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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'.

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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'

By

Catherine Margaret Whitman

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ABSTRACT

INFLUENCE OF PHOTOPERIOD AND TEMPERATURE ON FLOWERING OF *CAMPANULA CARPATICA* 'BLUE CLIPS', *COREOPSIS GRANDIFLORA* 'EARLY SUNRISE', *RUDBECKIA FULGIDA* 'GOLDSTURM' AND *LAVANDULA ANGUSTIFOLIA* 'MUNSTEAD'

By

Catherine Margaret Whitman

Effectiveness of supplementary light from cool white fluorescent, high-pressure sodium, incandescent, and metal halide lamps for flowering in *Campanula carpatica* 'Blue Clips', *Coreopsis grandiflora* 'Early Sunrise', *Coreopsis verticillata* 'Moonbeam', and *Rudbeckia fulgida* 'Goldsturm' was compared. An irradiance of 1.0 μmol $m^{-2}s^{-1}$ from any lamp tested was adequate for uniform flowering in these species. The influence of 5C treatments on flowering in *C. carpatica* was determined. Time to flower was unaffected by cold treatments in 12- to 16-node plants, but decreased by $\approx$10 days in 10- to 12-node plants cooled 14 weeks. The influence of 5C treatments and photoperiod on flowering in *Lavandula angustifolia* 'Munstead' was determined. Larger initial plant size and increased duration of cold storage were associated with increased percent flowering and decreased time to flower. Cold treatments reduced the photoperiodic response in *L. angustifolia*. *C. carpatica* and *L. angustifolia* were forced under 15, 18, 21, 24, or 27C, and the linear relationship between temperature and rate of progress to flowering was determined. Base temperatures and degree-days for developmental stages were calculated and can be used to predict flowering.

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LITERATURE REVIEW

LITERATURE REVIEW

Introduction and definitions.

Most biological processes proceed more quickly as temperatures rise. An exception is the promotion of flowering upon exposure to low temperatures which is found in a wide range of plant species. As early as the 1800s, research revealed that the cold temperatures of winter were the factor that enabled biennials and winter annuals, such as many grains, to flower promptly after the return of warmer temperatures (Chouard, 1960). Early studies emphasized the influence of low temperatures on germinating seeds. A cool, moist pretreatment of grain seeds is described in crop production reports by J.H. Klippart from Ohio State University in the mid 1800s (summarized by Whyte, 1948). After imbibition and exposure to an artificial cold treatment, winter wheat seeds planted in the spring grew and flowered quickly like the spring wheat varieties (Chouard, 1960). This strategy was used extensively in Russia during the 1930s to hasten the development of grain crops, especially in regions with a short growing season. "Jar" is a Russian name for the god of spring, and the phenomenon was termed "jarovization" by the Russian Lysenko . The English translation is "vernalization", "vernum" meaning "spring" in Latin (Chouard, 1960).

Direct and indirect effects of low temperatures.

Environmental factors can influence plant development either directly or inductively. Direct effects evoke the plant response during exposure to the

environmental condition. Inductive effects are associated with plant responses that occur some time after exposure to the environmental condition. Exposure to low temperature can influence flowering in several different ways.

Cold temperatures promote flowering in many plants by breaking the dormancy of existing buds, when reproductive structures are present prior to the onset of low temperatures. Insufficient duration of cold eliminates or reduces the flowering response. This response is found in many spring-flowering woody perennials and flowering bulbs such as *Tulipa* and *Narcissus* (Chouard, 1960; LeNard and DeHertogh, 1993). Floral primordia of *Paeonia* are also initiated soon after anthesis of the current year's flowers and require a minimum of four weeks at 5.6C to break dormancy (Byrne and Halevy, 1986).

Flower induction, initiation, and development occur during exposure to low temperatures in some species. Temperatures below 11C are required for flower initiation in *Brassica oleracea* gongylodes L. (kohlrabi), with the optimum being between 2 and 8C (Wiebe et al., 1992). Flower initiation and development occurred during 3C cold treatments in brussels sprouts (Stokes and Verkerk, 1951). Low temperatures are also required during floral initiation in *Allium cepa* (onion), *Iris* cv. Wedgewood, and *Matthiola incana* (stocks) (Vince-Prue, 1975). In *M. incana*, it was found that low-temperature conditions must continue until the buds are visible in order for their development to continue upon return to warmer temperatures (Kohl, 1957). Floral bud initiation and development occur in *Astilbe* during storage at 2C (Pemberton, 1992), and in *Dicentra spectabilis* during storage at 5 and 10C

(Hanchek,1989).

In contrast to these direct effects, exposure of some species to low temperatures induces the subsequent initiation and development of floral primordia. This inductive influence of low temperatures (often -2 to 5C) is the phenomenon known as vernalization, generally defined as a cold treatment that induces or hastens the capacity for flowering in a plant (Chouard, 1960; Vince-Prue, 1975; Zeevaart, 1963). Floral primordia are not initiated until after the return of warmer temperatures. In many species initiation will not occur until photoperiodic requirements are met as well. Species exhibiting a vernalization response encompass a wide range of winter annuals, biennials, and herbaceous perennials (Vince-Prue, 1975).

While promotion of flowering by cold temperatures is readily observed, often it is not possible to categorize the nature of this promotion in the absence of definitive knowledge on the time of flower initiation. In a diverse group of plants such as herbaceous perennials, a spectrum of mechanisms may exist which do not fit into the categories described above. Studies of flowering bulbs have established that the bulbs or corms are never completely at rest, but are physiologically active even in the absence of visible organogenesis. A similar situation may be present in other types of plants (LeNard and DeHertogh, 1993).

In addition, it can be difficult to determine if flowering was truly hastened by a cold treatment when forcing conditions for the plants are not constant through the course of the experiment. Temperatures and irradiance in greenhouses change as the seasons change, and this will influence the developmental rates of plants emerging from

cold treatments of different durations (Baskin and Baskin, 1989; Preston et al., 1983; White et al., 1989). One way to document a hastening of flowering is to count the number of leaves formed before flowering, but this is often not done.

Vernalization is defined as the acquisition of the ability to flower, or reduction in time to flower, and a range of obligate and facultative responses exists. No flowering will occur until the qualitative or obligate requirement for a cold treatment has been fulfilled in some biennial and herbaceous perennial plants, including members of the Umbelliferae family, *Hyoscyamus, Beta* spp., *Brassica* spp., *Campanula* spp., *Oenothera* spp., *Dianthus* spp., and many others (Lang, 1965; Vince-Prue, 1975).

Facultative or quantitative responses are found in annuals and herbaceous perennials, including many cereal grains, *Brassica* spp., *Pisum sativum*, *Oenothera* spp., *Dianthus* spp., and many others (Lang, 1965; Vince-Prue, 1975). Effectiveness of vernalization in these plants is measured as a reduction of leaves formed before flowering, or a reduction in days to flowering, which often becomes more pronounced as the duration of low-temperature conditions increases. Unvernalized winter rye will flower after forming 22 leaves, but in vernalized plants, flowering occurs after only six to seven leaves are formed (Purvis, 1961). Vernalization does not influence subsequent leaf production rate in *Arabidopsis*, and the cold treatment hastens flowering by reducing the number of leaves formed before anthesis (Bagnall, 1993).

A range of responses can be found within a species. Different cultivars of winter wheat reveal obligate, facultative, and neutral responses to the cold treatment (Gardner and Barnett, 1990). Some wheat cultivars classified as spring wheats show

slight but significant vernalization responses (Jedel et al., 1986). Evaluation of 32 *Arabidopsis* ecotypes also revealed a variety of responses (Karlsson et al., 1993). In *Lilium longiflorum*, a qualitative requirement for low temperatures must be fulfilled before a subsequent quantitative response becomes apparent (Miller, 1993).

Seed vernalization.

Different species are capable of being vernalized in many different ways. The seeds of many species exhibiting a facultative response, such as cereal crops, *Brassica* spp., *Pisum*, and others, can be vernalized after they have begun imbibition. A water content of 40-50 percent of the seed dry weight is required in cereals, 70 percent in radish, and 60-160 percent in *Arabidopsis* (Chouard, 1960; Purvis, 1961; Vince-Prue, 1975). The vernalized condition generally persists through drying of the seeds in many species, including cereal grains (Lang, 1965; Purvis, 1961).

The seeds of some species can become vernalized during development on the mother plant. Developing ears of cereal grains including rye can be vernalized at any stage after fertilization has occurred (summarized by Purvis, 1961). *Pisum* plants were successfully vernalized while developing in pods on the maternal plant (Reid, 1979). In studies with wheat, plants with developing heads were transferred to cold temperatures at various intervals following anthesis. The seeds from these plants were planted, and the flowering response was observed. The developing seeds were most responsive to the cold treatment approximately 10-12 days after fertilization, during the early stages of embryogenesis, and became less sensitive to the low-temperature treatment as they matured (Krekule, 1987).

In biennials, cold treatment of the seeds does not completely fulfill the vernalization requirement. Seed vernalization of *Lunaria* and *Daucus carota* (carrot), was associated with a higher percentage of flowering and more rapid flowering after subsequent plant vernalization (Wellensiek, 1965). Effectiveness of seed vernalization in genotypes of wheat varies, with some varieties capable of being completely vernalized as an imbibed seed, and others requiring at least some exposure to low temperatures as a growing plant (Salisbury et al., 1979).

Requirements of the vernalization process.

In all plant tissues that have been studied, oxygen, carbohydrates, and water must be present for vernalization to occur (Chouard, 1960). Exclusion of oxygen by submerging cereal grain tissues in water or exposing them to a nitrogen atmosphere during vernalization treatments delayed flowering. Excised embryos of winter cereals or radishes and meristematic tissues of carrot or cabbage respond optimally to vernalizing temperatures only if supplied with carbohydrates (Lang, 1965; Purvis, 1961). Some level of respiratory activity appears to be necessary for vernalization.

Plant age and vernalization.

Sensitivity to vernalization varies in plants as they develop. The duration of vernalization required to saturate the response in wheat decreases as the plants germinate and develop to the eight- leaf stage (Wang et al., 1995). *Lilium longiflorum* bulbs that are harvested later in the season are more responsive to vernalization, perhaps because they are more mature (Miller, 1993). Wild-type *Arabidopsis* plants responded maximally to vernalization when treatments were given to imbibed seeds,

and minimally when treatments were given to plants 5 - 10 days after germination. In *fca-1* mutants, the phase of maximal sensitivity lasted for 25 days after germination (Chandler and Dean, 1994).

Many biennials and perennials must attain a certain size before they are capable of any vernalization response. These plants must complete a " juvenile" period before they will respond to a cold treatment. The juvenile period of *Hyoscyamus niger* is approximately 10 days (Sarkar, 1958); of *Lunaria*, eight weeks (Zeevaart, 1963). In *Centaurea diffusa*, 50 percent of the plants responded to vernalization at 4C after 13 leaves had formed (Thompson and Stout, 1991). Juvenility in carrot cv. Chantenay Red Cored ended after 8-12 leaves were initiated (Atherton et al., 1990). Length of juvenility in *Aquilegia* x *hybrida* varied among cultivars, as did requirements for cold treatment. To obtain 100 percent flowering in 'McKana's Giant' plants, at least 12 leaves and 10 weeks of storage at 4.5C were required. For 'Fairyland,' 15 leaves and only four weeks of cold storage were required for 100 percent flowering to occur. 'Crimson Star' reached 100 percent flowering after at least 15 leaves were formed and eight weeks of cold storage were completed (Shedron and Weiler, 1982).

Conditions that promote growth can shorten the juvenile period. High-intensity supplemental lighting of *Lunaria* plants prior to vernalization increased subsequent flowering and reduced time to flower after vernalization, responses attributed to increased photosynthesis (Wellensiek, 1965; Zeevaart, 1963). Timing of flowering in some facultative biennials may be related to the accumulation of a critical amount of food reserves. However, work with *Oenothera erythrosepala* showed that flowering

would not occur until the diameter of the rosette exceeded 9 centimeters, regardless of chronological age or dry weight of the taproot. In this species, a critical leaf area seems to be necessary to perceive inductive photoperiods after the vernalization requirement has been met (Kachi and Hirose, 1983).

Temperature.

Vernalization is a cumulative process, the effectiveness of which depends on the temperature experienced and the duration of the vernalization period. As in many biochemical reactions, an optimum temperature range exists (often -2 to 5C), and higher or lower temperatures are less effective. In *Secale cereale* (winter rye), exposure to any temperatures between 1 and 7C will be equally effective (Purvis, 1961). Optimum temperatures in wheat differ among cultivars, ranging from 0 to 15C (Berry et al., 1986). In carrots, rates of bolting and flowering increased linearly with vernalization temperatures from -1 to 6.5C and decreased linearly as temperatures increased from 7 to 16C (Atherton et al., 1990). Base, optimum, and maximum vernalization temperatures were determined to be -1, 6.5, and 16C, respectively (Atherton et al., 1990). Studies of *Lilium longiflorum* showed that temperatures below 21C can fulfill the vernalization requirement of the bulbs (Weiler and Langhans, 1968). Exposure to temperatures of 2 to 10C accelerates flowering and decreases the number of leaves and flowers formed (Miller, 1993). In *Hyoscyamus niger*, temperatures between 0C and 17C are effective but the optimum temperature for vernalization varies with the duration of treatment. The optimum temperature was 10C when treatments lasted 7-15 days, and 3C to 6C for treatments of 42 days. (Lang, 1965). The

vernalization response becomes saturated after a particular duration of cold which ranges from 10 to 100 days between species (summarized by Thomas and Vince-Prue, 1984).

Alternation of vernalization temperatures with moderately warmer temperatures does not diminish the vernalization response already accumulated, and will enhance the response in some species (Chouard, 1960; Wellensiek, 1964). Wheat plants can be vernalized while growing under cool night temperatures with a 20C day temperature, although the influence of low temperatures on overall development rate confounded the response in some genotypes (Berry et al., 1986).

Devernalization.

High temperatures during or soon after vernalization can reduce or reverse the inductive effect. This process is termed devernalization and, like vernalization, is a cumulative process that is influenced by the temperature experienced and the duration of the exposure. The ranges of inductive and devernalizing temperatures can be very close together, as in some winter cereals in which only a narrow range of temperatures (12 to 18C) has neither vernalizing nor devernalizing effects (Lang, 1965). Typically, temperatures approaching 30C or higher result in devernalization (Thomas and Vince-Prue, 1984). Flower stalks on *Cheiranthus cheiri* plants vernalized at 2 or 5 C reverted to vegetative growth when plants were transferred to 22 C, and aborted when transferred to 32 C (Diomaiuto-Bonnand, 1972). Devernalization by short-day conditions has been described in *Beta* and *Oenothera biennis* (Vince-Prue, 1975).

Many plants become progressively less susceptible to devernalization as the

duration of vernalizing conditions increases. An interval of moderate temperatures between the low inductive temperatures and the high devernalizing temperatures also tends to stabilize the vernalized state (Lang, 1965). Interactions between light levels and stability of vernalization have also been described. In *Chrysanthemum*, high-temperature treatments did not devernalize basal shoots, but complete devernalization was induced by 8 weeks exposure to low intensity illumination (25 foot candles, 5.0 μmol $m^{-2}s^{-1}$) (Schwabe, 1955). In *Arabidopsis*, exposure to light during either vernalizing or devernalizing conditions reduces devernalization (Napp-Zinn, 1984). However, red or far-red irradiation during devernalization of winter rye did not significantly affect the amount of devernalization (Friend, 1965).

Site of vernalization.

Generally the apical meristem is considered the site of perception of vernalizing temperatures. Experiments with celery, beet, and chrysanthemum showed that flowering only occurred when the growing point was chilled (Vince-Prue, 1975). Localized temperature treatments confirmed that the shoot tip is the site of perception in *Thlaspi arvense* plants (Metzger, 1988). Warming the roots of Chinese cabbage plants had no influence on the effectiveness of vernalization (Rietze and Wiebe, 1988).

Other experiments suggest that dividing cells anywhere in the plant can be vernalized. Leaf and root cuttings of *Lunaria biennis* were given cold treatments, and plants regenerated from these cuttings flowered. When the basal 0.5 centimeter of the petiole was removed from the leaf cuttings, flowering did not occur. Cells in this region were regenerating and apparently were the site of perception of the cold

temperatures. When intact plants were vernalized, leaf cuttings from younger leaves that were expanding during the cold treatment were vernalized much more effectively than those from mature leaves. Vernalization was most effective when cells were dividing during the cold treatment (Wellensiek, 1964).

The presence of actively dividing cells may not be necessary for vernalization in *Thlaspi arvense*. The shoot tip was the site of perception in this species; however, leaf cuttings of mature leaves from vernalized plants developed flowering shoots. The presence of dividing cells during the cold treatment was minimized by treating intact plants, using mature leaves, and removing the basal 1 to 2 centimeters of the petiole. Many cell types may be capable of being vernalized in *Thlaspi arvense* (Metzger, 1988).

In some species, the vernalized state can be very stable and perpetuated through many mitotic divisions. Plants vernalized as embryos of peas, wheat, and rye maintain their thermoinduced state through maturation of the seed, germination, and subsequent growth of the plant (Krekule, 1987; Reid, 1979). Vernalized *Hyoscyamus* plants flowered promptly when exposed to long days even after more than 190 days under short-day conditions. No decrease in flowering response occurred until more than 300 days after the end of the cold treatment. All leaves present after 190 days had been formed after vernalization (Lang, 1986). Cells that are vernalized apparently transmit this condition to cells that arise from them mitotically. Vernalization is generally not considered to be maintained through a meiotic division, but experiments with peas revealed a small but significant effect on the progeny of vernalized parents (Reid,

1979).

Polycarpic or perennial plants.

Annuals and biennials are monocarpic plants that flower once and then die. In contrast to the considerable persistence of the vernalized state in some species, perennial or polycarpic plants must be revernalized each year if they are to bloom. Three hypotheses that can explain this requirement have been proposed.

The first hypothesis is based on the observation that some perennial plants grow vegetatively in a rosette form, and flowers are formed on long stems above the rosette. Some of the buds on the crown of these plants apparently do not become induced during natural vernalization. In *Geum urbanum,* the terminal bud produces vegetative growth, while axillary buds form the inflorescence. Under natural conditions, only axillary buds of a certain maturity are capable of being vernalized, while the terminal bud never differentiates into reproductive growth. If these plants are artificially chilled for 40-50 weeks, eventually all buds including the terminal will become vernalized and produce flowers, and the plant will die. In other perennials, the terminal bud becomes vernalized but axillary buds do not (Chouard, 1960; Vince-Prue, 1975).

The second hypothesis suggests that warm temperatures or other environmental conditions during the summer months may cause some buds to devernalize (Chouard, 1960). Buds located in the basal portion of chrysanthemum plants were found to be vernalized in the spring, but not vernalized at the end of the summer (Schwabe, 1955). Prolonged exposure to low intensity illumination (25 footcandles, 5.0 μmol $m^{-2}s^{-1}$) devernalized the basal shoots in chrysanthemum plants, so low light levels under the

plant canopy may influence the process (Schwabe, 1955).

The third hypothesis suggests that the vernalized state is not always transmitted indefinitely to all cells formed by a vernalized plant. While shoots arising from vernalized buds also are vernalized, the condition is sometimes not transmitted to the buds formed on those shoots (Chouard, 1960).

Interactions between vernalization and photoperiod.

Interactions between vernalization requirements and photoperiodic responses are varied and complex. Some plants respond most strongly to vernalization if they experience short days before the cold treatment, while others prefer long days or continuous light (reviewed by Napp-Zinn, 1984).

Exposure to certain daylengths during vernalization can modify the effectiveness of the cold treatment. Long days, short days plus night interruptions, or continuous light during vernalization can increase the vernalization effect in some species and decrease it in others (reviewed by Napp-Zinn, 1984). In seed-vernalized *Arabidopsis*, vernalization was more effective in darkness than in either eight-hour or 24-hour days, provided with fluorescent lamps (Chandler and Dean, 1994). In *Poa pratensis* and celery, long-day conditions during vernalization inhibited induction, although long days after vernalization promote flowering (Vince-Prue, 1975; Thomas and Vince-Prue, 1984). In winter wheat, some experiments have demonstrated that vernalization was more effective under long days than short days when irradiance levels were low (approximately 2000 lx). The influence of photoperiod was reduced when light intensity was increased, suggesting that a certain amount of carbohydrates

must be available for vernalization to take place (Krekule, 1961; Krekule, 1987). Increasing light intensity during vernalization increased the percentage of 10-week old *Cardamine pratensis* plants flowering, but had little influence on flowering percentage in 38-week old plants (Pierik, 1967).

Little information is available about the influence of light quality during vernalization. In *Cardamine pratensis*, long days during the cold treatment promoted flowering slightly when provided by incandescent lights, but not when fluorescent lights were used (Pierik, 1967). Red radiation delivered during vernalization of winter rye accelerated flowering slightly in several experiments, and far-red accelerated flowering slightly after 1, 3, or 4 weeks of irradiation. Radiation during vernalization did not influence flowering when given during treatments that fully vernalized the grain (Friend, 1965).

Many plants that respond to vernalization are long-day plants. Vernalization of the seed for 8 weeks lowered the critical photoperiod in spinach (var. Nobel) from 14 to 8 hours (Vlitos and Meudt, 1955). A similar response has been found in a number of herbaceous perennials, including *Iris* (Buxton and Mohr, 1969), *Dicentra spectabilis* (Lopes and Weiler, 1977), *Echinops* 'Taplow Blue', *Achillea millefolium* 'Rosea', and *Physostegia virginiana* 'Summer Snow' (Iversen, 1989), *Chrysanthemum* x *superbum* Bergmans (Shedron, 1980), and *Lavandula angustifolia* and *Lobelia speciosa* (Engle, unpublished data; Runkle, unpublished data). Lang (1965) has listed some modifications of photoperiodic requirements in a number of species.

Unvernalized late-flowering mutants of *Arabidopsis* showed a strong response

to light quality. Under a 16- hour photoperiod, time to flowering was doubled when fluorescent lamps were used, compared to fluorescent plus incandescent lamps. After vernalization, this response to light quality was largely eliminated. Studies with other ecotypes also showed that vernalization reduces the response to light quality and photoperiod (Bagnall, 1993).

