EFFECTS OF VARIOUS PLANT REGULATORS ON THE GROWTH AND DEVELOPMENT OF SELECTED HERBACEOUS ORNAMENTALS

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EFFECTS OF VARIOUS PLANT REGULATORS ON THE GROWTH AND DEVELOPMENT OF SELECTED HERBACEOUS ORNAMENTALS

By

CHARLES ALLEN FOUNTAIN

AN ABSTRACT

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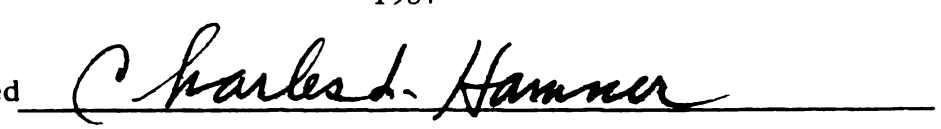
Approved 

CHARLES ALLEN FOUNTAIN ABSTRACT

The effects of various plant regulators on the growth, morphology, flowering and chemical composition of selected herbaceous ornamentals has been studied. In addition, tests were conducted to determine the effects of an interaction of regulators and vernalization and the effects of an interaction of growth regulators and photoperiods on plant development.

To determine the effect of an interaction of chemicals and vernalization, foliage sprays of 5, 25 and 100 parts per million of maleic hydrazide, 2, 3, 5-triiodobenzoic acid, and indoleacetic acid were applied to candytuft and snapdragon seedlings. Germinating seed were treated with concentrations of 1, 5 and 10 parts per million of the above regulators. Seedlings and germinating seed were subsequently exposed to a temperature of $40^{\pm}$ 2° F for 2 or 3 weeks.

The effects on plant development of sodium trichlorobenzoate, 2, 3, 5-tribromobenzoic acid, 5-chlorosalicylic acid, and 2, 3, 5-triiodobenzoic acid were determined by spraying wallflower and phlox plants with concentrations of 100, 500, and 1, 000 parts per million.

To determine the effects of repeated and single application of 2, 3, 5-triiodobenzoic to progressively older phlox plants, applications of 50, 100, 500 and 1, 000 parts per million were repeated three times at weekly intervals. To other plants these concentrations were applied as single treatments to 2-, 3-, and 4-week old phlox.

Effects of an interaction of plant regulator and various photoperiods were determined by spraying phlox seedlings, which were growing under natural, 8-hour 16-hour, and 24-hour photoperiods with 100, 500, and 1,000 parts per million of 2, 3, 5-triiodobenzoic acid.

Application of growth regulators did not affect the number of days from seeding to first flower of candytuft seedlings. During the spring application of plant regulators resulted in a decrease in number of days from seeding to flowering of snapdragons, however, when applications were made in late fall there was no significant effect on days to flowering. Generally, any acceleration of flowering was accompanied by an increase in nodes and weights of flowering plants.

An interaction of growth regulators and vernalization did not affect the number of days to flowering. However, vernalized seedlings required significantly fewer growing days to flowering than non-vernalized. Weights of plants were significantly reduced by vernalization. Chemically treated and vernalized germinating candytuft seeds generally flowered earlier than untreated vernalized seeds. Vernalization of treated germinating snapdragon seed gave varying results. Vernalized seed required fewer growing days to flowering.

All concentrations of chemicals resulted in delay of flowering in wallflower and phlox. Repeated and single applications of 2, 3, 5-triiodobenzoic acid

to phlox also resulted in delay of flowering and reduction of weight.

The interaction of photoperiods and 2, 3, 5-triiodobenzoic acid on flowering of phlox was promotive only under the 8-hour photoperiod. Flowering was delayed by chemical treatment under other photoperiods. Chemical composition of flowering plants was also affected under the 8-hour photoperiod where a decrease on carbohydrated was noted.

Pronounced morphological and teratological changes resulted from most chemical applications. The prevalence and magnitude of these changes were largely dependent upon chemical concentrations used, physiological activity of the chemical, plant type, and environmental conditions.

The results of the present research were discussed in view of the reports of others relative to the influence of chemical treatments, vernalization and photoperiods on the vegetative, flowering, morphological, and chemical responses in plants.

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INTRODUCTION

It is widely known that auxins play an important and often controlling role during the phenomena of vegetative and reproductive development. Thimann (1957) has concluded that the type and magnitude of responses obtained with growth regulating chemicals depend upon the amount of the compound absorbed by the plant, the amount translocated within the plant, and the inherent ability of the plant to respond to the stimulus of the particular chemical that is applied.

The ability of the plant to respond to the stimulus of a particular regulator is largely dependent upon the kind or variety of plant treated, the part of the plant treated, and its stage of development. In addition to the above factors, plant responses induced by growth regulators are modified and sometimes counteracted by the environmental factors to which the plant is exposed before, during, and after auxin application. Photoperiod and temperature are two of the most important environmental factors which affect subsequent growth and development of auxin treated plants.

Since Garner and Allard (1920) first recognized the importance of daylength as a major factor in growth and development, especially as it affects sexual reproduction, this environmental factor has been rather extensively investigated. There are now available a number of general reviews (Hamner,

1942; Hamner, 1944; Murneek and Whyte, 1948; Borthwick et al., 1952). These reviews have shown that as soon as chlorophyll is formed in leaves of the young seedlings, the photoperiodic influence of the environment can begin to operate, and from then on the behavior of plants appear to depend upon the interrelationship of temperature and light. Although day length may act to modify any and all structural parts of the plant, its influence is modified and sometimes counteracted by other environmental factors, especially temperature.

The role of temperature, particularly as it applies to early cold treatment of seeds and seedlings, has also been widely investigated. The report of Klippart (1857), in which it was shown that winter wheat could be converted into spring wheat by exposing slightly germinated seed to low temperature, were followed by numerous others (Gassner, 1918; Lysenko, 1946; Purvis, 1934; Gregory and Purvis, 1936; Purvis and Gregory, 1953).

The experiments which follow were conducted to determine some of the effects of selected plant regulators upon the growth and development of several herbaceous ornamentals. Also, an attempt was made to determine plant response to auxin as influenced by vernalization and photoperiodism.

REVIEW OF LITERATURE

Effect of Plant Regulators on Vegetative Development

Among the numerous responses of plants to natural and synthetic plant regulators are the quantitative inhibition or acceleration of vegetative development. Leopold (1955) stated that a remarkable "dualism" exists in the action of auxin. Auxin can either stimulate or inhibit the various growth functions. The effect obtained is primarily a function of the effective auxin concentration in the tissue.

A review of the literature indicates that auxins and other plant regulators sprayed onto plants, or added to their root media in dilute solutions, have given varying and sometimes conflicting results. Hitchcock and Zimmerman (1935) have reported that indoleacetic, indolepropionic, indolebutyric, naphthaleneacetic, phenylacetic and phenylpropionic acids applied to tomato and tobacco plants retarded top growth. Pearse (1937) has found that indoleacetic acid sprayed on broad bean plants caused a decrease in root weight and a decrease in top growth.

The inhibition of one plant part by applied plant regulators is not usually accompanied by any compensating growth elsewhere in the plant, and involves a real decrease in the total dry weight (Thimann 1937). The inhibition of

lateral bud development in pea seedlings was not reflected by greater growth of the central axis, nor was the inhibition of root elongation due to a corresponding increase in thickness. It was suggested that roots, buds, and stems all behave in a comparable way, their growth being inhibited by a relatively high and promoted by a relatively low auxin concentration. Differences between them are usually of a quantitative rather than a qualitative nature. Pearse (1937) observed that young tomato plants treated with a daily application of either phenylacetic acid or indolebutyric acid resulted in an increased height of plants with longer petioles and internodes. Phenylacetic acid depressed root and leaf growth, but increased the growth of stem and petiole, while indolebutyric acid depressed leaf growth, but increased that of root, stem, and petiole.

Grace (1937, 1938) found that progressive gradients of naphthaleneacetic acid solution produced a characteristic physiological growth curve. A marked stimulation in growth at low concentrations was followed by inhibition and damage as the amount was increased to an excess. Green weight of eight-week-old lettuce plants was increased more than three hundred percent by addition of an equivalent of 150 milligrams of naphthaleneacetic acid to an acre of soil. Total dry weight of treated plants was never higher than that of untreated.

Thimann and Lane (1938) and Audus (1953) have suggested that any sus-

tained acceleration of the general vegetative growth of plant shoots after treatment of young plants with auxins is probably an after effect due to the promotive effect of auxins on root systems. If the concentrations used are not too high, or the exposure too long sustained, then a more extensive root system could theoretically result with consequent benefit to the plant. Dry weight of plants, which may be increased more than fifty percent, is therefore, primarily due to the greater efficiency in uptake of minerals and water by a more extensive root system.

Zimmerman and Hitchcock (1942) described the various growth responses induced by substituted phenoxyacetic and benzoic acids. The most active were 2, 4-dichlorophenoxyacetic acid and its derivatives. Cell elongation of tomato plants has been induced with concentrations of 2, 4-dichlorophenoxyacetic acid as low as 0.0007 percent in lanolin paste. The ability of bromo-3-nitrobenzoic acid to induce cell elongation has also been noted. The straight growth method with Avena coleoptiles has shown high physiological activity for 2, 3, 6-trichlorobenzaldehyde (Bentley, 1950). In other tests, likewise, the physiological activity of these substances has been noted (Muir and Hansch, 1951; Thimann, 1951; Zimmerman and Hitchcock, 1951).

Thimann and Bonner (1948) have postulated that triiodobenzoic acid allows a small amount of endogenous growth substance to bring about a disproportionate amount of growth. Triiodobenzoic acid is believed to be

sufficiently like in structure to indoleacetic acid to be able to combine with the same substrate within the plant. This combination does not bring about growth, but (if the concentration of triiodobenzoic acid is not too high) it still leaves a small number of spaces or active groups open on the substrate with which the endogenous auxin can combine. The result is that growth takes place with an expenditure of a smaller number of auxin molecules than are normally required. Higher triiodobenzoic acid concentrations, however, take up all the spaces or active groups, so that indoleacetic acid is excluded and growth is inhibited.

The action of maleic hydrazide (1, 2-dihydro-3, 6-pyridazine-dione) was first reported as a unique growth regulant after six-inch Bonnie Best tomato plants which had been sprayed with 2, 000 parts per million failed to grow for a period of about two months. After one month some chlorosis developed on younger leaves, but otherwise the plants were normal in appearance. After the quiescent period, growth resumed mainly from lateral buds (Schoene, 1949). Wittwer (1954) has stated that maleic hydrazide appears to produce effects opposite to those induced generally by indoleacetic acid, naphthalene-acetic acid, and a number of other regulators which generally promote growth. It inhibits terminal growth and stem elongation, and destroys apical dominance, whereas the growth-promoting substances favor terminal growth and stem elongation, and promote apical dominance. Lateral bud development

is stimulated by maleic hydrazide and inhibited by growth-promoting substances.

Leopold and Klein (1951) employed the split-pea, straight growth, and the Avena straight growth test to determine the relation between indoleacetic acid level within the plant and the growth response induced by application of maleic hydrazide. It was observed that maleic hydrazide had a greater inhibitory effect on plant growth when the native auxin level was high. This suggested that the auxin may counteract the action of maleic hydrazide. Therefore, it was suggested that maleic hydrazide should be classified as an anti-auxin.

Currier and Crafts (1950) have demonstrated that various types of plants react differently and that the age of plants is critical, young plants respond to a greater extent, older plants show some response, but survive concentrations which may be lethal to younger plants. Thus, the effects of maleic hydrazide on vegetative growth are determined largely by the age and species of plants treated and the concentration of the chemical applied.

Recently gibberellin has been shown to promote the growth of a wide variety of plants, including grasses, vegetables, and ornamental plants. It induces rapid lengthening of stems or internodes, broadening or elongation of leaves, and an increase in height. No significant increase in dry weight was reported (Bukovac and Wittwer 1956; Wittwer and Bukovac 1957).

Effect of Plant Regulators on Morphology

Another characteristic response of plants to applied plant regulators is the tendency to produce a diversity of morphological abnormalities.

