This is to certify that the

thesis entitled

The Effects of Photoperiod and Cold Treatment on Flowering of Twenty-five Species of Herbaceous Perennials

presented by

Erik Sanford Runkle

has been accepted towards fulfillment of the requirements for

Master degree in Science

Royal D. Heins

Major professor

Date 10/29/96

THE EFFECTS OF PHOTOPERIOD AND COLD TREATMENT ON FLOWERING OF TWENTY-FIVE SPECIES OF HERBACEOUS PERENNIALS

By

Erik Sanford Runkle

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Horticulture

1996

ABSTRACT

THE EFFECTS OF PHOTOPERIOD AND COLD TREATMENT ON FLOWERING OF TWENTY-FIVE SPECIES OF HERBACEOUS PERENNIALS

By

Erik Sanford Runkle

Twenty-five herbaceous perennial species were treated at 5 °C for 0 or 15 weeks and placed under photoperiods of 10, 12, 13, 14, 16, or 24 hours of continuous light or 9 hours plus a four-hour night interruption. Species were categorized into several response groups based on the effects of cold and photoperiod on flowering. The cold treatment was required for flowering of seven species and improved flowering of 16 species. The perennials were obligate long-day, facultative long-day, or day-neutral plants. The effects of cold and photoperiod on the percentage of flowering, time to flower, node development, flower number, and plant height are presented.

A separate study was conducted to determine the effect of night-interruption duration and cyclic lighting on flowering of six long-day herbaceous perennial plants. Photoperiods were nine-hour natural days with night interruptions for the following durations: 0.5, 1, 2, or 4 hours; 6 min on, 54 min off for 4 hours (10% cyclic lighting); or 6 min on, 24 min off for 4 hours (20% cyclic lighting). Response to night interruptions varied by species, but five of the six species flowered most rapidly and uniformly under four-hour night interruption.

ACKNOWLEDGMENTS

Many thanks to my major professor, Dr. Royal Heins, for his support, encouragement, advice, and friendship throughout my program.

I would also like to express gratitude to Dr. Art Cameron and Dr. William Carlson, whose guidance and camaraderie are greatly appreciated, and to Dr. Jan Zeevaart for his valuable input and analysis. I would like to recognize the many greenhouse growers who supported this work, for their generosity and vision have made this research possible.

Thanks to all of the horticulture graduate students, past and present, who have provided me with valuable advice, support, and especially friendship. A special thanks to Bill Argo, Cheryl Hamaker, Paul Koreman, Bin Liu, Katie Nott, Shi-Ying Wang, Cathy Whitman, and Mark Yelanich. I also owe many thanks to Tom Wallace and his crew of students who provided the daily nurturing of the plants in these experiments, and to Cara Wallace for her masterful editing. Last but not least, I thank my family for their constant love and blessing.

TABLE OF CONTENTS

LIST OF TABLES

SECTION III

LIST OF FIGURES

SECTION III

SECTION I

LITERATURE REVIEW

Introduction

Some plants flower independent of the surrounding environmental conditions, which is known as autonomous flowering. Others flower in response to one or more environmental stimuli. The environmental conditions that induce flowering are species-specific. Plants of the same species but with different genotypes (varieties, subspecies, and cultivars) may have different flowering requirements (Vince-Prue, 1975). Some plants such as African violets, roses, and cyclamen flower only in response to temperature in the presence of adequate radiant energy. Other plants, including many herbaceous perennials, flower only after exposure to temperatures less than 7 °C for a certain period of time. This is known as vernalization. Many plants, including poinsettias and chrysanthemums, flower in response to the duration and timing of light and dark periods in a day or series of days, which is known as photoperiodism (Vince-Prue, 1984). Temperature and photoperiod interact to play significant roles in the flowering process of many plants.

Vernalization

Vernalization is a cold treatment given to an imbibed seed, bulb, or plant that promotes flowering at subsequent higher temperatures (Vince-Prue, 1975). Vernalization leads to flower induction sometime after the cold temperature treatment. In many plants, floral initials are not present immediately after a plant is vernalized; they differentiate only when the plant is exposed to higher

temperatures (Zeevaart, 1978). Other plants form floral initials during the cold temperature treatment. Vernalization does not affect the flowering process of all plants. Some plants flower only when vernalized; others flower faster if vernalized. For example, there are three types of vernalization responses in winter wheat (*Triticum aestivum* L.) cultivars: 1) cold-obligate, or qualitative, 2) cold-stimulated, or quantitative, and 3) cold-neutral, or unresponsive (Gardner and Barnett, 1990).

Vernalization occurs in apices of shoots. A cold treatment is perceived by shoot tips; the leaves of a plant do not affect vernalization. Chilling the roots of penny cress (*Thlaspi arvense* L.) was ineffective, whereas chilling only the shoot tips initiated reproductive development (Metzger, 1988). However, leaf cuttings taken from vernalized penny cress plants exhibited signs of flower development, while cuttings taken from unvernalized plants developed into vegetative rosettes (Metzger, 1988), which suggests the shoot apex is not the only tissue capable of being vernalized, and some new meristems are potential sites for vernalization.

The length and effective temperature range for vernalization varies by species. In general, plants require several weeks of cold to saturate the vernalization response. Forty-six percent of the 'Gloriosa' blazing-star (*Liatris spicata* Willd.) herbaceous perennials that received six weeks of 3 to 5 °C flowered, whereas 90% that received eight weeks of 3 to 5 °C flowered (Waithaka and Wanjao, 1982). This suggests that 'Gloriosa' blazing-star requires at least eight weeks of cold for most plants to become vernalized. The

most effective temperature range for vernalization of most plants is 1 to 7 °C (Lang, 1965), although higher and lower temperatures are effective for some plants. 'Nellie White' Easter lily bulbs (*Lilium longiflorum* Thunb.) vernalized for eight weeks at 5 °C had the highest flower induction index, a relationship that represents the relative flower-induction effectiveness of a cold treatment (Figure 1) (Lange, 1993). As the temperature varied from 5 °C and the length of vernalization decreased, the flower induction index rapidly decreased.

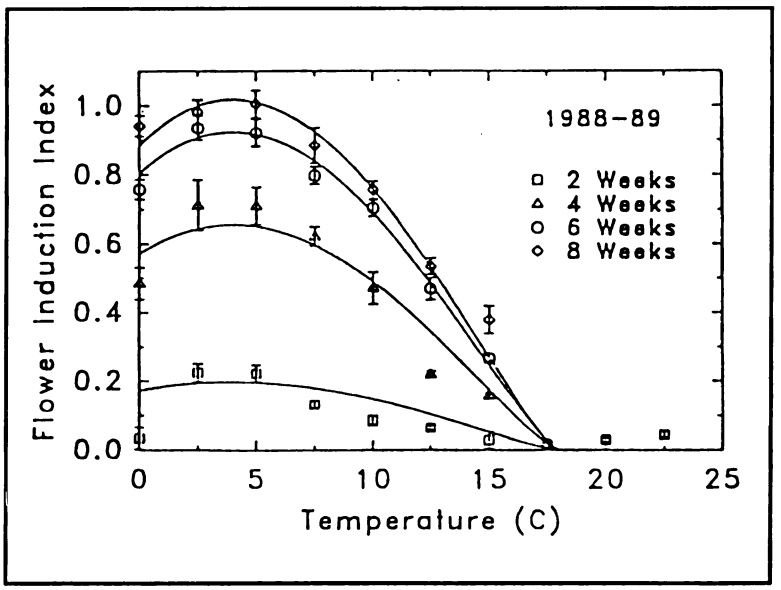


Figure 1. Flower induction index of *Lilium longiflorum* 'Nellie White' as a function of cold temperature and duration (Lange, 1993).

Vernalization is not effective for juvenile plants, and time to maturity is species dependent. Some seeds can be vernalized, but the juvenile phase may last weeks or months. In winter wheat cultivars, seeds became saturated with cold treatment (most were vernalized) after 49 days, while seedlings with two or seven leaves were saturated after 42 or 35 days of vernalization, respectively (Wang et al., 1995). The minimum vernalization duration required for saturation in winter wheat cultivars decreased linearly as plant age increased (Wang et al., 1995). In silver-dollar plant (*Lunaria annua* L.), a biennial, three- and five-week-

old plants did not flower after being vernalized, and were apparently juvenile. Plants nine weeks old and older were completely mature, and all flowered after being vernalized; those seven weeks old were judged intermediate, and half of them flowered (Wellensiek, 1958).

A plant may become devernalized, which means loss of the vernalized condition. The most common way is from a few days' exposure to high temperatures (30 to 35 °C) immediately following a vernalization treatment (Thomas and Vince-Prue, 1984). However, once the cold requirement becomes saturated, the vernalized condition is extremely stable, and devernalization is nearly impossible (Thomas and Vince-Prue, 1984).

Vernalization also can be defined as the biochemical processes that occur during a cold treatment (Napp-Zinn, 1987). The internal processes are controlled by the genetics of a plant and signaled by environmental conditions. Vernalization is triggered by either dominant or recessive alleles (Napp-Zinn, 1987). Garden peas' (*Pisum sativum* L.) dominant alleles cause synthesis of a flower inhibitor, which is not produced when only recessive alleles are present. Vernalization reduces flower inhibitor synthesis by the dominant gene that causes flowering (Napp-Zinn, 1987). Vernalization requirements may be caused by recessive alleles, as are those of winter wheat and mouse-ear cress (*Arabidopsis thaliana* Heynh.) (Napp-Zinn, 1987). In this case, a flower-promoting substance formed in the presence of the dominant allele is absent. Several genes are involved in vernalization, and the identity and function of each

is not well understood. Nearly genetically identical lines of a species may react differently to a cold treatment. After three near-isogenic lines of winter wheat were vernalized for zero to 11 weeks at 4 °C, one line showed a quantitative vernalization response, and two showed an all-or-nothing flowering response (Flood and Halloran, 1984).

Applying gibberellic acid (GA_3) may substitute for either vernalization or inductive photoperiods for some species (see summary by Lang, 1965). Vernalization of penny cress alters GA metabolism in the shoot tip, which may be the mechanism that induces flowering (Hazebroek and Metzger, 1990). The endogenous levels of kaurenoic acid, a GA precursor, in penny cress shoot tips decreased 10-fold and 50-fold two and 10 days, respectively, after plants were returned to 21 °C following four weeks of vernalization at 6 °C (Hazebroek et al., 1993). There was no change in the endogenous levels of kaurenoic acid in the leaves. The activity of an enzyme that dictates changes in the conversion of kaurenoic acid to 7-OH kaurenoic acid rapidly increased in shoots tips following the vernalization treatment; there was no increase in activity in the leaves. Hazebroek et al. (1993) have proposed that the conversion of kaurenoic acid to 7-OH kaurenoic acid is the primary step in GA metabolism regulated by vernalization in penny cress shoot tips.

Recently, it has been postulated that DNA methylation provides a developmental control that prevents flower initiation, and vernalization releases the block to flower initiation by demethylation. The demethylation of a promoter

of a gene responsible for flowering allows its transcription, and the plant is induced to flower. Mouse-ear cress and penny cress plants treated with 5-azacytidine, a DNA demethylating agent, induced unvernalized plants to flower significantly faster than untreated control plants (Burn et al., 1993). Plants insensitive to vernalization did not respond to the demethylating agent. In a separate experiment, 5-azacytidine induced flowering of penny cress cultivars significantly earlier than that of unvernalized plants, although not nearly as rapidly as that of plants vernalized for six weeks at 2 °C (Brock and Davidson, 1994). Gamma ray treatments also induced flowering rapidly compared with that of unvernalized 'Winco' penny cress plants, which suggests gamma rays may act as a demethylating agent similar to 5-Azacytidine (Brock and Davidson, 1994). Under certain conditions, both treatments partially substituted for cold treatment in promoting winter wheat flowering.

Photoperiodism

Plants sexually and asexually reproduce when environmental conditions are favorable for production and distribution of seeds and formation of bulbs, tubers, runners, etc. Many plants therefore have mechanisms that interpret seasonal changes by measurement of photoperiod. Photoperiod is the only completely reliable environmental signal with respect to calendar date at a given latitude. Plants that originate above or below around 30° north and south latitude, respectively, are exposed to pronounced changes in daylength as the

seasons change. Plants that originate closer to the equator are exposed to small changes in daylength as the seasons change, but there are examples of photoperiodic control of flowering even close to the equator. One often can predict accurately if and how photoperiod affects flowering by knowing from where a plant evolved.

Plants have been divided into three main categories on the basis of flowering in response to photoperiod (Figure 2). Day-neutral plants (DNP) flower regardless of the photoperiod to which they are exposed. Short-day plants (SDP) only flower, or flower most rapidly, when exposed to fewer than a certain number of hours of light in a 24-hour cycle. In contrast, long-day plants (LDP) only flower, or flower quicker, when exposed to

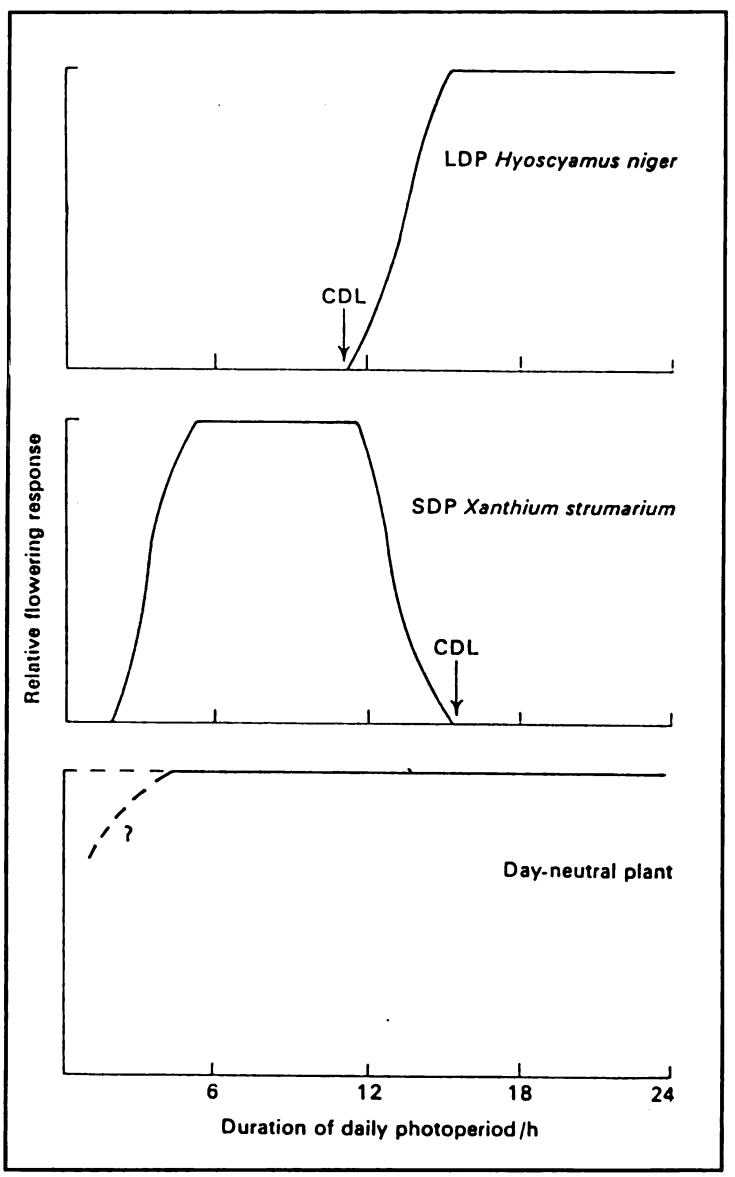


Figure 2. Graphical illustrations of long-day plants (LDP), short-day plants (SDP), and day-neutral plants. CDL = critical daylength. From Vince-Prue, 1975.

more than a certain number of hours of light in each 24-hour cycle. However, it has been shown that the length of the dark period is the critical factor for flower induction: SDP require uninterrupted nights longer than a certain duration, and LDP require a limited darkness duration. The number of photoperiod cycles required for flowering varies tremendously by species, from as little as one to more than 70. SDP and LDP can be subdivided further: plants may have either a qualitative or a quantitative response to photoperiod. A qualitative response, also known as an absolute or obligate response, means the plant requires daylengths that are either shorter or longer than a certain duration to flower. For example, a qualitative LDP must have photoperiods that meet or exceed a particular duration to flower. A quantitative photoperiodic response describes a particular daylength that hastens, but is not essential for, flowering. A quantitative LDP will flower under short days, but will flower quicker under long days.

Day-neutral Plants

Some plants exhibit little or no flowering response to daylength. DNP may flower any time of the year under any daylength. Virtually all DNP, including African violets, cyclamen, and roses have no specific environmental requirements for flower induction, other than adequate light levels and temperatures. 'Sentimental Blue' balloon flower (*Platycodon grandiflorus* A. DC. 'Sentimental Blue') plants grown under 10-hour (SD) or 16-hour (LD)

photoperiods flowered roughly simultaneously (Song et al, 1993). Because flowering was not affected by photoperiod, 'Sentimental Blue' is a DNP. Other DNP are cucumber, annual bluegrass, rice, tomato, and some varieties of corn and tobacco (Salisbury, 1981; Vince-Prue, 1975).

Some DNP are induced to flower by high or low temperatures or by temperature fluctuations. Bulbous plants have mechanisms to survive low and high temperatures, drought, or both. Shoots of bulbs that actively grow above the soil in the spring generally rest in the summer, when temperatures are high. Growth resumes in the fall but often is underground. Many bulbs, including *Tulipa, Freesia, Narcissus,* and *Hyacinthus*, require a warm-cold-warm sequence to complete their life cycle (LeNard and De Hertogh, 1993). Other bulbs, including *Allium, Gladiolus,* and *Lilium*, need a cold-warm-cold temperature sequence to flower and complete their life cycle (LeNard and De Hertogh, 1993). The three general stages of the life cycle of bulbous plants are the initiation of leaves in the bulb, flower formation in the bulb, and elongation, growth, and above ground development. Temperature is generally the most important environmental factor for bulb growth, development, and flowering (LeNard and De Hertogh, 1993).

Vegetative Growth

In most plants, some vegetative growth is required before flowering can take place (Vince-Prue, 1975). Photoperiod affects vegetative growth as well as

reproductive growth. Vertical growth of LDP generally is restricted by short days (SD) and is promoted by long days (LD). Many LDP develop only as leaf rosettes during short photoperiods. LD favor stem growth of gymnosperms and runner development of strawberries, and induce bulb formation in onions. Photoperiod also can influence the number of vegetative and reproductive stems. Dense-flowered loosestrife (*Lysimachia congestiflora* Hemsl.) averaged 27 vegetative stems and one flowering stem under 8-hour photoperiods, 22 vegetative and five flowering stems under 12-hour photoperiods, and one vegetative stem and 21 flowering stems under 16-hour photoperiods (Zhang et al., 1995). Leaf initiation and expansion also were affected by photoperiod. The minimum leaf number required before flowering can occur has been determined for some species. This vegetative phase is defined as "juvenile" or "basic" as discussed in the vernalization section, and is assumed insensitive to photoperiod for flowering. We are most concerned with the phases beyond the juvenile phase.

E.H. Roberts and R.J. Summerfield have distinguished four phases through which all seed plants that flower in response to photoperiod proceed (Roberts et al., 1986). First is a preemergence phase that lasts from germination to emergence through the soil surface. The seedlings are in darkness and therefore are presumably insensitive to photoperiodic stimulation. The second phase is the preinductive phase, also known as the juvenile or basic vegetative phase, that begins at shoot emergence and exposure to light. This phase is a

period of relative, if not complete, insensitivity to photoperiod. The length of the preinductive phase is species-specific and may either not exist if the first leaves are photoperiodically sensitive or last for several years, as is the case with many woody plants. In the quantitative SDP soybean (*Glycine max* Merrill) the duration of the photoperiod-insensitive preinductive phase lasted approximately 18 days (Ellis et al., 1992). Following the preinductive phase is an inductive phase in which the plant is very sensitive to photoperiod, and its duration varies too. The inductive phase persists in less-inductive regimes; for a quantitative SDP, LD increase the length of the inductive phase, and in quantitative LDP, SD increase the length of the inductive phase. Many, but not all, plants proceed through the fourth phase, called the postinductive phase. This phase extends through the flowering process and is insensitive to photoperiod. In studies with rice (*Oryza sativa* L.) the duration of the two photoperiod-insensitive phases decreased as temperature increased. No consistent effects of temperature were apparent for the duration of the photoperiod-sensitive inductive phase (Collinson et al., 1992).

Reproductive Growth

There are also several phases during the flowering process. Any of these stages may be affected by photoperiod, depending on the species. The first stage is flower induction, which is the biochemical change in a plant. The second stage is flower initiation, the first physical evidence of the morphological

change, in which one can discern the floral inflorescence, the buds, or both. A microscope allows this stage to be divided into many substages primarily by redifferentiation of the reproductive meristem and flower bud size (Salisbury and Ross, 1978). The next stage is flower development, in which the inflorescence and flowers develop and expand. The flowers then open, which is the fourth stage. The final stage is anthesis, when pollen is shed by the flower.

In studying the LDP spinach (*Spinacia oleracea* L.), Knott (1934) discovered that photoperiodism is perceived by the leaves of a plant. When a spinach plant had its leaves removed, exposure to LD photoinduction cycles did not cause floral initiation. If the plant was defoliated except for one leaf, the photoinduction cycle caused floral initiation. A leaf's sensitivity to daylength often varies with age. In general, plants become more sensitive to daylength as they grow older, perhaps because young leaves do not export carbohydrates (Vince-Prue, 1975). Other studies show that peak photoperiod sensitivity occurs in the newest leaves and those half-expanded. Photoperiodic sensitivity of the leaves of several cultivars of chrysanthemum gradually decreases with increasing age, until there is no sensitivity (Ochesanu and Barbat, 1965). According to Lang (1965), peak sensitivity in most plants is reached when a leaf has just attained full size.

Daylength

In photoperiodism, a plant perceives day and night duration and, in response to one or both, initiates flowering (Salisbury, 1981). There are substantial changes in the spectral composition of natural light as the day begins and ends, particularly in the red to far-red ratio (R:FR) (Hughes et al., 1984). However, it is most likely the change from night to day and vice versa is signaled by exceeding or falling below a particular value of irradiance or photon fluence rate, not by a change in the spectral quality (Hughes et al., 1984). Plants' sensitivity to light varies tremendously by species, but in general, they perceive a very low illuminance. The threshold light value may be defined as the lowest intensity at which a plant still perceives the light. The SDP Mexican bush sage did not flower when exposed to four-hour night breaks with an intensity of 2.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ or higher in the 400-700 nm wave band, but did flower under a night break intensity of 1.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ or lower; the results suggest the threshold light level for Mexican bush sage is somewhere between 1.3 and 2.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Armitage and Laushman, 1989).

The "natural daylength" commonly has been defined as the length of the day between civil twilights. Civil twilight begins in the morning when the center of the sun is 6° below the horizon and lasts until sunrise, and begins in the evening at sunset and lasts until the center of the sun is 6° below the horizon (Griffiths, 1976). The illuminance at the beginning of civil twilight in the morning and at the end of civil twilight in the evening is around 0.06 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Griffiths, 1976).

The higher the latitude, the longer the civil twilight. Civil twilight lasts 21 to 23 minutes at the equator, depending on the time of year (Griffiths, 1976); 27 to 33 minutes at 40° latitude; and 41 to 108 minutes at 60° latitude (Griffiths, 1976).

In East Lansing, Michigan, which is N 43° latitude, heavily overcast skies significantly reduced the length of daylight above 0.25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Faust and Heins, 1994). Under clear skies in a glass greenhouse in September, light levels exceeded 0.25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for nearly 20 minutes before sunrise through 20 minutes after sunset; under heavily overcast skies, the duration was only 5 minutes before sunrise through 5 minutes after sunset. Outside the greenhouse, light levels exceeded 0.25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ approximately 12 minutes longer before

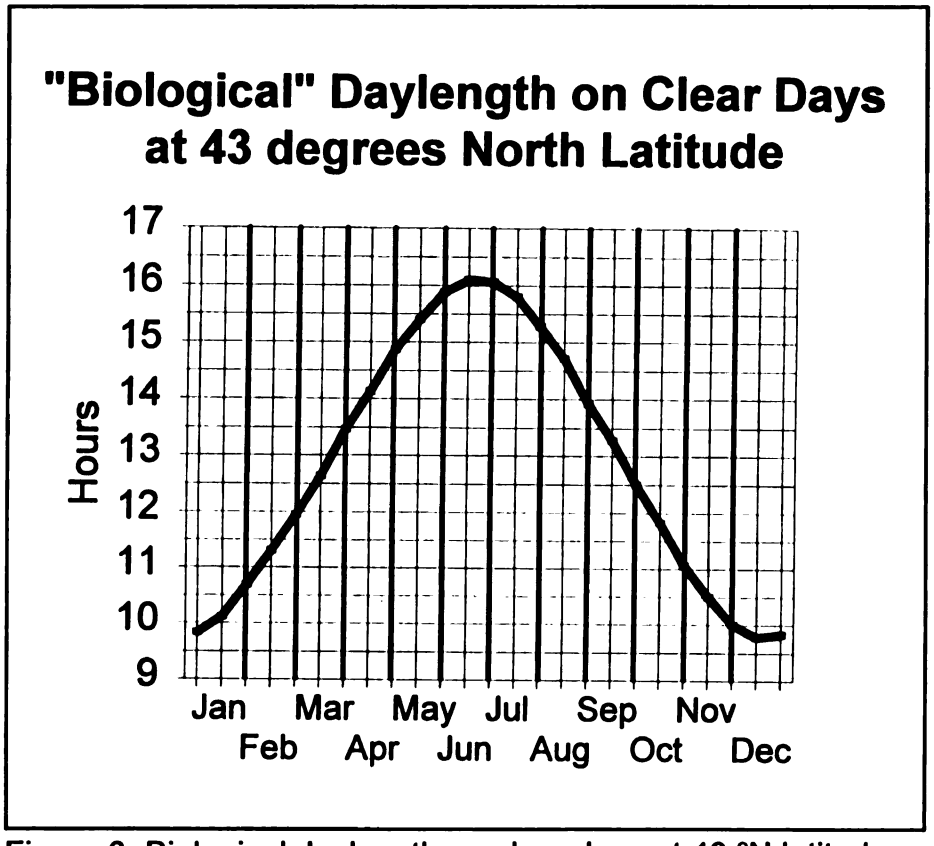


Figure 3. Biological daylength on clear days at 43 °N latitude.

and after sunrise and sunset than inside the greenhouse. Therefore, the natural daylength under clear skies for many plants at 40° latitude is roughly 40 minutes longer than the daylength duration from sunrise to sunset, and cloudy weathercan reduce the duration of the natural daylength. Figure 3 illustrates the biological daylength, the approximate duration that plants perceive light.

Manipulation of Daylength

In the greenhouse industry, the photoperiod often is shortened or lengthened artificially to keep plants vegetative or induce flowering. Under natural LD, SD are created by blocking out light; i.e., by covering the plants with blackcloth. Under natural SD, LD are created by adding light beyond the daylength. There are four ways to extend natural SD into LD: lighting before dusk and into the night (day extension), interrupting the night with a period of light (night interruption or night break), lighting before the end of the night until after dawn (predawn lighting), and lighting continuously (24 hours a day). Traditionally, night interruption has been the method of choice for delivering LD, and many of the studies of LDP, including that of the role of phytochrome, have been with night interruption. Plants respond differently to the timing of the light period at night; some methods of creating LD more effectively induce flowering of some LDP species than others. Continuously lighting baby's-breath, an LDP, caused plants to flower in 91 days; 4-hour predawn and 4-hour night-interruption

lighting caused plants to flower in 125 days; 4-hour day-extension lighting caused plants to flower in 148 days (Shillo and Halevy, 1982).

For most plants, yellow, and especially the red, regions of the spectrum most effectively promote flowering in LDP and prevent flowering in SDP when used to extend natural SD (Vince-Prue, 1975). When plants are irradiated with similar red-light intensities of blue, green, or violet, many hardly perceive the light, and in many instances, the light is equivalent to darkness (Vince-Prue, 1975). For some species, blue light must be 20 to 250 times more intense than red light to be equally effective for promoting or preventing flowering (Vince-Prue, 1975).

There are several types of electrical lamps used to provide supplemental greenhouse light to plants. The four most common lamps are fluorescent, metal halide, high-pressure sodium, and incandescent.

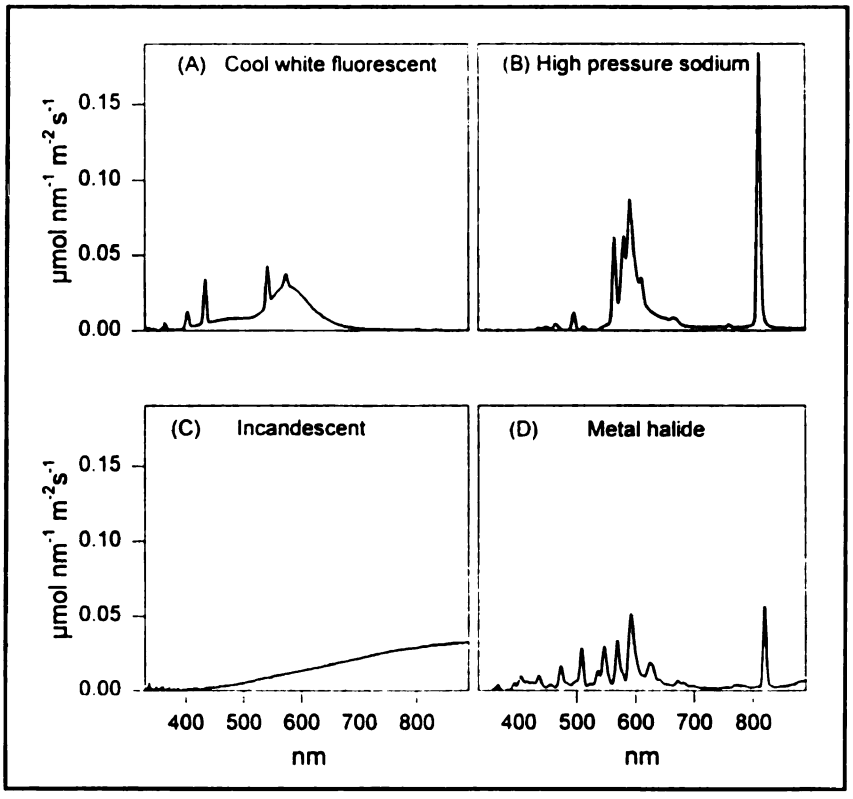


Figure 4. The spectral distribution of four lamp types (Whitman, 1995).

There are many differences among lamp types, including spectral distributions (Figure 4). Cool-white fluorescent lamps emit primarily blue, green, and yellow light. Metal halide lamps emit mostly blue and violet light and some green and yellow light. High-pressure sodium lamps, the most common for photosynthetic lighting in floriculture, emit yellow and orange light. Incandescent lamps emit relatively high amounts of red and far-red light. Because red light most effectively promotes flowering in LDP, the most effective artificial light source for extending the number of hours of natural light should be incandescent lamps. A blend of red and far-red light is desired for decreasing the length of the dark period, so incandescent lamps most effectively promote flower induction (Deitzer, 1984). However, the value of lighting with incandescent lamps must be weighed in relation to their effect on stem elongation (Vince-Prue, 1975).

It may be beneficial to use fluorescent lamps if the plants adequately perceive the light; fluorescent lamps emit very low amounts of far-red light, which may limit overall plant height. However, some plants do not respond to light from various sources. In a glass greenhouse, a 4-hour lighting treatment with cool-white florescent lamps to create LD caused all baby's-breath plants to remain vegetative, regardless of when the treatment was delivered (Shillo and Halevy, 1982). In contrast, LD delivered with incandescent lamps induced flowering. For inducing flowering, a combination of one 40-W cool-white fluorescent lamp and two 60-W incandescent lamps was equal to or better than only incandescent lamps of the same intensity (Shillo and Halevy, 1982). The LDP black-eyed

Susan (*Rudbeckia hirta* var. *pulcherrima* L.) perceived LD when grown under fluorescent illumination at 161 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Podol'nyi and Chetverikov, 1986). However, this high an intensity of fluorescent light easily would contain enough red light to elicit the flowering response. Whitman (1995) found that, even at low intensities (<1.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$), incandescent, cool white fluorescent, metal halide, and high pressure sodium lamps were effective for flower induction of four species of long-day herbaceous perennials: *Campanula carpatica* 'Blue Clips', *Coreopsis grandiflora* 'Early Sunrise', *Coreopsis verticillata* 'Moonbeam', and *Rudbeckia fulgida* 'Goldsturm'.

Critical Photoperiod

The critical photoperiod is defined by Vince-Prue as the daylength at which 50% of the same species flowers (Vince-Prue, 1975). The critical photoperiod marks the transition from vegetative growth to reproductive growth in a population of one genotype. This definition applies to SDP and LDP and does not consider time as a factor. Roberts and Summerfield (1987) define critical photoperiod in SDP as "that photoperiod at or below which the time to flower is minimal and is not affected by variations in daylength; photoperiods longer than [the critical photoperiod] delay flowering." Roberts and Summerfield (1987) propose several definitions for the critical photoperiod of LDP; of those, the following definition is useful: "that photoperiod above which time to flowering is minimal and not affected by further increases in photoperiod, and below which

flowering is delayed." From this definition, an LDP that flowers most rapidly under 24-hour continuous light would have a critical photoperiod of 24 hours. Horticulturally, percent flowering, time to flower, and uniformity are all required components of a definition. Thus, critical photoperiod will be referred to as that photoperiod that elicits a population of the same genotype to flower completely, rapidly, and uniformly. Thus, the critical photoperiod of LDP is that photoperiod which, if met or exceeded, elicits an identical population of plants to flower completely, rapidly, and uniformly. Plants provided daylengths shorter than the critical daylength may still flower, but more slowly, less uniformly, or only partially. The critical photoperiod can differ with different species, or even different cultivars within the same species.

Roberts and Summerfield (1987) also propose two additional flowering photoperiod concepts for SDP and LDP: the base photoperiod and the ceiling photoperiod. The base photoperiod for SDP is that photoperiod at which, if *lengthened*, plants remain permanently vegetative; for LDP, that photoperiod at which, if *shortened*, plants remain permanently vegetative. The base photoperiod concept can apply only to qualitative LDP or SDP, since quantitative SDP or LDP eventually flower under SD and LD. The ceiling photoperiod for SDP is that photoperiod *below* which flowering is hastened; for LDP, *above* which flowering is hastened. Again, the ceiling photoperiod can apply only to qualitative SDP or LDP.

The critical photoperiod of a species may change to some degree with changes in environmental conditions or plant age. As floriculturists, we are more concerned with what daylength keeps a species vegetative when one desires vegetative growth, and what daylength is required for flowering when one wants the plant to flower, perhaps most rapidly. Therefore, knowing the critical photoperiod of a plant is useful so that one can either prevent or initiate flowering, whichever is desired. Cuttings propagated under photoinductive cycles favor reproductive growth, not desired vegetative growth. Cuttings of two cultivars of obedience plant (*Physostegia virginiana* L. 'Summer Snow' and 'Vivid'), both LDP, rooted well under SD but rooted poorly under LD (Beattie et al., 1989). Production time decreased and plant quality increased when stock plants from which the cuttings were taken were grown under SD, and rooted cuttings then were forced to flower under LD (Beattie et al., 1989). For most LDP, exceeding the critical daylength induces a higher percentage of the same species to flower, and faster. For most SDP, reducing the critical daylength below the base photoperiod, yet still long enough for active photosynthesis, increases the percentage of plants that flower and hastens flowering.

Phytochrome

The quality of light describes the spectral energy distribution curve. The wavelengths of electromagnetic radiation (light) that humans can detect is similar to the photosynthetically active radiation wave band in plants: 400-700 nm. Light

quality has a profound influence on plant morphology and, thus, on the flowering process. Plants detect light quality through photoreceptors, particularly the major photoreceptors found in nearly all plants, phytochromes. The amounts of phytochromes in plants vary by species. Phytochrome is involved in many physiological responses, including seed germination, photomorphogenesis, bud dormancy, many enzyme activities, and flowering.

In unirradiated plants, phytochrome is present in a red light-absorbing form, P_R. This form is converted by red light to a far-red light-absorbing form, P_{FR}. The P_{FR} form can be converted to P_R by far-red light, so phytochrome is somewhat photoreversible, but most P_{FR} is metabolized. Phytochrome establishes a photoequilibrium based on the R:FR. Red light typically is defined as photon irradiance between 655 and 665 nm; far-red light, 725 and 735 nm (Smith, 1994). Interestingly, leaves absorb hardly any radiation between 700 and 800 nm; virtually all the incoming far-red radiation is either transmitted through or reflected from the leaf (Smith, 1994). The P_R form of phytochrome absorbs very little in the far-red region of the light spectrum, but the spectra of P_R and P_{FR} overlap significantly in the red region (Figure 5). The

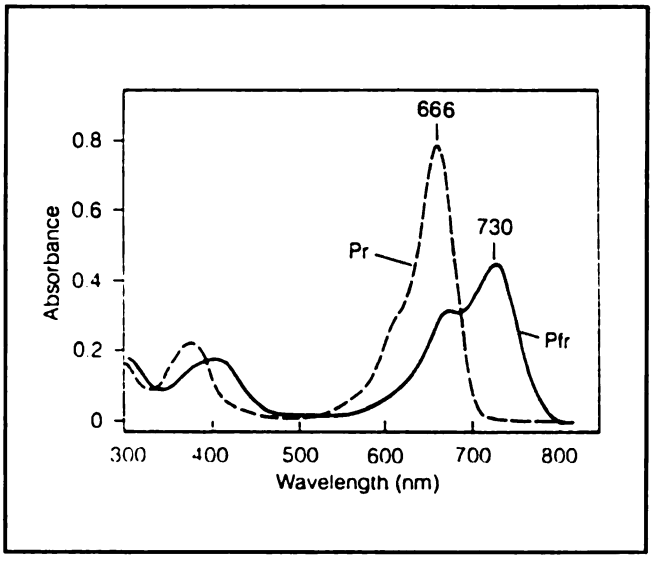


Figure 5. Phytochrome absorption spectrum (Vierstra and Quail, 1983).

proportion of the P_{FR} form, after saturating red light illumination, is only 85% (Taiz and Zeiger, 1991). Therefore, phytochrome never can be 100% in one form or another once a plant has been exposed to light.

Many problems arise when R:FR and estimates of phytochrome photoequilibrium are used to compare plant responses (Rajapakse and Kelly, 1994). First, the range of wavelengths chosen for peak absorbances of P_R and P_{FR} varies from a 5-nm wave band to over a 100-nm wave band. Smith (1982) used a 10-nm width centered around the peak absorbencies of red and far-red of 660 and 730 nm, respectively, while Mortensen and Stromme (1987) used broad widths of 100 nm, in which red was defined as 600-700 nm and far-red as 700-800 nm. Therefore, there is no consistency among researchers when relating R:FR to phytochrome-mediated responses. Second, the R:FR of a light source can vary considerably. For example, etiolated corn coleoptile tips exposed to cool-white fluorescent light, sunlight, and high-pressure sodium light contained 76%, 57%, and 74% P_{FR} at photochemical photoequilibrium, respectively, assuming that red light produces 80% P_{FR} at photoequilibrium (Gardner and Graceffo, 1982). This assumption can lead to erroneous conclusions when responses of plants grown under light sources with little red or far-red light are explained. Third, estimation methods for determining phytochrome equilibrium (P_{FR}:P_{TOTAL}, where $P_{TOTAL} = P_R + P_{FR}$) vary among researchers (Gardner and Graceffo, 1982; Mortensen and Stromme, 1987; Smith, 1982). Finally, poor understanding of the physiological roles and photochemical properties of

phytochromes may result in further erroneous phytochrome equilibrium estimates.

In all known cases, P_{FR} is the physiologically active form of phytochrome, but it is very unstable; most is destroyed when the plant is irradiated with red light. The amount of P_R and P_{FR} can be regulated by synthesis, breakdown, and dark reversion (Taiz and Zeiger, 1991). P_R is synthesized in darkness, and there may be some slow dark reversion from P_{FR} to P_R over a period of several hours. In many SDP, a flash of red light during a long night prevents flowering, which can be restored by a flash of far-red light. In a few LDP, (i.e. *Fuchsia hybrida* 'Lord Byron'), a flash of red light during a long dark period induces flowering, and the effect is reversed by a flash of far-red light (Vince-Prue, 1994). In general, however, most LDP require much longer periods (half an hour to several hours) of light to break up the long night and, thus, induce flowering.

Circumstantial evidence implied that phytochrome existed in more than one form. In garden peas (*Pisum sativum* L.) an initial level of phytochrome was detected in dark-grown seedlings, but once the plants were exposed to light, the phytochrome levels were no longer measurable, even though those plants still had phytochrome responses. The amount of phytochrome in plants varies by species, and those deficient in phytochrome, such as florist's chrysanthemum (*Dendranthema* x *morifolium* Ramat.), still may contain the pigment, but in undetectable levels or different forms (Lane et al., 1963). The physiological

functions of the different phytochromes are being elucidated slowly through the use of mutant plants with reduced phytochrome levels and transgenic plants.