In some cold-requiring long-day plants such as *Campanula medium*, short-day treatments can replace vernalization prior to the long-day conditions. The mechanisms of short-day and vernalization induction appear to be different because the young plants became sensitive to short days one month sooner than to vernalization. In addition, fewer long days were required for floral initiation when following short days than when following vernalization (Wellensiek, 1960). *Coreopsis grandiflora* Nutt. has also been classified as a short-long-day plant, in which vernalization can replace the short-day treatment. Seven weeks of vernalization was somewhat more effective than 7 weeks of short days in terms of flowering percentage (Ketellapper and Barbaro, 1966). Long days can substitute for quantitative vernalization responses in *Lilium longiflorum* once the initial qualitative requirement for two weeks of temperatures below 21C has been satisfied (Miller, 1993).

Light quality during long days influences the ability of photoperiod to substitute for vernalization in *Arabidopsis*. Time to flowering and leaf number at flowering increase as the ratio of red:far red light increases. Leaf production rate is not influenced by light quality (Bagnall, 1993).

Mechanisms.

Vernalization is an unusual phenomenon because it occurs more rapidly as temperatures decrease, unlike most other biological processes. Research has yielded descriptive information about the response and suggested a variety of hypotheses, but uncovered little information about the biochemical basis of vernalization. No substances that form during vernalization and induce flowering have yet been isolated. Analysis of unvernalized, partially vernalized, and fully vernalized wheat seeds showed that changes in rRNA synthesis occur during the cold treatment. An rRNA that is synthesized at low temperatures but decomposes at 25C was detected (Paldi and Devay, 1983).

Genetics.

Genes that influence vernalization have been identified in several species. In wheat, at least five loci may be involved, and there are also reports of extranuclear inheritance. Genes influencing photoperiodic responses are entirely separate from the vernalization genes. The situation is very complex since wheat is a hexaploid. In *Pisum*, six genes are implicated in flowering, and two of these are responsible for both photoperiodic and vernalization requirements. In *Arabidopsis*, up to 24 genes may be involved (Napp-Zinn, 1987). In *Secale cereale*, only one gene is responsible for the vernalization requirement, which results in a clear distinction between spring and winter rye (Purvis, 1939). One gene also determines the vernalization response in *Hyoscyamus niger* (Lang, 1986).

Researchers have suggested that the interaction of competing processes may control vernalization. If the optimum temperatures differ for the inhibitory and

promotive processes, there may be certain temperatures at which levels of promoters are greater than those of inhibitors (Lang, 1965). More recent work with peas has suggested that a low temperature influence on gene expression may play a part. Exposure to low temperatures or continuous light appears to repress activity of a gene (*Sn*) that may encode a flowering inhibitor. Other genes encode a promoter, and influence the ratio of inhibitor to promoter. Vernalization may also change the sensitivity of the shoot apex to the inhibitor or promoter (Reid and Murfet, 1975). Similar mechanisms have been suggested for *Lathyrus odoratus*. When one of two *Dn* alleles are present, a substance that delays flowering is produced. After vernalization, flowering is promoted. Vernalization also appears to alter the sensitivity of the shoot apex to floral initiation. Plants with only *dn* alleles show some vernalization response, suggesting that a floral promoter may be involved as well (Ross and Murfet, 1986).

The control of gene expression is not well understood, but patterns of DNA methylation appear to play a role. Methylation of cytosines in the promoter region of a gene may be associated with a lack of transcription of that gene. In *Arabidopsis* and cell cultures of *Nicotiana plumbaginifolia*, cold treatments resulted in a substantially reduced level of methylation. Treatment with the demethylating agent 5-azacytidine hastened flowering in *Thlaspi arvense* and late-flowering ecotypes and mutants of *Arabidopsis*, but had no effect on flowering in mutants that do not respond to vernalization (Burn et al., 1993). Gamma rays are a presumed demethylating agent, and in winter wheat, exposure to 5-azacytidine or to gamma rays partially substituted for the cold treatment and significantly hastened flowering (Brock and Davidson,

1994).

Grafting experiments.

In an effort to determine if a graft-transmissible substance is produced during vernalization, grafting experiments have been performed with a number of species (Lang, 1965). The long-day, cold-requiring variety of henbane has been used extensively. Nonvernalized henbane plants were induced to flower under long-day conditions when vernalized plants were grafted onto them, suggesting that a flower-promoting substance termed "vernalin" was produced during the cold treatment. The vernalized plants were photoinduced and flowering when the grafts were made. The majority of earlier successful grafting experiments were performed under conditions in which the donor tissue was already flowering, so it is possible that other flower-inducing substances that were not associated with vernalization were present (Chouard, 1960; Lang, 1965). One set of experiments with the short-day tobacco 'Maryland Mammoth', which does not require a cold treatment, showed that even under noninductive photoperiods, 'Maryland Mammoth' donors did overcome the cold requirement in henbane (Lang, 1965). Experiments with *Lathyrus odoratus* grown under noninductive photoperiods demonstrated that vernalization reduced the production of a graft-transmissible substance that inhibits flowering (Ross and Murfet, 1986). Similar results were obtained in *Pisum* (Reid and Murfet, 1975). Grafting experiments have been unsuccessful in many cases, however, and vernalization seems only to affect a small region of the apex in *Geum* and *Chrysanthemum morifolium* (Thomas and Vince-Prue, 1984). Whether the vernalized state leads to the production

of a mobile substance remains unclear (Burn et al., 1993).

Gibberellins.

Gibberellins have been associated with vernalization, but the nature of the relationship is not clear. Levels of gibberellins were found to be higher after vernalization in *Chrysanthemum*, *Althaea*, *Raphanus*, and winter wheat (Vince-Prue, 1975). Analysis of *Thlaspi arvense* showed that the level of one gibberellin-like substance was dramatically influenced by low temperatures, but could not be causally related to thermoinduced stem elongation (Metzger, 1985). Subsequent studies have found that vernalization induced the activity of an enzyme catalyzing the conversion of the gibberellin precursor kaurenoic acid to 7α-OH kaurenoic acid. This thermoinduced change in gibberellin metabolism occurred only in the shoot tip, which is the site of perception of vernalization in this species (Hazebroek et al., 1993). Preliminary evidence indicates that a correlation between vernalization and gibberellins exists in *Arabidopsis* (Burn et al., 1993). In *Lunaria*, no accumulation of gibberellin-like material during vernalization was found (Zeevaart, 1968).

Applications of exogenous gibberellins can induce flowering in some cold-requiring plants grown under long-day conditions such as *Hyoscyamus niger* (Sarkar, 1958). Applications of gibberellic acid could not substitute for vernalization in *Coreopsis grandiflora*, but could replace the requirement for long days (Ketellapper and Barbaro, 1966). In many cases, gibberellin treatments cause stem elongation, but no flowering. In some species, gibberellin treatments have no influence on flowering or inhibit the process. A table summarizing these responses has been published by

Lang (1965). In *Thlaspi arvense*, GA_3 treatments completely substituted for thermoinduced stem growth. In addition, application of a gibberellin biosynthesis inhibitor completely inhibited the elongation response (Metzger, 1985). Gibberellins may be associated more closely with elongation in response to cold rather than with flowering (Thomas and Vince-Prue, 1984).

Induction by application of gibberellins differs from environmental induction in several ways. When temperature or photoperiod induces flowering, shoot elongation and floral initiation occur simultaneously; but when gibberellins are used to induce the process, elongation occurs before initiation. In species that can be vernalized as imbibed seeds, gibberellin treatment is not effective as a substitute for low temperatures (Vince-Prue, 1975).

Clearly, flowering mechanisms are very complex. The enormous variety of reproductive strategies that plants have evolved reflects the wide range of environments they inhabit. Types of vernalization response vary within a species and sometimes correspond to patterns of climatic conditions. Varieties of wheat native to subtropical areas show very different vernalization responses than those from northern areas (Krekule, 1987). Often requirements for vernalization are coupled with a response to long days. A requirement for vernalization before flowering ensures that mature plants will flower at the time of year when conditions are most favorable for development and maturation of the seeds. Without this mechanism, seedlings might begin reproductive development during the same summer as their germination and flowering might occur in the fall when insufficient time remains for the seeds to develop.

LITERATURE CITED

Atherton, J., J. Craigon,and E.Basher. 1990. Flowering and bolting in carrot. I. Juvenility, cardinal temperatures, and thermal times for vernalization. J. Hort. Sci. 65:423-429.

Bagnall, D. 1993. Light quality and vernalization interact in controlling late flowering in *Arabidopsis* ecotypes and mutants. Ann. Bot. 71:75-83.

Baskin, J. and C. Baskin. 1989. Ecophysiology of seed germination and flowering in *Liatris squarrosa*. Bull.Torrey Bot. Club 116:45-51.

Berry, G., P. Salisbury, and G. Halloran. 1986. Wheat lines: effects of night temperature. Ann. Bot. 58:523-529.

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

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

Buxton, J. and H. Mohr. 1969. The effect of vernalization and photoperiod on flowering of tall bearded irises. HortScience 4:53-55.

Byrne, T. and H. Halevy. 1986. Forcing herbaceous peonies. J. Amer. Soc. Hort. Sci. 111:379-383.

Chandler, J. and C. Dean. 1994. Factors influencing the vernalization response and flowering time of late flowering mutants of *Arabidopsis thaliana* (L.) Heynh. J. Exp. Bot. 45: 1279-1288.

Chouard, P. 1960. Vernalization and its relations to dormancy. Annu. Rev. Plant Physiol. 11:191-238.

Diomaiuto-Bonnand, J. 1972. Réversions de l'état reproducteur à l'état végétatif, chez la Giroflée (*Cheiranthus cheiri* L., Cruciferes), sous l'action de températures moyennes ou élevées. C.R. Acad. Sci. Ser. D. Sci. Nat. (Paris) 274:372-375.

Friend, D. 1965. Interaction of red and far-red radiations with the vernalization process in winter rye. Can. J. Bot. 43:161-170.

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

Hanchek, A. 1989. Growth and development of *Dicentra spectabilis* in relation to storage temperature and harvest date. PhD Diss. Michigan State Univ., East Lansing.

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

Iversen, R. 1989. Greenhouse forcing of herbaceous garden perennials. PhD Diss. Cornell Univ., Ithaca.

Jedel, P., L. Evans, and R. Scarth. 1986. Vernalization responses of a selected group of spring wheat (*Triticum aestivum* L.) cultivars. Can. J. Plant Sci. 66:1-9.

Kachi, N. and T. Hirose. 1983. Bolting induction in *Oenothera erythrosepala* Borbas in relation to rosette size, vernalization, and photoperiod. Oecologia 60:6-9.

Karlsson, B., G. Sills, and J. Nienhuis. 1993. Effects of photoperiod and vernalization on the number of leaves at flowering in 32 *Arabidopsis thaliana* (Brassicaceae) ecotypes. Amer. J. Bot. 80:646-648.

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

Kohl, H. 1957. Flower initiation of stocks grown with several temperature regimens. Proc. Amer. Soc. Hort. Sci. 72:481-484.

Krekule, J. 1961. The effect of photoperiodic régime on vernalization of winter wheat. Biol. Plantarum 3:180-191.

Krekule, J. 1987. Vernalization in wheat, p. 159-169. In: J.G. Atherton (ed). Manipulation of flowering. Butterworths, London.

Lang, A. 1965. Physiology of flower initiation, p. 1380-1536. In: W. Ruhland (ed.). Handbuch der Pflanzenphysiologie. Springer-Verlag, Berlin.

Lang, A. 1986. *Hyoscyamus niger*, p. 144-186. In: A. Halevy (ed.). CRC handbook of flowering. CRC Press, Boca Raton.

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

Lopes, L. and T. Weiler. 1977. Light and temperature effects on the growth and flowering of *Dicentra spectabilis* (L.) Lem. J. Amer. Soc. Hort. Sci. 102:388-390.

Metzger, J. 1985. Role of gibberellins in the environmental control of stem growth in *Thlaspi arvense* L. Plant Physiol. 78:8-13.

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

Miller, W. 1993. *Lilium longiflorum*, p. 391-422. In: A. DeHertogh and M. LeNard (eds.). The physiology of flower bulbs. Elsevier Science Publishers, Amsterdam.

Napp-Zinn, K. 1984. Light and vernalization, p. 75-88. In: D. Vince-Prue, B. Thomas, K. Cockshull (eds.). Light and the flowering process. Academic Press,London.

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

Purvis, O. 1939. Studies in vernalization of cereals. V. The inheritance of the spring and winter habit in hybrids of Petkus rye. Ann. Bot., 3:719-729.

Purvis, O. 1961. The physiological analysis of vernalization, p. 76-122. In: W. Ruhland (ed.). Encyclopedia of Plant Physiology volume 16. Springer-Verlag, Berlin.

Paldi, E. and M. Devay. 1983. The changes in the nature of rRNA synthesis in the plumula of seedlings during vernalisation. Plant Sci. Lett. 30:69-75.

Pemberton, G. 1992. Factors affecting the growth and development of forced Dutch-grown *Astilbe*. MS Thesis, North Carolina State Univ., Raleigh.

Pierik, R. 1967. Effect of light and temperatue on flowering in *Cardamine pratensis* L. Z. Pflanzenphysiol. 56:141-152.

Preston, M., J. Buston, R. Anderson, and H. Mohr. 1983. Effect of vernalization duration and storage method on forcing of tall bearded irises. HortScience 18:455-456.

Reid, J. 1979. Flowering in *Pisum*: effect of the parental environment. Ann. Bot. 44:461-467.

Reid, J. and I. Murfet. 1975. Flowering in *Pisum*: the sites and possible mechanisms of the vernalization response. J. Expt. Bot. 26:860-867.

Rietze, E. and H. Wiebe. 1988. The influence of soil temperature on vernalization of Chinese cabbage. J. Hort. Sci. 63:83-86.

Ross, J. and I. Murfet. 1986. The mechanism of action of vernalization in *Lathyrus odoratus* L. Ann. Bot. 57:783-790.

Salisbury, P., G. Berry, and G. Halloran. 1979. Expression of vernalization genes in near-isogenic wheat lines: methods of vernalization. Can. J. Genet. Cytol. 21:429-434.

Sarkar, S. 1958. Versuche zur Physiologie der Vernalisation. Biol. Zentralbl. 77:1-49.

Schwabe, W. 1955. Factors controlling flowering in the chryanthemum. J. Exp.Bot. 6:435-450.

Shedron, K. 1980. Regulation of growth and flowering of four herbaceous perennials: *Aquilegia* x *hybrida* Sims, *Aurinia saxatilis* (L.) Desv., *Chrysanthemum* x *superbum* Bergmans, and *Lupinus* spp. `Russell.' MS Thesis, Purdue Univ., Lafayette.

Shedron, K. and T. Weiler. 1982. Regulation of growth and flowering in *Aquilegia* x *hybrida* Sims. J. Amer. Soc. Hort. Sci. 107:878-882.

Stokes, P. and K. Verkerk. 1951. Flower formation in brussels sprouts. Meded. Landbouwhogeschool, Wageningen 50: 143-160.

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

Tompson, D. and D. Stout. 1991. Duration of the juvenile period in diffuse knapweed (*Centaurea diffusa*). Can. J. Bot. 69:368-371.

Vince-Prue, D. 1975. Photoperiodism in plants. McGraw-Hill, Maidenhead.

Vlitos, A. and W. Meudt. 1955. Interactions between vernalization and photoperiod in spinach. Contr. Boyce Thompson Inst. 18:159-166.

Wang, S., R. Ward, J. Ritchie, R. 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.

Weiler, T. and R. Langhans. 1968. Determination of vernalizing temperatures in the vernalization requirement of *Lilium longiflorum* (Thunb.) cv `Ace.' Proc. Amer. Soc. Hort. Sci. 93:623-629.

Wellensiek, S. 1960. Flower formation in *Campanula medium*. Meded. Landbouwhogeschool, Wageningen 60:1-18.

Wellensiek, S. 1964. Dividing cells as the prerequisite for vernalization. Plant Physiol. 39:832-835.

Wellensiek, S. 1965. Recent developments in vernalization. Acta Bot. Neerl. 14:308-314.

White, J., D. Beattie, and E. Holcomb. 1989. Flowering studies with *Aquilegia* cultivars. Acta Hort. 252:219-226.

Whyte, R. 1948. History of research in vernalization, p. 1-38. In: A. Murneek and R. Whyte (eds.). Vernalization and photoperiodism. Chronica Botanica Co.,Waltham.

Wiebe, H., R. Habegger, and H. Liebig. 1992. Quantification of vernalization and devernalization effects for kohlrabi (*Brassica oleracea* convar. acephala var. gongylodes L.) Sci. Hort. 50:11-20.

Zeevaart, J. 1963. Climatic control of reproductive development, p. 289-310. In: L. Evans (ed.). Environmental control of plant growth. Academic Press, New York.

Zeevaart, J. 1968. Vernalization and gibberellins in *Lunaria annua* L., p. 1357-1370. In: F. Wightman and G. Setterfield (eds.). Biochemistry and physiology of plant growth substances. The Runge Press, Ltd., Ottawa.

SECTION II

INFLUENCE OF THE SPECTRAL QUALITY OF DAYLENGTH EXTENSIONS ON FLOWERING OF *CAMPANULA CARPATICA* 'BLUE CLIPS', *COREOPSIS GRANDIFLORA* 'EARLY SUNRISE', *COREOPSIS VERTICILLATA* 'MOONBEAM', AND *RUDBECKIA FULGIDA* 'GOLDSTURM'

Influence of the spectral quality of daylength extensions on flowering of *Campanula carpatica* 'Blue Clips', *Coreopsis grandiflora* 'Early Sunrise', *Coreopsis verticillata* 'Moonbeam', and *Rudbeckia fulgida* 'Goldsturm'.

Catherine M. Whitman[1], Royal D. Heins[2], Arthur Cameron[2], and William Carlson[2]

Department of Horticulture, Michigan State University, E. Lansing, MI 48824

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[1] Graduate student.

[2] Professor of Horticulture.

Abstract. The effectiveness of cool white fluorescent (CWF), high-pressure sodium (HPS), incandescent (INC), and metal halide (MH) lamps in inducing flowering in *Campanula carpatica* Jacq. 'Blue Clips', *Coreopsis grandiflora* Hogg ex Sweet.'Early Sunrise', *Coreopsis verticillata* L. 'Moonbeam', and *Rudbeckia fulgida* Ait.'Goldsturm' was compared. For each light source, lighting was delivered as a 7-hr day extension with PPF ranging from 0.05 to 2.0 μmol $m^{-2}s^{-1}$. Threshold irradiance values for flowering ranged from <0.05 to 0.37 μmol $m^{-2}s^{-1}$, depending on species. Saturation irradiance values for *C. carpatica* 'Blue Clips' and *C. grandiflora* 'Early Sunrise' were between 0.22 and 0.68 μmol $m^{-2}s^{-1}$ for all lamps tested. An irradiance of 1.0 μmol $m^{-2}s^{-1}$ was adequate for flowering in all species. Time to flower at irradiances above the saturation points did not differ significantly between lamp types in all species tested. *C. carpatica* 'Blue Clips' and *C. grandiflora* 'Early Sunrise' plants under INC lamps were significantly taller than those in any other treatment. *C. verticillata* 'Moonbeam' plants grown under CWF lamps were approximately 10% taller than those grown under HPS and INC. The heights of *R. fulgida* 'Goldsturm' plants did not differ significantly between light treatments.

The popularity of herbaceous perennials has increased in recent years. Combined wholesale, retail, and landscape sales in 1992 were estimated by the Perennial Plant Association at $222 million, with 81% of respondents reporting increases over 1991 levels (Rhodus, 1993). Traditionally perennials have been produced outdoors, and many are not in flower in the spring when the majority of garden plants are sold (Armitage, 1994a; Schwarze, 1993). A plant in bloom has much greater sales appeal than a non-flowering plant. Consequently, producers of herbaceous perennials are interested in production methods which will allow them to produce flowering plants at any season of the year.

Several popular species of herbaceous perennials are long-day plants (LDP), so photoperiods exceeding a certain minimum length either are required for flowering or hasten flowering (Beattie and German, 1985; Iversen and Weiler, 1994). Long days can be provided by extending the day length to 14 to 16 hours, or by providing a 4-hour night break (Armitage, 1994b; Vince-Prue and Canham, 1983).

Traditional photoperiodic lighting involves the use of incandescent lamps (INC) (Vince-Prue and Canham, 1983). Incandescent lights are effective, inexpensive, and simple to install; however their output in the 400-700 nm waveband is only 57-69 milliwatts per watt (≈6%) of input power compared to 204 mW, 261 mW, and 265 mW (≈20,26, and 27%) for cool white fluorescent (CWF), high pressure sodium (HPS), and metal halide (MH) lamps respectively (Thimijan and Heins, 1983). Use of

these other light sources in place of INC can reduce photoperiodic lighting energy costs.

The output of incandescent lamps is rich in far-red light, (700-800 nm), the ratio of red (600-700 nm):far-red being less than one (Lane et al., 1965). Far-red light has several horticulturally undesirable effects on plant morphology including the promotion of stem elongation, and suppression of lateral branching (Downs et al., 1958; Moe and Heins, 1990; Vince-Prue and Canham, 1983). Several other lamp types, such as CWF, HPS, and MH, deliver proportionately less far-red than red light compared to incandescent lamps (deGraaf-van der Zande and Blacquière, 1992; Thimijan and Heins, 1983). The use of photosynthetic lighting with lamps other than INC offers the potential for flower induction with less stem elongation.

Lighting used to extend the photoperiod must be of adequate intensity (Summerfield and Roberts, 1987; Vince-Prue, 1975). Each LDP has a threshold irradiance below which flowering is not hastened or induced by the light treatment, and a saturation irradiance above which the time to flower becomes constant (Summerfield and Roberts, 1987). Between these two light levels, the rate of progress to flowering (inverse of time to flower) for a LDP is often linearly related to the irradiance (Summerfield and Roberts, 1987). For incandescent lighting, the threshold irradiance for floral induction in many species of LDP lies between 1 lux (0.1 footcandle or 0.02 μmol $m^{-2}s^{-1}$) (400-700nm) and 50 lux (5 footcandles or 1 $\mu m^{-2}s^{-1}$) (Vince-Prue, 1975). For example, the threshold irradiance of incandescent lighting for floral induction in *Callistephus chinensis* Cass. was reported as 0.1 footcandle (0.02 μmol $m^{-2}s^{-1}$)

(Withrow and Benedict, 1936). In *Cicer arietinum* L., the threshold irradiance and saturation irradiance values under incandescent lamps are 1 to 2 lux and 3 to 8 lux (0.02 to 0.04 μmol $m^{-2}s^{-1}$ and 0.06 to 0.16 μmol $m^{-2}s^{-1}$), respectively (Summerfield and Roberts, 1987) while in *Lens culinaris* L. the values are 60 to 70 lux and 720 to 1150 lux (1.2 to 1.4 μmol $m^{-2}s^{-1}$ and 14.4 to 23 μmol $m^{-2}s^{-1}$) (Summerfield et al., 1984). Flowering response, determined by flower number, was saturated in *Gypsophila paniculata* L. at 60 to 100 lux (1.2 to 2.0 μmol $m^{-2}s^{-1}$) under incandescent lamps (Shillo and Halevy, 1982). Horticulturally, determination of threshold and saturation irradiances is important to avoid inadvertant induction in nearby greenhouse sections, and so that uniform flowering will be induced without providing surplus light.

