PHOTOPERIODIC RESPONSES ON SELECTED WOODY ORNAMENTAL SHRUBS

By

Harold Davidson

AN ABSTRACT

Submitted to the School for Advanced Graduate Studies of
Michigan State University of Agriculture and
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DOCTOR OF PHILOSOPHY

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Approved Charles L. Hamner

ABSTRACT

Six species of woody plants were grown under various photoperiods at East Lansing, Michigan to determine their response to photoperiod. *Buddleja davidi* and *Philadelphus coronarius aureus* were not sensitive to variation in photoperiod. *Taxus cuspidata* made significantly less growth under the short (8-hour) photoperiod than under the natural photoperiod, but no response was noted to an increased photoperiod.

Hibiscus syriacus, *Rhododendron catawbiense*, and *Weigela florida* were demonstrated to be very sensitive to variation in photoperiod. These three species made significantly more growth under a long (16-hour) photoperiod and significantly less growth under a short (8-hour) photoperiod than when grown under the natural photoperiod prevailing at East Lansing, Michigan (June 21 - October 17).

The critical period for *Rhododendron catawbiense* and *Weigela florida* was found to be between 12 and 16 hours. Maximum flower bud initiation occurred when these plants were grown under natural or long photoperiods. Photoperiods of 16 hours or greater resulted in phylloidy of the bracts of *Rhododendron catawbiense*. Continuous illumination resulted, in addition to phylloidy of the bracts, in the formation of petalloidy of the stamens and the development of shoots in the axils of bracts.

Short photoperiods (reduced daylength) induced dormancy of *Hibiscus syriacus*, *Rhododendron catawbiense* and *Weigela florida*, and as a result, plants possessed a high degree of resistance to cold temperature injury. Long photoperiods (increased daylength) delayed dormancy and resulted in considerable winter injury.

Long photoperiods (16-hours and greater) were effective in breaking the dormancy of one variety of *Rhododendron catawbiense*, but were ineffective in a second variety.

It was demonstrated that high temperature was the environmental factor that influenced the opening of *Rhododendron catawbiense* buds in the spring.

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To my

Parents

John and Tyne Davidson

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INTRODUCTION

The response of plants to variation in the length of day has excited the imagination of man for many years. John Ray (87) noted in 1686 in his publication "Historia Plantarum" that plants exhibited differences due to variation in light. Liberty Hyde Bailey (6, 7, 8) and many others experimented with electric arc lamps in the 1890's, to determine the effect upon the plant of extending the natural day length. It was not until 1920, however, when Garner and Allard (38) published their classical paper that a clear understanding was available of the effect that variation in day length (photoperiod) had upon plants. Garner and Allard called this effect photoperiodism, and they classified plants into various categories depending upon their response to the photoperiod (37). Plants that bloomed when the photoperiod was short, less than the critical, they called short-day plants; those that bloomed when the photoperiod was long, longer than the critical, they called long-day plants; those that did not appear to be affected by the length of the photoperiod they called indeterminate.

Since 1920, thousands of papers have been published on photoperiodism in both plants and animals. Most papers pertaining to plants have dealt with the effect that variation in photoperiod had upon the flowering response, and were primarily concerned with herbaceous species even though Garner and Allard (1) included a number of woody species in their early papers. A number of investigators have studied the effect of photoperiod upon seedling trees and in 1955, Downs (30) reported the effect of photoperiod on the vegetative growth of Weigela florida. To date, however, no systematic study has been made of this effect upon many woody ornamental shrubs.

An understanding of the effect of photoperiod on the behavior of woody shrubs might be useful to nurserymen in producing and adapting woody ornamental plants for landscape beautification. The purpose of the present investigation was to study what effect variation in the photoperiod had upon the woody ornamental shrubs: Buddleja davidi, Franch; Hibiscus syriacus, L.; Philadelphus coronarius aureus Rehd.; Rhododendron catawbiense, Michx.; Taxus cuspidata, Sieb. & Zucc.; and Weigela florida, A.DC.

REVIEW OF LITERATURE

Photoperiodism in General

Since 1920 when Garner and Allard (38) recognized the importance of the length of the light period (photoperiod) as a factor of the first importance in the growth and development of plants, particularly with respect to sexual reproduction, numerous papers have been published pertaining to photoperiodism. A number of general reviews were available, particularly with respect to the flowering response (14, 16, 19, 44, 45, 60, 64, 76, 79, 107). Papers to illustrate salient principles were selected in order to emphasize the most pertinent parts of these general reviews.

Hendricks and Borthwick (48) reported that in addition to the flowering response plants exhibit other photoperiodic responses: namely, seed germination, seedling elongation, leaf enlargement, plumular hook unfolding, epinasty, leaf abscission, bulb formation, rhizome formation, casparian strip formation, flower development, pigmentation, phylloidy of bracts, succulency, sex expression, root development and response to day and night temperatures.

Most of the literature on photoperiodism has been concerned with herbaceous plants; perhaps, because the data may be obtained within a short period of time. Nevertheless, there were a number of findings concerned with the effect of photoperiod upon woody plants, a topic which has been reviewed recently by Wareing (121), and earlier by Wareing (115) and Gevorkiantz and Roe (40).

The Flowering Response

It is at present, generally believed that the flowering response is hormonally controlled (43, 60, 65), that it consists of a series of partial processes (60, 64), and that the site of origin of the stimulus is in the leaves (46, 54).

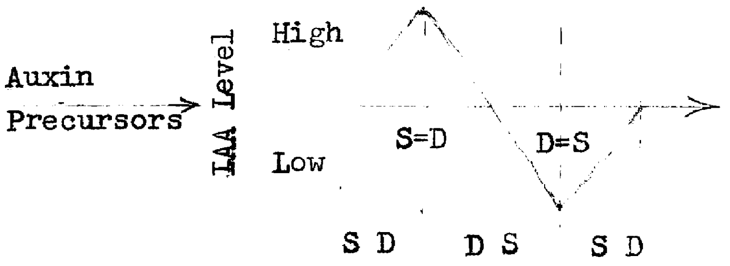
Hamner and Bonner (46) demonstrated in 1938 that the floral initiating substance had its genesis in the leaves. This has been confirmed by Khudairi and Hamner (54) who demonstrated that the youngest leaf blades of *Xanthium* gave no flowering response, but the response increased with the age of the expanding leaf, reaching a maximum when the leaves are of an area approximately one-half fully expanded.

Hamner (43) demonstrated in 1940 that Biloxi soybean and *Xanthium*, both of which are short day plants, must be exposed to cycles of light and darkness in which the light periods are of a certain intensity and length, and that the dark period must be of a definite minimum duration for photoperiodic induction to take place. His findings demonstrated a requirement for a high intensity light phase and a dark phase of some definite minimum length.

In 1944 Hamner (45) suggested his A, B, C hormonal relationship in which A accumulates during the light period and slowly decays during darkness, B increases during darkness and decreases rapidly during exposure to light, C develops from an interaction between A and B, and floral initiation takes place.

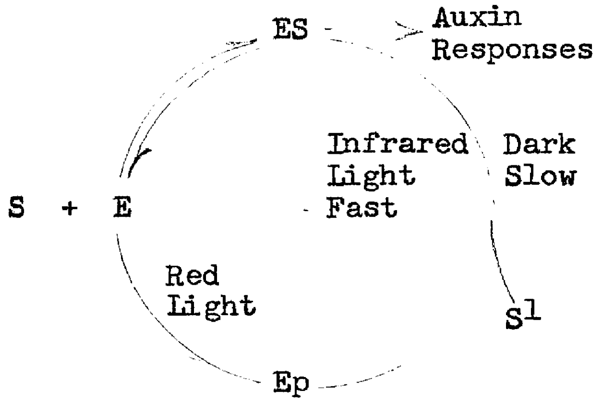
In 1953 Liverman and Bonner (65) interrelated auxin and light in growth responses of plants with their photocycle. They postulated that the flowering response is governed by the level of an auxin-receptor complex (ES) within the plant. During the light period an auxin-non-receptive precursor (Ep) is converted to an auxin receptive entity (E) which combines with auxin (S), when present, to form the ES complex. During the dark period the ES decays to Ep and S. If the dark period is sufficiently long, the level of ES drops below that critical for initiation of flowering in short day plants. If, however, the dark period is interrupted by a flash of red light, Ep is reconverted to E and the supply of ES is regenerated.

In 1954 Galston and Dalberg (35) proposed the biochemical mechanism for rhythmical changes in Indoleacetic acid (IAA) level which, when coupled with the photocycle, explains partially the flowering response of long and short day plants.



Rhythmical Changes in IAA Level

S = Synthesis
D = Destruction



Photocycle

The importance of red light with respect to producing a photoperiodic response was demonstrated in 1926 by Withrow and Biebel (125). This observation was confirmed and elaborated upon in 1952 by Borthwick et al who proposed the reversible photo reaction in which the action of red and infra red light are reversible in controlling floral initiation (18) and other photoperiodic responses (48). They suggest the presence of two pigments, one receptive to red irradiation, the other to infrared irradiation, and two reactants which control photoperiodic response. The reaction may be written:

$$\begin{array}{lcl} \text{Pigment + RX} & \xrightarrow{\text{Red}} & \text{Pigment X + R} \\ \quad\text{6500 max.} & & \quad\text{7300 max.} \\ & \xleftarrow{\qquad} & \\ \text{Floral long} & \text{Infrared} & \text{Vegetative long} \\ \text{night plants.} & \text{Darkness} & \text{night plant.} \\ \text{Dormant lettuce} & & \text{Germinating lettuce} \\ \text{seed.} & & \text{seed.} \end{array}$$

The exact nature of the pigments or the reactions RX and R are as yet unknown but are undoubtedly associated in some way with the auxin-receptor complex of Liverman and Bonner.

The importance of temperature with respect to the photoperiodic response, especially translocation, has been conclusively demonstrated (90, 91, 92, 104). Roberts and Struckmeyer (92) have indicated from their studies that photoperiod may be a primary factor for inducing blossom formation within a certain temperature range for a certain species, but in other species and at other temperatures it becomes a contributing factor along with other environmental factors which when taken together create a physiological condition that results in flower formation.

The flowering response may be summarized by the equation suggested by Liverman (64):

High Intensity Light Reaction → Dark Process → 2nd High Intensity Light Process

Translocation (Temp. dependent) → Flower Differentiation

Photoperiodism in Woody Plants

Flowering Response in Shrubs:

Early in the study of photoperiodism Allard (1) demonstrated that the flowering of woody shrubs might be susceptible to photoperiodic influences. It was shown that *Hibiscus syriacus* was a long-day plant, flowering when the photoperiod was 12 to 15 hours; *Bougainvillea glabra* was a short-day plant, flowering when the photoperiod was less than 10 hours; and that *Malvaviscus conzattii* was indeterminate (day-neutral).

