ppm)	Time of Application
1	Control	-	-
2	M.H.	250	November 26, 1951
3	M.H.	250	December 20, 1951
4	M.H.	250	January 7, 1952
5	T1BA	250	December 20, 1951
6	T1BA	250	January 7, 1952

Treatment Number	Chemical	Concentration (ppm)	Time of Application
7	ClPP	250	December 20, 1951
8	ClPP	250	January 7, 1952

All plants were subjected to a cold-induction treatment of $36^{\circ} \pm 3^{\circ}$ F. for forty-one days from November 27, 1951 through January 7, 1952. Observe in the list of treatments above that growth substances were applied to certain treatments before cold-induction, to others during cold-induction and to still others after cold-induction. Lighting for the plants throughout the induction treatment was the same as described in experiment 4.

After the induction treatment, all plants were returned to the greenhouse and transplanted to one-gallon tin cans January 10. The medium in the cans consisted of equal parts of soil, well-rotted manure, and well-rotted sawdust. Treatments were randomized in four replicates throughout the experiment.

To insure adequate nutrients for the growing plants 200 ml. of a nutrient solution consisting of one ounce of 10-52-17 soluble fertilizer and two ounces of ammonium nitrate dissolved in three and one-half gallons of water was applied every two weeks to each can. Nicotine sulfate and DDT were used to control insects. Diseases were not a problem. Data on growth and development were collected as described in previous experiments.

RESULTS

The data regarding the effect of time of application of ClPP, TlBA and MH on plant height are presented in Table 18. Average heights were essentially the same January 17, 1952. The average heights for two treatments were on February 29, statistically different from the controls. Plants sprayed with MH after cold-induction were not as high and plants which were sprayed during induction with ClPP were higher than the controls. The difference in average height of the plants in the former treatment and that of the control was highly significant.

Plants in the control were about twice as tall April 17 as plants sprayed with MH after cold-induction. Spraying TlBA before induction and TlBA and ClPP during induction produced taller plants than the control.

The only plants with average heights significantly different from the control on June 11 were those sprayed with MH after induction. Spraying with MH after induction inhibited growth and plants receiving this treatment were only half as high as the controls. The terminal bud died in most of these plants. Terminals that did not die made little or no growth. Several axillary buds developed but made very poor growth. At the end of the experiment when the data were collected on the head-core ratios and growth phase indices, five plants which had been sprayed with MH after induction were not dissected but left intact for further observation of their growth habit. The

Table 18. The Effect of 250 PPM of Certain Growth-Regulating Substances on Average Height of Cabbage Plants Partially Induced to Flower by Cold Temperature Exposure (Variety, Round Dutch).

Growth Substances		Height in cms. on dates specified.			
Chemical Symbol	Time of Application*	Jan. 17	Feb. 29	Apr. 17	June 11
Control		6.48	13.85	16.45	20.42
MH	Before	7.02	13.90	18.48	22.92
	During	7.05	12.85	17.90	20.82
	After	6.75	7.08	7.77	10.35
TlBA	Before	7.25	14.85	18.80	21.85
	During	7.05	14.98	18.85	22.42
ClPP	Before	7.45	13.70	18.22	20.18
	During	7.45	15.55	18.80	22.02
L.S.D.	@.05	N.S.	1.30	2.24	4.25
	@.01		1.77	3.05	5.79

* Time of application in respect to cold-induction.

average height of these five plants twelve months after treatment was 15.6 cms. During this twelve month period neither heads nor seed stalks developed on either of the five plants.

Data concerning time of applying MH, TlBA and ClPP on the head-core ratio and growth phase index of partially induced plants are shown in Table 19. Applying MH before cold-induction had no material effect on the head-core ratio but significantly increased the growth phase index over the control. The difference between each of these two values and the corresponding values for the controls were very apparent. Spraying plants either before or after induction with TlBA caused no change of the head-core ratio or growth phase index. The head-core ratio was reduced and the growth phase index increased by spraying plants before induction with ClPP. The difference in head-core ratios between the control and plants sprayed with ClPP before induction was outstanding. Growth phase indices for these two treatments were significantly different. The head-core ratio and the growth phase index of plants sprayed during induction were essentially the same as the control.

The absence from Table 19 of the data pertaining to plants sprayed with MH after induction should be noted. These data were omitted from the statistical analysis and were not included in the table. The head-core ratio for this treatment was 1. None of the growth phase indices employed in these studies fit the plants in this treatment and the plants were not scored.

Table 19. Head-Core Ratio and Growth Phase Index of Cabbage Plants Partially Induced to Flower by Cold Temperature Exposure as Influenced by Time of Application of MH, TlBA, and ClPP (Variety Round Dutch).

Growth Substances		Head-Core Ratio		Growth Phase Index	
Chemical Symbol	PPM	Time of Application*		Time of Application	
		Before	During	Before	During
Control		1.86	-	2.1	-
MH	250	1.68	1.29	3.1	4.5
TlBA	250	1.71	1.76	2.6	2.1
ClPP	250	1.42	1.72	3.2	2.2
L.S.D.** @.05		0.23		1.0	
@.01		0.31		1.4	

* Time of application in respect to the cold-induction treatment.

** L.S.D. values apply to time of application means within and among chemicals.

The general appearance of plants among the treatment in this experiment varied little except those sprayed with MH during and after induction. There was also variation among plants treated with MH during induction. Most plants sprayed during induction were reproductive in appearance but none of them produced flowers. The photographs shown in Figure 8 illustrate the type of growth made by these MH sprayed plants. The plant represented by D was the control. Note the well formed head. Plants sprayed during induction with MH did not form heads. The degree of apparent reproductiveness in this treatment varied as shown in A and B. The plant shown in A had all appearances of a reproductive plant except for the production of flowers. The plant shown in C was representative of those sprayed with MH after induction. Note the dead terminal bud and young withered leaves. Four lateral buds developed on this plant but three were removed just before this photograph was made.



A



B



C



D

Figure 8. Partially induced cabbage plants following treatment with MH. A and B sprayed during; and C after cold-induction. D, control.

MORPHOLOGICAL STUDIES

These studies were made with three objectives: (1) to ascertain the morphological changes occurring in the terminal growing points while the plants were being cold-induced, and after induction; (2) to determine the changes in terminal growing points caused by applying growth-regulating substances at varied times with respect to the cold-induction treatment; and, (3) to determine the time of seed stalk initiation among the various treatments. Such studies should reveal the morphological changes associated with the transformation from the vegetative to the reproductive growth phase, time of differentiation of the seed stalk and flowers, and any internal changes associated with application of growth-regulating substances.

MATERIALS AND METHODS

Samples consisting of terminal shoots¹ were harvested periodically throughout the season from each treatment in the three experiments conducted during the 1949-50 season. The first samples were collected December 12, 1949, and subsequent samples at approximately 15 day intervals through April 14, 1950. Each sample comprised four terminal shoots.

After the leaves and roots were removed from the selected plants, excess tissue was trimmed, with a sharp knife, from around

¹ See Terminology, page 24.

the terminal shoots. The terminal shoots were then placed in vials containing formalin - aceto - alcohol (FAA) solution for killing and fixing. Each 100 ml. of FAA formula used consisted of 6.5 ml. of formalin, 2.5 ml. of acetic acid and 91 ml. of 50 percent ethyl alcohol. The length of the preserved shoots varied from 8 to 12 mm. depending on the size of plant and character of growth.

Air was removed from the specimens in the vials by means of a suction pump. Vials containing the specimens were left in the vacuum chamber until the terminal shoots sank to the bottom of the killing and fixing solution with the vacuum off, which usually required 20 to 30 minutes. The vials were then sealed with air tight lids and stored until February, 1951.

After washing in running water for three hours the terminal shoots were dehydrated by the alcohol-xylene method as described by Johansen (42). These shoots were embedded in paraffin and sectioned longitudinally at a thickness of seven microns with a rotary microtome. Ten to thirty near-median sections were saved from the ribbon of each shoot and mounted on slides. After drying, the paraffin in and around the sections was removed with xylene. The sections were stained in safranin and aniline blue with Delafield's hematoxylin as described by Popham (67), and mounted in balsam. The sections were studied under a low and high power and oil immersion microscope. Gross and detail morphological changes induced by various treatments were observed.

The morphological study reported herein was conducted with the large, medium and small plants sprayed with 250 ppm of ClPP and 15 ppm of 2,4-D before, during and after the cold-induction treatment as described in experiment 4. Studies were limited to this experiment since no plants in other experiments were completely in the reproductive phase. In all, about 110 different samples were studied including about 440 terminal shoots.

The growing point¹ was divided into a zonal pattern for simplicity in discussing the morphological studies. The diagrammatic representation shown in Figure 9 will facilitate an understanding of the location of each of the four zones. The tunica consisting of only the two surface cell layers is represented in zone 1. The corpus initials are represented in zone 2. The peripheral or flanking tissue is represented in zone 3, and the rib meristem in zone 4. This method was employed with realization that certain tissues were not easily differentiated from others. For example, a distinction between the tunica and corpus in the shoot apex¹ was not easily made. There was a gradual transition from one tissue to the other rather than a distinct line of demarcation separating them. To further simplify the discussion the cell layers will occasionally be referred to as the first, second, third, fourth and so forth, progressing from

¹ See Terminology, page 24.

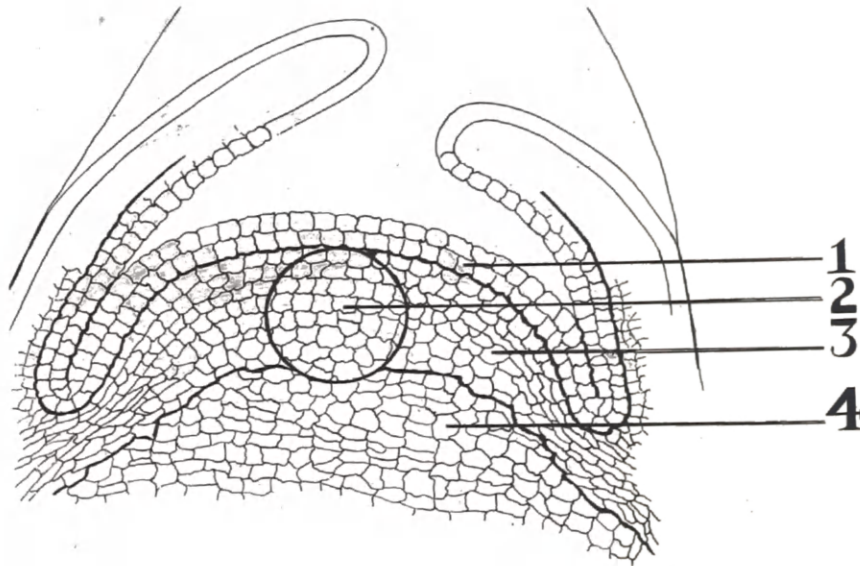


Figure 9. Diagrammatic representation showing four distinctive zones in the vegetative growing point of cabbage.
1. Tunica layer. 2. Corpus initials. 3. Peripheral or flank-ing tissues. 4. Rib meristem.

