FLORAL INITATION AND EXPRESSION IN *WEIGELA* AS AFFECTED BY PHOTOPERIOD AND EXOGENOUS APPLICATIONS OF GIBBERELLIN AND MALEIC HYDRAZIDE

Thesis for the Degree of M. S.
MICHIGAN STATE UNIVERSITY
David Cameron Maclean
1962

FLORAL INITIATION AND EXPRESSION IN WEIGELA AS AFFECTED BY PHOTOPERIOD AND EXOGENOUS APPLICATIONS OF GIBBERELLIN AND MALEIC HYDRAZIDE

By

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A THESIS

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

MASTER OF SCIENCE

Department of Horticulture

1962

ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation to Dr. Harold Davidson for his accurate guidance, invaluable suggestions and aid throughout this investigation.

The writer is also indebted to Dr. Donald P. Watson for his helpful suggestions concerning the anatomical studies, to Dr. M. John Bukovac for his constructive criticisms, and to Dr. Richard R. Dedolph for assistance with statistical methods.

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INTRODUCTION

The growth and development of plants can be modified in various ways. Two such methods are: by controlling the relative duration of darkness and illumination (photoperiod); and by the application of chemical substances with growth regulatory properties such as gibberellin and maleic hydrazide.

The numerous literature references germain to photoperiodism and to the responses of plants to applications of gibberellin and maleic hydrazide have, for the most part, been concerned with herbaceous species, and relatively little has been published of their effects on woody plants. Undoubtedly, the limited amount of research on woody plants is due to the time required to obtain valid results and the relatively small number of researchers concerned with woody plants. In the past decade there has been an increasing interest in the responses of woody plants to photoperiod and to plant growth substances, but there is much yet to be learned of these responses on both the theoretical and practical levels.

This investigation concerns the joint effects of photoperiod and maleic hydrazide or gibberellin on the initiation and expression of flowering in Weigela.

REVIEW OF LITERATURE

Photoperiodism

General

The use of the electric light to lengthen the daily duration of illumination in order to promote plant growth was reported as early as 1880 by Siemens (1880). Shortly thereafter, Bailey (1891, 1892, 1893) conducted an extensive series of experiments using the electric arc light on greenhouse plants. He noted that growth and maturity were hastened and that flower color was often intensified by these treatments.

Later Bonnier (1895) published a series of papers on the modifications of plant structure when grown under electric lights. He reported on the responses to different intensities, but not to different durations. Klebs (1914), in 1914 reported that European beech, oak, ash, and hornbeam grew all winter under continuous illumination.

The effect of the relative duration of day and night on plants was not conclusively demonstrated until Garner and Allard (1920) published their classical report. For this effect they suggested the term photoperiod, and to designate "the response of organisms to the relative length of day and night", the term photoperiodism was proposed. on the basis of their flowering responses, plants were

classified as: (a) long-day plants, those which flowered when the photoperiod was longer than the critical period (eg. that light period which is the dividing line between photoperiods favorable for flowering and photoperiods favorable for vegetative activity); (b) short-day plants, those which flowered only when the photoperiod was shorter than the critical period; and (c) indeterminate plants, those which flowered over a wide range of photoperiods (Garner and Allard, 1920). Later (Allard, 1935), a fourth group designated intermediate was added. Intermediate plants were those which flowered when the photoperiod was intermediate (12 to 14 hours), but remained vegetative at photoperiods longer than 12 to 14 hours. More recently, new terms have been introduced such as long-short-day plants, non-obligate short-day plants, and many others which more precisely describe their photoperiodic responses.

Role of the Dark Period

The first mention of the role of the dark period was made by Blackman (1936) who postulated that "in the case of short-day plants there is some reason to believe that it is...the period of darkness to which attention should be directed". Subsequently, it was realized that the length of the dark period was the primary determining factor for photoperiodic flower induction for both long- and short-day plants, and they might be more properly termed short- or long-night plants respectively (Hamner and Bonner, 1938). Short-night (long-day) plants have been defined as those

plants which require a dark period shorter than the critical period (Bonner, 1959a), and long-night (short-day) plants have been defined as those which require an uninterrupted dark period longer than the critical period. For convenience, the original terms long-day and short-day are still accepted and commonly used.

For photoperiodic responses it is the duration of light (or more accurately the duration of continuous darkness), and not light intensity, which is effective. Supplimentary artifical light of an intensity as low as 0.1 foot candles, which is only twice the intensity of bright moonlight, has been effective in hastening the flowering of *Callistephus chinensis* (Withrow and Benedict, 1936). Using bright moonlight itself for supplimentary illumination, Gaertner (1935) found that *Hordeum distichum*, *Triticum vulgare*, and *Iberis amara*, all long-day species, flowered earlier; he also noted that two short-day species, *Soja hispida* and *Pharbites hispida*, exhibited a delay in flowering when exposed to bright moonlight.

Working initially with tobacco and soybean, and later with a wide variety of plants, Garner and Allard (1920, 1923) observed various plant responses to photoperiods of different durations. For the most part, emphasis was placed on the influence of photoperiod on: increase in stature; tuberization and formation of bulbs and thickened roots; character and extent of branching; root growth; pubescence; pigment synthesis; senescence and rejuvinescence; abscission

and leaf fall; dormancy and death; and geographical distribution. Since then the influence of photoperiod on sex expression, root development, rhizome formation, seed germination, and seedling elongation have been reported (Hendricks and Borthwick, 1954). More recently, some teratological effects have been attributed to photoperiod by Youmis (1955), Davidson and Watson (1959), and Piringer and Borthwick (1961).

The Flowering Response

The most basic stage of flowering is induction, or the transition of a meristem from vegetative to reproductive development. If Xanthium, a short-day plant, which has been growing under long-days is exposed to one short-day followed by a long-night and then returned to long-day exposure, flowering will be initiated and expressed even if long-days are continued (Hamner, 1940). This phenomenon is photoperiodic induction, and the number of photoinductive cycles required for photoinduction varies from species to species.

The leaves are the loci of photoperiodic induction (Bonner, 1959b; Hamner and Bonner, 1938; Borthwick and Parker, 1938a; Hamner and Naylor, 1939; Naylor, 1941b) and the stimulus, which is interchangeable for both long- and short-day types, is of a hormonal nature (Lang, 1952; Bonner and Liverman, 1953).

