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THE INFLUENCE OF COLD TREATMENT, PHOTOPERIOD, AND FORCING TEMPERATURE ON THE DORMANCY, GROWTH, AND FLOWERING OF HOSTA

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THE INFLUENCE OF COLD TREATMENT, PHOTOPERIOD, AND FORCING TEMPERATURE ON THE DORMANCY, GROWTH, AND FLOWERING OF *HOSTA*

By

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ABSTRACT

THE INFLUENCE OF COLD TREATMENT, PHOTOPERIOD, AND FORCING TEMPERATURE ON THE DORMANCY, GROWTH, AND FLOWERING OF *HOSTA*

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Studies were conducted to determine the influence of cold treatment, photoperiod, and forcing temperature on the dormancy, growth, and flowering of *Hosta.* Plants consisting of single-eye divisions were used in 1997-1998 resulting in small shoots with low flowering percentages. Larger plants used in 1998-1999 were more uniform and yielded higher flowering percentages. Each hosta clone was cooled for 0, 3, 6, 9, 12, or 15 weeks at 5 °C then forced in a 20 °C greenhouse under a short day (9-h) or long day (NI) photoperiod. The duration of cold required to break crown dormancy varied with genotype. Long days were required for continual vegetative growth followed by flowering, and short days induced dormancy of all clones. The response of *Hosta* to photoperiod duration was further evaluated by growing plants having received 0 or 15 weeks of cold under 10, 12, 13, 14, 15, 16, 24-h photoperiods or NI lighting. Cooled plants grown under ≤13 h emerged yet developed only a single flush of leaves and became dormant. Mature plants of all clones actively grew and flowered under photoperiods ≥14 h and NI. In a separate experiment, cold-treated plants were grown in greenhouse sections set at 14, 17, 20, 23, 26, or 29°C with 16-h day-extension lighting. Time to flower decreased as temperature increased. Plant height, average leaf size, and leaf color were adversely affected by high temperatures, and plant quality was greatest for plants grown at ≤23°C.

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LITERATURE REVIEW

Hosta originated in the eastern Asian countries of China, Korea, and Japan. Collectively, 25 to 40 species evolved in these countries, with the greatest differentiation occurring in Japan (Chung et al., 1991; Grenfell, 1996). Mountain valleys, forest margins, grasslands, and rocky soils and slopes are home to different *Hosta* species (Fujita, 1976a). The diversity of plants within *Hosta* makes them premier perennials for any location in the garden or landscape. Their versatility and adaptability to different soil moisture content allow survival under adverse conditions. Culturally, hostas thrive in varying degrees of sun and shade, require minimal care, and endure vast climatological differences. Combined, these characteristics have made *Hosta* the most popular herbaceous perennial for decades.

Evolution

The progenitors of *Hosta* are thought to be lilylike ancestors from which *Hosta plantaginea,* the most primitive species, evolved (Schmid, 1991). These predecessors likely migrated from the Chinese mainland south through Korea to southern Japan and north through southeastern Russia to northern Japan. Speciation then occurred in the diverse climate and ecology of Japan. Chung et al. (1991) hypothesize that, based on morphology and plant distribution, *H. venusta* is a recent derivative of *H. minor*. *Hosta venusta* may have originated from a population of *H. minor* that moved to Cheju Island, Japan from southeastern Korea after the last ice age. *Hosta jonesii* and *H. tsushimensis* may have developed from elements of *H. minor* as well. Evidence suggests Tsushima Island, Japan and mainland Korea were connected during the Pleistocene Age (Chung et al., 1991). The progenitor of *H. tsushimensis* may have migrated to Tsushima Island

during the ice age where it adapted and differentiated into an endemic species. Cytological studies by Kaneko (1968) suggest that *H. ventricosa* and *H. clausa* descended from a common prototype. Morphological divergence studies by Chung et al. (1991) indicate the Korean species, *H. minor*, *H. clausa*, *H. capitata*, and *H. yingeri* have been isolated reproductively for long periods.

Investigations into pollen morphology show *Hosta* pollen has evolved into five distinct types that aid in species delimitation (Schmid, 1991). *Hosta plantaginea* and *H. ventricosa* can be identified by a unique pollen type not found in other hosta species. Korean and Japanese hosta, however, have similar pollen types; thus, differentiation of Korean and Japanese taxa by pollen type is difficult.

Genome

A genome is the monoploid set of chromosomes (x) for a species that contains one of each chromosome (Poehlman and Sleper, 1995). The haploid, or gametic, chromosome number (n) and the basic genome, or chromosome set (x), of hostas is n = x = 30 (Kaneko, 1968; Yasui, 1935). Five of these chromosomes are large and 25 are small (Yasui, 1935). However, work by Yasui (1935) revealed that hosta chromosome sizes are not absolute, and gradations do occur. The somatic or diploid number (2n) of most hostas species is 2n = 2x = 60 (Kaneko, 1968; Yasui, 1935).

Kaneko (1968) found evidence of polyploidy in *Hosta.* The somatic cells of polyploids possess multiples of the plant genome in excess of the diploid number (Poehlman and Sleper, 1995). The haploid chromosome number in a polyploid series is a multiple of x and increases in an arithmetic ratio (Jones and Luchsinger, 1986). *Hosta*

clausa, a triploid species in which 2n = 3x = 90, and *H. ventricosa*, a tetraploid species in which 2n = 4x = 120, have been identified (Chung et al., 1991; Kaneko and Maekawa, 1968).

Evidence suggests that hostas are allopolyploids (Kaneko, 1968). Allopolyploid species originate from two or more genome combinations of distinctly separate species, whereas autopolyploids form by gene duplication of a single species (Poehlman and Sleper, 1995). Polyploids with an uneven genome number are infertile, as is *H. clausa* (Poehlman and Sleper, 1995; Yasui, 1935). Infertile pollen grains, a degeneration of the embryo sac, and an inability of the corolla to open contribute to sterility of *H. clausa* (Yasui, 1935).

Historical Overview

Chinese and Korean plant exchanges with Japan enabled the Japanese cultivation of many nonnative hosta species (Schmid, 1991). The Edo Period lasted from1603 to1867 and opened trade between Japan and the West, allowing European scientists, botanists, and plant explorers to acquire plant material (Schmid, 1991). Englebert Kaempfer was the first Westerner to describe and draw the likeness of a hosta; his illustrations were published in *Amoenitates Exoticae* in 1712 (Grenfell, 1996; Schmid, 1991). Following Kaempfer, Carl Thunberg first assigned species names to hosta specimens by using the Linnaeus system of binomial nomenclature and published *Flora Japonica* in 1784 (Bailey, 1930).

The actual introduction of plant material to Europe from Asia did not begin until the latter part of the eighteenth century. Seeds of the Chinese species *H. plantaginea*

arrived in France between 1784 and 1789 (Grenfell, 1996; Schmid, 1991). Live specimens of another Chinese species, *H. ventricosa*, along with *H. plantaginea* entered Europe in 1790 through the aid of Thunberg (Grenfell, 1996; Schmid, 1991). Later in 1829, Phillip von Siebold imported Japanese species to Holland (Grenfell, 1996).

According to plant listings from early nineteenth-century garden directories, hostas entered the United States around 1839 (Schmid, 1991). By 1850 the United States gained access to trade with Japan, and by 1861, direct shipments of hostas from the Japanese archipelago had occurred (Schmid, 1991). Plant exchanges with Europe enabled the selection of hostas in America to rival that of European countries by 1900. The use of the hosta in American gardens and landscapes increased after 1930 as more nurseries offered and specialized in hosta plant material (Schmid, 1991). During the 1960s and 1970s, an extensive group of enthusiasts, hybridizers, growers, and gardeners avidly collected plant material and began the introduction of new hosta cultivars (Schmid, 1991). The formation of the American Hosta Society in 1968 nationally promoted the versatility and appeal of hostas. The American Hosta Society also provided an authoritative means for proper cultivar registration with the objective of preventing name misuse and duplication (Jones and Luchsinger, 1986). New species and cultivar introductions continually renew interest in hostas and increase the popularity of these versatile plants.

Nomenclature and Classification

The classification of plants within *Hosta* has undergone numerous changes since the introduction of hostas to Europe. Botanists initially employed names that lacked

uniformity, which led to incoherent classifications and a complex synonymy. *Hosta* was the first unique genus name proposed by Leopold Trattinick in 1812 to honor botanist Nicholas Thomas Host (Bailey, 1930). Five years later the name *Funkia* proposed by Kurt Sprengel was embraced by several European countries as the common name for the genus (Grenfell, 1996; Schmid, 1991). The International Botanical Congress in Vienna eventually restored the name *Hosta* to the genus in 1905 (Schmid, 1991).

Phylogeny. The phylogenetic placement of *Hosta* has also undergone several revisions. Originally, *Hosta* was placed with *Hemerocallis* in Liliaceae (Bailey, 1930). Taxonomists, noting karyotypic similarities with *Agave*, later transferred the genus to Agavaceae. After further review, these findings were considered inconclusive, and *Hosta* was taxonomically classified in Funkiaceae (Dahlgren et al., 1985). Recently, Mathew placed *Hosta* in the monotypic Hostaceae (Watson and Dallwitz, 1992).

Species Classification. A biological species typically has been defined as a reproductively isolated natural population of plants with distinct morphological boundaries (Jones and Luchsinger, 1986; Schmid, 1991). With *Hosta*, however, a proper species concept has not been defined, thus complicating the classification process (Chung et al., 1991; Jones, 1989; Schmid, 1991). Furthermore, existing herbarium specimens often provide few diagnostic characters for proper species identification (Jones, 1989). However, Schmid's (1991) redefined species criterion recently declared many species to be cultivars. Figure 1 presents the current classification of *Hosta* species and their present habitat.

Reproduction

Hostas, except for *H. plantaginea*, are receptive to pollen early in the morning (Schmid, 1991). Because of morphological differences, the nocturnal-blooming *H. plantaginea* is naturally reproductively isolated from the day-blooming Korean and Japanese hostas. Japanese and Korean taxa readily hybridize unless geographical, ecological, or seasonal reproductive barriers prevent pollination (Jones and Luchsinger, 1986; Schmid, 1991). However, no absolute barriers prevent the movement and exchange of genes within *Hosta* species (Schmid, 1991).

Hybridization. Breeding systems are associated with levels of genetic variability in plant groups, and several mating systems allow for gene flow in *Hosta*. Both intraspecific and interspecific hosta hybrids are produced through hybridization, which involves the cross-pollination and subsequent fertilization of two taxa (Schmid, 1991). The female parent is the pod parent and produces seed, while the male parent provides the pollen for pollination. Generally, uncontrolled hybridization is accomplished through random insect or wind pollination (Schmid, 1991). High levels of phenotypic variation within *Hosta* result from a predominantly outcrossing breeding system, gene duplications, and high haploid chromosome numbers (Chung et al.,1991).

Hybrids also can be produced by hand through controlled hybridization. Hand-pollination is useful on reproductively isolated plants that do not flower simultaneously (Janick, 1986). Plants are artificially pollinated by mechanically transferring pollen from one plant to the stamen of another. Breeders attempt to incorporate fragrance, leaf substance, heat and sun tolerance, slug resistance, compactness, leaf and flower color,

variegation, and increased vigor into existing hosta genomes through controlled hybridization (Crockett, 1996). By manipulating the photoperiod, *Hosta* species and cultivars that do not naturally flower simultaneously can be induced to do so, thus making hybridization possible. High-pressure sodium (HPS) or incandescent lighting can extend the natural photoperiod to provide the day length requirement (≥14 hours) needed for hosta flower induction (Fausey, 1998; Finical et al., 1997). Night interruption (NI) lighting (3 to 5 μmol m^{-2} s^{-1} from 2200 to 0200) with incandescent bulbs in addition to a nine-hour natural day also induces flowering of hosta.

Hosta species overlap, interbreed, and hybridize in the wild to create self-sustaining natural populations (Schmid, 1991). These populations interbreed and commonly backcross to a parental type (Jones and Luchsinger, 1986). This process, called introgressive hybridization, occurs as genes from one hosta species mingle with another's, thereby creating an intermediate type (Jones and Luchsinger, 1986; Schmid, 1991). The abundance of variable intermediate types increases the complexity and difficulty of classifying true hosta species (Chung et al., 1991; Schmid, 1991).

Self-fertilization. Most hosta species are self-compatible, permitting fertilization after self-pollination occurs (Schmid, 1991). Isolated hosta populations in the wild perpetuate through self-pollination and fertilization aided by open insect pollination (Schmid, 1991). Self-pollination is the process by where pollen from an anther is transferred to a stigma within the same flower or on the same plant (Poehlman and Sleper, 1995). Self-fertilization occurs when a sperm and an egg gamete produced on the same plant unite to form a zygote (Poehlman and Sleper, 1995). Self-fertilization of wild populations

increases their homozygous state, yields uniform individuals, and can decrease plant vigor over time (Jones and Luchsinger, 1986; Schmid, 1991). Natural populations of the Korean species *H. capitata* are predominantly self-pollinated because of the lack of surrounding pollinators (Schmid, 1991). These populations display a lack of vigor and adapt poorly to adverse environmental conditions.

Over an extended time, homozygosity appears to affect the distance, or spatial separation, between the anther and stigma of most Korean and Japanese species (Chung et al., 1991; Schmid, 1991). This separation in highly self-pollinated and self-fertilized hostas is quite small. In some cases, pollination and fertilization occur before the flower opens. However, a pronounced distance between the stigma and the anthers may impede self-pollination and promote outcrossing (Chung et al., 1991).

Genetics

The morphological characteristics of hostas, except for variegation, follow the general rules of Mendelian genetics (Schmid, 1991); both parents equally contribute chromosomal DNA to offspring (Vaughn, 1982). Recessive traits in the F_1 generation can be expressed by selfing or backcrossing the F_1 progeny to the recessive parent, thus expanding the range of possible gene combinations in the F_2 progeny (Crockett, 1996).

Vaughn (1982) found that flower color, color intensity, and the size and shape of blossoms and leaves are controlled by multiple genes. In particular, two complementary genes control the production of anthocyanin, which determines flower color, in *Hosta*. The production of lavender flowers requires two dominant genes, yet only one recessive gene is required to produce white flowers. Other dominant traits include fragrance and

lavender petiole color.

Variegation

The occurrence of variegated hostas in the wild is uncommon and nonperpetuating without human intervention (Schmid, 1997). Variegation, however, is common among cultivated hostas. Variegated hostas are often periclinal chimeras in which tissue of one genetic type is surrounded by that of another. Variegation arises in somatic cells near the apical dome and results from plastid or nuclear DNA mutations that prevent normal chlorophyll synthesis (Vaughn, 1979; Schmid, 1991). These mutations are fairly unstable and eventually will rearrange to a more stable form. The Benedict's Cross (Figure 1) illustrates four stable chimeral forms of hosta arising from unstable or streaky variegated types (Schmid, 1991). Plants having unstable variegation will eventually revert to forms having monochromatic dark leaves, monochromatic light leaves, dark-margined leaves with a light center, or light-margined leaves with a dark center. However, unstable variegation can be maintained by removing shoots with stable variegation, thus preventing the more vigorous, stable shoots from dominating the plant's growth (Nash, 1998; Schmid, 1991).

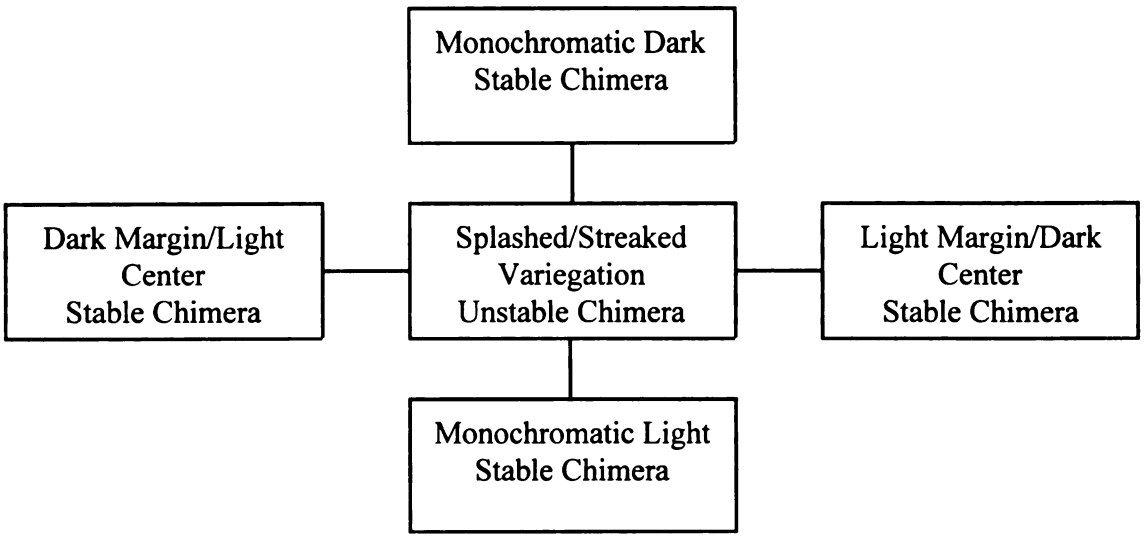

Figure 2. Benedict's Cross (Schmid, 1991).

Plastid Inheritance. Variegation is transferred maternally by plastids in the cytoplasm. The transfer process of cytoplasm and chloroplasts is a source of nonnuclear inheritance and is controlled by the female pod parent (Yasui, 1929). Plastid destruction occurs during pollen development in young pollen grain cells but does not occur in the female egg cell (Vaughn, 1979). Thus, the genetic composition of the plastid is transferred to progeny via the female pod parent.

Vaughn (1979) identified five unique classes of plastid mutants in *Hosta,* the marginata, mediovariegata, aurea, 'Snow Flurry', and mosaic. Marginata mutants have green leaves with white (albo) or yellow (aureo) leaf margins. When used as a pod parent, marginata mutants' progeny are green. Mediovariegated mutants have yellow or white central leaf tissue, and the resulting progeny are primarily yellow or white, depending on the original central leaf color. Seedlings of aurea (chartreuse to yellow) mutants are all aurea in color. Seedlings of selfed 'Snow Flurry' (white with green

flecks) emerge nearly all white and develop green sectors on the leaves. Backcrossing to 'Snow Flurry' provides white seedlings with green flecks or all-green plants. Mosaic mutants have no discernable color pattern, and self-fertilization gives a wide segregation of normal, variegated and mutant types.

Asexual Propagation

Today, over 2,500 named hosta cultivars exist (Chung and Kim, 1991). The term culton, or cultivar, applies to any member of a systematic group of cultivated plants whose origin or selection is due to the activities of mankind and is maintained for deliberate and continuous propagation (Schmid, 1996). A cultivar is distinguished by one or more characteristics and retains these distinguishing characteristics when reproduced sexually or asexually (Schmid, 1996; Zonneveld, 1997). Most *Hosta* cultivars and cultivated species do not come true from seed, except for the clonal seed of the apomictic *H. ventricosa* (Schmid, 1991). Neither variegation nor morphological characteristics are transferred reliably through sexual means. Therefore, hosta cultivars are propagated asexually or vegetatively to perpetuate their existence (Schmid, 1991). The most common forms of asexual propagation are rhizome divisions and tissue culture propagation. Interestingly, *H. clausa* reproduces asexually by rhizomes in the wild to compensate for inefficient sexual reproduction caused by unstable environmental conditions at flowering and seed set (Chung et al., 1991; Yasui, 1935).

Hosta Morphology

Form. Shape, height, and diameter combine to create a plant's overall form. Hostas typically have a mounding habit with fleshy, rhizomatous roots that form clumps (Schmid, 1991). A hosta clump can be classified into size categories by diameter and height. The diameter is measured from one lower leaf tip to another on the opposite side of the clump (Schmid, 1991). Diameters can range from fewer than four inches to more than several feet. Height also varies tremendously and can range from several inches to several feet.

Leaf Characteristics. A *Hosta* species cannot be identified solely by leaf characteristics; therefore, both vegetative and reproductive characteristics are used for proper *Hosta* identification and classification (Schmid, 1991; Schmid, 1997). Leaf characteristics are derived from mature hosta plantings to avoid developmental discrepancies found between juvenile and adult plants (Henson, 1984). According to Schmid (1991), a hosta is mature after six complete growing seasons.

Overall leaf shape is based upon the ratio of leaf blade length to width and includes the shape of the leaf base and tip. Leaves can be straplike (12:1), lance-shaped (6:1 to 3:1), ovate (2:1 to 3:2), heart-shaped (6:5), or round (1:1) (Schmid, 1991). Some hostas produce several leaf flushes within a year, while others such as *H.* 'Tokudama' produce only one (Schmid, 1991). Three different leaf types, vernal, juvenile, and summer, may originate from the same growing point of hostas that produce multiple flushes of growth (Schmid, 1991). Vernal leaves emerge in the spring following dormancy and are the first to mature. These leaves are used to determine leaf area, color,

texture, or shape (Schmid, 1991). Juvenile leaves emerge in late spring and, for some *Hosta*, are followed by a flush of summer leaves. Both juvenile and summer leaves are atypical of the mature leaf type (Schmid, 1991).

The positioning of veins within the leaf blade is important in the identification process. Hostas are monocotyledonous plants with parallel veins. Veins within the leaf blade curve outward from the base of the leaf as the blade widens and then curve inward as the blade narrows to the tip (Grenfell, 1996; Schmid, 1991). The number of vein pairs ranges from two to twenty and varies for leaves of different cultivars and species, and even for leaves on an individual plant (Grenfell, 1996; Schmid, 1991). An average number of veins is taken from several mature leaves on a single plant to determine the most accurate number of vein pairs present.

Hostas are identified according to primary and secondary leaf color. The primary leaf color covers at least 60% of the total leaf area, while the secondary color covers 40% or less and includes descriptions of marginal or streaky variegation (Schmid, 1991). Nonvariegated leaves do not have secondary coloration. The blue color of some hostas results from the bloom, a waxy, chalklike substance on the leaf epidermis (Schmid, 1991).

Leaf colors can be unstable and may change as a plant ages. Viridescence is a leaf's color change from white or yellow to green (Schmid, 1991). Heat-affected viridescence primarily occurs when daytime temperatures exceed 95°F (Pollack, 1997). Lutescence means green or chartreuse leaves change to yellow or whitish yellow, and albescence occurs when yellow or green leaves become white (Schmid, 1991). Blue leaves turn green when the leaf epidermal wax is lost through rain or when an increase in

the day and night temperature differential occurs (Hensen, 1984; Schmid, 1991).

Leaf surface describes texture and can be smooth and flat or rugose (Schmid, 1991). Rugose leaves have an uneven texture expressed through dimpling, puckering, pleating, and crinkling of the leaf surface and also may show cupping as the leaf edges turn upward (Schmid, 1991). Other variations in surface texture include wavy undulations, contortions, or piecrust and furrowed margins (Schmid, 1991).

Flower Stalk. The flower stalk, also called the scape, is another important means for species identification. Botanically, the flower stalk is a stem and not a scape because of the presence of modified leaves known as bracts (Pollack, 1997). The stalk of some species is horizontal, therefore, the stem length rather than height is measured (Schmid, 1991). The degree of stem foliation varies with species and cultivars. Some bracts are inconspicuous and tightly wrap about the stem, while others take on the appearance of true leaves. A hosta flower bud forms in a leaf axil where the leaf bract connects to the stem (Pollack, 1997). A fertile bract subtends a flower bud, whereas a sterile bract does not (Pollack, 1997).

Reproductive Structures. Typically, the reproductive features of a plant, not the vegetative features, are essential for proper identification and classification. The reproductive structures of the flower, the fruit, and the seed provide the basis for much of the classification of plants, especially that of *Hosta* (Jones and Luchsinger, 1986; Schmid, 1997). Hosta flowers are aggregated in an inflorescence called a raceme (Jones and Luchsinger, 1986; Watson and Dallwitz, 1992). A raceme is an arrangement of flowers

composed on a single main axis with pedicles, or short stalks, attached to each flower (Jones and Luchsinger, 1986; Watson and Dallwitz, 1992). The hosta inflorescence is indeterminate, meaning the flowering sequence begins at the base of the raceme and proceeds upward (Jones and Luchsinger, 1986).

Most flowers are funnel-shaped, bell-shaped, or possess a spiderlike form. For some *Hosta* such as *H. clausa*, the collective calyx and corolla, also known as the perianth, remain closed (Schmid, 1991; Yasui, 1935). Flower color ranges from the pure white of *H. plantaginea* to lavender and deep purple. These colors intensify in cooler climates and fade under warm conditions (Grenfell, 1996). The color of the anther of unopened flowers before pollen shed is yellow or purple for true species and bicolored for hybrids (Grenfell, 1996; Henson, 1984).

Hosta flowering occurs from early summer to late fall in North America and is species and cultivar dependent. Hostas can be grouped into general flowering categories: early season (before June 1), midseason (June 1 to July 15), mid- to late season (July 15 to September 1), and late season (after September 1) (Grenfell, 1996). Figure 3 illustrates the diverse flowering times of some Japanese *Hosta* in their native sites (Fujita, 1976b).

The hosta fruit contains many mature ovules, and seeds are borne in dehiscent, nonfleshy capsules (Schmid, 1991; Watson and Dallwitz, 1992). Hosta seeds are ovate and black when fertile, white when sterile (Schmid, 1991; Zonneveld, 1998).

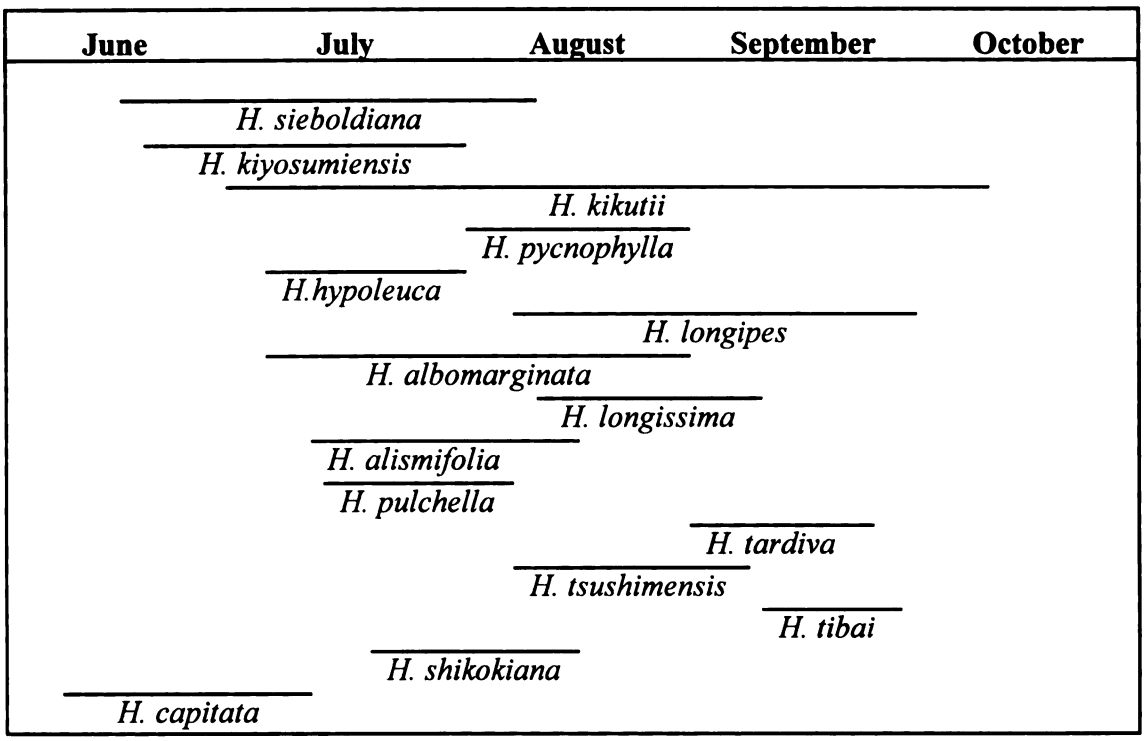

Figure 3. Flowering season of *Hosta* species in native sites (Fujita, 1976b).

Hostas in Thesis Experiments

In order to determine the effect of photoperiod, vernalization, and temperature on the development and flowering of *Hosta*, species and cultivars were selected to reflect the geographical distribution of their native habitat while acknowledging those plants important to the horticultural industry. All three subgenera, *Hosta*, *Bryocles*, and *Giboshi*, are represented. (A subgenus includes plant species that originated in the same geographical region [Jones and Luchsinger, 1986; Schmid, 1991]).

Subgenus Hosta. The first subgenus represented is that of *Hosta*, which solely includes *H. plantaginea* (Grenfell, 1996; Schmid, 1991). This hosta originated in southeastern China and has the most southerly native habit of any species (Schmid, 1991). *Hosta*

plantaginea was the first hosta to reach Europe, the first to receive taxonomic classification, and is a typic species--a specimen for which the genus name is permanently associated (Jones and Luchsinger, 1986; Schmid, 1991). It is referred to as the August lily and the plantain lily. Interestingly, it is prized as the only nocturnal flowering hosta with heavily fragrant, pure white blooms that produce abundant seed during warm, long summers (Grenfell, 1996).

Subgenus Bryocles. The subgenus *Bryocles* is represented by *H.* 'Golden Tiara' and *H.* 'Golden Scepter' (Schmid, 1991). *H*osta 'Golden Tiara' is a member of the Tiara group, which includes hybrids of *H. nakaiana* made by Robert Savory (Grenfell, 1996). *Hosta nakaiana*, the "ornamental hairpin hosta," evolved on the mainland of Korea. It is most closely related to and almost indistinguishable from another Korean hosta, *H. capitata* (Schmid, 1991). *Hosta* 'Golden Scepter' is a 1983 chartreuse sport of *H.* 'Golden Tiara', also made by Savory (Grenfell, 1996).

Subgenus Giboshi. The third subgenus, *Giboshi*, encompasses plant material from which many of today's most important hosta cultivars are derived (Schmid, 1991). 'Giboshi', the Japanese equivalent of the word 'hosta', also is subdivided into three groups (Group I, Group II, and Group III), each with section divisions (Schmid, 1991). (A section division assembles closely related species.)

Hostas in Group I are closely related to those in the Section Helipteroides originating in central to northern Japan (Grenfell, 1996). Members of this section include

H. montana, H. sieboldiana, H. 'Fortunei' and *H.* 'Tokudama' (Schmid, 1991). *Hosta montana* and *H. sieboldiana* are true species. *H.* 'Fortunei' and *H.* 'Tokudama' have been reduced from species classification to cultivar status (Schmid, 1991). *Hosta montana,* meaning "large-leaved hosta," is native to woodlands and forest margins and exhibits variable leaf form, variegation, and flower morphology (Grenfell, 1996; Schmid, 1997). Many plants offered as true *H. montana* are thought to be hybrids (Schmid, 1991).

Hosta 'Halcyon', a classic blue-grey hybrid, resulted from a cross made by Eric Smith and involved a late-flowering *H.* 'Elegans' and an early-flowering *H.* 'Tardiflora' (Grenfell, 1996). The first leaves to emerge from young clumps are characteristically lance-shaped and soon are followed by oval and eventually heart-shaped leaves as the clump matures (Grenfell, 1996).