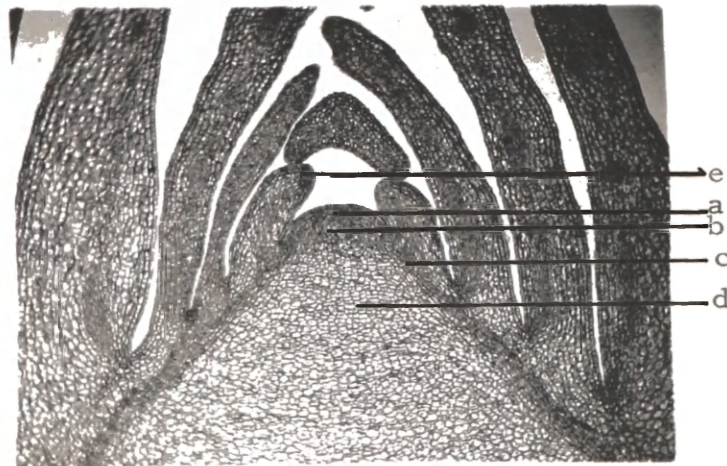


Figure 10. The growing point of a vegetative cabbage plant harvested February 6. (a) Tunica layer; (b) corpus initials; (c) procambial cells; (d) rib meristem; (e) young developing leaf. x64

the surface layer inward.

RESULTS

Familiarity with the changes that occur in the vegetative and reproductive growth phases as the plants developed from seedlings to maturity was the first objective. After this was accomplished any changes that might be caused by the applied growth-regulating substances could be more readily detected.

Seasonal Changes in the Terminal Growing Point of Vegetative Plants

Only slight changes were found in plants within a treatment between December 12, 1949, and February 6, 1950. On each sampling date the growing points in the large plants were larger than in the medium plants and in like manner those in the medium plants were larger than in the small plants. There was little difference in size of growing points in plants of the same size and little change occurred in the growing points during the cold-induction treatment.

After the plants were transplanted to the field the apices became more active. In Figure 10 can be seen a photomicrograph of a representative of the vegetative plants on February 6, 1950, about six weeks prior to the time of active plant growth. The cells in the different tissues were about the same size. Cells in the tunica were distinct. Cells in the third and fourth cell layers were less

distinct. The procambium cells were more active than the corpus initials as evidenced by differential staining. The rib meristem cells were arranged in a non-descriptive manner, and appeared to have been dividing in various planes. When active growth started after March 20, activity increased in each of the four zones (Figure 11). The cells in the tunica divided rapidly in an anticlinal plane (cell wall formed in a plane perpendicular to the outer surface). Corpus initials divided rapidly in various planes. Cells in this zone were easily distinguishable from those of adjoining zones. The division of the cells in the third and fourth cell layers in the outer part of zone 3 near the shoot apex was primarily anticlinally. However, occasionally, periclinal divisions occurred as will be discussed later. The procambium cells were dividing rapidly in a periclinal plane (cell wall formed in a plane parallel with the outer surface) and these cells were less distinct than before active growth began. Cell division in zone 4 occurred in various planes. The cells in each zone were slightly larger and the apices were broader than before the time of active growth.

As can be seen in Figure 12, no major gross change occurred in the terminal growing point of vegetative plants after growth started in the spring. This shoot was collected April 14. Shoots collected after this date showed that no gross changes had occurred in the growing points, other than a slight increase in size, as the plant heads reached market maturity.

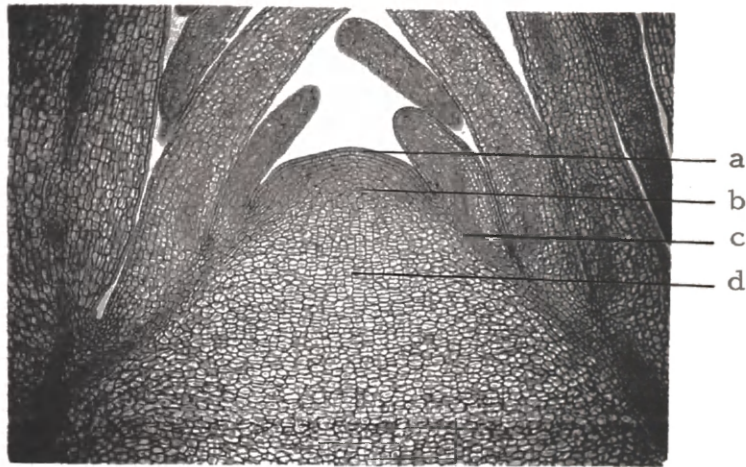


Figure 11. The growing point of a vegetative cabbage plant harvested March 27. (a) Tunica layer; (b) corpus initials; (c) procambial cells; (d) rib meristem. x 64

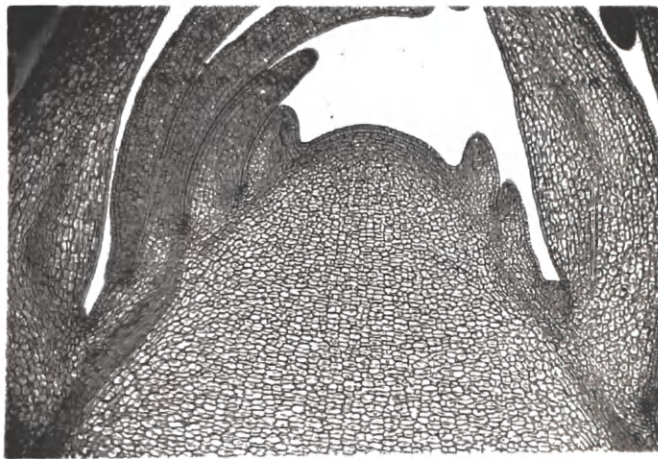


Figure 12. The growing point of a vegetative cabbage plant harvested April 14. x64

Leaf Development

Cells in the tunica divided anticlinally without exception. Those in the third and fourth cell layers divided anticlinally except during the initiation of a leaf or other later appendage. In the beginning of leaf initiation cells in the third and fourth layers just to either side of the corpus initials and in zone 3 began to divide periclinally to form the leaf initials. Early evidence of this phenomenon can be seen in Figure 13. Continued periclinal divisions followed shortly by periclinal and anticlinal divisions resulted in the formation of a leaf primordium, Figure 14. The cells in the tunica continued to divide anticlinally. In the leaf primordium, Figure 15, cells divided in various planes forming slight "humps" to either side of the shoot apex. In Figure 16 can be seen a photomicrograph of a cabbage terminal growing point with young developing leaves and advanced leaf primordia.

Some Changes Which Occur in the Terminal

Growing Point of Reproductive Plants

Several observable gross changes occurred in the terminal shoots during the transitional stages from the vegetative to the reproductive phase of growth. In the early stages of this gradual transformation it was difficult to morphologically detect with certainty when the reproductive phase was initiated. For example, the terminal growing point represented in Figure 17 only depicted indications that the reproductive phase was being initiated. The lateral

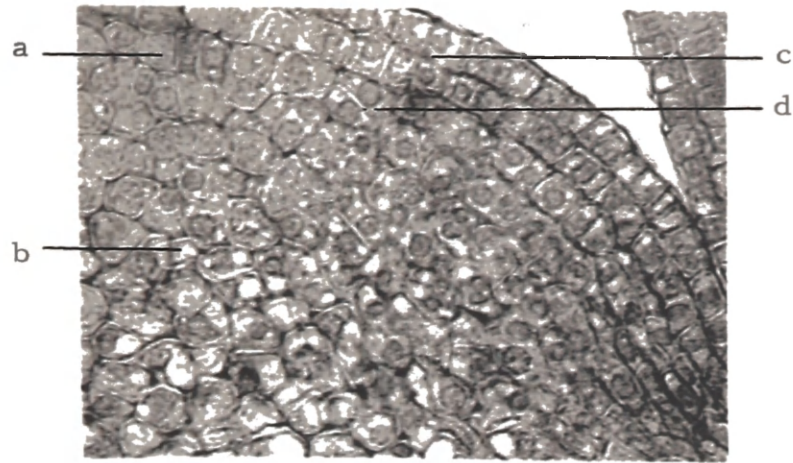


Figure 13. Leaf initiation in a vegetative cabbage plant.
(a) Shoot apex; (b) corpus initials; (c) tunica layer; (d) leaf
initial in third and fourth cell layers. x620

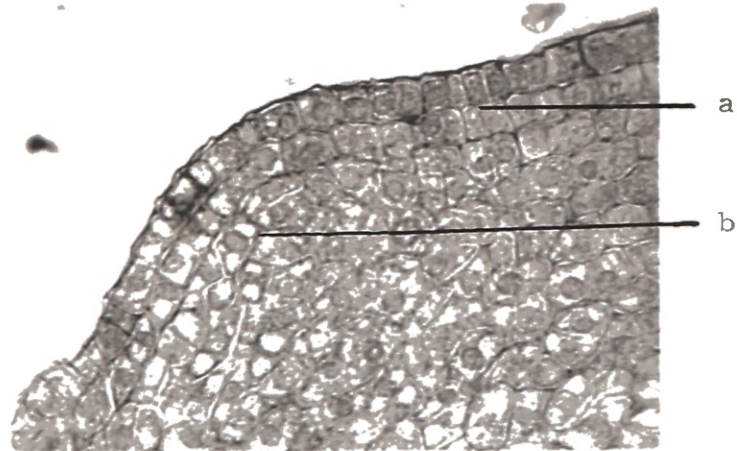


Figure 14. Development of a leaf primordium in a vegetative
cabbage plant. (a) Tunica layer; (b) leaf primordium developing by
periclinal cell division. x620

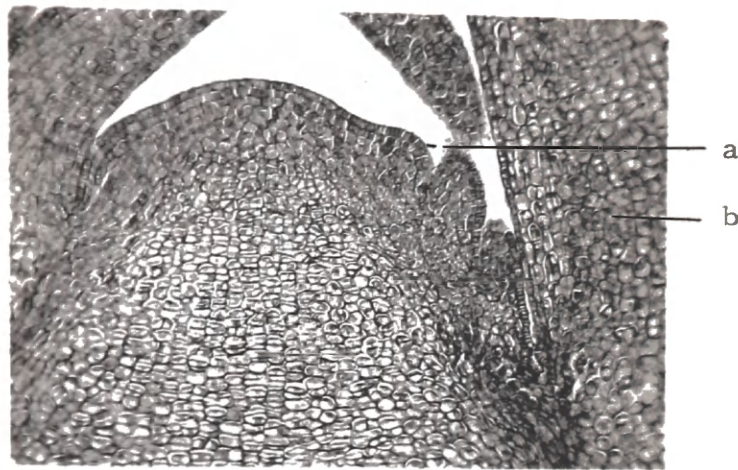


Figure 15. The growing point of a vegetative cabbage plant showing a leaf primordium. (a) Leaf primordium; (b) older leaf. x128

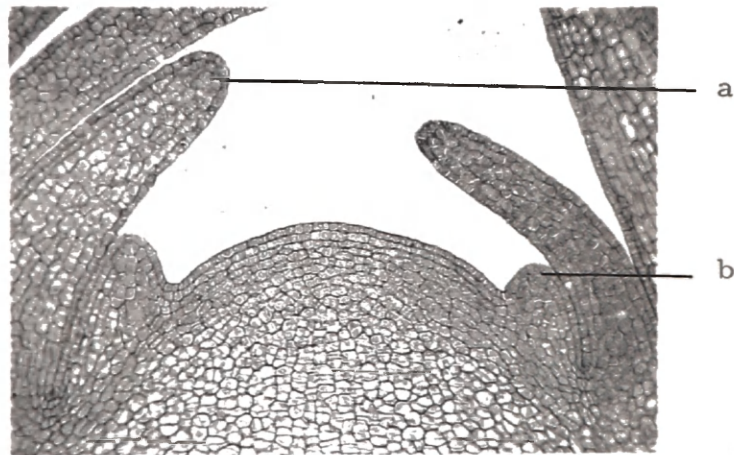


Figure 16. The growing point of a vegetative cabbage plant showing leaf development. (a) Young developing leaf; (b) advanced leaf primordium. x128