Types of Phytochromes

There are two known groups or types of phytochrome found in plants. Type I phytochrome, also called light-labile phytochrome, is abundant in dark-grown tissue and is present at low levels in light-grown tissue (Parks and Quail, 1993; Smith, 1995). The P_{FR} form of phytochrome I is unstable compared to the P_R form (Smith, 1995). Type II phytochromes, also called light-stable phytochromes, are present at relatively equal levels in dark- and light-grown tissue (Parks and Quail, 1993; Smith, 1995). Type II phytochromes are stable in the P_{FR} form (O'Neill, 1992). The genes that encode these phytochromes have been at least partially identified in several plants, including tomato, oat, cucumber, field mustard, and sorghum, while the most intensive study has been with *Arabidopsis* (Smith, 1995). To date, there have been five different phytochrome genes identified in this quantitative LDP, and, thus, five different phytochromes (Reed et al., 1994). Phytochromes A-E, which are encoded by genes PHY A-E, respectively, have very similar structures (Clack et al., 1994). The amino acid sequences of these five *Arabidopsis* phytochromes have been determined to be from 46 to 80% identical (Clack et al., 1994).

Phytochrome A is a type I phytochrome believed to play an important role in seed germination and early seedling establishment (Smith, 1994) and may be

the primary, if not exclusive, far-red photoreceptor (Parks and Quail, 1993). In addition, this phytochrome may regulate a component of photoperiodic perception in LDP (Smith, 1995). Phy A *Arabidopsis* mutants (plants that contained no or very low levels of phytochrome A) were significantly less responsive to night interruption than were wild-type plants (Reed et al., 1994). Under SD, wild-type and phy A plants flowered at the same time after producing the same number of vegetative leaves. When grown under night interruption to provide artificial long days, wild-type plants flowered six days earlier and grew eight fewer leaves than those grown without night interruption. Phy A mutants flowered only two days earlier and grew four fewer leaves under long days than those grown under short days. Because phy A mutants were less sensitive to daylengths than wild-type plants, PHY A may interact with the circadian rhythm involved in sensing daylengths (Reed et al., 1994). Phytochrome A also appears to play an important role in the flowering of winter wheat (Carr-Smith et al., 1994).

Phytochromes B, C, D, and E are considered type II phytochromes because they are all light-stable (Clack et al., 1994). Of these four phytochromes, most is known about phytochrome B, the most abundant form in green plants. Phytochrome B is believed to be at least partially responsible for detection of R:FR and the R/FR reversible responses (Smith, 1995). Phytochrome B has been implicated in flowering in two separate studies with mutants of two different plant species. However, in the first case (garden pea),

the light-stable phytochrome mutants, known as lv mutants, behaved similarly to phy A mutants of *Arabidopsis* which lack the light-labile phytochrome A. Garden pea, a quantitative LDP, showed a substantial reduction in flowering response to photoperiod in lv mutants compared to wild-type plants (Weller and Reid, 1993). The hastening of flowering under LD compared to SD was not as pronounced with mutant plants as it was with wild-type plants. Wild-type plants flowered six nodes earlier under 24-hour photoperiods than under 8-hour photoperiods; mutants flowered only 1.5 nodes earlier. Perhaps these mutants really lacked the light-labile phytochrome A, not the light-stable B. Alternatively, the phytochrome forms may have different functions in separate species.

In *Arabidopsis*, phy B mutants flowered earlier and with fewer rosette leaves than wild-type plants, regardless of photoperiod (Reed et al., 1993). The apical meristematic cells of mutants underwent vegetative to reproductive differentiation prematurely compared to wild-type plants. The experiment was repeated later and yielded similar results (Reed et al., 1994). This suggests that phytochrome B plays an inhibitory role in flowering, since plants that contained this phytochrome flowered significantly later than mutants.

Phytochromes A and B may interact to control flowering. Reed et al. (1994) believe phytochromes A and B act synergistically or antagonistically to affect flowering. Johnson et al. (1994) suggest phytochrome A action is antagonistic to the action of phytochrome B. However, Parks and Quail (1993)

postulate that phytochromes A and B have reciprocal and independent roles in mediating flowering.

Little is known about phytochromes C, D, or E, and only recently have the PHY D and PHY E sequences been elucidated in *Arabidopsis* (Clack et al., 1994). The physiological roles for genes PHY C, D, and E are not yet known, and mutants deficient in these phytochromes have not yet been identified (Smith, 1994). The proteins encoded by PHY D and E are more similar to phytochrome B than A or C (Clack et al., 1994). Phytochromes D and E are the least abundant forms of phytochrome in *Arabidopsis* (Clack et al., 1994).

The roles of the various phytochromes will be better understood as more phytochrome mutants are discovered and studied. Transgenic plants may be engineered that "turn on or off" certain phytochromes, and their subsequent responses could be monitored. However, other photoreceptors, such as blue-light and UV photoreceptors, may also be involved in the flowering process.

Short-day Plants

Short-day plants flower only, or flower more rapidly, under fewer than a certain number of hours of light in each 24-hour period. However, the length of the darkness is the critical factor for flower induction, not the length of the light period. Thus, these plants more accurately could be labeled long-night plants. Although the duration of night or darkness promotes or inhibits flowering, light must precede the dark period (Vince-Prue, 1975). The intensity and duration of

light required varies by species. In general, the amount of light required for inhibition of flower induction is much less than that needed for promotion of it (Cockshull, 1984). For some plants, including those in the genus *Chrysanthemum*, flowering may be delayed considerably if the light intensity is low. The length of illuminance required to initiate flowering, given the critical night length, varies tremendously by species, from one second to 8 to 12 hours (Vince-Prue, 1975). Thus, photoperiodism in SDP must be analyzed in terms of dark reactions counteracted by light and a light requirement, primarily for photosynthesis.

Hourglass Theory

There are two photoperiodism theories that attempt to explain how *short-day plants* perceive durations of light and darkness. The first, known as the "hourglass theory," holds that time is measured by a series of curves, which must be completed in sequence in order to measure the durations of light and darkness. The transfer to darkness initiates a noncyclic process or series of processes that function as an hourglass. The effective element in flower induction is the duration of darkness. When darkness begins, the hourglass is tipped upside down, and it continues to empty to the bottom half as long as there is darkness. If the darkness extends long enough for the hourglass to empty to the bottom half, the critical duration of darkness is completed and flower-induction processes are initiated. If light is perceived by the plant before the

hour-glass has emptied, the critical duration of darkness is not reached, and the plant is not induced to flower. The hourglass may represent the time taken for P_{FR} to fall below a critical threshold that no longer inhibits flowering in SDP (Vince-Prue, 1994).

The critical dark period may begin a few hours after the onset of darkness (Vince-Prue, 1975). As discussed previously, P_R is synthesized in darkness. When a low critical threshold of P_{FR} is reached, the hourglass then may be tipped, and the timing process may begin. If the plant is exposed to red light, P_{FR} is destroyed; this destruction may cease or reverse the flower-induction process. However, because phytochrome reversion does not always begin at the onset of darkness and may be delayed for several hours, it is difficult to associate it with the critical dark period (Vince-Prue, 1975).

If SDP receive red light several hours into the dark period, flowering is inhibited. This inhibition may be nullified by a subsequent exposure to far-red light. Reversibility is possible for several cycles; a plant repeatedly exposed to a red/far-red sequence will not flower. This reversibility is most effective when the far-red light is given soon after red light. The response becomes irreversible if time between the red/far-red sequence exceeds a critical duration, known as the escape time. Far-red light given at the end of the photoperiod or early in the dark period may inhibit flowering in some SDP species (Vince-Prue, 1975). Phytochrome may have a dual action on flowering in SDP. Within the first several hours of the dark period, a reaction that depends on the presence of P_{FR}

is required for floral induction. After this reaction is completed, further reactions leading to induction require reduction of P_{FR} below a certain threshold. When red light is given, these later reactions are interrupted or stopped, and floral induction fails. It is still unclear why far-red and red light are inhibitory at times, and some authors believe a second pigment may be involved (Thomas, 1993; Vince-Prue and Takimoto, 1987).

The hourglass theory is not considered correct, because plants' time-keeping mechanisms are not affected significantly by changes in temperature. All biological reactions are hastened with an increase in temperature to a certain point. If the theory were correct, raising the temperature should shorten the critical dark period required for flower induction; in other words, the hourglass would empty faster with an increase in temperature. In cocklebur and morning glory, changes in temperature only marginally affect the length of the critical photoperiod (Salisbury and Ross, 1969). Thus, evidence leads to dismissal of the theory.

Endogenous Oscillator Theory

The second theory that attempts to explain how SDP measure time is the "clock" or "endogenous oscillator" theory, in which an internal oscillator computes the daily durations of light and darkness. Time is measured on a circadian (24-hour) clock, and there is an oscillation between phases of inhibition and promotion of flowering by light. If flowering is to occur, the light and dark pattern

must be synchronized in some way with the internal oscillator. There may be a light-sensitive phase, known as external coincidence, in the photoperiodic rhythm (Vince-Prue, 1994). This proposition holds that there is a single photoperiodic rhythm, and light directly prevents flower induction in SDP when it coincides with a particular light-sensitive phase of the rhythm. Another proposition, for which there is more evidential support, is known as internal coincidence. This theory maintains that there is an interaction of two rhythms, and flower induction occurs only when critical phase points coincide (Vince-Prue, 1994).

Many organisms are subjected to daily alterations of light and darkness that often cause rhythmic behavior. Under long periods of darkness, the internal rhythm continues and is said to be free-running. Thus, the rhythms are innate but may need an initiation signal, such as a light-to-dark or dark-to-light transfer. The circadian rhythm is started by the first dark period, which will act as a long night for flower induction only if it coincides with the night phase of the circadian rhythm. Duckweed (*Lemna perpusilla* Torr.) flowers only when the dark period longer than the critical night length coincides with the circadian clock's night phase; darkness during the day ineffectively initiates flowering (Sweeney, 1987). The period of circadian rhythms is insensitive to temperature, strengthening the theory that the circadian clock is responsible for measuring the night length (Sweeney, 1987).

There are two essential components of the photoperiodic process in SDP (Vince-Prue, 1994). First, time is measured in darkness, and when SDP are

exposed to a sufficiently long dark period or succession of dark periods, flower induction occurs. Second, the night length must be preceded by a minimal photoperiod. Many rhythms respond identically to skeleton photoperiods, or recurrent pulses of light, and entire photoperiods (Vince-Prue, 1975). In the SDP pigweed (*Chenopodium rubrum* L.), the light-to-dark signal sets the phase, and the timing of the dark-to-light signal determines if flowering occurs (Cumming et al., 1965). Thus, it is the timing of "dawn" and "dusk" signals that is important. There are many other examples of similar rhythmic flowering responses (King, 1984; Vince-Prue, 1975). However, not all plants are dominated by light-on/light-off signals (King, 1984).

Phytochrome may be involved in light detection and, to some degree, inhibits or promotes flowering, depending on the circadian time. Phytochrome's link to the flowering clock is unknown, although night-break inhibition of flowering in SDP depends on P_{FR}. However, phytochrome apparently is not involved in photocontrol of the circadian rhythm in some species that respond identically to blue and red light (Vince-Prue, 1994). Plants that respond identically to blue and red light are all members of the Brassicaceae family (Thomas, 1993), one of many aspects of the "clock" theory that requires further study and explanation. Nevertheless, flowering in SDP appears to be connected to circadian rhythms, and the "clock" theory has received support from numerous experiments and is currently the accepted theory.

Long-day Plants

Long-day plants flower, or flower more rapidly, only when the length of irradiance exceeds a critical number of hours. Qualitative LDP remain vegetative when the duration of darkness exceeds a particular value and flower when it is less than a critical value. Again, the critical photoperiod varies among species and genotypes. 'Esther Read' daisy chrysanthemum (*Chrysanthemum maximum* Ramond 'Esther Read') remained vegetative under 12-hour photoperiods and flowered under photoperiods of 13 hours or longer; 'T.E. Killian' daisy chrysanthemum plants flowered only under 15-hour photoperiods and remained vegetative under 14-hour or shorter photoperiods (Griffin and Carpenter, 1964). Many LDP flower under continuous 24-hour light, which suggests there is not an absolute dark-period requirement for flowering in many LDP. Therefore, some people term LDP, perhaps more accurately, light-dominant plants.

'Moonbeam' tickseed (*Coreopsis verticillata* L. 'Moonbeam') is an example of a qualitative LDP; no plants grown with 8-hour photoperiods after receiving 0, 6, or 12 weeks of 4.5 °C cold treatment flowered, whereas all those grown under 16- or 24-hour photoperiods flowered, regardless of cold treatment (Iversen and Weiler, 1994). Many LDP show a quantitative response to light after the critical photoperiod until a maximum has been reached. Forty percent of a clone of shasta daisy (*Chrysanthemum* x *superbum* Bergmans) plants grown under 12-hour photoperiods flowered, and 80% of the plants under 14-hour photoperiods

flowered (Shedron and Weiler, 1982). Thus, the critical photoperiod as defined by Vince-Prue (1975) is between 12 and 14 hours. Plants were grown from seed for 80 days under 10-hour photoperiods, then transferred to 12-, 14-, 16-, or 18-hour photoperiods. As the photoperiod duration increased, the number of days to reach visible bud decreased: 100 at 12 hours, 92 at 14 hours, 49 at 16 hours, and 28 at 18 hours (Shedron and Weiler, 1982). Flowering was most rapid under 18-hour photoperiods, so horticulturally, the critical photoperiod is $\geq$18 hours.

Some LDP may be induced to flower by vernalization, exposure to cold temperatures, or LD. 'Bristol Fairy' baby's-breath (*Gypsophila paniculata* L. 'Bristol Fairy') can be induced to flower by LD or cool night temperatures (12C). Plants grown at 18 °C or above did not flower under 11-hour photoperiods (SD), whereas all plants flowered when grown under 24-hour continuous light (LD) (Moe, 1988). All plants grown under SD with cool night temperatures (12/18 °C night/day) flowered, but took 38 days longer than those grown under LD at the same temperature regime (Moe, 1988). The photoperiodic induction of flowering in LDP is much less well understood than that in SDP. The mechanism for the time-measuring process in LDP appears similar to that in SDP. It is theorized LDP perceive a critical nightlength that, if exceeded, prevents flowering, whereas in SDP it promotes flowering. Flowering may depend on whether light is given during a flowering-promotion phase of a circadian rhythm, although fewer species have been examined to test this theory (Vince-Prue, 1994). If there is a

circadian clock involved in flowering in LDP, the rhythm appears to be out of phase with that found in SDP (Vince-Prue, 1975). The differing rhythmic sensitivities to flower induction can be illustrated in the graph to the right in the LDP white mustard and the SDP pigweed (Sweeney, 1987).

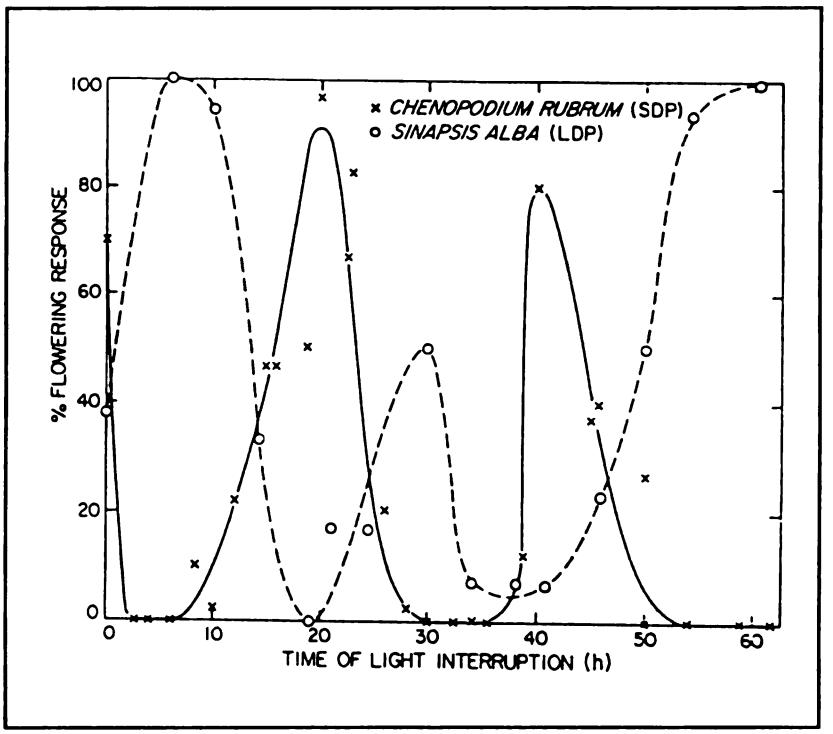


Figure 6. The differing rhythmic sensitivities to flower induction in the LDP white mustard and the SDP pigweed (Sweeney, 1987)

LDP can be divided into two flowering response types on the basis of the role of light and darkness in flowering (Vince-Prue, 1994). Flowering of some LDP is controlled primarily by dark processes, and a long night can be prevented by a short night break at an appropriate time. These plants are referred to as dark-dominant response types. For other LDP, a long light period to initiate flowering is very important. These plants can be labeled light-dominant LDP. LDP are usually less sensitive to night interruptions than SDP. Only a small number of LDP species is capable of flower induction with a single night break of fewer than 30 minutes, and then only under specific conditions (Deitzer, 1984).

LDP usually require longer light exposures, higher light intensities, or both to promote flowering than are required by SDP to inhibit flowering (Kasperbauer et al., 1963; Vince-Prue, 1975). For most species, the number of flowers increases as the amount of irradiance striking a plant increases. For many light-dominant LDP, earliness of flowering increases as the amount of irradiance striking the plant increases. The flowering process was accelerated in 'Bridal Veil' and 'Bristol Fairy' baby's-breath when the photosynthetic photon flux increased from 210 to 710 μmol·m^{-2}·s^{-1} at 12, 20, or 28 °C (Hicklenton et al., 1993).

The Role of Phytochrome in LDP

Similar to that in SDP, phytochrome conversion and reversion has been demonstrated in flowering of LDP. For some LDP, a brief exposure of far-red light immediately following a brief period of red light can reverse the promoting effect of red light on flower induction. However, brief night-breaks are often ineffective at promoting flowering in LDP. Most LDP require longer durations, higher intensities, or both, of light to interrupt the night and promote flowering than SDP require to interrupt the night and inhibit flowering. With long night breaks, the action spectrum for a maximal night-break effect to promote flowering in LDP is near 720 nm (Vince-Prue, 1994). If long photoperiods do not include far-red light, LDP either do not flower or flower more slowly (Vince-Prue, 1975). The addition of far-red light not only directly promotes flowering, but also affects the phase of the time-keeping mechanism that controls the sensitivity of

the plant for flower promotion (Deitzer, 1984). Flowering is frequently most rapid under continuous 24-hour light, as long as both red and far-red light are delivered.

The optimum R:FR for earliest flowering changes dramatically during the course of the daily cycle (Vince, 1969). Light-dominant LDP have a distinctive pattern of sensitivity to light quality (Thomas, 1993). Long periods of light given as a day extension with a blend of red and far-red light generally induce flowering in most LDP, including lettuce and carnation, far better than red light alone (Thomas, 1993). The addition of far-red light has a promoting effect on flowering when delivered from about the eight hour of the daily photoperiod through about the sixteenth hour (Vince-Prue, 1994). However, the addition of far-red light to the first eight hours of a 16-hour period of red light often had little or sometimes no effect on promotion of flowering in LDP (Vince-Prue, 1994). Far-red light's flowering promotion or lack thereof may be interpreted as a form of high-irradiance response, presumed to act through P_{FR}, and the far-red action spectrum for promotion of flowering in LDP by long light exposures may not apply solely in terms of P_{FR} (Weller and Reid, 1993). However, why far-red is required during photoperiods for optimal flowering in LDP is still unknown (Vince-Prue, 1994).

Vince-Prue suggests that, at the end of a short day of sunlight, a high concentration of P_{FR} in leaves inhibits flowering of LDP (Vince-Prue, 1975). Later in the night, P_{FR} is necessary for flower induction, and at this point the

addition of far-red light often has little or no effect on flowering (Vince-Prue, 1975). The results suggest a dual response to P_{FR}, as in SDP, except the sequence of promotion and inhibition by P_{FR} is reversed in LDP (Vince-Prue, 1975). Deitzer (1984) believes there is a low-P_{FR}- and a high-P_{FR}-requiring period involved in LDP flower induction. There may be two sequential phytochrome-mediated events necessary for flowering in LDP: one toward the middle of the dark period, requiring comparatively higher levels of P_{FR} to initiate flowering, and a relatively lower-P_{FR}-requiring period that occurs at the end of the day and promotes floral development (Deitzer, 1984). P_{FR} inhibits flowering of the LDP ryegrass (*Lolium temulentum* L.) at some phases of a circadian rhythm and promotes it in others (Vince-Prue, 1994). Photoperiodic sensing in LDP may be the result of two circadian rhythms (Vince-Prue and Takimoto, 1987). It is proposed that the first rhythm runs in the light, is responsive to far-red light, and may be related to the LD requirement. The second rhythm runs in darkness, is responsive to red light, is suspended in continuous light, and relates to the measurement of the critical night length. The role of phytochrome is not clearly understood in LDP; we know only that it plays some role in flowering or the lack thereof.

Recent evidence suggests that gene expression shows a rhythmic response that may be involved in flowering in LDP. The expression levels of distinct leaf mRNAs oscillated in a circadian rhythm with respect to photoperiod in mouse-ear cress (Lechner and Rau, 1993). In the LDP white mustard, levels

of an mRNA undergo circadian oscillations in light/dark cycles with maxima between 2000 HR and 2400 HR and minima around 0800 HR (Heintzen et al., 1994). The underlying oscillatory mechanism(s) operate(s) synchronously in different plant organs, including the epidermis and spongy parenchyma cells in the leaves and regions of the cortex in stems and petioles (Heintzen et al., 1994). No novel mRNA appeared and mRNA did not decrease to undetectable levels during changes from SD to inductive LD. After the onset of LD, there were alterations in the phase and amplitude of circadian oscillations of mRNA expression levels either within hours after the beginning of the extended light period or after the first LD was complete (Lechner and Rau, 1993). These findings indicate that a distinct time-measuring mechanism at least partially regulates levels of mRNA, which may participate in temporary processes in the leaves and thereby transform a photoperiodic perception into a flowering stimulus (Lechner and Rau, 1993).

Although there is strong evidence for the involvement of a circadian rhythm in flower induction, there is also strong evidence for the involvement of a semidian rhythm that cycles twice each day. The semidian rhythmic process persists in prolonged light with a period of about 12 hours and has a pronounced effect on flowering, at least in LDP (Heide et al., 1986). At various times before the beginning of the dark periods, mouse-ear cress plants exposed to 90 minutes of far-red light during continuous white light deficient of far-red displayed signs of distinct inhibitory and promotive effects on flowering (Heide et al., 1986).

Far-red light given for 90 minutes 4, 16, and 28 hours before the dark period promoted flowering, and when given 8, 22, and 34 hours before the dark period, it inhibited flowering. The semidian rhythm is set by a light-on signal, in contrast to the phasing of the circadian rhythm, which is set by a light-off signal. Far-red interruptions' effect on flower promotion increases with duration, and temperature may influence the period length of the semidian rhythm (Heide et al., 1986).

Flowering Stimulus Theory

There is evidence from many physiological experiments that leaves produce a flower-inducing hormone, or a floral stimulus, under photoinduced cycles. This proposed hormone was termed "florigen" by Chailakhyan around 1937 (see Lang, 1965). Despite decades of research, the floral stimulus has not yet been identified. Numerous grafting experiments demonstrate that the floral stimulus can be transmitted through a graft union. A plant kept under noninductive conditions could be induced to flower by a graft union with an induced leaf. Examples exist in SDP, LDP, and plants that require long then short days to flower (LSDP), within species, and between species of different families (Lang, 1965; Zeevaart, 1976). In some cases, a leaf that was taken from the graft-induced plant and was never under inductive conditions still could induce flowering indirectly when grafted onto another uninduced plant. Such grafts have been successful in the SDP cocklebur (*Xanthium strumarium* L.), the

LDP garden catchfly (*Silene armeria* L.), and the LSDP Devil's-backbone (*Kalanchoë daigremontiana* Hamet & Perr.) (Zeevaart, 1976). The floral stimulus may be the same or very similar in LDP, SDP, and DNP, since it can be transmitted from SDP to LDP, SDP to DNP, LDP to DNP, and vice versa (Lang, 1965). Transmission of the flower-promotiing stimulus has also been demonstrated between DNP (Lang, 1965). Additional evidence to support the existence of a floral stimulus comes from plants that initiate flowers after one inductive cycle. Immediate removal of the induced leaves after the end of the cycle can prevent a flowering response, but if the leaves are removed a certain number of hours after the end of the cycle, the plants flower as if their leaves still are intact (Lang, 1965).

The flowering stimulus appears to be translocated with the flow of carbohydrates, through the phloem, to the bud meristem (Vince-Prue, 1975). There was a rapid, dramatic increase in apical sap transmitted from the phloem during floral induction in the LDP white mustard (*Brassica hirta* Moench., formerly *Sinapis alba*) (Lejeune et al., 1993). These results suggest sucrose plays a messenger-type role in transmitting the floral stimulus from the leaves to the apex, since there is an accumulation of sucrose in the meristem early in the vegetative to reproductive process (Lejeune et al., 1993).

Once the floral stimulus arrives at the apex, cell activity increases; nucleic acid, RNA, and protein synthesis increase; and soon there is an increase in cell size (Vince-Prue, 1975). The increase in RNA synthesis in the LDP black-eyed

Susan (*Rudbeckia hirta* L.) is apparent after eight LD (Harkess and Lyons, 1993). The increase in RNA in other species occurs just before or on the arrival of the floral stimulus and is necessary for flowering (Harkess and Lyons, 1993). Genes that are inactive when the plant is vegetative may become activated once the floral stimulus arrives at the apex. Two major groups of white mustard genes whose expression was affected during flower formation were identified (Melzer et al., 1990). The first group of genes, present at low concentrations in the apex in uninduced plants, quickly accumulated after the end of the inductive photoperiod. The second group of genes was not detected in uninduced plants but was detected first 10 days after the onset of inductive photoperiods. The group rapidly accumulated, then dropped to undetectable levels before the flower reached maturity. Alterations in gene expression during photoperiodic induction appear to be temporary (Lechner and Rau, 1993). Following the floral stimulus, the apex reorganizes and differentiates floral organs. Once cells begin their increased activity, flowering moves into the initiation stage, and the distinct anatomical zonation in the meristem is lost (Harkess and Lyons, 1993).

After a sufficient number of favorable cycles, photoperiodically sensitive plants may continue to flower, even if returned to noninductive cycles (Vince-Prue, 1975). Nearly all seed plants transition from the vegetative to reproductive state is almost completely irreversible (Krishnamoorthy and Nanda, 1968). Dense-flowered loosestrife, a quantitative LDP, given one week of LD followed by SD flowered at the same time as those given two, three, or four weeks of LD

followed by SD, or continuous LD (Zhang et al., 1995). Therefore, this species requires seven or fewer LD to initiate 100% flowering. However, flower number decreased as the duration of LD decreased.

Some species' inflorescence requires continued favorable cycles through the late stages of flower development. The qualitative SDP garden balsam (*Impatiens balsamina* L.), must be exposed to an appropriate photoperiod until anthesis; if not, the plant will revert to vegetative growth, even after anthers and ovules have formed (Krishnamoorthy and Nanda, 1968). Mexican bush sage (*Salvia leucantha* Cav.) SDP exposed to five weeks of SD following flower initiation then were followed by LD and did not reach anthesis; 57% of plants exposed to six weeks of SD followed by LD reached anthesis; and all plants exposed to nine weeks of SD when the calyx became visible reached anthesis (Armitage and Laushman, 1989). Roberts and Summerfield (1987) proposed the existence of a postinductive phase, which is insensitive to photoperiod. However, initiation of the phase varies by species, from immediately after floral induction to the beginning of anthesis. Therefore, induction is not an "all or none" process; there are degrees. A plant exposed to inductive cycles less than the number that elicits a full flowering response may still flower, but in a different manner. For example, kalanchoe (*Kalanchoë blossfeldiana* Poelln.), when exposed to one or two fewer cycles than the number that would provide full flowering, flowers sparsely and from axillary shoots; terminal infloresences are absent (Carlson et al., 1979).

Inhibitory Process Theory

Another theory, for which there is less evidence, is that an inhibitory process occurs in plants under noninductive daylengths, which implies that a plant flowers when the inhibitor is absent. There are some examples of LDP and SDP that flower in noninductive cycles when their leaves are removed, suggesting an inhibitory substance originates in the leaves and acts at the apex. In a grafting experiment with the SDP morning glory (*Pharbitis nil* Choisy.), different strains produced different intensities of flowering stimuli or amounts of flowering hormone. In many cases, the productivity of the floral stimuli by the leaves was more important than the reactability of the bud. The experimenters concluded inhibitory factors, when transmitted through the graft, played some significant role in flowering (Imamura et al., 1966). As 'Marmalade' black-eyed Susan plants, an LDP, experienced longer periods of uninterrupted LD, the effect of photoperiodic inhibition diminished (Orvos and Lyons, 1989). The longer plants perceived the inductive photoperiod, the faster they came into flower, and the effects of photoperiodic inhibition on flowering were strongest for plants that received the fewest inductive days (Orvos and Lyons, 1989).

With many of the grafting experiments, non-induced, particularly mature, leaves were usually removed since their presence had an unfavorable effect on the flowering response, whereas removal of young leaves often had an adverse effect on flower initiation (Lang, 1965). The inhibitory action of non-induced leaves was reduced when they were provided low light intensity, complete

darkness, or extreme SD in the case of LDP (Lang, 1965). Thus, the inhibitory effect appears to be translocated and interferes with florigen transport from induced leaves to the buds. However, no recent evidence suggests that the removal of an inhibitor induces flowering.

Chemical Induction of Flowering

Application of a variety of substances can induce flowering in some plants, including the plant hormones gibberellin, cytokinin, auxin, abscisic acid, and ethylene, as well as sugars, growth retardants, and some mineral elements (Vince-Prue, 1975). However, most substances are effective at inducing flowering in only a small number of often related species. Numerous attempts have been made to extract from flowering plants various chemicals that would induce flowering in plants under noninductive conditions. To date, there has been very limited success, and no hormone that has an inductive effect over a broad range of plants has been discovered.

In the 1950s, gibberellic acid was discovered and was believed by some to be the flowering hormone. In some cases, GA can substitute for a cold requirement; in others, for LD to induce flowering. For example, application of GA to two cultivars of blanket flower (*Gaillardia* x *grandiflora* Van Houtte 'Dazzler' and 'Goblin') substituted for LD and promoted flowering under SD in the same amount of time untreated, photoperiodically induced plants required (Evans and Lyons, 1988). In some LDP, GA applications have little effect on

flowering. Flowering and stem elongation are induced by photoperiod in garden catchfly, but the flowering response mainly is LD-qualitative and is not induced by applied GA, and stem elongation is related to the duration of the LD treatment (Talon and Zeevaart, 1990). However, GA can replace either cold or LD, not both, and does not cause SDP to flower. Levels of GA increase in many LDP exposed to LD. The rate of accumulation of ent-Kaurene, a point of regulation in the GA pathway, was three times higher in the LDP spinach and two and one-half times higher in the LDP corn cockle (*Agrostemma githago* L.) when plants were grown under LD compared to SD (Zeevaart and Gage, 1993). Most of the plants that respond to GA are rosettes. The primary effect of GA is internode elongation; secondary, flowering. If GA biosynthesis inhibitors (growth retardants) are applied to LDP under LD, the plants do not bolt, but they flower. The growth retardant tetcyclacis, a GA biosynthesis inhibitor, inhibited stem elongation induced by LD in *Silene*, but had no effect on flowering (Talon and Zeevaart, 1990). Therefore, GA directly affected stem growth, and indirectly influenced flowering.

The Role of Temperature in Flowering

Many plants flower in response to photoperiod, and in a vast majority of those, temperature plays a significant role in the rate of flower induction, initiation, development, and maturation. The duration of the flowering process can be measured by either the number of days to flowering (F) or its inverse, the

rate of progress toward flowering (1/F). The rate of progress toward flowering is a positive linear function, extending from the base to optimum temperature of a species (Roberts and Summerfield, 1987). The base temperature (T_{base}) is species-specific and describes the temperature at which growth begins; below that base temperature there is no growth. The optimum temperature (T_{opt}) also varies by species and describes the point at which growth and the flowering process are most rapid; beyond T_{opt}, both are delayed and eventually aborted. The flowering process is accelerated as the average daily temperature increases from T_{base} to a maximal rate, T_{opt}. Herbaceous perennial 'Bristol Fairy' baby's-breath plants grown at 12 °C under 450 or 710 $\mu mol \cdot m^{-2} \cdot s^{-1}$ took 81 or 70 days to reach visible bud, respectively; at 20 °C, 63 or 43 days, respectively; and at 28 °C, 24 or 25 days, respectively (Hicklenton et al., 1993). There is a possibility that the increased light levels increased plant temperature and confounded the results. As the temperature increased, the average number of florets per plant decreased from 3,022 and 8,977 at 450 or 710 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 12 °C to 720 and 1,874 at 28C, respectively (Hicklenton et al., 1993). 'Sentimental Blue' balloon flower flowered earlier when plants were grown at 23/25 °C night/day (137 days) than at 15/17 °C (159 days) (Song et al., 1993).

High temperatures (25-35C) generally are inhibitory to SDP toward the end of the inductive night (Vince-Prue, 1975). In contrast, several LDP, including calamint (*Calamintha nepeta glandulosa* P.W. Ball), underwater rose (*Samolus parviflorus* Raf.), and garden catchfly flowered under SD with night temperatures

above 30 °C (Zeevaart, 1976). Over a wide range of temperatures, the rate of progress toward flowering increases usually in a linear manner with an increase in temperature until an optimum temperature is reached (Roberts and Summerfield, 1987). Beyond the optimum temperature, flowering is delayed as temperatures get warmer (Roberts and Summerfield, 1987). The optimum temperature varies by species.

Roberts and Summerfield (1987) have proposed mathematical equations that attempt to predict the time it takes a plant to flower based on temperature and photoperiod. Three factors that modulate the rate of progress toward flowering in the quantitative LDP lentil *(Lens culinaris* Medic.) were found: vernalization, postvernalization mean temperature, and photoperiod (Roberts et al., 1986). The photoperiodic sensitivity of lentil, defined in terms of the difference in days to flower between two different photoperiods, was affected markedly by temperature (Roberts et al., 1986). Roberts and Summerfield (1987) believe that the critical photoperiod of SDP decreases with an increase in temperature. Their results contradict those of Vince-Prue, who believes the critical photoperiod remains relatively resistant to changes in temperature (Vince-Prue, 1975). The majority of evidence suggest that temperature may shorten or lengthen the critical photoperiod of some species to at least a small extent. Photoperiodic responses in general often are modified by changes in temperature.

The interaction of daylength and temperature was investigated in three cultivars of the SDP poinsettia (*Euphorbia pulcherrima* Willd.). Langhans and Miller (1963) defined the critical daylength for SDP as that daylength above which the plant remains vegetative and below which the plant flowers. For all three cultivars studied, the critical daylength for flower initiation and development decreased as the temperature increased from 16 to 27 °C (Langhans and Miller, 1963). For example, the critical photoperiod of 'Barbara Ecke Supreme' shifted from above 12 hours at 16 °C to 11.5 hours at 21 °C to between 10 and 12 hours at 27 °C (Langhans and Miller, 1963).

A similar experiment was conducted on three cultivars of the SDP chrysanthemum (*Dendranthema grandiflora* Tzvelev): 'White Wonder', a 6-week variety; 'Encore', a 10-week variety; and 'Snow', a 15-week variety. Temperature altered the critical photoperiods required for flower initiation and flower development in all three cultivars (Cathey, 1957). Cathey (1957) defined the critical photoperiod of SDP as the minimum light length necessary for flowering. In 'Encore', as the temperature increased from 10 to 27 °C, the critical photoperiod for flower initiation increased from 13.75 to 15.25 hours and the critical photoperiod for flower development decreased from 13.75 to 12 hours (Cathey, 1957). In contrast, the critical photoperiods for flower initiation of 'Snow' decreased from 12 to 10 hours as temperatures increased from 10 to 27 °C and the critical photoperiod for flower initiation decreased from 12 to 9 hours (Cathey, 1957). The poinsettia and chrysanthemum examples provide evidence

that, at least in SDP, temperature modifies the critical photoperiods for flower initiation and development.

Describing the rate of progress toward flowering (the inverse of days to flower, or 1/F) is perhaps more useful than describing flowering as days to flower. These flowering rates vary by species and are affected by temperature and possibly photoperiod. In experiments with chickpeas (*Cicer arietinum* L.) and soybeans, there was no apparent correlation between relative sensitivity of temperature and photoperiod for flowering (Roberts et al., 1985; Upadhyay et al., 1994). These studies suggest that, although both factors affect time to flowering, they are under separate genetic control (Roberts et al., 1985; Upadhyay et al., 1994).

The rate of progress toward flowering can be related linearly to mean temperature, t, in °C by the equation

$$1/F=a + bt$$

where a and b are constants, a is the slope coefficient, and b is the intercept coefficient. The constants a and b vary by species. The base temperature, T_{base}, as described previously, can be determined by the equation

$$T_{base}=-a/b$$

At suboptimal temperatures, the flowering response rate decreases linearly until T_{base} is reached, at or below which the rate is zero (Upadhyay et al., 1994).

The rate of progress toward flowering is clearly a linear function of mean temperature for photoperiod-insensitive genotypes (DNP); daylength has no effect on the rate of flower development. SDP exhibit a basic temperature response similar to that of DNP and a photoperiodic response in which the rate of progress toward flowering is a negative linear function of photoperiod (Roberts and Summerfield, 1987). In soybean, increases in daylength beyond the optimal daylength in which flowering was most rapid progressively delayed flowering until the flowering response rate reached a minimum (Upadhyay et al., 1994). Temperature also may have some effect on the rate of progress toward flowering when the photoperiod exceeds the critical photoperiod for that genotype. The following equation describes the rate of progress toward flowering in SDP:

$$1/F=a' + b't + c'p$$

where t is the mean temperature in °C, p is photoperiod in hours, and a', b', and c' are species-specific constants that apply when photoperiods are shorter than the critical photoperiods (Roberts and Summerfield, 1987). For SDP, the temperature constant, b', always will be positive between T_{base} and T_{opt}, and the photoperiodic constant, c', always will be negative. In a photoperiod-sensitive genotype of the SDP soybean (TGx 46-3C), data from plants grown under various temperature and photoperiodic regimes yielded the top graph shown on the next page (Figure 7), which illustrates photothermal effects on flowering (Roberts and Summerfield, 1987).

The photothermal responses of LDP are essentially mirror images to those of the SDP soybean. However, the value of the photoperiodic constant, c', is positive; the longer the photoperiod in many LDP, the faster the rate of flowering. The lower graph in Figure 7 illustrates the effects of photoperiod and temperature on flowering in a photoperiod-sensitive genotype of the LDP lentil (ILL 4605) (Roberts and Summerfield, 1987). The response shown for lentil is similar to that of other LDP, including chickpeas, barley (*Hordeum vulgare* L.), and faba bean (*Vicia faba* L.) (Roberts and Summerfield, 1987). No critical photoperiod is apparent, and as the length of the photoperiod increases, flowering rates increase, so this genotype of lentil is likely a quantitative LDP.

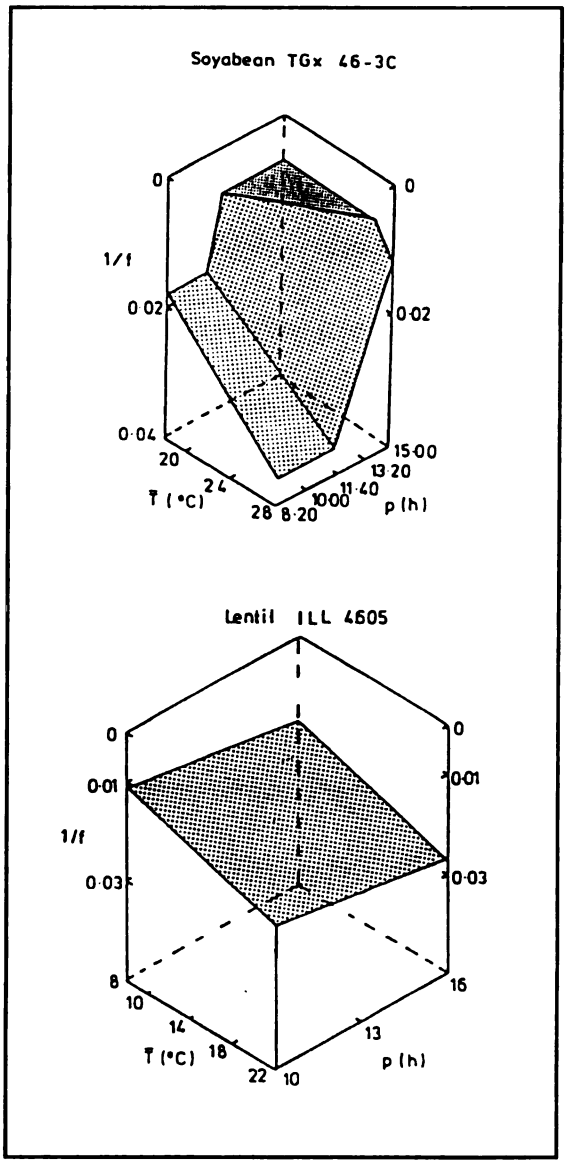


Figure 7. The photothermal effects on flowering of the SDP soyabean (top) and the LDP lentil (bottom) (Roberts and Summerfield, 1987).