Hosta 'Fortunei' encompasses a large group of sports and hybrids formerly cultivated in Europe (Schmid, 1991). *Hosta* 'Fortunei Hyancinthina' developed in von Siebold's garden and is considered to be a clone originally propagated in Holland (Schmid, 1991). *Hyacinthinus*, meaning violet, describes both the color of the leaves in early spring and the flower in summer (Schmid, 1991). Plant material is generally uniform and may produce fertile seed, though most seed is sterile (Grenfell, 1996). A white line traces the leaf edge of this cultivar, and plants are prone to bud mutations that produce variegated forms (Schmid, 1991).

The last hosta in the *Giboshi* subgenus is *H.* 'Tokudama'. The name means "well-rounded hosta" and describes the typical rounded leaf of the plant (Schmid, 1991). *Hosta* 'Tokudama' arrived in Europe around 1860 from plants Fortune received from von Siebold in Japan (Schmid, 1991). Tokudamas have been hybridized extensively in

cultivation, and most are considered similar clones with minor macromorphological differences (Schmid, 1991). They grow extremely slowly and are prone to variegation mutations.

Group III of the subgenus *Giboshi* includes two important hostas: *H.* 'Undulata', belonging to the Section Nipponosta A, and *H.* 'Lancifolia', belonging to the Section Tardanthae (Grenfell, 1996; Schmid, 1991). *Hosta* 'Lancifolia', meaning "little hosta," was reportedly the first hosta introduced into the United States (Schmid, 1991). Live plants first were sent to Holland by von Siebold in 1829 (Schmid, 1991). This ancient hybrid is sterile (Schmid, 1991). Live plants of *H.* 'Undulata,' meaning "striped hosta," also were imported by von Siebold around 1829 (Schmid, 1991). Clones of this pod-sterile hybrid of cultivated origin have unstable variegation, leaf forms, and flower scapes, especially on recently disturbed clumps (Schmid, 1991). The ratio of green to white tissue of *H.* 'Undulata' is 1:4. *Hosta* 'Undulata' eventually reverts to the all-green form, *H.* 'Undulata Erromena', after passing through the transitional *H.* 'Undulata Univittatal' (Vaughn, 1979).

Perennial Growth Habit

Hostas are perennial herbs with fleshy, rhizomatous root systems. The rhizome is a thickened underground stem composed of nodes and internodes from which root and shoot buds arise (Schmid, 1991). The rhizome functions as a perennating organ and enables a plant to survive unfavorable environmental conditions such as extreme temperature or severe water stress (Schmid, 1991). Hostas exhibit three rhizomatous growth types: stoloniferous and spreading, horizontal and tuberlike, or nearly vertical

(Schmid, 1991). The transitional area from the stem to the root system, including the rhizome, is called the crown. A division or section of the crown includes a fleshy bud plus the associated roots from which a new plant may arise. Hosta shoots emerge from buds that were formed in the leaf axils of the crown the previous growth season.

The Axillary Bud

The latent axillary bud of a hosta is an embryonic shoot consisting of an apical meristem, nodes, internodes, and leaf primordia enclosed within bud scales. Bud scales prevent desiccation, provide insulation, and restrict oxygen movement into the bud (Raven et al., 1992). Buds remain vegetative and slowly form leaf primordia while in this quiescent state.

Environmentally, the survival of perennial plants with rhizomatous growth is controlled by their ability to produce lateral shoots from existing axillary buds called reserve meristems (Stafstrom, 1995). Reserve meristems partially develop into shoots after a period of climate-induced dormancy. These meristems supplement existing shoots within a growing season by replacing shoots lost to herbivory, disease, or damage (Stafstrom, 1995).

Many buds, however, remain latent and are inhibited from emerging while the plant actively grows. This within-season dormancy is known as correlative inhibition (Stafstrom, 1995). By limiting shoot production through the inhibition of lateral buds, adequate food reserves stored in the rhizome allow future regenerative growth (McIntyre, 1990).

When plant foliage is destroyed, the resulting loss of leaf area may affect

carbohydrate reserves. Carbohydrate levels may decline, depending upon the time defoliation occurs within the growth season (Lubbers and Lechowicz, 1989). Plants can increase their photosynthetic rate to compensate for a loss in carbohydrate reserves. Additional compensatory growth by the parent shoot or previously latent buds may ensue; however, increases in leaf production in response to defoliation are at the expense of nutrients and carbohydrates stored in the rhizome (Archer and Tieszen, 1983). Consecutive defoliations of the graminoid *Eriophorum vaginatum* L. depleted the storage structure's reserves, resulting in a general decline in plant growth (Archer and Tieszen, 1983).

Correlative Inhibition of Lateral Buds

What factors promote or delay the outgrowth of hosta lateral buds? Shoot emergence from axillary buds is a correlative event and in *Hosta* is inhibited strongly by leaves and the flower stalk. Correlative inhibition involves the control of one plant part by another and is influenced directly or indirectly by leaves, shoots, inflorescences, or apices (Rubinstein and Nagao, 1976).

Inhibition by the Apex. The growing apex and apical portions of the shoot are partly responsible for inhibition of the outgrowth of axillary buds (Cline, 1991). This phenomenon is referred to as apical dominance, which controls a plant's growth and form; however, the degree of control varies among plant species.

The direct auxin theory of apical dominance contends auxin, as indole acetic acid (IAA), migrates from the apex down the stem and into the lateral buds, where it inhibits

growth (Cline, 1994). Excision of the growing point removes the source of auxin and growth of lateral buds ensues. Auxin's direct role in inhibition, however, remains unknown (Cline, 1991).

Inhibition by the Shoot and Stem. Smith and Rogan (1980) showed main shoot growth of quackgrass and that of axillary shoots, or tillers, are reciprocally suppressed. Axillary shoots impose a stress that inhibits main shoot growth and promotes tiller growth. In contrast, the removal of lateral buds or axillary shoots, also known as detillering, results in an increase in stem height, leaf number, and overall size of the main shoot.

A study by Clifford (1977) suggests that tiller buds of ryegrass, *Lolium multiflorum* Lam. cv. Westerwoldicum, are suppressed by auxin levels from adjacent internodes. A close source-sink relationship was identified between a leaf, the elongating internode below the leaf, and the tiller bud located in the leaf axil.

Inhibition by the Stem, Leaf, and Inflorescence. Immature, cotyledonary, and mature leaves inhibit lateral bud growth in dicotyledonous species during a plant's vegetative phase, while the inflorescence inhibits bud outgrowth during a plant's reproductive phase (Laidlaw and Berrie, 1974; Weiss and Shillo, 1988). Little research evaluating correlative inhibition by the leaves or inflorescence has been conducted with monocot species. It is suspected, however, that the mechanisms are similar (Smith and Rogan, 1980). For example, apical dominance is maintained in *L. multiflorum* by the apex and expanding leaves when the plant is vegetative (Laidlaw and Berrie, 1974). Upon flowering, apical dominance is released by excision of the young inflorescence. I

observed this phenomenon for *Hosta* as well (Fausey, 1998).

Weiss and Shillo (1988) evaluated the influence of the apex and young leaves on the inhibition of *Euphorbia pulcherrima* Willd. 'Brilliant Diamond' axillary buds. In this study, the apical bud or the immature, expanding leaves were removed (decapitation or defoliation, respectively) from a plant over a six-week period. Rapid lateral bud break occurred three to four days after defoliation. However, lateral bud break of decapitated plants was not visible until fifteen days after apical bud removal. The rate of shoot elongation also increased for defoliated plants compared with decapitated plants.

Weiss and Shillo (1988) also found that apical dominance in poinsettia is weakened upon transition to the floral phase. The three uppermost buds are released from inhibition, initiate floral buds, and develop into the inflorescence, while lower buds subtending the inflorescence remain inhibited. Removal of the poinsettia bract, cyathia, or both was compared to assess the source of axillary bud inhibition. The rate of lateral bud break depended on the organ removed. Rapid bud break followed by shoot elongation resulted with bract plus cyathia removal. Bract removal alone resulted in a similar yet slower response. Cyathia removal, however, resulted in fewer bud breaks that did not elongate. The authors concluded bracts and cyathia are the primary and secondary inhibitors of axillary bud outgrowth in poinsettia, respectively. Hosokawa et al. (1990) examined the inhibitory effects of upper shoot tissues, the apex, expanding leaves, and the stem segment of *Ipomoea nil* L. on lateral bud outgrowth. The apical region inhibited bud growth more than the basal portion, while the stem segment had as strong an influence on apical dominance as the upper leaves.

A synergistic effect on lateral bud growth also was identified between apex

removal and defoliation of *I. nil* (Hosokawa et al., 1990). The apical stem segments of all plants were removed. Subsequent defoliation resulted in a six- to seven-fold increase in lateral bud outgrowth after seven days compared with that of nondefoliated plants. The presence of leaves fewer than 5 cm in length inhibited lateral bud outgrowth, with smaller leaves having a greater control over growth. Results suggested the ability for small leaves to expand may be associated with their ability to inhibit bud growth.

Similarly, McIntyre and Hsiao (1990) showed fully expanded leaves inhibited growth of axillary buds located on the root and the shoot of common milkweed, *Asclepias syriaca* L. Stem decapitation and defoliation synergistically increased bud length compared with either used alone. The total bud lengths for decapitated, defoliated, and decapitated plus defoliated plants were 22.1 mm, 48.2 mm, and 154 mm, respectively.

Theron et al. (1987) identified two primary sources of bud inhibition in *Malus domestica* Borkh 'Granny Smith' trees. They reported buds were inhibited by either a decrease in the age of a subtending leaf or an increase in bud age. In contrast, axillary buds of *Rosa* are correlatively inhibited by mature leaves and stem tissue located above the bud (Zieslin and Halevy, 1976). Zieslin and Halevy (1976) pruned seven-node *Rosa hybrida* 'Baccara' branches to the fourth node. Buds located at the fourth node sprouted following pruning and removal of their subtending leaf. In contrast, stem segments with attached leaves above the fourth node did not sprout.

Inhibition by Scale Leaves. Quackgrass bud-scale leaves suppress bud development by producing an inhibitory substance (Robertson et al., 1989). Robertson et al. (1989) reported bud suppression limits the competition for nutrients between the bud and the

apex. Denudation of rhizome buds, however, removed the inhibitory growth factor and temporarily allowed bud growth.

Environmental Effects

Lateral bud development ultimately depends upon the environmental conditions imposed upon a plant. In *Hosta,* heavy fertilization, increased light levels, and copious amounts of water promote new flushes of growth from reserve meristems (Pollack, 1998). The degree of lateral bud outgrowth is influenced by interactions involving light quality and quantity, moisture availability, and nutritional levels.

Light Quantity. Light duration affects many aspects of plant development, such as flower initiation and dormancy. Plants are classified as long-day, short-day, or day-neutral according to their light and dark requirements within a 24-hour period. Short-day plants require longer dark periods, while long-day plants require shorter ones to achieve a particular response. Day-neutral plants are not affected by day length.

Climate-induced dormancy of many woody species and herbaceous perennials is promoted by short photoperiods (Stafstrom, 1995). Exposure to short photoperiods alters the developmental pathway of shoot meristems, resulting in a shift from production of vegetative leaves to bud scales (Villiers, 1975). Therefore, many herbaceous perennials require long day lengths to promote vegetative growth and induce flowering. In *Hosta*, flower induction occurs under photoperiods longer than or equal to fourteen hours, and vegetative leaf production terminates as the apex differentiates into a flower. Once flowering ensues, surrounding buds at the base of the flower stalk or on the crown are

released from apical control and are capable of growing under favorable conditions (Pollack, 1998).

Light Quality. Plants respond not only to light duration, but also to its spectrum (Thomas and Vince-Prue, 1997). Plant responses to the far-red to red (FR/R) ratio affect apical dominance with red light (R) from 600 to 700 nm, weakening dominance, and far-red light (FR) from 700 to 770 nm, strengthening dominance (Cline, 1991). Thus, a high FR/R ratio reduces lateral branching and promotes stem elongation (Smith, 1994).

Kasperbauer and Karlen (1986) investigated the effect of the FR/R ratio on the tillering of wheat, *Triticum aestivum* L. cv. Coker. Field-grown wheat at high densities averaged 2.9 tillers compared to that of widely spaced plants, which averaged 14. Kasperbauer and Karlen (1986) hypothesized that the reduction in tillering of closely spaced plants resulted from a higher percentage of FR light within the plant canopy. Further studies examined the effects of FR/R on tillering, leaf length, and the root-to-shoot biomass of wheat (Kasperbauer and Karlen, 1986). Exposure to FR light reduced the number of tillers per plant and increased the leaf length and the root-to-shoot biomass of wheat compared with the R light treatment.

Effects of Water, Relative Humidity, and Nutrition. *Hosta* cultivars commonly have several flushes of leaf growth or division increases within a single growing season. Midseason growth flushes in plants can be attributed to water regulation and starch breakdown by the roots (Stafstrom, 1995). Water potential also may affect lateral bud outgrowth since an increase in water supply often coincides with bud extension growth.

McIntyre (1990) hypothesizes the reduction in bud inhibition at high relative humidity results from a reduction in transpiration, which increases the water potential of the parent shoot. This theory is supported by the fact that lateral bud inhibition was prevented in quackgrass rhizomes grown under 100% relative humidity (McIntyre, 1990). However, reducing relative humidity to 98% resulted in the inhibition of the first five buds on the rhizome. Inhibition was completely eliminated when water was supplied freely to the rhizome.

Another theory postulates that correlative inhibition is based on an internal competition for nutrients between plant organs (Cline, 1991). The growing apex commands dominance by acting as a sink for nutrients that are diverted from other plant organs. After apex decapitation, lateral buds become new sites for nutrient accumulation. The theory holds the primary requirement for bud outgrowth is nutrient availability in the vicinity of the bud.

The most critical inorganic nutrient contributing to the growth and morphogenesis of axillary buds is nitrogen. Exposure to high nitrogen concentrations often promotes outgrowth of axillary buds in many species (McIntyre, 1990). McIntyre and Hsiao (1990) reported the inhibition of common milkweed axillary buds was released by increasing the nitrogen supply from 21 to 210 $mg \cdot L^{-1}$.

Methods to Increase Division of Hosta

Principles of correlative inhibition and apical dominance can be applied to existing production methods within the horticultural industry. Both chemical and mechanical methods to increase the number of plant divisions can be implemented by

growers and plant producers.

Mechanical Methods. A current method to increase shoot growth of *Hosta* is to remove the foliage and flower stalk when the flower stalk emerges (Schmid, 1991). This technique promotes lateral bud break and allows additional shoot growth. Alternatively, hosta leaves can be mowed 1/4 to 1/2 inch above the ground to elicit lateral shoot growth from latent buds (Grenfell, 1996). This bulking technique increases the number of shoots per plant and can be performed two times during a single growing season (Grenfell, 1996). Unlike mowing, the Ross method does not inhibit plant growth by removing actively photosynthesizing leaves. Instead, incisions in the rhizome induce division formation (Schmid, 1991). This technique is performed by inserting a sharp knife into the crown of a hosta plant and is favored by hosta gardeners because of its simplicity and effectiveness (Grenfell, 1996).

Chemical Branching Agents. Many chemical branching agents successfully promote lateral branching. Maleic hydrozide, fluorenols, fatty acid esters, and ethephon release axillary buds from inhibition by inhibiting the terminal bud (Cline, 1991). I observed the ethylene-releasing substance Florel effectively promoted lateral bud break of *Hosta* (Fausey, 1998).

Cytokinins. Cytokinin and cytokinin /gibberellin combinations can promote lateral branching of *Hosta* successfully. Cytokinins are synthesized primarily in root tips and are involved in cell division, promotion of shoot formation, delay of leaf senescence, and

release of apical dominance (Cline, 1991; Letham, 1994). Cytokinins interact with auxin to promote lateral bud growth when apical dominance is lessened or broken and auxin levels in the bud decline (Cline, 1994). Exogenous applications of cytokinin can induce endogenous cytokinin synthesis (Letham, 1994). King and van Staden (1988) suggest lateral bud response to exogenous cytokinin depends upon the capacity of a bud to use cytokinin.

Keever (1994) applied different rates of benzyladenine (BA) to *H. sieboldiana* to promote growth from axillary and rhizomic buds. No offsets formed on untreated plants; however, offset production increased with increasing rates of BA and was similar between foliar and drench applications. Additional work determined the optimum drench and foliar spray rate for plant growth was 40 mg BA/pot and 3000 ppm, respectively (Keever, 1994).

Garner et al. (1997) further examined the effect of foliar BA applications on ten *Hosta* cultivars and found that the cultivars responded differently in their ability to form offsets. Control plants of several cultivars readily formed offshoots without a BA application, yet others relied heavily on exogenous BA.

Garner et al. (1998) also evaluated the effects of multiple BA applications and repeated removal of offsets on single-eye divisions of *H.* 'Francee' and *H.* 'Frances Williams' at thirty-day intervals. The authors found that offset yields increased linearly with subsequent BA applications and repeated applications were necessary to achieve a continual increase in offset number.

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The Genus *Hosta*

A listing of Subgenera, Sections, and Species

Subgenus *Hosta* China	**Subgenus *Bryocles*** China/Korea	**Subgenus *Giboshi*** Japan		
		Group I	**Group II**	**Group III**
H. plantaginea	**Section *Eubryocles*** *H. ventricosa*	**Section *Helipteroides*** *H. crassifolia* *H. fluctuans* *H. montana* *H. nigrescens* *H. sieboldiana*	**Section *Picnolepis*** *H. aequinoctiiantha* *H. hypoleuca* *H. longipes* *H. okamotoi* *H. pulchella* *H. pycnophylla* *H. rupifraga* *H. takiensis*	**Section *Nipponosta A*** *H. atropurpurea* *H. callianthia* *H. clavata* *H. ibukiensis* *H. rohdeifolia* *H. sieboldii*
	Section *Lamellatae I* *H. capitata* *H. nakaiana*	**Section *Rynchophorae*** *H. kikutii* *H. shikokiana*		**Section *Nipponosta B*** *H. alismifolia* *H. rectifolia*
	Section *Lamellatae II* *H. minor* *H. venusta*	**Section *Intermediae*** *H. densa* *H. kiyosumiensis* *H. pachyscapa*		**Section *Nipponosta C*** *H. longissima*
	Section *Arachnanthe* *H. laevigata* *H. yingeri*			**Section *Tardanthae*** *H. cathayana* *H. gracillima* *H. jonesii* *H. takahashii* *H. tardiva* *H. tibae* *H. tsushimensis*
	Section *Stoloniferae* *H. clausa*			

Figure 1. Classification of *Hosta* (Grenfell, 1996).

SECTION II

THE INFLUENCE OF COLD-TREATMENT DURATION AND PHOTOPERIOD ON DORMANCY, GROWTH, AND FLOWERING OF *HOSTA*

The influence of cold-treatment duration and photoperiod on dormancy, growth, and flowering of *Hosta*.

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Production and Culture

The influence of cold-treatment duration and photoperiod on dormancy, growth, and flowering of *Hosta*.

Additional index words. Maturity, long-day plant, plantain lily, herbaceous perennial.

Abstract. Many dormant plants require a cold treatment to break vegetative dormancy and continue growth. Plants may also require cold for flower induction or to improve plant vigor and flowering characteristics. The cold requirement to break dormancy of *H. montana*, *H. plantaginea*, *H.* 'Golden Scepter', *H.* 'Golden Tiara', *H.* 'Hyacinthina', *H.* 'Lancifolia', *H.* 'Royal Standard', *H.* 'Tokudama' gold, *H.* 'Tokudama' green, and *H.* 'Undulata' clones was determined by exposing plants to 5°C cold for 0, 3, 6, 9, 12, or 15 weeks. Following cold treatment, plants were grown at 20°C under a 9-h photoperiod (short days) or with a 4-h night interruption from 2200 to 0200 (long days) in 1997-1998 and only under long days in 1998-1999. Plants consisting of single-eye divisions were used in 1997-1998 resulting in small shoots with low flowering percentages. Larger plants used in 1998-1999 were more uniform with higher flowering percentages. Hosta clones required 0, 3, or 6 weeks of cold for 100% emergence of all plants in both years. Noncooled and cooled plants grown under short days emerged and went dormant irrespective of cold-treatment duration. Cold was not required for flowering of hosta clones, and noncooled and cooled plants grown under long days actively grew and flowered.

INTRODUCTION

Herbaceous and woody perennial plants persist from season to season by experiencing a resting period known as dormancy during the winter. Perennials enter a dormant state when physiological or environmental factors temporarily suspend visible growth of plant structures containing meristems (Lang et al., 1987). Three specific dormancy types exist (Lang et al., 1987). Ecodormancy is regulated by unsuitable environmental factors that directly prevent growth. Paradormancy occurs when physical or biochemical factors are produced in the plant but are external to the dormant tissue. Endodormancy, often referred to as rest, results from physiological factors produced inside the dormant structure.

Dormancy is often accompanied by the formation of specialized structures in woody and herbaceous plants. Many herbaceous perennials form underground storage tissues that enable survival following exposure to extreme environmental conditions such as cold, heat, or drought when in a dormant state. The resting structure of hosta is called the crown and enables the plant to survive to USDA hardiness zone 3 where winter air temperatures may reach - 30 to -40°F (-34 to -40°C). The crown also enables hosta to survive summer temperatures above 95°F by entering a state of heat dormancy (Solberg, 1997).

Plants synchronize and optimize their growth and development according to environmental signals. The onset of dormancy and the formation of storage organs are inductive processes triggered primarily by seasonal fluctuations in daylength (Jones, 1992). The critical daylength necessary to induce these processes can vary between broadly distributed species and ecotypes of species as daylength varies considerably with

latitude. A plant's local environment is impacted by temperature and water availability which also play a role in initiating these processes.

Continuous exposure to inductive photoperiods are required by many plants to enter a state of true dormancy (Thomas and Vince-Prue, 1997). Many plant species enter a transitional state when initially exposed to a short series of inductive photoperiods. This transitional state can be reversed by noninductive photoperiods until continued exposure to inductive photoperiods renders the plant fully dormant. Long days may prevent or delay dormancy whereas short days hasten dormancy of alpine and woody temperate plants. In contrast, long photoperiods interact with high temperatures to induce summer dormancy of many herbaceous perennials including *Anemone coronaria*, a geophyte native to hot, dry Mediterranean regions (Ben-Hod et al., 1988). In some cases when plants prematurely enter dormancy before an inductive photoperiod is perceived endogenous factors override the need for an appropriate daylength (Thomas and Vince-Prue, 1997).

Periods of low temperatures may be required by some plants to continue growth and development. The thermoninductive temperatures required for flowering are often species and cultivar-specific. These temperatures range from below freezing to 16°C with an optimum range of 1 to 7°C for most cold-requiring plants (Lang, 1965; Roberts and Summerfield, 1987).

Exposure to cold temperatures affects plant development in several ways. Many dormant woody and herbaceous perennials require sufficient periods of low temperatures to break dormancy of vegetative or reproductive buds to resume growth or flowering. When dormancy is fully broken, the resumption of growth is usually independent of

photoperiod (Thomas and Vince-Prue, 1997). For example, six weeks of cold were required to break crown dormancy of *Platycodon grandiflorus* 'Mariesii', and 12 weeks of cold were required to break rhizome dormancy and achieve complete emergence of *Lysimachia clethroides* under 8, 12, and 16 h photoperiods (Iversen and Weiler, 1994). Cold exposure also increased the rate of emergence of both species. Although cold was not required for long day flower induction of *Lysimachia clethroides* under 12 and 16 h photoperiods, six weeks of cold were required for flowering of *Platycodon* under all photoperiods.

Cold temperatures may also be required by plants for vernalization, the induction of flowering by low temperatures. The requirement for vernalization is commonly found in long-day plants (LDP) and is followed by a requirement for long-day photoperiods (Napp-Zinn, 1984). For plants with an obligate vernalization requirement, flower initials form only after vernalization is complete and differentiate into floral organs when the plant is exposed to warmer growing conditions (Thomas and Vince-Prue, 1997). *Campanula persicifolia* and *Lavandula angustifolia* did not require cold for vegetative growth but required cold for inflorescence development (Iversen and Weiler, 1994; Whitman et al., 1996). Cold temperatures may also reduce the critical photoperiod of a species or eliminate it's photoperiodic requirement for flowering (Thomas and Vince-Prue, 1997). The critical photoperiod for *Rudbeckia fulgida* 'Goldsturm' shifted from 14 h prior to cold to 13 h following cold treatment (Runkle et al., 1999). *Leucanthemum* x*superbum* 'Snowcap' performed as a qualitative LDP prior to cold and a quantitative LDP following cold (Runkle et al., 1998a).

Finally, plants may exhibit a facultative response to cold. In this case, cold is not

absolutely required but accelerates growth and improves plant quality and uniformity. Cold was not required to break vegetative dormancy or for floral development of *Phlox* 'Fairy's Petticoat' and *Phlox paniculata* 'Eva Cullum'; yet exposure to cold accelerated flower development, increased plant height, and improved overall vigor (Iversen and Weiler, 1994; Runkle et al., 1998b).

Few researchers have investigated the effect of cold temperatures and photoperiod on *Hosta* dormancy, growth, and development. The regrowth of field-grown *Hosta* 'Honeybells' crowns stored at -10, -5, -2, 2, or 5°C for six months varied among the temperatures examined (Maqbool and Cameron, 1994). Plants stored at -10°C for six months failed to regrow, and regrowth was poor with reduced survival and plant height for plants stored at -5°C. However, plant growth after storage at -2, 2, or 5°C was not impacted by exposure to cold temperatures. Improved emergence, growth, and flowering of *Hosta* 'Francee' occurred when dormant divisions received 15 weeks of 5°C compared with noncooled divisions (Finical et al., 1997).

Hosta is comprised of 40 species native to China, Korea, and Japan and contains over 2,500 named cultivars (Chung and Kim, 1991). Because of the large diversity within *Hosta*, the objectives of this research were to determine the amount of cold necessary to break vegetative dormancy of a diverse group of hosta clones and to determine the effects of cold temperature on vegetative and reproductive growth characteristics.

MATERIALS AND METHODS

Plant material. *1997-1998.* Hostas were received from commercial producers (Table 1) in fall 1997 and were separated into single-eye divisions. Divisions were placed upright into 23 x 15 x 7 cm (6.8 L) bulb crates or planted individually in 13-cm (1.1 L) square containers filled with a commercial soilless medium composed of composted pine bark, vermiculite, Canadian sphagnum peat, and coarse perlite with a wetting agent, lime, and starter fertilizer charge (High Porosity Mix, Strong-Lite Products, Pine Bluff, AR). Potted divisions were placed directly in a glass greenhouse, while bulb crates were placed in a cooler set at 5°C. Plants were watered as required with well water acidified with citric acid to a pH of 6.0. Divisions were removed from the bulb crates after 3, 6, 9, 12, or 15 weeks of cold, planted into 13-cm square containers as described above, and placed in the greenhouse.

1998-1999. Hostas from the 1997 experiments were grown outdoors from May 15 to October 16, 1998 in 13-cm (1.1 L) square containers under 50% shade created by alternate strips of wood lath at the Michigan State University Horticultural Teaching and Research Center, East Lansing, MI. An exception was *Hosta* 'Royal Standard' where single-eye divisions were taken from 3 year-old crowns grown in 8-cm (350 ml) containers. Plants showed visible signs of dormancy (leaf senescence) and had the foliage removed prior to first frost on October 16, 1998. Pots were placed in a 20°C glass greenhouse or in a cooler at 5°C for 0, 3, 6, 9, 12, or 15 weeks.

Following cold treatment, plants were placed under a 9-hour short day (SD) or a 9-hour plus 4-hour night interruption (NI) in 1997, but only under NI in 1998. Plants were covered with opaque black cloth from 1700 to 0800, and NI lighting was provided

from 2200 to 0200 with 60-W incandescent lights delivering 3 to 5 μmol $m^{-2}s^{-1}$.

General Procedures. Plants were fertilized at every irrigation with a nutrient solution of well water (EC of 0.70 $mS \cdot cm^{-1}$ and 105, 35, and 23 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively) acidified with H_2SO_4 to a titratable alkalinity of 130 $mg \cdot L^{-1}$ $CaCO_3$ and water soluble fertilizer providing 125-12-125-13 N-P-K-Ca $mg \cdot L^{-1}$ (30% ammonical N) plus 1.0-0.5-0.5-0.5-0.1-0.1 (Fe, Mn, Zn, Cu, B, Mo) $mg \cdot L^{-1}$ (MSU Special, Greencare Fertilizers, Chicago, IL).

Four-hundred-watt high-pressure sodium (HPS) lamps provided a photosynthetic photon flux (PPF) of 100 $\mu mol \cdot m^{-2}$ s^{-1} when the ambient greenhouse PPF dropped below 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from 800 to 1700. Supplemental lighting was terminated when PPF exceeded 400 $\mu mol \cdot m^{-2}$ s^{-1}. In 1998, the average daily light integral was measured with a quantum sensor (LI-COR) connected to a CR-10 datalogger (Campbell, Scientific, Logan, UT). Greenhouse air temperature was monitored on each bench with 36-gauge type E thermocouples connected to a CR-10 datalogger (Campbell, Scientific, Logan, UT). Temperatures and light measurements were collected every 10 seconds and the hourly average recorded. Supplemental heat was provided at night as needed to maintain 20°C by 1500-W electric heaters (Model T771, Rival Manufacturing Co, Sedalia, MO) located under each bench. In 1998, the average daily temperature and daily light integral from force to flower for each species and cultivar were calculated for each cold treatment (Table 2).

Experiments were conducted in the Plant and Soil Sciences Research Greenhouses at Michigan State University, East Lansing, MI. The experiment was a factorial design

study with two factors, photoperiod and cold duration, in 1997-1998. In 1998-1999, the experiment only examined one factor, cold duration. Each treatment was completely randomized with ten replications in both years. Unless otherwise indicated, the greenhouse air temperature was a constant 20°C. All plants were forced under the specified treatments for fifteen weeks.

Data collection and analysis. Emergence and flowering percentages were calculated for each hosta clone in both years. Flowering percentages were calculated as the number of flowering plants divided by the number of emerged plants in each treatment. The date of visible flower bud was collected for all reproductive plants; the date of flower anthesis, plant height (cm), inflorescence height (cm), flower number, scape leaf number, leaf number, and shoot number were collected when the first flower opened. Plant height, leaf number, and shoot number were collected for nonreproductive plants fifteen weeks after forcing. Leaf area was taken on all plants fifteen weeks after the start of forcing with a LI-300 portable leaf area meter (LI-COR, Lincoln, NB).

Days to visible bud, days to flower, and days from visible bud to flower were calculated for all reproductive plants. Data were analyzed using SAS's (SAS Institute, Cary, NC) analysis of variance (ANOVA) and general linear models (GLM) procedures.

RESULTS

General responses. Emergence of dormant plants when grown under short-day photoperiods depended upon the cold-treatment duration and genotype. Of those that did emerge following cold, plants developed only one flush of leaves and then became

dormant irrespective of cold treatment. Growth under long-day photoperiods was more vigorous and, depending upon cold duration, led to flowering.