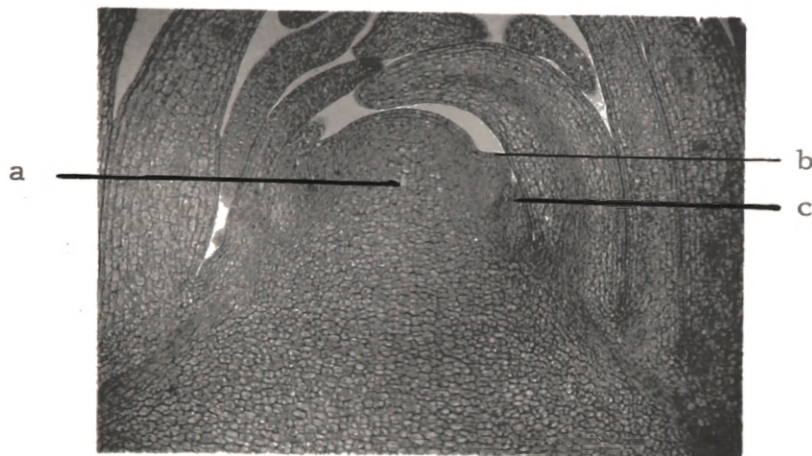


Figure 17. The growing point of a cabbage plant harvested February 6 which is probably reproductive. (a) Cells forming in longitudinal rows; (b) leaf primordium; (c) lateral growing point. x64

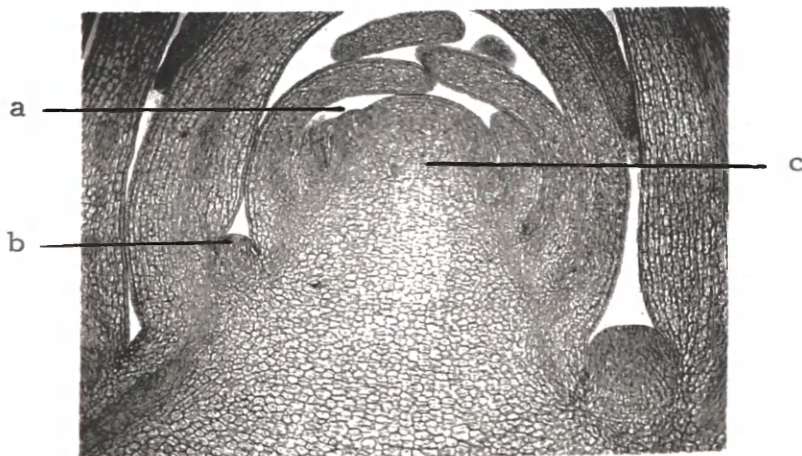


Figure 18. The growing point of a reproductive cabbage plant harvested February 24. (a) Lateral growing point primordium developing in the axil of a leaf primordium; (b) an older growing point primordium; (c) cells forming in longitudinal rows. x64

growing points were beginning to differentiate and grow in the axils of each of two leaf primordia. The cells in the rib meristem zone underneath the corpus initials were beginning to form in longitudinal rows when this specimen was collected. As will be seen later, the growth of the lateral growing points and the tendency of cells to be arranged in longitudinal rows in zone 4 were two gross changes found in this study to be definitely associated with the reproductive phase. In contrast to the numerous studies reported for many crops, the shoot apices of the cabbage plants examined in this study did not become "flattened and broadened at the tip" prior to seed stalk or floral initiation but remained slightly dome-shaped throughout the study irrespective of the growth phase.

Gross changes occurring in the growing point in the early stages of initiation of the reproductive phase can be seen more clearly in Figure 18. Growth had initiated in a few lateral growing points. Cells in the rib meristem zone were being arranged in more distinct longitudinal rows when this shoot was collected. On the left side of the terminal growing point just beneath the apex was a leaf primordium with a lateral growing point primordium in its axis. Note that the primordium of the lateral growing point had made about the same growth as that of the leaf. The two uppermost lateral growing point primordia shown in Figure 19 had also made growth equal to their adjacent leaf primordia. The terminal growing point shown in Figure 19 was slightly more advanced in the reproductive

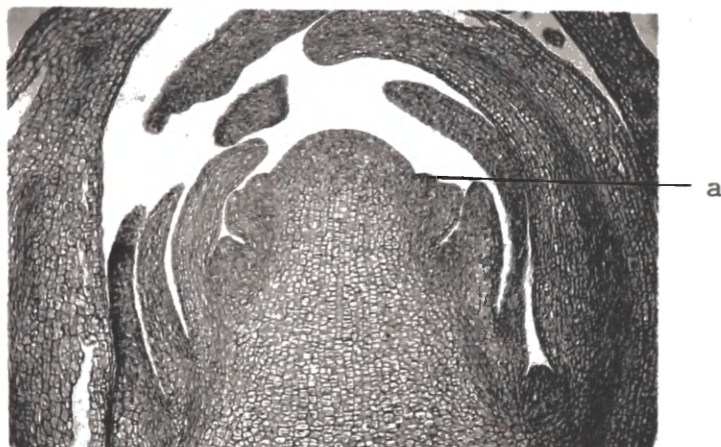


Figure 19. The growing point of a reproductive cabbage plant harvested March 10. (a) Lateral growing point primordium. x64

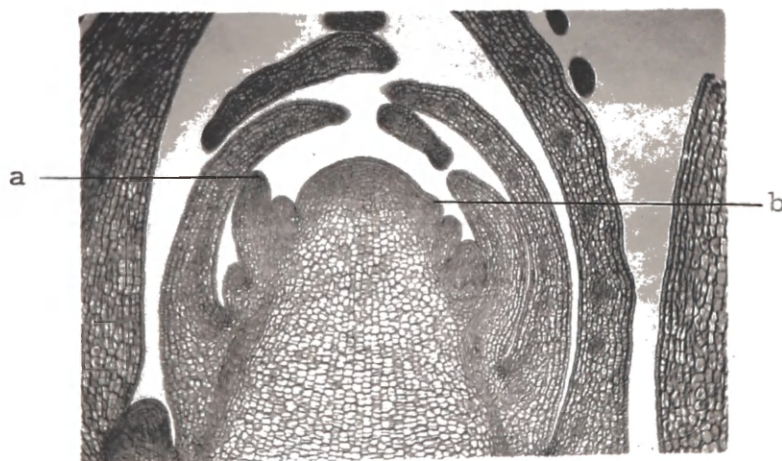


Figure 20. The growing point of a reproductive cabbage plant harvested March 27 showing a probable flower primordium. (a) Leaf making limited growth; (b) probable flower primordium. x64

phase than the one shown in Figure 18. The younger leaves were not developed so well in the shoot shown in Figure 19 as in Figure 18. The cells in the rib meristem were in longitudinal rows.

In Figure 20 is shown an advanced stage in the reproductive growth phase. Lateral growing points had been initiated throughout the length of the shoot. More newly developed leaves had made limited growth and cells in the rib meristem were in longitudinal rows. As will be shown in detail later in this discussion it was difficult to distinguish between a floral initial or primordium and a leaf initial or primordium. By thoroughly studying type of leaf growth and number of lateral growing points which have been initiated one can become proficient in distinguishing floral primordia from leaf primordia. One outstanding feature found in this study was the first flower primordium to be initiated was found in the axil of a much dwarfed leaf primordium. After several flower primordia were initiated the leaves became rudimentary. Based on these observations the uppermost primordium on the right side of the terminal growing point in Figure 20 was labeled as a probable flower primordium.

In Figure 21 is shown a developing young flower. Sepal primordia were clearly distinct. Initiation of the other floral parts had not occurred.

Lateral Shoot Development

In the development of a lateral shoot which may be either

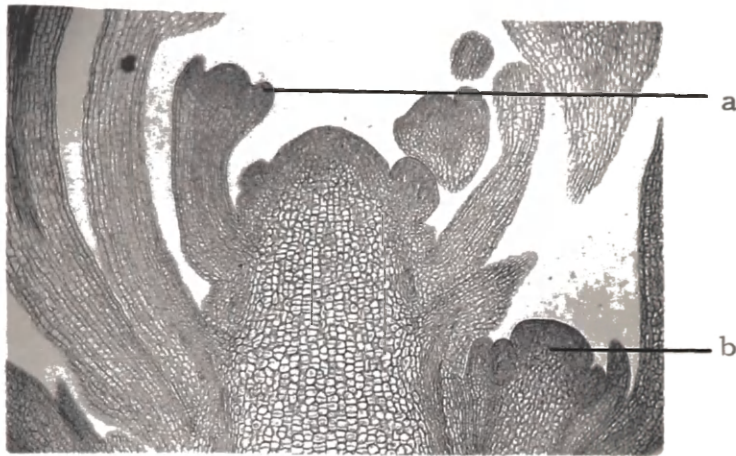


Figure 21. The growing point of a reproductive cabbage plant harvested March 27. (a) Developing flower; (b) lateral growing point. x64

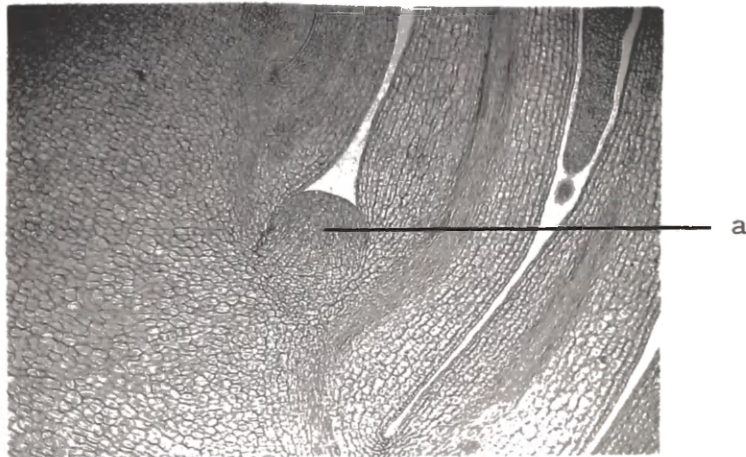


Figure 22. A developing lateral shoot primordium in cabbage. (a) A lateral shoot primordium. x128

vegetative or reproductive the meristematic bud in the axil of a leaf began to differentiate. As growth proceeded the growing point of the lateral shoot assumed an architectural design and gross morphology identical with that in the growing point of the terminal shoot.

The tunica in the lateral shoot was formed by the two surface cell layers in the early stages of growth. Shown in Figure 22 is a young lateral growing point in the leaf axil of a terminal shoot. The tunica was distinct, and the corpus initials were detectable but less distinct. The planes of cell division in the lateral growing point were identical with those in the terminal growing point. In the tunica, cell divisions were anticlinal, the corpus initials divided anticlinal and periclinal, and the cells in the rib meristem divided in various planes. Divisions were anticlinal in the third and fourth cell layers of the peripheral zone except during the initiation of a lateral organ when they were periclinal. A young lateral shoot is shown in Figure 23. The rib meristem cells were in longitudinal rows which indicates this lateral was in the reproductive phase.

In Figure 24 is a more advanced stage in the growth of a lateral shoot. This lateral shoot had a growing point morphologically characteristic of the early stages of the reproductive growth phase. The lateral shoot shown in Figure 25 was rapidly initiating floral primordia when it was collected.

