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thesis entitled

INFLUENCE OF PHOTOPERIOD AND TEMPERATURE ON FLOWERING OF
ASCLEPIAS TUBEROSA, CAMPANULA CARPATICA 'BLUE CLIPS',
COREOPSIS GRANDIFLORA 'EARLY SUNRISE', COREOPSIS VERTICILLATA
'MOONBEAM', LAVANDULA ANGUSTIFOLIA 'MUNSTEAD', AND
PHYSOSTEGIA VIRGINIANA 'ALBA'

presented by

CHERYL KAY HAMAKER

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William H. Carlson
Major professor

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INFLUENCE OF PHOTOPERIOD AND TEMPERATURE ON FLOWERING OF *ASCLEPIAS TUBEROSA, CAMPANULA CARPATICA* 'BLUE CLIPS', *COREOPSIS GRANDIFLORA* 'EARLY SUNRISE', *COREOPSIS VERTICILLATA* 'MOONBEAM', *LAVANDULA ANGUSTIFOLIA* 'MUNSTEAD', AND *PHYSOSTEGIA VIRGINIANA* 'ALBA'

By

Cheryl Kay Hamaker

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ABSTRACT

INFLUENCE OF PHOTOPERIOD AND TEMPERATURE ON FLOWERING OF *ASCLEPIAS TUBEROSA, CAMPANULA CARPATICA* 'BLUE CLIPS', *COREOPSIS GRANDIFLORA* 'EARLY SUNRISE', COREOPSIS VERTICILLATA 'MOONBEAM', *LAVANDULA ANGUSTIFOLIA* 'HIDCOTE BLUE', AND *PHYSOSTEGIA VIRGINIANA* 'ALBA'

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Five methods for long-day (LD) lighting for flowering in *Asclepias tuberosa, Campanula carpatica*, *Coreopsis grandiflora*, and *Lavandula angustifolia* were compared. LD treatments consisted of a 7-hour pre-dawn extension (PD), 7-h day extension (DE), 4-h night interruption (4-h NI), 7-h night interruption (7-h NI), and 24-h continuous lighting (24-h). NI and DE were superior to PD for all species. The 4-h NI treatment was adequate as a LD delivery. The influence of 5C treatments and photoperiod on flowering in *Coreopsis verticillata* and *Physostegia virginiana* was determined. Cold decreased time to flower in *Coreopsis* by ≈10 days. In *Physostegia*, cold increased flowering percentage and decreased time to flower. Both *Coreopsis* and *Physostegia* required LD to flower. *Coreopsis* and *Physostegia* were forced under 15, 18, 21, 24, or 27C, and the linear relationship between temperature and rate of progress to flowering was determined. Base temperatures and degree-days were calculated and can be used to predict flowering.

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LITERATURE REVIEW

The Effect of Photoperiod on Flowering

Introduction and definitions

Plants respond to a variety of environmental conditions that promote plant growth. The response to different environmental stimuli is species-specific. Even different cultivars or varieties within the same species can have quite different growth and flowering requirements. The environmental conditions that most frequently promote flowering are photoperiod and low temperatures (Thomas *et al.*, 1984). Hillman (1969) defined photoperiodism as a response to the timing of light and darkness. Thomas and Vince-Prue (1984) defined vernalization as the effect on flowering brought about by exposure to cold.

In many cases, photoperiod and vernalization interact to enable plants to adapt to seasonal changes. Response to various combinations of photoperiod and vernalization can give certain advantages to an organism. A plant can respond to these two factors in a way that will avoid or prevent adverse effects of unfavorable environments that can affect reproduction, growth, and ultimately, survival (Evans, 1975). For example, some plants drop leaves and enter dormancy in response to the combination of short days and decreasing air temperature which precede winter. Other adaptations involving reproduction include: synchrony of reproduction within a population to increase out-breeding; synchrony of reproduction with favorable conditions, such as availability of water, favorable temperatures or a high daily light integral; or avoid unfavorable environments, such as water stress or low temperature (Thomas *et al.*, 1984). These adaptations enable a species to initiate flowering and subsequent seed maturation at appropriate times of the year to satisfy necessary requirements, such as vernalization or moisture needs.

Direct and indirect effects of photoperiod

Photoperiod is the most reliable of environmental stimuli to which plants respond in that it changes regularly throughout the year. The absolute daylength is affected by latitude and time of year. The range of daylength varies from 6 to 19 h at 60°, from 9 to 15.5 h at 45°, and from 10 to 14 h at 30°. The average rates of photoperiodic change for the above latitudes for April and August are 40 $\text{min}\cdot\text{wk}^{-1}$ at 60°, 25 $\text{min}\cdot\text{wk}^{-1}$ at 45°, and 12 $\text{min}\cdot\text{wk}^{-1}$ at 30°. Depending on geographical location, a plant needs to differentiate between these photoperiodic changes in order to time environmental responses.

The greatest precision of timing occurs in plants that originate or are located near the equator, where the range of daylengths is very small in comparison with greater latitudes. Nevertheless, the flowering of tropical plants is strongly affected by photoperiod, and tropical plants respond to smaller changes in the daylength than those in temperate latitudes. In addition to flowering, photoperiod also influences a number of other developmental responses, such as the formation of storage organs, leaf development, stem elongation, and germination. Due to the enormous range of photoperiodic responses, this review will primarily consider the flowering response with respect to photoperiod.

Garner and Allard (1920) were the first to demonstrate that response to daylength was a major environmental factor controlling flowering. Garner (1933) classified plants into three groups based upon their flowering response to photoperiod. These groups were indeterminate, short-day, and long-day types (see Figure 1). Long-day plants (LDP) only flower, or flower more rapidly, when exposed to days in excess of a critical duration. Short-day plants (SDP) only flower, or flower more rapidly, when exposed to daylengths shorter than a critical duration. Indeterminate, or day neutral, plants (DNP) were found to be indifferent to daylength, flowering at the same time irrespective of photoperiodic conditions.

The long-day and short-day groups are further subdivided into either a qualitative or quantitative photoperiodic response (see Figure 2). A qualitative response,

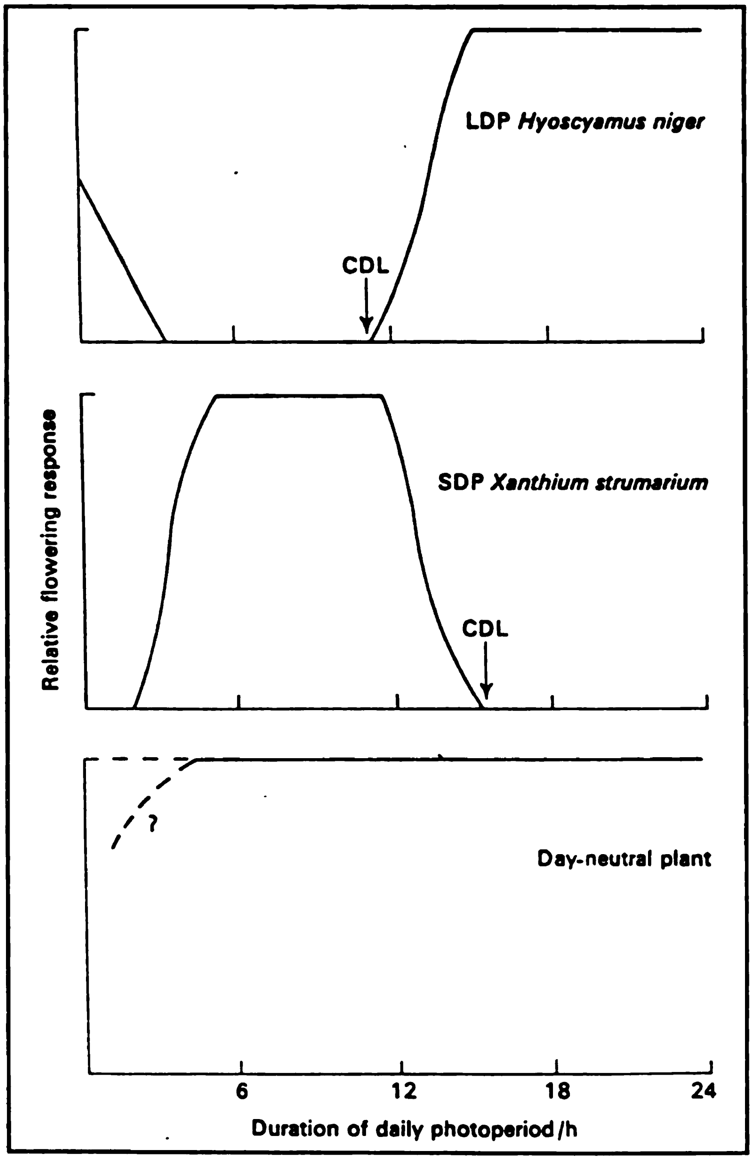


Figure 1. Plants are divided into three categories, LD, SD, or DN, depending on their photoperiodic requirements for flowering. Taken from Photoperiodism in Plants, Vince-Prue, D. 1975.

otherwise known as an absolute or obligate response, occurs when a particular daylength is essential for flowering. A quantitative response occurs when a particular daylength promotes, or hastens, but is not essential for flowering (Summerfield *et al.*, 1987). It is best to consider these two response types not as two distinct groups, but as a continuum with a slight acceleration of flowering by favorable daylengths at one end and a indefinite delay of flowering by unfavorable conditions at the other (Vince-Prue, 1975).

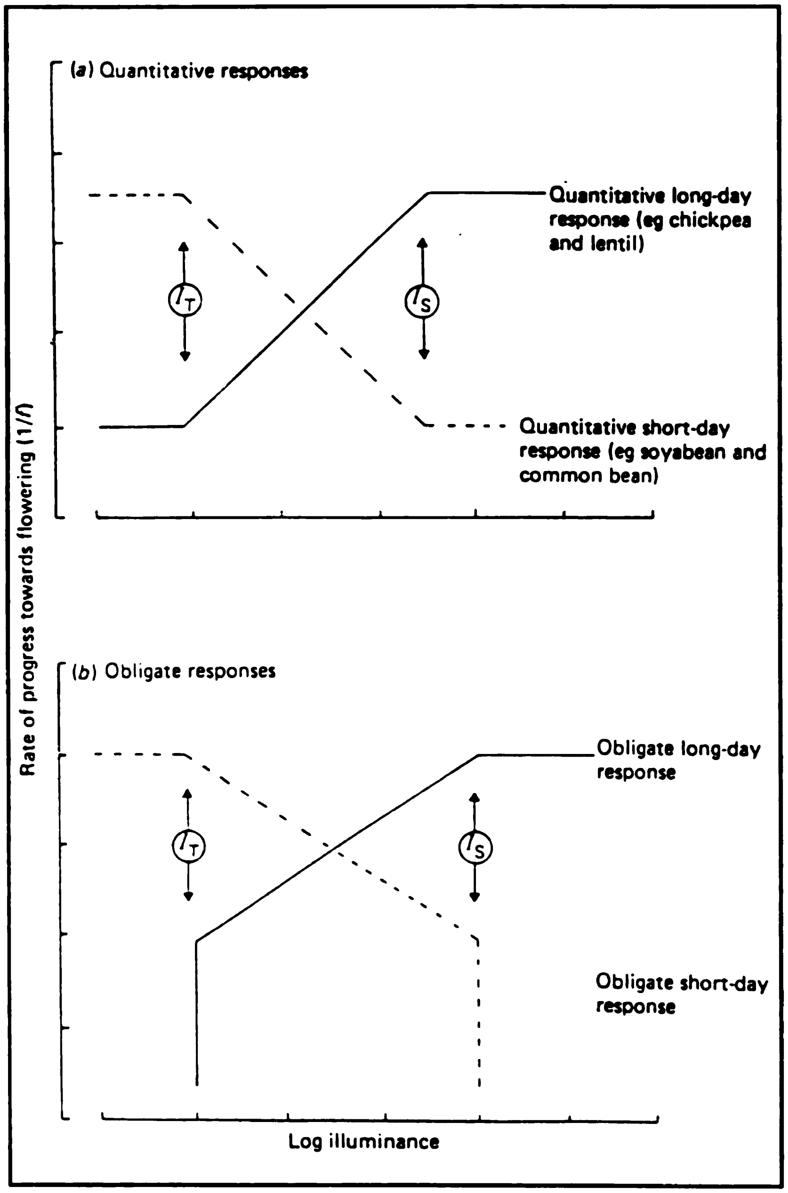


Figure 2. Photoperiodic categories are further divided into either quantitative or obligate response.
Taken from Manipulation of Flowering, Atherton, 1987.

Initially, plants were thought to rely on a critical daylength (CDL) to differentiate between reproductive and vegetative photoperiods. However, it was found that the length of the dark period was the decisive factor when measuring photoperiodic response for the above response groups.

Vegetative and Reproductive Growth

Depending on their photoperiodic classification, plants can respond to photoperiod with two distinct growth habits, vegetative and reproductive. In LDP, vegetative growth is promoted and reproductive growth is restricted by short days (SD), or more specifically, daylengths less than the critical daylength required for flowering. Under long days (LD), when considering a mature plant, reproductive growth is promoted while vegetative growth is restricted. The converse would apply to SDP.

In some species of LDP, vegetative growth is necessary before flower initiation can take place. In many cases this requirement is the same as the number of leaf primordia already present within the seed (Vince-Prue, 1975). However, it may be necessary for additional leaves to form before flower initiation can occur. Plant species with a minimum leaf number requirement are found to be insensitive to environmental stimuli affecting flowering until the minimal leaf requirement is satisfied. The minimum leaf numbers have been determined for several different species of plants including *Chrysanthemum superbum* 'Marconii' and 'Snow Lady' (Damann *et al.*, 1995), *Eschscholzia californica* (Lyons *et al.*, 1986), and *Gaillardia pulchella* (Bourke, 1990).

There are three phases of plant growth and morphology which have been differentiated by Roberts and Summerfield (Roberts *et al.*, 1987). The first phase is known as the pre-inductive phase, or juvenile phase, and requires a minimum number of leaves in order for the plant to sense inductive conditions. Juvenility is considered to be the early phase of growth from seed during which flowering cannot be induced by any treatment (Vince-Prue, 1975). The need for a juvenile period is species-specific and the length of the juvenile phase can vary from one week after germination, as in *Xanthium*, to several years, as in many woody species. The second growth phase is known as the inductive phase. During this phase, the plant becomes sensitive to photoperiod and as a result can be induced to flower. The inductive phase also has been found to vary in duration. Some LDP species, such as *Asclepias tuberosa*, require LD from forcing until flower or development will cease and the plant will go dormant (Whitman, 1995). Other LDP species, such as *Coreopsis grandiflora* (Lyons, 1992) or *Coreopsis verticillata* (Koreman, unpublished data), require a minimum of three weeks of LD for flower initiation to occur and then will develop under SD conditions until flower. The third phase is called the post-inductive phase, which includes the flowering process. Like the juvenility phase, the post-inductive phase is generally insensitive to photoperiod.

The reproductive growth phase can be separated into the following major stages: 1) floral initiation, 2) floral organization, 3) floral maturation, and 4) anthesis (Lang, 1952). The floral initiation stage involves the differentiation of floral primordia. Differentiation of the individual flower parts then occurs in the floral organization stage. The floral maturation stage consists of several processes, such as growth of the flower parts, differentiation of the sporofeneous tissues, meiosis, and pollen and embryo sac development. The final stage of the flowering process results in anthesis, when pollen is shed by the flower (Lang, 1952).

Photoperception

It has been extensively demonstrated that daylength is perceived by the leaves of a plant and that it is immaterial whether or not the apex is exposed to inductive conditions. Knott (1934) first demonstrated the concept of leaf sensitivity to daylength in an experiment where only the leaves of the LDP spinach, *Spinacia oleracea*, were exposed to long photoperiods. This procedure resulted in initiation of floral primordia at the terminal growing point. Later studies involving the SDP cocklebur, *Xanthium strumarium*, confirmed the results found by Knott (Ferry *et al.*, 1959). Floral initiation did not occur when defoliated cocklebur plants were exposed to a SD photoinduction cycle. Ferry discovered that if all but one of the leaves were removed, the SD photoinduction cycle resulted in floral initiation. Perhaps Chailakhyan (cited in Vince-Prue, 1975) most effectively illustrated that the site of perception occurs in the leaves through his work with the SDP, *Dendranthemum* x*grandiflorum* (see Figure 3).

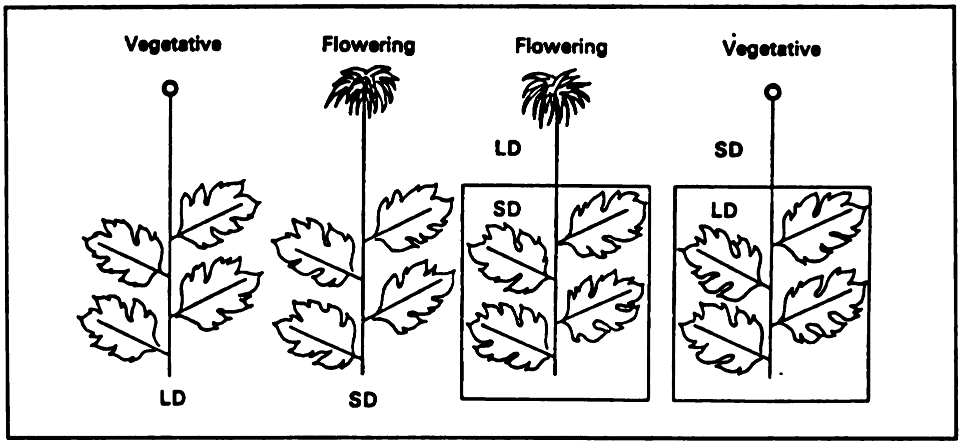


Figure 3. The effect of photoperiodic treatments to the leaves or apex on flowering response of *Dendranthema* x*grandiflorum*.
Taken from Photoperiodism in Plants, Vince-Prue, 1975.