Short-day Plants

In short-day plants it is the long night that controls photoperiodic induction (Hamner and Bonner, 1938). Hamner (1942) postulated a hormonal theory in which substance "A" increases in amount when plants are exposed to light, and another substance, "B", that increases during dark periods and is destroyed by brief periods of light. When "B" reaches a threshold value, it interacts with "A" resulting in the substance "C", and floral initiation occurs.

Later, Liverman and Bonner (1953), suggested that the presence of an auxin-receptor complex controls the flowering response. When exposed to light, an auxin non-receptive precursor becomes receptive and combines with auxin resulting in the auxin-receptor complex. In the dark, this complex begins to decompose below the threshold level required for short-day plant induction. However, a flash of red light during the dark period interrupts this decomposition and the auxin-receptor complex is formed again.

More recently, Bonner (1959b) summarized the events which occured during photoperiodic treatments of short-day plants as: (a) the conversion of a pigment from a predominately far-red absorbing form to a red absorbing form during the early stages of the dark period; (b) the occurance of a temperature insensitive time-measuring reaction of which little is known; (c) the formation of the "flowering hormone" in the leaf in the dark; (d) the stabilization of the product of the dark period; and (e) the translocation of

the hormone from the leaf.

Long-day Plants

Unlike short-day plants, the dark period is not necessarily a critical factor in the photoinduction of long-day plants. In fact, flowering of many long-day plants is optimal under continuous light (Hamner and Bonner, 1938; Naylor, 1941a). Experiments with *Hyoscymus niger* show that it is the period of illumination and not the short-night that determines photoperiodic induction, and other evidence indicates that long dark periods exert an inhibitory effect on photoperiodic responses (Lang, 1952). Long-day plants exposed to short-days can be induced to flower by interruptions of the dark period by low intensity light (Bonner and Liverman, 1953). Lang (1952) states that the action of light in controlling floral initiation in long-day plants is the "counteraction of the inhibitory effect of dark periods in the formation of the floral stimulus".

The Action Spectra

Measurements of the action spectra of photoperiodic responses have given mich to the understanding of the flowering response. Barley, a long-day plant, has an action spectrum for flowering which is the same as the action spectrum for flower inhibition of *Xanthium*, a short-day plant. The action spectra have two parts; one favors the photoperiodic response and the other nullifies it, indicating that the mechanism of flowering of both types is the same

(Hendricks and Borthwick, 1954). Radiation of 540 to 695 mμ with a maximum at 660 mμ (red) favors the flowering of barley, but inhibits flowering of cocklebur. The induction of these responses can be reversed before the actual response occurs by far-red (695 to 800 mμ) radiation (Borthwick and Hendricks, 1960; Butler *et al*, 1959). The antagonism between red and far-red light is completely reversible. This photoreversibility is due to phytochrome, a blue or blue-green pigment which can exist in either red or far-red absorbing forms. Upon exposure to red light it is converted to the far-red absorbing form, which if irradiated with far-red light, changes back to the red absorbing form (Borthwick *et al*, 1952; Borthwick and Hendricks, 1960).

The reversible photoreaction which applies to most observed photoperiodic phenomena can be written, with some uncertainty, as

$$\text{Pigment } RH_2 + A \xrightleftharpoons[\text{720-740 m}\mu\text{ max}]{\text{650-660 m}\mu\text{ max}} \text{Pigment} + FR + AH_2$$

where R refers to the red absorbing form, FR to the far-red absorbing form, and A to the hydrogen acceptor (Hendricks, 1959).

The above reaction has been shown to control; flowering of both long- and short-day plants, seed and fern spore germination, elongation, plumular hook unfolding, and anthocyanin formation. Evidence indicates that it may also

be involved with epinasty, leaf abscission, bulbing, sex expression, root development, and plastid generation (Hendricks, 1959).

Photoperiodism in Woody Plants

Vegetative Responses

In 1914, before the discovery of photoperiodism, Klebs (1914) noted that European beech, oak, ash, and hornbeam grew all winter when given continuous illumination. In one of their early reports Garner and Allard (1923) reported that long-days promoted and short-days retarded or caused a cessation of vegetative growth of Rhus glabra, Acer negundo, and Liriodendron tulipifera. They also reported that Malus sylvestris grew better under short-days than long-days. However, since these early reports there have been relatively few publications concerning the effects of photoperiod on trees and shrubs. Nevertheless, vegetative responses such as root and shoot extension, the induction and breaking of dormancy, cambial activity and leaf abscission, all of which are affected by photoperiod, have been reported. Two general reviews by Nitsch (1957b) and Wareing (1956) have summarized these photoperiodic responses of woody plants.

In general, photoperiods longer than the critical photoperiod favor shoot growth by increases in length and node number, and short photoperiods usually result in reduced extension due to earlier cessation of apical growth

and reduced internode extension (Garner and Allard, 1923; Wareing, 1941; Nitsch and Nitsch, 1959; Waxman, 1958). The response of roots to photoperiod has received little attention other than on the rooting of cuttings (see later).

Leaf abscission of a number of deciduous species can be prolonged by lengthening the photoperiod and hastened by short photoperiods (Garner and Allard, 1923). Short-days can also bring about the onset of dormancy (eg. imposed dormancy) and long-days are capable of breaking dormancy of many woody plants (Wareing, 1949, 1956). Imposed dormancy is much more readily broken by long photoperiods than is winter dormancy (Wareing, 1956).

The natural reduction in the length of day prior to the onset of freezing temperatures in the Northern Hemisphere retards growth and thereby reduces the probability of winter injury. Wareing (1949) reported that southern species grown in northern latitudes were susceptible to low temperature injury due to the effect of the longer photoperiod. By reducing the natural daylength, Davidson (1957) found that *Hibiscus syriacus*, *Rhododendron catawbiense*, and *Weigela florida* became highly resistant to freezing temperatures. Conversly, *Abelia* grown under long-days was killed by low temperature (Kramer, 1937).

Flowering

The limited information concerning the effects of photoperiod on flowering of woody plants has, for the most part, been restricted to the determination of the photo-

periods favorable for flowering, and they have been summarized by Wareing (1956).

Propagation

Caspary in 1860 was the first to report on the beneficial influence of light on seed germination (Borthwick and Hendricks, 1960). But it was not until 1955 however, when Black and Wareing (1955) reported their findings on Betula pubescens, that the effect of photoperiod on the germination of woody plant seeds was known. They found that germination occured when exposed to long photoperiods. This eliminated the chilling requirement and chilled seeds were found to be unaffected by long-days. Shortly thereafter, Waxman (1957) found that the germination of Sciadopitys verticillata was similar to the flowering response of short-day plants. Germination was inhibited by continuous light, but when exposed to short-days germination was earlier and at a significantly higher percentage.