Plants grown under long-day photoperiods in 1997-1998 were significantly smaller with lower flowering percentages compared to plants grown in 1998-1999 (Figures 1B; 2B, F; 3B; 4B, F; 6B, F). Plant height, average leaf size, and flower number were generally greater for plants grown in 1998-1999 than in 1997-1998 (Table 3). Time to visible bud and time from visible bud to flower were generally less in 1998-1999 when compared to 1997-1998 (Table 4). Time to flower for all hosta clones decreased or did not change between years (Figures 1C; 2C, G; 3C; 4C, G; 6C, G). The following results and discussion are based upon growth and development of plants grown under the long-day photoperiod in 1998-1999 because plants under these experimental conditions were larger and more typical of established hostas.

Cold requirement for emergence. Each hosta clone evaluated in this study was placed in one of three categories based on the cold requirement for 100% of the plants to emerge from dormancy. These categories were 0, 3, or 6 weeks of cold (Figure 1A, E; 2A, E; 3A; 4A, E; 5A; 6A, E). A smaller percentage of plants in each category emerged with less cold.

H. plantaginea, 'Royal Standard', and 'Lancifolia' did not require a cold treatment to break dormancy. Essentially all plants emerged and actively grew after exposure to any cold duration, including none (Figure 1A, E; 2A). Both *H. plantaginea* and 'Royal Standard' plants receiving no cold displayed more vigorous growth than cooled plants as evidenced by maximum plant height and average leaf size (Figure 1D, H;

Table 4).

A diverse group of hosta clones required at least three weeks of cold to achieve complete emergence of all plants. This group included 'Golden Scepter', 'Golden Tiara', 'Hyacinthina', *H. montana*, and 'Undulata'. Greater than 50% of *H. montana* and 'Undulata' plants (Figure 3A, E), a smaller percentage of 'Golden Scepter' and 'Golden Tiara' plants (Figure 4A, E), and no 'Hyacinthina' plants (Figure 5A) emerged without exposure to cold temperatures. However, each clone displayed increased vigor following 3 weeks of cold.

H. 'Tokudama' gold and 'Tokudama' green required six weeks of cold for 100% emergence (Figure 6A, E). One 'Tokudama' gold and one 'Tokudama' green plant did emerge without cold, and emergence rates for both cultivars were 40% after exposure to 3 weeks of cold.

Vegetative and reproductive characteristics. The flowering characteristics of noncold-requiring hosta clones varied with cold treatment. Flowering percentage of *H. plantaginea* was less than or equal to 50% for each cold treatment (Figure 1B). Flowering of *H. plantaginea* did not occur when plants were exposed to 3 weeks of cold although some plants flowered when exposed to 0 or 6 weeks of cold. Maximum flowering occurred after plants were exposed to 9 or more weeks of cold. Ninety percent of 'Royal Standard' plants flowered with six weeks of cold, yet other cold treatments yielded lower flowering percentages ($\leq$40%) (Figure 1F). All 'Lancifolia' plants flowered after 9 or more weeks of cold (Figure 2A). Time to flower increased 10 days for 'Lancifolia' (Figure 2C) after 3 weeks of cold then declined slightly with further cold.

Days to visible bud decreased and days from visible bud to flowering increased for 'Lancifolia' with increasing cold duration (Table 5). Cold duration did not affect days to visible bud, days to flower, or days from visible bud to flower for either *H. plantaginea* or 'Royal Standard' (Figure 1C, G; Table 5).

Cold-treatment duration affected the average height and leaf size of 'Lancifolia', *H. plantaginea*, and 'Royal Standard' plants. Plant height and average leaf size increased 33 and 36%, respectively for 'Lancifolia' plants exposed to 15 weeks of cold (Figure 2D; Table 4). However, *H. plantaginea* and 'Royal Standard' plant height decreased 6 to 8 cm from a maximum for noncooled plants to a minimum after 15 weeks of cold (Table 6). Average leaf size of *H. plantaginea* varied considerably for noncooled and cooled plants (Figure 1D), and 'Royal Standard' average leaf size declined after 15 weeks of cold (Figure 1H). Potted 'Royal Standard' crowns were dry when removed from the cooler after 9, 12, and 15 weeks of cold and were slow to initiate growth when placed in the greenhouse. This may account for the unusually low vigor and flowering percentage of 'Royal Standard' plants compared with *H. plantaginea* plants exposed to 9, 12, and 15 weeks of cold.

The flowering percentages of hosta clones requiring 3 weeks of cold for complete emergence varied with cold duration. The flowering percentage of *H. montana* generally increased with cold but never exceeded 60% (Figure 3A). Flowering of noncooled 'Undulata' plants was 14% and increased with cold but never exceeded 80% (Figure 3E). Flowering of all 'Hyacinthina' plants occurred after 12 or more weeks of cold (Figure 5A). Flowering percentage of emerged 'Golden Scepter' plants ranged from 60 to 100%, while flowering of 'Golden Tiara' reached 100% for plants in all treatments (Figure

4A,E). In 1998-1999, 40% of 'Golden Scepter' plants failed to flower after fifteen weeks of cold. These plants appeared to be in a vegetatively dormant state for much of the forcing duration and did not produce a second flush of growth commonly observed in plants belonging to the 'Tiara' series (Pollock, 1997).

Time to flower generally decreased with increasing cold for most clones. However, days to visible bud, days to flower, and days from visible bud to flower were not affected by cold duration for the *H. montana* plants that flowered (Figure 3C, Table 5). Time to visible bud and flower increased for 'Undulata' (Figure 3G) after 3 weeks of cold then declined slightly with further cold. Time to flower decreased 5 weeks for 'Hyacinthina', 2 weeks for 'Golden Tiara', and 6 weeks for 'Golden Scepter' as cold duration increased from 0 to 15 weeks (Figure 4C, G; 5C). The decrease in time to flower is primarily attributed to a decrease in time to visible bud and a decrease in time from visible bud to flower (Table 5) as forcing temperature only increased slightly as cold duration increased (Table 2). The average daily light integral may have contributed to the decrease in time to flower as light levels more than doubled for plants having received 15 weeks of cold versus noncooled plants (Table 2).

Plant height and average leaf size of plants requiring 3 weeks of cold also varied with cold treatment. 'Undulata' and 'Golden Scepter' average leaf size were not affected by cold duration (Figures 3H; 4D). The average leaf size of 'Golden Tiara' and 'Hyacinthina' plants increased as cold duration increased (Figure 4H, 5D), and the average leaf size of *H. montana* plants more than doubled with increasing cold (Figure 3D). Plant height was greatest for 'Golden Scepter', 'Hyacinthina', and *H. montana* plants following nine weeks of cold, although absolute differences were only 4 to 6 cm

(Table 4). 'Undulata' plant height was not affected by cold duration (Figure 4H; Table 6). The responses of 'Golden Scepter' and 'Golden Tiara' to cold treatments were less uniform than anticipated despite their nearly identical genetic background as 'Golden Scepter' is a chartreuse sport of the prolific green and gold variegated 'Golden Tiara' (Savory, 1985).

'Tokudma' gold and 'Tokudama' green plants varied in their response to cold-treatment duration. Complete flowering of 'Tokudama' gold did not occur under any cold treatment (Figure 6B). 'Tokudama' green reached 100% flowering following 15 weeks of cold (Figure 6F). Days to flower declined 3 weeks for 'Tokudama' gold and 5 to 6 weeks for 'Tokudama' green, respectively with increasing cold (Figure 6C, G). Inflorescence height of 'Tokudama' gold was not affected by length of cold treatment (Table 4). However, inflorescence height of 'Tokudama' green plants increased as cold duration increased.

Although plant height increased as the length of cold treatment increased for both hosta clones, 'Tokudama' gold plants were 4 to 9 cm shorter than 'Tokudama' green plants in all treatments (Table 4). Cold did not affect 'Tokudama' green average leaf size (Figure 6D) while the average leaf size of 'Tokudama' gold plants exposed to cold temperatures increased over 50% after 15 weeks of cold (Figure 6H).

DISCUSSION

This study provides evidence that plant size, photoperiod, exposure to cold temperatures, and genotype interact to impact growth, development, and flowering of *Hosta*. Flowering is controlled in part by plant size and crown maturity. Flowering

percentages of single-eye divisions were low for noncooled and cooled plants in 1997-1998. Not all bulked plants flowered in 1998-1999 despite larger shoot sizes and a greater number of divisions per container. Hostas are considered mature and attain a mature leaf size and shape when they have completed six growing seasons after being started from one- or two-year-old divisions (Schmid, 1991). Thus, the plants that did not flower under inductive conditions are considered juvenile and may be physiologically incapable of flowering. Complete flowering percentages would be expected of mature plants.

The foliage of experimental plants was removed prior to first frost but after leaf senescence began in early-to-mid autumn. However, some or all the plants may not have entered a fully dormant state as the foliage had not died back to the crown. For many of the hosta clones examined, a small percentage of noncooled plants emerged irrespective of photoperiod and exhibited low vigor. Developmentally these plants may not have completed the transition into dormancy when outdoors under natural short days in the lath house. Artificial long days provided in the greenhouse apparently promoted emergence and subsequent growth. Therefore, the cold duration necessary to break dormancy for plants experiencing deep dormancy induced in late-autumn or winter may be longer than for the plants examined in this experiment.

Short-day photoperiods alone induced vegetative dormancy of hosta clones. Plants grown under short-day photoperiods with and without a cold treatment produced an initial flush of leaves, then entered a state of dormancy where vegetative growth ceased and no flowering occurred. Leaf senescence only occurred in the greenhouse under short-day photoperiods for 'Golden Scepter' and 'Golden Tiara'. This suggests

that cold temperatures may be required by other genotypes to promote the leaf senescence that is observed outdoors. Exposure to cold temperatures breaks crown dormancy of hosta clones, yet long-day photoperiods must follow the cold treatment to promote continued growth and subsequently induce flowering (Figures 1B; 2B, F; 3B; 4B, F; 6B, F).

Growth of *H. plantaginea* and 'Royal Standard' plants appears to be inhibited solely by unfavorable environmental factors (short days), a form of ecodormancy. *H. plantaginea* and 'Royal Standard' plants produced an initial flush of leaves under short-day photoperiods then entered a dormant state. When transferred to long-day photoperiods after 15 weeks of short days, *H. plantaginea* and 'Royal Standard' plants resumed growth (personal observation). For the remaining hosta clones, growth was not observed upon transfer from short-day to long-day photoperiods and must be inhibited by physiological factors within the crown (paradormancy or endodormancy).

The range of effective low temperatures required to break vegetative dormancy of hosta clones and their duration are unknown. All clones examined had cold requirements of 0, 3, or 6 weeks at 5°C to break vegetative dormancy and achieve complete emergence in both years. In the natural environment, hostas are remarkably hardy plants and tolerate long durations of cold temperatures (e.g. up to five months of temperatures at 5°C or below in climates similar to Michigan) when dormant. Plants having longer cold requirements may have a selective advantage in areas where warm temperatures favorable for growth follow periods of cold temperatures in autumn and early winter. The longer cold requirement would prevent plants from emerging prematurely and dying when conditions for growth turn unfavorable. Longer durations of cold generally decreased the

time to flower and improved percent flowering under long-day photoperiods (Figures 2B, C, F, G; 3B, C; 4B, C, F, G; 6B, C, F, G). For most hosta clones, time to flower of plants exposed to long days did not vary for photoperiods ≥14 h and NI (personal observation). These characteristics would ensure emergence in areas with long winters followed by short growing seasons and enable plants to complete their life cycle from emergence to seed set within the shortest amount of time possible. Thus, a decrease in time to flower would be advantageous for the survival of seedling progeny and existing plants.

Cold temperatures were not absolutely required by 'Lancifolia', *H. plantaginea*, or it's seedling derivitive 'Royal Standard' (Pollock, 1989) to break dormancy or for flower initiation as flowering of these clones occurred without a cold treatment. The disparity in size between noncooled and cooled plants in 1998-1999 suggests that *H. plantaginea* was not dormant and continued growth from the summer season when brought into the greenhouse. *H. plantaginea* is presumably native to Zheijing province or provinces further south in China (Schmid, 1991). These areas are located between 20°N and 30°N latitude (similar to Houston, TX and New Orleans, LA) and experience annual average low temperatures of -6.6 to 4.4°C (20 to 40°F) (Widrlechner, 1997). Temperatures below 5°C in these areas would not persist for long durations, therefore it is not surprising these hosta clones do not require cold periods to initiate or maximize growth. 'Lancifolia', *H. plantaginea* and 'Royal Standard' plants naturally bloom in late summer (Solberg, 1988), and a greater percentage of flowering of these plants might be achieved with forcing periods longer than 15 weeks or with larger, more mature plant material.

The remaining hosta clones benefitted from cold exposure with improved emergence and percent flowering, reduced time to flower, and increased vigor as

evidenced by greater plant height and average leaf size. Many of these clones are cultivars of unknown origin, therefore the native locations of their parents are difficult to determine and mostly hypothesized. However, most *Hosta* species are native to Korea and the Japanese archipelago which span from 35°N to 45°N latitude (similar latitudes as Memphis, TN and Minneapolis, MN) (Graves, 1992) and experience a temperate continental climate much similar to North America (Schmid, 1991). The parental species of 'Golden Tiara' and 'Golden Scepter' is *H. nakaiana*, a species native to central and southern Korea (Schmid, 1991). 'Tokudama' gold and green are hypothesized hybrids of *H. sieboldiana*, a species native to Japan (Schmid, 1991).

In a comparative study of *Hosta* across the United States, the emergence patterns of several genotypes closely parallel their cold requirements as established in this study (Solberg, 1988). *H. plantaginea* emerged earlier than other hostas in southern gardens and later than most in northern gardens; 'Lancifolia', *H. montana*, and 'Undulata' were first to emerge in all gardens; *H. nakaiana* and 'Fortunei' emerged mid-to-late in all gardens; and 'Tokudama' emerged late in all gardens. Early emergence would be expected for hostas with a minimum cold requirement, such as *H. plantaginea*, 'Lancifolia', *H. montana*, and 'Undulata'. Presumably these hostas are native to areas that experience short durations of cool or cold temperatures. *H. montana* and 'Undulata' exhibited $\geq$50% emergence without cold and may require fewer than 3 weeks of cold to saturate the cold requirement for emergence. 'Golden Scepter', 'Golden Tiara' (a *H. nakaiana* hybrid), and 'Hyacinthina' (a 'Fortunei') appear to require an absolute minimum of 3 weeks of cold, as evidenced by poor emergence without cold and mid-to-late emergence in relation to other hostas. The 'Tokudamas' are set apart from other

hosta clones by having the longest cold requirement (6 weeks). The parental species of 'Golden Scepter', 'Golden Tiara', 'Hyacinthina', and 'Tokudama' originated in areas of Japan and Korea that presumably experience a longer duration of cold temperatures.

Long periods of cold appeared to alter the emergence pattern and delay emergence of *H. plantaginea* (Solberg, 1988). Emergence of hostas such as *H. plantaginea* which do not have a cold requirement to break dormancy may be controlled by temperature. These plants may emerge only when the root zone temperature warms above a clonal-specific base temperature. This would explain early emergence in southern climates with warm soil temperatures and late emergence in cooler climates where the soil takes a longer period of time to warm in the spring. However, this hypothesis needs to be tested as the base soil temperature was not determined in this experiment.

Most hosta clones required or benefitted from a period of cold temperatures although the optimum temperature and it's required duration remain unknown. These experiments indicate that clonal divisions of hosta harvested in early to late autumn should be cooled up to 6 weeks at 5°C to maximize vigor and growth. The cold requirement for divisions harvested in winter and early spring should be naturally fulfilled, and no artificial cold would be required. Emergence of cooled divisions occurred irrespective of photoperiod in 1 to 3 weeks at 20°C, depending upon genotype. When continuously grown under short-day photoperiods, hostas entered a vegetatively dormant state and further growth ceased. Therefore, it is recommended that long-day photoperiods $\geq$14 h be provided to promote vegetative and reproductive development. When forcing for foliage, hostas reach a saleable size in approximately six weeks at 20°C. It is recommended that large, mature plants be used when forcing plants to flower

as incomplete flowering will result with small plants. Flower buds form in 8 to 13 weeks for mature plants given the minimum amount of cold required for emergence (Table 7). Greater durations of cold generally decreased time to flower and improved percent flowering.

Because many commercially available hosta clones are closely related, approximations for the cold requirement of other genotypes not examined in this study can be made based upon their growth characteristics and genetic background. For example, members of the 'Tiara' series share a close relationship with 'Golden Scepter' and 'Golden Tiara.' It can be inferred that these hostas would require at least three weeks of cold for maximum emergence. However, the vegetative and flowering responses to cold temperature duration of plants not examined warrants further investigation.

Table 7. Cold temperature and greenhouse forcing requirements for hosta clones in 1998-1999.

Clone	Weeks of 5°C cold for 100% emergence	Weeks to flower at 20°C[z]
'Golden Scepter'	3	10-12
'Golden Tiara'	3	10-12
'Hyacinthina'	3	11-13
'Lancifolia'	0	13-15
H. montana	3	10-12
H. plantaginea	0	14-16
'Royal Standard'	0	16-18
'Tokudama' gold	6	8-9
'Tokudama' green	6	9-11
'Undulata'	3	10-12

[z] With NI lighting provided from 2200 to 0200 h.

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Table 1. Plant material characteristics for 1997 and 1998 cold-treatment duration experiments. All plants in 1998-1999 were grown in containers and originated from 1997 experimental plant material, except for *H. montana* and 'Royal Standard'.

Clone	Source Location (latitude)	Arrival Date	Starting material	Starting date of cold treatment 1997	Starting date of cold treatment 1998
'Golden Scepter'	Walters Gardens Zeeland, MI (42.9°N)	10/09/97	clump	10/14	10/16
'Golden Tiara'	Walters Gardens	10/09/97	clump	10/14	10/16
'Hyacinthina'	Wade and Gatton Nursery Bellville, OH (40.6°N)	10/31/97	bare root	11/01	10/16
'Lancifolia'	Sunnybrook Farms Chesterland, OH (41.5°N)	10/08/97	clump	10/14	10/16
montana	Walters Gardens	11/06/97	seed	—	10/16
plantaginea	Sunny Border Nursery Kensington, CT (41.6°N)	11/03/97	bare root	11/04	10/16
'Royal Standard'	Twixwood Nursery Berrien Springs, MI (41.9°N)	08/24/97	container	—	10/16
'Tokudama' gold	Klehm Nursery Champaign, IL (40.1°N)	10/13/97	bare root	10/14	10/16
'Tokudama' green	Klehm Nursery	10/13/97	bare root	10/14	10/16
'Undulata'	Walters Gardens	10/09/97	bare root	10/14	10/16

Table 2. Average daily temperatures and daily light integrals from date of forcing to average date of flowering for hosta clones in 1998-1999.

Clone	Average air temperature (°C)						Average daily light integral[z] ($mol \cdot m^{-2} \cdot d^{-1}$)					
	Weeks of 5°C											
	0	3	6	9	12	15	0	3	6	9	12	15
'Golden Scepter'	20.4	20.3	20.8	20.4	20.7	21.5	6.2	5.9	6.2	7.3	11.2	12.9
'Golden Tiara'	20.4	20.3	20.8	20.4	20.6	21.4	6.2	6.1	6.3	7.3	10.0	13.3
'Hyacinthina'	--[y]	20.5	20.8	20.4	20.8	21.4	--	6.9	6.9	9.1	11.3	13.8
'Lancifolia'	20.4	20.5	20.9	20.5	20.3	21.4	6.1	6.8	8.3	10.1	12.1	14.5
montana	--	20.3	20.8	20.4	20.8	21.4	--	5.9	6.5	7.3	11.2	13.7
plantaginea	20.4	--	20.9	20.6	20.3	21.4	6.2	--	8.6	10.2	13.2	14.5
'Royal Standard'	20.5	20.5	20.9	20.1	20.4	21.4	6.5	6.9	6.5	11.0	13.2	13.8
'Tokudama' gold	--	20.3	20.8	20.4	20.6	21.5	--	6.1	6.5	7.1	9.5	13.0
'Tokudama' green	20.4	20.4	20.8	20.4	20.6	21.5	6.2	6.2	6.2	7.5	9.4	13.0
'Undulata'	20.5	20.3	20.8	20.4	20.6	21.4	6.2	6.1	6.4	7.5	10.1	13.3

[z] Light measurements were recorded at roof level then reduced 22% for approximate integrals at bench level.
[y] No plants flowered (--).

Table 3. Differences in characteristics of hosts alones between 1987–1988

Table 3. Differences in characteristics of hosta clones between 1997-1998 and 1998-1999.

Clone	Plant Height (cm)							Inflorescence Height (cm)							Flower number						
	Weeks of 5°C																				
	0	3	6	9	12	15	Sign[z]	0	3	6	9	12	15	Sign	0	3	6	9	12	15	Sign
'Golden Scepter'	+5	+5	+5	+8	+6	+7	***	-[y]	-	-6	-4	-7	-	NS	-	-	-7	-6	+4	-	NS
'Golden Tiara'	+8	+5	+10	+10	+8	+10	***	+1	-1	-1	+7	+13	+7	NS	-1	-6	-1	-1	-1	+3	NS
'Hyacinthina'	--[x]	+8	+16	+21	+16	+14	***	-	-	+11	+11	+18	+36	***	-	-	+6	+9	+9	+4	***
'Lancifolia'	+6	+10	+9	+11	+12	+12	***	-3	-	-1	+11	+7	-	NS	+1	-	+6	+6	+3	-	***
montana	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	
plantaginea	+21	+10	+5	+3	+9	+9	***	-	-	-9	-	-	-	NS	-	-	+2	-	-	-	NS
'Royal Standard'	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	
'Tokudama' gold	0	+2	+5	+6	+4	+7	***	-	-	+9	+8	+9	+10	**	-	-	+16	+14	+11	+18	**
'Tokudama' green	+9	+5	+12	+13	+14	+11	***	-	-	-	-	+14	+17	***	-	-	-	-	+20	+24	***
'Undulata'	+6	+10	-	+10	+12	+13	***	-	-	-	-	+11	+20	**	-4	+7	-	+4	+1	+6	NS

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

[y] No first-year data available (-).

[x] No second-year data available (--).

Table 4. Differences in flowering characteristics of hosta clones between 1997-1998 and 1998-1999.

Clone	Days to visible bud							Days from visible bud to flower						
	Weeks of 5°C													
	0	3	6	9	12	15	Sign[z]	0	3	6	9	12	15	Sign
'Golden Scepter'	-[y]	-	-43	-45	-48	-	***	-	-	-7	-1	+3	-	NS
'Golden Tiara'	-30	-48	-47	-5	-5	-24	***	-5	-6	-2	0	-2	-2	**
'Hyacinthina'	-	-	-27	-21	-24	-35	***	-	-	0	-1	-2	+1	NS
'Lancifolia'	-12	-	-6	-18	-7	-	***	0	-	-2	+4	+2	-	NS
montana	-	-	-	-	-	-		-	-	-	-	-	-	
plantaginea	-	-	+4	-	-	-		-	-	+1	-	-	-	
'Royal Standard'	-	-	-	-	-	-		-	-	-	-	-	-	
'Tokudama' gold	-	-	-23	-8	+25	+1	NS	-	-	+3	+4	-33	0	***
'Tokudama' green	-	-	-	-	-9	-6	**	-	-	-	-	-2	-2	NS
'Undulata'	-1	-22	-	+5	-7	-6	*	+6	+2	-	-1	0	+1	NS

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

[y] No first-year data available (-).

Table 5. Average days to visible bud and average days from visible bud to flower for hosta clones in 1998-1999.

Clone	Days to visible bud							Days from visible bud to flower						
	Weeks of 5°C													
	0	3	6	9	12	15	Sign[z]	0	3	6	9	12	15	Sign[z]
'Golden Scepter'	81 (2)[y]	55 (10)	49 (10)	48 (10)	53 (10)	40 (10)	Q*	29	28	25	27	27	25	L*
'Golden Tiara'	64 (4)	57 (10)	49 (10)	51 (10)	43 (10)	44 (10)	L**	26	27	26	27	28	27	NS
'Hyacinthina'	--[x] (0)	91 (10)	66 (10)	69 (10)	64 (10)	57 (10)	L***	--	27	24	23	22	23	NS
'Lancifolia'	77 (9)	87 (9)	84 (10)	75 (10)	72 (10)	71 (10)	Q**	23	22	23	26	26	26	L*
montana	-- (6)	39 (9)	49 (10)	43 (10)	52 (10)	45 (10)	NS	--	36	29	33	32	34	NS
plantaginea	90 (10)	-- (10)	86 (10)	85 (10)	87 (10)	79 (10)	NS	24	--	26	22	23	21	NS
'Royal Standard'	97 (10)	91 (10)	84 (10)	96 (10)	89 (10)	88 (10)	NS	29	28	29	27	27	27	NS
'Tokudama' gold	-- (1)	64 (4)	55 (10)	48 (10)	43 (10)	44 (10)	L***	--	23	23	25	23	23	NS
'Tokudama' green	90 (1)	70 (4)	48 (10)	52 (10)	41 (10)	39 (10)	Q***	18	27	21	26	22	24	NS
'Undulata'	44 (7)	55 (10)	48 (10)	49 (10)	43 (10)	42 (10)	NS	30	29	29	29	29	29	NS

[z] NS, *, **, ***Nonsignificant or significant linear (L) or quadratic (Q) trend at $P \leq 0.05$, 0.01, or 0.001, respectively.

[y] Sample size for each observation.

[x] No plants flowered (--).

Table 6. Effect of cold duration on subsequent plant height, inflorescence height, and average leaf number per flowering shoot of hosta clones in 1998-1999. Plants were grown at 20°C for 15 weeks under a 9-h natural day plus a 4-h night interruption photoperiod following cold treatment.

Clone	Plant Height (cm)							Inflorescence Height (cm)							Leaves per Flowering Shoot						
	Weeks of 5°C																				
	0	3	6	9	12	15	Sign[z]	0	3	6	9	12	15	Sign	0	3	6	9	12	15	Sign
'Golden Scepter'	10	12	12	15	13	13	Q*	43	33	30	33	36	31	Q*	12	7	7	6	9	6	Q**
'Golden Tiara'	12	12	17	16	15	17	L**	39	41	40	41	41	42	NS	8	8	8	7	7	8	NS
'Hyacinthina'	-[y]	14	21	27	23	16	Q***	--[x]	42	49	51	53	42	Q*	--	7	7	8	7	7	NS
'Lancifolia'	14	16	17	18	17	19	L**	38	47	43	49	43	43	Q*	8	8	10	10	9	10	NS
montana	14	14	20	22	20	20	Q*	--	74	53	45	46	53	NS	--	5	5	6	7	6	NS
plantaginea	32	25	22	26	25	24	Q*	39	--	36	42	49	35	Q*	7	--	8	7	7	7	NS
'Royal Standard'	26	26	23	15	22	20	Q**	60	60	51	40	57	59	Q**	10	8	7	7	10	9	NS
'Tokudama' gold	2	5	12	10	11	13	Q*	--	26	21	26	22	26	NS	--	8	8	9	8	9	NS
'Tokudama' green	16	11	16	18	19	17	L*	29	22	27	34	33	34	L*	5	9	6	7	8	9	NS
'Undulata'	16	18	18	19	19	18	NS	65	63	63	65	62	68	NS	7	8	7	9	9	9	NS

[z] NS, *, **, ***Nonsignificant or significant linear (L) or quadratic (Q) trend at $P \leq 0.05$, 0.01, or 0.001, respectively.

[y] No plants emerged (-).

[x] No plants flowered (--).

