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MANAGEMENT AND PRODUCTION OF NINE
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JANELLE ELIZABETH GLADY

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M. Suzanne Young
Major Professor's Signature

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MANAGEMENT AND PRODUCTION OF NINE HERBACEOUS PERENNIAL SPECIES

By

Janelle Elizabeth Glady

A THESIS

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ABSTRACT

MANAGEMENT AND PRODUCTION OF NINE HERBACEOUS PERENNIAL SPECIES

By

Janelle Elizabeth Glady

Commercial floriculture growers require economically efficient ways of propagation and production for many different species of herbaceous perennials to meet consumer demand for variety and floral blooms at retail sale. However, propagation and production strategies are both species dependent and affected by juvenility, photoperiod, and temperature requirements. This work tested the hypothesis that environmental conditions could be utilized to control key developmental phases for "quick production" schedules. The plant growth regulator ethephon (Florel®) was applied to manage vegetative stock plants for the purpose of propagation in perennials. Under a 13-h photoperiod, ethephon application at 600 ppm biweekly increased the number of vegetative cuttings and decreased the number of floral buds in *Coreopsis verticillata* L. 'Moonbeam'; 400 ppm weekly was effective for *Veronica longifolia* L.'Sunny Border Blue'. Ethephon application had limited beneficial effects on *Dianthus caryophyllus* L. 'Cinnamon Red Hots'™ and had no or detrimental effects on four other species. To test the requirement for sufficient vegetative development prior to floral induction, four bulking durations under 10- or 16-h were provided prior to 0 or 8 weeks at 5 °C for six species. Days to flower decreased and the number of floral buds increased after increased bulking and chilling for several species tested.

To my grandm

DEDICATION

To my grandma, Elda Glady, and all the strong women who have been examples and inspiration for my life.

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SECTION I

LITERATURE REVIEW

Introduction

Herbaceous perennial plant production involves the management of plant growth, development, and flowering. Production management for the diverse selection of plant material, due to expanding consumer demand, continues to pose challenges for the industry. The promotion of vegetative growth is useful for stock plant management (to produce vegetative cuttings) and for sufficient vegetative growth to obtain plant size (i.e., bulking) prior to inducing flowering.

The United States Department of Agriculture reported a 15% increase in value for potted herbaceous perennial crops in 2002 (USDA, 2003). Perennials crops, other than *Hosta* and *Chrysanthemum*, increased by 18% and are valued at $416,704,000.00. The state of Michigan is a large producer of floriculture crops. In the 'other' (e.g., *Coreopsis grandiflora*) potted herbaceous perennials sector, Michigan produced $44,957,000 (wholesale value), and leads the nation in the number of pots sold. Thus, the importance of the floriculture industry, specifically potted herbaceous perennials, to Michigan is significant. Due to the extreme temperature range and periods of low light levels experienced in Michigan, managing optimum plant growth and flowering requires implementation of lighting and temperature regulation systems for successful commercial production. Further control of plant development can be accomplished through additional growth management tools including application of growth regulating chemicals. Understanding the factors that influence plant growth and reproductive development (e.g., juvenility, vernalization, and photoperiod) is essential for the development of commercial plant production schedules.

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Juvenility is the term given to an early phase of growth during which flowering cannot be induced under any treatment (Thomas and Vince-Prue, 1997). This insensitivity to floral stimuli, i.e. photoperiod and cold, is prevalent in angiosperms and gymnosperms, and prevents flowering before the required energetic capacity to do so (Thomas and Vince-Prue, 1997).

The duration of the juvenile phase varies greatly among species and cultivars, usually lasting longer in woody plants than herbaceous ones. Some plants have no juvenile phase, as flower primordia are found in the seed (Thomas and Vince Prue, 1997). For example, *Pharbitis nil* (L.) Roth becomes responsive to photoperiod 2 days after germination (Imamura, 1967). In contrast, some forest trees are juvenile for 30 to 40 years (Robinson and Wareing, 1969).

Juvenility is responsible for a certain degree of unpredictability in the floriculture industry; therefore it is important to understand so that propagation and production schedules can be developed. The ability to propagate herbaceous perennials through many different sexual and asexual methods, (e.g., seed, stem or root cuttings, division, and tissue culture), results in plants at different stages of maturation when they enter the production system. This difference in maturation can stagger time to anthesis within a crop or force the sale of a vegetative plant, both of which are not conducive to efficient crop management or desired marketing strategies. Seed-propagated plugs are often more cost effective to produce than field-grown plants, but also less predictable because they can be at various stages of maturation, and anthesis requires the

correct timing of photoperiodic treatments, cold treatments, or both (Heins et al., 1997). Exposure to flower induction treatments (i.e., cold or photoperiod) at the adult stage of maturation can improve crop management and flowering characteristics, such as percentage and uniformity.

Juvenility is the first of three growth phases in the maturation process, and is followed by adult vegetative and adult reproductive phases. Plant shoot characteristics, such as leaf shape, and physiological ones, such as the ability to initiate roots easily, change as plants mature. These phases are independently regulated, yet overlapping, allowing a single plant part to express different developmental phases at the same time (Poethig, 1990). In some plant systems, juvenile tissues at the base of a plant are able to continue as juvenile in conjunction with a stable, adult apical meristem (Thomas and Vince-Prue, 1984). For example, basal cuttings of *Hedera helix* L. give rise to plants with juvenile characters, while cuttings from the top of a mature vine show adult characters; those cuttings taken from the transition zone, between the apex and base, exhibit both maturity levels (Wareing and Frydman, 1976).

Minimal leaf number can be used to quantify juvenility in some plants, as measured by the number of vegetative nodes, (i.e. leaves) produced before the inflorescence (Lang, 1965). For example, *Aquilegia* x *hybrida* Sims requires 12 leaves to be responsive to cold induced flowering (Shedron and Weiler, 1982). The juvenile phase of *Coreopsis grandiflora* Hogg ex Sweet ends when approximately eight leaves have formed (Yuan et al., 1998). Many perennials that require cold for floral induction must reach a minimum leaf or node number

before cold perception is possible (Heins et al., 1997). The biennial *Centaurea diffusa* Lam. will not respond to vernalization treatments before rosettes have more than 12 leaves (Thompson and Stout, 1990). A required leaf number for floral induction is not restricted to plants that require cold. Two daylength responsive cultivars of *Salvia splendens* Sello ('Bonfire' and 'Red Pillar') become responsive to photoperiod when the juvenile phase ends at a stem node number between four and six (Lai and Weiler, 1975).

When plants have passed the juvenile phase, they are 'ripe-to-flower', meaning that they are capable of flowering (Lang, 1965), or receptive to floral induction. However, flowering may still be delayed or sporadic due to the absence of other necessary floral inducing stimuli such as temperature and/or photoperiod. For example, flowering percentage in mature *Aquilegia* x *hybrida* is greatly increased after a vernalization period (Shedron and Weiler, 1982). *Rudbeckia fulgida* Ait. 'Goldsturm' is an obligate long-day plant and will not flower under short days, even when the required 10 nodes have been developed (Yuan et al., 1998).

Maturation that results in a growth phase change from juvenile to adult phases over time commonly occurs with aging; however, the gradual and irreversible decline in vigor associated with aging is not directly responsible for maturation and phase change (Wareing and Frydman, 1976). There is no specific morphological characteristic that gives a plant the ability to flower or indicates the capacity to flower, and different plant characteristics (e.g., leaf phyllotaxy) (Table 1) do not change all at once (Thomas and Vince-Prue, 1984).

Additionally, among these characteristics, no single character has been indisputably connected with the transition to adult reproductive growth and flowering. It has been postulated that the duration of the juvenile stage is determined by one of three factors: plant size, endogenous gibberellins, or perception of a floral stimulus (Wareing and Frydman, 1976).

Table 1. Juvenile and adult characters of *Hedera helix* L. (English ivy) (Wareing and Frydman, 1976).

Juvenile characteristics	Adult characteristics
• Three- or five-lobed, palmate leaves	Entire, ovate leaves
• Alternate phyllotaxy	Spiral phyllotaxy
• Anthocyanin pigmentation of young leaves and stems	No anthocyanin pigmentation
• Stems pubescent	Stems glabrous
• Climbing and plagiotropic growth habit	Orthotropic growth habit
• Shoots show unlimited growth and lack terminal buds	Shoots show limited growth terminated by buds with scales
• Absence of flowering	Presence of flowers

Plant Size

Plant size appears to be a very important factor in the transition from juvenile to adult growth. Therefore, the environmental conditions that increase plant growth will consequently decrease the length of the juvenile phase (Thomas and Vince-Prue, 1997). Unlike commercial means to measure plant size (e.g., height or trunk girth) in relation to maturity level, size is best measured by leaf or node count, in herbaceous and woody plants alike. Node number is a function of temperature and time, and is a more reliable indicator of maturity than time alone (Holdsworth, 1956).

In general, plant species become more sensitive to inductive conditions as they increase in size and maturity (e.g. node number). In herbaceous perennials, such as *Coreopsis* and *Rudbeckia*, plants with a greater number of nodes before inductive stimuli flower faster, develop fewer subsequent nodes before flowering, and produce more floral buds (Yuan et al., 1998). This increased initial growth enables herbaceous plants to establish enough photosynthetic leaf area to support the large energy demands of reproductive development (Schwabe, 1976).

Gibberellins

Gibberellins are a family of terpenoid compounds derived from the *ent*-kaurene ring structure that are responsible for, or precursors or metabolites to, physiological responses such as internode elongation, juvenility changes, and flower sexuality. Although 120 gibberellins have been identified in plants, only a few (GA_1, GA_3, GA_4) are biologically active as hormones. In addition to

molecules that are derived from the previously defined chemical classification, other compounds have been referred to as gibberellin-like substances. A "gibberellin-like substance" is a compound or extract that has biological activity similar to gibberellins, but without a defined chemical structure (Taiz and Zeiger, 1998).

Actively growing roots produce gibberellin-like substances. These substances are also found in adventitious, internodal, and regenerated roots at the base of cuttings. Similar to the influence of gibberellin-like substances on the generation of new growth, exogenous GA_3 has the ability to rejuvenate adult plants when applied to shoots (Robbins, 1957; Robbins, 1960). In addition, gibberellin-like substances were detected in extractions from root apices in *Hedera helix* L. and displayed a similar peak to GA_1 and GA_3 when chromatographed (Frydman and Wareing, 1973). Thus, gibberellins and gibberellin-like substances are similar in structure and mode of action.

The influence of gibberellic acid on juvenility is apparent in *H. helix* where concentrations of gibberellic acid are higher in juvenile apical buds than their adult counterparts (Frydman and Wareing, 1973). It has been postulated that as plants grow and the distance from shoot apices to the roots increases, the effect of gibberellins on inhibiting maturity decreases. Although relatively high levels of endogenous gibberellins in the shoot apices can promote and maintain juvenility (Wareing and Frydman, 1976), GA_4 can promote juvenile conifers to enter into the reproductive phase (Metzger, 1988).

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The state of shoot maturation is influenced by the location of the gibberellin-like substances in the roots in relation to shoot apices. Flowering in black current (*Ribes nigrum* L.) was delayed due to the close proximity of roots to the shoot apices (Schwabe, 1976). Rogler and Hackett (1975) showed that roots with high concentrations of gibberellic acid not only have the ability to influence the juvenile phase, but also keep nearby shoots in this juvenile state for an indefinite amount of time.

Perception Ability

Plant maturity can be influenced by the ability to perceive a floral stimulus, thus changing from juvenile or vegetative to reproductive. Changes in both the leaves and shoot apices may be needed to perceive this signal. There are two different hypotheses that support the perception of a floral stimulus as critical to growth phase transition: (1) the plant needs to be large enough in size for the leaves to transmit one or more signals to the apex or (2) the apical meristem is independent and undergoes a phase transition before it can respond to any phase changing stimulus (Thomas and Vince-Prue, 1984).

Leaves are the primary sites of photoperiodic perception, and the state of maturation influences what can or cannot be perceived. Juvenile plant leaves are insensitive to daylength and therefore cannot produce a floral stimulus. This was demonstrated through work on *Bryophyllum daigremontianum* (R. Hamet et Perr.) Berg. conducted by Zeevaart (1962). Shoot apices from juvenile plants flowered when grafted onto adult plants, indicating that the growing points are capable of flowering, but the leaves are not able to produce a floral stimulus.

This was also demonstrated in the short-day plant *Ipomaea batatas* (L.) Lam. Immature seedlings flowered when grafted onto adult *Pharbitis nil* under short days, but not when originally exposed to inductive cycles (Takeno, 1991).

In contrast, there are several arguments that suggest the apical meristem is independent, changing in composition before becoming responsive to any leaf signals. The proposed autonomous change in the apical meristem could be dependent upon age and the number of cell divisions that have occurred since germination (Wareing and Frydman, 1976). Experiments with *Larix leptolepis* Murray (Robinson and Wareing, 1969) and *Mangifera indica* L. (Kulkarni, 1988) demonstrate the inability of juvenile scions to flower even when grafted onto adult stock plants with sufficient nutrient reserves and floral stimuli. Similar results through numerous grafting experiments in woody and herbaceous plant systems support the hypothesis that the apical meristem must undergo a phase transition prior to floral stimulus perception.

In *Nicotiana silvestris* L. (tobacco), age of the plant providing the scion is important, as only mature tobacco scions are able to perceive any promoter or inhibitor signal gradients for floral development (Singer et al., 1992). A competent terminal bud from a tobacco plant with 26 nodes will initiate 10 to 12 new nodes before anthesis when grafted onto a mature stock plant, while a scion from a seedling with only 7 nodes will initiate 22 new nodes. In *Ribes nigrum*, apical parts were able to flower even after sequential decapitations inhibited the plant from gaining the minimum number of leaves necessary for photoperiodic responsiveness (Robinson and Wareing, 1969). In this plant system, size

appeared to be relative and not the primary factor determining phase change. In addition to the morphological changes of node and leaf development, metabolic changes are also present. For example, polypeptide changes in *Silene coeli-rosa* L. are evident in mature meristems, which consequently flower faster than juvenile ones (Nougarede et al., 1989).

Results from grafting experiments between juvenile scions and adult stock plants, or vise versa, suggest that a possible juvenile hormone is acting as a trigger for phase change and is being translocated within the plant. Rejuvenation occurred when mature *Hedera helix* scions were grafted onto juvenile stocks if the leaves from the mature scions were removed as to not interfere with the juvenile signal (Clark and Hackett, 1980). Thus perhaps juvenile leaves produce a substance that promotes reversion while adult leaves inhibit it. However, not all grafting experiments conform to this postulation. Young mango seedlings could not be induced to flower when grafted onto adult plants (Kulkarni, 1988).

Maturity is a stable-state growth phase in most plant systems and can be retained through vegetative propagation. However, although maturity is stable, it is not irreversible. External factors, such as nutrition inadequacies, low light, water stress, defoliation, low temperature, and application of exogenous hormones, such as GA_3, can cause rejuvenation of adult shoots (Taiz and Zeiger, 1998).

Vernalization

The natural correlation of flowering time with the seasons in temperate climates is essential for the survival of a plant species, as reproductive development is unfavorable during colder temperatures. Therefore, the timing of the transition between vegetative and reproductive growth is critical. Temperature is a major environmental cue plants perceive to coordinate flowering with changing seasons (Michaels and Amasino, 2000). Although species dependent, warm temperatures (≈ 20 °C) influence flower development, while low temperatures (≈ 0 °C) influence dormancy and vernalization.

During dormancy, the growth of any developing organ is arrested due to internal factors, and upon release, this growth is resumed instead of new growth activities being introduced (Chouard, 1960). Dormancy can be defined as the temporary suspension of visible growth of any plant structure containing a meristem and consists of three types: endodormancy, paradormancy, and ecodormancy (Lang, 1987). Endodormancy is the specific induction of a morphological response solely within the affected structure. Paradormancy is the specific induction of a morphological response originating in a structure other than the affected structure. Ecodormancy is the growth limitation associated with inadequate environmental factors necessary for plant growth.

Thus, dormancy can affect the germination of seeds, breaking of buds, and floral development of some trees, shrubs, and herbaceous perennials located in temperature climates (Hartmann et al., 1997). Perception of cold by the apical meristem is an example of endodormancy; photoperiodic responses perceived by the leaves and related to the apical meristem is an example of

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paradormancy; water stress is an example of ecodormancy (Lang et al., 1987). Also, dormancy is not solely influenced by cold, and may be broken (i.e., removal of inhibitors) by external stimuli other than cold, such as heat, long days, or sublethal treatments (i.e., application of hydrogen-cyanomide based chemicals).

Unlike dormancy, which affects growth or vegetative and floral development, vernalization affects the physiology of reproductive development and influences plant competence towards floral initiation. This promotion of flowering after a cold period was observed and reported in cereals during the late nineteenth century. The word "Jarovization" (from "Jar" meaning god of spring and "Jarovoe" meaning spring cereals) was termed by the Russian scientist Lysenko. In English, "vernalization" is derived from the Latin word *vernum*, meaning spring (Chouard, 1960). Early research by G. Gassner and A. Lang has generated a base of research for understanding the vernalization process that more recent genetic and molecular research has built upon.

Vernalization is commonly defined as the specific promotion of flowering by a cold treatment provided to an imbibed seed or young plant (Thomas and Vince-Prue, 1984). Genetic and quantitative environmental factors influence the development of the vernalization processes that lead to "ripeness-to-flower" (Napp-Zinn, 1987). Vernalization is distinguished from other environmental factors in flowering because floral initials are not yet present after vernalization, and further inductive conditions are required for flower initiation (Vince-Prue, 1975). This phenomenon is described in *Triticum* (wheat), where both floral and

terminal spikelet initiation are affected by temperature and photoperiod after vernalization (Pinthus, 1985).

Effective temperatures for vernalization have traditionally been cited between 1 to 7 °C (Chouard, 1960). However, in *Beta vulgaris* (L.) (sugar beet), the effective temperature range is –2 °C to 10 °C; Petkus winter rye (*Secale cereale* L.) has a range between –5 °C to 15 °C (Vince-Prue, 1975). Additionally, a determined temperature optimum is relative since the optimum temperature may shift depending upon duration of the cold treatment. Temperatures that may not be inductive at the start of cold may be influential towards the end. For example, the optimum vernalization temperature for *Hyoscyamus* shifted from 10 °C during days 7 thru 15 of cooling to 3 to 6 °C at day 42 (Lang, 1965).

The length of cold exposure required for completion of the vernalization process is species dependent. Flowering percentage in *Aquilegia* x *hybrida* 'McKana's Giant' increased from 0 to 100 percent when cold treatment (4.5 °C) increased from 0 weeks to 12 (Shedron and Weiler, 1982). Rooted cuttings of *Veronica longifolia* L. 'Sunny Border Blue' with four to five nodes flower most uniformly and rapidly after nine weeks at 5 °C (Engle, 1994). In most plant species, flowering is delayed, or plants fail to flower, when exposed to an inadequate duration of cold (Thomas and Vince-Prue, 1984).

Overall, an adequate amount of time at an effective temperature range will allow for the progression of vernalization processes to occur (Lang, 1965). The subsequent vernalized state is considered to be stable, as change in the genetic pattern serves as a "permanent memory" controlling plant growth. For example,

Hyocyamus niger L. remains vernalized 300 days after cold (Taiz and Zeiger, 1998). However, the perpetuation of vernalization through mitosis requires that progeny be re-exposed to cold for vernalization to occur.

Required chilling for the development of reproductive organs and subsequent flowering varies greatly between species. For example, winter annuals (e.g., wheat) can be vernalized as imbibed seeds with subsequent flowering in the spring; biennial plants (e.g., *Hyoscyamus niger*) cannot be vernalized as seeds and must grow to a certain size before cold is perceived. Cold-requiring perennials (*Lolium perenne* L.) overwinter and require vernalization every year (Vince-Prue, 1975). Vernalization can be further classified by whether it is absolutely required for flowering. Winter annuals, such as rye, are considered facultative because flowering is hastened, but not determined, by cold; biennials, such as some sugar beets, are considered obligate because a cold period is required for flowering (Michaels and Amasino, 2000).

The stage of development at which plants have the ability to perceive cold is dependent on the presence of a juvenile phase. Cereal seeds with adequate moisture (Purvis, 1961) and rye embryos (Chouard, 1960) are capable of responding to cold. The biennial *Hyoscyamus* is insensitive to cold before an age of 10 days (Lang, 1965); most other biennials and herbaceous perennials require more time to reach the necessary size requirement and grow as rosettes until they are sensitive to vernalization. The perennial *Coreopsis grandiflora*

'Sunray' must have more than 16 leaves (8 nodes) before vernalization can occur in a population of plants (Yuan et al., 1997).

The strong interaction between vernalization and photoperiod suggests that these two environmental signals act simultaneously yet independently to induce flowering (Lang, 1965). The most common interaction is the combination of vernalization and long days, with many plant species requiring a cold period followed by long days to initiate flowers (e.g., winter wheat) (Taiz and Zeiger, 1998). For some of these species, short days can substitute partly or entirely for cold. For example, the normal flowering response of a low temperature/long day induction treatment in *Campanula medium* L. can be substituted by a short day/long day treatment (Vince-Prue, 1975). Therefore, although the relationship is not fully understood, short days and cold seem to be different alternative mechanisms that lead to flowering in some plants.

Additionally, exogenous GA_3 can substitute for cold and induce flowering in some long day plants (Vince-Prue, 1975). However, it does not substitute for cold in most plants and, unlike vernalization where shoot elongation and flower initiation occur simultaneously, GA_3 will promote shoot elongation before flower initiation. Here, cold may lead to the biosynthesis of GA_3, which may be further required for the flowering process. However, this role in flower initiation in mature plants contradicts previous statements about the ability of GA_3 to promote juvenility. Regardless, different forms of gibberellins influence various physiological events, and there are no data to suggest that juvenility is promoted by GA_3 in all plants or that GA_3 has a role in flower induction for all plants.

Numerous reviews have cited research that demonstrates cold perception occurs in the actively dividing cells of the shoot apical meristem (Chouard, 1960; Wellensiek 1964; Lang, 1965; Vince-Prue, 1975). Thus, vernalization would occur when only the shoot apex is exposed to cool temperatures, irrespective of plant temperature elsewhere. In addition, cells dividing in young leaves, particularly at the petiole base, are also receptive to cold and able to produce a floral stimulus (Vince-Prue, 1975; Crosthwaite and Jenkins, 1993). Cuttings of *Lunaria biennis* L. with fully expanded leaves before a cold treatment generated only vegetative plants while those cuttings with leaves that had not fully expanded before cold regenerated into flowering shoots (Wellensiek, 1964).

The developmental processes that lead to flowering as a result of vernalization require further investigation. Numerous grafting experiments between vernalized and non-vernalized plants (e.g., *Hyoscyamus niger*, *Beta vulgaris*, *Lunaria biennis*) showed that induction can be transferred to non-vernalized plants, which suggest the presence and ability of some floral inducing substance to be translocated throughout the plant (Lang, 1965). Although specific translocation pathways have not been determined, further experimentation suggests that cold temperatures induce the production of a transmissible substance (termed vernalin), which is proposed to be a precursor to a theoretical flowering hormone, florigen. However, despite numerous grafting experiments that demonstrate the translocation of a floral inducing hormone, florigen is still only theoretical, as no concrete evidence has been found to support its existence.

More recent hypotheses have focused on the concept that the purpose of a cold treatment is to induce changes in the cells. The vernalized state is perpetuated through the continued divisions of vernalized cells, as the vernalized condition is also a property of the daughter cells (Thomas and Vince-Prue, 1984). Hence, the ability of leaves initiated from a vernalized meristem to respond to long days and produce a floral stimulus is presumably greater than those leaves initiated before cold. However, research in biennial sugar beet concluded that plants do not need leaves initiated from a vernalized apical meristem, but that young, expanding leaves are capable of responding to low temperatures and consequently, produce a floral stimulus under long days (Crosthwaite and Jenkins, 1993).

The flowering process is influenced by environmental factors (e.g., vernalization and photoperiod), biochemical substances (e.g., gibberellic acid), and genetic regulation (e.g., FLOWERING LOCUS C, FLC) (Michaels and Amasino, 2000). Genetic research has utilized *Arabidopsis* mutants to investigate the autonomous pathway of flowering and the induction of genes that regulate it. A major repressor of flowering is the FLC gene, as its mutant *flc* results in early flowering (Michaels and Amasino, 1999). It appears that the vernalization response in *Arabidopsis* is primarily due to the suppression of FLC, which decreases the level of *FLC* transcript and subsequent biosynthesis of the specific protein that it encodes (Sheldon et al., 2000).

Another repressor of flowering is a methyl block in the promoter region of a critical flowering initiation gene, which prevents its transcription and

subsequent flowering. Therefore, it has been proposed that vernalization removes this block through its natural demethylating effect to allow for consequent transcription and flowering (Burn et al., 1993). One theory is that prolonged exposure to low temperature will increase DNA demethylation and promote subsequent flowering (Finnegan et al., 1998). This may be accomplished through the uncoupling of DNA replication and cold sensitive maintenance methylation strands, to synthesize new, unmethylated DNA strands. This theory is supported by studies showing that the DNA demethylating agent 5-azacytidine (5-azaC) can partially substitute for cold in the promotion of flowering (Burn et al., 1993). *Arabidopsis* and *Thlaspi* plants treated with 5-azaC induced nonvernalized plants to flower earlier than untreated control plants. Additionally, non-vernalized, transformed *Arabidopsis* plants with the methyltransferase (*METI*) antisense gene flowered faster than non-transformed control plants (Finnegan et al., 1998). Thus, the parallel between vernalization and DNA demethylation systems to activate the same flowering pathway is supported by more recent research.

Devernalization is the partial or full erasure of the cold effect triggered by exposure to warm temperatures (> 30 °C) or short days during or after vernalization (Bernier et al., 1981). In *Chrysanthemum* x *morifolium* Ramat., plants can become devernalized during the high temperatures of summer. In addition to warm temperatures, two other potential causes of devernalization have been observed: insufficient maturation of axillary buds to a specific developmental stage influence cold perception as exhibited in *Geum urbanum* L.;

and vernalization is not perpetuated indefinitely through cell division (e.g., perennial grasses) (Vince-Prue, 1975).

Photoperiod

Photoperiod is the duration of light a plant receives that then determines the amount of light energy available to the plant for photosynthesis and physiological responses, independent from light intensity (Thomas and Vince-Prue, 1997). Literally meaning 'light' and 'duration of time', photoperiodism, the developmental response of the plant, is actually a plant response to the length of the uninterrupted night period. In addition to juvenility and vernalization, it provides another way for plants to correlate developmental processes with the changing seasons. Daylength influences flower initiation in the long-day plant *Hyoscyamus niger* L. (Parker et al., 1950) and the short-day plant *Xanthium saccharatum* Wallr. (Parker et al., 1946). Photoperiod manipulation in the floriculture industry is an important tool for management of plant growth since daylength can be controlled to strategically influence vegetative growth, floral initiation, or floral development.

There are three main categories of photoperiod responses in respect to floral initiation: long-day plants (LDP), short-day plants (SDP), and day-neutral plants (DNP). Long-day plants flower when the dark period is shorter than a critical length; SDP flower when the dark period is longer than a critical length; and DNP flower irrespective of night length (Thomas and Vince-Prue, 1997). For example, *Coreopsis grandiflora* 'Early Sunrise' is an LDP requiring a photoperiod

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> 14 hours (Damann and Lyons, 1993). *Salvia leucantha* L. is a SDP, requiring 10-hour days (or shorter) for flower development (Armitage and Laushman, 1989).

In addition, plants may have an obligate (qualitative) or facultative (quantitative) photoperiod requirement. Plants with an obligate requirement flower only when a specific length of day is reached. Flowering in plants that have a quantitative requirement is accelerated, but not dependent upon, a certain daylength. This critical daylength is defined by Thomas and Vince-Prue (1997) as the photoperiod that marks the transition between flowering and non-flowering. Plant response to the critical daylength can be sensitive to a difference in minutes or hours and is influenced by plant age, air temperature, the number of inductive cycles, and the variability among plant species. Perception of the critical daylength is accomplished through a "biological inner clock" to measure the duration of light and a photoreceptor to distinguish between light and dark.

Biological Rhythms

The measurement of time must be independent of all other environmental factors, mainly temperature and light intensity, to guarantee the right plant processes occur at the right time. In response to the daily light-dark cycles on Earth, living organisms have developed circadian rhythms. An endogenous oscillator or circadian clock within plants may be coupled to plant processes, such as floral initiation (Taiz and Zeiger, 1998). This self-sustaining pacemaker is independent of ambient temperatures. The period length is close to 24 hours

and is synchronized by environmental signals, mainly the red (600 – 700 nm)/far red (700 – 800 nm) light ratio transitions at dawn and dusk, as described by a model for timekeeping in *Pharbitis* (Thomas and Vince-Prue, 1997).

Thus, the measurement of time by biological rhythms is an important and independent pathway to floral induction that, when coupled with other mechanisms such as juvenility and vernalization, enables plants to determine the correct ecological time to flower in their specific environmental niche. Some plant species in temperate climates require that adult plants receive a cold treatment followed by long days for flower initiation (Lang, 1965). Although biological rhythms are mainly associated with floral induction, they may also play an important role in other plant processes such as sex expression, plant dormancy, vegetative storage, asexual propagation, and seed germination (Thomas and Vince-Prue, 1984). The induction of plant dormancy during fall is partly induced by short days (Smith and Kefford, 1964). However, flower initiation is not solely determined by the ability of a "biological clock" to measure daylength, but also by light quality and the photoreceptor pigments that discriminate between light and darkness.

Light Quality and Phytochrome

Light quality is the combination of wavelengths of light available for plant processes. The ratio between red (R) light and far red (FR) light influences plant morphological characteristics. A high R:FR ratio is responsible for short, well-branched plants; a low R:FR ratio increases stem elongation and leaf area, decreases lateral branching, and decreases leaf and flower color (Thomas and

Vince-Prue, 1997). Chlorophyll screening (i.e., the absorption of red light by chlorophyll and reflection of far red light) influences light quality through an increase of far red light relative to red light that reaches the photoreceptor pigment (Cathey and Borthwick, 1964; Thomas and Vince-Prue, 1997).

Both R and FR light serve as a way to measure the length of the light and dark periods, which are important stimuli for regulation of plant growth. The R:FR ratio has a strong influence on many plant responses, including seed germination, plant architecture, and developmental sequences. For example, flowering is promoted and inhibited in LDP and SDP, respectively, under a low R:FR (Lane et al., 1965). Stem extension is promoted by a low R:FR in most plant species. Light environments deficient in R light during production cycles increased plant height from forcing to visible bud by 65% in *Campanula carpatica* Jacq.; while those deficient in FR light inhibited flowering in *Viola* x *wittrockiana* Gams. (Runkle and Heins, 2001).

The interaction between the "inner clock" and the R:FR ratio received by the photoreceptor is an important feature in the flower induction process. The site of this interaction is in the plant leaves, as they are the principle organs of light perception and consequent floral induction (Lang, 1965). Phytochrome is the primary light absorbing, protein pigment that is responsive to the red (660 nm) and far-red (730 nm) range of the electromagnetic spectrum (Taiz and Zeiger, 1998). Phytochrome is the major photoperiodic receptor responsible for mediating plant responses to light through gene regulation or biophysical changes (Thomas and Vince-Prue, 1997).

Phytochrome exists in a photoreversible state between a red-absorbing form (P_R) and a far-red absorbing form (P_{FR}), where $P = P_R + P_{FR}$. Exposure to red light converts P_R to the physiologically active, yet unstable, P_{FR}, which in turn reverts back to P_R upon exposure to far red light (Taiz and Zeiger, 1998). The hypothesis that inductive responses are determined by the phytochrome state at the end of the light sequence or dark period was proven in lettuce, as dark germination of lettuce seeds depended upon the last exposure in the sequence of alternating R and FR light (Borthwick et al., 1952). Seeds exposed to R light as the final treatment had a germination rate close to 100 percent, while germination in those that received FR light as the final treatment was strongly inhibited. The researchers proposed that there was only one light absorbing pigment able to exist in two interconvertible forms: a R light absorbing form and a FR light absorbing form. Further research with plant extracts demonstrated these photoreversible properties of phytochrome (Butler et al., 1959), thereafter, dark germination of lettuce seed was the model system for phytochrome. *Xanthium saccharatum* Wallr. (cocklebur) is a short-day plant in which even seconds of night interruption prevent flowering due to an increase in P_{FR}, (Parker et al., 1946); however, this interruption of R light to *Xanthium* can be reversed with an exposure to FR light (Borthwick et al., 1952).

Flowering in Short-Day Plants

Short-day plants are commonly considered to flower specifically or most rapidly in response to daylength exposure shorter than a certain number of hours of light. Velvet sage (*Salvia leucantha* L.) is a short-day plant with a different

critical photoperiod for floral initiation (12 hours) and subsequent development (10 hours) (Armitage and Laushman, 1989). More importantly, it is the critical night length that promotes flower initiation, thus, plants would be more effectively termed "long-night plants." Although light counteracts the required darkness for flowering in SDP, it is not without a purpose, as a preceding exposure to light is necessary for a subsequent dark period to be inductive (Thomas and Vince-Prue, 1997). This light period is not just photosynthetic, but an important component to timekeeping, as it serves as a signal to set the phase of the circadian rhythm. Photoperiodic induction under photosynthetically insignificant light levels has been accomplished in *Xanthium* and *Pharbitis*.

There are two hypotheses for the perception of light and darkness in SDP. First, the "hourglass theory" proposed that the transfer to darkness initiates a noncyclic process that must be completed in sequential order to measure durations of light and dark. The "hourglass" tips upon darkness and continues to empty as long as there is darkness, resulting in floral initiation; if this process is interrupted by a light period, floral initiation is inhibited. *Xanthium saccharatum* Wallr. (cocklebur) is an SDP in which night interruption periods as brief as a few seconds, dependent upon intensity, prevents flowering (Parker et al., 1946). The proposed "sands" in the hourglass are P_{FR}, which must fall below a certain level as to not inhibit flowering in SDP. However, the hourglass theory has been disregarded because, unlike all other biological processes that are influenced by temperature, it is not, and therefore not considered a true biological process.

The second hypothesis is that time is measured by an internal clock with an oscillation between inductive and non-inductive phases. For flowering to occur, the light and dark periods must be in sync with this rhythm (Thomas and Vince-Prue, 1997). This internal rhythm is free running, meaning it continues even under long periods of darkness. Thus, it may need an initiation signal to start, such as the change from light-to-dark or dark-to-light transfer. The dark period starts the circadian rhythm, and flowering is induced only if it coincides with the right phase of the circadian rhythm. Darkness during the day does not effectively initiate flowering in duckweed (*Lemna perpusilla* Torr.), as the dark period does not coincide with the circadian clock's night phase (Sweeney, 1987).

Phytochrome may be linked to circadian time. Light breaks during dark periods inhibit flowering in SDP because of an increased amount of flower inhibiting P_{FR}. Thus, SDP require a larger amount of P_{FR} at the beginning of the dark period, but smaller amounts during the last part to promote flowering (Zeevaart, 1976). The decreased amount of P_{FR}, and thus floral initiation in SDP, is accomplished through long, uninterrupted periods of darkness preceded by a minimal photoperiod.

Photoperiodism is perceived in the leaves, which, in response to changing phytochrome forms, are believed to produce and translocate a floral inducing stimulus to the apex, where transition to flowering takes place (Lang, 1965). This theoretical hormone was termed "florigen" by Chailakhyan (Taiz and Zeiger, 1998), which despite numerous research activities, has not been identified. The translocation properties of florigen have been demonstrated through grafting

experiments. For example, leaves of the SDP *Xanthium* induced under SD will continue to flower and induce other leaves when grafted onto a plant under LD (Thomas and Vince-Prue, 1984).