The rooting of cuttings is influenced by photoperiod in two ways; (a) directly upon the cutting, and (b) indirectly through the stock plant. In general, long-days provided during the rooting period result in an increase in the rate and extent of rooting. The effects of exposing stock plants to different photoperiods on the rooting of cuttings varies from species to species (Nitsch, 1957b).

EFFECTS OF GIBBERELLIN ON WOODY PLANTS

The first report on the effects of gibberellin, the generic name for nine distinct chemical structures, on woody plants was published in 1956 (Marth _et al_, 1956). This was immediately followed by numerous papers concerning its remarkable effects on woody plant behavior, and there is still much interest in this area.

Application of gibberellin results in increased length of internodes and accelerated shoot elongation of most deciduous fruit, shade and ornamental trees and of most shrubs (Marth _et al_, 1956; Nitsch, 1957a; McVey and Wittwer, 1958; Bukovac and Davidson, 1959). However, most conifers fail to exhibit this growth response (Nelson, 1957; McVey and Wittwer, 1958).

When applied to woody plants, gibberellin can: stimulate growth of physiological (Barton, 1956) and genetic (McVey and Wittwer, 1958) dwarfs; delay the setting of terminal buds and thereby delay dormancy (McVey, 1961); cause dormant buds to resume growth (Bukovac and Davidson, 1959); replace the cold treatment of dormant embryos(Marth _et al_, 1956); induce juvinility (McVey, 1961); and increase the rate of seed germination (Benjamin and Snyder, 1958).

Gibberellin also exerts an effect on some photoperiodic responses of woody plants. By replacing long-photoperiods, it can overcome the photoinduced dormancy of _Weigela_ (Bukovac and Davidson, 1959) and _Rhus typhina_ (Nitsch, 1957a).

MALEIC HYDRAZIDE

The first report on the growth regulatory properties of maleic hydrazide (MH), or 6-hydroxy-3(2H)pyridazinone (Miller and White, 1956; Weller et al, 1957), was made in 1949 by Schoene and Hoffman (1949). Since that time many different morphological and physiological effects of this compound on plants have been published, and an extensive literature summary has been compiled by Zukel (1957).

Primarily, maleic hydrazide induces dormancy (Crafts et al, 1957) and brings about a temporary cessation of terminal meristem activity due to reduced or inhibited cell division (Naylor and Davis, 1950). Preliminary observations (Currier and Crafts, 1950) indicated that it might be an effective herbicide, but Crafts et al (1957), after extensive studies reported that its effectiveness as an herbicide without supplimental oil sprays or tillage did not warrant its use. However, maleic hydrazide can: cause abscission of fruits of Olea (Hartman, 1955); be used to prevent sprouting in storage of radishes (Dewey and Wittwer, 1955), potatoes,onions, sugar beets, and other vegetable root crops (Wittwer and Paterson, 1951); induce male sterility in Zea (Naylor and Davis, 1950) and acorn squash (Hillyer, 1956); shift the critical photoperiod of Xanthium (Naylor, 1950) and somewhat inhibit the photoperiodic induction of Biloxi soybean (Klein and Leopold, 1953); delay or inhibit flowering and fruiting (Miller and Erskine, 1949); and

overcome apical dominance (Beach and Leopold, 1953; Rai and Hamner, 1955). The effects of maleic hydrazide applications on unlike plant species is strikingly uniform (Naylor and Davis, 1950).

Responses of Woody Plants to Maleic Hydrazide

Exogenous applications of maleic hydrazide to woody plants generally results in the cessation of terminal activity. This is often accompanied by the removal of apical dominance and increased lateral growth (Freeman, 1952; Rai and Hamner, 1955; Reisch and Chadwick, 1955). Retardation of growth can be of practical significance, for applications of maleic hydrazide can: (a) reduce the number of clippings required for hedge plants (Knott, 1950); (b) result in smaller, more compact, higher quality shrubs; (c) enhance frost protection by delaying the opening of buds in early spring and retarding growth late in the season (Pinney and Chadwick, 1955); and (d) inhibit formation of undesirable fruits of Catalpa (Miller and Erskine, 1949).

Most investigators concerned with the effects of maleic hydrazide on flowering and fruiting of woody plants have reported that flower and fruit formation was either delayed or inhibited by maleic hydrazide (Miller and Erskine, 1949; White, 1950; Griesel, 1954; Zulel, 1957). However, Davidson and Bukovac (1961) recently reported that maleic hydrazide (3000 p.p.m.) treated Weigela plants exposed to long photoperiods produced an abundance of flowers twelve weeks after treatment.

Naylor (1950) reported that maleic hydrazide seemingly modified the photoperiodic effect. Applications of the chemical at 0.025% to cocklebur at the beginning of the photoinduction period slightly altered the critical daylength. Klein and Leopold (1953) reported that 4 X 10^{-5} M maleic hydrazide completely inhibited the formation of flower primordia in Wintrex barley, a long-day plant, but only partially supressed photoperiodic induction of soybean, a short-day plant. They suggested that the compound inhibits the production of flower primordia through its "inhibitory effect on growth, rather than by any specific action against the photoperiodic mechanism itself".

Ambiguous reports on the response of plants to maleic hydrazide can be attributed to the effect of relative humidity on absorption through the leaf surface. The rate of absorption is directly proportional to relative humidity, and turgid plants absorb maleic hydrazide at higher rates than do wilted plants. The rates of absorption by tomato plants exposed to either 18 hours light or 18 hours darkness are essentially the same (Smith, 1955). Once absorbed, it is translocated both basipetally and acropetally (Smith et al, 1957; Stone, 1957). Radioactive C^{14} maleic hydrazide applied to tobacco showed that the greatest quantity was translocated to the axillary buds and young leaves, with gradually decreasing amounts in older leaves and the least amount in the oldest leaves. The same distribution pattern was observed when applied to either young or old leaves

(Stone, 1957).

Desson and Rollen (1951) reported that maleic hydrazide inhibits cell division by preventing the cells from entering into mitosis, but Darlington and McLeish (1951) showed that concentrations of 0.0005 M did not completely inhibit mitosis, but caused breakage of chromosomes in Vicia. At concentrations greater than this mitosis was completely inhibited.