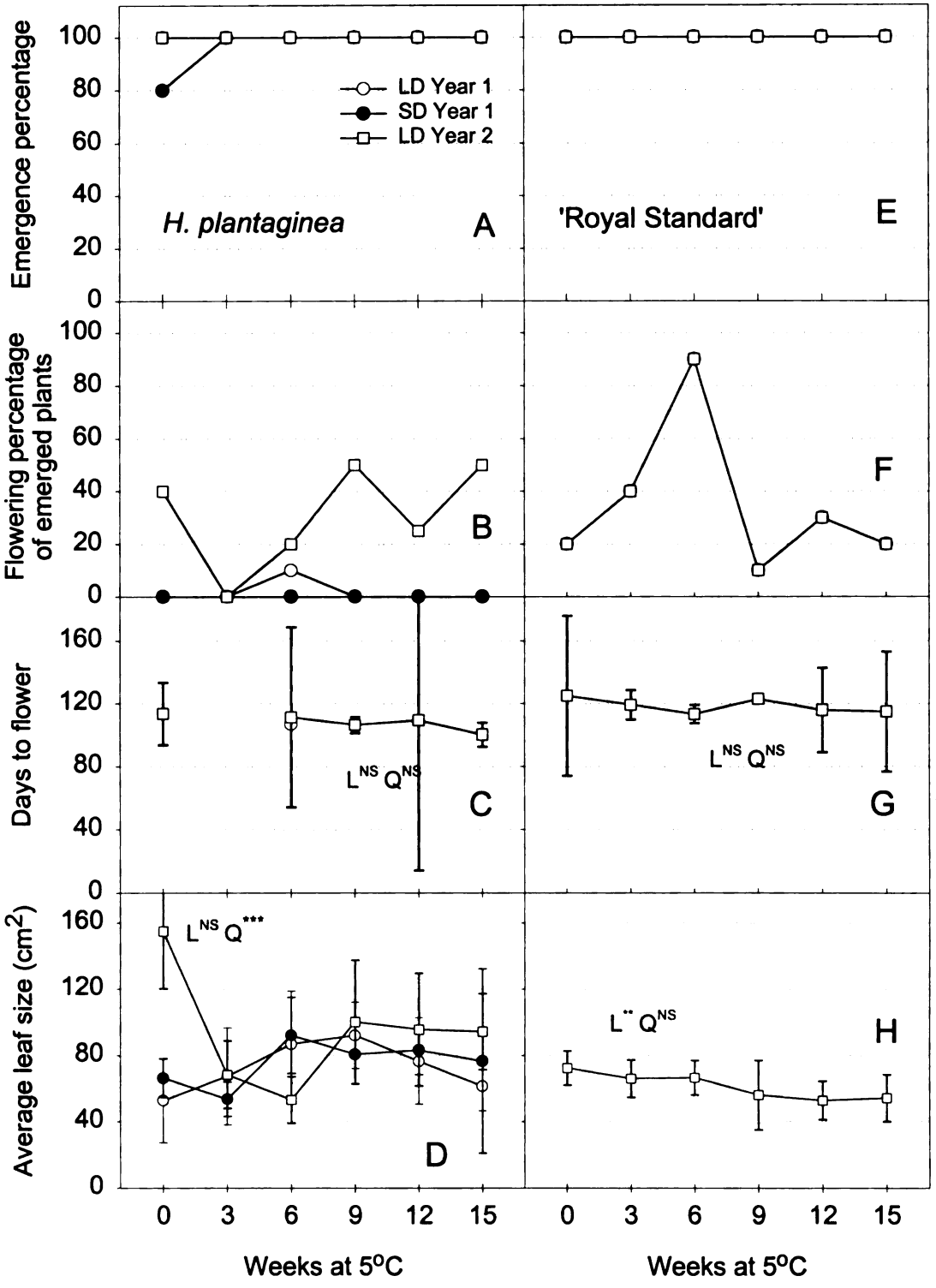

Figure 1. Percent emergence (A, E), percent flowering (B, F), days to flower (C, G), and average leaf size (D, H) of *Hosta plantaginea* and 'Royal Standard' after 0, 3, 6, 9, 12, or 15 weeks of 5°C cold under a 9-hour short day in year one (●) or a 9-hour day plus a 4-hour night interruption in year one (○)and year two (□). Error bars are 95% confidence intervals. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

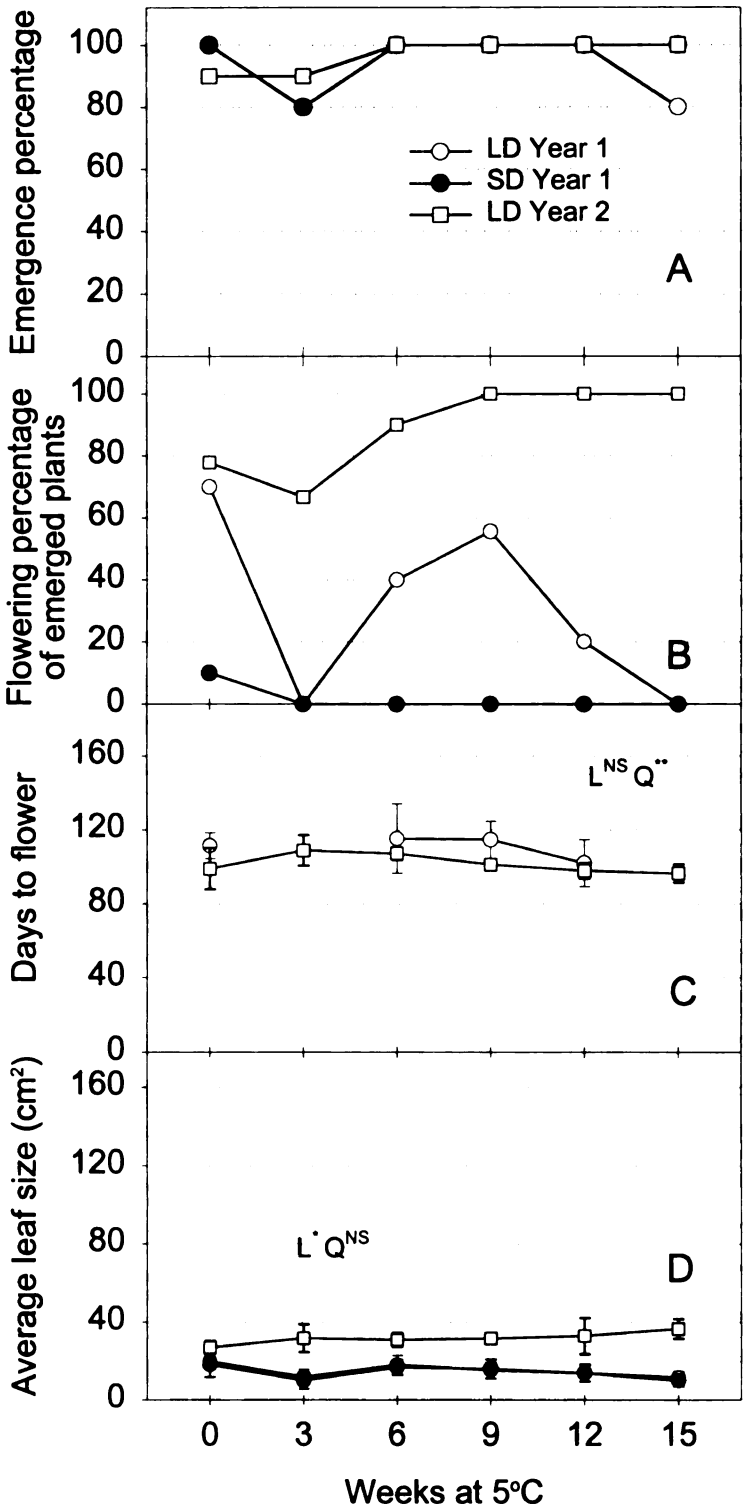

Figure 2. Percent emergence (A), percent flowering (B), days to flower (C), and average leaf size (D) of *Hosta* 'Lancifolia' after 0, 3, 6, 9, 12, or 15 weeks of 5°C cold under a 9-hour short day in year one (●) or a 9-hour day plus a 4-hour night interruption in year one (○) and year two (□). Error bars are 95% confidence intervals. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

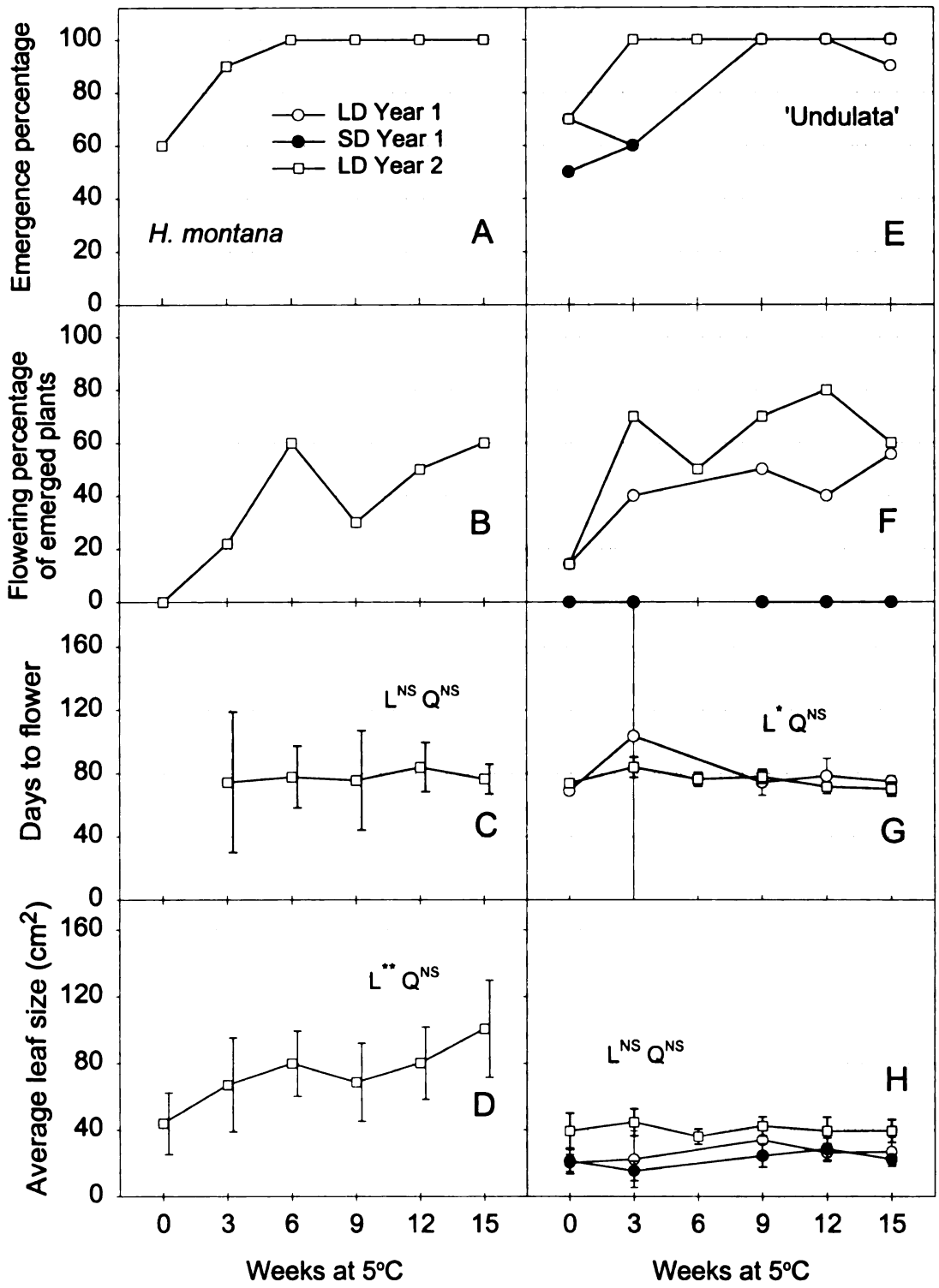

Figure 3. Percent emergence (A, E), percent flowering (B, F), days to flower (C, G), and average leaf size (D, H) of *Hosta montana* and 'Undulata' after 0, 3, 6, 9, 12, or 15 weeks of 5°C cold under a 9-hour short day in year one (●) or a 9-hour day plus a 4-hour night interruption in year one (○) and year two (❑). Error bars are 95% confidence intervals. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

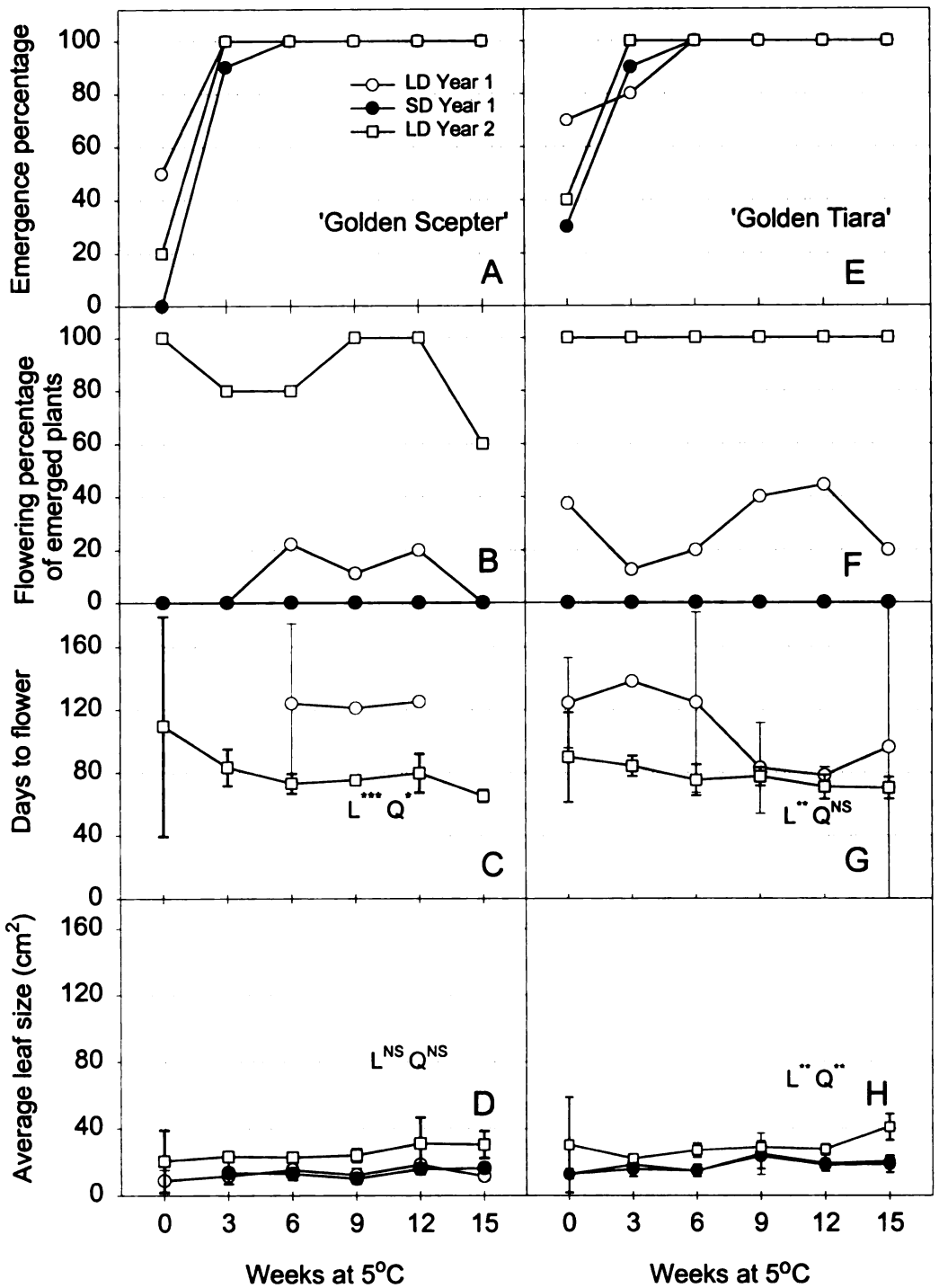

Figure 4. Percent emergence (A, E), percent flowering (B, F), days to flower (C, G), and average leaf size (D, H) of *Hosta* 'Golden Scepter' and 'Golden Tiara' after 0, 3, 6, 9, 12, or 15 weeks of 5°C cold under a 9-hour short day in year one (●) or a 9-hour day plus a 4-hour night interruption in year one (○) and year two (□). Error bars are 95% confidence intervals. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

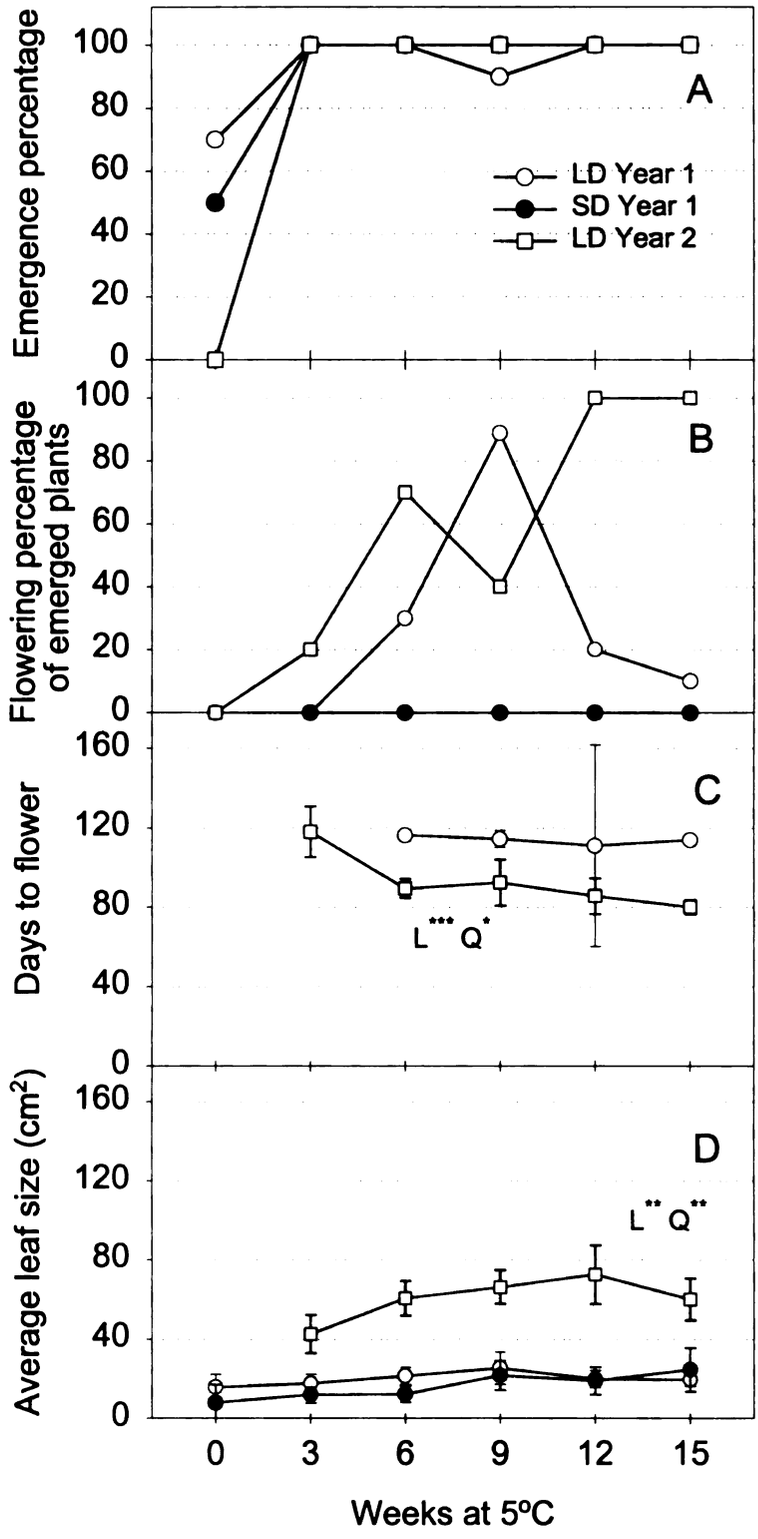

Figure 5. Percent emergence (A), percent flowering (B), days to flower (C), and average leaf size (D) of *Hosta* 'Hyacinthina' after 0, 3, 6, 9, 12, or 15 weeks of 5°C cold under a 9-hour short day in year one (●) or a 9-hour day plus a 4-hour night interruption in year one (○) and year two (□). Error bars are 95% confidence intervals. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

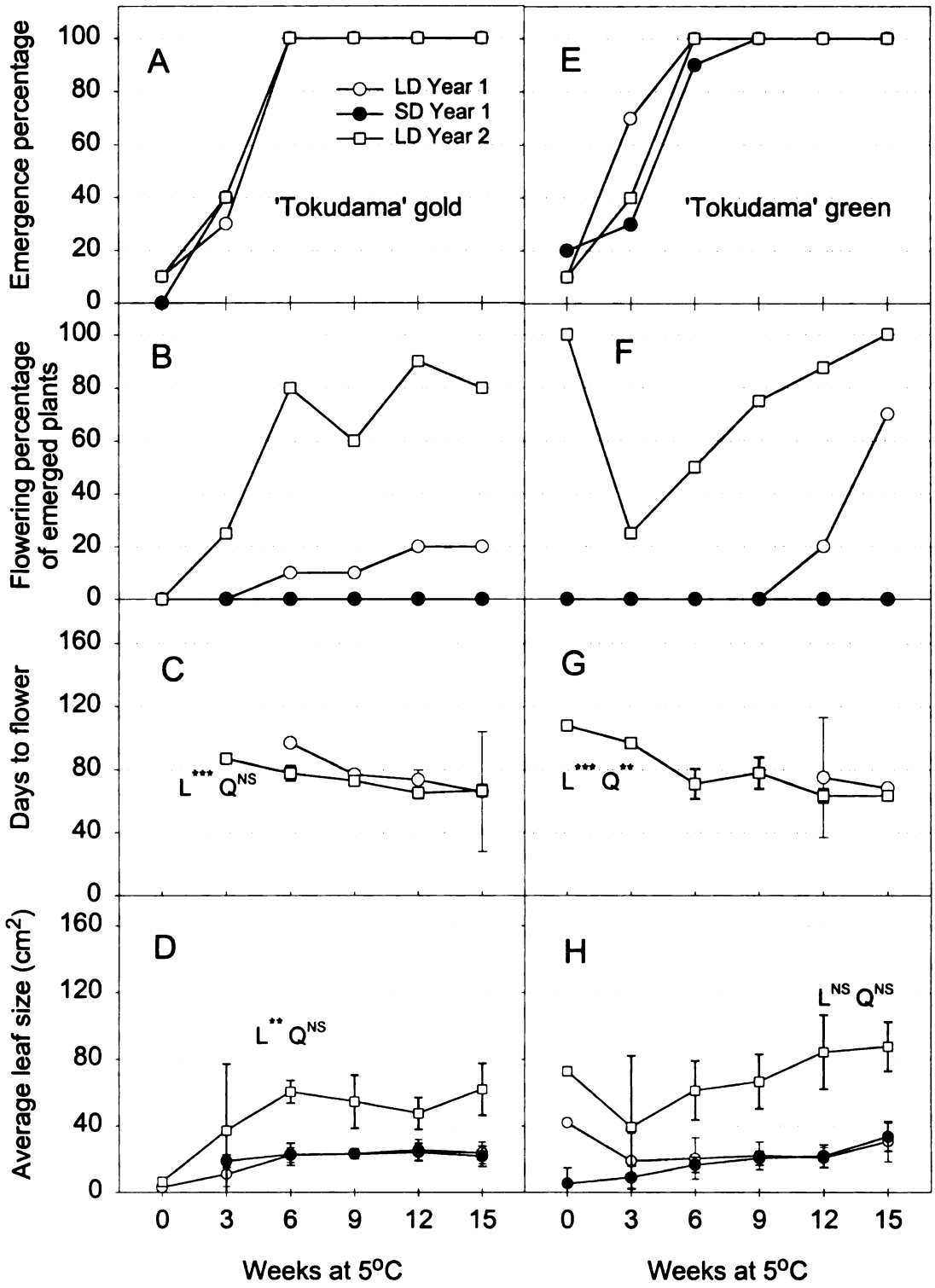

Figure 6. Percent emergence (A, E), percent flowering (B, F), days to flower (C, G), and average leaf size (D, H) of *Hosta* 'Tokudama' gold and 'Tokudama' green after 0, 3, 6, 9, 12, or 15 weeks of 5° C cold under a 9-hour short day in year one (●) or a 9-hour day plus a 4-hour night interruption in year one (○) and year two (□). Error bars are 95% confidence intervals. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P< 0.05$, 0.01, or 0.001, respectively.

SECTION III

THE INFLUENCE OF COLD TREATMENT AND PHOTOPERIOD DURATION ON GROWTH AND FLOWERING OF *HOSTA*.

The influence of cold treatment and photoperiod duration on growth and flowering of *Hosta*.

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Production and Culture

The influence of cold treatment and photoperiod duration on growth and flowering of *Hosta*.

Additional index words. Herbaceous perennial, critical photoperiod, plantain lily.

Abstract. Single-eye divisions of *H. montana*, *H. plantaginea*, *H.* 'Golden Scepter', *H.* 'Golden Tiara', *H.* 'Hyacinthina', *H.* 'Lancifolia', *H.* 'Royal Standard', *H.* 'Tokudama' gold, *H.* 'Tokudama' green, and *H.* 'Undulata' were grown under seven photoperiods following 0 or 15 weeks of 5°C to determine the effects of cold treatment and photoperiod duration on growth and flowering in 1997-1998. Plants were bulked during the summer, and the experiment was repeated in 1998-1999. Photoperiods were a 9-h natural day extended with incandescent bulbs to 10, 12, 13, 14, 15, 16, or 24 hours. An additional night interruption treatment (NI) was a 9-h natural day with a 4-h night break from 2200 to 0200. Larger plants used in 1998-1999 were more uniform with higher flowering percentages than single-eye divisions, suggesting that plant size and crown maturity influence flowering of hosta clones. Not all plants emerged from a dormant state and grew without exposure to cold. A small percentage of noncooled plants emerged under photoperiods ≤13 h then went dormant without flowering. A greater percentage of noncooled plants emerged under photoperiods ≥14 h or with a 4-h NI and flowered. All plants emerged following cold and were more vigorous. Cooled plants under ≤13 h emerged yet developed only a single flush of leaves and became dormant. Vegetative growth led to flowering of mature plants of all clones under photoperiods ≥14 h and NI. Plant height was greater for plants under photoperiods ≥14 h and NI. Average

leaf size and leaf number generally did not vary with photoperiod following cold. Time to flower decreased as photoperiod duration increased, but differences between photoperiods $\geq$ 16 h and NI were not significant.

INTRODUCTION

The specific vernalization, forcing temperature, and photoperiodic requirements for growth and flowering of herbaceous perennials must be determined in order to devise production schedules to force plants for sale on a specific date. Although hosta are primarily grown for their foliage, the scheduling of hosta in flower is of interest to producers wanting to force plants for retail sale or show, for breeders wishing to cross plants with incongruent flowering habits, and for propagators wishing to increase shoot production by releasing lateral buds from apical dominance. Many questions concerning the physiology of *Hosta* remain, and it is necessary to determine the environmental conditions required for growth, floral induction, and development.

Plants optimize growth and adapt to seasonal changes by synchronizing their development to environmental signals (Rees, 1987). Many physiological processes, such as flower initiation, are determined or influenced by a plant's interaction with temperature and photoperiod. The photoperiod duration and effective low temperature requirements for flower induction are often species- and cultivar-specific. Effective temperatures for flower induction range from below freezing to 16°C with an optimum range of 1 to 7°C for most cold-requiring plants (Lang, 1965; Roberts and Summerfield, 1987). Plants are categorized according to their flowering response to photoperiod. Short day plants (SDP) flower or flower faster when the daylength is less than a critical duration; long day plants

(LDP) flower or flower faster when the daylength is greater than a critical duration; and day neutral plants (DNP) flower irrespective of daylength.

Exposure to cold temperatures affects plant development in several ways. Many dormant woody and herbaceous perennials require sufficient periods of low temperatures to break dormancy of vegetative or reproductive buds to resume growth or flowering. When dormancy is fully broken, the resumption of growth is usually independent of photoperiod (Iversen and Weiler, 1994). Plants may also require vernalization, the induction of flowering by low temperatures, to continue growth and flower. For plants with an obligate vernalization requirement, flower initials form only after vernalization is complete and differentiate into floral organs when the plant is exposed to warmer growing conditions (Thomas and Vince-Prue, 1997). Finally, plants may exhibit a facultative response to cold where cold is not absolutely required but accelerates growth and flowering and improves plant quality and uniformity.

The cold requirement for flowering is often coupled with a photoperiodic requirement. Many herbaceous perennials are LDP native to temperate regions and require cold temperatures followed by long daylengths for spring and summer flowering (Roberts and Summerfield, 1987). Long day plants are induced to flower when the daylength is greater than a critical length, also known as the critical photoperiod. This critical photoperiod marks the transition from vegetative growth to reproductive growth in obligate plants. For some plants such as *Gaura lindheimeri* and *Geranium dalmaticum*, the response to daylength is facultative, and flowering occurs under all photoperiods but more rapidly when plants are exposed to long days (Finical et al., 1998a; Finical et al., 1998b). In this case, the critical photoperiod would be the photoperiod

where time to flower is minimal and not affected by further increases in photoperiod, and below which flowering is delayed (Roberts and Summerfield,1987). The critical photoperiod can also be defined as the photoperiod required for 50% flowering of a population, or the photoperiod that induces complete, rapid, and uniform flowering when met or exceeded (Runkle et al., 1998b; Thomas and Vince-Prue, 1997).

Cold and photoperiod interact to impact several aspects of flowering. Cold temperatures may reduce the critical photoperiod for particular species or cultivar. The critical photoperiod for *Rudbeckia fulgida* 'Goldsturm' shifted from 14 hours without cold to 13 hours following 15 weeks of cold (Runkle et al., 1999). Cold temperatures may also eliminate a plant's photoperiodic requirement for flowering (Runkle et al., 1998a; Thomas and Vince-Prue, 1997). *Lavandula angustifolia* 'Munstead' flowered only under LD prior to cold yet flowered under LD and SD following 10 or more weeks of cold temperatures (Whitman et al., 1996). Finally, short photoperiods followed by long photoperiods can replace or partially replace the cold requirement for some LDP (Thomas and Vince-Prue, 1997).

Few studies have examined the influence of cold treatment and photoperiod on flowering of *Hosta*. Improved emergence, growth, and flowering of *Hosta* 'Francee' occurred when dormant divisions received 15 weeks of 5°C compared with noncooled divisions (Finical et al., 1997). All plants failed to flower without cold, and flowering only occurred with photoperiods $\geq$ 14 h following cold. Because of the diversity within commercially available *Hosta*, the objectives of this research were to examine the effects of photoperiod duration on vegetative and reproductive development and determine the critical photoperiod necessary for flower induction of a diverse group of hosta clones.

MATERIALS AND METHODS

Plant material. *1997-1998.* Hostas were received from commercial producers (Table 1) in fall 1997 and were separated into single-eye divisions. Divisions were placed upright into 23 x 15 x7 cm (6.8 L) bulb crates or planted individually in 13-cm (1.1 L) square containers filled with a commercial soilless medium composed of composted pine bark, vermiculite, Canadian sphagnum peat, and coarse perlite with a wetting agent, lime, and starter fertilizer charge (High Porosity Mix, Strong-Lite Products, Pine Bluff, AR). Potted divisions were placed directly in a glass greenhouse, while bulb crates were placed in a cooler set at 5°C. Plants were watered as required with well water acidified with citric acid to a pH of 6.0. Divisions were removed from the bulb crates after 15 weeks of cold, planted into 13-cm square containers as described above, and placed in the greenhouse.

1998-1999. Hostas from the 1997 experiments were grown outdoors from May 15 to October 16, 1998 in 13-cm (1.1 L) square containers under 50% shade created by alternate strips of wood lath at the Michigan State University Horticultural Teaching and Research Center, East Lansing, MI. An exception was *Hosta* 'Royal Standard' where single-eye divisions were taken from 3 year-old crowns previously grown in 8-cm (350 ml) containers, potted in the spring of 1998, and bulked in the lath house until fall. Plants showed visible signs of dormancy (leaf senescence) and had the foliage removed prior to first frost on October 16, 1998. Pots were placed in a 20°C glass greenhouse or in a cooler at 5°C without supplemental lighting for 15 weeks prior to photoperiod treatments.

Plants were placed under 10, 12, 13, 14, 15, 16, or 24 hours of continual light or under a 9-h day plus 4-h night interruption (NI) from 2200 to 0200. Photoperiods were

established by covering benches with opaque black cloth from 1700 to 0800 to eliminate natural light. The 9-h natural daylength was then extended from 1700 until photoperiod completion with 60-W incandescent lights delivering 3 to 5 $\mu mol \cdot m^{-2} s^{-1}$ under the opaque black cloth.

General Procedures. Plants were fertilized in the greenhouse at every irrigation with a nutrient solution of well water (EC of 0.70 $mS \cdot cm^{-1}$ and 105, 35, and 23 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively) acidified with H_2SO_4 to a titratable alkalinity of 130 $mg \cdot L^{-1}$ $CaCO_3$ and water soluble fertilizer providing 125-12-125-13 N-P-K-Ca $mg \cdot L^{-1}$ (30% ammonical N) plus 1.0-0.5-0.5-0.5-0.1-0.1 (Fe, Mn, Zn, Cu, B, Mo) $mg \cdot L^{-1}$ (MSU Special, Greencare Fertilizers, Chicago, IL).

Four-hundred-watt high-pressure sodium (HPS) lamps provided a photosynthetic photon flux (PPF) of 100 $\mu mol \cdot m^{-2} s^{-1}$ starting at 0800 and continuing until the outside PPF exceeded 400 $\mu mol \cdot m^{-2} s^{-1}$. If the outside PPF then dropped below 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ lamps were again turned on until 1700. In 1998, the average daily light integral was also measured from the start of forcing to the average date of flowering with a quantum sensor (LI-COR) connected to a CR-10 datalogger (Campbell, Scientific, Logan, UT) (Table 2). Greenhouse air temperature was monitored on each bench with 36-gauge type E thermocouples connected to a CR-10 datalogger (Campbell, Scientific, Logan, UT). Temperatures and light measurements were collected every 10 seconds and the hourly average recorded. Supplemental heat was provided by 1500-W electric heaters (Model T771, Rival Manufacturing Co, Sedalia, MO) located under each bench at night as needed to maintain a 20°C air temperature under the black cloth. In 1998, the average

daily temperature and daily light integral from the start of greenhouse forcing to flower for each clone was calculated for each cold and photoperiod treatment (Table 2).