Chouard (23, 24) has indicated that *Caryopteris mastacanthus*, *Rosa* (Pernetiana), *Calluna vulgaris*, and *Ribes rubrum* failed to initiate flowers under short days but flowered normally in long or continuous photoperiods. *Syringa vulgaris* and *Vinca minor* were relatively indifferent to photoperiod.

Poinsettia (*Euphorbia pulcherrima*) exhibited good flower development when the photoperiod was about 8 to 9 hours in length. Photoperiods greater than 12 hours inhibited flower formation (80). It must also be noted, however, that flower development in poinsettia was also temperature dependent (90).

Information relative to the flowering of gardenia is somewhat contradictory. Baird and Laurie (9) report that short days (9-hours) during July and August are responsible in part for bud initiation, whereas Keyes (53) indicates that supplementary illumination (5 to 9 P.M.) did not consistently increase the number of buds formed. Arthur et al (2) indicated that long days hasten bud development and flower production following cold nights.

Camellia japonica is apparently responsive to long days for flower bud initiation (13, 69). The reports on the response of Rhododendron are not clear. Azalea (Rhododendron obtusum) has been found not to be affected by day length (86). Skinner (99) has reported, however, that exposure to short days resulted in more flower buds on Rhododendron carolinianum and R. mucronulatum, but had little effect on the other species tested (R. ponticum, R. roseum elegans).

Coffea arabica was found to be a short-day plant with respect to flower initiation (84), the critical photoperiod being between 13-14 hours.

A different mechanism was recently demonstrated by Sachs (93) for floral initiation in Cestrum nocturnum. His conception is that the plant must be exposed to long days followed by short days for floral initiation to take place.

Photoperiodism in Woody Plants

Vegetative Response in Trees:

Stem elongation of woody plants was associated with the length of the light period as early as 1914 when Klebs (55) maintained Fagus sylvatica in a state of continuous growth during the winter by supplementary illumination. Garner and Allard (39) noted in 1923 that Acer negundo made vegetative growth under long days as contrasted to poor growth under a day length of 10 hours. On the other hand, Malus sylvestris grew well on a 10-hour photoperiod and made less growth under long days. They noted that for each species there was an optimal light period for maximum upward elongation of the stem.

Seedlings of Robinia pseudoacacia and Phellodendron amurense and cuttings of Salix lantana and S. babylonica produced maximum growth under long days (70). Robinia, a representative of the lower latitudes of Russia, exhibited a rapid growth rate under long days and continued growth until killed by frost, but decreased its growth rate under short days. Moshkov (71) indicated that subjecting Prunus armeniaca, Juglans regia, Robinia pseudoacacia, from the Southern Caucasia and from Moscow, and Salix babylonica to short day periods increases their frost resistance.

It was also indicated in the species tested that those which are indigenous to the Northern latitudes require less shortening of the photoperiod to become frost resistant than those which are indigenous to southern areas.

Artificial shortening of the day at Leningrad, Russia (5) reduced the vegetative period of seedlings of Robinia pseudoacacia, Acer negundo, Ailanthus glandulosa, Rhus cotinus, and Phellodendron amurense, but resulted in less height growth, a more rapid development of young shoots, and earlier leaf fall. The seedlings exhibited a greater hardiness with respect to early autumn frosts and winter cold. Aesculus hippocastanum, Alnus glutinosa, Fraxinus excelsior, Caragana arborescens, Corylus arellama, and Ulmus montana did not have their vegetative period seriously reduced.

Experimenting with white and green ash, beech, yellow locust, yellow poplar, red gum, post oak, northern red oak, white oak, and loblolly pine, Kramer (56) found that the plants grown under short days made less growth and became dormant sooner than plants grown under normal day length. When grown under a long day, all but ash and red oak made more growth than did plants under a normal day. He also noted that all the species ceased growth at about the same time when grown under normal length of day in a warm greenhouse or out of doors.

Jester and Kramer (51) reported that black locust, slash pine, and red maple seedlings made their greatest height growth under long days, whereas short days retarded height growth. Southern red oak was not significantly affected by day length, whereas chestnut oak made poor growth under both long or short days.

An interrupted dark period was reported by Zahner (127) to be effective means of producing growth in Liriodendron tulipifera and Pinus taeda.

Ulmus americana, Cornus florida, Aesculus hippocastanum, Acer rubrum, Liquidambar styraciflua, Liriodendron tulipifera, Paulownia tomentosa, Betula mandshurica, Catalpa bignonioides, C. speciosa, Pinus taeda, P. virginiana, and P. sylvestris when grown at Beltsville, Maryland (29) responded to long days by a prolonged period of growth. Short days (8 hours), in general, induced dormancy. Most species required about 4 weeks on 8-hour days to stop growth. Catalpa, elm birch, red maple and dogwood grew continuously on a photoperiod of 16 hours, whereas paulownia, sweet gum and horse chestnut became dormant.

Liriodendron tulipifera and Fagus sylvatica responded to long days (122), but like the three last plants stated above, they showed periodicity of growth.

Aleurites fordii and Aleurites cordata (32) responded to changes in photoperiod. The normal vegetative growth was reduced under short days with a 60 percent decrease in protective sugars and greater hardiness. Long days, on the other hand, brought about an accumulation of sugars and greater vegetative growth.

Studies with Populus (84, 112) demonstrated that it was sensitive to daylength. Photoperiods of 9- and 12-hours caused growth to cease in about 4 to 6 weeks, whereas long photoperiods and continuous light kept the plants vegetative. It was concluded by Pauley and Perry (84) as a result of an extensive study, that the adaptation of Populus species to various habitats differing in length of the frost-free season, was effected by a genetic mechanism which controlled the duration of their seasonal period of growth. The photoperiod, which was the only factor of the environment with a uniform seasonal variation that was constant from year to year, functioned as the timing device for this mechanism. One month old seedlings of *Quercus pedunculata* when grown under continuous light were 15-20 times as tall, the stem was twice as thick, and produced about 20 times as many leaves as the control plants (62). Three year old seedlings when grown for 10 months under continuous illumination produced plants that were equal in size to 8-10 year old seedlings grown in the field.

Transplanting these plants to the field did not result in any serious winter injury even though temperatures of -22° C. were recorded.

Under continuous illumination oak seedlings did not grow continuously, but exhibited periods of growth and rest which vary with the species (61).

Somewhat similar results were reported by Wareing (116, 117, 118) for *Pinus sylvestris*. Under a 10-hour photoperiod, first-year seedlings ceased growth earlier, with fewer needles formed than on seedlings exposed to a 15-hour photoperiod. Needle length and internode extension was reduced under short days, maximum growth being obtained when the plants were grown on a 20-hour photoperiod.

When *Pinus sylvestris* and *P. sibirica* were grown (63) under continuous illumination, there was an increase in stem and needle length.

Vaartaja (111) demonstrated in Finland that there are ecotypes for *Pinus sylvestris* and *Alnus incana* and that under a 24-hour photoperiod seedlings from the Northern latitudes grow best. He also demonstrated that short photoperiods hasten the onset of dormancy for *Pinus sylvestris*, *Picea abies*, *Betula pubescens*, *B. verrucosa*, and *Alnus incana* (110).

Karschan's results (52) in Switzerland also demonstrated ecotypes for Pinus sylvestris. He states that frost-hardiness, needle-volume, growth period, internode, and hypocotyl length are closely related to light exposure. Similar results are reported for hemlock (77).

The reason for poor winter survival of Larix leptolepis in the nurseries on the coast of Norway has been shown to be related to photoperiod (89). Plants exposed to short days survived the winter better than those on normal day length.

Subjecting seedlings of Picea glehnii, P. abies, Abies sachalinensis, Larix leptolepis, Cryptomeria japanica, Chamaecyparis obtusa, Pinus densiflora, P. thunbergii, Cinnamamum camphara, Paulawnia tomentosa, and Citrus spp. to short days resulted in a high osmotic pressure with a high degree of resistance to cold but less total growth (96).

The length of the day was effective in inducing dormancy and in breaking dormancy in the case of Pinus taeda, and Thuja occidentalis (83). Supplemental red irradiation was effective in the breaking of dormancy when the plants were grown on an 18-hour photoperiod. Blue irradiation was ineffective.

Information relative to breaking dormancy in the spring is somewhat conflicting. Daubenmire (25) from his studies with deciduous and evergreen trees in Idaho suggests that day length is more important than temperature in stimulating the trees studied to resume cambial growth. Whereas, experiments (84) on the breaking of dormancy in Populus spp. in the spring, indicated that temperature, rather than photoperiod, was the controlling factor.

Wareing (119, 120) was able to induce growth in dormant buds of *Betula pubescens*, *Larix decidua*, and *Fagus sylvatica* when they were exposed to long days, whereas *Acer pseudoplatanus*, and *Robinia psuedoacacia* remained dormant. It was shown that both the buds and leaves must be exposed to continuous illumination in order to bring about a resumption of growth in *Betula pubescens*. In other species the photoperiodic perception is mediated through the leaves. In *Fagus sylvatica* exposure of the buds to an 18-hour photoperiod at 1000 lux was shown to be effective in breaking dormancy. Gustafson (41) found that if seedlings of *Pinus resinosa* are not exposed to the cold temperature of winter, they failed to grow or made only slight growth during the following summer unless they were grown under a photoperiod of about 16 hours.

Wareing (120) postulated that a growth inhibitor is produced by the leaves during long dark periods. Hemberg (49) has shown that the resting buds of *Fraxinus* contained a growth inhibiting substance which disappeared by spring. It has been demonstrated (3) by the agar block technique that dormant winter buds of *Aesculus* and *Malus* do not contain a growth hormone, but during the period of swelling of the terminal buds a growth hormone was detectable in increasing amounts.

van der Veen (112) has shown that plants grown under short days are difficult to "awaken" from dormancy even when exposed to long days, suggesting that the state of dormancy increases with time. This time factor may in part explain somewhat the conflicting reports about dormancy. Downs and Borthwick (29) reported that *Catalpa* becomes progressively more delayed in its response to the stimulus of long days as the plants remained for longer periods on short days. The fact that many species exhibit ecotypes (81, 111) may also explain, in part, the varying results.

It has been observed that leaf abscission is associated with photoperiod (11, 22, 67, 78). Benassi (11) noted that leaf fall was retarded on *Platanus* when the tree or branches were exposed to illumination from electric street lights. Similar results have been reported for *Platanus acerifolia*, *P. occidentalis*, *Populus canadensis* and *Salix fragilis* (67). Cappelletti (22) reported that illuminated *Platanus orientalis* in the streets of Rome, Italy maintained their leaves long after their non-illuminated neighbors, but that this was not true of *Platanus orientalis* when grown in the streets of Turin, Italy. In a controlled experiment with *Acer saccharum*, Olmsted (78) reported that the amount of leaf drop was positively related to length of photoperiod.