Maleic hydrazide has been classified as an anti-auxin by Leopold and Klein (1951), and Hillyer (1956) considered this anti-auxin property as a probable cause of its selective inhibition of staminate flowers, while permitting simultaneous development of pistillate flowers of acorn squash. It has also been suggested that growth inhibition due to maleic hydrazide applications resulted from excessive oxidation of indoleacetic acid (Andreae and Andreae, 1953).

MATERIALS AND METHODS

Experiments to determine (a) the effects of photoperiod and gibberellin and (b) the effects of photoperiod and maleic hydrazide on the initiation and expression of flowering of *Weigela* were conducted in the Plant Science Greenhouse at Michigan State University, from January 1961 to August 1961.

Plant Material and Culture

Plants of *Weigela* clone 'Vanicek' grown from rooted cuttings were used in all experiments. All plants in each of the experiments were exposed to comparable temperatures of 21°C or greater for the duration of the experiments.

Photoperiods

Photoperiods employed in these experiments were provided by extending or reducing the duration of the prevailing natural daylength. The high intensity light phase consisted of nine hours of natural irradiation daily (8am to 5pm). Long photoperiods (16 hours) were obtained by supplimentary low intensity irradiation provided by 60 watt incandescent bulbs for a period of seven hours (5pm to 12pm) following the high intensity light phase. Short photoperiods (9 hours) were obtained by excluding light from the plants for fifteen hours daily (5pm to 8am) by covering with black greenhouse shade cloth.

Bud Analysis

Representative samples of buds were removed for microscopic examination from alternate nodes of all stems exposed to short-days in the photoperiod-gibberellin experiment, and from like nodes of all plants of the photoperiod-maleic hydrazide experiment. Buds removed were killed and fixed in FAA (50 parts 95% ethyl alcohol, 5 parts glacial acetic acid, 10 parts formaldehyde, 35 parts water); dehydrated in a series of ethanol-tertiary butyl alcohol solutions of increasing TBA concentrations from 50 to 100%; imbedded in paraffin; longitudinally sectioned 10 microns thick; and microscopically observed to determine the presence or absence of floral primordia.

PHOTOPERIOD-GIBBERELLIN EXPERIMENT

Six 2-stem and six 3-stem plants of Weigela cl.'Vanicek' in 6 inch clay poys were selected for uniformity of size and vigor, removed from long-day exposure, and 3 plants were subjected to each of the following treatments:

A. 3-stem plants: 1 stem exposed to long-days; 2 stems and pot exposed to short-days

B. 3-stem plants: 1 stem exposed to short-days; 2 stems and pot exposed to long-days

C. 2-stem plants: 1 stem exposed to long-days; 1 stem and pot exposed to short-days

D. 2-stem plants: 1 stem exposed to short-days; 1 stem and pot exposed to long-days

Each of the four treatments was replicated 3 times.

Providing unlike photoperiods to a single plant was accomplished by the use of double thickness black greenhouse shade cloth mounted on a wooden frame. Once the stems had been inserted through the light barrier, the openings were sealed so as to be light-tight. All leaves of stems placed through the light barrier, arising from nodes below the barrier, were removed, and any new leaves arising from these nodes were removed when first observed.

Shoot elongation was measured at 7-day intervals for 7 weeks following treatment and the results are presented in Figure 1.

Seventy-two days after being exposed to the above treatments, all plants were removed and re-staked. Stems previously exposed to long-days were pinched below the

terminal pair of expanding leaves, and a foliar spray of 1000 p.p.m. (acid equivalent) potassium gibberellate was applied to all plants. After treatment with gibberellin, one half of each of the above treatments was subjected to long-day exposure, and the remaining plants were exposed to short-days.

Observations on the expression of flowering were made periodically for 16 weeks, at which time final measurements were recorded and representative samples of buds were removed for microscopic examination.

PHOTOPERIOD-MALEIC HYDRAZIDE EXPERIMENT

Thirty completely vegetative one-stem plants of Weigela cl. 'Vanicek' previously grown from rooted cuttings were removed from long-day exposure and divided into 3 groups of 10 plants each. One group was exposed to short-days (9 hours), another to long-days (16 hours), and the third group received a foliar spray to run-off of maleic hydrazide, supplied as 3000 p.p.m. (acid equivalent) of the diethanolamine salt of 6-hydroxy-3(2H)pyridazinone (MH), and then exposed to long-days (16 hours).

Increases in stem length and incidence of flowering were recorded at 7-day intervals for 10 weeks (Figure 7). At the end of this 10 week period, representative samples of buds were removed for microscopic analysis.

RESULTS

PHOTOPERIOD-GIBBERELLIN EXPERIMENT

Vegetative Responses

Growth rates of Weigela for the first seven weeks after photoperiodic treatment were determined and are presented in Figure 1. Growth rates, as measured by shoot elongation, of stems exposed to long photoperiods increased in a linear fashion with time, whereas stems under short photoperiodic regimes ceased growing by the third week following light treatment. Providing short-days to one portion of the plant and long-days to the other had no effect on growth (Figures 2 and 3).

Stems treated with gibberellin, which were previously under short-day exposure and which had not been growing for seven weeks, resumed growth. This occured when these treated, dormant stems were placed under either long- or short-days (Figure 4: A,b; B,d). Resumption and extent of growth was of a greater magnitude under long photoperiods.

Shoots from the node nearest the pinch on stems formerly exposed to long photoperiods began to elongate by the second week following pinching and treatment with gibberellin. Stems which remained under long-day exposure showed an average elongation of 70.4 cm. sixteen weeks after treatment as compared to 10.8 cm. for those placed under short-days following treatment (Figure 4: A,a; B,c).

Figure 1.

Growth rates of Weigela grown under long- and short-day exposure. Points are the mean elongation values of long- or short-day stems of the four treatments. Curves were fitted to these means by appropriate orthogonal polynomials (Anderson and Houseman, 1942; Dedolph, 1960) or regression methods (Snedecor, 1956).