Flowering in Long-Day Plants

Long-day plants flower specifically or most rapidly in response to daylengths longer than a given threshold duration. The specific daylength required for flowering may be dependent upon variables such as exposure to cold, and can vary between and within species. For example, 'Eva Cullum' phlox (*Phlox paniculata* Lyon ex Pursh) is an LDP flowering most rapidly under continuous light; 13 hours is required for flowering in noncooled plants, while only 10 hours is needed for plants cooled at 5 °C for 15 weeks (Runkle et al., 1998). 'Ester Read' daisy chrysanthemum (*Chrysanthemum* x *superbum* Bergmans) flowered under photoperiods of 13 hours or longer while a different cultivar, 'T. E. Killian', only flowered under photoperiods greater than 15 hours (Griffin and Carpenter, 1964). Although the mechanism for measuring time is unknown in LDP, it is thought to be similar to SDP. However, unlike SDP, flowering in LDP is inhibited by long nights and requires a long duration of exposure to light (Lane, 1965). Additionally, the critical night length is measured, but not the overriding factor as in dark-dominant SDP (Thomas and Vince-Prue, 1997). Continuous (24-hour) periods of light promote, but are not required for complete flowering in LDP.

In LDP, flower initiation is promoted by far-red light and inhibited by red light. Night breaks are most effective at flower promotion when they are long (>

30 minutes), at high intensities, and include both R and FR light. Plants exposed to night breaks without FR light flower slower, if at all (Vince-Prue, 1994). For example, *Coreopsis verticillata* L. 'Moonbeam' is an LDP, flowering fastest under photoperiods greater than 14-hours or provided with 2 hours of night interruption lighting during a long night (Runkle et al., 1998).

Similar to SDP, phytochrome conversion and reversion has been demonstrated in flowering of LDP. Phytochrome sensitivity to R and FR light during different phases of the circadian rhythm influence floral initiation, and may be due to two sequential phytochrome-mediated events necessary for flowering in LDP. The first event may occur towards the middle of the dark period and require a relatively high level of P_{FR} to initiate flowering; the second lower P_{FR} requiring period might occur at the end of the day to promote floral development (Deitzer, 1984). This diurnal fluctuation of P_{FR} level in LDP is possibly related to the endogenous circadian rhythm (Zeevaart, 1976) or may be the result of two circadian rhythms (Vince-Prue and Takimoto, 1987). The first rhythm may be responsive to FR light during the light period and responsible for measuring light duration. The second R light responsive rhythm may run in the darkness, become suspended during the light period, and is accountable for the measurement of the critical night length. Thus, the timekeeping mechanism in LDP is not as clear as in SDP.

Flowering in Day-Neutral Plants

Day-neutral plants flower irrespective of daylength. Examples of day-neutral plants include Coleus (*Coleus blumei* Princeton strain) and African violet

(*Saintpaulia ionantha*) (Thomas and Vince-Prue, 1997). Other DNP species include cucumber, annual bluegrass, and rice (Salisbury, 1981).

Control of flowering in DNP species is dependent upon juvenility and temperature, but not daylength. Three phases of reproductive development include a biochemical change in the plant (induction), a morphological change when organs, such as the inflorescence or buds, can be recognized (initiation), and development and expansion of the inflorescence and flowers (development). The two final stages of floral development, bloom and pollen shed at anthesis, are generally not significantly affected by photoperiod, but by temperature. Thus, temperature can have a significant role in floral development in DNP. Bulbs such as *Tulipa*, *Freesia*, and *Allium* primarily rely on temperature fluctuations to control bulb growth, development, and flowering (Le Nard and De Hertogh, 1993).

Ethylene

Ethylene is one of the five classes of endogenous plant hormones (Bleeker and Kende, 2000). Significantly affecting many physiological plant growth processes, it is the most widely used plant hormone in commercial agriculture, representing a multimillion-dollar industry (Beaudry and Kays, 1988a).

The Russian scientist Dimitry Neljubow discovered ethylene in the early 20th century after observing specific morphological plant responses to coal gas lamps, including decreased height, radial growth instead of terminal, and increased stem thickness. This reaction to ethylene is termed the "triple

response". Despite the identification of ethylene as a natural plant product and hormone, it was considered to have an indirect physiological role mediated by auxin because plant responses to ethylene are similar to auxin (e.g., adventitious root formation; Taiz and Zeiger, 1998). However, advanced chemical techniques and gas chromatography have established ethylene as an important endogenous plant hormone due to its significant independent and combined affects with other plant hormones on plant growth and plant processes.

Ethylene is an olefin, meaning it is an unsaturated, open chain hydrocarbon that has only one double carbon bond. A gas in its natural state, ethylene is flammable, easily oxidized, and active at very low concentrations. Due to these properties, ethylene is very easily released from tissues and can move through intercellular spaces, directly affecting nearby plant organs (Bleeker and Kende, 2000). All plant tissues have the ability to produce ethylene, although major concentrations are found in nodal and meristematic regions and senescing tissues (Taiz and Zeiger, 1998).

Methionine is the sole precursor for ethylene formation and is kept in constant supply through the Yang cycle (Adams and Yang, 1979). In addition, ACC (1-aminocyclopropane-1-carboxylic acid) is the direct precursor to ethylene. The catalytic enzymes needed for ethylene production are ACC synthase and ACC oxidase. Coded from multigene families, their biosynthesis can be promoted by fruit ripening, stress factors (e.g., wounding, flooding, chilling), and auxin. Silver, cobalt, carbon dioxide, aminoethoxyvinylglycine (AVG) and

aminooxyacetic acid (AOA) interrupt ethylene production by blocking ACC enzyme functions.

Ethylene promotes plant growth processes such as seed germination, cell expansion, cell differentiation, flowering, senescence, and organ abscission with new growth showing the greatest sensitivity to ethylene. It is found in the highest concentration in plants that have not received a vernalization treatment, such as wheat seedlings (Bernier et al., 1981) and has been shown to break seed dormancy in peanuts and potato tubers (Taiz and Zeiger, 1998).

Ethylene also interacts with other plant hormones. During leaf senescence, ethylene counteracts cytokinin by increasing the rate of senescence, as indicated by decreased levels of chlorophyll, and accelerates formation of abscission zones. It is believed that the auxin concentration gradient controls cell sensitivity to ethylene in specific tissue regions and thus the rate of abscission (Taiz and Zeiger, 1998).

Plant cells have the ability to perceive ethylene and further translate this stimulus to create some physiological response. This is accomplished through a complex pathway of genes that code for the synthesis of specific proteins needed for the perception and consequent physiological response towards ethylene. The *ETR1* gene codes proteins for ethylene-receptors; the *EIN3* gene codes for transcription factors involved in regulating the expression of ethylene-responsive genes; and *CTR* genes are involved with transduction and development of signaling pathways (Bleeker and Kende, 2000).

Specific *Arabidopsis* mutants of these genes have contributed to the understanding of ethylene biosynthesis and response translation. The ethylene insensitive *etr1* (*e*thylene –*r*esistant *1*) mutant fails to code for the ethylene receptor protein ETR1; the *ein* (*e*thylene-*in*sensitive) mutants *ein2* and *ein3* are blocked during the signal transduction pathway (Bleeker and Kende, 2000). Due to these failures, mutant plants cannot perceive or respond to exogenous ethylene, and therefore, grow 'normal' despite high concentrations of ethylene. Constitutive *ctr1* (*c*onstitutive *t*riple *r*esponse *1*) mutants display the triple response in the presence or absence of ethylene. The activation of ethylene sensitivity in this mutant suggests that the *CTR* gene product (protein) acts as a negative regulator of ethylene response pathways (Kieber et al., 1993).

Due to pronounced physical effects (triple response, apical hook position), mutants are a valuable means of confirming specific pathways and the receptors involved. From these visual reactions and analysis of the epistatic relationships between the mutants, a preliminary model in *Arabidopsis* lists ETR1, CTR1, EIN2, and EIN3, in that order, to be involved with the ethylene signal pathway (Kieber et al., 1993).

Commercially, ethylene is used beneficially in orchards to thin fruit (e.g., cherries), induce flowering and consequently fruit (e.g., pineapple), ripen fruit (e.g., apples and tomatoes), and influence flower sex (e.g., female flowers in cucumber) (Beaudry and Kays, 1988a). However, ethylene can have negative effects on plant growth and post harvest longevity, such as epinastic effects on plant growth, climacteric effects in bananas and apples, and flower color fading.

The tremendous effects ethylene has on plant growth are important to understand so that it can be controlled and utilized as a commercial plant growth regulator in the horticulture industry.

Ethephon

Exogenous growth regulators are important in many horticulture industries because of their abilities to modify plant growth or development through either the inhibition or production of a target hormone. For example, ancymidol (A-Rest) is a growth regulator used to inhibit gibberellin biosynthesis to reduce internode elongation and therefore create a more compact, marketable plant for the floriculture industry (Taiz and Zeiger, 1998). In contrast, a crop system can be improved through ethylene production by a shift of plant energy towards desirable plant organs. This is achieved through the induction of ethylene formation by the target tissue, or the release of ethylene held by an absorbent (Beaudry and Kays, 1988a). For example, (2-chloroethyl)phosphonic acid (ethephon), can stimulate lateral branching in geranium for the production of cuttings or induce flowering in pineapple (Morgan, 1980). Commercially sold under the brand name Florel®, it is used primarily in the floriculture industry to inhibit reproductive bud development, reduced internode elongation, and stimulate branching for optimum management of herbaceous cuttings, stock plants, and potted crops. Ethephon has become popular for its proven ability to reduce or eliminate hand pinching, promote and maintain vegetative growth, and streamline crop production schedules in several annual bedding plant crops,

(e.g., *Pelargonium peltatum* (L.) L'Her. (ivy geranium) and *Fuchsia* x *hybrida* (fuchsia) (Konjoian, 1994a).

Correct ethephon application rate and timing is important because plant health, environmental factors, and mechanical factors all affect its subsequent performance in altering plant growth. Ethylene promotes tissue senescence and will exaggerate the negative consequences of any stress a plant is under. Therefore, it is important not to apply ethephon during periods of high temperature, deficit or surplus water stress, high light, or insect or disease pressures. Application during environmental stress (e.g., water stress), uneven spray coverage, or a high application rate, can result in uneven plant growth, stunting, or yellowing of leaves (Konjoian, 1998). For example, fuchsia plants treated with 500 ppm ethephon exhibited leaf blades that reflexed downwards and curled at the tips (Konjoian, 1994b). Direct use of the chemical ethephon caused leaf necrosis in *Monarda didyma* L. 'Blue Stocking' under 1000 $mg \cdot l^{-1}$ applied once, twice, or three times during a 4-week period (Hayashi et al., 2001).

Application of ethephon can mimic a "soft pinch" (i.e., death of apical meristem and some subtending leaf primordia) when applied early in the plant cycle or during active plant growth. For example, to maximize branching, rooted garden mum cuttings are treated 3 to 5 days after transplant or unrooted cuttings 15 to 17 days after sticking (Konjoian, 1995a). Additionally, most healthy and actively growing plants can be treated with ethephon sprays at two to three week intervals to maintain vegetative growth and branching.

Caution must be taken by commercial growers to avoid excessive stress or phytotoxic symptoms such as leaf burn or loss of plant vigor. Stock plants should not be treated one to two weeks before or after cutting-harvest so as to allow for subsequent vegetative growth (Konjoian, 1994c). It is recommended for growers to adjust the frequency of a constant application concentration instead of altering the concentration in order to adjust for variations in temperature or relative humidity levels to: avoid stock plant stress before and after cutting-harvest date; avoid stress on new cuttings after sticking or transplant; and allow for natural flowering before ship date in bedding plants.

Temperature is an environmental factor that has a major influence on ethylene release from (2-chloroethyl)phosphonic acid, the active ingredient in ethephon. This is because ethephon has a relatively high energy of activation (32 kcal·mol^{-1}) (Olien and Bukovac, 1978). This dependence upon temperature exists because compounds with high activation energies need more energy for degradation and optimum performance. Chemical uptake and subsequent breakdown and release of ethylene are hastened at high temperatures, while these processes, although continued over time, are slow at low temperatures. Thus, the same applied concentration of ethephon can either elevate concentrations of ethylene to phytotoxic levels at high temperatures or inhibit activity at low temperatures.

For example, four hours after an ethephon (Ethrel®) application of 10,000 ppm (256 ml·L^{-1}) at 21 °C, the ethylene produced in ethephon treated tomato plants at a post-treatment temperature of 32 °C was 125 and 8 times greater

than the amount of ethylene produced in plants under post-treatment temperatures of 13 or 21 °C, respectively. After 28 hours, ethylene production was the greatest in plants at 13 °C (Lougheed and Franklin, 1972). Ethylene release is greatly accelerated at high temperatures for fruit abscission in sour cherry (30 °C) (Olien and Bukovac, 1982), and inadequate at low temperatures (16 °C) (Flore and Bukovac, 1982). As in other plant systems, the increased release of ethylene at high temperatures can be phytotoxic, causing leaf abscission or gummosis in cherry (Bukovac et al., 1971).

In addition to temperature, relative humidity can also influence the rate of ethylene release from ethephon and subsequent plant response (e.g., leaf abscission). Low humidity decreases droplet drying time, and therefore, decreases the length of time for ethylene release and penetration into leaf tissue. Therefore, high humidity generally elicits a stronger response. For example, a relative humidity of 62 percent at 25 °C enhanced the release of ethylene from ethephon applied to a glass slide (Beaudry and Kays, 1987).

The effect of ethylene depends on penetration into leaf tissue. Leaf stomata are the main entry port for any gas, and little or no ethylene entry is achieved on a leaf side that either lacks stomata or where stomata are tightly closed (Beaudry and Kays, 1988b). Experiments involving stomata aperture demonstrate that ethylene evolution from ethephon (Ethrel®) takes place primarily on the surface to which it was applied, and this evolution is at the highest rate when passed through open stomata during times of low air velocities ($< 33 \times 10^{-4}$ $m \cdot s^{-1}$) (Beaudry and Kays, 1988b).

In addition to physiological and environmental factors, the effect of ethephon depends on application technique. Application with a hand sprayer is desirable to ensure uniform and complete coverage of all plant material. Spray solution pH should not exceed 4.5, should not sit for long periods of time, or sit in direct sun. These events cause ethylene-releasing compounds, such as ethephon, to become unstable and release ethylene before plant contact due to the dianionic formation of the parent molecule (Beaudry and Kays, 1987). Surfactant use is not used by the majority of surveyed growers (Konjoian, 1996).

The ability of ethephon to influence reproductive and shoot growth is enhanced as ethephon concentration and exposure time on plant tissue increase. The recommended concentration for most herbaceous crops is 500 ppm at a rate of 2 L·10 m^2 of crop area (Konjoian, 1995b), and the length of time ethephon is exposed to plant tissue can be maximized by controlling watering, temperature, and relative humidity. Ethylene is released by ethephon within 10 minutes after spray, yet ethephon needs to be exposed to plant tissue for at least 20 minutes to be effective (Konjoian, 1995c). For example, after 24 hours, 'Dazzler White' impatiens plants exposed to ethephon for 30, 60, and 120 minutes abscised 86%, 79%, and 92% of flowers, respectively (Konjoian, 1995c). Although floral organs respond to ethephon application within 24 hours, effects on internode length can take up to one week (Konjoian, 1997).

Thus, understanding the effects that interactions between physiological, environmental, and mechanical factors have on plant response to ethephon application is important to determine correct ethephon application rate and

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frequency for quality plant material. These rates are plant specific, as the effects of ethephon application and consequent release of ethylene vary between plant species and cultivars due to basic morphological and biochemical properties of individual plants. Due to the large diversity and uniqueness within perennial species, stock plant management of these plants with ethephon is challenging.

Research Plant Material

Plant species were chosen for research because they are popular perennial garden plants that perform well in the northern latitudes (e.g., >35 °N), yet pose specific problems with stock plant management or commercial production. The following descriptions of plant species are an introduction to their botanic history; morphological characteristics; general known requirements for juvenility, photoperiod, or vernalization; and commercial propagation techniques. Plant descriptions and physiological responses to environmental stimuli are also listed for specific plant cultivars. Plants are listed by plant family according to evolutionary order as described by Cronquist (1988).

Aquilegia x *hybrida* Sims

A member of the Ranunculaceae family, *Aquilegia* x *hybrida* Sims produces beautiful flowers on mounded, gray-green foliage. The botanical name *Aquilegia* refers to *aquila*, like an eagle, referring to the beak or claw shape of the spur like petals (Armitage, 1997). Being of hybrid origin, *A.* x *hybrida* was created through crosses between *A. canadensis*, *A. chrysantha*, *A. caerulea*, *A. longissima*, and *A. vulgaris* (Shedron and Weiler, 1982).

Aquilegia has two to three ternately compound leaves on long, softly pubescent petioles. Characteristic terminal flowers with long, hollow, nectariferous backward-projecting spurs hang or are erect on one to three foot tall stalks during spring and early summer (Still, 1994). Plants do best outdoors in full sun to moderate shade with plenty of moisture in rich, well-drained soil. *Aquilegia* is commercially propagated from seed, and is a short-lived perennial, lasting only up to three years.

Plants have an obligate juvenile phase, satisfied by the development and maturation of a specific leaf count. In addition, mature plants flower most consistently after a cold treatment, regardless of photoperiod. Cold temperatures at 4.5 °C for 4 weeks stimulate inflorescence formation at the 12-leaf stage for *A.* x *hybrida* 'Fairyland', while 10 weeks at this temperature is required for *A* x *hybrida* 'McKana's Giant' (Shedron and Weiler, 1982).

The Songbird Mix is a popular *A.* x *hybrida* series that consists of large, upright, and vibrant pastel colored flowers, including white, pink, and lavender. Bulking is recommended before a required chilling period of 3 to 6 weeks at 5 °C for fast and complete flowering within 3 to 7 weeks (Finical, unpublished data). Despite the impressive aesthetic value of the flowers, post harvest potential is poor, as plants hold flowers for only a week at room temperature.

Dianthus caryophyllus L.

Dianthus are literally 'flowers of the gods'; the botanical name *Dianthus* is derived from Latin *dios* being 'divine' or 'of Zeus' and *anthos* 'flower', and *caryophyllus* is derived from 'clove leaved' (Smith, 1972). It is one of the oldest

and most treasured flowers in garden history. Over 300 species cover a wide geographic range in the temperate world from Great Britain to Siberia, primarily in southern Europe and decreasing in number in hot or wet areas of their range (Hughes, 1993).

Its cultivation dates to as early as the first century A.D. by people of diverse cultures. The Muslims of northern Africa grew them, they were favorites in many English gardens, and Pliny wrote that the Spaniards used *Dianthus* to flavor beverages (Coats, 1968). Additionally, the *Dianthus* flower appears in many Christian artistic works of late medieval and Renaissance Europe, because its 'fleshy' color signifies a representation of the death and rising of Christ (Hughes, 1993). Along with the common name carnation, the spicy scented *Dianthus* flowers have also been called 'ginger' or tansy, gromwell, and even Shakespeare referred to them as 'gillyvore' (Coats, 1968).

Dianthus is a member of the Caryophyllaceae family with opposite leaves and conspicuous nodes. It has few requirements for flower initiation and development. The developmental phase change from juvenility and exposure to cold temperatures of 5 °C may promote flowering, but they are not absolutely necessary (Bunt and Cockshull, 1985). *Dianthus* is considered to be a qualitative long day plant (Blake and Harris, 1960). The plant grows and flowers best in high light and cooler temperatures, preferring moist, well-drained soil (Still, 1994). Increased solar radiation and increased continuous light cycles decreased time to visible bud, therefore, high daily light integrals are necessary for adequate photosynthetic assimilate distribution and flower initiation to occur (Bunt et al.,

1981). Commercial propagation is by seed, vegetative cuttings (Still, 1994), or tissue culture (Perry, unpublished data).

Dianthus 'Cinnamon Red Hots'™ has very fragrant, bright crimson petals and are appropriate for mixed containers and baskets. It is a recent introduction from the Proven Selections plant line (Four Star Greenhouse, Carleton, Mich.), which is a focused marketing effort to bring plants under different brand names together. Despite wonderful aesthetic qualities, propagation of this plant presents challenges because plants do not remain vegetative for intervals that are compatible for harvesting cuttings due to the lack of a required exposure to specific environmental cues for flower initiation.

Penstemon digitalis Nutt.

Penstemon digitalis is a North American native, herbaceous plant found in drier regions of the southwest. Considered to be the European 'Foxglove' of the New World because of similar plant habit and flower characteristics, *Penstemon* was heavily introduced to England during the nineteenth century where additional cultivars were bred for the cooler and wetter conditions (Coats, 1968). The botanical name *Penstemon* comes from *penta*, five, and *stemon*, stamen, referring to the five stamens in a penstemon flower; *digitalis*, meaning 'finger like', refers to the elongated flower shape, morphologically similar to Foxglove (Smith, 1972). *Penstemon* is a member of the Scrophulariaceae family, which are mostly herbs that exhibit bisexual, zygomorphic flowers and corollas with 4 to 5 lobes, sometimes 2-lipped.

The dark red foliage and bright white flowers of *Penstemon digitalis* 'Husker Red' provides a great visual contrast to many other colors in any garden. In 1976, Dale Lindgren of the University of Nebraska found an ecotype of *P. digitalis* growing in Hardy, Nebraska, from which he collected seeds and selected for deeper pigmentation. *Penstemon digitalis* 'Husker Red' soon became a popular plant, becoming the Perennial Plant Association's 1996 Perennial Plant of the Year. It flowers early to mid-summer and does well in full sun and well-drained soil (Still, 1994).

Juvenility does not appear to influence flower initiation or development in *P. digitalis* 'Husker Red'. However, flower induction is greatly influenced by a vernalization requirement. Cold decreases the time to flower from 100 days at 20 °C in unchilled plants to about 50 days after 15 weeks at 5 °C (Clough, 1999). However, total production time is not reduced due to the additional amount of chilling time. Chilled plants are day-neutral. *P.* 'Husker Red' does not retain its characteristic and desired qualities through seed propagation, thus making vegetative propagation via stem cuttings, division, or tissue culture required.

Veronica longifolia L.

Veronica longifolia is a native of Europe and Asia commonly known as long-leaf speedwell. The origin of its epithet is somewhat unclear. Some believe it is named after St. Veronica, because the markings of the flower resemble those of her sacred handkerchief (Armitage, 1997). It could also be argued that the name comes from *Ver*, meaning spring, or *Vetonica*, a province in Spain

(Coats, 1968). The specific epithet, *longifolia*, refers to the plants' long, narrow leaves (Smith, 1972). *Veronica* is also a member of the Scrophulariaceae family.

Veronica longifolia 'Sunny Border Blue' grows to a height of 60.5 cm and produces many dark blue flowers on a terminal raceme. It performs best in full sun and well-drained soil. Named the 1993 Perennial Plant of the Year, it is a popular cultivar originally selected from a group of seedlings from a cross between *V. spicata* and *V. longifolia* by Robert Bennerup of Sunny Border Nurseries, Inc., in Kensington, Connecticut (Still, 1994). Its dark green, wrinkled foliage gives a pleasant contrast to the inflorescence.

Juvenility is not mentioned in the literature as a concern for flowering of *V.* 'Sunny Border Blue', but a cold period of 5 to 10 weeks at 5 °C is necessary for flower initiation, with longer exposure producing more uniform and full flowered plants (Runkle, 1996). Plants are day neutral following cold and *V.* 'Sunny Border Blue' is propagated by stem cuttings.

Salvia nemorosa L.

Salvia has traditionally been grown more as a medicinal plant than for ornamental purposes. It is native to many parts of the globe, including Mexico, the Mediterranean region, and Asia. The genus *Salvia* includes over 700 herbs, annual, and perennial species (Armitage, 1989). Commonly referred to as sage, these plants bloom throughout the growing season and offer a wide selection of color, foliage, and scent to the garden.

The distinct scent and a characteristic flower lip define these plants as a member of the Lamiaceae family. The genus *Salvia* is derived from *salvus*,

referring to its medicinal properties to save; *nemorosa* means 'of the woods' (Smith, 1972). Primarily listed as *S. nemorosa*, the lineage of hybrids of this genus is somewhat confusing. Most commercial trade catalogues list *Salvia* x *superba* as *S. nemorosa* (Still, 1994), with *S. superba* being a hybrid of *S. nemorosa*, *S. pratensis*, and *S. villicaulis* (Armitage, 1989).

Salvia is tolerant of dry conditions and does well in full sun. Opposite leaves and square stems are characteristic of the Lamiaceae family. Dense flowers of red, yellow, blue, purple, or white form on long, spike-like racemes. Vegetative propagation is accomplished through stem cuttings or division.

Salvia nemorosa 'May Night' is one of the most commonly used *Saliva* in the United States. It was introduced by Karl Foerster in 1956 as 'Mainacht' (Still, 1994) and was named by the Perennial Plant Association the 1997 Perennial Plant of the Year. Plants produce countless flowering racemes of vibrant indigo-blue flowers without any specific juvenility, cold, or photoperiod requirements (Finical, unpublished data). For this reason, *S. nemorosa* 'May Night' poses challenges for propagation because of the difficulty in maintaining vegetative plants for cutting harvest.

Achillea millefolium L.

Known as common yarrow, *Achillea millefolium* is a member of the Asteraceae or sunflower family and native to Europe and Western Asia (Still, 1994). It is common in meadows and roadsides because of its natural ability to spread quickly due to vigorous rhizomes. The Greek name *Achillea* honors the Trojan war hero Achilles and his use of the plant leaves to heal soldiers' wounds

(Smith, 1972). The finely dissected leaves give the illusion of thousands of leaves; hence the Latin species name *millefolium*. Early Europeans used the herb as a remedy for toothache and believed drinking the tea everyday was a great benefit to a person's health (Armitage, 1997).

The leaves of *Achillea* are strongly aromatic, alternating along a tall stem of up to 1.5 meters. The many ray and disk flowers are arranged in terminal, corymb inflorescences that can be an array of colors of yellow, lavender, red, or white. Blooming throughout the summer, full sun and well-drained soils provide the best growing conditions. Despite the nice display of color and fernlike foliage, tall *Achillea* stems are prone to lodging and plants can become invasive in the garden (Still, 1994).

Juvenility does not appear to be involved in reproductive development for *Achillea*. Like most *Achillea* species, *A. millefolium* is a facultative long-day plant, flowering fastest and most uniformly under photoperiods greater than 13 hours. Cold is beneficial, although not required for flower initiation and development. Commercially, propagation is accomplished asexually through stem cuttings or division (Nausieda et al., 2000).

One of the most prominent cultivars in the floriculture industry is *A. millefolium* 'Paprika'. Many red-orange flowers top bright green foliage to produce a showy plant within 6 to 8 weeks after inductive treatments are applied (Nausieda, 2000).

Coreopsis - Coreopsis grandiflora Hogg ex Sweet, *Coreopsis verticillata* L.

Coreopsis is native to North America and is another member of the Asteraceae family. Although native to the southern and eastern United States, some species are native to tropical regions such as Hawaii and parts of Africa (Still, 1994). This genus includes over 100 species of annuals and perennials with single or double, yellow daisy-shaped flowers, perfect to make any garden setting look more like the natural environment.

Bright yellow ray and disk flowers terminate long peduncles of full, mounded plants. *Coreopsis* grows most successfully in full sun and well-drained soils, even growing well in dry conditions (Still, 1994). Plants can become floppy and proper maintenance to remove spent flowers ensures rebloom and disease control. Referring to the size and color of the seed, the genus *Coreopsis* translates to 'like a bug', and from that meaning, the common name, tickseed, was introduced (Armitage, 1997).

C. grandiflora 'Early Sunrise' is an All-American Award winner (1989) valued for its many, large, double yellow flowers, lending to the *grandi* (large) *flora* (flower) specific epithet (Still, 1994). It has a long bloom season and is believed to be a cross between *C. grandiflora* and *C. lanceolata* (Yuan et al., 2000). It requires long days (>14-hours) or 9-hour natural days with night-interruption lighting for 4 hours from 10 p.m. to 2 p.m. to initiate flowering (Yuan et al., 2000). Plants grown under 9-hour days did not flower without night interruption lighting of at least 1 hour (Runkle et al., 1998). Unlike most *C. grandiflora* cultivars, 'Early Sunrise' does not require a cold treatment to initiate reproductive growth.

C. verticillata 'Moonbeam' is another well-known cultivar that was selected by the Perennial Plant Association as the 1992 Perennial Plant of the Year. Recognized by its characteristic fern like foliage, as described by the *verticillata* epithet, and pale yellow flowers, it has a long bloom time, is excellent in a natural garden setting, and is drought tolerant (Armitage, 1997).

As with *C. grandiflora* 'Early Sunrise', *C.* 'Moonbeam' does not require a cold treatment and is a qualitative long-day plant. Two hours or more of night interruption with short days (9 hours) increases flowering percentage and decreases time to flower (Runkle et al., 1998). However, cold temperatures at 5 °C for 10 to 15 weeks may decrease time to flower by 1 to 2 weeks and increase final bud count (Hamaker et al., 2000). Plants grow very poorly under short days (<13 hours) and produce very little vegetative or reproductive growth.

Coreopsis 'Moonbeam' is difficult to propagate by cuttings because of the dramatic impacts photoperiod has on both vegetative and reproductive plant growth. Long days provide more vegetative growth to harvest from, yet result in poor rooting percentage because bud development competes with root growth in induced cuttings. Short days eliminate floral induction thereby increasing rooting percentage. However, the total number of cuttings harvested is very low due to the lack of vegetative growth under short day conditions (Hamaker et al., 2000).

Echinacea purpurea Moench

The purple cone flower, *Echinacea purpurea*, is a wonderful native of the dry plains of North America and is a popular choice for American gardens (Finical et al., 2000). Its purple to white ray flowers and golden brown, cone-like disk

flowers are characteristic of the Asteraceae family to which it belongs. The name *Echinacea* is from the Greek *echinos*, meaning hedgehog, referring to the prickly scales of the disk flowers (Still, 1994). The specific epithet *purpurea* alludes to the purple color of the ray petals of some ecotypes (Smith, 1972). Sturdy terminal flowers top stalks that can reach up to 1.2 meters in length (Finical et al., 2000). *E. purpurea* has alternate leaves that are pubescent and dark green. A long summer bloomer, *E. purpurea* thrives in full sun and well-drained soil, and is able to tolerate drought (Still, 1994).

Juvenility does not seem to pose a problem in the induction of reproductive growth of *Echinacea*, as seedlings with only four leaves flowered under a 14-hour photoperiod (Finical et al., 2000). In addition, cold is not necessary for anthesis, but can decrease time to flower by 2 to 3 weeks (at 20 °C) if plants are chilled for 10 weeks at 0 to 7 °C. *Echinacea* falls into an unusual intermediate day photoperiod category, flowering poorly with less than 12- or greater than 16-hours of light. Night interruption can be provided and exposure to night interruption between 0.5- and 2-hours of light delivered to plants under 9-hour photoperiods is necessary for flowering (Runkle et al., 1998). Plants are propagated by seed, clump division, or vegetative cuttings.

Echinacea 'Magnus' is among the most popular commercially produced cultivars and in 1998 was awarded the Perennial Plant Association's Perennial Plant of the Year. Its unique deep pink ray petals remain more upright than the drooping petals of many other *Echinacea* cultivars (Finical et al., 2000).

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SECTION II

EFFECTS OF ETHEPHON ON STOCK PLANT MANAGEMENT OF SEVEN HERBACEOUS PERENNIAL SPECIES

Effects of Ethephon on Stock Plant Management of Seven Herbaceous Perennial Species

Janelle E. Glady[1], N. Suzanne Lang[2], and Erik S. Runkle[3]

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

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[1]Graduate Student

[2]Associate Professor

[3]Assistant Professor

Abstract

Commercial growers can benefit economically by providing a means to manage and propagate their own plant material. However, the ability to retain vegetative stock plants for cutting propagation is a challenge for some herbaceous perennial species that initiate floral buds under most environmental conditions. Ethephon (2-chloroethylphosphonic acid) is an ethylene-releasing chemical used to control height, induce branching, and prevent flowering of floriculture crops. The objective of this research was to determine if ethephon is effective at maintaining vegetative growth and increasing the number of cuttings harvested for seven perennial species. Treatment applications of ethephon were applied for 10 weeks biweekly and weekly at 0, 400, 600, or 800 ppm. Ethephon did not influence the number of flower buds, branching, or plant height in *Campanula* 'Kent Belle', *Salvia nemorosa* 'May Night', *Scabiosa* 'Giant Blue', and *Thalictrum kiusianum* plants. Biweekly applications at 600 ppm or weekly applications at 400 ppm increased branching and the number of vegetative cuttings in *Coreopsis verticillata* 'Moonbeam' and *Veronica longifolia* 'Sunny Border Blue', respectively. Ethephon application increased branching in *Dianthus caryophyllus* 'Cinnamon Red Hots'™, but decreased leaf area made cutting harvest difficult. Therefore, ethephon application has potential to maintain vegetative stock plants of *Coreopsis* 'Moonbeam' and *Veronica* 'Sunny Border Blue', but not *Campanula* 'Kent Belle', *Dianthus* 'Cinnamon Red Hots'™, *Salvia* 'May Night', *Scabiosa* 'Giant Blue', or *Thalictrum*.

Introduction

The management of herbaceous perennial species as stock plants for asexual propagation can be economically beneficial to commercial growers. Two ideal qualities of stock plants are uniform vegetative growth and numerous shoots from which to take cuttings. To accomplish these criteria, the environmental conditions (e.g., photoperiod or cold) that induce flowering in most perennials would be eliminated or reversed. Thus, the ability to maintain vegetative growth is a challenge with some perennial species in which flowering is not environmentally controlled. For example, *Salvia nemorosa* L. 'May Night' initiates flowers under most environmental conditions, making it difficult to propagate asexually. Material from which cuttings can be taken is limited by strong apical dominance that does not allow for branching. The strong induction to flower decreases the quality and rooting ability of the cuttings. Another example is *Dianthus caryophyllus* L. 'Cinnamon Red Hots'™, which is a day-neutral plant that perpetually develops flowers under most environmental conditions (Bunt and Cockshull, 1985).

In contrast to plants that do not respond to cold or photoperiod, other perennial plants are clearly responsive to such environmental cues, such as temperature and photoperiod. For example, *Coreopsis verticillata* L. 'Moonbeam' does not require a cold treatment, but is an obligate long-day plant that flowers most rapidly under photoperiods of at least 14 hours or a 4-hour night interruption (Hamaker et al., 2000).

Commercially, most stock plants are grown under natural days with regular irrigation and fertilization practices. Flowering occurs under short or long days in both *Salvia* and *Dianthus*, which makes it difficult to maintain highly branched, vegetative plants for quality cuttings. Vegetative propagation in *Coreopsis* is even more challenging because vegetative growth is limited under short days less than 12 hours. Photoperiods longer than 13 hours promote growth but also increase the number of reproductive buds, which may compete with the rooting process. Consequently, a limited number of cuttings from *Coreopsis* can be harvested under photoperiods less than 14 hours (Hamaker et al., 2000).

The lack of environmental factors that regulate desired plant growth in some species has led to attempts to control these processes chemically. The control of plant height through the inhibition of gibberellin biosynthesis is used throughout the United States. For example, the height of annual and perennial crops have been managed with plant growth regulators (PGR), such as A-Rest (ancymidol) and Bonzi (paclobutrazol) to create compact plants that are easy to ship and aesthetically pleasing.

Other classes of compounds, such as the PGR ethephon, release ethylene and are used in many different sectors of the horticulture industry. In addition to height and reproductive development control, ethephon has the potential to increase branching, and therefore, also increase the number of cuttings per plant. During propagation, it is also used to keep harvested cuttings vegetative.

Ethylene, one of the five classes of endogenous plant hormones, affects many significant physiological processes of plant growth (Bleeker and Kende, 2000). It is also one of the most widely used plant hormones in commercial agriculture (Beaudry and Kays, 1988). This is because ethylene promotes plant growth processes such as seed germination, cell expansion, cell differentiation, flowering, senescence, and organ abscission with new growth showing the greatest sensitivity to its presence.

Ethylene also interacts with other plant hormones. During leaf senescence, ethylene counteracts cytokinin by increasing the rate of senescence, as indicated by decreased levels of chlorophyll. Ethylene accelerates the formation of abscission zones. The auxin concentration gradient may control cell sensitivity to ethylene in specific tissues and thus the rate of abscission (Taiz and Zeiger, 1998). These plant processes occur because plant cells have the ability to perceive ethylene concentrations and further translate this stimulus to create the appropriate physiological response.