The spectral quality of photoperiodic lighting is also important. In LDP, research has shown that light in the far-red portion of the spectrum is important for flower induction (reviewed by Thomas, 1993). Mixtures of red (600-700nm) and far-red (700-800) light, when delivered as day extensions following eight hours of natural daylight, were more effective in hastening the flowering of *Dianthus caryophyllus* L. 'Puritan' and *Lactuca sativa* L.'Cheshunt Vb' than either light source alone (Vince et al., 1964). After eight hours of natural daylight, eight-hour day extensions with far-red did not induce flowering in *Lolium temulentum* L., and the response to red-light day extensions was limited, but mixtures of red and far-red light resulted in rapid flowering (Vince, 1965). The action spectrum for floral development, quantified as apex elongation, in light-grown *Triticum aestivum* L. under 16-hour day-extensions showed two maxima, one at 660 nm and one at 716 nm (Carr-Smith et al., 1989).

Artificial light sources vary in the ratio of red:far-red light they deliver, and in their effectiveness for inducing flowering of LDP when used as day extensions following natural daylight. Flowering of *Anethum graveolens* L., *Triticum compactum* Host var. Little Club, and *Hordeum vulgare* L. Var. Colsess I were compared under eight-hour day extensions with incandescent and cool white fluorescent lamps at 6.0 μmol $m^{-2}s^{-1}$, and flowering was delayed under fluorescent lamps by 28, 20, and 44 days respectively (Downs et al., 1958). Experiments with *Hyoscyamus niger* L., *Beta vulgaris* L., *Anethum graveolens* I., and *Petunia hybrida* Vilm. found that cool white fluorescent lamps delayed flowering by 10 to 20 days compared to three other light sources with lower ratios of red:far-red light, when delivering 8-hour day extensions (Lane et al., 1965). At the 0.2 μmol $m^{-2}s^{-1}$ level, eight-hour day extensions with incandescent lamps hastened flowering by 20 to 40 days in *Petunia hybrida* Vilm. 'Pink Cascade', when compared to high pressure sodium, cool white fluorescent, metal halide, and mercury lamps (Cathey and Campbell, 1975) while cool-white fluorescent lamps did not induce flowering in *Gypsophila paniculata* L, but were effective when combined with incandescent lamps (Shillo and Halevy, 1982). However, *Callistephus chinensis* 'Kometa pink' displayed similar flowering responses under incandescent, cool white fluorescent, low pressure sodium, or compact discharge lamps (deGraaf-van der Zande and Blacquière, 1992). The flowering response in *Campanula isophylla* Moretti was similar under either incandescent lamps or fluorescent lamps (Moe and Heins, 1990).

In this study, experiments were conducted to compare the effectiveness of four lamp types on flower induction in LDP by establishing threshold and saturation light intensities, and to determine the effect of lamp type on plant height.

Materials and Methods

Plant Culture. Seedlings of *C. carpatica* Jacq. 'Blue Clips' and *C. grandiflora* Hogg ex Sweet. 'Early Sunrise' were acquired from a commercial plug producer approximately four weeks after sowing. Seedlings of *R. fulgida* Ait. 'Goldsturm' growing in fifty-cell trays (85 ml cell volume) were acquired when approximately 20 weeks old. Cuttings of *C. verticillata* L. 'Moonbeam' were propagated on 28 June 1994 for use in experiment I, and plants in 72-cell trays (50 ml cell volume) were acquired from a commercial producer for use in experiment II. Characteristics of the plant material are presented in Table 1. Seedlings were subsequently transplanted into 10-cm pots (470 ml), or 13 cm (1.1 liter) for *R. fulgida* 'Goldsturm', using a commercial soilless media containing 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 as necessary with 7 mM N from a 20 N-4.4 P-16.6 K all-purpose water soluble fertilizer (20-10-20), Peter's professional Peat-lite special (Grace-Sierra Horticultural Products Company, Milpitas, CA). Prior to the start of long-day treatments, plants were maintained under a 9-hr photoperiod (SD) which was provided by pulling blackcloth from 1700 to 0800 daily. When ambient greenhouse light levels dropped below 400 μmol $m^{-2}s^{-1}$ during the 0800 to 1700 time period, HPS lights were

turned on automatically by an environmental control computer, providing ≈ 50 μmol $m^{-2}s^{-1}$ of supplemental light at plant level.

Light Sources & Treatments. Lights were installed at one end of four benches, 75-90 cm above the bench, so that an irradiance gradient from 0.05 to 2.0 μmol $m^{-2}s^{-1}$ (400-700 nm) was established as measured by a LI-Cor quantum sensor model LI-189 (Li-COR Inc., Lincoln, Nebraska), oriented horizontally at plant height. Irradiance was measured at the beginning of each of the experiments, and checked midway through the first experiment.

The spectrum of each light source was determined at the 2 μmol $m^{-2}s^{-1}$ bench position using a Li-Cor LI-1800 portable spectroradiometer (Li-COR Inc., Lincoln, Nebraska) with the remote sensor pointed directly toward the lamp, and oriented 45° from the horizontal position. Calculations of R:FR ratio used band widths of 600-700 nm for red radiation, and 700-800 nm for far-red radiation. The data in Figure 1 represent the average of 3 scans.

Fifteen plants of each species were arranged along the length of each bench, with 15 plants also remaining in SD. Black cloth was pulled at 1700 and opened at 0800 on all benches. Lights were turned on at 1700 and remained on until 2400, providing a 7-hr day extension.

The experiment was replicated in time with experiments I, II, and III starting on 16 Sept. 1994, 15 Dec.1994, and 15 March 1995, respectively. *C. carpatica* 'Blue Clips' and *C. grandiflora* 'Early Sunrise' were included in all three experiments, *C. verticillata* 'Moonbeam' was included in experiments I and II, and *R. fulgida*

'Goldsturm' was included in experiment II. Date of the first visible bud and date of opening of the first flower were recorded for each plant, and days to visible bud and flowering were calculated. At the time of flowering, total plant height, number of visible flower buds, and number of leaves on the main stem were determined.

Temperature control. Air temperatures on each bench were monitored with two 36-gauge thermocouples connected to a CR10 datalogger (Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 10 seconds and recorded the hourly average. Nighttime air temperatures under blackcloth on solid aluminum benches can be 3.5C cooler than greenhouse air temperatures due to radiant heat loss to the greenhouse glazing material (Heins and Faust, 1994). To provide uniform temperature conditions, the datalogger controlled a 1500W electric heater under each bench which provided supplemental heat as needed throughout the night. Actual average daily air temperature was 20.6C for all three experiments. The maximum difference in average daily air temperature between any two benches within each experiment was 0.8C, 0.6C, and 0.2C for Experiments I, II, and III, respectively.

Data Analysis

Days to flower was converted to the rate of progress to flowering by taking the reciprocal. To determine the saturation irradiance, the relationship between irradiance and rate of progress to flowering was developed using a multiphase function with two linear components as proposed by Argo and Biernbaum (1995) . The functions used were

$$I_{intersection} = \frac{b_2 - b_0}{b_1 - b_3} \quad [1]$$

$$\text{if : } I < I_{intersection} \text{ then } \quad R_1 = b_0 + b_1 I \quad [2]$$

$$\text{if : } I > I_{intersection} \text{ then } \quad R_2 = b_2 + b_3 I \quad [3]$$

where the I value is log irradiance and R is the rate of progress to flowering. $I_{intersection}$ is the intersection point of the two lines where the R values are equal and is calculated using Eq. [1]; b_1 and b_3 are the slopes, and b_0 and b_2 are the y-intercepts of Eqs. [2] and [3] respectively. Initial estimates for the parameters were obtained from a graph of the observed data. Estimates for b_0, b_1, b_2, and b_3, based on irradiance, were obtained using the SAS nonlinear regression procedure NLIN (SAS Institute, 1989). In cases where b_3 was <0, data were reanalyzed with b_3 set at 0.

In cases where two functions could not be fit to the data, linear regression was used to develop the relationship between irradiance and rate of progress to flowering.

Results

Campanula carpatica 'Blue Clips'. None of the plants under SD flowered. Some individuals flowered at the 0.05 to 0.1 μmol $m^{-2}s^{-1}$ levels under all light sources, indicating that the threshold irradiance for flowering in this species is below 0.05 μmol $m^{-2}s^{-1}$ (Fig. 2). As irradiances increased, flowering was hastened, with the response becoming saturated at irradiances of 0.44, 0.37, 0.25, and 0.68 μmol $m^{-2}s^{-1}$ under CWF, HPS, INC, and MH lamps respectively (Table 2). Time to flower at irradiances

above the saturation point averaged 51 days for all treatments, and did not differ significantly between lamp types. Plants in INC light treatments were significantly taller than those under CWF, HPS, or MH lamps (Table 3).

Coreopsis grandiflora 'Early Sunrise'. None of the plants under SD flowered. Some individuals flowered at the 0.05 to 0.1 μmol $m^{-2}s^{-1}$ levels under all light sources, indicating that the threshold irradiance for flowering in this species is below 0.05 μmol $m^{-2}s^{-1}$ (Fig.3). At higher light intensities, flowering was hastened, with the response becoming saturated at irradiances of 0.22, 0.25, 0.43, and 0.50 μmol $m^{-2}s^{-1}$ under CWF, HPS, INC, and MH lamps respectively (Table 2). Time to flower at irradiances above the saturation point averaged 60 days, and did not differ significantly between lamp types. Some plants at irradiances above I_{sat} did not flower within the time frame of these experiments. Plants treated with INC light were significantly taller than those under CWF, HPS, and MH lamps (Table 3).

C. verticillata 'Moonbeam'. None of the plants under SD flowered. Flowering response was somewhat dissimilar between the two replications, so the data were analyzed separately. In Experiment I (Fig. 4), all plants under CWF and HPS treatments flowered at approximately the same time, with a saturation irradiance apparently $\leq$ 0.05 μmol $m^{-2}s^{-1}$. Under INC lamps, some individuals flowered at the 0.05 to 0.1 μmol $m^{-2}s^{-1}$ level, and as irradiance increased, flowering was hastened until the response became saturated at the 0.27 μmol $m^{-2}s^{-1}$ level (Table 2). All individuals under MH lamps flowered, but flowering was delayed at irradiances below 0.19 μmol $m^{-2}s^{-1}$. Time to flower at irradiances above the saturation point averaged 57 days and

did not differ significantly between lamp types. In Experiment II (Fig. 5), flowering was not induced in individuals exposed to light levels less than 0.17, 0.22, 0.37, and 0.17 μmol $m^{-2}s^{-1}$ under CWF, HPS, INC, and MH lamps, respectively. Under CWF and HPS lamps, rate of progress to flowering increased linearly as light levels increased, so saturation irradiance apparently was not reached. Time to flowering for plants in the CWF treatment decreased from approximately 70 days to 60 days as irradiance increased from 0.17 to 2.0 μmol $m^{-2}s^{-1}$, and averaged 65 days. In the HPS treatment, time to flower decreased from 66 to 58 days as irradiance increased from 0.22 to 2.0 μmol $m^{-2}s^{-1}$, and averaged 63 days. Rate of progress to flower under INC and MH lamps did not increase significantly at irradiances above 0.37 and 0.17 μmol $m^{-2}s^{-1}$, respectively. At irradiances above the saturation points, time to flower averaged 66 days under INC and MH lamps, and did not differ significantly between the treatments.

Under the conditions of these experiments, the threshold irradiance in *C. verticillata* 'Moonbeam' was below 0.37 μmol $m^{-2}s^{-1}$. The saturation irradiance values were dissimilar between the two experiments, apparently below 0.05 μmol $m^{-2}s^{-1}$ in some cases and above 2.0 μmol $m^{-2}s^{-1}$ in others. Plants treated with CWF lamps were approximately 3.6 cm taller than those grown under HPS and INC. The average height of plants treated with MH lamps was 2 cm greater than those of the HPS and INC treatments (Table 3).

R. fulgida 'Goldsturm'. None of the plants under SD flowered. Plants exposed to light levels less than 0.37, 0.37, 0.28, and 0.28 μmol $m^{-2}s^{-1}$, under CWF, HPS,

INC, and MH lamps respectively, did not flower(Fig. 6). These results indicate that the threshold irradiance for this species is approximately 0.28 to 0.37 μmol $m^{-2}s^{-1}$. Rate of progress to flowering increased linearly under HPS and MH lamps as light intensity increased throughout the range tested (Table 2). Under HPS lamps, time to flower decreased from approximately 142 to 97 days as irradiance increased from 0.37 to 2.0 μmol $m^{-2}s^{-1}$. Time to flower for plants in the MH treatments decreased from 138 to 97 days as irradiance increased from 0.28 to 2.0 μmol $m^{-2}s^{-1}$. Time to flower under CWF and INC lamps did not change significantly as irradiance increased above 0.37 and 0.28 μmol $m^{-2}s^{-1}$, respectively. Time to flower under CWF and INC lamps averaged 118 days, and was not significantly different between the two lamps. The saturation irradiance for HPS and MH lamps was not reached under the conditions of this experiment. The saturation irradiance for CWF and INC lamps could not be distinguished from the threshold irradiance in those treatments. The average heights of plants in all light treatments were not significantly different (Table 3).

Discussion

Under the conditions of this experiment, all tested lamps were effective for flower induction in these species of LDP. When saturation irradiances could be determined for a species, they differed by more than 100% between lamps. However, days to flower at irradiances above the saturation points did not differ significantly between lamps in any species tested. Horticulturally, all the lamps tested are adequate for floral induction in these crops.

Lowest saturation irradiance values were obtained under INC lamps for *C. carpatica 'Blue Clips'* and under CWF for *C. grandiflora* 'Early Sunrise'. Previous research with other species has often found that lamps with a high red:far-red ratio, such as CWF, were less effective than lamps with a low red:far-red ratio, such as INC (Cathey and Campbell, 1975; Downs et al, 1958; Lane et al., 1965; Shillo and Halevy, 1982). Mixtures of red and far-red light are highly effective (Vince et al., 1964; Vince, 1965). All lamps included in this work emit some radiation in both the red and far-red wavebands, which apparently was sufficient for floral induction in these species. These findings are similar to results reported by deGraaf-van der Zande and Blacquière, (1992) and Moe and Heins (1990).

Threshold irradiance values in this experiment (<0.05 to 0.37 μmol $m^{-2}s^{-1}$) are similar to values published for other LDP. The sensitivity of these species to low light levels indicates that growers of herbaceous perennials should consider the potential for light pollution, which may promote flowering at times when vegetative growth is desired. In The Netherlands, light levels up to 0.10 μmol $m^{-2}s^{-1}$ were measured in greenhouses adjacent to those using supplemental lighting during the night (Bakker and Blacquière, 1992).

Saturation irradiance values in this experiment were between 0.22 to 0.68 μmol $m^{-2}s^{-1}$ for all lamps for *C. carpatica* 'Blue Clips' and *C. grandiflora* 'Early Sunrise'. These values are within the range of 0.02 to 1.0 μmol $m^{-2}s^{-1}$ described by Vince-Prue (1975) for many species of LDP, and similar to those reported for *C. arietinum* (Summerfield and Roberts, 1987) and *G. paniculata* (Shillo and Halevy, 1982).

An irradiance of 1.0 μmol $m^{-2}s^{-1}$ is more than adequate for floral induction in *C. carpatica* 'Blue Clips', *C. grandiflora* 'Early Sunrise', *C. verticillata* 'Moonbeam', and *R. fulgida* 'Goldsturm'. In *R. fulgida*, flowering was hastened by up to 30 days by increasing the irradiance from 1.0 to 2.0 μmol $m^{-2}s^{-1}$, so producers of this crop could benefit by providing at least 2.0 μmol $m^{-2}s^{-1}$. Although not tested here, further increases in irradiance may reduce the time to flower for *R. fulgida* since saturation irradiance values of 14 to 23 μmol $m^{-2}s^{-1}$ have been reported for other LDP, such as *Lens culinaris* (Summerfield et al., 1984).

A light level of 10 footcandles, or 2.0 μmol $m^{-2}s^{-1}$, is commonly used for photoperiodic control of crops such as poinsettias and chrysanthemums (Ecke and Hartley, 1991; Ball, 1991). Producers who currently utilize photoperiodic lighting for poinsettias and chrysanthemums can also use their equipment for these species of herbaceous perennials.

Far-red light strongly enhances stem elongation and suppresses lateral branching (Moe and Heins, 1990). INC lamps have the lowest red:far-red ratio of the lamps tested in these experiments, and both *C. carpatica* 'Blue Clips' and *C. grandiflora* 'Early Sunrise' were significantly taller when treated with INC lamps compared to all other lamps. Stem elongation in *R. fulgida* 'Goldsturm' was apparently unaffected by the red:far-red ratio. In *C. verticillata* 'Moonbeam', plants grown under HPS and INC were shorter than those treated with CWF and MH, a pattern of response that did not correspond with the red:far-red ratios of the lamps. For at least some crops, use of

lamps with a high red:far-red ratio can reduce final plant height compared to lamps with a low red:far-red ratio.

Use of CWF, HPS, or MH lamps in place of INC lighting offers benefits in energy savings as well. For example, using values presented by Campbell and Cathey (1980); to provide 1 μmol $m^{-2}s^{-1}$ (400-700 nm) the electrical input that must be provided per square meter of growing space are 2.4, 1.5, and 2.4 W for CWF, HPS, and MH lamps, respectively, compared to 7.0 W for INC.

LITERATURE CITED

Argo, W. and J. Biernbaum. 1995. The effect of lime, irrigation-water source, and water-soluble fertilizer on root-zone pH, EC, and macronutrient management of container root media with impatiens. J. Amer. Soc. Hort. Sci. (In review).

Armitage, A. 1994a. Spring into forcing perennials. Greenhouse Grower 12: 77-78.

Armitage, A. 1994b. Spring into perennials. Greenhouse Grower 13:92-94.

Bakker, J. and T. Blacquière. 1992. Reflected supplementary lighting can affect the crops of neighbours. Acta Hort. 327:95.

Ball, V. 1991. Chrysanthemums, p. 435-467. In: V. Ball (ed.). Ball Red Book. Ball Publishing, West Chicago, IL.

Beatty, D. and R. German, Sr. 1985. Perennials, p. 510-525. In: J. Mastalerz and E. Holcomb (eds.). Bedding Plants III. Pennsylvania Flower Growers.

Carr-Smith, H., Johnson, C., and B. Thomas. 1989. Action spectrum for the effect of day-extensions on flowering and apex elongation in green, light-grown wheat (*Triticum aestivum* L.). Planta 179: 428-432

Cathey, H. and L. Campbell. 1975. Effectiveness of five vision-lighting sources on photo-regulation of 22 species of ornamental plants. J. Amer. Soc. Hort. Sci. 100:65-71.

Cathey, H. and L. Campbell. 1980. Light and lighting systems for horticultural plants, p. 491-537. In: J. Janick (ed.). Horticultural reviews. AVI publishing, Westport, CN.

De Graaf-van der Zande,M. and T. Blacquière. 1992. Light quality during longday treatment for poinsettia and china aster. Acta Hort. 327:87-93.

Downs, R., Borthwick, H., and A. Piringer. 1958. Comparison of incandescent and fluorescent lamps for lengthening photoperiods. Proc. Amer. Soc. Hort.Sci. 71:568-578.

Ecke, P. and D. Hartley. 1991. Poinsettias, p. 695-734. In: V. Ball (ed.). Ball Red Book. Ball Publishing, West Chicago, IL.

Heins, R. and J. Faust. 1994. Radiant cooling leads to cooler temperatures under black cloth. HortScience 29:503. (Abstr.)

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

Lane, H., Cathey, H., and L. Evans. 1965. The dependence of flowering in several long-day plants on the spectral composition of light extending the photoperiod. Amer. J. Bot. 52:1006-1014.

Moe, R. and R. Heins. 1990. Control of plant morphogenesis and flowering by light quality and temperature. Acta Hort. 272:81-89.

Rhodus, T. 1993. Views on management. Perennial Plants; The quarterly newsletter of the Perennial Plant Association, Summer 1993 26-34.

SAS Institute. 1989. SAS/STAT user's guide, version 5, vol. 2, SAS Institute, Inc., Cary, N.C.

Schwarze, D. 1993. Perennials. Minn. Flower Growers Bull. 42:30-39.

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

Summerfield, R., Muehlbauer,F., and E. Roberts. 1984. Controlled environments as an adjunct to field research on lentils (Lens culinaris). III. Photoperiodic lighting and consequences for flowering. Expl. Agric. 20:1-18.

Summerfield, R. and E. Roberts. 1987. Effects of illuminance on flowering in long- and short-day grain legumes: a reappraisal and unifying model, p. 203-223. In: J.G. Atherton (ed.). Manipulation of flowering. Butterworth's, London.

Thimijan, R. and R. Heins. 1983. Photometric, Radiometric, and Quantum light units of measure: a review of procedures for interconversion. HortScience 18:818-822.

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

Vince, D., Blake, J., and R. Spencer. 1964. Some effects of wave-length of the supplementary light on the photoperiodic behavior of the long-day plants, carnation and lettuce. Physiol. Plant. 17:119-125.

Vince, D. 1965. The promoting effect of far-red light on flowering in the long day plant *Lolium temulentum*. Physiol. Plant 18: 474-482

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

Vince-Prue, D. and A. Canham. 1983. Horticultural significance of photomorphogenesis, p. 518-544. In: W. Shropshire, Jr. and H. Mohr (eds.). Photomorphogenesis. Springer-Verlag, Heidelberg.

Withrow, R. and H. Benedict. 1936. Photoperiodic responses of certain greenhouse annuals as influenced by intensity and wavelength of artificial light used to lengthen the daylight period. Plant Physiol. 11:225-249.

Table 1. Characteristics of plant material. Experiments I, II, and III started on 16 Sept. 1994, 15 Dec. 1994, and 15 March 1995, respectively.