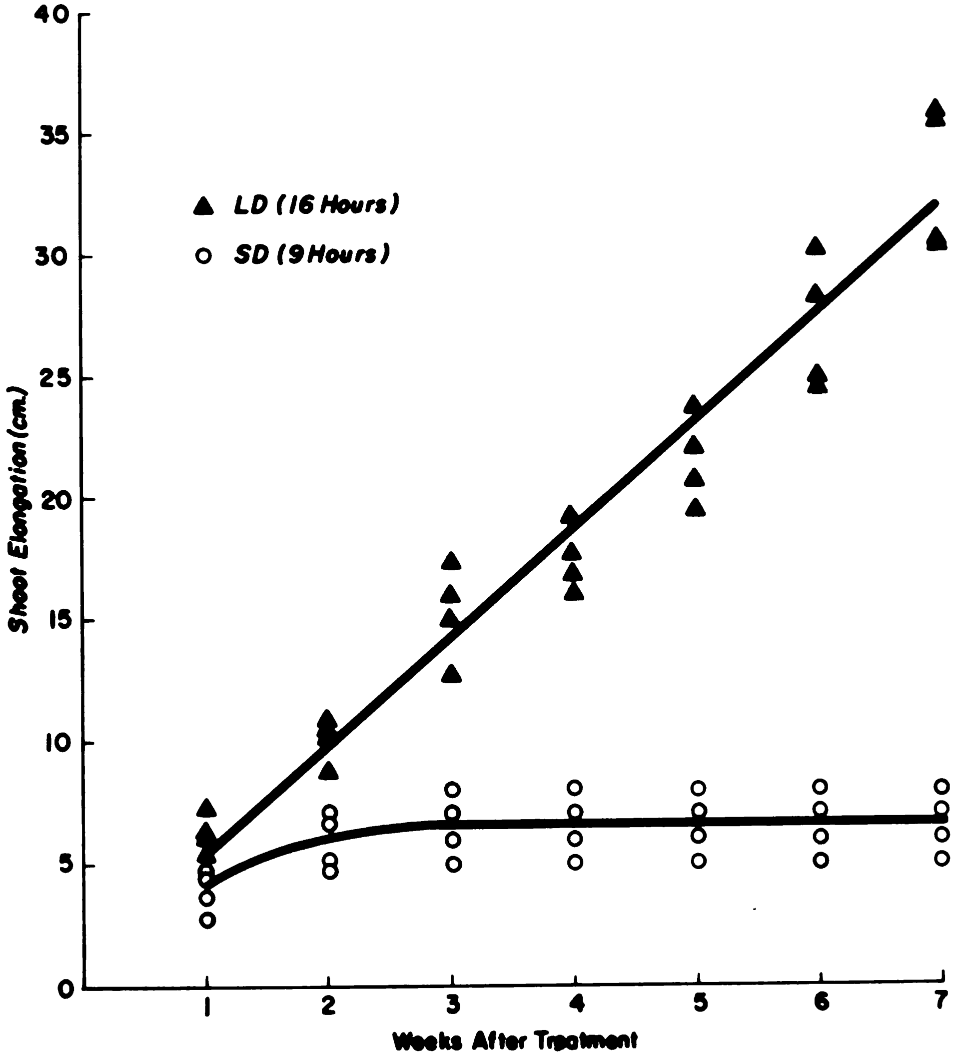

40
35
30
25
20
15
10
5
0
Shoot Elongation (cm.)
▲ LD (16 Hours)
○ SD (9 Hours)
1
2
3
4
5
6
7
Weeks After Treatment

Figure 2.

Effect of long- and short-days on serarate stems of the same plant. (Photographed 10 weeks after placement into light treatments.)

Figure 3.

Three-stem which received photoperiodic treatments.

Left: One stem exposed to short-days, and two stems and pot exposed to long-days.
Right: One stem exposed to long-days, and two stems and pot exposed to short-days.

Figure 4.

Effect of pinching, gibberellin, and photoperiod on the growth of Weigela.

A. Two stems previously exposed to long-days, and one stem exposed to short-days, which after pinching and treatment with gibberellin were exposed to long photoperiodic regimes.
    a. Point of pinching
    b. Point where growth ceased under short-days
B. Same as A, but following pinching and treatment with gibberellin, was exposed to short-days.
    a. Point of pinching
    b. Point where growth ceased under short-days

Figure 5.

Responses of Weigela after three weeks exposure to long-days, short-days, and long-days plus 3000 p.p.m. maleic hydrazide. (Left to right; SD, LD, LD + MH)

2

3

4

5

Floral Responses

Simultaneous exposure of stems of a single plant to different photoperiods had no effect on flowering.

No flowers were expressed at any time from stems which were maintained under short-days both before and after gibberellin treatment; nor were any flowers expressed from stems exposed to long-days prior to pinching and gibberellin treatment, and short-days thereafter. However, buds removed and analyzed at the end of the 26 week period (16 weeks after pinching and gibberellin treatment) revealed that 87.5 percent of the stems continually under short-days, and 62.5 percent of the stems exposed to short-days prior to, and long-days following treatment with gibberellin possessed well defined flower primordia (Figure 6).

Stems which resumed growth after treatment and exposure to long-days expressed flowers, on the average, from 23.3 percent of the nodes produced after treatment. These were invariably from the 3 to 5 most terminal nodes. An occasional flower was observed arising from nodes just below the point from which growth resumed.

New shoots arising from the pinch of plants continually exposed to long photoperiods expressed flowers, on the average, from 36.6 percent of the nodes. Here again, flowering was from the more terminal nodes.

Figure 6.