Experiments were conducted in the Plant and Soil Sciences Research Greenhouses at Michigan State University, East Lansing, MI. The experiment was a factorial design study with two factors, photoperiod and cold duration. Each treatment was completely randomized with ten replications. Unless otherwise indicated, the greenhouse air temperature was a constant 20°C. All plants were forced under the specified treatments for fifteen weeks.

Data collection and analysis. Emergence and flowering percentages were calculated for each hosta clone. Flowering percentages were calculated as the number of flowering plants divided by the number of emerged plants in each treatment. The date of visible flower bud was collected for all reproductive plants; the date of flower anthesis, plant height (cm), inflorescence height (cm), flower number, scape leaf number, leaf number, and shoot number were collected when the first flower opened. Plant height, leaf number, and shoot number were collected for nonreproductive plants fifteen weeks after forcing. Leaf area was taken on all plants fifteen weeks after the start of forcing with a LI-300 portable leaf area meter (LI-COR, Lincoln, NB).

Days to visible bud, days to flower, and days from visible bud to flower were calculated for all reproductive plants and no data were available for these parameters on nonflowering plants. Data were analyzed using SAS's (SAS Institute, Cary, NC) analysis of variance (ANOVA) and general linear models (GLM) procedures.

RESULTS

General responses. In both years, not all plants emerged from a dormant state and grew under the photoperiod treatments without prior exposure to cold. A small percentage of plants emerged under photoperiods ≤13 h but then went dormant without flowering. The greatest percentage of noncooled plants emerged under photoperiods ≥14 h or with a 4-h NI, and many of these plants flowered. The actual emergence and flowering percentages of noncooled plants varied with genotype. Essentially all plants, except several 'Lancifolia' plants in 1997-1998, emerged in both years under all photoperiods following cold. Cooled plants grown under 10-h and 12-h photoperiods developed a single flush of leaves and then became dormant. Irregular flowering of some plants occurred under 10-h and 12-h photoperiods following cold treatment in 1998-1999. 'Golden Scepter' and 'Golden Tiara' plants flowered uniformly under 13 h in 1998-1999, but other hosta clones went dormant. Vegetative growth led to flowering of all clones under photoperiods ≥14 h in both years.

Emergence. Emergence rates of depended upon genotype, cold treatment, and photoperiod in both years. Trends in emergence were generally the same between years although absolute percentages differed. Emergence percentage of noncooled plants increased as photoperiod increased from 10 h to 24 h without exception. Emergence under 10-h and 12-h photoperiods was dramatically different between years for noncooled *H. plantaginea* and 'Lancifolia' plants with both having little emergence in 1998-1999 compared to 1997-1998. Following cold treatment, essentially all plants emerged and formed leaves.

Noncooled clones were compared for emergence under long-day photoperiods by averaging the percent emergence for the 16, 24, and NI photoperiod treatments in 1998-1999. The NI treatment was included because emergence under NI was often similar to emergence under the 16 and 24-h photoperiods. Ninety to 100% of *H. plantaginea*, 'Royal Standard', and 'Lancifolia' plants (Figures 1A, 2A, 3A); fifty to 90% of 'Hyacinthina', 'Golden Scepter', *H. montana*, and 'Undulata' plants (Figures 4A, 5A, 6A, 7A); and less than 50% of 'Golden Tiara', 'Tokudama' green, and 'Tokudama' gold emerged under the 16-h, 24-h, and NI photoperiod treatments prior to cold (Figures 8A, 9A, 10A).

Vegetative Characteristics. Noncooled plants of all hosta clones under 10, 12, and 13 h entered a dormant state after emergence in both years. Plants grown under ≥14-h and NI photoperiods produced new leaves, and some flowered. Plants developed similarly under the photoperiod treatments following cold although cooled plants under 10, 12, and 13 h grew to a taller height, were more robust than noncooled plants under the same photoperiods, and eventually became dormant. Cooled plants of all clones under ≥14 h emerged and actively produced new leaves followed by flowering.

Several vegetative characteristics of *Hosta* were influenced by plant size, cold treatment, and photoperiod. Average leaf size and plant height were generally greater for plants grown in 1998-1999 than in 1997-1998. Noncooled plants grown under 10, 12, and 13-h photoperiods had fewer and smaller leaves and were shorter compared with plants grown under ≥14-h and NI photoperiods (Figures 1-10B, C, D, F, G, H). Statistically, leaf size of 'Golden Scepter', *H. montana, H. plantaginea,* 'Royal Standard',

and 'Undulata' plants increased with increasing photoperiod duration prior to cold (Figures 5D, 6D, 1D, 2D, 7D). However, leaf size of all hosta clones except 'Golden Scepter' did not vary with photoperiod following cold in 1998-1999 (Figure 5D). Leaf size of cooled *H. plantaginea* was smaller under photoperiods ≥14 h and NI compared with noncooled plants (Figures 1D, H). Average leaf size of cooled 'Lancifolia' was similar to noncooled plants (Figures 3D, H). Cooled 'Hyacinthina', *H. montana,* 'Tokudama' gold and 'Tokudama' green plants had larger leaves under all photoperiods than noncooled plants (Figures 4H, 6H, 9H, 10H).

The effects of photoperiod and cold treatment on plant height varied for hosta clones. Cooled 'Hyacinthina', 'Tokudama' gold, and 'Tokudama' green plants under photoperiods ≥14 h were taller than noncooled plants in 1998-1999 (Figures 4B, F; 9B, F; 10B, F). Plant heights were similar for noncooled and cooled 'Golden Scepter', 'Golden Tiara', 'Lancifolia', *H. montana*, and 'Undulata' under 16-h, 24-h, and NI photoperiods (Figures 5B, F; 8B, F; 3B, F; 6B, F; 7B, F). However, cooled *H. plantaginea* and 'Royal Standard' plants grown under photoperiods ≥14 h were shorter than noncooled plants only in 1998-1999 (Figures 1B, F; 2B, F).

The average number of leaves per shoot was generally similar between years. The leaf number for noncooled plants in 1998-1999 progressively increased as photoperiod increased and was greatest under 16 h, 24 h, or NI (Figures 1C-10C). Plants under 10, 12, and 13 h produced an initial flush of leaves and went dormant. Plants under ≥14 h continued to produce leaves until flowering occurred. Following cold, the average number of leaves per shoot did not vary significantly with photoperiod except for 'Golden Scepter', 'Lancifolia', *H. plantaginea*, and 'Royal Standard' plants(Figures 1G-10G).

'Golden Scepter', *H. plantaginea*, and 'Royal Standard' leaf number increased with increasing photoperiod while 'Lancifolia' leaf number was inconsistent in 1998-1999 (Figures 5G, 1G, 2G, 3G).

Flowering. Flowering was influenced by genotype, plant size, photoperiod, and cold treatment. Without exception, more plants of each clone flowered in 1998-1999 than in 1997-1998, and flowering percentages of many hosta clones increased dramatically following cold (e.g. 'Golden Scepter' increased from 0 to 100% following cold under a 13-h photoperiod). Noncooled and cooled plants in 1998-1999 generally required less time to flower than plants in 1997-1998.

Photoperiod was the primary determinate of flowering. Only 3 plants of 800 flowered under ≤12-h photoperiods in 1998-1999 (Figures 16E, 19E). Several clones flowered to varying degrees under the 13-h photoperiod following cold (Figures 16E, 20E, 15E, 18E). The 13-h and 14-h photoperiods appear to be transitional photoperiods for growth and flowering. Maximum flowering percentages of several clones occurred under ≥15-h and NI photoperiods. Flowering percentages for 'Hyacinthina', *H. plantaginea*, 'Tokudama' gold, and 'Tokudama' green were lower under continuous light than the 16-h treatment; while flowering percentages under NI were often as high or higher than the continuous photoperiod treatment.

No *H. montana* plants flowered without exposure to cold (Figure 16A). No flowering occurred under 12 h, and incomplete flowering occurred under all other photoperiods for cooled plants (Figure 16E). Time to flower ranged from 60 to 86 days and was not affected by cold or photoperiod. However, flowering of one cooled plant

occurred in 45 days under the 10-h photoperiod, thus suggesting that the flower bud was initiated prior to cooling (Figure 16F; Table 3).

No 'Hyacinthina' plants flowered in 1997-1998, and only noncooled plants flowered in 1998-1999 under the 24-h photoperiod. After cold, 'Hyacinthina' required photoperiods ≥14 h and NI for flowering (Figure 14A, E). Time to flower decreased following cold but did not vary with photoperiod (Figures 14B, F; Table 3).

Flowering of 'Tokudama' gold improved in 1998-1999 although complete flowering was never achieved under any photoperiod treatment. 'Tokudama' gold plants flowered without cold under 24 h in 1997-1998 and under 16 h in 1998-1999 (Figure 19A, E). Following cold treatment, flowering percentages were ≥70% under ≥14-h photoperiods and NI, except for the 24-h photoperiod (Figure 19E). One noncooled plant and all cooled plants grown in 1998-1999 flowered in 8 to 9 weeks irrespective of photoperiod (Figures 19B, F; Table 3). Flower buds formed on several 'Tokudama' gold plants grown under 10-, 12-, and 13-h photoperiods in 1998-1999; however, the buds of 10-h and 13-h plants aborted prior to anthesis while the buds of 12-h plants developed to anthesis (Figure 19E).

Noncooled 'Tokudama' green plants did not flower in 1997-1998, and only 30% flowered under 16-h and 24-h photoperiods in 1998-1999 (Figure 20A, E). Following cold, flowering in 1998-1999 occurred under ≥13-h photoperiods with 100% flowering under 16 h (Figure 20E). Time to flower decreased from 105 days for noncooled plants to 64 days for cooled plants (Figure 15F). The reduction in time to flower resulted from a decrease in days to visible bud (Table 4).

'Lancifolia', *H. plantaginea*, and 'Royal Standard' plants flowered to varying

degrees under photoperiods ≥14 h prior to and following cold in 1998-1999. Flowering of 'Lancifolia' was greater in 1998-1999 than the previous year. Essentially all noncooled 'Lancifolia' plants flowered under 24-h and NI photoperiods, and all cooled plants flowered under ≥14 h and NI (Figures 13A, E). Time from forcing to visible bud was two weeks longer under the 14-h and 15-h photoperiods than for photoperiods ≥16-h (Figure 13B, F; Table 4). *H. plantaginea* did not flower in 1997-1998, and incomplete flowering of noncooled and cooled plants reached a maximum under 16-h and 24-h photoperiods in 1998-1999 (Figure 11A, E). All 'Royal Standard' plants flowered under 16-h photoperiods prior to cold and under NI following cold (Figures 12A, E). Flowering of noncooled and cooled *H. plantaginea* and 'Royal Standard' plants occurred in 14 to 15 weeks and did not vary with photoperiod (Figures 12B, F; 13B, F, Table 3).

No treatment combination resulted in 100% flowering of 'Undulata', yet flowering percentages were generally greater for larger plants in 1998-1999 (Figures 17A, E). Flowering occurred under ≥15-h photoperiods prior to cold and under ≥13-h photoperiods following cold with some exceptions. Maximum flowering occurred under 24 h in 1998-1999 (Figures 17A, E). Time to flower decreased following cold in 1998-1999 but did not vary with photoperiod treatment (Figure 17B, F; Table 3). The reduction in time to flower resulted from a 2 to 5 week decrease in time to visible bud (Table 4). The most rapid uniform flowering of 'Undulata' occurred in 10 weeks under continuous light following cold treatment.

Flowering percentages for 'Golden Scepter' and 'Golden Tiara' increased in 1998-1999. Flowering of both clones occurred under ≥14-h photoperiods prior to cold and under ≥13-h photoperiods following cold (Figures 15A, E; 18A, E). Essentially all

noncooled and cooled 'Golden Scepter' plants flowered under ≥16 h and NI (Figures 15A, E). Time to flower of cooled 'Golden Scepter' plants decreased 2 to 3 weeks under these photoperiods due to a decrease in time to visible bud (Table 4). Flowering percentage of noncooled 'Golden Tiara' plants varied for photoperiods ≥14 h and NI, and essentially all cooled plants flowered under photoperiods ≥ 13 h and NI (Figure 17E). Time to flower of 'Golden Tiara' plants decreased 6 to 7 weeks under photoperiods ≥16 h following cold (Figure 18B, F). Uniform flowering of cooled 'Golden Tiara' plants occurred in 9 to 10 weeks for ≥13-h photoperiods (Figure 18E; Table 4).

Reproductive characteristics. Neither cold nor photoperiod consistently affected flower number or inflorescence height (Table 5). Flower number and inflorescence height were highly variable for *H. montana*, *H, plantaginea*, 'Tokudama' gold, and 'Tokudama' green plants following cold in 1998-1999. Flower number and inflorescence height of *H. plantaginea* decreased following cold in 1998-1999 (Figures 11C, D, G, H) while 'Royal Standard' flower number and inflorescence height were slightly greater for cooled plants than for noncooled plants (Figures 12C, D, G, H). Flower number and inflorescence height did not vary with photoperiod for *H. plantaginea* or 'Royal Standard' plants (Table 5). Flower number and inflorescence height of noncooled 'Lancifolia' plants were greater than cooled plants and decreased from 14 h to 24 h following cold in 1998-1999 (Figure 13C, D, G, H). Flower number and inflorescence height of 'Golden Tiara', 'Hyacinthina', *H. montana*, and 'Undulata' plants were not affected by cold treatment or photoperiod in either year (Table 5).

DISCUSSION

Hosta species are herbaceous perennials native to the temperate regions of China, Japan, and Korea (Schmid, 1991). They are long-day plants that naturally flower as the daylength increases in early-to-mid summer. Most hostas require a period of cold temperatures to break dormancy and long-day photoperiods for flowering. Each hosta clone in this study was previously determined to require 0, 3, or 6 weeks of cold for complete emergence (Fausey, 1999). The minimum duration of cold for emergence was required for uniform growth of all plants followed by flowering under long-day photoperiods.

Emergence of dormant buds was low under all photoperiod treatments prior to cold, and flowering responses of emerged plants were variable. Noncooled plants that emerged in both years may not have been fully dormant at the start of forcing. Hosta leaves were cut back to the crown prior to first frost after plants exhibited signs of leaf senescence. Further exposure to natural fall and winter conditions might have driven plants into a more-fully-dormant state where emergence would only occur following exposure to cold temperatures. Fifteen weeks of 5°C generally decreased time to flower and improved flowering percentage of hostas in this study. Cooled plants were taller, more vigorous, and typically had larger leaves than noncooled plants.

Average leaf size and leaf number were smaller under SD than LD for noncooled plants but did not vary appreciably following cold. Cooled plants emerged in response to the greenhouse temperature, and plants produced an initial flush of leaves irrespective of photoperiod following cold. Plants were not initially receptive to photoperiodic stimuli following emergence although prolonged exposure ($\geq$ 6 weeks) to short-day photoperiods

appeared to induce vegetative dormancy of all selections. Emergence in response to temperature is important for long-day plants that emerge early in the spring when short photoperiods might inhibit growth. Hostas naturally emerge in mid-to-late March and April in the southern United States (approximately 33°N) and in late April and May in the northern United States (approximately 42°N) (Solberg, 1988). The daylength including civil twilight as perceived by most plants ranges from 10 to 16 h at 40°N and from 11 to 15 h at 30°N throughout the year (Roberts and Summerfield, 1987). These latitudes closely correspond to the native habitat range of *Hosta* species. Consequently, hostas may be exposed to photoperiods ≤13 h upon emergence, yet the daylength would be sufficiently long to promote leaf production and induce flowering when plants become receptive to photoperiodic stimuli.

Some *H. montana* and 'Undulata' plants exhibited episodic growth patterns under long-day photoperiods. Leaf production ceased for an undetermined period of time. In many cases, these plants did not flower in the 105-day forcing time but might have flowered if grown for longer durations under long days. The mechanisms underlying this with-in season dormancy are unclear, although many hostas experience growth flushes in the natural environment (Pollock, 1997).

All hosta clones responded as obligate long-day-plants for flowering before and following cold in both years. There was a clear division between photoperiods which induced dormancy and those which allowed for continual growth and flowering. Essentially all clones remained vegetative and then went dormant under short-day photoperiods (≤13 h) with or without a cold treatment. Several clones had irregular flowering of single plants under photoperiods ≤13 h following cold, but the remaining

plants in the treatment went dormant. Flower buds may have been initiated in these plants prior to the start of the experiment. Only 'Golden Scepter' and 'Golden Tiara' had a high percentage of flowering plants under 13 h in 1998-1999. Emerged plants grown under ≥14 h and NI generally produced new vegetative growth and flowered with or without a cold treatment, although 100% flowering of each clone was not always achieved during the 15-week forcing period.

Complete flowering of many clones did not occur as flowering of *Hosta* appears to be influenced by plant size and crown maturity. Flowering percentages of single-eye divisions were low for noncooled and cooled plants in 1997-1998 and increased in 1998-1999. All plants had larger leaves in the second year. However, not all bulked plants flowered in 1998-1999 despite larger shoot sizes and a generally larger plant with multiple growing points. One- or two-year-old hosta divisions are considered immature and attain a mature leaf size and shape after completing six growing seasons (Schmid, 1991). Thus, nonflowering plants grown under inductive conditions in this experiment would be considered juvenile and physiologically incapable of flowering. Photoperiods which induced flowering of mature plants would be expected to induce flowering of juvenile plants upon reaching maturity.

For obligate photoperiodic responses, the photoperiod can be described as a base, transitional, or critical photoperiod according to it's effect on plant growth and development. The base photoperiod is the photoperiod where plants remain vegetative and at which progress towards flowering is zero (Roberts and Summerfield, 1987). Hostas clones grown under base photoperiods produced an initial flush of leaves then entered a vegetatively dormant state. Photoperiods that induce only a percentage of

mature plants to flower while other plants in the population remain vegetative are called transitional photoperiods (Runkle et al., 1998). The critical photoperiod marks the transition from vegetative growth to reproductive growth in obligate plants. The critical photoperiod for hosta clones in this experiment is identified as the photoperiod where mature plants are induced to flower and juvenile plants remain actively vegetative and not dormant.

The response of *Hosta* to cold and photoperiod treatments varied between years with larger plants yielding more uniform growth and flowering following cold in 1998-1999. Therefore, the base and critical photoperiods are defined for cooled plants in 1998-1999 only. The base photoperiod was 12 h for 'Golden Tiara', 'Golden Scepter', and 'Tokudama' green plants; and 13 h for 'Hyacinthina', 'Lancifolia', *H. montana*, *H. plantaginea*, 'Royal Standard', Tokudama' gold, and 'Undulata' plants following cold in 1998-1999.

The critical photoperiod varied between 13 and 14 h for all cooled hosta clones in 1998-1999. The critical photoperiod was ≥13 h for cooled 'Golden Scepter', 'Golden Tiara', and 'Tokudama' green plants with a high percentage of flowering in 9 to 10 weeks. *H. montana*, 'Tokudama' gold, and 'Undulata' plants also flowered in 9 to 10 weeks; 'Hyacinthina' plants flowered in 11 to 12 weeks; 'Lancifolia' and *H. plantaginea* plants flowered in 14 to 15 weeks; and 'Royal Standard' plants flowered in 15 to16 weeks under ≥14 h following cold. The highest flowering percentages and lowest time to flower generally occurred under photoperiods ≥16 h and NI. Time to visible bud generally did not change with increasing photoperiod.

Flowering of *Hosta* varies with latitude as photoperiod varies. Consequently, the

flowering season for hostas is generally divided into early, mid, mid-to-late, and late flowering periods (Grenfell, 1996). *H. montana* and 'Tokudama' naturally flower in early-to-mid summer; 'Golden Scepter', 'Golden Tiara', 'Hyacinthina', and 'Undulata' naturally flower in mid summer; and 'Lancifolia', 'Royal Standard', and *H. plantaginea* naturally flower in mid-to-late summer (Grenfell, 1996). The early-to-mid and mid season flowering clones are induced to flower under ≥13-h or ≥14-h photoperiods flowered in 10 to 12 weeks. However, the mid-to-late season clones flowered under ≥14-h photoperiods, and flowering of these plants took 3 to 6 weeks longer.

This experiment indicates that flowering of small hosta plants is undesirable as complete, rapid, and uniform flowering of these plants may not occur. Cooled plants will produce a vigorous flush of growth under all photoperiods. However, hosta clones should be grown under long-day (≥14 h and NI) photoperiods because plants will eventually go dormant under short-day (≤13 h) photoperiods. Photoperiods ≤13 h may limit the growth of *Hosta* in lower latitudes where short days during the growing season would induce dormancy and a lack of cold winter temperatures would ultimately prevent the breaking of crown dormancy and long-term plant survival.

For greenhouse production of hostas, long-day lighting ≥14 h should be provided when the natural daylength is ≤14 h in late winter or early spring. The photoperiod for complete, rapid flowering varies with genotype, but is generally ≥16 h or NI. Foliage plants of salable size can be produced in approximately six weeks at 20°C. The forcing of hostas to flower will take 3 to 12 weeks longer depending upon the genotype grown.

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Table 1. Plant material characteristics for 1997 and 1998 photoperiod experiments. All plants in 1998-1999 were grown in containers and originated from 1997 experimental plant material except for *H. montana* and 'Royal Standard'.

Clone	Source	Arrival Date	Starting material	Starting date of photoperiod treatments 1997	1998
'Golden Scepter'	Walters Gardens Zeeland, MI (42.9°N)	10/09/97	clump	10/14	10/14
'Golden Tiara'	Walters Gardens	10/09/97	clump	10/14	10/14
'Hyacinthina'	Wade and Gatton Nursery Bellville, OH (40.6°N)	10/31/97	bare root	11/01	10/14
'Lancifolia'	Sunnybrook Farms Chesterland, OH (41.5°N)	10/08/97	clump	10/10	10/14
montana	Walters Gardens	11/06/97	seed	—	10/14
plantaginea	Sunny Border Nursery Kensington, CT (41.6°N)	11/03/97	bare root	11/03	10/14
'Royal Standard'	Twixwood Nursery Berrien Springs, MI (41.9°N)	08/24/97	container	—	10/14
'Tokudama' gold	Klehm Nursery Champaign, IL (40.1°N)	10/13/97	bare root	10/14	10/14
'Tokudama' green	Klehm Nursery	10/13/97	bare root	10/14	10/14
'Undulata'	Walters Gardens	10/09/97	bare root	10/14	10/14

Table 2. Average air temperatures and average daily light integrals from start of forcing to the average date of flowering for cooled and noncooled *Hosta* clones under various photoperiods in 1998-1999.

Clone	Weeks of 5°C	Average air temperature (°C)								Average daily light integral[z] ($mol \cdot m^{-2} \cdot d^{-1}$)							
		Photoperiod															
		10	12	13	14	15	16	24	NI	10	12	13	14	15	16	24	NI
'Golden Scepter'	0	--[z]	--	--	20.7	20.7	20.7	21.6	21.1	--	--	--	6.5	6.5	6.5	6.5	6.5
	15	--	--	20.7	20.9	20.1	20.6	20.7	21.4	--	--	14.8	14.0	14.2	14.4	14.2	13.9
'Golden Tiara'	0	--	--	--	20.7	20.7	20.7	21.5	21.1	--	--	--	6.5	6.5	6.8	6.5	6.7
	15	--	--	20.7	20.9	20.0	20.6	20.7	21.4	--	--	14.5	14.2	14.5	14.2	14.0	14.0
'Hyacinthina'	0	--	--	--	--	--	--	21.5	--	--	--	--	--	--	--	6.7	--
	15	--	--	--	20.9	20.1	20.5	20.5	21.4	--	--	--	15.2	15.7	15.0	14.8	15.0
'Lancifolia'	0	--	--	--	20.8	20.7	20.7	21.5	21.0	--	--	--	6.5	6.5	6.6	6.5	6.5
	15	--	--	--	21.2	20.1	20.4	20.5	21.6	--	--	--	15.4	13.8	15.7	15.7	15.9
montana	0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	15	20.9	--	20.7	20.0	20.1	20.5	20.7	21.5	11.9	--	14.8	14.3	14.2	15.2	14.1	16.0
plantaginea	0	--	--	--	20.8	20.6	20.7	21.5	21.0	--	--	--	6.6	6.6	6.5	6.6	6.6
	15	--	--	--	21.1	19.9	20.4	20.5	21.6	--	--	--	15.5	14.5	15.5	15.6	15.8
'Royal Standard'	0	--	--	--	20.8	20.6	20.7	21.5	21.1	--	--	--	6.8	6.5	6.6	6.7	6.6
	15	--	--	--	21.1	20.1	20.5	20.6	21.7	--	--	--	15.6	13.8	15.2	15.4	15.3
'Tokudama' gold	0	--	--	--	--	--	20.9	--	--	--	--	--	--	--	6.5	--	--
	15	--	21	--	20.9	20.1	20.6	20.7	21.4	--	14.1	--	14.1	13.9	13.9	13.9	14.1
'Tokudama' green	0	--	--	--	--	--	20.7	21.5	--	--	--	--	--	--	6.8	6.5	--
	15	--	--	20.7	20.8	20.1	20.6	20.7	21.4	--	--	14.1	14.0	14.1	14.1	14.1	13.9
'Undulata'	0	--	--	--	--	20.6	20.7	21.5	21.0	--	--	--	--	6.5	6.6	6.5	6.5
	15	--	--	--	20.9	20.0	20.5	20.7	21.4	--	--	--	14.5	14.3	14.5	14.2	14.3

[z] No plants flowered (--).

Table 3. Cold treatment and photoperiod effects on time to flower of *Hosta* clones in 1998-1999.

Clone	Days to visible bud			Days to flower			Days from visible bud to flower		
	Significance[z]								
	C[y]	P	CxP	C	P	CxP	C	P	CxP
'Golden Scepter'	NS	NS	NS	***	*	NS	**	*	NS
'Golden Tiara'	***	*	**	***	*	*	*	***	**
'Hyacinthina'	***	NS	NS	***	NS	NS	NS	NS	NS
'Lancifolia'	NS	NS	NS	**	NS	NS	NS	NS	NS
montana	NS	NS	NS	NS	NS	NS	NS	NS	NS
plantaginea	NS	NS	NS	NS	NS	NS	NS	**	NS
'Royal Standard'	**	NS	NS	NS	NS	NS	***	NS	*
'Tokudama' gold	NS	NS	NS	NS	NS	NS	NS	*	NS
'Tokudama' green	***	NS	*	***	*	**	NS	NS	NS
'Undulata'	***	NS	NS	***	NS	NS	NS	NS	NS

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

[y] C, cold treatment; P, photoperiod; CxP, cold treatment by photoperiod interaction

Table 4. Average days to visible bud and from visible bud to flower of 10

Table 4. Average days to visible bud and from visible bud to flower of *Hosta* clones in 1998-1999 having received zero or fifteen weeks of 5°C cold followed by various photoperiod treatments.

Clone	Weeks of 5°C	Days to visible bud									Days from visible bud to flowering								
		Photoperiod									Photoperiod								
		10	12	13	14	15	16	24	NI	Sign[z]	10	12	13	14	15	16	24	NI	Sign
'Golden Scepter'	0	--[y]	--	--	66	63	64	59	51	NS	--	--	--	24	27	28	23	26	L*
	15	--	--	49	40	40	41	41	39	Q**	--	--	29	27	28	28	27	26	NS
'Golden Tiara'	0	--	--	--	67	67	92	87	91	NS	--	--	--	26	26	29	29	26	NS
	15	--	--	44	41	44	41	41	40	NS	--	--	26	27	27	27	26	27	NS
'Hyacinthina'	0	--	--	--	--	--	--	97	--		--	--	--	--	--	--	21	--	
	15	--	--	--	63	66	60	61	58	NS	--	--	--	23	23	24	23	25	NS
'Lancifolia'	0	--	--	--	71	76	74	75	74	NS	--	--	--	24	26	23	27	25	NS
	15	--	--	--	84	89	77	77	71	Q***	--	--	--	28	30	28	26	31	NS
montana	0	--	--	--	--	--	--	--	--		--	--	--	--	--	--	--	--	
	15	--	--	49	39	37	37	34	35	NS	--	--	25	34	33	49	27	31	Q*
plantaginea	0	--	--	--	89	88	82	75	85	NS	--	--	--	21	23	23	22	22	NS
	15	--	--	--	88	76	86	85	82	NS	--	--	--	22	26	25	22	20	NS
'Royal Standard'	0	--	--	--	90	87	89	90	81	NS	--	--	--	28	26	26	27	28	NS
	15	--	--	--	78	79	85	81	84	Q*	--	--	--	29	36	31	30	30	NS
'Tokudama' gold	0	--	--	--	--	--	42	--	--		--	--	--	--	--	26	--	--	
	15	40[x]	40	45[x]	40	40	42	43	39	NS	--	22	--	24	26	23	22	24	NS
'Tokudama' green	0	--	--	--	--	--	95	85	--		--	--	--	--	--	26	20	--	
	15	--	--	42	43	43	40	41	42	NS	--	--	23	22	23	24	22	23	NS
'Undulata'	0	--	--	--	--	78	57	78	72	NS	--	--	--	--	26	27	27	28	NS
	15	--	--	39	41	43	43	41	43	NS	--	--	31	29	29	30	29	29	NS

[z] NS, *, **, ***Nonsignificant or significant linear (L) or quadratic (Q) trend at $P \leq 0.05$, 0.01, or 0.001, respectively.
[y] No plants flowered (--).
[x] Flower bud aborted before anthesis.

Table 5. Cold treatment and photoperiod effects on vegetative and reproductive characteristics of *Hosta* clones in 1998-1999.

