This is to certify that the

thesis entitled

Effect of Juvenility, Temperature and Cultural Practices on Flowering of Coreopsis, Gaillardia, Heuchera, Leucanthemum and Rudbeckia

presented by

Mei Yuan

has been accepted towards fulfillment
of the requirements for

M.S degree in Horticulture

William H. Carlson

Major professor

Date 11/16/1995

[redacted]

EFFECT OF JUVENILITY, TEMPERATURE AND CULTURAL PRACTICES ON FLOWERING OF *COREOPSIS*, *GAILLARDIA*, *HEUCHERA*, *LEUCANTHEMUM* AND *RUDBECKIA*

By

Mei Yuan

A THESIS

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

MASTER OF SCIENCE

Department of Horticulture

1995

ABSTRACT

EFFECT OF JUVENILITY, TEMPERATURE AND CULTURAL PRACTICES ON FLOWERING OF *COREOPSIS*, *GAILLARDIA*, *HEUCHERA*, *LEUCANTHEMUM* AND *RUDBECKIA*

By

Mei Yuan

Most plants have a post-germination juvenile phase in which they are insensitive to flower induction conditions. The juvenile phases of *Coreopsis* x *grandiflora* 'Sunray', *Gaillardia grandiflora* 'Goblin', *Heuchera sanguinea* 'Bressingham' and *Rudbeckia fulgida* 'Goldsturm' were decided by exposing plants to cold treatments at 5C with node numbers varying from 0 to 20. After 0, 10, or 15 weeks cold treatment, plants were grown at 20C under LD or SD. Based on flowering percentage and time to flower, the juvenile phase of *Coreopsis*, *Gaillardia*, *Heuchera,* and *Rudbeckia* ended when plants had about 8, 16, 19, and 10 nodes, respectively. Scheduling plants to flower on specific dates requires a knowledge of the relationship between temperature and time to flower. *Coreopsis, Gaillardia, Leucanthemum* x *superbum* and *Rudbeckia* were forced under 15, 18, 21, 24, or 27C after cold treatments. The linear relationship between temperature and rate of progress toward flowering was determined for each species. Base temperatures and degree-days of each developmental stage were calculated. For *Coreopsis, Leucanthemum* and *Rudbeckia,* flower size, flower bud number, and plant height decreased as temperature increased from 15 to 27C. Plant size and three-week's growth before cold period influenced time to FLW and final plant quality.

DEDICATION

To my parents *Shuzhi Yuan* and *Qiou Ouyang*, for their love and trust.

To my brother *Yi Yuan*, for his inspiration.

ACKNOWLEDGMENTS

I want to express my sincere thanks to my major professor, Dr. William H. Carlson, for giving me this great opportunity to work with him, and for his patience and support. The guidance, advice and support of Dr. Royal Heins is greatly appreciated. I can hardly complete this project without his help. Thanks to other members of my committee, Dr. Arthur Cameron and Dr. Jan Zeevaart, for their time and advice.

Thanks to all my friends and colleagues and other individuals who have helped me in many different ways. Their friendship, encourage and assistance are deeply appreciated.

Very special thanks to my dear husband, Wei Song, for his support, both moral and practical, throughout the period of my study and thesis writing.

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Introduction

Many plant species will not flower after germination until they reach a certain size or age. Among species in which flower initiation is regulated by daylength, many are unable to respond to photoperiod at an early stage. For instance, SD (short day) plant *Perilla ocymoides* will not initiate flowers until it has formed at least three pairs of leaves (Zeevaart, 1958). Some species that require chilling for flowering cannot be vernalized until they have attained a certain minimum size (Wareing, 1987). 'New Dwarf' celery cannot be induced to flower before it has initiated 17 leaves, even when subjected to chilling at 5C for nine weeks (Ramin et al., 1991). The early developmental phase during which the plant is totally insensitive to conditions that later promote flower initiation is termed juvenility (Bernier et al., 1981). A juvenile phase in the plant is an evolutionary strategy where size is important for success, for instant, in the forest. A juvenile phase in the life cycle ensures maximum survival of the largest number of offspring (Schwabe, 1976). Plants therefore become reproductive at a later stage when they are able to produce viable seeds.

The transition from juvenile to adult phase is referred to as phase change. The term phase change is applicable when there are stable differences between the juvenile and adult phase that are maintained through vegetative propagation. Usually, phase changes are more distinct in woody species than in herbaceous species. Plants attain the ability to flower when the juvenile phase is complete and will form flowers if they are exposed to

the appropriate environment. The appearance of flowers and the end of the juvenile phase may not always coincide. The term 'ripe to flower' is used for plants that have completed the juvenile phase but have not experienced the appropriate conditions for flowering.

The phase change of many plants tends to be gradual (Zimmerman et al., 1985). For many photoperiodic herbaceous species, phase change is characterized by a period of increased sensitivity to daylength rather than a total inability to flower. In *Sinapis*, for example, the number of LD (long day) required for flower induction is six to seven at fifteen days from sowing, two at thirty days, and one at sixty days (Bernier et al., 1981). Other LD plants such as California poppy and *Coreopsis* 'Early Sunrise' also become more sensitive to inductive LD as they age (Lyons and Booze-Daniels, 1986). Although these plants do not have a true juvenile phase, they are usually called juvenile during their early growth period when they exhibit a poor photoperiodic response. In some extreme cases, plants are fully sensitive to inductive conditions at the cotyledon stage. *Chrysanthemum* x *superbum* 'Snow Lady' (LD plants) flowered fastest when transferred from SD to LD at the cotyledon stage compared to other plants transferred later, and they had the fewest number of stem leaves and total leaves at first flower (Damann and Lyons, 1995). The SD plants *Pharbitis nil* and *Chenopodium* have similar characteristics (Zeevaart, 1962b). These plants do not have a juvenile phase at all. On the other hand, some photoperiodic species exhibit a typical juvenile phase. According to Zeevaart (1962b), the long-short day plant *Bryophyllum* cannot respond to the change from LD to SD until they have at least ten to twelve pairs of leaves.

Many cold-requiring biennial or perennial species exhibit a juvenile phase and do not respond to chilling treatments at the seed stage or during germination. Atherton et al. (1990) showed that the juvenility of carrot cv. Chantenay Red Cored ended when the plant had initiated eight to twelve leaves. Plants with fewer than 7.5 leaves did not show a vernalization response. The juvenile phase of *Centaurea diffusa* (diffuse knapweed) ends at the formation of the thirteenth leaf (Thompson, 1991). *Lunaria biennis*, which is a typical biennial plant, shows a clear juvenile phase too (Wellensiek, 1957). But in this species seed vernalization increases the percentage of flowering in young plants when followed by a relatively short period of plant vernalization.

The juvenility period is also cultivar dependent. *Aquilegia* x *hybrida* 'McKana's Giant' transitions to adult phase when it has seven to twelve leaves, whereas 'Fairyland' or 'Crimson Star' loses its juvenility when it has twelve to fifteen leaves (Shedron and Weiler, 1982).

The duration of the juvenile phase is better described in terms of developmental stage rather than chronological age because juvenility may be reached more or less quickly depending on factors such as temperature, light intensity, or fertilizer. In herbaceous species, the number of leaves is often used as a measurement of the length of the juvenile phase. The concept of minimal leaf number was postulated to be the irreducible vegetative growth produced before flower initiation in plants held in optimal conditions for flowering from the very beginning of germination (Holdsworth, 1956). The original

concept was based on the idea that an apex would have to initiate a minimum number of leaf primordial before becoming capable of initiating floral organs (Schwabe, 1976). Efforts have been made to determine this number in some species, but it is difficult to be sure that the leaf numbers are really irreducible. Holdsworth (1956) showed that the lowest leaf number was obtained not only under optimal conditions for flowering, but also under extreme nutrient starvation. However, it is leaf number that shows the closest approximation to constancy; therefore, it is a good measurement of the physiological stage.

Characteristics of the juvenile and adult phase

Inability to flower is the most distinct characteristic of the juvenile phase. Attainment of the ability to flower indicates the end of the juvenile phase. The only practical way to identify the end of the juvenile phase is by the production of flowers. Plants that are ripe to flower but have not actually formed flowers because of environmental factors cannot be distinguished from those still in juvenile phase. Thus, first flowering is used as an indicator of the end of the juvenile phase. However, there are some exceptions. Seedlings of several conifer species can be readily induced to flower by exogenous application of GAs when they are only two to three months old (Zimmerman et al.,1985). But they will not continuously flower once the GA applications stopped. Apparently, they do not undergo a phase change. Based on this fact and other observations, Zimmerman (1985) suggested that one could only say the phase change occurred if a plant was induced to

flower and continued to flower in its natural environment without any artificial stimulation.

In addition to the difference in flowering behavior, the juvenile and adult phase may differ in other physiological characteristics such as rooting ability and cold resistance. Studies on the woody plants English ivy (Frydman and Wareing, 1973) and *Ficus pumila* (Davies, 1984) showed that cuttings from juvenile plants formed adventitious roots more rapidly and with more stability. The same results were obtained for poinsettias (Siraj, 1990), an herbaceous species.

Phase change in woody plants is frequently, but not always, accompanied by morphological changes such as leaf shape (heterophylly), phyllotaxy, pigmentation and thorniness. Morphological differences between the juvenile and adult phase are usually less distinct in herbaceous plants, but they do occur. Heterophylly and phyllotaxy differed in young and old poinsettia plants (Siraj et al., 1990). Younger plants produced predominantly elliptical or ovate leaves, while older plants generated a higher percentage of lobed leaves. However, no particular morphological character is associated with flowering ability. Thus, any changes observed do not necessarily indicate that the plant has undergone a phase change.

The differences between the juvenile and adult phase are associated with characteristics in the shoot apical meristem. Stein and Fosket (1969) showed that mature English ivy

apices had a larger meristematic area consisting of smaller cells than juvenile apices did. In contrast, the subapical region was larger in the juvenile shoot, and cell division continued longer, resulting in longer internodes. Hackett and Cordero (1987) found that the rates of initiation and emergence of leaves and nodes were very different in juvenile and adult ivy. Adult shoots produced leaves and nodes more rapidly than juvenile shoots. These results indicate that apical meristem activity is markedly different in the two phases.

Usually the apex gets larger as it ages. A gradual increase in the apex size with age is also demonstrated in grasses (Podolnyi, 1992). The apex of the *Abies alba* seedling is narrow and slightly protruding, while the adult tree has a wide flattened apex. In the LD plant *Lolium temulentum*, a relationship between the height of the apex and transition to flowering has been demonstrated (Evans, 1960). A drastic increase in the apex height indicates the beginning of the transition to adult phase.

Once the transition from juvenility to maturity has occurred, the adult phase is highly stable and cannot be reversed by common propagation methods (except sexual reproduction). Cuttings taken from juvenile ivy develop into juvenile plants, whereas those from the mature phase develop into mature plants. The characteristics of the mature phase are maintained through all subsequent cell divisions. Stem calluses originating from juvenile and mature sections of the ivy stem consistently develop different characteristics (Thomas and Vince-Prue, 1984).

Although the adult phase is quite stable, it is possible to restore juvenile characteristics under certain conditions. Rejuvenation, which implies a reversal of the maturation process (Hackett and Murray, 1992), has been demonstrated on many woody plants. Applying GAs to ivy induced morphological reversion of the mature form to the juvenile form (Rogler and Hackett, 1975). The effects of GA_3 increase as the dose increases from 0.1 ug/plant to 10 ug/plant. Individual characteristics show different sensitivity to GA_3. Doorenbos (1954) demonstrated that a juvenile stock of ivy caused an adult scion to lose the capacity to flower and show juvenile characteristics.

Similar results have been obtained on tree species. Repeatedly grafting shoot tips from an adult *Sequoia sempervirens* tree onto juvenile rootstocks in vitro results in gradual restoration of juvenile characteristics (Huang et al., 1992). Monteuuis (1991) successfully rejuvenated a 100-year-old *Sequoiadendron giganteum* through the culture of apical meristem removed during budbreak in vitro. The juvenile characteristics were maintained in vitro and in outdoor conditions. A gradual rejuvenation was obtained in grape when apices of the adult plant were subcultured repeatedly in vitro (Mullins et al., 1979).

Physiological and molecular basis of phase change

The mechanism of phase change is still unclear, but it is generally agreed that plant size is an important factor in phase change. In the biennial *Oenothera lanceolata*, bolting occurred only when rosette diameter was greater than 9 cm. Percent bolting increased with increasing rosette size (Kachi and Hirose, 1983). Black currant (*Ribes nigrum*)

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seedlings were unable to initiate flowers until they had attained a minimum stem height (Robinson and Wareing, 1969). The results indicated that the minimum stem height was about 100 cm and the percentage of plants that initiate flowers increased with average stem height.

Although many data suggest that the plant size is important, it is unclear what component of size has critical effects on phase change. One postulation is that plants transmit one or more signals to the apex, which determines the transition to maturity. A juvenile stock of ivy causes rejuvenation of the mature scion (Doorenbos, 1954), which indicates that juvenility in ivy may be influence by substances from the plant rather than the apex. However, when a juvenile scion of Japanese larch (*Larix leptolepis*) was grafted onto a mature bearing tree, only one out of fifty-six flowered (Robinson and Wareing, 1969). The result suggests that phase change is not determined by signals from the plant, but rather by events in the apex.

A number of observations suggest that 'root factors' play important roles in control of phase change. Schwabe and Al-Doori (1973) showed that juvenility of black currant shoots was associated with the proximity of the shoot tips to the roots. Adventitious roots were induced to form by air-layering at various positions on the shoots. None of the plants with adventitious roots initiated flowers, while all control plants flowered. Furthermore, shoot cuttings that were exposed to SD before being rooted flowered, and

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those that rooted before SD treatment never formed flowers. These results strongly support the view that roots, or signals from roots, inhibit the transition to maturity.

Other evidence supports the hypothesis that the apical meristem behaves independently and undergoes the phase change at a particular time. Tips of black currant were cut and rerooted (Robinson and Wareing, 1969). This process was repeated several times so that the plants never attained the minimum height for flower initiation. After three or four such decapitations, the plants flowered in response to SD, indicating that phase change is intrinsic to the apex and may occur after the apex has passed through a certain number of cell divisions.

The size of the apex is related to the transition to maturity. Flower initiation in *Chrysanthemum polaris* occurs in response to light intensity changes or temperature changes when the apex diameter is 0.26 mm (Horridge and Cockshull, 1979). Similar results have been obtained for *Amaranthus retroflexus* (Koller et al., 1977). These data support the view that transition can only occur after the apex reaches a certain size. On the other hand, growing the apices in vitro does result in gradual rejuvenation in some species, which may be due to the cessation of divisions in the apical meristem and a drastic decrease in cell number (Nozeran, 1984). Therefore, Podolnyi postulated (1992) that at the level of the apex, the phase change could be determined by the apex's size and number of cells in it. However, when ivy plants were induced to revert to the juvenile

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phase by GA_3 application, there was no significant reduction in the apical meristem size (Hackett and Srinivasani, 1983).

There is very little information on the physiological aspects of juvenility in herbaceous plants. One experiment showed that the tips of juvenile *Bryophyllum* were induced to flower by grafting to flowering donor stocks (Zeevaart, 1962b), indicating that inability to flower is due to the lack of a floral stimulus from the rest of the plant.

There is much evidence suggesting that GAs may be involved in phase change. But their roles are unclear, and data from different species conflict. Some researchers suggest that GAs from the roots prevent flowering in juvenile plants. Experiments with ivy (Wareing and Frydman, 1976) and black currant (Schwabe and Al-Doori, 1973) provide evidence. The adventitious roots of ivy have a high concentration of GAs, and removing the roots decreases the amount of GA-like substances in the shoot apices. But there are no convincing data indicating that GAs are synthesized in the roots and transported from the roots to the apex. Other parts of plants (like leaves) are also capable of synthesizing GAs (Crozier and Reid, 1971).

It has been shown that the leaves of *Bryophyllum* perceive the transfer from LD to SD. Applying GA_3 on the leaves of juvenile plants will induce flowering under SD (Metzger, 1987). This indicates that juvenility in *Bryophyllum* may result from their inability to biosynthesize GA following a transfer from LD to SD.

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In contrast with *Bryophyllum*, exogenous GA_3 causes reversion of many adult woody plants to the juvenile state; for example, ivy (Rogler and Hackett, 1975). A high GA level is necessary in ivy to maintain the juvenile phase. It appears that GAs play a different role in cases of *Bryophyllum* and ivy. Experiments with ivy demonstrate that phase change is a property of the apex, while in *Bryophyllum*, it is a property of the leaves. It is possible that one or more juvenile factors from the rest of the plant may have to be removed before phase change can occur. But the transition itself may require some additional factors intrinsic to the apex (Thomas and Vince-Prue, 1984).

The differences in the structure and growth rates between the juvenile and adult phase (Stein and Fosket, 1969; Hackett and Cordero, 1987) indicate that there are intrinsic differences in the meristem cells of the two phases. Thus Wareing (1987) postulates that phase change in woody plants is determined by these intrinsic differences in the meristem cells of juvenile and adult shoots and is epigenetic in nature. Epigenetic changes take place in response to inductive conditions and are reversible. They are not carried through meiosis (Wareing, 1987; Podolnyi, 1992).