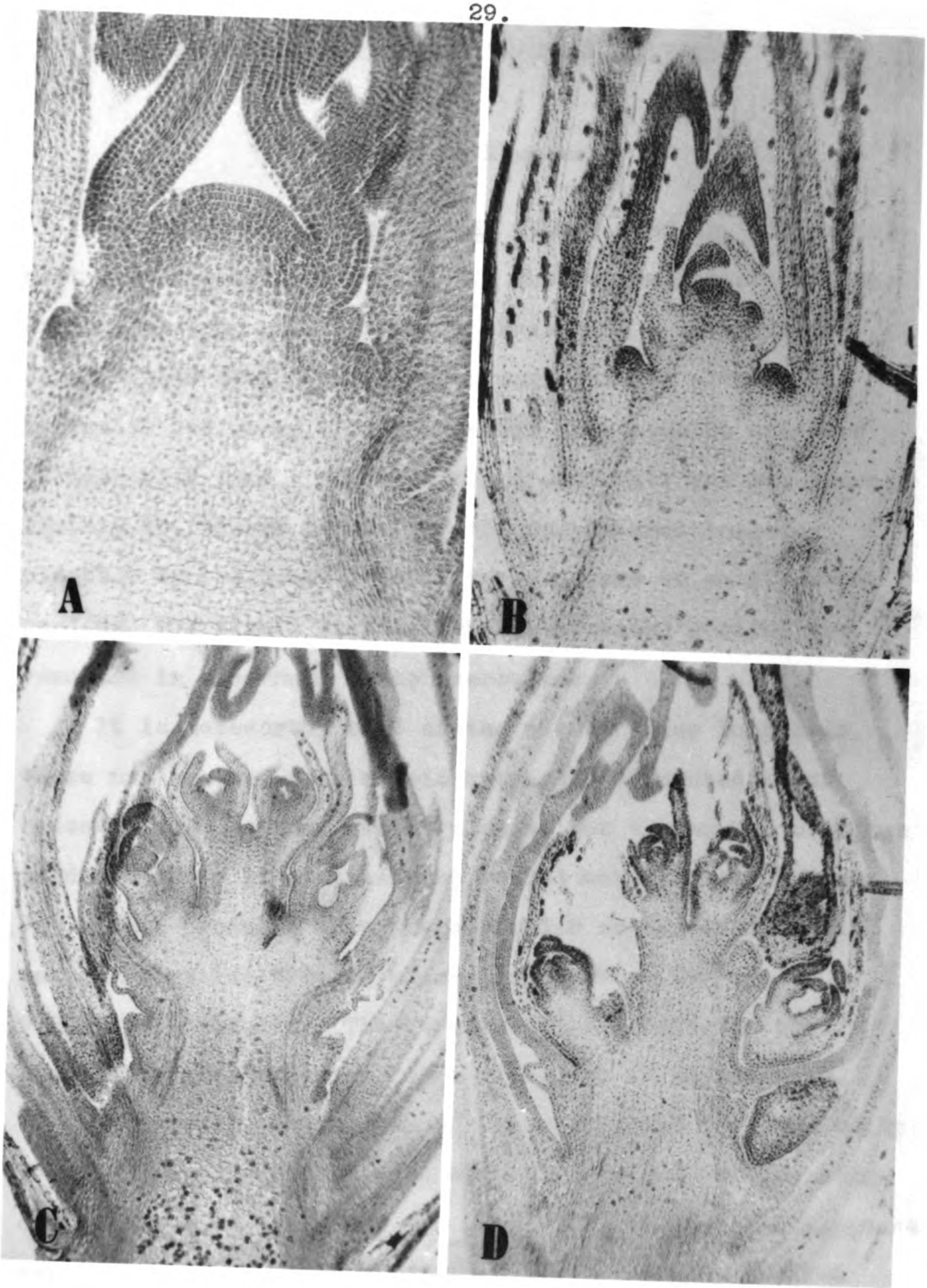
Photomicrographs of longitudinal sections of buds of Weigela.

A. Typical vegetative bud developed under short-day exposure (150 X).

B. Bud from plant treated with 3000 p.p.m. maleic hydrazide and grown under long-days (45 X).

C. Well defined floral primordia contained in bud from stem which was exposed to short-days throughout the experiment (45 X).

D. Well defined floral primordia contained in bud from stem which was exposed to short-days for 10 weeks, followed by 16 weeks under long-days (45 X).


A
B
C
D

PHOTOPERIOD-MALEIC HYDRAZIDE EXPERIMENT

Vegetative Responses

Growth rates of the Weigela plants used in this experiment are presented in figure 7. Shoot elongation of plants exposed to long photoperiods increased in a curvilinear fashion with time. Those which were treated with maleic hydrazide and grown under long-days increased in a linear fashion with time. However, the growth rate was but approximately 50 percent of that of the non-treated long-day plants. By the fourth week after exposure to short photoperiods, the plants in this treatment ceased growing and remained in a dormant state thereafter.

It is noteworthy that of the plants under long-days, those not treated with maleic hydrazide elongated about twice as much as the treated plants, but the number of nodes produced after light treatment varied but slightly. Long-day plants produced an average of 11.8 nodes, whereas the maleic hydrazide-treated plants produced an average of 9.8 nodes (Table I). The terminal 4 to 6 nodes of the chemically treated plants were extremely close together.

In general, by the end of the experiment the chemically treated long-day plants were compact, the non-treated long-day plants were tall, and the plants under short-day exposure were short, but not as compact as the chemically treated plants (Figure 5).

Figure 7.

Growth rates of *Weigela* subjected to long-days, short-days, and long-days plus 3000 p.p.m. maleic hydrazide. Points are the mean elongation values for 10 plants. Curves were fitted to these values by appropriate orthogonal polynomials (Anderson and Houseman, 1942; Dedolph, 1960) or regression methods (Snedecor, 1956).