Kraus et al. (1936) found that the response of different tissues varies when decapitated Red Kidney beans were treated with thirty milligrams of indoleacetic acid per gram of lanolin paste. In general, there was a very great speeding up of nuclear division and derived cells remained meristematic for a prolonged period. Epidermal cells became somewhat enlarged and underwent a few divisions in the radial plane. Cortical parenchyma cells enlarged and those near the endodermis became meristematic. Endodermal cells underwent accelerated nuclear division and walls formed in all planes, especially in the tangential. Derived cells differentiated into xylem, phloem and into large, often multinucleate parenchymatous cells. Many remained meristematic, others gave rise to adventitious roots, and into long strands of vascular tissues, especially over the vascular bundles, where they frequently enlarged to rupture exterior tissues, and appeared as tumors in rows along the stem. Cells of the pericycle and parenchyma of the primary phloem proliferated slightly while the parenchyma of the secondary phloem, the ray cells and pith proliferated greatly. Similar responses have been obtained by Borthwick et al. (1937) when decapitated tomato plants were treated with

twenty milligrams of indoleacetic acid per gram of lanolin. Skoog and Tsui (1948) with tobacco tissues and Ropp and Markley (1955) with sunflower seedlings noted comparable results.

The formative activities of substituted benzoic and phenoxy acids have been rather widely reported. Zimmerman and Hitchcock (1942) and Hitchcock and Zimmerman (1952) reported that all chlorophenoxy compounds having growth activity also induced morphogenic responses. The new organs which developed after treatments were modified as to size, shape, and pattern of venation. Triiodobenzoic acid did not induce immediate rapid cell elongation, but the ultimate results resembled those of indole and naphthalene regulators. Leaves or parts present at the time of treatment were not modified. The influence was, therefore, of a formative nature, effective on growing organs. Affected tomato plants grew odd-shaped leaves with translucent veins and pronounced pubescence. Stems showed odd curvatures as growth progressed.

Snyder (1948) has observed that five to two hundred and fifty parts per million of triiodobenzoic acid inhibited rooting of terminal cuttings of coleus and stimulated axillary bud development on Red Kidney beans and California privet. Coleus tissue was injured by repeated treatments of twenty-five or more parts per million, and by a single treatment of one hundred parts per million or more; however, no formative effects were noted. In beans, shortening of internodes and production of more trifoliate leaves on the main shoot

occurred when the chemical was applied above the primary leaves. The results were negative curvature of the stem at the point of application, abnormal leaf development, and premature death and abscission of apical and in some cases axillary buds.

Some months after Kalanchoe blossfeldiana had been treated with triiodobenzoic acid, various anomalies appeared, particularly the growing together of leaves originally opposite. There was also more or less growing together of the main axis with both of the well developed highest lateral shoots (Thimann and Bonner, 1948).

Triiodobenzoic acid applied to tomato plants altered the shape and structure of their growing points in such a way that they lost their capacity to split off leaf primordia. Instead, they grew out in straight cones which were characterized by irregular systems of noticeable thick-walled cells. This peculiar abnormality, ring fasciation, has been described as resulting from the connate growth of several apices. It is characterized by a ring-like growing point, which gives rise to a hollow stem with an internal cavity lined by an internal epidermis. Both outside and inside epidermis may produce leaves, bracts, and irregularly axillary buds (Gorter, 1949, 1951).

Wardlaw (1953) has suggested that triiodobenzoic acid causes a cessation of growth in the most distal cells of the apex, but admits slow growth in the subjacent region. As a result, apices of unusual configuration and organ-

ization are produced. It was also suggested that a ring fasciation can develop both from a single apex or from the connation of two or more leaves. Similar results have been reported by Kraus and Mitchell (1947); Whiting and Murray (1948); Niedergang et al. (1952); and Waard and Forsahultz (1948).

The formative effects of maleic hydrazide was first reported by Schoene and Hoffman (1949). When the inhibited terminal buds of tomato plants began to grow formative effects were produced. Fillmore (1950) found that maleic hydrazide inhibited growth of Paul Scarlet rose cuttings and after eleven weeks only abnormally elongated leaves were produced. Darlington and McLeish (1951) have reported that the growth restricting effect of maleic hydrazide destroyed apical dominance of shoots, inhibited root growth, destroyed germ cells, and stopped mitosis at higher concentrations. Lower concentrations did not stop mitosis, but caused breakage of chromosomes at mitosis. This effect has also been reported by Compton (1952).

Results from tests by Tatum and Crume (1951) showed pronounced differential response of various strains of corn to different concentrations of maleic hydrazide. In some strains treatment resulted in one or two aborted branches, and upper leaves were narrow and abnormal in appearance. Currier and Crafts (1950) also observed a selectivity of action by maleic hydrazide. In addition, the age of plant was critical, young plants responded to a greater extent than did older.

Maleic hydrazide has been found to cause nuclear aberrations in the cells of the protoderm and ground meristem. Normally meristematic apical cells became large and vascoulated, this caused a broadening of the apical region. Precocious differentiation of all cells in the developing shoot axis and leaves occurred, cell walls of the ground parenchyma and phloem became thickened, and later extensive obliteration of phloem and xylem accompanied general necrosis in mesophyl and pith. Premature growth of axillary buds was caused almost exclusively by cell enlargement (Compton 1952; Greulack and Atchison 1950, 1952; Gifford 1956; Watson 1952; and Beach and Leopold 1953).

The action of other growth regulatos on morphology has been reported. Watson (1948) found that 2, 4-dichlorophenoxyacetic acid caused distortion of leaves of bean plants. A delayed expression was associated with the stage of development of a leaf at the time of treatment. Dersheid (1952) observed several types of abnormalities when barley seedlings were sprayed with 2, 4-dichlorophenoxyacetic acid. There were tubular leaves, blasted florets, tweaked spikes, double spikes, and multiple spikelets. Other workers have reported chemically induced morphological changes with various growth regulators (Hamner et al. 1946; Felber 1948; and Skoog and Tsui 1948).

Applegate (1956) has demonstrated with Zinnia that one thousand parts per million 5-chlorosalicylic acid causes the production of abnormal leaves which may be strap-like, or fused, or have proliferated vascular tissue.

Effect of Plant Regulators on Flowering

Because of its great economic importance, the control of flowering by external application of growth regulators has attracted the attention of many investigators. Results from several independent sources have suggested that growth-regulating substances might be used supplementary to temperature and day length adjustments as a means of regulating flowering in many horticultural crops (Wittwer 1954).

Stier and DuBerry (1938) have shown that treatment of tomato seeds and subsequent treatment of plants with either indolebutyric or naphthaleneacetic acid at transplanting time can with certain combinations and proper concentrations result in marked acceleration of flower anthesis. On the other hand, marked inhibition of flowering occurs when high concentrations are employed. Clark and Kerns (1942) and VanOverbeek (1946) found that 0.006 percent water sprays of naphthaleneacetic acid and other naphthalene compounds sprayed on the foliage of pineapple plants hastened the formation of flower two months in advance of the normal flowering date. However, one-tenth percent sprays of the same chemicals delayed flowering beyond the normal flowering date. The above results agree with those of Wittwer et al. (1947) who demonstrated that for a given plant the same growth substance may accelerate or retard flowe ing, depending on the concentration used.

Green and Fuller (1948) treated petunia plants with two hundred parts

per million indoleacetic acid as they were approaching the flowering stage. Not only was further floral initiation prevented, but the opening of buds which had formed previous to auxin treatment was also delayed.

Galston (1946) found that no vegetative plants of Peking soybeans were induced to flower by application of triiodobenzoic acid, however, chemical treatment of photo induced plants produced a ten-fold increase in the number of flower buds formed.

Salisbury (1955) reported that applied auxin exerted two qualitatively different effects upon the flowering of Xanthium. Auxin applied before, during, or for some time after an inductive dark period inhibited subsequent flowering. Auxin applied after translocation of the flowering hormone from the leaf had been completed, promoted flowering by increasing the rate of flower bud development. He suggested that the promotive effect of the applied auxin was independent of the leaf, and appeared to be exerted directly upon the bud; whereas, the inhibitory effect of auxin on induction occurred only in the leaf where it induced the disappearance of the flowering hormone. It was further suggested that auxin applied after induction can substitute for active buds or young leaves which are normally required during and after induction. Lang (1952) has suggested that auxin applied before or during the induction period of short-day plants inhibits the formation of the floral stimulus. Comparable results with Biloxi soybeans and cocklebur have been obtained by deZeeuw and Leopold (1956).

Khudairi and Hamner (1954) induced flowering in Xanthium grown continuously under long-day conditions by exposing the plants to gaseous ethylene chlorohydrin, an agent which lowered the auxin content in plants. Thus, floral initiation depended on a reduction of the physiological auxin level in the plant. High auxin level seems to inhibit floral stimulus during photo-induction, especially if present at the beginning of the photo-induction period (Lang 1952).

Wittwer et al. (1954) have found that fifty to one hundred parts per million maleic hydrazide applied before cold induction of celery plants having eight to ten true leaves induced flowering in many plants which otherwise would have remained vegetative. A concentration of five hundred to one thousand applied at a later stage (thirty-seven true leaves) retarded the development of seedstalks.

Leopold and Thimann (1948) reported that low concentrations of naphthaleneacetic and indoleacetic acids promoted the floral expression of winter barley. However, Hussey and Gregory (1954) in later experiments of a similar nature, found that floral initiation was not promoted by low auxin treatments, but the number of flower primordia was increased. It was suggested that the role of auxin in the promotion of flowering as had been reported by Leopold and Thimann was probably a post initiation effect.

Recently it has been reported that twenty micrograms of gibberellin applied to stem apices as a foliar spray of ten to one hundred parts per million hastened flowering in stocks, petunia, larkspur, English daisy, China aster and gerbera from 10 days to four weeks when grown in the greenhouse during the fall and winter (Lindstrom et al. 1957).

Effect of Plant Regulators on the Chemical Composition of Plants

Changes in the chemical composition of a plant resulting from application of plant regulators may be direct or indirect expressions of any one of several responses, such as reduced growth, increase growth, flower bud initiation, inhibition of flower bud formation, increased respiration, and an increased pigmentation of the foliage (Weller et al. 1950). Alexander (1938) reported that the dry weight and percent of starch of bean plants treated with indoleacetic acid were less than that of unreated plants. The chemical caused simple carbohydrates to be condensed into complex polysaccharides. Stuart (1938) reported that treatment of Phaseolus vulgaris with indoleacetic acid brought about a directional shift of large amounts of nitrates and carbohydrates from leaves and other parts, principally to the treated area. Freeland (1949) found that growth regulators tended to decrease the rate of photosynthesis and increased the rate of respiration in beans. This action was reflected in loss of dry weight of treated plants. Audus (1949) also reported a stimulation of respiration and a shift in the starch-sugar equilibrium as a secondary action of auxin treatment. In addition, he found that auxin had a dissociating action on the complex plasma proteins.

Greulach (1952) after finding an abundance of starch in leaves of tomato and bean plants five weeks after treatment with 2,000 parts per million maleic hydrazide concluded that its delayed disappearance was probably due to a slowing down of the processes of hydrolysis and phosphorolysis by the chemical, or

that its high content may have been due to a lower rate of respiration and assimilation and to the interference of translocation in treated plants. McIlrath (1950) found that maleic hydrazide favored the accumulation of carbohydrates in treated plants, while the non-carbohydrate constituents, such as proteins, were reduced by chemical treatment. Wittwer and Patterson (1951) have found that foliar sprays of maleic hydrazide at five hundred to 2,500 parts per million made in the field two weeks before harvest increased the sugar content and reduced loss of sucrose in storage of root crops.