Commercially, ethylene is used beneficially in orchards to thin fruit trees (e.g., cherries), induce flowers and consequently fruit (e.g., pineapple), ripen fruit (e.g., apples and tomatoes), and promote flower sex (e.g., female flowers in cucumber) (Beaudry and Kays, 1988). Ethylene released from ethephon is primarily used in the floriculture industry to reduce internode elongation, stimulate branching, and inhibit reproductive bud development to manage herbaceous cuttings, stock plants, and potted crops. Due to these plant responses, ethephon, commercially sold as Florel®, has become popular for its ability to

eliminate hand pinching, promote and maintain vegetative growth, and streamline crop production schedules in several annual bedding plant crops, (e.g., *Pelargonium peltatum* (L.) L'Her. (ivy geranium) and *Fuchsia* x *hybrida* (fuchsia), therefore reducing labor by an estimated 80 percent (Konjoian, 1994a).

The interaction between many factors, (i.e., physiological, environmental, and mechanical), and their affect on plant response to ethephon application is important to understand to determine correct application rate, time of application, and application frequency of ethephon for quality plant material. These rates and times are plant specific, as the effects of ethephon application and consequent release of ethylene vary between plant species and cultivars due to basic morphological and biochemical properties of individual plants. Therefore, the variable response within perennials does not facilitate one general production protocol.

The objective of this research is to investigate the use of ethephon as a tool to maintain vegetative stock plants for perennial species that cannot be maintained in a vegetative state using environmental manipulation, such as photoperiod and chilling. In addition, we tested the hypothesis that ethephon application will increase the number of cuttings harvested, cutting quality, and rooting ability of the cuttings.

Materials and Methods

Plant material. Year 1: All plant species were received as commercially propagated, rooted, vegetative plugs. *Campanula* L. 'Kent Belle' and dormant

Coreopsis verticillata L. 'Moonbeam' were received in 32-cell (0.18-L) plugs from Bluebird Nursery, Inc., Clarkson, Neb.; *Dianthus caryophyllus* L. 'Cinnamon Red Hots'™ and *Scabiosa columbaria* L. 'Giant Blue' in 84-cell (0.02-L) plugs from Four Star Greenhouse, Inc., Carleton, Mich.; and *Salvia nemorosa* L. 'May Night' in 54-cell (0.08-L) plugs and dormant *Veronica longifolia* L. 'Sunny Border Blue' in 72-cell (0.04-L) plugs from Green Leaf Perennials, Lancaster, Pa. Twenty-five dormant *Thalictrum kiusianum* L. plants were received from Walters Gardens in Zeeland, Mich. Upon arrival in January 2002, all plugs were transplanted to 13-cm square plastic containers (1.1-L) filled with a peat and perlite soil mix (Sure-mix Perlite; Michigan Grower Products, Galesburg, Mich.; 70% peat moss, 21% perlite, 9% vermiculite).

Year 2: *Coreopsis verticillata* L. 'Moonbeam' and *Veronica longifolia* L. 'Sunny Border Blue' were received as dormant 32-cell (0.18-L) or 72-cell (0.04-L) plugs, respectively, from Green Leaf Perennials, Lancaster, Pa. Vegetative, rooted *Dianthus caryophyllus* L. 'Cinnamon Red Hots'™ were received as 84-cell (0.02-L) plugs from Four Star Greenhouse, Inc, Carleton, Mich. Plugs were transplanted as in Year 1, and were held in a glass greenhouse under 11-h photoperiods, maintained at 20 °C (day/night), for 4 weeks prior to the first ethephon application. Floral buds that formed on *Coreopsis* were hand-pinched when visible.

Photoperiod Treatments (Expt. 1): Beginning 6 February 2002, 10 plants of each species were randomly assigned to greenhouse benches under 11-, 12-, 13-, 14- and 15-h photoperiods for the duration of 15 weeks to determine

photoperiodic responses. Photoperiods consisted of 9-h days completed with day-extension lighting (≈ 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at canopy level) provided by incandescent lamps. Lamps were turned on at 1700 HR and turned off when each photoperiod was completed. Opaque black cloth was pulled at 1700 HR and opened at 0800 HR everyday on all benches so that plants received a similar daily light integral.

Plants were grown in a glass greenhouse section set at 20 °C during both the day and night. Temperatures on each bench were measured by a thermocouple in an aspirated tube every 10 s, and hourly averages were recorded by a CR-10 datalogger (Campbell Scientific, Logan, Utah). Average daily light integral was calculated using a line light quantum sensor (Apogee Instruments, Inc., Logan, Utah).

Plants were irrigated as necessary with well water (containing 95, 34, and 29 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively) supplemented with water-soluble fertilizer to provide the following ($mg \cdot L^{-1}$): 125 N, 12 P, 125 K, 15 Ca, 1.0 Fe, 0.1 B and Mo, and 0.5 Mn, Zn, and Cu (MSU Special, Greencare Fertilizers, Chicago, Ill.). Water was acidified with H_2SO_4 to a titratable alkalinity of 140 $mg \cdot L^{-1}$ $CaCO_3$. Days to visible bud, days to flower, plant height at anthesis, node number at anthesis, and bud number at anthesis were recorded.

Ethephon Treatments (Expt. 2): Species that were not significantly influenced by photoperiod (Expt. 1) were selected for a second series of experiments. Beginning 14 May 2002, shoot material was removed to a height of 5 cm, and plants were grown for 8 d prior to ethephon (Florel®; Rhone-Poulenc)

application on 22 May 2002. Development of the experimental design during year 2 was built upon results and important points from year 1, to yield better information on the impact of ethephon as a tool to maintain perennial stock plants for commercial production systems. Therefore, the experiment was replicated in time, beginning 18 March 2003 (Year 2 non-chilled plants) and 11 May 2003 (Year 2 chilled plants) with the following changes: 1) photoperiod treatments were not replicated in time, as only species that did not respond to photoperiod during year 1 were selected for year 2; 2) commercial grown plugs were received and grown for 3 weeks prior to ethephon application; 3) ethephon experiments for *Campanula*, *Scabiosa*, *Salvia*, and *Thalictrum* were not replicated due to their lack of response to ethephon.

Cold Treatment: An additional set of *Veronica* plugs were transplanted into 13-cm square plastic containers (1.1-L) containing the commercial medium previously described, and placed in a cooler at 5 °C, lighted from 0800 to 1700 HR by cool-white fluorescent lamps (F96T 12/CW/VHO, Phillips, Somerset, N.J.) for 8 weeks. The photosynthetic photon flux (*PPF*) from the lamps was approximately 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. Plants were watered as needed. After this cold treatment, plants were transferred to the same greenhouse benches and environment as non-chilled plants and grown for 4 weeks prior to the first ethephon application.

Ten plants of each species were randomly assigned to greenhouse benches in each repetition and were treated with ethephon applications at: 0 ppm (control); 400 ppm (10.3 $ml \cdot L^{-1}$) weekly and biweekly; and 800 ppm (20.5 $ml \cdot L^{-1}$)

weekly and biweekly. Additional treatments of 0 ppm ethephon (water spray) and 600 ppm (15.4 $ml \cdot L^{-1}$) weekly and biweekly were applied during year 2. No surfactants were used. Ethephon was applied during the late afternoon (4:00 p.m.) using a hand-pump sprayer (1.9 L per 9.3 m^{-2}) to wet foliage and stems of all plants uniformly (approximately 2 L per 10 m^{-2}). Plants were grown under similar photoperiod and temperature conditions as previously described for photoperiod treatments. Environmental conditions were also measured with previously described equipment. Actual average daily temperatures and daily light integrals for the 10 weeks of ethephon application are presented in Table 1.

Year 2 plants were irrigated as necessary with reverse osmosis water supplemented with water-soluble fertilizer to provide the following ($mg \cdot L^{-1}$): 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo.

Cutting Harvest: Time of cutting harvest was determined when *Coreopsis*, *Dianthus*, and *Veronica* had 3, 4, and 2 nodes available per cutting, respectively, and when each plant had enough vegetative growth to take cuttings without removing more than 50 to 60 percent of total photosynthetic leaf area. These dates were staggered within species and treatments due to differences in plant uniformity; a schedule of cutting harvest dates is presented in Table 2. Basal portions of each cutting were dipped in a 1500 ppm solution of liquid auxin (Dip'n Grow; Astoria-Pacific, Clackama, Ore.), and propagated in 72-cell (0.04-L) plug trays (Landmark Plastic Corporation, Akron, Ohio) in a 50% commercial peat (Suremix Perlite; Michigan Grower Products, Galesburg, Mich.) and 50% perlite (Therm-O-Rock, East, Inc.; New Eagle, Pa.) mix. Plug trays were propagated

under natural photoperiods in a mist house with air temperature set at 23 °C. Cuttings were rooted for 2 or 3 weeks before cutting quality was assessed. Cuttings taken at the same time intervals but not used in propagation were placed into individual paper bags, labeled, and transferred to a dryer oven maintained at 60 °C for approximately 3 d before dry weights were measured.

Data Collection: Initial data collection prior to ethephon applications included plant height (PH) and number of primary shoots (PS) (> 1.0 cm in length). The PH was measured from the soil base to the growing point for all species during both years except for Year 1 *Dianthus*, where PH was measured from the soil base to the tip of the longest leaf. The PH, PS, and number of reproductive buds per plant (RB) were taken one day prior to each cutting harvest and at the end of the 10 week period; these data, with the substitution of shoot length (SL) instead of PH, were taken weekly during year 2. Data for control *Coreopsis* plants during Year 1 were taken from only two plants at the first cutting harvest and only one plant for final data because others died during the experiment. Five *Veronica* plants died during year 2 due to stress from ethephon application during the first week of the experiment and were discarded.

The number of vegetative cuttings (VC) and number of cuttings with floral buds (RC) were recorded at cutting harvest; these data, with the addition of cutting dry weight (DW), were also taken during year 2. The total number of cuttings per treatment was calculated. Cutting quality was observed 2 (*Coreopsis*, *Dianthus*) or 3 (*Veronica*) weeks after propagation and was quantified based on cutting height, number of floral buds per cutting, and the

rooting percentage. In year 2, a scale from 1 (poor) to 6 (excellent) was used to quantify cutting quality by these factors.

A complete randomized design was used that included 10 observations for each ethephon treatment. Data were analyzed using SAS (SAS Institute, Cary, N.C.) mixed model procedure (PROC MIXED) for analysis of variance. Data were not pooled and were analyzed separately for each year due to the differences in time of data collection and cutting harvest.

Results

Year 1: Ethephon was not effective at maintaining vegetative stock plants for *Campanula* 'Kent Belle', *Salvia nemorosa* 'May Night', *Scabiosa columbaria* 'Giant Blue', or *Thalictrum kiusianum* (data not shown). In addition to the lack of beneficial response, ethephon application was also phytotoxic to these plants at each application rate (i.e., deformed growth or necrosis occurred after ethephon application). Ethephon was toxic to *Thalictrum* and all plants died within three weeks.

Plant height in *Campanula*, *Salvia*, and *Scabiosa* significantly decreased as ethephon concentration increased (data not shown). Harvesting suitable cuttings from ethephon-treated plants remained difficult because flower buds were produced under all treatments (*Campanula* and *Salvia*) and internode length was stunted (*Scabiosa*) by ethephon application (data not shown). In addition, the slow growth rate allowed for a minimum of one cutting harvest at week 9 for *Salvia* and *Scabiosa*. Cuttings from all ethephon treated plants

weighed less than cuttings taken from control plants, and continued evaluation of rooting ability for cuttings showed no significant difference between treatments and controls (data not shown).

Coreopsis verticillata 'Moonbeam'. There was a significant interaction between ethephon concentration and treatment duration on PH. As ethephon concentration increased, PH decreased. During week 10, plants that received 800 ppm biweekly and weekly applications were 20.2 and 19.2 cm shorter, respectively, than control plants; height was also decreased at this time by 7.0 and 19.6 cm at application rates of 400 ppm biweekly and weekly, respectively (Table 3A). Over the 10-week duration, PH in control plants increased by 43.8 cm, while PH for plants that received 800 ppm biweekly or weekly only increased by 19.6 or 20.7 cm, respectively. No ethephon concentration increased the number of PS from control plants. However, at week 10, plants treated with 800 ppm biweekly had significantly more PS than in previous weeks (Table 3B).

The interaction between ethephon concentration and treatment duration decreased the number of RB that developed on each plant (Table 3C). When ethephon concentration increased, especially when applied weekly at 800 ppm, RB number decreased. At week 4, control plants had an average of 46 RB while plants treated with ethephon had 67 to 98 percent fewer RB, respectively, with 400 ppm biweekly to 800 ppm weekly. At week 10, a similar trend was demonstrated.

Increased treatment duration, illustrated as week of data collection, also increased the number of RB in all plants (Table 3C). However, the rate of bud

development in control plants was rapid and significantly greater each subsequent week, and was not as rapid in treated plants. The number of RB in plants treated with biweekly applications of 800 ppm and weekly applications of 400 ppm were only significantly greater at week 10. Treatment duration had no significant affect on the number of RB developed in plants treated with weekly applications of 800 ppm.

Although ethephon concentration did not significantly affect the number of VC, it did significantly decrease the number of RC harvested from each treated plant by 65 to 92 percent (Table 3D and E). Cuttings from control and plants treated biweekly continued flower bud development while in the propagation house (Table 4A). The number of roots after propagation was significantly greater for plants that received 800 ppm biweekly, and root length was significantly less for control plants as compared to treated plants.

Dianthus caryophyllus 'Cinnamon Red Hots'™. Plant height was significantly affected by ethephon concentration and treatment duration. When ethephon concentration increased, PH decreased (Table 5A). At week 10, plants treated with 400 ppm and 800 ppm weekly were 2.1 and 3.8 cm shorter than control plants, respectively. As time increased, the number of PS increased for all control and ethephon treated plants by 10 to 14 shoots (Table 5B). The number of VC harvested from control and ethephon treated plants was not significantly different (Table 5C).

No flowers or buds were formed on *Dianthus caryophyllus* 'Cinnamon Red Hots'™ and, thus, data are not shown. Ethephon concentration significantly

decreased cutting quality, as the number of roots and root length were reduced compared to the control (Table 4B). No RB were formed during propagation on cuttings harvested from control or ethephon treated plants.

Veronica longifolia 'Sunny Border Blue'. Ethephon application significantly influenced all measured variables in *Veronica* plants, except for the number of RC (Table 6). Plant height increased the most for control plants, which significantly increased in height each week of data collection, and was 39.5 cm after 10 weeks (Table 6A). In contrast, plants that received biweekly or weekly applications of 800 ppm attained an overall height of 23.7 or 20.2 cm, respectively.

Ethephon application increased the number of PS (Table 6B). Plants that received 800 ppm biweekly had 13 and 8 more shoots than control plants at weeks 8 and 10, respectively. Over time, plants treated weekly with 400 and 800 ppm ethephon developed 14 and 23 shoots, respectively, from week 4 to week 10, while control plants developed only 10.

Weekly ethephon applications significantly reduced the number of RB, and plants provided with weekly applications at 400 or 800 ppm had only 3 RB at week 10 (Table 6C). In contrast, at week 10, control plants had 9 RB, and 400 and 800 biweekly treated plants had 8 and 7, respectively. Biweekly treated plants at 400 were never significantly different from control plants.

The number of VC increased over time in ethephon treated plants, but not for control plants (Table 6D). Although control and ethephon treated plants yielded the same number of VC at the first cutting harvest, the number of cuttings

for ethephon treated plants significantly increased by the second cutting harvest date. Seven and 10 more cuttings were harvested at this time from plants treated with 400 and 800 ppm weekly than from control plants. In addition, the weekly treated plants had 9 or 13 more VC than control plants, respectively. The number of RC in 400 ppm biweekly treated plants was greater at the second harvest than other ethephon treated plants (Table 6E).

Ethephon did not significantly affect rooting quality in terms of root length or number of flower buds (Table 4C). Plants treated biweekly at 800 ppm had fewer roots than control and other ethephon treated plants, except for plants treated biweekly at 400 ppm; however, this difference was only by 1 to 4 roots.

Year 2: *Coreopsis verticillata* 'Moonbeam'. The statistical similarity between the two control treatments (0 ppm ethephon application and 0 ppm ethephon application plus water spray) allowed them to be pooled for SL, PS, and number of VC and RC harvested. However, the number of RB was significantly different between these plants, and data were not pooled for this parameter.

There was a significant interaction between treatment duration and ethephon concentration that influenced SL (Figure 1). Although SL in both control and ethephon treated plants increased prior to each harvest, shoot elongation was more rapid for control plants than ethephon treated plants. For example, during the period between week 5 and week 7, SL in control plants increased by 6.7 cm while plants that received weekly applications of 400 ppm, 600 ppm, and 800 ppm only increased by 3.2, 1.6, and 2.4 cm, respectively.

Plants that received 800 ppm of ethephon biweekly and weekly developed 25 or 24 shoots, respectively, during the period between week 7 and week 10, which were significantly greater than that in control plants that gained only 4 shoots (Figure 2). At week 10, plants that received 800 ppm biweekly, 600 ppm weekly, or 800 ppm weekly had 31, 26, or 25 more shoots than controls, respectively. Plant shoot number in treated plants that received only 400 ppm remained the same as control plants.

All ethephon applications significantly decreased the number of RB per plant in comparison to the control plants, with the greatest affect from concentrations of 600 ppm or 800 ppm after three weeks of ethephon application (Figure 3). Plants that received 600 ppm biweekly or weekly averaged only 1 RB while control plants retained an average of 16 RB during this period.

The number of VC harvested per plant significantly increased as date of cutting harvest and ethephon concentration increased, with the greatest number of cuttings harvested from 600 ppm and 800 ppm of ethephon-treated plants at the third harvest interval (Figure 4A). For all ethephon-treated plants, the number of cuttings by the third harvest ranged from 4 to 18 more cuttings than control plants. The number of VC combined from all three harvest events totaled 308 for the control treatments, while cutting totals ranged from 344 at 400 ppm weekly ethephon to 740 at 600 ppm weekly ethephon treatments (Appendix A Figure 1). Despite the significance in cutting number by the third harvest, there was no significant difference between the first or second harvest or between control and ethephon treated plants at those times (Figure 4A).

When time and ethephon concentration increased, the number of cuttings per plant with reproductive buds decreased (Figure 4B). The number of RC from plants that received 600 ppm biweekly or 400 ppm weekly averaged 1 for all three harvest events. Similar to other measured variables, the number of RC was affected the most by 600 ppm and 800 ppm concentrations. Percent decrease from the control in RC at the third cutting harvest for biweekly and weekly ethephon treatments was 93 and 73 percent at 600 ppm, respectively, and 93 and 100 percent at 800 ppm, respectively. The total number of RC over the three cutting harvest events was 506 for control plants, and was <250 when treated with ethephon regardless of rate or application frequency (Appendix A figure 1).

Cuttings from ethephon-treated plants were stronger, shorter, and had fewer flower buds in the propagation house than untreated plants (Table 7A). On the performance scale of 1 to 6, (6 being excellent), control plants were often ranked between a score of 1 to 3, while cuttings from ethephon-treated plants generally received scores between 4 and 5. The DW of cuttings taken from control and ethephon treated plants was only statistically different during the first and third cutting harvest event, when cuttings from control plants weighed more than treated plants (Figure 5A). Although cutting DW significantly increased from the first to third harvest date for control cuttings, DW for cuttings from ethephon treated plants generally decreased over the same time interval.

Dianthus 'Cinnamon Red Hots'™. The two control treatments (0 ppm ethephon application and 0 ppm ethephon application plus water spray) were

statistically similar and, thus, data for SL, PS, and number of RB, VC, and RC were pooled. The number of RB was not affected by any ethephon concentration or frequency, and although the number of RC was significantly influenced by ethephon concentration, the difference was only by 1 cutting (data not shown). Therefore, data for these parameters are not presented.

Shoot length, the number of PS, the number of VC, and cutting quality were either negatively affected by ethephon application or not significantly different from control plants. Shoot length did not differ between control and ethephon-treated plants (Appendix A Figure 2). In general, the number of PS in ethephon-treated plants were statistically similar to control plants for all weeks except week 10, when plants treated with ethephon had statistically more shoots than controls (Appendix A Figure 3). The exceptions to this trend were plants that received 800 ppm weekly. These plants had consistently fewer shoots than controls between week 0 and week 6 and did not develop as many shoots over time as other ethephon-treated plants, which developed 8 to 13 shoots from week 0 to week 10.

The number of VC per plant was significantly reduced from harvest date 1 to harvest date 2 and by weekly ethephon treatments of 800 ppm as compared to control plants (Figure 6). The 800 ppm weekly ethephon application negatively affected plant growth, as plants significantly produced 40 percent fewer cuttings than control plants at the first harvest date and no cuttings at the second harvest date. The total number of VC was similar for control and ethephon-treated

plants, except for plants that received weekly ethephon concentrations of 800 ppm, which yielded significantly fewer cuttings (Appendix A figure 4).

Cutting quality varied between the two harvest events. At the first harvest, cuttings from control plants and plants that received 800 ppm of ethephon weekly scored ≈ 2.7 on the performance scale from 1 to 6, (6 being excellent). Cuttings from other ethephon-treated plants scored ≈ 4.7. However, the quality of cuttings from ethephon treated plants (≈ 3.9) was similar to cuttings from control plants (≈ 3.7) at the second cutting harvest (Table 7B). Cuttings from plants receiving the 800 ppm weekly treatment were the most difficult to harvest because of severely decreased leaf area, internode length, and lack of shoots. Cutting dry weight was significantly greater for control and 600 ppm biweekly cuttings than other ethephon treatments (Figure 5B). Only cuttings from control plants and plants that received 800 ppm biweekly had significantly different DW at the different cutting harvest dates (Figure 5B).

Veronica 'Sunny Border Blue'. The control treatments (0 ppm ethephon application and 0 ppm ethephon application plus water spray) were statistically similar, and thus were pooled for all measured variables. Prior to week 10, all control and ethephon treated plants had no RB, therefore, data are not shown. Although ethephon concentration significantly reduced the number of RB at week 10, actual numerical differences were ≤ 3. No RC were harvested.

Veronica SL significantly decreased as ethephon concentration increased from week 6 to 10 (Figure 7). Following the first harvest date from week 3 to week 6, SL in control and ethephon treated plants failed to regain original shoot

growth observed in the first two weeks of the experiment. During the last three weeks, SL increased by 3.0 cm in controls while plants treated with weekly concentrations of 400 ppm, 600, or 800 ppm ethephon only increased by 2.1, 1.3, or 0.6 cm, respectively.

Control and ethephon treated plants had a statistically similar PS number prior to week 8, but PS number increased in ethephon-treated plants over the last two weeks of the experiment (Figure 8). At week 10, plants that received 800 ppm biweekly, 600 ppm weekly, or 800 ppm weekly had 9, 12, or 17 more shoots than controls, respectively. However, the number of shoots developed was greater in ethephon treated plants (with the single exception of 400 ppm biweekly treated plants) than control plants from week 6 to 8.

The number of VC harvested per plant significantly increased as ethephon concentration increased, with the greatest number of cuttings harvested from 600 ppm and 800 ppm treatment plants at the second harvest interval (Figure 9). At the first harvest date, only plants that received 800 ppm biweekly yielded significantly more VC than control plants; in contrast, plants that received biweekly and weekly applications of 400 ppm actually had statistically fewer VC as compared to control plants. By the second cutting harvest, cutting yield from plants that received 400 ppm weekly was similar to control plants, while plants that received 400 ppm biweekly actually had significantly fewer VC than controls. The total number of VC combined from both harvest dates totaled 192 for the control treatment, while ethephon treatment totals ranged from 150 at 400 ppm biweekly to 252 at 600 ppm weekly treatment (Appendix A figure 5).

Cutting quality was similar for control and treated plants for both harvest events (Table 7C). Cuttings from control plants had the greatest DW during both harvest events, while cuttings from all ethephon treatments were similar, except for plants treated weekly at 800 ppm. Regardless of treatment, cutting DW was greater during cutting harvest 1 than harvest 2 (Figure 5C).

Veronica 'Sunny Border Blue' (cold treated). Chilled *Veronica* control plants exhibited similar trends in measured variables as compared to non-chilled plants. However, SL, PS, RB, and RC were significantly greater, and VC was significantly less, for chilled versus non-chilled *Veronica* controls.

Ethephon concentration reduced SL in cold treated *Veronica* (Figure 10). In addition, shoot elongation was significantly greater in weekly ethephon-treated plants compared to control plants (Figure 11). For example, SL significantly increased from week 3 to week 6 by 8.0 cm in control plants while plants that received weekly applications of 400 ppm, 600 ppm, or 800 ppm ethephon only increased by 2.1, 0.8, or 0.6 cm, respectively.

The number of PS increased as treatment duration and ethephon concentration increased (Figure 12). Although control and ethephon-treated plants were not significantly different for the first five weeks, at week 6, ethephon-treated plants had up to 14 more shoots than controls; at week 10, treated plants had up to 36 more shoots than controls. This increased amount of development was most apparent during weeks 3 to 6 for plants that were treated weekly with 600 ppm or 800 ppm ethephon, or biweekly with 800 ppm (Figure 13). However,

plant foliage exhibited phytotoxic symptoms (i.e., necrotic tissue) at week 4 with 600 ppm and 800 ppm weekly applications.

Control and ethephon treated plants formed no RB during the first four weeks of the experiment, and ethephon applications greater than 400 ppm biweekly consistently kept the number of RB ≤1 for the first nine weeks (data not shown). From week 5 to week 9, control plants had up to 7 more RB than other ethephon applications. Only plants that received biweekly applications of 400 ppm had a similar number of RB as control plants at week 10.

The number of VC significantly increased at the second cutting harvest with increased ethephon concentration, except for plants treated with 600 ppm ethephon weekly (Figure 14). There were no RC at the first cutting harvest from any plant or at the second harvest from plants that received weekly ethephon applications of 600 ppm or 800 ppm (data not shown). Total number of VC and RC are shown in Appendix A figure 6.

On the performance scale from 1 to 6, (6 being excellent), cutting quality at harvest 1 was similar for control and all ethephon treated plants at ≈ 3.8, except those that received 600 ppm or 800 ppm weekly, which scored ≈ 2.9 (Table 7D). Cuttings from these treated plants were difficult to harvest because of severely decreased shoot size. In addition, foliage displayed ethephon phytotoxicity. Although cuttings from control and ethephon-treated plants were similar at the second harvest, cuttings from 600 ppm and 800 ppm were of lower quality.

Cutting DW significantly decreased from the first to the second cutting harvest in cuttings taken from control and ethephon-treated plants, except plants treated weekly at 600 and 800 ppm (Figure 5D). Cutting DW from weekly treated plants was statistically greater than biweekly treated plants at the same rate or controls at the second harvest.

Discussion

Dianthus and *Veronica* are day-neutral plants, which eliminated daylength as a means to maintain vegetative stock plants in these species. However, *Coreopsis* did respond strongly to daylength and remained primarily vegetative under days ≤ 12 h, but branching was not adequate for cutting harvest. Therefore, a photoperiod of 13 h was implemented during ethephon treatment in an effort to promote vegetative growth, yet suppress reproductive initiation in *Coreopsis*.

The industry standard for ethephon (Florel®), application on annual crops is 500 ppm (Konjoian, 1995), hence year 1 protocol focused on concentrations above and below this rate. However, applications of 400 ppm did not have a strong influence on vegetative growth in *Coreopsis* while 800 ppm often had negative impacts on *Dianthus* and *Veronica* growth. Therefore, additional biweekly and weekly treatments of 600 ppm were implemented during year 2. An additional control treatment at 0 ppm plus a water spray was also added during year 2 to simulate the spray action that ethephon treated plants were exposed to.

Ethephon is primarily used in the floriculture industry on annual bedding plants or hanging baskets to increase lateral branching and control height (i.e., shoot length). These affects of ethephon on plant growth and development are also beneficial for stock plant management, such as geraniums and mums, to maintain vegetative plants with potential for increased cutting yield. Although the common rate is 500 ppm, effective ethephon concentration varies between species. For example, *Heliotrope* requires concentrations greater than 500 ppm to eliminate flowering (Konjoian, 1999a), while double impatiens require only 200 to 300 ppm to effectively increase branching and eliminate reproductive growth (Konjoian, 1999b). In this experiment, height, branching, and reproductive development for *Coreopsis* and *Veronica* stock plants were most significantly affected by ethephon weekly applications rates of 600 ppm and 800 ppm. However, ethephon treatments greater than 600 ppm biweekly were phytotoxic to *Veronica* leaves. Ethephon application had minimal effects on *Dianthus* plants during both years, as there was no significant effect on reproductive bud reduction (data not shown), and only slight effects on height and branching. In fact, branching and the number of VC harvested decreased in *Dianthus* plants that received weekly treatments of 800 ppm ethephon. Cutting quality and cutting dry weight was only minimally influenced by ethephon application in all species.

The overall effectiveness of ethephon application is dependent upon the interactions between chemical, plant, and environmental factors. In general, the chemistry of the parent molecule (e.g., stability, activation energy, ethylene

evolution), plant factors (e.g., species and cultivar differences, physical characteristics, and physiological status), and environmental conditions e.g., temperature and relative humidity) lead to increased potential for variability within application (Beaudry and Kays, 1988). For example, leaf surface area is important because only the spray droplets retained on the plant surface are effective (Bukovac et al., 1995). In these experiments, increased ethephon application decreased PH, SL, RB, and RC, and increased the number of PS and number of VC in *Coreopsis* and *Veronica*. The variance in data between years and within treatments could be contributed to the interactions between chemical, plant, and environment. This is important for developing industry recommendation due to the specific environmental parameters that influence commercial production schedules

Successful use of ethephon is also dependent upon the quality and condition of the cutting received (Konjoian, 1993). In this experiment, plant quality prior to and after ethephon application influenced the difference in plant growth and cutting yield between the two years that experiments were completed. Overall, the stage of development at which all species started was different each year. Year 1 plants had been grown for 15 weeks and flowered prior to ethephon treatment, while year 2 plants started ethephon treatments as plugs with 2 to 6 nodes. Specifically, the plant habit of *Coreopsis* plants was influenced by previous photoperiod treatments during year 1, i.e., plants from an 11-h photoperiod had minimal vegetative growth, while those from 14- and 15-h had adequate vegetation to respond favorably to subsequent ethephon

treatments. Thus, lack of uniformity in starting material could be a reason for large variation in plant response represented by the data from year 1 and year 2.

In addition to initial plant age, the intervals at which ethephon was sprayed affected plant health and the ability to rejuvenate after cutting harvest. It is recommended to allow one to two weeks prior to and after a cutting event before resuming ethephon application (Konjoian, 1994b). In this experiment, ethephon was applied only 10 d after plant material was removed at the beginning of year 1; while year 2 plugs were grown for 3 weeks prior to ethephon sprays. The continued stress of ethephon application within one week of cutting harvests resulted in deformed vegetative growth in some species that was not suitable for cuttings, particularly in *Dianthus* and *Veronica*.

Temperature, relative humidity, and solution pH are listed in the literature as major influences on ethephon performance. However, light intensity and quality also have significant effects on plant growth (Thomas and Vince-Prue, 1997). The difference in the daily light integral (DLI) between year 1 and year 2 as well as between year 2 and pre-chilled *Veronica* plants varied by as much as 7 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 1). This may have had an effect on plant branching habit and thus the number of cuttings harvested from each plant. For example, all species studies in this experiment showed a dramatic increase in the number of harvest events, and thus the total number of VC during year 2. However, pre-chilled *Veronica* plants under a greater DLI did not have more VC than non-chilled *Veronica* plants. One possibility for this similarity between chilled and non-chilled *Veronica* plants are the increased phytotoxic effects associated with

higher ethephon applications that made cuttings difficult to harvest, despite an increased number of PS.

Plant height was also dependent upon cutting harvest, as when plant material was removed, PH decreased. There was only one cutting harvest during year 1, but three during year 2, thus the amount of vegetative material removed was significantly greater and shoot growth appeared to decrease over time during year 2. Therefore, SL was measured during year 2 in addition to PH, because it was not dependent upon cutting harvest. The number of RB was also particularly influenced by cutting harvest, as most buds were removed during the cutting event.

Despite the variation in data between years and within treatments, ethephon application did have significant impacts on plant vegetative growth. The number of PS increased the most over the experiment interval with weekly ethephon concentrations of 600 ppm and 800 ppm in *Coreopsis* and *Veronica* (Figures 2, 8, and 12). This agrees with previous work that illustrated the ability of ethephon to increase branching in geraniums (Carpenter and Carlson, 1970; Tayama and Carver, 1990).

In addition to stimulating branching, ethephon has the ability to induce flowering, such as in pineapple (Dole and Wilkins, 1999), or abort or delay flowering in any other plants. In this work, the number of RB was reduced in *Coreopsis* by 95 and 100 percent at 800 ppm weekly during year 1 and year 2, respectively. The pre-chilled *Veronica* treated plants also had a decrease in the number of RB by 88 percent during year 2. These results support previous work

in which ethephon reduced the number of inflorescences in *Hebe* x *franciscana* 'Variegata' plants (Kristensen and Adreansen, 1988). Flowering of the first and second inflorescences was delayed 5 to 10 d, respectively, in seed propagated geraniums sprayed with 1000 mg l^{-1} ethephon (Ethrel®) (Carpenter and Carlson, 1970). Additionally, flowering was delayed in the perennials *Achillea*, *Echinacea*, *Monarda*, and *Physostegia* by 2, 6, 7 and 9 d, respectively with three ethephon applications at 1000 mg l^{-1} (Hayashi et al., 2001).

Although ethephon increased branching and thus more harvestable cuttings were available in *Coreopsis* (Figure 4), the ethephon concentrations and frequencies studied caused *Veronica* shoots and leaves to become small (3.0 cm) and deformed. Therefore, the increased number of PS was negated because cutting quality and yield actually decreased. Ethephon phytotoxicity can be a problem in other plants as well, for example, ethephon treatment of 1000 mg l^{-1} caused necrosis of *Monarda* foliage (Hayashi et al., 2001). In *Dianthus*, the impact of treatment duration and ethephon concentration on branching was only significant during year 2, but negatively so, as the number of PS and number of VC remained the same or actually decreased from the control by weeks 2 and 6. These decreases in cuttings were due to the increased difficulty of physically taking a cutting from the stunted vegetative growth.

Results from these experiments suggest that application rates of 600 ppm biweekly are adequate to increase the number of PS and VC, as well as decrease PH, SL, and the number of RB and RC in *Coreopsis* 'Moonbeam'. Weekly applications of 400 ppm weekly were effective to decrease PH, SL, and

number of RB yet increase number of PS and VC for *Veronica*; rates greater than 600 ppm weekly were phytotoxic to *Veronica* plant material and should be used with caution. Ethephon application did not have a positive affect on *Dianthus*, as plants became undesirably stunted for propagation purposes. Ethephon had no residual effects on harvested cuttings. This is an important point to consider not only during production and propagation when continuous applications would be necessary to maintain control over both vegetative and reproductive growth, but also during retail sales and ultimate use by the consumer when plants grow beyond the restrictive effects.

The objective of this study was to see if ethephon application can improve stock plant management in perennials, specifically to maintain vegetative growth and improve cutting quality and yield. Based on the findings of this experiment, ethephon has potential for this purpose in *Coreopsis* and *Veronica*, but not *Campanula*, *Dianthus*, *Salvia*, *Scabiosa*; or *Thalictrum* (Table 8).

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Table 1. Actual average daily temperatures (°C) and average daily light integral (DLI) ($mol \cdot m^{-2} \cdot d^{-1}$) during ethephon application.

Year	Experiment duration	Temperature	DLI
1 (2002)	22 May - 26 July	23.0	12
2 (2003)	18 March - 23 May	22.0	14
Veronica [z]	13 May - 18 July	23.0	19

[z] Plants in 2003 were chilled for 8 weeks at 5 °C prior to ethephon application.

Table 2. Schedule of cutting harvest dates for *Coreopsis verticillata* 'Moonbeam', *Dianthus caryophyllus* 'Cinnamon Red Hots'™, and *Veronica longifolia* 'Sunny Border Blue' that received 0 ppm and biweekly or weekly applications of 400 ppm or 800 ppm ethephon during year 1 (2002); and 0 ppm, 0 ppm plus water spray, and biweekly or weekly applications of 400 ppm, 600 ppm, or 800 ppm ethephon during year 2 (2003). The first week of ethephon application was week 1.