Photoperiodism in Woody Plants

Vegetative Response in Shrubs:

Information pertaining to the vegetative responses of woody ornamental shrubs when grown under various photoperiods is limited. One of the earliest references, other than flowering responses, was that of Kramer's in 1937 in which he reported the observation that Abelia grandiflora when growning in the vicinity of electric lights was killed during the winter due to the photoperiodic stimulation of the light (57).

Increased stem elongation as a result of long days was reported for rhododendron and azaleas by Skinner in 1939 (99). This has been confirmed for greenhouse azaleas (20). Stem elongation in Hydrangea macrophylla has been shown to be under photoperiodic stimulus. Plants grown under a 16-hour photoperiod made more growth than similar plants under a 9-hour light period (98). It was noted during a period of storage that all plants lost their leaves except those grown under the long photoperiods (85, 98). Final plant height, number of nodes, length of internode, and bud size have been reported (85) to be influenced by the length of the photoperiod for Hydrangea macrophylla. Photoperiod had no effect in overcoming the need for a period of chilling before forcing Hydrangea macrophylla.

Long photoperiods have been reported (34) to increase the shoot growth of Juniperus chinensis columnaris, and Spirea vanhouttei, and to inhibit the growth of Euonymus vegetus and Taxus media hicksii.

Long photoperiods have promoted, and short photoperiods have inhibited the shoot growth of the following shrubs and small trees: Weigela florida, Weigela florida variegata, Cornus florida, Cornus florida rubra, Viburnum carlesi, V. opulus, V. burkwoodii, V. chenaultii, V. plicatum var. tomentosum, V. juddii, Magnolia soulangeana, and Juniperus horizontalis plumosa (30, 31, 34, 123, 124).

The following species have been reported to be unresponsive to photoperiod: Buxus sempervirens, Syringa vulgaris, and Viburnum prunifolium (124).

Long days have been reported to be advantageous in forcing flower buds into bloom for the following plants: Camellia japonica (69), Gardenia veitchii (9, 68), Rhododendron catawbiense (27), and Forsythia intermedia spectabilis (26). Doorenbos (27) reports that dormant buds of Rhododendron catawbiense album commenced growth after 30 days under continuous illumination as contrasted to 75 days under an 8-hour photoperiod. Under long days he was able to flower Rhododendron hybrids in a period of 2 years and 9 months as contrasted to twice this time when the same hybrids were grown under normal day length.

Perlmutter and Darrow (82) reported that the vegetative growth made by blueberry seedlings in the field was greatly stimulated by supplemental light for as short a period as a month prior to transplanting.

Moshkov (73) reported an interesting observation relative to disease immunity in 1938 for Ribes. It was his observation that Ribes nigrum was very resistant to Cronartium ribicola when the plants were grown under a photoperiod less than 11 or greater than 16 hours, but that these plants were susceptible to the disease when grown on photoperiods between 11 and 16 hours.

Photoperiodism in Woody Plants

Propagation:

It has been demonstrated that germination of seeds may be influenced by variations in the photoperiod. Gardner (36) as early as 1921 reported that some seeds are promoted in germination by additional light. Borthwick, et al (17, 18) have shown that the photoreaction effective for floral initiation is also effective in the germination of lettuce seed. Unchilled seeds of Betula pubescens are very responsive to the photoreaction; red irradiation stimulates, whereas infrared inhibits germination (12). Dormant seed of Scotch pine also responds to additional illumination (33).

Lammerts (59) has demonstrated that peach seedlings with long chilling requirements make more rapid growth instead of forming rosettes, when placed under continuous illumination.

Artificial illumination to lengthen the period of natural radiation has been reported to be beneficial for root formation in Ilex glabra, I. crenata (128), Rhododendron spp. (100), and Acalypha wilkesiama (105).

The exposure of stock plants to additional illumination has resulted in increased rooting of cuttings of Populus robusta (88) and Gordonia axillaris (106).

Snyder (102) has recently reported that the lateral buds of Taxus cuspidata can be prevented from developing in the cutting bench by exposing the cuttings to 8-hour days. The reduced day length had no significant effect on the rooting of cuttings, but as a result of preventing bud development, the young plants made significantly more top growth during the following season.

EXPERIMENTAL PROCEDURE AND RESULTS

Plant Materials and Methods

A number of experiments to determine the effect of photoperiod upon the behavior of woody ornamental shrubs were organized and conducted within the vicinity of, and in the Plant Science Greenhouse at Michigan State University, East Lansing, Michigan, during the period May 1955 to February 1957.

Plant Materials:

Six species of plants representing six families, including four deciduous shrubs, one broadleaved and one narrow leaved evergreen, were selected for study to represent species of economic importance in Michigan. These plants were chosen also for their diverse periods of flower display and degrees of winter hardiness for the vicinity (Table I). In addition to these characteristics, the plants were selected for uniformity of size and shape within each species. The *Rhododendrons* were obtained from Westcroft Gardens, Grosse Ile, Michigan. The *Buddleja*, *Hibiscus*, *Philadelphus*, *Weigela*, and *Taxus* were obtained from the Ilgenfritz Nursery in Monroe, Michigan.

Photoperiods:

Photoperiods used in the experiments consisted primarily of reducing or increasing the prevailing natural day length. Reduced (short) photoperiods were obtained by excluding light from the plants after a given period of natural, high-intensity irradiation. Increased (long) photoperiods were obtained by extending the natural day length by supplementary

TABLE I

Characteristics of Woody Ornamental Shrubs Used in Photoperiodic Studies

Species	Family	Foliage	Hardiness*	Time of Bloom*
Buddleja davidi, *Franch*	Loganiaceae	Deciduous	Semi Hardy	Late Summer
Hibiscus syriacus, L.	Malvaceae	Deciduous	Hardy	Late Summer
Philadelphus coronarius aureus, Rehd.	Saxifragaceae	Deciduous	Hardy	Late Spring
Weigela florida, A.DC.	Caprifoliaceae	Deciduous	Semi Hardy	Late Spring
Taxus cuspidata, Sieb & Zuuc.	Taxaceae	Evergreen, Narrow-leaved	Hardy	Early Spring
Rhododendron catawbiense, Michx.	Ericaceae	Evergreen, Broad-leaved	Semi Hardy	Late Spring

* At East Lansing, Michigan

artificial, low intensity irradiation. The lights were turned on and off automatically by a General Electric time clock which was adjusted weekly to supply the photoperiod.

Culture:

Plants were grown in various types of containers to accommodate the root mass, with soil media adjusted to suit the edaphic requirements of the species (103), (Table II). They were watered as required and fertilized once every three weeks with a 15-30-15 fertilizer. The pH of the rhododendron media was maintained at about 4.5 - 6.0 by periodic application of flowers of sulphur.

Climatological Data:

Climatological data covering the period of the investigation is presented in Table III.

Temperature data pertaining to the East Lansing Experiment Station was extracted from "Climatological Data", published monthly by the U. S. Department of Commerce.

The data relative to day length was calculated from the Weather Bureau table, "The Time of Sunrise and Sunset for East Lansing", which is located on the 75th meridian. Calculations were limited to the 21st day of each month.

TABLE II

Cultural Conditions for Woody Plants Grown in the Photoperiod Investigation

Species	Size of Crown	Root System	Type of Container	Soil	
				Type	pH
Buddleja davidi	18"	Bare Root	Tar paper pot	Greenhouse Compost	6.0 - 7.0
Hibiscus syriacus	18"	Bare Root	Tar paper pot	"	6.0 - 7.0
Philadelphus coronarius aureus	12"	Bare Root	No. 10 Can	"	6.0 - 7.0
Weigela florida	18"	Bare Root	Tar paper pot	"	6.0 - 7.0
Taxus cuspidata	15-18"	Balled & Burlapped	14" Clay pots	"	6.0 - 7.0
Rhododendron catawbiense	12-15"	Balled & Burlapped	14" Clay pots	1-1 Mixture greenhouse compost & Michigan peat	4.5 - 6.0

TABLE III

Climatological Data
East Lansing Experiment Station, 1955-1956

	Months of the Year											
	J	F	M	A	M	J	J	A	S	O	N	D
					Temperature (Degrees F) 1955							
Average Maximum	31	32	41	64	71	77	88	84	75	63	41	30
Average	26	25	33	53	60	67	76	74	62	63	34	25
Average Minimum	20	18	24	41	48	56	65	64	50	44	27	19
					1956							
Average Maximum	29	31	36	53	64	78	77	77	70	67	46	36
Average	23	24	29	43	54	68	68	68	58	55	38	31
Average Minimum	16	16	23	33	43	58	58	58	46	42	30	25
					Day Length (All Years) (hours-minutes)							
21st day of month	9:35	10:50	12:11	13:29	14:49	15:20	14:52	13:40	12:14	10:49	9:34	9:02

Responses of Selected Shrubs to Photoperiod

In order to determine the effect of increasing or decreasing the natural photoperiod on the total growth of woody shrubs, an experiment was designed utilizing a number of economically important, woody, ornamental shrubs. Six plants each of *Buddleja davidi*, *Hibiscus syriacus*, *Philadelphus coronarius aureus*, *Weigela florida*, *Taxus cuspidata*, and *Rhododendron catawbiense* var Roseum Elegans were grown under three photoperiods from June 21 to October 17, 1955. The photoperiod treatments consisted of (1) a natural day length, (2) a decreased day length, and (3) an increased day length.

Sixteen hours of light, the increased photoperiod, were obtained by supplementing the natural day length with light from 120 watt mazda lamps contained within 12-inch metal reflectors suspended over the plants. The light intensity averaged between 20 to 40 foot-candles at the growing points. Eight hours of light, the decreased photoperiod, was obtained by constructing a wire trellis over the plants upon which was placed a sheet of black-white laminated polyethylene film that was drawn over the plants at 4:30 P.M. and removed at 8:30 A.M. daily. The black film provided total darkness within and the white film on the outside reflected the heat energy of the sun.

Measurements of the total stem elongation, and counts of the number of nodes and flushes of growth were recorded during the last week in September. Five shoots were selected at random from each plant for the specific measurements.

Average stem elongation and number of nodes for *Buddleja davidi*, *Hibiscus syriacus*, *Philadelphus coronarius aureus*, and *Weigela florida* were recorded (Table IV). Similarly, elongation and number of flushes of growth were recorded for *Rhododendron catawbiense* and *Taxus cuspidata* (Table IV).

The number of flower buds produced by *Rhododendron catawbiense* were compared to the number of shoot buds to determine if photoperiod had an effect on flower bud initiation (Table V).

Vegetative Response:

The vegetative growth of *Weigela*, *Hibiscus*, *Rhododendron*, and *Taxus* was influenced by photoperiod, whereas *Buddleja*, and *Philadelphus* showed no significant difference (Figures 1, 3, 5).

Rhododendron catawbiense made three flushes of growth on the long photoperiod, two on the natural day length and only one on the short (8-hour) photoperiod. Short days significantly reduced the vegetative growth of *Weigela*, *Hibiscus*, *Rhododendron*, and *Taxus* and long days significantly increased the growth of *Hibiscus*, *Weigela*, and *Rhododendron*. *Taxus cuspidata*, when grown under a long day (16-hours), produced about the same amount of growth as plants grown under a natural photoperiod.