Other chemical changes which have been reported after treatment with growth regulators are: (1) reduced percentages of protein, certain amino acids, and non-reducing sugars in the leaves and roots of kidney beans, but no significant change in reducing sugar, starch, polysaccharides, crude fiber, total ash, ether extract, or saponifiable material (Weller 1950); (2) an accumulation of protein and amino acids, a decrease in crude fiber, reducing and non-reducing sugars, and an increase in ash, ether extract, unsaponfiable material, and fatty acids in kidney bean stems (Sell et al. 1949); and (3) increased concentration of sucrose, hemicelluloses and decreased reducing sugars and organic acids in the main stalk of cotton plant (Ergle and Dunlap 1949). These results show that the changes induced may vary according to the plant part which is examined.

Wittwer and Sell (1955) have stated that biochemical studies of growth regulators used to induce rooting of cuttings, fruit set, and fruit maturity

have revealed that changes in composition are essentially the same as those processes that occur naturally in the plant. Application of the growth regulators tends to hasten the mobilization of carbohydrate and protein by hydrolysis to yield simpler forms and produce the above responses at an earlier date.

That the uptake of minerals from the root medium may be influenced by auxin treatments has been observed by several workers (Hamner, 1942; Nance, 1949; Rhodes, 1950; Loustalot et al., 1953; and Wildon et al., 1957). Uptake of minerals, as influenced by growth regulators, is largely dependent upon th complex interactions induced within the plant.

Effect of Vernalization and Photoperiods on the Response of Plants to Regulators

It has been stated that the two conditions which most frequently control plant development in a specific manner are day length and low temperature (Lang 1952). Since auxins are also known to be involved, it seems reasonable to assume the existence of an interaction between these three factors. This is especially true in regards to the flowering process.

Following this assumption, Leopold and Guernsey (1953a, 1953b) performed tests which demonstrated that an interaction between auxin (naphthaleneacetic acid) and temperatures in floral initiation existed in all types of floral initiation known, namely, photoperiodic initiation, vernalization, and indeterminate initiation. In each instance auxin either promoted or inhibited flowering, depending on the temperature and day length exposure following auxin treatment.

To demonstrate the interaction between auxin and vernalization, seeds of long-day Winter barley and short-day Biloxi soybean were treated with auxin after which they were given three or 18 degrees centigrade exposures for two weeks. When subsequently grown in the greenhouse under their respective inductive day length, it was found auxin treatment followed by the three-degree temperature exposure caused a fifty percent increase in the number of flower primordia, whereas, the same auxin treatment followed by eighteen-degree temperature exposure did not increase, and may have inhibited flower initiation.

The results were similar with both plant species.

To demonstrate the interaction during photoinduction, foliar application of auxin was made to Biloxi soybeans during this period. It was shown that floral initiation can be promoted by auxin with appropriate temperature control, since low temperature and auxin promoted floral initiation, whereas, floral initiation was inhibited at higher temperature by auxin treatment.

To demonstrate the interaction in indeterminate initiation, Alaska pea seeds were treated with auxin followed by three to ten degrees centigrade temperature exposure for one group, and 20 degree centigrade exposure for another group. At three to ten degrees, a quantitative promotion of flowering resulted, whereas, the same auxin treatment resulted in a quantitative inhibition of earliness at 20 degrees.

Purvis (1934) has also suggested that differentiation of flower primordia is subject to an interaction between day length and temperature during germination. It was concluded that these factors determine both the minimal number of leaves which must be formed before differentiation of flower primordia begins and rate of growth of meristematic tissue.

It has been hypothesized (Gregory and Purvis 1937) that during vernalization a flower forming substance or its precursor (named vernalin by Melcher 1939) increases in concentration so that a critical level is reached earlier. During short days a portion of this flower forming substance is converted into

a leaf forming substance, but, as the day lengthens beyond a certain minimum the leaf forming substance is retarded, therefore, the flower forming substance which now accumulates promotes the formation of flowers. Nevertheless, it was found that a certain minimum number of leaves must be formed regardless of day length before flower primordia formation is accumplished. From later experiments with excised mature embryos of winter rye, Gregory and Purvis (1938) concluded that the process of vernalization was localized in the embryo itself, and was entirely independent of changes which took place in other parts of the seed during germination. Purvis (1940) later found that whole grains of rye responded more rapidly than excised embryos to vernalization treatment. Thus, it was concluded that the embryo probably received some substances from the endosperm which accelerated vernalization.

Melchers and Lang (1942) suggested that the role of vernalization in flower induction is the prevention of removal by the leaves of the flowering-hormone during long dark periods in an intact plant. The inhibitory effect of leaves was related to an exhaustion of carbohydrates. It was suggested that low temperature might conserve the carbohydrates, thereby removing the restrictive effect of leaves.

The interaction between auxins and low temperature has also been noted by Rappaport and Wittwer (1956a, 1956b) with endive and lettuce, and by Chakravarti (1954) with Linum usitatissimum Linn.

Bukovac and Wittwer (1957) have reported that gibberellin seemed to partially, or in a few instances completely, substitute for the normal cold requirement for flowering in biennials, when applied as one or several foliar sprays of one hundred to one thousand parts per million, or as weekly doses of one hundred micrograms to the stem apices.

The effect of photoperiodic stimulus on the response of plants to applied auxins has been reported by several investigators. Zimmerman and Hitchcock (1937) found that prolonged dark periods caused plants to become more sensitive to growth substances. Plants in light when treated with low concentrations made maximum response in a relatively short time, and then tended to recover, but plants placed in the dark upon treatment showed more pronounced response and in many instances treated parts did not recover. Those in bright light tolerated higher concentrations than plants in partial shade.

Bonner (1949) and Bonner and Thurlow (1949) working with Xanthium, a short-day plant, found that indoleacetic acid or naphthaleneacetic acid sprayed on foliage during the photo-induction period suppressed initiation of florescence primordia. However, 2, 4-dichloroanisole and 2, 3, 5-triiodobenzoic acid applied to vegetative Xanthium plants induced the formation of flower-like buds under condition of long days in which untreated plants remained in the vegetative condition. The flower-like buds did not develop into mature flower and fruits as

in photoperiodically induced plants.

Lockhart and Hamner (1954) observed that when Xanthium plants were treated with indoleacetic acid at the beginning of the second dark period, immediately following the inductive dark period, the inhibitory effect on flowering of that period was greatly inhanced. It was suggested that the second dark period and indoleacetic acid acted either to destroy the flowering stimulus or prevented intermediate reactions in the production of the stimulus.

EXPERIMENTAL

General

These investigations were conducted in the Plant Science Greenhouses at Michigan State University, East Lansing, Michigan, and in the Campus Greenhouses of Hampton Institute, Hampton, Virginia.

The principal parts were concerned with the effects of various growth regulators upon the growth, morphology, and flowering of selected herbaceous ornamentals. In addition, tests were conducted to determine the effects of an interaction of growth regulators and vernalization, and the effects of an interaction between growth regulators and various photoperiods.

All plant species selected have been generally found to be definite in their temperature and photoperiodic requirements. Candytuft produces short flowering plants in summer, but are tall if grown in winter at lower temperatures. Phlox requires long days and high temperatures for earlier flowering. Summer-flowering snapdragon requires long days or high temperature for flower bud formation. Wallflower requires low temperature for flower bud formation.

Growth regulating chemicals used in these experiments were obtained from the Eastman Kodak Company, B. F. Goodrich Company, and the Dow Chemical Company. Selection were based upon their reported physiological activities. Indoleacetic acid, the native auxin, maleic hydrazide, a known

growth inhibitor, and the substituted benzoic and salicylic acids, which affect flowering, were used. Desired quantities of the chemicals were accurately weighed on analytical balances, dissolved in five milliliters of alcohol, and then diluted with distilled water to the desired parts per million concentrations.

Vernalization of seed and seedlings was accomplished by pregerminating seed in sterilized clay pots filled with a mixture of sterilized loam and peat, or on moistened filter paper in sterilized petri dishes. Seedlings or germinating seeds were then stored for a given time in a room which was continuously lighted and thermostatically controlled at 40± 2° F.

Increased photoperiods were obtained by supplementing the natural day length with Mazda lamps contained in reflectors suspended over the plants. The decreased photoperiod was obtained by drawing a black sateen cloth over the plants at 4:00 p. m., and removing it at 8:00 a. m. daily.

Plant responses to the various treatments were measured as given under the material and methods of each experiment. The analysis of variance was used to evaluate statistical differences of measurements.

Response of Candytuft to Application of Plant Regulators and Vernalization to Seedlings

Methods and Materials. Seed of Candytuft (Iberis umbellata var. Alba) obtained from Vaughn's Seed Company, Chicago, Illinois were sown February 28, 1955 in five-inch clay pots, which contained a mixture of steam sterilized loam and peat. Three pots were used for each of thirty treatments. After seeding, the pots were labeled according to a proposed treatment outline and then placed at random in a 65° F greenhouse for germination. On March 8, at which time the cotyledons were fully expanded, a water solution of either maleic hydrazide (1, 2-dihydro-3, 6-pyridazine-dione), 2, 3, 5-triiodobenzoic acid, or indoleacetic acid was applied as a foliar spray. The concentrations of each chemical used were 5, 25, and 100 parts per million. These were applied with a hand sprayer until the upper surfaces of the cotyledons were covered with a thin film of the solution. Plants used as controls were sprayed with distilled water to which had been added five milliliters of 95 percent alcohol in each one hundred milliliter volume.

On March 9 the pots were stored in a lighted room thermostatically controlled at 40 ± 2° F. One-half of the seedlings were vernalized for two weeks, and the other half for three weeks. At the same time non-vernalized (control) seedlings were placed in a 60° F greenhouse. At the end of the two-

week vernalization period, one group of seedlings was removed from cold storage and transplanted to a bench of a 60° F house. Each treatment was spaced four inches apart in rows four inches apart. Each row represented a random block which contained ten plants. The entire experiment was to consist of thirty treatments replicated three times. Non-vernalized controls were also planted at this time. One week later the remaining seedlings were removed from cold storage and transplanted to the bench in predetermined block locations.

Plants were observed daily for any significant morphological changes. When the first flower on a plant opened that plant was removed by severing the stem at the soil level. Data were recorded for the date of blooming, fresh weight, and the number of nodes. To compare treatments, all data were statistically analyzed.

Results. The chemicals used in this experiment in most instances did not significantly affect candytuft plants in such a manner that the number of days from seeding to first flower was influenced (Table I). Maleic hydrazide at 100 parts per million exhibited the greatest ability to hasten flowering under non-vernalized treatments. There appeared to be no highly significant interaction of chemical treatment and vernalization in regards to the acceleration or delay of flowering. However, when considered separately, flowering was generally delayed by vernalization. There was a highly significant delay in

TABLE I

Effect on Number of Days from Seeding to First Flower of Application of Growth Regulators and Vernalization to Candytuft Seedlings (1955).

Chemicals	Concentration (ppm)	*Average Number of Days Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		80.9	81.7	85.0
Maleic hydrazide	5	81.1	81.0	86.5
	25	80.5	81.0	--
	100	78.3	82.3	86.9
2, 3, 5-Triiodobenzoic acid	5	80.0	82.1	86.0
	25	80.2	81.4	85.8
	100	80.3	81.1	85.7
Indoleacetic acid	5	80.8	80.2	86.7
	25	80.3	82.2	85.3
	100	80.5	81.4	86.1
L. S. D. at 5% level		1.6		
L. S. D. at 1% level		2.1		

*All values are averages from three replicates of 10 plants.

most instances by the three-week vernalization period.

Chemical treatments varied in their effects on number of nodes at flowering. These effects were mostly dependent upon concentration of the particular chemical. Plants treated with 100 parts per million of 2, 3, 5-triiodobenzoic acid had significantly fewer nodes than controls, and those treated with lower concentrations of the same chemical. Higher concentrations of maleic hydrazide and 2, 3, 5-triiodobenzoic acid produced fewer nodes under two weeks vernalization while lower concentrations of indoleacetic acid caused the production of a smaller number of nodes under this vernalization period. Three weeks vernalization caused a significant reduction in the number of nodes in most instances (Table II).

Table III shows that there was considerable variations of fresh weights within chemical groups. In general, an increase in concentration resulted in a decrease in fresh weight. Vernalization tended to decrease weight in accordance to its duration.