The experiment involved four different treatment groups. The first and second groups involved entire plants exposed to either long or short days. The third group had only the leaves exposed to LD while the growing point was exposed to SD. The fourth group had the leaves exposed to SD while the growing point was exposed to LD. Of the plants that were treated in their entirety, only the SD treatment resulted in flowering. The plants with the LD leaf treatment and the SD growing point treatment remained vegetative while the plants with the SD leaf treatment and the LD growing point treatment flowered. These results downplay the role of the apex and suggest a direct role of leaves in the perception of photoperiod.

Plant age can often affect daylength sensitivity. For instance, older plants are often more inducible. Originally this was thought to be caused by the increased leaf area of older plants. Research has shown that the same number of cycles are required to induce an intact plant as one defoliated to a single leaf (Vince-Prue, 1975).

Other experiments have demonstrated that leaves are not all equally sensitive to photoperiod. Hamner and Bonner (1938) discovered that induced leaves are effective in causing flowering only when they are relatively young. Their experiments concluded that the leaves' effectiveness in promoting flowering declined with age. Khudairi and Hamner (1954) found that in *Xanthium*, the peak of photoperiodic sensitivity occurred in leaves that were approximately half of their final length. A later study showed that, in *Perilla crispa*, the youngest, fully expanded leaf was found to have the most sensitivity to photoperiod (Ochesanu, 1965).

The role of leaves in the perception of daylength is confirmed by removing leaves from induced plants and grafting them to vegetative receptors to induce those receptors. Zeevaart (1958) discovered that induced leaves of *Perilla* could be grafted and regrafted to different receptors and still retain their capacity to induce flowering on the receptors. In later studies, Zeevaart (1969) demonstrated that the leaves of *Perilla* could be induced after they had been removed from a donor plant. These leaves were then grafted to a vegetative receptor, which then was induced to flower. Also in 1969, Zeevaart illustrated that grafted donor leaves of the SDP, *Xanthium strumarium*, will cause a flowering response on receptors that are maintained in long-day conditions.

Flower-promoting Theory vs. Flower-inhibiting Theory

The ability to induce receptors through grafting of induced leaves shows that under inductive conditions, changes take place in the plant which actively promote flower initiation. In fact, all of the chemicals necessary for floral initiation can be synthesized within the leaves alone. Two distinct theories have evolved which attempt to explain flower induction.

The first theory postulates the existence of a flower-promoting substance produced by the leaves and translocated to the terminal growing point. Experiments have shown that the substance which promotes flowering can move across graft unions and induce flowering in the scion. Lang (1965) reviewed results that demonstrated transmission of a floral stimulus to the growing points of both LDP and SDP through grafts of photoperiodically sensitive plants.

Indirect experiments, again involving grafting, have provided evidence that there may be a universal floral hormone that is interchangeable between LDP, SDP, and DNP (Lang, 1965). Grafts can be made not only of induced and noninduced plants of the same photoperiodic classifications, but also between plants belonging to different photoperiodic classifications. The SDP, *Xanthium*, was induced to flower in LD by grafting with any of the LDP, *Rudbeckia bicolor*, *Erigeron annuus*, or *Centaurea cyanus* (Okuda, 1953). The above experiments demonstrate a transfer of a floral stimulus between LD and SD plants but only if the donor leaves have been photoperiodically induced prior to grafting. Lang (1965) was unsuccessful in his attempts to induce the SDP, *Nicotiana* 'Maryland Mammoth', with the donor LDP, *Hyoscyamus niger*, which was maintained in SD. Lang also found the converse to be unsuccessful as well. A flowering-promoting stimulus, or 'florigen' as it has been called, has not yet been identified chemically. However, there is a great deal of circumstantial evidence that leaves maintained in the appropriate photoperiods produce a substance that is capable of promoting flowering in plants of different photoperiodic classifications.

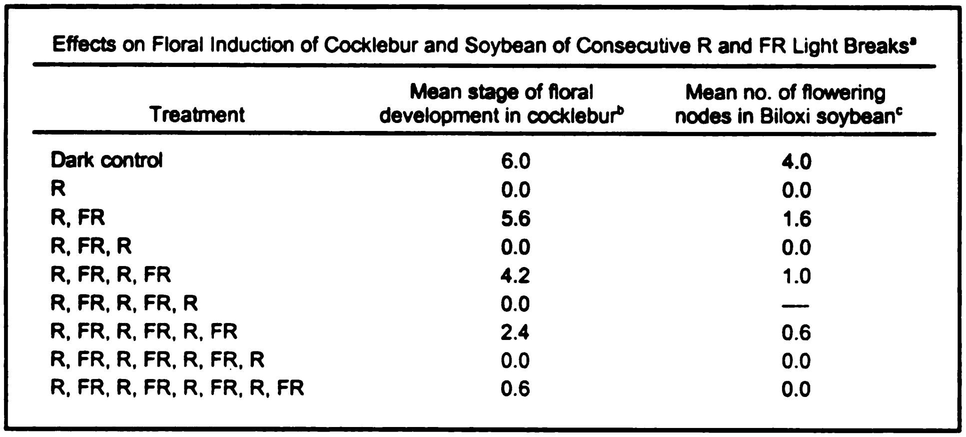
Failures in the attempt to extract and identify a universal flowering hormone led to the theory of the existence of a flowering inhibitor that may be antagonistic in some way to the processes occurring within the leaves or at the apex. The evidence advanced for a flowering hormone may be explained by the production of an inhibitor in non-inductive daylength instead of the production of a promoter in inductive daylengths. Borthwick and Parker (1938) found it necessary to defoliate a non-induced receptor branch to induce the transfer of the floral stimulus. In such cases, the presence of non-induced leaves may interfere with the translocation process. However, this inhibitory effect was only observed when non-induced leaves were between the induced leaves and the receptor meristem in *Silene armeria* (Wellensiek *et al.*, 1967).

Introduction to Phytochrome

Laurie (1931) demonstrated that flowering of several photoperiodic greenhouse crops could be controlled by providing supplemental lighting or shading to obtain the desired response. In the SDP, *Glycine max* 'Biloxi', flowering was inhibited by the use of a night interruption period (Parker *et al.*, 1945). Plants were debladed to one leaf and individual plants were given a night interruption of various wavelengths. The results showed that red light (R) was more effective than far-red light (FR) in inhibiting flowering in short days. This method was repeated with the LDP barley, *Hordeum vulgare* 'Wintex' (Borthwick *et al.*, 1948). Red light was found to be most effective in promoting flowering. The most effective region of the spectrum for both prevention of floral induction in SDP and the promotion of floral induction in LDP was between 600 and 660 nm. These results indicated that the same type of pigment was responsible for the absorption of effective spectrum regions for both SDP and LDP (Borthwick *et al.*, 1948). The similarities in the action spectrums led to the pursuit of a photoreceptor(s) that was partially or solely responsible for the observed results.

A key breakthrough in the history of the photoreceptor was the discovery that the effect of a red light treatment (650-680 nm) on morphogenesis could be negated with a similar light treatment of longer wavelengths (710-740 nm), known as far-red light (Downs, 1956). The first example of the red/far-red light photo-reversibility was demonstrated on the germination of lettuce seed 'Grand Rapids' (Borthwick *et al.*, 1952). In this experiment, a far-red light treatment given immediately following a FR light treatment was found to reverse the effects of the R light treatment and successfully inhibit germination. The wavelength of the final treatment was the critical factor in determining whether the previous light treatment was negated and germination was inhibited.

In 1956, Downs tested the apparent photoreversibility of red and far-red light treatments for flower induction (see Figure 4). Red light treatments were given to inhibit flowering in order to test a far-red light treatment for reversal and subsequent floral formation. Short periods of FR were again found to reverse the effect of R on *Xanthium*. However, as the number of successive cycles increased between the treatments FR, reversal lessened.

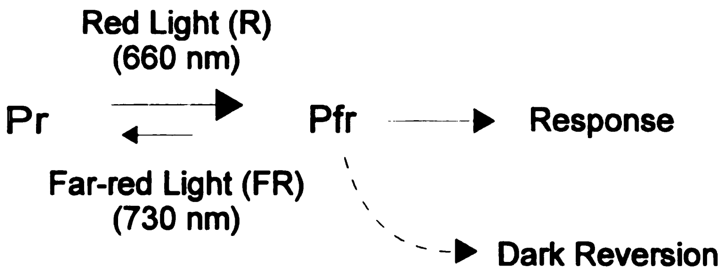


Effects on Floral Induction of Cocklebur and Soybean of Consecutive R and FR Light Breaks[a]

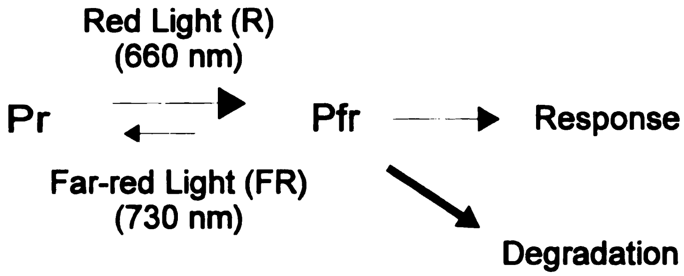
Treatment	Mean stage of floral development in cocklebur[b]	Mean no. of flowering nodes in Biloxi soybean[c]
Dark control	6.0	4.0
R	0.0	0.0
R, FR	5.6	1.6
R, FR, R	0.0	0.0
R, FR, R, FR	4.2	1.0
R, FR, R, FR, R	0.0	—
R, FR, R, FR, R, FR	2.4	0.6
R, FR, R, FR, R, FR, R	0.0	0.0
R, FR, R, FR, R, FR, R, FR	0.6	0.0

Figure 4. The photoreversibility of red and far-red light treatments suggested that only one pigment was involved in flower induction.
Taken from Pigment of the Imagination, Sage, 1992.

Hendricks and Borthwick (1952) proposed that there was only one pigment involved in these responses. In addition, the photoreceptor for this photoreversible system must itself be photoreversible and would change its own absorption properties by changing color reversibly in response to red and far-red treatments. They theorized that the pigment, phytochrome, occurred in two forms: P_r, the red absorbing form, and P_{fr}, the far-red absorbing form. They proposed that P_{fr} was the active form of phytochrome and mediated all responses. Thus, the R-absorbing form, when exposed to R, would convert to the FR-absorbing form and the response would be promoted. Similarly, the FR-absorbing form, when exposed to FR, would convert back to the R-absorbing form and the response would be inhibited. The general scheme created by Hendricks and Borthwick was the following:



It was thought that the P_{fr} slowly reverted back to the P_r form in the dark. The dark reversion was found to be reversible only to a point. With etiolated seedlings the phytochrome can only change back and forth between the P_r and P_{fr} forms a few times because the P_{fr} form deteriorates. Since P_{fr} is relatively unstable, most is destroyed. Light was found necessary to synthesize new P_r, thereby replenishing the supply of phytochrome. In view of these findings, the original model was modified to the following which still stands as the accurate model to this day. The improved model is as follows:



Special instruments were designed to detect the photoreversible color changes in plants and the proposal advanced by Hendricks and Borthwick was verified (Butler *et al.*, 1959).

When the pigment was isolated, it was found to actually exist in two forms (Sage, 1992). Phytochrome in the red absorbing form (P_r) was found to be green, while the phytochrome in the far-red absorbing form (P_{fr}) was found to be green-blue. In etiolated plants that have had no prior irradiation, only phytochrome in the P_r form was present. If a red light treatment was given, then the P_r form was found to convert to P_{fr}. P_r absorbs red light maximally at 660 nm and is converted to P_{fr}, while P_{fr} absorbs far-red light maximally at 730 nm and is converted back to P_r (see Figure 5). When the absorption spectra of these two forms were compared, a significant overlap in the red region was discovered (Taiz *et al.*, 1991). During a treatment of red light (~660 nm), not all of the P_r is converted to the P_{fr} form. There is approximately 15% of the pigment remaining

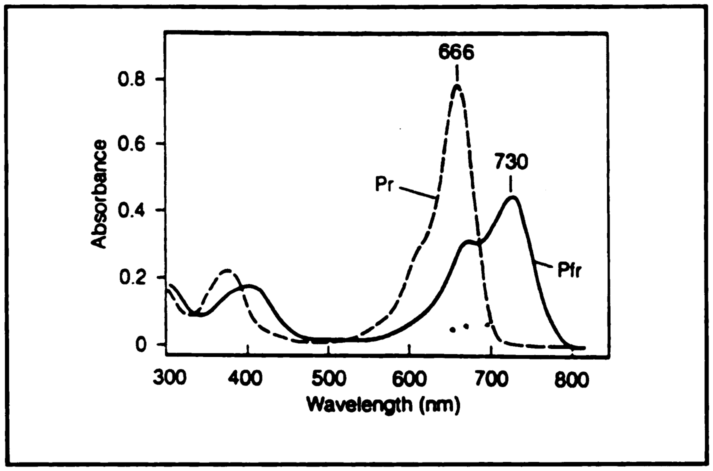


Figure 5. An absorption spectrum showing the overlap between the red and far-red regions.
Taken from Plant Physiology, Taiz and Zeiger, 1991.

in the P_r form since P_{fr} will also absorb the red light and be converted back to P_r. Likewise, if a treatment of far-red light is given (~730 nm), 97% of the phytochrome in the P_{fr} form will convert to the P_r form. The other 3% remains in the P_{fr} form because the small amount of far-red light absorbed by P_r makes it impossible to convert P_{fr} entirely to P_r. In some cases this remaining 3% is enough to drive some responses (Taiz *et al.*, 1991).

Phytochrome is made up of two parts, a protein and a chromophore. The protein is a holoprotein, which consists of two identical subunits that come together at the binding site. The chromophore, a tetrapyrole, is responsible for the absorption of light. When phytochrome is irradiated with red light, the configuration of the chromophore changes through a cis-trans rearrangement caused by an absorption of a photon. The conformation change brings about a change in the polypeptide which is thought to initiate the reactions that lead to a given response (Taiz *et al.*, 1991).

LD Response

Photoperiodic induction of flowering in long-day plants has not been as extensively studied as that of short-day plants. This is due to the relative insensitivity of most LDP to floral promotion by a brief light interruption of a non-inductive long dark period (Deitzer, 1984). Only a few genera of LDP respond to a few number of night breaks, such as *Hyoscyamus niger* (Downs *et al.*, 1982) and *Lolium temulentum* (Evans, 1960).

Delivery of Long Days

In the greenhouse industry, manipulation of the photoperiod is often employed to artificially shorten or lengthen natural daylengths in order to obtain either vegetative or reproductive growth (Laurie, 1931). For example, cuttings of the LDP *Physostegia virginiana* 'Summer Snow' and 'Vivid' were exposed to either SD or LD (Beattie *et al.*, 1989). The cuttings that were exposed to SD rooted well. In contrast, the cuttings that were exposed to LD rooted poorly, and approximately 20% of both cultivars had to be discarded due to poor growth habit. Days to flower can be greatly reduced in many plant species when grown under LD rather than SD (Carpenter *et al.*, 1973; Carpenter, 1974; Gagnon *et al.*, 1990). Short-days can be achieved when the daylengths are naturally long by eliminating the light that reaches the plant. This can be accomplished by manually or electrically pulling blackcloth over individual benches or entire greenhouses. Under natural SD, it is possible to lengthen the daylength by supplying additional light. There are four basic methods to extend photoperiod:

1) day extension lighting (DE) -- extending the natural day through the evening

2) night interruption lighting (NI) -- interrupting the night

3) pre-dawn lighting (PD) -- extending the natural day before dawn

4) continuous lighting (24-h) -- lighting 24 hours a day.

The photoperiod can be further manipulated by varying the duration of the artificial lighting. In early experiments, a brief irradiation of red light near the middle of a 12 to 12.5 hour non-inductive dark period was sufficient to induce flowering in the LDP, *Hyoscyamus niger* and *Hordeum vulgare* (Downs, 1956). However, with an 8-h photoperiod (e.g. 16-h night), a brief night break was no longer found to be effective in inducing LDP, *Hyoscyamus niger* (Lane *et al.*, 1965). Night breaks of several hours were found to be effective while increased extensions of the photoperiod were still more effective. The results suggest that most LDP require an extended period of light when using night interruption lighting for maximum flower induction.

The effectiveness of the different LD delivery methods for floral induction varies between LD genera. Long-days were traditionally delivered by a 4-h night interruption to initiate flowering (Borthwick *et al.*, 1948; Parker *et al.*, 1950). Lane *et al.* (1965) compared an 8-h day extension with an 8-h pre-dawn extension. For all species tested, the 8-h pre-dawn extension was most effective for floral induction. For instance, *Beta vulgaris*, a LDP, flowered in both the PD and the DE, but time to flower was decreased by approximately 7 days when a pre-dawn treatment was utilized. In 1966, Hughes and Cockshull determined that a 4-h night interruption from 2200 hours until 0200 hours was as effective as an 8-h extension to the natural photoperiod. In a later study, all four LD delivery methods were compared using the LDP *Gypsophila paniculata* (Shillo *et al.*, 1982). Again, all light treatments resulted in flowering but time to flower was reduced under 24-h continuous lighting. The 4-h NI and 4-h PD treatments were found to be equal in effectiveness, but both appeared to be superior to the 4-h DE.