Species	Sow date	Age at forcing (wks)	Average leaf # at start of treatment
Expt. I			
Campanula carpatica 'Blue Clips'	7 June 1994	14	16.3
Coreopsis grandiflora 'Early Sunrise'	7 June 1994	14	24.5
Coreopsis verticillata 'Moonbeam'	Cuttings propagated 28 June 1994.	11	[z]
Expt. II			
Campanula carpatica 'Blue Clips'	8 Sept. 1994	14	11.4
Coreopsis grandiflora 'Early Sunrise'	8 Sept. 1994	14	16.7
Coreopsis verticillata 'Moonbeam'	[z]	[z]	[z]
Rudbeckia fulgida 'Goldsturm' [y]	June 1994	≈28	11.1
Expt. III			
Campanula carpatica 'Blue Clips'	7 Dec. 1994	14	8.6
Coreopsis grandiflora 'Early Sunrise'	7 Dec. 1994	14	13.6

[z] Not recorded.
[y] LD started 3 Feb. 1995.

Table 2. Parameters of nonlinear and linear regression analysis relating rate of progress to flowering to quantum flux (400-700nm). b1 and b3 are slopes and b0 and b2 are intercepts. For nonlinear regression, b_0, b_1, b_2, and b_3 represent values for Eqs. [2] and [3]. $I_{intersection}$ is the irradiance at the intersection point of the two lines in μmol $m^{-2}s^{-1}$ and is calculated using Eq. [1].

Species	Lamp	b_0 1/DTF	b_1 (1/DTF)/log(1+ μmol $m^{-2}s^{-1}$)	b_2 1/DTF	b_3 (1/DTF)/log(1+ μ mol $m^{-2}s^{-1}$)	$I_{intersection}$ μmol $m^{-2}s^{-1}$	No.[z]	R^2 [y]
C. carpatica 'Blue Clips'	CWF	0.015±0.002[x]	0.027 ±0.026	0.019 ±0.004	0.001 ±0.013	0.44	40	0.30
	HPS	0.013 ±0.003	0.047 ±0.047	0.019 ±0.000	0[w]	0.37	33	0.46
	INC	0.012 ±0.004	0.076 ±0.067	0.019 ±0.003	0.002 ±0.009	0.25	38	0.39
	MH	0.014 ±0.002	0.026 ±0.002	0.020 ±0.001	0[w]	0.22	33	0.47
C. grandiflora 'Early Sunrise'	CWF	0.012 ±0.003	0.056 ±0.058	0.017 ±0.002	0.002 ±0.01	0.22	35	0.36
	HPS	0.013 ±0.003	0.041 ±0.055	0.017 ±0.001	0[w]	0.25	35	0.22
	INC	0.013 ±0.002	0.039 ±0.027	0.019 ±0.001	0[w]	0.43	34	0.43
	MH	0.013 ±0.002	0.02 ±0.024	0.017 ±0.002	0[w]	0.50	29	0.26
C. verticillata 'Moonbeam' Ex.I	CWF	-	-	0.017 ±0.001	-0.003 ±0.002	-	15	0.13[v]ns
	HPS	-	-	0.017 ±0.001	0.002 ±0.004	-	14	0.01[v]ns
	INC	0.014 ±0.004	0.042 ±0.061	0.019 ±0.002	0[w]	0.27	11	0.52
	MH	0.009 ±0.005	0.123 ±0.115	0.018 ±0.000	0[w]	0.19	15	0.62
C. verticillata 'Moonbeam'Ex.II	CWF	-	-	0.014 ±0.001	0.008 ±0.003	-	9	0.49[v] **
	HPS	-	-	0.015 ±0.000	0.005 ±0.001	-	7	0.75[v] *
	INC	-	-	0.014 ±0.001	0.005 ±0.005	-	6	0.17[v] ns
	MH	-	-	0.015 ±0.001	-0.0002 ±0.003	-	9	0.001[v] ns
R. fulgida 'Goldsturm'	CWF	-	-	0.007 ±0.001	0.006 ±0.002	-	6	0.63[v] ns
	HPS	-	-	0.007 ±0.001	0.01 ±0.002	-	9	0.76[v] **
	INC	-	-	0.008 ±0.001	0.004 ±0.002	-	6	0.62[v] ns
	MH	-	-	0.006 ±0.000	0.009 ±0.001	-	7	0.92[v] ***

[z] Number of observations in the data set.

[y] The R^2 value was calculated as $1\text{-}SS_{residual}/SS_{corrected\ total}$

[x] Asymptotic standard error.

[w] b_3 was defined as zero to avoid a negative slope.

[v] r^2

Table 3. Influence of light quality on mean total plant height at the time of flowering. Data includes the height of all plants that flowered.

Lamp	*C. carpatica* 'Blue Clips' (cm)	*C. grandiflora* 'Early Sunrise' (cm)	*C. verticillata* 'Moonbeam' (cm)	*R. fulgida* 'Goldsturm' (cm)
CWF	13.6b[z]	26.0b	41.1a	33.0a
HPS	13.3b	25.1b	37.7b	29.6a
INC	16.2a	31.9a	37.5b	36.7a
MH	12.5b	23.7b	39.9ab	31.4a

[z] mean separation in columns by Duncan's multiple range test, $P \leq 0.05$.

Figure 1. Spectral characteristics of light sources, average of 3 scans. Calculations of R:FR (red:far-red) ratio are based on the 1.0 μmol $m^{-2}s^{-1}$ level (400-700 nm). Band widths of 600-700 nm were used for red radiation, and 700-800 nm for far-red radiation. (A) Cool white fluorescent, Philips F48T12, 60 watts. Photon flux in 600-700 nm waveband = 0.25 μmol $m^{-2}s^{-1}$; R:FR = 8.8. (B) High pressure sodium, General Electric Lucolox LU70/MED, 70 watts. Photon flux in 600-700 nm waveband = 0.40 μmol $m^{-2}s^{-1}$; R:FR = 5.9. (C) Incandescent, Philips 100 watt bulb. Photon flux in 600-700 nm waveband = 0.58 μmol $m^{-2}s^{-1}$; R:FR =0.7. (D) Metal halide, VENTURE MH70W, 70 watts. Photon flux in 600-700 nm waveband = 0.27 μmol $m^{-2}s^{-1}$; R:FR = 3.3.

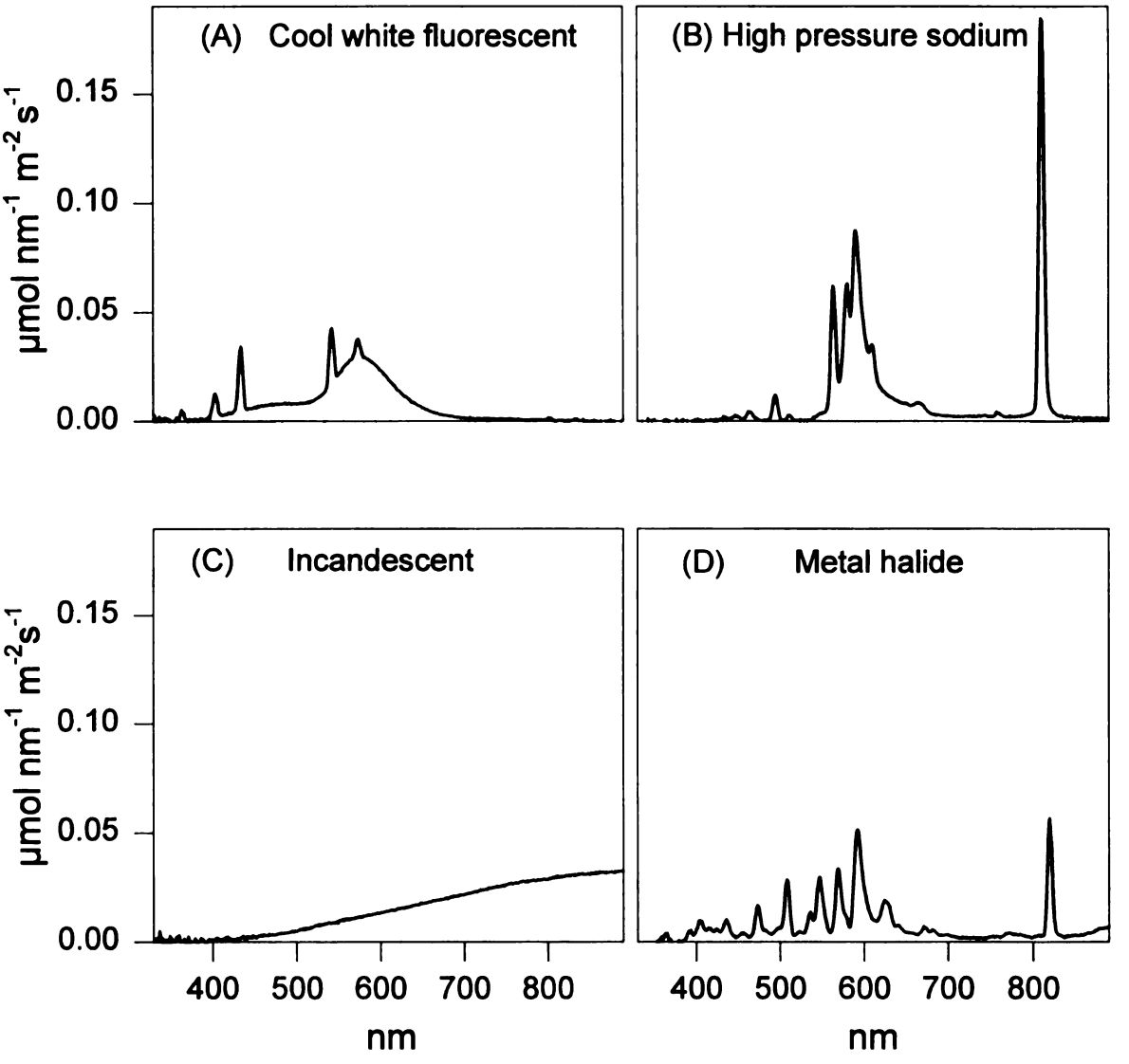

(A) Cool white fluorescent
(B) High pressure sodium
(C) Incandescent
(D) Metal halide
µmol nm-1 m-2 s-1
0.15
0.10
0.05
0.00
400
500
600
700
800
nm

Figure 2. Effect of light source and intensity on rate of progress to flowering in *Campanula carpatica* 'Blue Clips'. Each symbol (●) represents one plant. Data from the three replications were combined. The solid line (—) represents the predicted rate of progress to flowering based on Eqs. [2 and 3]. Plants which did not flower were not included in the analysis. The saturation illuminance (I_{sat}) is the quantum flux at the point of intersection between the two lines. The rate of progress to flowering is constant at irradiances above I_{sat}. None of the plants under SD flowered. Statistical analysis is presented in Table 2.

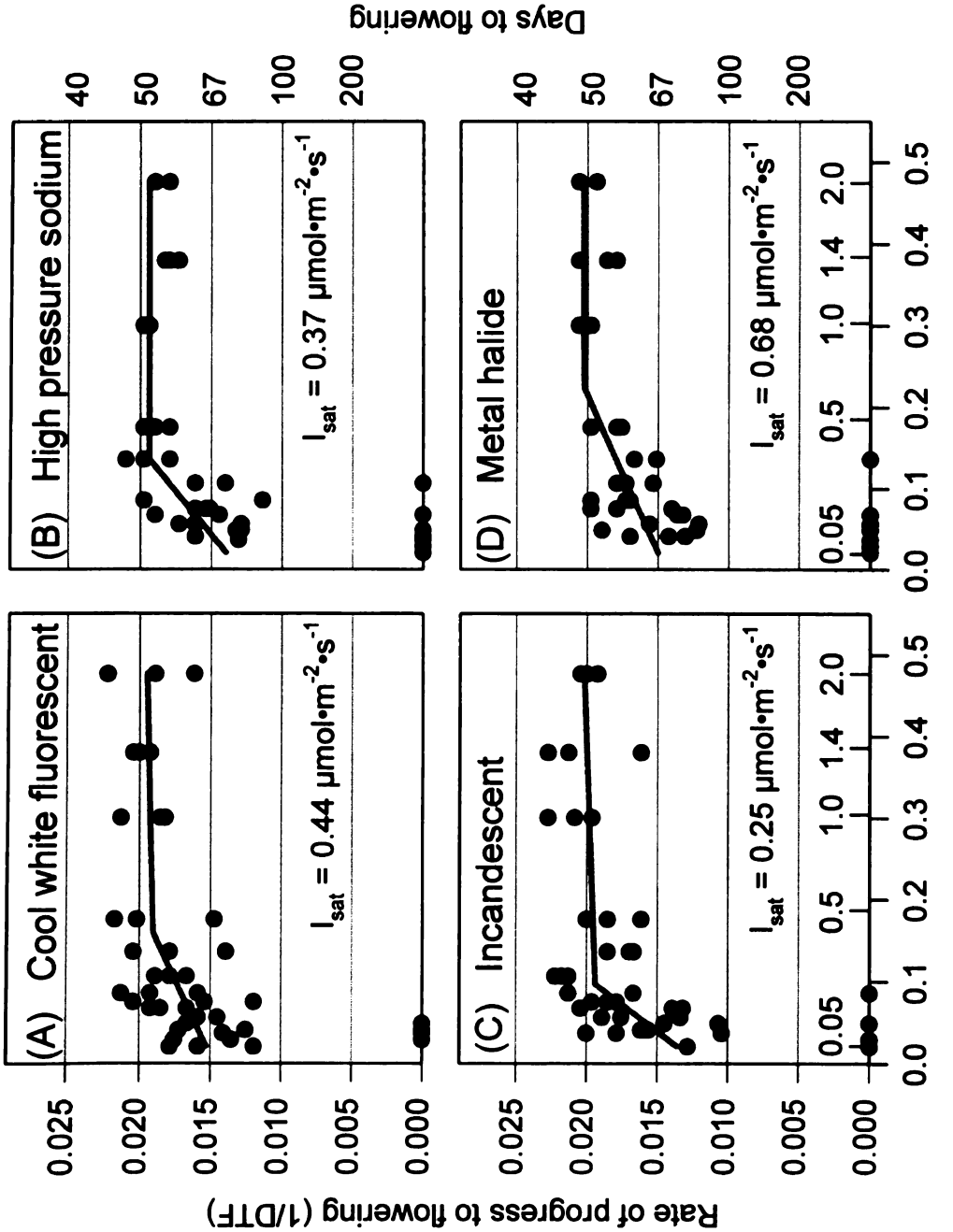

(A) Cool white fluorescent
(B) High pressure sodium
(C) Incandescent
(D) Metal halide
I_{sat} = 0.44 µmol•m^{-2}•s^{-1}
I_{sat} = 0.37 µmol•m^{-2}•s^{-1}
I_{sat} = 0.25 µmol•m^{-2}•s^{-1}
I_{sat} = 0.68 µmol•m^{-2}•s^{-1}
Rate of progress to flowering (1/DTF)
Days to flowering
Quantum flux
[log (µmol•m^{-2} •s^{-1} +1) below; µmol•m^{-2}•s^{-1} above]

Figure 3. Effect of light source and intensity on rate of progress to flowering in *Coreopsis grandiflora* 'Early Sunrise'. Each symbol (●) represents one plant. Data from the three replications were combined. The solid line (—) represents the predicted rate of progress to flowering based on Eqs. [2 and 3]. Plants which did not flower were not included in the analysis. The saturation illuminance (I_{sat}) is the quantum flux at the point of intersection between the two lines. The rate of progress to flowering is constant at irradiances above I_{sat}. None of the plants under SD flowered. Statistical analysis is presented in Table 2.

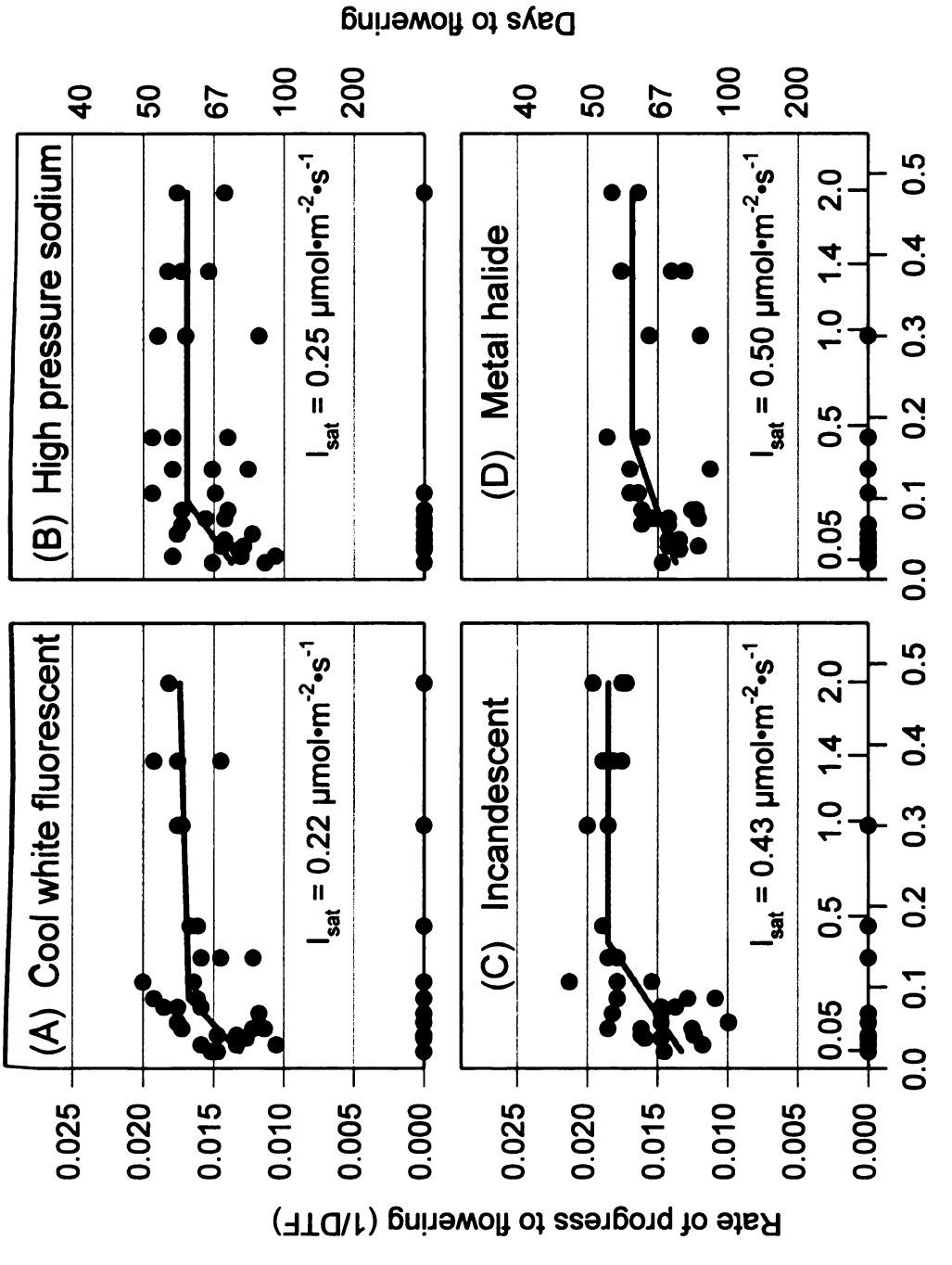

(A) Cool white fluorescent
(B) High pressure sodium
(C) Incandescent
(D) Metal halide
I_{sat} = 0.22 µmol•m^{-2}•s^{-1}
I_{sat} = 0.25 µmol•m^{-2}•s^{-1}
I_{sat} = 0.43 µmol•m^{-2}•s^{-1}
I_{sat} = 0.50 µmol•m^{-2}•s^{-1}
Rate of progress to flowering (1/DTF)
Days to flowering
Quantum flux
[log (µmol•m^{-2} •s^{-1} +1) below; µmol•m^{-2}•s^{-1} above]

Figure 4. Effect of light source and intensity on rate of progress to flowering in *Coreopsis verticillata* 'Moonbeam', experiment I. Each symbol (●) represents one plant. For (A) and (B), the solid line (—) represents the predicted rate of progress to flowering based on linear regression. For (C) and (D), the solid line (—) represents the predicted rate of progress to flowering based on Eqs. [2 and 3]. Plants which did not flower were not included in the analysis. The saturation illuminance (I_{sat}) is the quantum flux at the point of intersection between the two lines. The rate of progress to flowering is constant at irradiances above I_{sat}. None of the plants under SD flowered. Statistical analysis is presented in Table 2.