It was suggested that the stable differences between meristematic cells of the juvenile and adult phase are related to gene expression. Out of 542 polypeptides found in *Chrysanthemum segetum* apex, only two were specific for the vegetative apex. After the transition, these two disappeared and four new ones appeared (Rembur and Nougarede,

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1989). Qualitative differences in RNA between juvenile and adult apices of ivy indicate that phase change may involve differences in the rate of transcription of specific genes (Thomas and Vince-Prue, 1984). Some DNA sequences transcription in the adult phase appears to be inactive in the juvenile phase.

Control of the duration of juvenile phase

The juvenile phase delays flowering. From a horticultural point of view, it is usually desirable to terminate the juvenile phase as soon as possible. Since plants attain maturity only after they have reached a certain size, raising plants under favorable conditions that accelerate growth will shorten the juvenile phase.

Light intensity and photoperiod are the primary techniques used to shorten the juvenile phase (Zimmerman, 1972). Higazy (1962) worked with several herbaceous species that required specific flower-inducing treatments. High light intensity increased early growth of the seedlings and reduced the duration of the juvenile phase, and the seedlings responded to flowering-induction at a younger age than normal.

Jonkers (1958) shortened the life cycle of strawberries by treating seeds with sulfuric acid to speed germination and applying inductive SD as soon as the seedlings became sensitive. Brussels sprouts are induced to flower by application of NAA (DeZeeuw and Leopold, 1955).

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species.

Temperature and fertilization, as well as some other methods such as grafting, girdling, pruning, etc., are used to control the juvenile phase. However, most research has been conducted with fruit and forest trees. There is very little information on herbaceous species.

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Section I

Determining the Duration of the Juvenile Phases of *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Heuchera sanguinea* (Engelm.) and *Rudbeckia fulgida* (Ait.)

Determining the Duration of the Juvenile Phases of *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Heuchera sanguinea* (Engelm.) and *Rudbeckia fulgida* (Ait.)

Mei Yuan [1], William H. Carlson [2], Royal D. Heins [3], and Arthur C. Cameron [4]

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

Received for publication _____. Accepted for publication _____. We acknowledge the financial support of the Agriculture Experiment Station of Michigan State University and greenhouse growers supportive of Michigan State University floriculture research.

[1] Graduate Assistant.

[2, 3, 4] Professor

Production and Culture

Determining the Duration of the Juvenile Phases of *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Heuchera sanguinea* (Engelm.) and *Rudbeckia fulgida* (Ait.)

Additional index words. Juvenility, maturity, phase change, vernalization, photoperiod, tickseed, blanket flower, coralbells, orange coneflower

Abstract. Most plants have a post-germination juvenile phase in which flower induction will not occur. Some species require a cold period for flower induction and will not respond to the cold treatments during the juvenile phase. The juvenile phases of *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin', *Heuchera sanguinea* 'Bressingham', and *Rudbeckia fulgida* 'Goldsturm' were characterized by exposing plants with node numbers varying from 0 to 20 to cold treatments at 5C. After 0, 10, or 15 weeks cold treatment, plants were grown at constant 20C under 4-h night interruption lighting (LD) or under a 9-h photoperiod (SD). Based on flowering percentage and time to flower, it was concluded that the juvenile phase of *Coreopsis*, *Gaillardia*, *Heuchera,* and *Rudbeckia* ended when they had about 8, 16, 19, and 10 nodes, respectively. Ten weeks cold treatment were required for flower induction of *Coreopsis*. Cold treatments were not required for flowering of *Gaillardia* and *Rudbeckia*, however, it improved flowering percentage and greatly accelerated flowering on *Gaillardia*. It accelerated flowering on *Rudbeckia* too. Increasing cold duration from 10 to 15 weeks did not influence time to flower on *Coreopsis, Gaillardia* and *Rudbeckia*, however, enhanced flowering percentage on *Coreopsis* and *Gaillardia*, and hastened flowering on *Heuchera*. *Heuchera* was a day neutral plant after ten weeks cold treatment, *Rudbeckia* was an obligate LDP, and *Gaillardia* and *Coreopsis* were quantitative LDP.

Introduction

The commercial production of herbaceous perennial plants, especially as flowering potted plants, has greatly increased in recent years (Schwarze,1993). Many species are forced from seed-propagated plugs because forcing seedlings is more cost effective than forcing field-grown plants. But the results of forcing seedlings are usually described as undependable due to lack of the knowledge of flowering requirements on many herbaceous perennials plants. Traditionally plants were sold green with color pictures and descriptive labels. However, plants in bloom are more attractive and desired by the consumers.

Flowering of seed-propagated herbaceous perennials requires the correct timing of cold or/and photoperiodic treatments. Many herbaceous perennials have a juvenile phase following germination. Exposing plants to inductive environmental conditions (e.g. cold or/and LD) before plants attain maturity will not induce flowering. The loss of juvenility in a population is a gradual process in herbaceous plants such as *Coreopsis* 'Early sunrise' (Damann and Lyons, 1993), *Gaillardia pulchella* and *Rudbeckia hirta* (Bourke, 1990). These plants flowered faster as they became older when they were exposed to inductive LD. Leaf (or node) number is usually used to measure plant age because it is more constant than other measurements such as time (Holdsworth, 1956). For many cold requiring species, a minimum leaf number is necessary before plants are full sensitive to a cold period. For instance, flowering percentage of *Aquilegia* x *hybrida* increased as leaf number increased (Shedron and Weiler, 1982). The duration of juvenile phase varies considerably among species and cultivars. Three cultivars of *Aquilegia* showed different duration of juvenile phases (Shedron and Weiler, 1982).

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Coreopsis grandiflora 'Sunray', *Gaillardia* x *grandiflora* 'Goblin' and *Rudbeckia fulgida* 'Goldsturm' belong to the Composite family (Asteraceae). They are all rosette plants and bolt before flowering. Ketellapper and Barbaro (1966) suggested that *Coreopsis grandiflora* 'Single Mayfield Giant' was a short-long-day plant. The SD could be replaced by vernalization and cold treatment was more effective than SD in inducing flowering. They also reported that the *C. grandiflora* had a juvenile phase during which the plants exhibited little sensitivity to inductive treatments. *Gaillardia* x *grandiflora* 'Goblin' is a hybrid of *G. aristat* and *G. pulchella* and was reported to be a quantitative LD plant which exhibited juvenility (Evans and Lyons, 1988). However, its juvenile phase was not determined. Chilling *G.* x *grandiflora* prior to LD enhanced flowering (Bourke, 1990). *Rudbeckia* plants are reported as LD plants (Tanimoto and Harada, 1985) and *R. hirta* are obligate LD plants that pass the juvenile phase when they have 19 leaves (Bourke, 1990). *Heuchera sanguinea 'Bressingham'* (Saxifragaceae) was a day neutral plant which required vernalization for flower initiation (Engle, 1994). *Heuchera* also showed a juvenile phase. Besides this information, there is no knowledge of the duration of the juvenile phases of these species.

The objectives of these experiments were to determine the duration of the juvenile phase of *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin', *Heuchera sanguinea* 'Bressingham' and *Rudbeckia fulgida* 'Goldsturm' and to verify their cold and photoperiodic requirements for flowering.

Materials and Methods

Year I. Seedlings of *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin', and *Rudbeckia fulgida* 'Goldsturm' in 128-cell (10 cm^3) trays were received from a commercial grower on Oct. 5, 1993. They were transplanted into 10-cm diameter (450 cm^3) round plastic pots on Oct. 7, 1993. A commercial growing medium containing composted pine bark, horticulture vermiculite, Canadian sphagnum peat moss, processed bark ash, and washed sand (Metro Mix 510, Scotts-Sierra Horticultural Products Company, Marysvill, Ohio) was used. Plants were grown in a glass greenhouse at a temperature setpoint at constant 24C under LD (natural day + 4-hr night interruption) until they were ready for cold treatments. Night interruption was provided by incandescent lamps at a photosynthetic photon flux (PPF) of 3 - 5 $\mu mol\ s^{-1}m^{-2}$. Plants were exposed to 5C for 0, 10 or 15 weeks at the following node counts: *Coreopsis:* 3, 6, 9, 12; *Gaillardia:* 5, 10, 15, 20; *Rudbeckia:* 4, 8, 12, 16 nodes. To determine the ontogeny prior to cold treatments, 15 plants were chosen randomly from each species. Node number on these plants was counted twice a week. A node was counted when the attached leaf was equal or longer than 1cm. Sample means of each species were calculated and used as an indicator to determine the average node number of each species. When the sample means were equal or very close to a designed node number, plants with the same (or closest) node count were chosen from the population and moved to coolers with a temperature setpoint at 5C. In the coolers, a 9-hr photoperiod was provided by cool-white fluorescent lamps (VHOF96T12; Philips, Bloomfield, N.J.) at PPF around 20 $\mu mol\ s^{-1}m^{-2}$. After cold treatments, plants were grown in a greenhouse at a temperature setpoint of constant 20C. Ten plants from each cold treatment were grown under LD (9-hr daylength + 4-hr night interruption provided by incandescent light) and ten under SD (9-hr daylength).

Dates of first visible flower bud (VB) and first flower reaching anthesis (FLW) were recorded for each plant. At the time of FLW, total leaf number on the main stem was recorded for *Coreopsis grandiflora* 'Sunray' and *Rudbeckia fulgida* 'Goldsturm'. Any plants that did not reach FLW or show VB at the end of a 20-week forcing period were considered as non-flowering plants.

One cooler malfunctioned on Mar. 8, 1994, resulting in a two-day high temperature period. Most *Rudbeckia* with 16 nodes died resulting in missing data of this treatment.

Year II. Seeds and seedlings of *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin' and *Rudbeckia fulgida* 'Goldsturm' in 128-cell (10 cm^3) trays were received from the same commercial grower on Sept. 5, 1994. Seeds had been sown in 338-cell trays and grown under natural photoperiodic condition. Seedlings of *Heuchera sanguinea* 'Bressingham' in 128-cell trays were received on Nov. 94. Upon arrival, seedlings of all species were transplanted into 11-cm diameter round pots (500 cm^3) and grown under 12-hr photoperiod at a temperature setpoint of constant 24C. Plants of each species were divided into groups for uniformity and each group was randomly assigned to one cold treatment. Plants were exposed to 5C for 10 or 15 weeks at the following stages: *Coreopsis*: cotyledon (0), 2, 4, 6, 8 and 10; *Heuchera*: 8, 12, 16 and 20; *Gaillardia*: cotyledon (0), 4, 8, 12, and 16; and *Rudbeckia:* cotyledon (0), 5, 10, 15 and 20 nodes. Fifteen plants of *Gaillardia* and *Rudbeckia* at each stage were forced without cold treatment. The same method as Year I was used to determine the average node number for cold treatments except that plants were randomly chosen within each group when they were ready for cold treatments. Node number of each plant was counted and recorded prior to cold treatments. The temperature and lighting set-up in the coolers were the same as Year I. Fifteen plants of *Coreopsis, Gaillardia* and *Rudbeckia* were forced under LD, *Heuchera* under both LD and SD at 20 C when cold treatments were

completed. During forcing period, supplemental light was provided by high pressure sodium (HIP) lamps when the ambient PPF at the greenhouse roof dropped below 200 $\mu mol\ s^{-1}m^{-2}$ and lights were turned off when PPF level was higher than 400 $\mu mol\ s^{-1}m^{-2}$.

Dates of VB and FLW were recorded. At time of FLW, unopened flower bud (or inflorescence for *Heuchera*) number and plant height were recorded for each plant. Total node number on the main stem was counted in *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin', and *Rudbeckia fulgida* 'Goldsturm'. Since *Heuchera* has tufted basal leaves with axillary inflorescences, it is very difficult to precisely count node number below the first inflorescence without destroying plants. Therefore, total node number was not collected on *Heuchera*. The forcing period for *Coreopsis, Gaillardia* and *Heuchera* was 15 weeks, and for *Rudbeckia,* 20 weeks.

The experimental design for both years were completely randomized designs. Data were analyzed using SAS (SAS Institute. Cary, NC) general linear models (PROC GLM) for analysis of variance and non-linear regression procedure (PROC NLIN) for regression models.

Results

***Coreopsis grandiflora* 'Sunray'** Year I. Ten or zero percent of all non-cold treated plants flowered under LD or SD, respectively (Table 1). Plants grown under LD after 10 or 15 weeks cold treatment flowered much faster (average 72 days) than those under SD (average 120 days) and at a higher flower percentage. Plants grown under SD had more total and new nodes (nodes formed during forcing after cold) than those under LD. New node number of plants under LD decreased as node count increased prior to cold treatments. Days to VB and FLW of plants under LD and plants with 15-week cold treatment under SD decreased as node number at start of cold treatments increased. Average days from VB to FLW were 3.5 days longer under SD than under LD. The effect of node number at the start of cold treatments on flowering percentage was inconsistent.

Year II. Days to VB and FLW decreased as the node number increased from 0 to 10 at the start of cold treatments (Fig. 1A). For example, plants receiving cold treatments at the six or eight nodes stage flowered 40 - 50 days faster than plants with less node count. New node number decreased while total node number increased when nodes count at the start of cold treatments increased (Table 2). Flowering percentage, unopened flower bud number, and plant height at time of FLW (Table 2) also increased with the increasing of node count at start of cold treatments. Highest flowering percentage occurred when plants received cold treatment at 8-node or older stage (Figure 1B).

The duration of cold treatments had no effect on days to VB and FLW, total and new node number, and plant height (Table 2). However, the plants with 15-week cold treatment had higher flower bud count (Table 2) and flowering percentage than the plants with 10-week cold treatment (Figure 1B). Days from VB to FLW was not affected by plant age or cold treatment duration (Table 2).

***Gaillardia* x *grandiflora* 'Goblin'** Year I. There is large variation on time to FLW under both LD and SD (Figure 2: A1-3, B1-3). For example, when plants were forced under LD after 10 or 15 weeks cold treatment, some flowered in about 40 - 70 days, others flowered over 100 days (Figure 2: A2-3). Generally, the average time to VB, from VB to FLW and to FLW was less for plants grown under LD. However, some 15 or 20-node plants flowered faster under SD. Days from VB to FLW were not influenced by node number at start of cold treatments or duration of cold treatments. After plants showed VB, they flowered in average 25 days under LD, which was 1 day faster in average than those under SD. A higher percent of plants grown under LD flowered than those grown under SD (Figure 2: A4, B4).

Year II. Ten or 15-week cold treatments accelerated flowering by about 55 days. Overall, cold treated plants flowered in only half the time of non - cold treated plants under LD (Figure 3A). Increasing cold duration from 10 to 15 weeks had no effect on days to FLW. Days to VB and FLW decreased with increasing node number at start of cold treatments (Figure 3A). The fastest flowering occurred when plants received cold or LD at 12 or 15 node stage. Non-cold treated plants flowered randomly. However, flowering percentage of cold-treated plants increased as node number at start of cold treatment increased (Figure 3B). Flowering percentage under LD reached 100% when plants had 15 or 12 nodes after 10 or 15 weeks cold treatments, respectively.

Cold treatments reduced the total and new node number on plants (Table 3). Non-cold treated plants had average 70 nodes, while plants with 10 or 15-week cold treatments had 36 or 37 nodes, respectively. Total node number increased with increasing node count at start of cold treatments, however new node number was not affected. Flower bud number increased as the cold duration and node count at start of cold treatment increased. Plant

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***Rudbeckia fulgida* 'Goldsturm'** In year I, no plants with 4, 8, or 12 nodes flowered when transferred to SD from LD regardless of cold treatments. Half of the 16 node plants flowered when they were transferred to SD without cold (data not shown). Under LD, cold treatments accelerated flowering and reduced total and new node number at time of FLW in both years but did not enhance flower percentage, flower buds or plant height (Table 4, 5). Combining the data of 0, 10 and 15-week cold treatments, the response of flowering percentage to node number at start of cold treatments was determined (Figure 4).

Days to VB and FLW decreased as node number at start of cold treatments increased in both years. Days from VB to FLW were not affected by node number at start of cold treatment in Year I but increased in Year II (Table 4, 5). Flower buds and plant height increased as the node number at start of treatments increased but were not affected by cold treatments (Table 5).

***Heuchera sanguinea* 'Bressingham'** Photoperiod did not influence days to VB or FLW, inflorescence number or flowering percentage, however, plants were slightly taller under LD (Table 6). Node number at start of cold treatments significantly affected days to VB and FLW, and days from VB to FLW, although the effects were random. Flowering percentage was positively related to node number at start of cold treatments (Figure 5). Increasing the cold period from ten to 15 weeks accelerated flowering about one week (Table 6). Time from VB to FLW was about 1.5 days longer for 15-week cold treated plants compared to 10-week cold treated plants. Plant height and inflorescence number increased with the increased cold duration and node number at start of cold treatments.