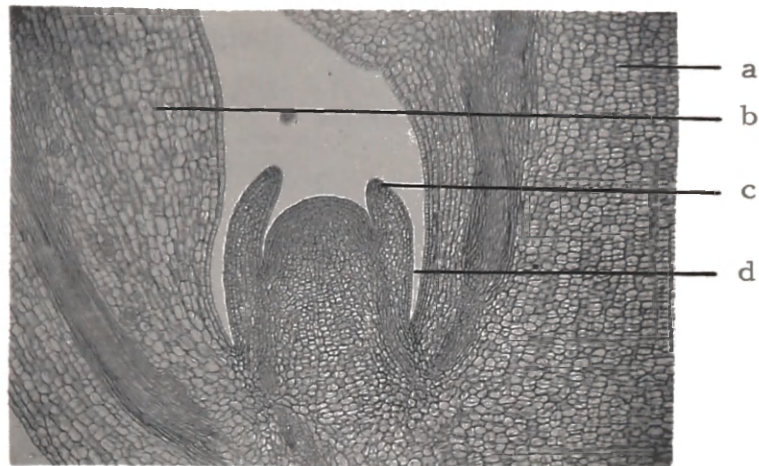


Figure 23. A developing lateral shoot showing first pair of leaves in cabbage. (a) Portion of terminal shoot; (b) old leaf; (c) young leaf; (d) lateral growing point. x128

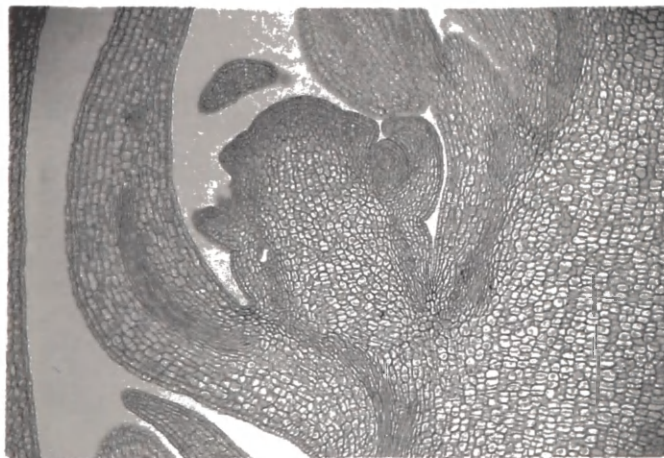


Figure 24. A developing lateral shoot in cabbage. This lateral shoot is morphologically characteristic of the early stages of the reproductive growth phase. x128

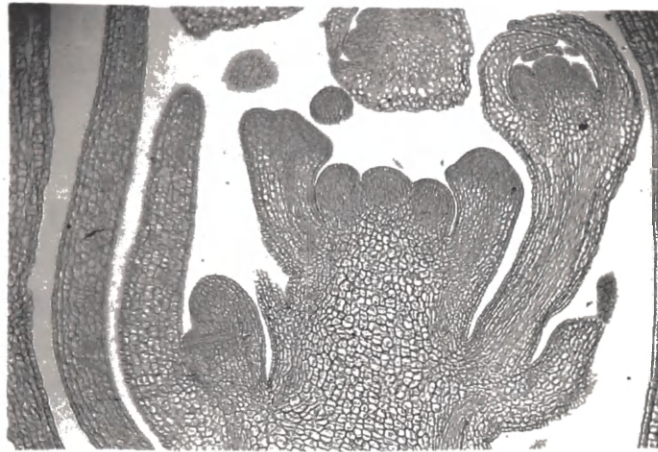


Figure 25. A reproductive lateral shoot in cabbage. x128

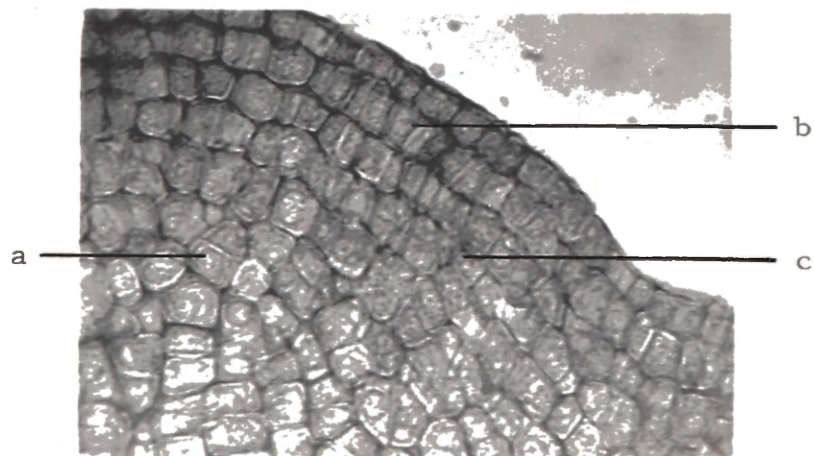


Figure 26. Flower initiation in cabbage. (a) Corpus initials; (b) tunica layer; (c) flower initial in third and fourth cell layer. x620

Flower Development

Floral initials arose in the uppermost part of the peripheral zone of the growing point. The principal plane of cell division in the third and fourth cell layers of this area was anticlinal. When floral initials were being differentiated a few of the cells divided in a periclinal plane. Early evidence of periclinal cell division in the third and fourth cell layers is shown in Figure 26. In Figure 27 is shown a flower bud initial resulting from periclinal cell division from the third and fourth layers. It was evident that this was a floral initial, because the terminal shoot from which it was selected was developing only floral initials. Continued periclinal and anticlinal divisions of the floral initials resulted in the formation of the flower primordium, Figure 28, and the young developing flower, Figure 29. The order of appearance of the floral parts, Figure 30, 31 and 32, was found to be sepals, stamens, pistil and lastly petals. A cross section of a flower is shown in Figure 33.

It has been generally intimated in the literature that flowering in cruciferea is terminal. In this study, cabbage flowers were initiated laterally on either side of the shoot apex in the same manner as leaves and lateral shoots. Furthermore, the gross shape and cellular appearance of the shoot apex in a reproductive plant was not different from that of a vegetative plant. The growing points of the vegetative and reproductive plants were different. To attest the belief that the apices of the plants in the two growth phases were alike,

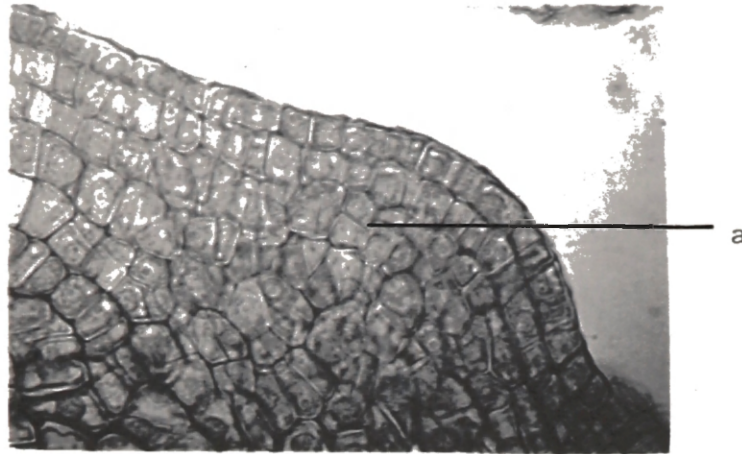


Figure 27. A developing flower initial in cabbage.
(a) Periclinal cell divisions in the third and fourth cell layers. x620

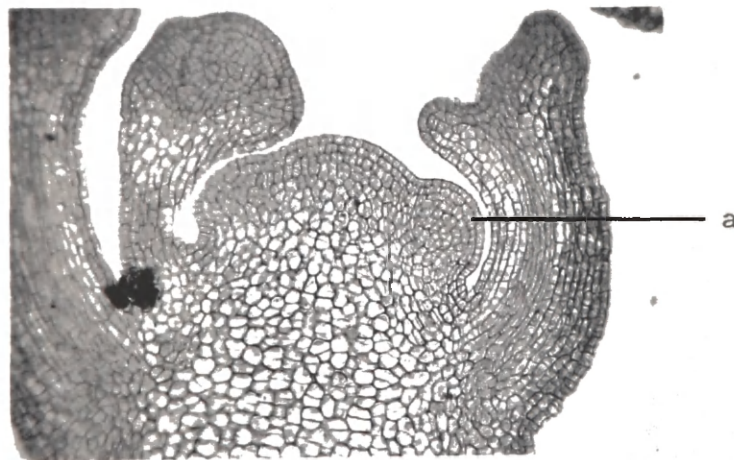


Figure 28. The developing flower primordium in cabbage. (a) Flower primordium. x128

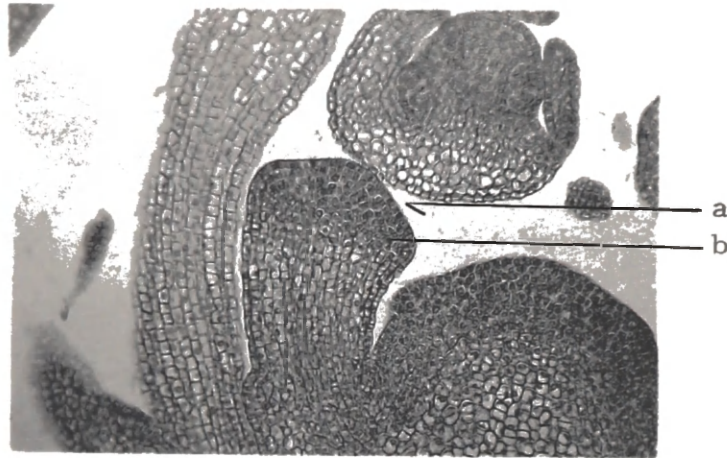


Figure 29. The development of a flower showing sepal initials in cabbage. (a) Advanced flower primordium; (b) sepal initials. x128

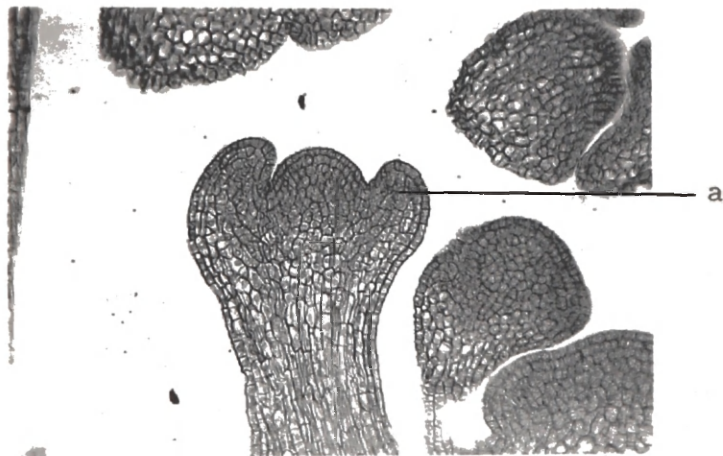


Figure 30. The development of a flower showing sepal primordium in cabbage. (a) Sepal primordium, the first flower part to develop. x128

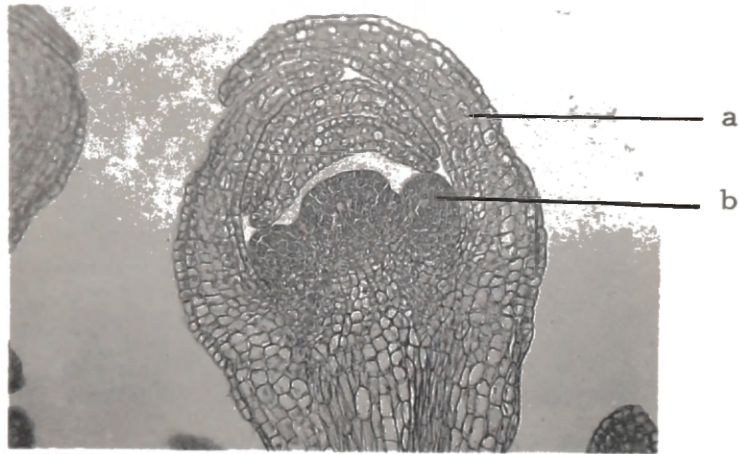


Figure 31. The development of a flower showing stamen primordium in cabbage. (a) Sepal; (b) stamen primordium.