Recent experiments have focused on what effect, if any, carbon dioxide (CO_2) levels have on annual plants' development toward flowering. Reekie et al.

(1994) suggested that the effect of CO_2 on flowering is a function of the photoperiodic response of a species. In four SDP, increasing levels of CO_2 delayed flowering somewhat, whereas in four LDP, increasing levels of CO_2 hastened flowering (Reekie et al., 1994). Flowering was delayed by one, two, four, and five days in chrysanthemum, cocklebur (*Xanthium pensylvanicum* Gandoger), kalanchoe, and morning glory, respectively, when plants were grown at 350 μmol CO_2/mol of air compared to those grown at 1000 μmol CO_2/mol of air (Reekie et al., 1994). Flowering was hastened by 6, 8, 10, and 14 days in the LDP common yarrow (*Achillea millefolium* L.), China aster (*Callistephus chinensis* Nees), throatwort (*Trachelium caeruleum* L.), and Italian bellflower (*Campanula isophylla* Moretti), respectively, when plants were grown at 350 μmol CO_2/mol of air compared to those grown at 1000 μmol CO_2/mol of air (Reekie et al., 1994). In another study, as CO_2 levels increased from 210 to 720 μmol CO_2/mol of air, flowering was delayed by 17 or 19 days in two cultivars of the SDP sorghum (*Sorghum bicolor* Moench.) and by three days in soybean (Ellis et al., 1995). Flowering was hastened by two days in the SDP cowpea (*Vigna unguiculata* Walp.) (Ellis et al., 1995). For the two genotypes of sorghum studied, as CO_2 concentrations increased, panicle initiation occurred 17 to 22 days earlier at 210 than at 720 μmol CO_2/mol of air (Ellis et al., 1995). The effects of CO_2 concentrations on rates of development clearly vary by species, and no significant generalizations can be made (Ellis et al., 1995).

The preceding equations that attempt to quantify and predict the rate of progress toward flowering are perhaps the best (and only) models developed to date. Upon analysis, the models have several faults. First, each assumes that plants are sensitive to photoperiod throughout the four phases of plant growth and development. As described earlier, most SDP and LDP go through phases in which they are relatively insensitive to photoperiod. Second, the three constants, a', b', and c', vary by genotype, and these constants must be derived for application. Third, little research delineates the effect of vernalization on the models. Roberts and Summerfield (1987) predict modeling of crop phenology will become more simplified and reliable when thermal and photoperiodic time are integrated into models.

Quantification of the effects of photoperiod on rates of flowering is not as well understood, but some conclusions have been reached. Several LDP flower faster as the length of the photoperiod increases beyond the critical photoperiod (Roberts and Summerfield, 1987). However, in the LDP garden pea, photoperiods longer than the critical photoperiod have no effect on flowering, and the time to flowering is solely a function of mean temperature (Roberts and Summerfield, 1987). These LDP contradictions may be explained if species in which flowering is hastened as the photoperiod increases are light-dominant plants, and garden pea plants are an example of a dark-dominant LDP. In 10 genotypes of soybean, a SDP, the rate of progress toward flowering increased as the photoperiod decreased below the critical photoperiod (Roberts and

Summerfield, 1987). In cowpea and soybean, both SDP, there is a temperature-dependent critical photoperiod until there is no longer a photoperiodic-hastening response, when time to flower is solely a function of mean temperature (Roberts and Summerfield, 1987). The rate of progress toward flowering is not affected by photoperiod in DNP, as expected. Thus, rates of progress toward flowering tend to be nearly linear functions of temperature, photoperiod, or both (Roberts and Summerfield, 1987).

Summary

There is not yet a clear understanding of how plants flower in response to photoperiod; we are only beginning to explain this very complex issue. To date, we know that leaves respond to light and dark and transmit the signals to the apex. Depending on the plant and its internal oscillator, the signal either promotes or inhibits flowering. Phytochrome is involved in the flowering process, but exactly how is unknown. If a universal plant hormone that induces flowering exists and can be synthetically replicated, then it may be applied to plants, which would make them flower. Conversely, a hormone that inhibits flowering and thus promotes vegetative growth may be identified. The idea of bringing a crop to flower with a chemical is fascinating and would change the plant world as we know it today drastically.

References

Armitage, A.M. and J.M. Laushman. 1989. Photoperiodic control of flowering of *Salvia leucantha*. J. Amer. Soc. Hort. Sci. 114(5):755-758.

Beattie, D.J., C.F. Deneke, E.J. Holcomb, and J.W. White. 1989. The effects of photoperiod and temperature on flowering of *Physostegia virginiana* 'Summer Snow' and 'Vivid' as potted plants. Acta Hort. 252:227-233.

Brock, R.D. and J.L. Davidson. 1994. 5-Azacytidine and gamma rays partially substitute for cold treatment in vernalizing winter wheat. Environ. Expt. Bot. 34:195-199.

Burn, J.E., D.J. Bagnall, J.D. Metzger, E.S. Dennis, and W.J. Peacock. 1993. DNA methylation, vernalization, and the initiation of flowering. Proc. Natl. Acad. Sci. 90:287-291.

Carlson, W.H., C.A. Turner, and J. Schnabel. 1979. Effect of inductive photoperiodic cycles on flowering of kalanchoe cultivars. HortScience 14(1):62-63.

Carr-Smith, H.D., C.B Johnson, C. Plumpton, G.W. Butcher, and B. Thomas. 1994. The kinetics of type I phytochrome in green, light-grown wheat (*Triticum aestivum* L.). Planta 194:136-142.

Cathey, H.M. 1957. Chrysanthemum temperature study. F. The effect of temperature upon the critical photoperiod necessary for the initiation and development of flowers of *Chrysanthemum morifolium*. Proc. Amer. Soc. Hort. Sci. 69:485-491.

Clack, T., S. Mathews, and R.A. Sharrock. 1994. The phytochrome apoprotein family *Arabidopsis* is encoded by five genes: the sequences and expression of *PHYD* and *PHYE*. Plant Mol. Biol. 25:413-427.

Cockshull, K.E. 1984. The photoperiodic induction of flowering in short-day plants, p. 33-49. In: D. Vince-Prue, B. Thomas, and K.E. Cockshull (eds.). Light and the flowering process. Academic Press, San Diego.

Collinson, S.T., R.H. Ellis, R.J. Summerfield, and E.H. Roberts. 1992. Durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering in four cultivars of rice (*Oryza sativa* L.). Ann. Bot. 70:339-346.

Cumming, B.G., S.B. Hendricks, and H.A. Borthwick. 1965. Rhythmic flowering responses and phytochrome changes in a selection of *Chenopodium rubrum*. Can. J. Bot. 43:825-853.

Deitzer, G.F. 1984. Photoperiodic induction in long-day plants, p. 51-63. In: D. Vince-Prue, B. Thomas, and K.E. Cockshull (eds.). Light and the flowering process. Academic Press, San Diego.

Ellis, R.H., P.Q. Craufurd, R.J. Summerfield, and E.H. Roberts. 1995. Linear relations between carbon dioxide and rate of development towards flowering in sorghum, cowpea, and soyabean. Ann. Bot. 75:193-198.

Ellis, R.H., S.T. Collinson, D. Hudson, and W.M. Patefield. 1992. The analysis of reciprocal transfer experiments to estimate the durations of the photoperiod-sensitive and photoperiod-insensitive phases of plant development: An example in soya bean. Ann. Bot. 70:87-92.

Evans, M.R. and R.E. Lyons. 1988. Photoperiodic and gibberellin-induced growth and flowering responses of *Gaillardia* x *grandiflora*. HortScience 23(3):584-586.

Faust, J.E. and R.D. Heins. 1994. Determining the effect of cloud conditions on the variation in daylength perceived by plants. HortScience 29(5):504.

Flood, R.G. and G.M. Halloran. 1984. The nature and duration of gene action for vernalization response of wheat. Ann. Bot. 53:363-368.

Gardner, F.P. and R.D. Barnett. 1990. Vernalization of wheat cultivars and a triticale. Crop Sci. 30:166-169.

Gardner, G. and M.A. Graceffo. 1982. The use of a computerized spectoradiometer to predict phytochrome photoequilibria under polychromatic irradiation. Photochem. Photobiol. 36:349-354.

Griffin, C.W. and W.J. Carpenter. 1964. Photoperiodic response of shasta daisy clones Esther Read and T. E. Killian. Proc. Amer. Soc. Hort. Sci. 85:591-593.

Griffiths, J.F. 1976. Sunrise, sunset. Weather 31:427-429.

Harkess, R.L. and R.E. Lyons. 1993. Anatomical changes in *Rudbeckia hirta* L. during transition to flowering. J. Amer. Soc. Hort. Sci. 228(6):835-839.

Hazebroek, J.P. and J.D. Metzger. 1990. Thermoinductive regulation of gibberellin metabolism in *Thlaspi arvense*. Plant Physiol. 94:154-165.

Hazebroek, J.P., J.D. Metzger, and E.R. Mansager. 1993. Thermoinductive regulation of gibberellin metabolism in *Thlaspi arvense*. Plant Physiol. 102:547-552.

Heide, O.M., R.W. King, and L.T. Evans. 1986. A semidian rhythm in the flowering response of *Pharbitis nil* to far-red light. Plant Physiol. 80:1020-1024.

Heintzen, C., R. Fischer, S. Melzer, S. Kappeler, K. Apel, and D. Staiger. 1994. Circadian oscillations of a transcript encoding a germin-like protein that is associated with cell walls in young leaves of the long-day plant *Sinapis alba* L. Plant Physiol. 106:905-915.

Hicklenton, P.R., S.M. Newman, and L.J. Davies. 1993. Growth and flowering of *Gypsophila paniculata* L. 'Bristol Fairy' and 'Bridal Veil' in relation to temperature and photosynthetic photon flux. Scientia Hort. 53:319-331.

Hughes, J.E., D.C. Morgan, P.A. Lambton, C.R. Black, and H. Smith. 1984. Photoperiodic time signals during twilight. Plant Cell Environ. 7:269-277.

Imamura, S., M. Muramatsu, S.I. Kitajo, and A. Takimoto. 1966. Varietal difference in photoperiodic behavior of *Pharbitus nil*. Bot. Magazine, Tokyo 79:714-721.

Iversen, R.R. and T.C. Weiler. 1994. Strategies to force flowering of six herbaceous garden perennials. HortTechnology 4(1):61-65.

Johnson, E., M. Bradley, N.P. Harberd, and G.C. Whitelam. 1994. Photoresponses of light-grown *phy*A mutants of *Arabidopsis*. Plant Physiol. 105:141-149.

Kasperbauer, M.J., H.A. Borthwick, and H.M. Cathey. 1963. Cyclic lighting for promotion of sweetclover, *Melilotus abla* Desr. Crop Sci. 3:230-232.

King, R.W. 1984. Light and photoperiodic timing, p.91-105. In: D. Vince-Prue, B. Thomas, and K.E. Cockshull (eds.). Light and the flowering process. Academic Press, San Diego.

Knott, J.E. 1934. Effect of localized photoperiod on spinach. Proc. Amer. Soc. Hort. Sci. 31:152-154.

Krishnamoorthy, H.N. and K.K. Nanda. 1968. Floral bud reversion in *Impatiens balsamina* under non-inductive photoperiods. Planta (Berlin) 80:43-51.

Lane, H.C., H.W. Siegelman, W.L. Butler, and E.M. Firer. 1963. Detection of phytochrome in green plants. Plant Physiol. 38:414-416.

Lang, A. 1965. Physiology of flower initiation, p.1380-1535. In: W. Ruhland (ed.). Encyclopedia of plant physiology. Springer-Verlag, Berlin.

Lange, N.E. 1993. Modeling flower induction in *Lilium longiflorum*. MS Thesis, Michigan State University, East Lansing.

Langhans, R.W. and R.O. Miller. 1963. Influence of daylength, temperature, and number of short days on the flowering of poinsettia (*Euphorbia pulcherimma*). Proc. Amer. Soc. Hort. Sci. 75:753-760.

Lechner, F.J., and W. Rau. 1993. A complex pattern of changes in polysomal mRNA populations is evident in the leaves of *Arabidopsis thaliana* (L.) Heynh. during photoperiodic induction of flowering. Planta 189:522-532.

Lejeune, P., G. Bernier, M. Requier, and J. Kinet. 1993. Sucrose increase during floral induction in the phloem sap collected at the apical part of the shoot of the long-day plant *Sinapis alba* L. Planta 190:71-74.

Le Nard, M. and A.A. De Hertogh. 1993. Bulb growth and development and flowering, p. 29-43. In: A. De Hertogh and M. Le Nard (eds.). The physiology of flower bulbs. Elsevier Science Publishers, Amsterdam, Netherlands.

Melzer, S., D.M. Majewski, and K. Apel. 1990. Early changes in gene expression during the transition from vegetative to generative growth in the long-day plant *Sinapis alba*. Plant Cell 2:953-961.

Metzger, J.D. 1988. Localization of the site of perception of thermoinductive temperatures in *Thlaspi arvense*. Plant Physiol. 88:424-428.

Moe, R. 1988. Flowering physiology of *Gypsophila*. Acta Hort. 218:153-158.

Mortensen, L.M. and E. Stromme. 1987. Effects of light quality on some greenhouse crops. Scientia Hort. 33:27-36.

Napp-Zinn, K. 1987. Vernalization--environmental and genetic regulation, p. 123-132. In: J.G. Atherton (ed.). Manipulation of flowering. Robert Hartnoll, Bodmin, Cornwall.

Ochesanu, C. and I. Barbat. 1965. The photoperiodical sensitivities of leaves depending on their age. Revue Roumaine de Biologie, serie de Botanique 10:403-409.

O'Neill, S.D. 1992. The photoperiodic control of flowering: progress toward understanding the mechanism of induction. Photochem. Photobiol. 56(5):789-801.

Orvos, A.R. and R.E. Lyons. 1989. Photoperiodic inhibition of stem elongation and flowering in *Rudbeckia hirta* 'Marmalade'. J. Amer. Soc. Hort. Sci. 114(2):219-222.

Parks, B.M. and P.H. Quail. 1993. *hy8*, a new class of Arabidopsis long hypocotyl mutants deficient in functional phytochrome A. Plant Cell 5:39-48.

Podol'nyi, V.Z. and A.G. Chetverikov. 1986. Influence of photoperiodic induction and gibberellin on growth of young coneflower leaves and formation of their photosynthetic apparatus. Soviet Plant Physiol. 33:686-692.

Rajapakse, N.C. and J.W. Kelly. 1994. Problems of reporting spectral quality and interpreting phytochrome-mediated responses. HortScience 29(12):1404-1407.

Reed, J.W., A. Nagatani, T.D. Elich, M. Fagan, and J. Chory. 1994. Phytochrome A and phytochrome B have overlapping but distinct functions in *Arabidopsis* development. Plant Physiol. 104:1139-1149.

Reed, J.W., P. Nagpal, D.S. Poole, M. Furuya, and J. Chory.1993. Mutations in the gene for the red/far-red light receptor phytochrome B alter cell elongation and physiological responses throughout Arabidopsis development. Plant Cell 5:147-157.

Reekie, J.Y.C., P.R. Hicklenton, and E.G. Reekie. 1994. Effects of elevated CO_2 on time to flowering in four short-day and four long-day species. Can. J. Bot.72:533-538.

Roberts, E.H. and R.J. Summerfield. 1987. Measurement and prediction of flowering in annual crops, p.17-50. In: J.G. Atherton (ed.). Manipulation of flowering. Robert Hartnoll, Bodmin, Cornwall.

Roberts, E.H., P. Hadley, and R.J. Summerfield. 1985. Effects of temperature and photoperiod on flowering in chickpeas (*Cicer arietinum* L.). Ann. Bot. 55:881-892.

Roberts, E.H., R.J. Summerfield, F.J. Muehlbauer, and R.W. Short. 1986. Flowering in lentil (*Lens culinaris* Medic.): The duration of the photoperiodic inductive phase as a function of accumulated daylength above the critical photoperiod. Ann. Bot. 58:235-248.

Salisbury, F.B. 1981. Responses to photoperiod, p. 135-167. In: O.L. Lange, P.S. Nobel, C.B. Osmund, and H. Ziegler (eds.). Physiological plant ecology, vol. I: Responses to the physical environment. Springer-Verlag, New York.

Salisbury, F.B. and C.W. Ross. 1969. Plant physiology. Wadsworth Publishing, Belmont, California.

Salisbury, F.B., and C.W. Ross. 1978. Plant physiology. 2nd ed. Wadsworth Publishing, Belmont, California.

Shedron, K.G. and T.C. Weiler. 1982. Regulation of growth and flowering in *Chrysanthemum* x *superbum* Bergmans. J. Amer. Soc. Hort. Sci. 107(5):874-877.

Shillo, R. and A.H. Halevy. 1982. Interaction of photoperiod and temperature in flowering-control of *Gypsophila paniculata* L. Scientia Hort. 16:385-393.

Smith, H. 1982. Light quality, photoperception, and plant strategy. Ann. Rev. Plant Physiol. 33:481-518.

Smith, H. 1994. Sensing the light environment: the functions of the phytochrome family, p. 377-416. In: R.E. Kendrick and G.H.M. Kronenberg (eds.). Photomorphogenesis in plants. 2nd ed. Kluwer Academic Publishers, Netherlands.

Smith, H. 1995. Physiological and ecological function within the phytochrome family. Annu. Rev. Plant Physiol. Plant Mol. Biol. 46:289-315.

Song, C.Y., M.S. Roh, S.K. Chung, and R.H. Lawson. 1993. Effect of temperature and light on growth and flowering of potted plant production of *Platycodon*. J. Korean Soc. Hort. Sci. 34(6):446-453.

Sweeney, B.M. 1987. Rhythmic phenomena in plants. 2nd ed. Academic Press, San Diego.

Taiz, L. and E. Zeiger. 1991. Plant physiology. Benjamin/Cummings Publishing, Redwood City, California.

Talon, M. and J.A.D. Zeevaart. 1990. Gibberellins and stem growth as related to photoperiod in *Silene armeria* L. Plant Physiol. 92:1094-1100.

Thomas, B. 1993. The role of phytochrome and other photoreceptors in the control of flowering in long-day plants. Flowering Newsletter 16:6-10.

Thomas, B, and D. Vince-Prue. 1984. Juvenility, photoperiodism and vernalization, p. 408-439. In: M.B. Wilkins (ed.). Advanced plant physiology. Pitman Publishing, London.

Upadhyay, A.P., R.H. Ellis, R.J. Summerfield, E.H. Roberts, and A. Qi. 1994. Characterization of photothermal flowering responses in maturity isolines of soyabean [*Glycine max* (L.) Merrill] cv. Clark. Ann. Bot. 74:87-96.

Vierstra, R.D. and P.H. Quail. 1983. Purification and structural characterization of 124-kDa phytochrome from *Avena*. Biochemistry 22:2498-2505.

Vince, D. 1969. The regulation of flowering in long-day plants. Acta Hort. 14:91-95.

Vince-Prue, D. 1975. Photoperiodism in plants. McGraw, London.

Vince-Prue, D. 1984. Light and the flowering process--setting the scene, p. 3-15. In: D. Vince-Prue, B. Thomas, and K.E. Cockshull (eds.). Light and the flowering process. Academic Press, San Diego.

Vince-Prue, D. 1994. The duration of light and photoperiodic responses, p. 447-490. In: R.E Kendrick and G.H.M. Kronenberg (eds.). Photomorphogenesis in plants. 2nd ed. Kluwer Academic Publishers, Netherlands.

Vince-Prue, D. and A. Takimoto. 1987. Roles of phytochrome in photoperiodic floral induction, p.259-273. In: M. Furuya (ed.). Phytochrome and photoregulation in plants. Academic Press, London.

Waithaka, K. and L.W. Wanjao. 1982. The effect of duration of cold treatment on growth and flowering of liatris. Scientia Hort. 18:153-158.

Wang, S., R.W. Ward, J.T. Ritchie, R.A. Fischer, and U. Schulthess. 1995. Vernalization in wheat: I. A model based on the interchangeability of plant age and vernalization duration. Field Crops Res. 41:91-100.

Wellensiek, S.J. 1958. Vernalization and age in *Lunaria biennis*, p. 561-571. In: Proc. koninklijke nederlandse akademie van wetenschappen, vol. 61.

Weller, J.L. and J.B. Reid. 1993. Photoperiodism and photocontrol of stem elongation in two photomorphogenic mutants of *Pisum sativum* L. Planta 189:15-23.

Whitman, C.M. 1995. Influence of photoperiod and temperature on flowering of *Campanula carpatica* 'Blue Clips; *Coreopsis grandiflora* 'Early Sunrise', *Coreopsis verticllata* 'Moonbeam', *Rudbeckia fulgida* 'Goldsturm' and *Lavandula angustifolia* 'Munstead'. MS Thesis, Michigan State University, East Lansing.

Zeevaart, J.A.D. 1976. Physiology of flower formation. Annu. Rev. Plant Physiol. 27:321-348.

Zeevaart, J.A.D. 1978. Phytohormones and flower formation. P. 291-327. In: Letham, Goodwin, and Higgins (eds.). Phytohormones and related compounds--a comprehensive treatise, vol. II. Elsevier/North-Holland Biomedical Press.

Zeevaart, J.A.D. and D.A. Gage. 1993. ent-Kaurene biosynthesis is enhanced by long photoperiods in the long-day plants *Spinacia oleracea* L. and *Agrostemma githago* L. Plant Physiol. 101:25-29.

Zhang, D., A.M. Armitage, J.M. Affolter, and M.A. Dirr. 1995. Environmental control of flowering and growth of *Lysimachia congestiflora* Hemsl. HortScience 30(1):62-64.

SECTION II

THE EFFECTS OF PHOTOPERIOD AND COLD TREATMENT ON FLOWERING OF TWENTY-FIVE SPECIES OF HERBACEOUS PERENNIALS

Introduction

Herbaceous perennials continue to increase in popularity. Between 1993 and 1994, 86% of firms surveyed saw an average increase of 33% in their sales of perennials (Rhodus and Hoskins, 1995). In the northern states most herbaceous perennials are sold in the spring, when a majority are not in flower. Herbaceous perennials in flower have much more appeal and marketing potential than those sold green, but the flowering requirements of most garden herbaceous perennials are unknown. The flowering requirements for the herbaceous perennials *Dendranthema* spp. and Easter lily (*Lilium longiflorum* Thunb.) have been intensely studied. This knowledge has enabled greenhouse growers to schedule crops to flower on a certain date with desired flowering characteristics. By knowing the flower induction requirements of other species of perennials, a greenhouse grower could force a variety of perennials into flower on a predetermined date.

Some plants flower only after exposure to temperatures less than 7 °C for a certain period of time (Lang, 1965). This is known as vernalization. Other plants flower faster following a cold temperature treatment (e.g., Easter lily), while for others, a cold temperature treatment does not affect flowering. The length and effective temperature range for vernalization varies by species. In general, plants require several weeks of cold to saturate the vernalization response. For example, forty-six percent of the 'Gloriosa' blazing-star (*Liatris spicata* Willd.) herbaceous perennials that received six weeks of 3-5 °C flowered, whereas 90% that received eight weeks of 3-5 °C flowered (Waithaka and

Wanjao, 1982). This suggests that 'Gloriosa' blazing-star requires at least eight weeks of cold for most plants to become vernalized. The most effective temperature range for vernalization of most plants is 1 to 7 °C (Lang, 1965).

Many herbaceous plants flower in response to the duration and timing of light and dark periods in a day or series of days, which is known as photoperiodism (Vince-Prue, 1984). Plants have been divided into three main categories on the basis of flowering in response to photoperiod. Day-neutral plants flower regardless of the photoperiod to which they are exposed. For example, 'Sentimental Blue' balloon flower (*Platycodon grandiflorus* A. DC. 'Sentimental Blue') plants grown under 10-hour (short day) or 16-hour (long day) photoperiods flowered roughly simultaneously; thus, the plant is considered day-neutral (Song et al, 1993). Short-day plants (e.g. Chrysanthemums) only flower, or flower most rapidly, when exposed to fewer than a certain number of hours of light in a 24-hour cycle. In contrast, long-day plants only flower, or flower quicker, when exposed to more than a certain number of hours of light in each 24-hour cycle. It has been shown that the length of the dark period is the critical factor for flower induction: short-day plants require uninterrupted nights longer than a certain duration, and long-day plants require a limited darkness duration. The number of photoperiod cycles required for flowering varies tremendously by species, from as little as one to more than 70 (Vince-Prue, 1975).

Short- and long-day plants can be subdivided further: plants may have either a qualitative or a quantitative response to photoperiod. A qualitative response, also known as an absolute or obligate response, means the plant

requires daylengths that are either shorter or longer than a certain duration to flower. For example, a qualitative long-day plant must have photoperiods that meet or exceed a particular duration to flower. 'Moonbeam' tickseed (*Coreopsis verticillata* L. 'Moonbeam') is an example of a qualitative long-day plant; no plants grown with 8-hour photoperiods after receiving 0, 6, or 12 weeks of 4.5 °C cold treatment flowered, whereas all those grown under 16- or 24-hour photoperiods flowered, regardless of cold treatment (Iversen and Weiler, 1994). A quantitative photoperiodic response describes a particular daylength that hastens, but is not essential for, flowering. Dense-flowered loosestrife (*Lysimachia congestiflora* Hemsl.) is an example of a quantitative long-day plant; days to visible bud decreased from 61 to 27 and flower number increased from 21 to 416 as the photoperiod increased from 8 to 16 hours (Zhang et al., 1995).

The objectives of these experiments were to determine 1) the effects of a vernalizing cold-treatment on flowering, 2) the photoperiodic response category for flowering, 3) the influence of photoperiod on flower number and plant height, and 4) the photoperiod(s) that induced the most complete, rapid, and uniform flowering. The herbaceous perennial species were chosen based on popularity, greenhouse grower interest, and suitability as a potted plant.

Materials and Methods

Plant material. The species studied, plug size, and age of plant material are provided in Table 1. To eliminate juvenility problems, *Coreopsis grandiflora* 'Sunray', *Gaillardia xgrandiflora* 'Goblin', and *Rudbeckia fulgida* 'Goldsturm' were

Tab

Sp

Ar

Ar

As

Ca

Ca

Co

Co

Co

Ec

Ec

G

G

H

H

La

Lu

Lu

Lu

C

P

P

P

P

R

S

S

V

V

a

b

c

d

e

a

P

P

Table 1. Species studied and characteristics of starting material.

Species	Propagation			Plug size[y]	Avg. nodes
	Date	Method	Environment[z]		
Armeria xhybrida 'Dwarf Ornament Mix'	10/3/94	seed	a	128	12.0
Armeria pseudarmeria Mansf.	6/20/94	seed	b	50	35.6
Asclepias tuberosa L.	7/10/94	seed	c	50	0
Campanula carpatica Jacq. 'Blue Clips' (94-5)	9/26/94	seed	a	128	4.9
Campanula carpatica Jacq. 'Blue Clips' (95-6)	8/7/95	seed	d	70	13.0
Coreopsis grandiflora Hogg ex Sweet 'Sunray'	6/25/95	seed	b	50	7.9[xw]
Coreopsis verticillata L. 'Moonbeam' (no cold)	unknown	cutting	unknown	128	2.7[x]
Coreopsis verticillata L. 'Moonbeam' (with cold)	unknown	cutting	unknown	70	3.3[x]
Echinacea purpurea Moench. 'Bravado' (94-5)	10/17/94	seed	a	128	4.2
Echinacea purpurea Moench. 'Bravado' (95-6)	10/9/95	seed	a	128	4.1
Gaillardia xgrandiflora Van Houtte 'Goblin'	6/25/95	seed	b	50	18.8[w]
Gypsophila paniculata L. 'Double Snowflake'	10/17/94	seed	a	128	8.2[x]
Helenium autumnale L.	6/15/95	seed	b	50	5.1
Hibiscus xhybrida 'Disco Belle Mixed'	11/7/94	seed	a	128	4.5
Lavandula angustifolia Mill. 'Munstead Dwarf'	6/10/94	seed	b	50	21.8[x]
Leucanthemum xsuperbum 'Snow Cap'	unknown	tissue culture	unknown	8 cm	11.9
Leucanthemum xsuperbum 'White Knight'	10/9/95	seed	a	128	6.1
Lobelia x *speciosa* Sweet 'Compliment Scarlet'	10/3/94	seed	a	128	6.6
Oenothera missouriensis Sims	10/10/94	seed	a	128	4.4
Phlox paniculata 'Eva Cullum'	6/95	cutting	d	50	8.8[x]
Phlox paniculata 'Tenor'	unknown	cutting	d	50	4.7[x]
Phlox subulata L. 'Emerald Blue'	unknown	cutting	d	70	15.5[x]
Physostegia virginiana Benth 'Alba'	10/10/94	seed	a	128	4.9[x]
Rudbeckia fulgida Ait. 'Goldsturm'	6/1/95	seed	b	50	10.0[w]
Salvia xsuperba 'Blue Queen'	10/17/94	seed	a	128	4.7[x]
Scabiosa columbaria L. 'Butterfly Blue'	8/94	tissue culture	e	8 cm	5.8[x]
Veronica longifolia L. 'Sunny Border Blue'	8/94	cutting	b	50	4.6[x]
Veronica spicata L. 'Blue'	10/24/94	seed	a	128	7.0

[z]a = natural photoperiods, temperatures beginning at 24 °C and gradually decreasing to 19 °C.
b = natural photoperiods, minimum temperatures of 19 °C until last two weeks, when minimum temperatures decreased to 13 °C.
c = same as b, but with 4-hour night interruption lighting from 8/25 to 10/1.
d = natural daylengths, no exposure to temperatures below 12 to 15 °C.
e = natural photoperiods, propagated at 18 °C, held at four weeks with 7 °C night temperatures and 7 to 21 °C day temperatures, then grown at 18 °C for final two weeks.
[y]Volume of 128-, 70-, and 50-cell trays or 8-cm containers are 10, 50, 85, or 350 ml, respectively.
[x]Plants have opposite phyllotaxy, so the number of leaves is twice the number of nodes; all others have alternate phyllotaxy, so the number of nodes equals the number of leaves.
[w]Plants were grown under photoperiods <11 hours for 6 or 7 weeks to attain indicated node count.

grown under natural short-day photoperiods (approximately 10 to 11 hours of light) for seven, six, or six weeks, respectively, before cold treatment or forcing so that they met the recommendations of Yuan (1995).

Plant culture. Plants were grown in a commercial soilless medium composed of composted pine bark, horticultural vermiculite, Canadian sphagnum peat moss, processed bark ash, and washed sand (MetroMix 510, Scotts-Sierra Horticultural Products Company, Marysville, Ohio). Plants were top-watered with well water acidified (two parts H_3PO_4 plus one part H_2SO_4, which provided ≈2.5 mol $P \cdot m^{-3}$) to a titratable alkalinity of approximately 130 mg calcium bicarbonate per liter and fertilized with 14N-0P-6K_2O ($mol \cdot m^{-3}$) from potassium nitrate (14N-0P-55K_2O) (Vicksburg Chemical Co., Vicksburg, MS) and ammonium nitrate (34N-0P-0K_2O) (Cargill, Lexington, KY). Fertilization and acidification rates were adjusted in response to weekly soil test results, so regimes varied during experiments. High-pressure sodium lamps provided a photosynthetic photon flux (*PPF*) of approximately 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant level when the ambient greenhouse *PPF* was lower than 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Cold treatments. Plants received either no cold treatment or were placed in a controlled-environment chamber for 15 weeks at 5 °C. The chamber was lit from 0800 to 1700 HR at approximately 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from cool-white fluorescent lamps (VHOF96T12; Philips, Bloomfield, N.J.), as measured by a LI-COR quantum sensor (model LI-189; LI-COR, Inc., Lincoln, NE). Plants were cold-treated in the containers in which they were received. While in the cooler,

plants were watered with well water acidified (H_2SO_4) to an approximate pH of 6.0.

Photoperiod treatments. In 1994-95, sixty plants of each species and cold treatment were removed from their containers, thinned to a single plant per cell (singulated), and transplanted into 10-cm round containers (470 ml). In 1995-96, seventy plants of each species and cold treatment were removed from their containers, singulated, and transplanted into 13-cm square containers (1.1 liters). Ten plants were placed under each photoperiod treatment that was assigned randomly to benches in the greenhouse. In 1994-95, photoperiods were 10, 12, 14, 16, or 24 hours of continual light or 9 hours with a 4-hour night interruption (NI) from 2200 to 0200 HR. In 1995-96, photoperiods were 10, 12, 13, 14, 16, or 24 hours of continual light or 9 hours with a 4-hour NI. Black cloth was pulled at 1700 HR and opened at 0800 HR every day on all benches to provide similar daily light integrals. Photoperiods were completed with incandescent lamps at 1 to 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For the continual photoperiodic treatments, lamps provided day-extensions; they were turned on at 1700 HR and turned off after each photoperiod was completed.

Greenhouse temperature control. All plants were grown in glass greenhouses set at 20 °C. Air temperatures on each bench were monitored with 36-gauge (0.013-mm-diameter) type E thermocouples connected to a CR10 datalogger (Campbell Scientific, Logan, UT). To provide uniform temperatures, the datalogger controlled a 1500-watt electric heater under each bench, which provided supplemental heat as needed throughout the night. The datalogger collected temperature data every 10 seconds and recorded the hourly average.

Actual average daily air temperatures from the beginning of forcing to the average date of flowering under every photoperiod were calculated for each species and are presented in Table 2.

Data collection and analysis. The leaves of each plant were counted at the onset of forcing. Date of the first visible bud or inflorescence and date of opening of the first flower were recorded for each plant. At flowering, the number of visible flower buds or inflorescences, the number of leaves on the main stem below the first flower, and total plant height were determined. Plants that did not have visible buds or inflorescences after 15 weeks of forcing were discarded and considered nonflowering, but those with visible buds or inflorescences were kept until flowering. Days to visible bud, days from visible bud to flower, days to flower, and increase in node count were calculated.

For each species, a randomized complete block design was used in which blocks were photoperiods with ten observations for each cold treatment. Data were analyzed using SAS's (SAS Institute, Cary, NC) analysis of variance and general linear models procedures.

Presentation of results. For each species, a page with six figures provides illustrations of means and trends; the following apply to these figures. Unless otherwise indicated, all data points represent means of the number of plants that flowered out of ten. (A) and (B) show days to visible bud, days to flower, and percentage of flowering in non-cold treated and cold-treated plants, respectively. (C) shows the average number of initial nodes (n=120) and nodes at flower for non-cold treated plants. (D) shows the number of initial nodes (n=120), nodes

Table 2.

date of flowering

Table 2. Plug size, propagation date, dates of forcing, and average air temperatures from date of forcing to average date of flowering for each species under each photoperiod.

Species	Date of forcing	Weeks of 5C	Average temperature during forcing (°C)						
			Photoperiod (hours)						
			10	12	13	14	16	24	NI[z]
Armeria xhybrida 'Dwarf Ornament Mix'	12/19/94	0	20.6	20.4	-[y]	20.9	20.8	20.6	20.4
	4/4/95	15	20.7	20.6	-	21.1	22.6	21.4	20.4
Armeria pseudarmeria	11/5/94	0	20.5	20.3	-	21.2	21.0	20.8	20.4
	2/19/95	15	20.7	20.4	-	20.9	20.9	20.7	20.7
Asclepias tuberosa	11/5/94	0	--[x]	--	-	--	--	--	--
	2/19/95	15	--	--	-	20.9	21.1	20.7	20.5
Campanula carpatica 'Blue Clips'	12/19/94	0	--	--	-	20.8	20.7	20.6	20.3
	4/4/95	15	--	--	-	21.2	21.6	21.0	20.3
Campanula carpatica 'Blue Clips'	12/6/95	0	--	--	20.6	20.9	20.1	20.4	20.6
	3/29/96	15	--	--	--	21.4	20.9	22.2	21.0
Coreopsis grandiflora 'Sunray'	12/15/95	0	--	20.6	-	20.7	20.1	20.3	20.6
	3/23/96	15	20.8	20.4	21.2	20.9	20.9	21.6	20.8
Coreopsis verticillata 'Moonbeam'	2/19/95	0	20.5	20.3	-	20.9	20.7	20.7	20.7
	2/19/95	15	20.5	20.2	-	21.0	21.0	20.8	20.7
Echinacea purpurea 'Bravado'	12/19/94	0	--	--	-	20.8	20.9	--	20.5
	4/4/95	15	21.5	21.0	-	21.1	22.0	--	20.7
Echinacea purpurea 'Bravado'	12/15/95	0	--	20.7	20.7	21.0	20.3	20.8	20.7
	3/29/96	15	--	--	--	21.9	21.3	--	22.1

[z]Four-hour night interruption.
[y]Photoperiod not included in experiment.
[x]No plants flowered.

Table 2 (cont'd).

Species	Date of forcing	Weeks of 5C	Average temperature during forcing (°C)						
			Photoperiod (hours)						
			10	12	13	14	16	24	NI[z]
Gaillardia xgrandiflora 'Goblin'	12/6/95	0	20.8	–[y]	20.7	21.0	20.3	20.6	20.7
	3/23/96	15	20.6	20.4	21.3	20.9	20.9	21.7	20.9
Gypsophila paniculata 'Double Snowflake'	12/19/94	0	–	–	-[x]	20.9	20.9	20.6	20.4
	4/4/95	15	21.1	–	-	21.7	22.6	21.2	21.1
Helenium autumnale	11/9/95	0	–	–	–	–	20.3	20.5	20.7
	2/1/96	15	–	–	–	21.1	20.7	21.3	20.8
Hibiscus xhybrida 'Disco Belle Mixed'	12/19/94	0	–	20.3	-	20.8	20.7	20.7	20.4
	4/4/95	15	–	–	-	–	–	–	–
Lavandula angustifolia 'Munstead Dwarf'	11/5/94	0	–	–	-	–	–	20.7	20.4
	2/19/95	15	20.7	20.2	-	20.9	21.1	20.8	20.7
Leucanthemum xsuperbum 'Snow Cap'	11/9/95	0	–	–	–	–	20.3	20.6	20.6
	2/1/96	15	21.0	20.9	21.1	21.4	20.6	21.2	20.8
Leucanthemum xsuperbum 'White Knight'	12/15/95	0	–	20.6	20.7	21.0	20.2	20.4	20.8
	3/29/96	15	21.3	20.8	22.0	21.7	21.3	22.4	21.2
Lobelia xspeciosa 'Compliment Scarlet'	12/19/94	0	–	–	-	20.7	20.7	20.5	20.3
	4/4/95	15	21.0	20.8	-	21.1	21.9	20.8	20.4
Oenothera missouriensis	12/19/94	0	–	–	-	20.8	20.7	20.6	20.3
	4/4/95	15	20.5	20.4	-	21.0	21.4	20.5	20.1

[z]Four-hour night interruption.
[y]No plants flowered.
[x]Photoperiod not included in experiment.

Table 2 (cont'd).

Species	Date of forcing	Weeks of 5C	Average temperature during forcing (°C)						
			Photoperiod (hours)						
			10	12	13	14	16	24	NI[z]
Phlox paniculata 'Eva Cullum'	11/9/95	0	–[y]	–	–	20.8	20.2	20.6	20.6
	2/1/96	15	–	20.7	21.1	21.2	20.5	21.1	20.8
Phlox paniculata 'Tenor'	11/9/95	0	–	–	20.5	20.9	20.3	20.6	20.6
	2/1/96	15	–	20.6	21.1	21.2	20.5	21.1	20.8
Phlox subulata 'Emerald Blue'	11/9/95	0	20.6	20.5	20.5	20.9	20.6	21.0	20.6
	2/1/96	15	21.0	20.7	20.6	20.8	20.2	20.5	21.0
Physostegia virginiana 'Alba'	12/19/94	0	–	20.4	-[x]	–	20.7	20.5	20.5
	4/4/95	15	21.5	21.2	-	21.5	22.1	20.8	20.4
Rudbeckia fulgida 'Goldsturm'	12/6/95	0	–	–	–	21.0	20.2	20.6	20.7
	3/23/96	15	–	21.5	21.7	21.3	21.1	22.4	20.8
Salvia xsuperba 'Blue Queen'	12/19/94	0	20.6	–	-	–	–	20.6	20.4
	4/4/95	15	20.3	20.1	-	21.0	21.4	20.4	20.1
Scabiosa columbaria 'Butterfly Blue'	11/5/94	0	20.4	20.3	-	21.1	21.1	20.8	20.4
	2/19/95	15	20.8	20.4	-	21.0	20.9	21.0	20.7
Veronica longifolia 'Sunny Border Blue'	11/5/94	0	–	–	-	–	–	–	–
	2/19/95	15	20.6	20.2	-	20.9	21.1	20.7	20.5
Veronica spicata 'Blue'	12/19/94	0	20.5	20.4	-	20.8	20.7	20.6	20.4
	4/4/95	15	20.2	20.1	-	21.0	21.4	20.6	20.1

[z]Four-hour night interruption.
[y]No plants flowered.
[x]Photoperiod not included in experiment.

after cold treatment (n=60), and nodes at flower for cold-treated plants. (E) and (F) show the number of inflorescences per plant and plant height at flower.