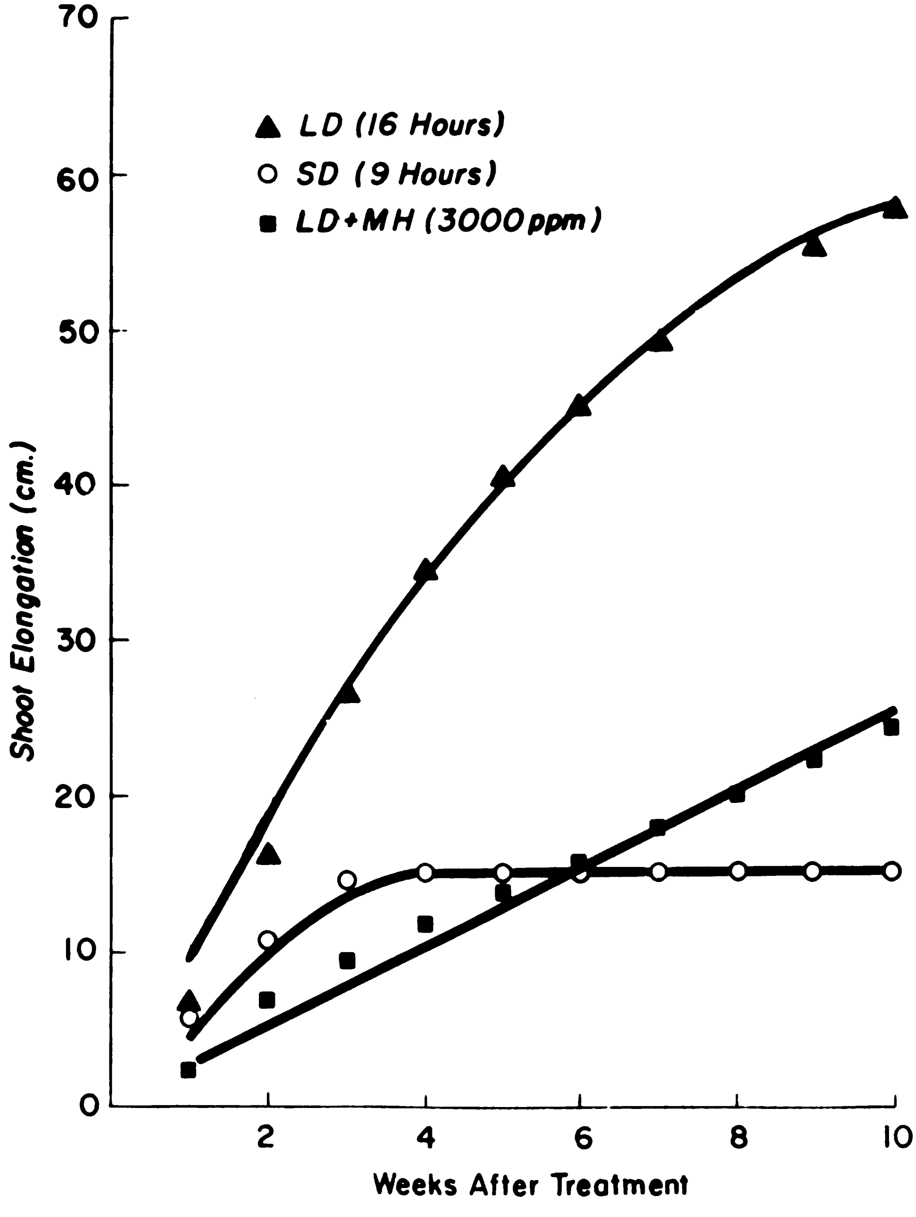

▲ LD (16 Hours)
○ SD (9 Hours)
■ LD+MH (3000 ppm)
Shoot Elongation (cm.)
0
10
20
30
40
50
60
70
2
4
6
8
10
Weeks After Treatment

Table 1. Comparisons of Plants Exposed to Long-days, Short-days, and Long-days plus Maleic Hydrazide.[a/]

	Long-days	Long-days plus Maleic Hydrazide	Short-days
Shoot elongation (cm.)	57.7	24.1	15.0
Nodes produced after treatment	11.8	9.8	2.8
Nodes which expressed flowers (%)	52.2	90.9	0.0
Nodes not expressing flowers, but possessing reproductive buds (%)	80.0	81.8	11.8

[a/] Values for 10 plants over the 10-week period.

Floral Responses

Flower Expression

No flowers were expressed by plants receiving short photoperiods in this experiment. Plants under long-days produced a small amount of sporadic flowering from lower nodes by the sixth week, and thereafter only flowered from nodes produced following treatment. Long-day - maleic hydrazide-treated plants were all flowering by the eleventh week and incidence of flowering increased with time.

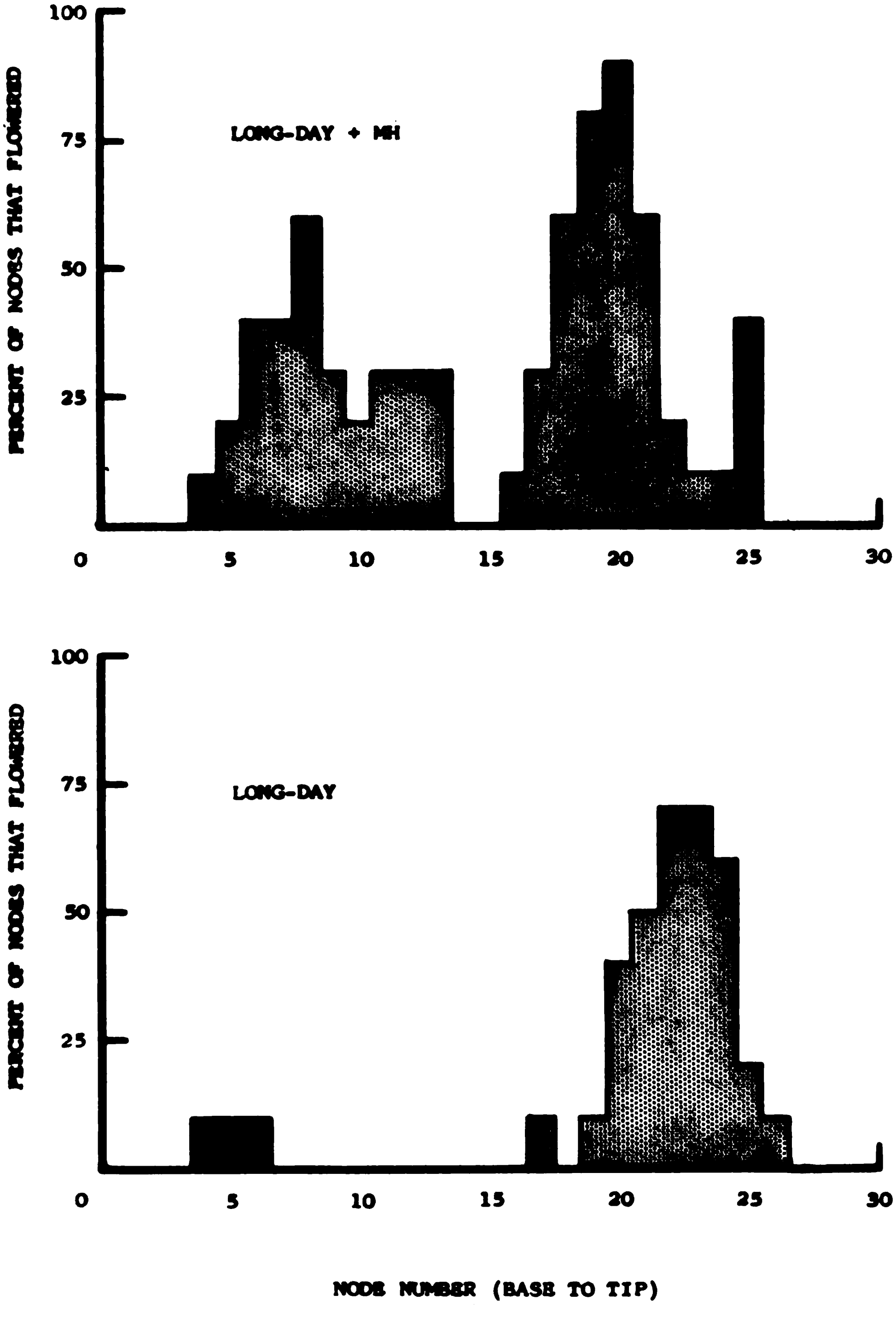
At no time did the non-treated long-day plants express flowers from terminal nodes. However, plants treated with the chemical expressed flowers (in the colored bud stage) from approximately 30 percent of the nodes which were terminal at the end of the experiment.