It was observed that maleic hydrazide tended to suppress terminal bud development of the central axis. Upon suppression of the terminal axis one, in many plants two or more, strong lateral shoots developed which resulted in vigorous flowering plants.

TABLE II

Effect on Number of Nodes Before Flowering of Application of Growth Regulators and Vernalization to Candytuft Seedlings (1955).

Chemicals	Concentration (ppm)	*Average Number of Nodes Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		37.6	37.0	25.7
Maleic hydrazide	5	37.4	35.0	26.5
	25	39.1	34.2	--
	100	35.9	32.5	20.4
2, 3, 5-Triiodobenzoic acid	5	39.1	36.2	27.8
	25	37.4	36.7	25.0
	100	34.5	32.9	35.7
Indoleacetic acid	5	37.1	33.2	27.1
	25	36.6	38.2	26.4
	100	37.9	36.6	27.4
L. S. D. at 5% level		2.9		
L. S. D. at 1% level		3.8		

*All values are averages from three replicates of 10 plants.

TABLE III

Effect on Fresh Weight of Application of Growth Regulators and Vernalization to Candytuft Seedlings (1955)

Chemicals	Concentration (ppm)	*Average Fresh Weight (gms) Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		46.27	35.73	11.70
Maleic hydrazide	5	47.13	31.10	6.77
	25	59.23	41.53	--
	100	45.53	23.87	3.80
2, 3, 5-Triiodobenzoic acid	5	46.87	44.63	5.50
	25	43.47	40.03	6.67
	100	35.83	30.97	4.30
Indoleacetic acid	5	52.60	39.87	9.40
	25	43.30	34.67	6.93
	100	41.53	35.63	10.17
L.S.D. at 5% level		13.40		
L.S.D. at 1% level		17.82		

*All values are averages from three replicates of 10 plants.

Response of Snapdragon to Application of Growth Regulators and Vernalization to Seedlings

Methods and Materials. Seed of snapdragon (Antirrhinum majus var. Shasta) obtained from Vaughn's Seed Company, Chicago, Illinois were sown on February 28, 1955 in five-inch clay pots which contained a mixture of steam sterilized loam and peat. Three pots were used for each of thirty treatments. After seeding the pots were labeled according to the proposed treatment outline and placed at random in a 65° F greenhouse for germination. By March 12 the cotyledons were well developed. Thereafter, the methods and materials were the same as outlined in the preceding candytuft experiment.

Later this experiment was repeated in the campus greenhouses of Hampton Institute, Hampton, Virginia. There snapdragon seed were planted on November 18, 1955. Therefrom, the methods and materials were the same as had been used previously at Michigan State University.

Results. According to the data presented in Table IV, chemical treatment of snapdragon seedlings had a positive influence upon the number of days from seeding to first flower of non-vernalized plants. These differences were only of slight significance, and there were only small differences between the different concentrations of a particular chemical. Moreover, variation of differences in the effects obtained with different chemicals was not significant. The effects of the interaction of chemicals and vernalization did not in any instance hasten flowering and with several combinations

TABLE IV

Effect on Days from Seeding to First Flower of Application of Growth Regulators and Vernalization to Snapdragon Seedlings (1955)

Chemicals	Concentration (ppm)	*Average Number of Days Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		87.6	87.7	88.2
Maleic hydrazide	5	83.7	88.6	86.5
	25	81.8	91.7	89.4
	100	82.6	86.9	91.6
2, 3, 5-triiodobenzoic acid	5	83.3	87.0	88.7
	25	83.3	87.0	--
	100	85.4	87.4	91.2
Indoleacetic acid	5	83.8	87.4	90.9
	25	83.9	87.2	91.8
	100	82.2	87.9	91.6
L. S. D. at 5% level		3.1		
L. S. D. at 1% level		4.1		

*All values are averages from three replicates of 10 plants.

flowering was significantly delayed.

Chemical treatments when applied without vernalization also influenced the number of nodes (Table V). A general increase in node number was noted when compared with non-vernalized controls, vernalized controls, and chemically treated vernalized plants. There seemed to be no close correlation between date of flowering and node number as influenced by chemicals or chemical concentrations. Vernalization generally resulted in a decrease in node number.

Table VI shows that chemicals varied in their influence upon growth as measured by the fresh weights of flowering plants. In non-vernalized groups lower concentrations of maleic hydrazide and 2, 3, 5-triiodobenzoic acid tended to stimulate plant growth, whereas, growth was stimulated by an increased concentration of indoleacetic acid. Table VI shows that exposure of seedlings to low temperature for two or three weeks resulted in significant decrease in fresh weight of flowering plants as compared to non-vernalized controls.

Data from a duplicate experiment conducted at Hampton Institute are given in Tables VII, VIII, and IX. The data in these tables differ somewhat from those presented for the previous experiment. It should be noted before comparing the two sets of data that in addition to differences in geographic locations, there was also a difference in the season of the year during which the experiments were conducted (as listed in the methods and materials above). Under these conditions vernalization and chemical treatments generally exerted adverse influences upon vegetative growth and flowering.

TABLE V

Effect on Number of Nodes Before First Flower of Application of Growth Regulators and Vernalization to Snapdragon Seedlings (1955)

Chemicals	Concentration (ppm)	*Average Number of Nodes		
		Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		21.5	21.3	19.3
Maleic hydrazide	5	24.0	20.8	19.8
	25	22.3	19.0	20.0
	100	21.4	19.8	18.9
2, 3, 5-Triiodobenzoic acid	5	23.3	18.0	20.2
	25	22.6	19.4	--
	100	21.6	19.7	19.6
ndoleacetic acid	5	23.9	21.8	20.7
	25	22.3	19.5	20.5
	100	24.1	20.2	19.8
. D. at 5% level		2.6		
D. at 1% level		3.5		

ll values are averages from three replicates of 10 plants.

TABLE VI

Effect on Fresh Weight of Application of Growth Regulators and Vernalization to Snapdragon Seedlings (1955)

Chemicals	Concentration (ppm)	*Average Fresh Weight (gms) Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		41.00	25.90	27.26
Maleic hydrazide	5	51.99	25.13	23.43
	25	51.53	15.73	18.27
	100	47.50	21.43	14.33
2, 3, 5-Triiodobenzoic acid	5	54.66	28.26	24.03
	25	48.83	25.36	--
	100	33.96	25.40	18.63
Indoleacetic acid	5	50.93	31.10	24.96
	10	51.66	26.23	15.20
	100	55.69	27.73	19.80
L.S.D. at 5% level		11.24		
L.S.D. at 1% level		14.94		

*All values are averages from three replicates of 10 plants.

TABLE VII

Effect on Number of Days from Seeding to First Flower of Application of Growth Regulators and Vernalization to Snapdragon Seedlings[1] (1956)

Chemicals	Concentration (ppm)	Average Number of Days[2]		
		Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		139.2	143.0	147.8
Maleic hydrazide	5	143.3	145.9	148.8
	25	141.5	146.7	143.9
	100	140.8	157.2	157.9
2, 3, 5-Triiodobenzoic acid	5	141.5	147.0	156.0
	25	140.9	148.8	146.2
	100	141.2	144.1	150.0
Indoleacetic acid	5	144.2	146.3	150.0
	25	138.8	149.6	146.3
	100	143.0	144.0	149.5
L. S. D. at 5% level		7.0		
L. S. D. at 1% level		9.4		

[1]Experiment conducted at Hampton Institute, Hampton, Virginia.

[2]All values are averages from three replicates of 10 plants.

TABLE VIII

Effect on Number of Nodes Before First Flower of Application of Growth Regulators and Vernalization to Snapdragon Seedlings[1] (1956)

Chemicals	Concentration (ppm)	Average Number of Nodes[2] Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		44.3	44.5	42.2
Maleic hydrazide	5	45.0	45.6	41.6
	25	43.4	40.4	36.9
	100	46.0	49.6	41.6
2, 3, 5-Triiodobenzoic acid	5	45.2	48.7	46.3
	25	48.4	47.5	38.4
	100	44.3	41.0	43.1
Indoleacetic acid	5	48.4	43.2	41.9
	25	43.2	46.6	40.3
	100	44.4	41.5	39.6
L. S. D. at 5% level		4.2		
L. S. D. at 1% level		5.5		

[1]Experiment conducted at Hampton Institute, Hampton, Virginia.

[2]All values are averages from three replicates of 10 plants.

TABLE IX

Effect on Fresh Weight of Application of Growth Regulators and Vernalization to Snapdragon Seedlings[1] (1956)

Chemicals	Concentration (ppm)	Average Fresh Weight (gms)[2]		
		Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		96.9	59.5	49.8
Maleic hydrazide	5	82.4	61.2	43.4
	25	83.4	62.6	40.1
	100	100.7	33.9	31.1
2, 3, 5-Triiodobenzoic acid	5	84.6	81.9	47.8
	25	92.4	69.5	38.8
	100	96.7	68.7	52.2
Indoleacetic acid	5	78.6	70.7	41.0
	25	91.8	60.5	28.4
	100	71.7	60.5	41.0
L. S. D. at 5% level		25.2		
L. S. D. at 1% level		33.5		

[1]Experiment conducted at Hampton Institute, Hampton, Virginia.

[2]All values are averages from three replicates of 10 plants.

Response of Candytuft to Application of Plant Regulators and Vernalization to Germinating Seed

Methods and Materials. Seed of candytuft (Iberis umbellata var. Alba) obtained from Vaughn's Seed Company, Chicago, Illinois were used in this experiment. On February 26, 1955, seeds were uniformly distributed upon two pieces of moistened Whatman No. 1 filter paper in each of sixty-three petri dishes. Three sterilized petri dishes were used for each of the twenty-one treatments. The seeds were germinated four days at 70° F. At this time the radicle had emerged from most and in others swelling and splitting of the seed coat had occurred. This was considered as an indication that radicle emergence would soon follow.

The filter paper was then impregnated with five milliliters of solution of a predetermined concentration of the compound to be used. The concentrations used were one, five, and ten parts per million. The growth regulators used were maleic hydrazide, 2, 3, 5-triiodobenzoic acid, and indoleacetic acid. Non-treated seeds served as controls. On the following day the petri dishes were placed in a continuously lighted room which was thermostatically controlled at 40±2° F. However, before placing the non-treated petri dishes in cold storage, a sufficient number of seeds were randomly selected from them to serve as unvernalized controls. These were subsequently planted two by two inches apart in flats, which were placed in a 60° F greenhouse.

After a two-week vernalization period one-half of the seeds were selected at random from each treatment and planted in rows four by four inches apart on a bench of a 60° F greenhouse. Each row represented a random block which contained ten plants. The entire experiment was to consist of twenty-one treatments replicated three times. Unvernalized controls were also transplanted to the bench at this time. At the end of three weeks the remaining seeds were removed from cold storage and transplanted to the bench in predetermined locations.

Plants were observed daily for any significant morphological change. When the first flower on a plant opened, that plant was removed by severing the stem at the soil level. Data were recorded for the date of blooming, fresh weight, and the number of nodes. The data of each treatment were compared statistically.

Results. The data, as presented in Table X, indicated that application of indoleacetic acid and 2, 3, 5-triiodobenzoic acid to germinating candytuft seed, which were subsequently vernalized, in most instances significantly decreased the number of days from seeding to first flower as compared with vernalized controls. One part per million maleic hydrazide and 2, 3, 5-triiodobenzoic acid caused a delay in flowering. In general, it was observed that flowering was delayed by both two and three weeks vernalization.

TABLE X

Effect on the Number of Days from Seeding to First Flower of Application of Growth Regulators to Germinating Candytuft Seed (1955)

Chemicals	Concentration (ppm)	*Average Number of Days Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		82.7	83.8	85.0
Maleic hydrazide	1		84.7	87.4
	5		--	--
	10		--	--
2, 3, 5-Triiodobenzoic acid	1		84.7	83.3
	5		82.8	83.7
	10		83.7	84.1
Indoleacetic acid	1		82.3	84.1
	5		82.3	83.3
	10		82.8	83.4
L.S.D. at 5% level			0.7	
L.S.D. at 1% level			0.9	

*All values are averages from three replicates of 10 plants.