Species	Cutting harvest date	Weeks after first ethephon application
A. Year 1 (2002) [z]		
Coreopsis	12 June [y]	3
	19 June [x]	4
Dianthus	18 June [y]	4
	28 June [x]	5
Veronica	11 June [y]	3
	18 June [x]	4
	10 July	7
B. Year 2 (2003) [w]		
Coreopsis	1 April	2
	17 April	4
	9 May	7
Dianthus	1 April	2
	29 April	6
Veronica	1 April	2
	22 April	5
Veronica [v]	19 May	1
	20 June	5

[z] Ethephon was first applied on 22 May 2002.

[y] Cuttings were only harvested from five plants under each treatment.

[x] Cuttings were only harvested from the five plants not harvested from the previous week.

[w] Ethephon was first applied on 18 March 2003.

[v] Plants were chilled 8 weeks at 5 °C prior to ethephon application, which was first applied on 13 May 2003.

Table 3. Effects of ethephon on growth of *Coreopsis verticillata* 'Moonbeam' during year 1 (2002).

	Ethephon concentration (ppm)				
		Biweekly		Weekly	
Treatment duration	0	400	800	400	800
A. Plant height (cm)					
Week 0	1.0 A[z] a[y]	4.3 A a	5.0 A a	4.4 A a	4.9 A a
Week 4	25.7 B b	15.2 B a	14.9 B a	15.6 B a	9.8 A a
Week 10	44.8 C b	37.8 C b	24.6 C a	25.2 C a	25.6 B a
B. No. of primary shoots/plant					
Week 0	3 A	6 A	14 A	15 A	13 A
Week 4	37 A	50 A	36 A	26 A	35 A
Week 10	5 A	22 A	70 B	54 A	54 A
C. No. of reproductive buds/plant					
Week 0	0 A a	0 A a	0 A a	0 A a	0 A a
Week 4	46 B c	15 B b	6 A a	5 A a	1 A a
Week 10	88 C c	22 B b	23 B b	19 B b	4 A a
D. No. of vegetative cuttings/plant					
Harvest 1	8 a	11 a	7 a	7 a	7 a
E. No. of reproductive cuttings/plant					
Harvest 1	26 c	9 b	5 ab	6 ab	2 a

[z]For each variable, upper case letters next to means in the same column represent mean separation by LSMeans ($P \leq 0.05$).

[y]For each variable, lower case letters next to means in the same row represent mean separation by LSMeans ($P \leq 0.05$).

Table 4. Effects of ethephon on cutting quality of *Coreopsis verticillata* 'Moonbeam', *Dianthus caryophyllus* 'Cinnamon Red Hots'™, and *Veronica longifolia* 'Sunny Border Blue' during year 1 (2002).

Ethephon concentration	No. of roots	Root length (cm)	No. of flower buds
A. *Coreopsis*			
0 ppm	11 a [z]	4.8 a	2 b
400 ppm biweekly	11 a	6.8 b	1 a
800 ppm biweekly	16 b	6.8 b	1 a
400 ppm weekly	12 a	7.6 b	0 a
800 ppm weekly	13 a	6.8 b	0 a
Significance			
Ethephon concentration	**	**	***
B. *Dianthus*			
0 ppm	8 c	15.6 b	0 a
400 ppm biweekly	6 b	8.7 a	0 a
800 ppm biweekly	5 ab	3.8 a	0 a
400 ppm weekly	4 ab	6.9 a	0 a
800 ppm weekly	3 a	5.2 a	0 a
Significance			
Ethephon concentration	***	**	***
C. *Veronica*			
0 ppm	14 b	5.0 a	1 a
400 ppm biweekly	11 ab	6.5 a	1 a
800 ppm biweekly	10 a	6.2 a	1 a
400 ppm weekly	13 b	6.5 a	1 a
800 ppm weekly	12 b	6.1 a	1 a
Significance			
Ethephon concentration	*	NS	NS

[z]For each species, letters next to means in the same column represent mean separation by LSMeans ($P \leq 0.05$).

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

Table 5. Effects of ethephon on growth of *Dianthus caryophyllus* 'Cinnamon Red Hots'™ during year 1 (2002).

	Ethephon concentration (ppm)				
		Biweekly		Weekly	
Treatment duration	0	400	800	400	800
A. Plant height (cm)					
Week 0	5.0 A[z]a[y]	5.0 A a	5.0 A a	5.0 A a	5.0 A a
Week 5	12.0 B c	10.6 B b	8.2 B a	8.9 B a	8.4 B a
Week 10	16.1 C c	15.5 C c	-[x]	14.0 C b	12.3 C a
B. No. of primary shoots/plant					
Week 0	14 A a	15 A a	13 A a	13 A a	17 A a
Week 5	26 B a	22 B a	22 B a	23 B a	25 B a
Week 10	24 B a	28 C a	-	26 C a	31 C a
C. No. of vegetative cuttings/plant					
Harvest 1	18 a	15 a	14 a	13 a	17 a

[z]For each variable, upper case letters next to means in the same column represent mean separation by LSMeans ($P \leq 0.05$).

[y]For each variable, lower case letters next to means in the same row represent mean separation by LSMeans ($P \leq 0.05$).

[x]Data not available.

Table 6. Effects of ethephon on growth of *Veronica longifolia* 'Sunny Border Blue' during year 1 (2002).

	Ethephon concentration (ppm)				
		Biweekly		Weekly	
Treatment duration	0	400	800	400	800
A. Plant height (cm)					
Week 0	5.0 A[z]a[y]	5.0 A a	5.0 A a	5.0 A a	5.0 A a
Week 4	17.9 B a	14.9 B a	13.8 B a	11.5 B a	12.1 B a
Week 8	28.4 C d	23.5 C c	13.9 B a	18.3 C b	16.7 C b
Week 10	39.5 D c	33.0 D b	20.9 C a	23.7 D a	20.2 C a
B. No. of primary shoots/plant					
Week 0	4 A a	4 A a	5 A a	4 A a	3 A a
Week 4	7 A a	10 B a	11 B a	10 B a	10 B a
Week 8	12 B a	22 C c	25 C c	13 B ab	17 C b
Week 10	14 B a	21 C bc	26 C c	18 C ab	26 D c
C. No. of reproductive buds/plant					
Week 0	0 A a	0 A a	0 A a	0 A a	0 A a
Week 4	1 A a	2 A a	1 A a	1 A a	1 A a
Week 8	6 B b	6 B b	1 A a	1 A a	1 A a
Week 10	9 B b	8 B b	7 B a	3 A a	3 A a
D. No. of vegetative cuttings/plant					
Harvest 1	6 A a	7 A a	9 A a	8 A a	9 A a
Harvest 2	6 A a	13 B ab	18 B bc	15 B b	19 B c
E. No. of reproductive cuttings/plant					
Harvest 1	1 A a	2 A a	1 A a	1 A a	1 A a
Harvest 2	5 B ab	7 B b	2 A a	3 A a	2 A a

[z]For each variable, upper case letters next to means in the same column represent mean separation by LSMeans ($P \leq 0.05$).

[y]For each variable, lower case letters next to means in the same row represent mean separation by LSMeans ($P \leq 0.05$).

Table 7. Effect of ethephon application on cutting quality based on cutting height, number of reproductive buds, and rooting percentage 2 (*Coreopsis verticillata* 'Moonbeam' and *Dianthus caryophyllus* 'Cinnamon Red Hots'™) or 3 (*Veronica longifolia* 'Sunny Border Blue') weeks after propagation during year 2 (2003).

	Cutting quality		
Treatment duration	Harvest 1	Harvest 2	Harvest 3
A. *Coreopsis*			
0 ppm	2.2	2.1	1.0
0 ppm water spray	3.4	2.5	1.8
400 ppm biweekly	2.9	3.7	3.0
600 ppm biweekly	4.1	4.7	3.6
800 ppm biweekly	3.6	4.3	4.2
400 ppm weekly	3.7	4.3	3.9
600 ppm weekly	2.7	4.3	3.9
800 ppm weekly	3.9	5.2	3.6
B. *Dianthus*			
0 ppm	2.7	3.3	
0 ppm (water spray)	2.7	4.1	
400 ppm biweekly	4.7	4.3	
600 ppm biweekly	4.8	3.9	
800 ppm biweekly	2.6	3.8	
400 ppm weekly	4.8	3.9	
600 ppm weekly	4.5	3.7	
800 ppm weekly	4.5	3.3	
C. *Veronica*			
0 ppm	-[z]	4.9	
0 ppm (water spray)	-	4.5	
400 ppm biweekly	4.3	4.5	
600 ppm biweekly	-	4.1	
800 ppm biweekly	-	3.8	
400 ppm weekly	4.1	4.5	
600 ppm weekly	5.6	4.1	
800 ppm weekly	-	3.8	
D. *Veronica*[y]			
0 ppm	3.9	4.3	
0 ppm (water spray)	3.6	4.7	
400 ppm biweekly	3.7	4.1	
600 ppm biweekly	4.2	3.9	
800 ppm biweekly	3.6	4.5	
400 ppm weekly	3.5	3.9	
600 ppm weekly	2.9	4.4	
800 ppm weekly	2.8	3.6	

[z]Data not available

[y]Plants were chilled at 5 °C for 8 weeks prior to ethephon applications.

Table 8. Summary of photoperiod and vernalization requirements, and recommended ethephon application rates and frequencies on *Campanula* 'Kent Belle', *Coreopsis verticillata* 'Moonbeam', *Dianthus caryophyllus* 'Cinnamon Red Hots'™, *Salvia nemorosa* 'May Night', *Scabiosa columbaria* 'Giant Blue', *Thalictrum kiusianum*, and *Veronica longifolia* 'Sunny Border Blue'.

Species	Photoperiod	Chilling at 5 °C	Ethephon (ppm)
Campanula	DN [z]	Yes	NE [x]
Coreopsis	LD [y]	No	600 biweekly
Dianthus	DN	No	NE
Salvia	DN	No	NE
Scabiosa	DN	NT [w]	NE
Thalictrum	DN	Yes	NE
Veronica	DN	Yes	400 weekly

[z]Day-neutral plant
[y]Long-day plant (≥ 14 h)
[x]Not effective
[w]Not tested

Figure 1. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on shoot length in *Coreopsis verticillata* 'Moonbeam' during year 2 (2003). Cutting harvests occurred during week 2, week 4, and week 7. Data for week 9 were not taken. Error bars represent SE.

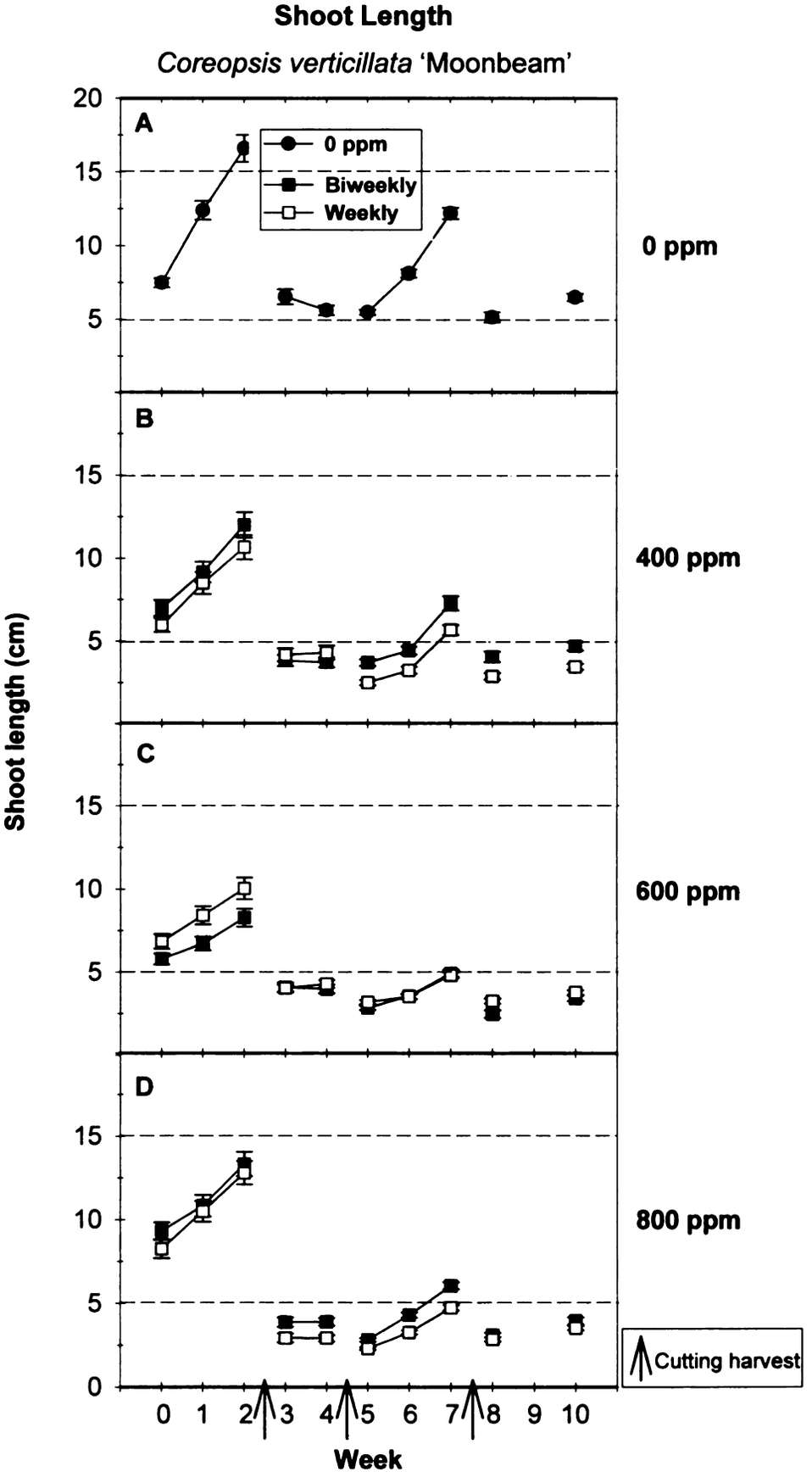

Shoot Length
Coreopsis verticillata 'Moonbeam'
A
B
C
D
0 ppm
Biweekly
Weekly
0 ppm
400 ppm
600 ppm
800 ppm
Shoot length (cm)
Week
Cutting harvest

Figure 2. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on the number of primary shoots in *Coreopsis verticillata* 'Moonbeam' during year 2 (2003). Cutting harvests occurred during week 2, week 4, and week 7 Data for week 9 were not taken. Error bars represent SE.

Primary Shoots
Coreopsis verticillata 'Moonbeam'

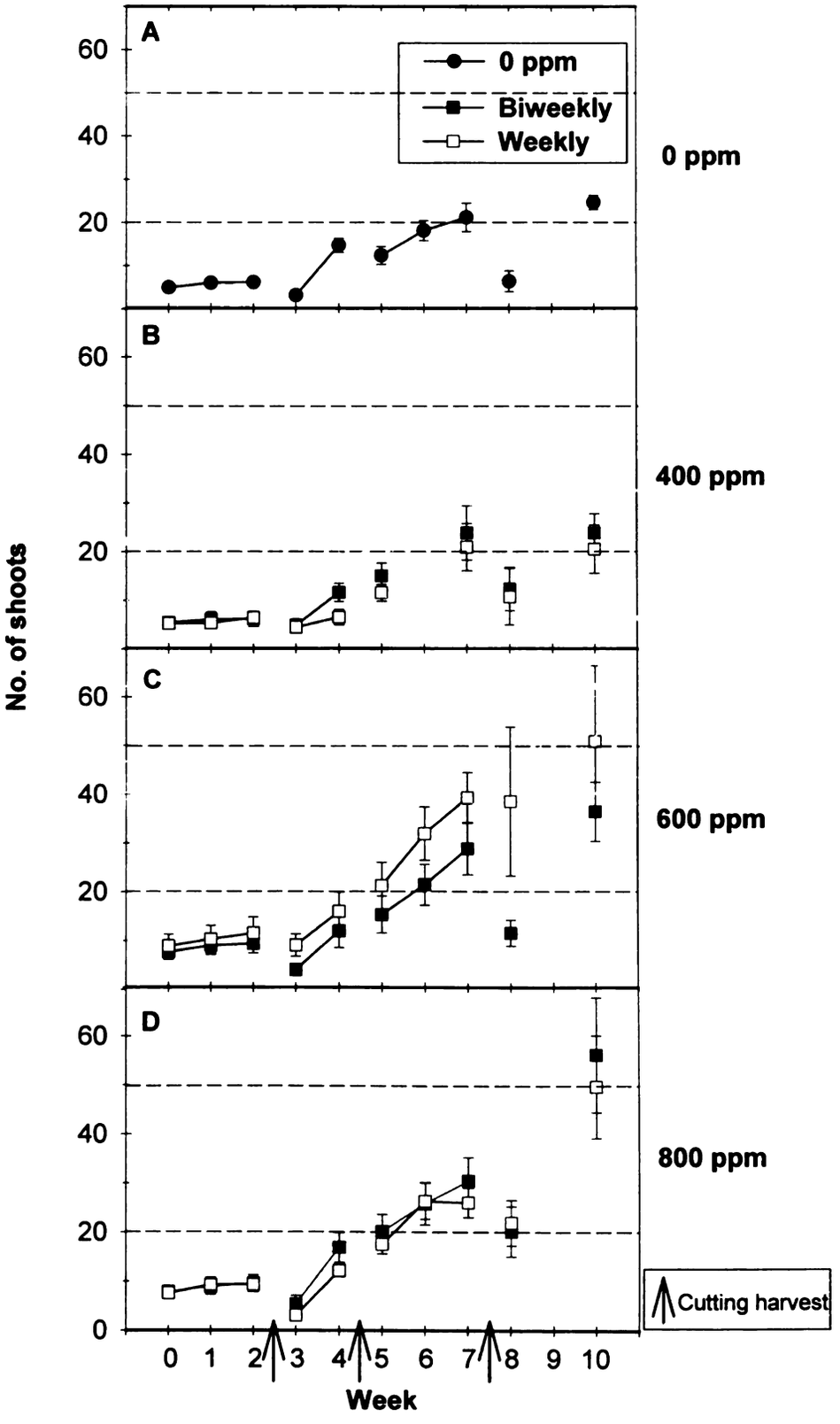
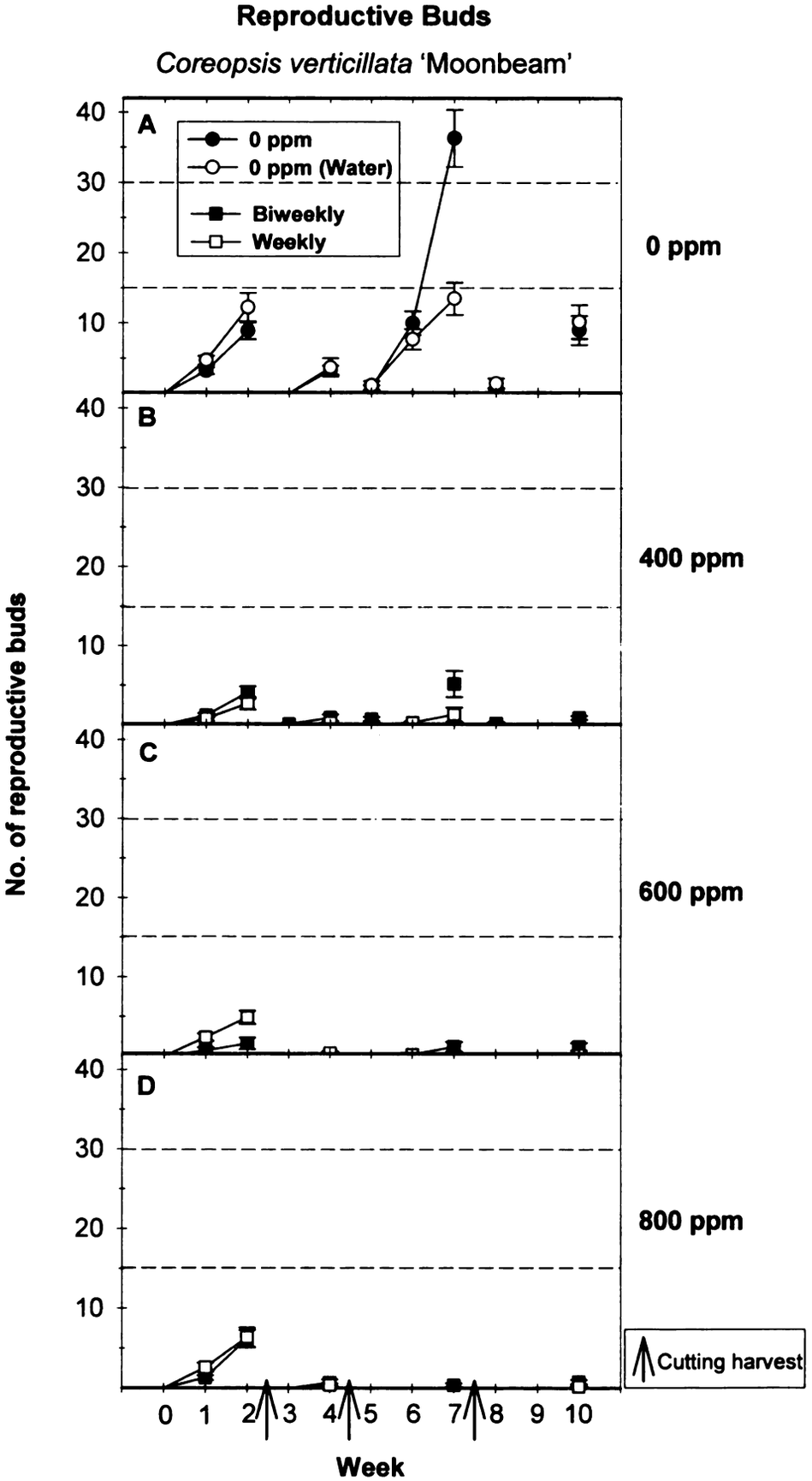


Figure 3. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on the number of reproductive buds in *Coreopsis verticillata* 'Moonbeam' during year 2 (2003). Cutting harvests occurred during week 2, week 4, and week 7. Data for week 9 were not taken. Error bars represent SE.


Reproductive Buds
Coreopsis verticillata 'Moonbeam'
A
B
C
D
0 ppm
0 ppm (Water)
Biweekly
Weekly
0 ppm
400 ppm
600 ppm
800 ppm
Cutting harvest
No. of reproductive buds
Week
0 1 2 3 4 5 6 7 8 9 10
10 20 30 40

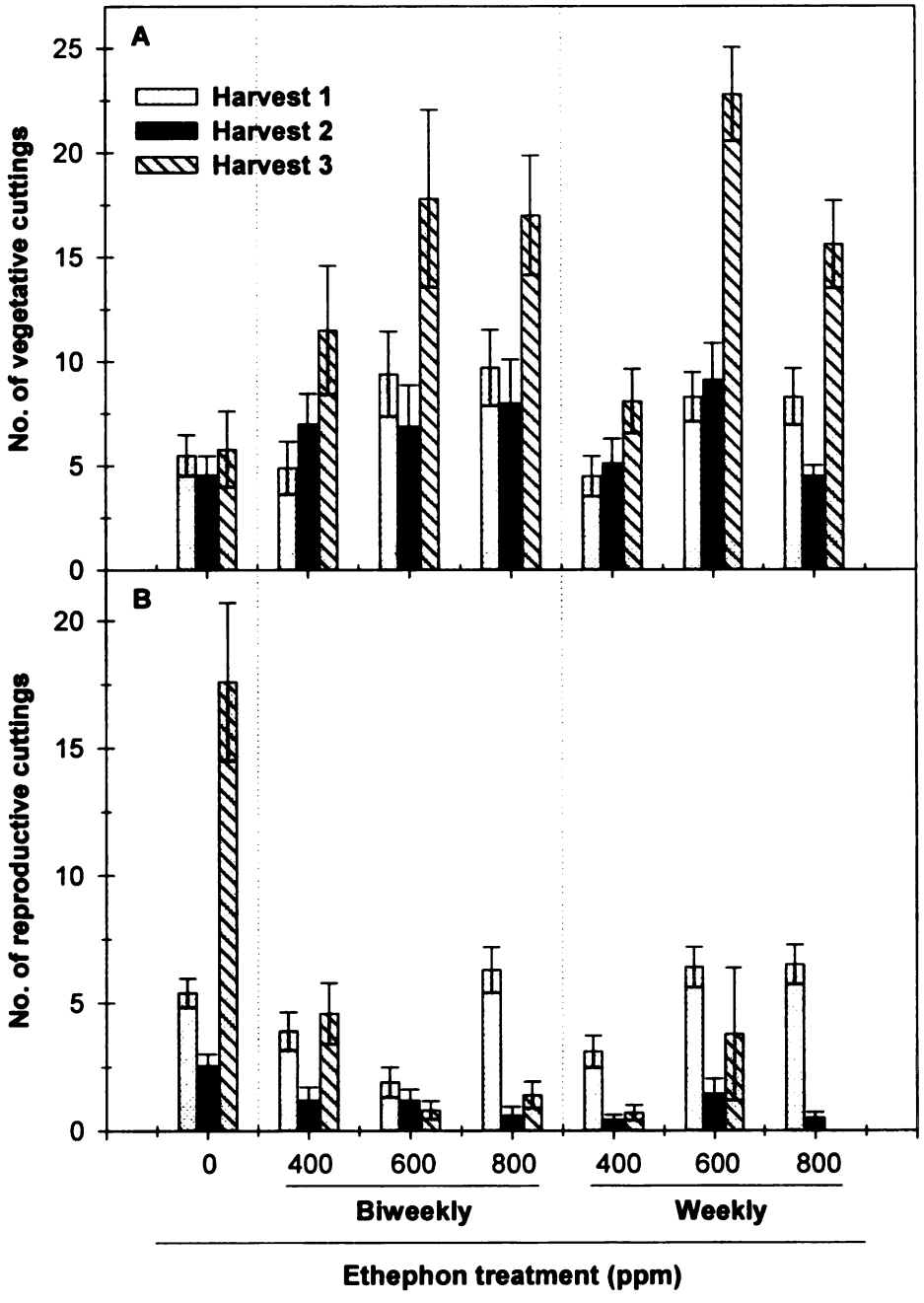
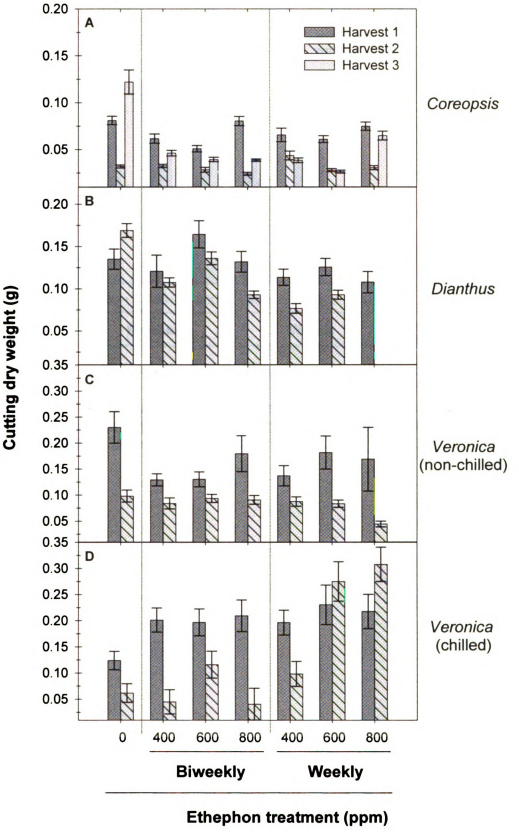


Figure 4. Effects of ethephon on the average number of vegetative (A) and reproductive (B) cuttings per plant at each cutting harvest date of *Coreopsis verticillata* 'Moonbeam' during year 2 (2003).

Figure 5. The effect of ethephon application on cutting dry weight of *Coreopsis verticillata* 'Moonbeam' (A), *Dianthus caryophyllus* 'Cinnamon Red Hots'™ (B), *Veronica longifolia* 'Sunny Border Blue' (C), and chilled (8 weeks at 5 °C) *Veronica longifolia* 'Sunny Border Blue' (D) during year 2 (2003). Error bars represent SE.


A
B
C
D
Harvest 1
Harvest 2
Harvest 3
Coreopsis
Dianthus
Veronica
(non-chilled)
Veronica
(chilled)
Cutting dry weight (g)
0.20
0.15
0.10
0.05
0.35
0.30
0.25
0
400
600
800
Biweekly
Weekly
Ethephon treatment (ppm)

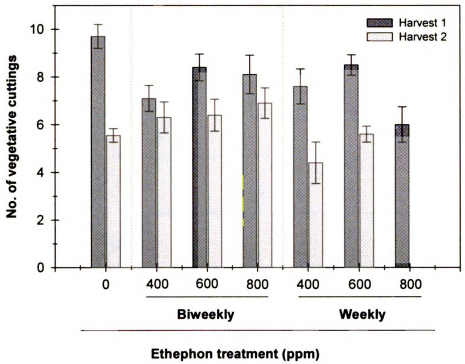


Figure 6. Effects of ethephon on the average number of vegetative cuttings per plant at each cutting harvest date of *Dianthus caryophyllus* 'Cinnamon Red Hots'™ during year 2 (2003).

Figure 7. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on shoot length in *Veronica longifolia* 'Sunny Border Blue' during year 2 (2003). Cutting harvests occurred during week 2 and week 5. Data for week 3 and week 9 were not taken. Error bars represent SE.

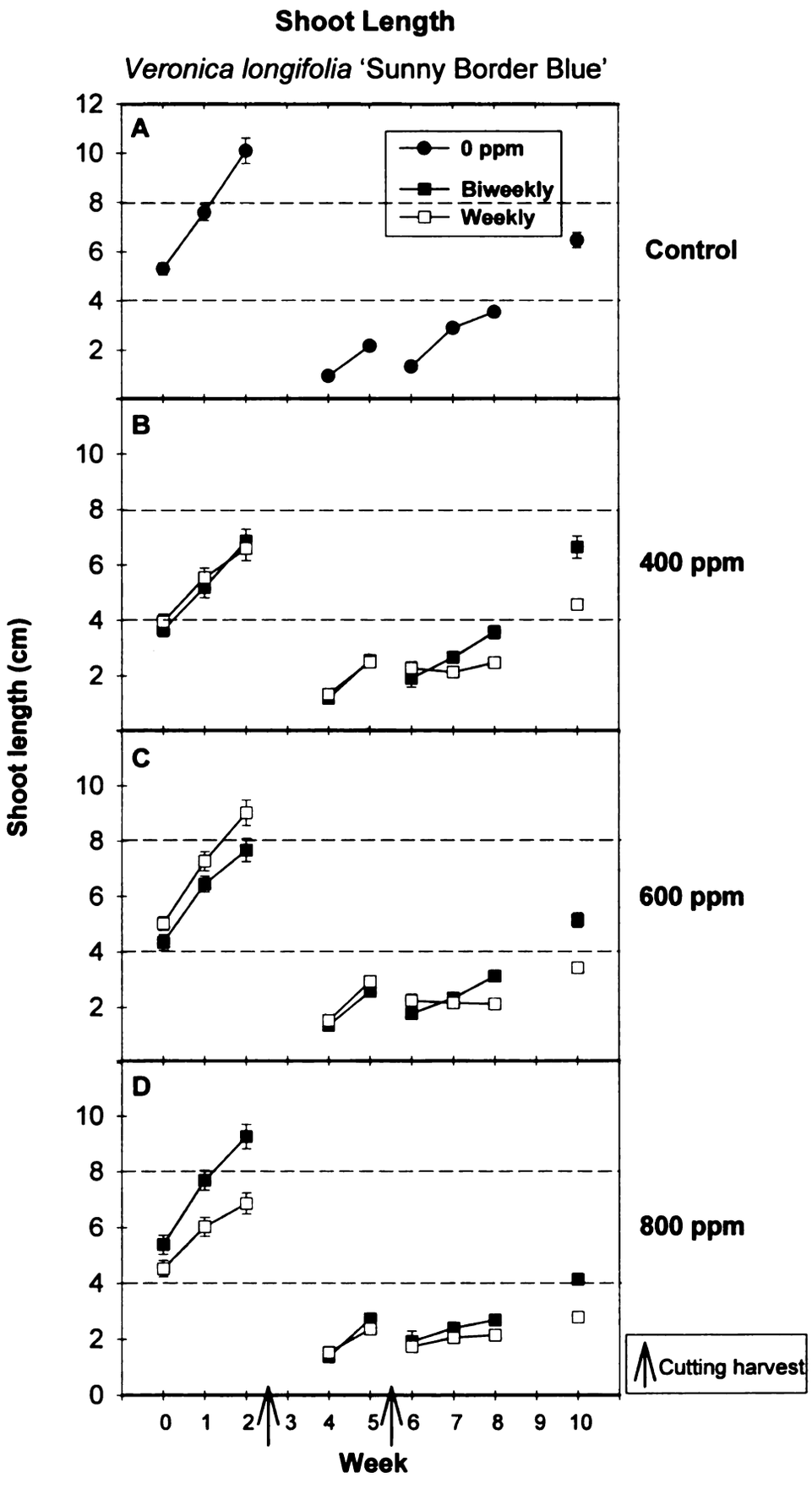
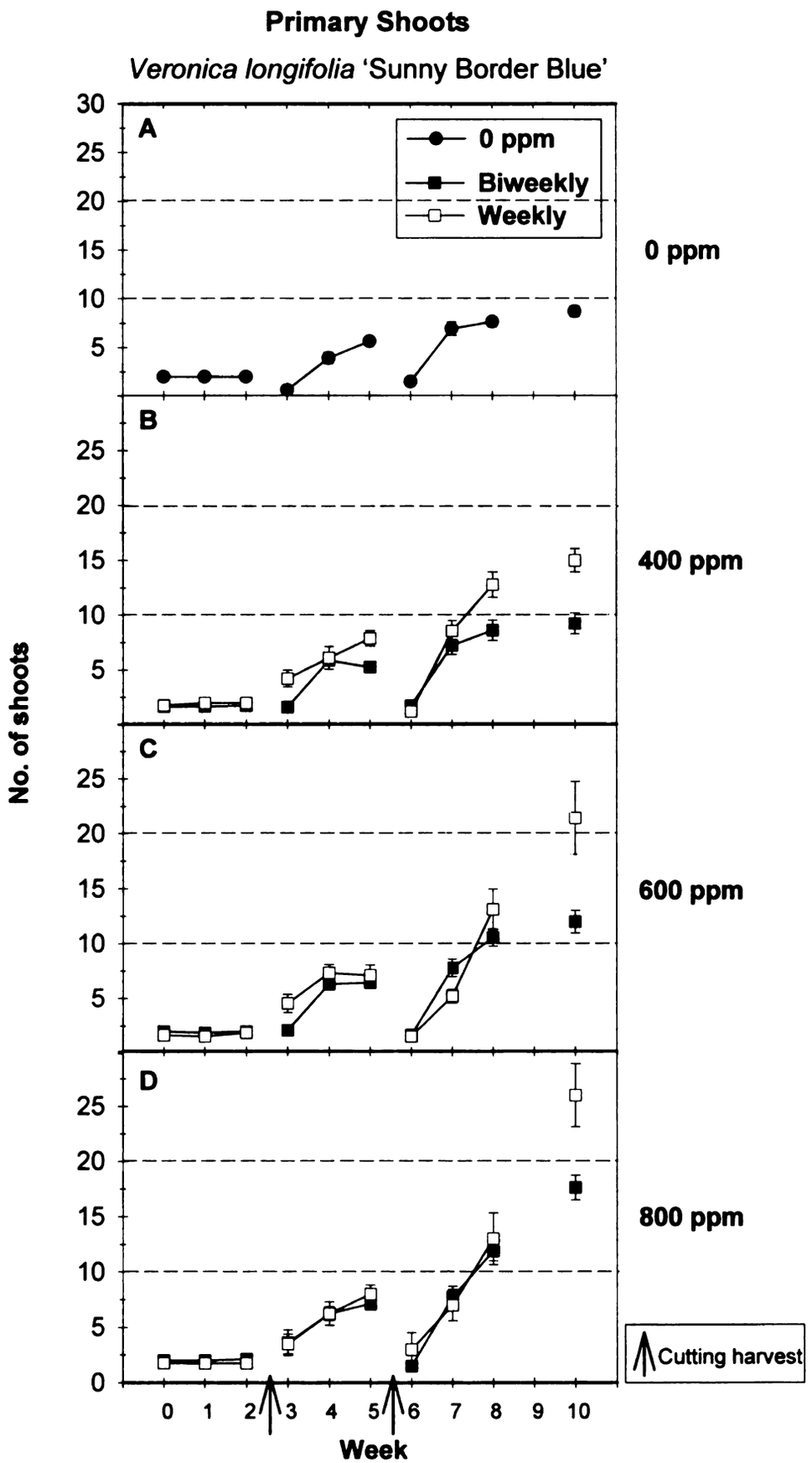

Shoot Length
Veronica longifolia 'Sunny Border Blue'
A
B
C
D
0 ppm
Biweekly
Weekly
Control
400 ppm
600 ppm
800 ppm
Shoot length (cm)
Week
Cutting harvest

Figure 8. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on the number of primary shoots in *Veronica longifolia* 'Sunny Border Blue' during year 2 (2003). Cutting harvests occurred during week 2 and week 5. Data for week 9 were not taken. Error bars represent SE.