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Discussion

Juvenility is defined as an early age during which a plant will not response to flower inductive conditions (Bernier et al., 1981). According to this definition, *Coreopsis, Gaillardia* and *Rudbeckia* do not have a true juvenile phase because some plants having only cotyledons responded to inductive treatments and flowered. However, in all these species, plants showed a gradual increase in sensitivity to inductive conditions as they had more nodes. The flowering percentage increased as plants became older before they received cold or LD treatments. The early growth phase of herbaceous plants during which they are less sensitive to inductive condition is usually called juvenile phase (Bernier et al. 1981). For an individual plant, it is either juvenile or mature. However, within a population, some plants may be juvenile and some may be mature. As the average age (node number) of the population increased, more and more plants in the population will become mature until the node number reaches a point where all (or most) plants become mature. Since attaining maturity of a plant can only be demonstrated by flowering, the flowering percentage of a population is a good measurement to describe whether the population is juvenile or mature. In this paper, flowering percentage of a population will be used as the primary criteria to determine the end of juvenile phase of the four species.

In *C. grandiflora* 'Sunray', flowering percentage reached a maximum and new node number was at the lowest level when plants had about eight nodes or more. Time to anthesis decreased dramatically and number of flower buds increased at the same node range, suggesting plants became mature when they had about eight nodes. *G.* x *grandiflora* plants became fully sensitive to vernalization and reached 100% flowering when they had 12 to 16 nodes, indicating the end of juvenile phase (Figure 3B). In *Rudbeckia*, flowering percentage increased very rapidly with plant age and reached 99%

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when plants had ten nodes or more according to the regression relationship (Figure 4). Also, days to anthesis decreased about 60 to 70 days as node count at start of cold treatments increased from five to ten, but only about 20 days when node count increased from 10 to 20 (Table 5). This suggests that the juvenile phase of *R. fulgida* ends at the ten node stage. *Heuchera* plants with an average seven nodes did not respond to cold treatments and did not flower. (Engle, 1994). However, under the condition of the current experiment, about 50% of seven-node plants flowered (Figure 5). The flowering percentage increased gradually with plant age at the start of cold treatment and exceeded 95% when plants had about 19 nodes. It suggests the juvenile phase of *Heuchera sanguinea* ends when plants have about 19 nodes. Plant age at start of cold treatments influenced time to FLW in *Heuchera* (Table 6). However, the maximum difference in days to anthesis among treatments was no more than four days. From a horticultural point of view, plant age at the start of cold treatments can be considered as having no influence on time to FLW in *Heuchera.*

Chouard (1960) showed that some plants undergo a phase change during vernalization. When the required chilling time of five weeks at 5 C for *Geum urbanum* is extended for 10 to 15 weeks, more meristem are vernalized, especially those which are too young at the beginning of the cold treatment. We observed that *Coreopsis*, *Gaillardia, Heuchera* and *Rudbeckia* continued growing and formed some new nodes during cold treatment, but data were not collected. *Coreopsis* plants with only cotyledons formed true leaves and some seeds germinated at 5C. Increasing cold duration from 10 to 15 weeks enhanced flowering percentage in *Coreopsis* and *Gaillardia* (Figure 1B, 3B). It may indicate that some young plants underwent phase changes during extended cold period.

Cold treatments have different effects on flowering of these species. A cold period is required for flower initiation of *Coreopsis grandiflora* 'Sunray'. Few plants flowered

without cold treatments even after extended time under LD (Table 1). Cold periods enhanced the flowering percentage and greatly accelerated flowering in *Gaillardia. Rudbeckia* did not require a cold period to flower. However, cold hastened flowering and shortened time from VB to anthesis (Table 4, 5). Increasing the cold duration from 10 to 15 weeks resulted in more flower buds on *Coreopsis, Gaillardia* and *Heuchera*, but had no effect on *Rudbeckia.*

C. grandiflora 'Sunray', unlike the other cultivar 'Single Mayfield Giant', behaved as a quantitative LD plant with an obligated vernalization requirement for flower induction (Table 1). *G.* x *grandiflora* 'Goblin' also behaved as a quantitative LD plant (Figure 2). Under SD condition, not only time to anthesis, but also time from VB to anthesis were delayed on *Coreopsis* and *Gaillardia. H. Sanguinea* 'Bressingham' is a day neutral plant because photoperiod has no effect on time to flower or flowering percentage after cold treatments.

It has been shown in *Rudbeckia hirta*, *R. bicolor* and *R. speciosa*, that flower initiation can be induced only under LD, and that normal flower development will continue even if plants are transferred subsequently to SD condition. However, stem elongation ceases under SD (Harkess and Lyons, 1994; Tanimoto and Harada, 1985). Under the condition of the experiment in year I, some 16 - node *Rudbeckia* plants flowered when they were transferred to SD and the plants were quite short compared with those grown under continuous LD. It is most likely that those plants had already been induced under LD before transferred to SD. So we suggest that *R. fulgida* , like *R. hirta*, is an obligate LD plant.

Breeding and selection of herbaceous perennial plants has not progressed to the same level as many annual flower crops. Their flower initiation requirements usually vary

among cultivars and even among different seed lots (Schwarze, 1993). Shedron and Weiler (1982) showed that seedlings of *Chrysanthemum* (*Leucanthemum)* x *superbum* 'G. Marconi' varied greatly in cold and photoperiod requirements for flowering. The difference on time to flowering and flowering percentage between the two years in *Coreopsis* and *Gaillardia* may reflect such variation.

Based on the results in these experiments, the juvenile phases of *C. grandiflora* 'Sunray', *G.* x *grandiflora* 'Goblin'. *H. sanguinea* 'Bressingham' and *R. fulgida* 'Goldsturm' end when plants have about 8, 16, 19, or 10 nodes, respectively. Generally, older plants flower faster with fewer new nodes and more flower buds than younger plants. The exception is *Heuchera* which does not show distinct change on time to FLW.

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Table 1. Effect of node number at start of cold treatments, duration of cold treatments and photoperiod on flowering percentage, days to visible bud (VB) and anthesis (FLW), days from VB to FLW, total node and new node number at time of FLW in *Coreopsis grandiflora* 'Sunray' in year I.

Cold (weeks)	Node no. at start of cold trt.	Photoperiod	Flowering percentage	Node		Days		
				Total	New	VB	FLW	VB to Flw
0	3	LD	0	.	.	.	.	.
0	6	LD	20	44	32	150	172	22
0	9	LD	20	47	29	101	125	24
0	12	LD	0	.	.	.	.	.
10	3	LD	90	31	25	59	79	21
10	6	LD	90	30	18	40	61	21
10	9	LD	80	33	15	44	66	22
10	12	LD	50	41	17	37	72	22
	Statistic			L***,Q***	L***,Q***	L*	ns	ns
15	3	LD	90	31	25	58	82	23
15	6	LD	70	28	16	36	58	23
15	9	LD	80	38	20	45	71	23
15	12	LD	90	40	16	29	52	22
	Statistic			L***	L**	L**	L*	ns
0	3	SD	0	.	.	.	.	.
0	6	SD	0	.	.	.	.	.
0	9	SD	0	.	.	.	.	.
0	12	SD	0	.	.	.	.	.
10	3	SD	70	45	39	116	143	27
10	6	SD	60	41	29	98	121	29
10	9	SD	20	54	36	119	140	21
10	12	SD	20	.	.	116	149	22
	Statistic			ns	ns	Q*	Q*	ns
15	3	SD	70	41	35	95	120	25
15	6	SD	60	42	30	97	124	29
15	9	SD	90	54	36	88	113	26
15	12	SD	50	58	34	64	86	22
	Statistic			L***	ns	L**	L***,Q*	ns
		Significance						
		age (a)		***	***	***	***	ns
		chill (c)		**	**	***	***	ns
		photoperiod (p)		***	***	***	***	***
		a x c		ns	ns	**	**	ns
		a x p		ns	ns	ns	ns	*
		c x p		ns	ns	**	**	ns
		a x c x p		ns	ns	ns	ns	ns

NS, *, **, *** Nonsignificant or significant at P≤ 0.05, 0.01, or 0.001, respectively. L or Q indicate linear or quadratic trend.

Table 2: Effect of node number at start of cold treatments and duration of cold treatments on total and new node number, unopened flower bud number and plant height at the time of FLW, days from VB to FLW in *Coreopsis grandiflora* 'Sunray' in year II. Data represent plants forced under LD.

cold (weeks)	node no. at start of cold trt.	node number		unopened flower bud	plant height	days VB to FLW
		total	new			
10	0.0	9	9	17	43	24
10	2.2	11	9	13	44	26
10	4.7	17	12	0	30	20
10	5.9	13	7	12	56	23
10	8.2	17	9	23	52	24
10	9.7	17	8	24	47	24
15	0.0	12	12	16	41	26
15	2.3	14	12	12	37	23
15	4.4	14	9	17	40	22
15	5.7	14	8	23	48	23
15	7.9	16	8	33	50	23
15	9.6	17	8	36	53	23
Average	0.0	11	11	17	42	25
	2.2	14	12	12	38	23
	4.6	15	10	13	37	21
	5.8	14	8	21	49	23
	8.1	16	8	28	51	24
	9.7	17	8	31	50	23
	Statistic	L***	L***	L**	L***	ns
	Significance					
	node	***	***	*	***	ns
	cold	ns	ns	*	ns	ns
	node x cold	ns	ns	ns	ns	ns

NS, *, **, *** Nonsignificant or significant at P≤ 0.05, 0.01 or 0.001, respectively. L indicates linear trend.

Table 3. Effect of node number at start of cold treatments and duration of cold treatments on total and new node number, unopened flower bud number and plant height at the time of anthesis in *Gaillardia* x *grandiflora* 'Goblin' in year II. Data represent plants forced under LD.

cold (weeks)	node No. at start of cold trt.	node number		unopened flower buds	plant height	Days VB to FLW
		total	new			
0	0.0	77	77	1	28	25
0	4.5	70	65	8	31	26
0	8.2	68	59	10	34	28
0	12.8	70	57	6	33	26
0	14.6	72	58	6	26	27
Statistic		ns	ns	Q*	ns	ns
10	0.0	.	.	.	.	
10	5.0	29	24	9	38	24
10	8.5	34	24	10	35	24
10	11.4	34	22	14	36	22
10	15.4	40	25	16	40	25
Statistic		ns	ns	ns	ns	ns
15	4.6	24	20	17	34	20
15	8.7	37	28	14	36	28
15	12.5	36	24	30	34	24
15	15.2	40	25	28	36	25
Statistic		L**	ns	L*	ns	ns
	Significance					
	node	**	ns	***	ns	ns
	cold	***	***	***	ns	ns
	node x cold	ns	***	**	ns	ns

NS, *, **, *** Nonsignificant or significant at P≤ 0.05, 0.01, or 0.001, respectively. L or Q indicate linear or quadratic trend.

Table 4. Effect of node number at start of cold treatments and duration of cold treatments on flowering percentage, days to visible bud (VB) and anthesis (FLW), days from VB to FLW, total and new nodes at time of FLW in *Rudbeckia fulgida* 'Goldsturm' in year I. Data represent plants forced under LD.

cold	node No. at	Flowering	node number		Days		
(weeks)	start of cold trt.	percentage	Total	New	VB	Flw	VB to Flw
0	5.5	100	33	27	149	189	40
0	8.0	100	33	25	104	148	43
0	12.0	100	40	28	87	127	41
0	16.0	100	34	18	61	98	38
Statistic			Q*	L**,Q*	L***,Q**	L***,Q*	ns
10	4.0	100	34	30	126	160	34
10	8.0	100	34	26	99	137	38
10	12.0	90	34	22	80	112	32
10	16.0	100	38	22	61	93	33
Statistic			ns	ns	L***	L***	ns
15	4.0	70	33	29	127	160	33
15	8.0	100	28	20	88	123	36
15	12.0	100	29	17	53	85	31
Statistic			ns	L***	L***	L***	ns
	Significance						
	node		***	ns	***	***	ns
	cold		**	**	***	***	***
	node x cold		ns	ns	*	**	ns

NS, *, **, *** Nonsignificant or significant at P≤ 0.05, 0.01, or 0.001, respectively. L or Q indicate linear or quadratic trend.

Table 5. Effect of node number at start of cold treatments and duration of cold treatments on flowering percentage, total and new nodes, unopened flower buds and plant height at time of anthesis (FLW), days to visible bud (VB) and FLW, days from VB to FLW in *Rudbeckia fulgida* 'Goldsturm' in year II. Data represent plants forced under LD.

cold	node No. at	flowering	node number		unopened	plant	days		
(weeks)	start of cold trt.	percentage	total	new	flower buds	height	VB	FLW	VB to FLW
0	0.5	14	28	27	10	24	129	164	35
0	4.7	87	36	31	20	37	127	161	35
0	9.5	100	32	23	31	32	86	125	43
0	14.6	100	35	20	31	31	48	92	43
0	18.9	100	38	19	33	27	56	97	40
Statistic			L*	L***	L**	Q**	L***	L***	L**
10	4.7	85	29	24	22	35	129	159	31
10	9.8	100	25	15	16	30	61	97	36
10	14.7	100	30	15	38	30	40	78	38
10	19.5	100	39	20	45	29	38	74	36
Statistic			L***,Q***	L**,Q***	L***,Q***	ns	L***,Q***	L***,Q***	L***,Q**
15	4.9	82	30	25	31	46	126	156	30
15	9.8	100	24	14	30	26	53	88	35
15	14.3	100	26	12	27	27	42	77	35
15	19.4	93	37	18	34	35	34	69	34
Statistic			L***,Q***	L***,Q***	ns	L***,Q***	L***,Q***	L***,Q***	L**,Q**
	significance								
	node		***	***	***	***	***	***	***
	cold		***	***	ns	ns	***	***	***
	node x cold		**	**	***	***	***	***	ns

NS, *, **, *** Nonsignificant or significant at P≤ 0.05, 0.01, or 0.001, respectively. L or Q indicate linear or quadratic trend.

Table 6. Effect of node number at start of cold treatments, duration of cold treatments and photoperiod on days to visible bud (VB) and anthesis (FLW), days from VB to FLW, unopened flower buds and plant height at time of FLW in *Heuchera sanguinea* 'Bressingham'.

cold (weeks)	node No. at start of cold trt.	photoperiod	flowering percentage	days			inflorescence number	plant height (cm)
				VB	FLW	VB to FLW		
10	8.3	LD	53	24	37	13	0	36
10	7.7	SD	40	20	35	15	0	31
10	11.9	LD	60	22	37	15	0	39
10	11.5	SD	100	21	36	15	1	35
10	15.6	LD	93	19	36	16	1	43
10	15.5	SD	100	20	35	15	2	39
10	19.6	LD	100	20	36	16	2	42
10	19.8	SD	87	26	41	15	1	39
	Statistic			ns	ns	L***	L***	L***
15	7.8	LD	87	10	26	16	1	46
15	7.7	SD	40	15	30	15	1	31
15	10.9	LD	80	16	32	16	1	36
15	10.9	SD	67	15	32	17	2	36
15	15.8	LD	93	9	26	18	3	49
15	15.6	SD	100	11	28	18	2	42
15	19.6	LD	93	15	32	16	1	42
15	19.7	SD	100	12	29	16	2	47
	Statistic			ns	ns	Q**	ns	L**
		significance						
		node (n)		***	**	***	***	***
		cold (c)		***	***	***	***	***
		photoperiod (p)		ns	ns	ns	ns	***
		n x c		ns	ns	ns	ns	ns
		n x p		ns	ns	ns	ns	ns
		c x p		ns	ns	ns	ns	ns
		n x c x p		ns	ns	ns	ns	ns

NS, **, *** Nonsignificant or significant at P≤ 0.01, or 0.001, respectively. L or Q indicate linear or quadratic trend.

Figure 1. The effect of node number at start of cold treatments in *Coreopsis grandiflora* 'Sunray' in Year II on A) Days to visible bud (●) and days to anthesis (■). Vertical bars represent ±SE of means. B) Flowering percentage with 10 (●) or 15 (■) weeks cold treatments at 5C.