There was a general tendency for chemically treated plants to have fewer nodes at flowering than those to which chemicals were not applied. An increased vernalization period caused a corresponding decrease in node number in all cases (Table XI). Table XII shows that application of solutions of indoleacetic acid to germinating seed caused a significant increase in fresh weight of flowering plants under two-week vernalization. The results obtained with other chemicals gave varying results. Ten parts per million 2, 3, 5-triiodobenzoic acid under conditions of two weeks vernalization caused a significant decrease in fresh weight, while maleic hydrazide caused a decrease in weight under both two and three weeks vernalization periods. In all cases vernalization caused a decrease in fresh weight, as compared with non-vernalized controls.

As with maleic hydrazide treated seedlings, terminal growth was inhibited by all concentrations of the chemical. The flowering plants developed in most cases from the growing out of lateral buds.

TABLE XI

Effect on Number of Nodes Before First Flower of Application of Growth Regulators and Vernalization to Germinating Candytuft Seed (1955)

Chemicals	Concentration (ppm)	*Average Number of Nodes Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		36.8	34.6	31.6
Maleic hydrazide	1		31.7	27.7
	5		--	--
	10		--	--
2, 3, 5-Triiodobenzoic acid	1		33.5	32.0
	5		31.3	28.1
	10		31.1	27.9
Indoleacetic acid	1		32.1	31.8
	5		31.8	30.8
	10		31.8	27.7
L.S.D. at 5% level			1.6	
L.S.D. at 1% level			2.1	

*All values are averages from three replicates of 10 plants.

TABLE XII

Effect on Fresh Weight of Application of Growth Regulators and Vernalization to Germinating Candytuft Seed (1955)

Chemicals	Concentration (ppm)	*Average Fresh Weight (gms) Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		61.03	37.30	28.47
Maleic hydrazide	1		19.33	19.63
	5		--	--
	10		--	--
2, 3, 5-Triiodobenzoic acid	1		36.73	35.37
	5		39.33	31.00
	10		27.37	31.00
Indoleacetic acid	1		43.43	32.17
	5		45.47	29.70
	10		47.00	29.23
L. S. D. at 5% level			4.53	
L. S. D. at 1% level			6.11	

*All values are averages from three replicates of 10 plants.

Response of Snapdragon to Application of Plant Regulators and Vernalization to Germinating Seed

Methods and Materials. Seed of snapdragon (Antirrhinum majus var. Shasta) obtained from Vaughn's Seed Company, Chicago, Illinois were used. On March 13, 1955 seed were uniformly distributed upon two pieces of moistened Whatman No. 1 Filter paper in each of sixty-three sterilized petri dishes. Three petri dishes were used for each of twenty-one treatments. The seeds were germinated at 70° F until the radicle had emerged from most and in others swelling and splitting of the seed coat had occurred.

The germinated seed were treated March 21 as outlined in the preceding experiment for germinating candytuft seed. After this point the methods and materials were the same.

Results. The effect on the number of days from seeding to first flower of application of growth regulators and vernalization to germinating snapdragon seed is presented in Table XIII. It is clear that when germinating seed were vernalized there was a general tendency for flowering to be delayed. This was especially true when the seed were subsequently exposed to a three-week vernalization period. The effects of an interaction of chemical treatment and vernalization were outstanding only with 2, 3, 5-triiodobenzoic acid and three weeks vernalization. In this instance flowering was significantly

TABLE XIII

Effect on the Number of Days from Seeding to First Flower of Application of Growth Regulators and Vernalization to Germinating Snapdragon Seed (1955)

Chemicals	Concentration (ppm)	*Average Number of Days		
		Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		87.2	87.5	89.7
Maleic hydrazide	1		87.1	90.0
	5		87.1	87.1
	10		86.8	89.6
2, 3, 5-Triiodobenzoic acid	1		86.9	90.5
	5		87.7	91.7
	10		89.1	91.4
Indoleacetic acid	1		86.5	91.7
	5		87.8	--
	10		87.8	90.3
L.S.D. at 5% level			0.8	
L.S.D. at 1% level			1.0	

*All values are averages from three replicates of 10 plants.

elayed by all concentrations of the chemical. These results differed from nose obtained in the preceding experiment with candytuft (Table X). In that est it was noted that the same treatments resulted in earlier flowering of hemically treated plants than in untreated three-week vernalized controls.

Plants from seed treated with one part per million of indoleacetic acid and those which developed from seed treated with five parts per million maleic hydrazide and three weeks vernalization were the only ones which flowered significantly earlier than non-chemically treated, but similarly vernalized controls. It should be recalled that indoleacetic acid also tended to cause earlier flowering in candytuft under similar conditions (Table VII).

The effect on number of nodes before first flower of application of growth regulators and vernalization to germinating snapdragon seed is presented in Table XIV. The average number of nodes was influenced by duration of vernalization. The two-week period tended to increase the number, whereas a decrease was noted in three weeks vernalization. Chemical treatments with two weeks vernalization generally resulted in a decrease in number, while the effect of chemical treatments with three weeks vernalization caused an increase in node number. The interaction of chemical and concentration of chemical was infrequently significant.

From the data presented in Table XV it is clear that vernalization caused highly significant reduction in growth, as measured by fresh weights.

TABLE XIV

Effect on Number of Nodes Before First Flower of Application of Growth Regulators and Vernalization to Germinating Snapdragon Seed (1955)

Chemicals	Concentration (ppm)	*Average Number of Nodes		
		Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		19.0	20.1	17.2
Maleic hydrazide	1		20.2	17.5
	5		19.6	17.2
	10		23.0	17.3
2, 3, 5-Triiodobenzoic acid	1		19.5	17.4
	5		18.5	18.8
	10		19.3	17.6
Indoleacetic acid	1		18.6	18.1
	5		18.0	--
	10		18.8	17.7
L.S.D. at 5% level			1.4	
L.S.D. at 1% level			1.8	

*All values are averages from three replicates of 10 plants.

TABLE XV

Effect on Fresh Weight of Application of Growth Regulators and Vernalization to Germinating Snapdragon Seed (1955)

Chemicals	Concentration (ppm)	*Average Fresh Weight (gms)		
		Period of Vernalization		
		None	2-Week	3-Week
H_2O-control		40.97	28.57	15.07
Maleic hydrazide	1		44.80	19.03
	5		27.37	26.07
	10		29.97	18.67
2, 3, 5-Triiodobenzoic acid	1		32.43	18.37
	5		29.43	26.13
	10		27.10	20.40
Indoleacetic acid	1		39.73	17.53
	5		25.73	--
	10		24.43	18.23
L.S.D. at 5% level			2.57	
L.S.D. at 1% level			3.44	

*All values are averages from three replicates of 10 plants.

is also evident that the lowest concentration (1 ppm) of maleic hydrazide imulated growth in a significant manner in the two-week vernalized group. t seemed that low concentrations of the chemicals tended to overcome the inhibitory effect of this vernalization period. With three weeks vernalization it was observed that a small increase in chemical concentration (5 ppm) caused the greatest counteraction of the inhibitory effect of vernalization. When these results are compared with those obtained with candytuft (Table XII), it was noted that the response of the two plant species differed in their reaction to different concentrations of a particular chemical. No significant teratological or morphological changes occurred in this experiment.

Response of Wallflower and Phlox to Application of Plant Regulators

Methods and Materials. Seed of wallflower (Cheiranthus cheiri) and phlox (Phlox drummondii var. Scarlet) obtained from George Tait Seed Company, Norfolk, Virginia were planted on September 13, 1956 in flats containing a mixture of sterilized loam and peat at Hampton Institute, Hampton, Virginia. The plants were transplanted to three-inch pots on September 27. The following day water solutions of sodium trichlorobenzoate, 2, 3, 5-tribromobenzoic acid, 5-chlorosalicylic acid, and 2, 3, 5-triiodobenzoic acid were applied as foliar sprays to the wallflower. Phlox plants were sprayed with solutions of 5-chlorosalicylic acid and 2, 3, 5-tribromobenzoic acid. Concentrations of solutions used were 100, 500, and 1, 000 parts per million. Each treatment consisted of twenty plants.

After the plants had been sprayed they were placed in rows on a greenhouse bench where they were grown at a night temperature of 65±5° F until flowering. Day temperatures varied according to the seasonal conditions of the area.

Plants were observed daily for any significant morphological changes. When the first flower on a plant opened, that plant was removed by cutting at the ground level. Data were recorded for the date of blooming, dry weight and number of nodes.

Results. The results as presented in Table XVI indicated that the chemicals used in this experiment varied in their ability to affect the flowering response of wallflower. It was also clear that in addition to variations in response to different chemicals, flowering was also affected by different concentrations of the same chemical. Solutions of 5-chlorosalicylic acid and 2, 3, 5-triiodobenzoic acid when applied at concentrations of 100 to 1000 parts per million did not cause a significant difference in time of flowering. The response to 100 and 500 parts per million concentrations of sodium triichlorobenzoate was about the same, but at 1, 000 parts per million growth and flowering was completely inhibited and many of the plants died during the test period. There were also significant differences in the time of flowering according to the concentration of 2, 3, 5-tribromobenzoic acid. Chemical applications in all instances produced some delay in flowering.

Chemical treatments, in general, did not significantly affect the number of nodes at flowering (Table XVII). Applications of 100 and 500 parts per million of 2, 3, 5-triiodobenzoic acid caused a significant increase in the number of nodes.

Chemical treatments in most instances did not cause significant differences in dry weight (Table XVIII). A notable exception was the decreased dry weight which resulted from applications of 500 and 1, 000 parts per million of sodium trichlorobenzoate. This difference in growth is apparent in Figure 1.

Wallflower showed considerable morphological and teratological

TABLE XVI

Effect on Number of Days from Seeding to First Flower of Application of Growth Regulators to Wallflower Seedlings (1956)

Chemicals	*Average Days to First Flower			
	Concentrations of Solution (ppm)			
	0	100	500	1000
H_2O-control	101.9			
Sodium trichlorobenzoate		120.6	120.8	--
2, 3, 5-Tribromobenzoic acid		102.3	112.0	116.8
5-Chlorosalicylic acid		108.5	103.7	104.7
2, 3, 5-Triiodobenzoic acid		125.8	126.9	121.8
L.S.D. at 5% level		6.4		
L.S.D. at 1% level		8.4		

*All values are averages of fifteen plants.

TABLE XVII

Effect on Number of Nodes Before First Flower of Application on Growth Regulators to Wallflower Seedlings (1956)

Chemicals	*Average Number of Nodes			
	Concentrations of Solution (ppm)			
	0	100	500	1000
H_2O-control	39.4			
Sodium trichlorobenzoate		42.6	40.7	--
2, 3, 5-Tribromobenzoic acid		40.4	41.5	42.6
5-Chlorosalicylic acid		42.1	38.9	42.3
2, 3, 5-Triiodobenzoic acid		45.1	46.5	41.2
L. S. D. at 5% level		4.3		
L. S. D. at 1% level		5.7		

*All values are averages of fifteen plants.

TABLE XVIII

Effect on Dry Weight of Application of Growth Regulators to Wallflower Seedlings (1956)

Chemicals	*Average Dry Weight of Stems (gms)			
	Concentrations of Solutions			
	0	100	500	1000
H_2O-control	7.67			
Sodium tribromobenzoate		6.41	4.30	--
2, 3, 5-Tribromobenzoic acid		5.81	6.33	6.45
5-Chlorosalicylic acid		6.14	5.57	6.12
2, 3, 5-Triiodobenzoic acid		7.21	8.19	7.48
L. S. D. at 5% level		2.06		
L. S. D. at 1% level		2.71		

*All values are averages of fifteen plants.

Figure 1. The response of Cheiranthus cheiri to applications of sodium trichlorobenzoate.

Left to right: Control, 100, 500 and 1,000 ppm.

response to the different chemicals. However, with the exception of sodium trichlorobenzoate, there were no pronounced and consistent modifications in the overall habit of growth. With 2, 3, 5-triiodobenzoic acid and 5-chloro-salicylic acid there was a slight tendency toward more profuse development of the lower axillary buds at concentrations of 100 and 500 parts per million. Leaf formation and terminal growth was relatively unaffected.