Results and Discussion

Plants were placed into one of six categories based on the effects of photoperiod and cold treatment on flowering (Figure 8). Most plants fit into one of two cold treatment response categories: cold treatment was either beneficial or required for flowering. Plants fit into one of three photoperiodic response categories for flowering; species were day-neutral, facultative (quantitative) long-day, or obligate (qualitative) long-day plants. No species required both cold treatment and long days for flowering. Percent flowering, days to flower, flower number, and uniformity in time to flower were the four primary flowering parameters considered when species were placed into categories.

Several species responded to photoperiod differently before or after cold treatment. For example, *Lobelia xspeciosa* 'Compliment Scarlet' flowered as an obligate long-day plant without a cold treatment, and a facultative long-day plant after cold treatment. For these situations, plants were placed into response categories based on the photoperiodic responses after cold treatment.

Day-Neutral Species That Benefit from a Cold Treatment

***Armeria xhybrida* 'Dwarf Ornament Mix'**. Time to flower in 'Dwarf Ornament Mix' was highly variable, regardless of photoperiod or cold treatment

	Day-neutral Plant	Facultative Long-day Plant	Obligate Long-day Plant	
Cold Beneficial	*Armeria xhybrida* 'Dwarf Ornament Mix'	*Leucanthemum xsuperbum* 'Snow Cap'	*Asclepias tuberosa*	*Helenium autumnale*
	Armeria pseudarmeria	*Leucanthemum xsuperbum* 'White Knight'	*Campanula carpatica* 'Blue Clips'	*Oenothera missouriensis*
	Scabiosa columbaria 'Butterfly Blue'	*Lobelia xspeciosa* 'Complement Scarlet'	*Coreopsis verticillata* 'Moonbeam'	*Phlox paniculata* 'Eva Cullum'
	Veronica spicata 'Blue'		*Echinacea purpurea* 'Bravado'	*Phlox paniculata* 'Tenor'
			Gypsophila paniculata 'Double Snowflake'	*Rudbeckia fulgida* 'Goldsturm'
			Hibiscus xhybrida 'Disco Belle Mixed'	
Cold Required	*Lavandula angustifolia* 'Munstead Dwarf'	*Coreopsis grandiflora* 'Sunray'		
	Phlox subulata 'Emerald Blue'	*Gaillardia xgrandiflora* 'Goblin'		
	Veronica longifolia 'Sunny Border Blue'	*Physostegia virginiana* 'Alba'		
		Salvia x superba 'Blue Queen'		

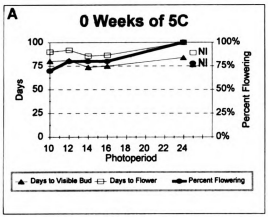
Figure 8. Flowering response categories of herbaceous perennial plants.

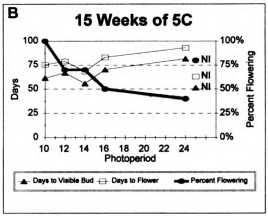
(Figure 9, Table 3). For example, the 95% confidence intervals (CI) of days to flower for plants under the NI treatment were ± 17 or ± 18 days, without or with cold treatment, respectively.

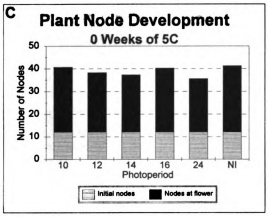
Percentage of flowering increased from 70 to 100 as photoperiod increased from 10 to 24 hours for plants that did not receive 15 weeks of cold treatment. However, the percentage decreased from 100 to 40 as photoperiod increased for plants that did receive the cold treatment. Cold treatment significantly reduced (by approximately two weeks) days to visible bud and flower. It also reduced the number of new nodes formed before flowering from 27 to 21 but did not affect days from visible bud to flower, final plant height, or number of inflorescences.

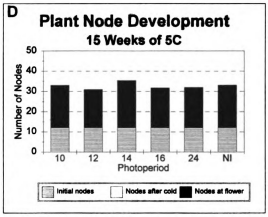
There were no photoperiodic trends in days to visible bud or flower for unchilled plants, but for cold-treated plants time to flower increased linearly as photoperiod increased. This trend suggests that 'Dwarf Ornament Mix' is day-neutral before cold treatment and is a quantitative short-day plant thereafter. However, the latter conclusion is not supported by a reduction in nodes formed under shorter daylengths. There was a linear increase in final plant height as photoperiod increased in unchilled plants. Photoperiod had no effect on flower number.

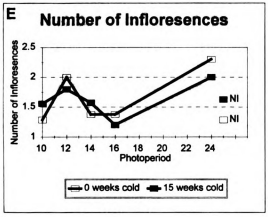
In *Armeria maritima* Willd. 'Düsseldorfer Stolz', 34% of plants flowered (in approximately 25 weeks) when forced under natural photoperiods in a 14 to 16 °C greenhouse beginning in November (Christensen et al., 1989). In January,











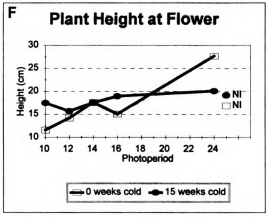


Figure 9. The effects of photoperiod and cold treatment on flowering of *Armeria* x*hybrida* 'Dwarf Ornament Mix'.

Table 3. The effects of photoperiod and cold treatment on flowering of *Armeria xhybrida* 'Dwarf Ornament Mix'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	81	78	12	91	27	17	1.6
15	-	68	65	12	77	21	18	1.6
-	10	85	71	12	83	25	15	1.4
	12	75	74	12	86	23	15	1.9
	14	75	65	12	77	24	18	1.5
	16	65	73	12	85	24	17	1.3
	24	70	83	14	97	22	24	2.2
	NI[z]	79	64	12	76	25	18	1.5
0	10	70	80	10	90	29	12	1.3
	12	80	81	11	92	26	14	2.0
	14	80	74	12	86	25	18	1.4
	16	80	75	12	87	28	15	1.4
	24	100	84	16	100	24	28	2.3
	NI	78	76	13	89	29	17	1.3
15	10	100	62	14	76	21	17	1.6
	12	70	67	12	79	19	16	1.8
	14	70	56	13	68	23	18	1.6
	16	50	70	12	83	20	19	1.2
	24	40	82	12	93	20	20	2.0
	NI	80	51	12	63	21	19	1.6
Significance								
Weeks cold (WC)			***	NS	***	**	NS	NS
Photoperiod (P)			*	NS	*	NS	*	NS
WC × P			NS	*	NS	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			14	3.8	17	6.8	3.7	0.5
15 weeks 5C			18	1.9	18	4.5	2.8	0.6
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	*	NS	NS	***	NS
P_{Linear} (10 to 24 h)			NS	***	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			*	NS	*	NS	NS	NS
NI vs. 24			**	NS	**	NS	NS	NS
P_{Linear} (10 to 24 h)			*	NS	*	NS	NS	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS
0 and 15 weeks 5C								
P_{Linear} (10 to 24 h)			*	NS	*	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS

[z]NI = 4-h night interruption.

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

89% of plants flowered in an average of 14 weeks, and 75% flowered (in about seven weeks) when forced at similar temperatures in March.

Armeria pseudarmeria. Flowering characteristics of *A. pseudarmeria* were highly variable, regardless of photoperiod or cold treatment (Figure 10 and Table 4). The 95% CI of days to flower for plants under NI was reduced after cold treatment, but was still ± 21 days. The relatively large error bars in time to flower in Figure 11 illustrate the nonuniformity of flowering under all photoperiods with both cold treatments.

The 15 weeks of cold treatment increased the percentage of flowering by about one-half. The cold treatment significantly reduced (by approximately 20 days) days to visible bud and flower, increased final plant height by 30%, and increased the average number of inflorescences by 0.5. Cold treatment also reduced the number of new nodes formed before flowering, particularly under the longer photoperiods. After cold treatment, days from visible bud to flower increased an average of two days.

Photoperiod did not affect time to visible bud or flower without or with cold treatment; thus, *A. pseudarmeria* is a day-neutral species with a quantitative response to cold treatment. There was a linear increase in total plant height at flower as photoperiod increased.

***Scabiosa columbaria* 'Butterfly Blue'**. *Scabiosa* flowered uniformly under all photoperiods, especially after cold treatment (Figure 12, Table 5). For example, the 95% CI of days to flower for cold-treated plants under NI was ± 1 day.

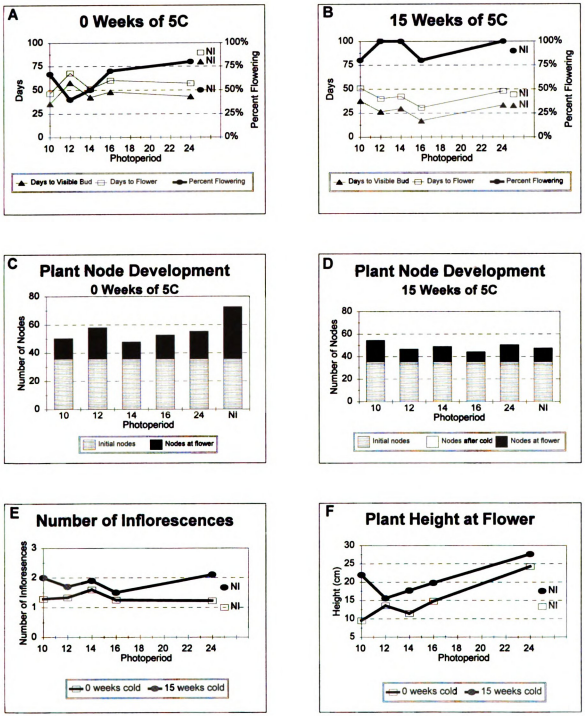


Figure 10. The effects of photoperiod and cold treatment on flowering of *Armeria pseudarmeria*.

Table 4. The effects of photoperiod and cold treatment on flowering of *Armeria pseudarmeria*.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	60	51	11	62	21	14	1.3
15	-	92	30	13	43	13	20	1.8
-	10	74	37	12	49	17	16	1.6
	12	70	42	12	54	17	15	1.5
	14	75	36	11	47	13	15	1.8
	16	75	32	13	45	13	17	1.4
	24	90	38	14	52	17	26	1.7
	NI[z]	70	57	11	67	24	15	1.3
0	10	67	35	11	46	15	10	1.3
	12	40	58	10	68	23	14	1.3
	14	50	42	9	51	12	11	1.6
	16	70	48	12	60	17	15	1.3
	24	80	43	14	57	20	24	1.3
	NI	50	80	10	90	37	13	1.0
15	10	80	38	13	51	19	22	2.0
	12	100	26	14	40	11	16	1.7
	14	100	30	13	43	13	18	1.9
	16	80	17	13	31	9	20	1.5
	24	100	33	15	48	15	28	2.1
	NI	90	33	11	44	12	18	1.7
Significance								
Weeks cold (WC)			***	***	***	**	***	*
Photoperiod (P)			NS	**	NS	NS	***	NS
WC × P			NS	NS	NS	*	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			27	1.9	27	24	13	0
15 weeks 5C			20	2.1	21	5	3	0.8
Contrasts								
Zero weeks 5C								
NI vs. 16			*	NS	NS	**	NS	NS
NI vs. 24			*	**	*	**	**	NS
P_{Linear} (10 to 24 h)			NS	**	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	*	NS	NS	***	NS
P_{Linear} (10 to 24 h)			NS	NS	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	*	NS
0 and 15 weeks 5C								
P_{Linear} (10 to 24 h)			NS	**	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	*	NS

[z]NI = 4-h night interruption.

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

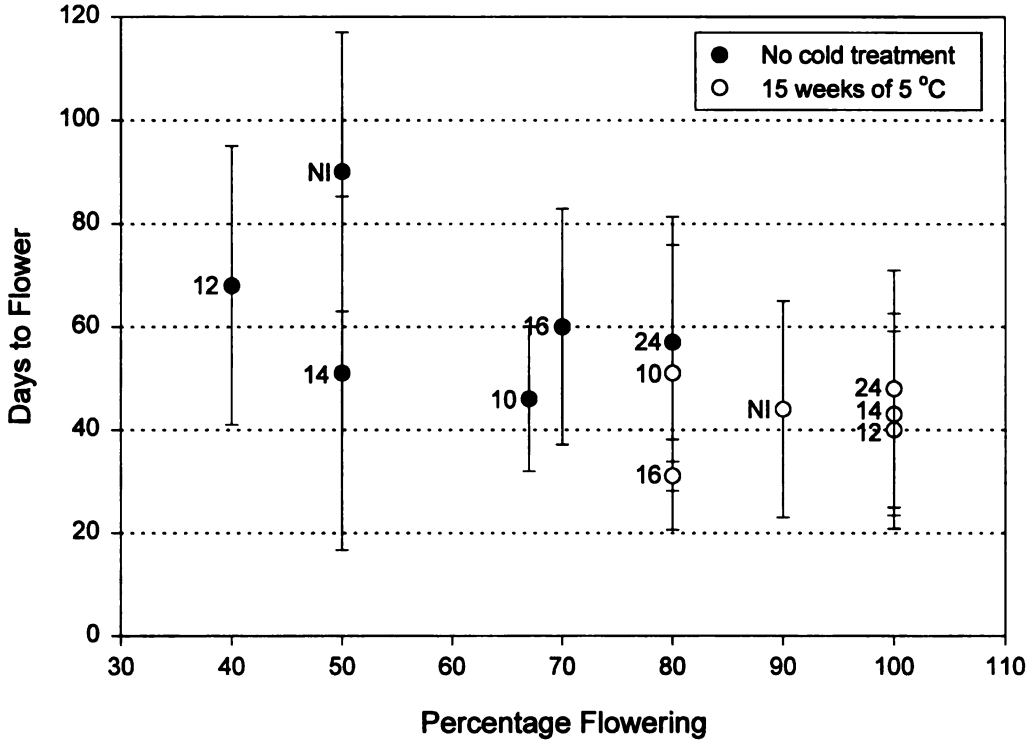


Figure 11. Percentage flowering, time to flower, and flowering uniformity of *Armeria pseudarmeria* under different photoperiods with or without cold treatment. Numbers next to symbols represent photoperiods consisting of nine-hour natural days that were extended with incandescent lamps. NI = nine-hour natural days with four hours of night interruption. Error bars are 95% confidence intervals.

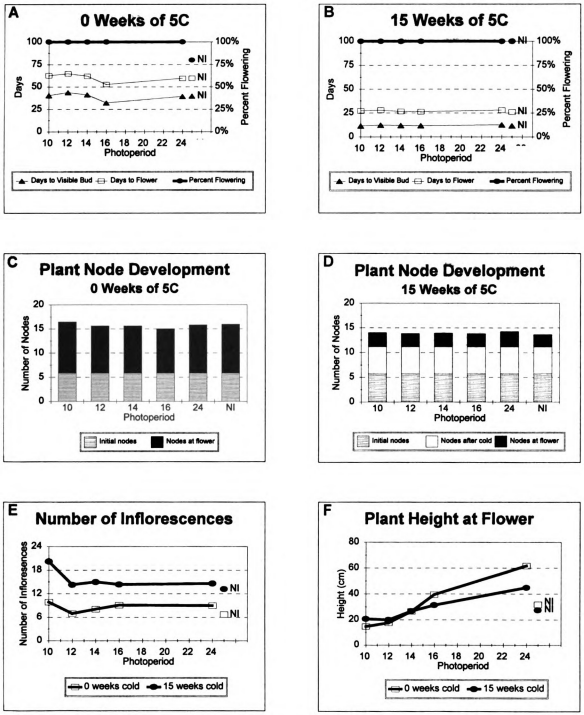


Figure 12. The effects of photoperiod and cold treatment on flowering of *Scabiosa columbaria* 'Butterfly Blue'.

Table 5. The effects of photoperiod and cold treatment on flowering of *Scabiosa columbaria* 'Butterfly Blue'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	100	39	21	60	10	32	8
15	-	100	12	15	27	3	28	15
-	10	100	26	19	45	7	18	15
	12	100	28	18	46	6	19	11
	14	100	27	18	44	6	27	12
	16	100	22	18	40	6	35	12
	24	100	26	18	44	7	53	12
	NI[z]	100	26	17	43	6	30	10
0	10	100	40	22	63	11	15	10
	12	100	44	21	65	10	17	7
	14	100	41	21	62	10	26	8
	16	100	32	21	53	9	39	9
	24	100	39	20	60	10	62	9
	NI	100	40	20	60	10	32	7
15	10	100	12	16	27	3	21	20
	12	100	12	16	28	3	20	14
	14	100	12	15	27	3	27	15
	16	100	12	15	26	3	31	14
	24	100	13	16	28	3	45	15
	NI	100	12	15	26	3	28	13
Significance								
Weeks cold (WC)			***	***	***	***	***	***
Photoperiod (P)			NS	*	NS	NS	***	***
WC × P			NS	NS	NS	NS	***	NS
95% Confidence interval for NI								
Zero weeks 5C			6.8	1.8	7.6	0.6	3.4	2.6
15 weeks 5C			1.0	0.9	1.0	0.5	3.1	3.8
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	*	NS	NS	***	NS
NI vs. 24			NS	NS	NS	NS	***	NS
P_{Linear} (10 to 24 h)			NS	NS	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	*	NS	NS
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	*	NS
NI vs. 24			NS	NS	NS	NS	***	NS
P_{Linear} (10 to 24 h)			NS	NS	NS	NS	***	*
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	**
0 and 15 weeks 5C								
P_{Linear} (10 to 24 h)			NS	*	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	*	NS	*

[z]NI = 4-h night interruption.

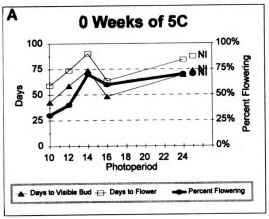
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

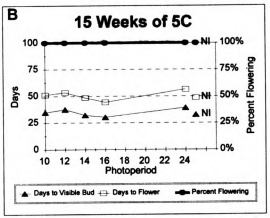
All plants flowered, irrespective of cold treatment or photoperiod. Cold treatment cut time to flower in half, reduced the number of new nodes formed from ten to three, and increased flower number nearly two-fold. Plants developed an average of five nodes (ten leaves) during cold treatment, which partially explains the reduction in nodes formed after cold.

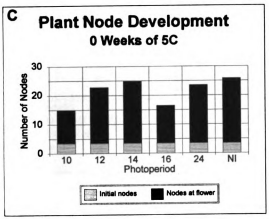
Photoperiod did not affect days to visible bud or flower, which suggests that 'Butterfly Blue' is day-neutral. Final plant height increased over four-fold as photoperiod increased from 10 to 24 hours without a cold treatment and two-fold with the cold treatment.

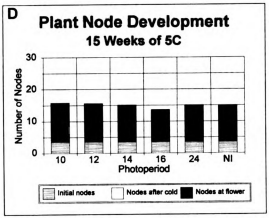
***Veronica spicata* 'Blue'**. Cold treatment dramatically increased the percentage of flowering and improved uniformity of all flowering characteristics measured (Figure 13, Table 6). Only half of the plants flowered without cold treatment, but all plants flowered after cold treatment. Under NI, cold treatment reduced the 95% (CI) for days to flower from about 16 to 2 days. Cold treatment also reduced plant height by an average of 13 cm. Engle (1994) observed a similar effect of cold treatment on flowering; 43% or 98% of plants flowered without or with 15 weeks of 5 °C cold treatment, respectively.

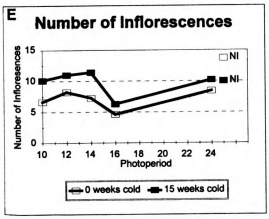
Final plant height increased linearly as photoperiod increased for plants that did not receive cold. Cold treatment and photoperiod interacted with each of the following: days to visible bud, days to flower, and increase in node number. Without cold treatment, days to visible bud and flower increased linearly as photoperiod increased. However, the percentage of flowering increased as photoperiod increased. If plants had remained on the benches longer, more











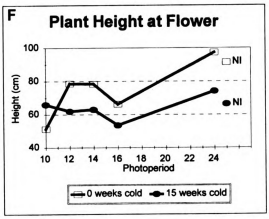


Figure 13. The effects of photoperiod and cold treatment on flowering of *Veronica spicata* 'Blue'.

Table 6. The effects of photoperiod and cold treatment on flowering of *Veronica spicata* 'Blue'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	57	61	15	76	36	77	8
15	-	100	34	16	50	23	64	10
-	10	65	39	16	55	24	59	8
	12	70	48	16	64	31	70	10
	14	85	53	16	69	33	71	9
	16	80	39	15	54	23	60	5
	24	85	54	16	70	32	86	9
	NI[z]	85	53	15	68	34	79	12
0	10	30	43	16	59	23	51	7
	12	40	59	15	74	39	79	8
	14	70	74	17	90	43	78	7
	16	60	48	15	64	26	66	5
	24	70	69	15	84	40	97	8
	NI	70	73	14	87	45	91	14
15	10	100	35	17	51	25	66	10
	12	100	38	16	54	24	62	11
	14	100	32	16	49	23	63	11
	16	100	30	14	44	20	54	6
	24	100	39	17	56	23	74	10
	NI	100	33	16	49	23	66	10
Significance								
Weeks cold (WC)			***	NS	***	***	**	NS
Photoperiod (P)			**	NS	***	***	***	***
WC × P			**	NS	**	***	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			16.5	1.6	16.4	10.8	25.1	7.5
15 weeks 5C			2.7	1.5	2.4	2.8	5.0	1.3
Contrasts								
Zero weeks 5C								
NI vs. 16			***	NS	***	***	**	***
NI vs. 24			NS	NS	NS	NS	NS	*
P_{Linear} (10 to 24 h)			*	NS	*	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	*	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			NS	NS	NS	NS	NS	NS
$P_{Quadratic}$ (10 to 24 h)			NS	*	NS	NS	*	NS
0 and 15 weeks 5C								
P_{Linear} (10 to 24 h)			*	NS	*	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS

[z]NI = 4-h night interruption.

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

would have flowered, which would have increased the average time to flower, particularly under the shorter photoperiods. After cold treatment, plants were day-neutral because their flowering was unaffected by daylength. The number of new nodes formed decreased after cold treatment, but the reduction varied with photoperiod.

Day-Neutral Species That Require a Cold Treatment

***Lavandula angustifolia* 'Munstead Dwarf'.** Few plants flowered without cold treatment (Figure 14, Table 7), and those that did required more than 80 days and were rangy. After cold treatment, all plants flowered uniformly, in about 50 days. Cold treatment reduced the number of new nodes formed before flower by 14 (28 leaves). 'Munstead' plants grown under NI from 50-cell plugs that received 15 weeks of 5 °C flowered over 40 days earlier than non-cold treated plants (Whitman, 1995). Engle (1994) found that 15%, 15%, 17%, 35%, 56%, or 84% of 'Munstead' plants flowered after receiving 0, 2, 4, 6, 8, or 10 weeks of 5 °C cold treatment, respectively.

After cold treatment, photoperiod did not significantly affect days to flower; thus, 'Munstead Dwarf' is day-neutral. Photoperiod also did not influence the number of new nodes formed or the number of inflorescences. Plant height increased linearly from 32 to 41 cm as the photoperiod increased from 10 to 24 hours. Whitman (1995) found that 'Munstead' plants grown under 4-hour NI had a greater percentage of flowering and flowered three to seven days earlier than plants grown without NI.

A

125

10

Days

7

C

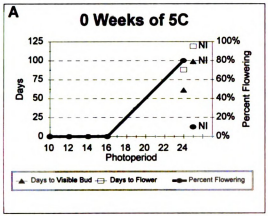
Number of Nodes

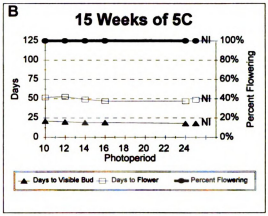
E

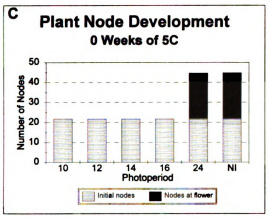
Number of Interseccos

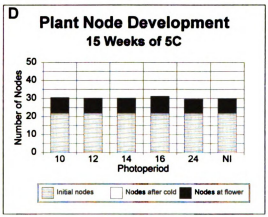
F

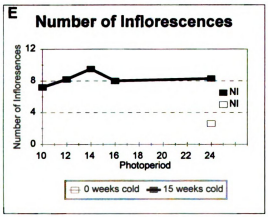
La











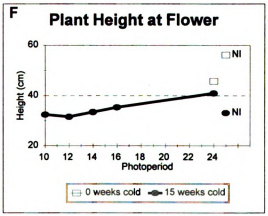


Figure 14. The effects of photoperiod and cold treatment on flowering of *Lavandula angustifolia* 'Munstead Dwarf'.

Table 7. The effects of photoperiod and cold treatment on flowering of *Lavandula angustifolia* 'Munstead Dwarf'.

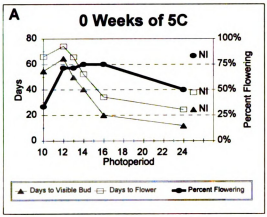
Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	15	65	26	92	23	47	2.9
15	-	100	19	30	49	9	34	8.0
-	10	50	21	31	52	9	32	7.2
	12	50	20	33	53	9	32	8.2
	14	50	19	30	49	9	33	9.5
	16	50	19	28	47	10	35	8.0
	24	90	37	28	65	15	43	5.8
	NI[z]	55	26	30	55	10	35	6.4
0	10	0	--[y]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	0	--	--	--	--	--	--
	16	0	--	--	--	--	--	--
	24	80	61	27	88	23	46	2.6
	NI	10	99	20	119	23	56	5.0
15	10	100	21	31	52	9	32	7.2
	12	100	20	33	53	9	32	8.2
	14	100	19	30	49	9	33	9.5
	16	100	19	28	47	10	35	8.0
	24	100	18	29	47	8	41	8.3
	NI	100	18	31	49	8	33	6.5
Significance								
Weeks cold (WC)			***	***	***	***	***	NS
Photoperiod (P)			*	***	NS	NS	NS	NS
WC × P			**	**	*	NS	**	NS
95% Confidence interval for NI								
15 weeks 5C			3.3	2.7	5.0	1.1	3.0	3.6
Contrasts								
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	***	NS
P_{Linear} (10 to 24 h)			NS	**	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS

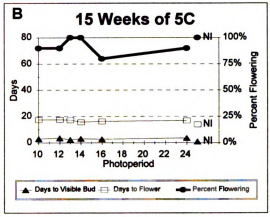
[z]NI = 4-h night interruption.
[y]-- = No plants showed visible bud after 105 days of forcing.
[NS, *, **, ***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

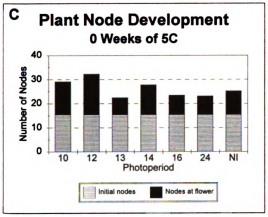
***Phlox subulata* 'Emerald Blue'**. Cold treatment increased percentage of flowering, flower number, and flowering uniformity (Figure 15, Table 8). Two-thirds of plants flowered without cold treatment, but flowering was sporadic and sparse; plants averaged less than 10 flowers per plant. After the cold treatment nearly all plants flowered and flower number increased by over four-fold. The 95% CI of days to flower for plants under NI was reduced by over 8-fold.

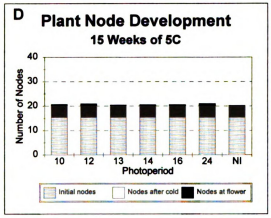
There was an interaction with cold treatment and photoperiod for days to visible bud, days to flower, the number of new nodes formed, and final plant height. Without cold treatment, flowering was progressively hastened as the photoperiod increased, which suggests that 'Emerald Blue' is a quantitative long-day plant. Flower buds were immediately visible on plants in all photoperiods after cold treatment, so photoperiod did not influence time to flower. Thus, 'Emerald Blue' is day-neutral after cold. Flower number showed a quadratic response to photoperiod, reaching a maximum under the 14-hr photoperiod.

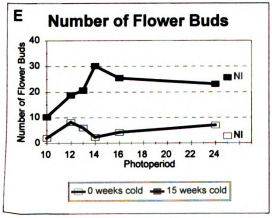
***Veronica longifolia* 'Sunny Border Blue'**. No plants flowered without cold treatment and all plants flowered uniformly after cold treatment (Figure 16, Table 9). Plants developed approximately two nodes (four leaves) during the cold treatment. Photoperiod did not influence days to visible bud, days to flower, the number of new nodes formed, or flower number. Plant height at flower increased from 33 to 38 cm as the photoperiod increased from 10 to 24 hours. Engle (1994) found that a cold treatment of five weeks at 5 °C increased the percentage of flowering from 3 to 100.











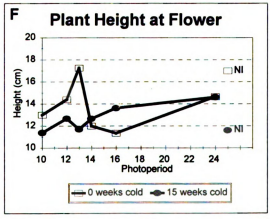
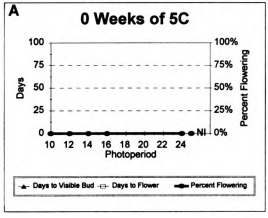


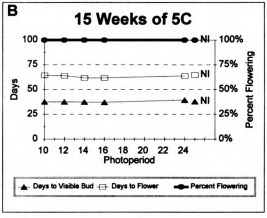
Figure 15. The effects of photoperiod and cold treatment on flowering of *Phlox subulata* 'Emerald Blue'.

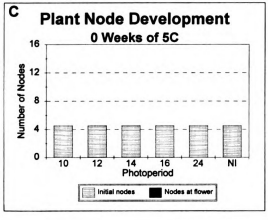
Table 8. The effects of photoperiod and cold treatment on flowering of *Phlox subulata* 'Emerald Blue'.

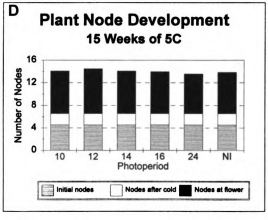
Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	64	38	12	51	11	14	5
15	-	93	3	14	16	5	13	22
-	10	63	29	13	42	8	12	6
	12	82	34	12	46	10	14	13
	13	88	26	14	41	6	14	13
	14	93	22	12	34	7	12	16
	16	78	11	13	25	6	12	15
	24	75	8	13	21	6	15	15
	NI[z]	94	13	13	26	6	14	14
0	10	33	55	11	66	14	13	2
	12	71	65	10	74	17	14	8
	13	71	50	12	66	7	17	6
	14	75	40	12	52	12	12	2
	16	75	20	13	34	8	12	4
	24	50	12	13	24	8	15	7
	NI	83	24	12	38	10	17	3
15	10	90	3	14	18	5	11	10
	12	90	4	14	18	6	13	19
	13	100	2	15	17	5	12	21
	14	100	3	13	16	5	13	30
	16	80	3	14	16	5	14	25
	24	90	4	13	17	6	15	23
	NI	100	1	13	14	5	12	26
Significance								
Weeks cold (WC)			***	***	***	***	***	***
Photoperiod (P)			***	NS	***	***	*	NS
WC × P			***	NS	***	**	***	NS
95% Confidence interval for NI								
Zero weeks 5C			11.8	5.0	17.7	5.7	0	1.5
15 weeks 5C			1.0	1.5	2.1	0.7	1.2	9.0
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	***	NS
NI vs. 24			*	NS	*	NS	NS	NS
P_{Linear} (10 to 24 h)			***	NS	***	**	NS	NS
$P_{Quadratic}$ (10 to 24 h)			*	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	*	NS
NI vs. 24			NS	NS	NS	NS	***	NS
P_{Linear} (10 to 24 h)			NS	NS	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	**
0 and 15 weeks 5C								
P_{Linear} (10 to 24 h)			***	NS	***	*	*	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS

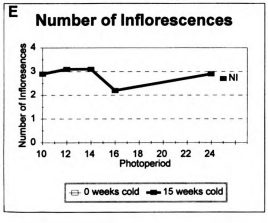
[z]NI = 4-h night interruption.
NS,*,**,*** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.











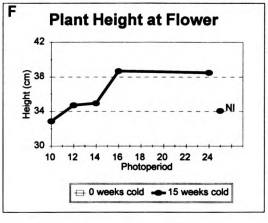


Figure 16. The effects of photoperiod and cold treatment on flowering of *Veronica longifolia* 'Sunny Border Blue'.

Table 9. The effects of photoperiod and cold treatment on flowering of *Veronica longifolia* 'Sunny Border Blue'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	0	–[z]	–	–	–	–	–
15	-	100	38	26	63	7	36	2.8
15	10	100	38	27	64	8	33	2.9
	12	100	38	26	64	8	35	3.1
	14	100	37	25	62	8	35	3.1
	16	100	37	25	62	7	39	2.2
	24	100	39	25	64	7	38	2.9
	NI[y]	100	38	27	65	7	34	2.7
Significance								
Photoperiod (P)			NS	**	NS	NS	***	NS
95% Confidence interval for NI								
15 weeks 5C			3.8	1.2	3.7	0.6	2.8	0.6
Contrasts								
15 weeks 5C								
NI vs. 16			NS	*	NS	NS	**	NS
NI vs. 24			NS	**	NS	NS	**	NS
P_{Linear} (10 to 24 h)			NS	*	NS	NS	***	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	*	NS

[z]–No plants showed visible bud after 105 days of forcing.
[y]NI = 4-h night interruption.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Facultative Long-day Species That Benefit from a Cold Treatment

***Leucanthemum* x*superbum* 'Snow Cap'**. Without a cold treatment, no plants flowered under photoperiods ≤14 hours, but at least 60% of plants flowered under photoperiods ≥16 hours or NI (Figure 17, Table 10). All plants flowered after cold treatment. Cold accelerated (by approximately ten days) time to visible bud and flower, reduced final plant height by four to six cm, and improved flowering uniformity (Figure 18). Under photoperiods ≥16 hours or NI, cold treatment more than doubled the number of inflorescences.

Days to visible bud and flower, days from visible bud to flower, and the number of new nodes formed decreased linearly as photoperiod increased. Plant height increased linearly from 10 to 17 cm as the photoperiod increased from 10 to 24 hours. Flower number was greatest under photoperiods ≥16 hours or NI.

The effects of cold treatment and photoperiod on flowering of *L.* x*superbum* (formerly *Chrysanthemum* x *superbum* or *C. maximum*) varies considerably by cultivar or clone. Non-cold treated 'Esther Read' daisy chrysanthemum (*C. maximum* Ramond, 'Esther Read') remained vegetative under 12-hour photoperiods and flowered under photoperiods of 13 hours or longer (Griffin and Carpenter, 1964). Non-cold treated 'T.E. Killian' daisy chrysanthemum plants flowered only under 15-hour photoperiods and remained vegetative under 14-hour or shorter photoperiods (Griffin and Carpenter, 1964). Shedron and Weiler (1982) propagated five clones of 'G. Marconi' shasta daisy

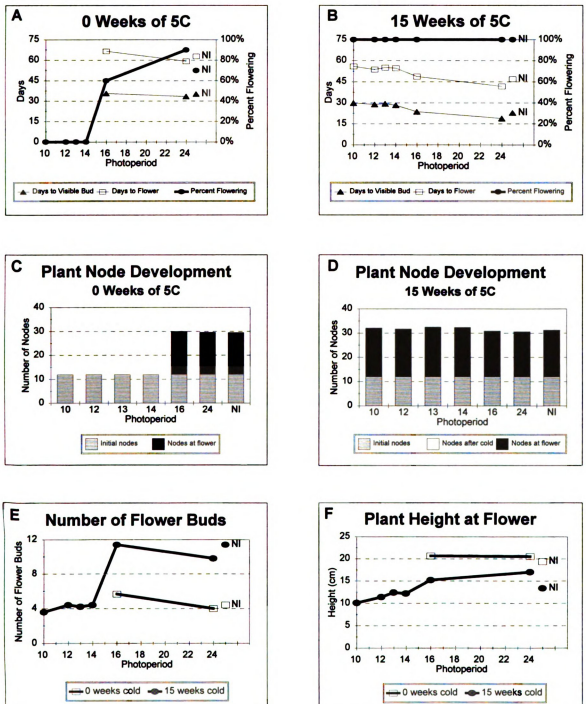


Figure 17. The effects of photoperiod and cold treatment on flowering of *Leucanthemum xsuperbum* 'Snow Cap'.

Table 10. The effects of photoperiod and cold treatment on flowering of *Leucanthemum xsuperbum* 'Snow Cap'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	31	35	28	62	18	20	5
15	-	100	26	25	51	20	13	7
-	10	50	30	26	56	20	10	4
	12	50	29	25	54	20	11	4
	13	50	29	26	55	21	12	4
	14	50	28	26	55	20	12	4
	16	80	30	28	58	18	18	9
	24	95	26	24	51	18	19	7
	NI[z]	85	29	26	55	18	16	8
0	10	0	--[y]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	0	--	--	--	--	--	--
	14	0	--	--	--	--	--	--
	16	60	36	31	67	18	21	6
	24	90	33	26	59	18	21	4
	NI	70	35	28	63	18	19	4
15	10	100	30	26	56	20	10	4
	12	100	29	25	54	20	11	4
	13	100	29	26	55	21	12	4
	14	100	28	26	55	20	12	4
	16	100	24	25	49	19	15	11
	24	100	19	23	42	19	17	10
	NI	100	23	24	47	19	13	11
Significance								
Weeks cold (WC)			***	***	***	*	***	***
Photoperiod (P)			***	***	***	NS	***	***
WC × P			NS	*	NS	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			3.3	1.4	3.2	1.3	2.3	1.5
15 weeks 5C			1.1	0.8	1.0	0.9	0.8	1.4
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	**	NS	NS	NS	NS
NI vs. 24			NS	*	*	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	*	NS
NI vs. 24			*	NS	**	NS	***	NS
P_{Linear} (10 to 24 h)			***	***	***	*	***	***
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	*	***

[z]NI = 4-h night interruption.
[y]-- = No plants showed visible bud after 105 days of forcing.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

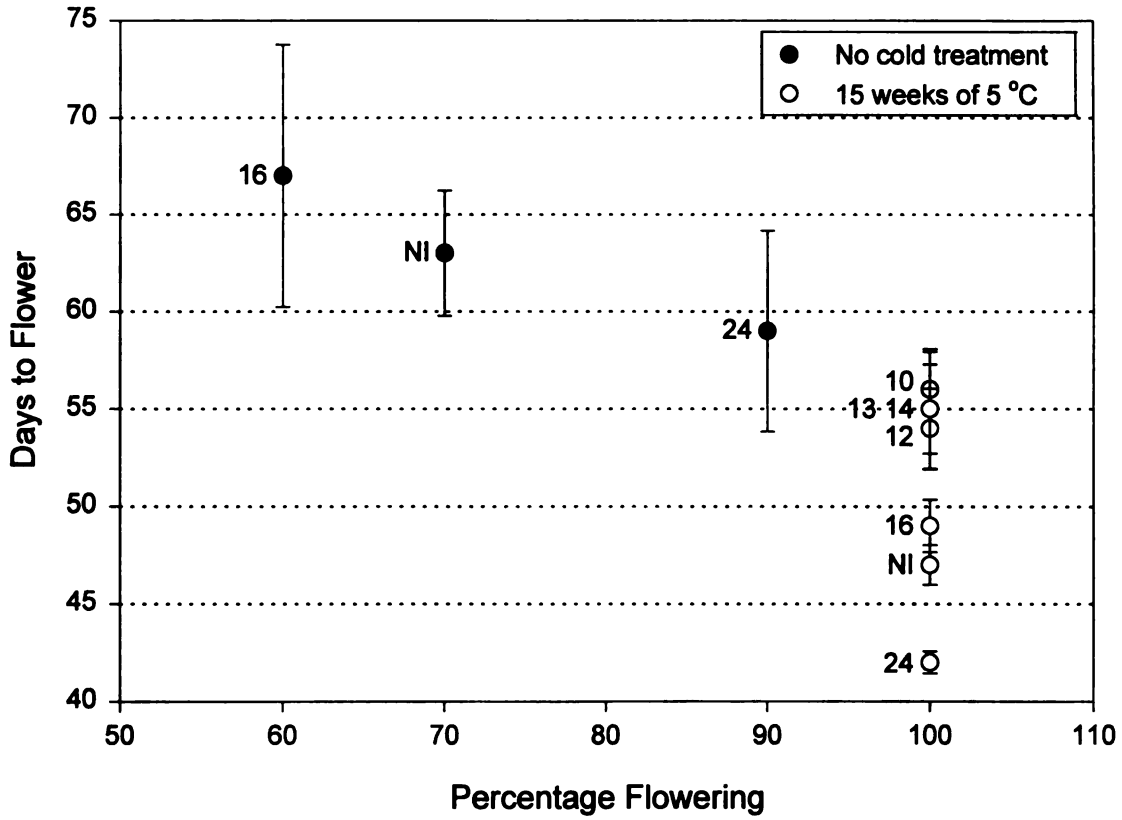


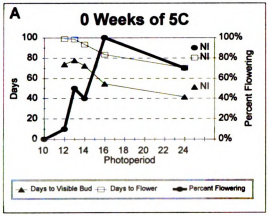
Figure 18. Percentage flowering, time to flower, and flowering uniformity of *Leucanthemum xsuperbum* 'Snow Cap' under different photoperiods with or without cold treatment. Numbers next to symbols represent photoperiods consisting of nine-hour natural days that were extended with incandescent lamps. NI = nine-hour natural days with four hours of night interruption. Error bars are 95% confidence intervals.