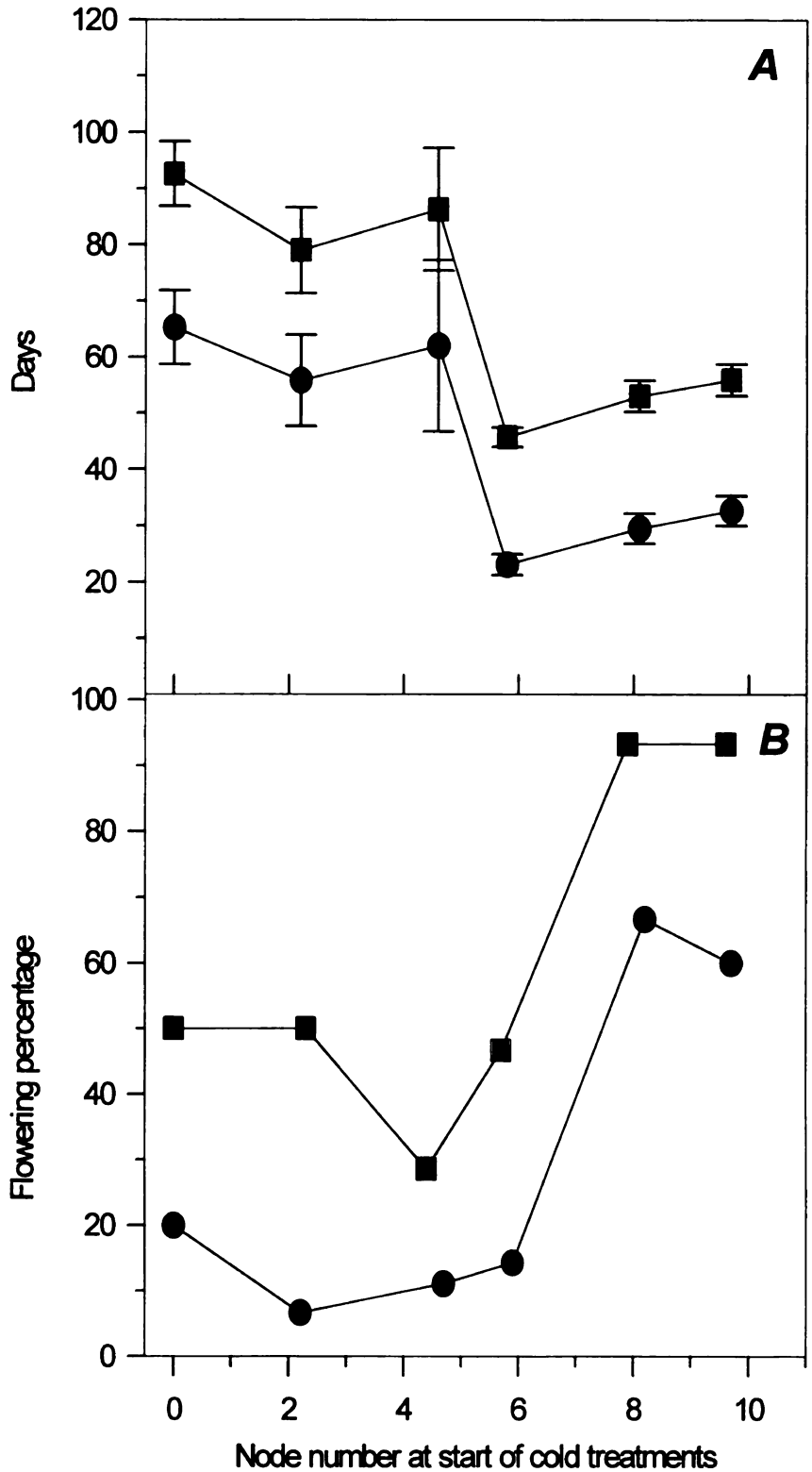

A
B
Days
Flowering percentage
Node number at start of cold treatments
120
100
80
60
40
20
0
2
4
6
8
10

Figure 2: The effect of node number at start of cold treatments and duration of cold treatments in *Gaillardia* x *grandiflora* 'Goblin' in year I on A1-4) Days to anthesis and flowering percentage under LD with 0 (O), 10 (□) or 15 (△) weeks cold treatment at 5C. B1-4) Days to anthesis and flowering percentage under SD with 0 (●), 10 (■) or 15 (▲) weeks cold treatment at 5C.

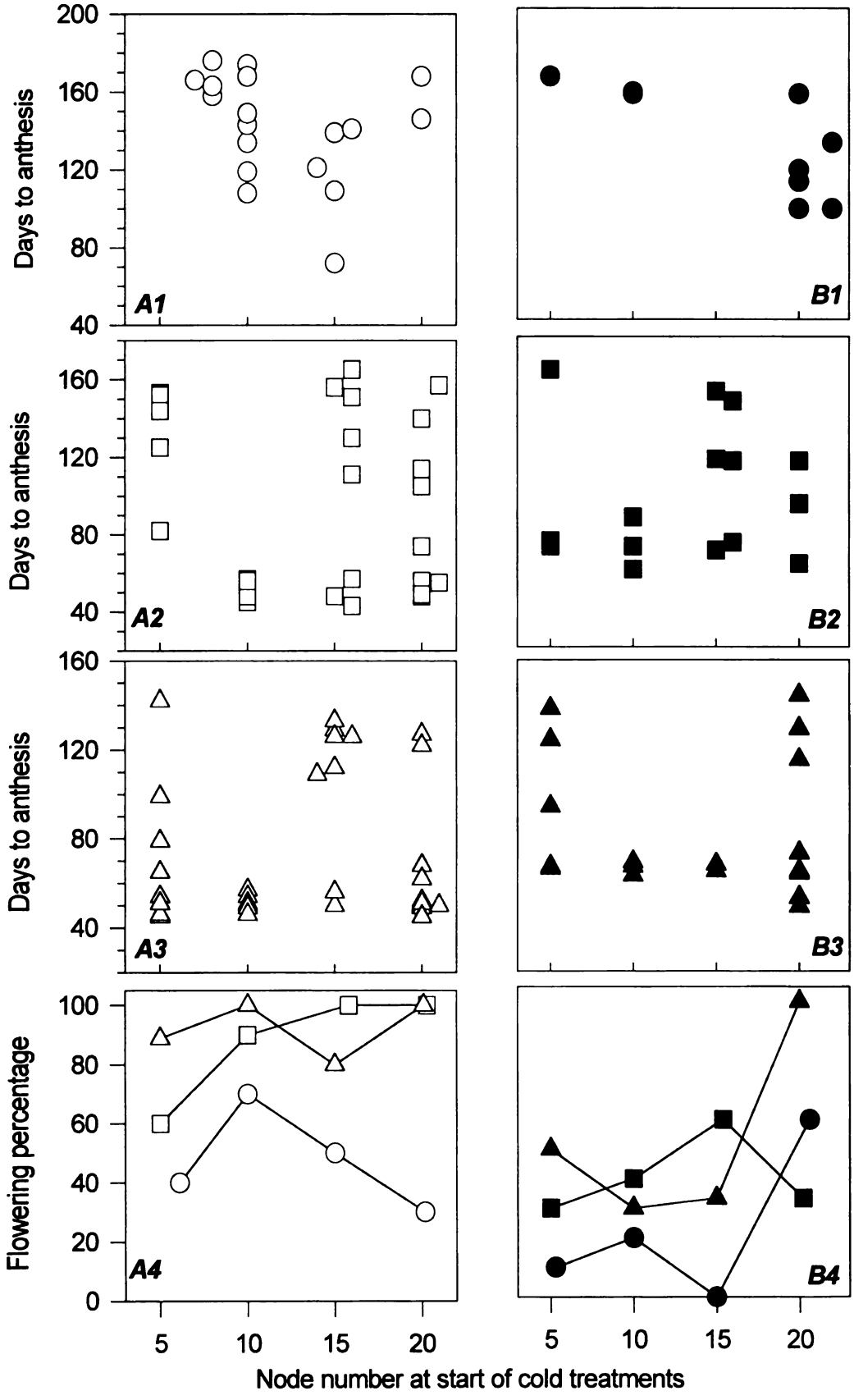

Days to anthesis
Days to anthesis
Days to anthesis
Flowering percentage
A1
B1
A2
B2
A3
B3
A4
B4
Node number at start of cold treatments

Figure 3: The effect of node number at start of cold treatments and duration of cold treatments in *Gaillardia* x *grandiflora* 'Goblin' in year II on A) Days to anthesis with 0 (●), 10 (■), or 15 (▲) weeks cold treatment at 5C. B) Flowering percentage with 0 (●), 10 (■) or 15 (▲) weeks cold treatment at 5C. Vertical bars represent ±SE of means.

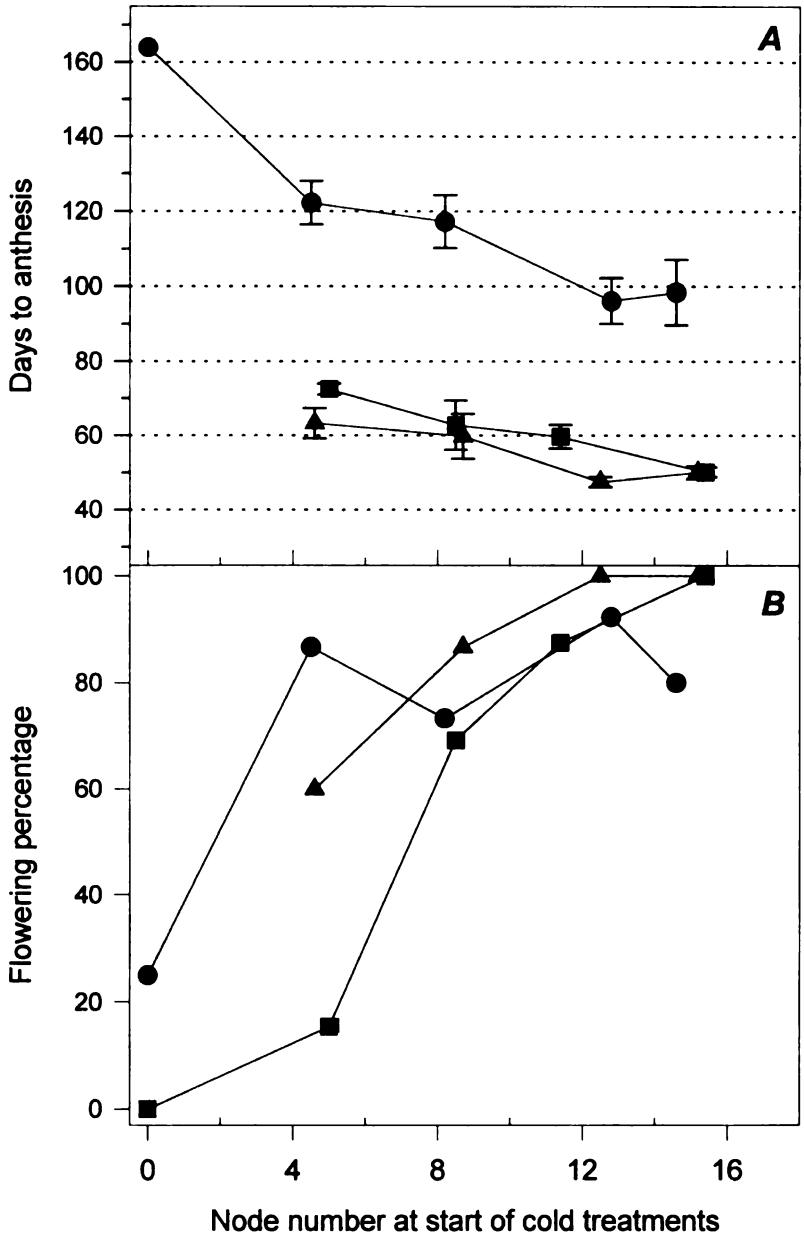

A
B
Days to anthesis
Flowering percentage
160
140
120
100
80
60
40
100
80
60
40
20
0
0
4
8
12
16
Node number at start of cold treatments

Figure 4: The effect of node number at start of cold treatments on flowering percentage (combined data of 0, 10, 15 weeks cold treatments of two years' data) in *Rudbeckia fulgida* 'Goldsturm'. The regression line is: $y = 1 - e^{-0.446x}$. $r^2 = 0.899$ which was calculated as $1 - SS_{residual} / SS_{corrected\ total}$.

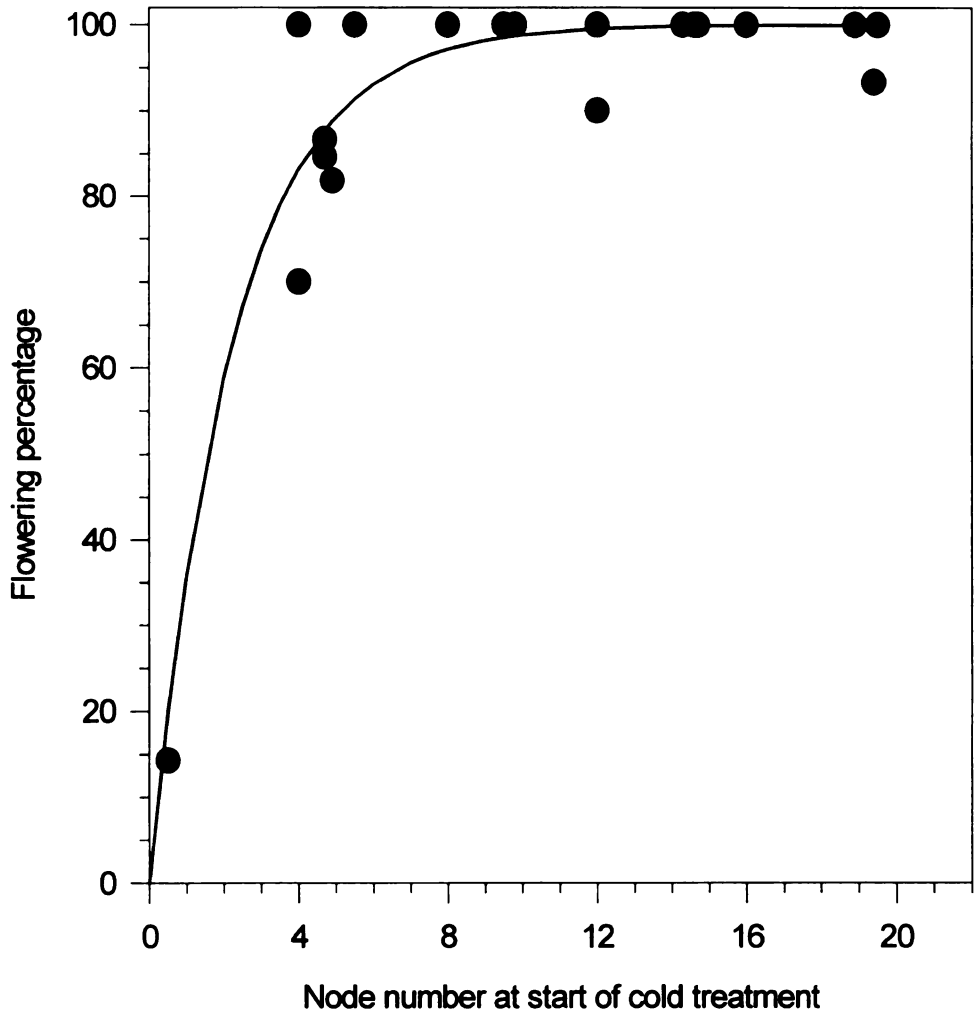
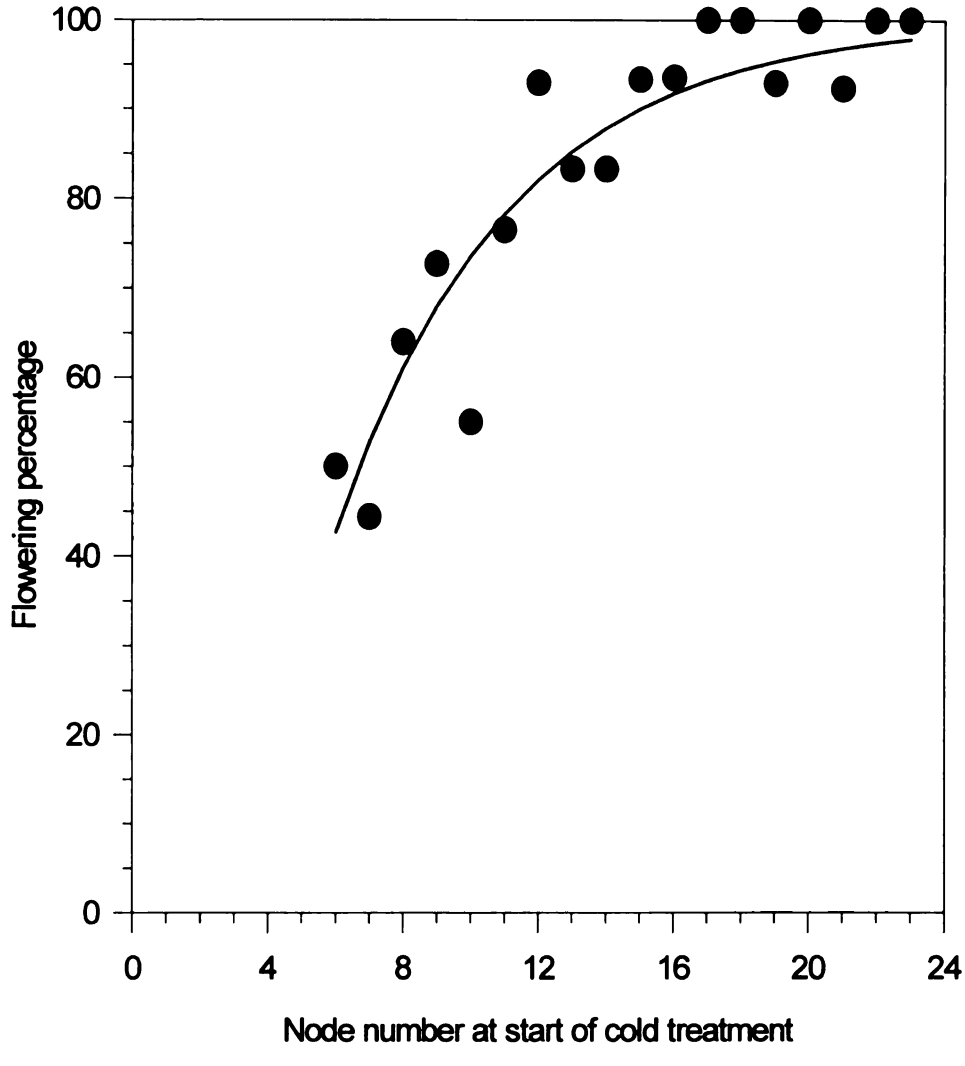

Flowering percentage
100
80
60
40
20
0
0
4
8
12
16
20
Node number at start of cold treatment

Figure 5: The effect of node number at start of cold treatments (combined data of 10 and 15 weeks cold treatments) on flowering percentage in *Heuchera sanguinea* 'Bressingham'. The regression line is: $y=1-1.836\ e^{-0.194x}$. $r^2 = 0.86$ which was calculated as $1- SS_{residual} / SS_{corrected\ total}$.