Flower Response:

Buddleja davidi flowered on or about the fourteenth node and at the same time regardless of photoperiod. *Rhododendron catawbiense* produced significantly more flower buds under the natural and long photoperiod than on the short photoperiod. Fifty-two percent of the flower buds formed under the 16-hour day length exhibited a malformation. (This malformation is discussed in detail in the section on teratological effects of photoperiod.)

TABLE IV

Mean Stem Length and Mean Number of Nodes or Flushes of Growth Produced by Various Woody Ornamental Shrubs When Grown Under Different Photoperiods. June 21, 1955 - October 17, 1955.

Species	Stem Length (Cm.)			Number of Nodes		
	16-Hour	Natural	8-Hour	16-Hour	Natural	8-Hour
Weigela florida	53.7 ±7.2	44.4 ±5.4	27.4 ±5.5	13.2 ±0.6	13.3 ±1.4	9.2 ±0.7
Hibiscus syriacus	41.0 ±6.9	16.4 ±4.4	6.9 ±1.9	17.6 ±1.9	12.4 ±1.1	8.7 ±1.3
Buddleja davidi	81.3 ±20.0	77.1 ±17.8	74.8 ±15.5	14.8 ±1.0	13.9 ±1.5	14.5 ±1.7
Philadelphus coronarius	31.0 ±3.3	26.8 ±4.6	24.0 ±5.7	10.7 ±0.9	9.9 ±1.7	11.5 ±1.8
	Stem Length (Cm.)			Flushes of Growth		
Rhododendron catawbiense	31.8 ±6.1	22.0 ±1.3	12.9 ±0.8	3	2	1
Taxus cuspidata	20.9 ±7.7	18.9 ±1.5	8.3 ±2.2	1	1	1

TABLE V

Mean Number of Flower and Shoot Buds Produced on *Rhododendron catawbiense* Under Different Photoperiods. June 21, 1955 - October 17, 1955

Photoperiod	Average Number of Buds Per Plant Per Treatment				Percent of Flower Buds Per Photoperiod	Percent of Flower Buds Distorted Per Photoperiod
	Flower		Shoot	Total		
	Normal	Distorted				
16- Hour	3.50	3.83	14.83	22.16	33.07	52.25
8-Hour	1.20	0	11.20	12.40	9.68	0
Natural	12.33	0.33	8.50	21.16	59.83	2.61

When this experiment was repeated the following summer, the results were similar except it was noted that the Hibiscus plants grown under the short (8-hour) photoperiod flowered for three weeks and the flowers opened one week earlier than on plants under the longer photoperiods. In contrast, plants under the long and natural photoperiods as well as blooming one week later, produced the greatest number of flowers per stem (Table VI) which lasted for a period of ten and eight weeks respectively.

TABLE VI

Summation of the Average Number of Flowers per Stem Produced on *Hibiscus syriacus* When Grown Under Different Photoperiods

	Average Number of Flowers/Stem/Photoperiod		
Week	16-Hour	Natural	8-Hour
1	0	0.12	2.13
2	1.55	0.88	3.44
3	5.50	4.94	3.94
4	17.05	8.77	--
8	17.50	9.16	--

Effect of Photoperiod on Winter Hardiness

In October 1955 the shrubs (Table I) exhibited various gross morphological differences as a result of 15 weeks exposure to an increased, reduced, and natural photoperiod. Since a number of investigators (57, 72, 89, 96) have indicated that winter injury may be influenced by the exposure of plants to a long photoperiod prior to winter temperatures, an experiment was designed to test this hypothesis upon these plants and to attempt to establish a relationship between morphological characteristics and winter hardiness.

Morphology and Winter Hardiness:

Two indices of winter hardiness were established for each species grown under each of the three photoperiods on the basis of morphological characteristics. One was based on a high, medium or low degree of hardiness established by visual inspection of each species within each photoperiod (Table VIII).

The second winter hardiness index was a percentage measure of succulence based on the mean amount of immature growth compared to total growth. Five stems per treatment were measured with a centimeter scale to determine the average (Table VIII).

In October 1955 the pots were mulched and the plants left exposed to the natural prevailing temperature of winter. The temperature was below 32° F. for 160 days with a minimum temperature of 5° F.

In April 1956 an index of winter injury was established for each species as described in Table VII and the results recorded (Table VIII).

TABLE VII

Index of Winter Injury

Index	Degree of Injury	Characteristics
1	None	No visible injury
2	Slight	Leaf burn of some leaves of evergreen plants; slight die-back on deciduous plants
3	Medium	Much die-back of stem
4	Extensive	Severe die-back of stem
5	High	Plants dead

TABLE VIII

Winter Hardiness and Winter Injury Indices for Selected Ornamental Shrubs as Related to Photoperiod
October 1955 - April 1956

Species	Winter Hardiness Indices/Photoperiod						Winter Injury Index*		
	Subjective			% Succulent Growth					
	16-Hour	Natural	8-Hour	16-Hour	Natural	8-Hour	16-Hour	Natural	8-Hour
Buddleja davidi	Low	Low	Low	70	72	67	3.2	3.6	3.5
Hibiscus syriacus	Low	Medium	High	47	31	0	3.7	2.7	1.1
Philadelphus coronarius	High	High	High	25	24	19	1	1	1
Rhododendron catawbiense	Medium	High	High	25	0	0	3.0	1.5	1.2
Taxus cuspidata	High	High	High	--	--	--	1.0	1.0	1.0
Weigela florida	Low	Medium	High	60	55	13	4.8	3.3	**

* See Table VII.
** Destroyed by rodents.

The shrubs which had previously shown a photoperiodic response (*Hibiscus syriacus*, *Weigela florida*, and *Rhododendron catawbiense*) exhibited a perfect relationship between degree of winter injury and length of the photoperiod under which they had been grown prior to the onset of winter (Figures 2, 4, 6). Long (16-hour) photoperiods resulted in a high degree of winter injury to the plants, whereas plants grown under a short (8-hour) photoperiod were only slightly injured. *Taxus cuspidata* and *Philadelphus coronarius aureus* which had been assigned high winter hardiness classification showed no winter injury, and *Buddleja davidi* which had been assigned a low winter hardiness classification exhibited considerable injury.

Moisture Content and Winter Hardiness:

The morphological characteristics of the plant material when grown under different photoperiods suggested that there may be differences in the moisture content which might have an influence upon winter hardiness. To investigate this premise and to attempt to relate moisture content with winter injury, four samples of the stem and foliage from the apical six inches of shoots from *Rhododendron catawbiense*, *Hibiscus syriacus* and *Taxus cuspidata* growing under long, short and natural photoperiods were selected at random. Each sample was weighed on a torsion balance to a tenth of a gram, dried in a forced air oven for three hours, and reweighed. The average percent moisture content was computed and tabulated (Table IX).

The plants were exposed to existing winter temperatures with a minimum temperature of -10° F.

TABLE IX

Percent Moisture Content of Selected Plant Tissue as Influenced by Photoperiod

Species	Percent Moisture Content/Photoperiod 16-Hour	 Natural	 8-Hour
Rhododendron catawbiense	64.9* ±1.03	59.1 ±1.66	58.8 ±0.86
Hibiscus syraicus	66.2* ±2.33	65.9* ±1.16	62.4 ±0.40
Taxus cuspidata	63.6 ±0.98	61.2 ±1.08	61.5 ±0.76

* Exhibited winter injury

The results were similar to those obtained the previous year by the index method. Rhododendron grown under the long (16-hours) photoperiod had a relatively higher moisture content and exhibited winter injury as contrasted to those plants grown on shorter photoperiods. Hibiscus syriacus exhibited a relatively higher moisture content when grown on the long and natural photoperiod as contrasted to plants grown under the 8-hour photoperiod. Hibiscus exhibited winter injury on plants grown under the longer photoperiods. Taxus cuspidata had approximately the same moisture content regardless of photoperiod and exhibited no winter injury.

Effect of Photoperiod on Breaking Dormancy, Periodicity of Growth and Bud Formation

Long photoperiods have been reported to be an effective agent in the breaking of winter dormancy, caused by an inhibitory system within the buds as contrasted to summer dormancy (26), in *Acer saccharum* (78), *Betula pubescens* (120), *Fagus sylvatica* (120), and *Pinus resinosa* (42).

Doorenbos (26) has recently shown that winter dormancy in *Forsythia* may be broken by continuous light and that *Rhododendron* has shown a similar response to continuous irradiation.

An experiment was designed to determine the effect of an increased photoperiod on breaking the winter dormancy of *Rhododendron*, to study the malformation of the *Rhododendron* flower buds, and to observe the periodicity of its growth.

In November 1955 two varieties of *R. catawbiense* were potted (Table II) and placed in a 50° F. greenhouse until December 21, when they were moved to a 60° F. greenhouse and placed under three photoperiodic treatments. Three plants of each variety were grown under: continuous illumination, 16 hours of light, and natural day length.

Observations were made daily to gather the data. Measurements were made weekly of the stem elongation and counts of bud malformations were made periodically as they developed.

The Breaking of Dormancy:

Rhododendron catawbiense var. American Beauty broke dormancy and was in full bloom within 20 days on both the 24-and 16-hour photoperiods. The plants under the 8-hour photoperiod bloomed 35 days later. *R. catawbiense* var. 1004 bloomed under all photoperiods 24 weeks after the beginning of treatment (Figure 8).

Periodicity of Growth:

Both the rhododendron varieties exhibited a periodicity of growth in that a shoot elongated for approximately 4 weeks followed by a three to five week rest period during which time a new terminal bud was developed (Figure 10). During the 26 week period the plants on all photoperiods made at least three flushes of growth.

Bud Formation:

The malformation of the *Rhododendron* flower bud which was observed previously developed extensively under continuous illumination. Eighty-seven percent of the flower buds developed under continuous illumination were malformed as contrasted to 20 percent under the 16-hour and the natural photoperiod (Figures 11, 12, 13).

Effect of Photoperiod on Inducing Dormancy, Periodicity of Growth and Bud Formation

During summer of 1956 an attempt was made to determine the critical photoperiod for shoot growth in Rhododendron, to examine further the periodicity of its growth, and to study the onset of dormancy. On July 12, when buds had formed terminating the first flush of growth, eighteen plants were divided randomly into six groups of three plants each. One group was placed under each of the following photoperiods: 24-hours, 20-hours, 16-hours, 12-hours, 8-hours and natural daylength. In one greenhouse the plants received 24-hours, 16-hours and natural photoperiods, and in another they received the 20-, 12- and 8-hour photoperiod. The average night temperature was 60° F. The number of terminal buds which grew and developed was recorded weekly. The percent of terminal buds which grew with each subsequent flush of growth is recorded in Table X. The average amount of stem elongation produced by the plants under the various photoperiods is shown in Figure 9.