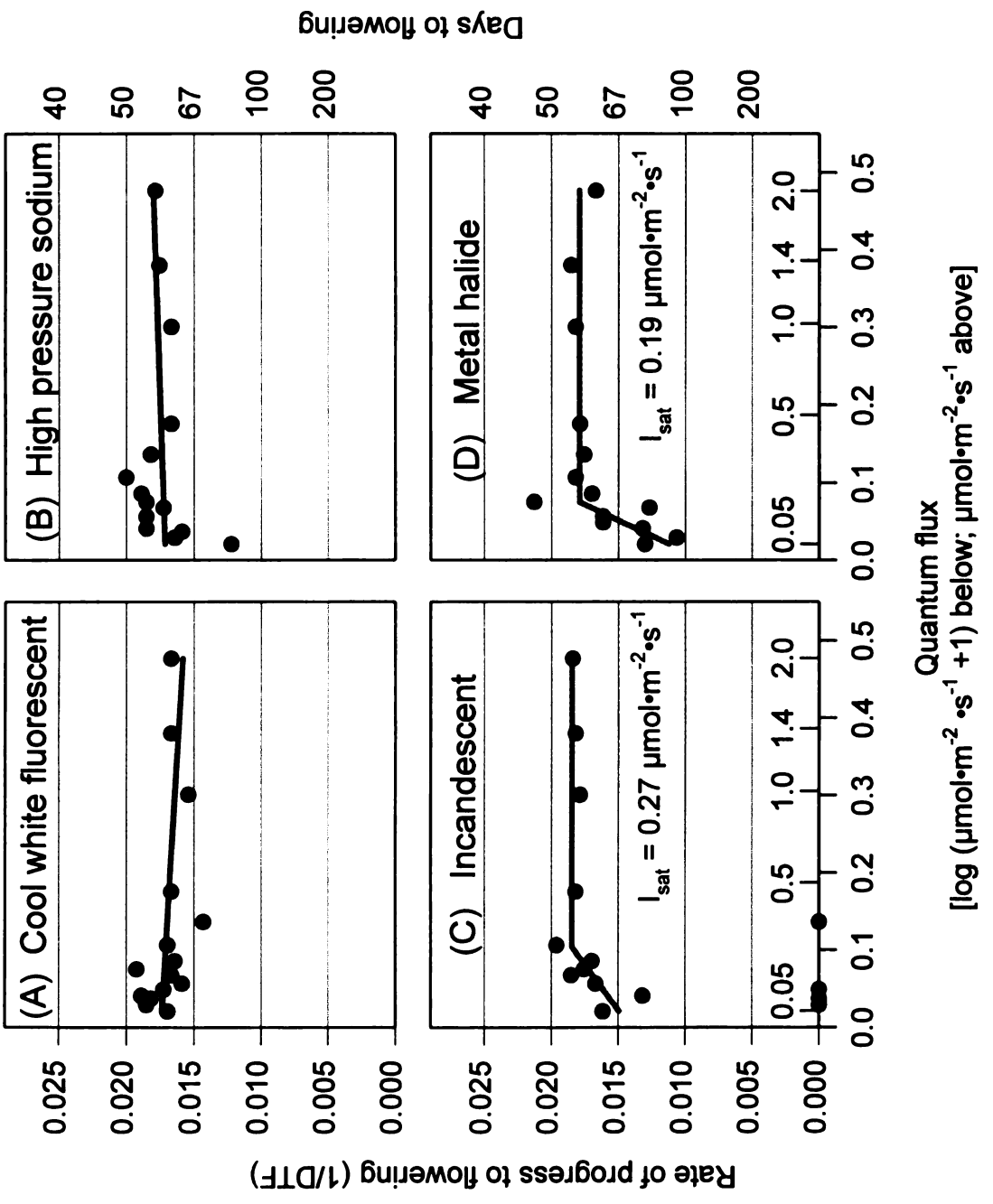

(A) Cool white fluorescent
(B) High pressure sodium
(C) Incandescent
(D) Metal halide
I_{sat} = 0.27 µmol•m^{-2}•s^{-1}
I_{sat} = 0.19 µmol•m^{-2}•s^{-1}
Rate of progress to flowering (1/DTF)
Days to flowering
Quantum flux
[log (µmol•m^{-2} •s^{-1} +1) below; µmol•m^{-2}•s^{-1} above]

Figure 5. Effect of light source and intensity on rate of progress to flowering in *Coreopsis verticillata*'Moonbeam', experiment II. Each symbol (●) represents one plant. The solid line (—) represents the predicted rate of progress to flowering based on linear regression. Plants which did not flower were not included in the analysis. Statistical analysis is presented in Table 2.

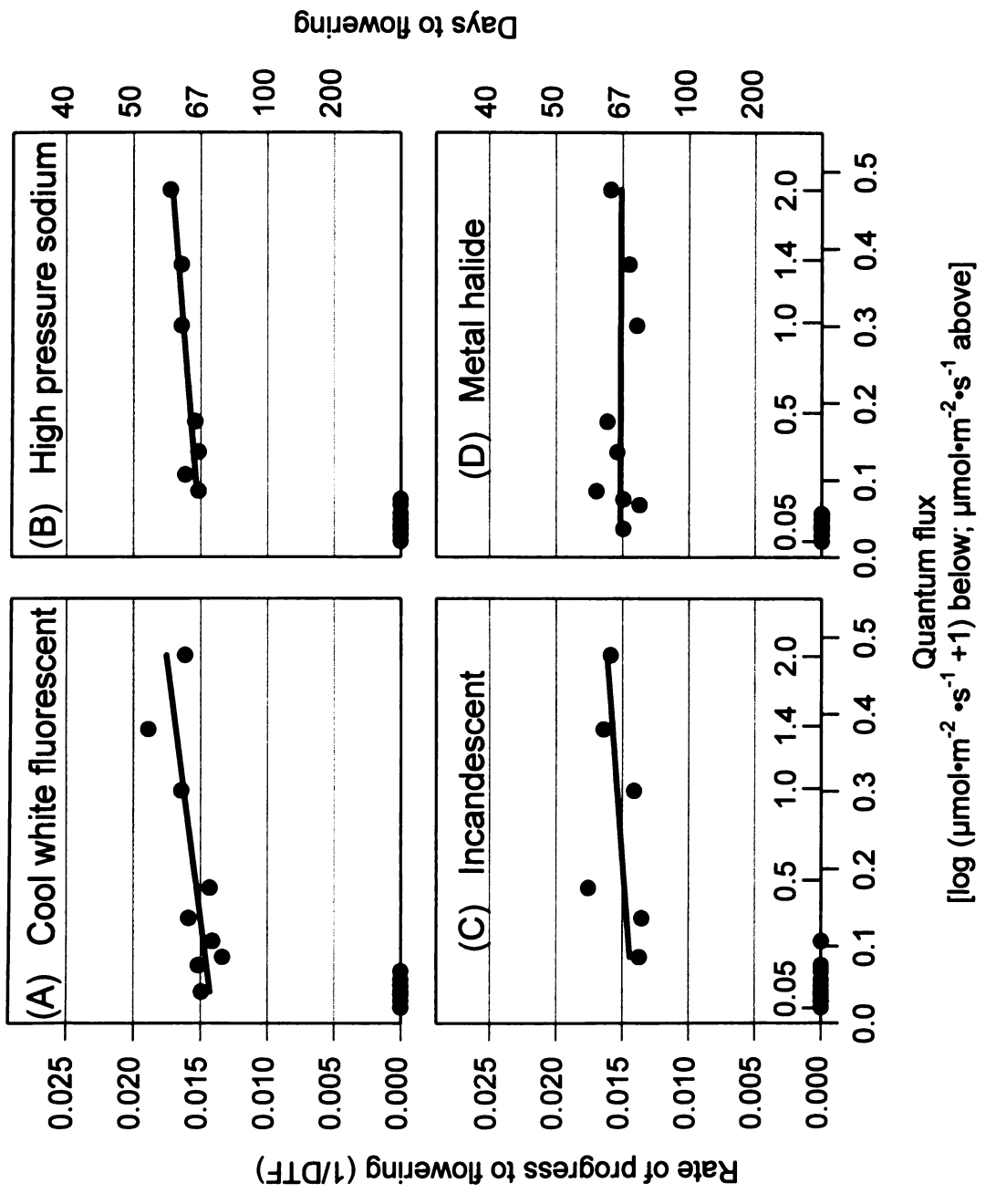
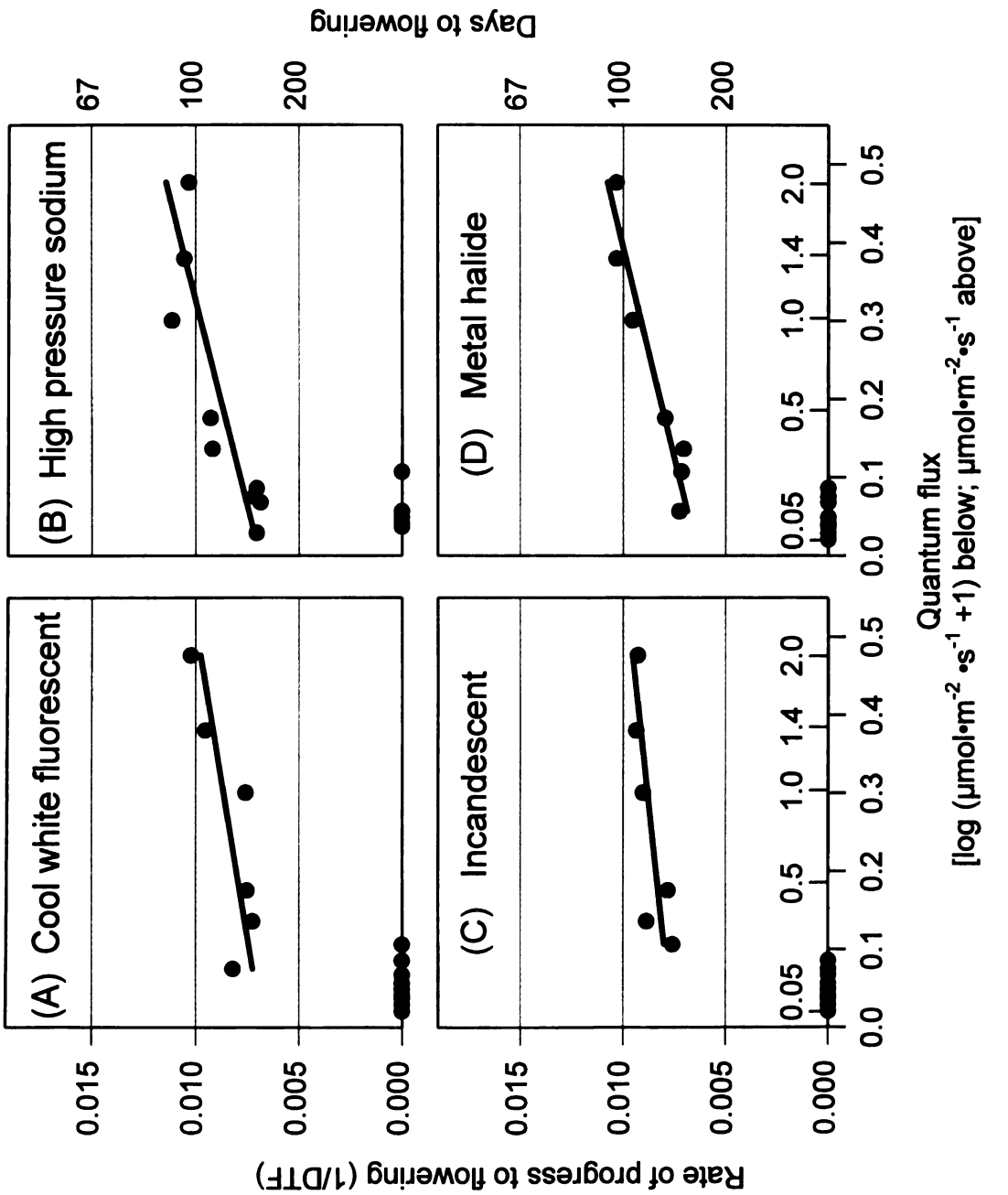

(A) Cool white fluorescent
(B) High pressure sodium
(C) Incandescent
(D) Metal halide
Rate of progress to flowering (1/DTF)
Days to flowering
Quantum flux
[log (µmol•m-2 •s-1 +1) below; µmol•m-2•s-1 above]

Figure 6. Effect of light source and intensity on rate of progress to flowering in *Rudbeckia fulgida* 'Goldsturm'. Each symbol (●) represents one plant. The solid line (—) represents the predicted rate of progress to flowering based on linear regression. Plants which did not flower were not included in the analysis. Statistical analysis is presented in Table 2.


(A) Cool white fluorescent
(B) High pressure sodium
(C) Incandescent
(D) Metal halide
Rate of progress to flowering (1/DTF)
Days to flowering
0.000
0.005
0.010
0.015
67
100
200
0.0
0.1
0.2
0.3
0.4
0.5
1.0
1.4
2.0
0.05
0.5
Quantum flux
[log (µmol•m-2 •s-1 +1) below; µmol•m-2•s-1 above]

SECTION III

INFLUENCE OF COLD TREATMENT AND FORCING TEMPERATURE ON FLOWERING OF *CAMPANULA CARPATICA* 'BLUE CLIPS'

Influence of cold treatment and forcing temperature on flowering of *Campanula carpatica* 'Blue Clips'.

Catherine M. Whitman[1], Royal D. Heins[2], Arthur Cameron[2], and William Carlson[2]

Department of Horticulture, Michigan State University, E. Lansing MI 48824

Additional index words: *vernalization, herbaceous perennial, long-day plant*

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[1] Graduate student.

[2] Professor of Horticulture

Abstract. The influence of cold treatments on flowering in *Campanula carpatica* Jacq. 'Blue Clips' was determined. Plants with 10 to 12 nodes and 12 to 16 nodes, in 128-cell (10 ml cell volume) and 50-cell (85 ml cell volume) trays, respectively, were stored at 5C for 0, 2, 4, 6, 8, 10, 12, or 14 weeks. They were then transplanted and forced in a 20C greenhouse under a 4-hr night interruption (2200-0200) long day. Time to visible bud and time to flowering in 128-cell plants decreased approximately 10 days after 14 weeks at 5C, but the trends were not significant in 50-cell plants. The number of flower buds on 128-cell plants showed no significant response to cold treatments, while flower bud number increased by approximately 60% in 50-cell plants as duration of cold treatments increased. Final plant height at flowering of 128-cell plants showed no significant trends, but height of 50-cell plants decreased 20% with increasing cold.

To determine the relationship between forcing temperature and time to flower in *C. carpatica* 'Blue Clips', 3 plant sizes were forced under a 4-hr night interruption (2200-0200) at setpoints of 15C, 18C, 21C, 24C, and 27C. Plants flowered more quickly at higher temperatures, but number of flowers and diameter of flowers were reduced. Days to visible bud and flowering were converted to rates, and base temperature (T_b) and thermal time to flowering (°days), were calculated. Average T_b for forcing to visible bud stage was 2.1C and for forcing to flower, 0.0C. Calculated °days to visible bud were 455, and°days to flower, 909. These values can be used to predict time to flower at different forcing temperatures.

The Campanulaceae family includes over 700 species of annual, biennial, and perennial plants. There are over 300 species within the *Campanula* genus, many of which are popular garden plants (Bailey et al., 1976). *Campanula* is one of the 20 top selling genera of herbaceous perennials grown in the United States (Rhodus, 1993).

Campanula carpatica Jacq. is a popular herbaceous perennial which grows as a compact mound, with numerous blue or white bell-shaped flowers. The species is native to the Carpathian Mountains of Eastern Europe and is hardy from USDA zones 3 to 8 (Nau, 1993). In North America, *C. carpatica* has traditionally been produced outdoors and is not in bloom in the spring when the majority of garden plants are sold. Consumers prefer to purchase plants in flower, consequently producers are interested in understanding the flowering requirements of this species and developing production schedules.

Exposure to a period of low temperatures is one of the environmental cues that regulates development and flowering in many plant species native to temperate latitudes (Roberts and Summerfield, 1987). Some species of herbaceous perennials require a cold treatment for flowering, while in others, low temperatures hasten or improve uniformity of flowering (Iversen, 1994). In some cases, cold temperatures promote flowering by breaking the dormancy of existing buds. Floral primordia of *Paeonia* are initiated soon after anthesis of the current year's flowers and require a minimum of four weeks at 5.6C to break dormancy (Byrne and Halevy, 1986). Flower induction, initiation, and development occur during exposure to low temperatures in some species. Floral bud initiation and development occurred in *Astilbe* during storage at 2C

(Pemberton, 1992) and in *Dicentra spectabilis* during storage at 5 and 10C (Hanchek,1989).

In some species, low temperatures induce the subsequent initiation and development of floral primordia. This response is termed vernalization, generally defined as a cold treatment that induces or hastens the capacity for flowering in a plant (Chouard, 1960). Hastening of flowering can be measured directly by calculating time to flower, and has also been correlated with a reduction of the number of leaves formed before flowering in grains (Chouard, 1960) and *Arabidopsis thaliana* L. (Bagnall, 1993). A cold treatment is not required for flowering in *C. carpatica*, but Armitage (1995) reported that cooling the cultivar 'White Clips' at 2C for 12 weeks accelerated subsequent flowering by ≈ 50 days compared to uncooled plants, under a 16-hr photoperiod provided with day-extension lighting. In preliminary experiments, we have not observed this response to cold treatments in *C. carpatica* 'Blue Clips' when grown under a 4-hr night interruption, but observed a hastening of flowering of approximately 10 days when plants were forced under day-extension lighting (unpublished).

Many species native to temperate latitudes are long-day plants (LDP), so photoperiods exceeding a certain minimum length either are required for flowering or hasten flowering (Roberts and Summerfield, 1987). *C. carpatica* is an obligate LDP (Drushal, 1991). Recommended forcing conditions include extending the daylength to a minimum of 16 hours, or providing a 4-hr night-break with incandescent lamps, at 10-20 footcandles (2 to 4 μmol $m^{-2}s^{-1}$) (Drushal, 1991).

Production time for any crop is related to temperatures supplied during forcing. At temperatures below a species-specific minimum, T_b, the time to flower (*f*) is infinity. Temperatures above a ceiling value, T_{ce}, are detrimental to development and will delay flowering. In the range of temperatures between T_b and T_{ce} , the relationship between mean temperature and rate of development is often linear (Roberts and Summerfield, 1987). Base and optimum temperatures vary within species and between species, and are related to climatic origin (Roberts and Summerfield, 1987). The T_b calculated for leaf unfolding in *Hibiscus rosa-sinensis* was 9.8C (Karlsson et al., 1991); minimum temperature for leaf growth of *Saintpaulia ionantha* was 8C (Faust and Heins, 1993); and T_b was ≈8.5C in three cultivars of *Phaseolus vulgaris* (Roberts and Summerfield, 1987). *H. rosa-sinensis, S. ionantha*, and *P. vulgaris* are all native to tropical or sub-tropical climates. For *Lilium longiflorum*, native to temperate climates, the base temperature was estimated to be approximately 1.1C (Karlsson et al., 1988).

Temperatures which result in most rapid flowering may not optimize plant appearance. Recommended forcing temperatures for *C. carpatica* are approximately 13 to 17C (Armitage, 1994; Drushal, 1991; Madsen and Madsen, 1986; Nau, 1993); however, the actual time to flower at different forcing temperatures has not been quantified.

Information on the time required for flowering is critical for development of effective production schedules for any crop. In order to predict time to flower, it is important to determine if *C. carpatica* 'Blue Clips' exhibits a vernalization response, and how forcing temperature influences development. The objectives of these

experiments were to clarify the influence of cold treatments on subsequent flowering, and to understand the relationship between temperature and time to flower in *C. carpatica* 'Blue Clips'.

Materials and Methods

General. During forcing, plants were grown in a commercial soilless media containing 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 as necessary with 7 mM N from a 20N-4.4P-16.6K all-purpose water soluble fertilizer (20-10-20), Peter's professional Peat-lite special (Grace-Sierra Horticultural Products Company, Milpitas, CA). When the ambient greenhouse photosynthetic photon flux (PPF) dropped below 400 μmol $m^{-2}s^{-1}$, high pressure sodium lights were turned on automatically by an environmental control computer, providing $\approx$ 50 μmol $m^{-2}s^{-1}$ PPF at plant level.

All cold treatments were delivered in a 5C cooler, lighted for 9 hours per day with cool white fluorescent lamps (VHOF96T12; Philips, Bloomfield, N.J.) at approximately 10 μmol $m^{-2}s^{-1}$. While in the cooler, plugs were watered with well water (340 mg calcium bicarbonate per liter) acidified (93% H_2SO_4) to a titratable alkalinity of 100 mg calcium bicarbonate per liter.

Experiment 1 - cold treatments. Two plug sizes were tested. Seedlings grown in 50-cell trays (85 ml cell volume) were received from a commercial producer on 27 October 1994 when they were approximately 20 weeks old, and had 12 to 16 nodes. Seedlings grown in 128-cell trays (10 ml cell volume) were received 21 December

1994, and had 10 to 12 nodes. Upon arrival, ten plants of each size were removed from the plug tray, thinned to a single plant per cell (singulated), and transplanted. The 128-cell seedlings were transplanted into 10-cm containers (470 ml), and the 50-cell plants into 2.2-liter containers. Plants were placed in the greenhouse at 20 C, and grown under a 4-hr night interruption (NI) from 2200 to 0200. The NI was supplied with 60 W incandescent lamps at a PPF of 3 to 5 μmol $m^{-2}s^{-1}$ as measured by a LI-Cor quantum sensor model LI-189 (Li-COR Inc., Lincoln, Nebraska). Black cloth was pulled at 1700 and opened at 0800 on all benches. The remaining plants in the plug trays were placed in a 5C cooler. Ten plugs of each size were removed from the cooler at two-week intervals, singulated, transplanted, and placed under NI in the greenhouse. Date of the first visible bud (when flower bud was approximately 2 mm long) and date of opening of the first flower were recorded for each plant, and days to visible bud and flowering were calculated. At the time of flowering, total plant height, number of visible flower buds, and number of nodes under the terminal flower on the main stem were determined. The number of nodes formed on the main stem during forcing was calculated.

Temperature control. Air temperatures on each bench were monitored with two 36-gauge thermocouples connected to a CR10 datalogger (Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 10 seconds and recorded the hourly average. Night time air temperatures under blackcloth on solid aluminum benches can be 3.5C cooler than greenhouse air temperatures due to radiant heat loss to the greenhouse glazing material (Heins and Faust, 1994). To provide uniform

temperature conditions, the datalogger controlled a 1500W electric heater under each bench which provided supplemental heat as needed throughout the night. Actual average daily air temperature was 20.4 C. The maximum difference in actual average daily air temperature between any two treatments throughout the experiment was 0.6C.

Data analysis. Analysis of variance was used to determine the relationship between duration of cold treatment and time to visible bud, time to flowering, number of buds and nodes at flowering, nodes formed during forcing, and total plant height.

Experiment 2 - Forcing temperature. Three plant sizes were tested. The 50-cell seedlings were received from a commercial producer on 27 October 1994 when they were approximately 20 weeks old, and had 12 to 16 nodes. They were placed into a 5C cooler for 13 weeks until 23 January 1995, then singulated, transplanted into 13-cm square containers (1.1 liter), and moved into the different treatments. The 128-cell seedlings were received 21 December 1994, and had 10 to 12 nodes. They were placed in a 5C cooler for 15 weeks until 7 April 1995, when they were singulated, transplanted into 10-cm containers, and placed into the different treatments. The 5.5 cm plants (190 ml cell volume) were received on 17 January 1995, transplanted into 2.2-liter containers, and placed into the different greenhouses on 4 February 1995. Ten plants of each size were placed into each of five greenhouses set to 15C, 18C, 21C, 24C, and 27C. Plants received natural daylengths with a 4-hr NI, 2200 to 0200, provided by HPS lamps which delivered approximately 90 μmol $m^{-2}s^{-1}$.

Temperature control. Temperatures in each greenhouse were controlled with a Priva environmental computer. Actual air temperatures were recorded every fifteen minutes

by a CR-10 datalogger. Actual average daily air temperatures were determined, and used in all calculations.