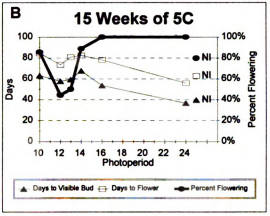
(*Chrysanthemum* x *superbum* Bergmans) and placed them under photoperiods of 10, 12, 14, 16, or 18 hours. Two clones were photoperiodic, one responded to cold temperatures, and two responded to cold treatment and photoperiod. Damann and Lyons (1995) found that *C.* x*superbum* 'Snow Lady' flowered as a facultative long-day plant .

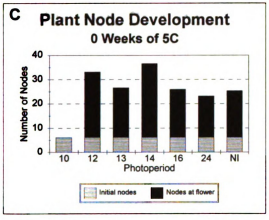
***Leucanthemum* x*superbum* 'White Knight'**. Flowering of 'White Knight', propagated from seed, was not as rapid, complete, or uniform as 'Snow Cap', which was a tissue-cultured clone (Figures 18 and 20). One-half of the plants flowered without cold treatment, and three-fourths flowered after cold treatment (Figure 19, Table 11). The uniformity of time to flower increased nearly two-fold after cold treatment. Cold treatment hastened flowering by about nine days but had no effect on the number of new nodes formed, final plant height, or flower number.

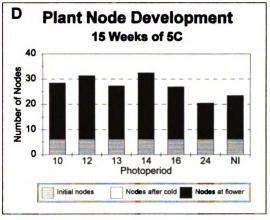
Under photoperiods of ≤14 hours, many plants did not flower without cold treatment; after cold treatment, while more plants flowered, flowering was not uniform. The greatest percentage of flowering was achieved under photoperiods ≥16 hours or NI, regardless of cold treatment. Days to visible bud and flower and the number of new nodes formed decreased linearly as the photoperiod lengthened. Therefore, 'White Knight' responded as a quantitative long-day plant. Photoperiod did not influence plant height or flower number.

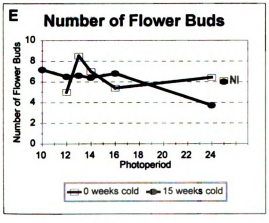
***Lobelia* x*speciosa* 'Compliment Scarlet'**. Cold treatment did not accelerate flowering or improve flowering uniformity, but it did increase flower











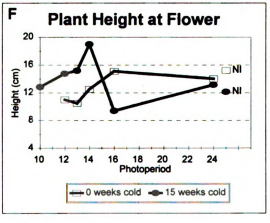


Figure 19. The effects of photoperiod and cold treatment on flowering of *Leucanthemum xsuperbum* 'White Knight'.

Table 11. The effects of photoperiod and cold treatment on flowering of *Leucanthemum xsuperbum* 'White Knight'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	52	57	29	82	20	14	6
15	-	75	53	22	73	20	14	6
-	10	38	63	22	85	22	13	7
	12	26	61	26	80	26	14	6
	13	50	69	23	86	21	14	7
	14	63	69	25	86	28	17	7
	16	100	54	28	82	20	13	6
	24	82	39	24	63	16	14	5
	NI[z]	85	46	27	72	18	14	6
0	10	0	--[y]	--	--	--	--	--
	12	10	74	25	99	27	11	5
	13	50	78	28	99	21	11	9
	14	40	73	29	94	31	13	7
	16	100	55	29	84	20	15	5
	24	70	41	29	70	17	14	6
	NI	90	51	29	80	19	15	6
15	10	86	63	22	85	22	13	7
	12	44	58	26	74	25	15	7
	13	50	59	21	81	21	15	7
	14	89	68	23	83	26	19	6
	16	100	54	25	78	21	9	7
	24	100	37	19	56	14	13	4
	NI	80	40	24	63	17	12	6
Significance								
Weeks cold (WC)			**	***	***	NS	NS	NS
Photoperiod (P)			***	NS	***	***	NS	NS
WC × P			NS	NS	NS	NS	**	NS
95% Confidence interval for NI								
Zero weeks 5C			9.6	3.5	10.2	3.2	2.7	2.0
15 weeks 5C			5.9	1.5	5.7	1.9	2.0	2.3
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	*	NS	NS	NS
P_{Linear} (12 to 24 h)			***	NS	***	***	NS	NS
$P_{Quadratic}$ (12 to 24 h)			NS	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			*	NS	**	NS	NS	NS
NI vs. 24			NS	**	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			***	*	***	***	NS	*
$P_{Quadratic}$ (10 to 24 h)			NS	*	NS	NS	NS	NS

[z]NI = 4-h night interruption.
[y]-- = No plants showed visible bud after 105 days of forcing.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

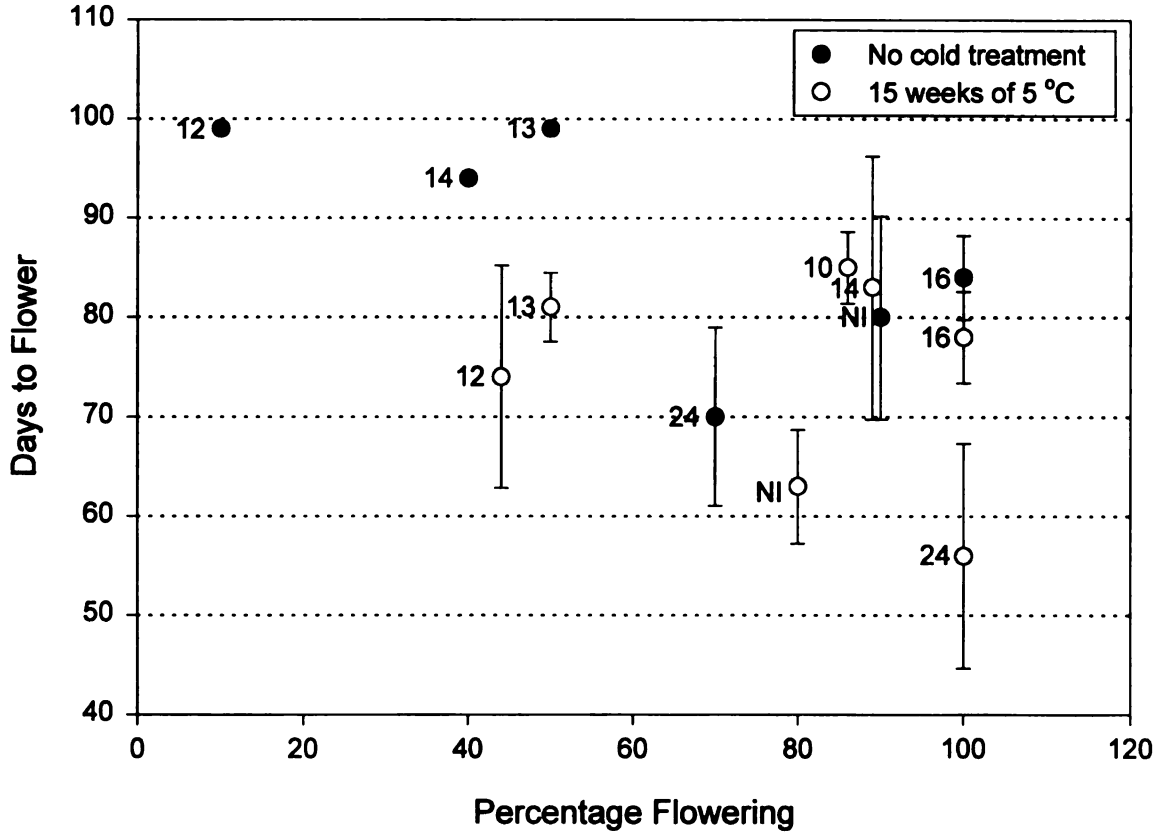


Figure 20. Percentage flowering, time to flower, and flowering uniformity of *Leucanthemum* x*superbum* 'White Knight' under different photoperiods with or without cold treatment. Numbers next to symbols represent photoperiods consisting of nine-hour natural days that were extended with incandescent lamps. NI = nine-hour natural days with four hours of night interruption. Error bars are 95% confidence intervals. Symbols without error bars indicate that the confidence intervals were too large for the graph.

number and the number of new nodes formed (Figure 21, Table 12). Plants without or with the cold treatment averaged 21 and 48 flowers, respectively. Some of this increase is likely due to naturally higher light levels when cold-treated plants were grown.

'Compliment Scarlet' flowered as an obligate long-day plant before cold treatment and as a facultative long-day plant after cold treatment. Without cold treatment, 'Compliment Scarlet' only flowered under photoperiods ≥14 hours or NI. In contrast, all cold-treated plants flowered and as the photoperiod duration increased, days to visible bud and flower and the number of new nodes formed decreased linearly. For example, as the photoperiod increased from 10 to 24 hours, days to flower decreased from 83 to 64. The number of flower buds and plant height were greatest under 14-hour photoperiods and both decreased under shorter or longer photoperiods.

Engle (1994) found that no 'Compliment Scarlet' plants flowered without a cold treatment. After 15 weeks of 5 °C, 80 or 100% of plants flowered without or with a 4-hour NI, respectively. However, 'Queen Victoria' flowered completely under NI without a cold treatment (Engle, 1994).

Facultative Long-day Species That Require a Cold Treatment

***Coreopsis grandiflora* 'Sunray'**. 'Sunray' requires a cold treatment for flowering (Yuan, 1995). However, plants that were not cold-treated but exposed to seven weeks of short days prior to transfer to the experimental photoperiods flowered under all but 10-hour photoperiods (Figure 22, Table 13). Exposure to

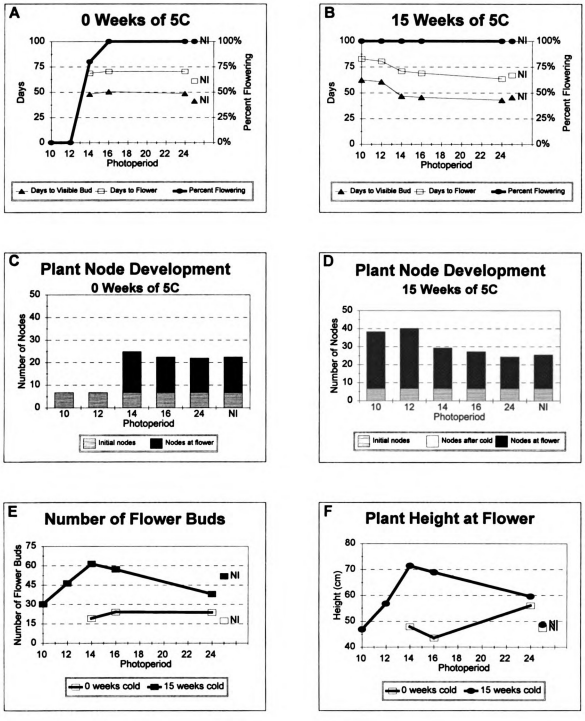


Figure 21. The effects of photoperiod and cold treatment on flowering of *Lobelia* x*speciosa* 'Compliment Scarlet'.

Table 12. The effects of photoperiod and cold treatment on flowering of *Lobelia xspeciosa* 'Compliment Scarlet'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	76	47	21	68	16	49	21
15	-	100	51	22	73	24	59	48
-	10	67	62	21	83	32	47	30
	12	67	61	20	81	34	57	46
	14	90	47	23	70	21	62	44
	16	100	48	22	70	18	56	40
	24	100	46	21	67	16	58	31
	NI[z]	100	44	21	64	17	48	35
0	10	0	--[y]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	80	48	21	69	18	48	19
	16	100	51	20	71	16	44	24
	24	100	49	22	71	15	56	24
	NI	100	41	20	61	16	47	17
15	10	100	62	21	83	32	47	30
	12	100	61	20	81	34	57	46
	14	100	47	24	71	23	71	61
	16	100	46	23	69	21	69	57
	24	100	43	21	64	18	60	38
	NI	100	46	21	67	19	49	52
Significance								
Weeks cold (WC)			NS	**	NS	*	***	***
Photoperiod (P)			***	*	**	***	**	*
WC × P			NS	*	NS	NS	**	NS
95% Confidence interval for NI								
Zero weeks 5C			7.1	1.3	6.4	3.0	9.7	5.9
15 weeks 5C			5.8	2.0	6.3	3.2	10.9	23.3
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (14 to 24 h)			NS	NS	NS	NS	NS	NS
$P_{Quadratic}$ (14 to 24 h)			NS	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	***	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			***	NS	***	***	NS	NS
$P_{Quadratic}$ (10 to 24 h)			*	***	NS	*	***	***

[z]NI = 4-h night interruption.
[y]-- = No plants showed visible bud after 105 days of forcing.
[NS, *, **, ***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

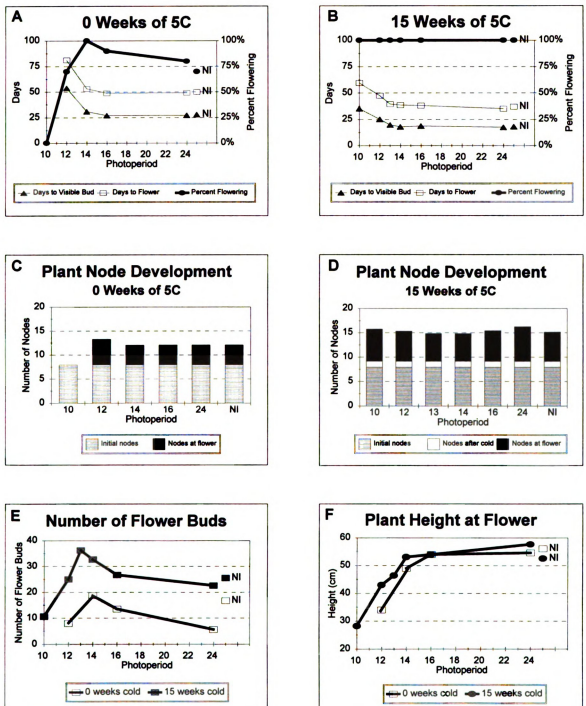


Figure 22. The effects of photoperiod and cold treatment on flowering of *Coreopsis grandiflora* 'Sunray'.

Table 13. The effects of photoperiod and cold treatment on flowering of *Coreopsis grandiflora* 'Sunray'.

Weeks of 5C[z]	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	68	33	23	56	4	50	13
15	-	100	22	20	42	6	48	26
-	10	50	35	24	60	7	28	11
	12	85	39	25	64	6	38	17
	14	100	24	21	46	5	51	26
	16	95	23	21	43	5	54	20
	24	90	22	20	42	6	56	14
	NI[y]	85	23	21	44	5	54	21
0	10	0	–[x]	–	–	–	–	–
	12	70	54	27	81	5	34	8
	14	100	31	22	53	4	49	19
	16	90	27	22	49	4	54	13
	24	80	27	22	49	4	55	6
	NI	70	28	22	50	4	56	17
15	10	100	35	24	60	7	28	11
	12	100	25	22	47	6	43	25
	13	100	20	20	40	6	46	36
	14	100	18	21	39	6	53	33
	16	100	19	19	38	6	54	27
	24	100	18	18	35	7	58	23
	NI	100	18	19	37	6	53	26
Significance								
Weeks cold (WC)			***	***	***	***	NS	***
Photoperiod (P)			***	***	***	NS	***	***
WC × P			***	NS	***	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			3.2	2.9	3.1	3.5	4.8	6.7
15 weeks 5C			0.9	1.0	1.2	1.5	2.8	5.4
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	**
P_{Linear} (12 to 24 h)			***	***	***	NS	***	*
$P_{Quadratic}$ (12 to 24 h)			***	***	***	*	***	**
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	*	NS	NS
P_{Linear} (10 to 24 h)			***	***	***	*	***	NS
$P_{Quadratic}$ (10 to 24 h)			***	**	***	*	***	***

[z]All plants were grown under natural short-day photoperiods for 51 days prior to forcing or cold treatment.
[y]NI = 4-h night interruption.
[x]– = No plants showed visible bud after 105 days of forcing.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

short days can be substituted by a cold requirement, or vice-versa (Ketellapper and Barbaro, 1966). However, in another experiment, 'Sunray' plants that received 10 weeks of nine-hour short days followed by long days did not flower, perhaps because of heat stress from warm day temperatures (26 to 30 °C) (Damann and Lyons, 1993).

Cold treatment increased the percentage of flowering from 68 to 100, improved flowering uniformity, doubled the flower number, but did not influence plant height. Cold treatment reduced the time to visible bud and flower by approximately 30 days under 12-hour photoperiods and by 10 to 15 days under photoperiods ≥13 hours or NI.

Days to visible bud and flower decreased at a decreasing rate as the photoperiod increased from 12 to 24 hours in non-cold-treated plants and from 10 to 24 hours in cold-treated plants. For example, as the photoperiod increased, time to flower decreased from 81 to 49 days or 60 to 35 days for non-cold-treated or cold-treated plants, respectively. Plant height increased at a decreasing rate as photoperiods increased, but photoperiod did not significantly affect the number of nodes formed. Plants had the most flowers under 13- and 14-hour photoperiods.

***Gaillardia* x*grandiflora* 'Goblin'**. Only 43% of non-cold-treated plants flowered, and those that did flowered sporadically (Figure 23, Table 14). For example, without cold treatment, the 95% CI of days to flower for plants under NI was ± 14 days. After cold treatment, 91% of the plants flowered and much more

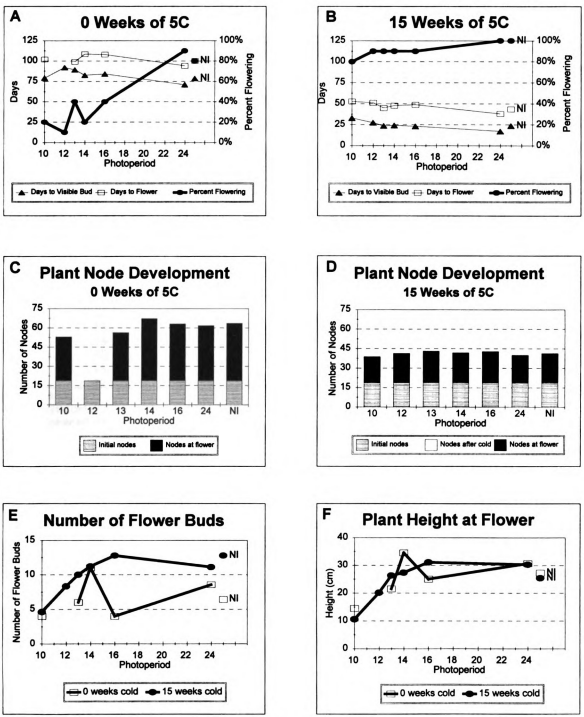


Figure 23. The effects of photoperiod and cold treatment on flowering of *Gaillardia xgrandiflora* 'Goblin'.

Table 14. The effects of photoperiod and cold treatment on flowering of *Gaillardia xgrandiflora* 'Goblin'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	43	79	24	100	43	27	7
15	-	91	24	22	47	23	25	10
-	10	50	42	21	63	23	11	5
	12	50	34	24	51	23	20	8
	13	65	44	21	55	27	25	9
	14	55	35	24	59	28	29	11
	16	65	42	25	59	29	29	10
	24	95	43	22	64	30	30	10
	NI[z]	90	48	23	68	31	26	10
0	10	20	79	23	102	34	15	4
	12	10	92	–[y]	–	–	–	–
	13	40	89	19	99	38	22	6
	14	20	83	26	109	49	35	11
	16	40	84	24	108	44	25	4
	24	90	71	23	94	43	31	9
	NI	80	79	25	100	45	27	6
15	10	80	33	20	53	20	11	5
	12	90	27	24	51	23	20	8
	13	90	24	21	45	24	26	10
	14	90	24	24	48	23	27	11
	16	90	23	25	49	24	31	13
	24	100	17	21	38	21	30	11
	NI	100	24	21	44	22	25	13
Significance								
Weeks cold (WC)			***	NS	***	***	NS	**
Photoperiod (P)			NS	*	NS	NS	***	NS
WC × P			NS	NS	NS	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			16.7	3.5	13.9	14.2	5.5	4.4
15 weeks 5C			5.0	2.1	4.1	2.7	3.7	4.2
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			NS	NS	NS	NS	*	NS
$P_{Quadratic}$ (10 to 24 h)			NS	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	**	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			***	NS	*	NS	***	*
$P_{Quadratic}$ (10 to 24 h)			***	***	NS	NS	***	**

[z]NI = 4-h night interruption.
[y]The only plant with visible bud died before flowering.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

uniformly (the 95% CI for plants under NI was ± 4 days)(Figure 24). Cold treatment reduced days to flower from 100 to 47 days, reduced the number of new nodes formed from 43 to 23, and increased flower number from seven to ten. Cold treatment did not affect final plant height. Evans and Lyons (1988) found that multiple gibberellin applications (100 ppm GA_{4+7}) could replace the cold-treatment requirement for 'Goblin'.

As the photoperiod increased from 10 to 24 hours, cold-treated plants flowered faster, had more flowers, and were taller. Days to flower decreased from 53 to 38, flower number increased from 5 to 13, and plant height increased from 11 to 31 cm. Photoperiod did not significantly affect the number of new nodes formed. Thus, 'Goblin' requires cold treatment and photoperiods ≥13 hours or NI for complete, rapid, and uniform flowering.

***Physostegia virginiana* 'Alba'**. Cold treatment increased the percentage of flowering from 47% to 90%, increased flower number from an average of 2.9 to 7.0, and improved flowering uniformity (Figure 25, Table 15). Without a cold treatment, all plants flowered only when under continual light; ≤ 50% of the plants flowered under other photoperiods.

Sixty, 80, or 100 percent of cold-treated plants flowered under 10-, 12-, or ≥14-hour photoperiods or NI, respectively. Days to visible bud and flower decreased linearly as the photoperiod increased from 10 to 24 hours. The number of new nodes formed decreased from 23 nodes (46 leaves) under 12 hours to 12 nodes (26 leaves) under continual light. Flower number increased linearly from 3.0 to 9.5 as the photoperiod increased from 10 to 24 hours. An

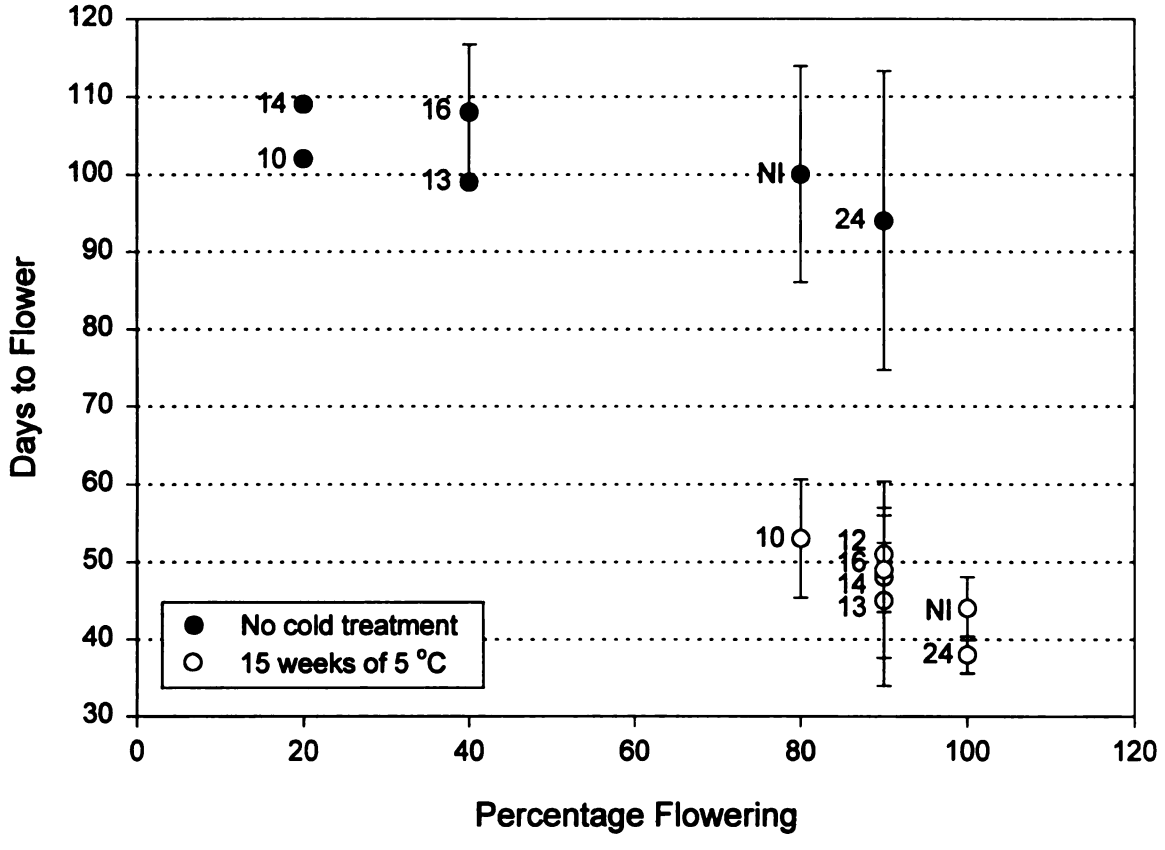


Figure 24. Percentage flowering, time to flower, and flowering uniformity of *Gaillardia xgrandiflora* 'Goblin' under different photoperiods with or without cold treatment. Numbers next to symbols represent photoperiods consisting of nine-hour natural days that were extended with incandescent lamps. NI = nine-hour natural days with four hours of night interruption. Error bars are 95% confidence intervals. Symbols without error bars indicate that the confidence intervals were too large for the graph.

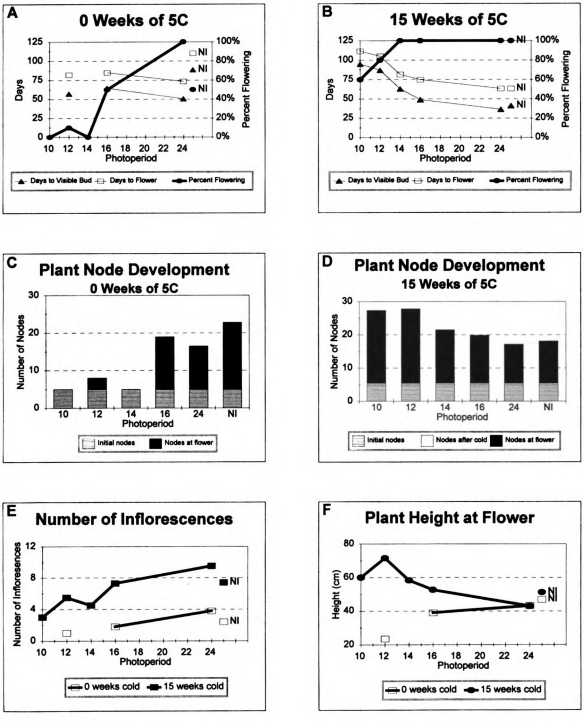


Figure 25. The effects of photoperiod and cold treatment on flowering of *Physostegia virginiana* 'Alba'.

Table 15. The effects of photoperiod and cold treatment on flowering of *Physostegia virginiana* 'Alba'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	47	63	22	85	13	42	2.9
15	-	90	59	22	80	14	53	7.0
-	10	40	95	16	111	22	60	3.0
	12	60	84	19	102	16	56	4.0
	14	67	63	19	82	16	58	4.5
	16	75	54	24	78	14	48	5.5
	24	100	43	25	68	12	43	6.7
	NI[z]	75	57	22	79	14	50	5.7
0	10	0	—[y]	—	—	—	—	—
	12	20	57	25	82	3	24	1.0
	14	0	—	—	—	—	—	—
	16	50	65	20	85	14	39	1.8
	24	100	50	23	73	12	43	3.8
	NI	50	89	22	110	18	47	2.4
15	10	60	95	16	111	22	60	3.0
	12	80	87	18	105	23	72	5.5
	14	100	63	19	82	16	58	4.5
	16	100	49	26	75	15	53	7.3
	24	100	36	27	63	12	43	9.5
	NI	100	41	22	64	13	51	7.4
Significance								
Weeks cold (WC)			***	NS	***	***	***	***
Photoperiod (P)			***	***	***	***	NS	***
WC × P			***	**	***	***	***	NS
95% Confidence interval for NI								
Zero weeks 5C			6.6	2.1	6.8	5.7	6.5	2.6
15 weeks 5C			2.4	1.3	3.2	2.4	4.4	1.4
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	***	*	NS
NI vs. 24			**	NS	*	*	NS	NS
15 weeks 5C								
NI vs. 16			***	***	***	***	***	***
NI vs. 24			***	NS	**	**	**	*
P_{Linear} (10 to 24 h)			***	***	***	***	NS	**
$P_{Quadratic}$ (10 to 24 h)			NS	***	NS	*	***	NS

[z]NI = 4-h night interruption.
[y]— = No plants showed visible bud after 105 days of forcing.
[NS, *, **, ***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

experiment with *P. virginiana* 'Summer Snow' and 'Vivid' also concluded that this species is a quantitative long-day plant: percentage of flowering decreased and days to flower increased as exposure to long-days increased (Beattie et al., 1989).

***Salvia* x *superba* 'Blue Queen'**. Only 22% of the plants that were not treated with cold flowered, and those that did took an average of 101 days to flower (Figure 26, Table 16). In contrast, all cold-treated plants flowered. In a separate experiment, all 'Blue Queen' flowered regardless of cold treatment or photoperiod (Engle, 1994).

Plants under photoperiods $\geq$14 hours or NI flowered uniformly (the 95% CI of days to flower for cold-treated plants under NI was ± 2 days). As the photoperiod increased from 10 to 24 hours, days to flower decreased from 58 to 29, final plant height increased linearly from 29 to 47 cm, and the number of new nodes formed decreased from 13 (26 leaves) to seven (14 leaves). Cold and photoperiod had no effect on flower number.

Obligate Long-day Species That Benefit from a Cold Treatment

***Campanula carpatica* 'Blue Clips'**. Plants grown from 50-cell plug trays in 1995-96 flowered 12 to 15 days faster than plants grown from 128-cell plug trays in 1994-95 (Figures 27 and 28, Tables 17 and 18). The following results and discussion apply to both years in which *Campanula* was studied.

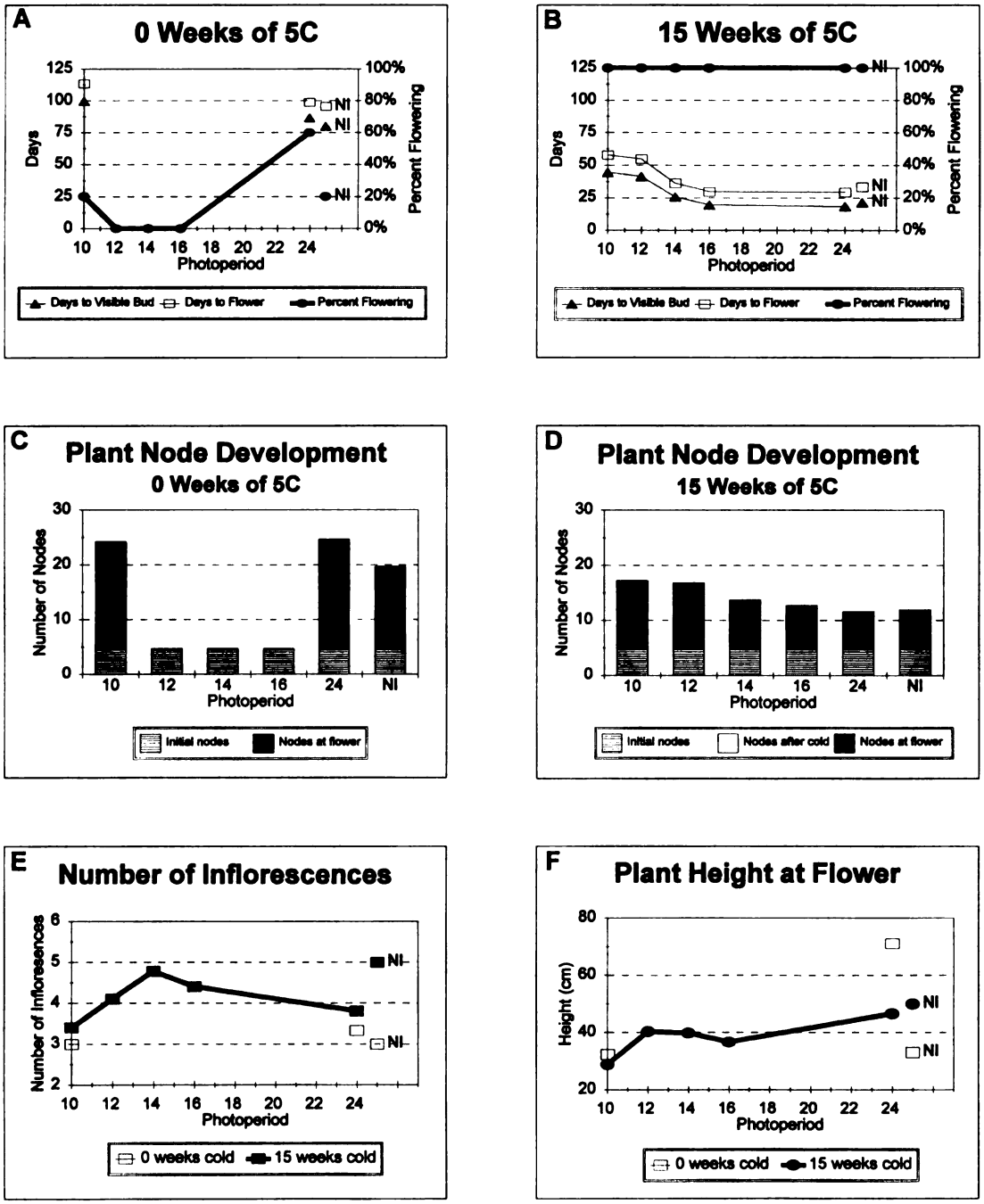


Figure 26. The effects of photoperiod and cold treatment on flowering of *Salvia* x *superba* 'Blue Queen'.

Table 16. The effects of photoperiod and cold treatment on flowering of *Salvia* x *superba* 'Blue Queen'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	22	88	13	101	19	56	3.2
15	-	100	29	12	40	9	40	4.2
-	10	60	54	14	67	14	29	3.3
	12	67	41	13	55	12	40	4.1
	14	67	26	11	36	9	40	4.8
	16	67	20	10	30	8	37	4.4
	24	80	44	11	55	12	56	3.6
	NI[z]	60	31	13	44	9	47	4.7
0	10	20	100	14	114	20	32	3.0
	12	0	--[y]	--	--	--	--	--
	14	0	--	--	--	--	--	--
	16	0	--	--	--	--	--	--
	24	60	87	12	99	20	71	3.3
	NI	20	80	16	96	15	33	3.0
15	10	100	45	13	58	13	29	3.4
	12	100	41	13	55	12	40	4.1
	14	100	26	11	36	9	40	4.8
	16	100	20	10	30	8	37	4.4
	24	100	19	11	29	7	47	3.8
	NI	100	22	12	33	7	50	5.0
Significance								
Weeks cold (WC)			***	*	***	***	NS	NS
Photoperiod (P)			***	***	***	***	***	NS
WC × P			*	NS	NS	***	***	NS
95% Confidence interval for NI								
15 weeks 5C			2.0	0.7	1.9	1.1	4.6	0.8
Contrasts								
Zero weeks 5C								
NI vs. 24			NS	*	NS	***	***	NS
15 weeks 5C								
NI vs. 16			NS	*	NS	NS	***	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			***	**	***	***	***	NS
$P_{Quadratic}$ (10 to 24 h)			***	***	***	***	NS	NS

[z]NI = 4-h night interruption.
[y]-- = No plants showed visible bud after 105 days of forcing.
[NS, *, **, ***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

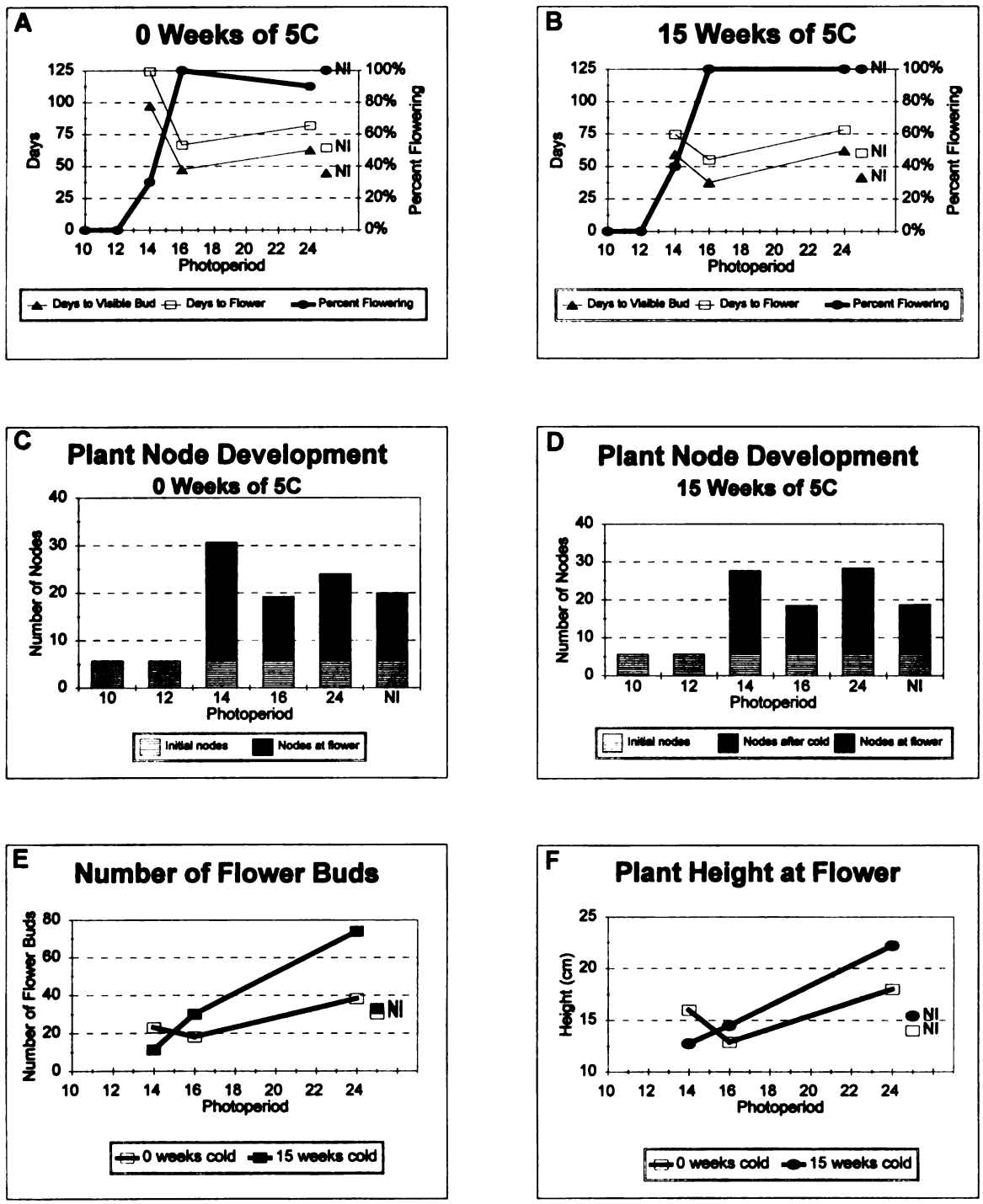


Figure 27. The effects of photoperiod and cold treatment on flowering of *Campanula carpatica* 'Blue Clips'. 1994-95.

Table 17. The effects of photoperiod and cold treatment on flowering of *Campanula carpatica* 'Blue Clips': 1994-95.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	64	56	20	76	16	15	28
15	-	67	48	17	65	17	17	41
-	10	0	--[z]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	35	78	21	100	24	14	17
	16	100	43	18	61	13	14	24
	24	95	62	18	80	21	20	56
	NI[y]	100	43	19	62	14	15	32
0	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	30	97	27	124	25	16	23
	16	100	48	19	67	14	13	18
	24	90	63	19	82	18	18	38
	NI	100	45	20	64	14	14	30
15	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	40	59	16	75	22	13	11
	16	100	38	18	55	13	15	30
	24	100	62	16	78	23	22	74
	NI	100	42	19	60	13	15	33
Significance								
Weeks cold (WC)			***	***	***	NS	NS	*
Photoperiod (P)			***	***	***	***	***	***
WC × P			**	***	***	***	*	***
95% Confidence interval for NI								
Zero weeks 5C			5.0	1.1	5.7	1.3	2.3	5.9
15 weeks 5C			5.6	1.3	5.0	1.8	1.5	10.2
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	*
NI vs. 24			***	NS	***	***	**	NS
P_{Linear} (14 to 24 h)			**	***	***	*	*	*
$P_{Quadratic}$ (14 to 24 h)			***	***	***	***	*	NS
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			***	**	***	***	***	***
P_{Linear} (14 to 24 h)			*	NS	NS	**	***	***
$P_{Quadratic}$ (14 to 24 h)			***	*	***	***	NS	NS
0 and 15 weeks 5C								
P_{Linear} (14 to 24 h)			NS	***	NS	NS	***	***
$P_{Quadratic}$ (14 to 24 h)			***	**	***	***	NS	NS

[z]-- = No plants showed visible bud after 105 days of forcing.
[y]NI = 4-h night interruption.
[NS,*,**,***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

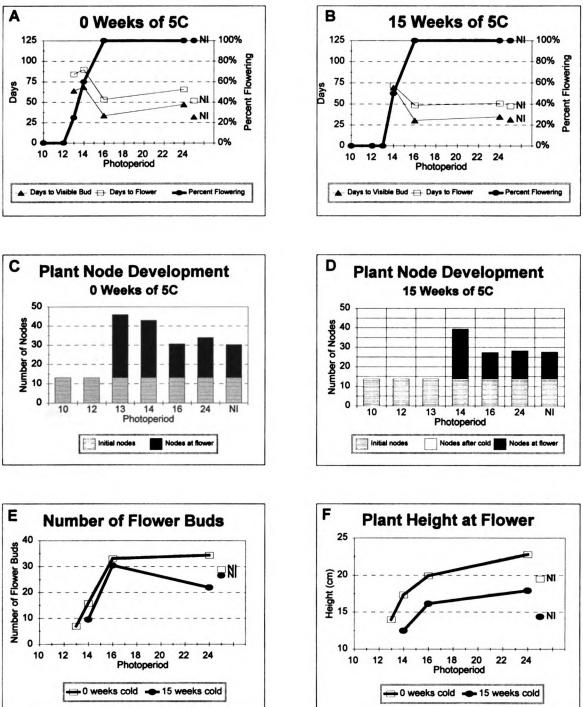


Figure 28. The effects of photoperiod and cold treatment on flowering of *Campanula carpatica* 'Blue Clips'. 1995-96.