x128

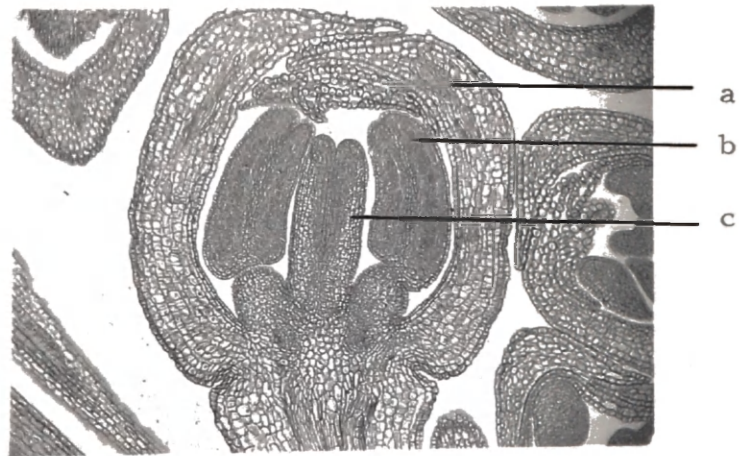


Figure 32. Longitudinal section of a cabbage flower. (a) Sepal; (b) stamen; (c) pistil. The petal, not shown is the last flower part to develop. x64

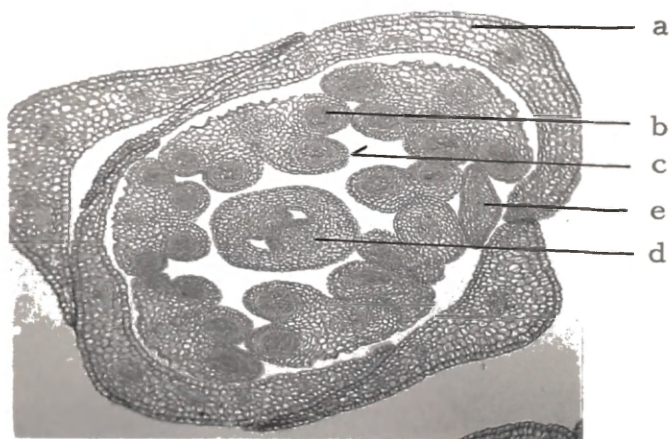


Figure 33. Cross section of a cabbage flower showing floral diagram. (a) Sepal; (b) anther lobe, 2; (c) stamen; (d) pistil, 2 carpels; (e) petal tip. x100



Figure 34. Photograph of a cabbage plant which was devernalized by high temperature. After six weeks of temperatures above 85° F. this plant ceased to flower and produced a small firm head at the summit of the seed stalk.

ten reproductive plants were devernallized by subjecting them to temperatures above 85° F. in the greenhouse for six weeks. As a result of this treatment the plants ceased to flower and were transformed from the reproductive to the vegetative growth phase. The plant shown in Figure 34 had seed pods on a "seed stalk" which bore a small but firm cabbage head at the summit of the seed stalk.

Certain morphological changes which occur as a plant transforms from the vegetative to the reproductive phase have been discussed above. It should be noted that the first evidence of initiation of the reproductive growth phase was about February 24. A study of the shoots collected on that date from the various treatments was then made.

Effect of Growth-Regulating Substances Upon

Time of Flower Initiation

It was found that the morphological characteristics of the growing points within a treatment were similar but great differences among the various treatments were observed. Seed stalk initiation had occurred in certain treatments on February 24 while in other treatments it had not.

Plant size at the time of cold-induction had no effect upon the time of initiation in reproductive plants. Initiation occurred in medium size plants as early as in large plants. The growing points of the small plants were vegetative and consequently no seed stalk ini-

tiation occurred.

Large Plants

There was little evidence on February 24 to indicate that initiation of the reproductive growth phase had occurred in any of the large control plants. Lateral growing points in the axils of the leaves were not enlarging. The only indication was the cells in the rib meristem just beneath the corpus initials were being formed in longitudinal rows, Figure 35. Figure 36 represents a growing point collected February 24 from a plant sprayed with ClPP before induction. The reproductive phase had been initiated in the growing points of all plants examined for this treatment. Cells in the rib meristem were in longitudinal rows, and lateral growing points were differentiating throughout the length of the shoot.

No evidence of initiation existed on February 24 in any of the plants sprayed during induction with ClPP, Figure 37. The cells in the rib meristem were not arranged in longitudinal rows but in a non-descriptive manner. No lateral growing points were differentiating in any plants examined. In Figure 38, evidence of initiation can be seen. This figure is representative of the large plants on February 24 which were sprayed after induction with ClPP.

Based on this study the order of initiation among the large plants sprayed at various times with ClPP follows: first, in plants sprayed before induction; second, in plants sprayed after induction; third, in

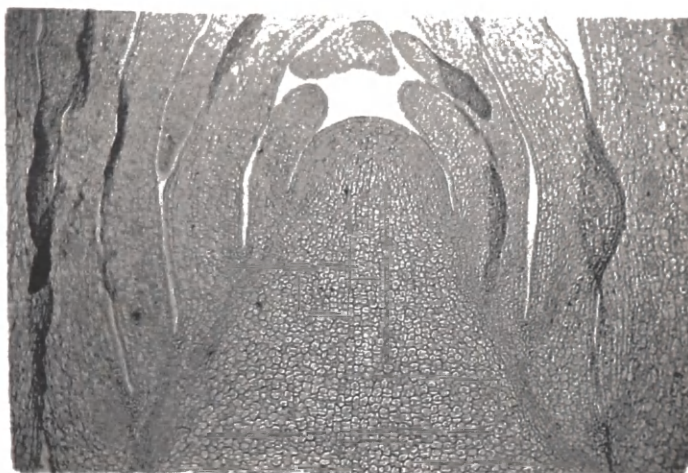


Figure 35. The growing point of a cabbage plant (large size) harvested February 24. There is little evidence of the reproductive phase. x64

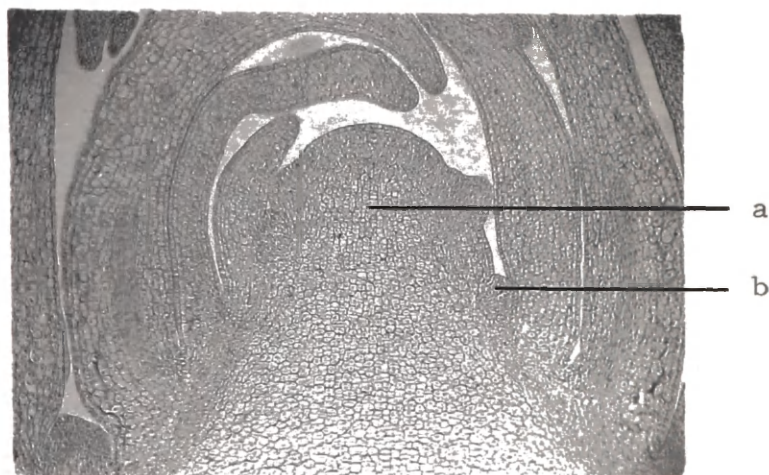


Figure 36. The growing point of a cabbage plant (large size) sprayed with ClPP before cold-induction and harvested February 24. (a) Rib meristem cells forming in longitudinal rows and (b) lateral growing points developing in the leaf axils are indicative of the reproductive phase. x64

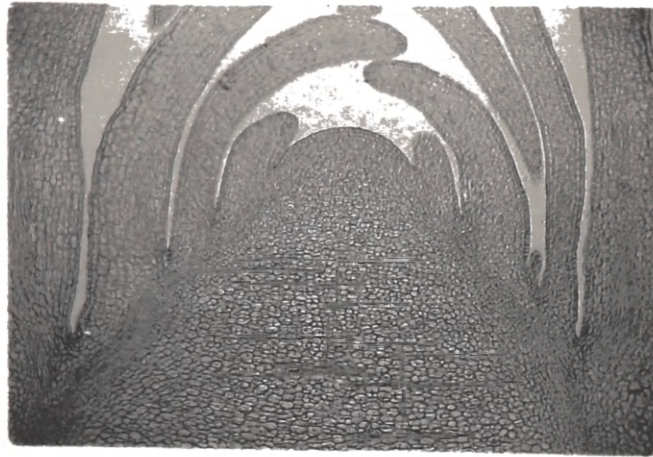


Figure 37. The growing point of a cabbage plant (large size) sprayed with ClPP during cold-induction and harvested February 24. There is no evidence of the reproductive phase. x64

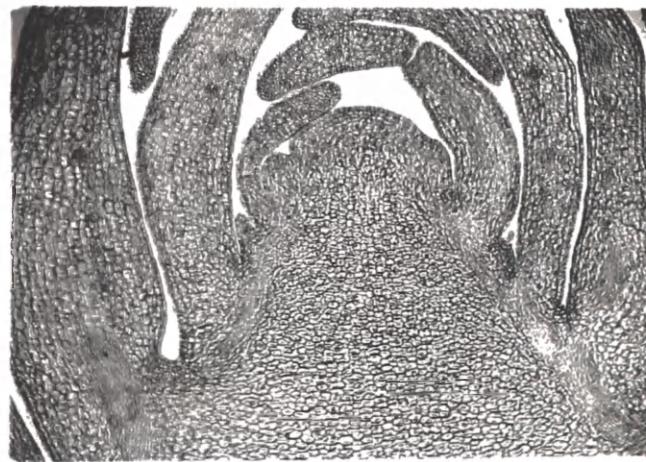


Figure 38. The growing point of a cabbage plant (large size) sprayed with ClPP after cold-induction and harvested February 24. The rib meristem cells were forming in longitudinal rows and a few lateral growing points were developing when this terminal shoot was harvested. x64

control plants; and fourth, in plants sprayed during induction.

Photomicrographs of the growing points of large plants sprayed with 2,4-D before, during and after the induction treatment are presented in Figures 39, 40 and 41, respectively. These shoots showed little indication that the reproductive phase had been initiated when the shoots were collected on February 24. Studies made of shoots collected two weeks later indicated that initiation occurred earliest in plants sprayed before induction and latest in plants sprayed during induction. The difference in time of initiation between the plants sprayed before and those sprayed after induction was negligible. Plants sprayed during cold-induction were considerably less advanced in the reproductive phase than plants sprayed before or after induction.