Data analysis. Date of the first visible flower bud (when bud was approximately 2 mm long) and date of opening of the first flower were recorded for each plant, and days to visible bud and flowering were calculated. At the time of flowering, total plant height and number of visible flower buds were determined. Base temperature (T_b) and thermal time, or degree-days, were calculated using equations presented by Roberts and Summerfield (1987). The mean time to flower in each treatment was converted to a rate by taking the reciprocal, and the relationship between the rate of progress to flowering ($1/f$) and the mean temperature T in °C was determined:

$$\frac{1}{f} = b_0 + b_1 \overline{T} \qquad [1]$$

where b_0 and b_1 are constants. Once b_0 and b_1 had been calculated, the base temperature, T_b, was calculated as:

$$T_b = -\frac{b_0}{b_1} \qquad [2]$$

and thermal time, or degree-days was determined by:

$$^{\circ}Cd = \frac{1}{b_1} \qquad [3]$$

Within each developmental stage, slopes and intercepts of regression equations for the three plant sizes were compared using the procedure by Snedecor and Cochran (1967).

Results

Experiment 1 - Screen. The number of new nodes formed on the main stem during forcing did not change significantly after cold treatments in plants from either 128-cell or 50-cell trays (Table 1). No other trends were common to both plant sizes. Time to visible bud and time to flowering decreased significantly in 128-cell plants after cold treatments, whereas the trends were not significant in 50-cell plants. The number of flower buds on 128-cell plants showed no significant response to cold treatments, while flower bud number increased significantly in 50-cell plants as duration of cold treatments increased. Final plant height at flowering of 128-cell plants showed no significant trends, but height of 50-cell plants decreased significantly with increasing cold.

Experiment 2 - Forcing Temperatures. Actual average daily air temperatures during forcing are presented in Table 2. Plants flowered more quickly at higher temperatures (Figure 1). Time to flower at ≈16C averaged approximately 57 days, and at ≈26C, 36 days.

Rates of progress to visible bud and flowering were linear within the range of temperatures tested (Figure 1). There were small but significant differences in estimated T_b values for the different plant sizes (Table 3). Since the regression parameters showed significant differences between the plant sizes in only 5 out of 18 comparisons (Table 4), the data for the 3 plant sizes were pooled and the average actual

daily temperatures used in the calculations. Average base temperatures for all sizes and developmental stages were between -1.0 and 2.0C (Table 3). Within each developmental stage, the slopes of regression lines for the three plant sizes were not significantly different, indicating that the °days required for each stage were the same for all plant sizes tested.

The average number of flower buds per plant decreased as forcing temperatures increased (Figure 3). Flower diameter on both 50-cell and 5.5-cm plants decreased as forcing temperatures increased from ≈16C to ≈26C. Average plant height in 50-cell plants and 5.5-cm plants did not vary with temperature. The 128-cell plants forced at ≈16 and 19C were approximately 2 to 4 cm taller than those in all other treatments.

Discussion

Time to visible bud and time to flower in the 128-cell plants decreased after 14 weeks cooling at 5C, but time to visible bud and time to flower in the 50-cell plants did not change. These findings contrast with those of Armitage (1995), who reported a reduction in time to flower from ≈ 150 days for uncooled plants to ≈ 100 days after 12 weeks at 2C for the cultivar 'White Clips'. According to temperature data provided by Armitage, forcing temperatures in the greenhouse were not consistent throughout the course of his experiment. Plants that were cooled experienced warmer forcing temperatures than uncooled plants, which would certainly hasten flowering in the cooled plants. A forcing schedule for *C. carpatica* 'Karl Foerster' suggested by Madsen and Madsen (1986) states that plants will be ready for sale 8 to 10 weeks after the start of forcing under long days at 15C, similar to the time to flower we observed.

A hastening of flowering in *C. carpatica* after cold treatments may be more evident when plants are subsequently forced under day-extension treatments (DE) rather than NI treatments. Preliminary experiments have revealed a reduction of time to flower after 15 weeks at 5C of approximately 10 days when 128-cell plants were forced under DE, and approximately 4 days when plants were forced under NI (E. Runkle, personal communication).

Flower bud number on the 50-cell plants increased with cold treatment but since time to flowering was not reduced, it is difficult to conclude that this is a vernalization response. An increase in flower number after vernalization was reported in some species of *Dianthus*, but was accompanied by a hastening of flowering (Chouard, 1960). The increase in flower bud number reported here may reflect the higher natural light levels experienced by plants forced in the spring, although 128-cell plants did not respond similarly.

The two plant sizes tested displayed conflicting responses to the cold treatments. However, in general, holding plugs of *C. carpatica* 'Blue Clips' at 5C for up to 14 weeks influenced subsequent time to flower by 10 days or less. Exposure to cold temperatures had no detrimental effects on any of the characteristics evaluated in this work.

To complete a developmental process in a plant, the plant must experience a specific number of units of thermal time (°days) above the base temperature characteristic of that process (Roberts and Summerfield, 1987). Once the base temperature and the amount of thermal time required for a developmental stage are

known, predicted time for the developmental stage can be calculated. Thermal time is commonly used to schedule planting and harvest of fruit and vegetable crops (Roberts and Summerfield, 1987). For *C. carpatica* 'Blue Clips', calculated °days to visible bud were 455 and°days to flower, 909. To calculate time to visible bud or flower at any temperature between T_b and T_{ce}, the degree-days required for that developmental stage are divided by the degrees provided above the T_b . For example, time to flower for plants forced at 18C (T_b = 0.0C) is estimated to be 909°days/18.0° C ≈ 50 days.

C. carpatica 'Blue Clips' is native to temperate alpine regions, and the plants in this experiment were most attractive, in terms of the number and size of flowers, when forced at temperatures at or below 21C. For growers, plant appearance must be balanced against the longer production time required with cooler forcing temperatures. Forcing at 20C will hasten flowering by approximately 5 days compared to forcing at 18C.

Plants from the 50-cell trays bloomed approximately five days earlier than either the larger or smaller seedlings. The 5.5-cm plants had been pruned back before shipment, which apparently delayed their development. We expect that cutting back plants of any size would delay their flowering comparably. Slopes of the regression lines for each stage of development did not differ significantly between plug sizes, indicating that all plant sizes responded similarly to the forcing temperatures.

Larger plugs generally resulted in taller plants with more flowers. Seedlings from 128-cell trays developed into well-proportioned flowering potted plants in the 10-cm containers, and larger plugs were appropriate for the 2.2-liter containers. *C.*

carpatica is grown extensively as a flowering pot plant in Northern Europe (Madsen and Madsen, 1986), and could certainly occupy a similar niche in the marketplace in North America.

LITERATURE CITED

Armitage, A. 1994. Spring into perennials. Greenhouse Grower 13:92-94

Armitage, A. 1995. Forcing perennials for early spring sales. Bedding Plants Foundation Inc. Res. Rpt. F-9501.

Bagnall, D.J. 1993. Light quality and vernalization interact in controlling late flowering in *Arabidopsis* ecotypes and mutants. Ann. Bot. 71: 75-83.

Liberty Hyde Bailey Hortorium, 1976. Hortus Third. Macmillan, New York.

Byrne, T. and H. Halevy. 1986. Forcing herbaceous peonies. J. Amer. Soc. Hort. Sci. 111:379-383.

Chouard, P. 1960. Vernalization and its relations to dormancy. Annu. Rev. Plant Physiol. 11: 191-238.

Drushal, N. 1991. Campanulas. p. 422-423 in Ball Red Book, V. Ball, Ed., Ball Publishing, Chicago.

Faust, J. and R. Heins. 1993. Modeling leaf development of the African violet (*Saintpaulia ionantha* Wendl.) J. Amer. Soc. Hort. Sci. 118:747-751.

Hanchek, A. 1989. Growth and development of *Dicentra spectabilis* in relation to storage temperature and harvest date. PhD Diss. Michigan State Univ., East Lansing.

Heins, R. and J. Faust. 1994. Radiant cooling leads to cooler temperatures under black cloth. HortScience 29:503. (Abstr.)

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

Karlsson, M., Heins, R., and J. Erwin. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. J. Amer. Soc. Hort. Sci. 113:70-74.

Karlsson, M., Heins, R., Gerberick, J., and M. Hackmann. 1991. Temperature-driven leaf unfolding rate in *Hibiscus rosa-sinensis*. Scientia Hort. 45:323-331.

Madsen, P. and K. Madsen. 1986. Campanula- a bright star in the future. BPI News. May, p. 7.

Nau, J. 1993. Ball Culture Guide. Ball Publishing, Batavia, Illinois.

Pemberton, G. 1992. Factors affecting the growth and development of forced Dutch-grown *Astilbe*. MS Thesis, North Carolina State Univ., Raleigh.

Rhodus, T. 1993. Views on management. Perennial Plants. Summer 1993 p.26-34.

Roberts, E. and R. Summerfield. 1987. Measurement and prediction of flowering in annual crops. p. 17-51. In: J.G. Atherton (ed.). Manipulation of flowering. Butterworth's, London.

Snedecor, G. and W. Cochran. 1967. Statistical methods. 6th edition. The Iowa State Univ. Press, Ames.

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

Weeks	Plug	Days			Nodes			FLW	Height
of 5C	size	VB	FLW	VB to FL	Planting	Final	New	Count	(cm)
0	128	31	48	17	11	25	14	28	16
2		34	56	21	12	28	16	17	16
4		34	54	20	11	27	16	32	18
6		25	51	26	10	25	15	22	18
8		32	53	21	12	30	18	21	16
10		24	42	18	10	25	14	23	14
12		25	44	19	13	29	16	26	15
14		25	42	17	12	27	15	25	16
Average		29	49	20	11	27	16	24	16
Significance									
Weeks 5C		***	***	***			NS	NS	NS

Weeks	Plug	Days			Nodes			FLW	Height
of 5C	size	VB	FLW	VB to FL	Planting	Final	New	Count	(cm)
0	50	26	48	21	15	34	20	33	22
2		27	48	21	17	34	18	31	22
4		27	49	22	15	30	15	33	19
6		29	50	21	12	30	18	26	20
8		26	47	20	14	31	17	32	18
10		30	50	20	12	28	16	35	18
12		28	47	19	12	30	18	45	20
14		25	47	20	13	30	17	52	18
Average		27	48	20	13	31	18	36	19
Significance									
Weeks 5C		NS	NS	NS			NS	***	***

NS, *, **, *** not significant, significant at $P<0.05$, 0.01, and 0.001, respectively.

Table 2. Actual average daily air temperatures during the indicated developmental stages, during forcing of *C. carpatica* 'Blue Clips'.

Plant size	Force date	Set point temperature C	Forcing to visible bud C	Visible bud to flower C	Forcing to flower C
128-cell	7 April 1995	15.0	16.3	17.2	16.7
		18.0	19.4	19.2	19.4
		21.0	21.1	21.2	21.1
		24.0	23.6	23.7	23.6
		27.0	27.7	26.9	27.4
50-cell	23 Jan 1995	15.0	15.5	16.0	15.6
		18.0	18.4	19.4	18.7
		21.0	20.7	21.3	20.9
		24.0	22.8	22.9	22.9
		27.0	25.9	26.1	25.9
5.5-cm	4 Feb 1995	15.0	15.4	15.9	15.6
		18.0	18.5	19.1	18.8
		21.0	20.6	21.2	20.8
		24.0	22.8	23.1	22.9
		27.0	25.8	26.6	26.1

Table 3. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud and flowering in *C. carpatica* 'Blue Clips'. Intercept and slope were used in Eqs. [2] and [3] to calculate base temperature (T_b) and degree-days, or thermal time (°days). Visible bud and flowering data for 128-cell plants forced at setpoint 27C were not included in the calculations because the plants were damaged by heat stress.

Plant size	Developmental stage	Intercept (b_0) (1/dev.stage)	Slope (b_1) (1/dev.stage)/ °C	T_b (C)	°days	r^2 [z]
128-cell	forcing to visible bud	-0.0030 ±[y]0.0111	0.0022 ±0.0005	1.4	455	0.89NS
(10-12 nodes)	visible bud to flower	0.0062 ±0.0115	0.0024 ±0.0006	-2.6	417	0.90NS
	forcing to flower	-0.0009 ±0.0028	0.0012 ±0.0001	0.8	833	0.98*
50-cell	forcing to visible bud	-0.0029 ±0.0064	0.0020 ±0.0003	1.5	500	0.93**
(12-16 nodes)	visible bud to flower	-0.0112 ±0.0126	0.0031 ±0.0006	3.6	323	0.90*
	forcing to flower	-0.0032 ±0.0007	0.0012 ±0.0000	2.7	833	0.99***
5.5 cm	forcing to visible bud	-0.0041 ±0.0021	0.0024 ± 0.0001	2.0	417	0.99***
	visible bud to flower	0.0039 ±0.0139	0.0023 ±0.0006	-1.7	435	0.80**
	forcing to flower	0.0015 ±0.0022	0.0011 ±0.0001	-1.4	909	0.97**
Pooled	forcing to visible bud	-0.0025 ± 0.0046	0.0022 ±0.0002	2.1	455	0.97**
	visible bud to flower	0.0017 ± 0.0065	0.0025 ±0.0030	-0.7	400	0.97*
	forcing to flower	0.0002 ± 0.0013	0.0011 ±0.0001	0	909	0.99***

[z] NS, *, **, *** not significant, significant at $P<0.05$, 0.01, and 0.001, respectively.
[y] Standard error.

Table 4. Influence of forcing temperature on time to flower in *C. carpatica* 'Blue Clips'. Comparison of regression lines within each developmental stage, between the 3 plant sizes tested.

Rate to visible bud	128 vs 50-cell	slopes	F = 0.1649 (df = 1,5)	NS
		intercepts	F = 8.4410 (df = 1,6)	*
	128 vs 5.5-cm	slopes	F = 0.2302 (df = 1,5)	NS
		intercepts	F = 6.7647 (df = 1,6)	*
	50-cell vs 5.5-cm	slopes	F = 2.0000 (df = 1,6)	NS
		intercepts	F = 46.141 (df = 1,7)	**
Rate visible bud to flower	128 vs 50-cell	slopes	F = 0.6347 (df = 1,5)	NS
		intercepts	F = 0.5245 (df = 1,6)	NS
	128 vs 5.5-cm	slopes	F = 0.0033 (df = 1,5)	NS
		intercepts	F = 1.7824 (df = 1,6)	NS
	50-cell vs 5.5-cm	slopes	F = 0.8763 (df = 1,6)	NS
		intercepts	F = 0.5597 (df = 1,7)	NS
Rate to flower	128 vs 50-cell	slopes	F = 0.0173 (df = 1,5)	NS
		intercepts	F = 50.828 (df = 1,6)	**
	128 vs 5.5-cm	slopes	F = 0.4493 (df = 1,5)	NS
		intercepts	F = 0.0758 (df = 1,6)	NS
	50-cell vs 5.5-cm	slopes	F = 1.5398 (df = 1,6)	NS
		intercepts	F = 20.815 (df = 1,7)	**

NS, *, **, *** not significant, significant at $P<0.05$, 0.01, and 0.001, respectively.

Figure 1. Influence of forcing temperature on time to flower in *C. carpatica* 'Blue Clips'. Each symbol (●, ■, or▲) represents the mean of 10 plants. Open symbols (Δ) represent data not included in the calculations because the plants were damaged by heat stress. (A), (B), and (C) show days for the indicated developmental stage. For (D), (E), and (F): solid lines (—) represent predicted values for the rate of progress to the indicated developmental stage, based on linear regression. Statistical analysis and calculations are presented in Table 3.

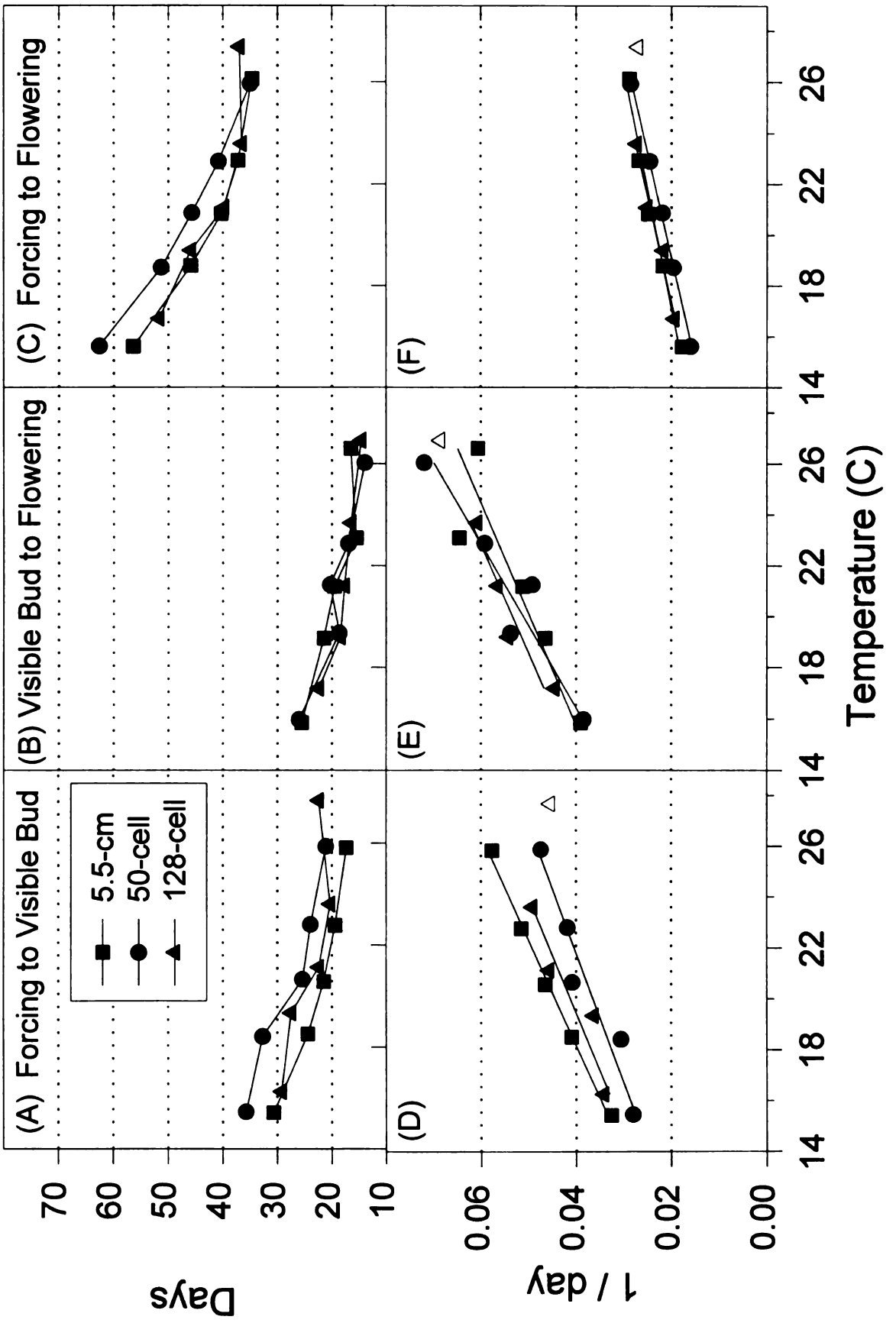
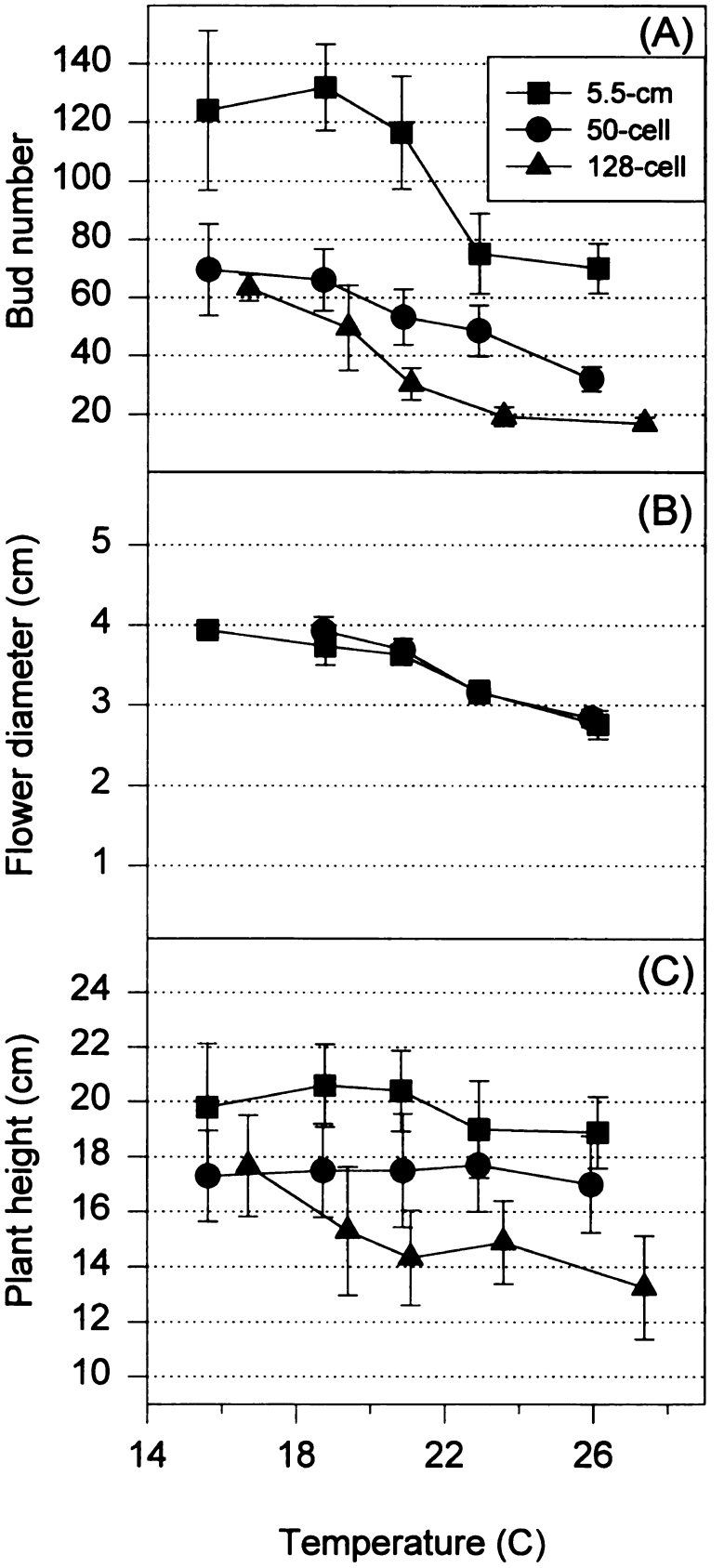

(A) Forcing to Visible Bud
(B) Visible Bud to Flowering
(C) Forcing to Flowering
(D)
(E)
(F)
5.5-cm
50-cell
128-cell
Days
1 / day
Temperature (C)
70
60
50
40
30
20
10
0.06
0.04
0.02
0.00
14
18
22
26

Figure 2. Influence of forcing temperature on (A) number of flower buds, (B) average flower diameter, and (C) total plant height in *C. carpatica* 'Blue Clips'. For (A) and (C), each symbol (●,■, or▲) represents the average of 10 plants. For average flower diameter (B), each symbol (● or ■) represents the average of 50 flowers. Flowers on plants from 128-cell trays were not measured. Error bars represent 95% confidence intervals.