There are many different types of artificial lamps of varying wavelengths used to provide supplemental lighting. Four of the most commonly used lights are incandescent (INC), cool white fluorescent (CWF), metal halide (MH), and high pressure sodium (HPS). The spectral emission curves for these lamps are shown in Figure 6. Incandescent lamps are the most common type used in altering photoperiod because they emit relatively high amounts of red and far-red

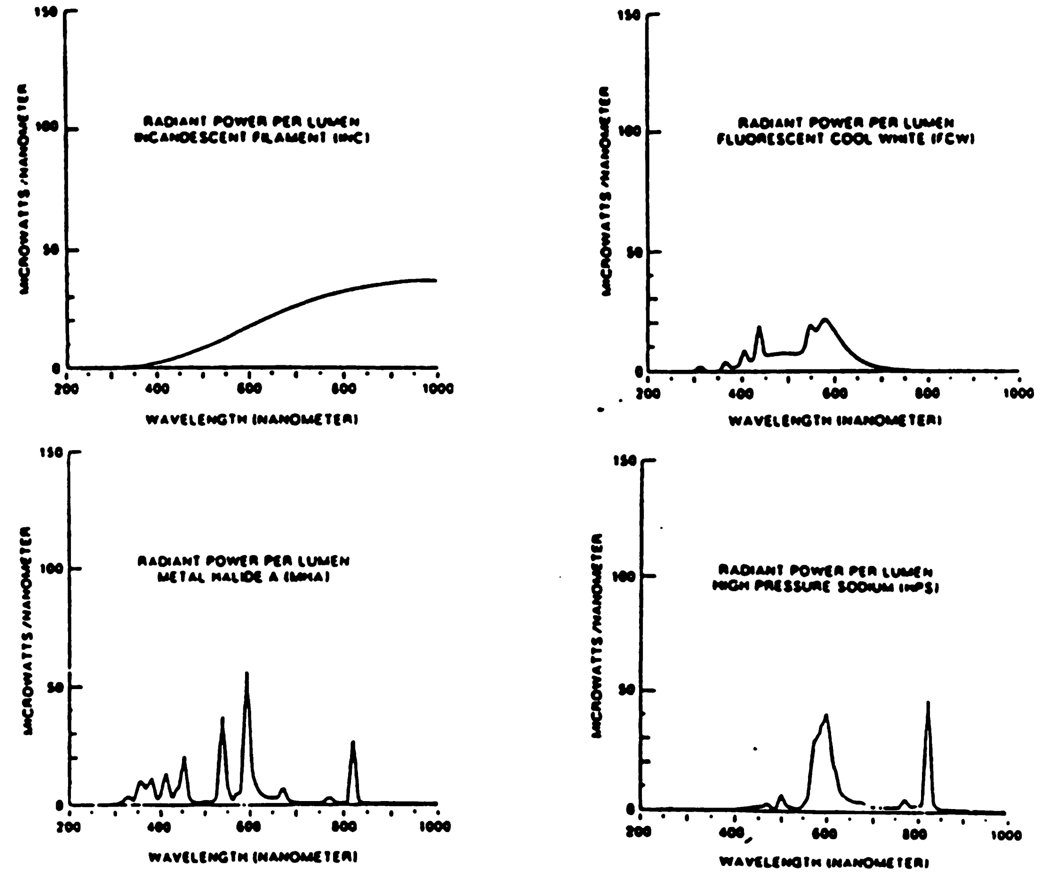


Figure 6. The spectral energy emission curves of incandescent, cool white fluorescent, metal halide, and high pressure sodium lamps. Taken from Campbell et al., 1975.

wavelengths and are an inexpensive source of photoperiodic lighting. Night-breaks and day-extensions with a mixture of red + far-red have been found to be more effective at promoting floral induction (Schneider *et al.*, 1967; Carr-Smith *et al.*, 1989). However, incandescent lights promote stem elongation and may suppress lateral branching. They should not be used for photoperiodic lighting when compact, well-branching plants are desired (Moe *et al.*, 1990). Fluorescent lamps are not commonly used alone due to the fact that they emit wavelengths mostly in the blue, green, and yellow regions and little from the red and far-red regions. Metal halide lamps emit mostly blue and violet light with a small amount of emission in the green and yellow regions. High pressure sodium lamps are most commonly used for photosynthetic lighting and emit primarily yellow and orange light.

Light Quality

LDP can be induced to flower by either extending the photoperiod or interrupting the night with low intensity lighting. Originally, the most effective region of the spectrum for both prevention of floral induction in SDP and the promotion of floral induction in LDP was thought to be between 600 nm and 660 nm (Parker *et al.*, 1945; Borthwick *et al.*, 1948). Later experiments show that the action spectra differed based upon the method of LD delivery.

Red light is generally most effective for brief night interruptions but far-red light has been found to be more effective for day extensions (Lane *et al.*, 1965). However, in the LDP, *Lolium temulentum*, 8-h DE with far-red did not promote floral induction while an 8-h DE with red light had limited effectiveness (Vince, 1965). Vince determined that the addition of far-red light greatly enhanced the effectiveness of DE with only red light. A DE with a mixture of red + far-red was superior to either red or far-red alone.

Further research has shown that a mixture of red + far-red light is also more effective when used as a long night break on flower induction of LDP (Carr-Smith *et al.*, 1989). Schneider *et al.* (1967) found that a 8-h night-break response curve differed substantially from a 15-min night-break response curve (Parker *et al.*, 1950) for the promotion of flowering in the LDP, *Hyoscyamus niger.* The results showed a peak in the response curve at approximately 718 nm for an 8-h night-break. A similar action spectrum for the promotion of flower induction by day-extension was found for the LDP, *Triticum aestivum* (Carr-Smith *et al.*, 1989) (see Figure 7) and the LDP, *Brassica campestris* (Tanada, 1984). Again, the most effective wavelength for floral promotion of LDP using DE was near 716 nm.

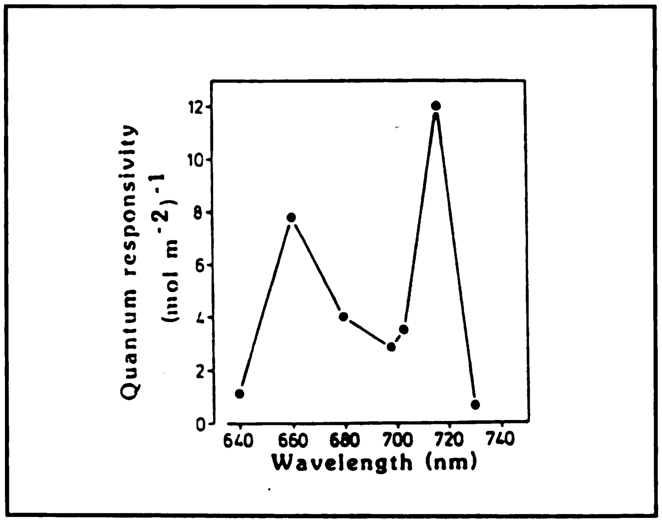


Figure 7. An action spectrum for the promotion of flowering by DE in the LDP, *Triticum aestivum.* Taken from Planta, Carr-Smith et al., 1989.

Sequential light treatments with different wavelengths have also been found to be effective in promoting floral induction. A 15-minute exposure to fluorescent light at the end of an 8-h daylight period significantly reduced the effectiveness of a 4-h incandescent night-break in *Beta vulgaris* and

Hyoscyamus niger (Lane *et al.*, 1965). Similar 15-minute exposures of a far-red light source apparently enhanced the effectiveness of a fluorescent 4-h night-break on *Hyoscyamus niger* or an incandescent 4-h night-break on *Hordeum vulgare*. Lane *et al.* (1965) also found that when an 8-h day extension was split between two different light treatments, fluorescent light during the first four hours resulted in inhibition of flowering regardless of the light treatment during the last four hours. A further experiment involving 8-h day extension showed that a 7-h exposure to FR followed by 1-h of R accelerated flowering as much as an 8-h exposure to R+FR in *Lolium temulentum* (Vince, 1965). Vince also discovered that a 1-h R night break was almost as effective in promoting flowering as long as it was preceded by a 7-h period of darkness.

Phytochrome in LDP

The results of several studies have indicated that long-day plants show a change in sensitivity to red light but not to far-red light (Vince, 1965). Day extensions consisting of a 7-h FR exposure followed by 1-h R exposure promoted flowering significantly more than a 7-h R exposure followed by 1-h FR exposure in *Lolium temulentum* (Vince, 1965). In fact, the 7-h R/1-h FR day extension had as little effect in flower promotion as an 8-h R day extension. Red light was found to have an inhibitory effect when given from 4 pm until midnight, while far-red light promoted flowering at this time. During the latter part of the dark period, midnight until 8 am, red light was found to strongly promote flowering while far-red only slightly enhanced flowering.

These results suggest that there are two different Pfr concentration requirements that must be satisfied for flower induction to occur in LDP. A low concentration of Pfr is necessary during the early part of the 8-h period for flowering to occur most rapidly, but a high concentration of Pfr is also necessary at some stage. The low level of Pfr would be achieved by providing either a dark period or by irradiating with a far-red light treatment prior to the red night-break.

Examination of this theory reveals conflicting methodologies in which flowering occurs. The requirement of a high concentration of Pfr promotes flowering but an exposure to far-red light, which reduces the proportion of Pfr, also promotes flowering in many situations. Downs *et al.* (1982) discovered that plants may respond differently to concentrations of Pr and Pfr depending on their current stage of development. In the LDP, *Hyoscyamus niger*, different action spectra were found during the initiation and development phases. The initiation phase was set in motion by ten LD and required large amounts of Pfr to be present near the middle of long dark periods. Plants were then returned to SD for development. A FR irradiation at the end of each SD was found to accelerate flowering. Therefore, a light treatment which has a mixture of red + far-red would satisfy both stages of floral initiation and development and their respective periods of sensitivity (Downs *et al.*, 1982; Deitzer, 1984).

Another possible theory is that flowering in LDP is due to two photoreceptors, phytochrome and an unknown pigment with far-red, green photoreversible properties (Tanada, 1984). Tanada established that 710 nm was the most effective region whereas the 730 nm region was the least effective in promoting flowering in the LDP, *Brassica campestris* (see Figure 8). Radiation at 550, 660, and 750 nm resulted in little or no flowering. However, the effectiveness of both 710 and 730 nm radiation to induce flowering was completely negated by 550 nm treatments given simultaneously. In contrast, radiation at 660 nm had no inhibitory effect on flower induction brought about by either the 710 or 730 nm radiation treatments.

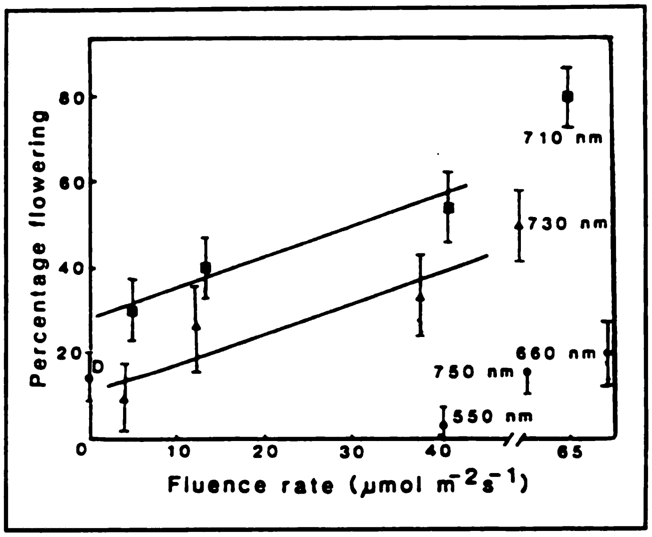


Figure 8. Comparison of regions 710 and 730 nm for effectiveness at flower promotion.
Taken from Tanada, 1984.

Conclusion

Photoperiod has a dramatic effect on growth and development of a wide range of plant species. It is possible to force plants to bloom by studying plant response to photoperiod and using that knowledge to manipulate their environment. The economic benefits that may be reaped from this knowledge are immeasureable. Research suggests that a chemical signal(s) to induce flowering exist. However, further research is still necessary to isolate this elusive compound.

Even though the chemical signal to induce flowering has not been isolated, the application of photoperiodism is already being implemented in the floriculture industry. Because many perennials are LDP, it is possible to bring them into bloom at any time of year through the control of photoperiod.

Understanding the basics of photoperiod and its effect on plant growth and development allows growers to anticipate the needs of the market place and plan production schedules appropriately. In the industry today, offering perennials in bloom has dramatically increased sales and also filled a niche in the floricultural market place.

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SECTION II

THE EFFECT OF LONG-DAY LIGHTING STRATEGIES ON FLOWER INDUCTION OF *ASCLEPIAS TUBEROSA, CAMPANULA CARPATICA* 'BLUE CLIPS', *COREOPSIS GRANDIFLORA* 'EARLY SUNRISE', AND *LAVANDULA ANGUSTIFOLIA* 'HIDCOTE BLUE'

The Effect of Long-day Lighting Strategies on Flower Induction of *Asclepias tuberosa, Campanula carpatica* 'Blue Clips', *Coreopsis grandiflora* 'Early Sunrise', and *Lavandula angustifolia* 'Hidcote Blue'

Cheryl K. Hamaker[1], William H. Carlson[2], Royal D. Heins[2], and Arthur C. Cameron[2]

Department of Horticulture, Michigan State University, East Lansing, MI 48824

Additional index words: photoperiod, long-day plant, LDP, herbaceous perennial, *Campanula*, *Campanula carpatica*, *Coreopsis*, *Coreopsis grandiflora*, Tickseed, Lavender, Butterfly Weed, *Asclepias*

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[1] Graduate Student.

[2] Professor.

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***Abstract*.** To investigate effective lighting strategies for flower induction of long-day (LD) plants, 4 herbaceous perennial species were chilled at 5°C for either 0 or 12 weeks and then forced at 20°C under the following photoperiod treatments: short day, 4-h night interruption (4-h NI), 7-h night interruption (7-h NI), 7-h day extension, 7-h pre-dawn (7-h PD), and 24-h continuous light (24-h). All treatments consisted of a 9-h photoperiod of sunlight supplemented with 50 μmol m^{-2}s^{-1} from HPS lamps. LD lighting treatments were delivered by incandescent lights at approximately 1.8 μmol m^{-2}s^{-1}. All LD lighting treatments induced flowering in obligate LD plants tested. Rate of flowering, height, and bud number at first flower varied among species and LD treatments. Although flowering was accelerated under 24-h and 7-h NI for most species, flowering was delayed under 24-h for *Campanula carpatica* 'Blue Clips'. For unchilled plants of most species, flowering was delayed under 7-h PD as compared to other LD treatments. Chilling decreased time to flower and resulted in more uniform flowering among plants in LD treatments. *Coreopsis verticillata* 'Moonbeam' and *Coreopsis grandiflora* 'Early Sunrise' were shorter at first flower when grown under 4-h NI than 7-h treatments.

Photoperiodic induction of flowering in long-day plants (LDP) has not been as extensively studied as that of short-day plants (SDP). This is due to the relative insensitivity of most LDP to floral promotion by a brief light interruption of a non-inductive long dark period (Deitzer, 1984). Only a few genera of LDP are able to be induced with relatively few night breaks, such as *Hyoscyamus niger* (Downs *et al.*, 1982) and *Lolium temulentum* (Evans, 1960).

In the greenhouse industry, manipulation of the photoperiod is often employed to artificially shorten or lengthen natural daylengths in order to obtain either vegetative or reproductive growth (Laurie, 1931). For example, cuttings of the LDP *Physostegia virginiana* 'Summer Snow' and 'Vivid' were exposed to either short days (SD) or long days (LD) (Beattie *et al.*, 1989). The cuttings that were exposed to SD rooted well. In contrast, the cuttings that were exposed to LD rooted poorly, and approximately 20% of both cultivars had to be discarded due to poor growth habit. Days to flower can be greatly reduced in many long-day plant species when grown under LD rather than SD (Carpenter *et al.*, 1973; Carpenter, 1974; Gagnon *et al.*, 1990).

When the daylengths are naturally long, short-days can be achieved by eliminating the light that reaches the plant. This can be accomplished by pulling blackcloth over individual benches or entire greenhouses. Under natural SD, daylengths have been extended using four basic methods: 1) day extension lighting (DE) -- extending the natural day through the evening, 2) night interruption lighting (NI) -- interrupting the night, 3) pre-dawn lighting (PD) -- extending the natural day before dawn, and 4) continuous lighting (24-h) --

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lighting 24 hours a day. The photoperiod can be further manipulated by varying the duration of the day extensions.

In early experiments, a brief irradiation of red light near the middle of a 12 to 12.5 hour non-inductive dark period was sufficient to induce the LDP, *Hyoscyamus niger* and *Hordeum vulgare* (Downs, 1956). However, with an 8-h photoperiod (e.g. 16-h night), a brief night break was not effective in inducing flowering in the LDP, *Hyoscyamus niger* (Lane *et al.*, 1965). Night breaks of several hours were found to be effective while increased extensions of the photoperiod were still more effective. The results suggest that most LDP require an extended period of light for maximum induction.