Onset of Dormancy:

Plants under the 8-hour photoperiod did not grow. Those under the 12-hour and normal photoperiods made one flush of growth. Plants under photoperiods of 16-hours or more made two or more flushes of growth, depending upon the temperature in which they were growing. The plants under the 20-hour photoperiod failed to make a third flush of growth. This was apparently due to low temperature, 50° F., in which they were maintained after their second flush of growth. Plants growing under the 16-hour and 24-hour photoperiods made four flushes of growth.

TABLE X

Percent of Terminal Buds of *Rhododendron catawbiense* that Developed With Each Subsequent Flush of Growth Under Different Photoperiods. July - December, 1956

Flush of Growth	Percent of Shoot Buds that Grew With Each Subsequent Flush of Growth Under Different Photoperiods					
	24-Hour	20-Hour	16-Hour	12-Hour	8-Hour	Normal
1	100	100	100	100	0	100
2	83	85	43	0	0	0
3	41.8	X	26.2	--	--	--
4	18.4	X	19.0	--	--	--

The average temperature was maintained at 60° F. for these plants. These results indicate that the critical photoperiod for growth of Rhododendron catawbiense is between 12 and 16 hours, and that short photoperiods hasten the on-set of dormancy.

Periodicity of Growth:

Data relative to the number of buds which developed with each subsequent flush of growth indicated that there was a decrease of approximately 50 percent with each subsequent flush. Plants under 20-and 24-hour photoperiods exhibited only a 15 percent decrease in activity on the second flush, whereas plants under the 16-hour photoperiod exhibited a 57 percent decrease. On the third and fourth flushes of growth, the decrease in the number of new shoots formed was greatest on the plants under the 24-hour photoperiod so that at the end of the fourth flush of growth plants under the-24 hour photoperiod had approximately the same number of active shoots as the plants growing under the 16-hour photoperiod.

Total Growth:

The greatest amount of growth was made by plants grown under the 16-hour photoperiod (Figure 9). However, artificially extending the natural photoperiod caused the plants to develop a very "leggy" appearance due to the reduced number of buds that developed with each subsequent flush of growth.

Teratological Effects of Photoperiod on Rhododendron catawbiense

Morphological Observations:

The flower buds and flowers which developed under photoperiods of 16-hours or longer exhibited various degrees of malformation. A morphological examination of the buds identified the malformation as phylloidy of the bracts. The phylloid bracts were pinnately veined on the 16-hour and natural photoperiods (Figure 12), whereas they were primarily palmately veined on the 24-hour photoperiod (Figure 11). The phylloids developed by an expansion of the apical area of the bract, to develop the blade, accompanied by a sloughing off part of the bract on each side of the basal area, leaving a petiole-like structure (Figure 14).

Morphological examination of the inflorescence revealed that those developed under continuous illumination exhibited petaloidy of the stamens, an elongation of the peduncle to form a raceme-like inflorescence and in a number of cases stems replaced flowers in the axils of bracts (Figures 11, 15, 16).

Anatomical Observations:

An anatomical study of the bracts and phylloids was made to determine the vascular development.

Permanent microscope slides were made of the rhododendron bracts and petiole by the established method of paraffin imbedding, cutting sections on a rotary microtone to ten microns in thickness, and staining with fast green. Cross sectional diagrams were made with the aid of a low power microscope.

The cross section of the bract revealed the presence of 15 vascular strands, all of which were not completely differentiated (Figure 17), whereas the cross section of the phylloid petiole, in approximately the same location, possessed nine well-developed amphicribral bundles (Figure 18). The cross section of the petiole of a normal rhododendron leaf, in a similar location, revealed the presence of one large amphicribral bundle and two small bundles (Figure 19).

Effect of Photoperiod and High Temperature on Breaking of Winter Dormancy Following Exposure to Cold Temperature

To determine whether photoperiod influences the opening of the flower buds of Rhododendron catawbiense in the spring after exposure to cold temperatures, four plants were exposed to the following treatments: Two plants were placed under a 16-hour photoperiod (natural day length plus artificial light), and two under natural day length. Each plant was subjected from 4:00 P.M. to 8:00 A.M. daily to the following conditions: (1) Three buds were covered with a black polyethylene cap, (2) three buds and branches were covered, (3) three branches were covered with flower buds exposed, and (4) three branches and buds were left uncovered. When flower buds showed color they were assigned a number designating date of flowering. For example, the first buds to show color were designated 1, representing the first day of flower display. Those that developed color on the second day were designated by number 2, representing the second day, etc. When all buds had flowered, totals for each treatment were obtained (Table XI).

The results of the experiment clearly showed that photoperiod is not the factor that controls the opening of flower buds of Rhododendron catawbiense in the spring after exposure of the plants to the cold temperatures of winter.

To determine the importance of temperature relative to the opening of the flower buds of Rhododendron catawbiense after exposure to cold temperatures, six 30-inch plants were placed in temperature controlled greenhouses so that two plants each were exposed to 50°, 60°, and 70° F.

TABLE XI

Summation Index of the Effect of Photoperiod on the Spring Flowering of *Rhododendron catawbiense* Following Exposure to Winter Temperature

Photoperiod	Replicate	Treatments				Total
		Buds Covered	Foliage Covered Buds Exposed	Buds and Foliage Covered	Buds and Foliage Exposed	
16-Hour						
	1	8	7	4	7	26
	2	10	10	10	9	36
Natural						
	1	9	10	5	6	30
	2	8	9	11	9	37
Total		35	36	30	31	132

temperature. In addition, each plant was divided vertically by a black polyethylene screen, method of Garner and Allard (39), so that one half of each plant was exposed to a continuous photoperiod while the other half was exposed to a natural photoperiod.

Plants exposed to the 70°, 60°, and 50° F. temperatures were in full bloom after 48, 55 and 87 days respectively, regardless of photoperiod, indicating that warm temperature is more important than photoperiod as an ecological pressure controlling the opening of rhododendron flower buds in the spring.

These results are similar to those of Skok (101) who found that temperature was the more important factor in breaking dormancy of *Syringa hybrida*, *Cornus stolonifera*, and *Viburnum opulus*.

Effect of Photoperiod on Summer Dormancy of Weigela florida

An attempt to break summer dormancy in woody plants by alteration or manipulation of the photoperiod was tested by the following experiment.

On October 13, 1956, twelve single stem plants of Weigela florida which had been grown under natural day length and had been exposed to one killing frost were brought into the greenhouse. Two plants were placed under each of the following photoperiods: 24-, 20-, 16-, 12-, 8-hour and natural. The night temperature in the 24-hour, 16-hour and natural photoperiod house had a minimum of 60° F., while the 20-, 12- and 8-hour house had a minimum of 50° F. Within seven days the plants under the 24-, 20- and 16-hour photoperiods had commenced to grow, while those under the 12-hour, 8-hour and normal photoperiods remained dormant (Figure 20).

To determine the effect of short-day treatment upon the plants relative to dormancy, these plants were transferred to a long-day treatment on December 29. Those that had been growing on an 8-hour photoperiod were placed on a 16-hour photoperiod, and those that had been growing on the 12-hour day were transferred to a 24-hour day (Figure 20).

In each treatment one plant was left with its leaves intact and from another plant all leaves were removed to determine the effect of the foliage for mediating the photo response.

To determine what effect shortening the photoperiod had upon plants previously grown on a long-day, the plants that were under a 20-hour photoperiod were transferred to a natural day length on December 29 (Figure 20).

Summer dormancy in Weigela florida was broken within one week by photoperiods of 16-hours or greater. Plants under the 12-hour, 8-hour and natural photoperiods remained dormant. This indicates that the critical photoperiod is within the range of 12- to 16-hours.

When the plants which had grown on short days for eleven weeks were transferred to long days, they commenced growth within two weeks. Plants transferred from long days to short days ceased growth within three weeks.

The Effect of Photoperiod on Apical Dominance

The theory of apical dominance has been well established for plants, and Hemberg (49) has reported the presence of an inhibiting substance in the dormant buds of *Fraxinus*, but information on the relationship of the apical bud to dormancy produced by short photoperiods is not available.

An experiment was made to determine if removing the apical bud would affect growth of *Rhododendron catawbiense* and to determine whether an inhibitor was present in the apical buds of plants grown under a short (8-hour or 12-hour) photoperiod contrasted with buds produced under a long (20-hour) photoperiod

On September 14, 1956, five terminal buds were removed from each of three plants under 8-hour, 12-hour, 12-hour and natural photoperiods. Five terminal buds were marked on each plant for comparison. The buds were placed into separate vials, by treatment, and immediately quick frozen for biological assay. Weekly observations and measurements were made relative to: number of lateral shoots developed, length of shoot, and size of leaves.

Apical Dominance:

Removal of the terminal bud from shoots of *Rhododendron catawbiense* allowed lateral shoots to develop under all photoperiods tested. However, the degree of response varied with the photoperiod (Table XII and Figure 7). All of the disbudded shoots from plants growing under a 12- or 20-hour photoperiod produced laterals that averaged 13.0 centimeters in length.

TABLE XII

The Effect of Removing the Apical Buds of <u>Rhododendron catawbiense</u> When Grown Under Various Photoperiods

Photoperiod	Treatment	Percent of Shoots	Number of Laterals Per Shoot	Average Stem Length (cm.)	Character of Growth
8	Disbudded*	27	1	4.1	Leaves small, 3-4 per shoot
	Check	0	-	-	- - - - - - -
12	Disbudded	100	1-3	13.0	Leaves normal, 5-7 per shoot
	Check	0	-	-	- - - - - - -
20	Disbudded	100	3-4	13.0	Leaves normal, 5-7 per shoot
	Check	100	1	8.3	Leaves normal, 8-9 per shoot
Natural	Disbudded	87	2-4	4.2	Leaves small, 3-4 per shoot
	Check	0	-	-	- - - - - - -

* Based on 15 buds

Disbudded shoots growing under the 12-hour photoperiod produced one to three laterals, whereas those growing under the 20-hour photoperiod produced three to four laterals.

Disbudded shoots grown under the 8-hour and the natural photoperiods showed 27 percent and 87 percent activity, respectively. Although the length of the laterals averaged 4.1 centimeters under each treatment, the plants under the 8-hour photoperiod produced only one lateral contrasted with two to four laterals under natural photoperiod. The only check buds to develop were under the long (20-hour) photoperiod.

Biological Assay:

Buds which had been collected and quick frozen were extracted with peroxide-free-ether at 4° C. for two hours to obtain any free auxins. The ether extracts were then partitioned with 5 percent $NaHCO_3$ to obtain the acid auxins. The bicarbonate layer was separated and acidified with HCl to a pH of 2.8, extracted with ether, and concentrated.

The solutions were chromatographed on Whatman No. 1 filter paper with a water solvent. The chromatographs were sectioned and bioassayed by the Avena straight growth method. No significant difference in growth was noted.