Applications of 2, 3, 5-tribromobenzoic acid to wallflower resulted in the appearance of strap-like and fused leaves (Figure 2). The fused leaves possessed two distinct midribs and were of approximately the same length as normal leaves. The tips were separate and normal in appearance. This appearance seems to indicate that the chemical caused an inhibition in the formation or development of the marginal meristems. The prevalence of abnormal leaves were in accordance to chemical concentrations, being nearly absent at 100 parts per million.

Sodium trichlorobenzoate produced profound morphological and tera-logical changes within the entire plant. Concentration of 500 parts per mil- caused connate coalescing of terminal leaves, thereby producing a broad, -shaped structure (Figure 3). There was also pronounced swelling of em immediately below the second node. Upon complete inhibition of al growth a nearly normal size flowering plant developed from the of axillary buds. With treatments of 1,000 parts per million growth

e 2. **Variations** in leaf form of phlox and wallflower induced by application of 2, 3, 5-tribromobenzoic acid.

Upper: Leaves from Phlox drummondii treated with 2, 3, 5-tri-**bro**mobenzoic acid. Normal leaf on left.

Lower: Leaves from Cheiranthus cheiri treated with 2, 3, 5-tri-**bro**mobenzoic acid. Normal leaf on left.

e 3. **Cheiranthus** cheiri treated with 500 ppm of sodium trichloro-
benzoate.

in most cases was nearly or completely inhibited. Terminal leaves were extremely deformed and reduced in size. Lower leaves, including the cotyledon, were abnormally curved and extremely pendulous. There was also pronounced swelling of the stem beneath the second node (Figure 4).

Results with Phlox. Treatment of phlox seedlings with 5-chloro-salicylic acid did not result in a significant difference in the time of flowering, number of nodes, or general appearance of the plant, as compared with controls. Even though differences in dry weights resulted from the use of different concentrations of the chemical, they were not highly significant when compared with each other and controls (Table XIX).

Applications of 100, 500 and 1, 000 parts per million of 2, 3, 5-tribromobenzoic acid resulted in retardation of growth and highly significant delay in flowering (Figure 5, and Table XIX). This was especially true at concentrations of 500 and 1, 000 parts per million. These concentrations also caused significant decrease in dry weights, but the number of nodes was only slightly affected (Table XIX). Fused leaves and abnormally developed terminals were apparent (Figure 2).

re 4. *Cheiranthus* cheiri treated with 1, 000 ppm of sodium trichloro-benzoic. Picture taken 30 days after treatment.

TABLE XIX

Response of Phlox to Applications of 5-Chlorosalicylic Acid and 2, 3, 5-Tribromobenzoic Acid (1956)

Chemicals	Concentration (ppm)	*Measurements		
		Days to Flowering	Number of Nodes	Dry Weight (gms)
H_2O-control		125.1	39.1	5.00
5-Chlorosalicylic acid	100	129.4	41.7	4.76
	500	125.3	39.7	3.76
	1000	128.3	38.5	4.17
, 3, 5-Tribromobenzoic acid	100	133.9	42.3	5.14
	500	142.2	42.3	3.80
	1000	144.3	43.3	3.12
S. D. at 5% level		4.7	4.4	1.04
. D. at 1% level		6.2	5.8	1.39

*All values are averages from eighteen plants.

Figure 5. Response of Phlox drummondii to applications of 2, 3, 5-tribromobenzoic acid.

Left to right: Control, 100, 500 and 1, 000 ppm.

Response of Phlox to 2, 3, 5-Triiodobenzoic Acid as Influenced by Repeated and Single Applications to Progressively Older Plants

Methods and Materials. Seed of phlox (Phlox drummondii var. Scarlet) were planted June 29, 1955 in a greenhouse bench in rows eight inches apart. The seed were spaced so that several plants grew approximately four inches apart in the row. On July 24 one seedling was selected in each space for treatment and all others destroyed. Care was exercised to select seedlings of uniform size and stage of development. Each row represented one treatment and the entire experiment consisted of 19 treatments replicated three times.

On July 24 one-half of the seedlings were treated with water solutions of 2, 3, 5-triiodobenzoic acid at concentrations of 100, 500 and 1,000 parts per million. One week later two thirds of the previously sprayed seedlings were given another application of the above concentrations. The following week one-half of those which had received two applications were given a third application of 2, 3, 5-triiodobenzoic acid of the same concentrations.

Meanwhile, one-third of the seedlings which had not been treated on July 24 were treated one week later, August 1, with the above concentrations. Another third was treated the following week, and the remainder were treated one week thereafter. Non-treated plants served as controls.

Plants were observed daily for any significant morphological change. ıta were recorded for the date of first flower.

A similar experiment was performed in the campus greenhouses of ımpton Institute. There phlox seed were planted February 14, 1956. The ʻst treatments of 2, 3, 5-triiodobenzoic acid were applied March 10 and ɔther group sprayed one week later. Concentrations of chemical used ere 50, 100, 500 and 1, 000 parts per million.

Results. According to the results presented in Table XX it is appar- ıt that applications of 500 and 1, 000 parts per million of 2, 3, 5-triiodobenzoic ʻid to phlox seedlings one week after germination significantly delayed ɔwering. Moreover, it can also be noted that flowering was further delayed ʼ applications the second and third weeks after germination; however, at ɔse times there was less response to increased concentrations of chemical. ʃter the third week there was a general decline in responsiveness to chem- al applications as reflected by earlier flowering of plants which were eated at a more advanced stage of development.

Repeated application resulted in further delay in further delay in the ɔwering response with all concentrations. But there was no significant esponse to a third treatment to more fully developed seedlings, except ith the relatively high concentration of 1, 000 parts per million.

The result from a similar test is presented in Table XXI. It can be

TABLE XX

Effect of Repeated and Single Applications of 2, 3, 5-Triiodobenzoic Acid on the Flowering of Phlox (1955)

Treatments	Average Number of Days to First Flower[1]			
	Concentration of Solutions (ppm)			
	0	100	500	1000
nber of applications[2]				
One	79.5	77.4	84.7	89.3
Two		95.0	97.1	97.7
Three		94.0	97.8	104.9
ne of applications[3]				
Two weeks		91.2	93.5	92.7
Three weeks		88.7	88.2	87.0
Four weeks		81.3	84.8	86.1
S.D. at 5% level			2.8	
S.D. at 1% level			3.8	

[1] All values are averages from three replicates of 10 plants.

[2] Applications repeated at weekly intervals beginning one week after germination.

[3] Refers to number of weeks following germination.

TABLE XXI

fect on Number of Days to Flowering and Fresh Weight of Applications of 2, 3, 5-Triiodobenzoic Acid to Phlox Plants One and Two Weeks After Germination (1956)[1]

reatments (ppm)	Days to First Flower[2]		Fresh Weight (gms)[2]	
	Time of Applications			
	One Week	Two Week	One Week	Two Week
trol	100.7		21.93	
0	102.5	101.2	21.47	26.00
00	103.9	100.8	20.43	25.67
00	112.2	110.8	13.57	16.43
00	112.1	113.2	12.73	14.83
.S.D. at 5% level	2.9		4.69	
..S.D. at 1% level	3.9		6.83	

[1] Experiment conducted at Hampton Institute, Hampton, Virginia, February-June, 1956.

[2] All values are averages from three replicates of 10 plants.

seen that the response of plants to chemical treatments was somewhat similar, however, in this case there was no significant difference in the time of flowering of plants treated one and two weeks after germination. This was probably due to a seasonal influence.

Higher concentrations of chemical caused a significant decrease in fresh weights whether applied one or two weeks after germination.

Delayed tratements tended to cause an increase in fresh weight over controls and earlier treated plants. It is suggested that this was probably due to a stimulation in production and growth of axillary shoots, as some inhibition of apical dominance was obvious with all concentrations above 50 parts per million (Figure 6).

Teratological and morphological changes included the production of strap-like leaves, epinasty of leaves, the more or less growing together of opposite leaves to form connate structures, and proliferation of vascular tissues (Figures 6 and 7).

Time of chemical treatment was reflected by the location of teratological disturbances on the plant. In earlier treated plants the first pair of leaves following the cotyledons was most affected. With later treatments, at which time the first true leaves were well developed, greatest deviation from the normal occurred in the first two pairs of leaves above the initial true

leaves. Axillary shoots which developed had one pair of strap-like leaves near their bases and abnormally thin and elongated stem sections were terminated by hollow cones which were formed by what appeared to be the connate fusion of leaves (Figure 6). Leaves and stem sections present at the time of treatments appeared to be only slightly affected. Treated plants, in general, produced darker and more succulent leaves.

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Figure 6. **Response of** Phlox drummondii **to one and two applications of 1, 000 ppm 2, 3, 5-triiodobenzoic acid.**

Left to right: Control, one application, and two applications.

Figure 7. Leaf and stem variations from Phlox drummondii treated with 2, 3, 5-triiodobenzoic acid.

Normal leaf and stem on the left.

Response of Phlox to Application of Plant Regulators as Influenced by Various Photoperiods

Methods and Materials. In order to determine the effect of increasing or decreasing the natural photoperiod on the response of phlox plants to application of growth regulators, an experiment was designed in which plants treated with 100, 500 and 1, 000 parts per million of 2, 3, 5-triiodobenzoic acid were grown under different day lengths. Photoperiod treatments consisted of a natural, an eight-hour, a sixteen-hour, and a twenty-four-hour day length.

Seed obtained from Tait's Seed Company, Norfolk, Virginia were planted in flats of sterilized loam and peat on November 30, 1956 at Hampton Institute, Virginia. Upon germination seedlings in flats were exposed to various day lengths. When their cotyledons were fully expanded, they were transplanted to three-inch pots, subsequently sprayed with auxin solutions, and continued under the proper light regime. Twenty-five plants were grown in each of 16 treatments. Non-chemically treated plants served as controls under each photoperiod.

When the first flower on a plant opened, that plant was harvested and data were recorded for the dates of blooming, fresh weight, length of main stem, and dry-weight. Previously, a record had been made of the

umber of fused leaves, strap-like leaves, cone-like growing points, primary axillary shoots, and fasciated branches. The data of each treatment were compared statistically.

Results. When various concentrations of 2, 3, 5-triiodobenzoic acid were applied to phlox seedlings growing under several photoperiods, flowering was significantly affected (Table XXII). Highly significant reduction of the number of days from seeding to first flower resulted from all concentrations of the chemical solution under the eight-hour photoperiod. The lowest concentration (100 parts per million) was most significant, whereas there was a decrease in the promotive effect as the concentration of solutions was increased. An increase in the duration of photoperiods also caused a significant decrease in the number of days to first flower. However, chemical treatments to plants growing under all durations of the light period, other than eight hours, resulted in significant delay of flowering.

The data in Table XXIII indicate that an increase in day length has considerably stimulated elongation of the central axis (Figures 8-11). Maximum stimulation was obtained with twenty-four hours of light, and decreased as the photoperiods shortened. Under the longer photoperiods chemical treatments were inhibitory, but under the shorter light periods chemical treatments tended to stimulate stem elongation. This effect was not apparent during earlier stages of development (Figure 8), nevertheless, upon advent of

TABLE XXII

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on Days from Seeding to First Flower of Phlox (1957)

Concentration (ppm)	*Average Days to First Flower				
	Length of Photoperiods				
	Natural	8 Hours	16 Hours	24 Hours	Means
Control	140.7	180.6	114.1	108.9	136.1
100	146.4	160.2	138.6	122.8	142.0
500	143.8	168.2	137.4	122.0	142.9
1000	144.4	171.6	131.7	127.8	143.9
Means	143.8	170.2	130.5	120.4	141.2
L.S.D. at 5% level		2.7			
L.S.D. at 1% level		3.8			

*All values are averages from 25 plants.