Medium Plants

In the control plants of medium size certain morphological changes, associated with the initiation of the reproductive growth phase, were noticed in terminal shoots collected February 24. Cells in the rib meristem were beginning to form longitudinal rows and lateral growing point primordia were differentiating in the axils of the leaf primordia, Figure 42. A comparison of the terminal growing point shown in Figure 42 with the one in Figure 43 shows that initiation of the reproductive phase was slightly more advanced in plants sprayed with ClPP before induction than in the control plants. Lateral growing points were growing in the axils of the older leaves of plants sprayed

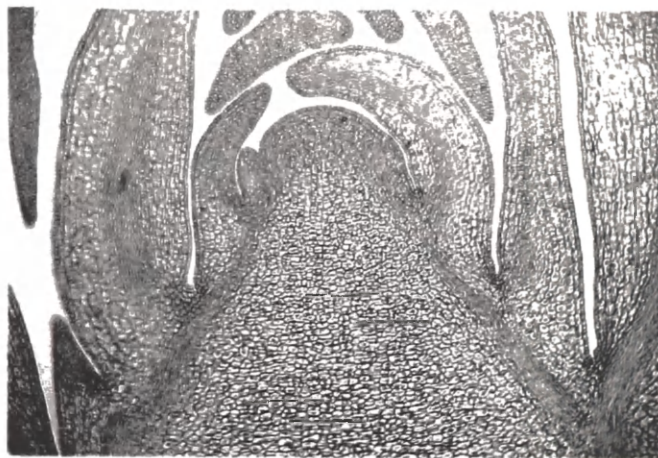


Figure 39. The growing point of a cabbage plant (large size) sprayed with 2,4-D before cold-induction. Rib meristem cells were forming in longitudinal rows when harvested February 24. x64



Figure 40. The growing point of a cabbage plant (large size) sprayed with 2,4-D during cold-induction. A few lateral growing points were developing when harvested February 24. x64

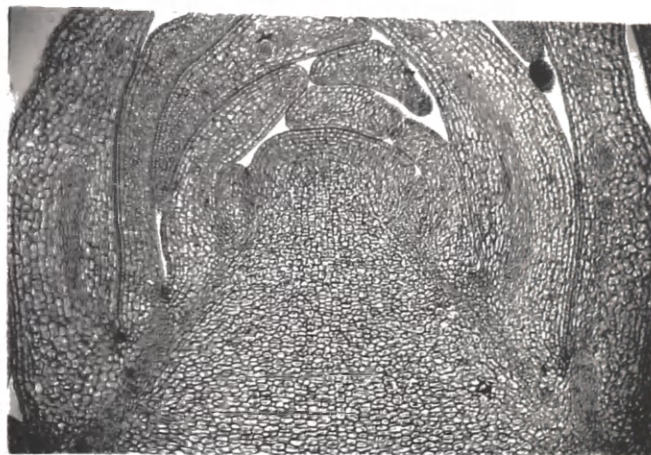


Figure 41. The growing point of a cabbage plant (large size) sprayed with 2,4-D after cold-induction. A few lateral growing points were developing and the rib meristem cells were forming in longitudinal rows when harvested February 24. x64

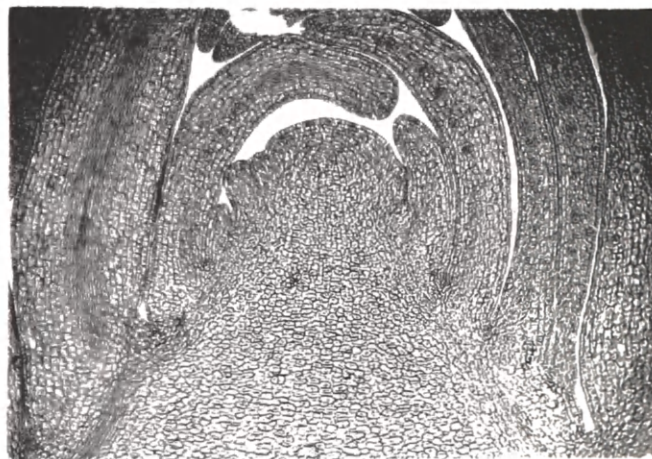


Figure 42. The growing point of a cabbage plant (medium size) in the control. Lateral growing points were beginning to develop and rib meristem cells were forming in longitudinal rows when harvested February 24. x64

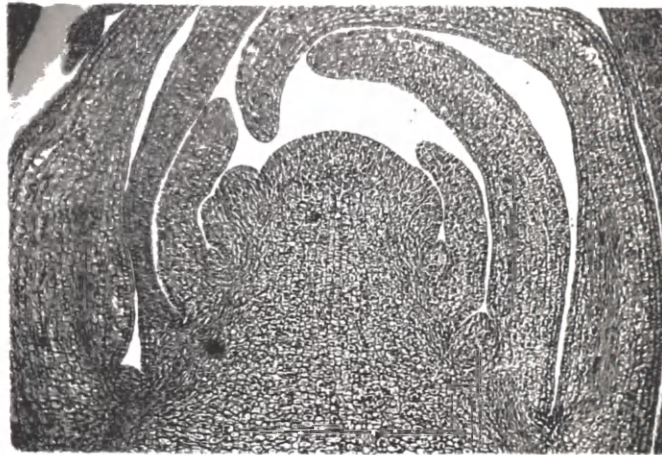


Figure 43. The growing point of a cabbage plant (medium size) sprayed with ClPP before cold-induction. Lateral growing points were developing and rib meristem cells were forming in longitudinal rows when harvested February 24. x64

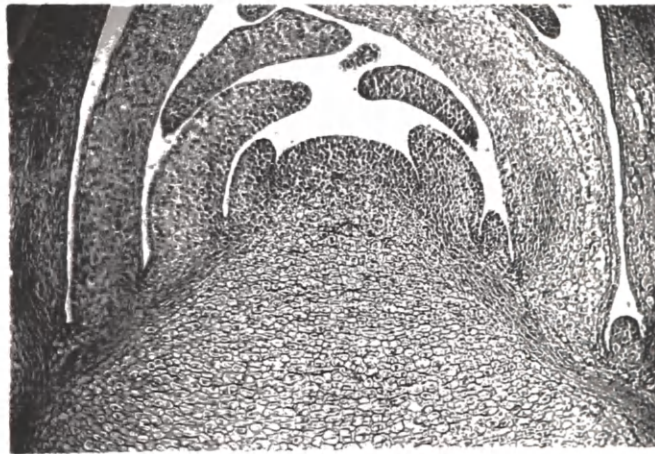


Figure 44. The growing point of a cabbage plant sprayed with ClPP during cold-induction. General disorganization of the cells occurred in all shoots harvested February 24 from this treatment but no evidence of initiation of the reproductive phase was observed. x64

before induction.

No evidence of initiation was found in any terminal shoots examined of plants sprayed during induction, Figure 44. A general lack of organization of the cells was observed especially in the apices of all shoots collected February 24 from plants sprayed during induction with ClPP, Figure 44. Shoots collected from all treatments were similarly handled throughout the histological procedure for any one sampling date. Those harvested on different dates were handled as nearly alike as possible. One might assume that ClPP applied during induction interferes with normal cellular organization during the period of initiation. As will be pointed out later such pronounced disorganization of the cells was not observed in shoot apices harvested from any treatments before or after February 24. A similar but less pronounced response was observed in the apices of terminal shoots collected February 24 of plants sprayed after the induction treatment, Figure 45. Lateral growing points were differentiating in these terminal shoots which indicates initiation of the reproductive phase.

Initiation of the reproductive growth phase appeared to have occurred earliest in the plants sprayed before induction. The plants in the control were next in order followed by those sprayed after induction.

Terminal shoots of medium size plants sprayed with 2,4-D before, during and after the induction treatment are shown in Figures 46, 47 and 48, respectively. Initiation of the reproductive phase was more

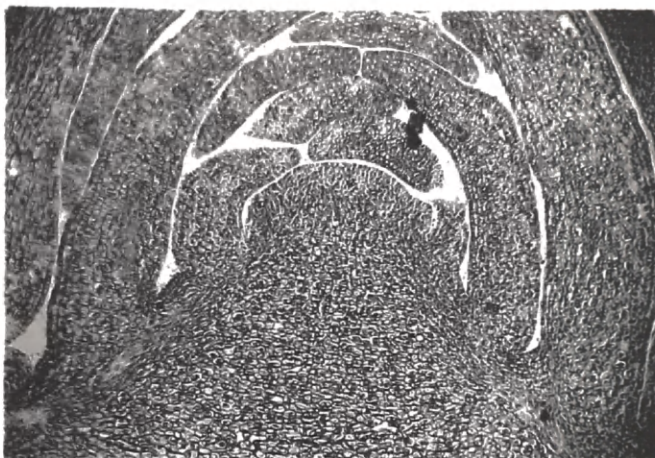


Figure 45. The growing point of a cabbage plant (medium size) sprayed with ClPP after cold-induction. There was slight cellular disorganization in the shoots harvested February 24 from this treatment and slight evidence of initiation of the reproductive phase. x64

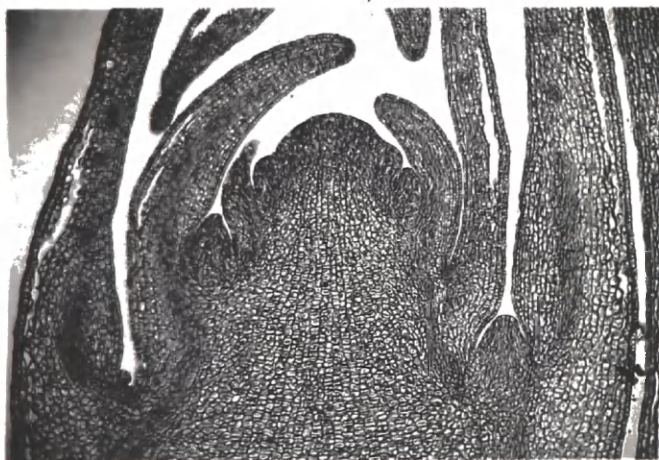


Figure 46. The growing point of a cabbage plant (medium size) sprayed with 2,4-D before cold-induction. Harvested February 24. x64

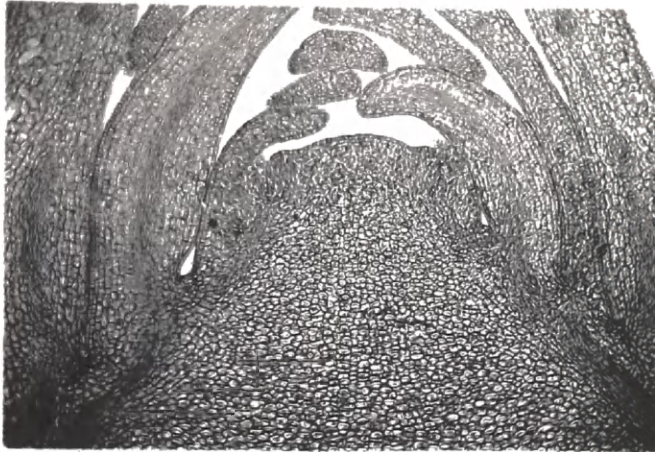


Figure 47. The growing point of a cabbage plant (medium size) sprayed with 2,4-D during cold-induction. Harvested February 24. x64

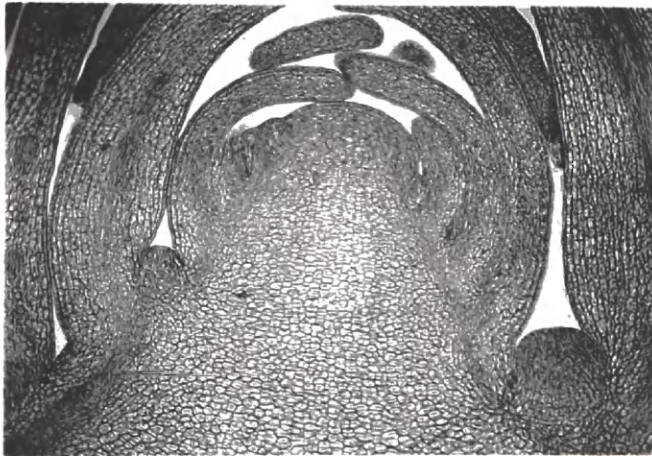


Figure 48. The growing point of a cabbage plant (medium size) sprayed with 2,4-D after cold-induction. Harvested February 24. x64

advanced in plants sprayed before (Figure 46) and after the induction treatment (Figure 48) than in the control (Figure 42). There was no observable difference between plants sprayed before and those sprayed after the induction treatment. Plants sprayed with 2,4-D during induction showed almost no evidence of initiation on February 24. A study of the shoots harvested two weeks later revealed that initiation had occurred. These morphological observations hardly corroborate the data in Table 16 dealing with the growth phase index. These inconsistencies may be attributed to variation in auxin content of the two groups of plants at or immediately following initiation.