Table 18. The effects of photoperiod and cold treatment on flowering of *Campanula carpatica* 'Blue Clips': 1995-96.

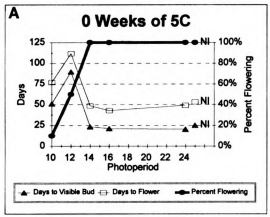
Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	77	43	20	63	21	20	29
15	-	72	38	17	50	15	16	25
-	10	0	--[z]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	13	64	20	84	33	14	7
	14	55	69	20	85	29	16	14
	16	100	32	19	51	16	18	32
	24	100	41	17	58	18	20	28
	NI[y]	100	32	18	50	15	17	28
0	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	25	64	20	84	33	14	7
	14	60	69	21	90	30	17	16
	16	100	34	20	54	18	20	33
	24	100	47	18	66	21	23	34
	NI	100	32	20	52	17	20	29
15	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	0	--	--	--	--	--	--
	14	50	70	17	72	26	13	10
	16	100	30	18	49	14	16	31
	24	100	35	16	51	14	18	22
	NI	100	32	16	47	14	14	27
Significance								
Weeks cold (WC)			NS	***	***	***	***	NS
Photoperiod (P)			***	NS	***	***	**	**
WC × P			NS	NS	NS	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			4.4	1.1	3.9	0.9	2.4	6.5
15 weeks 5C			4.8	1.1	4.6	2.0	1.0	4.7
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			***	NS	***	**	*	NS
P_{Linear} (13 to 24 h)			**	NS	***	***	**	**
$P_{Quadratic}$ (13 to 24 h)			***	NS	***	***	NS	*
15 weeks 5C								
NI vs. 16			NS	*	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	*	NS
P_{Linear} (14 to 24 h)			***	NS	**	***	NS	NS
$P_{Quadratic}$ (14 to 24 h)			***	NS	***	***	NS	*

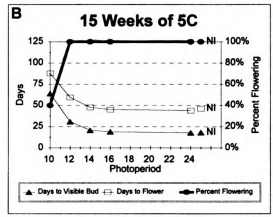
[z]-- = No plants showed visible bud after 105 days of forcing.
[y]NI = 4-h night interruption.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

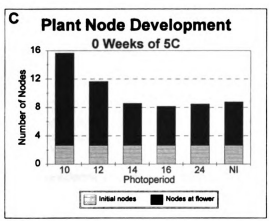
Cold treatment did not affect the percentage of flowering but reduced days to flower by five to fifteen days under photoperiods ≥16 hours or NI. However, slightly warmer bench temperatures (0.5 to 1 °C) likely contributed to this hastening of flowering. Based on experiments by Whitman (1995), a temperature increase of 1 °C would have accelerated days to flower by 1.5 days. Cold treatment did not consistently affect any other flowering characteristic measured. Whitman (1995) found that plants grown from 128-cell plugs that received 14 weeks of 5 °C flowered approximately 10 days faster than plants that did not receive a cold treatment, but cold did not hasten flowering of plants grown from 50-cell plugs.

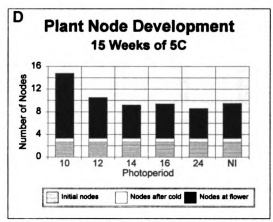
Campanula is an obligate long-day plant; no plants flowered under photoperiods ≤12 hours and essentially all plants flowered under photoperiods ≥16 hours or NI. Under continual light, flowering was delayed and nonuniform. Thirty to 60% of plants flowered under 14-hour photoperiods and flowering was delayed by at least 30 days compared to plants under 16-hour photoperiods. Thus, photoperiods ≥16 hours, but not continual light, or NI are recommended for rapid, uniform flowering. Plant height increased linearly from 14 to 20 cm as photoperiod increased from 14 to 24 hours. There were no consistent photoperiodic trends for flower number.

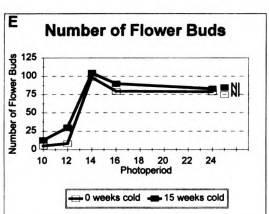
***Coreopsis verticillata* 'Moonbeam'**. Horticulturally, 'Moonbeam' is an obligate long-day plant. Flowering was complete, rapid, and uniform under photoperiods ≥14 hours or NI, regardless of cold treatment (Figure 29, Table 19). Plants flowered in 45 to 50 days, developed an average of five to six nodes (10











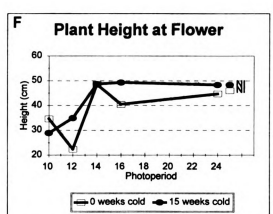


Figure 29. The effects of photoperiod and cold treatment on flowering of *Coreopsis verticillata* 'Moonbeam'.

Table 19. The effects of photoperiod and cold treatment on flowering of *Coreopsis verticillata* 'Moonbeam'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	77	38	25	64	7.6	39	57
15	-	90	28	27	55	7.0	43	67
-	10	25	58	25	83	12.3	32	9
	12	75	60	25	86	8.1	29	19
	14	100	22	26	48	5.9	49	101
	16	100	20	24	44	5.8	45	85
	24	100	19	27	47	5.6	47	81
	NI[z]	100	22	28	50	6.2	47	80
0	10	10	51	26	77	13.0	35	5
	12	50	90	22	112	9.0	22	8
	14	100	23	25	49	5.9	49	98
	16	100	21	22	43	5.5	41	80
	24	100	20	29	49	5.8	45	79
	NI	100	25	28	53	6.1	46	75
15	10	40	64	24	88	11.5	29	13
	12	100	30	29	59	7.2	35	30
	14	100	21	27	48	5.9	49	104
	16	100	20	26	45	6.1	49	90
	24	100	18	26	44	5.3	48	83
	NI	100	18	28	46	6.2	48	85
Significance								
Weeks cold (WC)			***	NS	***	*	**	*
Photoperiod (P)			***	***	***	***	***	***
WC × P			***	***	***	*	**	NS
95% Confidence interval for NI								
Zero weeks 5C			1.8	1.8	2.7	0.2	4.1	8.0
15 weeks 5C			2.2	1.5	2.1	0.6	3.1	13.5
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	***	***	NS	*	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			***	*	***	***	***	***
$P_{Quadratic}$ (10 to 24 h)			***	*	***	***	NS	***
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	*	NS	NS
P_{Linear} (10 to 24 h)			***	NS	***	***	***	***
$P_{Quadratic}$ (10 to 24 h)			***	NS	***	***	***	***
0 and 15 weeks 5C								
P_{Linear} (10 to 24 h)			***	NS	***	***	***	***
$P_{Quadratic}$ (10 to 24 h)			***	NS	***	***	***	***

[z]NI = 4-h night interruption.
[NS, *, **, ***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

to 12 leaves), grew 40 to 50 cm tall, and averaged 75 to 100 flowers. Iversen and Weiler (1994) found that 'Moonbeam' plants did not flower under 8-hour photoperiods after receiving 0, 6, or 12 weeks of 4.5 °C cold treatment, whereas all those grown under 16- or 24-hour photoperiods flowered, regardless of cold treatment.

The cold treatment shifted the minimum photoperiod under which all plants flowered from 14 hours to 12 hours. Under photoperiods ≥14 hours, cold treatment did not dramatically affect time to flower. The cold treatment increased the average flower number from 57 to 67, increased plant height by an average of four cm, and slightly reduced the number of new nodes formed. However, the effects of cold treatment on plant height and the number of new nodes formed varied by photoperiod, with differences primarily under 10- or 12-hour photoperiods.

Photoperiod influenced all flowering characteristics measured but, except for flower number, the effects varied with cold treatment. As the photoperiod increased, days to visible bud and flower and the number of new nodes formed decreased at a decreasing rate. For example, for cold-treated plants, time to flower decreased from 88 to 44 days as the photoperiod increased from 10 to 24 hours. Plant height increased linearly as photoperiod increased from 10 to 24 hours. Plants had few flowers under 10- or 12-hour photoperiods and had the greatest number of flowers under 14-hour photoperiods.

***Echinacea purpurea* 'Bravado'.** The following results and discussion apply to both years in which *Echinacea* was studied. The cold treatment

reduced days to visible bud and flower by 15 to 25 days and decreased the number of new nodes formed by one or two (Figures 30 and 31, Tables 20 and 21). Cold treatment did not consistently affect any other flowering characteristic measured.

Echinacea has an optimum photoperiod at or near 14 hours for complete, rapid, and uniform flowering. Regardless of cold treatment, all plants flowered under 14-hour photoperiods, and the percentage of flowering decreased as photoperiods decreased or increased. The percentage of flowering plants under NI never reached 100%, and only one plant in forty flowered under continual light. Photoperiodic trends are difficult to establish because of the variable percentage of flowering plants under all but the 14-hour photoperiods.

Plants grown under 14-hour photoperiods flowered more uniformly than plants grown under NI. For example, in 1994-95, the 95% CI of days to flower for plants under 14-hour photoperiods were ± 8 or ± 3 days, without or with the cold treatment, respectively. The same intervals for plants under NI were ± 15 or ±7 days, respectively. In another experiment, 2% of 'Bravado' plants flowered under 9-hour short days and 98% flowered under 4-hour NI (Engle, 1994).

***Gypsophila paniculata* 'Double Snowflake'**. Flowering of *Gypsophila* was highly variable, regardless of cold treatment or photoperiod (Figure 32, Table 22), and those that did flower were rangy and unattractive. Cold treatment doubled the percentage of flowering and reduced the time to flower by an average of 25 days. Days from visible bud to flower decreased from 22 to 16 for cold-treated plants, but part of this acceleration may have been due to higher

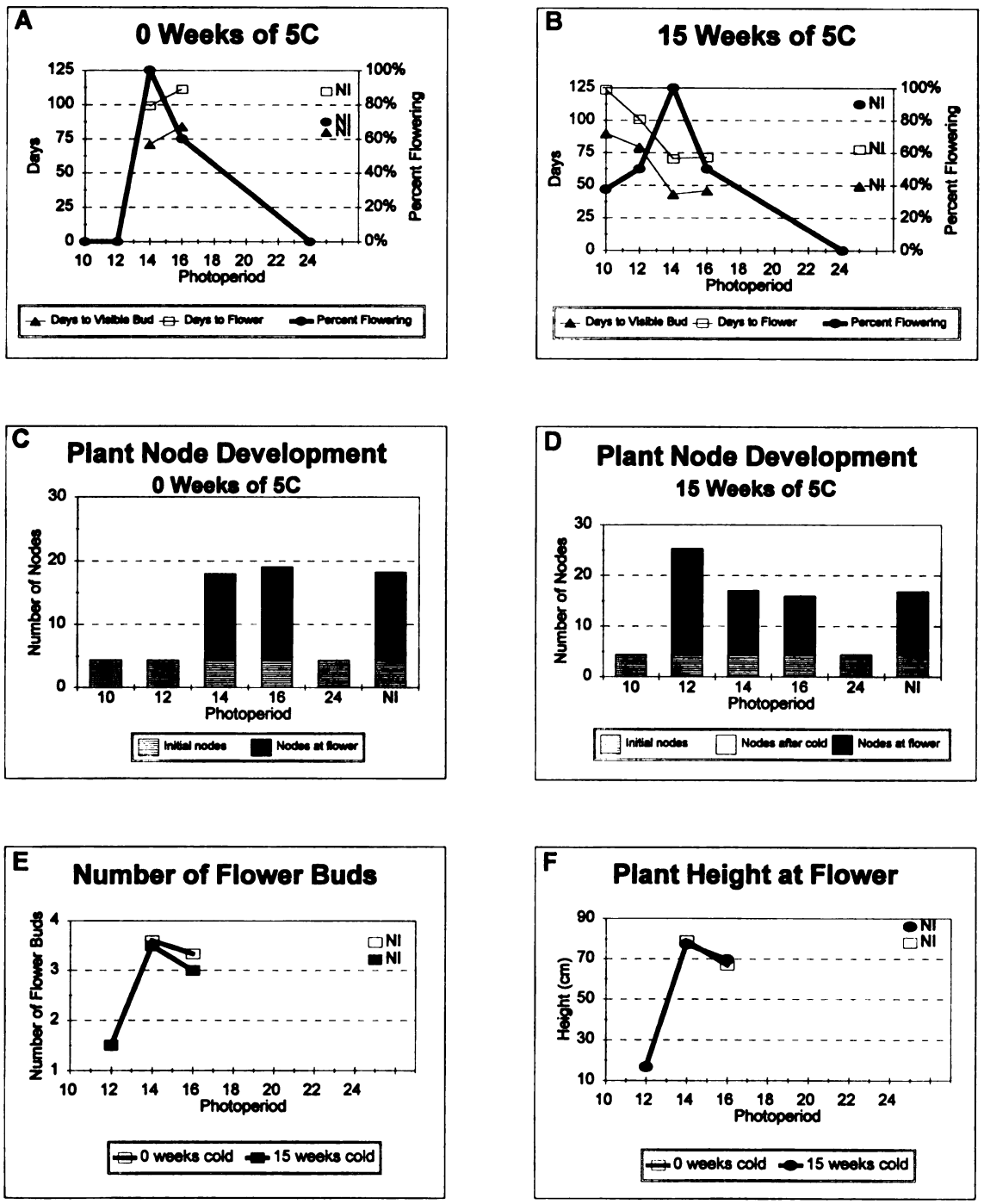


Figure 30. The effects of photoperiod and cold treatment on flowering of *Echinacea purpurea* 'Bravado'. 1994-95.

Table 20. The effects of photoperiod and cold treatment on flowering of *Echinacea purpurea* 'Bravado': 1994-95.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	38	77	28	105	14	76	3.5
15	-	55	55	26	79	13	74	3.2
-	10	17	90	---[z]	---	---	---	---
	12	22	80	22	101	21	17	1.5
	14	100	57	28	85	13	78	3.6
	16	55	67	26	93	13	68	3.2
	24	0	--[y]	--	--	--	--	--
	NI[x]	80	63	29	92	13	83	3.4
0	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	100	71	28	99	14	79	3.6
	16	60	84	27	111	15	67	3.3
	24	0	--	--	--	--	--	--
	NI	70	80	30	110	14	78	3.6
15	10	38	90	---	---	---	---	---
	12	50	80	22	101	21	17	1.5
	14	100	43	27	71	13	77	3.5
	16	50	46	26	72	12	70	3.0
	24	0	--	--	--	--	--	--
	NI	90	49	28	78	12	86	3.2
Significance								
Weeks cold (WC)			***	NS	***	**	NS	NS
Photoperiod (P)			***	***	***	***	***	**
WC × P			NS	NS	NS	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			12.8	3.1	14.7	1.5	6.9	1.3
15 weeks 5C			6.4	0.9	6.5	1.5	5.3	0.3
95% Confidence interval for 14 h								
Zero weeks 5C			8.5	1.4	8.4	1.6	7.3	0.5
15 weeks 5C			3.1	1.9	3.0	0.9	5.7	0.4
Contrasts								
Zero weeks 5C								
14 vs. 16			*	NS	*	NS	*	NS
14 vs. NI			NS	NS	NS	NS	NS	NS
15 weeks 5C								
14 vs. 16			NS	***	***	NS	NS	NS
14 vs. NI			NS	**	***	NS	*	NS
P_{Linear} (12 to 16 h)			***	NS	***	***	NS	NS
$P_{Quadratic}$ (12 to 16 h)			NS	***	**	***	***	*

[z]--- = Experiment was terminated before plants flowered.
[y]-- = No plants showed visible bud after 105 days of forcing.
[x]NI = 4-h night interruption.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

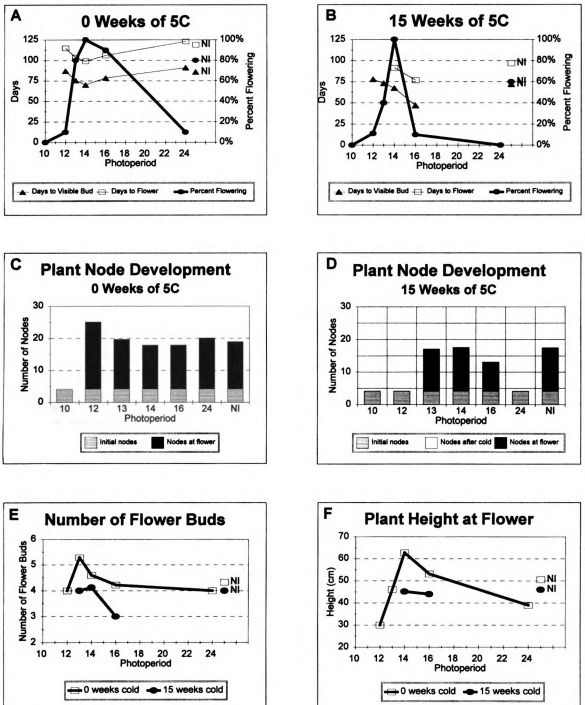


Figure 31. The effects of photoperiod and cold treatment on flowering of *Echinacea purpurea* 'Bravado'. 1995-96.

Table 21. The effects of photoperiod and cold treatment on flowering of *Echinacea purpurea* 'Bravado': 1995-96.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	53	78	29	106	15	53	4.6
15	-	32	69	31	90	13	45	4.0
-	10	0	--[z]	--	--	--	--	--
	12	11	83	28	115	21	30	4.0
	13	60	75	29	104	15	46	5.1
	14	100	69	30	97	14	56	4.4
	16	50	75	28	103	13	52	4.1
	24	5	91	32	123	16	39	4.0
	NI[y]	70	80	29	115	14	50	4.2
0	10	0	--	--	--	--	--	--
	12	10	87	28	115	21	30	4.0
	13	80	76	29	104	16	46	5.3
	14	100	70	29	99	14	63	4.6
	16	90	78	28	106	14	53	4.2
	24	10	91	32	123	16	39	4.0
	NI	80	86	30	119	15	51	4.3
15	10	0	--	--	--	--	--	--
	12	11	78	---[x]	---	---	---	---
	13	40	73	---	---	---	---	---
	14	100	68	33	92	14	45	4.1
	16	10	47	30	77	9	44	3.0
	24	0	--	--	--	--	--	--
	NI	60	72	24	97	13	46	4.0
Significance								
Weeks cold (WC)			*	NS	**	*	NS	*
Photoperiod (P)			*	NS	NS	*	NS	**
WC × P			NS	NS	NS	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			12.2	6.1	17.5	2.7	9.2	1.1
15 weeks 5C			18.8	2.2	w	1.8	w	0.9
95% Confidence interval for 14 h								
Zero weeks 5C			5.3	1.9	6.3	1.0	5.1	1.1
15 weeks 5C			6.8	7.7	5.2	1.7	6.4	0.5
Contrasts								
Zero weeks 5C								
14 vs. 16			NS	NS	NS	NS	NS	**
14 vs. NI			**	NS	**	NS	NS	**
P_{Linear} (12 to 24 h)			NS	NS	NS	NS	NS	NS
$P_{Quadratic}$ (12 to 24 h)			NS	NS	NS	***	NS	***

[z]-- = No plants showed visible bud after 105 days of forcing.
[y]NI = 4-h night interruption.
[x]--- = Experiment was terminated before plants flowered.
w = Insufficient data.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

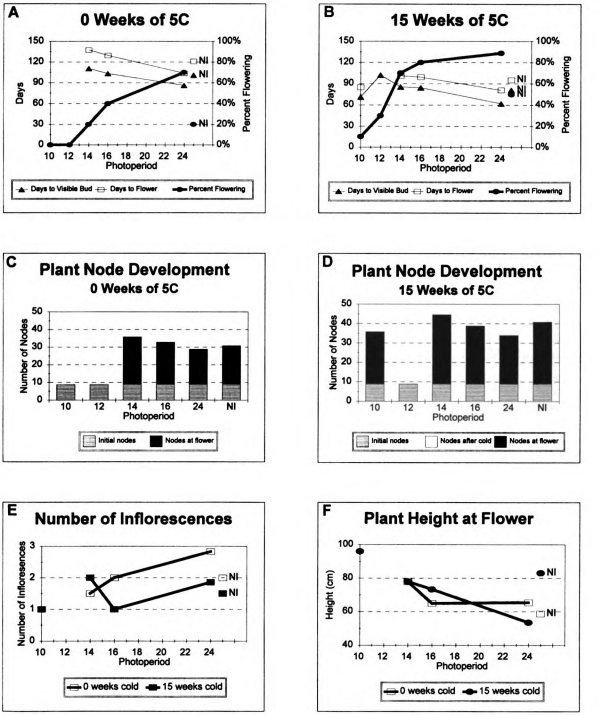


Figure 32. The effects of photoperiod and cold treatment on flowering of *Gypsophila paniculata* 'Double Snowflake'.

Table 22. The effects of photoperiod and cold treatment on flowering of *Gypsophila paniculata* 'Double Snowflake'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	25	96	22	118	23	66	2.3
15	-	54	80	16	93	30	71	1.6
-	10	5	71	14	85	27	96	1.0
	12	15	102	z	z	z	z	z
	14	45	91	18	109	33	78	1.8
	16	60	91	19	109	27	69	1.5
	24	79	73	18	91	23	59	2.3
	NI[y]	35	87	16	103	29	75	1.7
0	10	0	--[x]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	20	111	27	138	27	78	1.5
	16	40	103	26	130	24	65	2.0
	24	70	86	17	104	20	65	2.8
	NI	20	101	20	121	22	59	2.0
15	10	10	71	14	85	27	96	1.0
	12	30	102	z	z	z	z	z
	14	70	85	16	101	36	78	2.0
	16	80	84	15	99	30	73	1.0
	24	89	62	19	81	25	53	1.9
	NI	50	81	14	95	32	83	1.5
Significance								
Weeks cold (WC)			***	***	***	*	NS	NS
Photoperiod (P)			***	NS	**	NS	***	NS
WC × P			NS	*	NS	NS	***	NS
95% Confidence interval for NI								
15 weeks 5C			12.3	3.1	13.7	11.1	8.2	0.9
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (14 to 24 h)			*	**	**	NS	NS	*
$P_{Quadratic}$ (14 to 24 h)			NS	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	NS	*	*	***	NS
NI vs. 24			NS	NS	*	NS	***	NS
P_{Linear} (14 to 24 h)			NS	NS	NS	NS	*	NS
$P_{Quadratic}$ (14 to 24 h)			*	NS	NS	NS	NS	NS
0 and 15 weeks 5C								
P_{Linear} (14 to 24 h)			NS	NS	NS	NS	**	NS
$P_{Quadratic}$ (14 to 24 h)			NS	NS	NS	NS	*	NS

[z]Experiment terminated before plants reached anthesis
[y]NI = 4-h night interruption.
[x]-- = No plants showed visible bud after 105 days of forcing.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

plant temperatures. Cold-treated plants were more vigorous and developed approximately five to seven more nodes before visible bud than non-cold-treated plants.

For plants that did not receive cold treatment, the percentage of flowering increased from zero to 70 as the photoperiod increased from 12 to 24 hours, and days to flower decreased linearly from 138 to 104 as photoperiods increased from 14 to 24 hours. For cold-treated plants, the percentage of flowering increased from 10 to 90 as the photoperiod increased from 10 to 24 hours, with fastest flowering occurring under continual light. Plant height decreased linearly as photoperiods increased, regardless of cold treatment.

Several experiments have been conducted on the effects of photoperiod and cold treatment on flowering of *Gypsophila*. Moe (1988) found that long-days were required for flower initiation and development of 'Bristol Fairy', except for plants grown at 12 °C, where flowering was complete but delayed relative to plants grown under long days. For seven selections of 'Bristol Fairy', few or no plants flowered under photoperiods of eight or ten hours, and as photoperiods increased from 12 to 24 hours, days to visible bud decreased (Kusey et al., 1981). Cold treatment for 2 to 8 weeks at 5 °C hastened days to visible bud but did not affect percentage of flowering.

Helenium autumnale. Cold treatment shifted the minimum daylength required for flowering from 16 to 14 hours, hastened days to visible bud and flower by approximately 20 days, and reduced the number of new nodes formed (Figure 33, Table 23). On average, cold-treated plants were 15 cm shorter and

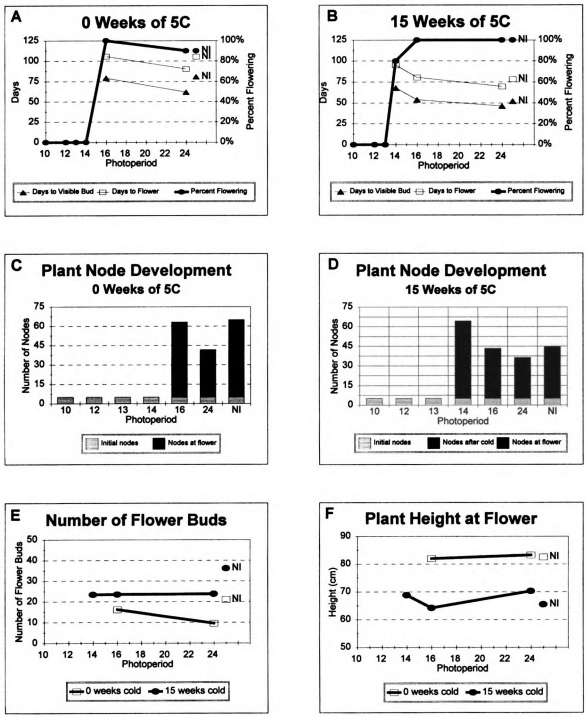


Figure 33. The effects of photoperiod and cold treatment on flowering of *Helenium autumnale*.

Table 23. The effects of photoperiod and cold treatment on flowering of *Helenium autumnale*.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	40	74	26	101	52	83	16
15	-	55	54	25	82	42	67	27
-	10	0	--[z]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	0	--	--	--	--	--	--
	14	40	68	24	95	59	69	23
	16	100	67	27	96	51	75	19
	24	95	54	27	85	35	79	14
	NI[y]	95	66	25	94	52	76	27
0	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	0	--	--	--	--	--	--
	14	0	--	--	--	--	--	--
	16	100	79	26	106	58	82	16
	24	90	62	28	90	36	83	9
	NI	90	81	25	105	60	83	21
15	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	0	--	--	--	--	--	--
	14	80	68	24	95	59	69	23
	16	100	54	27	81	38	64	24
	24	100	46	21	70	31	70	24
	NI	100	52	26	78	40	66	36
Significance								
Weeks cold (WC)			***	NS	***	***	***	***
Photoperiod (P)			***	NS	***	***	NS	*
WC × P			**	*	NS	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			5.2	1.7	6.0	8.4	7.5	6.7
15 weeks 5C			3.4	3.4	6.3	9.6	8.9	13.3
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			***	*	***	***	NS	*
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	*
NI vs. 24			*	NS	NS	NS	NS	NS
P_{Linear} (14 to 24 h)			***	NS	***	***	NS	NS
$P_{Quadratic}$ (14 to 24 h)			***	NS	*	**	NS	NS

[z] -- = No plants showed visible bud after 105 days of forcing.
[y] NI = 4-h night interruption.
[NS, *, **, ***] Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

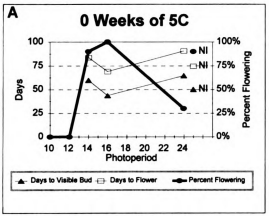
had nine more flowers than plants that did not receive the cold treatment. Cold treatment did not improve flowering uniformity.

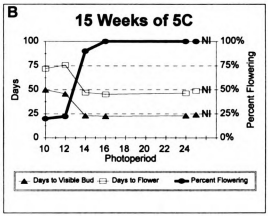
Without cold, no plants flowered under photoperiods ≤14 hours; after cold, 80% of plants flowered under 14-hour photoperiods but none flowered under shorter photoperiods. Nearly all plants flowered under photoperiods ≥16 hours or NI. For cold-treated plants, days to flower decreased linearly from 95 to 70 and the number of new nodes formed decreased linearly from 59 to 31 as the photoperiod increased from 14 to 24 hours. There were no photoperiodic trends for plant height or flower number.

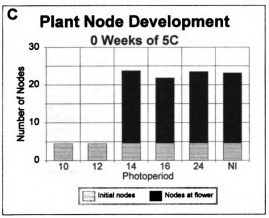
Oenothera missouriensis. The cold treatment increased the percentage of flowering from 62 to 72, hastened flowering by 25 days, reduced the number of new nodes formed by two or three, and improved flowering uniformity (Figure 34, Table 24). For example, the 95% CI of days to flower for plants under NI decreased from ± 10 to ± 4 after cold treatment.

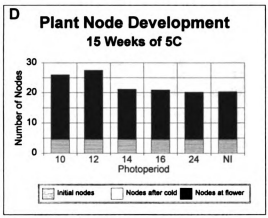
Fewer than 15% of the plants flowered under photoperiods of 10 or 12 hours, and except for non-cold-treated plants under continual light, ≥90% of plants flowered under photoperiods ≥14 hours or NI. Only 30% of non-cold-treated plants under continual light flowered.

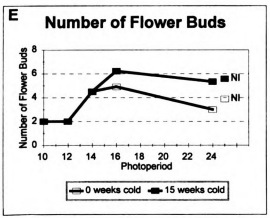
For cold-treated plants, days to visible bud and flower, the number of new nodes formed, plant height, and flower number were similar under photoperiods ≥14 hours or NI. On average, plants that flowered under 10- or 12-hour photoperiods flowered 30 days later, developed six more nodes, were six cm











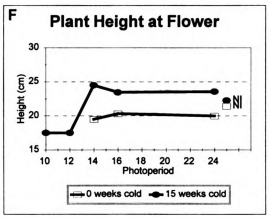


Figure 34. The effects of photoperiod and cold treatment on flowering of *Oenothera missouriensis*.

Table 24. The effects of photoperiod and cold treatment on flowering of *Oenothera missouriensis*.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	62	52	25	77	18	20	4.3
15	-	72	27	25	52	17	23	5.0
-	10	13	50	22	72	22	18	2.0
	12	14	46	30	76	23	18	2.0
	14	90	42	24	65	18	22	4.5
	16	100	34	24	58	17	22	5.5
	24	65	33	24	57	16	23	4.9
	NI[z]	95	36	25	61	17	22	4.6
0	10	0	--[y]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	90	60	24	84	19	20	4.5
	16	100	44	25	69	17	20	4.9
	24	30	65	26	91	19	20	3.0
	NI	90	50	24	75	19	21	3.9
15	10	20	50	22	72	22	18	2.0
	12	22	46	30	76	23	18	2.0
	14	90	23	24	47	17	25	4.5
	16	100	23	23	45	16	24	6.2
	24	100	23	23	46	16	24	5.3
	NI	100	24	25	49	16	22	5.6
Significance								
Weeks cold (WC)			***	NS	***	***	***	*
Photoperiod (P)			***	***	***	***	***	*
WC × P			*	NS	NS	NS	*	NS
95% Confidence interval for NI								
Zero weeks 5C			9.8	2.3	10.3	2.2	1.5	0.8
15 weeks 5C			2.6	2.6	3.6	2.2	1.5	2.2
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			*	NS	*	NS	NS	NS
P_{Linear} (14 to 24 h)			NS	NS	NS	NS	NS	NS
$P_{Quadratic}$ (14 to 24 h)			***	NS	**	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			***	NS	***	***	***	**
$P_{Quadratic}$ (10 to 24 h)			**	NS	**	*	***	*

[z]NI = 4-h night interruption.
[y]-- = No plants showed visible bud after 105 days of forcing.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

shorter, and had less than half as many flowers as plants under other photoperiods.

***Phlox paniculata* 'Eva Cullum'**. Cold treatment increased percentage of flowering and improved the uniformity of time to flower (Figures 35 and 36, Table 25). For example, without cold treatment, 70% of plants under NI flowered in an average of 69 days with a 95% CI of ± 9 days. After cold treatment, all plants flowered under NI in an average of 73 days with a 95% CI of ± 3 days. Plants treated with cold had many more flowers and were more vigorous than non-cold-treated plants, which may be partly due to higher light levels. Cold treatment also increased plant height by approximately one-half and increased the number of new nodes formed by four to six (eight to twelve leaves).

For plants that did not receive cold treatment, no plants flowered under photoperiods ≤13 hours and the percentage of flowering increased from zero to 78 as the photoperiod increased from 14 to 24 hours. For cold-treated plants, 0%, 50%, or 100% of plants flowered under 10-, 12-, or ≥13-hour photoperiods or NI. For plants that received the cold treatment, days to flower decreased linearly from 88 to 61 and the number of new nodes formed decreased from 21 to 14 as the photoperiod increased from 12 to 24 hours. Plants under continual light flowered nonuniformly. Photoperiod did not affect days from visible bud to flower, final plant height, or flower number.

***Phlox paniculata* 'Tenor'**. Flowering of 'Tenor' was similar to 'Eva Cullum'. Cold treatment doubled the percentage of flowering and improved time-to-flower uniformity (Figures 37 and 38, Table 26). For example, the 95% CIs of

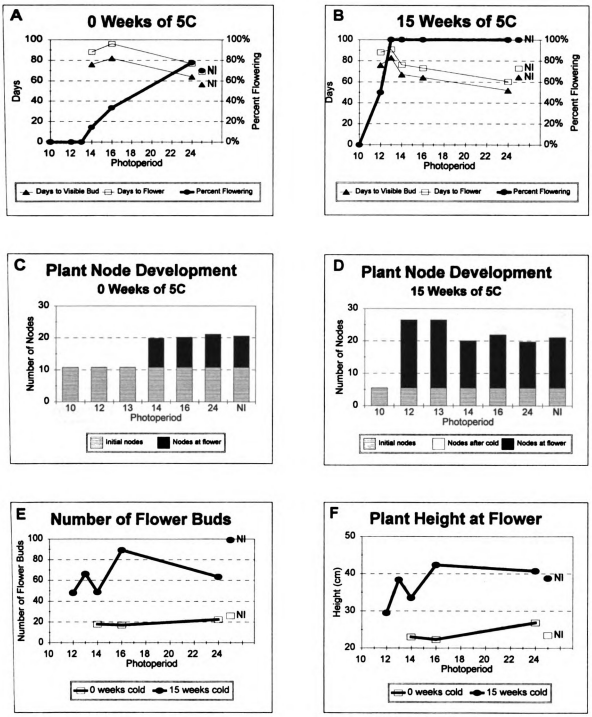


Figure 35. The effects of photoperiod and cold treatment on flowering of *Phlox paniculata* 'Eva Cullum'.

Table 25. The effects of photoperiod and cold treatment on flowering of *Phlox paniculata* 'Eva Cullum'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	29	65	13	77	10	25	23
15	-	80	67	9	76	17	38	73
-	10	0	--[z]	--	--	--	--	--
	12	14	76	12	88	21	30	48
	13	40	84	8	91	21	38	66
	14	54	68	10	78	14	32	44
	16	60	70	11	81	14	36	65
	24	87	58	11	69	12	33	41
	NI[y]	82	61	10	71	12	31	63
0	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	0	--	--	--	--	--	--
	14	14	76	12	88	9	23	18
	16	33	82	14	96	9	22	17
	24	78	64	13	77	10	27	22
	NI	70	56	12	69	10	23	26
15	10	0	--	--	--	--	--	--
	12	50	76	12	88	21	30	48
	13	100	83	8	91	21	38	66
	14	100	67	9	76	15	34	49
	16	100	64	9	73	16	42	89
	24	100	52	9	61	14	41	63
	NI	100	65	8	73	16	39	99
Significance								
Weeks cold (WC)			NS	***	**	***	***	***
Photoperiod (P)			***	NS	***	**	NS	NS
WC × P			*	NS	*	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			8.6	2.4	8.8	0.7	4.0	11.0
15 weeks 5C			2.2	0.9	3.0	1.5	3.7	29.8
Contrasts								
Zero weeks 5C								
NI vs. 16			***	NS	***	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (14 to 24 h)			NS	NS	NS	NS	NS	NS
$P_{Quadratic}$ (14 to 24 h)			NS	NS	NS	NS	NS	NS
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			*	NS	*	NS	NS	*
P_{Linear} (12 to 24 h)			***	NS	***	**	NS	NS
$P_{Quadratic}$ (12 to 24 h)			NS	NS	NS	NS	NS	NS

[z]-- = No plants showed visible bud after 105 days of forcing.
[y]NI = 4-h night interruption.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

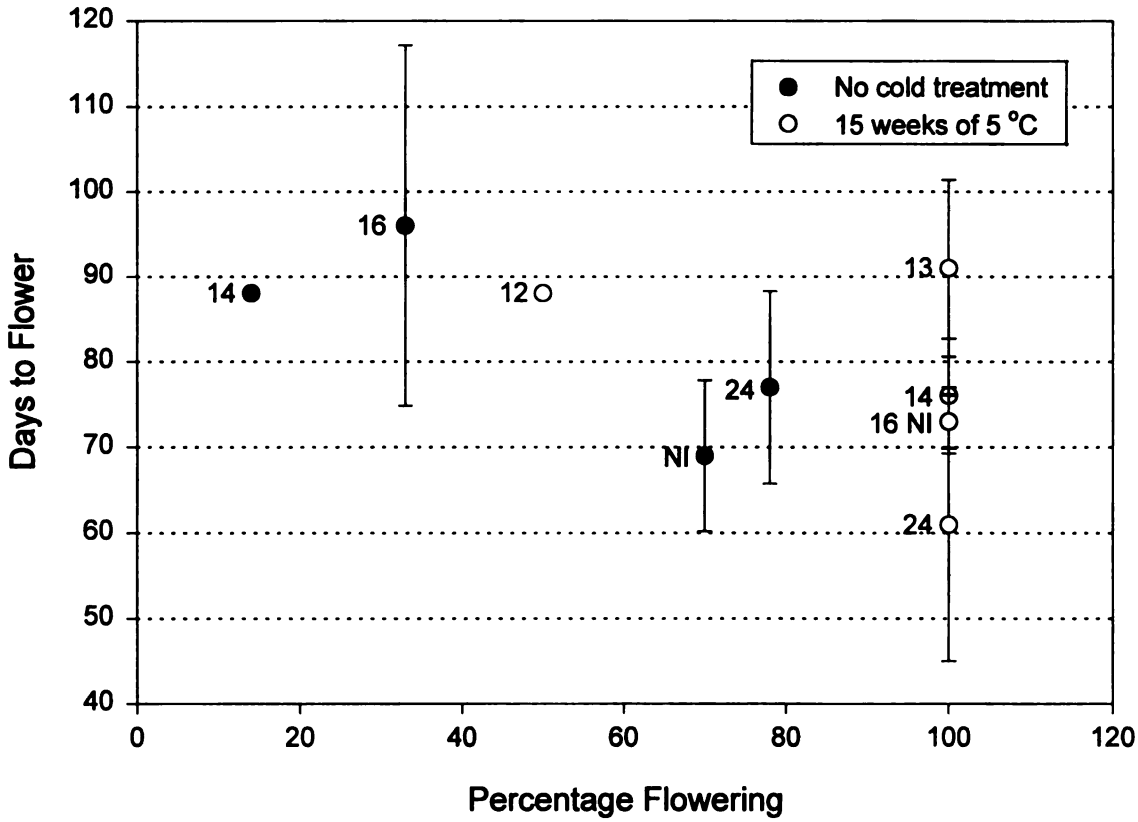
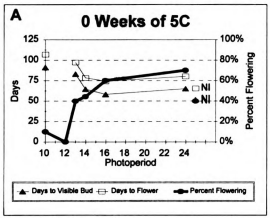
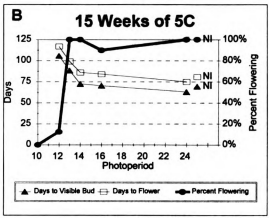
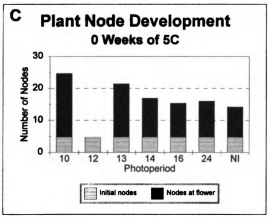
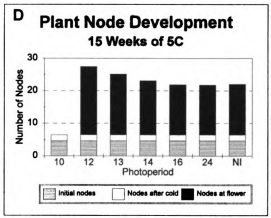


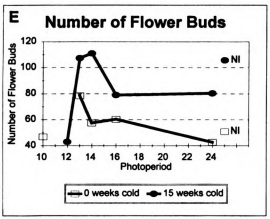
Figure 36. Percentage flowering, time to flower, and flowering uniformity of *Phlox paniculata* 'Eva Cullum' under different photoperiods with or without cold treatment. Numbers next to symbols represent photoperiods consisting of nine-hour natural days that were extended with incandescent lamps. NI = nine-hour natural days with four hours of night interruption. Error bars are 95% confidence intervals. Symbols without error bars indicate that the confidence intervals were too large for the graph.