The various extracts were also tested for auxin activity by the cucumber root test. Ten seeds of cucumber (Cucumus sativus var. Marketer) were uniformly distributed upon a piece of Whatman No. 1 filter paper in petri dishes. The paper was impregnated with five ml. of solution and the seeds were allowed to germinate for five days under laboratory conditions (temperature 70-75° F.). The length of the primary roots was measured to determine biological activity. No significant results were obtained.

Figure 1.

Weigela florida previously grown for 15 weeks under 16-hour, 8-hour, and natural photoperiods.

Figure 2.

Winter injury on *Weigela florida* previously grown for 15 weeks under 16-hour, 8-hour, and natural photoperiods. (Center plant destroyed by rodents.)

Figure 3.

Hibiscus syriacus previously grown for 15 weeks under 16-hour, 8-hour, and natural photoperiods.

Figure 4.

Winter injury on *Hibiscus syriacus* previously grown for 15 weeks under 16-hour, 8-hour, and natural photoperiods.

Figure 5.

Rhododendron catawbiense previously grown for 15 weeks under 16-hour, 8-hour, and natural photoperiods.

Figure 6.

Winter injury on *Rhododendron catawbiense* previously grown for 15 weeks under 16-hour, 8-hour, and natural photoperiods.

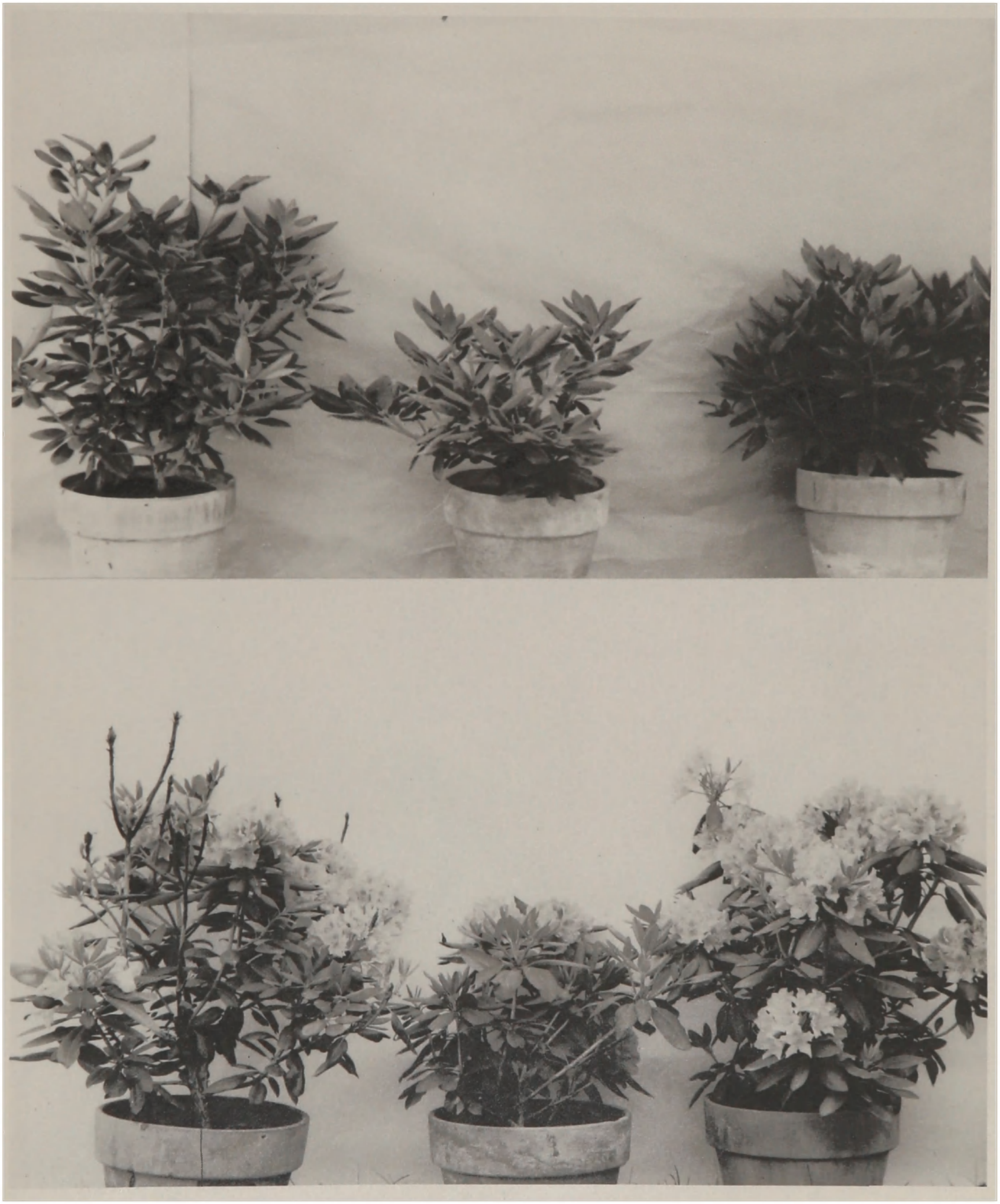


Figure 7.

Shoots produced on branches of Rhododendron catawbiense previously grown under 8-, 12-, and 20-hour photoperiods for 10 weeks. Apical bud removed in September, photo taken 5 weeks later.

A - Represents an average shoot produced under a natural photoperiod in June
B - Shoot produced under 8-hour photoperiod in October
C - Shoots produced under 16-hour photoperiod in October
D - Shoots produced under 20-hour photoperiod in October

Figure 8.

Flower development on two varieties of Rhododendron catawbiense under continuous illumination. American Beauty on left flowered within two weeks, var. 1004 on right flowered after 24 weeks.

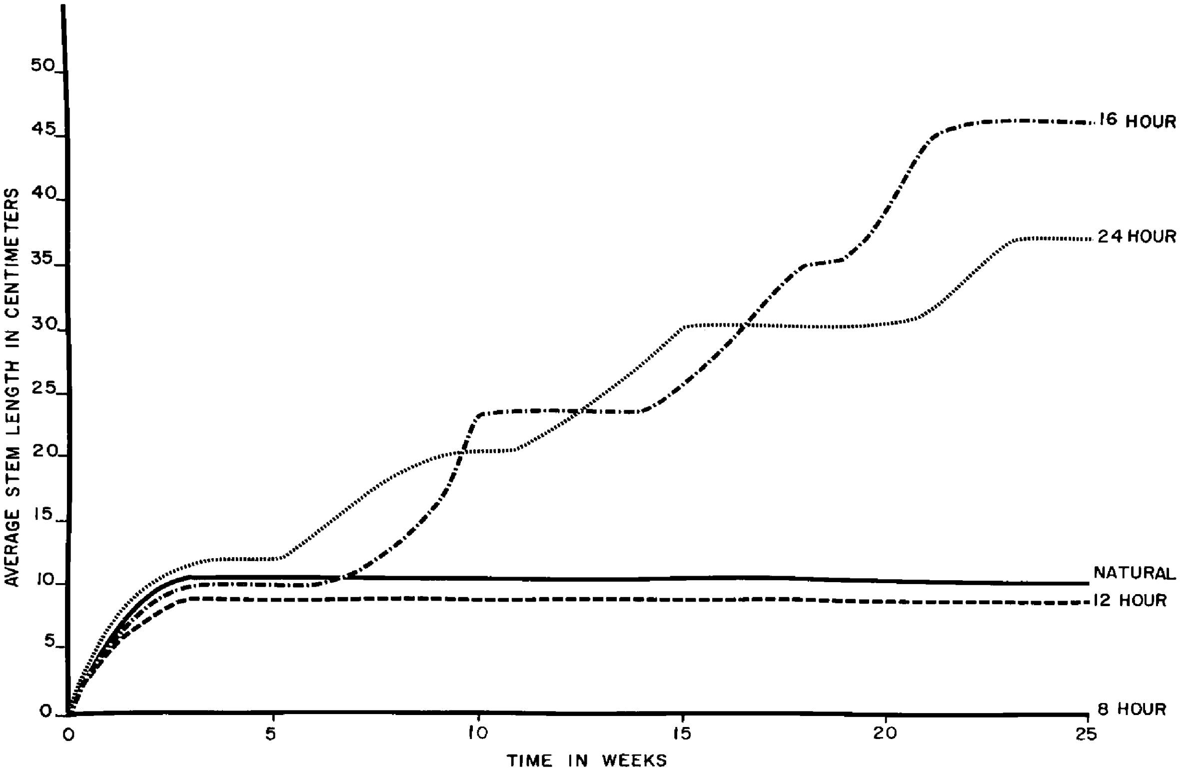

A
B
C
D

Figure 9.

Mean rate of growth of Rhododendron catawbiense grown under different photoperiods July - December 1956. Means based on fifteen determinations.

Figure 10.

Mean rate of growth of Rhododendron catawbiense grown under different photoperiods January - July 1956. Means based on fifteen determinations.


AVERAGE STEM LENGTH IN CENTIMETERS
0
5
10
15
20
25
30
35
40
45
50
TIME IN WEEKS
0
5
10
15
20
25
16 HOUR
24 HOUR
NATURAL
12 HOUR
8 HOUR

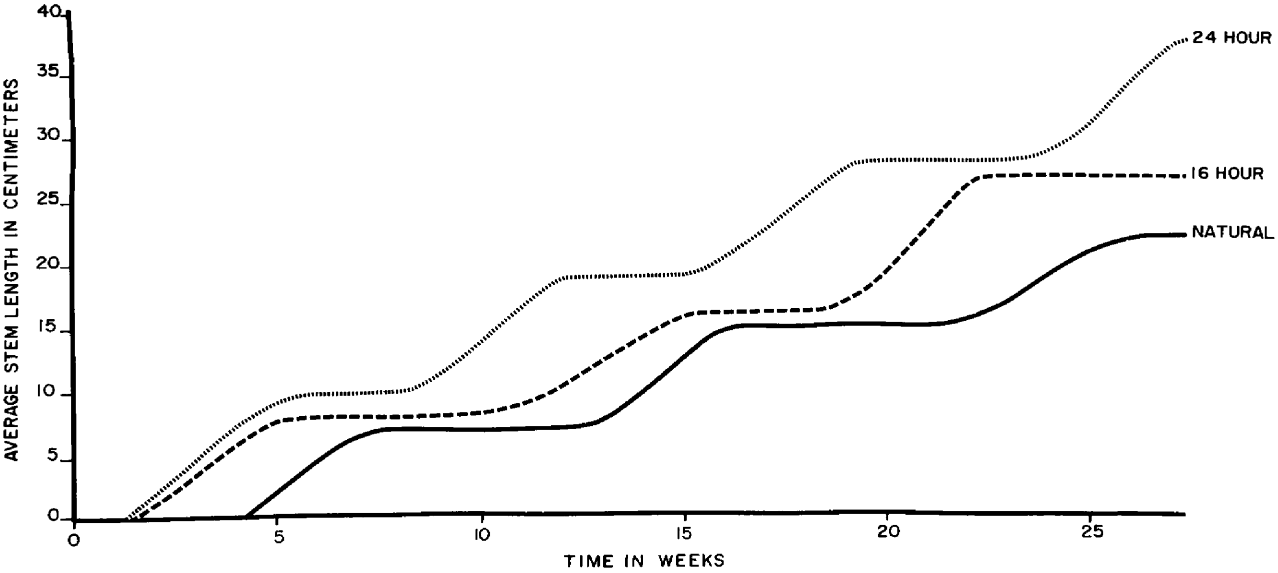

AVERAGE STEM LENGTH IN CENTIMETERS
0
5
10
15
20
25
30
35
40
TIME IN WEEKS
0
5
10
15
20
25
24 HOUR
16 HOUR
NATURAL

Figure 11.