Clone	Plant height			Leaves per shoot			Average leaf size			Flower number			Inflorescence height		
	Significance[z]														
	C[y]	P	CxP	C	P	CxP	C	P	CxP	C	P	CxP	C	P	CxP
'Golden Scepter'	***	***	**	***	***	**	***	**	*	*	*	*	*	**	**
'Golden Tiara'	***	**	*	***	***	***	***	*	NS	*	NS	NS	NS	NS	NS
'Hyacinthina'	***	**	**	***	***	***	***	NS	NS	NS	NS	NS	NS	NS	NS
'Lancifolia'	***	***	**	**	NS	*	NS	NS	NS	***	**	***	NS	**	NS
montana	***	**	**	***	***	*	***	NS	NS	NS	NS	NS	NS	NS	NS
plantaginea	NS	***	***	***	***	***	***	***	***	**	NS	NS	***	NS	NS
'Royal Standard'	***	***	***	NS	***	***	NS	***	***	*	NS	NS	**	NS	*
'Tokudama' gold	***	NS	NS	***	***	**	***	*	NS	NS	*	NS	NS	**	NS
'Tokudama' green	***	***	NS	NS	NS	NS	**	**	NS	NS	**	NS	NS	NS	NS
'Undulata'	***	***	***	NS	***	***	NS	***	**	NS	NS	NS	NS	NS	NS

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

[y] C, cold treatment; P, photoperiod; CxP, cold treatment by photoperiod interaction

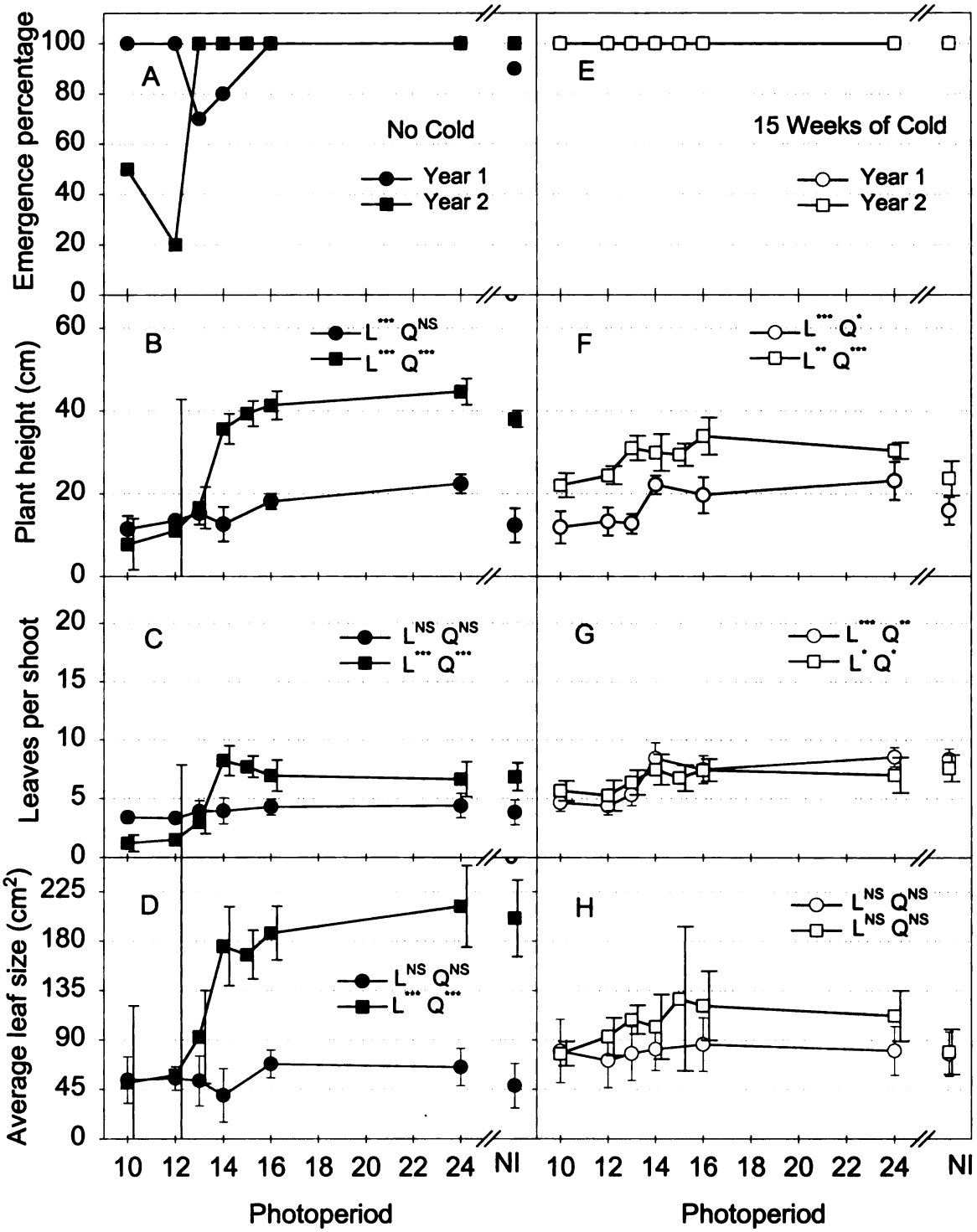

Figure 1. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta plantaginea* under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5° C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

Average leaf size (cm^2) Leaves per shoot Plant height (cm) Emergence percentage

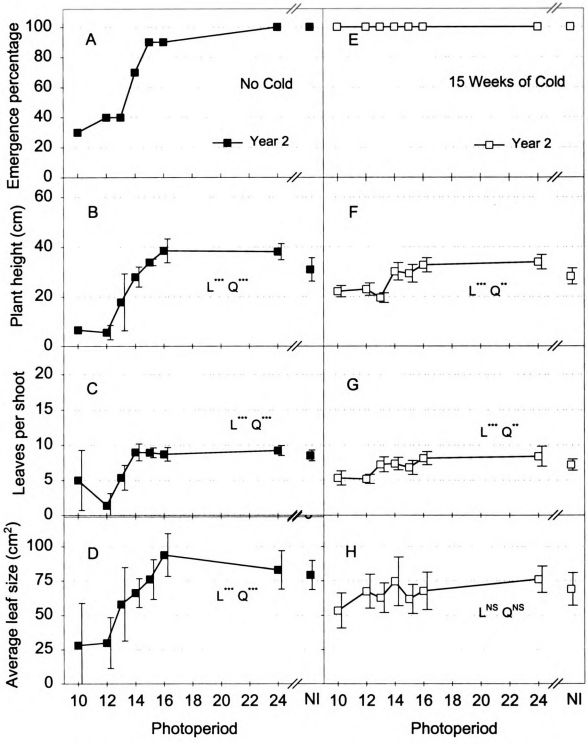

Figure 2. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta* 'Royal Standard' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.


Average leaf size (cm²)
Leaves per shoot

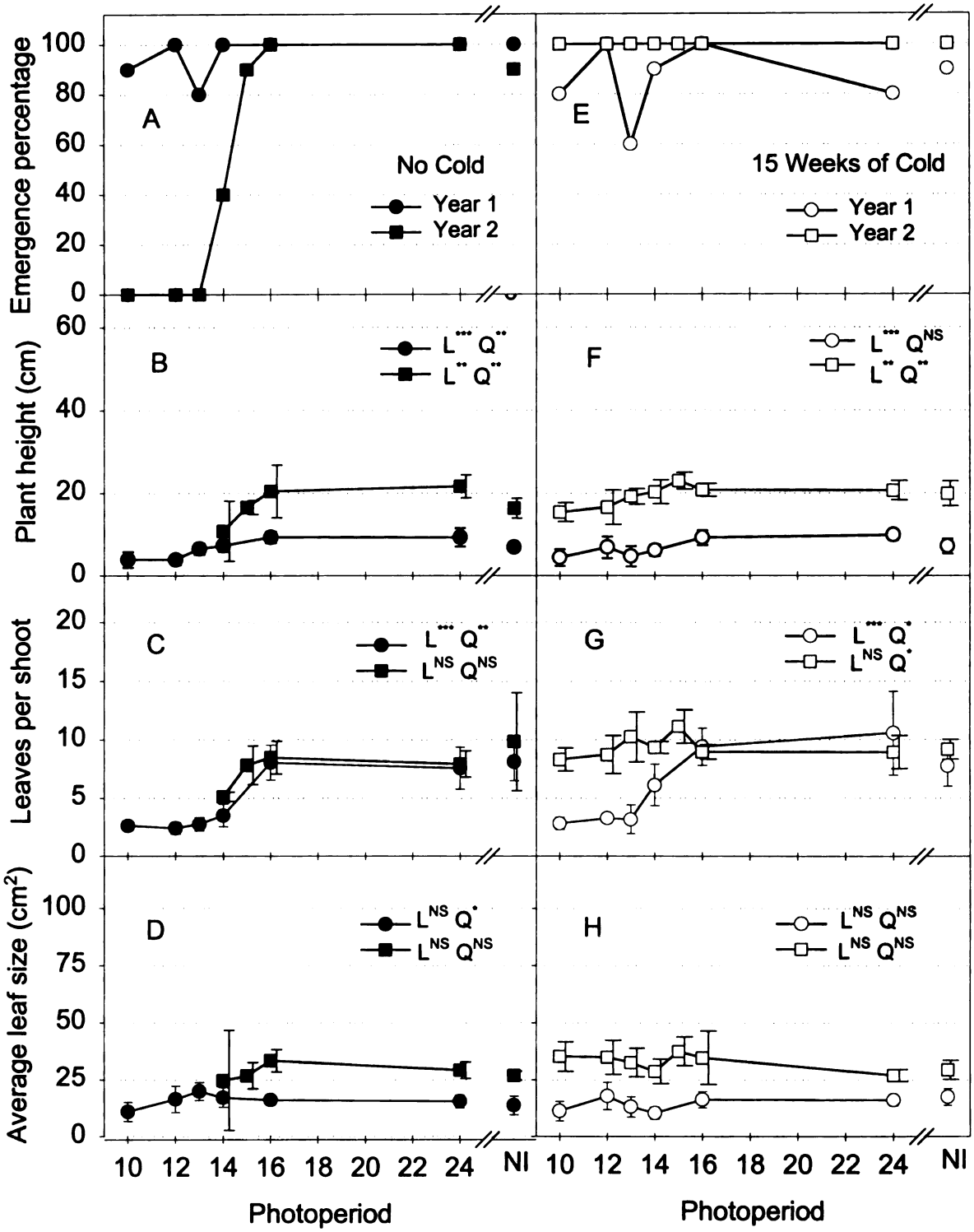

Figure 3. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta* 'Lancifolia' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

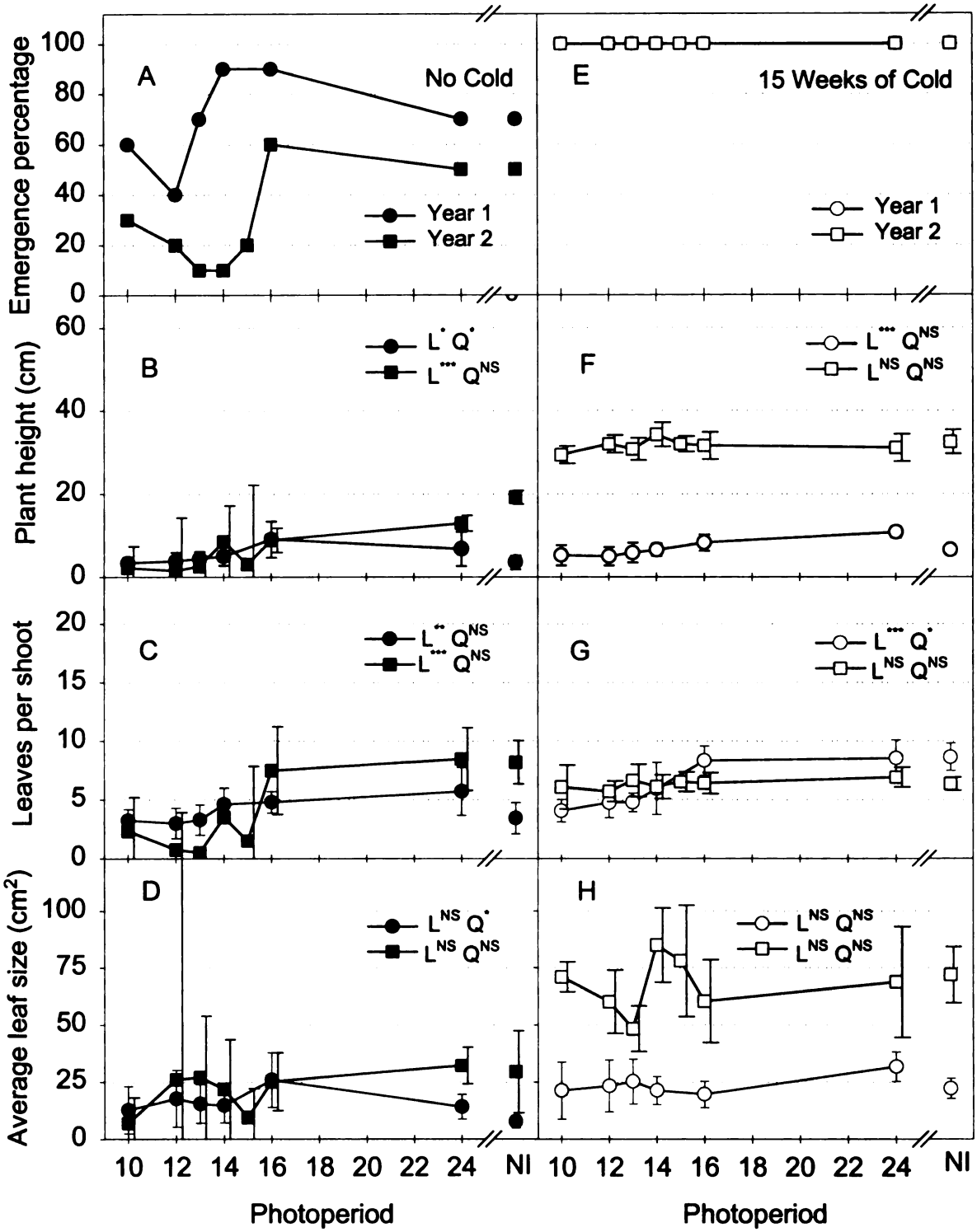

Figure 4. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta* 'Hyacinthina' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

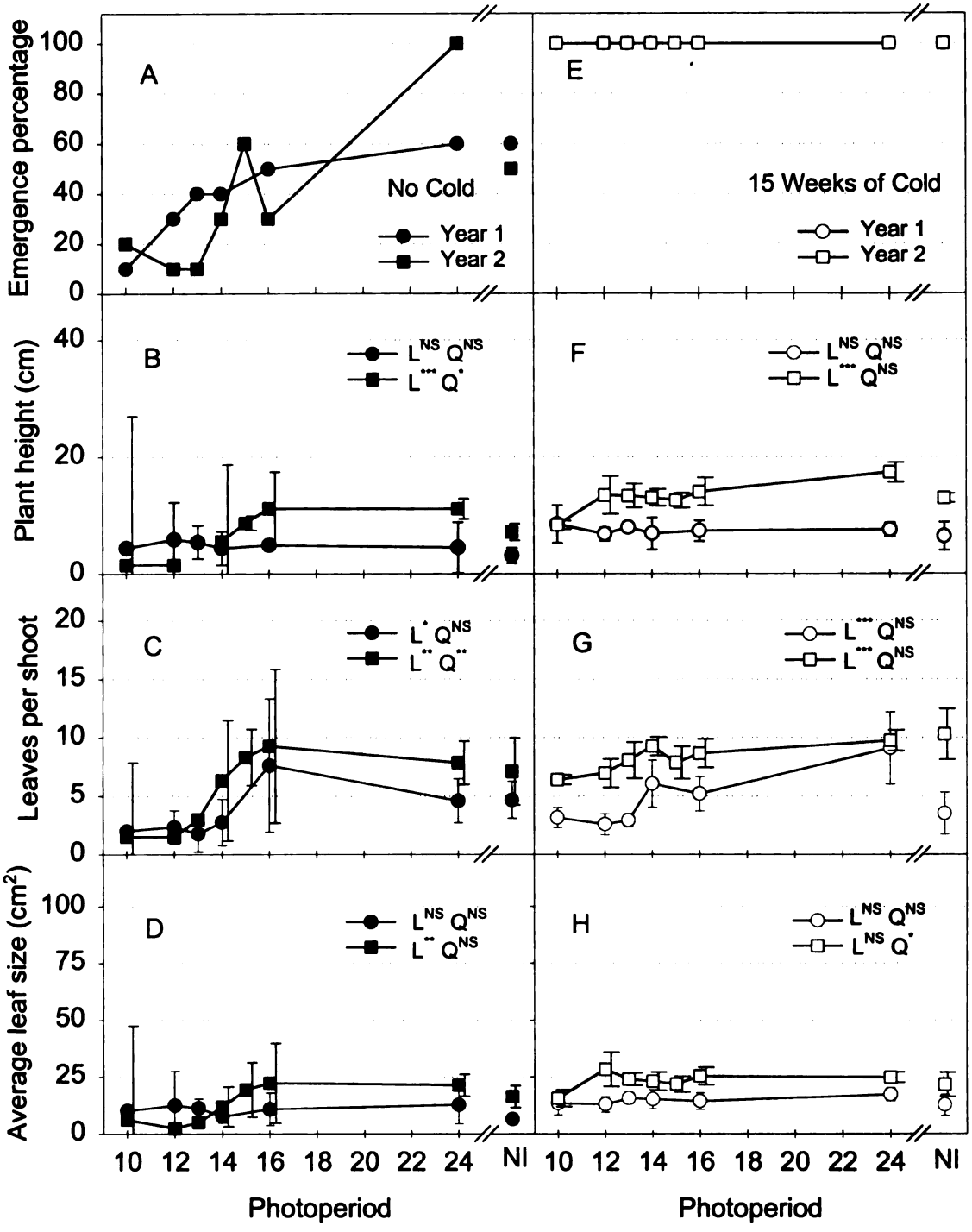

Figure 5. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta* 'Golden Scepter' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

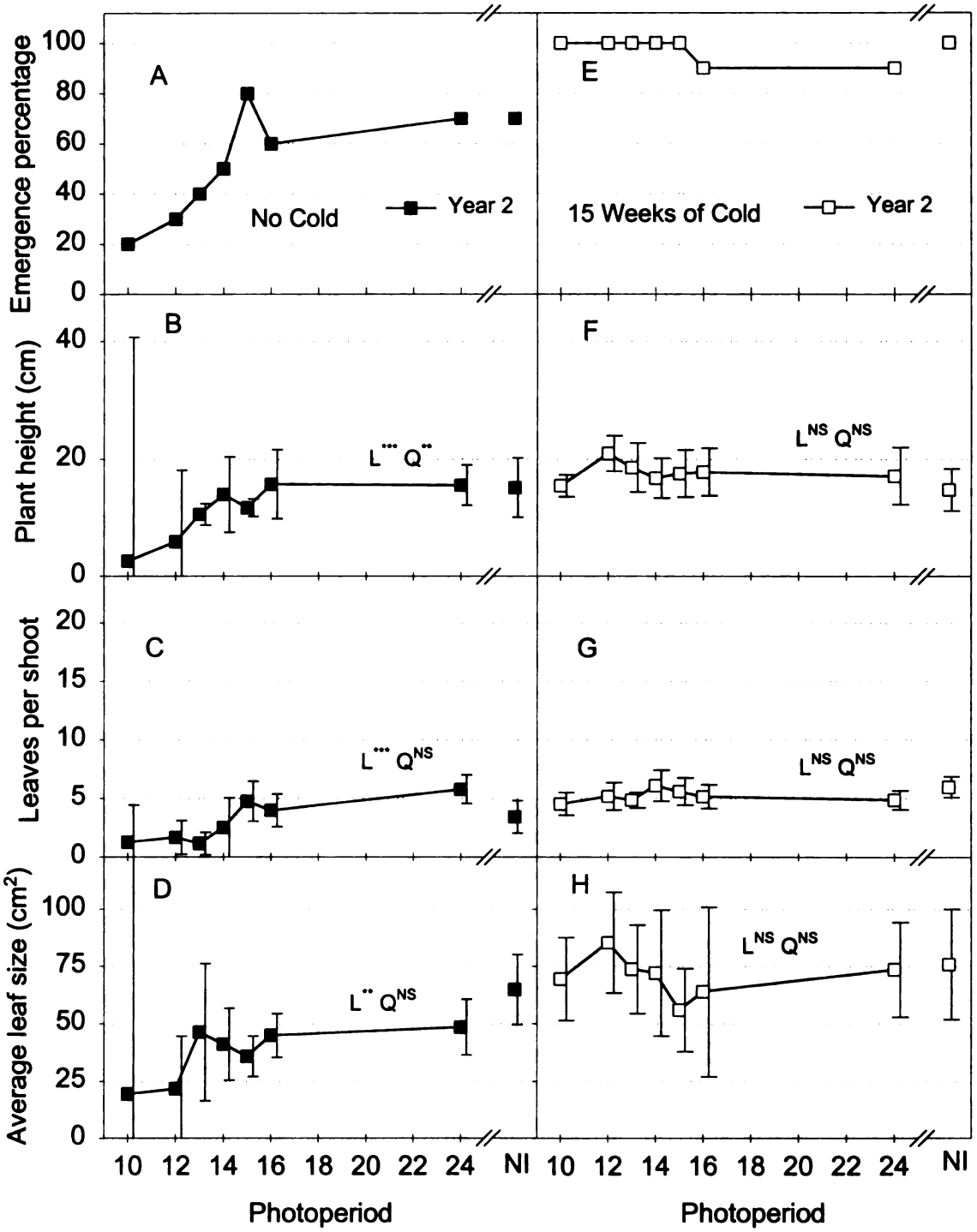

Figure 6. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta montana*under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P< 0.05$, 0.01, or 0.001, respectively.


Average leaf size (cm²)
Leaves per shoot

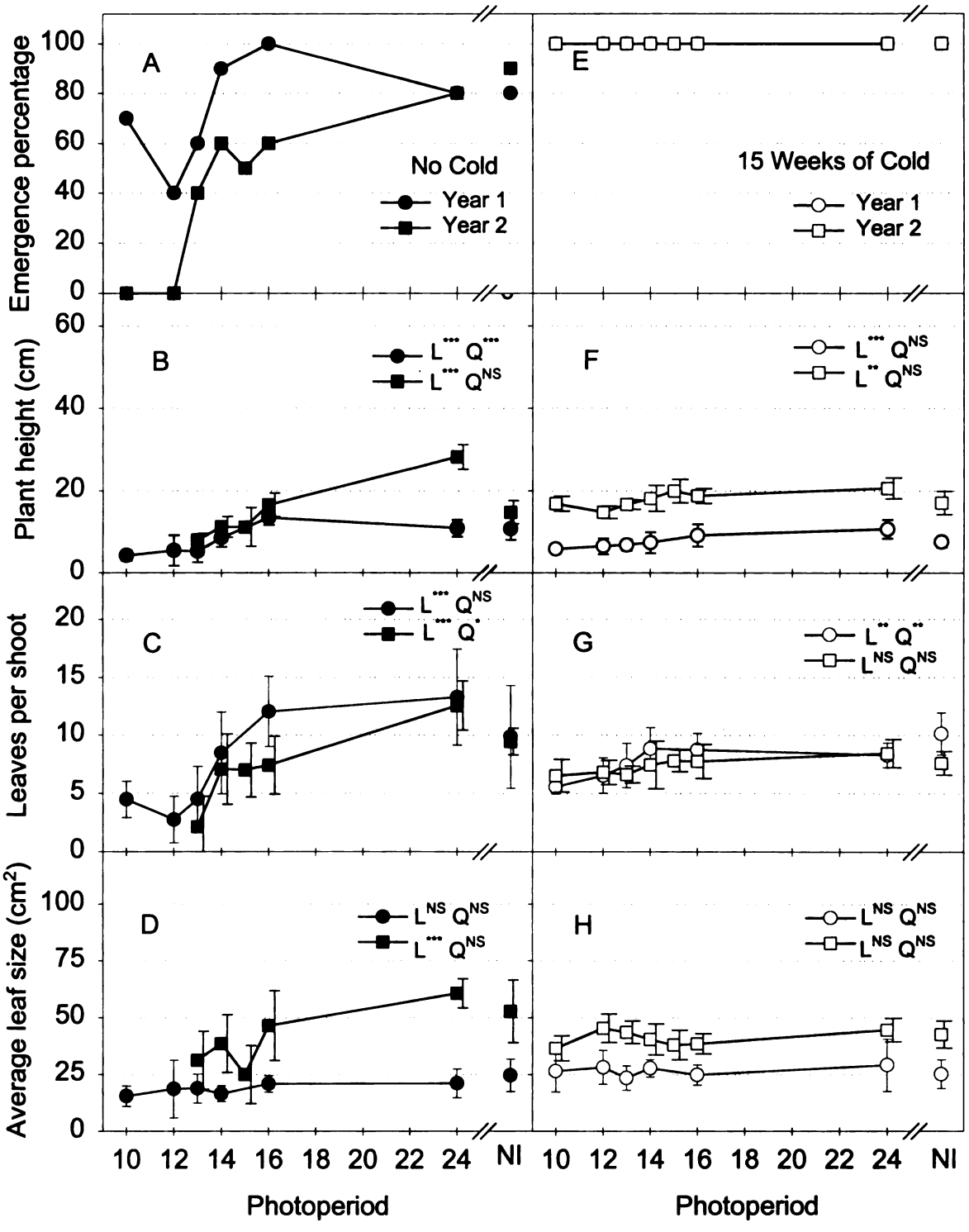

Figure 7. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta* 'Undulata' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificantor significant at $P < 0.05$, 0.01, or 0.001, respectively.

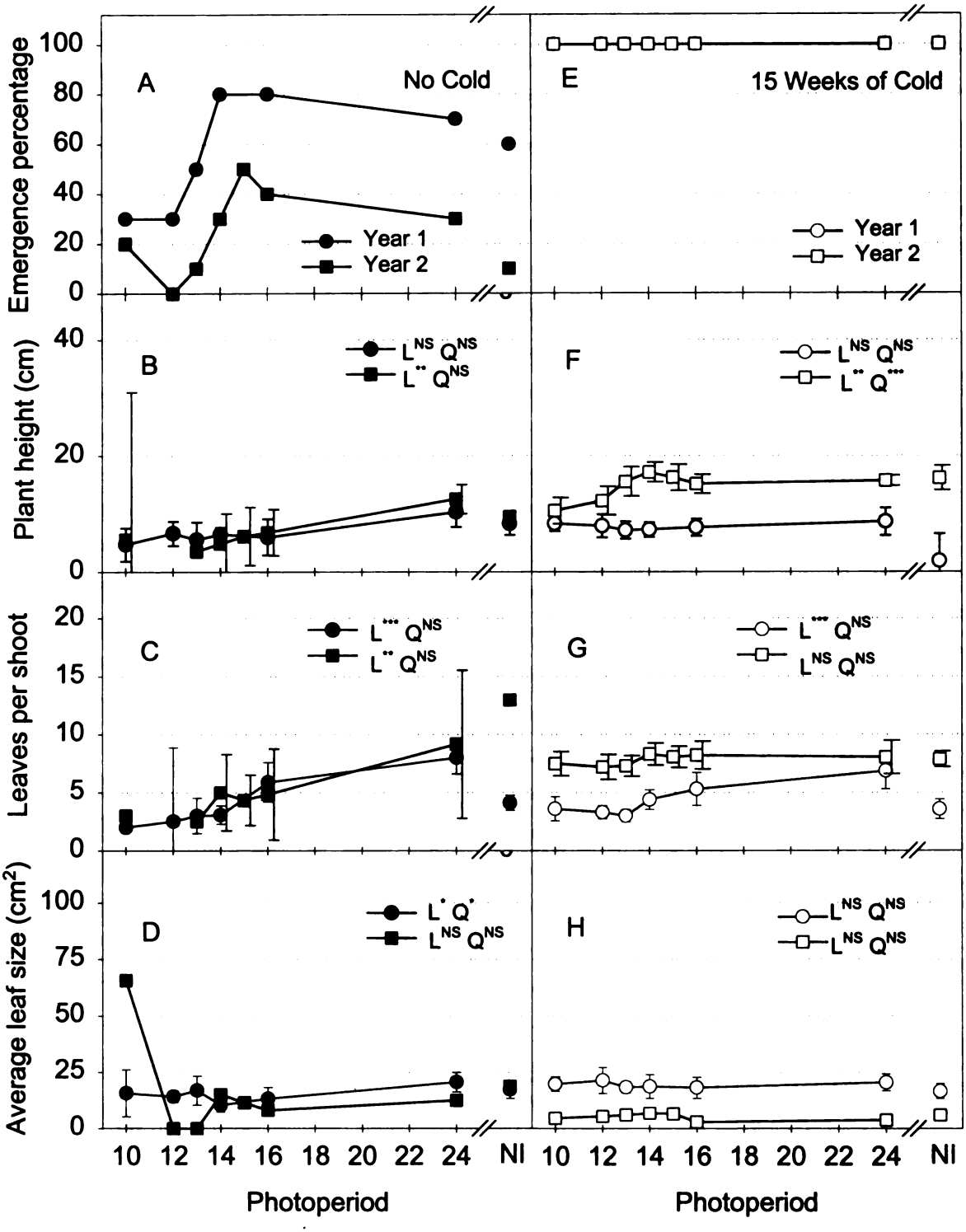

Figure 8. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta* 'Golden Tiara' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

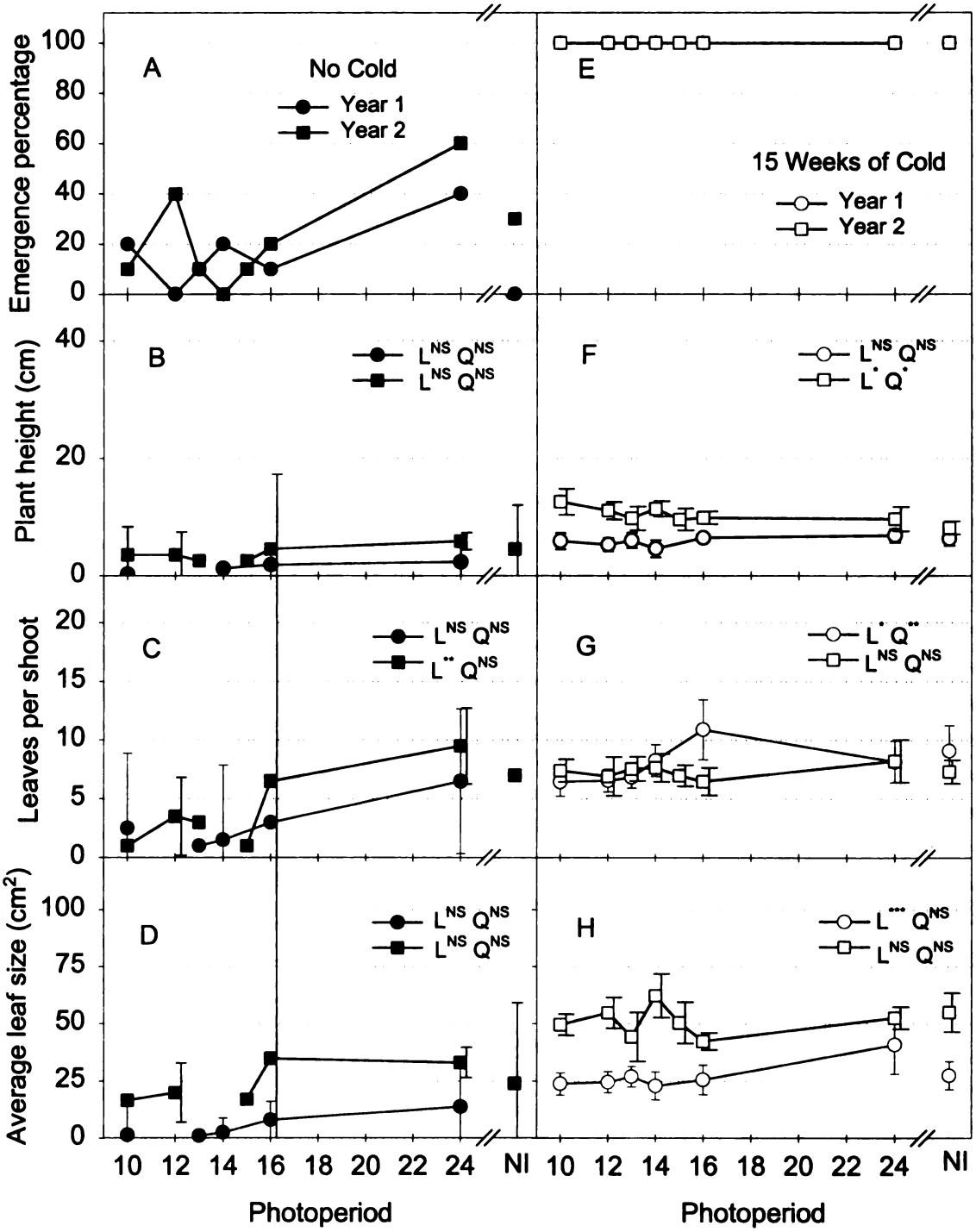

Figure 9. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta* 'Tokudama' gold under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