(A)
5.5-cm
50-cell
128-cell
Bud number
140
120
100
80
60
40
20
(B)
Flower diameter (cm)
5
4
3
2
1
(C)
Plant height (cm)
24
22
20
18
16
14
12
10
14
18
22
26
Temperature (C)

SECTION IV

INFLUENCE OF COLD TREATMENTS, PHOTOPERIOD, AND FORCING TEMPERATURE ON FLOWERING OF *LAVANDULA ANGUSTIFOLIA* 'MUNSTEAD'

Influence of cold treatments, photoperiod, and forcing temperature on flowering of *Lavandula angustifolia* 'Munstead'.

Catherine M. Whitman[1], Royal D. Heins[2], Arthur Cameron[2], and William Carlson[2]

Department of Horticulture, Michigan State University, E. Lansing MI 48824

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[1] Graduate student.
[2] Professor of Horticulture

Abstract. The influence of cold treatments and photoperiod on flowering of 8-to 11-node and 18-to 23-node *Lavandula angustifolia* Mill. 'Munstead' plants from 128-cell (10 ml cell volume) and 50-cell trays (85 ml cell volume), respectively, was determined. Plants were stored at 5C for up to 15 weeks, then forced under a 9-hr photoperiod (SD), or under a 4-hr night interruption (NI) (2200-0200) photoperiod at 20C. Increasing durations of cold treatment were associated with an increase in flowering percentage in plants from both 128-cell and 50-cell trays. Flowering percentage was greater under NI than SD. Time to visible bud (VB) and to flowering (FLW) generally decreased with increasing durations of cold treatment. Plants under NI reached FLW 3 to 7 days before those under SD. The 128-cell plants that flowered produced 1 to 2 infloresences in all treatments. Infloresence number in the 50-cell plants increased with increasing durations of cold treatment, and in those cooled for 15 weeks, was increased under NI compared to those under SD.

To determine the relationship between forcing temperature and time to flower in *Lavandula angustifolia* 'Munstead', plants growing in 3 sizes of plugs were forced under a 4-hr NI (2200-0200) at setpoints 15C, 18C, 21C, 24C, and 27C. Plants generally flowered more quickly at higher temperatures, time to FLW decreasing from 77, 71, and 60 days at the lowest temperature (≈15.6C) to 46, 40, and 36 days at the highest temperature (≈ 26C) for 128-cell, 50-cell, and 5.5-cm (190 ml pot volume) plants respectively. The 128-cell plants flowered 5 to 10 days later than 50-cell plants, and plants from 50-cell trays flowered 5 to 10 days later than plants from 5.5 cm pots, under all forcing temperatures. The T_b for forcing to VB stage was 7.1C, 10.7C, and

8.7C for 128-cell, 50-cell, and 5.5-cm plants, respectively, and for forcing to FLW, T_b was 4.7C, 5.4C, and 5.6C respectively. Calculated thermal time, or °days required for forcing to VB were 357 days, 178 days, and 178 days for 128-cell, 50-cell, and 5.5-cm plants, respectively; and for forcing to FLW, 833 days, 769 days, and 625 days, respectively.

Lavandula angustifolia Mill. is native to the Mediterranean region, and is cultivated both for its aromatic oil which is used in perfumery, and as an ornamental for its purple flowers and attractive grey-green foliage (Bailey, 1976). It is hardy in USDA zones 5 to 9 (Ball, 1991). Botanically, *L. angustifolia* is considered a shrub (Bailey, 1976), but is commonly produced and marketed with herbaceous perennials (Ball, 1991). Like most herbaceous perennials in North America, *L. angustifolia* has traditionally been produced outdoors and is not in bloom in the spring when the majority of garden plants are sold. Since current consumers prefer to purchase plants in flower, producers are interested in understanding the flowering requirements of this species.

Exposure to a period of low temperatures is one of the environmental cues that regulates development and flowering in many plant species (Roberts and Summerfield, 1987). Some species of herbaceous perennials require a cold treatment for flowering, while in others, low temperatures hasten or improve uniformity of flowering (Iversen, 1994). We have been unable to find information in the literature on the response of *L. angustifolia* to cold treatments. In preliminary experiments, we found that *L. angustifolia* required exposure to low temperatures for subsequent flowering in the greenhouse, and that larger seedlings are more sensitive to the inductive influence of cold treatments (unpublished data).

A requirement for a period of low temperatures is frequently coupled with a photoperiodic requirement, generally for long-days, so photoperiods exceeding a certain minimum length either are required for flowering or hasten flowering (Roberts

and Summerfield, 1987). In preliminary experiments, we found that *L. angustifolia* demonstrated a facultative response to night-interruption (NI) lighting (unpublished data).

Production time for any crop is related to temperatures supplied during forcing. At temperatures below a species-specific minimum, T_b, the time to flower (*f*) is infinity. Temperatures above a ceiling value, T_{ce}, are detrimental to development and delay flowering. In the range of temperatures between T_b and T_{ce} , the relationship between mean temperature and rate of development is often linear (Roberts and Summerfield, 1987). However, temperatures that result in most rapid flowering may not optimize plant appearance. We were unable to find any recommended temperatures for production of *L. angustifolia* as a flowering plant, but for greenhouse production as an herb, temperatures of 15 to 18C are suggested (Laskey, 1991).

We are unaware of any information in the literature on the flowering requirements of *L. angustifolia*, or on time to flower. The objectives of these experiments were to determine the influence of plant size, cold temperatures, and photoperiod on subsequent flowering; and to quantify the effect of forcing temperature on time to flower.

Materials and Methods

General. Plants were grown in a commercial soilless media containing 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 as necessary with 7

mM N from a 20N-4.4P-16.6K all-purpose water soluble fertilizer (20-10-20), Peter's professional Peat-lite special (Grace-Sierra Horticultural Products Company, Milpitas, CA). When the ambient greenhouse photosynthetic photon flux (PPF) dropped below 400 μmol $m^{-2}s^{-1}$, high pressure sodium lights were turned on automatically by an environmental control computer, providing $\approx$ 50 μmol $m^{-2}s^{-1}$ PPF at plant level.

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

Experiment 1 - cold treatments. Two plug sizes were tested. Seedlings growing in 50-cell trays (85 ml cell volume) with 18 to 23 nodes were received from a commercial producer on 27 October 1994, approximately 20 weeks after sowing. Seedlings in 128-cell trays (10 ml cell volume) with 8 to 11 nodes were received 27 October 1994. Upon arrival, twenty plants of each size were removed from the plug tray, thinned to a single plant per cell (singulated), and transplanted. The 128-cell seedlings were transplanted into 10-cm containers (470 ml), and the 50-cell plants into 2.2-liter containers. Plants were placed in the greenhouse at 20 C. Ten plants of each size were placed under a 9-hr photoperiod (SD). The remaining ten were placed under a 9-hr photoperiod with a 4-hr night interruption (NI) from 2200 to 0200. The NI was supplied with incandescent lamps at a PPF of 3 to 5 μmol $m^{-2}s^{-1}$ as measured by a LI-Cor quantum sensor model LI-189 (Li-COR Inc., Lincoln, Nebraska). Black cloth was

pulled at 1700 and opened at 0800 on all benches. Twenty plugs of each size were removed from the cooler at five-week intervals, singulated, transplanted, and placed in the greenhouse. Half were placed under SD and half under NI. Date of the first visible bud (VB) (when infloresence was approximately 2 mm long), and date of opening of the first flower (FLW) were recorded for each plant, and days to visible bud and flowering were calculated. At the time of opening of the first flower, total plant height, number of visible infloresences, and number of nodes on the main stem were determined.

Temperature control. Air temperatures on each bench were monitored with two 36-gauge thermocouples connected to a CR10 datalogger (Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 10 seconds and recorded the hourly average. Nighttime air temperatures under blackcloth on solid aluminum benches can be 3.5C cooler than greenhouse air temperatures due to radiant heat loss to the greenhouse glazing material (Heins and Faust, 1994). To provide uniform temperature conditions, the datalogger controlled a 1500W electric heater under each bench which provided supplemental heat as needed throughout the night. Actual average daily air temperature throughout the course of the experiment was 20.4 C. The maximum difference in actual average daily air temperature between any two treatments throughout the experiment was 0.7 C.

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

Experiment 2 - Forcing temperature. Three plant sizes were tested. Seedlings in 50-cell trays with 19 to 23 nodes were received from a commercial producer on 27 October 1994, approximately 20 week after sowing. They were placed into a 5C cooler for 13 weeks until 22 January 1995, then transplanted into 13-cm square containers (1.1 liter), and moved into the different treatments. Seedlings in 128-cell trays were received 27 October 1994, with 7 to 9 nodes. They were placed in a 5C cooler for 13 weeks until 21 January 1995, when they were transplanted into 10-cm containers and placed into the different treatments. Plants growing in 5.5 cm pots (190 ml pot volume) were received on 17 January 1995, transplanted into 2.2-liter containers, and placed into the different greenhouses on 4 February 1995. Ten plants of each size were placed into each of five greenhouses set to 15C, 18C, 21C, 24C, and 27C. Plants received natural daylengths with a 4-hr NI, 2200 to 0200, provided by HPS lamps which delivered approximately 90 μmol $m^{-2}s^{-1}$.

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

Data analysis. Date of the first visible bud (when infloresence was approximately 2 mm long) and date of opening of the first flower were recorded for each plant, and days to visible bud and flowering were calculated. At the time of opening of the first flower, total plant height, number of additional visible infloresences, and number of nodes on the main stem were determined. Base temperature (T_b) and thermal time, or

degree-days, were calculated using equations presented by Roberts and Summerfield (1987). The average time to visible bud or flower within each treatment was converted to a rate by taking the reciprocal, and the relationship between the rate of progress to visible bud or flowering ($1/f$) and the mean temperature T in °C was determined:

$$\frac{1}{f} = b_0 + b_1 \overline{T} \qquad [1]$$

where b_0 and b_1 are constants. Once b_0 and b_1 had been calculated, the base temperature, T_b, was calculated as:

$$T_b = -\frac{b_0}{b_1} \qquad [2]$$

and thermal time, or degree-days was determined by:

$$^{\circ}Cd = \frac{1}{b_1} \qquad [3]$$

Results

Experiment 1 - Cold treatments and photoperiod. Flowering percentage in the 8-to 11-node plants from 128-cell trays did not reach 100 in any treatment (Figure 1). Increasing durations of cold treatment were associated with an increase in flowering percentage in plants from both 128-cell and 50-cell trays. Flowering percentage for both plant sizes tested was greater under NI than SD.

Time to VB and to FLW generally decreased with increasing durations of cold treatment (Figure 1). Plants under NI generally reached FLW 3 to 7 days before those under SD.

The 128-cell plants that flowered produced 1 to 2 infloresences in all treatments (Figure 2). Infloresence number in the 50-cell plants cooled for 15 weeks was increased under NI compared to those plants forced under SD.

The final node number and height in 128-cell plants under NI were similar whether plants were cooled for 10 or 15 weeks (Figure 2). Final node number and height in 50-cell plants generally decreased as duration of cold treatment increased.

Experiment 2 - Forcing temperatures. Actual average daily air temperatures during forcing are presented in Table 1. Plants generally flowered more quickly at higher temperatures (Figure 3). Time to flower at ≈16C averaged approximately 69 days, and at ≈26C, 41 days.

The 128-cell plants flowered 5 to 10 days later than 50-cell plants, and plants from 50-cell trays flowered 5 to 10 days later than plants from 5.5-cm pots, under all forcing temperatures.

All plants flowered in all treatments except for plants at ≈26C, where only 40% of plants flowered and 128-cell plants at 23C, where 70% flowered. Since flowering was adversely affected in those treatments, and Eqs. [2] and [3] are only valid for temperatures below the optimum or ceiling temperature, visible bud and flowering data for those plants were not included in the calculations. Rates of progress to visible bud and flowering were linear between 16C and 21C for 128-cell plants, and

between 16C and 23C for 50-cell and 5.5-cm plants (Figure 3). The T_b for forcing to visible bud stage were between 7.1C and 10.7C, and for forcing to flower, between 4.7 and 5.6C (Table 2). Slopes of regression lines for the 3 plant sizes were not significantly different from each other within each developmental stage (Table 3), indicating that the °days required for each stage were the same for all plant sizes tested.

The average number of infloresences per plant increased as initial plant size increased and forcing temperatures decreased (Figure 4). Final plant height in 128-cell, 50-cell, and 5.5-cm plants was 5, 6, and 12 cm greater respectively when forced at ≈15C than when forced at ≈26C. The 5.5-cm plants had been cut back before shipping, resulting in a final plant height below that of the 50-cell plants.

Discussion. Preliminary experiments had suggested that plant size influences the flowering response of *L. angustifolia* 'Munstead'. The results of these experiments also indicate that 128-cell plants with 8 to 11 nodes required a longer cold treatment to induce flowering than 50-cell plants with 18 to 23 nodes. Flowering percentage did not reach 100% for the 128-cell plants in any treatment.

Many biennials and perennials must attain a certain size before they are capable of floral induction. Juvenility is defined as an early developmental phase during which a plant is insensitive to conditions that later promote flower initiation (Bernier et al., 1981). A juvenile phase has been described in several herbaceous perennials including some cultivars of *Aquilegia* x *hybrida*. To obtain 100 percent flowering in 'McKana's Giant' plants, at least 12 leaves and 10 weeks of storage at 4.5C were required while

for 'Fairyland,' 15 leaves and only four weeks of cold storage were required. (Shedron and Weiler, 1982). For maximum flowering in *Heuchera sanguinea*, plants should have approximately 19 nodes before cold storage (Yuan,1995). A juvenile phase appears to exist in *L. angustifolia* 'Munstead', but its duration can not be determined from these experiments.

Exposure to a period of low temperatures is a primary factor influencing flowering in *L.angustifolia* 'Munstead'. Flowering percentage, time to flower, number of infloresences, number of nodes present at flowering, and total plant height all were influenced by cold treatments.

Exposure to low temperature can influence flowering of herbaceous perennials in several different ways. Cold temperatures promote flowering in many plants by breaking the dormancy of existing buds. Floral primordia of *Paeonia* are initiated after anthesis of the current year's flowers and require a minimum of four weeks at 5.6C to break dormancy (Byrne and Halevy, 1986). Flower induction, initiation, and development occur during exposure to low temperatures in some species. Floral bud initiation and development occurred in *Astilbe* during storage at 2C (Pemberton, 1992) and in *Dicentra spectabilis* during storage at 5 and 10C (Hanchek,1989).

In many species, exposure to low temperatures induces the subsequent initiation and development of floral primordia. Vernalization is generally defined as a cold treatment that induces or hastens the capacity for flowering in a plant (Chouard, 1960). Floral primordia are not initiated until after the return of warmer temperatures.

We observed vegetative growth from the apical meristem on uncooled

L.angustifolia 'Munstead' plants that did not flower. Since the infloresence of this plant is a terminal infloresence, it is unlikely that flower buds were present prior to cold treatments. While low temperatures clearly influence flowering of *L.angustifolia* 'Munstead', we did not determine in these experiments whether initiation occurs during or after cold treatments.

When 50-cell plants were cooled for 10 or 15 weeks, flowering percentages in plants forced under SD were 60% and 100%, respectively. Extended exposure to 5C apparently eliminated any photoperiodic requirement for flowering of *L.angustifolia* 'Munstead'. A similar response has been found in a number of herbaceous perennials, including *Iris* (Buxton and Mohr, 1969), *Dicentra spectabilis* (Lopes and Weiler, 1977), *Echinops* 'Taplow Blue,' *Achillea millefolium* 'Rosea,' and *Physostegia virginiana* 'Summer Snow' (Iversen, 1989), and *Chrysanthemum* x *superbum* Bergmans (Shedron, 1980).

Forcing temperatures have a significant effect on rates of development in all plants. At temperatures below a certain species-specific value, no growth will occur, and at temperatures above optimum, development is delayed or ceases. Optimum temperature ranges vary within species and between species, and are related to climatic origin (Roberts and Summerfield, 1987). The T_b calculated for *Hibiscus rosa-sinensis* was 9.8C (Karlsson et al., 1991), minimum temperature for leaf growth of *Saintpaulia ionantha* was 8C (Faust and Heins, 1993), and T_b was ≈8.5C in three cultivars of *Phaseolus vulgaris* (Roberts and Summerfield, 1987). *H. rosa-sinensis, S. ionantha,* and *P. vulgaris* are all native to tropical or sub-tropical climates. The base temperature

was estimated to be approximately 1.12C in *Lilium longiflorum* (Karlsson et al., 1988), a species native to temperate climates. Calculated base temperatures for *L.angustifolia* 'Munstead' for forcing to the visible bud stage were 7.1 to 10.7C, and for forcing to flower, 4.7 to 5.6C. These values reflect the moderate Mediterranean climate in the regions where *L. angustifolia* is native. Slopes of regression lines for the 3 plant sizes were not significantly different from each other within each developmental stage, indicating that different plant sizes responded similarly to forcing temperatures (Table 3). Intercepts of regression lines were significantly different in some comparisons, reflecting the fact that the plants were at different physiological stages at the start of forcing.

To complete a developmental process in a plant, the plant must experience a specific number of units of thermal time (°days) above the base temperature characteristic of that process (Roberts and Summerfield, 1987). Once the base temperature, and the amount of thermal time required for a developmental stage are known, predicted time for the developmental stage can be calculated. Thermal time is commonly used to schedule planting and harvest of fruit and vegetable crops (Roberts and Summerfield, 1987) and field crops such as maize (Tollenaar et al., 1979).

In *L. angustifolia*, degree days required for reaching the visible bud stage varied between 178 and 357, and for flowering, 625 to 833 between 15C and 22C. The 128-cell plants required more thermal time than the 50-cell or 5.5-cm plants, because they were at a less advanced physiological starting point when forcing began. In order to calculate time to visible bud or flower at any temperature between T_b and T_{cc}, the

degree-days required for that developmental stage are divided by the degrees provided above the T_b. For example, time to flower in 50-cell plants forced at 18C (T_b = 5.4C) is 769°days/12.6° C ≈ 60 days.

In conclusion, recommendations for flowering *L. angustifolia* 'Munstead' in approximately 8 weeks include using initial plant material with more than 11 nodes. Plants with 18 to 23 nodes are adequate. For rapid uniform flowering, provide a minimum of 10 weeks of 5C. Flower number will be increased if the plants are subsequently forced under a 4-hr NI. To reach flowering in 8 weeks, forcing temperatures should be approximately 14 degrees above the T_b of 5C, or 19C (769°days/ 56 days = 14) Infloresence number decreased with higher forcing temperatures.

The 5.5-cm plants used in this experiment had been cut back before shipping, and we observed that their regrowth was compact, uniform, and attractive. Although not specifically tested in this work, observations suggest that pruning or pinching may be beneficial when forcing other sizes of *L. angustifolia* 'Munstead' as flowering plants.

LITERATURE CITED

Armitage, A. 1994. Spring into perennials. Greenhouse Grower 13:92-94.

Liberty Hyde Bailey Hortorium, 1976. Hortus Third. Macmillan, New York.

Ball, V. 1991. Perennials. p. 677-689 in Ball Red Book 15th edition, V. Ball, Ed., Ball Publishing, Chicago.

Bernier, G., Kinet, J., and R. Sachs. 1981. Age and flower initiation. p. 106-115 in The physiology of flowering, Vol.1. CRC Press, Boca Raton, FL.

Buxton, J. and H. Mohr. 1969. The effect of vernalization and photoperiod on flowering of tall bearded irises. HortScience 4:53-55.

Byrne, T. and H. Halevy. 1986. Forcing herbaceous peonies. J. Amer. Soc. Hort. Sci. 111:379-383.

Chouard, P. 1960. Vernalization and its relations to dormancy. Annu. Rev. Plant Physiol. 11: 191-238.

Faust, J. and R. Heins. 1993. Modeling leaf development of the African violet (*Saintpaulia ionantha* Wendl.) J. Amer. Soc. Hort. Sci. 118:747-751.

Hanchek, A. 1989. Growth and development of *Dicentra spectabilis* in relation to storage temperature and harvest date. PhD Diss. Michigan State Univ., East Lansing.

Heins, R. and J. Faust. 1994. Radiant cooling leads to cooler temperatures under black cloth. HortScience 29:503. (Abstr.)

Iversen, R. 1989. Greenhouse forcing of herbaceous garden perennials. PhD Diss. Cornell Univ., Ithaca.

Karlsson, M., Heins, R., and J. Erwin. 1988. Quantifying temperature-controlled leaf unfolding rates in 'Nellie White' Easter lily. J. Amer. Soc. Hort. Sci. 113:70-74.

Karlsson, M., Heins, R., Gerberick, J., and M. Hackmann. 1991. Temperature-driven leaf unfolding rate in *Hibiscus rosa-sinensis*. Scientia Hort. 45:323-331.

Laskey, M. 1991. Herbs. p. 577-581 in Ball Red Book 15th edition, V. Ball, Ed., Ball

Publishing, Chicago.

Lopes, L. and T. Weiler. 1977. Light and temperature effects on the growth and flowering of *Dicentra spectabilis* (L.) Lem. J. Amer. Soc. Hort. Sci. 102:388-390.

Pemberton, G. 1992. Factors affecting the growth and development of forced Dutch-grown *Astilbe*. MS Thesis, North Carolina State Univ., Raleigh.

Roberts, E. and R. Summerfield. 1987. Measurement and prediction of flowering in annual crops. p. 17-51. In: J.G. Atherton (ed.). Manipulation of flowering. Butterworth's, London.

Shedron, K. 1980. Regulation of growth and flowering of four herbaceous perennials: *Aquilegia* x *hybrida* Sims, *Aurinia saxatilis* (L.) Desv., *Chrysanthemum* x *superbum* Bergmans, and *Lupinus* spp. `Russell.' MS Thesis, Purdue Univ., Lafayette.

Shedron, K. and T. Weiler. 1982. Regulation of growth and flowering in *Aquilegia* x *hybrida* Sims. J. Amer. Soc. Hort. Sci. 107:878-882.