Phylloidy of the bracts and petalloidy of the stamens on *Rhododendron catawbiense* previously grown for 20 weeks under a 24-hour photoperiod.

Figure 12.

Phylloidy of the bracts of *Rhododendron catawbiense* previously grown for 20 weeks under a 16-hour photoperiod.

Figure 13.

A flower bud of *Rhododendron catawbiense* previously grown for 20 weeks under a natural photoperiod.

Figure 14.

Sequence to show formation of phylloid-like bract when *Rhododendron catawbiense* was grown under a 24-hour photoperiod. Normal bract on right. Normal leaf on left.

Figure 15.

Phylloidy of the bract and petalloidy of the stamens when *Rhododendron catawbiense* was grown under a 24-hour photoperiod. Normal flower and bract on left.

Figure 16.

Sequence to show petalloidy of the stamens when *Rhododendron catawbiense* was grown under a 24-hour photoperiod. Normal petal shown on left. Petalloid stamens on right.

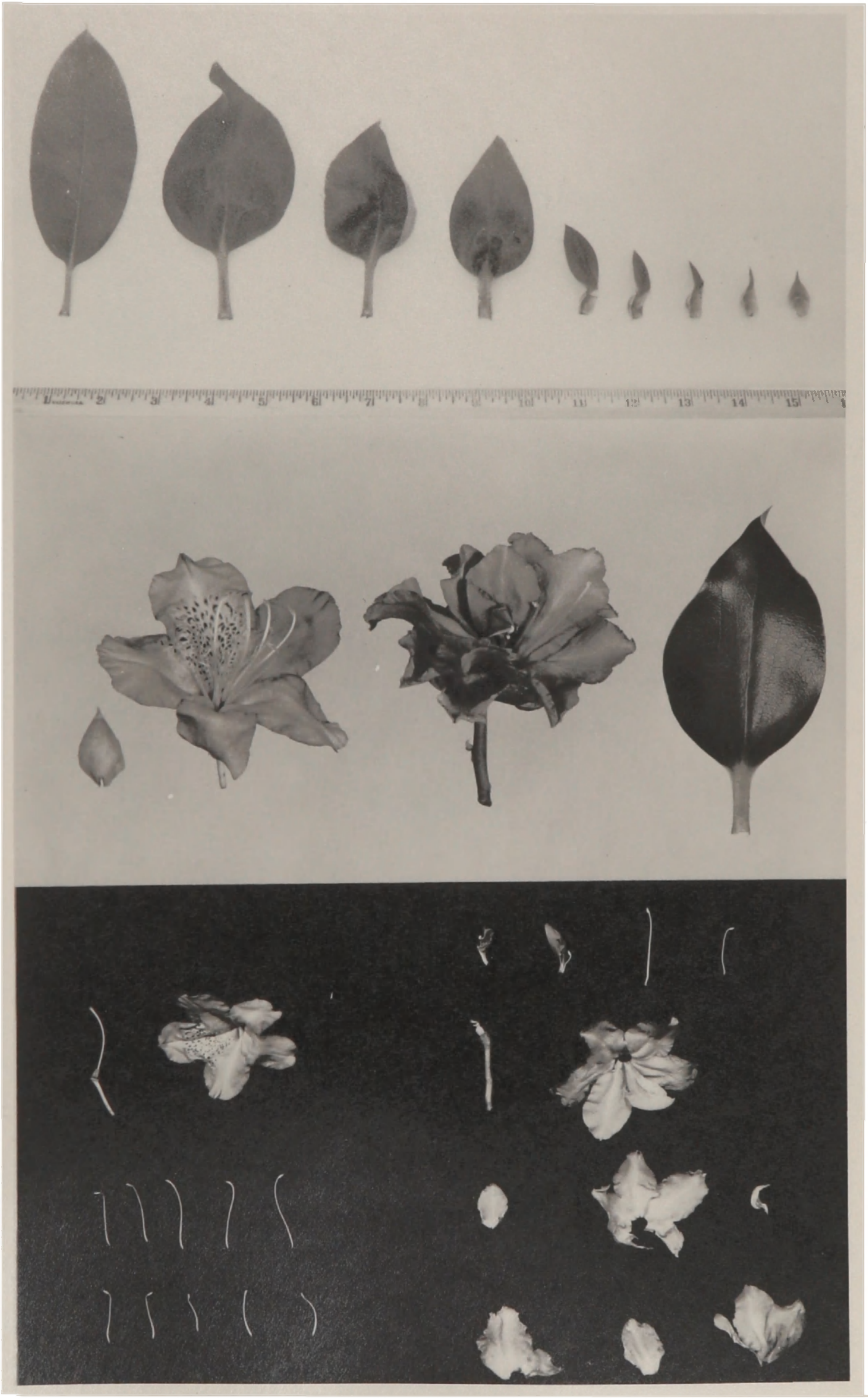


Figure 17.

Diagrammatic cross section of a typical bract (X8) of *Rhododendron catawbiense*. Bract is normal size.

Figure 18.

Diagrammatic cross section of a petiole (X10) of a phylloid bract from *Rhododendron catawbiense*. Bract is one-third normal size.

Figure 19.

Diagrammatic cross section of a typical petiole (X15) of a leaf of *Rhododendron catawbiense*. Leaf is one-third normal size.

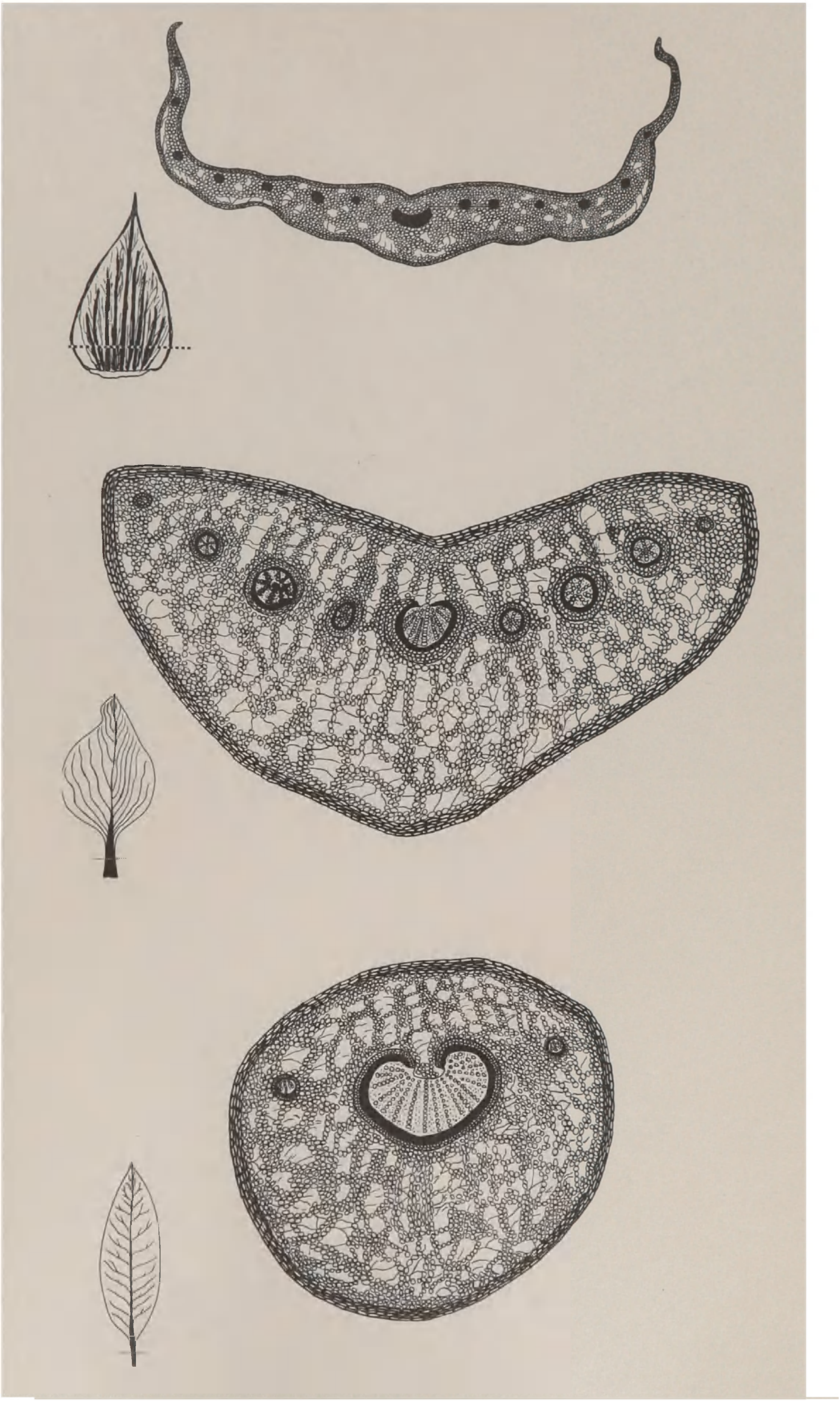
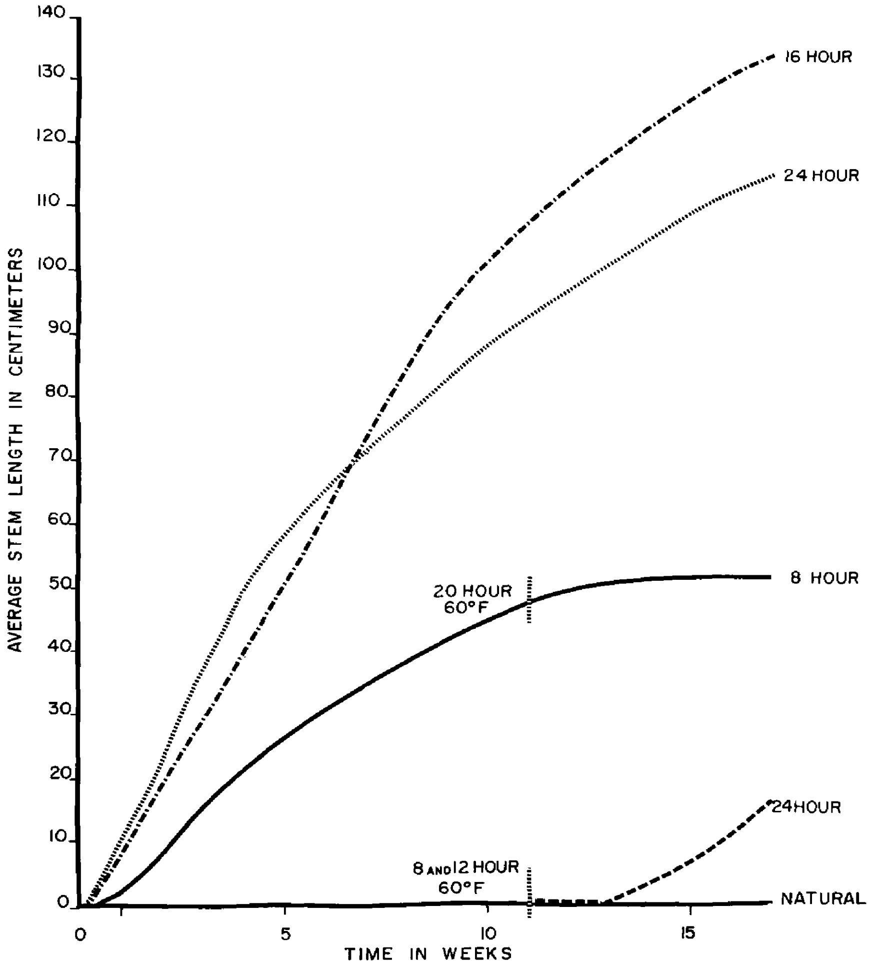