Primary Shoots
Veronica longifolia 'Sunny Border Blue'
A
B
C
D
0 ppm
Biweekly
Weekly
0 ppm
400 ppm
600 ppm
800 ppm
No. of shoots
Week
Cutting harvest

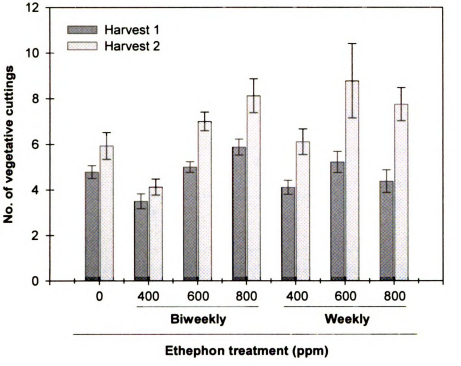
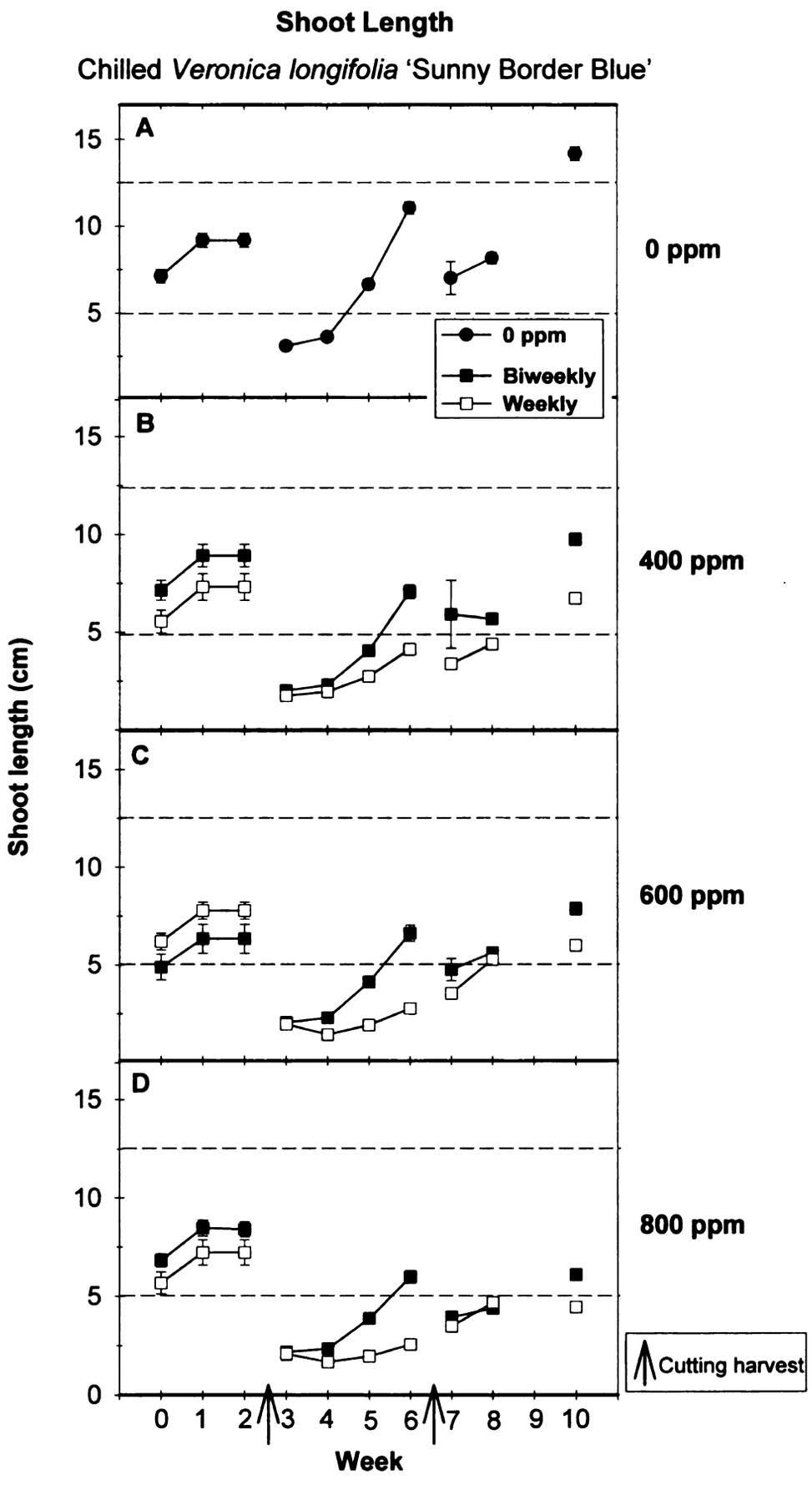


Figure 9. Effects of ethephon on the average number of vegetative cuttings per plant at each cutting harvest date of *Veronica longifolia* 'Sunny Border Blue' during year 2 (2003). Error bars represent SE.

Figure 10. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on shoot length in *Veronica longifolia* 'Sunny Border Blue' that received 8 weeks at 5 °C prior to ethephon application during year 2 (2003). Cutting harvests occurred during week 2 and week 6. Data for week 9 were not taken. Error bars represent SE.


Shoot Length
Chilled Veronica longifolia 'Sunny Border Blue'
A
B
C
D
0 ppm
400 ppm
600 ppm
800 ppm
0 ppm
Biweekly
Weekly
Cutting harvest
Shoot length (cm)
Week
0 1 2 3 4 5 6 7 8 9 10
0 5 10 15

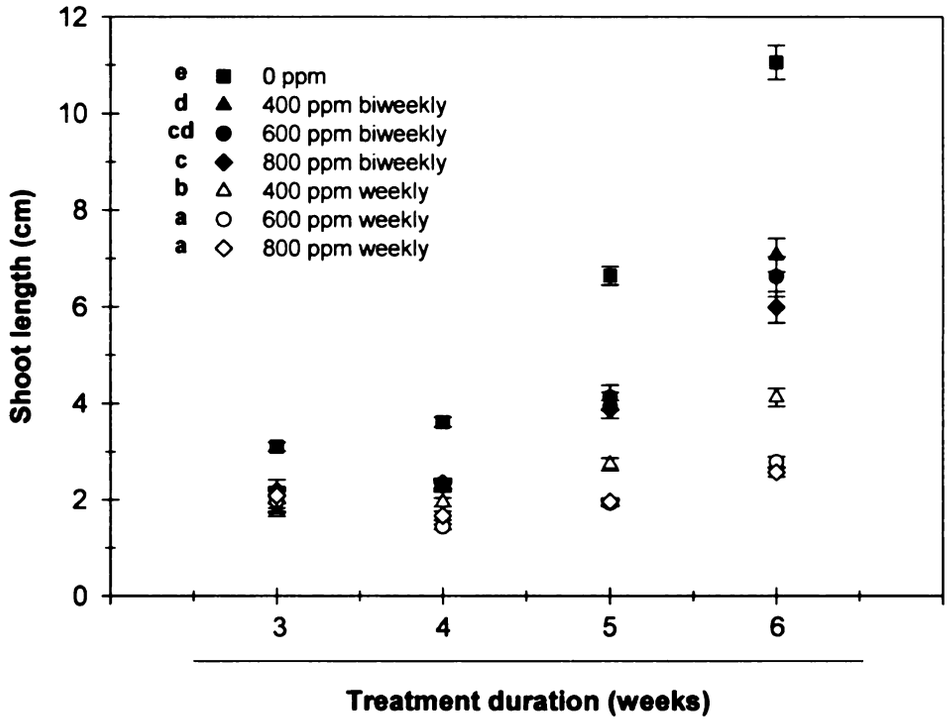
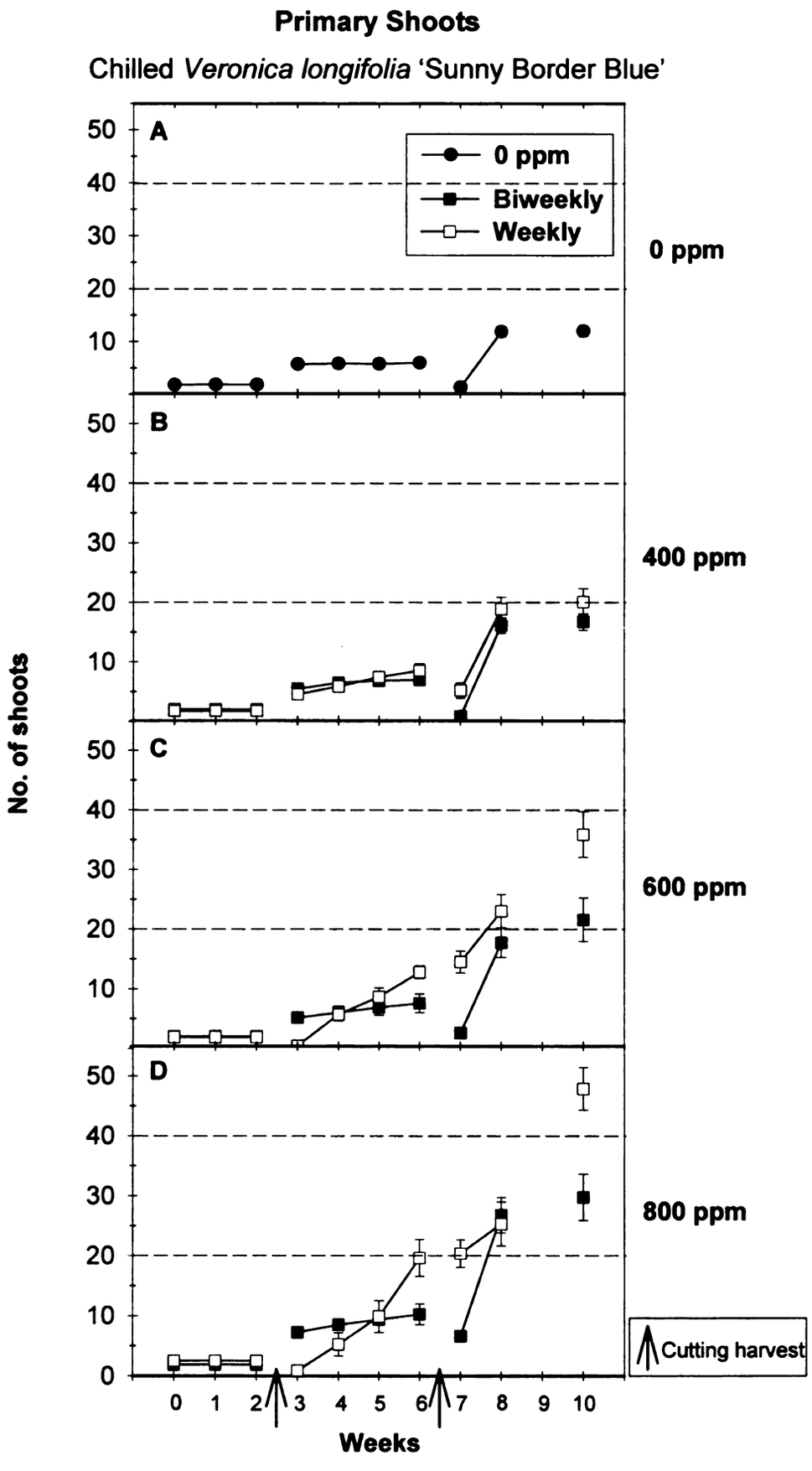


Figure 11. The relationship between ethephon application and shoot length in *Veronica longifolia* 'Sunny Border Blue' that received 8 weeks at 5 °C prior to ethephon application during year 2 (2003). Letters next to application rates represent mean separation by LSMeans ($P \leq 0.05$) for the slope of each line.

Figure 12. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on the number of primary shoots in *Veronica longifolia* 'Sunny Border Blue' that received 8 weeks at 5 °C prior to ethephon application during year 2 (2003). Cutting harvests occurred during week 2 and week 5. Data for week 9 were not taken. Error bars represent SE


Primary Shoots
Chilled Veronica longifolia 'Sunny Border Blue'
A
B
C
D
0 ppm
Biweekly
Weekly
0 ppm
400 ppm
600 ppm
800 ppm
No. of shoots
Weeks
Cutting harvest

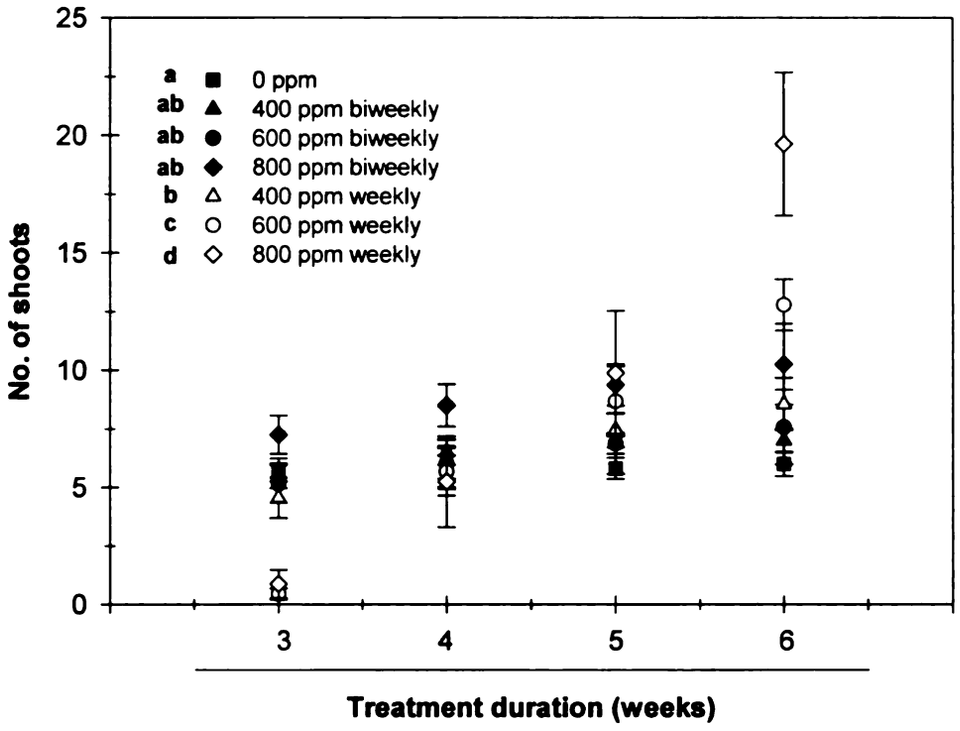


Figure 13. The relationship between ethephon application and the number of primary shoots developed in *Veronica longifolia* 'Sunny Border Blue' that received 8 weeks at 5 °C prior to ethephon application during year 2 (2003). Letters next to application rates represent mean separation by LSMeans ($P \leq 0.05$) for the slope of each line.

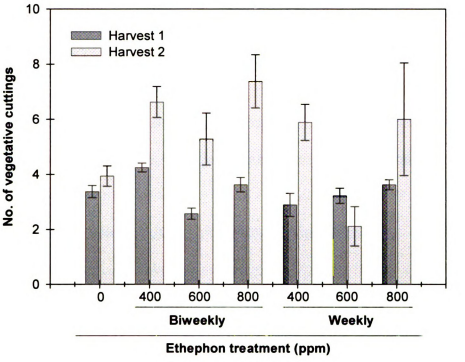


Figure 14. Effects of ethephon on the average number of vegetative cuttings per plant at each cutting harvest date of *Veronica longifolia* 'Sunny Border Blue' that received 8 weeks at 5 °C prior to ethephon application during year 2 (2003).

SECTION III

THE EFFECT OF BULKING DURATION, BULKING PHOTOPERIOD, AND VERNALIZATION ON PRODUCTION SCHEDULING OF EIGHTEEN HERBACEOUS PERENNIAL SPECIES

The Effect of Bulking Duration, Bulking Photoperiod, and Vernalization on Production Scheduling of Eighteen Herbaceous Perennial Species

Janelle E. Glady[1], N. Suzanne Lang[2], and Erik S. Runkle[3]

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

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[1]Graduate Student

[2]Associate Professor

[3]Assistant Professor

Abstract

Consumer demand for a variety of flowering, herbaceous perennial plants increased from 2001 to 2002 by 18%. However, scheduling various species to flower for a particular market date poses challenges to commercial growers, as production time is dependent upon species' responses to juvenility, photoperiod, and vernalization. Four bulking durations under 10- or 16-h photoperiods were provided prior to 0 or 8 weeks at 5 °C to investigate the effects of vegetative growth on flower initiation. Species studied included: *Achillea millefolium* L. 'Paprika', *Aquilegia* x *hybrida* Sims 'Songbird Mix', *Coreopsis grandiflora* Hogg ex Sweet 'Early Sunrise', *Echinacea purpurea* Moench 'Magnus', *Penstemon digitalis* Nutt. 'Husker Red', and *Salvia nemorosa* L. ' May Night'. As the bulking duration increased, plant height and the number of nodes increased in all species. Although *Echinacea* flowered under all treatments, total production time was too long (10 weeks) for a quick crop schedule. Juvenility and vernalization requirements were apparent in *Aquilegia* and *Penstemon*, as increased bulking (≥ 5 weeks) and cold exposure were essential for complete and uniform flowering. *Achillea*, *Coreopsis*, and *Salvia* flowered in less than 8 weeks with no requirement for bulking or vernalization. However, during year 2, time to flower was significantly reduced from 69 to 43 d and the number of floral buds was increased 70% in *Coreopsis* after 8 weeks of 5 °C. Recommended schedules for total production time (i.e., weeks bulking, chilling, and forcing) of each species are presented.

Introduction

Herbaceous perennial plant production involves the management of plant growth, development, and flowering. Production management for a diverse selection of plant material continues to pose challenges for the commercial industry. Obtaining sufficient vegetative growth (i.e., bulking) ideal for forcing flowering for retail sale is one of these challenges.

The state of Michigan is a major producer of floriculture crops, including potted herbaceous perennials. However, due to the extreme temperature range and periods of low light levels in Michigan, managing optimum plant growth and flowering requires implementation of lighting and temperature management systems for successful commercial production. In addition, marketing studies have shown that plants with open blooms sell better than plants that are vegetative, as consumers can experience the flower qualities, instead of relying on what is printed on a tag (Behe and Barton, 2000). Thus, understanding the factors that control plant vegetative and reproductive development (i.e., juvenility, photoperiod, and vernalization) is essential for the development of commercial plant production schedules.

The quality and condition of propagated plant material is important for the uniformity and overall growth of a crop that must be in flower at a specific market date. The ability to propagate herbaceous perennials by different sexual and asexual methods (e.g., seed, stem or root cuttings, division, and tissue culture) can result in plants at different stages of maturation when they enter the production system, thus staggering their final market date. Many of these young

propagules are still juvenile, and thus remain in an early phase of growth during which flowering cannot be induced under any environmental condition (Thomas and Vince-Prue, 1997). For example, two daylength responsive cultivars of *Salvia splendens* Sello ('Bonfire' and 'Red Pillar') only become sensitive to photoperiod when the juvenile phase ends at a stem node number between four and six (Lai and Weiler, 1975). Additionally, many perennials that require cold for floral induction must reach a minimum leaf or node number before cold perception is possible (Heins et al., 1997). For example, *Aquilegia* x *hybrida* Sims requires a minimum of 12 leaves to be responsive to a vernalization treatment (Shedron and Weiler, 1982). However, a required leaf number for floral induction is not restricted to plants that require cold for flowering.

Juvenility can be responsible for a certain degree of unpredictability and lack of uniformity during production cycles in the floriculture industry. Therefore, it is important to understand the impact of juvenility during the development of propagation material to have uniform flowering crops. Bulking is the termed used to describe the time period during which young plants are grown to attain adequate vegetative growth prior to floral inductive conditions. As a mature plant, a specific amount of chilling or daylength may be required to subsequently induce flowering.

Temperature perception is a major environmental cue that plants have evolved to help control flowering in response to the changing seasons (Michaels and Amasino, 2000). In temperate crops, low temperatures that are sufficient to provide a vernalization response are often between 1 and 7 °C (Chouard, 1960).

This amount of chilling, or vernalization, is the specific promotion of flowering by a cold treatment given to an imbibed seed or young plant (Thomas and Vince-Prue, 1984). Unlike dormancy, which affects growth or vegetative and floral development, vernalization affects the physiology of reproductive development and influences plant competence towards floral initiation. In regards to floral development, vernalization is further distinguished from other environmental induction processes because floral initials are not yet present after vernalization and often further inductive conditions are required (Vince-Prue, 1975).

The length of cold exposure is critical and species dependent. For example, flowering percentage in *Aquilegia* x *hybrida* 'McKana's Giant' increased from 0 to 100 percent when cold treatment (4.5 °C) increased from 0 weeks to 12 (Shedron and Weiler, 1982). Rooted cuttings of *Veronica longifolia* 'Sunny Border Blue' with four to five nodes flowered most uniformly and rapidly after 9 weeks at 5 °C (Engle, 1994). When exposed to an inadequate amount of cold, flowering is delayed, if initiated at all, in many plant species that require vernalization (Thomas and Vince-Prue, 1984).

In addition to vernalization, photoperiod can regulate flowering, and can act simultaneously yet independently with cooling to induce flowering (Lang, 1965). Meaning 'light' and 'duration of time', photoperiodism is a developmental plant response to the length of the uninterrupted night period. Photoperiod manipulation in the floriculture industry is an important tool for management of plant growth since daylength can be controlled to strategically influence vegetative growth, floral initiation, or floral development.

The most common interaction between vernalization and photoperiod occurs in many temperate plant species that require a cold treatment prior to long days for flower initiation (Lang, 1965). For some species, short days can substitute partly or entirely for cold. For example, the normal flowering response of a low temperature/long day induction treatment in *Campanula medium* can be substituted by a short day/long day treatment (Vince-Prue, 1975). Therefore, although the relationship is not fully understood, short days and cold seem to be alternative mechanisms that lead to flower induction.

This work tests the hypothesis that increased bulking time is necessary for some herbaceous perennials to fulfill the juvenility requirement prior to exposure to further floral induction factors such as chilling. The objectives of this study are to quantify the effects that length of bulking time, bulking photoperiod, and exposure to a cold period have on plant quality (i.e., good color and good plant habit) and total finish time (i.e., fast and easy to grow) in herbaceous perennial crops to develop production schedules for commercial growers.

Materials and Methods

Plant Material: Eighteen different herbaceous perennial species (Table 1) were received as vegetative, rooted plugs in 306 trays (0.15–L) (East Jordan Plastics, Inc., East Jordan, Mich.) for year 1 (2002) experiments. For year 2, (2003), plants were received as vegetative, rooted, 72–cell (0.04–L) plugs and immediately transplanted into 306 trays using a peat and perlite soil mix (Sure-mix Perlite; Michigan Grower Products, Galesburg, Mich.; 70 % peat moss, 21%

perlite, 9% vermiculite). Only *Salvia nemorosa* 'May Night' was received as a 54-cell (0.08–L) plug during year 2. Twelve species that were screened during 2002 were not replicated in time, as they did not meet the desired production criteria of being fast and easy to grow with good color and plant habit. Complete schedules of treatment durations are listed in Table 2A for year 1 and Table 2B for year 2.

Bulking treatments: The experiment was replicated in time, beginning 8 Aug. 2002 and 17 July 2003. Ten plants of each species were randomly placed on greenhouse benches for the duration of 2, 5 or 8 weeks as a 306 plug under 10- or 16-h photoperiods; an additional treatment of 0 weeks bulking was added in year 2. Continuous photoperiods consisted of 9-h days completed with 1 or 7 h of extension lighting (≈ 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at canopy level) provided by incandescent lamps. Lamps were turned on at 1700 HR and turned off when each photoperiod was completed. Opaque black cloth was pulled at 1700 HR and opened at 0800 HR everyday on all benches. Floral buds that formed on *Achillea*, *Coreopsis*, and *Salvia* during the bulking interval were removed by hand.

Plants were grown in a glass greenhouse set at a constant 20 °C. Temperatures on each bench were measured by a thermocouple in an aspirated tube every 10 s, and hourly averages were recorded by a CR-10 datalogger (Campbell Scientific, Logan, Utah). Average daily light integral (DLI) was monitored by a line light quantum sensor (Apogee Instruments, Inc., Logan, Utah).

Plants were irrigated as necessary with reverse osmosis water supplemented with water-soluble fertilizer to provide the following ($mg \cdot L^{-1}$): 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo.

Cold treatment: Following the respective bulking treatment, plants in 306 trays were placed in a cooler set at 5 °C for eight weeks; a cold treatment for plants that received 0 weeks bulking was added during 2003. Five plants from each respective bulking treatment that did not receive a cold treatment were treated as controls (non-cooled); 10 plants per treatment were used during 2003. The cooler was lighted from 0800 to 1700 HR by cool-white fluorescent lamps (F96T 12/CW/VHO, Phillips, Somerset, N.J.) with a photosynthetic photon flux (*PPF*) of approximately 6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. Plants were watered as needed. *Achillea* plant leaves and stems were cut back to ≈10 cm above the soil line prior to cold for most bulking durations to reduce the potential of a pathogen infection in the cooler, due to the large amount of vegetative material produced during bulking. However, *Achillea* plants that were bulked for 2 weeks during 2002 were not cut back. One to two plants each of *Aquilegia*, *Echinacea*, and *Penstemon* died in the cooler, were discarded, and were not included in the results.

Finish environment: Plants that did not receive a bulking or a cold treatment (control) were immediately transplanted into 15-cm (3.8-L) containers (Dillen Products, Middlefield, Ohio) using a peat and perlite soil mix (Sure-mix Perlite; Michigan Grower Products, Galesburg, Mich.; 70% peat moss, 21% perlite, 9% vermiculite). Non-cooled plants remained in 306 trays under 10- or

16- h days until cold-treated plants were removed from the cooler. Thus, the flower start date was the same for non-cooled and cooled bulking treatments. Immediately prior to the beginning of forcing, bulked plants were transplanted into containers with medium as previously described. In 2003, non-cooled plants were transplanted as previously described and placed directly under flowering conditions after the bulking treatment. Thus, the flower start date was 8 weeks prior to that of cold treated plants.

Ten plants from each bulking and cooling treatment were randomly placed on greenhouse benches and forced to flower under 16-h photoperiods. Day extension lighting was provided by high-pressure sodium lamps with an approximate *PPF* of 85 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. High-pressure sodium lamps were also used for supplemental light until natural light levels exceeded 120 $\mu mols \cdot m^{-2} \cdot s^{-1}$. Temperature and light intensity were measured with sensors previously described. Actual average daily temperatures and average DLI for each bulking and flower treatment are presented in Table 3A for year 1 and Table 3B for year 2.

Data Collection: Plant height (PH), number of nodes (NN), and number of primary shoots (PS) were recorded upon plant arrival and are presented in Table 4. These data were also recorded after completion of each bulking treatment. The dates of visible bud (VB) and open flower (FLW) were recorded, and on the flower date, PH, the NN, and number of reproductive buds (RB) were recorded. In addition, the number of vegetative shoots (VS) and flowering shoots (FS) were recorded on the flower date in 2003.

Plant height was measured from the soil base to the growing point, except for *Achillea* 2002 initial data, where it was measured from the soil base to the tip of the longest leaf. Node development was tracked and presented as the number of nodes gained during the flowering treatment (NG), (from the end of the bulking duration to anthesis). Shoot development for 2003 was calculated similarly and presented as the number of shoots gained (SG) during the flowering treatment. Days to VB and FLW were calculated as the number of days from the start of force to visible bud or anthesis, respectively. Days from VB to FLW (VBF) were calculated as the days to VB subtracted from the days to FLW.

Those plants without visible bud after 10 weeks at forcing conditions were considered non-flowering. Data recorded on non-flowering plants were final plant height, final number of nodes, and final number of vegetative shoots (data not shown).

A complete randomized design was used that included 10 plants for each bulking treatment. Data were analyzed using SAS (SAS Institute, Cary, N.C.) mixed model procedure (PROC MIXED) for analysis of variance and mean comparisons. The two control treatments added during 2003 were compared using a paired t-test and presented separately from the other treatments. Data were not pooled and analyzed separately for each year due to the significant year x bulking interaction and the difference between years regarding exposure to 10- and 16-h photoperiods prior to flower treatments for control bulking treatments.

Results

Achillea. *Year 1*. Plant vegetative growth significantly increased with bulking duration, and was the greatest after 8 weeks of bulking with 17 more nodes (Figure 1) than initial data measurements. Plant height and the number of PS also significantly increased over time (Appendix B Table 1).

Flowering percentage was not influenced by any bulking duration, bulking photoperiod, or vernalization, as nearly all plants initiated flowers (Table 5). In addition, the significant difference between the days to VB, VBF, and FLW varied by only 4 to 9 d between all treatments, which may have limited commercial importance. For example, vernalized plants flowered 1 week faster than non-vernalized plants ($P \leq 0.0011$). There was no significant difference between the numbers of FS developed between the different bulking and vernalization treatments.

Plant height measured at anthesis was greatest for those plants bulked 5 or 8 weeks. Plants bulked for 8 weeks were 12.0 cm taller than plants bulked for 2 weeks and vernalized for 8 weeks (Table 5). In addition, plants bulked for 2, 5, or 8 weeks had 37, 42, or 65 nodes at anthesis, respectively, (Figure 1). This reflects the significant number of NG during the 8-week bulking period over the 2-week one.

Year 2. The PH, NN, and number of PS were significantly greater after 8 weeks of bulking (data not shown). Plants bulked for 8 weeks under both 10- and 16-h photoperiods were 1.5 cm taller than plants bulked for only 2 weeks. Regardless of bulking duration, plants grown under 10-h photoperiods were 0.7

cm shorter at bulking completion than those grown under 16-h photoperiods (data not shown). Plants gained 7 nodes (Figure 2) and 6 shoots (Figure 3) after 8 weeks of bulking under 10-h photoperiods.

Flowering percentage was not influenced by any bulking duration, bulking photoperiod, or vernalization, as all plants initiated flowers (Figure 4). However, the days to VB, VBF, and FLW increased after 8 weeks of bulking and 8 weeks of chilling. The number of FS did not differ between plants bulked for 0 weeks, regardless of chilling duration, and significantly increased when plants were bulked under 10-h days and received no vernalization treatment (from Table 6).

Plant height at anthesis increased as bulking duration increased, and was significantly greater for non-vernalized plants as compared to vernalized plants (from Table 6). Plants bulked under 10-h photoperiods for 5 or 8 weeks had up to 11 more nodes than plants bulked for 2 weeks (Figure 2). The number of NG also increased from 17 to 20 as bulking duration increased from 2 to 8 weeks, but decreased by one after cold (data not shown). The number of PS was greatest for non-vernalized plants (Figure 3). After 8 weeks of bulking and no vernalization, plants had developed 32 shoots as compared to only 22 shoots after 5 weeks of bulking and vernalization.

Aquilegia. *Year 1*. Although significant, PH for plants bulked under 16-h photoperiods increased by only 1.0 cm from plants bulked for 2 weeks after 8 weeks of bulking (data not shown). Plants bulked for 5 or 8 weeks had 8 more nodes than plants bulked for only 2 weeks (Figure 5). Bulking duration and

bulking photoperiod had no significant effect on the number of PS (data not shown), with 2 shoots developed in each treatment.

Bulking duration and vernalization had the greatest influence on plant reproductive development (Figure 6). As bulking duration increased from 2 to 8 weeks, flower initiation increased from 25 to 80 percent without chilling, and 60 to 100 percent following chilling. Plants reached VB earlier after 5 or 8 weeks of bulking and vernalization, and chilled plants flowered significantly faster than non-chilled plants. The average number of days from VBF was 11 d for all treatments, except 5 weeks of bulking followed by vernalization, which required 14 d (Figure 6). Plants bulked for 8 weeks had significantly more RB than plants bulked for only 2 weeks (Table 7).

Bulking duration and vernalization also increased PH and the NN. The PH at anthesis for 8-week, chilled plants was 10.0 cm greater than 2-week, chilled plants (from Table 7). Although the NN increased from 29 to 34 after 5 or 8 weeks of bulking, respectively, the number of NG was not affected by bulking duration (from Figure 5).

Year 2. The PH significantly increased from 1.1 cm after 0 weeks of bulking to 2.5 cm after 8 weeks of bulking (data not shown). The NN also increased with bulking duration, as plants had 15 and 19 nodes after 5 and 8 weeks, respectively (Figure 7).

Bulking duration and vernalization had a significant influence on floral initiation, as plants that were not bulked and plants that did not receive chilling flowered poorly, if at all (Figure 8). The flowering percentage for plants bulked 2

weeks prior to chilling was 50 to 80 percent (16- and 10-h photoperiods, respectively), while the percentage for plants bulked 5 to 8 weeks with the same chilling treatment was 90 to 100 percent, regardless of photoperiod (Figure 8). After chilling, the days to VB and FLW were similar regardless of bulking duration or photoperiod (Figure 8). Increased bulking also increased RB and FS (Appendix B Table 2). Plants bulked for 2, 5, and 8 weeks had 9, 17, and 20 buds, respectively, and were significantly related to the NN at bulking completion by an r^2 value of 0.798 (Figure 9). Thus, as the NN prior to chilling increased, so did the number of RB.

Bulking treatments did not significantly influence vegetative growth after chilling. The PH was similar in all treatments except plants bulked for 8 weeks under 10-h photoperiods, which were the tallest at 46.4 cm. The number of PS and SG were not influenced by any treatment (Appendix B Table 2). Bulking duration and photoperiod length had the greatest influence on the NN and NG. At anthesis, plants bulked for 0, 2, 5, or 8 weeks had 23, 24, 32, or 39 nodes, respectively, and had gained 14, 14, 18, or 21 nodes, respectively (Figure 7). In addition, plants bulked under 10-h photoperiods had 4 more nodes than plants bulked under 16-h (from Appendix B Table 2).

Coreopsis. *Year 1*. Plants bulked under 16-h photoperiods were 2.5 cm taller than plants bulked under 10-h photoperiods (Table 8). Bulking photoperiod also significantly influenced the number of PS, as plants bulked under 16-h photoperiods had 4 fewer shoots than 10-h plants.

Flowering percentage increased from an average of 60 to 100 percent after plants were exposed to 8 weeks of 5 °C (Table 8). Plants that were chilled reached VB and FLW earlier than others (Appendix B Figure 1). For example, plants bulked for 2 weeks under 10- or 16-h photoperiods reached VB and FLW by 16 and 43 d, respectively, while non-chilled plants took 43 and 69 d to reach VB and FLW, respectively. However, after cold, 5- and 8-week bulking durations did not hasten days to VB or FLW. In fact, plants bulked for 2 weeks and chilled reached FLW significantly faster than 8-week, chilled plants by ≈ 13 d, respectively. Days from VBF were the same under every treatment. Plants that received 8 weeks of bulking under 16-h followed by chilling had 29 more RB as compared to those that were only bulked for 2 weeks under the same photoperiod (from Table 8).

From 2 to 5 weeks, PH increased by 10.0 cm (Table 8). The NN and number of NG were not influenced by any treatment factor.

Year 2. Similar to year 1, plants bulked under 16-h photoperiods were 1.9 cm taller than plants bulked under 10-h photoperiods, independent of bulking duration (Table 9). The NN significantly increased with bulking duration, with 8, 10, 12, and 14 nodes for 0, 2, 5, and 8 weeks, respectively. Plants gained 10 shoots between 0 and 8 weeks of bulking (Table 9).