100
80
60
40
20
0
Flowering percentage
0
4
8
12
16
20
24
Node number at start of cold treatment

Section II

Effect of Forcing Temperature on Time to Flower of *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Leucanthemum* x *superbum* (Bergm. ex J. Ingram) and *Rudbeckia fulgida* (Ait.)

Effect of Forcing Temperature on Time to Flower of *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Leucanthemum* x *superbum* (Bergm. ex J. Ingram) and *Rudbeckia fulgida* (Ait.)

Mei Yuan [1], William H. Carlson [2], Royal D. Heins [3], and Arthur C. Cameron [4]

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

Received for publication _____. Accepted for publication _____. We acknowledge the financial support of the Agricultural Experiment Station of Michigan State University and greenhouse growers supportive of Michigan State University floriculture research.

[1] Graduate Assistant.

[2, 3, 4] Professor

Production and Culture

Effect of Forcing Temperature on Time to Flower of *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Leucanthemum* x *superbum* (Bergm. ex J. Ingram) and *Rudbeckia fulgida* (Ait.)

Additional index words. Base temperature, degree day, herbaceous perennials

Abstract. Scheduling crops to flower on specific dates requires a knowledge of the relationship between temperature and time to flower. Our objective was to quantify the effect of temperature on time to flower and plant appearance of four herbaceous perennials. Field-grown, bare-root *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin' and *Rudbeckia fulgida* 'Goldsturm'; tissue-culture-propagated *Leucanthemum* x *superbum* 'Snowcap' plants were exposed to 5C for 10 weeks and then grown in a greenhouse with temperature setpoints at 15, 18, 21, 24, or 27C under 4-h night-interruption lighting until they reached anthesis. Days to visible bud (VB), days to anthesis (FLW), and days from VB to FLW decreased as temperature increased. The rate of progress toward flowering increased linearly with temperature and base temperatures and degree-days of each developmental stage were calculated. For *Coreopsis, Leucanthemum* and *Rudbeckia,* flower size, flower bud number, and plant height decreased as temperature increased from 15 to 26C.

Introduction

Temperature is one of the critical factors controlling developmental processes such as flowering in plants. Time to flower usually decreases as forcing temperature increases until it reaches an optimum. In many circumstances, without the effect of other factors such as photoperiod, the rate of development increases linearly with temperature (Roberts and Summerfield, 1987). Thus the relationship between the rate toward flowering (1/DTF), where DTF is the days to flower, and temperature can be described as follows:

$$1 / DTF = b_0 + b_1 * T \quad (1)$$

Using the two constants b_0 and b_1, the base temperature, T_b, and degree-day (^{o}days), can be calculated as follow:

$$T_b = - b_0 / b_1 \quad (2)$$

$$^o \text{days} = 1 / b_1 \quad (3)$$

Base temperature is the maximum temperature at or below which the rate of progress toward flowering is zero. Degree-days represent the thermal time required for flowering.

Temperature not only influences time to flower, but also influences plant appearance. For instance, stem length, spike length, and number of florets of *Antirrhinum majus* L. 'Jackpot' increased as temperature was decreased from 21 to 10C (Maginnes and Langhans, 1961). Flowers of *Lysimachia congestiflora* Hemsl. grown at 18C last longer than those grown at 26C (Zhang et al., 1995). Temperature also affects plant morphological characteristics such as height and leaf color in *Dicentra spectabilis* (L.) Lem (Lopes and Weiler, 1977).

Growing herbaceous perennials as flowering potted plants is a new trend in the horticulture industry. *Coreopsis grandiflora* 'Sunray', *G.* x *grandiflora* 'Goblin', *L.* x

superbum 'Snowcap' and *R. fulgida* 'Goldsturm' are popular commercial-grown herbaceous perennial plants. *Coreopsis, Leucanthemum* and *Rudbeckia* ranked in the top 10 best selling perennials in 1992 and 1993 (Rhodus, 1995). *Coreopsis grandiflora, G.* x *grandiflora, L.* x *superbum* and *Rudbeckia* are reported as long-day plants, and cold treatments enhanced flowering of *Coreopsis* and *Gaillardia* (Engle, 1994; Evans and Lyons, 1988; Ketellaper and Barbaro, 1966; Tanimoto and Harada, 1985.). Another cultivar of Shasta daisy, 'G. Marconi', required about four weeks to reach first visible flower bud after cold treatments under LD (Shedron and Weiler, 1982). However, there is little information on the effect of forcing temperature on time to flower of these species. Scheduling crops to flower on a specific date is usually desirable in greenhouse production, and requires knowledge of the relationship between forcing temperature and time to flower. The objectives of these experiments were to quantify the effect of forcing temperature on time to flower and plant appearance (flower size, flower bud number, and plant height) of *C. grandiflora* 'Sunray', *G. grandiflora* 'Goblin', *L.* x *superbum* 'Snowcap', and *R. fulgida* 'Goldsturm' to provide a means by which production of these crops can be scheduled.

Materials and Methods

Experiments were conducted twice over two years. In the first year, field-grown, bare-root *C. grandiflora* 'Sunray' and *R. fulgida* 'Goldsturm', tissue-culture-propagated *L.* x *superbum* 'Snowcap' growing in 5.7-cm-diameter square pots (1090 cm^3) and *Gaillardia* x *grandiflora* 'Goblin' in 5.7 cm square pots, were received from a commercial grower and transplanted into 15-cm diameter (2570 cm^3) round pots on 24, Oct. 1993. Plants were grown under LD (9-h daylength + 4-h night interruption provided by incandescent light bulbs at photosynthetic photon flux (PPF) aroung 3 - 5 $\mu mol.s^{-1}.m^{-2}$) at 20C for three weeks. They then were exposed to 5C for 10 weeks in coolers with light provided by cool-white fluorescent lamps for 9-h a day from 0800 to 1700 HR at a PPF about 20$\mu mol\ s^{-1}m^{-2}$. After cold treatment, 10 plants of each species were grown in greenhouse sections with temperature setpoints of 15, 18, 21, 24, and 27C under LD. LD were created by 4-h night interruption lighting at PPF about 90 $\mu mol\ s^{-1}m^{-2}$ using high-pressure sodium lamps.

In the second year, similar plant material was used except for *Gaillardia* (bare-root plants instead of 5.7-cm potted plants). Bare-root plants were dug from field on 11 Nov. 1994. They then were sealed in boxes and held at 0C for 10 weeks; *Leucanthemum,* at 5C. Plants were transplanted into "one-gallon" (3402 cm^3) pots after cold treatments and grown in the same conditions as those during the first year.

Date of first visible bud (VB) and first flower reaching anthesis (FLW) were recorded for each plant in both years. The diameter of the first-opened flower, number of unopened flower buds, and plant height also were recorded at FLW in the second year.

The experimental designs for both years were completely randomized. Data were analyzed using SAS (SAS Institute, Cary, N.C.) general linear models (PROC GLM) procedure for analysis of variance and linear regression procedure (PROC REG) for the regression models. Mean days to VB, from VB to FLW, and to FLW were used to calculate regression models.

Temperatures in each greenhouse section were controlled with a Priva environmental computer. The actual temperature for each treatment was recorded every 15 min. by a CR-10 datalogger, and average temperatures from the start of forcing to VB and FLW, and from VB to FLW of were calculated for each species and used in data analyses.

The bare-root *Gaillardia* plants did not tolerate cold storage, and more than half died in the coolers. The surviving plants lacked vigor through out the entire experiment. Therefore, only the first year's (1994) data on *Gaillardia* are presented.

Results and Discussion

Days to VB, days from VB to FLW, and days to FLW of all species decreased as temperature increased. The relationship between time to VB and FLW, time from VB to FLW, and temperature generally followed a quadratic pattern (Figs. 1A, 2A, 3A, 4A). Increasing temperature from 15 to 21C accelerated flowering more than from 21C to 27C in all species. For example, days to FLW for *Coreopsis* decreased from 75 to 47 days (28 days) as temperature increased from 15.5 to 20.3C but only decreased from 47 to 33 days (14 days) as temperature increased from 20.3 to 25.9C (Fig. 1). Under the conditions of these experiments, all plants flowered. The effect of temperature on time to FLW was species dependent. Increasing temperature from 15 to 26C shortened days to FLW about 40, 25, 20, or 50 days for *Coreopsis, Gaillardia, Leucanthemum* and *Rudbeckia*, respectively.

In the first year, some *Leucanthemum* plants showed VB in a few days (one plant in only three days) from the end of cold treatment (Fig. 5). The distribution of plants related to days to VB exhibited a binomial distribution. *Leucanthemum (Chrysanthemum)* x *superbum* varies greatly in their requirements for flowering (Shedron and Weiler, 1982). Some clones required cold to flower; some did not, however, they usually responded to LD (Engle, 1994). In other experiments (Yuan, 1995), we showed ' Snowcap' does not require cold treatment for flowering. Under the experimental conditions of year one, some plants must have initiated flowers before or during cold treatments since they showed VB shortly after returned to warm temperatures. Therefore, we think it is inappropriate to use the data, and only the second year's data were used to estimate base temperature and ^{o}days.

There were linear relationships between temperature and rate of progress toward flowering of all species in the studied temperature range. For *Coreopsis*, the regression analysis was based on the combination of two years' data (Fig. 1B), and the parameters of the equation are given in Table 1. In *Gaillardia*, the rate of progress toward VB, VB to FLW, and FLW at 27C was slower than that at 24C. Since the rate to flowering increases linearly with temperature only at sub-optimal ranges (Roberts, 1987), the data at 27C were excluded from regression analysis (Fig. 2B). For *Rudbeckia,* regression lines for each year were calculated and their slopes and intercepts were compared using the F test (Table 2). Although the slopes and intercepts for equation related rate of the progress to VB and FLW was different in each year, the rate from VB to FLW was the same. When the reciprocal of the linear regression lines were plotted against original data, they matched well (Figs. 1A, 2A, 3A, 4A). It suggested that linear regression lines describe the relationship of temperature and developmental rate well and can be used to predict flowering time.

Base temperature and degree-days of each developmental stage of each species were determined using equation (2) and (3). For *Coreopsis*, the results are similar for the different growth phases. The estimated base temperature ranged from 6.4 to 7.2C, and the degree-days to FLW were 627 when days to FLW data were used alone, and 643 when the combined days from to VB and days VB to FLW data were used. For *Rudbeckia*, the estimated base temperature ranged from 5.2 to 10.2C in the first year; and from -1.3 to 5.1 in the second year. Base temperature (T_b) and degree-days can be used to predict flowering date in commercial greenhouse environments in which temperatures fluctuate. Fulfilling a developmental process in a plant requires a certain amount of thermal time (degree-days) above the base temperature. If the average daily temperature is T_a, the days necessary to complete a growth phase can be calculated as ^{o}days / (T_a - T_b). For example, 353 or 627 degree-days are required for *Coreopsis* plants to show VB or reach FLW from

the start of forcing when the base temperature is 6.5 or 7.2C, respectively. If the average forcing temperature is 20C, days from forcing to VB or FLW will be 26 or 49, respectively. By the same way, the time required to complete a developmental stage can be obtained for the other species when the average forcing temperature is available. The predicted days to complete a developmental stage are similar to the observed days in all species.

The rate of progress toward VB and FLW was different between the two years for *Rudbeckia* (Figure 4). Plants flowered about 20 days faster with three weeks of growth under LD prior to cold treatment. *Rudbeckia* is an obligate LD plant that does not require vernalization for flower induction (Yuan, 1995). In the first year, we speculate that plants had been induced during the three weeks of LD prior to the cold treatment. When they were returned to warm temperatures after cold treatment, they flowered faster than non-induced plants from the second year. It is interesting that the average time to FLW was 20 days fewer the first year, which is almost equal to the three-week precold growth period. In other words, the total growing time in the greenhouse was the same both years for *Rudbeckia*.

Coreopsis grandiflora 'Sunray' has an obligate vernalization requirement for flower initiation (Yuan, 1995). Plants cannot be induced to flower without cold treatment, even under extended LD. In the first year, field-grown bare-root plants were shipped to us in late October and had received little cold in the field prior to harvesting. Therefore they were insensitive to LD during the three-week precold LD treatment. They flowered at the same time as plants that did not have three-week LD growth period before cold the second year.

Flower bud number, flower diameter, and plant height decreased in *Coreopsis, Leucanthemum,* and *Rudbeckia* as temperature increased from about 16 to 26C (Fig. 6). Flower bud number of *Coreopsis, Leucanthemum,* and *Rudbeckia* decreased about 80%, 75%, and 55%, respectively, when temperature increased from 16 to 26C (Fig. 6A). Temperature had a greater effect on flower size of *Leucanthemum* and *Rudbeckia* than *Coreopsis* (Fig. 6B). Flower diameter was 2.7cm smaller on *Leucanthemum* and *Rudbeckia*, but only 0.9 cm smaller on *Coreopsis* as temperature increased from 16 to 26C. Temperature affected plant height of *Rudbeckia* the most (Fig. 6C). Plant height decreased 50% when temperature increased from 16 to 26C. In *Coreopsis,* only plants grown at 16C were significantly taller than those grown under higher temperatures such as 23C or 26C. Height of *Leucanthemum* decreased about 9cm as temperature increased from the lowest to highest.

Overall, plants grown in cooler temperatures had more numerous, larger flowers and are taller but took longer to reach FLW. On the other hand, plants flowered faster in higher temperatures, but flower bud numbers and flower size were smaller. *Leucanthemum* plants grown under the two highest temperatures tended to be too short for "1 gallon" pots. *Coreopsis* and *Rudbeckia* grown under the lowest temperature tended to be too tall for "1 gallon" pots. Temperatures from 18 to 21C are recommended to force *C. grandiflora* 'Sunray', *G.* x *grandiflora* 'Goblin', *L.* x *superbum* 'Snowcap', and *R. fulgida* 'Goldsturm'. Plants flowered faster in this temperature range compared to that at lower temperatures, and they were more attractive. The time required to bring each species to flower under the same temperature varies. To schedule *Coreopsis*, *Gaillardia*, *Leucanthemum,* and *Rudbeckia* to flower on the same day at 20C, for example, they should be forced 50, 45, 45, and 85 days, respectively, before the schedule date if they are transplanted after cold treatment.

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Table 1. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud (VB), from VB to anthesis (FLW) and to FLW in *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin' and *Leucanthemum* x *superbum* 'Snowcap'. Intercept and slope were used to calculate base temperature (T_b) and degree-days (^{o}days).

Species	Developmental stage (days)	Intercept (b_0) 1/days	Slope (b_1) (1/days) / C	T_b (C)	^{o}days	r^2
Coreopsis	forcing to VB	- 0.0182 ± 0.0018 [z]	0.0028 ± 0.0001	6.5	353	0.94 ***
	VB to FLW	- 0.0222 ± 0.0018	0.0035± 0.0001	6.4	290	0.90 ***
	forcing to FLW	- 0.0114 ± 0.0060	0.0016 ± 0.0003	7.2	627	0.96 ***
Gaillardia	forcing to VB	0.0008 ± 0.0074	0.0015 ± 0.0004	-0.5	667	0.88 *
	VB to FLW	-0.0621 ± 0.0284	0.0065 ± 0.0014	9.6	154	0.91 *
	forcing to FLW	-0.0043 ± 0.0045	0.0013 ± 0.0002	3.3	769	0.94 *
Leucanthemum	forcing to VB	0.0170 ± 0.0051	0.0013 ± 0.0002	-13.1	769	0.90 *
	VB to FLW	-0.0042 ± 0.0047	0.0022 ± 0.0002	0.9	455	0.95 **
	forcing to FLW	0.0031 ± 0.0025	0.0009 ± 0.0001	-3.4	1111	0.97 **

*, **, *** Significant at P <0.05, 0.01, or 0.001, respectively.

[z] Standard error

Table 2. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud (VB), from VB to anthesis (FLW) and to FLW in *Rudbeckia fulgida* 'Goldsturm'. Intercept and slope were used to calculate base temperature (T_b) and degree-days (°days).