TABLE XXIII

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on Length of the Main Stem of Phlox (1957)

Concentration (ppm)	*Average Length of Main Stems (cms)				
	Length of Photoperiods				
	Natural	8 Hours	16 Hours	24 Hours	Means
Control	59.1	34.3	69.4	81.2	61.0
100	61.7	42.5	58.8	66.6	57.4
500	63.8	43.3	59.1	69.0	58.8
1000	59.6	33.6	59.9	66.2	54.8
Means	61.1	38.4	61.8	70.7	58.0
L.S.D. at 5% level		3.3			
L.S.D. at 1% level		4.4			

*All values are averages from 25 plants.

flowering it was obvious that elongation of the flowering stem had been effectively stimulated by 100 and 500 parts per million of 2, 3, 5-triiodobenzoic acid.

Data pertaining to fresh and dry weights are presented in Tables XXIV and XXV. It is evident that greater production of total plant material occurred from exposure to natural and eight-hour light periods than from the 16- and 24-hour periods. Since longer stems were produced under extended photoperiods (Table XXIII), it can be concluded that the shorter photoperiods led to the production of stockier and more numerous vegetative elements (Figure 11). Furthermore, it is evident that chemical treatments of 100 and 500 parts per million tended to promote growth under the eight-hour photoperiod, but inhibited growth under other photoperiods.

The number of axillary shoots produced indicated significant influence of light duration and chemical concentrations (Table XXVI). Exposure of plants to eight-hour and natural photoperiods resulted in the highest production of shoots. Under these periods chemical applications tended to inhibit shoot production, whereas under 16- and 24-hour photoperiods chemical treatments encouraged axillary shoot production. Another effect of short photoperiods was the tendency for plants to assume a more prostrate habit of growth (Figures 8 and 11).

Morphological and teratological changes were evident in chemically

TABLE XXIV

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on Fresh Weight of Phlox (1957)

Concentration (ppm)	*Average Fresh Weights (gms) Length of Photoperiods				
	Natural	8 Hours	16 Hours	24 Hours	Means
Control	30.10	14.57	13.35	19.32	19.34
100	28.08	29.30	11.02	10.50	19.73
500	29.31	22.16	10.10	14.32	18.97
1000	28.41	17.34	11.10	11.90	17.19
Means	28.97	20.84	11.39	14.01	18.81
L. S. D. at 5% level		1.19			
L. S. D. at 1% level		1.56			

*All values are averages from 25 plants.

TABLE XXV

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on Dry Weight of Phlox (1957)

Concentration (ppm)	*Average Dry Weights (gms)				
	Length of Photoperiods				
	Natural	8 Hours	16 Hours	24 Hours	Means
Control	3.69	2.21	1.63	2.19	2.43
100	3.50	3.57	1.36	1.25	2.42
500	3.60	3.12	1.26	1.57	2.39
1000	3.44	2.37	1.32	1.38	2.13
Means	3.56	2.82	1.39	1.60	2.34
L.S.D. at 5% level		0.18			
L.S.D. at 1% level		0.24			

*All values are averages from 25 plants.

TABLE XXVI

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on Number of Axillary Shoots of Phlox (1957)

Concentration (ppm)	*Average Number of Axillary Shoots				
	Length of Photoperiods				
	Natural	8 Hours	16 Hours	24 Hours	Means
Control	6.6	7.9	1.5	1.8	4.5
100	4.7	6.7	1.9	2.3	3.9
500	5.2	6.2	1.7	2.2	3.9
1000	4.2	5.2	1.7	2.2	3.3
Means	5.2	6.5	1.7	2.1	3.9
L. S. D. at 5% level			0.2		
L. S. D. at 1% level			0.3		

*All values are averages from 25 plants and included all shoots which were over 3 inches in length.

treated plants. Changes induced were related to both chemical concentrations and length of photoperiods. The number of cone-like growing points (Table XXVII) were more numerous under the longer photoperiods and higher concentration of solutions, whereas the number of strap-like leaves (Table XXVIII) and fused leaves (Table XXIX) were most numerous under the natural photoperiod and higher chemical concentrations.

Abnormal plants were characterized by terminal growth in the form of tight to flaring cone-like structures (Figures 12, 13, 14). These structures were formed by the connate growing together of opposite leaves. They were found at the terminus of the central shoot and also in the axils of lower leaves (Figures 13, 14). Plant parts presented at the time of chemical application were relatively unaffected. In some plants the terminal growing point emerged through the end of the cones and in others through the ruptured side of cones. In other plants growth of the central shoot was completely inhibited; consequently the flowering plant developed from the growing out of axillary shoots. Other abnormalities were one or several pairs of strap-like leaves, fused leaves, and fused stems.

Chemical composition of phlox plants treated with various concentrations of 2, 3, 5-triiodobenzoic acid and exposed to photoperiods of different length was as presented in Table XXX. The data indicate that photoperiods, other than 8-hour period, had little effect upon chemical

TABLE XXVII

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on the Number of Cone-Like Growing Points of Phlox Plants (1957)

Concentration (ppm)	*Average Number of Cone-Like Structures				
	Length of Photoperiods				
	Natural	8 Hours	16 Hours	24 Hours	Means
Control	0.0	0.0	0.0	0.0	0.0
100	0.7	0.7	1.6	1.7	1.2
500	2.1	1.3	1.4	1.7	1.6
1000	2.4	1.5	2.7	2.8	2.4
Means	1.7	1.5	1.9	2.1	1.8
L. S. D. at 5% level			0.1		
L. S. D. at 1% level			0.2		

*All values are averages from 25 plants.

TABLE XXVIII

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on the Number of Strap-Like Leaves of Phlox (1957)

Concentration (ppm)	*Average Number of Strap-Like Leaves				
	Length of Photoperiods				
	Natural	8 Hours	16 Hours	24 Hours	Means
Control	0.0	0.0	0.0	0.0	0.0
100	2.6	2.0	2.6	3.2	2.6
500	4.3	2.1	2.5	4.2	3.3
1000	5.2	2.1	4.5	4.0	3.9
Means	4.0	2.0	3.2	3.8	3.3
L. S. D. at 5% level			0.1		
L. S. D. at 1% level			0.2		

*All values are averages from 25 plants.

TABLE XXIX

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on the Number of Fused Leaves of Phlox (1957)

Concentration (ppm)	*Average Number of Fused Leaves				
	Length of Photoperiods				
	Natural	8 Hours	16 Hours	24 Hours	Means
Control	0.0	0.0	0.0	0.0	0.0
100	1.8	1.2	1.2	1.5	1.4
500	2.6	1.3	0.7	1.2	1.5
1000	3.4	1.8	1.2	1.4	2.0
Means	2.6	1.4	1.1	1.4	1.6
L. S. D. at 5% level			0.1		
L. S. D. at 1% level			0.2		

*All values are averages from 25 plants.

TABLE XXX

Effect of Various Concentrations of 2, 3, 5-Triiodobenzoic Acid and Photoperiods on the Chemical Composition of Phlox Plants (1957)

Photoperiods / Concentrations	Percent of Oven-Dry Weight of Samples*				
	Ash	Crude Fiber	Ether Extract	Proteins	N-Free Extract
Normal					
0	11.85	24.78	3.88	15.25	44.24
100	13.78	24.66	3.77	16.56	41.23
500	11.65	25.86	3.63	14.56	44.32
1000	13.00	23.40	4.40	17.75	41.45
Means	12.57	24.68	3.92	16.03	42.81
8-Hour					
0	24.70	18.24	4.09	18.81	40.63
100	16.49	19.97	4.10	18.63	36.95
500	21.32	19.13	3.97	19.06	34.98
1000	22.79	19.06	4.11	18.93	34.34
Means	21.33	19.10	4.07	18.86	36.73
16-Hour					
0	13.18	24.34	3.30	20.19	38.99
100	14.84	21.05	3.55	18.00	42.56
500	12.44	23.91	3.44	18.50	41.71
1000	12.60	25.09	3.59	18.81	39.91
Means	13.27	23.60	3.47	18.88	40.79
24-Hour					
0	13.46	27.23	3.15	18.69	37.47
100	15.50	27.08	3.37	21.25	34.80
500	13.67	25.14	3.39	22.06	35.74
1000	13.77	26.26	3.15	19.25	37.57
Means	13.60	26.43	3.27	20.31	36.40
.. S. D. at 5% level	3.37	2.15	0.32	2.12	3.27
. S. D. at 1% level	5.24	3.09	0.46	3.05	4.71

*Averages of results from duplicated determinations expressed on oven-dry basis.

composition. It was found that when the duration light was reduced to eight hours there was significant increase in total ash and significant decrease in crude fiber. Chemical application caused a significant decrease in nitrogen-free extract under eight-hour photoperiod.

Figure 8. Response of Phlox drummondii to applications of 2, 3, 5-triiodobenzoic acid and an 8-hour photoperiod.

Left to right: 100, 500, 1,000 and 0 ppm.

Figure 9. Response of Phlox drummondii to application of 2, 3, 5-triiodobenzoic acid and a 16-hour photoperiod.

Left to right: 100, 500, 1, 000 and 0 ppm.

Figure 11. Response of Phlox drummondii to various photoperiods.

Left to right: 8-hour, 16-hour, 24-hour, and normal.

Figure 12. Phlox drummondii treated with 500 ppm 2, 3, 5-triiodobenzoic acid showing abnormally elongated hollow stem.

Figure 13. Phlox drummondii treated with 500 ppm 2, 3, 5-triiodobenzoic acid showing cone-like terminal, pair of strap-like leaves, and distorted cotyledonary shoots.

Figure 14. Phlox drummondii treated with 500 ppm 2, 3, 5-triiodobenzoic acid showing abnormally narrow petioles of first true leaves and flaring cone-like terminal.

Figure 15. Normal plant of Phlox drummondii.

GENERAL DISCUSSION

Effect of Plant Regulators on the Vegetative Development of Selected Herbaceous Ornamentals

The results of these investigations clearly show that application of growth regulators to germinating seed and foliar sprays to seedlings had pronounced effects upon subsequent vegetative development of herbaceous ornamentals. The effects obtained were dependent largely upon the concentration of chemical applied, the physiological activity of the chemical, the species of plant treated, the morphological age of the plant when treated, and the environmental conditions to which the plant was exposed after treatment.

As measured by weights of flowering plants, it was observed that application of low concentrations generally tended to promote growth while higher concentrations resulted in retardation of growth. This trend of vegetative development in accordance to chemical concentration is shown Tables III and VI. In addition, it has been shown that different species of plants did not show the same degree of response to a particular concentration of a given chemical. This is apparent in Tables XVIII and XIX. With 2,3,5-tribromobenzoic acid wallflower plants showed an increase in weight with increased concentration of this chemical, whereas increased concen-

tration resulted in a decrease in phlox weights. These and other results seem to indicate that for each plant there was an optimum level at which beneficial effects were derived and a critical level at which the effects became inhibitory. Thus, it becomes clear that if desired effects are to be assured, one must consider the many influencing factors and adjust applications accordingly.

The type and magnitude of response obtained with growth regulators depended on the amount of the compound absorbed by the plant, and the amount translocated within the plant (Mitchell and Marth, 1950). This was evident from Table XXI, which showed that response of plants to chemical treatment was affected by the total absorptive surface area present at the time of chemical applications. Plants treated with low concentrations of 2, 3, 5-triiodobenzoic acid when two weeks old, at which time greater surface area was present, were more responsive than plants treated one week earlier. This effect could also have been due to the presence of a greater number of young expanding meristematic tissues with a rapid rate of growth in the slightly older plants. This would be especially true as it pertains to young buds and leaves. Since the auxin level in the terminal of a plant is a primary factor in the inhibition of lateral buds, treatments which reduced the auxin level stimulated branching. Thus, it can be concluded that increased weights were due largely to auxin stimulated development

of lateral shoots. On the other hand, there is a tendency for somewhat older terminal buds to yield proportionally more diffusible native auxin than smaller, young apices. Since the synergistic action of low concentrations of an anti-auxin (TIBA) with auxin tends to stimulate growth to a greater extent when the auxin level is relatively high, it is probable that this relationship was contributory with plants having an increased number of young, active leaves.