The effectiveness of the different LD delivery methods at inducing flower initiation varies between LD genera. Long-days were traditionally delivered by a 4-h night interruption in order to initiate flowering in LDP (Borthwick *et al.*, 1948; Parker *et al.*, 1950). Lane *et al.* (1965) compared an 8-h day extension with an 8-h pre-dawn extension. For all species tested, the most effective method of lengthening the natural day was an 8-h pre-dawn extension. For instance, *Beta vulgaris*, a LDP, flowered in both the PD and the DE, but time to flower was decreased by approximately 7 days when a pre-dawn treatment was utilized. In 1966, Hughes and Cockshull determined that a 4-h night interruption from 2200 hours until 0200 hours was as effective as providing an 8-h extension to the natural photoperiod. In a later study, all four LD delivery methods were compared using the LDP *Gypsophila paniculata* (Shillo *et al.*, 1982). All light treatments resulted in flowering, but time to flower was affected by the timing of the LD delivery. The quickest time to flower occurred under 24-h continuous lighting. The 4-h NI and 4-h PD treatments were found to be equal in effectiveness, and both were superior to the 4-h DE.

Traditionally, LD have been delivered using a 4-h NI in order to initiate flowering in LDP. Preliminary observations suggested that this method of light delivery was not completely effective for flower induction in all species. Because the results of many comparisons of LD-lighting treatments in the literature are inconsistent, further experimentation was needed in order to draw firm conclusions on lighting strategies for LDP. In this study, experiments were conducted to determine and compare the effectiveness of five LD-lighting strategies on flower induction of several LDP.

Materials and Methods

Plant Culture. Seedlings of *Asclepias tuberosa*, *Campanula carpatica* Jacq. ‘Blue Clips’, *Coreopsis grandiflora* Hogg ex Sweet. ‘Early Sunrise’, and *Lavandula angustifolia* ‘Hidcote Blue’ were acquired from a commercial plug producer approximately four weeks after sowing. Seedlings were transplanted into 10-cm pots (470 ml) using MetroMix 510, a commercial soilless media that contains composted pine bark, horticultural vermiculite, Canadian sphagnum peat moss, processed bark ash, and washed sand (Scotts-Sierra Horticultural Products Company, Marysville, Ohio). Plants were top-watered as necessary with approximately 100 ppm N from a 20N-4.4P-16.6K all-purpose water-soluble fertilizer (20-10-20), Peter’s professional Peat-lite special (Grace-Sierra Horticultural Products Company, Milpitas, CA).

Prior to the start of each experiment, *C. carpatica* ‘Blue Clips’, *C. grandiflora* ‘Early Sunrise’, and *L. angustifolia* ‘Hidcote Blue’ were maintained for 9 weeks under a 9-hr photoperiod (SD) which was provided by pulling blackcloth from 1700 to 0800 daily. When the ambient photosynthetic photon flux (PPF) in the greenhouse dropped below 400 μmol $m^{-2}s^{-1}$, computer-controlled, high pressure sodium lights turned on during the 9-h photoperiod to provide supplemental lighting of approximately 50 μmol $m^{-2}s^{-1}$ PPF at plant level. *Asclepias tuberosa* was immediately put under the 5 LD-lighting treatments because seedlings went dormant when exposed to SD conditions.

Cold and Light Treatments. Campanula carpatica ‘Blue Clips’, *C. grandiflora* ‘Early Sunrise’, and *L. angustifolia* ‘Hidcote Blue’ received 0 and 12 v

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weeks of cold in a 5°C cooler, lighted for nine hours, from 0800 to 1700, with a mixture of cool white fluorescent (VHOF96T12; Philips, Bloomfield, N.J.) and incandescent lamps at approximately 10 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$. While in the cooler, plugs were watered with well water (340 mg calcium bicarbonate per liter) acidified (93% H_2SO_4) to a titratable alkalinity of 100 mg calcium bicarbonate per liter. *Asclepias tuberosa* was not chilled.

Plants were forced at 20°C under 9-h SD or one of five LD-lighting treatments for 12 weeks. The five LD-lighting methods consisted of 1) 7-h day extension (7-h DE), 2) 4-h night interruption (4-h NI), 3) 7-h night interruption (7-h NI), 4) 7-h pre-dawn extension (7-h PD), and 5) 24-h continuous light (24-h). All treatments received 9-h natural daylengths before blackcloth was pulled. LD treatments were delivered by incandescent lamps at ≈ 1.8 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$.

The experiment was replicated twice in time. Starting dates for *C. carpatica* and *C. grandiflora* were 16 September, 1994 and 15 December, 1994. Starting date for *L. angustifolia* was 15 December, 1994. Starting dates for *A. tuberosa* were 16 October, 1994 and 16 January, 1995.

Date of first visible bud (when inflorescence was detectable to the naked eye) and date of anthesis were recorded for each plant, and days to visible bud and flowering were calculated. At the time of first flower, total plant height, number of visible infloresences or flower buds, and number of nodes on the main stem were determined.

Temperature control. Air temperatures on each bench were monitored with two 36-gauge thermocouples connected to a CR10 datalogger (Campbell

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Scientific, Logan, Utah). The datalogger collected temperature data every 15 seconds and recorded the hourly average. Nighttime air temperatures under blackcloth on solid aluminum benches have been known to drop as many as 3.5°C below greenhouse air temperatures due to radiant heat loss to the greenhouse glazing material (Heins and Faust, 1994). To maintain uniform temperature conditions, the datalogger controlled a 1500 W electric heater under each bench, which provided supplemental heat as needed throughout the night. Actual average daily air temperature throughout the course of both experiments was 20.6°C. The maximum difference in average daily air temperature between any two benches within each experiment was 0.5°C and 0.4°C for experiment I and II, respectively.

Data analysis. Analysis of variance was used to relate weeks of cold and LD-delivery light treatments to time to flower, number of inflorescences and nodes present at flowering and final plant height. Duncan's Multiple Range Test was used to define significant differences between lighting treatments.

Results

Asclepias tuberosa. *Asclepias tuberosa* was an obligate LDP. None of the plants flowered under SD and vegetative growth was limited. Flowering percentage varied from 40% for the 7-h PD treatment to 80% for the 7-h NI and 24-h treatments (Table 1). Time to visible bud and flower for flowering plants were not significantly different (Table 1). The 7-h DE plants were significantly shorter than the 24-h treated plants.

Campanula carpatica. *Campanula carpatica* 'Blue Clips' was an obligate r

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LDP that has no requirement for cold in order to flower. None of the plants flowered under SD. There was 100% flowering under all LD-light treatments. However, noncold-treated plants in the 24-h treatment reached anthesis approximately two weeks later than plants in the other light treatments (Table 2). After cold, plants flowered uniformly among all lighting treatments. The average number of flower buds at first flower was reduced by 36% for noncold-treated plants grown under 7-h PD compared to those grown under 24-h. Plants that received cold were generally taller than plants that received no cold treatment. Plants grown under 24-h continuous lighting were significantly taller compared to other lighting treatments. Plants that did not receive cold were shortest under 7-h PD and 7-h DE. Plants that received cold were shortest under 7-h DE.

Coreopsis grandiflora. *Coreopsis grandiflora* 'Early Sunrise' was an obligate LD plant without cold and a quantitative LD plant with cold. None of the noncold-treated plants flowered under SD. However, plants that received cold flowered under SD, but 30 to 40 days later than plants in the LD treatments (Table 3). There was 100% flowering under all LD-light treatments. Plants given a cold treatment flowered ≈15 days faster in all LD-delivery treatments compared to plants that received 0 weeks of cold (Table 3). Regardless of cold duration, 7-h PD delayed flowering compared to other LD treatments. Final inflorescence number was decreased in plants under 7-h PD and was increased 4-h NI and 7-h DE, regardless of cold treatment. Final plant height was increased after cold for plants grown under all LD-lighting treatments.

Lavandula angustifolia. *Lavandula angustifolia* 'Hidcote Blue' has been classified as an obligate LD plant that requires a cold treatment in order to flower. However, some flowering occurred under all LD-lighting treatments for plants that received no cold treatment; flowering varied from 30 to 90%. No plants that received cold flowered under 7-h PD. After plants received cold, time to flower was significantly decreased for all LD treatments (Table 4). Time to visible bud and flower was consistently decreased for plants grown under 24-h continuous lighting as compared to other LD-lighting treatments, regardless of cold duration. Flowering was hastened by ≈37 days for non cold-treated plants grown under 24-h compared to those grown under 4-h NI. For cold-treated plants, flowering was hastened by ≈21 when grown under 24-h compared to 4-h NI. Final plant height was not significant between LD-lighting treatments, regardless of cold treatment.

Discussion

Under the conditions of this experiment, each LD-lighting strategy effectively induced flowering to some degree. Plant response to the LD-delivery methods varied slightly by species. In general, 7-h PD was less effective than other LD treatments. Generally, 24-h continuous lighting is not normally used horticulturally to force plants due to energy cost and increased height of the final plants. In both *A. tuberosa* and *L. angustifolia*, 7-h PD treatment failed to induce flowering consistently. Before cold treatment, flowering percentage was low for *A. tuberosa* and *L. angustifolia*, and no flowering occurred in *L. angustifolia* after the cold treatment. Flowering was delayed in *C. grandiflora* grown under 7-h PD before and after cold treatment and final inflorescence number was reduced in both *C. carpatica* and *C. grandiflora*.

The cold treatment appeared to interact with the LD treatments by altering plant response. Cold treatments will often shift the critical photoperiod of many LDP, such as *Iris* (Buxton and Mohr, 1969); *Dicentra spectabilis* (Lopes and Weiler, 1977); *Leucanthemum xsuperbum* Bergmans (Shedron, 1980); *Achillea millefolium* 'Rosea', *Echinops* 'Taplow Blue', and *Physostegia virginiana* 'Summer Snow' (Iversen, 1989); and *Coreopsis verticillata, Lavandula angustifolia,* and *Lobelia speciosa* (Engle unpublished data; Runkle, 1996). The cold treatment may have increased the plants' sensitivity to inductive conditions; either reducing or enhancing plant response. Flowering percentage in *L. Angustifolia* grown under 7-h PD was reduced after cold. Flowering was no longer delayed in *C. carpatica* grown under 24-h continuous lighting, and the delay in time to flower for *C. grandiflora* grown under 7-h PD was reduced.

Overall, both NI and DE were superior to PD treatments for three out of four species tested. A 4-h NI was horticulturally similar to both a 7-h DE or 7-h NI. Results of this experiment showed that a 4-h NI was an adequate method for supplying LD in order to induce flowering.

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Table 1. Effect of LD delivery methods on days to visible bud and anthesis, number of inflorescences, and final plant height of Asclepias tuberosa

Table 1. Effect of LD delivery methods on days to visible bud and anthesis, number of inflorescences, and final plant height of *Asclepias tuberosa*.

Cold Duration	LD-delivery Methods	Flowering Percentage	Days			Nodes		Flower Count	Height (cm)
			VB	VB to FLW	FLW	New	Final		
0 weeks	4-h NI	60	44a	26a	70a	30ab	36ab	1ab	41ab
	7-h NI	80	40a	25a	65a	33a	39a	1b	41ab
	7-h DE	60	43a	23a	66a	29ab	36ab	1ab	36b
	7-h PD	40	38a	26a	64a	23b	29b	2a	37ab
	24-h	80	41a	27a	70a	28ab	34ab	1ab	43a

[z] Mean separation within columns of each cold duration by Duncan's multiple range test (P=0.05).

Table 2. Effect of cold and LD delivery methods on days to visible bud and anthesis, number of inflorescences, and final plant height of Campanula carpatica 'Blue Clips'.

Table 2. Effect of cold and LD delivery methods on days to visible bud and anthesis, number of inflorescences, and final plant height of *Campanula carpatica* 'Blue Clips'.

Cold Duration	LD-delivery Methods	Flowering Percentage	Days			Nodes		Flower Count	Height (cm)
			VB	VB to FLW	FLW	New	Final		
0 weeks	4-h NI	100	27b	20a	47b	15b	33a	30ab	19b
	7-h NI	100	28b	20a	48b	15b	31a	33ab	18bc
	7-h DE	100	28b	21a	49b	15b	32a	28bc	16c
	7-h PD	100	28b	19a	47b	13b	26b	23c	14d
	24-h	100	39a	23a	62a	19a	34a	36a	21a
12 weeks	4-h NI	100	24b	18c	42b	8a	23a	37a	19ab
	7-h NI	100	23b	20a	43b	9a	25a	39a	19ab
	7-h DE	100	26a	21a	47a	9a	24a	35a	18b
	7-h PD	100	24b	20ab	44b	8a	23a	32a	20ab
	24-h	100	25bc	18bc	43b	6a	23a	39a	21a

^{z} Mean separation within columns of each cold duration by Duncan's multiple range test (P=0.05).

Table 3. Effect of cold and LD delivery methods on days to visible bud and anthesis, number of inflorescences, and final plant height of *Coreopsis grandiflora* 'Early Sunrise'.

Cold Duration	LD-delivery Methods	Flowering Percentage	Days			Nodes		Flower Count	Height (cm)
			VB	VB to FLW	FLW	New	Final		
0 weeks	SD	-------	-------	-------	-------	-------	-------	-------	-------
	4-h NI	100	30b	21b	51b	16a	36a	11ab	36c
	7-h NI	100	30b	24a	54b	14b	36a	8b	45b
	7-h DE	100	30b	23ab	53b	15ab	36a	12a	43b
	7-h PD	100	34a	25a	59a	17a	36a	9b	46ab
	24-h	100	29b	23ab	52b	10c	36a	9b	51a
12 weeks	SD	100	41a	31a	72a	20a	38a	3c	17c
	4-h NI	100	18bc	19c	37cd	15b	31b	12a	53ab
	7-h NI	100	18bc	20c	38c	14b	31b	12a	55a
	7-h DE	100	18bc	19c	38c	18ab	32b	12a	54a
	7-h PD	100	19b	22b	41b	14b	31b	8b	51b
	24-h	100	17c	20c	36d	14b	30b	11a	56a

[z] Mean separation within columns of each cold duration by Duncan's multiple range test ($P=0.05$). Data for 0 week plants grown under SD is not included in Duncan's test.

Table 4. *Effect of cold and LD delivery methods on days to visible bud and anthesis, number of inflorescences, and final plant height of Lavandula angustifolia*

Table 4. Effect of cold and LD delivery methods on days to visible bud and anthesis, number of inflorescences, and final plant height of *Lavandula angustifolia* ‘Hidcote Blue’.

Cold Duration	LD-delivery Methods	Flowering Percentage	Days			Nodes		Flower Count	Height (cm)
			VB	VB to FLW	FLW	New	Final		
0 weeks	4-h NI	40	85a	31a	116a	29a	43ab	1ab	52a
	7-h NI	90	63ab	30a	93ab	21b	33c	1ab	56a
	7-h DE	30	59b	30a	89b	22b	36bc	3a	61a
	7-h PD	30	72ab	30a	102ab	30a	44a	1b	56a
	24-h	90	49b	30a	79b	19b	35c	2ab	64a
12 weeks	4-h NI	40	39a	30a	69a	8a	21a	2a	54a
	7-h NI	70	40a	22a	62ab	6a	19a	2a	44a
	7-h DE	60	33a	29a	62ab	8a	22a	2a	49a
	7-h PD	0	-------	-------	-------	-------	-------	-------	-------
	24-h	100	18a	30a	48b	5a	16a	1a	39a

[z] Mean separation within columns of each cold duration by Duncan’s multiple range test (P=0.05).

SECTION III

INFLUENCE OF COLD TREATMENTS, PHOTOPERIOD, AND FORCING TEMPERATURE ON FLOWERING OF *COREOPSIS VERTICILLATA* ‘MOONBEAM’

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Influence of Cold Treatments, Photoperiod, and Forcing Temperature on Flowering of *Coreopsis verticillata* 'Moonbeam'

Cheryl K. Hamaker[1], William H. Carlson[2], Royal D. Heins[2], and Arthur C. Cameron[2]

Department of Horticulture, Michigan State University, East Lansing, MI 48824

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[1] Graduate Student.

[2] Professor.

***Abstract*.** The influence of cold treatments, photoperiod and forcing temperature on flowering of *Coreopsis verticillata* 'Moonbeam' from two sizes of vegetatively propagated plant material was determined. Plants from 72-cell trays were stored in plug trays at 5°C for 0, 5, 10, or 15 weeks and then transplanted into 10-cm diameter pots. Field-grown material was potted into 1.9-liter containers and stored at 5°C for 0, 5, or 10 weeks. After cold treatment, plants were forced under a 9-h natural photoperiod (SD) with or without a 4-h night interruption (NI) (2200-0200 HR) at 20°C. All plants flowered with or without a cold treatment provided that the plants were forced under LD. However, sporadic flowering occurred under SD after a cold treatment of 10 or 15 weeks. Time to flower of plants from 72-cell trays and field-grown divisions decreased approximately two weeks after 15 weeks of storage at 5°C. The number of buds at first flower increased from 207 to 413 on field-grown plants as cold duration increased from 0 to 10 weeks. To determine the relationship between forcing temperature and time to flower, two plant sizes were forced under a 4-h NI photoperiod at temperature settings of 15, 18, 21, 24, or 27°C. Plants generally flowered more quickly at higher temperatures, but flower number and final height were reduced. Days to first visible bud and anthesis were converted to rates, and base temperature (T_b) and thermal time to flowering (degree-days) were calculated. Various pretreatments of photoperiod and cold were tested for their effect on time to flower, bud number, and plant height at flower.