	Developmental stage (Days)	Intercept (b_0) 1/days	Slope (b_1) (1/days) / C	T_b (C)	°days	r^2
Year one	forcing to VB	-0.0317 ± 0.0029 [z]	0.0031 ± 0.0001	10.2	323	0.99 ***
year two	forcing to VB	0.0013 ± 0.0048	0.0010 ± 0.0002	-1.3	1000	0.86 *
Comparison		F = 6.81 *	F = 71.23 **			
Year one	VB to FLW	0.0076 ± 0.0018	0.0009 ± 0.0001	8.4	1111	0.99 ***
year two	VB to FLW	0.0051 ± 0.0019	0.0010 ± 0.0001	5.1	1000	0.98 **
Comparison		F = 1.81 NS	F = 0.38 NS			
year one	forcing to FLW	-0.0047 ± 0.0011	0.0009 ± 0.0001	5.2	1111	0.98 ***
Year two	forcing to FLW	0.0007 ± 0.0014	0.0005 ± 0.0001	-1.4	2000	0.96 **
Comparison		F = 9.4 *	F = 20.9 **			

*, **, *** Significant at P <0.05, 0.01, or 0.001, respectively.

[z] Standard error.

Figure 1. Effect of temperature on (A) time and (B) rate of progress toward flowering in *Coreopsis grandiflora* 'Sunray' for year one (■) and year two (●). The parameters of linear regression lines are presented in Table 1. The quadratic regression lines in graphs A are the reciprocal of correlated linear regression lines in graphs B.

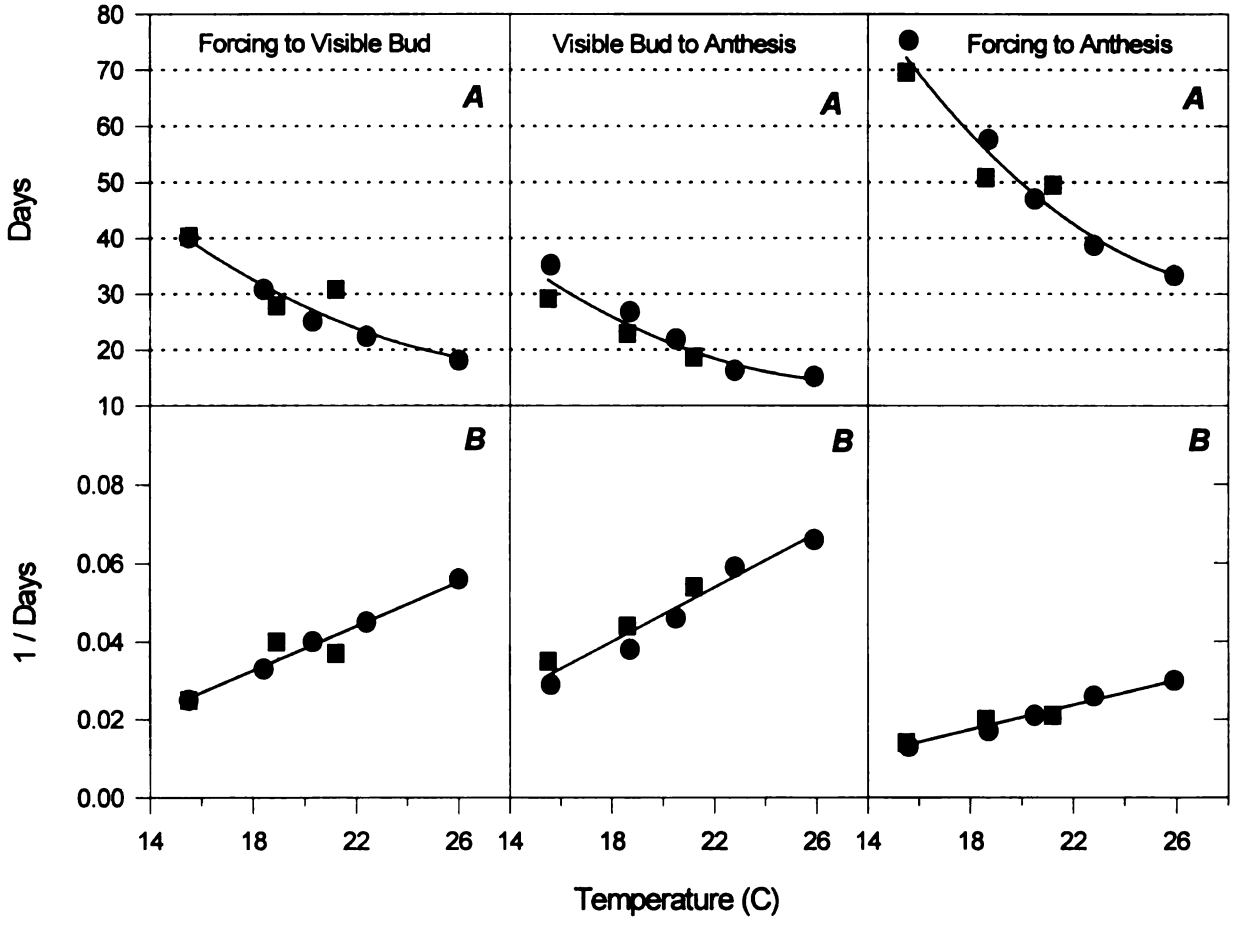

Forcing to Visible Bud
Visible Bud to Anthesis
Forcing to Anthesis
A
B
Days
1 / Days
Temperature (C)
80
70
60
50
40
30
20
10
0.08
0.06
0.04
0.02
0.00
14
18
22
26

Figure 2. Effect of temperature on (A) time and (B) rate of progress toward flowering in *Gaillardia* x *grandiflora* 'Goblin' for year one. The parameters of linear regression lines are presented in Table 1. Data represented by □ is not included in regression analysis. The quadratic regression lines in graphs A are the reciprocal of correlated linear regression lines in graphs B.

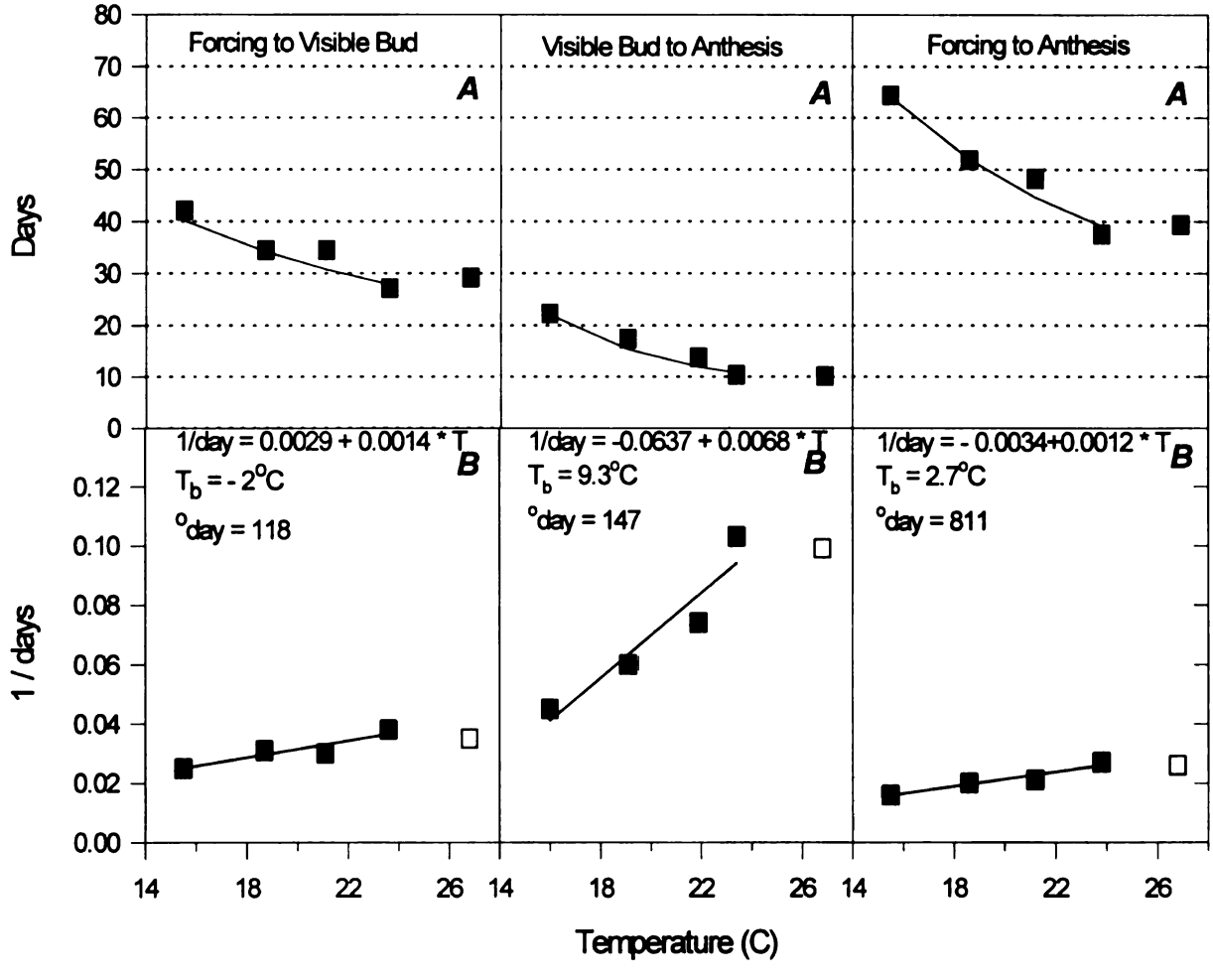

Forcing to Visible Bud
Visible Bud to Anthesis
Forcing to Anthesis
A
B
Days
1 / days
1/day = 0.0029 + 0.0014 * T
T_b = - 2°C
°day = 118
1/day = -0.0637 + 0.0068 * T
T_b = 9.3°C
°day = 147
1/day = - 0.0034+0.0012 * T
T_b = 2.7°C
°day = 811
Temperature (C)

Figure 3. Effect of temperature on (A) time and (B) rate of progress toward flowering in *Leucanthemum* x *superbum* 'Snowcap' for year two. The parameters of linear regression lines are presented in Table 1. The quadratic regression lines in graphs A are the reciprocal of correlated linear regression lines in graphs B.

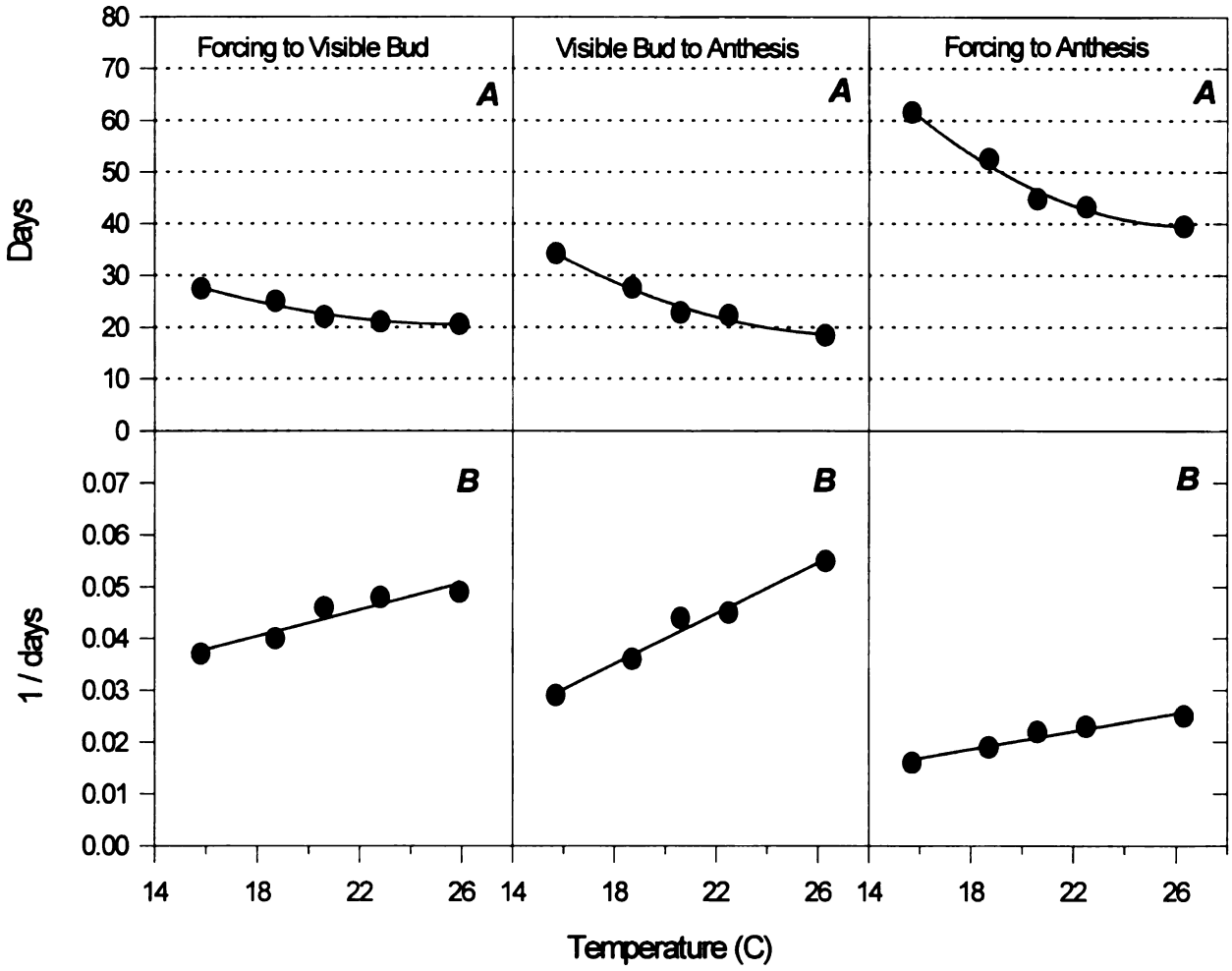

Forcing to Visible Bud
Visible Bud to Anthesis
Forcing to Anthesis
A
B
Days
1 / days
Temperature (C)
80
70
60
50
40
30
20
10
0
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
14
18
22
26

Figure 4. Effect of temperature on (A) time and (B) rate of progress toward flowering in *Rudbeckia fulgida* 'Goldsturm' for year one (■) and year two (●). The parameters of linear regression lines are presented in Table 2. The quadratic regression lines in graphs A are the reciprocal of correlated linear regression lines in graphs B.

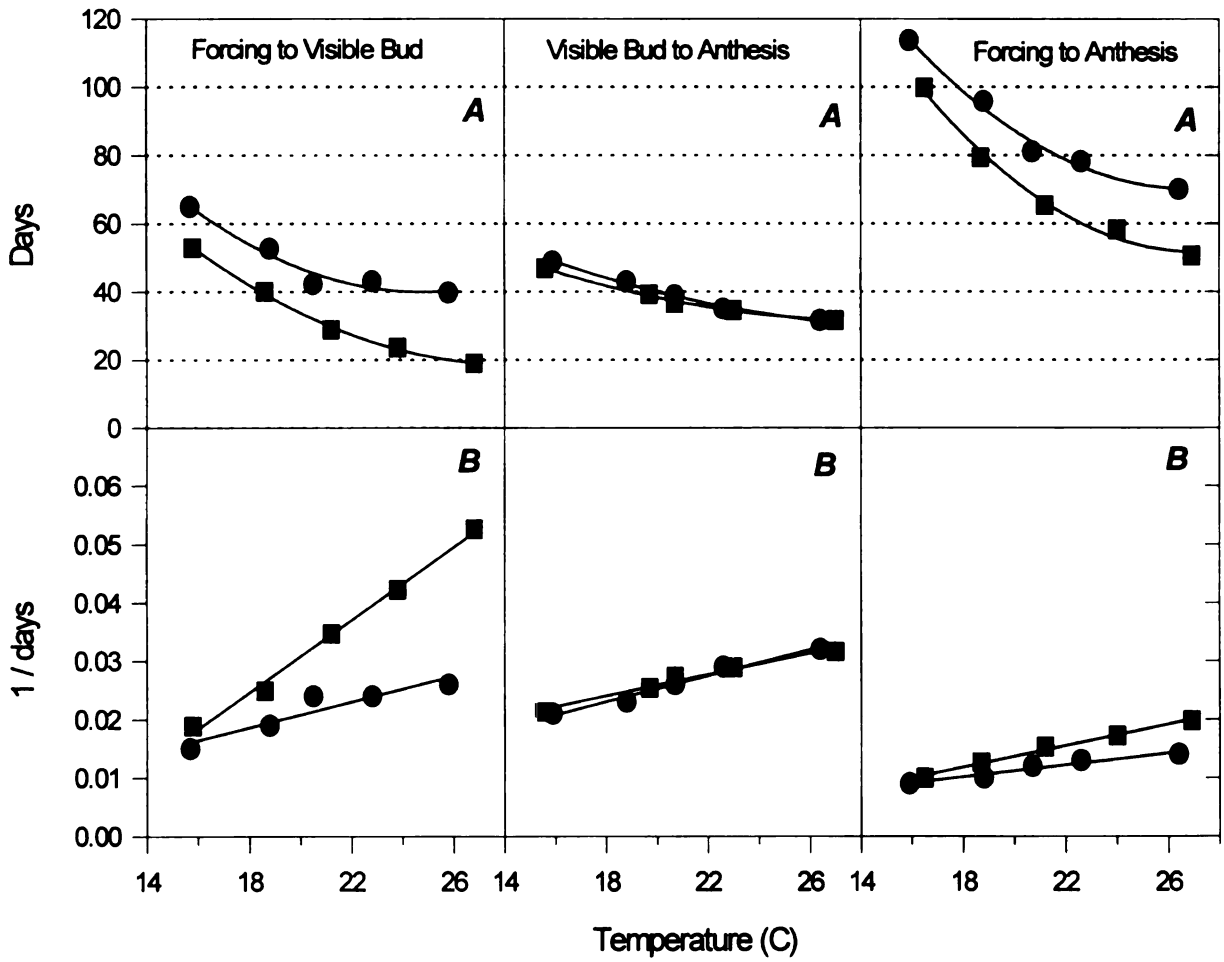

Forcing to Visible Bud
Visible Bud to Anthesis
Forcing to Anthesis
A
B
Days
1 / days
Temperature (C)
120
100
80
60
40
20
0
0.06
0.05
0.04
0.03
0.02
0.01
0.00
14
18
22
26

Figure 5. Distribution of *Leucanthemum* x *superbum* 'Snowcap' plants relating to days to visible bud after 10 weeks of cold treatment at 5C.