It was observed that those chemicals which exerted the greatest influence upon the growing points of plants tended to be most effective in influencing the whole course of plant development. Maleic hydrazide, sodium trichlorobenzoate, and 2, 3, 5-triiodobenzoic acid were found to have the greatest influence upon the growing points and also on overall vegetative development in these tests (Figures 1, 3 and 6). At lower concentrations inhibition of terminal growth caused pronounced development of axillary shoots, which in many cases tended to result in greater total vegetative development (Table XVII). Similar effects on vegetative development has been noted by Avery et al. (1937), Naylor and Davis (1950), and Applegate (1956).

The two main barriers to penetration of chemical sprays are the cuticle and plasma membrane (Overbeek, 1956). Therefore, it can be concluded that the physical structure of the foliage itself strongly affects the response of different plants to growth regulators applied as foliar sprays.

Waxy leaves which are difficult to wet present a more effective barrier to the accumulation and absorption of sprays than less protected leaves. Thus, the same concentration of spray may be less effective on plants having the former type of leaf than those with leaves of greater absorptive capacity. This may, in part, account for differences in response to 2, 3, 5-tribromobenzoic acid shown by phlox and wallflower (Tables XVIII and XIX).

It was observed that even low concentrations of more physiologically active regulators appeared to cause temporary inhibition of growth soon after their application. The duration of their effect was in direct proportion to the concentration applied. When growth resumed it proceeded at the same rate as controls, and in some instances the growth rate of controls was exceeded. It is suggested that the promotive effect of low concentrations of plant regulators on subsequent vegetative development is due to their effects on root development. It is generally concluded that very low concentrations of growth regulators tend to stimulate root elongation, thereby resulting in a more efficient root system, which would promote vegetative growth.

High chemical concentrations in general was inhibitory to vegetative development. With some chemicals, inhibition lasted for extended periods before growth resumed either from apical or lateral buds. This prolonged inhibition was reflected by extremely low weights of flowering plants. In instances where terminal growth was completely inhibited and no laterals

developed (Figure 4), it was apparent that the chemical exerted a persistent effect which prevented further division of meristematic cells of both terminal and axillary buds.

It was consistently observed that growing conditions to which plants were exposed following chemical treatments influenced their response. During the seasons of the year when all environmental factors (especially light intensity) favored rapid vegetative development, plants which were treated with low chemical concentrations of growth regulators were induced to greater growth than controls, and those similarly treated under more adverse environmental conditions. Reference to Table VI shows that growth of snapdragon plants under non-vernalized condition was effectively stimulated in a number of instances by chemical treatments. Table XI shows that the same concentrations did not stimulate growth, and in some instances inhibition of growth occurred. It should be noted that the data in Table VI were collected from plants started in early March, whereas those of Table IX were started in November. The limitation of carbohydrate production during the winter months was probably a strong influencing factor, since translocation and effectiveness of auxins are largely dependent upon this factor.

Another aspect of seasonal influence upon plants' response to growth regulators is the effect of light on endogenous auxin supply. The auxin supply tends to decrease in darkness and low light intensity (Zimmerman and

Hitchcock, 1937), while higher light intensity is conducive to auxin production and auxin induced growth. This was reflected by differences in response to applied regulators according to seasonal light conditions.

Differences in auxin levels are also influenced by length of photoperiods. Auxin level tends to be higher under long-day conditions than under short-day conditions. With phlox short photoperiods were associated with profuse branching, prostrate habit of growth, and less rapid elongation (Figure 11). This was an indication of low auxin level due to probable limitation of auxin production and greater auxin destruction by the extended dark period. Reference to Tables XXIV and XXV shows that stimulation of growth under 8-hour photoperiod by applications of 2, 3, 5-triiodobenzoic acid was highly significant. It is suggested that translocation of the chemical was delayed by the short photoperiod and low light intensity of the winter months, thus accounting for its persistent effect. With the high auxin level of spring the synergistic promotion of growth was enhanced.

Effects of vernalization on vegetative development as presented in the foregoing tables did not appear to be promotive. However, when it is considered that non-vernalized plants were placed under conditions favorable to vegetative development two and three weeks earlier than vernalized plants, it can be seen that growth was stimulated, especially so when the number of nodes before flowering is considered.

Effect of Plant Regulators on the Morphology of Selected Herbaceous Ornamentals

Numerous examples have been given which show that application of growth regulators can induce striking morphological abnormalities in plants. The responses obtained were dependent upon the formative activity of the chemical, concentration applied, the degree of tissue differentiation at time of application, plant species, and environmental factors.

The substituted benzoic acid and maleic hydrazide were found to be highly active, while 5-chlorosalicyclic acid and indoleacetic acid exerted less pronounced influence. The magnitude of effect was in direct proportion to concentrations used.

It has been shown that chemical treatments stimulated development of axillary buds, especially after continued growth of the terminal bud had been inhibited. In many instances this resulted in a plant without a strong central axis (Figure 6). This indicated that the applied regulator was antagonistic to indoleacetic acid, and effectively lowered its content in terminal bud (Naylor and Davis, 1950; Leopole and Klein, 1952). Since young leaves are the seat of auxin production, it is likely that suppression of terminal leaf production (Figures 12 and 13) contributed to reduction of auxin accumulation in the terminal bud, thereby encouraging axillary shoot growth.

Short internodes was also an expression of native auxin deficiency.

Strap-like leaves and distorted leaves with many closely placed veins were caused by development of replacement tissue and failures of normal lateral leaf expansion (Figures 2 and 7). The replacement tissue consisted of thick walled parenchyma-like cells, which replaced the normal chlorophyll-bearing mesophyll cells (Watson, 1948).

Cone-like structures reflected a cessation of growth in the most distal cells of the apex and continued growth in subjacent regions (Wardlaw, 1953). A prevalent type (Figure 14) was formed by the connate growing together of two or more leaves (Van Stevenick, 1956). Chemical application also altered the shape and structure of growing points in such a way that they lost their capacity to split off leaf primordia and grew out as straight cones (Figures 12 and 13). This type of abnormality has been described by Gorter (1951). Cone-like structures and funnel leaflets appeared at the ends of the central stem and axillary shoots. In many instances both axillary and terminal straight-cones were subtended by a pair of strap-like leaves.

The effect of growing conditions upon the formation of abnormalities was observed with phlox under different light durations. It was found that the photoperiods which allowed for more succulent growth and rapid stem elongation resulted in greater numbers of cone-like shoots. This was probably due to more immediate stimulation of basil laterals under the favorable environ-

ment. An increased number of strap-like and fused leaves were found under the natural photoperiod. Since the appearance of dused leaves reflects a milder physiological activity of growth regulators than other formative effects, it is condluded that under this photoperiod the chemical effect was milder, but of longer duration than under longer photoperiods.

Effect of Plant Regulators on the Flowering of Selected Herbaceous Ornamentals

It has been reported that the effects of plant regulators on flowering is dependent upon such factors as the chemical used, concentration applied, time of application with respect to plant development, type of plant, and environmental conditions. With proper timing and proper dosage, flowering may be accelerated, and in some instances chemically induced. On the other hand, by altering the time of application and dosage, flowering may be inhibited (Wittwer, 1954).

Results of the investigation herein reported showed that under several instances low concentrations of chemicals decreased the number of days from seeding to flowering. This was noted under non-vernalized conditions with snapdragons (Table IV). Comparison of these results with the data of Tables V and VI show that acceleration of flowering was associated with an increase in weight and node number. Therefore, it is clearly indicated that earlier flowering resulted from the stimulatory effect of more abundant vegetative development.

Comparison of data in Table IV with that of Table VII shows the seasonal influence upon the flowering response as noted previously with vegetative development. In the latter, the same chemicals and concentrations tended to

delay flowering as they did vegetative development.

Reference to Table XXII shows that flowering of phlox plants which were treated with 2, 3, 5-triiodobenzoic acid and grown under an eight-hour photoperiod flowered as much as twenty days earlier than controls under the same photoperiod. It should be recalled that seed of this long-day plant were sown November 30, and very little vegetative development occurred as long as the short photoperiod was maintained (Figures 8 and 11). However, upon exposure to the long days of spring, rapid vegetative development occurred (as indicated by weight measurements in Tables XXIV and XXV) and flowering soon followed. It is suggested that acceleration of flowering in this instance also resulted from the stimulatory effect of more rapid growth, and earlier attainment of minimal vegetative development for flowering. Increased growth rate was induced by the synergistic action of high auxin level and applied growth regulators as discussed previously.

Acceleration of flowering of herbaceous ornamentals with 2, 3, 5-triiodobenzoic acid has also been reported by Wildon and Hamner (1955) and Applegate (1956).

Even though the interaction of vernalization and chemical treatment did not indicate a consistent effect on time of flowering, the effect of vernalization when considered separately was highly effective. It was observed that although vernalized seedlings and germinating seed were exposed to

environmental conditions which permitted growth two and three weeks later than non-vernalized controls, in most instances there was only a slight difference in their flowering date. Thus, it was quite obvious that vernalization significantly reduced the number of growing days to flowering. It was also noted that flowering occurred on plants which were smaller in size than the controls. This observation agrees with the finding of Crafts et al. 1950, Andrews 1953, and Rappaport 1956).

Effect of Plant Regulators on the Chemical Composition of Selected Herbaceous Ornamentals

Applied growth regulators may have very different effects on chemical composition of plants, depending upon the concentration. Physiological concentrations which may stimulate vegetative growth would probably have less pronounced influence than higher concentrations which may exhibit strong herbicidal action. Therefore, it should be recognized that collected data was complicated by the fact that the actual dry weight of plant material was altered as the result of treatments. Consequently, when treated plant constituents are compared with, or expressed as percentages of unit dry weight of controls, the values may be somewhat misleading (Leopold 1955). However, such comparison does tend to indicate the general trends of plant response to growth regulators as reflected by their chemical composition.

Since the chemical composition determinations of this investigation were made on phlox plants, which were grown during an adverse season for their best development, it is likely that the data presented were affected by seasonal factors. As indicated in previous sections of this discussion, the eight-hour photoperiod, as handled in this investigation, would more nearly approach the natural growing conditions. This conclusion is understandable when it is recalled that growth was almost completely inhibited as long as

this short-day condition was maintained (Figure 11). Consequently, the plants accomplished most of their development during the spring months. The data of Table XXX for this photoperiod show that there was a trend towards a disappearance of the carbohydrate reactions as the result of application of 2, 3, 5-triiodobenzoic acid. This observation agrees with those of other workers (Alexander, 1938; Brown, 1946; Tukey et al., 1946; Sell et al., 1949; Klingman and Ahlgren, 1951). In general, conclusive observations were not made from other findings.

SUMMARY

Application of plant regulators to germinating seed and foliar sprays to seedlings influenced subsequent vegetative development of selected herbaceous ornamentals. The responses obtained were largely dependent upon the concentration of chemical applied, physiological activity of the chemical, species of plant treated, morphological age of the plant when treated, and environmental conditions following treatment.

For each plant there was an optimum level at which promotive effects occurred and a critical level at which effects became inhibitory. High concentration, in general, was inhibitory to growth and development.

Chemicals which exerted the strongest influence upon terminal growing points most effectively altered the future development.

In general, acceleration of flowering was associated with an increase in weight and node number, therefore, it was concluded that earlier flowering was an indication a stimulatory effect of more vigorous vegetative development and not an indication of earlier chemically induced floral initiation. Furthermore, delay of flowering was generally associated with decreased weight and node number.

The interaction of vernalization and growth regulators did not consistently affect floral expression; however, vernalized plants required a smaller

number of growing days from seeding to first flower.

An interaction of photoperiods and 2, 3, 5-triiodobenzoic acid on flowering of phlox was promotive only under the eight-hour duration. Flowering was delayed by chemical treatment under other photoperiods.

Chemical composition of phlox as influenced by 2, 3, 5-triiodobenzoic acid was affected only under eight-hour photoperiod where a decrease in carbohydrates was noted.

Pronounced morphological and teratological changes resulted from the use of most chemicals. The prevalence and magnitude of these changes were largely dependent upon chemical concentration used, physiological activity of the chemical, plant type, and environmental conditions.

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