Flower initiation ranged from 75 to 90 percent without cold, but was the most uniform and complete at 100 percent after cold (Figure 10). After a chilling treatment, the days to VB and FLW significantly decreased by 23 and 25 d, respectively. Days to VB and FLW also significantly decreased by 9 d under a

10-h bulking photoperiod ($P \leq 0.001$). The days from VBF did not differ between treatments. The number of RB for plants bulked for 2, 5, and 8 weeks was 33, 45, and 54 buds per plant, respectively. The relationship between the NN at bulking completion and the number of RB for plants that did or did not receive a chilling treatment showed that RB number increased as NN prior to chilling exposure increased (Figure 11). The number of RB and FS significantly increased by 71 and 91 percent, respectively, after chilling. The number of FS after chilling was 12, 14, and 19, respectively, for bulking durations of 2, 5, and 8 weeks (Figure 12).

Plants were 10.0 to 17.0 cm taller after 5 or 8 weeks of bulking and a chilling treatment (Table 9). Plants that were not bulked prior to vernalization were 18.3 cm taller than non-vernalized plants. However, the differences in the number of NN, NG, NS, and SG were not so dramatic. Most plants developed between 21 and 24 nodes at anthesis. The number of NG was also similar between treatments, with chilled plants gaining 2 to 4 fewer nodes than non-chilled plants (data not shown). Plants that received chilling had fewer PS and SG than non-chilled plants. At anthesis, vernalized plants that were bulked for 2, 5, or 8 weeks averaged 15, 20, or 27 shoots as compared to non-chilled plants that averaged 25, 23, or 26 shoots. Non-vernalized plants developed up to 9 more shoots than vernalized plants.

Echinacea. Year 1. Plant height significantly increased after 8 weeks of bulking under a 16-h photoperiod (Appendix B Table 3). Node number significantly increased with bulking duration from 9 nodes after 2 weeks to 16

nodes after 8 weeks (from Appendix B Table 3). Bulking duration and photoperiod had no significant effect on the number of PS.

Flower initiation was 100 percent for all treatments except 5 and 8 weeks of bulking without chilling (Figure 13). After chilling, time to VB and FLW decreased when bulking duration increased. Plants reached VB and FLW in 40 and 72 d, respectively, when bulked for 8 weeks followed by 8 weeks at 5 °C. Bulking duration and bulking photoperiod had little commercial importance on the number of RB developed (Appendix B Table 3).

Plant height at anthesis decreased as duration of bulking increased, with values of 101, 89, and 82 cm with 2, 5, and 8 weeks (from Appendix B Table 3). The NN for plants bulked 2 weeks prior to a chilling treatment was only 22, compared with 56 for plants bulked under 10-h photoperiods for 8 weeks with no subsequent chilling treatment (Appendix B Table 3). The NG for these two treatments was also significantly different, as plants developed 14 or 34 nodes, respectively.

Year 2. Similar to year 1, bulking duration and photoperiod had a minimal effect on PH and no affect on the number of PS (Table 10). However, PH was significantly taller under 16-h after 5 or 8 weeks of bulking (data not shown). The NN significantly increased as bulking duration increased, with 6, 8, 10, or 12 nodes after 0, 2, 5, or 8 weeks of bulking, respectively (Table 10).

Flower initiation was 90 to 100 percent, regardless of treatment (Table 11). Days to VB and FLW were only significantly decreased (by 3 or 4 d, respectively,) when bulked under 10-h photoperiods as compared to 16-h

photoperiods. Increased bulking duration decreased days to VB by 15 d as bulking duration increased from 0 to 8 weeks (Table 11). Days from VBF only varied by 4 or 5 d, and RB and FS were not significantly different among treatments.

Plant height at anthesis was not significantly different between treatments, and the number of PS and SG were similar (Table 11). The NN significantly increased from 23 to 31 as bulking increased from 2 to 8 weeks, respectively, and NG increased from 15 to 20 nodes, respectively.

Penstemon. Year 1. Greater bulking durations significantly increased PH and NN, although the number of PS was not significantly different between treatments. Plants bulked under 10-h photoperiods for 2, 5, or 8 weeks were 1.8, 2.1, and 3.2 cm tall, respectively, compared to plants under a 16-h photoperiod that were 2.1, 2.8, and 3.1 cm, respectively ($P \leq 0.0160$). The NN for the same treatments followed a similar trend, and are presented in Figure 14.

An average of only 56 percent of plants flowered without chilling, while 90 percent flowered after chilling, regardless of bulking duration (Table 12). Although days to VB and days from VBF were not significantly different between treatments, days to FLW was dependent upon bulking duration. Plants bulked for 8 weeks flowered in 64 d while those bulked for 2 or 5 weeks took 75 or 71 d, respectively. Bud number increased from 62 to 141 as bulking increased from 2 to 8 weeks, respectively (data not shown). Thus, the relationship between the NN at bulking completion and the number of RB at flower was found to have an r^2 value of 0.745 (Figure 15). Plant height was similar under all treatments, but

the NN and NG slightly increased after 8 weeks of bulking and no chilling (Table 12).

Year 2. From the initial measurement of 1.4 cm (Table 4), PH continued to increase with bulking duration to 1.9, 2.4, and 2.6 cm after 2, 5, and 8 weeks of bulking, respectively (data not shown, $P \leq 0.001$). The NN increased from 7 to 10 with bulking duration, independent of bulking photoperiod length (Figure 16). The number of PS increased from 1 to 2 or 3 as bulking duration increased from 2 to ≥ 5 weeks (Appendix B Figure 2).

Less than 10 percent of bulked plants flowered without cold. Flower initiation was 0 or 10 percent for 0-week plants without or with a chilling treatment, respectively; therefore, the data are not discussed, but presented in Table 13. Plants bulked for 2 weeks reached VB significantly faster (44 d) than plants bulked ≥ 5 weeks (55 d) (from Table 13). Days to FLW also increased after bulking durations ≥ 5 weeks. The days from VBF was not significantly different under any treatment. The number of RB significantly increased from 99 to 166 buds for plants bulked 2 or 8 weeks, respectively ($P \leq 0.0382$). The number of FS followed this same trend, developing 1 to 4 inflorescences, respectively ($P \leq 0.0004$).

The NN that developed on plants bulked for 2 to ≥ 5 weeks ranged from 22 to 27, respectively (Figure 16). The number of NG significantly increased from 14 to 16, respectively (data not shown). The number of PS and SG at anthesis increased by 5 and 4 shoots, respectively, for plants bulked 8 weeks compared to 2 weeks (Appendix B Figure 2). Plants that were under 10-h

bulking photoperiods had 2 or 3 more NG or SG, respectively (data not shown).

Salvia. *Year 1*. Plants bulked for 8 weeks had 9 nodes in comparison to 5 nodes following only 2 weeks of bulking (Appendix B Table 4). Additionally, the number of PS increased by 2 after 8 weeks of bulking under 10-h photoperiods.

Flower initiation was between 80 and 100 percent for most treatments; only those plants bulked for 2 weeks under 10-h photoperiods without a chilling treatment flowered poorly at 60 percent (Figure 17). After vernalization, plants bulked for ≥ 5 weeks under 10-h photoperiods reached VB and FLW faster than plants bulked under 16-h. Days from VBF were not affected by any experimental treatment. The number of RB increased from 9 to 30 after chilling (Figure 18). Bulking photoperiod also increased RB number from 16 under 10-h photoperiods to 24 under 16-h photoperiods (data not shown).

Plants bulked under 16-h photoperiods were significantly taller at anthesis than 10-h photoperiod plants by 5, 11, and 22 cm, respectively (Appendix B Table 4). In addition, PH height increased from 29 to 45 cm after chilling. The NN also increased after a chilling treatment, as non-chilled plants developed 8 nodes as compared to 11 nodes after chilling.

Year 2. Plant height was significantly greater than initial measurements after 5 of bulking under 16-h and 8 weeks of bulking under both 10- and 16-h photoperiods (data not shown). The NN also increased from 5 nodes at 0 weeks, to 10 nodes after 8 weeks of bulking (Figure 19). The number of PS (2) was not influenced by any bulking treatment (data not shown).

Flower initiation was 90 to 100 percent regardless of treatment (Table 14). Plants that were bulked under 10-h photoperiods generally reached anthesis earlier than those plants under 16-h photoperiods, but the response varied by bulking duration. Similar to year 1, the number of RB significantly increased after a chilling treatment, specifically for plants bulked under 16-h photoperiods (Table 15). For plants that were not bulked, the number of RB also increased after a chilling treatment. Although not influenced by chilling, the number of FS increased by 5 or 7 after 5 or 8 weeks of bulking, respectively, under 10-h photoperiods (data not shown).

Plants bulked under 10-h for 8 weeks followed by chilling were shorter than all other treatments (Table 14). The range for NN at anthesis was between 11 and 16 nodes (Figure 19), with 4 to 7 NG. Plants bulked 8 weeks had significantly more (6) PS than plants bulked for 2 weeks (3) (Table 14).

Discussion:

Bulking duration: For both years, the trend for increased plant height, node development, and shoot development with increased bulking duration was predicted, as plants had a longer amount of time to grow. In addition, for most plants, (e.g., *Aquilegia*, *Coreopsis*, and *Echinacea*), stem extension and petiole length were greatest when plants were exposed to 16-h photoperiods under incandescent lamps, which are high in far red wavelengths (Thomas and Vince-Prue, 1997) and have been shown to increase plant height. For example, a red light deficient environment increased *Campanula carpatica* 'Blue Clips' plant

height by 65 percent as compared to a neutral environment (Runkle and Heins, 2001).

The effect of bulking duration on rate of floral initiation and development was dependent upon species, and was most beneficial for those that have a longer juvenile phase (e.g., *Aquilegia* and *Penstemon*). Environmental conditions that increase plant growth consequently decrease the length of the juvenile phase (Thomas and Vince-Prue 1997). In general, plants that were bulked for 5 or 8 weeks had a higher flower percentage with fewer days to VB and FLW. Plants bulked 5 or 8 weeks had the most biomass and carbohydrate reserves prior to chilling or forcing.

Achillea 'Paprika' has been labeled a facultative long-day plant that does not require a cold treatment for floral initiaton (Nausieda et al., 2000). In this work, results from both years confirm these findings, as flowering percentage was ≥ 90 percent for all treatments, and the variation between treatments for the days to VB, days from VBF, and days to FLW was only 1 to 2 weeks. The minimal significance, if any, in the number of FS between treatments also indicates that exposure to cold does not enhance flowering.

Although treatments were all bulked under approximately the same light levels during both years, the difference in light levels between forcing times was much greater during year 2. For example, during year 1, all treatments were forced under ca. 9 $mol \cdot m^{-2} \cdot d^{-1}$. During year 2, non-chilled plants were forced under 11 to 15 $mol \cdot m^{-2} \cdot d^{-1}$, while 5- or 8-week, chilled plants were forced under only 7 to 8 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 2A and 2B). Light is obviously important for

photosynthesis and has also been shown to be an important factor in the modification of floral development (Thomas and Vince-Prue, 1997). Thus, plants that were forced under lower light levels may have taken longer to reach anthesis. Another explanation for the differences in the days to VB and FLW could be attriubted to the removal of initiated buds during the bulking period during both years to reduce competition between vegetative and reproductive growth. Thus, the calendar dates and consequent light levels at which plants started each phase of the experiment, (i.e., bulking, chilling, and forcing) could account for the slower developmental rate during year 2.

The increased PH, NN, and PS at anthesis were related to the fact that plants had a longer amount of time to grow, accumulate biomass, and carbohydrate reserves prior to forcing. Plant height and the number of PS were the greatest without chilling, and cold did not appear to influence the NN.

The limited responses of *Achillea* 'Paprika' to treatment conditions suggest that bulking and cold treatments are not necessary. The fact that young plants had initiated floral buds during the bulking period implies that juvenility is not a significant factor in *Achillea*. In addition, plants became very unmanageable during the bulking period due to dense foliage, and continued to be too tall for production and shipping activities. When received as a 72-cell plug, *Achillea* requires no bulking or chilling and will reach FLW within 6 to 8 weeks when placed under optimum forcing conditions.

Aquilegia x *hybrida* Songbird Mix has a chilling requirement to flower, as demonstrated during both years by low (0%) and inconsistent flowering response

when plants were not provided with 8 weeks at 5 °C. In addition, chilling hastened days to VB and days to FLW. These data agree with work by Finical (unpublished data), who found that *Aquilegia* Songbird series could be induced to flower after only 3 to 6 weeks at 5 °C. Chilling has also been found to be an important trigger for reproductive growth in other *Aquilegia* species. For example, most *A. hybrida* cultivars studied required 10 to 12 weeks at 4.5 °C for floral induction, except *A.* 'Faryland' and *A.* 'Crimson Star', in which 100% flowered after only 8 weeks of cooling (Shedron and Weiler, 1982).

However, even with chilling, flowering percentage was still not 100 percent for all treatments. The flower percentages were the lowest in plants bulked for 0 or 2 weeks with 9 or 10 nodes prior to chilling. This is below the required 12-node (leaf) mark suggested by Shedron and Weiler for floral induction by a chilling treatment at 4.5 °C for *Aquilegia* x *hybrida* Sims (1982). Thus, despite adequate cold duration, it could be possible that 0- and 2-week plants were still juvenile and therefore unable to perceive floral initiation signals. This is demonstrated by the positive relationship between the NN at bulking completion and the number of RB at anthesis (Figure 9). This response could also be attributed to the increased amount of carbohydrate reserves available for flower development after increased bulking durations and consequent node and leaf development.

Despite beneficial affects on flowering percentage and RB number, bulking duration only influenced days from VBF and days to FLW during year 2. In fact, 0- and 2-week plants reached VB and FLW earlier than plants bulked for

5 or 8 weeks during year 2. However, this again could be related to the light levels as described for *Achillea*, as during year 2, cooled plants bulked for 5 or 8 weeks were forced under light levels 8 $mol \cdot m^{-2} \cdot d^{-1}$ lower than in other treatments.

Although treatments did not promote lateral shoot development in *Aquilegia*, NN and NG increased when bulked under 10-h photoperiods. As previously mentioned, this increase in vegetative growth was a result of longer bulking durations, and necessary for maturity and accumulation of nutrient reserves. The importance of these factors is demonstrated in the relationships between the NN prior to cold treatment and eventual flower percentage or RB development.

The significant responses of *Aquilegia* to bulking duration and cold confirm that it has a juvenility and vernalization requirement Commercial production of this plant should include a bulking period until at least 15 leaves are formed prior to a cold treatment of 8 weeks at 5 °C for complete flowering within 6 to 7 weeks (at 20 °C). Photoperiod does not influence *Aquilegia* development, as plant responses to bulking photoperiods were not commercially significant and plants are day neutral following a cold treatment (Heins et al., 1997). Post-harvest quality of this plant is of concern, as flowers shatter within one week of anthesis

In *Coreopsis*, a chilling treatment at 5 °C for 8 weeks was beneficial, although not required, for floral initiation and reproductive development during both years. This is in agreement with previous research that lists *Coreopsis* 'Early Sunrise' as not having an obligate cold requirement (Yuan et al., 2000). Despite the ability of *Coreopsis* to flower without a cold treatment, flower

percentage, number of RB, and number of FS were significantly greater, and days to VB and days to FLW were significantly decreased after chilling (Figures 10–12). Chilled plants also flowered with fewer nodes and developed fewer shoots.

Increased bulking duration, and therefore the NN prior to forcing, greatly increased the number of RB and FS, particularly after chilling. However, even plants that were not bulked (0 weeks) still produced 55 buds per plant on 12 flowering shoots after chilling. In addition, buds were initiated upon arrival and throughout the bulking durations, mostly under 16-h photoperiods, with few nodes and prior to chilling. This suggests that initial starting material with 8 or 9 nodes had already passed the juvenile stage, which is similar to other findings in *Coreopsis grandiflora* 'Early Sunrise'. Damann and Lyons (1993) showed that *C.* 'Early Sunrise' was most sensitive to long days at a calculated expanded leaf count of 16 leaves (8 nodes). Yuan et al. (1998) also suggests that the juvenile phase in a similar cultivar, *Coreopsis grandiflora* 'Sunray', ends at 8 nodes, after which it flowers faster with fewer nodes gained during forcing, and produces more flower buds.

Although the number of flowers increased with bulking duration, the days to VB and FLW were not dependent upon the NN prior to chilling. Plants bulked for 0 or 2 weeks reached VB and FLW just as rapidly, or even prior to 5- or 8-week bulked plants, especially after chilling. This further supports the idea that plants had reached a mature state as initial plugs, with 8 nodes.

The days to VB and days to FLW decreased during both years when plants were bulked under a 10-h photoperiod compared to 16-h photoperiods, especially with non-chilled plants. It may be possible that the treatments replicated the natural environment of short, autumn days prior to the onset of cold temperatures, followed by the long days of summer when *Coreopsis* plants flower outdoors. Interestingly, some of the first flowering shoots came from lateral shoots. This may be a result of pinching flower buds during the bulking period.

The photoperiod requirement for floral initiation in *C. grandiflora* has been the discussion of other research projects. Early experiments labeled *C. grandiflora* as a short day/long day plant (i.e., requiring short days prior to long days for floral initiation) (Metzger, 1988). However, this is cultivar dependent, as C. 'Early Sunrise flowers under long days without cold, while C. 'Sunray' has a juvenile phase and requires either short days or cold prior to long days for floral initiation (Yuan et al., 1998). More recent studies have disregarded the necessary link between flowering and short days, and proved that plants can flower under continuous long days but not under continuous short days (Damann and Lyons, 1993). The data from this study would suggest that exposure to short days prior to inductive conditions is beneficial, but not required, as plants bulked for 0 weeks without any photoperiod treatment reached VB and FLW just as quickly as those bulked under 10-h photoperiods.

Coreopsis 'Early Sunrise' is a fast and easy plant to produce commercially because plants flower regardless of bulking or chilling treatments. Although

bulking and chilling hasten flower initiation, plants become unmanageable and large when bulking is increased, and the extra time incurred by the addition of a chilling treatment prolongs the production schedule. With 8 nodes and no chilling treatment, plants flowered within 8 to 9 weeks, which is a rapid production schedule. However, flower number is reduced. Adding a chilling period (possibly less than 8 weeks) would increase the total production time, but could also decrease days to FLW to 7 or 8 weeks and may initiate more flower buds.

Bulking duration, bulking photoperiod, and chilling had few significant effects on flowering of *Echinacea* 'Magnus', suggesting that juvenility and vernalization were not major factors in plant reproductive development. A study by Finical et al. (2000) showed that plants with as few as 4 leaves flowered when forced under a 14-h photoperiod. Plant material in this study had 9 or 6 nodes at the start of bulking treatments and up to 16 nodes after 8 weeks of bulking, definitely eliminating any problems with juvenility.

Similar to other species in this study, bulking *Echinacea* plants for a longer duration increased vegetative growth at bulking completion and at anthesis. Also, days to VB and days to FLW were significantly shortened after 5 or 8 weeks of bulking compared to 0 or 2 weeks. In addition, exposure to chilling shortened the days to VB and days to FLW during year 1.

The lack of requirements for maturity or vernalization makes *Echinacea* a relatively simple crop to grow. However, the extended amount of time it takes to flower (10 to 11 weeks) makes production time unsuitable for a quick crop schedule, and the limited increase in RB and FS number under any treatment

does not create a plant full with blooms. Plant height is also a negative attribute, as without additional growth regulators, plants may grow up to 1 m tall, which is not manageable for commercial production or shipping purposes.

Bulking duration, and therefore juvenility, significantly increased vegetative growth and was beneficial to the flowering process in *Penstemon*. In particular, the number of RB and FS increased as bulking increased. This relationship was strongest during year 1 (r^2=0.745) when NN were between 10 and 24, but weaker during year 2 (r^2=0.390) when NN were only between 8 and 10. The stage of plant maturity could also account for some of the low and inconsistent flowering percentages during year 2. Although all treatments surpassed the current maturity benchmark of 7 nodes (Clough, 1999), the treatments with lower NN during year 2 may not have been fully responsive to the inductive chilling treatment.

The relationship with chilling was an important factor in floral initiation, as plants flowered poorly (≤ 50 percent) or not at all without it. Eight weeks of chilling was a generic duration to fulfill the requirements of all tested species in this experiment, but may not have been enough for *Penstemon*. Clough (1999) recommended that *Penstemon* be exposed to 9 weeks of cold, which may be why treatments limited to only 8 weeks had low flowering percentages.

Despite the major influence on flower percentage, chilling did not influence other reproductive processes. The days to VB, days to FLW, and the numbers of RB and FS were not significantly affected by chilling, but were influenced by bulking. Although the days to VB were not significant, the days to FLW

decreased as bulking duration increased during year 1. However, days to VB and days to FLW were actually increased with increased bulking duration during year 2. This could again be a result of the difference in light levels as described for the previous species where 0- and 2-week plants flowered faster than 5- or 8-week plants despite beneficial increases in node gain and exposure to chilling conditions.

Overall, *Penstemon* has a long production time that includes allowances for juvenility and vernalization requirements. Bulking until 7 to 10 nodes (≈ 2 to 5 weeks) have developed will produce flowering plants, but allowing up to 8 weeks of bulking will increase the floral display. Bulking under a 10-h photoperiod will also increase flowering percentage (Table 13). A chilling period of at least 9 weeks at 5 °C is recommended for complete and uniform flowering, which takes ≈ 10 weeks from the start of force. Plants are day neutral after cold (Clough, 1999)

Salvia 'May Night' has been cited as a day-neutral plant that does not require a cold treatment for floral initiation (P. Koreman, unpublished data). This was confirmed by the data presented in this work, as flower percentage was near 100 percent during both years. Although *Salvia* initiates flowers under most environmental conditions, the interactions between the bulking duration, bulking photoperiod, and a chilling treatment were significant for the days to VB and days to FLW. During both years, plants bulked under 10-h photoperiods reached FLW ≈ 10 to 15 d earlier than plants bulked under 16-h, with the exception of plants bulked for 5 weeks under 10-h and no cold treatment.

Bulking duration and therefore juvenility was not a factor in the number of RB initiated, as even plants bulked for 0 weeks had an equal number of buds as bulked plants. However, unlike days to VB and days to FLW, a bulking photoperiod of 16-h was beneficial to bud formation. This could be because plants were already past the juvenile stage and initiated buds during the bulking period.

Plant height at anthesis was greater for plants bulked under 16-h photoperiods during both years, which could be due to the influence of far-red light, as described earlier for *Achillea*. Plants that did not receive chilling flowered with fewer nodes than chilled plants. This could be because there is no temperature requirement and the juvenile phase is satisfied when plants attain 5 to 8 nodes. This level of development allowed control plants that did not receive chilling to initiate flowers immediately.

The limited responses to treatment factors suggest that bulking and chilling treatments are not necessary for *Salvia* 'May Night'. Overall, *Salvia* produces many flowers on a nicely formed plant without much effort or time. The fact that young plants had initiated floral buds during the bulking period implies that juvenility is not a factor in *Salvia*. Additionally, high flower percentages without chilling indicate that vernalization is also not a requirement for reproductive growth. However, bulking under 10-h photoperiods may decrease time to FLW and chilling may increase the number of flowers. For quick production of *Salvia* 'May Night', 54-cell plugs require no bulking or chilling, and will reach FLW within 3 to 4 weeks.

Conclusion: The objectives of this study were to observe the effects that length of bulking time, bulking photoperiod, and exposure to a chilling period have on plant quality (i.e., color and plant habit) and total finish time (i.e., rapid and easy to grow) in herbaceous perennial crops with the goal of quantifying these parameters to create production schedules. Plants that had the quickest production time with limited problems and a good display of flowers were *Achillea*, *Coreopsis*, and *Salvia*. They had a short juvenile phase (≤ 8 nodes), no cold requirement for complete flowering (although it increased RB number), and a force time of 7 to 8 weeks for *Achillea* and *Coreopsis* or 3 to 4 weeks for *Salvia* (at 20 °C).

Despite the nice display of flowers and attractive foliage color and growth habit, *Aquilegia* and *Penstemon* had more stringent requirements to overcome juvenility and vernalization. Therefore, these two factors increased total production time to 20 to 21 weeks, depending upon the duration of the chilling period.

These five species could all be scheduled to flower for sale during May. Starting bulking treatments for *Aquilegia* and *Penstemon* in early January would allow for the bulking and chilling time needed to initiate flowering, while having adequate time for forcing during April and May. Chilling plants at this time could also be beneficial in terms of cost, because by providing a chilling treatment during the winter, plants could be kept in an unheated greenhouse rather than being cooled over the summer or heated in the winter. Also, cost for high light levels would not be a concern during vernalization. The force time for *Achillea*,

Coreopsis, and *Salvia* could also be started during late March or early April to ensure blooms by early or mid-May. Actual flower date for each species would be staggered throughout the month of May and possibly into June. The quick production time for *Saliva* could potentially allow for two crops to be forced in sequence. Therefore, a constant supply of flowering plants would be available during these months of high consumer demand.

Although *Echinacea* had limited requirements for juvenility or vernalization, the total production time was long (10 to 11 weeks) with limited floral development and a very tall and unmanageable plant habit. Thus, *Echinacea* was unsuitable for quick crop production.

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Table 1. List of herbaceous perennial species.

Species
Achillea millefolium L. 'Paprika' *
Ajuga reptans L. 'Catlin's Giant'
Ajuga reptans L. 'Chocolate Chip'
Aquilegia x *hybrida* Sims Songbird Mix *
Astilbe Hybrid Mix
Coreopsis grandiflora Hoggs ex Sweet 'Early Sunrise' *
Delphinium 'Butterfly Blue'
Echinacea purpurea (L.) Moench 'Magnus' *
Euphorbia hybrid 'Despina'
Lamium galeobdolon (L.) L. 'Herman's Pride'
Lavandula angustifolia Mill. 'Hidcote Blue'
Leucanthemum x superbum (Bergmans ex J.W. Ingram) D.H. Kent 'Alaska'
Penstemon digitalis Nutt. 'Husker Red' *
Rudbeckia fulgida Aiton 'Goldsturm'
Salvia nemorosa L. 'May Night' *
Salvia officinalis L. 'Icterina'
Salvia officinalis L. 'Tricolor'
Veronica spicata L. 'Red Fox'

*Species were replicated in time.

Table 2. Schedule for bulking, chilling, and finish dates.

A. Year 1 (2002)

Bulking duration (weeks)	Weeks at 5 °C	Bulking dates	Chilling dates	Finish dates
2	0	12 Aug. - 23 Aug.	-	18 Oct. - 31 Jan., 2003
2	8	12 Aug. - 23 Aug.	23 Aug. - 18 Oct.	18 Oct. - 31 Jan., 2003
5	0	12 Aug. - 13 Sept.	-	06 Nov. - 31 Jan., 2003
5	8	12 Aug. - 13 Sept.	13 Sept. - 06 Nov.	06 Nov. - 31 Jan., 2003
8	0	12 Aug. - 04 Oct.	-	27 Nov.- 28 Feb., 2003
8	8	12 Aug. - 04 Oct.	04 Oct. - 27 Nov.	27 Nov.- 28 Feb., 2003

B. Year 2 (2003)

Bulking duration (weeks)	Weeks at 5 °C	Bulking dates	Chilling dates	Finish dates
0	0	-	-	21 July - 26 Sept.
0	8	-	21 July - 12 Sept.	12 Sept. - 21 Nov.
2	0	21 July - 01 Aug.	-	01 Aug. - 10 Oct.
2	8	21 July - 01 Aug.	01 Aug. - 26 Sept.	26 Sept. - 05 Dec.
5	0	21 July - 22 Aug.	-	22 Aug. - 27 Oct.
5	8	21 July - 22 Aug.	22 Aug. - 17 Oct.	17 Oct. - 26 Dec.
8	0	21 July - 12 Sept.	-	12 Sept. - 21 Nov.
8	8	21 July - 12 Sept.	12 Sept. - 07 Nov.	07 Nov. - 16 Jan.

Table 3A. Average daily temperatures (°C) and average daily light integrals (DLI) ($mol \cdot m^{-2} \cdot d^{-1}$) for bulking duration and finish environment during year 1 (2002).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	Bulking dates	Temperature	DLI
2	10	0	12 Aug. - 18 Oct.	23.7	14.5
2	10	8	12 Aug. - 23 Aug.	24.2	14.4
2	16	0	12 Aug. - 18 Oct.	22.4	13.9
2	16	8	12 Aug. - 23 Aug.	24.1	13.6
5	10	0	12 Aug. - 06 Nov.	23.2	13.3
5	10	8	12 Aug. - 13 Sept.	24.4	16.8
5	16	0	12 Aug. - 06 Nov.	22.0	12.9
5	16	8	12 Aug. - 13 Sept.	23.4	15.4
8	10	0	12 Aug. - 27 Nov.	22.7	12.3
8	10	8	12 Aug. - 04 Oct.	24.0	14.9
8	16	0	12 Aug. - 27 Nov.	21.8	11.3
8	16	8	12 Aug. - 04 Oct.	22.8	14.0

	Finish dates	Temperature	DLI
2	18 Oct. - 31 Jan.	19.0	8.8
5	06 Nov. - 31 Jan.	18.0	8.7
8	27 Nov. - 28 Feb.	19.2	9.7

Table 3B. Average daily temperatures (°C) and average daily light integrals (DLI) ($mol \cdot m^{-2} \cdot d^{-1}$) for bulking duration and finish environment during year 2 (2003).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	Bulking dates	Temperature	DLI
0	-	0	-	-	-
0	-	8	-	-	-
2	10	0	21 July - 01 Aug.	22.7	11.4
2	10	8			
2	16	0	21 July - 01 Aug.	24.5	16.5
2	16	8			
5	10	0	21 July - 22 Aug.	23.0	10.5
5	10	8			
5	16	0	21 July - 22 Aug.	24.6	14.5
5	16	8			
8	10	0	21 July - 12 Sept.	22.6	10.3
8	10	8			
8	16	0	21 July - 12 Sept.	24.2	14.6
8	16	8			

			Finish dates	Temperature	DLI
0	-	-	21 July - 26 Sept.	23.0	14.8
0	-	8	12 Sept. - 21 Nov.	21 0	11.4
2	10	0	01 Aug. - 10 Oct.	22.0	13.6
2	10	8	26 Sept. - 05 Dec.	21.0	9.9
2	16	0	01 Aug. - 10 Oct.	22.0	13.6
2	16	8	26 Sept. - 05 Dec.	21.0	9.9
5	10	0	22 Aug. - 27 Oct.	21.0	12.6
5	10	8	17 Oct. - 26 Dec.	21.0	8.4
5	16	0	22 Aug. - 27 Oct.	21.0	12.6
5	16	8	17 Oct. - 26 Dec.	21.0	8.4
8	10	0	12 Sept. - 21 Nov.	21.0	11.4
8	10	8	07 Nov. - 16 Jan.	21.0	7.2
8	16	0	12 Sept. - 21 Nov.	21.0	11.4
8	16	8	07 Nov. - 16 Jan.	21.0	7.2

Table 4. Plant height (PH), number of nodes (NN), and number of primary shoots (PS) of *Achillea millefolium* 'Paprika', *Aquilegia* x *hybrida* Songbird Mix, *Coreopsis grandiflora* 'Early Sunrise', *Echinacea purpurea* 'Magnus', *Penstemon digitalis* 'Husker Red', and *Salvia nemorosa* 'May Night' at the beginning of experiment.

A. Year 1 (2002)

Species	PH (cm)	NN	Number of PS
Achillea	5	16	4
Aquilegia	1	11	2
Coreopsis	5	9	10
Echinacea	1	9	2
Penstemon	2	7	2
Salvia	3	8	1

B. Year 2 (2003)

Achillea	2	10	4
Aquilegia	1	9	2
Coreopsis	4	8	3
Echinacea	1	6	2
Penstemon	1	7	3
Salvia	4	5	1

Table 5. The effects of bulking duration, bulking photoperiod, and vernalization on percent flowering, days to visible bud (VB), days from visible bud to flower (VBF), days to flower (FLW), number of flowering shoots (FS), and plant height (PH) at anthesis of *Achillea millefolium* 'Paprika' during year 1 (2002).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	Flower (%)	Days to VB [z]	Days VBF	Days to FLW [z]	No. of FS [y]	PH (cm) [y]
2	10	0	90	33	29	51	19	65
	10	8	100	21	29	50	1	50
	16	0	100	27	29	56	2	60
	16	8	100	36	29	48	12	55
5	10	0	100	24	27	51	8	72
	10	8	100	21	27	48	10	57
	16	0	100	28	29	57	4	64
	16	8	100	27	27	54	5	56
8	10	0	100	30	22	52	NA [x]	66
	10	8	100	30	26	50	9	64
	16	0	100	38	25	64	4	63
	16	8	100	27	25	52	NA	66
Significance								
Bulking duration (D)				*	*	NS	NS	**
Bulking photoperiod (P)				NS	NS	NS	NS	NS
Cold (C)				NS	NS	**	NS	***
D X P				NS	NS	NS	NS	NS
D X C				NS	NS	NS	NS	**
D X P X C				**	NS	NS	NS	NS

[z]Data for days to VB and days to FLW are for the period from the start of forcing until visible bud and anthesis, respectively.

[y]Data for number of FS and PH are for the period from the start of bulking until anthesis.

[x]Data not available.

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

Table 6. The effects of bulking duration, bulking photoperiod, and vernalization on the number of flowering shoots (FS) and plant height (PH) at anthesis of *Achillea millefolium* 'Paprika' during year 2 (2003).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	No. of FS [z]	PH (cm) [z]
0	-[y]	0	10 a[w]	61 a
	-	8	8 a	52 b
2	10	0	14	59
	10	8	13	56
	16	0	14	59
	16	8	15	57
5	10	0	13	62
	10	8	12	52
	16	0	13	68
	16	8	10	49
8	10	0	16	60
	10	8	13	59
	16	0	14	63
	16	8	7	57
Significance				
Bulking duration (D)			**	NS
Bulking photoperiod (P)			*	NS
Cold (C)			***	***
D X P			**	NS
D X C			*	***
D X P X C			NS	NS

[z]Data for number of FS and PH are for the period from the start of bulking until anthesis.

[y]Plants were directly placed under forcing or chilling conditions.

[w]Letters next to means within the same column represent mean separation by LSMeans ($P \leq 0.05$).

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

Table 7. The effects of bulking duration, bulking photoperiod, and vernalization on the number of reproductive buds (RB) and plant height (PH) at anthesis of *Aquilegia* x *hybrida* Songbird Mix during year 1 (2002).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	No. of RB [z]	PH (cm) [z]
2	10	0	17	42
	10	8	5	26
	16	0	-	-
	16	8	9	38
5	10	0	9	38
	10	8	15	46
	16	0	12	36
	16	8	9	32
8	10	0	20	37
	10	8	19	43
	16	0	19	40
	16	8	15	41
Significance				
Bulking duration (D)			***	NS
Bulking photoperiod (P)			NS	NS
Cold (C)			**	NS
D X P			NS	***
D X C			**	**
D X P X C			NS	NS

[z]Data for the number of RB and PH are for the period from the start of bulking until anthesis.
NS, **, *** Nonsignificant or significant at $P \leq 0.01$, or 0.001, respectively.

Table 8. The effects of bulking duration, bulking photoperiod, and vernalization on plant height (PH), the number of nodes (NN), and the number of primary shoots (PS) at bulking completion and percent flowering, the number of reproductive buds (RB), PH, and NN at anthesis of *Coreopsis grandiflora* 'Early Sunrise' during year 1 (2002).

			Bulking completion			Anthesis			
Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	PH (cm)	NN	No. of PS	Flower (%)	No. of RB	PH (cm)	NN
2	10	0	5	10	11	100	18	46	23
	10	8	5	9	10	100	27	38	19
	16	0	5	9	8	60	26	48	24
	16	8	5	10	8	100	26	38	22
5	10	0	3	10	11	50	16	43	22
	10	8	3	8	11	100	34	53	17
	16	0	4	10	7	60	35	57	27
	16	8	5	9	7	100	43	58	19
8	10	0	3	11	11	100	44	59	31
	10	8	3	11	12	100	23	57	25
	16	0	4	9	7	0	NA [z]	NA	NA
	16	8	5	10	7	100	55	71	26
Significance									
Bulking duration (D)			***	**	NS		**	***	NS
Photoperiod (P)			***	NS	***		**	NS	NS
Cold (C)							NS	NS	NS
D X P			**	*	NS		**	NS	NS
D X C							*	NS	NS
D X P X C							NS	NS	NS

[z]Data not available.