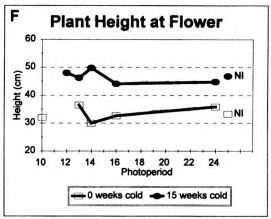


Figure 37. The effects of photoperiod and cold treatment on flowering of *Phlox paniculata* 'Tenor'.

Table 26. The effects of photoperiod and cold treatment on flowering of *Phlox paniculata* 'Tenor'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	38	65	15	80	12	34	56
15	-	75	74	12	86	16	46	96
-	10	5	91	16	107	20	32	47
	12	6	106	11	117	21	48	43
	13	70	87	12	99	18	43	99
	14	74	70	14	84	15	44	96
	16	75	66	15	80	14	40	72
	24	85	64	14	77	14	41	64
	NI[z]	70	65	12	77	14	43	90
0	10	10	91	16	107	20	32	47
	12	0	–[y]	–	–	–	–	–
	13	40	83	14	97	17	37	79
	14	44	65	14	78	12	30	58
	16	60	58	16	74	11	33	60
	24	70	65	15	80	12	36	43
	NI	40	52	14	66	10	33	51
15	10	0	–	–	–	–	–	–
	12	13	106	11	117	21	48	43
	13	100	88	11	99	19	46	107
	14	100	73	14	86	17	50	111
	16	90	71	14	84	15	44	79
	24	100	63	12	75	15	45	80
	NI	100	70	11	81	16	47	106
Significance								
Weeks cold (WC)			***	***	**	***	***	***
Photoperiod (P)			***	*	***	***	NS	*
WC × P			**	NS	**	NS	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			8.7	0.8	8.7	1.6	10.5	30.2
15 weeks 5C			3.1	1.0	2.8	1.0	3.1	23.3
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	*	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	NS	NS
P_{Linear} (10 to 24 h)			***	NS	***	***	NS	NS
$P_{Quadratic}$ (10 to 24 h)			***	NS	***	**	NS	NS
15 weeks 5C								
NI vs. 16			NS	**	NS	NS	NS	*
NI vs. 24			*	NS	NS	NS	NS	*
P_{Linear} (12 to 24 h)			***	NS	***	***	NS	NS
$P_{Quadratic}$ (12 to 24 h)			***	NS	***	**	NS	NS

[z]NI = 4-h night interruption.
[y]– = No plants showed visible bud after 105 days of forcing.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

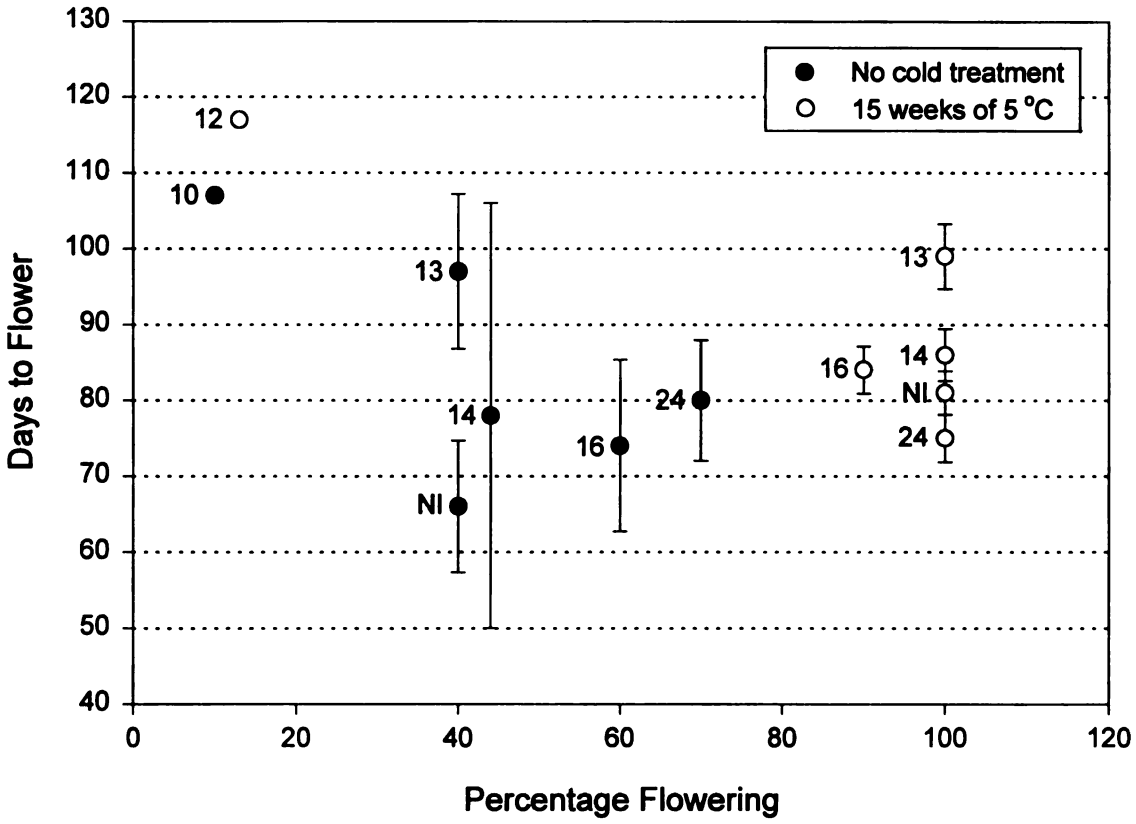
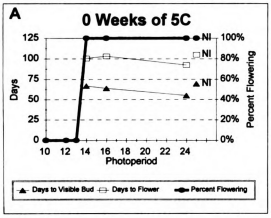


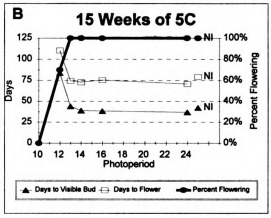
Figure 38. Percentage flowering, time to flower, and flowering uniformity of *Phlox paniculata* 'Tenor' under different photoperiods with or without cold treatment. Numbers next to symbols represent photoperiods consisting of nine-hour natural days that were extended with incandescent lamps. NI = nine-hour natural days with four hours of night interruption. Error bars are 95% confidence intervals. Symbols without error bars indicate that the confidence intervals were too large for the graph.

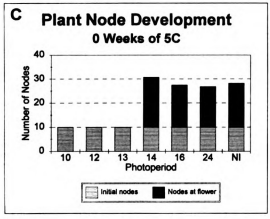
days to visible bud and flower for plants under NI were ± 9 and ± 3 without or with cold treatment, respectively. Plants that received the cold treatment were more vigorous, grew approximately four more nodes, averaged 12 cm taller, and were more floriferous than plants that did not receive the cold treatment. Cold treatment delayed flowering by an average of six days, but the delay varied by photoperiod.

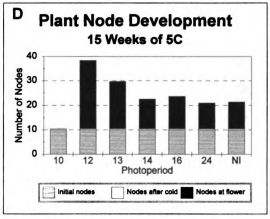
Few plants flowered under photoperiods ≤12 hours, so 'Tenor' requires short nights to flower. For non-cold-treated plants, the percentage of flowering increased from zero to 70 as the photoperiod increased from 12 to 24 hours. Nearly all cold-treated plants flowered under photoperiods ≥13 hours. Days to visible bud and flower and the number of new nodes formed decreased at a decreasing rate as the photoperiod increased. For example, for cold-treated plants, time to flower decreased from 117 to 75 days as the photoperiod increased from 12 to 24 hours. There were no photoperiodic trends for plant height or flower number.

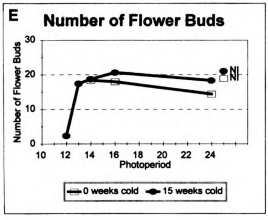
***Rudbeckia fulgida* 'Goldsturm'**. *Rudbeckia* flowered very uniformly, regardless of cold treatment (Figure 39, Table 27). However, cold treatment shifted the minimum photoperiod required for 100% flowering from 14 to 13 hours. Under photoperiods ≥14 hours or NI, cold treatment hastened time to flower by three to four weeks and plant height was reduced by an average of five cm. Cold-treated plants developed fewer nodes, but the reduction varied by photoperiod.











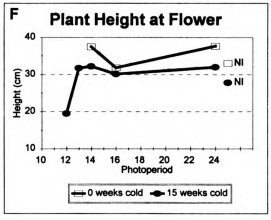


Figure 39. The effects of photoperiod and cold treatment on flowering of *Rudbeckia fulgida* 'Goldsturm'.

Table 27. The effects of photoperiod and cold treatment on flowering of *Rudbeckia fulgida* 'Goldsturm'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	57	64	36	100	18	35	17
15	-	81	45	34	79	15	30	17
-	10	0	--[z]	--	--	--	--	--
	12	35	84	27	111	28	20	2
	13	50	44	31	75	19	32	17
	14	100	53	34	87	16	35	19
	16	100	51	38	89	15	31	19
	24	100	46	36	82	13	35	16
	NI[y]	100	56	36	92	15	30	20
0	10	0	--	--	--	--	--	--
	12	0	--	--	--	--	--	--
	13	0	--	--	--	--	--	--
	14	100	67	34	101	21	38	18
	16	100	64	39	103	18	32	18
	24	100	55	38	93	17	38	14
	NI	100	70	35	105	18	33	19
15	10	0	--	--	--	--	--	--
	12	70	84	27	111	28	20	2
	13	100	44	31	75	19	32	17
	14	100	39	34	73	12	32	19
	16	100	38	37	76	13	30	21
	24	100	37	34	71	11	32	18
	NI	100	42	37	80	11	28	21
Significance								
Weeks cold (WC)			***	*	***	***	***	**
Photoperiod (P)			***	***	***	***	***	***
WC × P			***	***	*	*	NS	NS
95% Confidence interval for NI								
Zero weeks 5C			2.0	1.2	1.5	0.7	1.8	2.1
15 weeks 5C			2.4	1.5	3.0	2.0	1.5	3.1
Contrasts								
Zero weeks 5C								
NI vs. 16			***	***	NS	NS	NS	NS
NI vs. 24			***	*	***	NS	***	**
P_{Linear} (14 to 24 h)			***	**	***	**	NS	**
$P_{Quadratic}$ (14 to 24 h)			NS	***	**	**	***	NS
15 weeks 5C								
NI vs. 16			**	NS	*	*	NS	NS
NI vs. 24			***	***	***	NS	***	NS
P_{Linear} (12 to 24 h)			***	***	***	***	***	***
$P_{Quadratic}$ (12 to 24 h)			***	***	***	***	***	***

[z]-- = No plants showed visible bud after 105 days of forcing.
[y]NI = 4-h night interruption.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Without the cold treatment, no plants flowered under ≤13-hour photoperiods and all plants flowered under ≥14-hour photoperiods or NI. No cold-treated plants flowered under 10-hour photoperiods, 70% flowered under 12-hour photoperiods, and all flowered under ≥13-hour photoperiods or NI. Plants that flowered under 12 hours were delayed, had few flowers, and were short.

Days to visible bud and flower and the number of new nodes formed decreased as the photoperiod increased from 14 to 24 hours in non-cold-treated plants and from 12 to 24 hours in cold-treated plants. For example, the number of new nodes formed decreased at a decreasing rate from 28 to 11 as the photoperiod increased from 12 to 24 hours. With the exception of plants that flowered under 12-hour photoperiods, photoperiod did not dramatically affect plant height or flower number.

The critical daylengths for flowering of several other *Rudbeckia* spp. have been investigated (Kockankov and Chailakhyan, 1986). Without exception, all are obligate long-day plants with minimal critical photoperiods ranging from 10 to 14.5 hours.

Other Responses

Asclepias tuberosa. When plugs were received, plants had already been exposed to short days and induced into dormancy. Cold treatment was required to overcome dormancy. However, plants flower without a cold treatment if they are never exposed to short days (Whitman, unpublished data).

No cold-treated plants flowered under photoperiods ≤12 hours, and only 20% of the plants flowered under 14 hours (Figure 40, Table 28). Several plants under 14-hour photoperiods initiated flower buds that later aborted, and these were considered as nonflowering. Photoperiods ≥16 hours or NI induced complete flowering. *Asclepias* was only moderately uniform in time to flower: the 95% CI of days to flower for plants under NI was ±7.5 days. Flower number varied tremendously within each photoperiod.

Vernalized plants grown at 17/25 °C day/night under 4- or 8-hour NI during the middle of 15-hour dark periods flowered in 71 or 61 days, respectively (Albrecht and Lehmann, 1991). No plants flowered under 9-hour photoperiods. In contrast to the above findings, Lyons (1986) labeled *A. tuberosa* as a day-neutral plant with respect to flowering, but noted that photoperiod influenced vegetative and tuberous root development.

***Hibiscus* x*hybrida* 'Disco Belle Mixed'**. Cold-treated plants died from chilling injury. No plants flowered under 10-hour photoperiods and all plants flowered under photoperiods ≥14 hours or NI (Figure 41, Table 29). As photoperiod increased from 12 to 24 hours, days to flower decreased from 127 to 85, the number of new nodes formed decreased from 18 to 11, and the average flower number increased from 5.6 to 12.6. Photoperiod had no effect on final plant height.

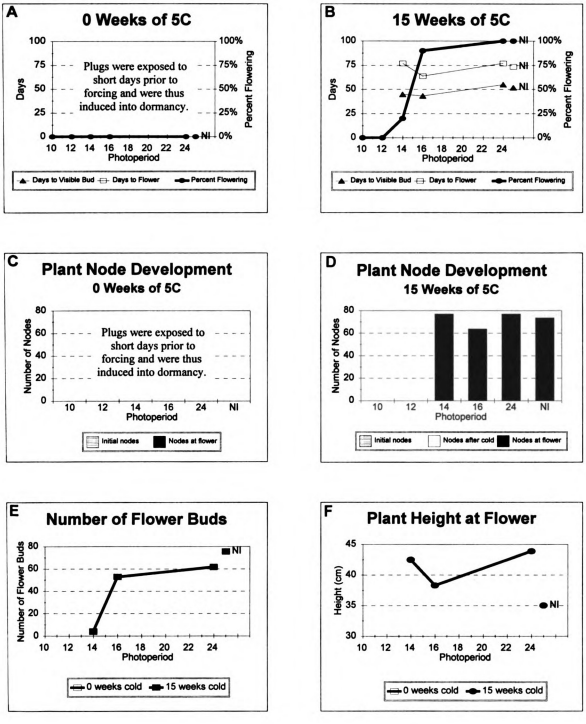
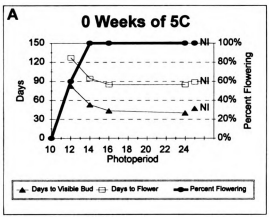


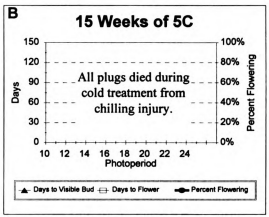
Figure 40. The effects of photoperiod on flowering of cold-treated *Asclepias tuberosa*.

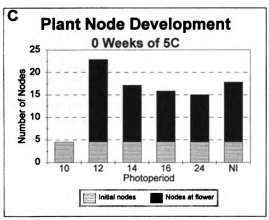
Table 28. The effects of photoperiod on flowering of cold-treated *Asclepias tuberosa*.

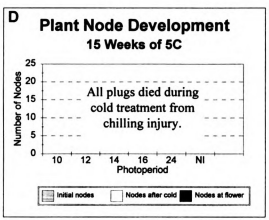
Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	0	z	z	z	z	z	z
15	-	52	49	24	73	68	40	49
15	10	0	--[y]	--	--	--	--	--
	12	0	--	--	--	--	--	--
	14	20	45	30	76	62	43	4
	16	90	43	20	64	64	38	53
	24	100	55	22	77	74	44	62
	NI[x]	100	52	22	74	72	35	76
Significance								
Photoperiod (P)			NS	**	NS	NS	*	NS
95% Confidence interval for NI								
15 weeks 5C			7.5	1.1	7.5	13	4.3	29
Contrasts								
15 weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	NS	NS	NS	**	NS
P_{Linear} (14 to 24 h)			NS	**	NS	NS	NS	NS
$P_{Quadratic}$ (14 to 24 h)			NS	***	NS	NS	NS	NS

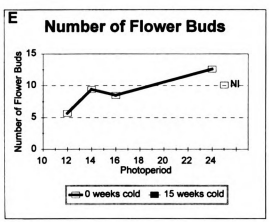
[z]Plugs were exposed to short days prior to forcing and were thus induced into dormancy.
[y]-- = No plants showed visible bud after 105 days of forcing.
[x]NI = 4-h night interruption.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.











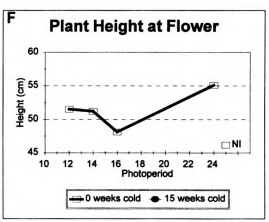


Figure 41. The effects of photoperiod on flowering of non-cold treated *Hibiscus xhybrida* 'Disco Belle Mixed'.

Table 29. The effects of photoperiod on flowering of *Hibiscus xhybrida* 'Disco Belle Mixed'.

Weeks of 5C	Photoperiod	Percentage flowering	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0	-	77	53	43	96	13	50	9.3
15	-	0	z	z	z	z	z	z
0	10	0	--[y]	--	--	--	--	--
	12	60	83	45	127	18	52	5.6
	14	100	53	42	95	13	51	9.4
	16	100	44	41	85	11	48	8.5
	24	100	40	45	85	11	55	12.6
	NI[x]	100	47	42	89	13	46	10.1
Significance								
Photoperiod (P)			***	*	***	***	NS	***
95% Confidence interval for NI								
0 weeks 5C			9.6	2.4	10.4	2.3	3.7	1.1
Contrasts								
Zero weeks 5C								
NI vs. 16			NS	NS	NS	NS	NS	NS
NI vs. 24			NS	*	NS	*	**	*
P_{Linear} (12 to 24 h)			***	NS	***	***	NS	***
$P_{Quadratic}$ (12 to 24 h)			***	**	***	***	NS	NS

[z]All plugs died during cold treatment from chilling injury.
[y]-- = No plants showed visible bud after 105 days of forcing.
[x]NI = 4-h night interruption.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Conclusions

The cold treatment was required for or improved flowering of all herbaceous perennial species studied. Horticulturally, seven of the 25 plants required a cold treatment for flowering; no plants flowered or flowering was erratic and sparse without a cold treatment. The cold treatment improved, but was not required for, flowering of sixteen plants by increasing the percentage of flowering, hastening flowering, improving uniformity, and/or increasing flower number.

Photoperiod did not affect the percentage of flowering, time to flower, or flower number of seven species studied, which were thus defined as day-neutral. The remaining eighteen plants were long-day plants. Seven species flowered as facultative long-day plants and eleven species required long days for flowering. Table 30 provides the photoperiods that induced the most complete, rapid, and uniform flowering of the long-day herbaceous perennials studied.

Table 30. The recommended photoperiods for the most complete, rapid, and uniform flowering of cold-treated long-day herbaceous perennial plants.

Species	Photoperiod
Asclepias tuberosa	≥16 or NI[z]
Campanula carpatica 'Blue Clips'	16 or NI
Coreopsis grandiflora 'Sunray'	≥14 or NI
Coreopsis verticillata 'Moonbeam'	≥16 or NI
Echinacea purpurea 'Bravado'	14
Gaillardia xgrandiflora 'Goblin'	24
Gypsophila paniculata 'Double Snowflake'	24
Helenium autumnale	24
Hibiscus xhybrida 'Disco Belle Mixed'	≥16
Leucanthemum xsuperbum 'Snow Cap'	24
Leucanthemum xsuperbum 'White Knight'	24
Lobelia xspeciosa 'Compliment Scarlet'	≥14 or NI
Oenothera missouriensis	≥14 or NI
Phlox paniculata 'Eva Cullum'	16 or NI
Phlox paniculata 'Tenor'	24
Physostegia virginiana 'Alba'	24 or NI
Rudbeckia fulgida 'Goldsturm'	≥13 or NI
Salvia x *superba* 'Blue Queen'	≥16 or NI

[z]NI = four-hour night interruption.

References

Albrecht, M.L. and J.T. Lehmann. 1991. Daylength, cold storage, and plant-production method influence growth and flowering of *Asclepias tuberosa*. HortScience 26(2):120-121.

Beattie, D.J., C.F. Deneke, E.J. Holcomb, and J.W. White. 1989. The effects of photoperiod and temperature on flowering of *Physostegia virginiana* 'Summer Snow' and 'Vivid' as potted plants. Acta Hort. 252:227-233.

Christensen, O.V., L.N. Kristensen, K. Friis, and O. Bøvre. 1989. Propagation and forcing of *Armeria maritima* as a pot plant. Danish J. Plant Soil Sci. 93:239-242.

Damann, M.P. and R.E. Lyons. 1995. Juvenility and photoperiodic flowering requirements of *Chrysanthemum xsuperbum* 'G. Marconi' and 'Snow Lady' grown under short- and long-day conditions. J. Amer. Soc. Hort. Sci. 120(2):241-245.

Damann, M.P. and R.E. Lyons. 1993. Juvenility, flowering, and the effects of a limited inductive photoperiod in *Coreopsis grandiflora* and *C. lanceolata*. J. Amer. Soc. Hort. Sci. 118(4):513-518.

Engle, B.E. 1994. Use of light and temperature for hardening of herbaceous perennial plugs prior to storage at -2.5C. MS Thesis, Michigan State University, East Lansing

Evans, M.R. and R.E. Lyons. 1988. Photoperiodic and gibberellin-induced growth and flowering responses of *Gaillardia xgrandiflora*. HortScience 23(3):584-586.

Faust, J.E. and R.D. Heins. 1994. Determining the effect of cloud conditions on the variation in daylength perceived by plants. HortScience 29(5):504.

Gardner, F.P. and R.D. Barnett. 1990. Vernalization of wheat cultivars and a triticale. Crop Sci. 30:166-169.

Griffin, C.W. and W.J. Carpenter. 1964. Photoperiodic response of shasta daisy clones Esther Read and T. E. Killian. Proc. Amer. Soc. Hort. Sci. 85:591-593.

Iversen, R.R. and T.C. Weiler. 1994. Strategies to force flowering of six herbaceous garden perennials. HortTechnology 4(1):61-65.

Ketellapper, H.J. and A. Barbaro. 1966. The role of photoperiod, vernalization and gibberellic acid in floral induction in *Coreopsis grandiflora* Nutt. Phyton 23(1):33-41.

Kochankov, V.G. and M.K. Chailakhyan. 1986. *Rudbeckia*, p. 295-320. In: A.H. Halevy (ed.). Handbook of flowering, vol. V. CRC Press, Boca Raton, Florida.

Kusey, W.E., T.C. Weiler, and P.A. Hammer. 1981. Seasonal and chemical influences on the flowering of *Gypsophila paniculata* 'Bristol Fairy' selections. J. Amer. Soc. Hort. Sci. 106(1):84-88.

Lang, A. 1965. Physiology of flower initiation, p.1380-1535. In: W. Ruhland (ed.). Encyclopedia of plant physiology. Springer-Verlag, Berlin.

Lyons, R.E. 1986. *Asclepias tuberosa*, p. 22-28. In: A.H. Halevy (ed.). Handbook of flowering, vol. V. CRC Press, Boca Raton, Florida.

Moe, R. 1988. Flowering physiology of *Gypsophila*. Acta Hort. 218:153-158.

Rhodus, T. And J. Hoskins. 1995. Views on management. Perennial Plants: Quarterly Journal of the Perennial Plant Association 3(4):28-38.

Shedron, K.G. and T.C. Weiler. 1982. Regulation of growth and flowering in *Chrysanthemum* x *superbum* Bergmans. J. Amer. Soc. Hort. Sci. 107(5):874-877.

Song, C.Y., M.S. Roh, S.K. Chung, and R.H. Lawson. 1993. Effect of temperature and light on growth and flowering of potted plant production of *Platycodon*. J. Korean Soc. Hort. Sci. 34(6):446-453.

Vince-Prue, D. 1975. Photoperiodism in plants. McGraw, London.

Vince-Prue, D. 1984. Light and the flowering process--setting the scene, p. 3-15. In: D. Vince-Prue, B. Thomas, and K.E. Cockshull (eds.). Light and the flowering process. Academic Press, San Diego.

Waithaka, K. and L.W. Wanjao. 1982. The effect of duration of cold treatment on growth and flowering of *Liatris*. Scanty Hort. 18:153-158.

Whitman, C.M. 1995. Influence of photoperiod and temperature on flowering of *Campanula carpatica* 'Blue Clips; *Coreopsis grandiflora* 'Early Sunrise', *Coreopsis verticillata* 'Moonbeam', *Rudbeckia fulgida* 'Goldsturm' and *Lavandula angustifolia* 'Munstead'. MS Thesis, Michigan State University, East Lansing.

Yuan, M. 1995. Effect of juvenility, temperature and cultural practices on flowering of *Coreopsis*, *Gaillardia*, *Heuchera*, *Leucanthemum*, and *Rudbeckia*. MS Thesis, Michigan State University, East Lansing.

Zeevaart, J.A.D. 1978. Phytohormones and flower formation. P. 291-327. In: Letham, Goodwin, and Higgins (eds.). Phytohormones and related compounds--a comprehensive treatise, vol. II. Elsevier/North-Holland Biomedical Press.

Zhang, D., A.M. Armitage, J.M. Affolter, and M.A. Dirr. 1995. Environmental control of flowering and growth of *Lysimachia congestiflora* Hemsl. HortScience 30(1):62-64.

SECTION III

EFFECT OF NIGHT INTERRUPTION DURATION AND CYCLIC LIGHTING ON FLOWERING OF LONG-DAY HERBACEOUS PERENNIAL PLANTS

Introduction

In the greenhouse industry, the photoperiod often is lengthened artificially to keep plants vegetative or to induce flowering. For most photoperiodic plants, the duration of the perceived uninterrupted dark period determines whether plant growth is vegetative or reproductive. Under natural short days (SD), long days (LD) are created by lighting during natural dark periods. Traditionally, a four-hour night interruption (NI) (e.g., from 2200 to 0200 HR) has been the most popular method of delivering LD.

The effectiveness of NI lighting primarily depends on timing, duration and intensity. For most plants, lighting during the middle of the dark period most effectively breaks up the long, dark period (Vince-Prue and Canham, 1983). To interrupt the dark period satisfactorily, long-day plants (LDP) often require longer durations and/or higher intensities of light for promotion of flowering than short-day plants (SDP) require for inhibition of flowering (Vince-Prue, 1975).

Many LDP show a quantitative response to the duration and intensity of the night-break exposure (Vince-Prue and Canham, 1983). For example, *Trachelium caeruleum* L. showed a quantitative relationship between duration and intensity of NI and the magnitude of the flowering response (Shillo, in press). However, Kadman-Zahavi (in press) found that for most SDP and LDP studied, NI of 15 min, 2, 4, or 10 hours were equally effective when provided at the same total light fluence. The light intensity required for effective NI may change during the year. To keep the SDP *Chrysanthemum xmorifolium* vegetative, Sachs et al.

(1980) found that plants grown during a period of high daytime irradiance (e.g., in July) required a greater intensity of NI lighting than plants grown during periods with a lower daytime irradiance (e.g., in January).

In contrast to continual NI lighting, cyclic, or intermittent, lighting is a strategy in which lamps are cycled, or flashed on, so that light and dark cycles are provided throughout the usual lighting period. The primary advantage of cyclic lighting is a savings of 60 to 80% in energy consumption compared to continual NI lighting (Bickford and Dunn, 1972; Canham, 1966). Cyclic lighting regimes have varied; lights may be on for 2 to 50% of the time for part or all of the dark period (Bickford and Dunn, 1972; Vince-Prue and Canham, 1983).

The efficacy of cyclic lighting at promoting or inhibiting flowering depends on the plant and the duration, frequency, and intensity of light. Cyclic lighting is frequently used to maintain vegetative growth in some SDP, such as *Chrysanthemum* spp. However, the effectiveness of cyclic lighting at initiating flowering in LDP has been investigated in only a few species and has been found to vary considerably.

In the LDP baby's breath (*Gypsophila paniculata* L. 'Bristol Fairy'), cyclic lighting of 5 min light and 10 min dark (33% cyclic) for four hours with incandescent lamps, which provided 2 μmol·m^{-2}·s^{-1}, induced flowering similarly to continual four-hour NI (Shillo and Halevy, 1982). In another study, the LDP sweet clover (*Melilotus alba* Desr.) was provided with five different 10% cyclic lighting treatments during 16-hour dark periods with incandescent lamps, which provided 8.6 μmol·m^{-2}·s^{-1}, (Kasperbauer et al., 1963). Plants provided with

shorter (1.5 min) but more frequent (every 15 min) cyclic lighting cycles flowered similarly to plants under continual light. The flowering response decreased as both the duration of light during each cycle increased and frequency decreased. Kasperbauer et al. (1963) found that days to flower decreased and flower number increased as the cyclic lighting intensity increased from 1 to 17 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

In two cultivars of the obligate LDP China aster (*Callistephus chinensis* Nees), very brief and infrequent cyclic lighting cycles (one minute every hour during 16-hour dark periods) induced flowering faster than plants under one hour of continual NI, but not as rapidly as plants under continual light (Cockshull and Hughes, 1969). Cyclic lighting also hastened flowering in the facultative LDP snapdragon (*Antirrhinum majus* L.); plants provided with at least 10 seconds of light per minute for four hours flowered simultaneously to those provided with a continual four-hour NI (Maginnes and Langhans, 1967).

The effectiveness of short durations (<4 hours) of NI lighting has been studied in a few LDP. In sweetclover, days to first flower decreased at a decreasing rate from >60 days to 32 days and average flower number increased as the NI duration increased from 2 to 16 hours (Kasperbauer et al., 1963). In the LDP carnation (*Dianthus caryophyllus* L.), plants were provided with 0.5-hour or two-hour NI treatments during the middle of 16-hour dark periods with incandescent lamps which emitted 7.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Harris, 1969). The 0.5-hour NI did not promote flowering but the two-hour NI was sufficient to produce a

long-day flowering response. Shillo (in press) reported that short durations (not specified) of NI induced flowering in butterfly weed (*Asclepias tuberosa* L.).

The objective of this experiment was to determine the effectiveness of various durations of NI or cyclic lighting at initiating flowering in six species of long-day herbaceous perennial species.

Materials and Methods

Plant material. The species studied, plug size, and age of plant material are provided in Table 31. The experiment was replicated in time with Experiments I and II beginning on 20 December, 1995 and 16 February, 1996, respectively. Plants were grown under natural short-day photoperiods (≤11.5 hours of light) until the beginning of each experiment.

Plant culture. Plants were grown in a commercial soilless medium composed of composted pine bark, horticultural vermiculite, Canadian sphagnum peat moss, processed bark ash, and washed sand (MetroMix 510, Scotts-Sierra Horticultural Products Company, Marysville, Ohio). Plants were top-watered with well water acidified (two parts H_3PO_4 plus one part H_2SO_4, which provided ≈2.5 mol $P \cdot m^{-3}$) to a titratable alkalinity of approximately 130 mg calcium bicarbonate per liter and fertilized with 14N-0P-6K_2O ($mol \cdot m^{-3}$) from potassium nitrate (14N-0P-55K_2O) (Vicksburg Chemical Co., Vicksburg, MS) and ammonium nitrate (34N-0P-0K_2O) (Cargill, Lexington, KY). Fertilization and acidification rates were adjusted in response to weekly soil test results, so regimes varied during experiments. High-pressure sodium lamps provided a *PPF* of approximately 50

Table 31. Species studied, characteristics of starting material, and average air temperatures from date of forcing to average date of flowering for each species under each photoperiod.

Species	Propagation[z]		Plug size[x]	Initial nodes	Expt.	Average temperature during forcing (°C)						
							Night interruption				Cyclic	
	Date	Environment[y]				SD[w]	0.5 h	1 h	2 h	4 h	10%[v]	20%[u]
Campanula carpatica Jacq. 'Blue Clips'	8/7/95	a	70	16.0	1	-[t]	-	20.4	20.6	20.4	20.3	20.3
				23.5	2	-	-	-	20.4	20.1	20.4	20.0
Coreopsis grandiflora Hogg ex Sweet 'Early Sunrise'	6/25/95	b	50	6.3	1	-	20.7	20.4	20.6	20.4	20.3	20.4
				8.4	2	-	20.6	20.2	20.4	20.1	20.4	20.0
Coreopsis verticillata L. 'Moonbeam'	8/14/95	a	70	≈3	1	-	20.7	20.3	20.5	20.4	20.3	20.3
				≈3	2	-	20.6	20.1	20.3	19.9	20.4	19.9
Echinacea purpurea Moench 'Bravado'	10/9/95	c	128	4.1	1	-	20.7	20.3	20.5	20.3	20.3	20.2
Hibiscus xhybrida 'Disco Belle Mixed'	10/30/95	c	128	4.8	1	20.4	20.6	20.2	20.4	20.2	20.3	20.2
				8.8	2	20.1	20.7	20.1	20.4	19.9	20.3	19.7
Rudbeckia fulgida Ait. 'Goldsturm'	6/1/95	b	50	11.0	1	-	-	20.3	20.4	20.4	20.3	20.3
				11.0	2	-	20.7	20.0	20.3	19.9	20.4	19.8

[z]All plants were propagated by seed, except for 'Moonbeam', which was propagated by stem cuttings.
[y]a = natural daylengths, no exposure to temperatures below 12 to 15 °C.
b = natural photoperiods, minimum temperatures of 19 °C until last two weeks, when minimum temperatures decreased to 13 °C.
c = natural photoperiods, temperatures beginning at 24 °C and gradually decreasing to 19°C.
[x]Volume of 128-, 70-, or 50-cell trays are 10, 50, or 85 ml, respectively.
[w]Nine-hour photoperiods.
[v]Lights on and off for 6 and 54 min, respectively, for 4 h.
[u]Lights on and off for 6 and 24 min, respectively, for 4 h.
[t]No plants flowered.

μmol·m^{-2}·s^{-1} at plant level when the ambient greenhouse *PPF* was lower than 400 μmol·m^{-2}·s^{-1}.

Cold treatments. R. fulgida 'Goldsturm' that averaged ≈11 nodes (leaves) received either no cold treatment (Experiment I) or were placed in a controlled-environment chamber for 8 weeks at 5 °C (Experiment II). The chamber was lit from 0800 to 1700 HR at approximately 10 μmol·m^{-2}·s^{-1} from cool-white fluorescent lamps (VHOF96T12; Philips, Bloomfield, N.J.), as measured by a LI-COR quantum sensor (model LI-189; LI-COR, Inc., Lincoln, NE). No other species received a cold treatment.

Light treatments. Seventy plants of each species were removed from their containers, singulated, and transplanted into 13-cm square containers (1.1 liters). Ten plants were placed under each treatment that was assigned randomly to benches in the greenhouse. Black cloth was pulled at 1700 HR and opened at 0800 HR every day on all benches to provide similar daily light integrals. During the middle of the dark period, benches were lighted with incandescent lamps at 1 to 3 μmol·m^{-2}·s^{-1} for the following durations: 0, 0.5, 1, 2, or 4 hours, 6 min on, 54 min off for four hours (10% cyclic lighting), or 6 min on, 24 min off for four hours (20% cyclic lighting).

Greenhouse temperature control. All plants were grown in a glass greenhouse set at 20 °C. Air temperatures on each bench were monitored with 36-gauge (0.013-mm-diameter) type E thermocouples connected to a CR10 datalogger (Campbell Scientific, Logan, UT). To provide uniform temperatures, the datalogger controlled a 1500-watt electric heater under each bench, which

provided supplemental heat as needed throughout the night. The datalogger collected temperature data every 10 seconds and recorded the hourly average. Actual average daily air temperatures from the beginning of forcing to the average date of flowering under every photoperiod were calculated for each species and are presented in Table 31.

Data collection and analysis. The leaves of each plant were counted at the onset of forcing. Date of the first visible bud or inflorescence and date of opening of the first flower were recorded for each plant. At flowering, the number of visible flower buds or inflorescences, the number of leaves on the main stem below the first flower, and total plant height were determined. Plants that did not have visible buds or inflorescences after 15 weeks of forcing were discarded and considered nonflowering. Days to visible bud, days from visible bud to flower, days to flower, and increase in node count were calculated.

For each species, I used a randomized complete block design in which blocks were light treatments with ten observations for each treatment and experiment. Data were analyzed using SAS's (SAS Institute, Cary, NC) analysis of variance and general linear models procedures.

Results and Discussion

Campanula carpatica 'Blue Clips'

Experiment 1. No plants flowered with ≤0.5 hours of NI. Flowering was similar with 2 or 4 hours of NI or the 20% cyclic lighting treatment: plants flowered in 49 to 59 days, developed 17 to 20 nodes, averaged 17 or 18 cm tall,

and had an average of 38 or 39 flowers (Figure 42, Table 32). Flowering was most uniform for plants under four hours of NI. For plants under one hour of NI or 10% cyclic lighting, flowering was incomplete, non-uniform, and delayed by 20 to 50 days. NI treatment did not affect days from visible bud to flower

Experiment 2. For plants provided with 2 or 4 hours of NI or 20% cyclic lighting, time to flower, flower number, and the number of new nodes formed were similar to those in Experiment 1. Although plants were more mature, they had approximately half the number of flowers as plants in Experiment 1. Few or no plants flowered with one hour of NI or 10% cyclic lighting.

***Coreopsis grandiflora* 'Early Sunrise'**

Experiment 1. No plants flowered without NI and all plants flowered with ≥0.5 hours of NI or 10 or 20% cyclic lighting (Figure 43, Table 33). Flowering was delayed under 0.5 hours of NI or 10 or 20% cyclic lighting compared to plants under four-hour NI. Plant height increased from 21 to 31 cm as the duration of NI increased. Plants under 0.5 hours of NI had the fewest flowers.

Experiment 2. All plants that received NI flowered. Plants flowered more uniformly and about ten days faster than plants in Experiment 1, which may be at least partially explained by the use of more developed (by ≈ two nodes, or four leaves) plants. Under 0.5 hours of NI or 10 or 20% cyclic lighting, days to visible bud and flower were delayed compared to those under four-hour NI. Flower number was reduced (by five to seven) and days from visible bud to flower was greatest for plants under 0.5 hours or 10% cyclic lighting.

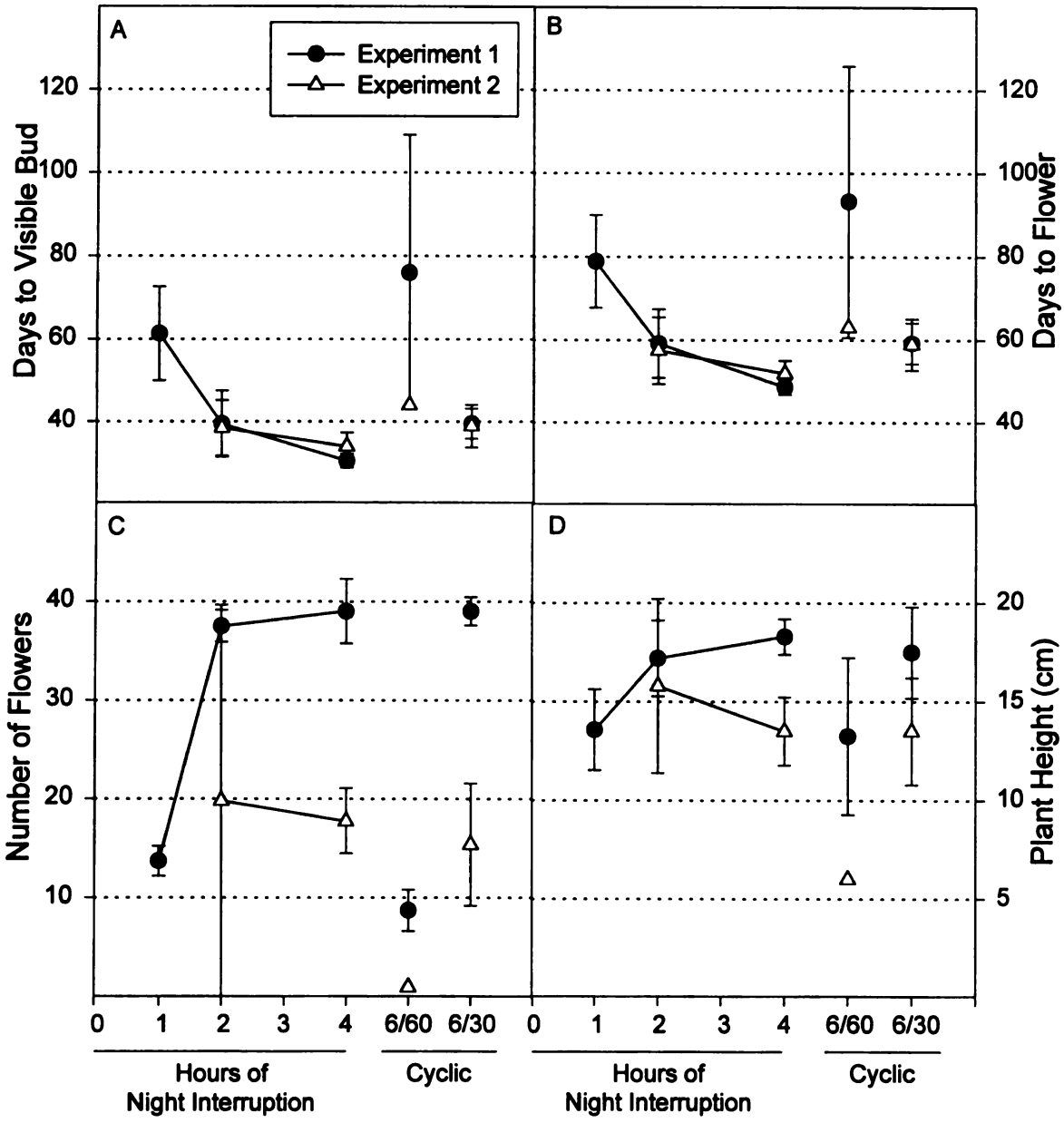


Figure 42. Flowering of *Campanula carpatica* 'Blue Clips' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-hour dark periods. For the cyclic lighting treatments, lights were on for six minutes every 30 or 60 minutes for a four hour period during the middle of the night. Error bars are 95% confidence intervals.