The *Coreopsis* spp. belong to the Asteraceae, or daisy, family and are known for their profuse single and double composite flowers. Many *Coreopsis* species are native to the dry climate of the prairie (Phillips *et al.*, 1995). Perhaps the most drought tolerant of the cultivated *Coreopsis* spp., *Coreopsis verticillata* is indigenous from Maine to Florida and as far west as Arkansas, and is hardy in USDA zones 3-9 (Nau, 1993).

Coreopsis verticillata 'Moonbeam' is a popular herbaceous perennial that grows as a low mound with profuse, single, lemon-yellow blooms. In North America, *Coreopsis* 'Moonbeam' has been traditionally produced outdoors and is not in flower during the early spring when the majority of potted perennials are sold. Producers are interested in understanding the flowering requirements of this species, which will allow for the development of forcing schedules to aid in the production of flowering plants at any time of the year.

The environmental conditions which most frequently promote flowering of plants are photoperiod and temperature (Thomas *et al.*, 1984). Of these factors, temperature affects the developmental rate of plants by directly controlling the timing of flower induction or by strongly interacting with photoperiodic requirements of each species to control flower induction.

Both cool and warm temperatures can have a direct effect on the flowering response. Many plants require a vernalization treatment for subsequent flowering. Vernalization is defined as a positive effect on flowering brought about by exposure to cold (Thomas *et al.*, 1984). Flower initiation does not occur during or even immediately following a cold temperature treatment.

Rather, the cold treatment prepares the plant to respond to the proper inductive environmental stimuli and the floral initials will differentiate once the plant has been exposed to these conditions (Taiz *et al.*, 1991).

While vernalization may have no impact on the flowering process in some plants, it may be absolutely necessary for flowering in others, even plants closely related (Roberts et al., 1987). For example, *Coreopsis grandiflora* 'Early Sunrise' does not require a cold treatment in order to flower (Lyons, 1992), while *Coreopsis grandiflora* 'Sunray' will only flower after receiving a vernalization treatment (Yuan, 1995). For species which require vernalization, the percentage of plants flowering without a cold treatment is insignificant compared to vernalized plants (Roberts *et al.*, 1987). For other plants, vernalization is not necessary for flowering but will greatly accelerate it.

To clarify this somewhat confusing issue, three responses have been observed in relation to vernalization in order to better define a plant's need for a cold treatment. The response categories are as follows: (i) cold obligate, or qualitative requirement, (ii) cold stimulated, or quantitative response to cold, and (iii) cold neutral, not stimulated by cold exposure (Gardner *et al.*, 1990). A plant with an obligate vernalization requirement will not flower unless given a cold treatment, as with the previous example of *Coreopsis grandiflora* 'Sunray'. Plants that have a quantitative response to cold will flower without a vernalization treatment. However, a cold treatment may be beneficial in such ways as hastening the time to flower or increasing the number of flower buds per plant. Plants which fall into the cold neutral response category do not require a cold treatment to flower and no benefits result from exposure to cold. We have been unable to find information in the literature on the cold response of *C. verticillata* 'Moonbeam'.

Regardless of a vernalization or cold requirement, many plants also respond to daylength. No literature has been found on the response of *C. verticillata* 'Moonbeam' to photoperiod. However, many species which flower in midsummer in their natural environment have been found to be long-day plants (LDP). A LDP only flowers, or flowers more rapidly, when daylengths are in excess of a critical duration. *Coreopsis* 'Moonbeam' naturally flowers in late June in northern latitudes, which suggests a LD photoperiod is required for flowering.

Production time for any crop is directly related to greenhouse temperatures during the time of forcing. Forcing temperature, defined as the temperature a plant is exposed to subsequent to the vernalization treatment (Roberts *et al.*, 1987), can impact the flowering response by influencing the rate of flowering. Roberts *et al.* (1987) suggest that the rate of development linearly increases as forcing temperature increases until an optimum temperature is reached. The optimum range of temperature is species-specific and lies in the area between the base temperature, T_b, and the ceiling temperature, T_{ce}. At optimal temperatures, the rate of flowering response decreases linearly with temperature, until the base temperature is reached (Upadhyay *et al.*, 1994). The base temperature is defined as the maximum temperature at or below which the rate of progress towards flowering (1/f) is zero. Temperatures at or above the ceiling value result in progressively delayed flowering until development halts (Roberts *et al.*, 1987).

Rates of development cannot be measured directly. Direct measurements or observations, such as time to flower, encompass a normal growth cycle which includes a lag, rapid growth, and plateau stage. These separate stages proceed at different rates over different time periods and are not linear with temperature. Therefore, if the relation between time taken to flower (f) and temperature is not linear, then the inverse, or rate of progress to flower (1/f), is linear with temperature.

The linear relationship between rate of progress towards flowering and temperature is mainly used to predict the amount of time required to reach flower in an environment of fluctuating temperatures. This concept allows the leaves per day rate to be determined for a particular species at a given temperature. In turn, the number of degree-days that are necessary can be determined in order to develop a forcing schedule for a particular plant.

The authors are unaware of any information in the literature on the flowering requirements of *Coreopsis verticillata* 'Moonbeam' or the flowering response to temperature. The objectives of these experiments were to determine the influence of cold temperatures and photoperiod on flowering, to quantify the effect of forcing temperature on time to flower, and to determine the effect of various light and temperature pretreatments on final plant size and quality.

Materials and Methods

General. Plants were grown in MetroMix 510, a commercial soilless media that contains composted pine bark, horticultural vermiculite, Canadian sphagnum peat moss, processed bark ash, and washed sand (Scotts-Sierra Horticultural Products Company, Marysville, Ohio). Plants were top-watered as necessary with approximately 100 ppm N from a 20N-4.4P-16.6K all-purpose water-soluble fertilizer (20-10-20), Peter's professional Peat-lite special (Grace-Sierra Horticultural Products Company, Milpitas, CA). When the ambient photosynthetic photon flux (PPF) in the greenhouse dropped below 400 μmol $m^{-2}s^{-1}$, computer-controlled, high pressure sodium lights turned on during the 9-h photoperiod to provide supplemental lighting of approximately 50 μmol $m^{-2}s^{-1}$ PPF at plant level.

Cold treatments were delivered in a 5°C cooler, lighted for nine hours, from 0800 to 1700, with a mixture of cool white fluorescent (VHOF96T12; Philips, Bloomfield, N.J.) and incandescent lamps at approximately 10 μmol $m^{-2}s^{-1}$. While in the cooler, plugs were watered with well water (340 mg calcium bicarbonate per liter) acidified (93% H_2SO_4) to a titratable alkalinity of 100 mg calcium bicarbonate per liter.

Experiment 1 -- cold treatments and photoperiod. **(1994)** Two sizes of plant material were tested. Rooted cuttings growing in 72-cell plug trays (58 ml cell volume) were received from a commercial producer on 27 October 1993 when they were approximately 8 weeks old. Field-grown divisions were received bare-root from a commercial producer on 3 November 1993 when they were two seasons old. Upon arrival, all field-grown divisions were immediately potted into 1.9-liter containers. Plants were placed in the greenhouse at 20°C under a 4-h night interruption (NI) for three weeks to allow for rooting and general establishment. Twenty 72-cell plugs were immediately potted when received. The 72-cell plugs were transplanted into 10-cm diameter containers (470 ml). Plants were placed in the greenhouse at 20°C. Ten plants of each size were placed under a 9-h photoperiod (SD). The remaining ten were placed under a long-day (LD) treatment consisting of a 9-h photoperiod with a 4-h night interruption from 2200 to 0200. Long-days were delivered with incandescent lamps at a PPF of approximately 1.8 μmol $m^{-2}s^{-1}$, as measured by a LI-Cor quantum sensor model LI-189 (Li-COR Inc., Lincoln, Nebraska). Black cloth was opened at 0800 and pulled at 1700 on all benches daily.

Plugs remained in plug trays and divisions were stored in their containers during cold treatments. At five-week intervals, twenty plants of each size were removed from the cooler, potted if necessary, and placed in the greenhouse. Half were placed under SD and half under LD. Date of first visible bud (when inflorescence was detectable to the naked eye) and date of first anthesis were recorded for each plant, and days to visible bud and flowering were calculated. At the time of first flower, total plant height, number of visible flowers or buds, and number of nodes on the main stem were determined.

Temperature control. Air temperatures on each bench were monitored with two 36-gauge thermocouples connected to a CR10 datalogger (Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 15 seconds and recorded the hourly average. Nighttime air temperatures under blackcloth on solid aluminum benches have been known to drop as much as 3.5°C below greenhouse air temperatures due to radiant heat loss to the greenhouse glazing material (Heins and Faust, 1994). To maintain uniform temperature conditions, the datalogger controlled a 1500 W electric heater under each bench, which provided supplemental heat as needed throughout the night. Actual daily air temperature throughout the course of the experiment was 20.4°C.

Data analysis. Analysis of variance was used to relate weeks of cold treatment and photoperiod to time to flower, number of visible buds and nodes present at flowering and final plant height.

Experiment 2 -- Forcing temperature. **(1994-95)** Two sizes of plant material were tested. Field-grown divisions were received bare-root from a commercial producer on 3 November 1993 when they were two seasons old. Upon arrival, field-grown divisions were immediately potted into 1.9-liter containers and placed in the greenhouse at 20°C under NI for a period of three weeks to allow plants to become established. Potted field-grown plants were placed into a 5°C cooler for 10 weeks, until 3 February 1994 and then moved into the different treatments. Rooted cuttings, growing in 50-cell plug trays (85 ml cell volume), were received from a commercial producer on 27 October 1994, when they were approximately 8 weeks old. Plugs were stored in a 5°C cooler in plug trays for 15 weeks, until 9 March 1995, potted into 1.1-liter pots, and then moved into the different temperature treatments. Ten plants of each size were placed into each of five greenhouses set to 15°C, 18°C, 21°C, 24°C, and 27°C.

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Plants received natural daylengths with a 4-h NI, from 2200 to 0200, provided by HPS lamps which delivered approximately 90 μmol $m^{-2}s^{-1}$. Date of first visible bud (when flower bud was detectable to the naked eye) and date of first anthesis were recorded for each plant, and days to visible bud and flowering were calculated. At the time of flowering, total plant height, number of visible buds, and number of nodes on the main stem were determined.

Temperature control. Temperatures in each greenhouse were controlled by a Priva environmental computer. Actual air temperatures were recorded every fifteen minutes by a CR-10 datalogger. Actual average daily air temperatures were determined and used in all calculations.

Data analysis. Analysis of variance was used to relate forcing temperatures to time to flower, number of infloresences, final plant height and nodes present at flowering. Base temperature (Tb) and thermal time, or degree days (°Cd), were calculated using equations presented by Roberts and Summerfield (1987). By using the inverse of time to visible bud or anthesis within each treatment, the rate of progress towards visible bud or flowering (1/f) was linearly related to mean temperature, T, by the following:

$$1/f = b_0 + b_1 T \qquad [1]$$

where b_0 and b_1 are constants, and T is in °C. Once b_0 and b_1 were determined, the base temperature, T_{base}, was calculated by the following:

$$T_b = -b_0 / b_1. \qquad [2]$$

The thermal time, or degree days necessary for flowering, was determined by the following:

$$°Cd = 1 / b_1. \quad [3]$$

Experiment 3 -- Forcing strategies. **(1995)** Two sizes of plant material were tested. Rooted cuttings growing in 72-cell plug trays (58-ml cell volume) were received from a commercial producer on 27 October 1994 when they were approximately 8 weeks old. Field-grown divisions were received bare-root from a commercial producer on 7 November 1994 when they were two seasons old. Upon arrival, both 72-cell plugs and field-grown divisions were planted into 2.7-liter containers. Plants were placed in the greenhouse at 20°C. Ten plants of each size were either forced immediately in the greenhouse, exposed to one of four lighting pretreatments prior to cold storage, or placed directly into cold storage. The six strategies were as follows: (1) immediate forcing in the greenhouse under NI at 20°C, 2) three weeks under SD at 20°C prior to cold storage, 3) three weeks of ND at 20°C prior to cold storage, 4) three weeks under a 3-hour day extension (DE) at 20°C prior to cold storage, 5) three weeks under NI at 20°C prior to cold storage, and 6) immediate cold treatment in a cool commercial greenhouse. Both the DE and NI pretreatments were delivered with incandescent lamps at a PPF of approximately 1.8 μmol m^{-2}s^{-1}. Black cloth was opened at 0800 and pulled at 1700 for SD, DE, and NI pretreatments. Plants without a cold treatment were forced under NI at 20°C. Plants that received a lighting pretreatment were stored in a 5°C cooler for approximately 15 weeks. Plants that went immediately into a commercial cold-frame were provided heat to keep plant temperature above 0°C and were exposed to natural photoperiods from November until March.

All plants were removed from coolers or the cool greenhouse on 15 March 1995, and were placed in a greenhouse at 20°C. Pretreated plants were forced under natural photoperiods plus 4-hour NI delivered by high pressure sodium lamps at a PPF of approximately 3-5 μmol $m^{-2}s^{-1}$. Date of first visible bud (when bud was detectable to the naked eye) and date of first anthesis were recorded for each plant, and days to visible bud and flowering were calculated. At the time of first flower, total plant height, number of visible inflorescences, and number of nodes on the main stem were determined.

Temperature control. Temperatures in the greenhouse were controlled by a Priva environmental computer. Actual daily air temperature throughout the course of the experiment was 20.8°C.

Data analysis. Analysis of variance was used to relate forcing strategies to time to flower, number of inflorescences, final plant height and nodes present at flowering. Duncan's Multiple Range Test was used to define significance between pretreatments.

Results

Experiment 1 -- Cold treatments and photoperiod. Plants from both 72-cell trays and field-grown divisions did not require cold in order to flower. In plants from 72-cell trays grown under SD, 30% flowering occurred after 10 weeks at 5°C. In plants from field-grown divisions, 30 and 10% of the plants flowered under SD after 10 and 15 weeks at 5°C, respectively. There was 100%

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In 72-cell plants forced under NI, time to anthesis (FLW) in plants cooled for 15 weeks was decreased 16 days compared to noncooled plants, although time from visible bud (VB) to FLW was similar (Table 1). Days to VB was decreased approximately two weeks for 72-cell plants forced under NI and cooled for 15 weeks compared to noncooled plants. The three plants that received 15 weeks at 5°C and flowered under SD flowered an average of 31 days later than plants grown under NI.

Field-grown divisions cooled for 15 weeks and forced under NI flowered 10 days faster than plants that did not receive cold (Table 1). Days to VB was decreased approximately one week for field-grown divisions forced under NI and cooled for 15 weeks compared to noncooled plants. Plants that flowered under SD after 10 and 15 weeks at 5°C reached FLW 9 and 6 days sooner, respectively, than plants under NI.

Plants from 72-cell trays that flowered under NI had an average of 103 flowers; plants that flowered under SD had an average of 3 inflorescences. The average number of flowers increased 58% for field-grown divisions grown under NI and cooled for 15 weeks compared to noncooled plants. Plants that flowered under SD after 10 and 15 weeks of cold had 9 and 11 inflorescences, respectively.

The final node number in 72-cell plants forced under NI differed only slightly with duration of cold treatment. Final plant height in 72-cell plants was similar for all cold treatments. The final node number for field-grown divisions under NI was similar for all cold treatments. Final plant height in field-grown divisions decreased slightly after 15 weeks of cold.

Experiment 2 -- Forcing temperatures. Actual average daily air temperatures during forcing are presented in Table 2. Field-grown plants flowered more quickly as temperatures increased (Figure 1); time to FLW was decreased approximately 40 days for plants grown at ≈26.8°C compared to those grown at ≈15.5°C. Increasing the forcing temperature from ≈15.5°C to ≈18.3°C decreased time to flower more than increasing temperatures from ≈18.3°C to ≈26.8°C. The difference in time to FLW for field-grown divisions was 32 days between ≈15.5°C and ≈18.3°C, and 10 days between ≈18.3°C and ≈26.8°C.

All plants flowered in all temperature treatments. Time from VB to FLW was delayed in field-grown divisions grown at ≈15.5°C. Visible bud and flowering data for the delayed plants were not included in the calculations for rates of the different developmental stages. Rates of progress to visible bud and flowering were linear between 16.2°C and 27.5°C for 50-cell plants and between 18.3°C and 26.8°C for field-grown divisions (Figure 1). The T_b for forcing to visible bud stage and from forcing to anthesis were -11.2°C and -20°C, respectively, for 50-cell plants (Table 3). Thermal time, or °days required for forcing to visible bud and forcing to flower were 1000 and 2500 days, respectively, for 50-cell plants. Due to the pretreatment of LD given prior to cold treatment, which may have induced plants prematurely, only data from the visible bud to flower stage can be used in calculations for field-grown divisions. The T_b

for visible bud to flower stage was 2°C for field-grown divisions. The required thermal time for visible bud to flower was 400 days for field-grown divisions.

Field-grown divisions grown at 15.5°C had significantly fewer flowers than plants grown at warmer temperatures. The average number of flowers per plant for field-grown divisions increased 50% for plants grown at 26.8°C compared to those grown at 15.5°C (Figure 2). Final plant height of field-grown plants was found to be nonsignificant for all temperature treatments. The average number of flowers per plant for 50-cell plants decreased when grown at higher temperatures (Figure 2). Final plant height of 50-cell plants significantly decreased as temperatures increased from 16.2 to 27.5°C.