Small Plants

There were no indications of initiation of the reproductive phase in any of the small plants examined.

Seasonal Changes in the Terminal Growing Points of Plants

Kept Vegetative by Growth-Regulating Substances

Little change occurred during the season in the general morphology of the growing points of plants sprayed with ClPP during the induction treatment. The general morphology of such plants is shown in Figures 49, 50 and 51. Specimens used in preparing these photographs were collected January 20, March 27 and April 14, respectively. It is to be recalled from the preceding discussion however that on February 24, the time of seed stalk initiation, marked cellular disorganization occurred in the growing points of the plants in this treat-

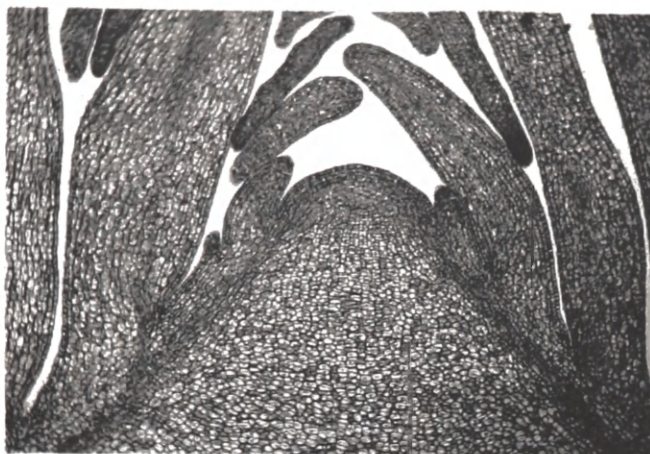


Figure 49. The growing point of a cabbage plant (medium size) sprayed with ClPP during cold-induction. Harvested January 20, 1950. x64

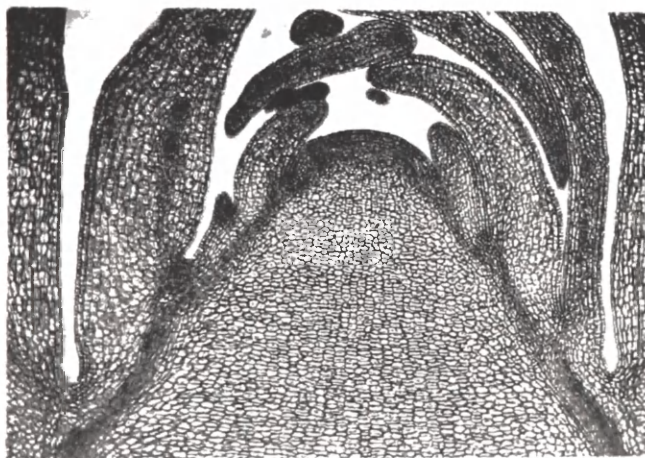


Figure 50. The growing point of a cabbage plant (medium size) sprayed with ClPP during cold-induction. Harvested March 27, 1950. x64



Figure 51. The growing point of a cabbage plant (medium size) sprayed with ClPP during cold-induction. Harvested April 14, 1950. x64

ment. Such disorganization did not prevail two weeks prior or two weeks subsequent to February 24.

In Figure 49, indications are that a few of the cells in the rib meristem region had formed in longitudinal rows. Terminal shoots collected March 27, Figure 50, appeared to be slightly elongated as compared with genuinely vegetative shoots. Even so, this shoot could not be classified as being in the reproductive phase. The shoot represented in Figure 51 was strictly vegetative and is characteristic of others collected April 14 from plants sprayed during cold-induction with 250 ppm ClPP.

DISCUSSION

Results of this study support the findings of Boswell (7) and Miller (59) that low temperature is the main environmental factor associated with precocious seeding in cabbage. In addition, the size of the plants when subjected to low temperatures is an important factor (7) and (48). Large plants have greater tendencies to shoot to seed than small ones. Plants with stem diameters 6 mm. or larger at cold-treatment of approximately 38° F. for 42 days bolted, whereas plants with diameters of 4 mm. did not bolt.

There was considerable difference in response by the two varieties to cold-induction treatment. Golden Acre plants having a stem diameter of 6 mm. or greater readily bolted after cold-induction. Round Dutch plants with stem diameters of 6 to 7 mm. did not bolt after a similar cold treatment. Although temperature had a pronounced effect on premature flowering in cabbage, this effect was influenced in both varieties by growth-regulating substances. These substances alone did not have sufficient influence to change the growth phase from vegetative to reproductive, but appeared to aid such changes when used in combination with the environment.

The influence of the substances applied varied with the chemicals, concentrations, plant sizes and times of application. Aside from formative effects and increased growth rate during the seedling stage the most outstanding chemical influences were noticed in plants treated with 2,4-D,

ClPP and MH. Vegetative growth rate was stimulated in young plants soon after treatment with low concentrations of NA, but this response was not noticeable a few weeks after treatment. Application of TIBA as used in these experiments had no apparent effect on plant growth.

Recent concepts concerning mechanisms involved in the transition of plants from the vegetative to the reproductive phase center around the hypothesis of existing flower-inducing and flower-inhibiting substances. Cailachjan (9) suggested that a hormonal substance which he called "florigen" was produced in the leaves and translocated to the growing point. According to the theory sufficient quantities of the substance must remain in the growing point for sufficient time for flower induction to occur. Cholodny (10, 11) made a different approach by suggesting that florigen might be an ordinary auxin or auxin-like substance and not a specific flower inducing substance.

Lang (51), in discussing the physiology of flowering in long and short day plants, visualized two basically different possibilities: 1, an inductive day length which promotes flowering and 2, a non-inductive day length which inhibits flowering. The former implies that plants are not capable of flowering unless photo-induced so as to build up a flowering stimulus. The latter implies that plants are capable of flowering but flowering is suppressed by non-inductive day lengths which builds up a flowering inhibitor. From these possibilities Lang concludes that floral initiation, in long day and short day plants, is determined by flowering stimuli generated in the leaves and translocated to the growing

point. He further concludes from results of grafting experiments with long and short day plants that the flowering stimuli of the two plants are similar and possibly the same. Definite proof has not been established, as pointed out by Lang, that substances extracted from flowering plants and introduced into non-flowering plants caused floral initiation.

Plants which require thermo-photoinduction build up two floral stimuli according to Lang (51). The stimulus produced during the cold treatment has been called "vernalinalin" and considered to be a precursor which acts as a catalyst of florigen formation. Purvis (68) believed the course of vernalization was autocatalytic. This could well be and if true explains why the stimulus cannot be extracted from living cells. The several hypotheses and possibilities set forth by Lang (51) can be explained on the basis of synthesis, level, economy and distribution of auxins or phytohormones¹. Many authors have preferred to explain their results with the phytohormone theory (4, 5, 6, 11, 14, 15, 25, 36, 41, 52, 55, 57, 92, 93, 94, 95). The recent work of Leopold and associates (52, 53, 55, 57) have rather conclusively shown that auxins exert an effect on flowering in Winter barley, Alaska pea, Biloxi soybean and Winter rye.

Data have been reported (14) to indicate that phytohormone content fluctuates in celery during and subsequent to cold-induction treatment. A low phytohormone level during induction followed by an

¹ See Terminology, page 24.

increase subsequent to induction appears to be associated with seed stalk initiation (14,51). Gustafson (36) presented data which show a reduction in phytohormones in plants grown at temperatures above 30° C. Brandis and McQuire (8) have shown that heat (52° C. for 20 minutes) destroys the geotropic response in crops with intercalary meristems such as sugar cane. This response was restored by soaking the plants in a solution containing 100 mg./l of indoleacetic acid. Their data strongly suggest that low temperature had a similar effect which indicates there are minimal, optimal and maximal temperature ranges for auxins and phytohormones. Leopold (57) presented data which conclusively show an interaction of auxin and temperature in flower initiation. He found a differential response to auxin applied to long day, short day and indeterminate plants which were grown under various temperatures. Auxin (NA) treated plants subsequently grown under low temperature conditions flowered earlier and more profusely than the controls. Under average temperatures (18-20° C.) applied auxin had no effect or inhibited flowering depending on the plant.

Van Overbeek et al (94) found that the stem apices of pineapple plants contained large quantities of free phytohormone (called free auxin by Van Overbeek) but small amounts of bound phytohormone (bound auxin); whereas, the leaf basis contained little free and large quantities of bound phytohormone. Skoog (80) considered cabbage leaves to contain relatively large amounts of bound phytohormone, or 4 mg. per kg. fresh weight. Van Overbeek et al (94) assumed the transformation of bound phytohormone

to free phytohormone to cause flowering in pineapple. Low temperatures may reduce the free or active phytohormone content in the apex, cause a change of phytohormone distribution in plants or modify the phytohormone mechanism so as to release the bound phytohormone in the leaves. This hypothesis takes into account the function of the leaves and stem tips in floral initiation. It finds support in experimental evidence with pineapple (94); celery (14,21); and barley, soybean, pea, and rye (57).

Results reported here with respect to cabbage appear to be readily explained by the auxin or preferably phytohormone theory. With this theory it becomes necessary to make certain assumptions. First, temperature alters the phytohormone mechanism. Such an assumption is feasible since an interaction between temperature and auxin and temperature and phytohormones have been demonstrated experimentally (14,21,57). Second, low temperatures (below 45° F.) and high temperatures (85° F. and above) tend to lower the free phytohormone level (8,14,21). Third, vegetative growth is favored by a static phytohormone supply, and reproductive growth is favored by a rather high phytohormone supply following a rather low one (14,21,94). Along with these assumptions, certain generalizations can be made. First, cabbage plants held at temperatures of 50° to 80° F. remain vegetative possibly as a result of an economic use of a static phytohormone supply. Second, plants held below 45° F. for sufficient time tend to bolt as a result of a reduction of free phytohormone in the apex followed by a sharp

increase brought about by a release of the bound form in the leaves. Third, the reason large cabbage plants bolt more readily than small ones might be elucidated by the possibility of a greater supply of bound phytohormone existing in large plants than in small. Such a thought is corroborated by the fact that temperatures below 45° F. for two to four weeks change the growth character in small plants (7), although such treatments are insufficient to induce the reproductive phase. Fourth, differences in bolting tendencies among varieties may be interpreted on the basis of a greater phytohormone stability existing in slow bolting varieties, such as Round Dutch, than in varieties which bolt readily, such as Golden Acre. The bound phytohormone might be released to the free form faster in Golden Acre than in Round Dutch. Such is the case in bolting and slow bolting celery varieties (14). If true with cabbage it explains why certain varieties require longer cold treatments than others to induce the reproductive phase.

The devernalization response brought about in cabbage as mentioned above by high temperatures may well be explained on the basis of a lowering of the phytohormone content by the high temperatures. Growth characteristics of devernalized plants were almost identical with plants treated with MH, which indicates that MH may be an anti-phytohormone as well as an anti-auxin as demonstrated by Leopold and Klein (54).