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

Table 9. The effects of bulking duration, bulking photoperiod, and vernalization on plant height (PH), the number of nodes (NN), and the number of primary shoots (PS) at bulking completion or at anthesis of *Coreopsis grandiflora* 'Early Sunrise' during year 2 (2003).

			Bulking completion			Anthesis		
Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	PH (cm)	NN	No. of PS	PH (cm)	NN	No. of PS
0	-[z]	0	4 a[y]	8 a	2 a	35 a	15 a	16 a
	-	8	4 a	9 a	4 a	53 b	17 a	16 a
2	10	0	5	10	4	41	21	24
	10	8	5	10	4	49	18	16
	16	0	5	10	5	40	21	26
	16	8	6	11	5	42	16	14
5	10	0	6	12	10	43	23	22
	10	8	6	12	11	51	21	23
	16	0	7	11	5	39	20	23
	16	8	6	11	5	58	20	18
8	10	0	6	15	12	49	23	27
	10	8	5	14	13	53	24	28
	16	0	7	13	8	42	21	25
	16	8	7	13	9	56	22	26
Significance								
Bulking duration (D)			NS	***	***	***	***	**
Bulking photoperiod (P)			**	NS	***	NS	**	NS
Cold (C)						***	**	**
D X P			NS	NS	***	NS	NS	NS
D X C						*	**	**
D X P X C						**	NS	NS

[z]Plants were placed directly under forcing or chilling conditions.

[y]Letters next to means within the same column represent mean separation by LSMeans ($P \leq 0.05$).

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

Table 10. The effects of bulking duration and bulking photoperiod on plant height (PH), number of nodes (NN), and number of primary shoots (PS) of *Echinacea purpurea* 'Magnus' at bulking completion for year 2 (2003).

Bulking duration (weeks)	Bulking photoperiod (h)	PH (cm)	NN	No. of PS
0	-[z]	1	6	2
2	10	1	7	2
	16	2	8	1
5	10	2	9	3
	16	3	10	2
8	10	2	12	2
	16	2	11	2
Significance				
Bulking duration (D)		***	***	NS
Bulking photoperiod (P)		**	NS	NS
D X P		NS	NS	NS

[z]Plants were placed directly under chilling or forcing conditions.
NS, **, *** Nonsignificant or significant at $P \leq 0.01$ or 0.001, respectively.

Table 11. The effects of bulking duration, bulking photoperiod, and vernalization on percent flowering, days to visible bud (VB), days from visible bud to flower (VBF), days to flower (FLW), and number of reproductive buds (RB), flowering shoots (FS), plant height (PH), nodes (NN), and primary shoots (PS) at anthesis of *Echinacea purpurea* 'Magnus' during year 2 (2003).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	Flower (%)	Days to VB[z]	Days VBF	Days to FLW[z]	No. of RB	No. of FS	PH (cm)	NN	No. of PS
0	-[y]	0	100	53 a[x]	28 a	81 a	6 a	1 a	89 a	23 a	7 b
	-	8	100	52 a	33 a	85 a	6 a	1 a	89 a	21 a	4 a
2	10	0	90	43	28	71	7	3	98	21	5
	10	8	90	40	34	74	7	2	83	21	4
	16	0	90	47	31	78	10	1	97	25	4
	16	8	100	39	33	72	10	1	100	23	4
5	10	0	100	37	29	66	10	2	102	25	5
	10	8	100	39	34	73	11	2	100	27	5
	16	0	90	45	32	77	8	2	102	27	7
	16	8	100	40	34	74	11	2	102	27	6
8	10	0	100	34	32	66	10	2	95	31	4
	10	8	100	37	31	68	9	2	103	30	3
	16	0	90	43	34	77	12	2	106	34	5
	16	8	100	37	33	69	10	2	100	30	5
Significance											
Bulking duration (D)				*	NS	NS	NS	NS	NS	**	**
Bulking photoperiod (P)				**	NS	**	NS	NS	NS	NS	NS
Cold (C)				*	**	NS	NS	NS	NS	NS	NS
D X P				NS	NS	NS	NS	NS	NS	*	*
D X C				NS	**	NS	NS	NS	NS	NS	NS
D X P X C				NS	NS	NS	NS	NS	NS	NS	NS

[z]Data for days to VB and days to FLW are for the period from the start of forcing until visible bud and anthesis, respectively.

[y]Plants were placed directly under forcing or chilling conditions.

[x]Letters next to means within the same column represent mean separation by LSMeans ($P \leq 0.05$).

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

Table 12. The effects of bulking duration, bulking photoperiod, and vernalization on percent flowering, days to visible bud (VB), days from visible bud to flower (VBF), days to flower (FLW), plant height (PH), and the number of nodes (NN) at anthesis of *Penstemon digitalis* 'Husker Red' during year 1 (2002).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	Flower (%)	Days VB [z]	Days VBF	Days FLW [z]	PH (cm) [y]	NN [y]
2	10	0	80	70	25	96	58	21
	10	8	90	53	23	75	69	21
	16	0	50	42	22	64	71	18
	16	8	80	58	24	82	66	20
5	10	0	50	54	24	78	80	19
	10	8	90	47	19	66	71	21
	16	0	40	52	23	75	67	22
	16	8	100	45	20	65	66	19
8	10	0	80	43	20	63	79	32
	10	8	100	42	21	63	83	22
	16	0	33	45	21	66	63	27
	16	8	73	43	20	63	89	19
Significance								
Bulking duration (D)				NS	NS	**	NS	**
Bulking photoperiod (P)				NS	NS	NS	NS	NS
Cold (C)				NS	NS	NS	NS	NS
D X P				NS	NS	NS	NS	NS
D X C				NS	NS	NS	NS	*
D X P X C				NS	NS	NS	NS	NS

[z]Data for days to VB and days to FLW are for the period from the start of forcing until visible bud and anthesis, respectively.

[y]Data for PH and NN are for the period from the start of bulking until anthesis.

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

Table 13. The effects of bulking duration and bulking photoperiod on percent flowering, days to visible bud (VB), days from visible bud to flower (VBF), days to flower (FLW), number of reproductive buds (RB), number of flowering shoots (FS), and plant height (PH) at anthesis after 8 weeks at 5 °C of *Penstemon digitalis* 'Husker Red' during year 2 (2003).

Bulking duration (weeks)	Bulking photoperiod (h)	Flower (%)	Days VB [z]	Days VBF	Days FLW [z]	No. of RB [y]	No. of FS [y]	PH (cm) [y]
0	- [x]	10	62	22	84	84	1	44
2	10	40	46	22	68	100	1	62
	16	50	41	20	61	99	1	54
5	10	80	51	22	73	110	2	59
	16	40	59	22	81	96	1	64
8	10	90	52	20	73	154	4	59
	16	60	52	23	76	178	5	64
Significance								
Bulking duration (D)			**	NS	**	*	**	NS
Bulking photoperiod (P)			NS	NS	NS	NS	NS	NS
D X P			NS	NS	*	NS	NS	NS

[z]Data for days to VB and days to FLW are for the period from the start of force until visible bud and anthesis, respectively.

[y]Data for number of RB, FS, and PH are for the period from the start of bulking until anthesis.

[x]Plants were placed directly under chilling conditions..

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

Table 14. The effects of bulking duration, bulking photoperiod, and vernalization on percent flowering, days to visible bud (VB), days from visible bud to flower (VBF), days to flower (FLW), number of flowering shoots (FS), plant height (PH), and number of primary shoots (PS) at anthesis of *Salvia nemorosa* 'May Night' during year 2 (2003).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	Flower (%)	Days to VB [z]	Days VBF	Days to FLW [z]	No. of FS	PH (cm)	No. of PS
0	-[y]	0	100	17 b [x]	8 a	25 a	4 a	31 a	3 a
	-	8	100	12 a	12 b	23 a	4 a	31 a	3 a
2	10	0	100	12	10	22	2	36	3
	10	8	100	10	12	22	4	29	3
	16	0	100	6	11	17	2	35	2
	16	8	100	9	14	23	5	33	4
5	10	0	100	7	11	19	3	29	3
	10	8	100	7	13	20	8	29	2
	16	0	90	13	12	25	3	36	6
	16	8	100	12	14	25	5	42	5
8	10	0	100	5	8	14	6	19	7
	10	8	100	4	12	15	9	21	5
	16	0	100	9	12	20	3	29	5
	16	8	100	13	12	25	7	35	6
Significance									
Bulking duration (D)				NS	*	**	***	***	***
Bulking photoperiod (P)				**	**	***	*	***	*
Cold (C)				NS	**	*	**	NS	NS
D X P				***	NS	***	**	**	**
D X C				NS	NS	NS	NS	*	NS
D X P X C				NS	NS	NS	NS	NS	NS

[z]Data for VB and FLW are for the period from the start of forcing until visible bud and anthesis, respectively.

[y]Plants were placed directly under forcing or chilling conditions.

[x]Letters next to means within the same column represent mean separation by LSMeans ($P \leq 0.05$).

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

Table 15. The effects of bulking duration, bulking photoperiod, and vernalization on the number of reproductive buds (RB) of *Salvia nemorosa* 'May Night' during year 2 (2003).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks of 5 °C	No. of RB
0	- [z]	0	17 A [y]
0	-	8	30 B
2	10	0	22 bcd [x]
2	10	8	31 de
2	16	0	10 a
2	16	8	36 e
5	10	0	12 ab
5	10	8	38 e
5	16	0	15 ab
5	16	8	36 e
8	10	0	14 ab
8	10	8	25 cd
8	16	0	17 abc
8	16	8	52 f

[z]Plants were placed directly under forcing or chilling conditions.

[y]Upper case letters next to means represent mean separation by LSMeans ($P \leq 0.05$).

[x]Lower case letters next to means represent mean separation by LSMeans ($P \leq 0.05$).

Table 16. Summary of bulking duration, vernalization requirements, and weeks to flower for *Achillea millefolium* 'Paprika', *Aquilegia* x *hybrida* Songbird Mix, *Coreopsis grandiflora* 'Early Sunrise', *Echinacea purpurea* 'Magnus', *Penstemon digitalis* 'Husker Red', and *Salvia nemorosa* 'May Night'.

Species	Starting plug size	Bulking duration (weeks)	Weeks at 5 °C	Weeks to flower (20 °C)
Achillea	72-cell	0	0	6 - 8
Aquilegia	72-cell	≥ 5	8	6 - 7
Coreopsis	72-cell	> 2	8 [z]	7 - 8
Echinacea	72-cell	0	0	10 - 11
Penstemon	72-cell	≥ 5	≥ 8	9 - 11
Salvia	54-cell	0	0	3 - 4

[z]Cold is beneficial, but not required.

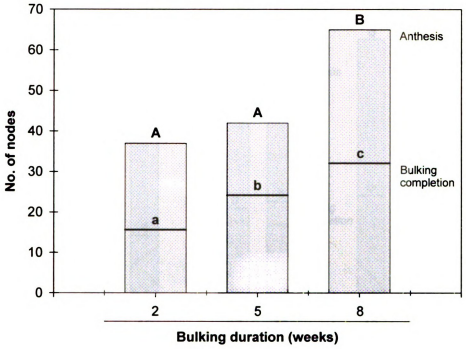


Figure 1. Node development responses of *Achillea millefolium* 'Paprika' bulked for 2, 5, or 8 weeks during year 1 (2002). Lower and upper case letters represent mean separation by LSMeans ($P \leq 0.05$) for the number of nodes at bulking completion and at anthesis, respectively.

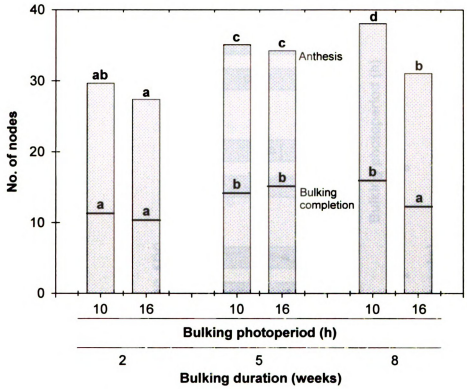


Figure 2. Node development responses of *Achillea millefolium* 'Paprika' bulked for 2, 5, or 8 weeks under 10- or 16-h photoperiods during year 2 (2003). Lower and upper case letters represent mean separation by LSMeans ($P \leq 0.05$) for the number of nodes at bulking completion and at anthesis, respectively.

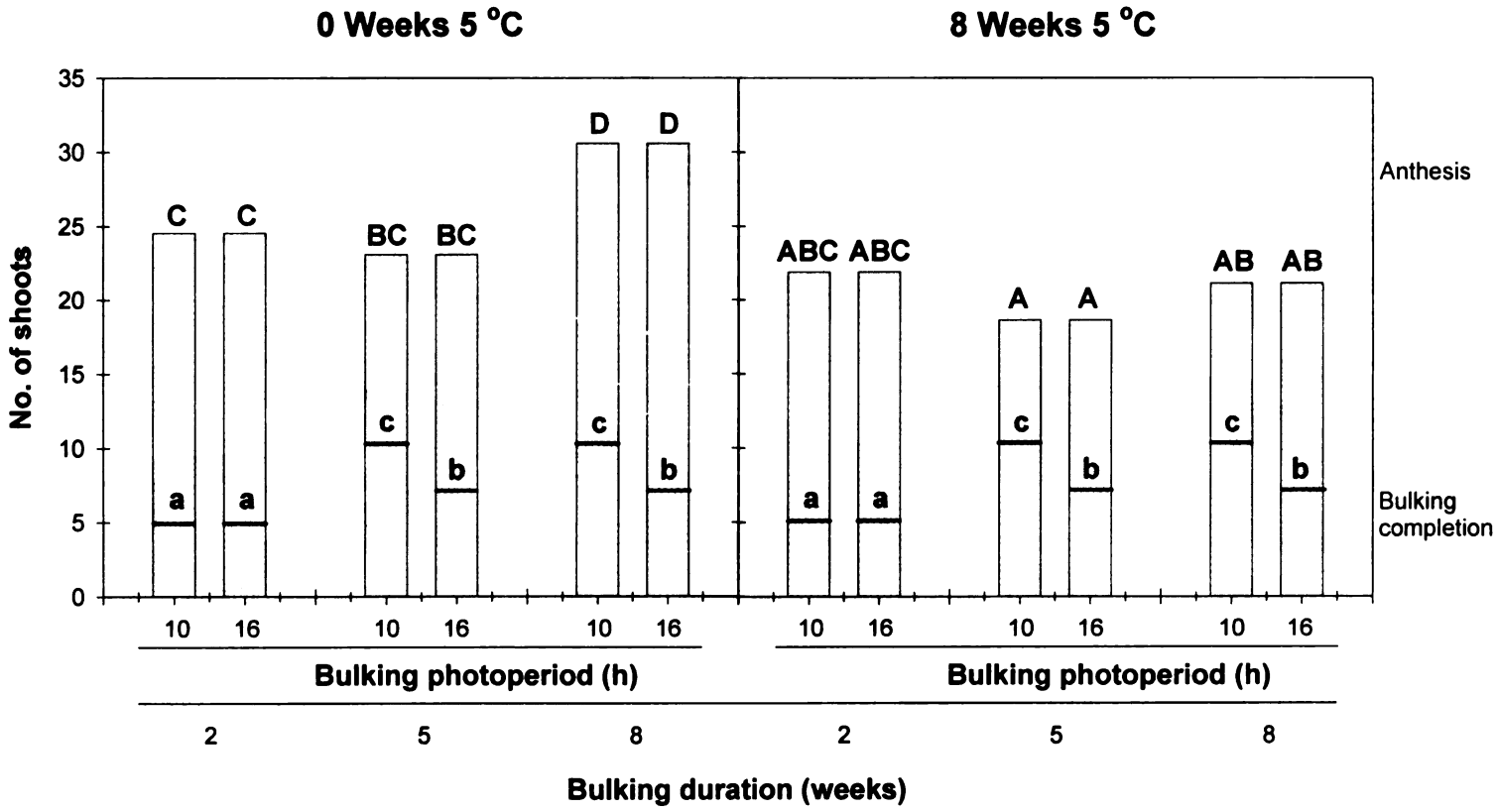


Figure 3. Shoot development of *Achillea millefolium* 'Paprika' bulked for 2, 5, or 8 weeks under 10- or 16-h photoperiods, followed by 0 or 8 weeks at 5 °C, during year 2 (2003). Lower and upper case letters represent mean separation by LSMeans ($P \leq 0.05$) for the number of primary shoots at bulking completion and at anthesis, respectively.

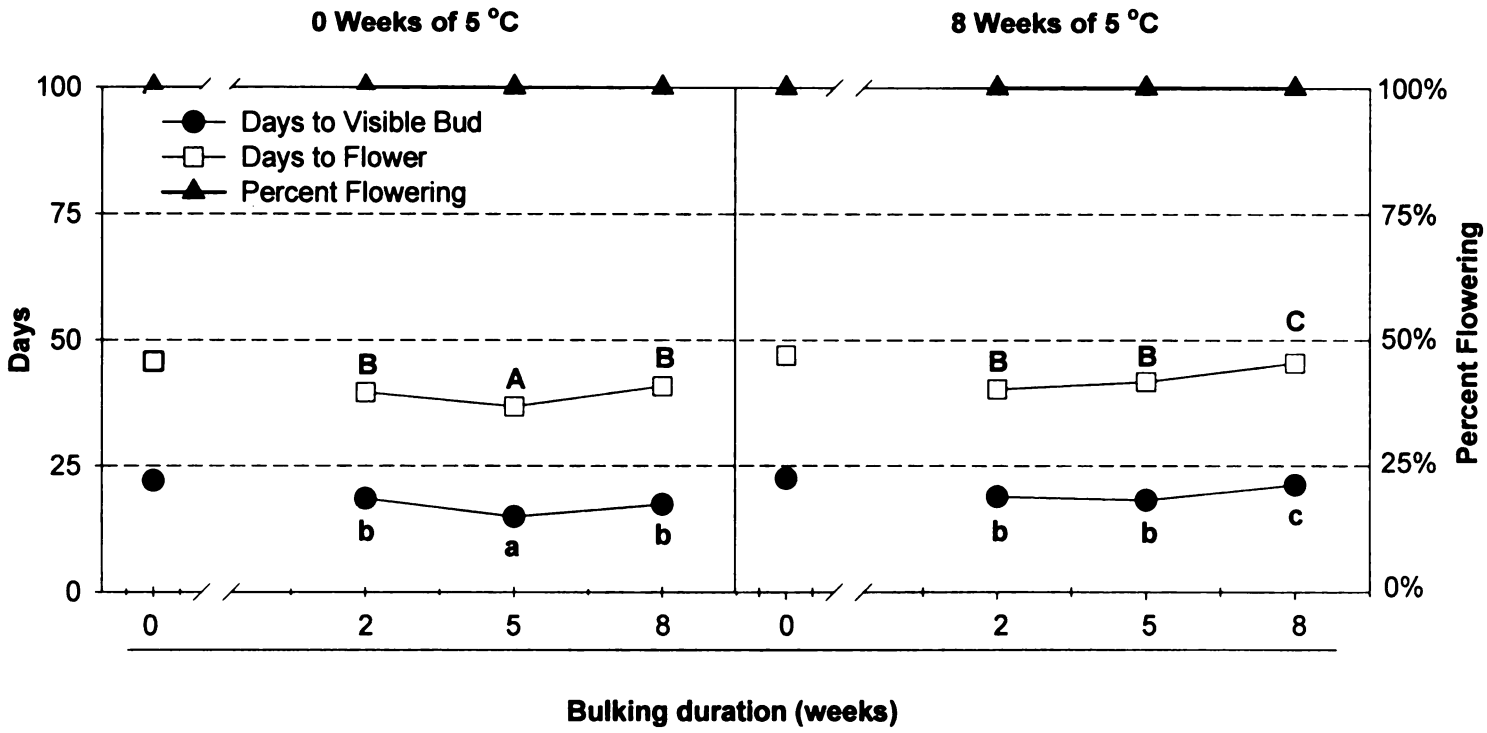


Figure 4. Flowering responses of *Achillea millefolium* 'Paprika' bulked for 0, 2, 5, or 8 weeks, followed by 0 or 8 weeks of vernalization, during year 2 (2003). Data for days to visible bud (VB) and days to flower (FLW) are for the period from the start of forcing until visible bud and anthesis. Lower and upper case letters next to symbols across graphs represent mean separation by LSMeans ($P \leq 0.05$) for days to VB and days to FLW, respectively.

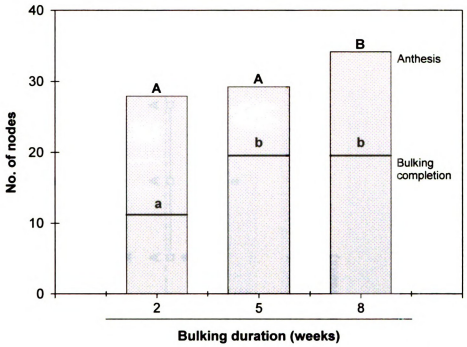


Figure 5. Node development responses of *Aquilegia* Songbird Mix bulked for 2, 5, or 8 weeks during year 1 (2002). Lower and upper case letters represent mean separation by LSMeans ($P \leq 0.05$) for the number of nodes at bulking completion and at anthesis, respectively.

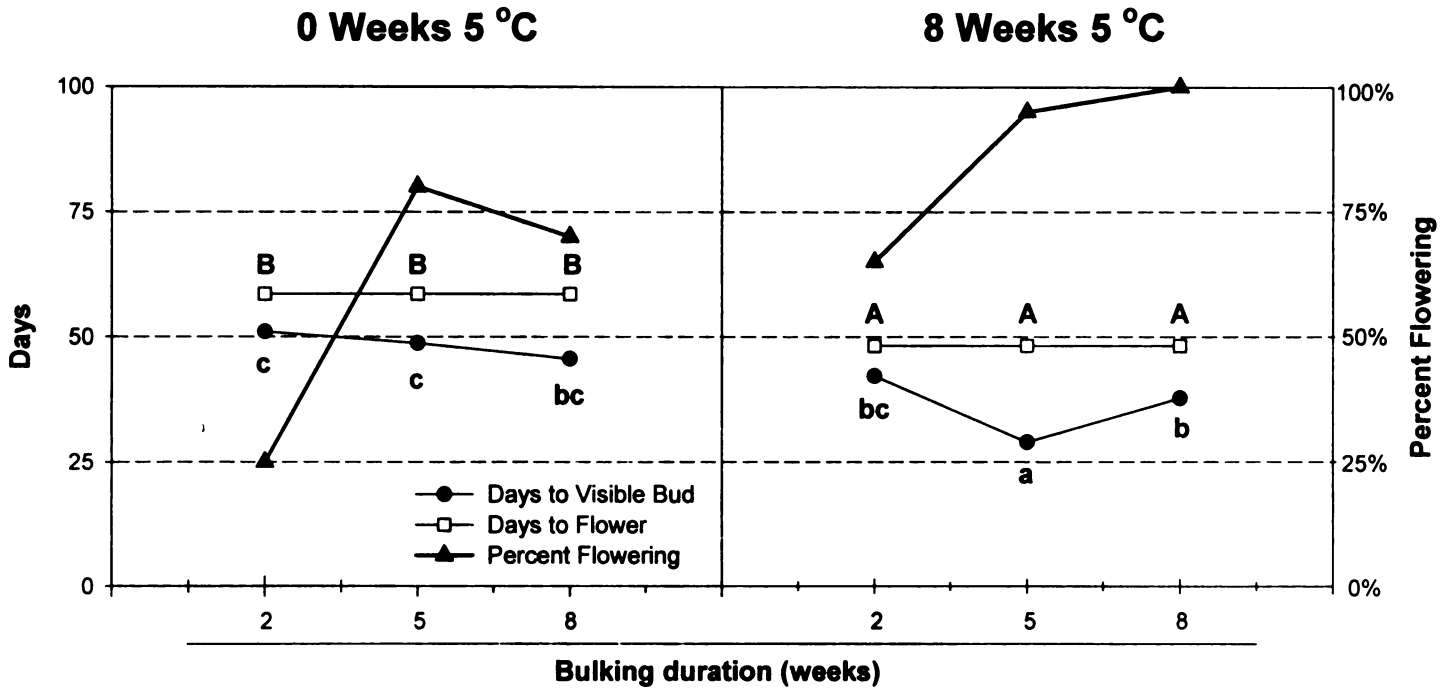


Figure 6. Flowering responses of *Aquilegia* Songbird Mix bulked for 2, 5, or 8 weeks, followed by 0 or 8 weeks of vernalization, during year 1 (2002). Data for days to visible bud (VB) and days to flower (FLW) are for the period from the start of forcing until visible bud and anthesis. Lower and upper case letters next to symbols across graphs represent mean separation by LSMeans ($P \leq 0.05$) for days to VB and days to FLW, respectively.

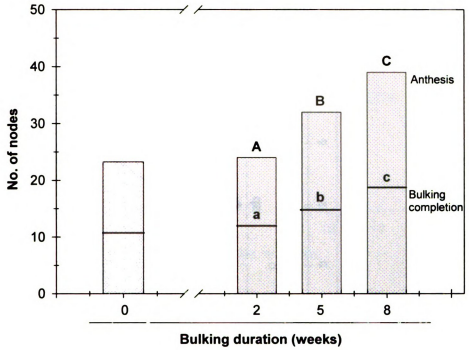


Figure 7. Node development responses of *Aquilegia* Songbird Mix Bulked for 0, 2, 5, or 8 weeks during year 2 (2003). Lower and upper case letters represent mean separation by LSMeans ($P \leq 0.05$) for the number of nodes at bulking completion and at anthesis, respectively.

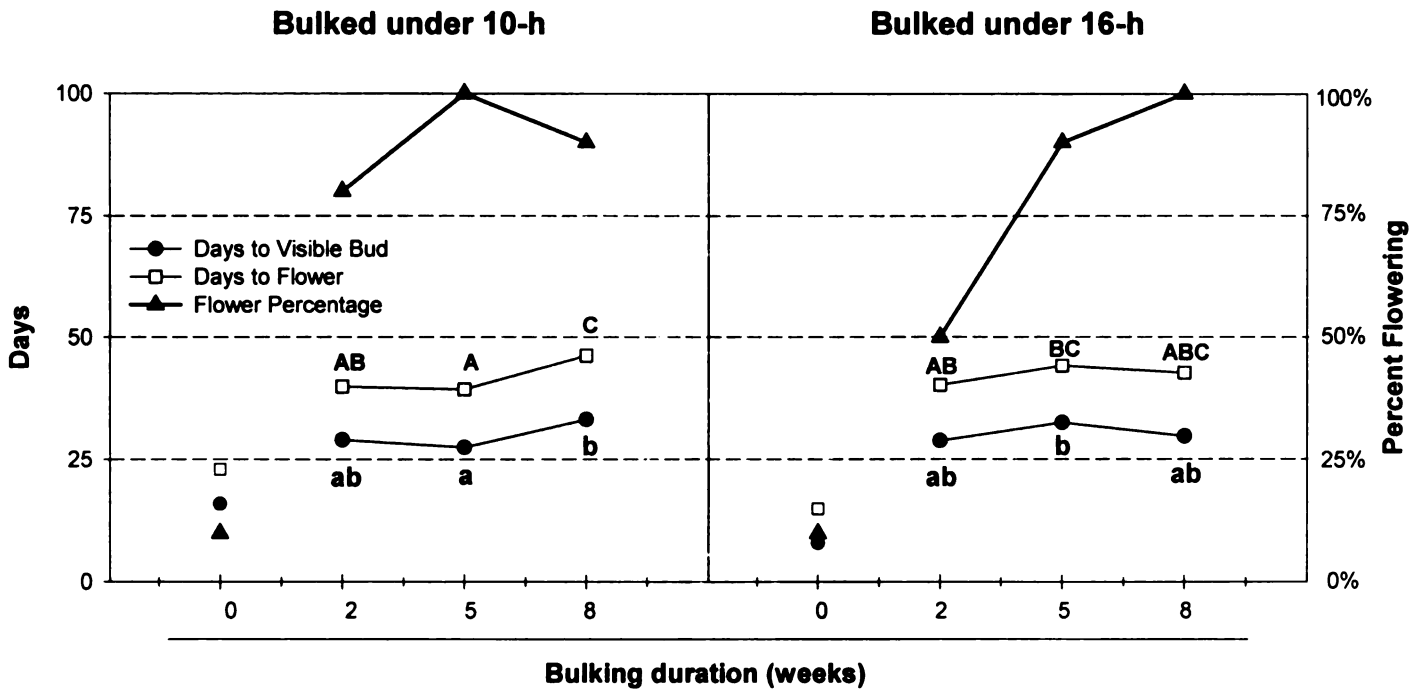


Figure 8. Flowering responses of *Aquilegia* Songbird Mix bulked for 2, 5, or 8 weeks under 10- or 16-h photoperiods, followed by 8 weeks at 5 °C, during year 2 (2003). Data for days to visible bud (VB) and days to flower (FLW) are for the period from the start of forcing until visible bud and anthesis. Lower and upper case letters next to symbols across graphs represent mean separation by LSMeans ($P \leq 0.05$) for days to VB and days to FLW, respectively.

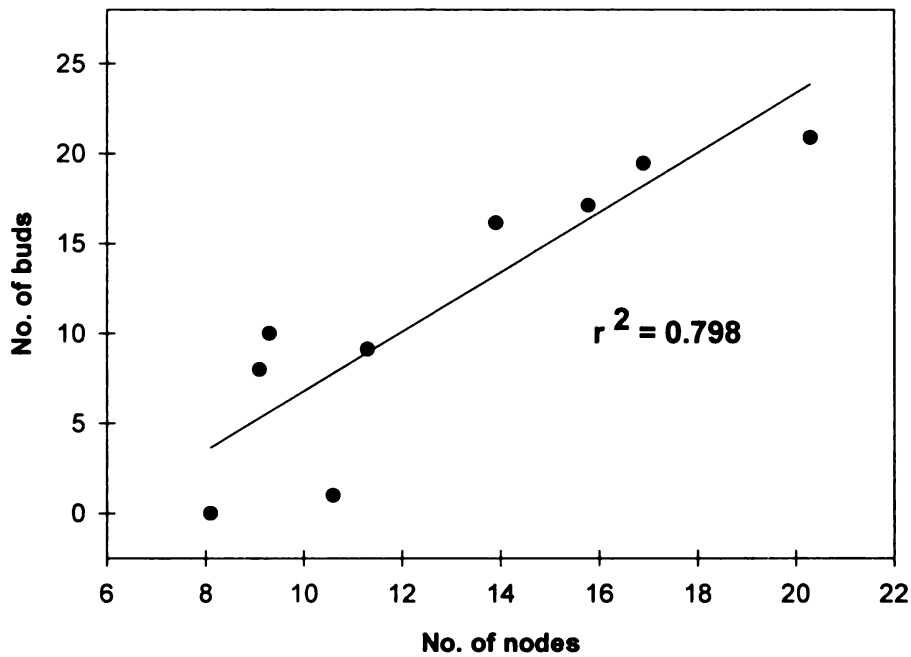


Figure 9. The relationship between the number of nodes at bulking completion and the number of reproductive buds at anthesis of *Aquilegia* Songbird Mix during year 2 (2003).

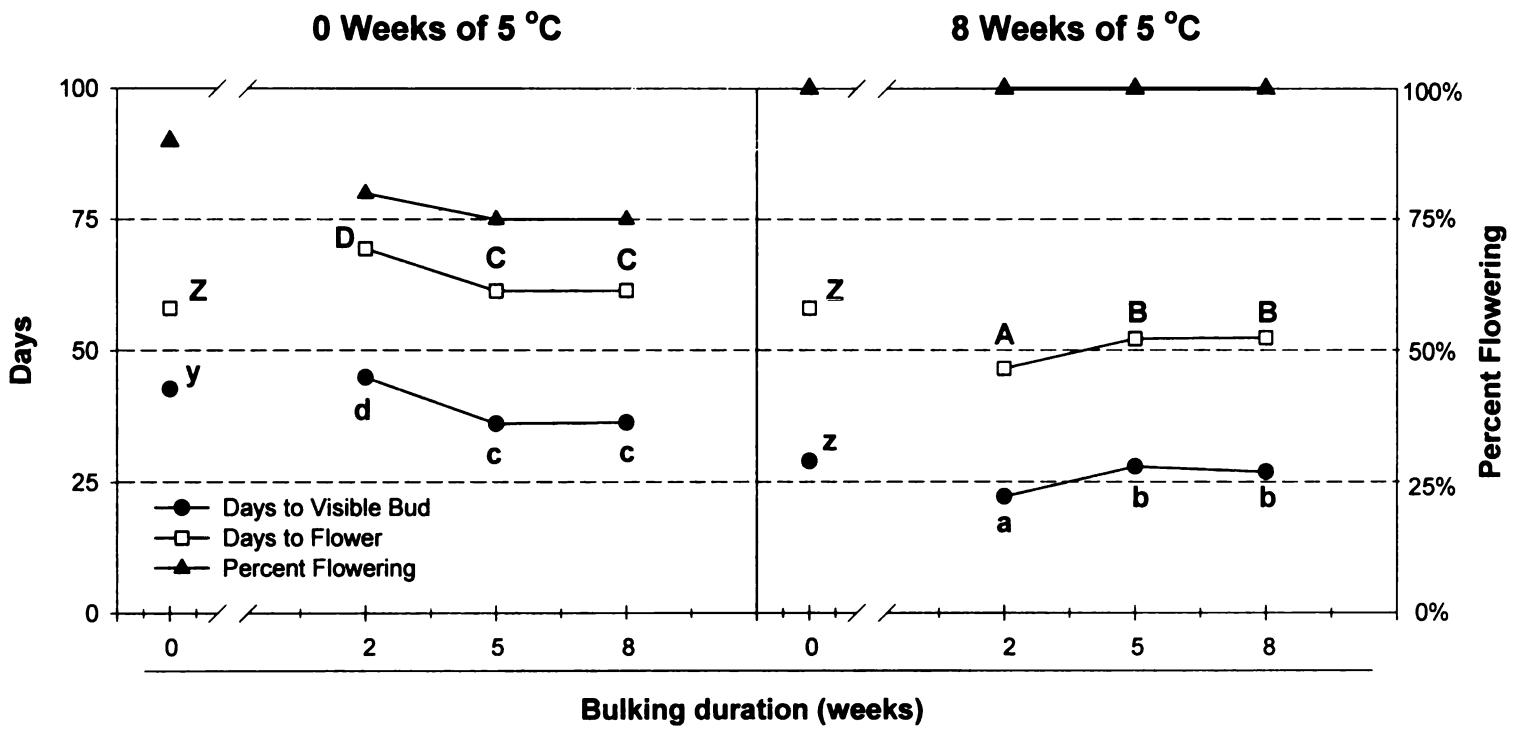


Figure 10. Flowering responses of *Coreopsis grandiflora* 'Early Sunrise' bulked for 0, 2, 5, or 8 weeks, followed by 0 or 8 weeks of vernalization, during year 2 (2003). Data for days to visible bud (VB) and days to flower (FLW) are for the period from the start of forcing until visible bud and anthesis. Lower and upper case letters next to symbols across graphs represent mean separation by LSMeans ($P \leq 0.05$) for days to VB and days to FLW, respectively.