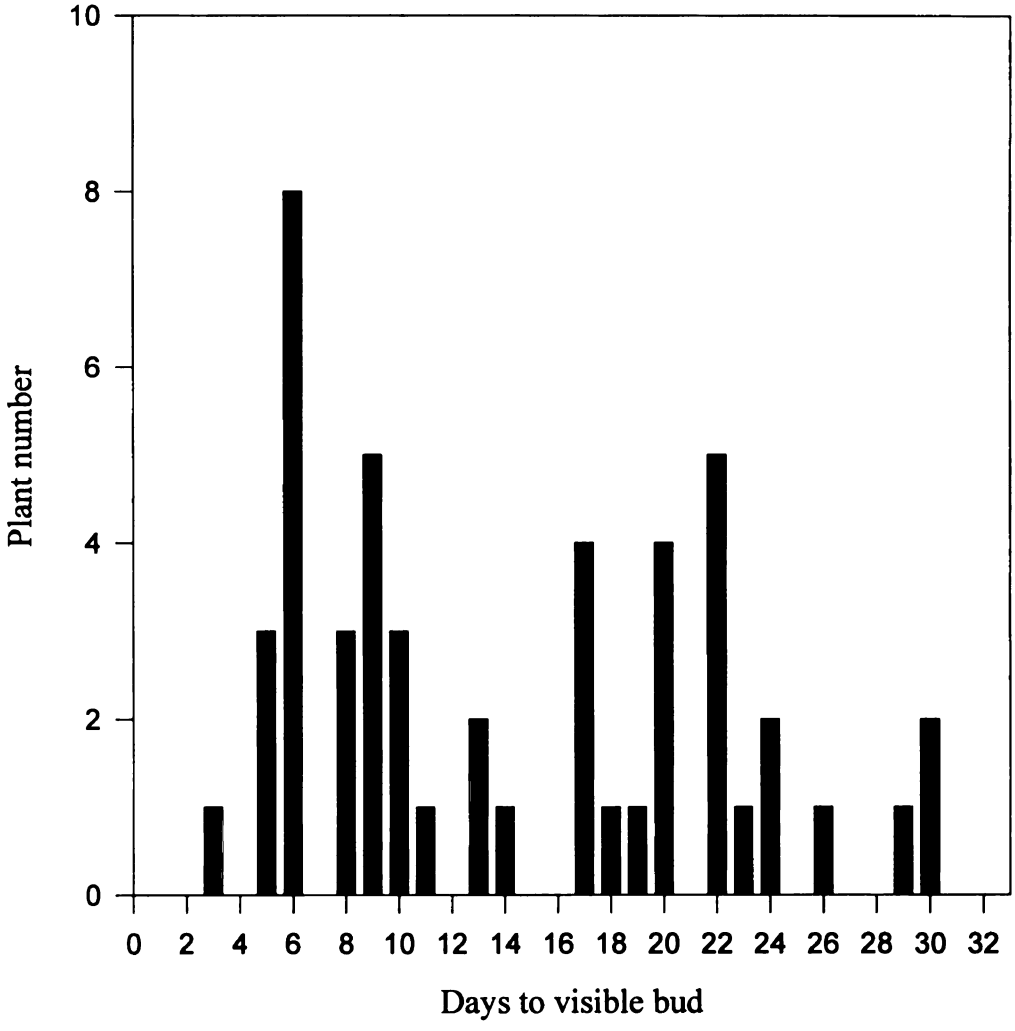
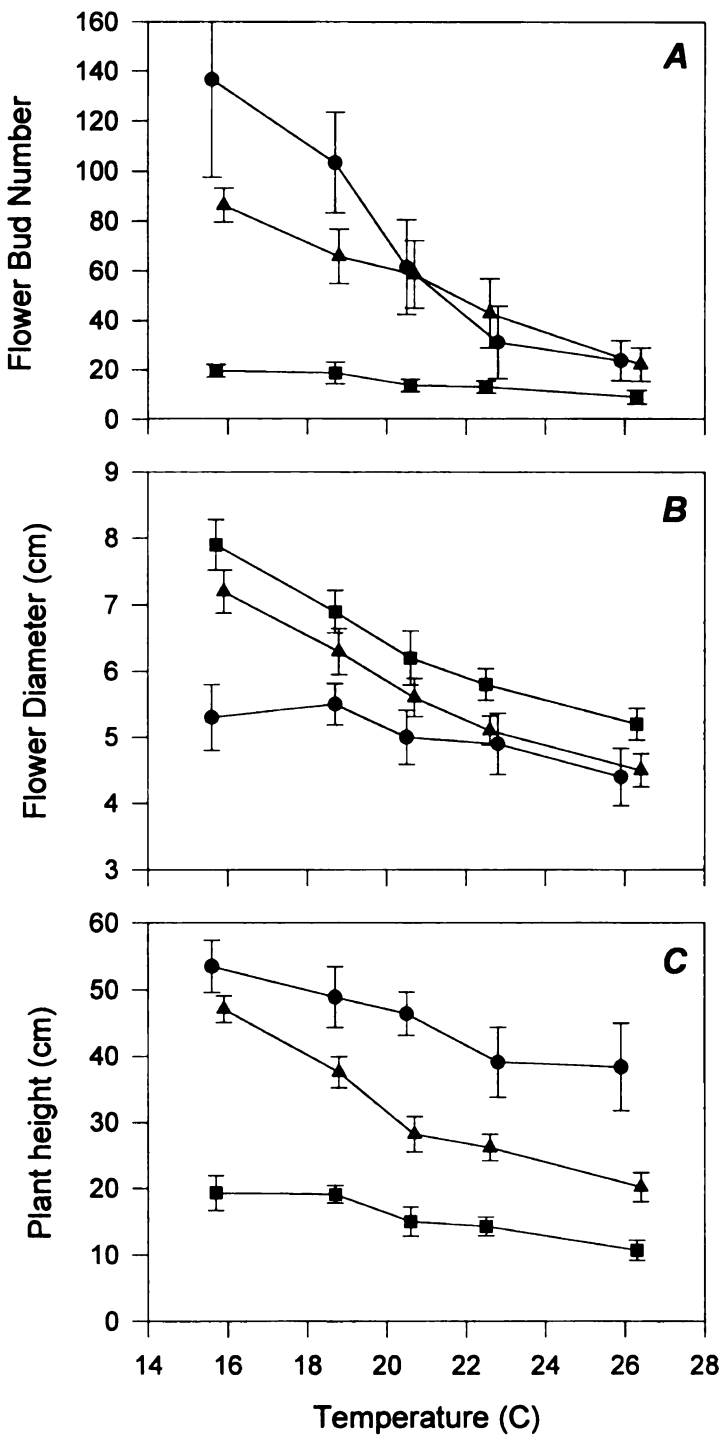

Plant number
0
2
4
6
8
10
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Days to visible bud

Figure 6. Effect of temperature on (A) unopened flower bud number, (B) flower diameter, and C) plant height in *Coreopsis grandiflora* 'Sunray' (●), ***Leucanthemum* x *superbum*** 'Snowcap'(■) and *Rudbeckia fulgida* 'Goldsturm' (▲). Error bars are 95% confidence intervals.


A
B
C
Flower Bud Number
Flower Diameter (cm)
Plant height (cm)
Temperature (C)
160
140
120
100
80
60
40
20
0
9
8
7
6
5
4
3
60
50
40
30
20
10
0
14
16
18
20
22
24
26
28

Section III

Strategies to Force *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Leucanthemum* x *superbum* (Bergm. ex J. Ingram) and *Rudbeckia fulgida* (Ait.) as Flowering Potted Plants

Strategies to Force *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Leucanthemum* x *superbum* (Bergm. ex J. Ingram) and *Rudbeckia fulgida* (Ait.) as Flowering Potted Plants

Mei Yuan [1], William H. Carlson [2], Royal D. Heins [3], and Arthur C. Cameron [4]

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

Received for publication _____. Accepted for publication _____.

We acknowledge the financial support of the Agriculture Experiment Station of Michigan State University and greenhouse growers supportive of Michigan State University floriculture research.

[1] Graduate assistant

[2, 3, 4] Professor

Production and Culture

Strategies to Force *Coreopsis grandiflora* (Hogg ex Sweet.), *Gaillardia* x *grandiflora* (Van Houtte), *Leucanthemum* x *superbum* (Bergm. ex J. Ingram) and *Rudbeckia fulgida* (Ait.) as Flowering Pot Plants

Additional index words. Shasta daisy, forcing, photoperiod

Abstract. Growing perennial plants under non-inductive conditions for some time before cold or photoperiodic treatment can result in more attractive finished plants. Plant size usually influence finial plant quality too. Field-grown bare-root plant, seedlings or tissue-culture-propagated plants of *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin', *Leucanthemum* x *superbum* 'Snowcap' and *Rudbeckia fulgida* 'Goldsturm' received three-week growth under different photoperiod before they were exposed to cold treatments at 5C. They were forced at 20C under LD after cold treatments. Plant size at start of forcing influenced time to FLW and final plant quality. Large plants flowered faster and had many more flower buds than seedlings. Three weeks of treatments prior to cold period resulted in higher flower bud number in *Leucanthemum* 'Snowcap' and bare-root *Rudbeckia,* however, had little effect on *Coreopsis, Gaillardia* and *Rudbeckia* seedlings.

Introduction

Herbaceous perennial plants have been widely used in gardens for many years. When appropriately planted, they persist for more than one years and are more permanent than annuals, therefore they usually require less care. A renewed interest in perennial plants has occurred in past ten years (Iversen and Weiler, 1994). Many perennial plants can be produced as potted plants, such as *Gaillardia* 'Goblin' and Shasta daisy 'Snow Lady' (Watt, 1989). The production of perennials has moved from field grown plants to container production in recent years (Schwarze, 1993). Producing perennials as flowering potted plants seems to have a lot of potential. Field grown plants, tissue-culture-propagated plants, divisions or mature seedlings can all be forced. Usually, large rootstock or field plants yield high quality flowering plants (Iversen, 1994). However, many perennials are forced from plugs because it is the most economical way.

Many perennial need a cold period to break dormancy and / or to initiate flowering. The traditional method is to place the potted plants outdoors under thermal blankets or bury them under mulch to protect crops from extreme cold (Campbell and Tayama, 1990). However, plants usually can not survive an extremely cold winter and the survived plants may be stunted in growth and flowering. Cold -requiring perennials can also be treated in refrigerator or walk in refrigerated room where precise temperature control can be achieved, or in a cold greenhouse with minimum heat provided.

Growing plants under non-inductive condition for some time after transplanting can allow plants to establish, thus usually result in better finished plants. Growing long-day (LD) plants under short-day (SD) for at least one months before cold exposure or forcing is recommended (Iversen, 1994). LD plants also are less apt to die during cold storage if they are first grown under SD conditions after transplanting. Growing LDP *Campanula carpatica* a few weeks under SD before LD or cold treatment promotes lateral shoots and results in more attractive finished plants with greater number of flowers (Whitman, et al. 1995).

Although an establishment period before cold or photoperiodic treatments is generally considered beneficial for plants, few experiments have been conducted to provide information for different species.

We selected *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin', *Leucanthemum* x *superbum* and *Rudbeckia fulgida* 'Goldsturm' for their popularity and great potential as pot plants. *Coreopsis grandiflora* is native north from Missouri and Kansas, and south to Florida and New Mexico (Bailey, et al. 1976). *Gaillardia* x *grandiflora* is a garden hybrid between *G. aristata* and *G. pulchella* and now it has naturalized in west parts of the United States. *Leucanthemum* x *superbum* presumably a hybrid between *Chrysanthemum lacustre* and *C. maeimum* Ramond. *Rudbeckia fulgida* is native east from Connecticut to West Virginia, and west to Michigan and down to Missouri. All the four cultivars are LD plants (Yuan, 1995).

The objectives of these experiments were to determine the effect of various precold treatments and plant size on time to flower and flower bud number.

Materials and Methods

Seedlings in 128-cell trays (10 cm^3), 50-cell trays (85 cm^3) and field grown bare roots plants of *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin' and *Rudbeckia fulgida* 'Goldsturm'; tissue-culture propagated *Leucanthemum* x *superbum* 'Snow cap' in 5.7-cm diameter square pots (1090 cm^3) were received from commercial growers. *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin' and *Rudbeckia fulgida* 'Goldsturm' were received and transplanted into "1-gallon" (3402 cm^3) pots on Nov. 7, 1994 and *Leucanthemum superbum* 'Snow cap' on Dec. 8. 1994. Seedlings were singled to one plant and the node numbers were recorded. Some plants were grown in the greenhouse for three-week before cold storage, other were exposed to cold before or immediately after transplanting. The treatments before forcing were as follow:

1: pot plants -- forcing

2: pot plant -- three weeks under LD at 20C – cold treatment -- forcing

3: pot plant -- three weeks under SD at 20C -- cold treatment -- forcing

4: pot plant -- three weeks under natural photoperiod at 20C -- cold treatment -- forcing

5: pot plant -- three weeks under 12-hr photoperiod at 20C -- cold treatment -- forcing

6: pot plants -- cool commercial greenhouse treatment -- forcing

7: cold treatment -- pot plants -- forcing

SD was 9-hr photoperiod created by covering benches with black cloth from 1700 to 0800 every day. LD was 9-hr photoperiod with 4-hr night interruption provided by incandescent light bulbs at photosynthetic photon flux (PPF) of 3 - 5 μmol $s^{-1}m^{-2}$. 12-Hr photoperiod was created by extending SD using incandescent light bulbs providing PPF of 3 - 5 μmol $s^{-1}m^{-2}$.

Field-grown *Leucanthemum* x *superbum* 'White knight', *Gaillardia* x *grandiflora* 'Goblin' and *Rudbeckia fulgida* 'Goldsturm' plants in 5.7-cm diameter round bottomless pots (1090 cm^3) from were received from a commercial grower and potted on Jan. 25, 1995. The plants were grown in Washington and were harvested in December. The four treatments before forcing were as follow:

1: pot plant -- forcing

2: pot -- cold treatment -- forcing

3: cold -- pot -- forcing

4: pot -- cool commercial greenhouse -- forcing

Plants without cold treatment were forced under LD as described above. Potted plants received cold treatment in coolers with a temperature setpoint at 5C under 9-hr photoperiod provided by cool-white fluorescent bulbs (VHOF96T12; Philips, Bloomfield, N.J.) at PPF about 20 μmol $s^{-1}m^{-2}$. In a cool commercial greenhouse, minimum heat was provided to keep plant temperature above 0C, and plants were exposed to natural photoperiod from November until March. Bare root plants were

packaged in plastic and held in a cooler with a temperature setpoint at 0C. All plants were removed from coolers or the cool greenhouse on March, 1. 1995 and forced in the greenhouse with a temperature setpoint of constant 20C under natural photoperiods plus 4h night interruption. Night interruption lighting was provided by high pressure sodium lamps at PPF about 2 - 5 $\mu mols^{-1}m^{-2}$. Date of first visible flower bud (VB) and first flower reaching anthesis (FLW) were recorded. At time of FLW, number of unopened flower bud was recorded. Plants that did not flower or show VB by the end of 15 weeks forcing period were considered as non-flowering plants.

The experimental design was completely randomized designs with ten plants for each treatment. Data were analyzed using SAS (SAS Institute. Cary, NC) general linear models (PROC GLM) for analysis of variance.

Field-grown Gaillardia in 5.7 cm bottomless pots were in poor condition when they arrived and only a few plants survived. This resulted in missing data in some treatments.

Results and Discussion

***Coreopsis grandiflora* 'Sunray'**. Vernalization is required for flower initiation and 50-cell and 128-cell plants did not flower without cold treatments (Table 1). Half of field-grown bare roots plants flowered without cold treatments. These plants were dug from field on Nov. 5, 1994. They had been exposed to some cold nights in the field in Michigan's weather, which presumably fulfilled some of the vernalization requirement. The larger the plant size at the start of experiments, the faster they flowered and more flower buds they had at time of FLW. Bare roots plants, 50-cell and 128-cell plugs flowered after an average of 46, 50, and 56 days of forcing, respectively, and had average 63, 33, and 31 flower buds at the time of flowering, respectively. Three weeks growth in the greenhouse prior to cold treatments did not influence flower buds number in any size of plants nor accelerate flowering in bare roots plants. However, it hastened flowering for about 10 days in both 50 and 128-cell plants. Days from VB to anthesis was not influenced by starting plant size nor any treatment.