Experiment 3 – Forcing strategies. There was no significant difference in time to anthesis among forcing treatments for field-grown divisions (Table 4). In 72-cell plugs, plants flowered slightly faster when overwintered in a cool greenhouse.

Final number of visible buds at anthesis varied between pretreatments. Both 72-cell plants and field-grown divisions pretreated with 3 weeks of SD had fewer bud numbers than plants pretreated with ND. Bud counts were greatest for plants overwintered in a cool greenhouse.

No trends were found between plant sizes for final height. Heights were greatest in 72-cell plants overwintered in a cool greenhouse.

Discussion

Regardless of size of starting material, all plants of *Coreopsis verticillata* 'Moonbeam' flowered when forced under LD. Plants flowered sporadically under

SD following a cold treatment of 10 to 15 weeks. Extended periods of cold have been shown to eliminate any photoperiodic requirement for flowering in *Dicentra spectabilis* (Lopes and Weiler, 1977). Similar responses have been found in a number of LD herbaceous perennials, such as *Iris* (Buxton and Mohr, 1969), *Leucanthemum* x*superbum* Bergmans (Shedron, 1980), *Achillea millefolium* 'Rosea', *Echinops* 'Taplow Blue', and *Physostegia virginiana* 'Summer Snow' (Iversen, 1989).

Prematurely induced starting material could be another explanation. Beattie *et al.* (1989) found that 25% of *Physostegia virginiana* cuttings flowered when placed under SD. Because *Physostegia* is a LDP, this suggested that LD before propagation initiated flowers. *Coreopsis* 'Moonbeam' is also vegetatively propagated. Many growers use a 4-h NI to root *C.* 'Moonbeam' in order to encourage growth. It is possible that the 72-cell plugs had been exposed to LD either in the stock plant environment or rooting environment, which would explain the sporadic flowering under SD conditions.

The concept of thermal time is used to calculate time to flowering and leaf unfolding rates in a number of crops (Karlsson *et al.*, 1988; Faust *et al.*, 1993; Roberts *et al.*, 1987). Plants must experience a specific number of units of degree days (°days) above the base temperature in order to complete a developmental process (Roberts and Summerfield, 1987). Once the base temperature and the amount of thermal time are known for a particular species, time to flower can be predicted at any temperature between T_b and T_{ce}. To calculate time to visible bud or flower at any temperature, the °days required for that developmental stage are divided by the degrees provided above the T_b. For *Coreopsis verticillata* 'Moonbeam', calculated °days to visible bud were 1000; to flower, 2500. For example, time to flower for plants forced at 20°C (T_b=-20°C) is estimated to be 2500 °days/40°C ≈ 62.5 days. In comparison, actual time to flower for plants forced at 20°C in Experiment I was ≈66 days.

Time to flower between the two plant sizes was notably different. Field-grown divisions flowered two to three weeks earlier than plugs. In Experiments I and II, all field-grown divisions were given three weeks of LD to establish. Later experiments have shown that once *C. verticillata* 'Moonbeam' has been induced, flowers will continue to develop after plants have been shifted back to SD. Experimental plants were established under inductive conditions prior to cold treatments and development may have continued during cold storage. In Experiment III, field-grown material did not necessarily flower more rapidly than plug material; rather, flowering of 72-cell plugs may have been delayed. During cold storage, plugs, unlike larger material, will often die back to ground level. Because cold acted as a pinch, development was believed to have been slowed compared to field-grown divisions, which remained green throughout the cold period.

Field-grown divisions typically had five times more inflorescences than 72- or 50-cell material. Plug material is suitable for 10-cm or 1.1-liter containers. However, bulking smaller plugs for 3 weeks in non-inductive photoperiods will increase flower number twofold. Growers will need to weigh the importance of plant appearance against longer production time required for bulking plug material. Multiple plugs or field-grown divisions are suitable to 1.8- or 2.7-liter containers.

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Table 1. Influence of 5C treatments on mean time to flower, number of nodes formed during forcing, number of flower buds present at flowering, and height at flowering of *Coreopsis verticillata* 'Moonbeam'.

Plant	Weeks	Days			Nodes	Flower	Height
Size	at 5C	VB	VB to FLW	FLW	Final	Count	(cm)
72-cell	0	36	32	68	14	91	50
	5	31	33	64	14	132	49
	10	31	35	66	17	84	47
	15	24	28	52	18	106	51
	Average	31	32	63	16	103	49
Significance							
Weeks 5C		***	***	***	**	***	NS
Linear		***	*	***	**	NS	NS
Quadratic		NS	***	**	NS	NS	NS
Field-grown	0	21	29	50	14	207	42
	10	18	28	46	14	413	43
	15	15	25	40	15	358	38
	Average	18	27	45	14	326	41
Significance							
Weeks 5C		NS	*	NS	NS	***	**
Linear		NS	*	NS	NS	***	*
Quadratic		NS	NS	NS	NS	**	*

^{NS}, *, **, *** Not significant or significant at P<0.05, 0.01, and 0.001, respectively.

Table 2. Actual average daily air temperatures during the indicated developmental stages, during forcing of *Coreopsis verticillata* 'Moonbeam'.

Plant size	Force date	Set point temperature (°C)	Forcing to visible bud (°C)	Visible bud to flower (°C)	Forcing to flower (°C)
50-cell	9 Mar 1995	15.0	15.9	16.7	16.2
		18.0	19.0	19.4	19.1
		21.0	20.8	21.1	21.0
		24.0	22.1	23.6	22.8
		27.0	27.4	27.7	27.5
Field-grown	27 Jan 1994	15.0	15.5	15.5	15.5
		18.0	18.4	18.3	18.3
		21.0	21.1	21.3	21.2
		24.0	23.2	24.2	23.7
		27.0	26.7	26.9	26.8

Table 3. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud and flowering in *Coreopsis verticillata* 'Moonbeam'. Intercept and slope were used in Eqs. [2] and [3] to calculate base temperature (T_b) and degree-days, or thermal time (°days). Visible bud and flowering data for field-grown material forced at setpoint 15C were not included in the calculations due to poor growth performance at the cooler temperature.

Plant size	Developmental stage	Intercept (b_0) (1/dev.stage)	Slope (b_1) (1/dev.stage)/°C	T_b (C)	°days	$r^{2\,z}$
50-cell	forcing to visible bud	0.0112 ± 0.0052^y	0.0010 ± 0.0002	-11.2	1000	0.84*
	visible bud to flower	0.0221 ± 0.0044	0.0007 ± 0.0002	-31.6	1429	0.78*
	forcing to flower	0.0080 ± 0.0023	0.0004 ± 0.0001	-20	2500	0.84*
Field-grown	forcing to visible bud	------	------	------	------	------
	visible bud to flower	-0.0050 ± 0.0151	0.0025 ± 0.0007	2.0	400	0.90ns
	forcing to flower	------	------	------	------	------

[z] * Significant at $P<0.05$.

[y] Standard error.

Table 4. Effect of plant size, and light and cold pretreatments on days to visible bud and anthesis, number of inflorescences, and final plant height of *Coreopsis verticillata* 'Moonbeam'.

Plant size	Treatments	Flowering percentage	Days to visible bud	Days visible bud to anthesis	Days to anthesis	Number of buds	Final height
72-cell	no cold	100	44d	34a	78d	92c	46.3b
	3-wks SD -- cold	100	55b	28b	83b	136b	44.7b
	3-wks ND -- cold	100	54bc	28b	82bc	172a	47.6ab
	3-wks 3-h DE -- cold	100	55b	28b	83b	135b	48.4ab
	3-wks 4-h NI -- cold	100	59a	28b	88a	104bc	38.5c
	cool greenhouse	100	52c	28b	80c	189a	51.2a
Field-grown	no cold	100	36b	32a	68a	606a	50.0a
	3-wks SD -- cold	100	40a	24b	64a	451b	38.1b
	3-wks ND -- cold	100	41a	27b	68a	521ab	36.9bc
	3-wks 3-h DE -- cold	100	40a	27b	67a	533ab	34.0c
	3-wks 4-h NI -- cold	100	41a	27b	68a	499b	39.6b
	cool greenhouse	100	41a	28b	68a	611a	36.9bc

^{z} Mean separation within columns of each size by Duncan's multiple range test (P=0.05).

Figure 1. Influence of forcing temperature on time to flower in *Coreopsis verticillata* 'Moonbeam'. Each symbol (◆ or) represents the mean of 10 plants. Lone symbols represent data not included in regression analysis due to poor growth at cooler temperatures. (A), (B), and (C) show days for the indicated developmental stage. For (D), (E), (F), lines represent predicted values for the rate of progress to the indicated developmental stage, based on linear regression. Statistical analysis and calculations are presented in Table 3.

Figure 1

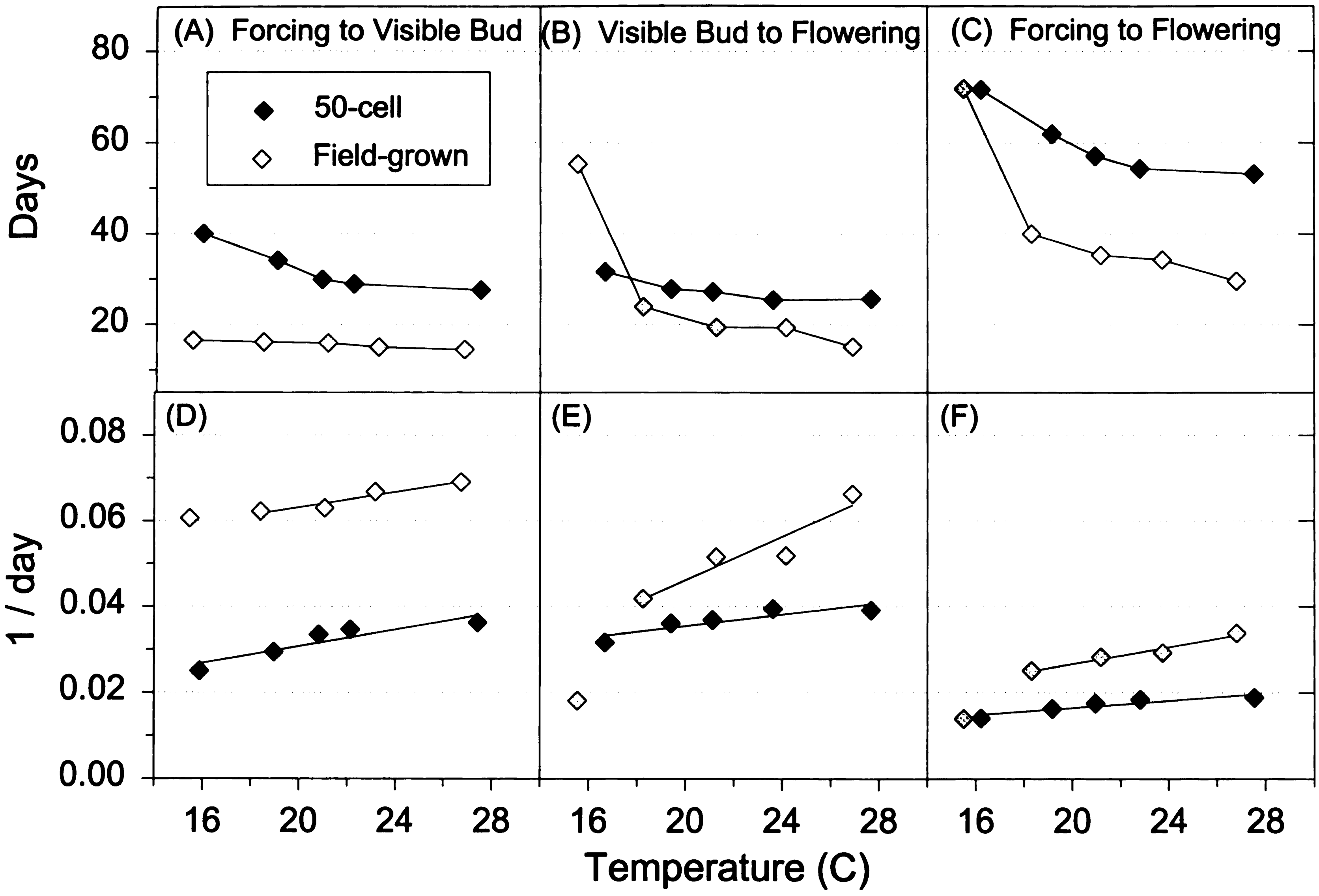
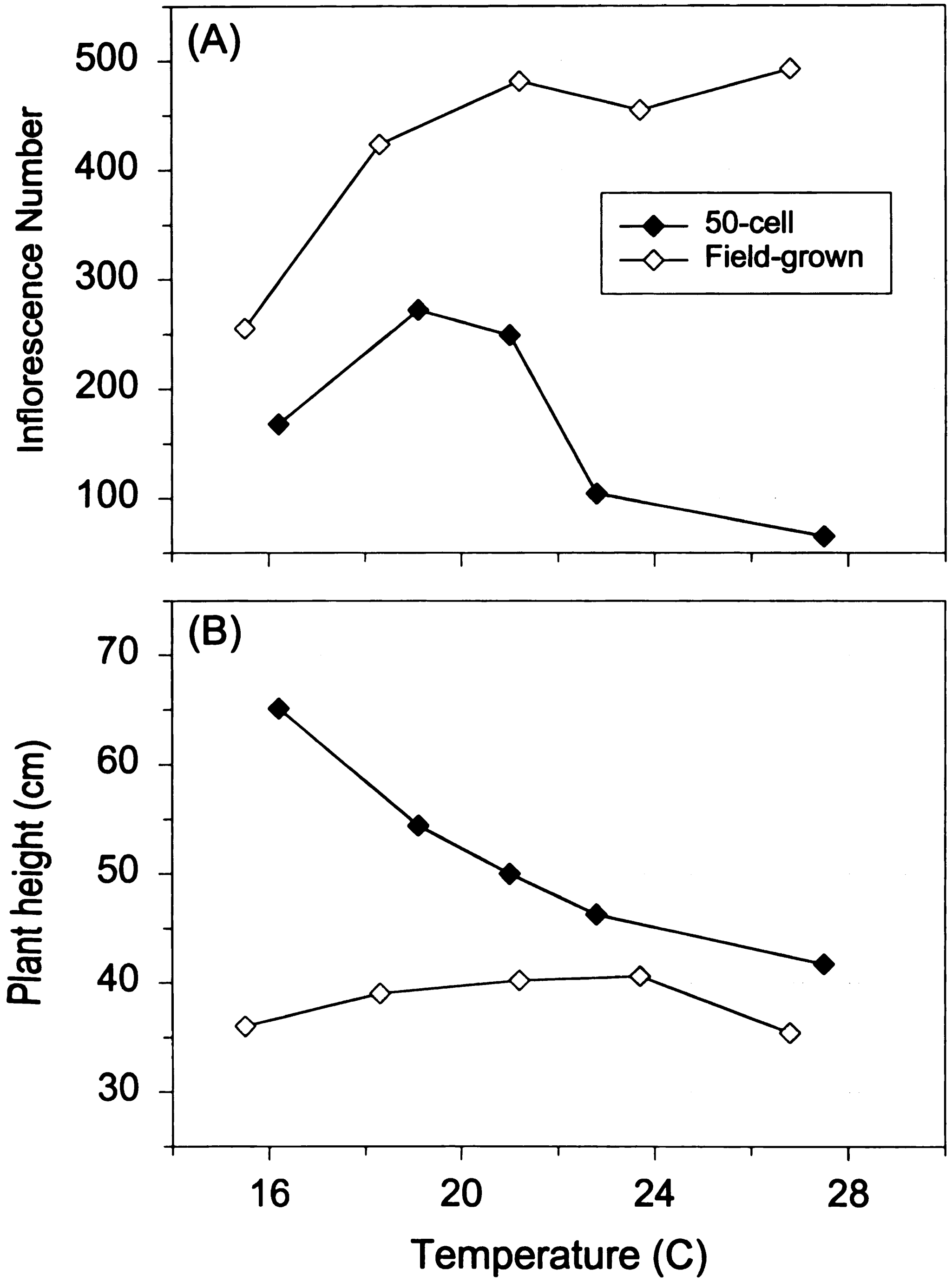

(A) Forcing to Visible Bud
(B) Visible Bud to Flowering
(C) Forcing to Flowering
(D)
(E)
(F)
50-cell
Field-grown
Days
80
60
40
20
1 / day
0.08
0.06
0.04
0.02
0.00
16
20
24
28
Temperature (C)

Figure 2. Influence of forcing temperature on (A) number of flower buds and (B) total plant height in *Coreopsis verticillata* 'Moonbeam'. Each symbol (◆ or [illegible]) represents the average of 10 plants.

Figure 2


(A)
Inflorescence Number
500
400
300
200
100
50-cell
Field-grown
(B)
Plant height (cm)
70
60
50
40
30
16
20
24
28
Temperature (C)

SECTION IV

INFLUENCE OF COLD TREATMENTS, PHOTOPERIOD, AND FORCING TEMPERATURE ON FLOWERING OF *PHYSOSTEGIA VIRGINIANA* 'ALBA' AND 'SUMMER SNOW'

Influence of Cold Treatments, Photoperiod, and Forcing Temperature on Flowering of *Physostegia virginiana* 'Alba' and 'Summer Snow'

Cheryl K. Hamaker[1], William H. Carlson[2], Royal D. Heins[2], and Arthur C. Cameron[2]

Department of Horticulture, Michigan State University, East Lansing, MI 48824

Additional index words: vernalization, herbaceous perennial, long-day plant, LDP, *Physostegia virginiana*, obedient plant, false dragonhead

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[1] Graduate Student.