Table 32. The effects of night-interruption duration and cyclic lighting on flowering of *Campanula carpatica* 'Blue Clips'.

Night interruption[z]	Flowering (%)	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
			Experiment 1				
0 h	0	–[y]	–	–	–	–	–
0.5 h	0	–	–	–	–	–	–
1 h	70	61 b[x]	18 a	79 b	27 a	14 a	14 a
2 h	100	39 c	20 a	59 c	20 b	17 b	38 b
4 h	100	30 c	18 a	49 c	17 b	18 b	39 b
10% cyclic[w]	40	76 a	17 a	93 a	29 a	13 a	9 a
20% cyclic[v]	100	40 c	20 a	59 c	20 b	18 b	39 b
			Experiment 2				
0 h	0	–	–	–	–	–	–
0.5 h	0	–	–	–	–	–	–
1 h	0	–	–	–	–	–	–
2 h	83	38 a	19 a	57 a	20 a	16 a	20 a
4 h	100	34 a	19 a	52 a	16 a	14 a	18 ab
10% cyclic	17	44 a	19 a	63 a	17 a	6 b	1 b
20% cyclic	89	39 a	20 a	59 a	19 a	14 a	15 ab

[z]9-h natural days with night-interruption lighting during the middle of the dark period.
[y]– = no plants showed visible bud after 105 days of forcing.
[x]Mean separation within each photoperiod by Duncan's multiple range test ($P = 0.05$).
[w]Lights on and off for 6 and 54 min, respectively, for 4 h.
[v]Lights on and off for 6 and 24 min, respectively, for 4 h.

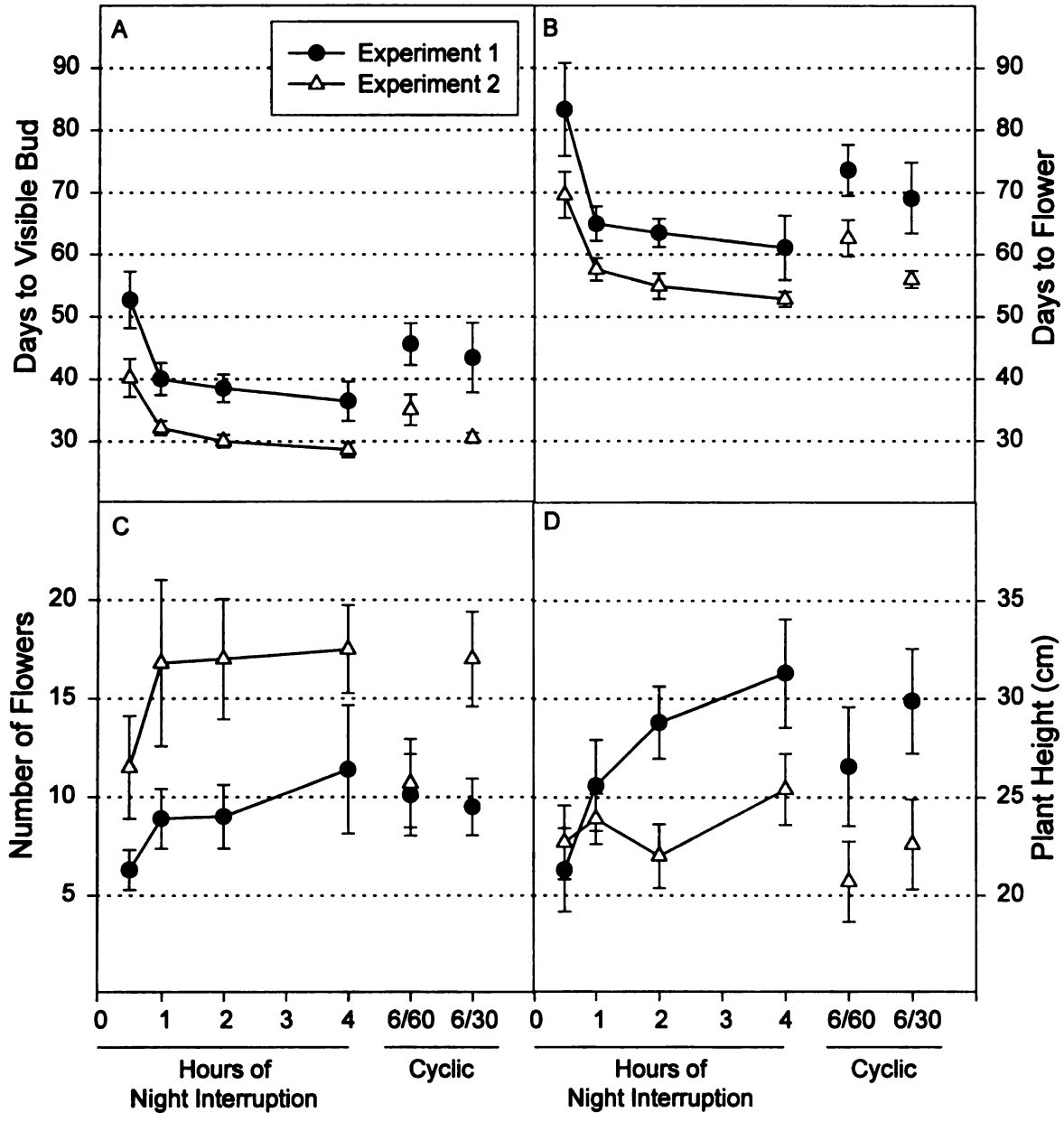


Figure 43. Flowering of *Coreopsis grandiflora* 'Early Sunrise' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-hour dark periods. For the cyclic lighting treatments, lights were on for six minutes every 30 or 60 minutes for a four hour period during the middle of the night. Error bars are 95% confidence intervals.

Table 33. The effects of night-interruption duration and cyclic lighting on flowering of *Coreopsis grandiflora* 'Early Sunrise'.

Night interruption[z]	Flowering (%)	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
			Experiment 1				
0 h	0	–[y]	–	–	–	–	–
0.5 h	100	53 a[x]	31 a	83 a	8 b	21 c	6 b
1 h	100	40 cd	25 b	65 cd	9 a	26 b	9 a
2 h	100	39 cd	25 b	64 cd	9 ab	29 ab	9 a
4 h	100	36 d	25 b	61 d	8 ab	31 a	11 a
10% cyclic[w]	100	46 b	28 b	74 b	9 ab	27 b	10 a
20% cyclic[v]	100	43 bc	26 b	69 bc	8 ab	30 a	10 a
			Experiment 2				
0 h	0	–	–	–	–	–	–
0.5 h	100	40 a	29 a	70 a	9 a	23 cb	12 b
1 h	100	32 c	26 b	58 c	8 b	24 ab	17 a
2 h	100	30 cd	25 b	55 cd	8 b	22 bc	17 a
4 h	100	29 d	24 b	53 d	8 b	25 a	18 a
10% cyclic	100	35 b	28 a	63 b	8 ab	21 c	11 b
20% cyclic	100	31 cd	26 b	56 c	8 b	23 bc	17 a

[z]9-h natural days with night-interruption lighting during the middle of the dark period.
[y]– = no plants showed visible bud after 105 days of forcing.
[x]Mean separation within each photoperiod by Duncan's multiple range test ($P = 0.05$).
[w]Lights on and off for 6 and 54 min, respectively, for 4 h.
[v]Lights on and off for 6 and 24 min, respectively, for 4 h.

***Coreopsis verticillata* 'Moonbeam'**

Experiment 1. No plants flowered without NI. Percentage of flowering increased from 40 to 100%, days to flower decreased from 114 to 68, and plant height increased from 31 to 77 cm as the duration of NI increased from 0.5 to 4 hours (Figure 44, Table 34). Furthermore, the 95% CI of time to flower decreased dramatically as the NI duration increased. All flowering characteristics measured under 20% cyclic lighting were similar to those under four-hour NI. Flowering under 10% cyclic lighting was incomplete and delayed by approximately four weeks compared to plants under four-hour NI. Plants under two hours of NI were delayed by approximately 17 days compared to plants under four hours of NI.

Experiment 2. No plants flowered without NI. All plants flowered under ≥1 hour of NI or either cyclic lighting treatment. NI duration did not influence days to flower as it did in Experiment 1. Flower number increased from 27 to 63 as the NI duration increased from 0.5 to 4 hours. Plants were shortest under 0.5 hours of NI or 10% cyclic lighting. Flowering under 20% cyclic lighting was similar to plants under four hours of NI.

***Echinacea purpurea* 'Bravado'**

Plant mortality was excessively high in Experiment 2, so only results of Experiment 1 are presented. No plants flowered without and essentially all flowered with NI (Figure 45, Table 35). All NI durations and cyclic lighting regimes induced plants to flower at approximately the same time. Plant height increased from 41 to 61 cm as the NI duration increased from 0.5 to 4 hours.

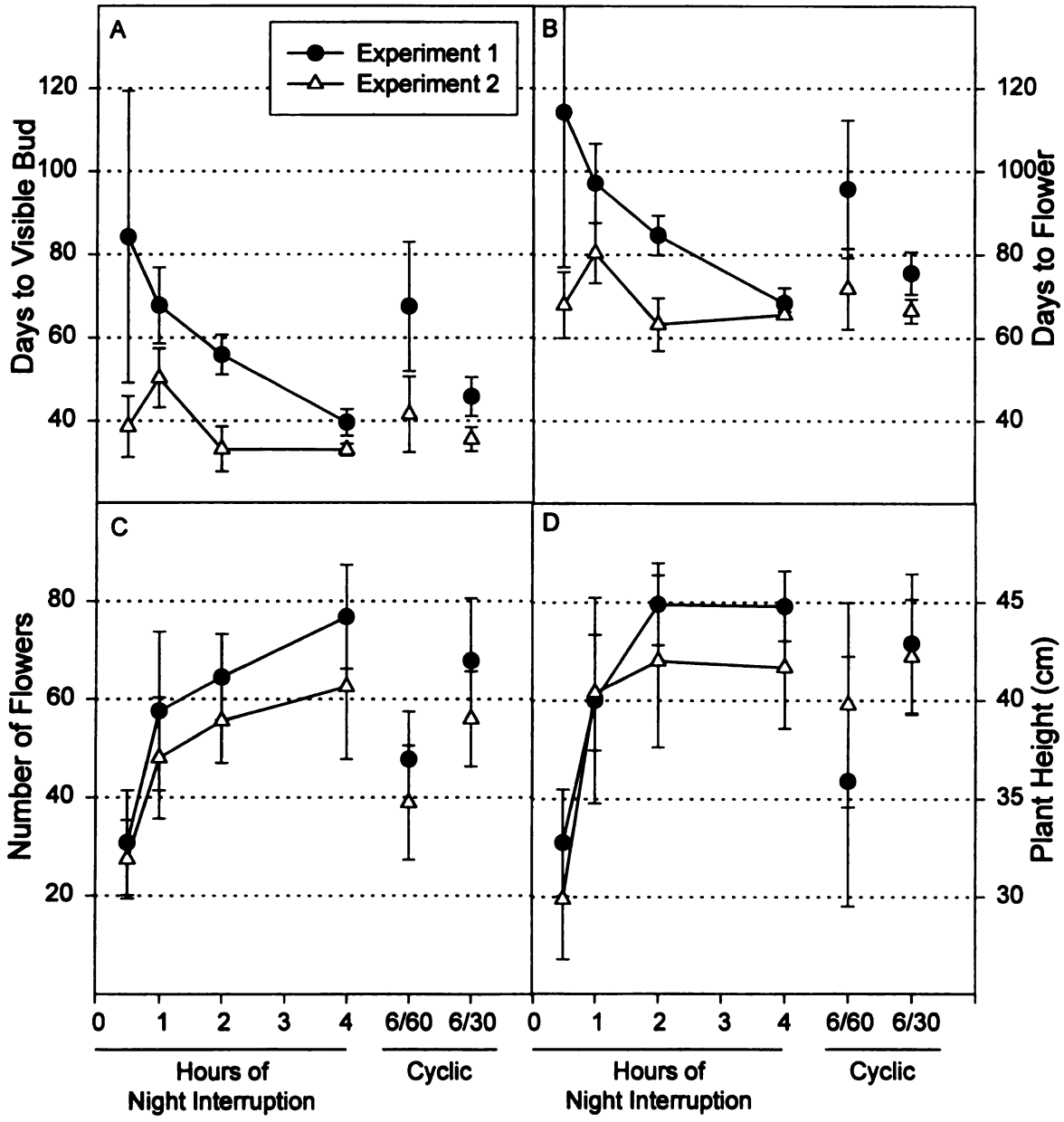


Figure 44. Flowering of *Coreopsis verticillata* 'Moonbeam' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-hour dark periods. For the cyclic lighting treatments, lights were on for six minutes every 30 or 60 minutes for a four hour period during the middle of the night. Error bars are 95% confidence intervals.

Table 34. The effects of night-interruption duration and cyclic lighting on flowering of *Coreopsis verticillata* 'Moonbeam'.

Night interruption[z]	Flowering (%)	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
			Experiment 1				
0 h	0	–[y]	–	–	–	–	–
0.5 h	40	84 a[x]	30 a	114 a	6 b	33 c	31 d
1 h	90	68 b	29 a	97 b	6 a	40 ab	58 bc
2 h	100	56 bc	29 a	85 bc	6 a	45 a	65 abc
4 h	100	40 d	29 a	68 d	7 a	45 a	77 a
10% cyclic[w]	80	68 b	28 a	96 b	6 a	36 bc	48 c
20% cyclic[v]	100	46 cd	30 a	76 cd	6 a	43 a	68 ab
			Experiment 2				
0 h	0	–	–	–	–	–	–
0.5 h	80	39 bc	29 c	68 b	5 a	30 b	27 c
1 h	100	50 a	30 bc	80 a	6 a	40 a	48 ab
2 h	100	33 c	30 bc	63 b	6 a	42 a	56 a
4 h	100	33 c	32 a	66 b	6 a	42 a	63 a
10% cyclic	100	42 b	30 bc	72 b	6 a	40 a	39 bc
20% cyclic	100	36 bc	32 ab	66 b	6 a	42 a	56 a

[z]9-h natural days with night-interruption lighting during the middle of the dark period.
[y]– = no plants showed visible bud after 105 days of forcing.
[x]Mean separation within each photoperiod by Duncan's multiple range test ($P = 0.05$).
[w]Lights on and off for 6 and 54 min, respectively, for 4 h.
[v]Lights on and off for 6 and 24 min, respectively, for 4 h.

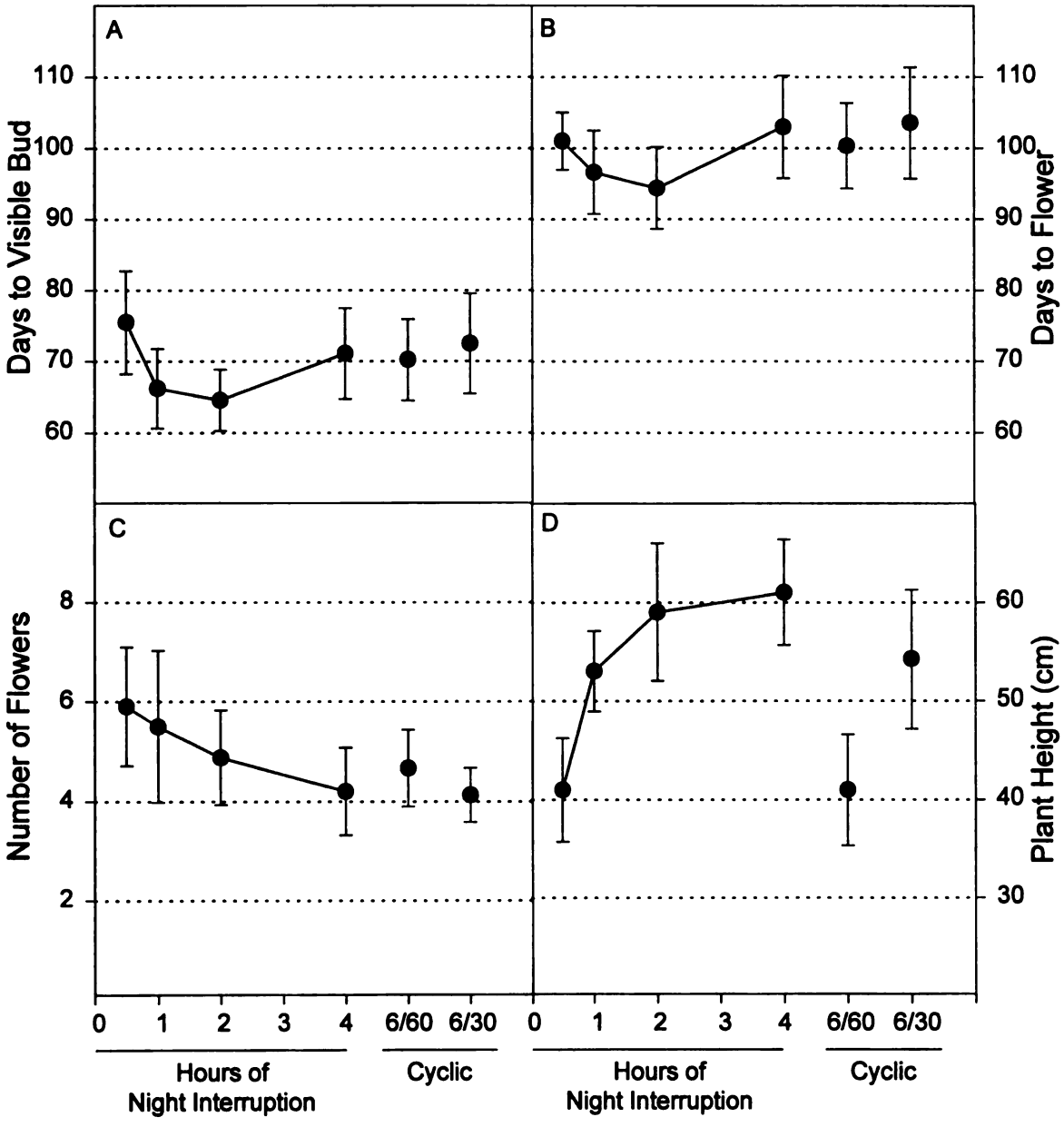


Figure 45. Flowering of *Echinacea purpurea* 'Bravado' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-hour dark periods. For the cyclic lighting treatments, lights were on for six minutes every 30 or 60 minutes for a four hour period during the middle of the night. Error bars are 95% confidence intervals.

Table 35. The effects of night-interruption duration and cyclic lighting on flowering of *Echinacea purpurea* 'Bravado'.

Night interruption[z]	Flowering (%)	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
0 h	0	–[y]	–	–	–	–	–
0.5 h	100	76 a[x]	26 b	101 ab	17 a	41 c	6 a
1 h	100	66 b	30 ab	97 ab	14 b	53 b	6 ab
2 h	90	65 b	29 ab	94 b	14 b	59 ab	5 ab
4 h	100	71 ab	32 a	103 ab	14 b	61 a	4 b
10% cyclic[w]	100	70 ab	30 ab	100 ab	14 b	41 c	5 ab
20% cyclic[v]	100	73 ab	32 a	104 a	13 b	54 ab	4 b

[z]9-h natural days with night-interruption lighting during the middle of the dark period.
[y]– = no plants showed visible bud after 105 days of forcing.
[x]Mean separation within each photoperiod by Duncan's multiple range test ($P = 0.05$).
[w]Lights on and off for 6 and 54 min, respectively, for 4 h.
[v]Lights on and off for 6 and 24 min, respectively, for 4 h.

Plants under 0.5 hours of NI had more flowers than plants under four hours of NI or 20% cyclic lighting.

***Hibiscus* x*hybrida* 'Disco Belle Mixed'**

Experiment 1. Ten percent of plants flowered without NI, 50% flowered with 0.5 hours of NI, and ≥80% flowered with ≥1 hour of NI or 10 or 20% cyclic lighting for four hours (Figure 46, Table 36). Days to flower decreased from 154 to 114 and flower number increased from 5 to 17 as the NI duration increased from 0 to 4 hours. Cyclic lighting induced flowering at approximately the same time as plants under the four hours of NI.

Experiment 2. Plants flowered more uniformly and 25 to 40 days earlier and than plants in Experiment 1, which may be at least partially due to starting with more mature plants. Seventy percent of plants flowered without and all plants flowered with a NI. All plants flowered at approximately the same time and developed approximately the same number of nodes.

***Rudbeckia fulgida* 'Goldsturm'**

Experiment 1. No plants flowered without NI or with 0.5 hours of NI (Figure 47, Table 37). All plants that received ≥1 hour of NI flowered, and 60 or 90% of plants flowered under 10 or 20% cyclic lighting, respectively. Plants under four hours of NI flowered earlier (≥19 days) and developed at least four fewer nodes than plants under other lighting treatments. Plants under one or two hours of NI or 20% cyclic lighting flowered simultaneously. For plants that

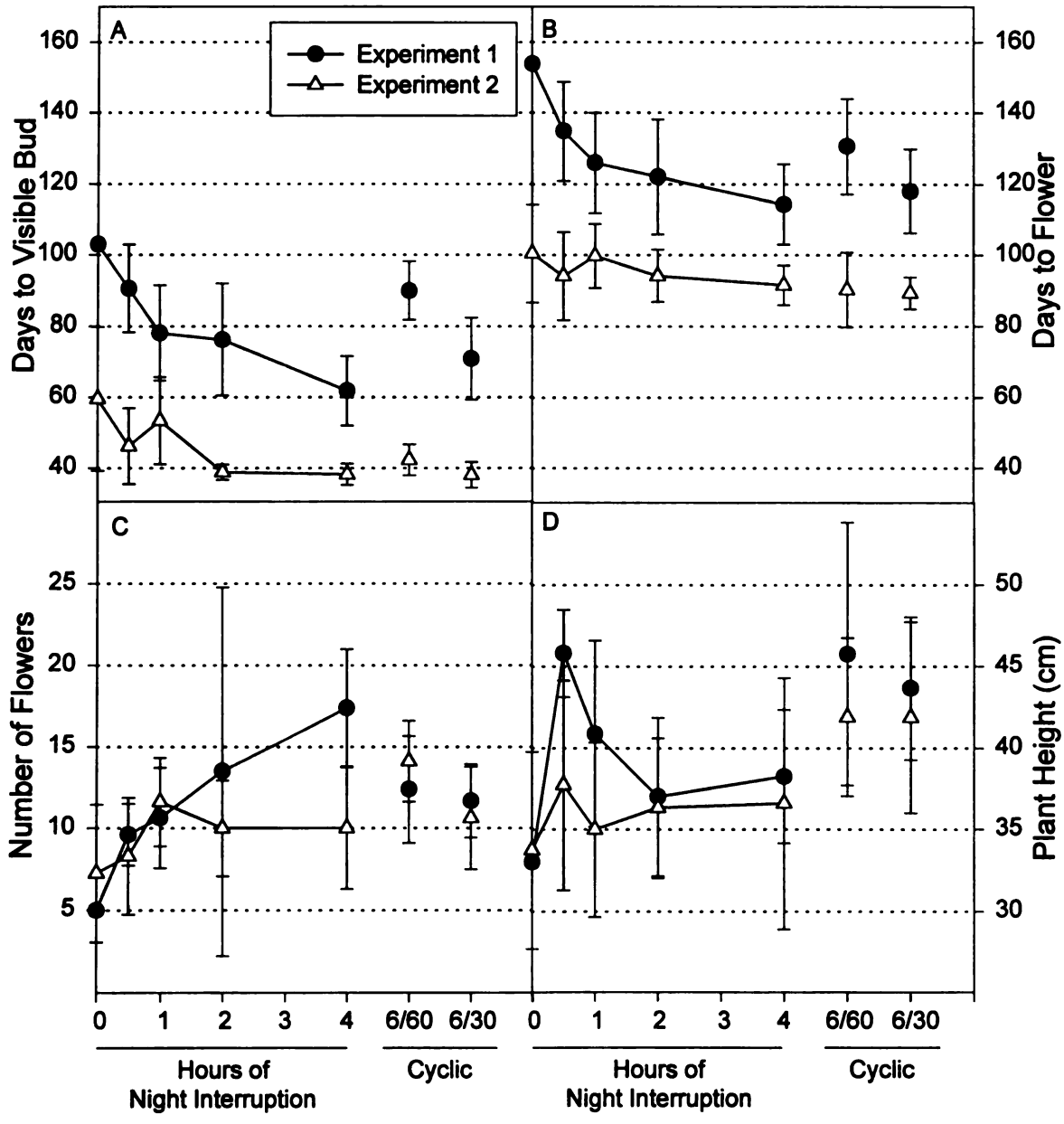


Figure 46. Flowering of *Hibiscus xhybrida* 'Disco Belle Mixed' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-hour dark periods. For the cyclic lighting treatments, lights were on for six minutes every 30 or 60 minutes for a four hour period during the middle of the night. Error bars are 95% confidence intervals.

Table 36. The effects of night-interruption duration and cyclic lighting on flowering of *Hibiscus xhybrida* 'Disco Belle Mixed'.

Night interruption[z]	Flowering (%)	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
			Experiment 1				
0 h	10	103 a[y]	51 a	154 a	21 a	33 b	5 b
0.5 h	50	91 ab	44 a	135 ab	19 a	46 a	10 ab
1 h	90	78 bc	46 a	126 b	15 a	41 ab	11 ab
2 h	90	76 bc	44 a	122 b	17 a	37 ab	14 ab
4 h	90	62 c	52 a	114 b	15 a	38 ab	17 a
10% cyclic[x]	80	90 ab	40 a	131 ab	17 a	46 a	12 ab
20% cyclic[w]	90	71 bc	47 a	118 b	15 a	44 a	12 ab
			Experiment 2				
0 h	70	60 a	52 a	101 a	14 a	34 b	7 b
0.5 h	100	46 bc	50 a	94 a	14 a	38 ab	8 b
1 h	100	53 ab	56 a	100 a	14 a	35 ab	12 ab
2 h	100	39 c	56 a	94 a	14 a	36 ab	10 ab
4 h	100	38 c	56 a	92 a	12 a	37 ab	10 ab
10% cyclic	100	42 bc	48 a	90 a	13 a	42 a	14 a
20% cyclic	100	38 c	51 a	89 a	12 a	42 a	11 ab

[z]9-h natural days with night-interruption lighting during the middle of the dark period.
[y]Mean separation within each photoperiod by Duncan's multiple range test ($P = 0.05$).
[x]Lights on and off for 6 and 54 min, respectively, for 4 h.
[w]Lights on and off for 6 and 24 min, respectively, for 4 h.

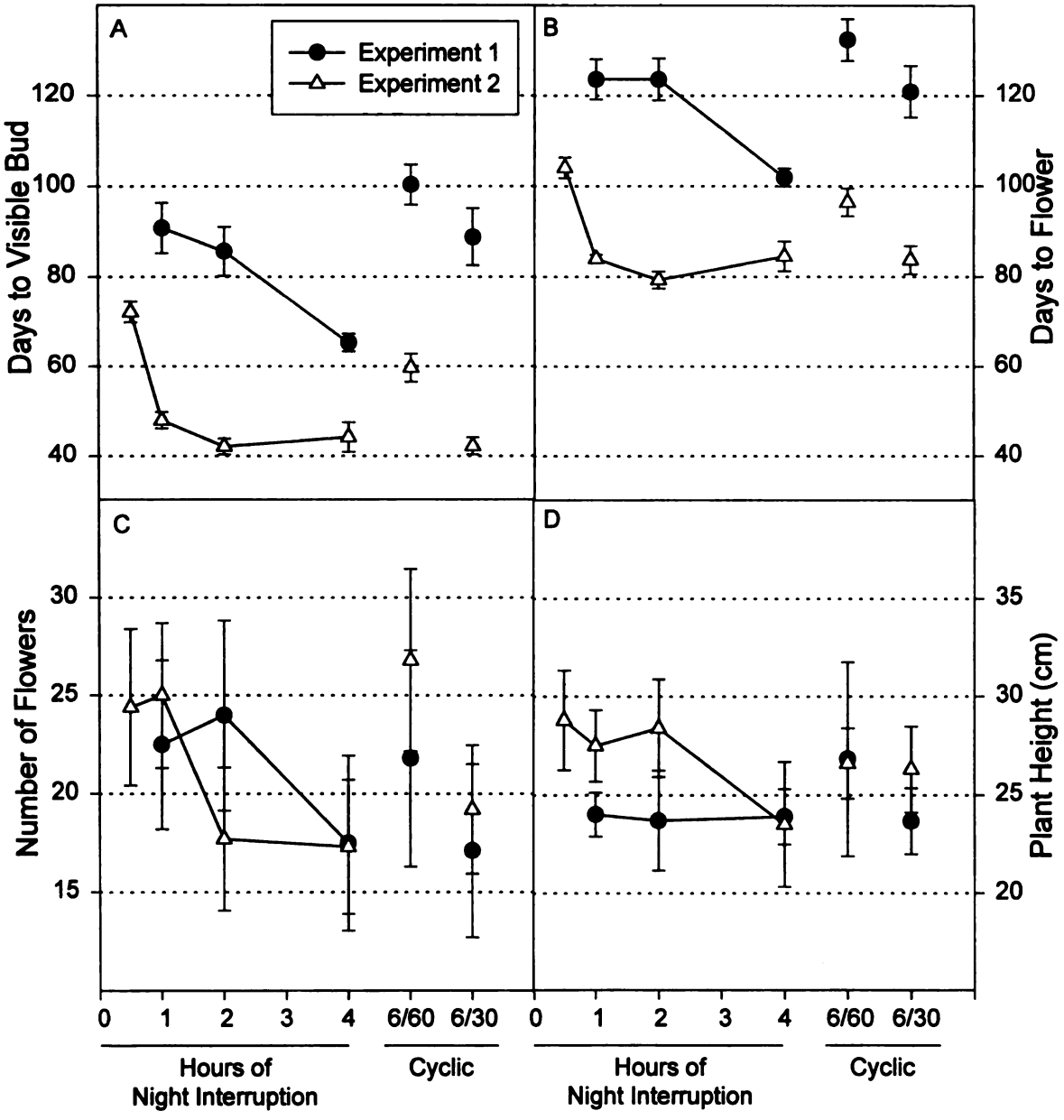


Figure 47. Flowering of *Rudbeckia fulgida* 'Goldsturm' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-hour dark periods. For the cyclic lighting treatments, lights were on for six minutes every 30 or 60 minutes for a four hour period during the middle of the night. Error bars are 95% confidence intervals.

Table 37. The effects of night-interruption duration and cyclic lighting on flowering of *Rudbeckia fulgida* 'Goldsturm'.

Night interruption[z]	Flowering (%)	Days to visible bud	Days from visible bud to flower	Days to flower	Increase in node number	Final plant height (cm)	Flower number
			Experiment 1				
0 h	0	–[y]	–	–	–	–	–
0.5 h	0	–	–	–	–	–	–
1 h	100	91 b[x]	33 b	124 b	23 a	24 b	23 ab
2 h	100	86 b	38 a	124 b	23 a	24 b	24 a
4 h	100	65 c	37 a	102 c	18 b	24 b	18 ab
10% cyclic[w]	60	100 a	32 b	132 a	24 a	27 a	22 ab
20% cyclic[v]	90	89 b	32 b	121 b	22 a	24 b	17 b
			Experiment 2				
0 h	0	–	–	–	–	–	–
0.5 h	100	72 a	32 c	104 a	22 a	29 a	24 a
1 h	100	48 c	36 b	84 c	18 c	28 a	25 a
2 h	100	42 d	37 b	79 d	15 de	28 a	18 b
4 h	100	44 d	40 a	85 c	13 e	24 b	17 b
10% cyclic	100	60 b	37 b	96 b	20 b	27 ab	27 a
20% cyclic	100	42 d	42 a	84 c	16 d	26 ab	19 b

[z]9-h natural days with night-interruption lighting during the middle of the dark period.
[y]– = no plants showed visible bud after 105 days of forcing.
[x]Mean separation within each photoperiod by Duncan's multiple range test ($P = 0.05$).
[w]Lights on and off for 6 and 54 min, respectively, for 4 h.
[v]Lights on and off for 6 and 24 min, respectively, for 4 h.

flowered under 10% cyclic lighting, flowering was delayed and plants were tallest.

Experiment 2. No plants flowered without and all plants flowered with NI. The cold treatment shifted the minimum duration of NI for flowering from 1 to 0.5 hours and hastened flowering by more than two weeks. Plants flowered earliest under two hours of NI, approximately five to six days earlier than plants under one or four hours of NI or 20% cyclic lighting. For most plants under four hours of NI and some plants under 20% cyclic lighting, the flowering phenotype was atypical: the inflorescence was branched at the base. This may explain why days from visible bud to flower was delayed under these two lighting treatments. Flowering under 10% cyclic lighting or 0.5 hours of NI was delayed by approximately 12 or 20 days, respectively. Plants under 0.5 or 1 hour of NI or 10% cyclic lighting had the most flowers.

Conclusions

The response of six species of long-day perennials to the six NI lighting treatments in Experiment 1 is illustrated in Figure 48. The continual four-hour NI induced complete, rapid, and uniform flowering of all species. For *Coreopsis verticillata* 'Moonbeam' and *Hibiscus xhybrida* 'Disco Belle Mixed' the 20% cyclic lighting treatment was nearly as effective as the continual four-hour NI. Except for *Echinacea*, which flowered at approximately the same time under all NI

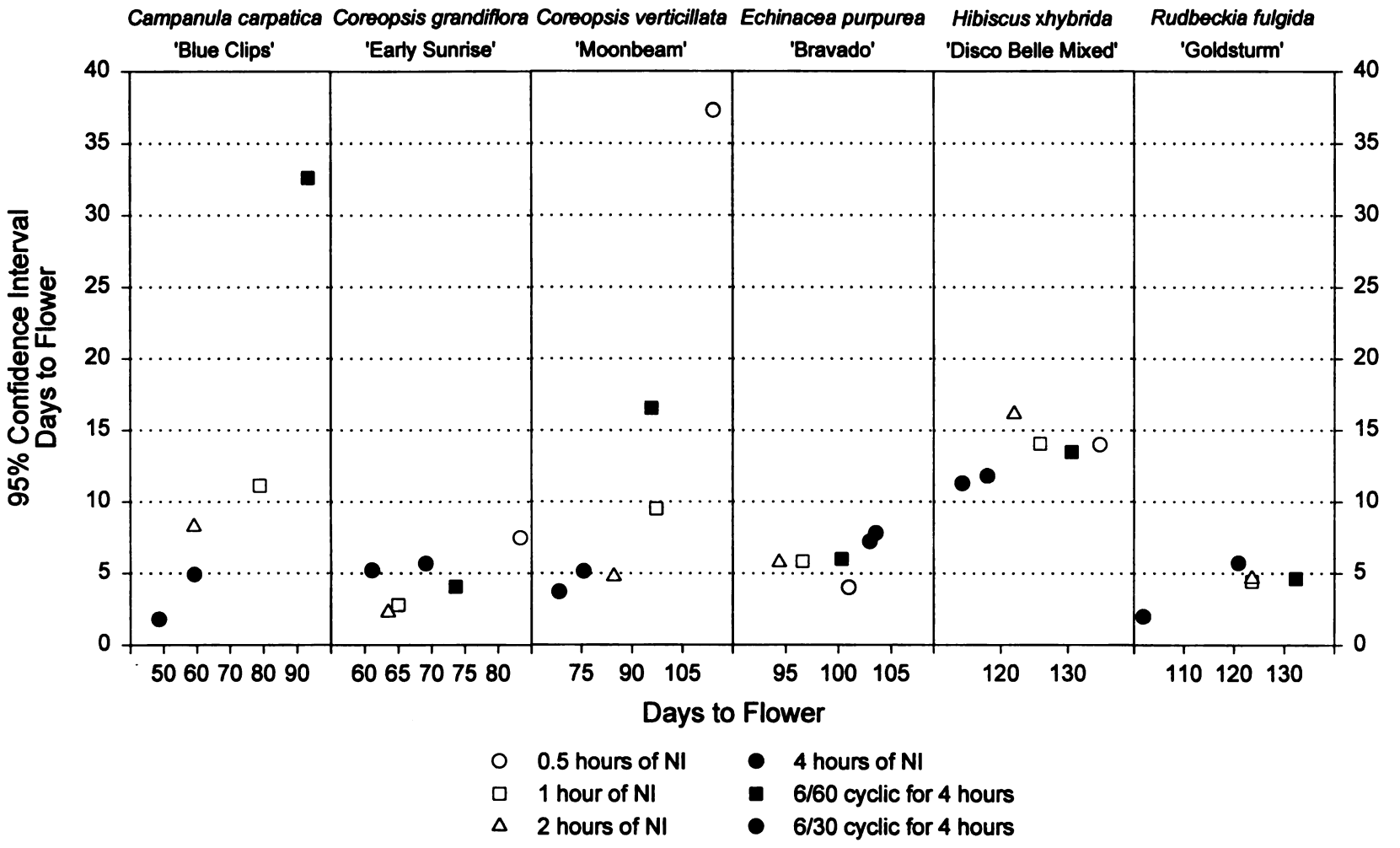


Figure 48. Time to flower and uniformity of flowering under the six night interruption treatments for six species of herbaceous perennials. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-hour dark periods. Cyclic lighting was for six minutes every 30 or 60 minutes for a four hour period during the middle of the night. Data are the results from Experiment 1. The absence of a point indicates that no plants flowered under that treatment.

treatments, NI durations of one hour or less or 10% cyclic lighting substantially delayed flowering and decreased uniformity.

The cold treatment increased the responsiveness of *Rudbeckia* to shorter durations of NI and to 10% cyclic lighting for four hours. This suggests that cold-treated herbaceous perennials may require shorter durations of NI for complete, rapid, and uniform flowering than plants not provided with a cold treatment. Further studies are needed to test this theory.

References

Bickford, E.D. and S. Dunn. 1972. Lighting for plant growth. Kent State Univ. Press.

Canham, A.E. 1966. The fluorescent tube as a source of night-break light. Exp. Hortic. 16:53-68.

Cockshull, K.E. and A.P. Hughes. 1969. Growth and dry-weight distribution in *Callistephus chinensis* as influenced by lighting treatment. Ann. Bot. 33:367-379.

Harris, G.P. 1968. Photoperiodism in the glasshouse carnation: the effectiveness of different light sources in promoting flower initiation. Ann. Bot. 32:187-197.

Kadman-Zahavi, A. 1994. Comparing lamps and timing of illumination to elicit a long-day response in long-day and short-day plants. Acta Hort. "(In press.)"

Kasperbauer, M.J, H.A. Borthwick, and H.M. Cathey. 1963. Cyclic lighting for promotion of flowering of Sweetclover, *Melilotus alba* Desr. Crop Sci. 3:230-232.

Maginnes, E.A. and R.W. Langhans. 1967. Flashing light affects the flowering of snapdragons. NY State Flower Grow. Bull.:261:1-3

Sachs, R.M., A.M. Kofranek, and J. Kubota. 1980. Radiant energy required for the night-break inhibition of floral initiation is a function of daytime light input in Chrysanthemum. HortScience 15(5):609-610.

Shillo, R. 1994. Flowering of some LDPs in response to photoperiodic lighting regimes. Acta Hort. "(In press.)"

Shillo, R. And A.H. Halevy. 1982. Interaction of photoperiod and temperature in flowering-control of *Gypsophila paniculata* L. Scientia Hort. 16:385-393.

Vince-Prue, D. 1975. Photoperiodism in plants. McGraw, London.

Vince-Prue, D. And A.E. Canham. 1983. Horticultural significance of photomorphogenesis, p. 518-544. In: Shropshire, W. and H. Mohr (eds.). Encyclopedia of plant physiology; new series, vol. 16. Springer-Verlag, Berlin.