An hypothesis is presented above with reference to a possible role played by phytohormones in the transformation from the vegetative

to reproductive growth phase in cabbage. The question arises as to the role of synthetic growth-regulating substances when applied to various plant sizes at varied times with respect to cold-induction. Apparently 2,4-D exerted an influence upon the phytohormone mechanism which tended to stabilize the free phytohormone supply, irrespective of the time it was applied. Responses were similar in large, medium, and small plants. The degree of effectiveness, however, was greater in small and medium than in large plants. These differences might be explained on the basis of a greater total quantity of bound phytohormone in large plants than in smaller ones. Possibly 2,4-D was more stable than the phytohormones to low temperatures.

Response to ClPP varied consistently with time of application. Flowering appeared to be stimulated when this substance was applied before or after the cold-induction treatment. In sharp contrast, flowering was inhibited or suppressed when ClPP was applied during cold-induction. The outstanding response from this chemical was obtained when plants were medium size. Plants treated before or after cold-induction flowered earlier and more profusely than the controls. Those treated during the induction treatment did not flower, and only 4 out of 20 plants tended to develop seed stalks. There appears to be no clear, all-encompassing explanation of these results. It might be assumed that low temperatures gradually lower the free phytohormone content. Apparently it is necessary for the relative level of free phytohormone to drop rather low, or to fluctuate widely before the reproductive

phase is induced. If such is the case, plants sprayed with ClPP before induction had a normal phytohormone content and a high auxin-like chemical content at the beginning of the cold storage treatment. As a result of low temperature the relative levels of these chemicals were reduced, followed by a sharp increase after the cold-induction treatment. The results suggest that within certain limits the range over which these substances fluctuates may be a more decisive factor than the actual quantity at any given level. Lack of seed stalk development and subsequent flowering in medium size plants sprayed during the cold-induction treatment may be similarly explained. The relative level of free phytohormone at the beginning of induction was biologically the same as in plants sprayed before induction. No chemical was applied however to raise the relative auxin level as with plants sprayed before induction. During the first 21 days of cold-induction treatment low temperatures did not reduce the free phytohormone to a level sufficiently low to induce the reproductive phase, or did not effect adequate release of the bound form. At the end of 21 days more auxin-like chemical (ClPP), was applied which may have raised the level of auxin-like substances in the plants. This substance (ClPP) in some way served at least some of the same functions as phytohormone. Then the remaining 21 days of cold-induction treatment were insufficient to effectively reduce these substances low enough to induce the reproductive growth phase. Another possibility is the application of ClPP during cold-induction prevented the wide fluctuation in phytohormone content

necessary to induce reproductive development. The stimulative response from ClPP applied after induction can therefore be explained on the basis of a low level of free phytohormone resulting from the low temperature treatment followed by an extremely high level of auxin brought about by the application of ClPP, and the release of bound phytohormone. This high auxin level following cold-induction stimulated growth and reproductive development.

The phytohormone theory is also applicable to the results obtained with MH applied to medium size plants at varied times with respect to the cold-induction treatment. Definite evidence has been presented that MH is an anti-auxin (53, 54) and this chemical might therefore be useful in reducing the free phytohormone level. Data reported here lends evidence to such a possibility. Round Dutch plants sprayed before a partial cold-induction treatment developed more open heads than the controls. Although these plants produced more open heads no seed stalks or flowers appeared. Such response may be interpreted as meaning that MH reduced the free phytohormone supply in the apex. In view of the fact that comparatively little growth occurred in the MH treated plants it seems likely that MH altered the entire phytohormone system to the extent that bound phytohormone in the leaves was not released to the free form, and translocated to the apex so as to effect growth. All plants sprayed with MH during cold-induction produced open heads, and about half of them developed elongated stems and leaves morphologically characteristic of reproductive plants. The lack of

flowering response in this treatment was due possibly to the same reason as those sprayed before induction. The terminal bud was killed in most plants sprayed after cold-induction. The reason for the lethal response obtained is believed to be due to the higher temperatures endured following chemical treatment by these plants than by those sprayed before or during induction. Plants sprayed before and during the cold treatment were subjected to approximately 38° F. following spray applications. Those sprayed after cold-induction were moved immediately to a greenhouse where the average temperature was above 65° F. More of the active MH chemical was probably absorbed by the plants at this higher temperature, resulting in severe stunting or killing of the terminal buds. Had MH sprayed plants been subsequently treated with an auxin or auxin-like substance the results might have been very different. Klein and Leopold (45) suggest that MH has no direct influence on flowering but alters the auxin mechanism which subsequently affects flowering. Results of these experiments indicate that MH alters the phytohormone system which subsequently affects flowering.

With respect to the morphological studies it will be recalled that large plants had correspondingly larger growing points than medium or small ones. Too, only slight changes occurred in the growing points while the plants were being cold treated. Then, after growth started in the spring there were no major gross changes in the terminal growing points of plants making vegetative growth, but cells elongated and lateral buds developed in plants making reproductive growth. The first

and most reliable morphological evidence of reproductive growth found in this study was longitudinal rows of cells in the rib meristem and growth of lateral buds. These morphological changes preceded flower initiation as much as 15 to 30 days, whereas experimental evidence presented (75,84) on cambial activity, limited phloem cell formation, increased cell wall thickness, freer staining of certain tissues, and the accumulation cell inclusions occur shortly before or concomitantly with flower initiation. Shoushan (79) found intra-cellular accumulation of starch granules just prior to flower initiation in Lillium. He also found that flower initials arose in the second the third cell layers of the flanking meristem, and leaf initials arose in the third and fourth cell layers. Examination of cabbage meristems in this study clearly demonstrated that all lateral appendages arose in the third and fourth cell layers of the flanking meristem. The last morphological evidence of reproductive growth was the origin of flower primordia in the axils of dwarf leaf primordia. Since these sessile leaf primordia eventually ceased to differentiate they signified the final stage of the gradual transition from vegetative to reproductive development. Apices of cabbage shoots remained unchanged as the stem axis elongated and produced lateral appendages. In vegetative plants these lateral appendages were leaves and in reproductive plants they were either dwarf leaves, lateral shoots, or flowers. The terminal apices did not differentiate into flowers, however, flowers arose so closely together near the apices of mature flowering stalks that they appeared to

the unaided eye to terminate the flowering stalk. The irregular order of appearance of flower parts (sepals, stamens, pistil and lastly petals) agrees with the findings of Thompson (89) and is the common order for the cruciferae family.

The findings in the morphological studies coincide with growth and flowering responses as discussed in the phytohormone theory. An important point concerning these studies was the general cellular disorganization in growing points harvested February 24 of medium size plants sprayed during the induction treatment. Auxins as well as the substituted phenoxy compounds have been found to activate growth by increasing cell division and cell elongation (2). Proliferation of various tissues, development of roots and shoots from callus, and general increase in growth resulting from the application of phenoxy compounds as reported by Beal (2) and shown in this study, strongly indicate that their main function morphologically is to encourage cell division and growth. There are indications that cellular organization during normal seed stalk initiation is involved in determining the growth phase which follows. Evidence presented in this study suggests that ClPP applied during a cold treatment influenced cellular organization. Until further work is conducted on this subject it would be presumptuous to claim that this phenomenon was brought about solely by the chemical treatment.

Maleic hydrazide appears to prevent cell division by inhibiting mitosis (16,22,24,34,69). Apparently this substance does not

interfere with cell elongation (34). Chelidonic acid (56) and alpha cyano-B (2,4, dichlorophenyl) acrylic acid (58) have also been found to inhibit plant growth. Plant response to the acrylic acid formulation appeared to be similar to that of maleic hydrazide. One major difference noted was that axillary bud development appeared not to be affected by alpha cyano-B (2,4, dichlorophenyl) acrylic acid. Further research with these chemicals is necessary before their auxin and anti-auxin properties are fully understood.

The genuine mechanism involved in the transformation from one growth phase to another remains obscure. Whether it be from the formation of a specific flower-inducing substance (florigen) or some other more complex phytohormone system affords intriguing speculation. The systemic nature of reproductive growth in cabbage is demonstrated first by the reproductive characteristics of young developing lateral shoots; second, by the production of numerous lateral seed-stalk branches; and third, by the devernalization response as accomplished by exposing mature flowering plants to high temperatures. The individual cell most likely encompasses the basic factor or factors involved. The course of development in cabbage is governed by temperature, light, water, and the food and nutrient supply. The genetic constitution plays a major role in the type and quantity of response. It is of importance to know that certain growth-regulatory substances used properly alter the quantity and quality of plant development. To this extent growth and development may be controlled or manipulated

in such a manner as to obtain the desired plant response.

SUMMARY

Response to 2,4-dichlorophenoxyacetic (2,4-D); alpha, ortho-chlorophenoxypropionic (ClPP); alpha naphthaleneacetic (NA); and 2,3,5-triiodobenzoic acid (TlBA); and maleic hydrazide (MH) varied with concentration, time of application and size of cabbage seedlings. Concentrations in ppm were: 5, 10, 15 and 20 2,4-D; 50, 100, 250 and 500 ClPP and TlBA; 100, 250, 500 and 1000 NA; and 250 MH. The three plant sizes were large (stem diameter 9 mm.), medium (6 mm.), and small (4 mm.). Most of the work dealt with the medium size.

Without an accompanying cold-induction of 38° F. for six weeks no chemical affected flowering. Almost complete inhibition of reproductive development was achieved in medium size Golden Acre sprayed during cold-induction with 250 ppm ClPP. Flower initiation and development was stimulated in large and medium plants by ClPP applied before or after induction. Response to 15 ppm 2,4-D was similar, but less pronounced. Spraying large plants during induction with 2,4-D or ClPP retarded flowering two weeks.

Sprays of 250 ppm of MH applied before partial induction of medium size Round Dutch plants induced open head development and when applied during partial induction promoted seed stalk development in many plants that otherwise would have remained vegetative. Although 50 percent of the plants in this treatment produced seed stalks, none flowered. Terminal buds were killed and subsequent growth suppressed for one year by MH applied after partial induction.

Low concentrations of auxin-like chemicals (2,4-D, ClPP, NA) applied before cold weather generally promoted vegetative development and stimulated growth in height for two months in medium size plants of both varieties. Proliferation of tissues, malformation of leaves, and shoot and root development in and around callus tissue were common with high concentrations of 2,4-D and ClPP. Plants sprayed with TIBA in concentrations up to 500 ppm resembled the controls.

The most reliable morphological changes indicative of reproductive development were the formation of longitudinal rows of cells in the rib meristem, lateral bud development and dwarfing of young leaves. Appearance of these changes varied among treatments but occurred about February 24 in large and medium size plants. Spraying large or medium plants with ClPP (250 ppm) before or after cold-induction hastened the appearance of these changes. Large plants sprayed during induction initiated reproductive growth two weeks later than controls. Plants of medium size sprayed with ClPP during induction showed no evidence of reproductive growth as late as April 27. The apices did not become dome-shaped but remained unchanged in the transition from vegetative to reproductive development.

Leaf and flower initials arose from periclinal cell division in the third and fourth cell layers of the flanking meristem just below the shoot apex. Flowers were produced laterally as were the leaves and did not terminate the seed stalk. Flower initials were distinguished from

leaf initials by gross changes associated with reproductive growth. When flower initiation began the subtending leaf became dwarfed. After several flowers were produced the leaf developed no further than the primordial stage.

A method for numerically evaluating the degree of reproduction was presented. Vegetative and reproductive growth, and floral development were histologically presented and discussed on the basis of synthesis, distribution and economy of phytohormones.

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