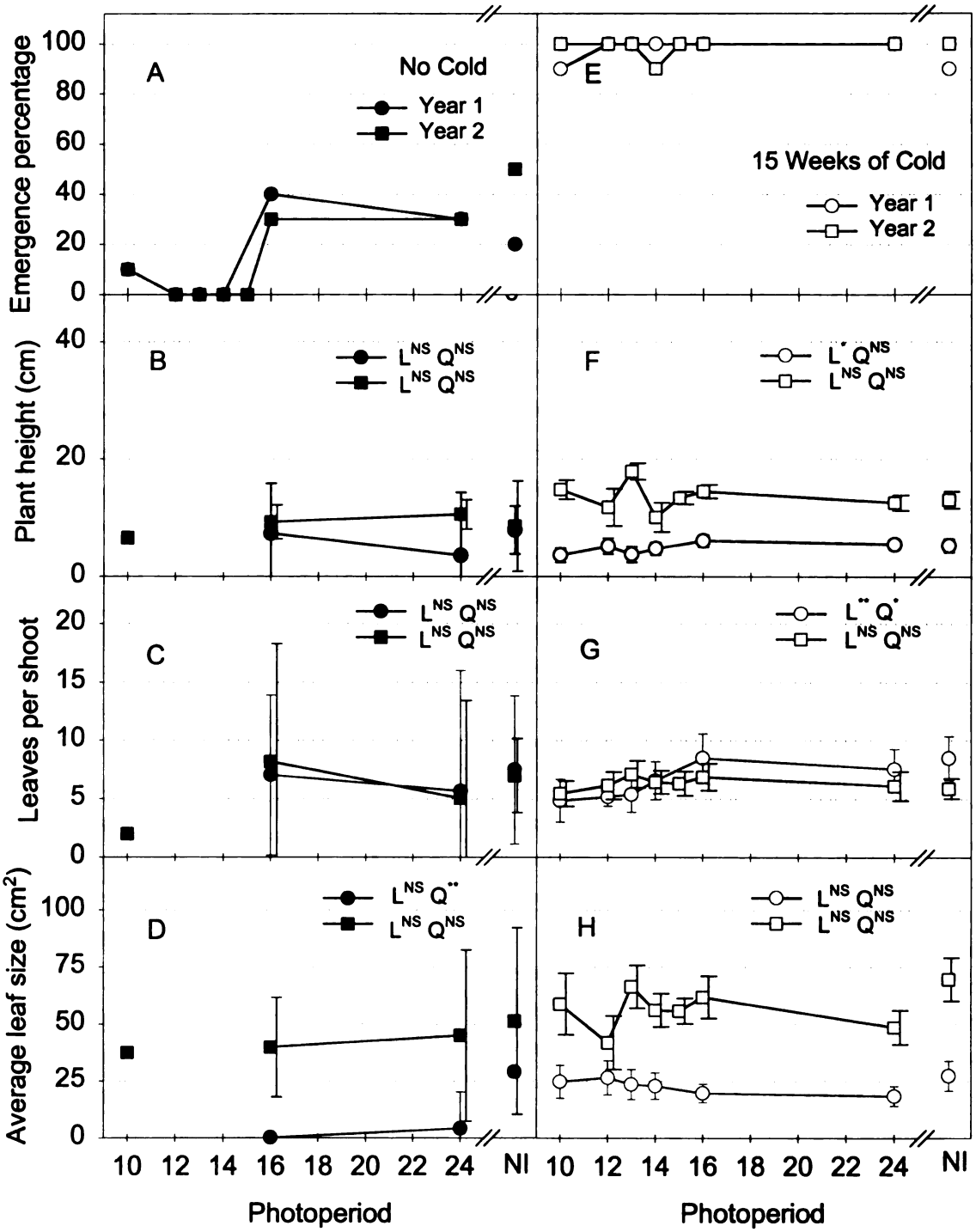

Figure 10. Percent emergence (A, E), plant height (B, F), average number of leaves per shoot (C, G), and average leaf size (D, H) of *Hosta* 'Tokudama' green under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

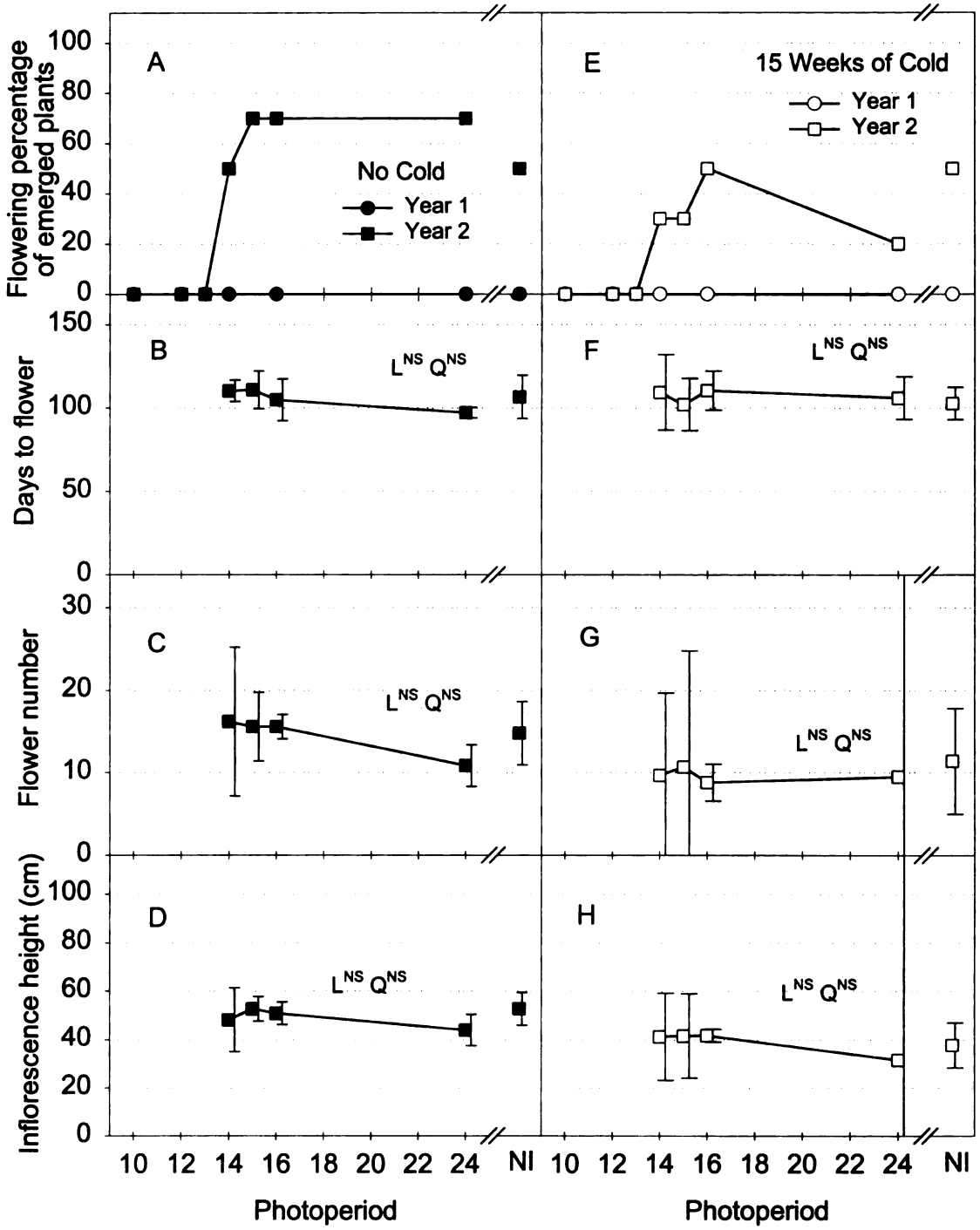

Figure 11. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta plantaginea* under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

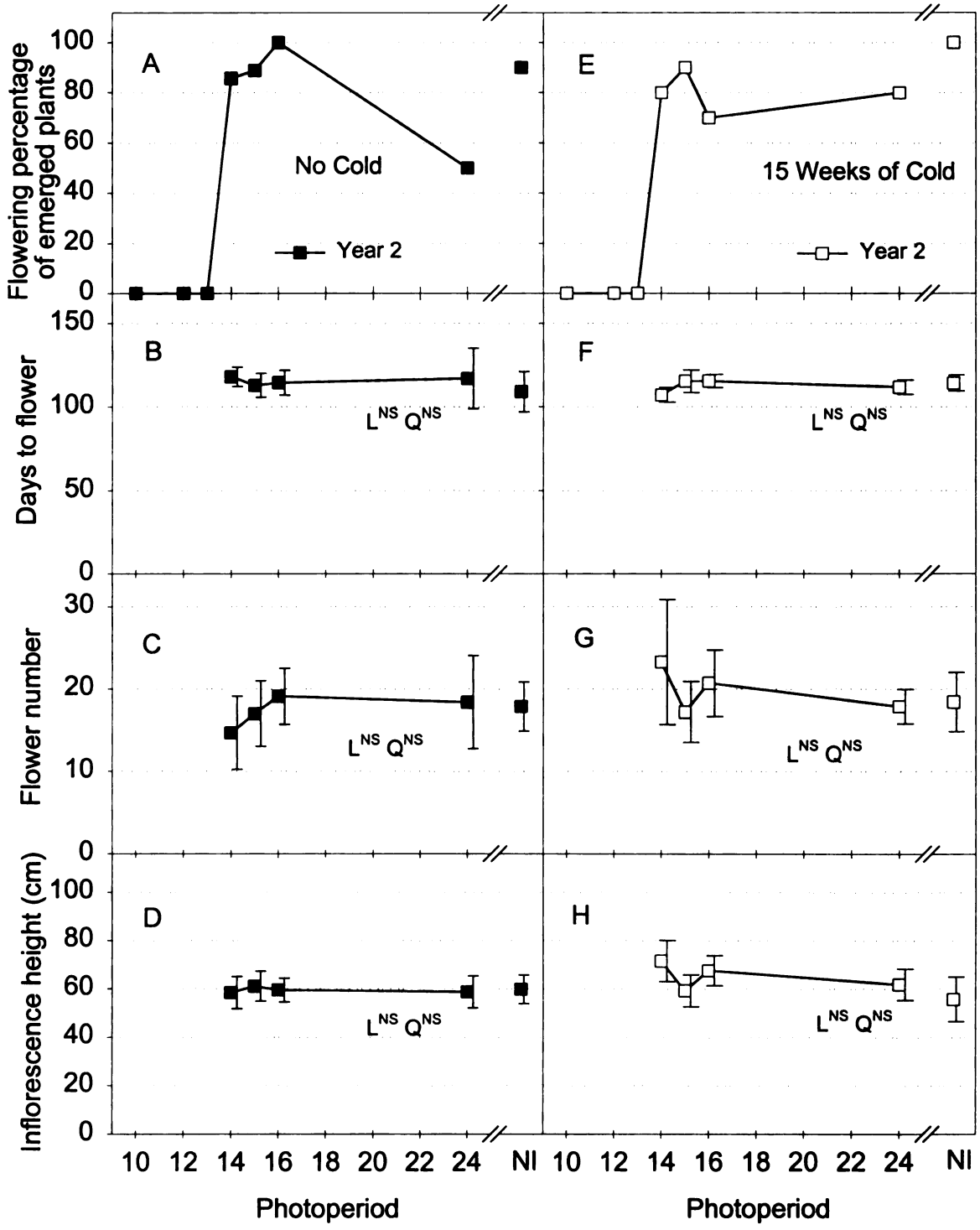

Figure 12. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta* 'Royal Standard' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

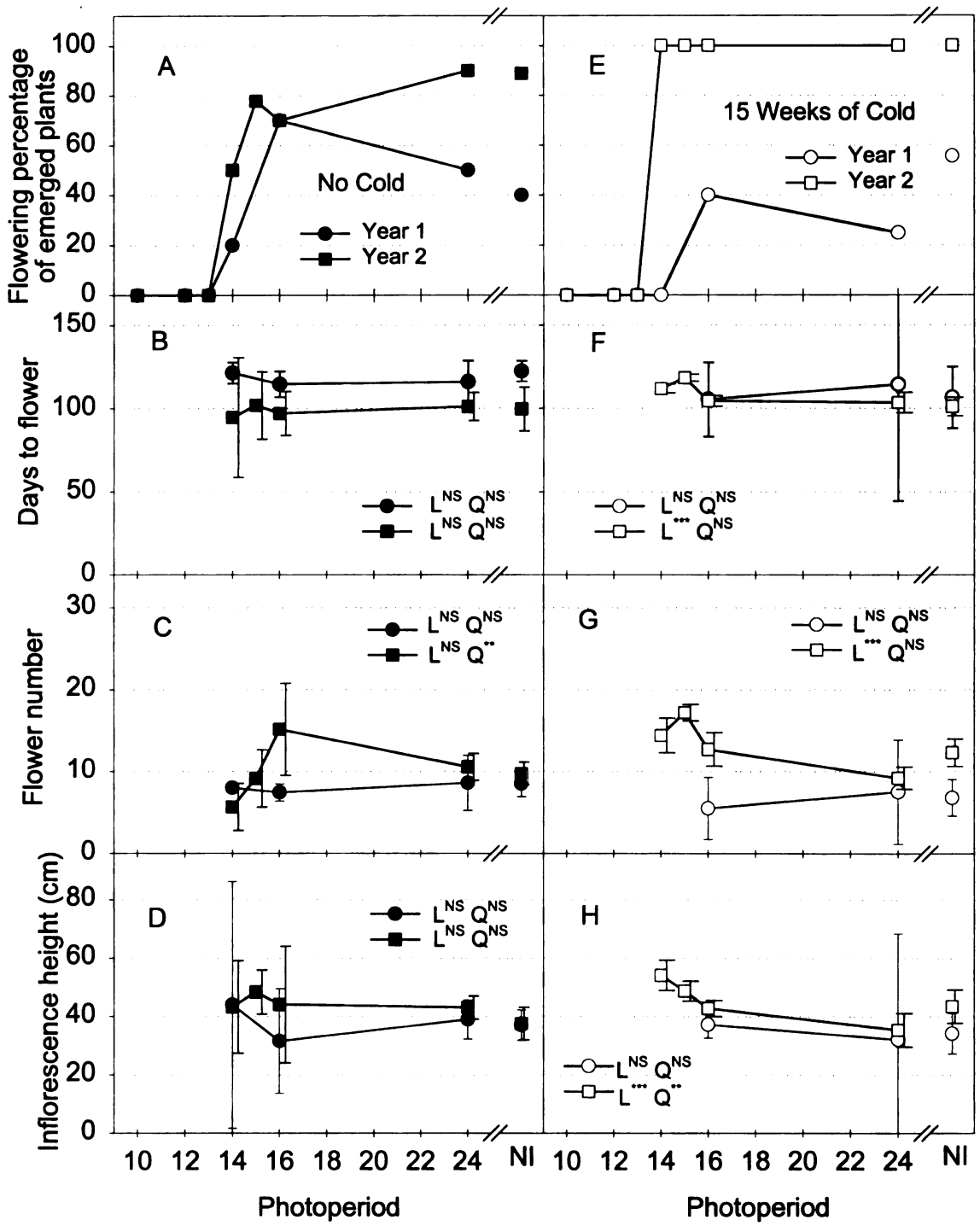

Figure 13. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta* 'Lancifolia' various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

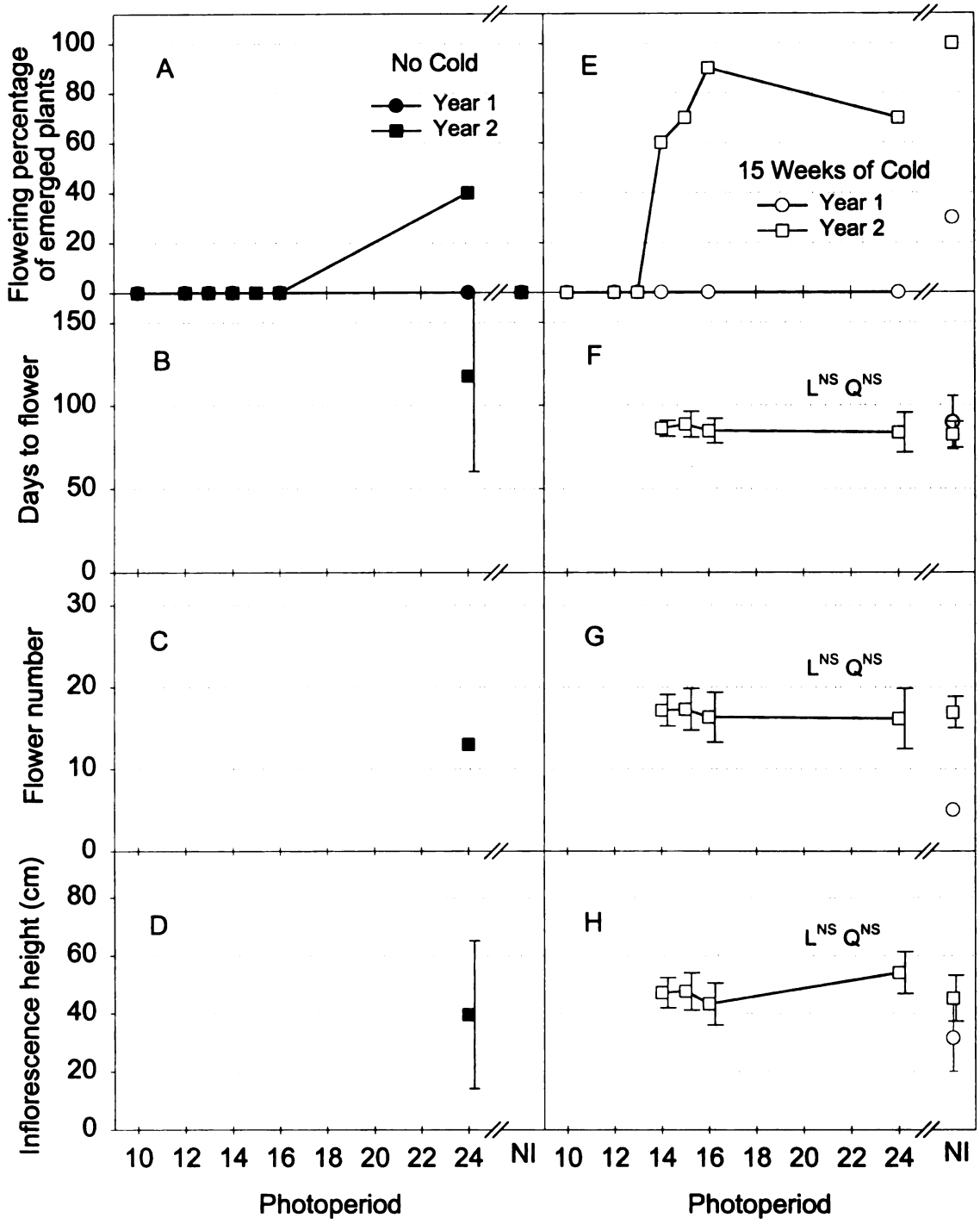

Figure 14. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta* 'Hyacinthina' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

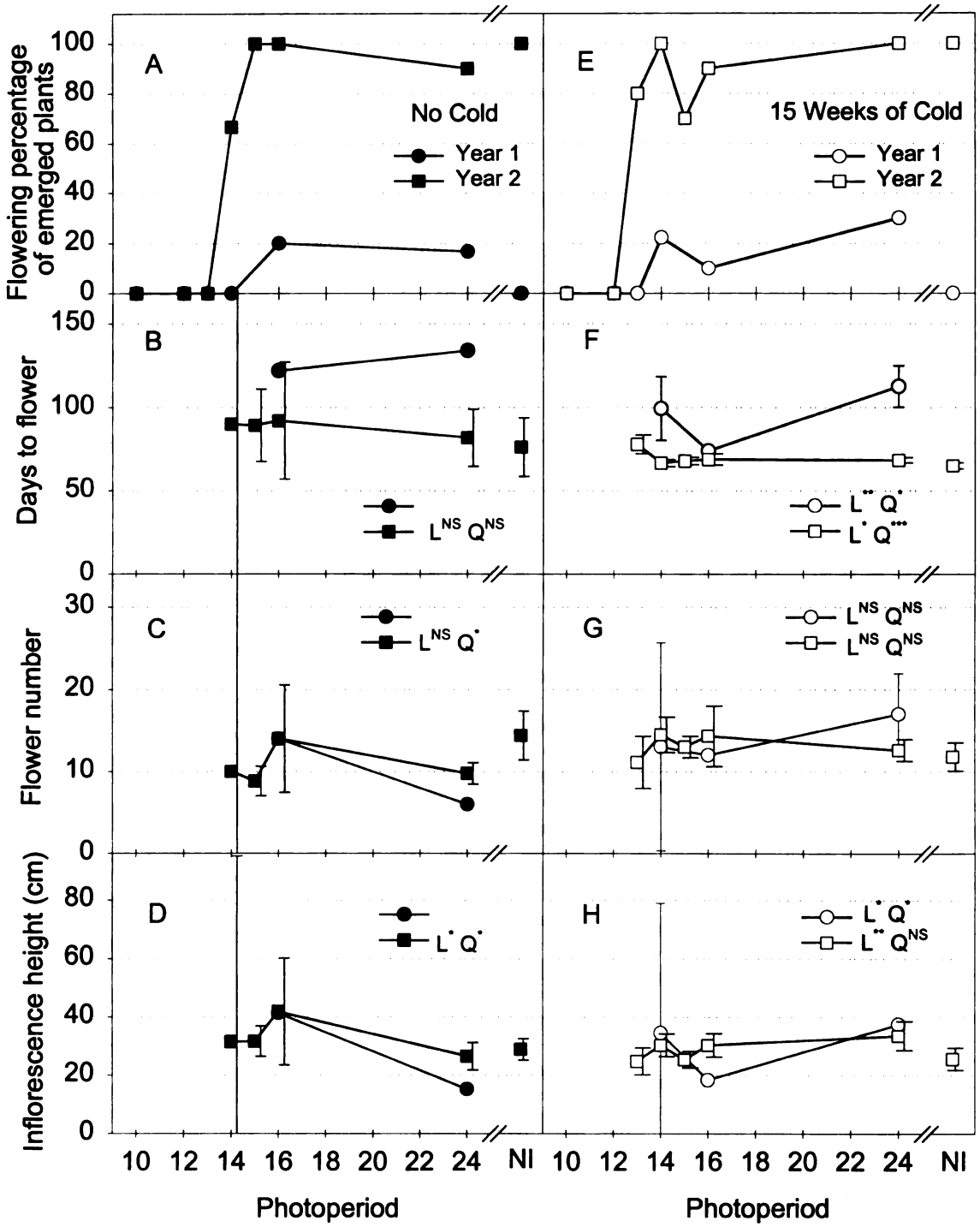

Figure 15. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta* 'Golden Scepter' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

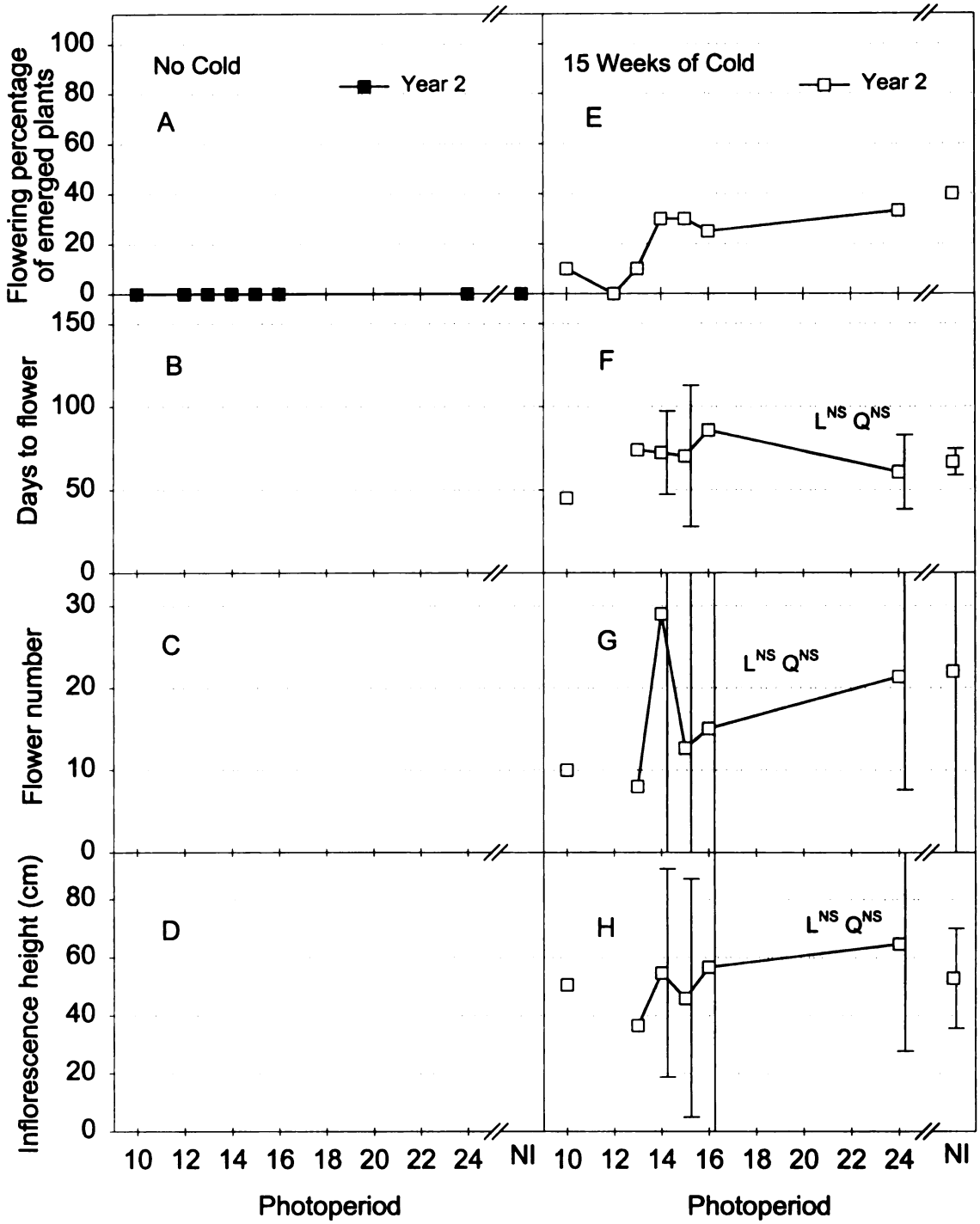

Figure 16. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta montana* under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one or and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

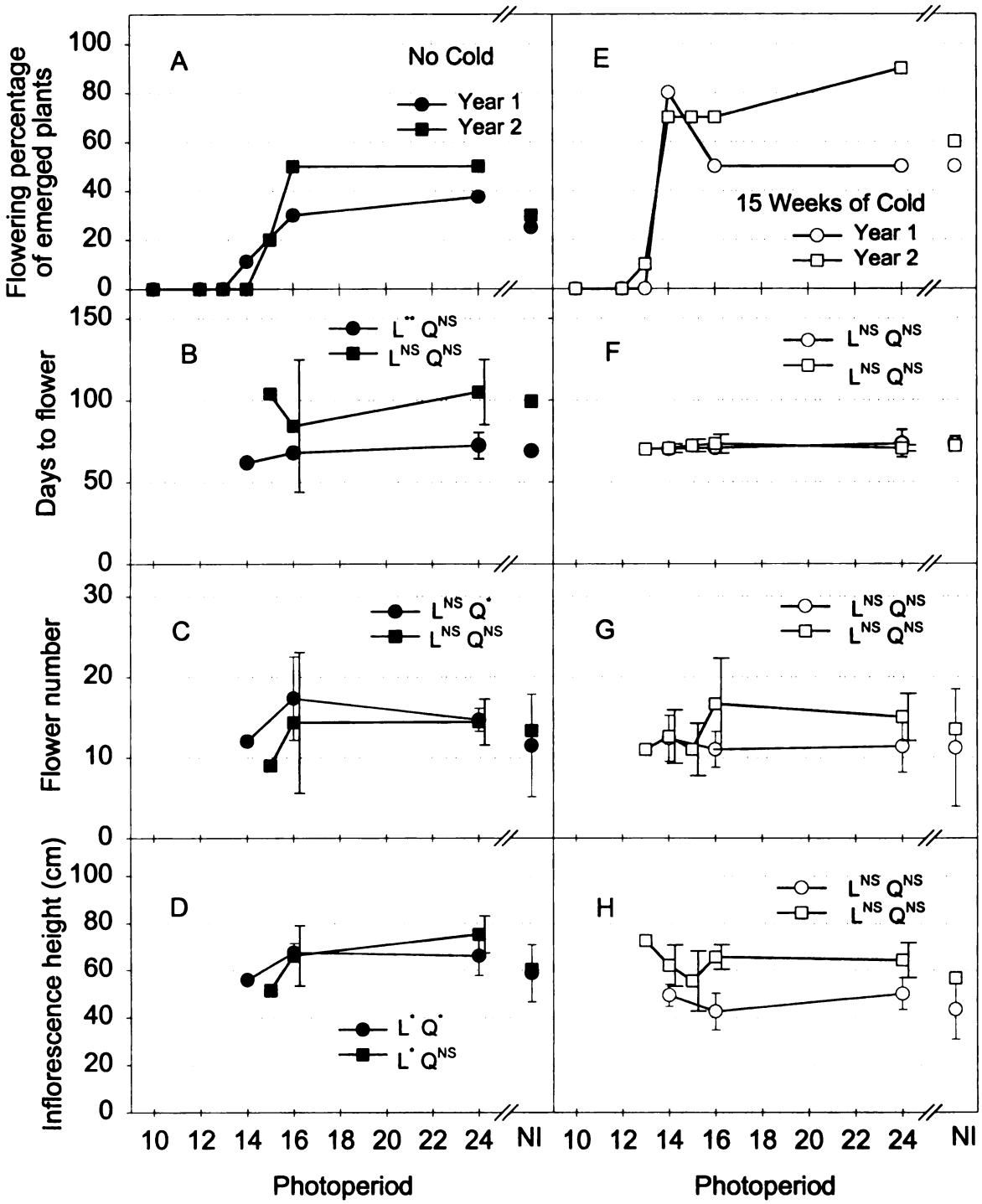

Figure 17. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta* 'Undulata' under various photoperiodafter 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificanbr significant at $P < 0.05$, 0.01, or 0.001, respectively.