Figure 20.

Mean rate of growth of *Weigela florida* under different photoperiods. The plants grown under 24-hour, 16-hour, and natural photoperiod were kept at 70° F. Plants grown under 20-, 12-, and 8-hour photoperiods were grown at 60° F. for the first 11 weeks, then transferred to 70° F. Plants previously grown under a 20-hour photoperiod were transferred to an 8-hour photoperiod. Plants previously grown under an 8- and 12-hour photoperiod were transferred to a 24-hour photoperiod.


AVERAGE STEM LENGTH IN CENTIMETERS
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
0
5
10
15
TIME IN WEEKS
16 HOUR
24 HOUR
8 HOUR
20 HOUR
60°F
24HOUR
8 AND 12 HOUR
60°F
NATURAL

DISCUSSION

Photoperiod was demonstrated to be an environmental factor of major importance in controlling growth, flowering, dormancy, winter hardiness, and teratological variation of a number of selected ornamental shrubs. The results of this study showed that a photoperiod longer than the natural was instrumental in producing greater total growth in *Hibiscus syriacus*, *Rhododendron catawbiense* and *Weigela florida*, whereas a photoperiod shorter than the natural caused these plants and *Taxus cuspidata* to produce less growth.

Buddleja davidi and *Philadelphus coronarius aureus* were not sensitive to variation in photoperiod, indicating that the growth of some woody shrubs like herbaceous plants may not be influenced by photoperiod. *Buddleja davidi* was established as an indeterminate (day-neutral) type of plant by the fact that regardless of photoperiod, it flowered on or about the fourteenth node, at the same time of the year, and made approximately the same amount of growth.

Rhododendron catawbiense developed the greatest number of flower buds when grown under a natural photoperiod and may belong to the class long-short day plants, suggested by Sachs (93) in his recent study on *Cestrum nocturnum* in which he found that floral induction takes place when the plants are grown under a long photoperiod followed by a short photoperiod. This may explain some of the conflicting reports concerning the flowering response of *Rhododendron* spp.

Hibiscus syriacus produced maximum flower initiation when grown under long (16-hour) photoperiods which is in agreement with the findings of Allard (1) who established the species as a long-day plant in 1935. Maximum flower response and vegetative growth were both made under the long (16-hour) photoperiod. These results indicate that vegetative growth and floral response need not necessarily be opposing mechanisms.

Dormancy in woody plants, recently reviewed by Samish (94), may be influenced by photoperiod. Short-days have induced dormancy (rest) in Populus spp. (81) and long-days have stimulated the breaking of winter dormancy (rest) in Betula pubescens (12), Fagus sylvatica (12), and Pinus resinosa (41).

It appears from the present study that photoperiod is an environmental factor of prime importance in inducing dormancy in some species of woody plants. Short (12-hours and less) photoperiods induced Hibiscus syriacus, Rhododendron catawbiense, and Weigela florida into dormancy, whereas under a long (16-hours or greater) photoperiod the plants remained vegetative.

Induced dormancy resulted in hastened maturity, low moisture content of tissues, and a high degree of winter hardiness (low amount of winter injury), whereas delayed dormancy resulted in delayed maturity, relatively high moisture content of tissues, and a low degree of winter hardiness (high amount of winter injury).

No dormancy or winter hardiness response could be correlated with photoperiod for Taxus cuspidata, Buddleja davidi and Philadelphus coronarius aureus which were also found to be insensitive to long photoperiods.

An attempt was made to determine the presence of a growth inhibitor or growth promoting substance in the terminal buds of Rhododendron catawbiense which had been previously grown under long (20-hour), short (8-and 12-hour), and natural photoperiods. The Avena straight growth and the cucumber root growth methods of biological assay failed to show the presence of an inhibitor in the dormant buds (8, 12 and natural photoperiods), or a growth promoting substance in the buds (20-hour photoperiod) that were about to commence growth. These results are similar to those of Avery et al (3) who were unable to detect an inhibitor or growth substance in the dormant buds of Aesculus and Malus. It is highly possible that the dormancy of rhododendron may be due to the adaptive formation of indoleacetic acid oxidase, which has been reported recently by Galston (35) to be the agent responsible for aging of cells and dormancy in plants.

It was demonstrated that long (16-hours or greater) photoperiods can substitute in some varieties of Rhododendron catawbiense for the cold temperature requirement in inducing winter dormant buds of this species into growth. It was also demonstrated, however, that high temperature rather than photoperiod is the primary environmental factor in inducing flowering of dormant buds of R. catawbiense following exposure of the buds to cold temperature.

The fact that some species of woody plants are not sensitive to photoperiod, and that other species exhibit ecotypes, may explain the variety of results reported with respect to woody plants and their photoperiodic response to dormancy.

Teratological variations have been observed in plants. Masters (66) devoted a book to the subject in 1869, but it was not until 1936 when Murneek (75) reported the development of "vegetative flowers" on Rudbeckia when exposed to short days following exposure to long days, that a relationship was established between teratological variations and photoperiod. Harder (47) and Youmis (126) have established the fact that phylloidy of the bracts in Kalanchoe blossfeldiana results from too short an induction period. These results indicate that the teratological response results from a deficient supply of the photoperiodic stimulus.

The present studies with Rhododendron catawbiense have shown that phylloidy of the bracts may also result from a photoperiod that is too long, and that continuous illumination intensifies this response and results in petalloidy of the stamens and "vegetative flowers" - where a shoot replaces a flower in the axil of a bract. These results indicate that too long an induction period also results in teratological variation.

This study, and the work of Bel'denkova (10) in Russia, strongly suggest that the length-of-day may be an important factor in regulating the distribution of many species of plants.

APPLICATIONS

The control of growth in some woody plants by manipulation of the daylength suggests a number of practical applications.

Increasing the natural day length by supplementary low intensity light might be used by nurserymen as a means of increasing the growth of those plants which are sensitive to changes in the photoperiod. It would be necessary, however, to provide a period just prior to freezing temperatures, during which these plants should be subjected to a short photoperiod, in order to mature the tissues to a condition where they could withstand freezing temperatures.

It has been observed that survival rates of many types of summerwood cuttings is extremely low in many northern nurseries. It is possible that a reduced photoperiod in late summer would hasten the on-set of dormancy in these cuttings, and thus bring about a higher resistance to cold temperature with a substantial increase in the survival rate. Sato (96) and Robak (89) have reported increased resistance to cold temperature in various forest tree seedlings by such a practice.

Photoperiodism might also be used as a tool in the screening of new hybrids and plant introductions to determine their ecological area of maximum production commensurate with their ability to mature by the end of the growing season, so that they will have maximum winter hardiness.

Pauley and Perry (81) and Hoffman (50) have demonstrated that photoperiodism is a hereditary factor. It might be practical to develop a genotype which would combine the various economic qualities present in a cultivated species hardy only in the southern latitudes with the quality of early dormancy found in the wild species indigenous to northern latitudes. By careful seedling selection, a cold-temperature-resistant ecotype possessing the qualities of the cultivated type might be obtained and established as a clone.

Increased photoperiods might also be used to hasten the breeding cycle of some plants similar to the method of Doorenbos (27) in which he flowered hybrids of _Rhododendron_ spp. in a period of thirty-three months contrasted to twice this period of time by older methods.

A thorough knowledge of photoperiodism in woody plants will be of an assistance in making possible the marketing of woody ornamental plants for special purposes, and aid in their propagation as has been shown by Snyder (102) for _Taxus cuspidata_, and by Downs and Borthwick (30) for _Weigela florida_ var. _variegata_.

SUMMARY

1. Six species of woody plants were grown under various photoperiods at East Lansing, Michigan to determine their response to photoperiod.

2. *Buddleja davidi* and *Philadelphus coronarius aureus* were not sensitive to variations in photoperiod. *Buddleja davidi* was established as a day-neutral plant.

3. *Taxus cuspidata* made less growth on the short (8-hour) photoperiod than under the natural photoperiod, and was not sensitive to an increase in daylength.

4. *Hibiscus syriacus*, *Rhododendron catawbiense*, and *Weigela florida* made maximum growth under long (16-hour and greater) photoperiods, and minimum growth under the short (8-hour) photoperiod.

5. The critical period for *Rhododendron catawbiense* and *Weigela florida* was found to be between 12- and 16-hours.

6. Maximum flower bud initiation occurred on *Rhododendron catawbiense* when grown under a natural photoperiod. Photoperiods in excess of 16 hours resulted in phylloidy of the bracts. Continuous illumination of *Rhododendron catawbiense* resulted, in addition to phylloidy of the bracts, in the formation of petalloidy of the stamens and "vegetative flowers", in which shoots replaced flowers in the axils of bracts.

7. Short photoperiods (reduced natural daylength) induced an early cessation of growth of *Hibiscus syriacus*, *Rhododendron catawbiense*, and *Weigela florida*, and as a result, plants possessed a high resistance to cold temperature injury.

8. Long photoperiods (16-hours and greater) were effective in breaking winter dormancy (rest) in the buds of *Rhododendron catawbiense* var. American Beauty, but they were ineffective on var. 1004*.

9. It was demonstrated that high temperature was the environmental factor that influenced the opening of *Rhododendron catawbiense* buds in the spring of the year.

* An unnamed hybrid, Westcroft Gardens, Grosse Ile, Michigan.

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