Snedecor, G. and W. Cochran. 1967. Statistical methods. 6th edition. The Iowa State Univ. Press, Ames.

Tollenaar, M., Daynard, T. and R. Hunter. 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Sci., 19:363-366.

Yuan, M. 1995. Effect of juvenility, temperature, and cultural practices on flowering of five herbaceous perennials. MS Thesis, Michigan State Univ., E. Lansing.

Table 1. Actual average daily air temperatures during the indicated developmental stage of *L. angustifolia* 'Munstead'.

Plant size	Force date	Set point temperature (C)	Forcing to visible bud (C)	Visible bud to flower (C)	Forcing to flower (C)
128-cell	21 Jan 1995	15.0	15.4	15.8	15.6
		18.0	18.5	19.1	18.7
		21.0	20.7	21.1	20.8
		24.0	22.9	23.1	23.0
		27.0	26.0	26.5	26.2
50-cell	22 Jan 1995	15.0	15.4	15.7	15.6
		18.0	18.2	19.0	18.7
		21.0	20.5	20.8	20.8
		24.0	22.6	23.0	22.8
		27.0	26.2	25.9	26.0
5.5 cm	4 Feb 1995	15.0	15.4	15.8	15.6
		18.0	18.4	19.1	18.8
		21.0	20.3	21.0	20.9
		24.0	22.7	23.1	22.9
		27.0	25.5	26.5	26.1

Table 2. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud and flowering in *L. angustifolia* 'Munstead'. Intercept and slope were used in Eqs. [2] and [3] to calculate base temperature (T_b) and degree-days, or thermal time (°days). Development was delayed in some plants in the highest temperature treatments, so data for 128-cell plants forced at 23 and 26.2C, and for 50-cell and 5.5-cm plants forced at 26C was not included in the calculations.

Plant size	Developmental stage (Days)	Intercept (b_0) 1/dev.stage	Slope (b_1) (1/dev.stage)/ °C	T_b (C)	°days	r^2
128-cell	forcing to visible bud	-0.0200 ±[z]0.0220	0.0028 ±0.0012	7.1	357	0.84NS[y]
(7-9 nodes)	visible bud to flower	0.0106 ±0.0033	0.0013 ±0.0002	-8.2	769	0.98NS
	forcing to flower	-0.0056 ±0.0053	0.0012 ±0.0003	4.7	833	0.94NS
50-cell	forcing to visible bud	-0.0599 ±0.0118	0.0056 ±0.0006	10.7	178	0.98*
(19-23 nodes)	visible bud to flower	0.0106 ±0.0018	0.0011 ±0.0001	-9.6	909	0.99**
	forcing to flower	-0.0070 ±0.0024	0.0013 ±0.0001	5.4	769	0.98**
5.5 cm	forcing to visible bud	-0.0485 ±0.0260	0.0056 ±0.0013	8.7	178	0.90NS
	visible bud to flower	-0.0121 ±0.0139	0.0025 ±0.0007	4.8	400	0.86NS
	forcing to flower	-0.0089 ±0.0061	0.0016 ±0.0003	5.6	625	0.93*

[z] Standard error

[y] NS, *, **, not significant, significant at $P<0.05$, and 0.01, respectively.

Table 3. Influence of forcing temperature on time to flower in *Lavandula angustifolia* 'Munstead'. Comparison of regression lines within each developmental stage, between the 3 plant sizes tested, followed procedures described by Snedecor and Cochran (1967).

Rate to visible bud	128 vs 50-cell	slopes	F = 5.5276 (df = 1,3)	NS
		intercepts	F = 9.4234 (df = 1,4)	*
	128 vs 5.5-cm	slopes	F = 1.8564 (df = 1,3)	NS
		intercepts	F = 19.649 (df = 1,4)	*
	50-cell vs 5.5-cm	slopes	F = 0.0000 (df = 1,4)	NS
		intercepts	F = 10.4373 (df = 1,5)	*
Rate visible bud to flower	128 vs 50-cell	slopes	F = 0.8220 (df = 1,3)	NS
		intercepts	F = 52.838 (df = 1,4)	**
	128 vs 5.5-cm	slopes	F = 1.5209 (df = 1,3)	NS
		intercepts	F = 0.0537 (df = 1,4)	NS
	50-cell vs 5.5-cm	slopes	F = 3.8447 (df = 1,4)	NS
		intercepts	F = 3.7091 (df = 1,5)	NS
Rate to flower	128 vs 50-cell	slopes	F = 0.4327 (df = 1,3)	NS
		intercepts	F = 10.445 (df = 1,4)	*
	128 vs 5.5-cm	slopes	F = 0.8185 (df = 1,3)	NS
		intercepts	F = 19.167 (df = 1,4)	*
	50-cell vs 5.5-cm	slopes	F = 0.6437 (df = 1,4)	NS
		intercepts	F = 14.688 (df = 1,5)	*

[z] NS, *, not significant, significant at $P<0.005$, respectively.

Figure 1. Influence of cold treatments on flowering of *L. angustifolia* 'Munstead'. (A) and (B) show flowering percentage for 128-cell and 50-cell plants, respectively. (C) and (D) show time to visible bud and flower for 128-cell and 50-cell plants, respectively. Error bars represent standard error of the means.

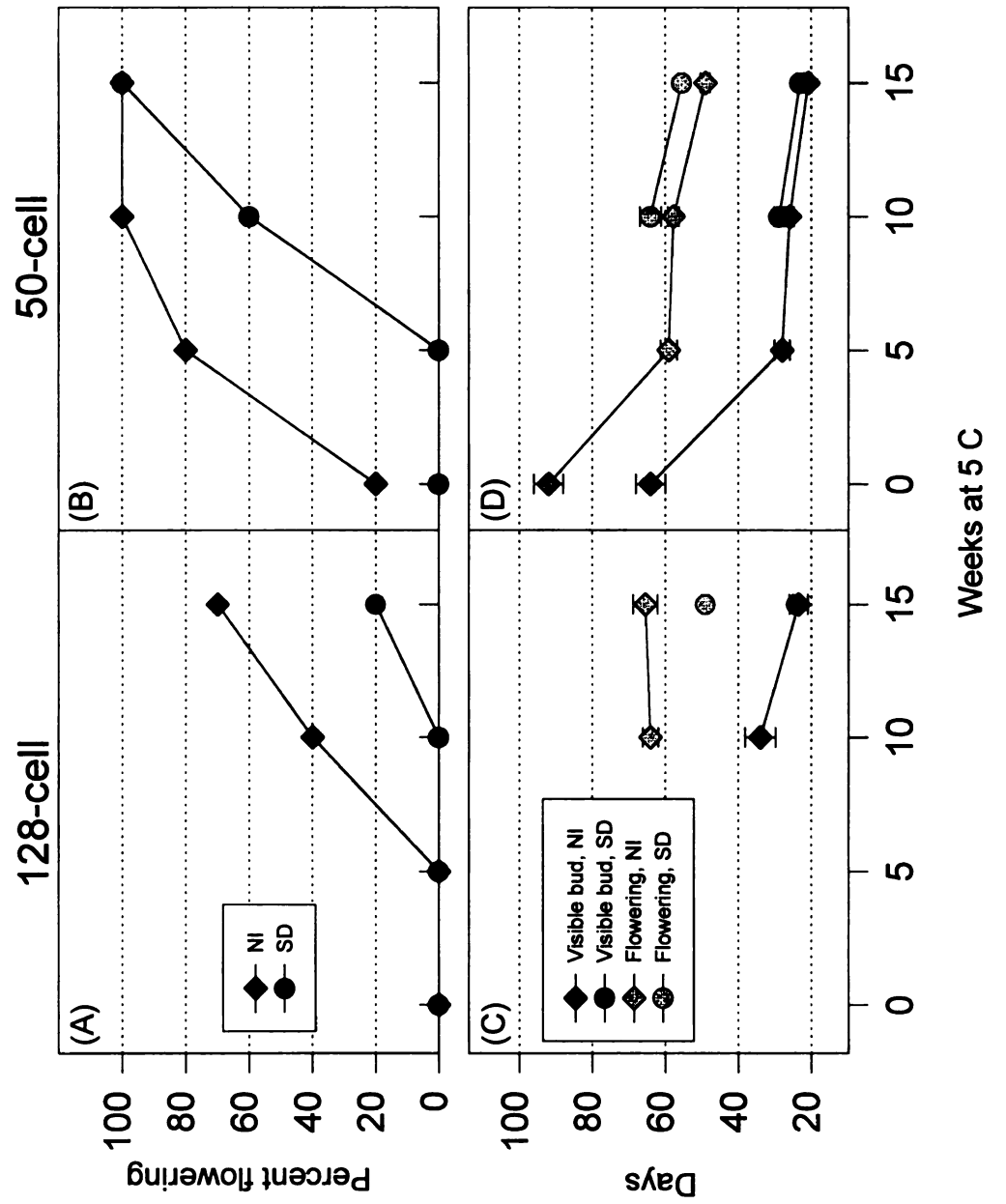

128-cell
50-cell
(A)
(B)
(C)
(D)
NI
SD
Visible bud, NI
Visible bud, SD
Flowering, NI
Flowering, SD
Percent flowering
Days
Weeks at 5 C
0
20
40
60
80
100
0
5
10
15

Figure 2. Influence of cold treatments on flowering of *L. angustifolia* 'Munstead'. (A) and (B) represent number of infloresences visible per plant at the time of first flower opening for 128-cell and 50-cell plants respectively. (C) and (D) show number of nodes present on the main stem at flowering for 128-cell and 50-cell plants respectively. (E) and (F) are total plant height at flowering for 128-cell and 50-cell plants respectively. Error bars represent standard error of the means.

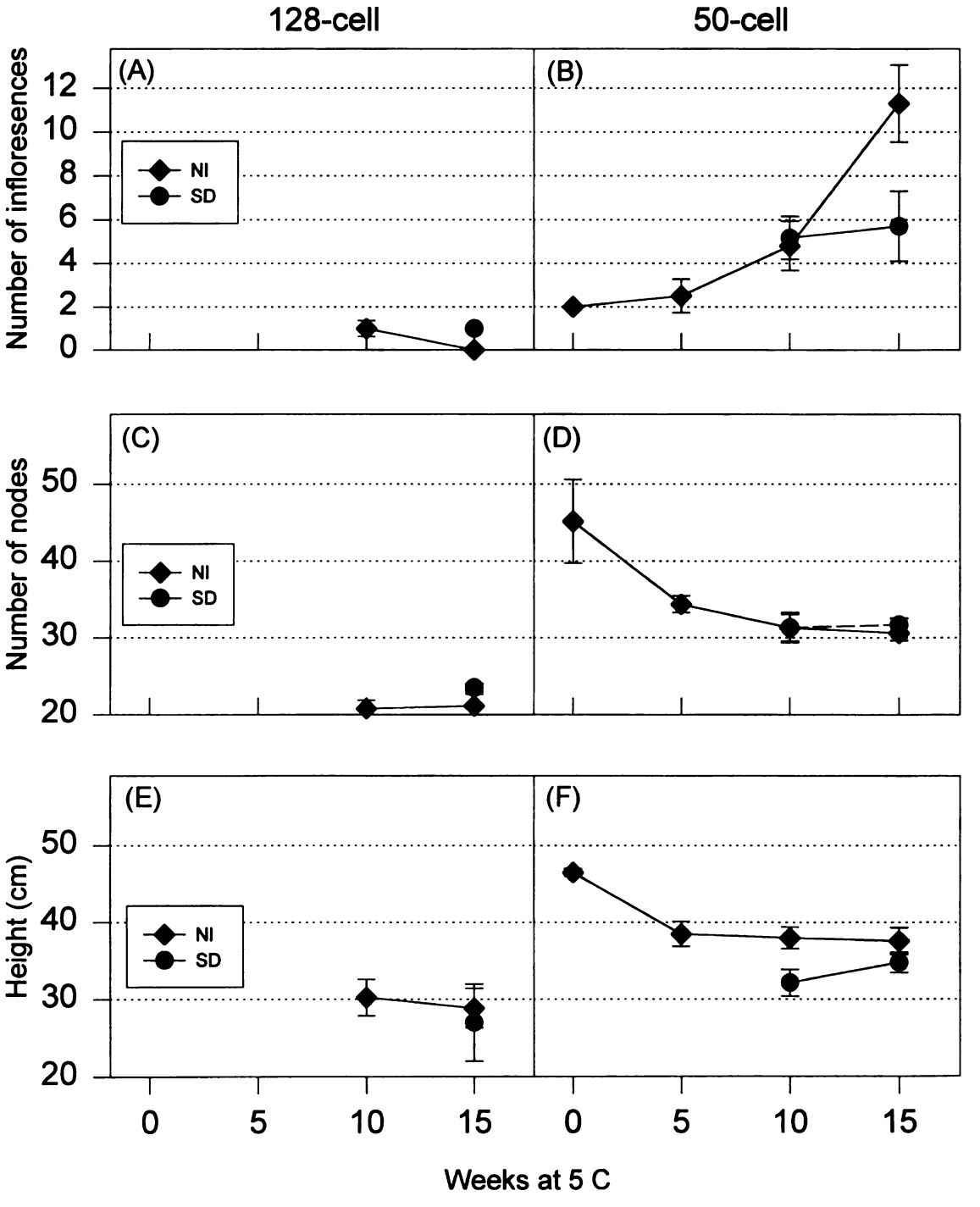

128-cell
50-cell
(A)
(B)
(C)
(D)
(E)
(F)
NI
SD
Number of inflorescences
Number of nodes
Height (cm)
0
2
4
6
8
10
12
20
30
40
50
0
5
10
15
Weeks at 5 C

Figure 3. Influence of forcing temperature on flowering of *L. angustifolia* 'Munstead'. Each symbol (▲, ●, or ■) represents the mean of 10 plants except for the 24-setpoint and 27-setpoint treatments of 128-cell plugs. Seven and four plants flowered in those treatments, respectively. Open symbols represent data not included in regression analysis. (A), (B), and (C) show days for the indicated developmental stage. For (D), (E), (F), solid lines (—) represent predicted values for the rate of progress to the indicated developmental stage, based on linear regression. Statistical analysis and calculations are presented in Table 2.

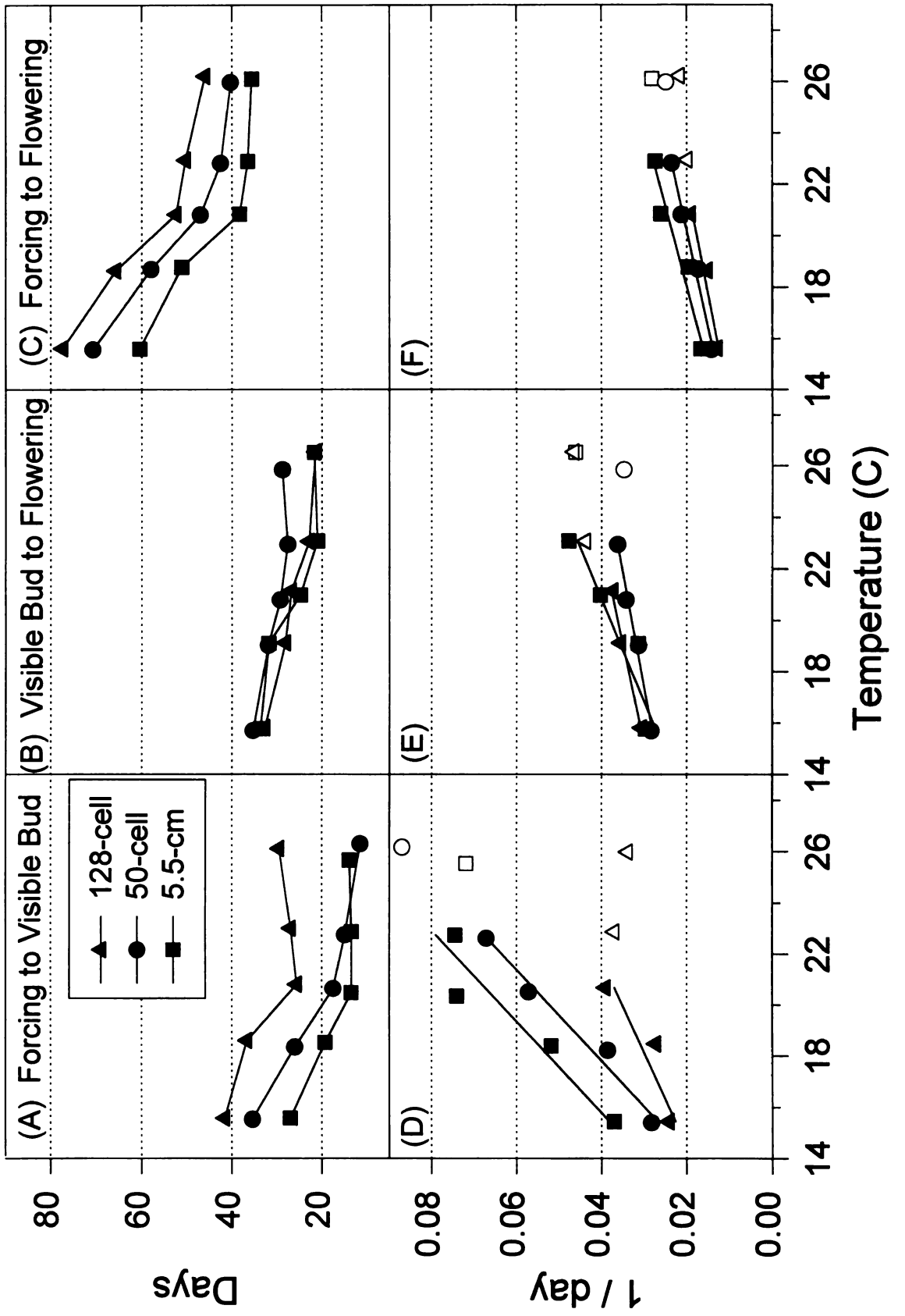
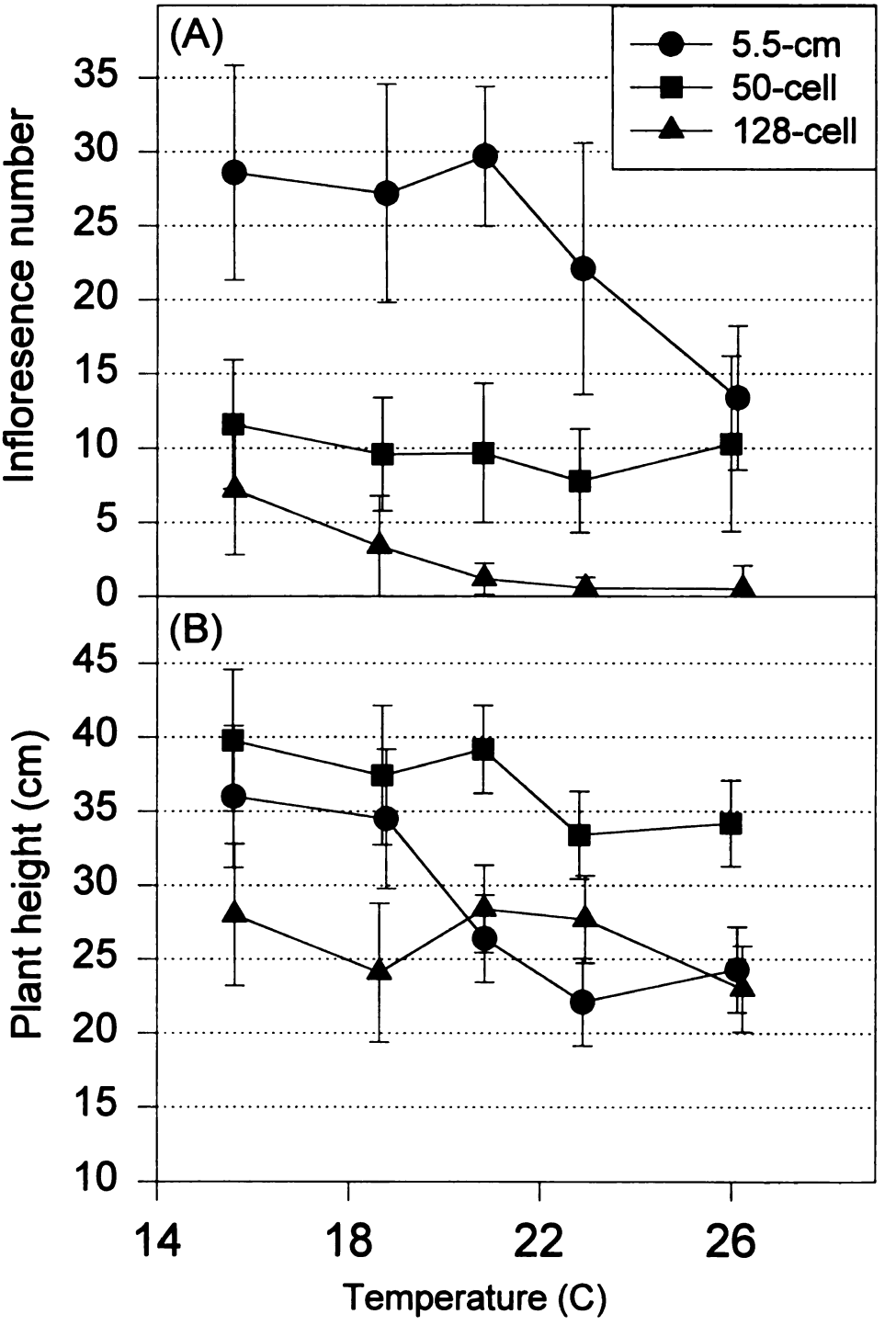

(A) Forcing to Visible Bud
(B) Visible Bud to Flowering
(C) Forcing to Flowering
(D)
(E)
(F)
128-cell
50-cell
5.5-cm
Days
1 / day
Temperature (C)
80
60
40
20
0.08
0.06
0.04
0.02
0.00
14
18
22
26

Figure 4. Influence of forcing temperature on (A) number of flower buds and (B) total plant height in *L. angustifolia* 'Munstead'. Each symbol (●,■, or▲) represents the mean of 10 plants, except in the 24-setpoint and 27-setpoint treatments for 128-cell plugs, where the symbols represent the mean of 7 and 4 plants, respectively. Error bars represent 95% confidence intervals.


(A)
5.5-cm
50-cell
128-cell
Inflorescence number
35
30
25
20
15
10
5
0
(B)
Plant height (cm)
45
40
35
30
25
20
15
10
14
18
22
26
Temperature (C)