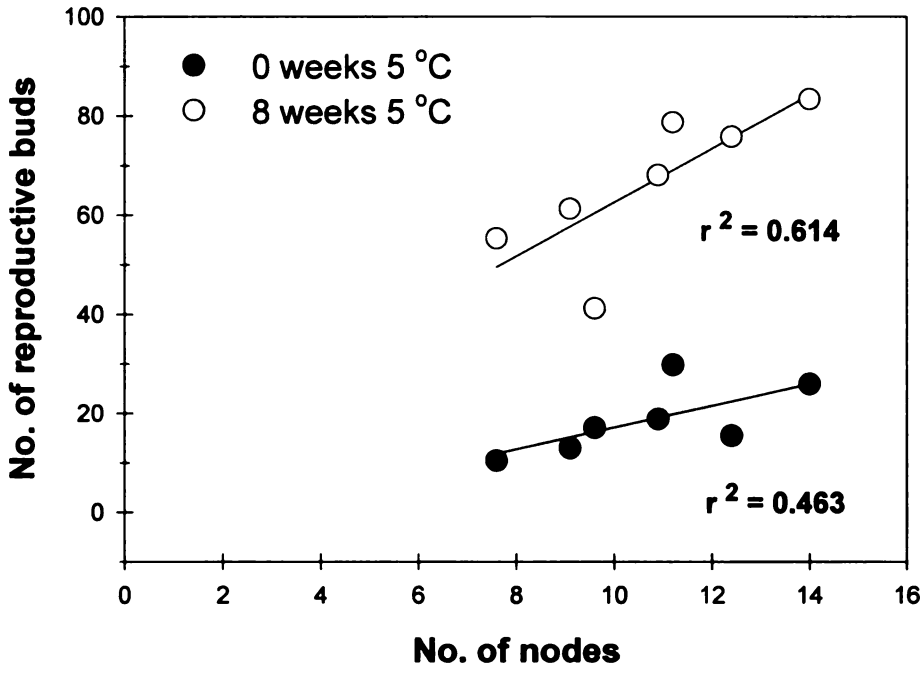


Figure 11. The relationship between the number of nodes at bulking completion and the number of reproductive buds at anthesis after 0 or 8 weeks of vernalization of *Coreopsis grandiflora* 'Early Sunrise' during year 2 (2003).

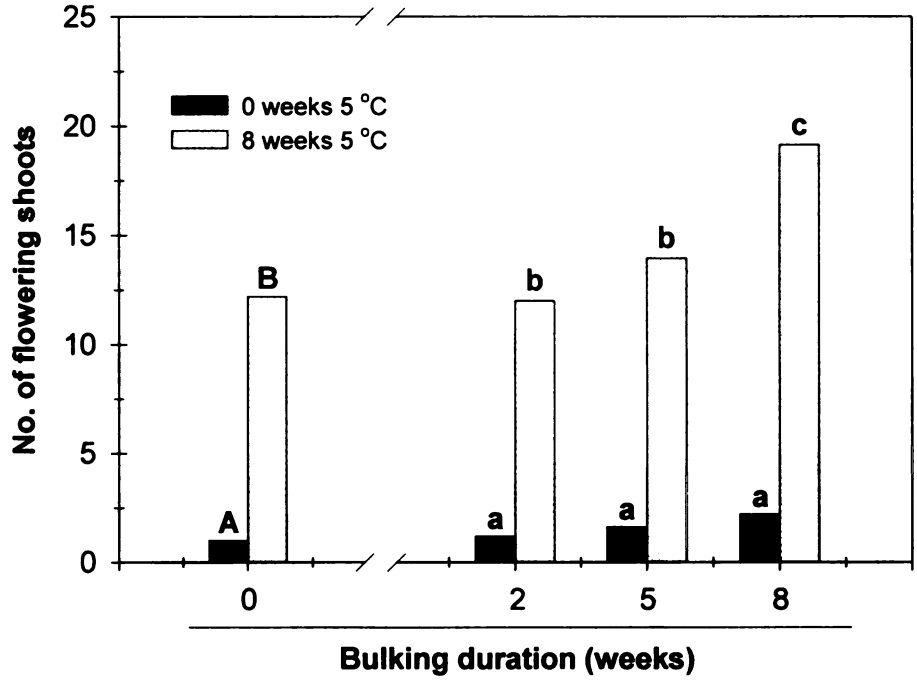


Figure 12. The effects of bulking duration and vernalization on the number of flowering shoots (FS) in *Coreopsis grandiflora* 'Early Sunrise' during year 2 (2003). Lower case letters next to bars represent mean separation by LSMeans ($P \leq 0.05$) for the number of FS at anthesis; data for plants bulked 0 weeks are separated by upper case letters.

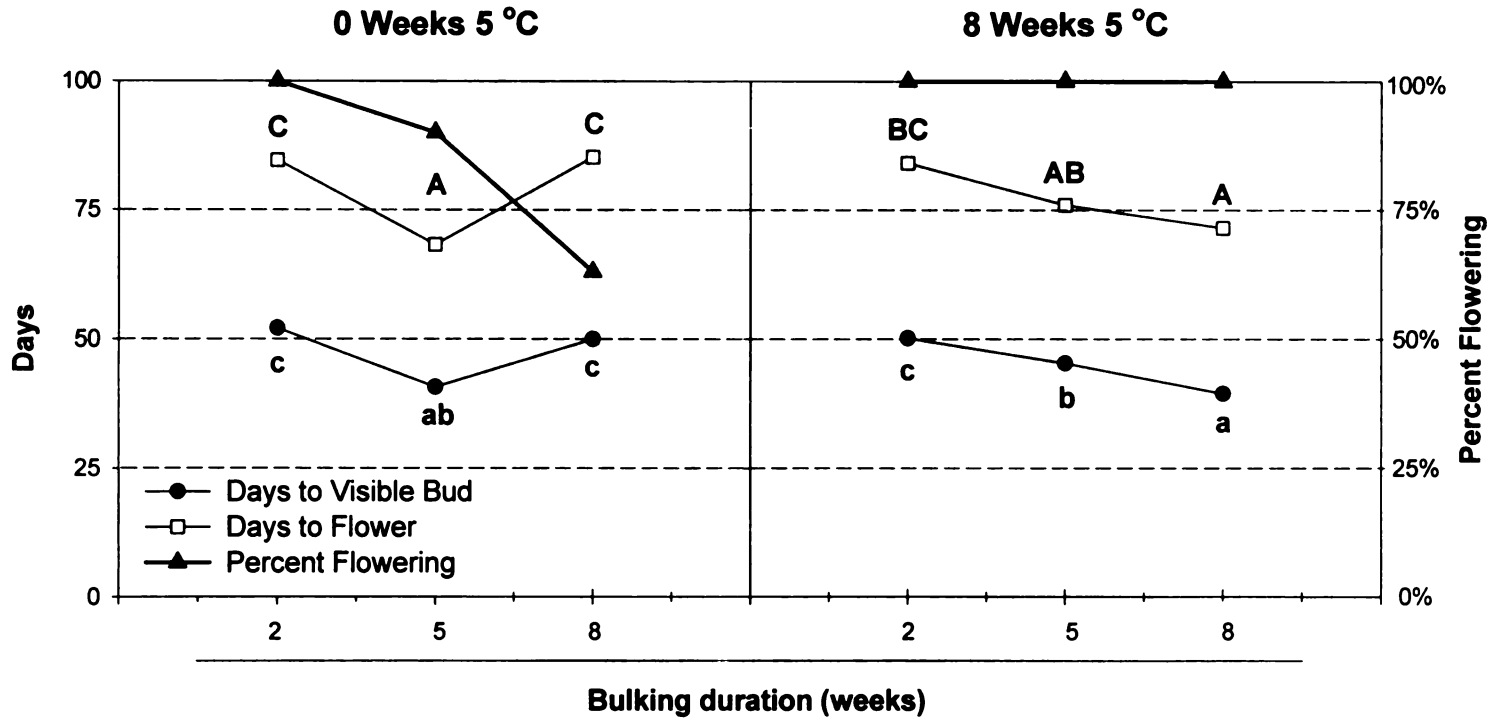


Figure 13. Flowering responses of *Echinacea purpurea* 'Magnus' bulked for 2, 5, or 8 weeks, followed by 0 or 8 weeks of vernalization, during year 1 (2002). Data for days to visible bud (VB) and days to flower (FLW) are for the period from the start of forcing until visible bud and anthesis. Lower and upper case letters next to symbols across graphs represent mean separation by LSMeans ($P \leq 0.05$) for days to VB and days to FLW, respectively.

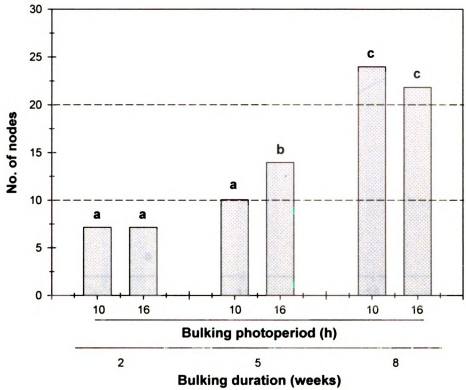


Figure 14. Node development responses of *Penstemon digitalis* 'Husker Red' bulked for 2, 5, or 8 weeks under 10- or 16-h photoperiods during year 1 (2002). Letters next to bars represent mean separation by LSMeans ($P \leq 0.05$) for the number of nodes at bulking completion.

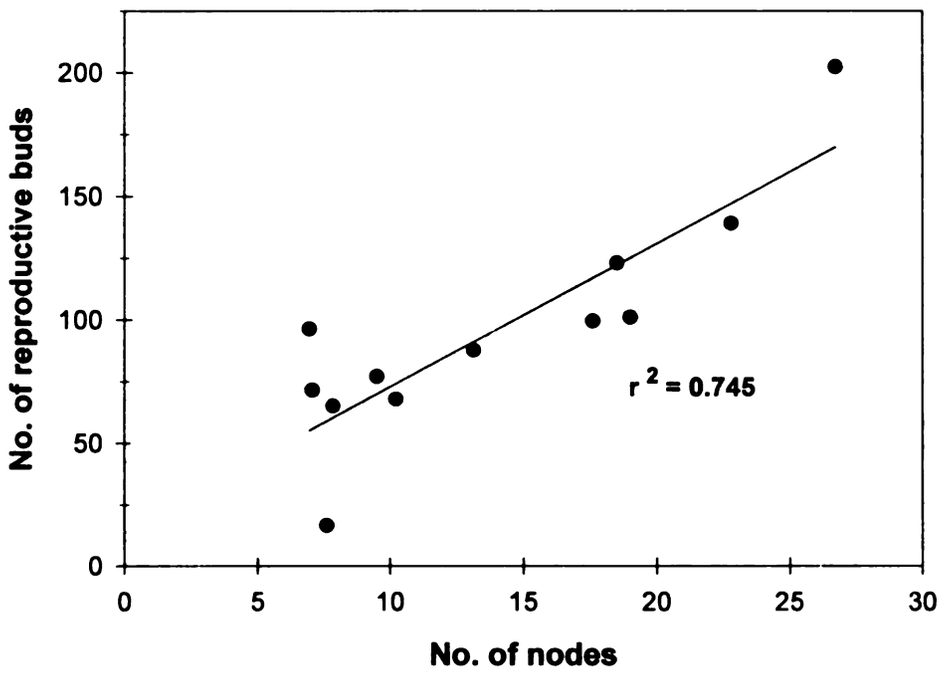


Figure 15. The relationship between the number of nodes at bulking completion and the number of reproductive buds at anthesis of *Penstemon digitalis* 'Husker Red' during year 1 (2002).

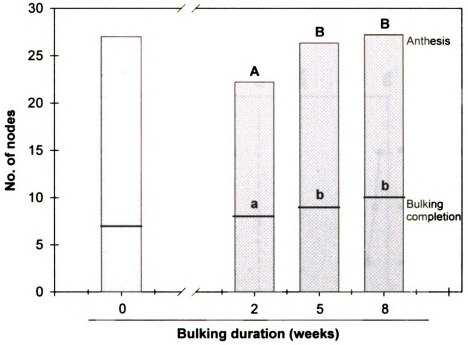


Figure 16. Node development responses of *Penstemon digitalis* 'Husker Red' bulked for 0, 2, 5, or 8 weeks during year 2 (2003). Lower and upper case letters represent mean separation by LSMeans ($P \leq 0.05$) for the number of nodes at bulking completion and at anthesis, respectively. For plants bulked 0 weeks, n=1.

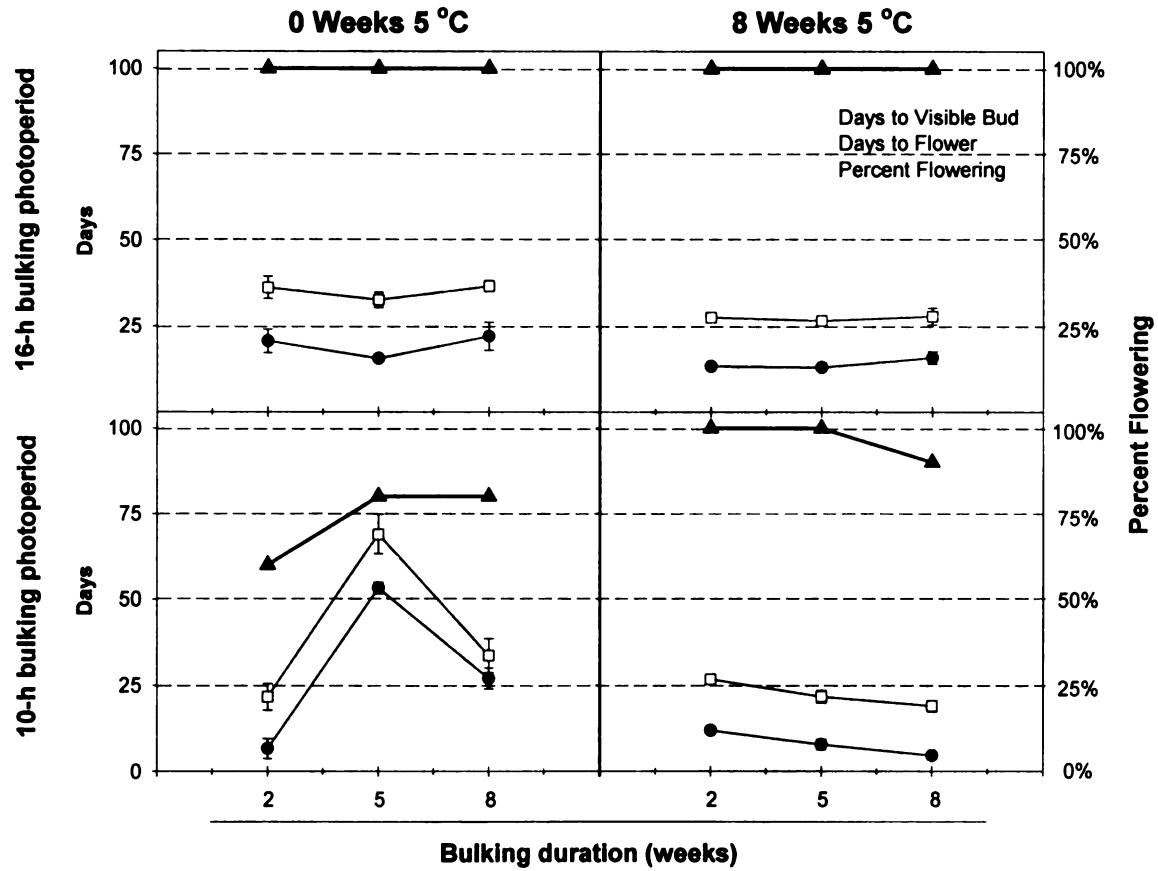


Figure 17. Flowering responses of *Salvia nemorosa* 'May Night' bulked for 2, 5, or 8 weeks under 10- or 16-h photoperiods, followed by 0 or 8 weeks of vernalization, during year 1 (2002). Data for days to visible bud and days to flower are for the period from start of forcing until visible bud or anthesis, respectively. Error bars represent SE.

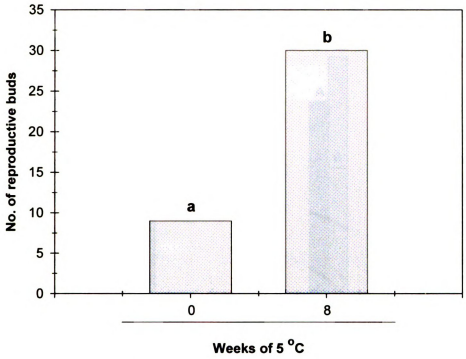


Figure 18. The response of reproductive bud development after 0 or 8 weeks of vernalization of *Salvia nemorosa* 'May Night' during year 1 (2002). Letters next to bars represent mean separation by LSMeans ($P \leq 0.05$) for the number of reproductive buds at anthesis.

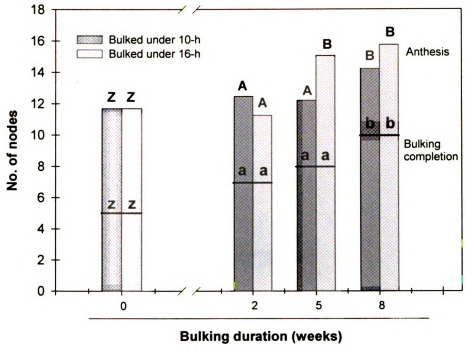


Figure 19. Plant node development responses of *Salvia nemorosa* 'May Night' to 0, 2, 5, or 8 weeks of bulking under 10- or 16-h photoperiods during year 2 (2003). Lower and upper case letters represent mean separation by LSMeans ($P \leq 0.05$) for the number of nodes at bulking completion and at anthesis, respectively.

APPENDIX A

EFFECTS OF ETHEPHON ON STOCK PLANT MANAGEMENT OF SEVEN HERBACEOUS PERENNIAL SPECIES

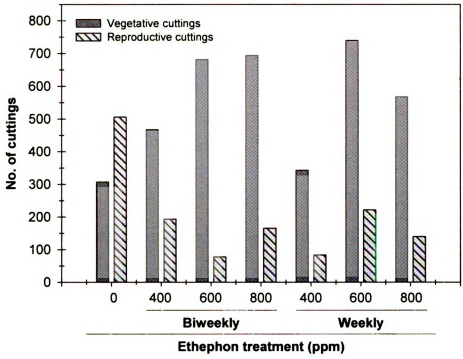


Figure 1. Total number of vegetative and reproductive cuttings harvested from *Coreopsis verticillata* 'Moonbeam' during year 2 (2003).

Figure 2. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on shoot length in *Dianthus caryophyllus* 'Cinnamon Red Hots'™ during year 2 (2003). Cutting harvests occurred during week 2 and week 6. Data for week 3 and week 9 were not taken. Error bars represent SE.

Shoot Length
Dianthus caryophyllus 'Cinnamon Red Hots'™

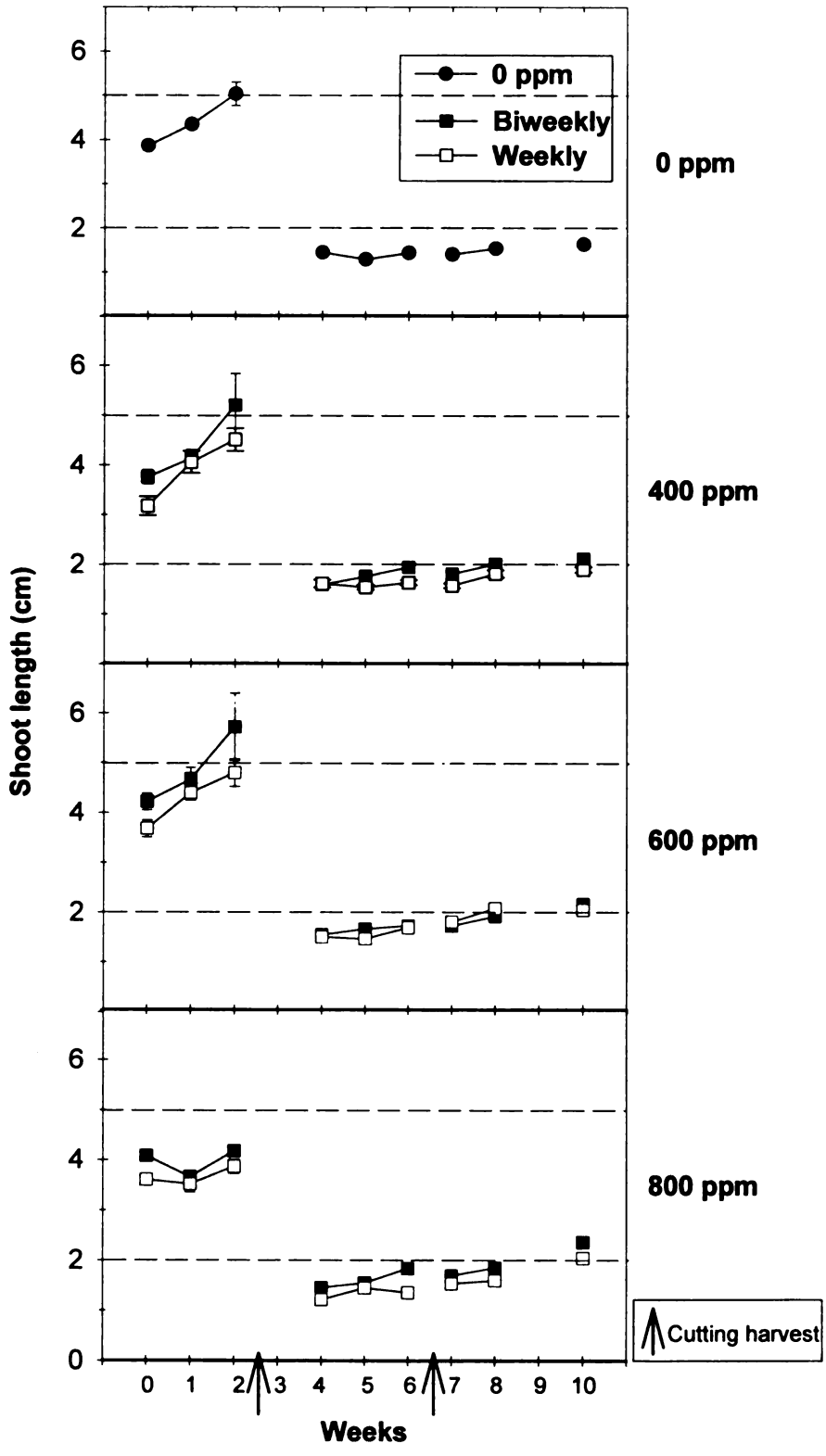
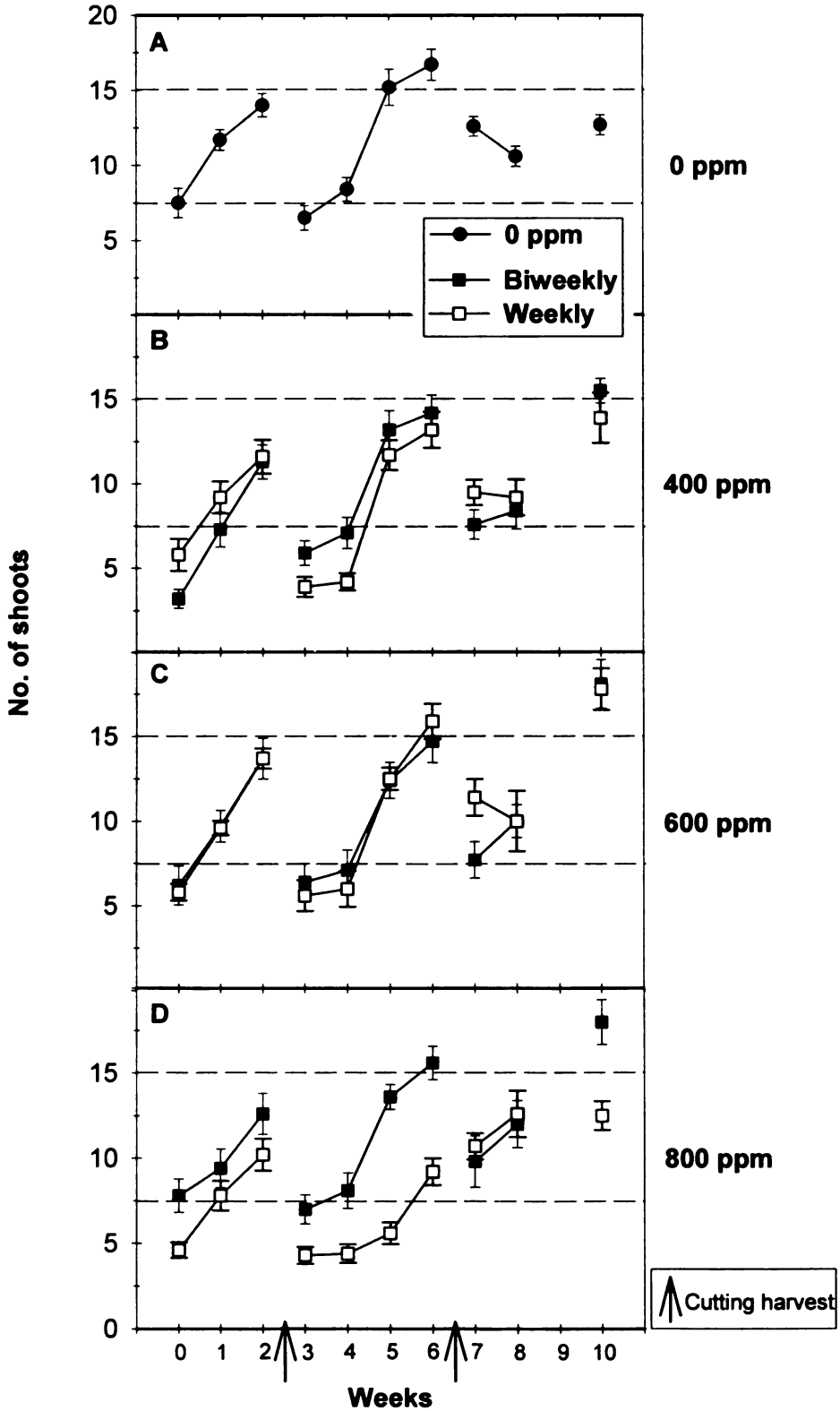


Figure 3. The effect of biweekly and weekly applications of 0 ppm (A), 400 ppm (B), 600 ppm (C), and 800 ppm (D) ethephon on the number of primary shoots in *Dianthus caryophyllus* 'Cinnamon Red Hots'™ during year 2 (2003). Cutting harvests occurred during week 2 and week 6. Data for week 9 were not taken. Error bars represent SE.

Primary Shoots

Dianthus caryophyllus 'Cinnamon Red Hots'™



of 0 ppm (A) 400 ppm

er of primary shoots

2 (2003). Cutting

ek 9 were not taken

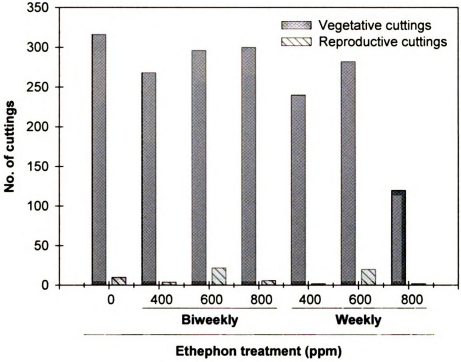


Figure 4. Total number of vegetative and reproductive cuttings harvested from *Dianthus caryophyllus* 'Cinnamon Red Hots'™ during year 2 (2003).

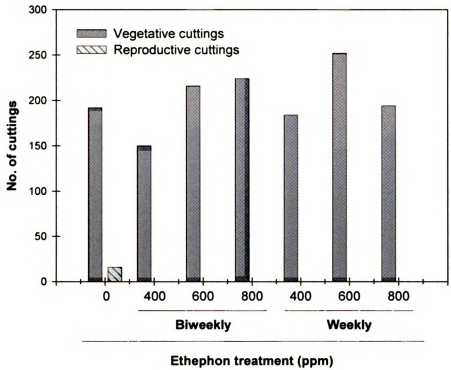


Figure 5. Total number of vegetative and reproductive cuttings harvested from *Veronica longifolia* 'Sunny Border Blue' during year 2 (2003).

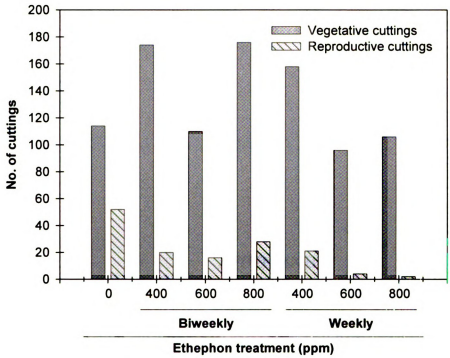


Figure 6. Total number of vegetative and reproductive cuttings harvested from *Veronica longifolia* 'Sunny Border Blue' that received 8 weeks at 5 °C for 8 weeks prior to ethephon application during year 2 (2003).

APPENDIX B

THE EFFECTS OF BULKING DURATION, BULKING PHOTOPERIOD, AND VERNALIZATION ON PRODUCTION SCHEDULING OF EIGHTEEN HERBACEOUS PERENNIAL SPECIES

Table 1. The effects of bulking duration and bulking photoperiod on plant height (PH), number of nodes (NN), and number of primary shoots (PS) of *Achillea millefolium* 'Paprika' at bulking completion during year 1 (2002).

Bulking duration (weeks)	PH (cm)	NN	No. of PS
2	4 b[z]	16 a	4 a
5	3 a	25 b	7 a
8	4 b	33 c	10 b

[z]Letters next to means represent mean separation by LSMeans ($P \leq 0.05$).

Table 2. The effects of bulking duration, bulking photoperiod, and vernalization on the number of reproductive buds (RB), flowering shoots (FS), plant height (PH), nodes (NN), and primary shoots (PS) at anthesis of *Aquilegia* x *hybrida* Songbird Mix during year 2 (2003).

Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	No. of RB [z]	No. of FS [z]	PH (cm) [z]	NN [z]	No. of PS [z]
0	- [y]	0	0 a [x]	1 a	20 a	21 a	4 a
	-	8	8 a	2 a	38 a	26 a	2 a
2	10	8 [w]	9	1	33	25	2
	16	8	10	1	39	23	1
5	10	8	17	6	38	35	2
	16	8	16	2	31	30	2
8	10	8	21	2	46	41	2
	16	8	19	2	38	37	1
Significance							
Bulking duration (D)			**	**	**	***	NS
Bulking photoperiod (P)			NS	*	NS	**	NS
D X P			NS	NS	*	NS	NS

[z]Data for the number of RB, FS, PH, NN and number of PS are for the period from the start of bulking until anthesis.

[y]Plants were placed directly under forcing or chilling conditions.

[x]Letters next to means within the same column represent mean separation by LSMeans ($P \leq 0.05$).

[w]Plants that received 0 weeks of chilling did not flower

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

Table 3. The effects of bulking duration, bulking photoperiod, and vernalization on plant height (PH), the number of nodes (NN), and the number of primary shoots (PS) at bulking completion and the number of reproductive buds (RB), PH, and NN at anthesis of *Echinacea purpurea* 'Magnus' during year 1 (2002).

			Bulking completion			Anthesis [z]		
Bulking duration (weeks)	Bulking photoperiod (h)	Weeks at 5 °C	PH (cm)	NN	No. of PS	No. of RB	PH (cm)	NN
2	10	0	1	9	2	11	105	29
	10	8	2	9	2	5	96	22
	16	0	2	9	2	19	107	34
	16	8	2	10	2	8	95	21
5	10	0	1	15	2	12	94	36
	10	8	1	18	2	8	84	31
	16	0	2	15	2	18	91	35
	16	8	1	11	2	10	87	30
8	10	0	2	17	2	12	88	56
	10	8	2	21	2	8	87	35
	16	0	3	16	2	3	64	23
	16	8	2	12	2	8	89	36
Significance								
Duration (D)			***	***	NS	NS	*	**
Photoperiod (P)			***	*	NS	NS	NS	*
Cold (C)					NS	**	NS	**
D X P			NS	NS	NS	*	NS	**
D X C					NS	NS	NS	NS
D X P X C					NS	NS	NS	**

[z]Data for the number of RB, PH, and NN are for the period from the start of bulking until anthesis.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 4. The effects of bulking duration, bulking photoperiod, and vernalization on plant height (PH), the number of nodes (NN), and the number of primary shoots (PS) at bulking completion and anthesis of *Salvia nemorosa* 'May Night' during year 1 (2002).

			Bulking completion			Anthesis [z]	
Bulking duration (weeks)	Bulking photoperiod (h)	Weeks of 5 °C	PH (cm)	NN	No. of PS	PH (cm)	NN
2	10	0	2	4	1	30	11
2	10	8	3	5	1	42	11
2	16	0	4	6	1	36	10
2	16	8	5	6	1	46	11
5	10	0	3	6	2	24	7
5	10	8	2	6	2	42	8
5	16	0	3	9	1	39	10
5	16	8	8	8	2	49	13
8	10	0	3	8	2	12	5
8	10	8	4	9	3	32	10
8	16	0	3	9	2	34	7
8	16	8	6	9	1	56	13
Significance							
Bulking duration (D)			NS	***	**	NS	NS
Bulking photoperiod (P)			***	***	**	***	**
Cold (C)						***	**
D X P			*	NS	NS	**	NS
D X C						NS	*
D X P X C						NS	NS

[z]Data for PH and NN are for the period from the start of bulking until anthesis.
NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

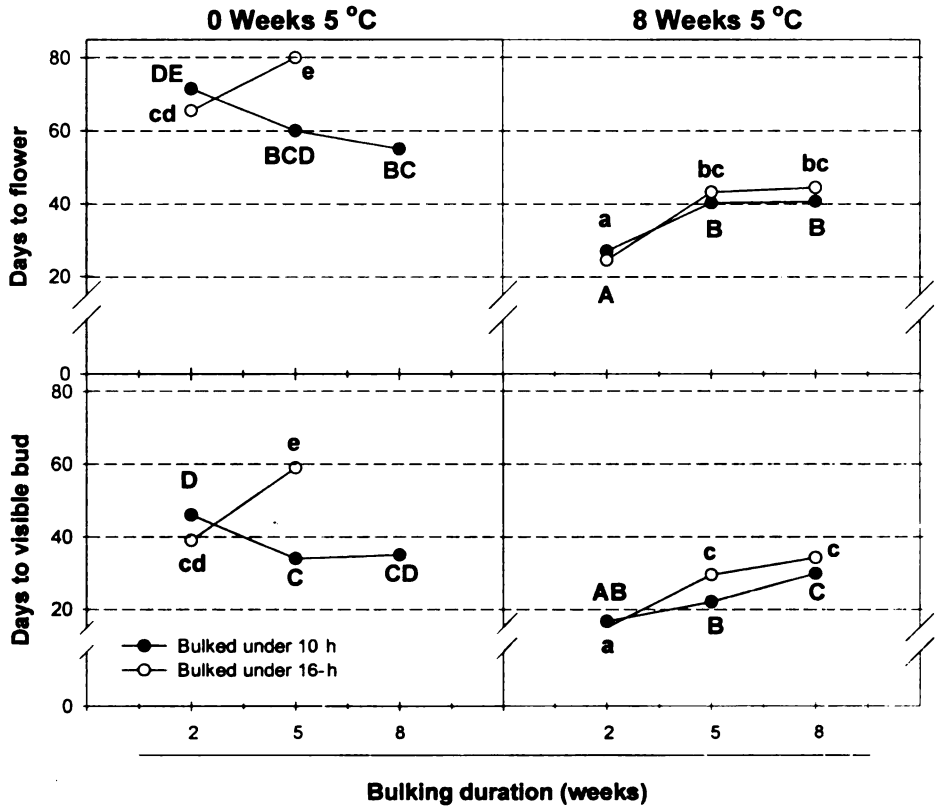


Figure 1. Flowering responses of *Coreopsis grandiflora* 'Early Sunrise' bulked for 2, 5, or 8 weeks under 10- or 16-h photoperiods, followed by 0 or 8 weeks of vernalization, during year 1 (2002). Data for days to visible bud (VB) and days to flower (FLW) are for the period from the start of forcing until visible bud and anthesis. Lower and upper case letters across graphs represent mean separation by LSMeans ($P \leq 0.05$) for days to VB or days to FLW under 10- or 16-h photoperiods, respectively.

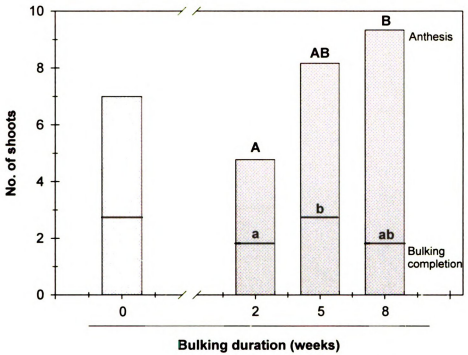


Figure 2. Shoot development responses of *Penstemon digitalis* 'Husker Red' bulked for 0, 2, 5, or 8 weeks during year 2 (2003). Lower and upper case letters represent mean separation by LSMeans ($P \leq 0.05$) for the number of primary shoots at bulking completion and at anthesis, respectively. For plants bulked 0 weeks, n=1.