Mode of Flowering

Differences in the flowering habit owing to exogenous applications of maleic hydrazide, as indexed by the nodes from which flowers were produced, were striking (Figure 8). Non-treated long-day plants expressed very few flowers from nodes produced prior to light treatment, whereas treated plants produced an abundance of flowers from corresponding nodes. Floral expression from nodes produced after treatment was similar for both treated and non-treated plants. However, the magnitude of flowering in the maleic hydrazide treated plants was greater. As mentioned above,

Figure 8.

Percent incidence of flower expression by nodes of *Weigela* exposed to long-days and long-days plus maleic hydrazide (3000 p.p.m.). Each percentage value based on 10 plants. (Node number 15 = node terminal at time of treatment)


PERCENT OF NODES THAT FLOWERED
100
75
50
25
LONG-DAY + MH
0
5
10
15
20
25
30
PERCENT OF NODES THAT FLOWERED
100
75
50
25
LONG-DAY
0
5
10
15
20
25
30
NODE NUMBER (BASE TO TIP)

terminal flowers were observed in treated, but not in the non-treated plants. No flowers were expressed from nodes which were terminal at the time of treatment (eg. node 15, Figure 8).

Floral Initiation

Upon microscopic examination, buds removed from plants under long photoperiods at the end of the experiment showed that of the buds at nodes which had not flowered, 80 percent contained flower primordia. Only 11.8 percent of the buds examined of the plants exposed to short photoperiods possessed flower primordia (Figure 6; Table I).

DISCUSSION AND CONCLUSIONS

PHOTOPERIOD-GIBBERELLIN EXPERIMENT

Vegetative Effects

Growth rates for the first seven weeks of Weigela plants in which different stems of the same plant were exposed to unlike photoperiods that the effect of photoperiod on one stem did not carry over and influence another. As reported by Downs and Borthwick (1956a), short-days inhibited, and long-days promoted growth of Weigela (Figure 1).

The most pronounced effect of treatment with gibberellin was its ability to cause a resumption in growth from the dormant short-day stems, or the ability to break "photo-induced dormancy" (Bukovac and Davidson, 1959).

Floral Effects

Flower expression was enhanced by long photoperiods and prevented by short photoperiods. However, flower primordia were differentiated under short-day exposure, but expression of these buds was supressed. No floral effects can here be attributed to exogenous applications of gibberellin, for all stems of all plants in the experiment were treated.

PHOTOPERIOD-MALEIC HYDRAZIDE EXPERIMENT

Vegetative Effects

Exogenous applications of 3000 p.p.m. maleic hydrazide drastically reduced the growth rate of Weigela as indexed by non-treated plants under the same photoperiodic regime (Figure 6).

Freeman (1952) and Reisch and Chadwick,(1955) reported that the chemical resulted in the cessation of meristematic activity in some woody species. But in this study, it was observed that although the length of internodes was greatly reduced, the rate of node formation was only slightly less than corresponding non-treated plants. These data suggest that cell enlargement, rather than cell division is inhibited. Furthermore, flowers were observed arising from nodes which were terminal at the end of the 10 week period, indicating that differentiation was not supressed by chemical treatment. In order for maleic hydrazide to cause complete cessation of terminal meristematic activity in Weigela, concentrations in excess of 3000 p.p.m. would be required.

Flowering Effects

Prior to flowering, Weigela produces "flower shoots" from axillary buds. These shoots consist of 3 to 5 pairs of opposite leaves, and flowers are produced from the axils of the 2 or 3 most terminal leaf pairs of the "flower shoot". This study has shown that completely differentiated flower

primordia exist in the axillary buds prior to the extension of the "flower shoot" (Figure 6-C; 6-D).

Short-day Plants: The flower primordia observed in plants exposed to short-days suggested that flowers may be differentiated in 10 weeks under these conditions. However, this has not been conclusively demonstrated, for the limited amount of flower primordia observed (11.8%), were at nodes which were present when the plants were removed from long-days. It is very possible that these had been initiated by that time. A typical short-day vegetative bud is illustrated in Figure 6-A.

Long-day Plants: In non-treated long-day plants, about 80 percent of the buds at nodes which had not expressed flowers by the end of the 10 week period contained flower primordia. The flowers expressed were produced, with but a few exceptions, from nodes laid down following placement into light treatment. Expression of these floral primordia was somehow inhibited.

Inhibition of this type did not occur when the plants were given exogenous applications of maleic hydrazide. Chemical treatment apparently overcame the inhibition of these buds. These data are graphically illustrated in Figure 8.

How maleic hydrazide negated this inhibition is not clearly understood. One possible explanation, that chemical treatment removed apical dominance resulting in the extension

of "flower shoots", is probably not too valid. Complete cessation of apical meristematic activity did not occur, for nodes were produced at a rate only slightly less than that of the non-treated long-day plants. If a partial loss of apical dominance did occur, then it is doubtful that such an effect would be expressed so far from the apex.

It appears that maleic hydrazide affected the buds present at the time of treatment and caused them to flower. Observed flower initiation and expression from growth produced after treatment suggested that the long photoperiods were more influencial than treatment with the chemical.

Thus, it was surmised that exogenous applications of maleic hydrazide to Weigela resulted in flower expression from buds present at the time of treatment, and in reduced growth rates due primarily to its effect of cell enlargement. The mode of flowering from nodes produced after chemical treatment was not shown to be materially affected.

SUMMARY

To ascertain the mode of floral initiation and expression, plants of Weigela clone 'Vanicek', grown under long and short photoperiods, were given exogenous applications of gibberellin or maleic hydrazide.

Shoot elongation under long-days (16 hours) was continuous, and under short-days (9 hours) plants ceased growing.

Applications of gibberellin stimulated shoot growth in general. When applied at 1000 p.p.m. to dormant stems under short-days, a resumption of growth occured.

Under long-days, exogenous applications of maleic hydrazide markedly inhibited shoot elongation, but the number of nodes produced was only slightly reduced. Cessation of meristematic activity did not occur. Rather, growth inhibition in these experiments was apparently due to reduced cell elongation and not to reduced cell division.

Flowering did not occur on plants under short-days, however, a limited amount of flower primordia were observed.

Evidence obtained indicated that applications of maleic hydrazide at 3000 p.p.m. caused flowers to be expressed from nodes present at the time of treatment, but flowering from nodes produced following chemical treatment was not materially affected.

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