[2] Professor.

Abstract. The influence of cold treatments, photoperiod and forcing temperature on flowering of *Physostegia virginiana* 'Alba' and 'Summer Snow' was determined. Plants from 128-cell trays were stored in plug trays at 5°C for 0, 5, 10, or 15 weeks and then transplanted into 10-cm diameter pots. Field-grown divisions were potted into 15-cm diameter pots and stored at 5°C for 0, 5, or 10 weeks. After cold treatment, plants were forced under a 9-h natural photoperiod (SD) with or without a 4-h night interruption (NI) (2200-0200 HR) at 20°C. Without a cold treatment, all field-grown divisions flowered while only 50% of the 128-cell plants flowered. All 128-cell plants flowered after 5-, 10-, and 15-week cold treatments under NI. Field-grown divisions did not flower under SD while 128-cell plants flowered sporadically under SD. Time to flower decreased approximately 60 and 10 days after 15 weeks at 5°C for 128-cell and field-grown divisions, respectively, compared to noncooled plants. To determine the relationship between forcing temperature and time to flower, 50-cell plants and field-grown divisions were forced at temperature settings of 15, 18, 21, 24, or 27°C. Plants generally flowered more slowly at higher temperatures, and flower number and plant quality were reduced. Days to visible bud and anthesis were converted to rates, and base temperature (T_b) and thermal time to flowering (degree-days) were calculated. Various pretreatments of photoperiod and cold were tested for their effect on time to flower, bud number, and plant height at flower.

The genus *Physostegia* belongs to the Lamiaceae, or mint family, which is characterized by square stems. *Physostegia virginiana* is indigenous to eastern North America and is hardy to USDA zones 3 through 9 (Bailey, 1976).

Physostegia virginiana, commonly known as obedient plant, is frequently used in the cut flower industry and is named for the tendency of its individual flowers to remain in any position to which they are shifted. *Physostegia virginiana* is a popular herbaceous perennial which grows approximately 4-feet tall and has terminal flower spikes that are 1 to 1½ feet tall. Each side of the four-sided stem is lined with 1-inch bilobed flowers (Phillips *et al.*, 1995). *Physostegia virginiana* 'Alba' is a seed-propagated cultivar with pure white blooms on 3- to 4-foot-tall stems. *Physostegia* 'Summer Snow' is a vegetatively propagated clone with a relatively low stature of only 3 feet and an earlier bloom time in the landscape than other *P. virginiana* cultivars.

In North America, *Physostegia virginiana* has been traditionally produced outdoors and is not in flower during the early spring when the majority of potted perennials are sold. Producers are interested in understanding the flowering requirements of this species, which will lead to the development of forcing schedules to aid in the production of flowering potted plants.

The environmental conditions that most frequently promote flowering of plants are photoperiod and temperature (Thomas *et al.*, 1984). Of these factors, temperature affects the developmental rate of plants by directly controlling the timing of flower induction or by strongly interacting with photoperiodic requirements of each species to control flower induction.

Both cool and warm temperatures can have a direct effect on the flowering response. Many plants require a vernalization treatment for subsequent flowering. Vernalization is defined as a positive effect on flowering brought about by exposure to cold (Thomas *et al.*, 1984). Flower initiation does not occur during or even immediately following a cold temperature treatment. Instead, the cold treatment prepares the plant to respond to the proper inductive environmental stimuli and the floral initials will differentiate once the plant has been exposed to these conditions (Taiz *et al.*, 1991).

While vernalization may have no impact on the flowering process in some plants, it may be absolutely necessary for flowering in others, even plants closely related (Roberts *et al.*, 1987). For example, *Coreopsis grandiflora* 'Early Sunrise' does not require a cold treatment in order to flower (Lyons, 1992), while *Coreopsis grandiflora* 'Sunray' will flower only after receiving a vernalization treatment (Yuan, 1995). For species which require vernalization, the percentage of plants flowering without a cold treatment is insignificant compared to vernalized plants (Roberts et al., 1987). For other plants, vernalization is not necessary for flowering but will greatly accelerate it.

To clarify this somewhat confusing issue, three responses have been observed in relation to vernalization in order to better define a plant's need for a cold treatment. The response categories are as follows: (i) cold obligate, or qualitative requirement, (ii) cold stimulated, or quantitative response to cold, and (iii) cold neutral, not stimulated by cold exposure (Gardner *et al.*, 1990). A plant with an obligate vernalization requirement will not flower unless given a cold treatment, as in the previous example of *Coreopsis grandiflora* 'Sunray'. Plants that have a quantitative response to cold will flower without a vernalization treatment. However, a cold treatment may be beneficial in such ways as hastening the time to flower or increasing the number of flower buds per plant. Plants which fall into the cold neutral response category do not require a cold treatment to flower and no benefits result from exposure to cold. We have been unable to find information in the literature on the cold response of *Physostegia virginiana* 'Alba'.

Regardless of a vernalization or cold requirement, plants also respond to daylength. *Physostegia virginiana* 'Summer Snow' has been characterized as a quantitative LDP (Beattie *et al.*, 1989). Cuttings taken from stock plants flowered fastest under LD. Beattie *et al.* (1989) found that the percentage flowering increased as the number of LD increased during forcing. Other research at MSU has also indicated that *Physostegia virginiana* is a quantitative LD plant (E. Runkle, personal communication).

Production time for any crop is directly related to greenhouse temperatures during the time of forcing. Forcing temperature, defined as the temperature a plant is exposed to subsequent to the vernalization treatment (Roberts *et al.*, 1987), can impact the flowering response by influencing the rate of flowering. Roberts *et al.* (1987) suggest that the rate of development linearly increases as forcing temperature increases until an optimum temperature is reached. The optimum range of temperature is species-specific and lies in the area between the base temperature, T_b, and the ceiling temperature, T_{ce}. At optimal temperatures, the rate of flowering response decreases linearly with temperature, until the base temperature is reached (Upadhyay *et al.*, 1994). The base temperature is defined as the maximum temperature at or below which the rate of progress towards flowering (1/f) is zero. Temperatures at or above the ceiling value result in progressively delayed flowering until development halts (Roberts *et al.*, 1987).

Rates of development cannot be measured directly. Direct measurements or observations, such as time to flower, encompass a normal growth cycle which includes a lag, rapid growth, and plateau stage. These separate stages proceed at different rates over different time periods and are not linear with temperature. Therefore, if the relation between time taken to flower (f) and temperature is not linear, then the inverse, or rate of progress to flower (1/f), is linear with temperature.

The linear relationship between rate of progress towards flowering and temperature is mainly used to predict the amount of time required to reach flower in an environment of fluctuating temperatures. This concept allows the leaves per day rate to be determined for a particular species at a given temperature. In turn, the number of degree-days that are necessary can be determined in order to develop a forcing schedule for a particular plant.

The authors are unaware of any information in the literature on the flowering response to temperature of *Physostegia virginiana* 'Alba' or 'Summer Snow'. The objectives of these experiments were to determine the influence of cold temperatures and photoperiod on flowering, to quantify the effect of forcing temperature on time to flower, and to determine the effect of various light and temperature pretreatments on final plant size and quality.

Materials and Methods

General. Plants were grown in MetroMix 510, a commercial soilless media that contains composted pine bark, horticultural vermiculite, Canadian sphagnum peat moss, processed bark ash, and washed sand (Scotts-Sierra Horticultural Products Company, Marysville, Ohio). Plants were top-watered as necessary with approximately 100 ppm N from a 20N-4.4P-16.6K all-purpose water-soluble fertilizer (20-10-20), Peter's professional Peat-lite special (Grace-Sierra Horticultural Products Company, Milpitas, CA). When the ambient photosynthetic photon flux (PPF) in the greenhouse dropped below 400 μmol $m^{-2}s^{-1}$, computer-controlled, high pressure sodium lights turned on during the 9-h photoperiod to provide supplemental lighting of approximately 50 μmol $m^{-2}s^{-1}$ PPF at plant level.

Cold treatments were delivered in a 5°C cooler, lighted for nine hours, from 0800 to 1700, with a mixture of cool white fluorescent (VHOF96T12; Philips, Bloomfield, N.J.) and incandescent lamps at approximately 10 μmol $m^{-2}s^{-1}$. While in the cooler, plugs were watered with well water (340 mg calcium bicarbonate per liter) acidified (93% H_2SO_4) to a titratable alkalinity of 100 mg calcium bicarbonate per liter.

Experiment 1 -- cold treatments and photoperiod. **(1994)** Two sizes of plant material were tested. Seedlings grown in 128-cell plug trays (10-ml cell volume) were received from a commercial producer on 3 November 1993 and had 5 nodes. Field-grown divisions were received bare-root from a commercial producer on 3 November 1993 when they were two seasons old. Upon arrival, all field-grown divisions were immediately potted into 1.9-liter containers. Plants were placed in the greenhouse at 20°C under a 4-h night interruption (NI) for three weeks to allow for rooting and general establishment. Twenty 128-cell plugs were immediately potted when received. The 128-cell plugs were transplanted into 10-cm containers (470 ml), thinned to a single plant per pot, and placed in the greenhouse at 20°C. Ten plants of each size were placed under a 9-h photoperiod (SD). The remaining ten were placed under a long day (LD) treatment consisting of a 9-h photoperiod with a 4-h night interruption from 2200 to 0200. Long-days were delivered with incandescent lamps at a PPF of approximately 1.8 μmol $m^{-2}s^{-1}$ as measured by a Li-Cor quantum sensor model LI-189 (Li-COR Inc., Lincoln, Nebraska). Black cloth was opened at 0800 and pulled at 1700 on all benches daily.

Plugs remained in plug trays and divisions were stored in their containers during cold treatments. At five-week intervals, twenty plants of each size were removed from the cooler, potted if necessary, and placed in the greenhouse. Half were placed under SD and half under LD. Date of first visible bud (when inflorescence was detectable to the naked eye) and date of first anthesis were recorded for each plant, and days to visible bud and flowering were calculated. At the time of first flower, total plant height, number of visible flowers or buds, and number of nodes on the main stem were determined.

Temperature control. Air temperatures on each bench were monitored with two 36-gauge thermocouples connected to a CR10 datalogger (Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 15 seconds and recorded the hourly average. Nighttime air temperatures under blackcloth on solid aluminum benches have been known to drop as much as 3.5°C below greenhouse air temperatures due to radiant heat loss to the greenhouse glazing material (Heins and Faust, 1994). To maintain uniform temperature conditions, the datalogger controlled a 1500 W electric heater under each bench, which provided supplemental heat as needed throughout the night. Actual daily air temperature throughout the course of the experiment was 20.6°C.

Data analysis. Analysis of variance was used to relate weeks of cold treatment and photoperiod to time to flower, number of visible buds and nodes present at flowering and final plant height.

Experiment 2 -- Forcing temperature. **(1994-95)** Two sizes of plant material were tested. Field-grown divisions were received bare-root from a commercial producer on 3 November 1993 when they were two seasons old. Upon arrival, field-grown divisions were immediately potted into 1.9-liter containers and placed in the greenhouse at 20°C under NI for a period of three weeks to allow plants to become established. Potted field-grown plants were placed into a 5°C cooler for 10 weeks until 3 February 1994 and then moved into the different treatments. Rooted cuttings growing in 50-cell plug trays (85 ml cell volume) were received from a commercial producer on 27 October 1994 when they were approximately 8 weeks old. Plugs were stored in a 5°C cooler in plug trays for 15 weeks until 9 March 1995, potted into 1.1-liter pots, and moved into the different temperature treatments. Ten plants of each size were placed into each of five greenhouses set to 15°C, 18°C, 21°C, 24°C, and 27°C. Plants received natural daylengths with a 4-h NI, from 2200 to 0200, provided by HPS lamps which delivered approximately 90 μmol $m^{-2}s^{-1}$. Date of first visible bud (when inflorescence was detectable to the naked eye) and date of first anthesis were recorded for each plant, and days to visible bud and flowering were calculated. At the time of first flower, total plant height, number of visible buds, and number of nodes on the main stem were determined.

Temperature control. Temperatures in each greenhouse were controlled by a Priva environmental computer. Actual air temperatures were recorded every fifteen minutes by a CR-10 datalogger. Actual average daily air temperatures were determined and used in all calculations.

Data analysis. Analysis of variance was used to relate forcing temperatures to time to flower, number of inflorescences, final plant height and nodes present at flowering. Base temperature (Tb) and thermal time, or degree days (°Cd), were calculated using equations presented by Roberts and Summerfield (1987). By using the inverse of time to visible bud or anthesis within each treatment, the rate of progress towards visible bud or flowering (1/f) can be linearly related to mean temperature, T, by the following:

$$1/f = b_0 + b_1 T \qquad [1]$$

where b_0 and b_1 are constants, and T is in °C. Once b_0 and b_1 were determined, the base temperature, T_{base}, was calculated by the following:

$$T_b = -b_0 / b_1. \qquad [2]$$

The thermal time, or degree days necessary for flowering, was determined by the following:

$$°Cd = 1/b_1. \qquad [3]$$

Experiment 3 -- Forcing strategies. **(1995)** One size of plant material was tested. Field-grown divisions were received bare-root from a commercial producer on 7 November 1994 when they were two seasons old. Upon arrival, field-grown divisions were planted into 2.7-liter containers. Plants were placed in the greenhouse at 20°C. Ten plants were either forced immediately in the greenhouse, exposed to one of four lighting pretreatments prior to cold storage, or placed directly into cold storage. The six strategies were as follows: (1) immediate forcing in the greenhouse under NI at 20°C, 2) three weeks under SD at 20°C prior to cold storage, 3) three weeks of ND at 20°C prior to cold storage, 4) three weeks under a 3-hour day extension (DE) at 20°C prior to cold storage, 5) three weeks under NI at 20°C prior to cold storage, and 6) immediate cold treatment in a cool commercial greenhouse. Both the DE and NI pretreatments were delivered with incandescent lamps at a PPF of approximately 1.8 μmol $m^{-2}s^{-1}$. Black cloth was opened at 0800 and pulled at 1700 for SD, DE, and NI pretreatments. Plants without a cold treatment were forced under NI at 20°C. Plants that received a lighting pretreatment were stored in a 5°C cooler for approximately 15 weeks. Plants that went immediately into a commercial cold-frame were provided heat to keep plant temperature above 0°C and were exposed to natural photoperiods from November until March.

All plants were removed from coolers or the cool greenhouse on 15 March

1995, and were placed in a greenhouse at 20°C. Pretreated plants were forced under natural photoperiods plus 4-hour NI delivered by high pressure sodium lamps at a PPF of approximately 3-5 μmol $m^{-2}s^{-1}$. Date of first visible bud (when bud was detectable to the naked eye) and date of first anthesis were recorded for each plant, and days to visible bud and flowering were calculated. At the time of first flower, total plant height, number of visible inflorescences, and number of nodes on the main stem were determined.

Temperature control. Temperatures in the greenhouse were controlled by a Priva environmental computer. Actual daily air temperature throughout the course of the experiment was 20.9°C.

Data analysis. Analysis of variance was used to relate forcing strategies to time to flower, number of inflorescences, final plant height and nodes present at flowering. Duncan's Multiple Range Test was used to define significance between pretreatments.

Results

Experiment 1 -- Cold treatments and photoperiod. Field-grown divisions did not require cold in order to flower. However, only 50% of the 128-cell plants flowered without a cold treatment. All 128-cell plants flowered after 5-, 10-, and 15-week cold treatments under NI. Field-grown divisions did not flower under SD regardless of cold treatment, while sporadic flowering occurred in 128-cell plants grown under SD.

Time to anthesis (FLW) in 128-cell plants cooled for 15 weeks and forced under NI was decreased approximately 50% compared to uncooled plants, although time from visible bud (VB) to FLW was similar (Table 1). Days to VB from 128-cell plants forced under NI was decreased 59 days for plants cooled for 15 weeks compared to noncooled plants.

Field-grown divisions cooled for 15 weeks and forced under NI flowered 8 days faster than plants which did not receive cold (Table 1). Days to VB from field-grown divisions forced under NI decreased slightly with increasing cold.

Plants from 128-cell trays that flowered under NI had about 4 inflorescences while the number of inflorescences per field-grown division grown under NI was 10 after 15 weeks of cold.

The number of new nodes developed under the flower spike on 128-cell plants forced under NI decreased with increasing cold duration (Table 1). The final plant height in 128-cell plants was similar for all cold treatments. The final node number for field-grown divisions under NI was similar for all cold treatments. Final plant height in field-grown divisions increased slightly after 15 weeks of cold.

Experiment 2 -- Forcing temperatures. Actual average daily air temperatures during forcing are presented in Table 2. Field-grown plants flowered more slowly at higher temperatures (Figure 1); time to FLW increased from 67 days at ≈21.2°C to 94 days at ≈27.0°C. The difference in time to FLW for 50-cell plants decreased 9 days between ≈16.8°C and ≈21.1°C.