All cold-treated bare-root plants flowered. However, 50 and 128-cell plants failed to reach 100% flowering under some treatment. The average flowering percentage of 128-cell plants was lower than that of 50-cell plants, suggesting the effect of juvenility. *Coreopsis grandiflora* 'Sunray' has a juvenile phase (Yuan, 1995). Plants required eight nodes or more before cold treatment for a stable high flowering percentage.

***Gaillardia* x *grandiflora* 'Goblin'** All field-grown bare root plants flowered regardless cold treatment (Table 2). Cold treatment increased flower bud number from about 7 to about 50, and reduced days to FLW from about 54 to 42 in non-cold treated plants or cold treated plants, respectively. Plants with three-week growth time under LD before cold treatment flowered faster than plants that received cold in the cool greenhouse. Cold treated plants had many more flower buds than non-cold treated plants at the time of FLW.

Cold treatment not only enhanced flowering percentage but also greatly accelerated time to flower in 50 or 128-cell plants. Days to FLW was decreased at least 60 days after cold treatment. Flower bud number of 50-cell plants was not affected by any treatment, however, for 128-cell plants, flower bud number increased 10 - 20 after cold treatment. Three-week growth under SD, natural or 12-hr photoperiod before cold storage accelerated flowering by about 10 days compared to those plants that received cold before or immediately after transplanting. Under many treatments, 50 and 128-cell plants did not reach 100% flowering, indicating the effects of juvenility. 50 or 128-cell plants had about 10 or 8 nodes at the start of experiment, which is less than the required node number for 100% flowering (Yuan, 1995). Time from VB to FLW varied slightly among treatments for about one week in bare root, 50 and 128-cell plants. Plants in 5.7-cm pots flowered within seven weeks after forcing regardless cold treatments or transplanting time. All cold treated plants flowered, while only 67% of non-cold treated plants flowered.

Field-grown bare root and 5.7-cm potted plants flowered in shorter time and had more flower buds resulting in more attractive finished plants. Three-week's growth prior to cold treatment did not increase flower bud number in bare root, 50 or 128-cell plants, and reduced on flowering time in 128-cell plants by just 10 days.

Leucanthemum* x *superbum Three cultivars - 'Snowlady', 'Snowcap' and 'White knight' were used in these experiments. 'Snowlady' was extremely sensitive to any kind of pesticides or fungicides, resulting in loss of most plants. Only non-cold treated plants survived and flowered within 60 days regardless start size (Table 3). Cold treatment was not required for flowering in this cultivar.

Cold treated 'Snowcap' plants flowered 4 -18 days faster and had 4-7 more flower buds compared to non-cold treated plants (Table 3). Plants with three-week growth before cold flowered within 40 - 48 days, while plants that received cold before or immediately after potting flowered in 54 days after forcing. Plants receiving three-week's LD before cold flowered fastest, while plants received three-week's SD or natural day had more flower buds compared to plants under other treatments. Three-week growth after transplanting allowed plants to establish and have some vegetative growth which might have resulted in more flower buds in 'Snowcap'.

Flower bud number decreased after cold treatments in 'White knight' plants. Plants that were hold in the cool greenhouse flowered most quickly. Transplanting plants before or after cold storage did not influence time to flower or flower bud number on plants.

Rudbeckia fulgida 'Goldsturm' Cold treated bare root plants flowered in 15 to 30 days earlier with 20 to 50 more flower buds than non-cold treated plants (Table 4). Plants that were grown under LD for three-week before cold treatment flowered faster than those that were transplanted after cold storage, however, they has similar flower bud number. Plants with three-week pre-cold growth under SD and those stored in the cool greenhouse had highest flower bud number at the time of anthesis. As an obligate LD plant (Yuan, 1995), *Rudbeckia* might have been induced during the LD period, therefore flowered faster after cold treatment.

Cold treatment hastened flowering in both 50 and 128-cell plants (Table 4). Flower bud number and days to flower of cold-treated plants were the same regardless of treatments prior to cold period. However, 128-cell plants with three-week growth before cold treatment flowered faster than plants under other treatment. 128-cell plants had only five nodes at the start of experiments. Since time to flower decreased as node number at start of cold treatment increased in *Rudbeckia* (Yuan, 1995), plants with three-week pre-cold growth had more node number at the time of cold treatment, therefore, flowered faster after cold.

50 and 128-cell plants did not reach 100% flowering under most treatments, indicating the effect of juvenility. Insufficient forcing time may be another reason of the low flowering percentage. In our other experiments (Yuan, 1995), plants with similar node number at the start of cold treatments flowered at higher percentage after 20 weeks forcing at 20C. Since *Rudbeckia* plants grow slowly a forcing period longer than 15 weeks may be necessary to force small plants into flower.

5.7cm-pot plants flowered within 68 to 75 days with 60 to 80 flower buds at the time of FLW. Transplanting plants before or after cold treatment did not influence days to FLW or flower bud number. Non-cold treated plants flowered slightly faster.

Plant size at the start of experiments had significant influence on days to anthesis and finished plant appearance. Field-grown bare-root and 5.7cm-pot plants flowered faster, more uniform and had much more flower buds than 50 or 128-cell plants. At time of FLW, 5.7cm-pot plants has 73 buds, which was more than twice of those on 50 or 128-cell plants, resulting in very attractive plants.

Based on the results of our experiments, three-week precold treatments did not enhance flower bud number in *Coreopsis grandiflora* 'Sunray', *Gaillardia* x *grandiflora* 'Goblin' or in 50 and 128-cell *Rudbeckia fulgida* 'Goldsturm'. A longer growth period might be required. These plants can be stored at 5C before transplanting if cooler space is limited. *L.* x *superbum* 'Snowcap' and bare root *Rudbeckia* should be grown under SD or natural

photoperiod in the fall for at least three weeks before cold or LD treatment for more attractive finished plants with greatly flower bud number.

Cold treatment accelerated flowering and increased flower bud number in all species. Plants can be exposed to cold treatments in a cooler or in a cool greenhouse.

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Table 1. Effect of start plant size and pre-cold treatments on flower percentage, unopened flower buds, days to visible bud and anthesis from the start of forcing in *Coreopsis grandiflora* 'Sunray'.[z]

Start plant size	Treatments	Node No. at start of treatment	Flowering percentage	Flower bud no.	Days to visible bud	Days to Anthesis	Days visible bud to anthesis
bare root	no cold	--	50	6 a	45 a	67 a	21 a
bare root	3-wks LD -- cold [1]	--	100	67 b	20 b	42 b	22 a
bare root	3-wks SD --- cold [1]	--	100	73 b	20 b	42 b	23 a
bare root	3-wks natural day --- cold [1]	--	100	65 b	20 b	42 b	22 a
bare root	3-wks 12-hr photo.--- cold [1]	--	100	65 b	19 b	43 b	24 a
bare root	pot - cool greenhouse [2]	--	100	65 b	25 b	48 b	24 a
bare root	cold - pot [3]	--	100	74 b	24 b	48 b	24 a
Avg	--	--	92	59	25	46	23
50 - cell	no cold	7	0	--	--	--	--
50 - cell	3-wks LD -- cold [1]	7	90	31 a	26 a	49 a	24 a
50 - cell	3-wks SD --- cold [1]	7	100	29 a	22 a	45 a	23 a
50 - cell	3-wks natural day --- cold [1]	7	90	29 a	25 a	48 a	24 a
50 - cell	3-wks 12-hr photo.--- cold [1]	7	100	40 a	25 a	47 a	22 a
50 - cell	pot - cool greenhouse [2]	7	100	28 a	29 a	53 ab	24 a
50 - cell	cold-pot [3]	7	100	33 a	37 a	58 b	22 a
Avg	--	7	82	31	27	50.2	23
128 - cell	no cold	6	0	--	--	--	--
128 - cell	3-wks LD -- cold [1]	6	100	50 a	29 a	54 a	23 a
128 - cell	3-wks SD --- cold [1]	6	100	34 ab	25 a	48 a	23 a
128 - cell	3-wks natural day --- cold [1]	6	80	27 ab	27 a	59 a	24 a
128 - cell	3-wks 12-hr photo.--- cold [1]	5.5	60	22 b	31 a	55 a	23 a
128 - cell	pot - cool greenhouse [2]	6	100	34 ab	32 a	54 a	23 a
128 - cell	cold-pot [3]	6	90	38 ab	46 b	68 b	22 a
Avg	--	6	74	32	32	55	23

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

[1]: Represent 14 weeks at 5C.

[2]: Represent 17 weeks in a cool commercial greenhouse.

[3]: Represent 17 weeks at 5C.

Table 2. Effect of start plant size and pre-cold treatments on flower percentage, unopened flower buds, days to visible bud and anthesis from the start of forcing in *Gaillardia* x *grandiflora* 'Goblin'.

Start plant size	Treatments	Node No. at start of treatment	Flowering percentage	Flower bud no.	Days to visible bud	Days to Anthesis	Days visible bud to anthesis
bare root	no cold	--	100	7 a	28 a	54 a	30 ab
bare root	3-wks LD -- cold [1]	--	100	30 ab	12 b	38 c	26 b
bare root	3-wks SD --- cold [1]	--	100	54 b	12 b	40 bc	28 ab
bare root	3-wks natural day --- cold [1]	--	100	54 b	11 b	39 bc	28 ab
bare root	3-wks 12-hr photo.--- cold [1]	--	100	48 b	14 b	43 bc	30 ab
bare root	pot -- cool greenhouse [2]	--	100	46 b	15 b	48 ab	33 a
Avg	--	--	100	44	15	44	29
50 - cell	no cold	10	10	12 a	98 a	123 b	25 a
50 - cell	3-wks LD -- cold [1]	10	90	23 a	30 b	54 a	28 ab
50 - cell	3-wks SD --- cold [1]	10	71	14 a	24 b	54 a	30 ab
50 - cell	3-wks natural day --- cold [1]	10	75	22 a	22 b	55 a	33 b
50 - cell	3-wks 12-hr photo.--- cold [1]	10	100	22 a	22 b	56 a	33 b
50 - cell	pot-cool greenhouse [2]	10	89	16 a	33 b	62 a	29 ab
50 - cell	cold-pot [3]	10	75	28 a	39 b	68 a	30 ab
Avg	--	10	73	20	38	68	30
128 - cell	no cold	8	50	10 b	99 a	124 b	26 a
128 - cell	3-wks LD – cold [1]	8	100	21 a	29 c	60 b	30 ab
128 - cell	3-wks SD --- cold [1]	9	90	25 a	17 d	47 c	31 ab
128 - cell	3-wks natural day --- cold [1]	9	100	24 a	21 d	51 c	30 ab
128 - cell	3-wks 12-hr photo.--- cold [1]	8	100	29 a	21 d	53 c	32 ab
128 - cell	pot-cool greenhouse [2]	9	90	20 a	29 c	62 b	33 c
128 - cell	cold-pot [3]	9	100	25 a	36 b	64 a	28 ab
Avg	--	8.3	90	22	36	66	30
5.7-cm pot	no cold	--	67	8 a	18 a	48 a	30 a
5.7-cm pot	cold-pot [4]	--	100	40 a	18 a	46 a	27 a
5.7-cm pot	pot-cold [4]	--	100	39 a	18 a	45 a	27 a
Avg	--	--	92	29	18	46	28

[2] Mean separation within columns of each size by Duncan's multiple range test (P = 0.05)

[1]: Represent 14 weeks at 5C.

[2]: Represent 17 weeks in a cool commercial greenhouse.

[3]: Represent 17 weeks at 5C.

[4]: Represent 6 weeks at 5C.

Table 3. Effect of start plant size and pre-cold treatments on flower percentage, unopened flower buds, days to visible bud and anthesis from the start of forcing in *Leucanthemum* x *Superbum*.

Cultivar	Start plant size	Treatments	Node No. at start of treatment	Flowering percentage	Flower bud no.	Days to visible bud	Days to Anthesis	Days visible bud to anthesis
Snowlady	50 - cell	no cold	16	100	4 a	30 a	60 a	31 a
Snowlady	128 - cell	no cold	11.3	100	4 a	31 a	60 a	32 a
Avg	--	--	13.7	100	4	31	60	31
Snowcap	5.7-cm pot	no cold	--	100	6 c	28 a	58 a	30 a
Snowcap	5.7-cm pot	3-wks LD -- cold [1]	--	100	11 ab	15 d	41 d	26 c
Snowcap	5.7-cm pot	3-wks SD --- cold [1]	--	100	14 a	17 cd	46 c	30 ab
Snowcap	5.7-cm pot	3-wks natural day --- cold [1]	--	100	15 a	21 b	49 c	28 bc
Snowcap	5.7-cm pot	3-wks 12-hr photo.--- cold [1]	--	100	12 ab	19 bc	48 c	29 ab
Snowcap	5.7-cm pot	pot-cool greenhouse [2]	--	100	12 ab	26 a	54 b	29 ab
Snowcap	5.7-cm pot	cold-pot [3]	--	100	9 bc	27 a	54 b	27 bc
Avg	--	--		100	11	22	50	28
White knight	5.7-cm pot	no cold	--	100	59 b	23 b	55 a	31 ab
White knight	5.7-cm pot	pot - cool greenhouse [4]	--	100	35 a	17 c	49 b	32 a
White knight	5.7-cm pot	cold-pot [5]	--	100	24 a	29 a	57 a	28 b
White knight	5.7-cm pot	pot-cold [5]	--	100	18 a	25 ab	57 a	31 ab
Avg	--	--	--	100	40	24	55	31

[z] Mean separation within columns of each cultivar by Duncan's multiple range test (P = 0.05).
[1]: Represent 9 weeks at 5C.
[2]: Represent 12 weeks in a cool commercial greenhouse.
[3]: Represent 12 weeks at 5C.
[4]: Represent 6 weeks in a cool commercial greenhouse.
[5]: Represent 6 weeks at 5C.

Table 4. Effect of start plant size and pre-cold treatments on flower percentage, unopened flower buds, days to visible bud and anthesis from the start of forcing in *Rudbeckia fulgida* 'Goldsturm'.

Start plant size	Treatments	Node No. at start of treatment	Flowering percentage	Flower bud no.	Days to visible bud	Days to Anthesis	Days visible bud to anthesis
bare root	no cold	--	100	19 d	57 a	10 a	46 a
bare root	3-wks LD -- cold [1]	--	100	59 abc	31 c	70 c	39 b
bare root	3-wks SD --- cold [1]	--	100	62 ab	39 bc	75 bc	35 b
bare root	3-wks natural day --- cold [1]	--	100	51 abc	44 b	80 b	37 b
bare root	3-wks 12-hr photo.--- cold [1]	--	100	44 bc	45 ab	78 bc	33 b
bare root	pot-cool greenhouse [2]	--	100	66 a	42 bc	80 bc	38 b
bare root	cold-pot [3]	--	100	42 c	47 ab	85 b	38 b
Avg	--	--	100	49	43	81	38
50 - cell	no cold	9	100	23 a	84 a	124 a	40 a
50 - cell	3-wks LD -- cold [1]	9	100	27 a	43 b	79 b	36 ab
50 - cell	3-wks SD --- cold [1]	9	90	30 a	55 bc	87 b	32 b
50 - cell	3-wks natural day --- cold [1]	9	86	29 a	56 c	88 b	32 b
50 - cell	3-wks 12-hr photo.--- cold [1]	9	63	28 a	47 bc	84 b	36 ab
50 - cell	pot-cool greenhouse [2]	9	78	21 a	55 bc	79 b	34 b
50 - cell	cold-pot [3]	9	75	27 a	46 bc	80 b	34 b
Avg	--	--	84	27	54	89	35
128 - cell	no cold	5	100	26 ab	112 a	151 a	39 a
128 - cell	3-wks LD -- cold [1]	5	50	24 ab	44 b	79 b	34 b
128 - cell	3-wks SD --- cold [1]	5	90	24 ab	46 b	79 b	33 bc
128 - cell	3-wks natural day --- cold [1]	5	70	24 ab	47 b	84 b	36 ab
128 - cell	3-wks 12-hr photo.--- cold [1]	5	90	18 b	51 b	86 b	35 ab
128 - cell	pot-cool greenhouse [2]	5	67	18 a	88 c	116 c	29 d
128 - cell	cold-pot [3]	5	60	32 a	91 c	122 c	30 bc
Avg	--	--	75	24	68	102	34
5.7-cm pot	no cold	--	100	60 a	35 ab	68 a	34 a
5.7-cm pot	pot - cool greenhouse [4]	--	100	75 b	30 c	69 a	39 bc
5.7-cm pot	cold-pot [4]	--	100	80 b	33 cb	74 b	41 c
5.7-cm pot	pot-cold [4]	--	100	77 b	37 a	75 b	38 b
Avg	--	--	100	73	34	72	38

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

[1]: Represent 14 weeks at 5C.

[2]: Represent 17 weeks in a cool commercial greenhouse.

[3]: Represent 17 weeks at 5C. [4]: Represent 6 weeks at 5C.