Plants from 50-cell plugs did not flower in the higher temperatures (23.1°C to 27.3°C) due to either heat stress or virus infection. Time from forcing to VB was delayed in field-grown divisions grown at ≈27.0°C. Visible bud and flowering data for the missing or delayed plants were not included in the calculations for rates of the different developmental stages. Rates of progress to visible bud and flowering were linear between 16.8°C and 21.1°C for 50-cell plants and between 15.5°C and 24.1°C for field-grown divisions (Figure 1). The T_b for forcing to visible bud stage and from forcing to flower were -14.6°C and -31°C, respectively, for 50-cell plants (Table 3). Thermal time, or °days required for forcing to visible bud and forcing to flower, was 2000 and 5000 days, respectively, for 50-cell plants. Due to the pretreatment of LD given prior to cold treatment, only data from the visible bud to flower stage can be used in calculations for field-grown divisions. The T_b for visible bud to flower stage was -25.6°C for field-grown divisions. The required thermal time for visible bud to flower was 1250 days for field-grown divisions.

Field-grown divisions grown at 27.3°C had significantly fewer inflorescences than plants grown at cooler temperatures. The average number of inflorescences per plant for field-grown divisions doubled for plants grown at 15.5°C compared to 27.0°C (Figure 2). The average number of inflorescences per plant for 50-cell plants decreased slightly at 27.0°C compared to lower growing temperatures. Final plant height of both size plant material decreased as temperature increased (Figure 2).

Experiment 3 -- Forcing strategies.

There was no significant difference in time to flower among pretreatments for field-grown divisions (Table 4). Time to flower was delayed for plants pretreated with 3 weeks of ND compared to other pretreatments (Table 4).

Plants that were forced immediately flowered significantly slower (≈20 days) compared to plants given a pretreatment.

Final number of inflorescences was not significant between pretreatments (Table 4). However, plants that were forced immediately had fewer inflorescences than those given any pretreatment. Differences in final plant height were not significant between plants given pretreatments (Table 4) while plants that were forced immediately were shorter than those given any pretreatment.

Discussion

All field-grown divisions of *Physostegia* 'Summer Snow' flowered with or without a cold treatment provided the plants were forced under LD. However, 5 weeks of cold were necessary in 128-cell plugs for 100% flowering. Field-grown material was harvested in late October. It is possible that divisions already had received ≈5 weeks of cool soil temperatures while out in the field. Long days were required to flower field-grown divisions while sporadic flowering occurred under SD in 128-cell plugs. Preliminary experiments and literature suggest that *Physostegia virginiana* is a quantitative LD plant (E. Runkle, personal communication; Beattie *et al.*, 1989). However, such a conclusion cannot be made decisively from the results of these experiments.

The concept of thermal time has been used to calculate time to flowering and leaf unfolding rates in a number of crops (Karlsson *et al.*, 1988; Faust *et al.*, 1993; Roberts *et al.*, 1987). Plants must experience a specific number of units of degree days (°days) above the base temperature in order to complete a developmental process (Roberts and Summerfield, 1987). Once the base temperature and the amount of thermal time are known for a particular species, time to flower can be predicted at any temperature between T_b and T_{ce}. To calculate time to visible bud or flower at any temperature, the °days required for that developmental stage are divided by the degrees provided above the T_b. For *Physostegia virginiana* 'Summer Snow', calculated °days to visible bud were 2000; to flower, 5000. For example, time to flower for plants forced at 20°C (T_b=-31°C) is estimated to be 5000 °days/51°C ≈ 98 days. In comparison, actual time to flower for plants forced at 20°C in Experiment I was ≈77 days.

Time to flower between the two plant sizes was notably different without cold. Field-grown divisions flowered four to five weeks earlier than plugs. In Experiments I and II, all field-grown divisions were established under inductive conditions prior to cold treatments and may have initiated flowers. Beattie *et al.* (1989) found that 25% of *Physostegia virginiana* cuttings flowered when placed under SD. Because *Physostegia* is a LDP, his results suggested that LD before propagation initiated flowers. Because field-grown divisions were established for three weeks under inductive conditions, it is possible that the plants had been induced and continued development in the cooler. During cold storage, field-grown divisions remained green and healthy.

Field-grown divisions typically had three times more inflorescences than 128 or 50-cell material. Plug material is suitable for 10-cm or 1.1-liter containers. However, bulking smaller plugs for at least 3 weeks in non-inductive photoperiods will increase inflorescence number. Growers will need to weigh the importance of plant appearance against longer production time required for bulking plug material. Multiple plugs or field-grown divisions are suitable to 1.8- or 2.7-liter containers.

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Table 1. Influence of 5C treatments on mean time to flower, number of nodes formed during forcing, number of flower buds present at flowering, and height at flowering of *Physostegia virginiana* 'Alba'.

Plant	Weeks	Days			Nodes		Flower	Height
Size	at 5C	VB	VB to FLW	FLW	New	Final	Count	(cm)
128-cell	0	93	28	121	29	39	1	39
	5	75	26	101	23	32	4	35
	10	50	27	77	20	30	5	42
	15	34	25	62	17	25	4	41
	Average	60	26	86	21	30	4	39
Significance								
Weeks 5C		***	NS	***	**	***	*	NS
Linear		***	NS	***	***	***	**	NS
Quadratic		NS	NS	NS	NS	NS	*	NS
Field-grown	0	53	20	72	-----	24	6	39
	10	47	29	75	-----	26	10	46
	15	41	23	64	-----	25	10	45
	Average	47	24	70	-----	25	8	43
Significance								
Weeks 5C		NS	***	NS	z	NS	*	NS
Linear		*	**	NS	z	NS	**	NS
Quadratic		NS	***	*	z	NS	NS	NS

^{NS}, *, **, *** Not significant or significant at $P<0.05$, 0.01, and 0.001, respectively.
z unavailable due to missing values

Table 2. Actual average daily air temperatures during the indicated developmental stages, during forcing of *Physostegia virginiana* 'Alba' (Field-grown) and 'Summer Snow' (50-cell).

Plant size	Force date	Set point temperature (°C)	Forcing to visible bud (°C)	Visible bud to flower (°C)	Forcing to flower (°C)
50-cell	9 Mar 1995	15.0	16.1	18.3	16.8
		18.0	19.2	19.9	19.5
		21.0	21.0	21.3	21.1
		24.0	22.8	23.5	23.1
		27.0	27.5	27.0	27.3
Field-grown	27 Jan 1994	15.0	15.5	15.6	15.5
		18.0	18.3	18.4	18.3
		21.0	21.2	21.2	21.2
		24.0	23.9	24.4	24.1
		27.0	27.0	27.2	27.0

Table 3. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud and flowering in *Physostegia virginiana* 'Alba' (field-grown) and 'Summer Snow' (50-cell). Intercept and slope were used in Eqs. [2] and [3] to calculate base temperature (T_b) and degree-days, or thermal time (°days). Visible bud and flowering data for 50-cell and field-grown plants forced at setpoints 24C and 27C were not included in the calculations because the plants were damaged by heat stress.

Plant size	Developmental stage	Intercept (b_0) (1/dev.stage)	Slope (b_1) (1/dev.stage)/°C	T_b (C)	°days	r^2 [z]
50-cell	forcing to visible bud	0.0073 ± 0.0003[y]	0.0005 ± 0.0000	-14.6	2000	0.99***
	visible bud to flower	0.0298 ± 0.0003	0.00003 ± 0.0000	-993.3	33333	0.81ns
	forcing to flower	0.0062 ± 0.0000	0.0002 ± 0.0000	-31	5000	0.99*
Field-grown	forcing to visible bud	------	------	------	------	------
	visible bud to flower	0.0205 ± 0.0153	0.0008 ± 0.0008	-25.6	1250	0.48ns
	forcing to flower	------	------	------	------	------

[z] * Significant at $P<0.05$.

[y] Standard error.

Table 4. Effect of light and cold pretreatments on days to visible bud and anthesis, number of inflorescences, and final plant height of *Physostegia virginiana* 'Alba'.

Plant size	Treatments	Flowering percentage	Days to visible bud	Days visible bud to anthesis	Days to anthesis	Number of buds	Final height
Field-grown	no cold	90	82a	23c	105a	6b	37.1b
	3-wks SD -- cold	100	54b	30b	84c	20a	55.2a
	3-wks ND -- cold	90	57b	33a	91b	23a	58.9a
	3-wks 3-h DE -- cold	90	53b	31b	84c	23a	57.3a
	3-wks 4-h NI -- cold	90	54b	33ab	87bc	18a	56.5a
	cool greenhouse	90	54b	32ab	86bc	22a	59.5a

^{z} Mean separation within columns of each size by Duncan's multiple range test (P=0.05).

Figure 1. Influence of forcing temperature on flowering of *Physostegia virginiana* 'Alba' (field-grown) and 'Summer Snow' (50-cell plug). Each symbol (◆ or) represents the mean of 10 plants except for plants from 50-cell trays at 23.1C and ≈27.3C. Lone symbols represent data not included in regression analysis because the plants were damaged by heat stress. (A), (B), and (C) show days for the indicated developmental stage. For (D), (E), and (F), lines represent predicted values for the rate of progress to the indicated developmental stage, based on linear regression. Statistical analysis and calculations are presented in Table 3.

Figure 1

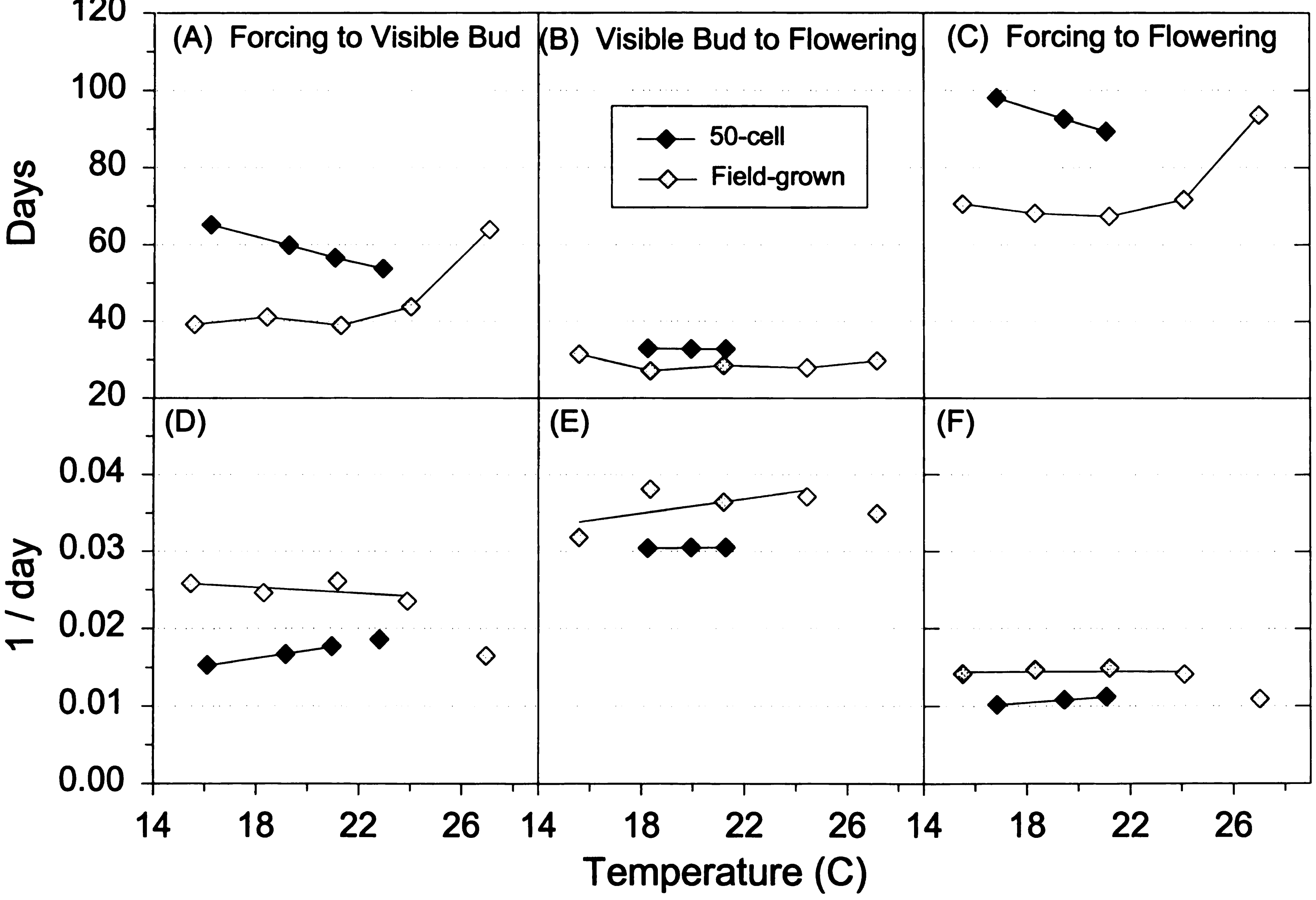
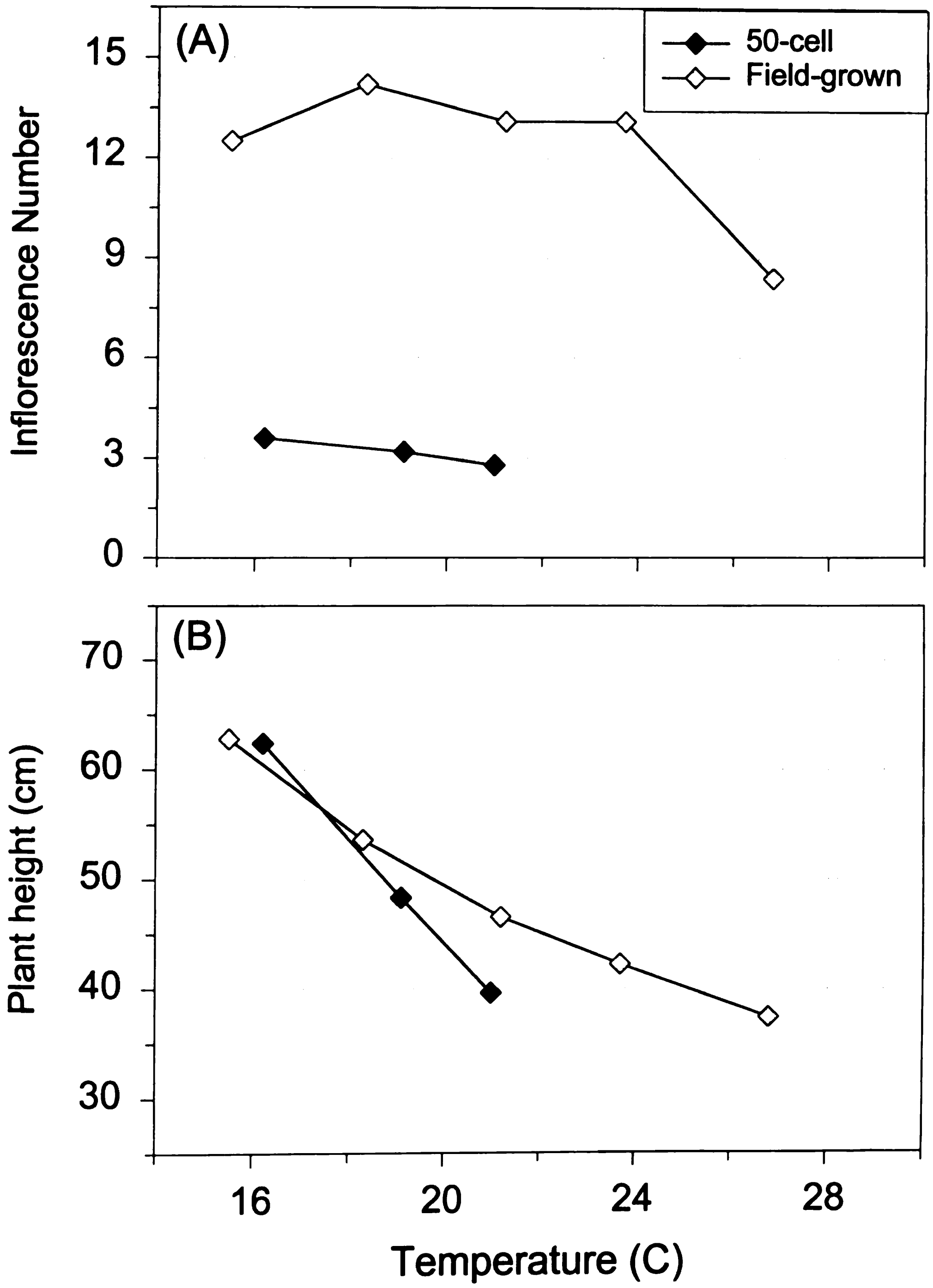

(A) Forcing to Visible Bud
(B) Visible Bud to Flowering
(C) Forcing to Flowering
(D)
(E)
(F)
50-cell
Field-grown
Days
1 / day
120
100
80
60
40
20
0.04
0.03
0.02
0.01
0.00
14
18
22
26
Temperature (C)

Figure 4. Influence of forcing temperature on (A) number of flower buds and (B) total plant height in *Physostegia virginiana* 'Alba' (field-grown) and 'Summer Snow' (50-cell plug). Each symbol (◆ or) represents the average of 10 plants.

Figure 2


(A)
50-cell
Field-grown
Inflorescence Number
0
3
6
9
12
15
(B)
Plant height (cm)
30
40
50
60
70
16
20
24
28
Temperature (C)