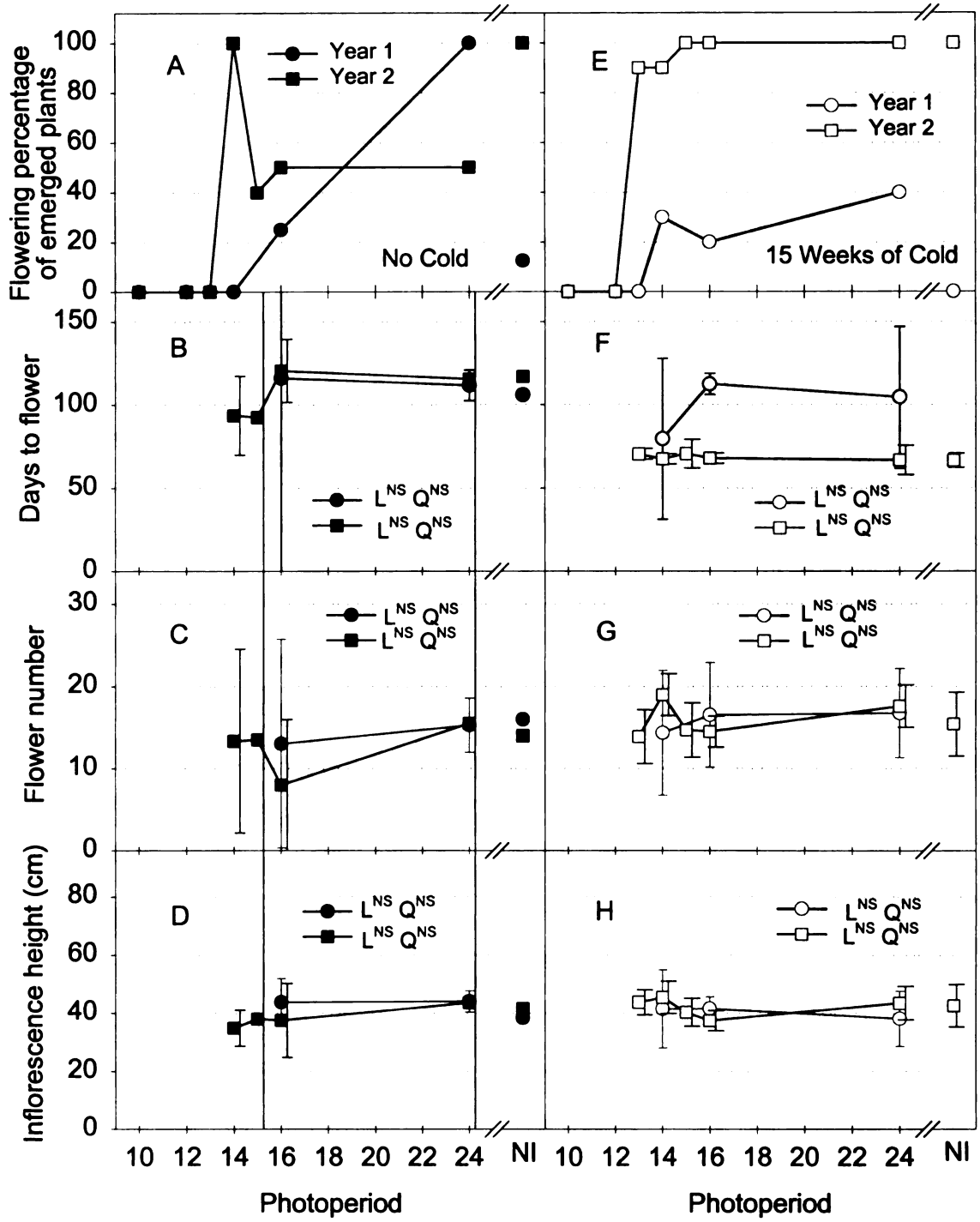

Figure 18. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta* 'Golden Tiara' under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

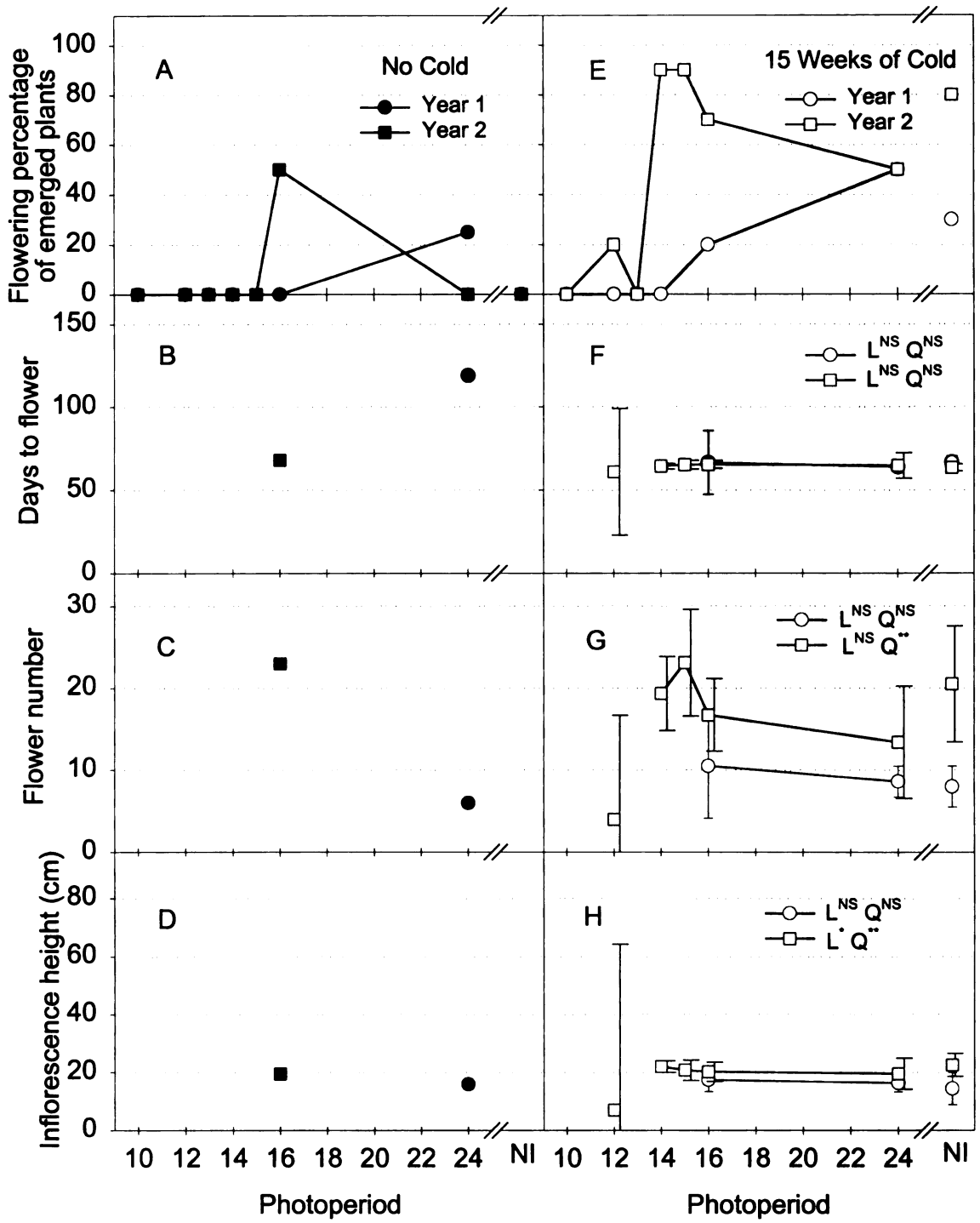

Figure 19. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta* 'Tokudama' gold under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

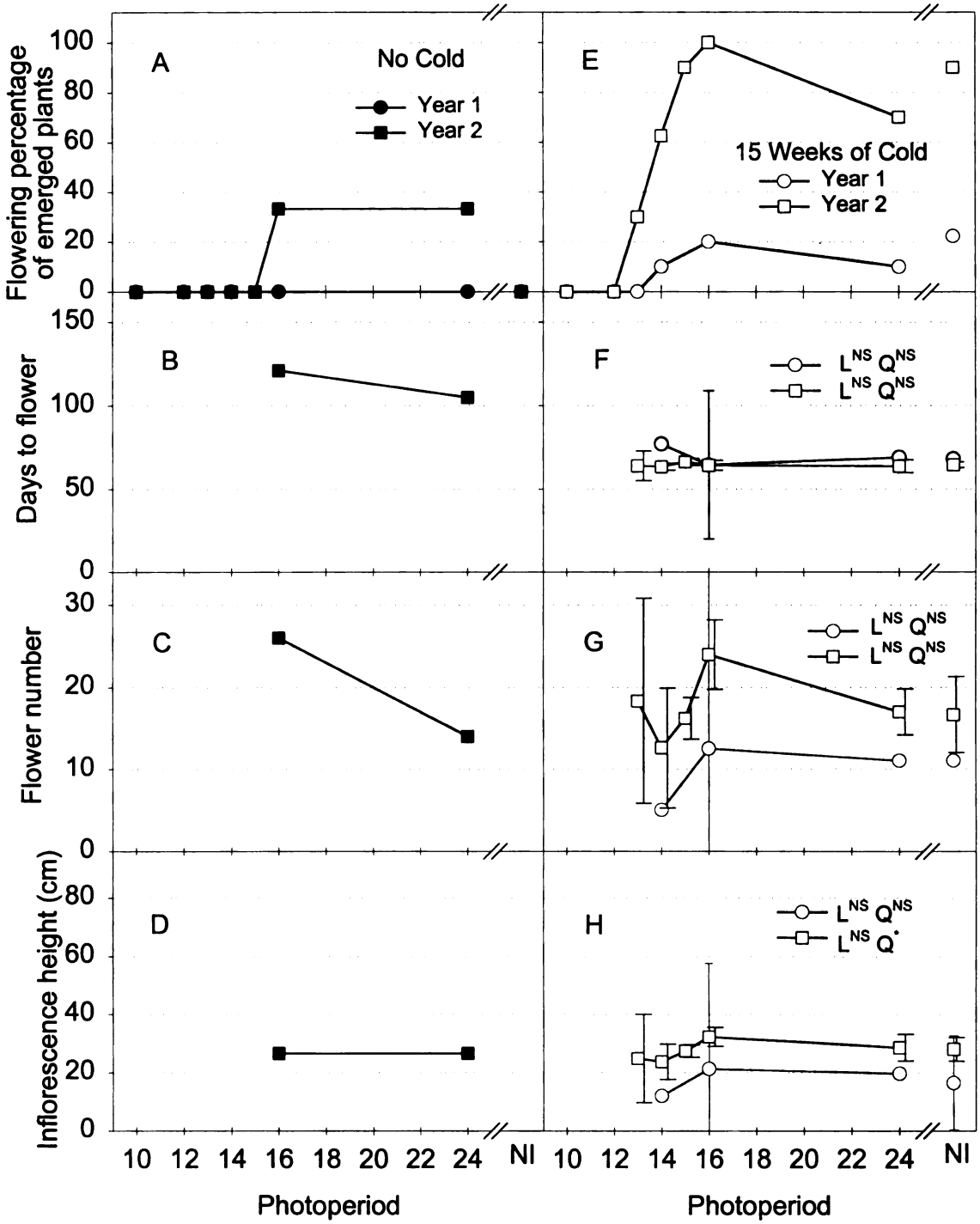

Figure 20. Percent flowering (A, E), number of days to flower (B, F), flower number (C, G), and inflorescence height (D, H) of *Hosta* 'Tokudama' green under various photoperiods after 0 (●, ■) or 15 (○, □) weeks of 5°C cold in year one and year two. Error bars are 95% confidence intervals and are offset to the right of year two data points for clarity. L=linear; Q=quadratic trends. NS, *, **,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

SECTION IV

THE EFFECTS OF FORCING TEMPERATURE FOLLOWING COLD TREATMENT ON GROWTH AND FLOWERING OF *HOSTA*.

The effects of forcing temperature following cold treatment on growth and flowering of *Hosta*.

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Production and Culture

The effects of forcing temperature following cold treatment on growth and flowering of *Hosta*.

Additional index words. Herbaceous perennial, base temperature, optimum temperature, plantain lily.

Abstract. The effects of forcing temperature following cold treatment on plant appearance and time to flower were evaluated for *Hosta* clones. *H. montana, H. plantaginea*, *H.* 'Francee', *H.* 'Golden Scepter', *H.* 'Golden Tiara', *H.* 'Hyacinthina', *H.* 'Lancifolia', *H.* 'Royal Standard', *H.* 'Tokudama' gold, *H.* 'Tokudama' green, and *H.* 'Undulata' plants were exposed to 5°C for 15 weeks. Plants were grown in greenhouse sections set at 14, 17, 20, 23, 26, or 29°C for 15 weeks with 16-h day-extension lighting. Days to visible bud (VB), days to anthesis (FLW), and days from VB to FLW decreased as temperature increased. The rate of progress toward visible bud and flowering increased as temperature increased for each clone. The base temperature and cumulative growing degree days for each hosta clone were calculated for each developmental stage. Plant height and average leaf size generally decreased as temperature increased from 14 to 29°C. Plant quality was greatest for plants grown at $\leq$23°C.

INTRODUCTION

Although photoperiod and vernalization typically control flower induction in herbaceous perennials, many developmental processes such as flower timing are temperature-dependent. Temperature directly determines the timing of floriculture crops by affecting the rate of plant development. The rate of development generally increases linearly with temperature until a maximum rate is achieved at an optimum temperature (Roberts and Summerfield, 1987). The general relationship between temperature and the rate of development toward flowering is measured by taking the reciprocal of days to flower (1/DTF). The linear relationship between the rate of progress towards flowering and the mean temperature T(°C) can be described as follows:

$$1/DTF = b_o + b_1 * T \qquad (1)$$

where b_o (intercept) and b_1 (slope) are species-specific constants. Both the base temperature and the cumulative thermal time (°days) required for flowering can be calculated from the constants in Equation 1:

$$T_b = -b_o/b_1 \qquad (2)$$

$$°days = 1/b_1 \qquad (3)$$

The base temperature (T_b) is the temperature at, or below which, the rate of progress toward flowering is zero (Roberts and Summerfield, 1987). Cumulative thermal time represents the number of thermal units above the base temperature required for flowering.

Forcing temperature not only affects flower timing but influences plant quality and appearance. Temperatures above 26°C reduced flower quality of *Echinacea purpurea* 'Bravado' and *Campanula* 'Birch Hybrid' (Finical et al., 1998a; Finical et al., 1998b). Flower-bud number for *Rudbeckia fulgida* 'Goldsturm' decreased 75% and flower

diameter decreased 2.7 cm as temperature increased from 16°C to 26°C (Yuan et al., 1998). Temperature also influenced plant height of *Achillea millefolium* 'Summer Pastels', *Coreopsis grandiflora* 'Sunray', and *Leucanthemum* x*superbum* 'Snowcap' as plants grown at 26°C were shorter than plants grown at 18°C (Zhang et al., 1996; Yuan et al., 1998).

Hostas are perennial shade plants commercially grown for their ornamental foliage. Limited information exists on the response of *Hosta* to temperature. Nau (1996) reported that divisions grown at 14°C night temperatures and 22 to 29°C day temperatures will have 8 leaves and be ready for sale in 7 to 9 weeks. Temperatures above 35°C reportedly promote heat-dormancy of hosta and may be responsible for heat-effected viridescence, the abrupt change of white or gold leaves to green in the summer (Pollack, 1997; Solberg, 1997). Therefore, the objective of this study was to characterize the vegetative responses of hosta clones to different temperatures and identify the relationship between temperature and time to flower.

MATERIALS AND METHODS

Plant material. *1997-1998.* Hostas were received from commercial producers (Table 1) in fall 1997 and were separated into single-eye divisions. Divisions were placed upright into 23 x 15 x 7 cm (6.8 L) bulb crates filled with a commercial soilless medium composed of composted pine bark, vermiculite, Canadian sphagnum peat, and coarse perlite with a wetting agent, lime, and starter fertilizer charge (High Porosity Mix, Strong-Lite Products, Pine Bluff, AR). Bulb crates were placed in a cooler set at 5°C for 12 weeks. Bulb crates were watered as needed with well water acidified with citric acid to a

pH of 6.0. Divisions were removed from the bulb crates after 12 weeks of cold, planted into 13-cm square containers, and placed in one of 6 greenhouses set to 14, 17, 20, 23, 26, or 29°C. Plants received a 16-h photoperiod provided by four-hundred-watt high-pressure sodium (HPS) lamps from 0500 to 0700 and from 1700 to 2300 that delivered approximately 90 $\mu mol \cdot m^{-2} s^{-1}$. HPS lamps provided a photosynthetic photon flux (PPF) of 100 $\mu mol \cdot m^{-2} s^{-1}$ when the ambient greenhouse PPF dropped below 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from 800 to 1700. Supplemental lighting was terminated when PPF exceeded 400 $\mu mol \cdot m^{-2} s^{-1}$. Greenhouse benches were covered with 50% aluminum shade cloth in 1997-1998 (LS Americas, Charlotte, NC). A vapor pressure deficit (VPD) of ~ 0.7 kPa was maintained by steam injection into greenhouse sections.

1998-1999. Hostas from the 1997 experiments were grown outdoors from May 15 to October 16, 1998 in 13-cm (1.1 L) square containers under 50% shade created by alternate strips of wood lath at the Michigan State University Horticultural Teaching and Research Center, East Lansing, MI. Plants displayed visible signs of dormancy (leaf senescence) and had the foliage removed prior to first frost on October 16, 1998. Pots were immediately placed in a cooler set at 5°C without supplemental lighting for 15 weeks. Multiple-eye 'Golden Scepter' divisions were received in the fall of 1998 and placed in bulb crates as previously described in 1997-1998. Single-eye *Hosta* 'Royal Standard' divisions were taken from 3 year-old crowns previously grown in 8-cm (350 ml) containers following cold treatment in the spring of 1998. Experimental conditions were as previously described in 1997-1998 although no shade cloth was provided in 1998-1999.

General Procedures. Plants were fertilized at every irrigation with a nutrient solution of well water (EC of 0.70 $mS \cdot cm^{-1}$ and 105, 35, and 23 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively) acidified with H_2SO_4 to a titratable alkalinity of 130 $mg \cdot L^{-1}$ $CaCO_3$ and water soluble fertilizer providing 125-12-125-13 N-P-K-Ca $mg \cdot L^{-1}$ (30% ammonical N) plus 1.0-0.5-0.5-0.5-0.1-0.1 (Fe, Mn, Zn, Cu, B, Mo) $mg \cdot L^{-1}$ (MSU Special, Greencare Fertilizers, Chicago, IL).

Greenhouse air temperature was monitored on each bench with 36-gauge type E thermocouples connected to a CR-10 datalogger (Campbell, Scientific, Logan, UT). Temperatures were collected every 10 seconds and the hourly average recorded. In 1998, the average daily temperature from start of the greenhouse forcing to flower for each clone was calculated for each forcing temperature (Table 2).

Experiments were conducted in the Plant and Soil Sciences Research Greenhouses at Michigan State University, East Lansing, MI. Each experiment was a completely randomized design with ten replications. All plants were forced under the specified treatments for fifteen weeks.

Data collection and analysis. Plant responses are reported in accordance with the treatment setpoint temperature as the actual average temperature from forcing to flower varied for each hosta clone (Table 2). Emergence and flowering percentages were calculated for each clone in both years. Flowering percentages were calculated as the number of flowering plants divided by the number of emerged plants in each treatment. The date of visible flower bud was collected for all reproductive plants; the date of flower anthesis, plant height (cm), inflorescence height (cm), flower number, scape leaf number,

leaf number, and shoot number were collected when the first flower opened. Plant height, leaf number, and shoot number were collected for nonreproductive plants fifteen weeks after forcing. Leaf area was taken on all plants fifteen weeks after the start of forcing with a LI-300 portable leaf area meter (LI-COR, Lincoln, NB).

Days to visible bud, days to flower, and days from visible bud to flower were calculated for all reproductive plants, and no data were available for these parameters on nonflowering plants. Data were analyzed using SAS's (SAS Institute, Cary, NC) analysis of variance (ANOVA) and general linear models (GLM) procedures.

All hostas exhibited a linear relationship between temperature and the rate of progress toward VB, from VB to FLW, and toward FLW up to an optimum temperature (T_{opt}) (Figures1-11D-F). The optimum temperature for flowering of *Hosta* appeared to be 23°C, except for *H. montana* (20°C), 'Tokudama' green (20°C), *H. plantaginea* (26°C), and 'Royal Standard'(26°C). The decision to include data points beyond these temperatures became arbitrary, and they were excluded from regression analysis. Slopes and intercepts of regression equations for the different developmental stages were calculated using SAS REG procedure. Base temperatures and cumulative thermal time were calculated for all clones according to Equations 2 and 3 (Roberts and Summerfield, 1987).

RESULTS AND DISCUSSION

To accurately predict flower timing, all plants in a population must be of a similar developmental stage at the start of forcing (Heins et al., 1997). Flowering of *Hosta* was previously demonstrated to be influenced by plant size and crown maturity (Fausey,

1999). Hostas forced under temperature treatments in 1998-1999 were larger and yielded more uniform vegetative and flowering responses than single-eye divisions forced in 1997-1998 (Table 3, 4, 5). Therefore, rates of development and plant characteristics in response to temperature are based upon 1998-1999 experimental data.

Flowering percentages of all clones under forcing temperatures were generally higher in 1998-1999 than in 1997-1998 (Table 3, 4). The lowest flowering percentage for each clone in 1998-1999 occurred at the low (14°C) or high (29°C) temperature extreme. However, plants grown at 14°C developed at a slower rate and may have eventually flowered if grown beyond the 105-day forcing period of this experiment. Flower development of plants grown at 29°C is unlikely beyond the 15-week forcing period as growth was reduced by high temperatures. Essentially all 'Francee', 'Golden Scepter', 'Golden Tiara', 'Hyacinthina', 'Lancifolia', 'Tokudama' gold, and 'Undulata' plants flowered under temperatures between 17°C and 26°C (Table 4). Flowering of *H. montana* and 'Tokudama' green plants decreased as temperatures increased above 20°C. Flowering of *H. plantaginea* and 'Royal Standard' plants was highest at 23 and 26°C but varied greatly for other temperatures.

H. plantaginea requires long growing seasons in temperate climates as it is presumably native to the Zheijing province or provinces further south in China (Schmid, 1991). These areas are located between 20°N and 30°N latitude (similar to Houston, TX and New Orleans, LA) and have humid, subtropical climates (Graves, 1992). No *H. plantaginea* plants flowered under 14°C after 15 weeks of forcing, but all plants flowered when grown at 26°C (Table 4).

Hosta shoots emerge in response to the root zone temperature, and emergence

may only occur when a clonal-specific minimum base temperature is exceeded. The base temperature for emergence could not be identified for the range of temperatures examined in this experiment. The number of days to emergence significantly decreased as temperature increased for about half of the clones (Table 6). Time to emergence decreased 10 days for 'Tokudama' gold plants, 6 days for 'Tokudama' green and 'Francee' plants, and 5 days for 'Hyacinthina' plants as temperature increased from 14 to 26°C (Table 6).

Days to visible bud (VB), days to flower (FLW), and days from VB to FLW for all clones decreased as temperature increased from 14°C to ≥23°C (Table 2, 6). Flowering accelerated more rapidly when temperature increased from 14°C to 20°C than from 20°C to 29°C (Table 2). For all hostas except *H. plantaginea*, 'Royal Standard', and 'Undulata' increasing the temperature from 20°C to 29°C resulted in an increase in days to VB and in days to FLW (Table 2, 6). Increasing the temperature from 20°C to 26°C also increased the time to VB and time to FLW for *H. montana* plants (Table 2, 6).

Flowering uniformity varied with temperature and genotype (Figures 1-11A-C). Variability in time to VB and FLW increased for 'Francee' and *H. montana* plants as the temperature increased from 14°C to 26°C (Figures 1A, C; 3A, C). Days from VB to FLW were generally uniform for all hosta clones except 'Tokudama' green (Figures 1-11B). However, the variability in time to VB and FLW, and from VB to FLW of 'Tokudama' green plants can in part be explained by a smaller sample size of 3 to 5 plants per treatment (Figure 2A-C).

The parameters of linear regression equations relating forcing temperature to plant development are presented in Table 7. There was a significant linear relationship

between temperature and the rate of progress toward VB, from VB to FLW, and toward FLW for most hostas (Table 7). However, the rates of progress toward VB and FLW for 'Royal Standard', toward VB for 'Undulata', and toward FLW for 'Tokudama' green were not significant (Table 7).

The reciprocal of the linear regression line was plotted against original data points. The regression line fit well with the original data for all clones except 'Royal Standard', 'Tokudama' green, and 'Undulata' (Figures 1-11A, B, C). The relationship between forcing temperature and the rate of progress toward visible bud and flowering were weak for these cultivars. However, the original data did fit the reciprocal of the linear regression line for the rate of progress from visible bud to flowering well.

The base temperature and the cumulative thermal time required for each developmental process can be used to predict flowering in greenhouse environments where temperatures fluctuate by using the average forcing temperature (T_f). The number of days required to complete a developmental event can be calculated as °days/(T_f-T_b). The calculated base temperatures of significant lines for flowering of hosta clones ranged from -28.8°C to 8.7°C (Table 7). The cumulative thermal time to flower ranged from 723 units above a base temperature of 8.7°C for *H. montana* to 3663 thermal units above a base temperature of -28.8°C for 'Undulata'. The calculated base temperatures and thermal times required for flowering for most hosta clones were physiologically unrealistic, and the relationship between time to flower and temperature should be examined over a wider range of cool temperatures.

Temperature has been shown to impact floral characteristics of many herbaceous plant species (Whitman et al., 1997; Yuan et al., 1998). The average number of flowers

per inflorescence of most clones was not affected by temperature (Table 4). However, twice as many flowers were formed on 'Hyacinthina' and 'Lancifolia' plants grown at 14°C than on plants grown at 29°C (Table 4). The lavender color of 'Golden Scepter', 'Golden Tiara', and 'Lancifolia' flowers intensified at 14°C and faded under temperatures ≥26°C (personal observation). The inflorescence height of all clones at first open flower was greatest at 14°C or 17°C and decreased with increasing temperature (Table 4).

Plant height generally decreased in 1998-1999 with increasing temperature for all hostas except 'Tokudama' gold and 'Undulata' (Table 3). 'Francee', 'Hyacinthina', *H. plantaginea*, and 'Royal Standard' plants grown at 14°C were 9 to 13 cm taller than plants grown at 29°C. Differences in plant height of other clones were less. Height of 'Undulata' plants increased to a maximum at 26°C then sharply decreased at 29°C. Leaves of 'Tokudama' gold plants exhibited an uncharacteristic vertical orientation when grown at 29°C which elevated plant height at this temperature.

Gardeners typically plant hostas in shady areas for optimal performance as temperature and light intensity impact the physical characteristics of *Hosta*. Hostas grown in full sunlight are reportedly shorter, have a larger number of leaves per division, and suffer from marginal leaf burn (Solberg, 1988). Cultivars grown in full sun may also lose characteristics which make them distinctive, such as a decrease in leaf size, a narrowing of the leaf shape, or a change in coloration. The alteration in plant habit and physical characteristics of hostas grown in sunlight may be attributed to an elevated plant temperature and not necessarily light intensity as leaves exposed to sunlight may reach a higher temperature than the surrounding air (Serrano et al., 1995). Evidence to support this hypothesis can be found with the altered leaf color and uncharacteristically small

leaves of hostas grown in deep shade (Solberg, 1988).

Hostas grown at high temperature exhibited several characteristics commonly observed for plants grown in full sunlight. Temperature affected the average leaf size in this experiment but did not impact the number of leaves per shoot of most hosta clones (Table 5). Average leaf size decreased with increasing temperature for all hostas except 'Golden Scepter' (Table 5). Average leaf size of *H. montana* and *H. plantaginea* increased as temperature increased from 16°C, then declined when exposed to warmer temperatures (Table 5).

Temperatures $\geq$ 26°C greatly altered plant habit and the physical appearance of all clones. Plants grown under high temperatures exhibited a rosette growth habit with long, narrow leaves attached to short petioles. Foliage pigmentation was also adversely affected by high average daily temperatures. 'Tokudama' gold and 'Golden Scepter' plants lost their characteristic gold color when grown at 29°C, and all leaves of the white-variegated 'Undulata' and the yellow-variegated 'Golden Tiara' became green. The white marginal variegation of 'Francee' turned yellow and narrowed to the extreme edge of the leaves when grown at 29°C. The wax bloom which gives 'Tokudama' green and 'Hyacinthina' their blue or grey hue was lost or did not form under 26°C and 29°C.

Marginal leaf burn of *Hosta* may be a direct response to water stress of plants with poorly developed root systems. Shade cloth was raised in the spring of 1998 when marginal burn was observed on newly planted divisions grown at $\geq$ 23°C. Leaf burn was exacerbated on plants that appeared to be underwatered. Plants grown in 1998-1999 had well-established root systems at the start of forcing, and fewer incidents of marginal burn were observed.

Hostas are almost exclusively grown for their ornamental foliage. Temperatures $\leq$ 23°C produced the highest quality plants with large leaves and vibrantly colored foliage. Plants of a salable size can be forced in four to six weeks at 20 and 23°C, and in six to eight weeks at 14 and 17°C. Although plants of some clones flowered faster under $\geq$ 26°C temperatures, they exhibited undesirable qualities that would prevent their sale. The fastest flowering of plants without a reduction in plant quality will occur in 8 to 15 weeks at 20 or 23°C, depending upon the genotype grown.

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Table 1. Plant material characteristics for 1997 and 1998 temperature experiments. All plants in 1998-1999 were grown in containers and originated from 1997 experimental plant material except for 'Golden Scepter', *H. montana*, and 'Royal Standard'.

Clone	Source Location (latitude)	Arrival Date	Starting material	Starting date of temperature treatments 1997	1998
'Francee'	Twixwood Nursery Berrien Springs, MI (41.9°N)	not available	clump	—	01/22
'Golden Scepter'	Walters Gardens Zeeland, MI (42.9°N)	09/23/98	clump	—	01/22
'Golden Tiara'	Walters Gardens	10/09/97	clump	01/05	01/22
'Hyacinthina'	Wade and Gatton Nursery Bellville, OH (40.6°N)	10/31/97	bare root	01/09	01/22
'Lancifolia'	Sunnybrook Farms Chesterland, OH (41.5°N)	10/08/97	clump	01/06	01/22
montana	Walters Gardens	11/06/97	seed	—	01/22
plantaginea	Sunny Border Nursery Kensington, CT (41.6°N)	11/03/97	bare root	01/12	01/22
'Royal Standard'	Twixwood Nursery	08/24/97	container	—	01/22
'Tokudama' gold	Klehm Nursery Champaign, IL (40.1°N)	10/13/97	bare root	01/05	01/22
'Tokudama' green	Klehm Nursery	10/13/97	bare root	01/05	01/22
'Undulata'	Walters Gardens	10/09/97	bare root	01/06	01/22

Table 2. Average number of days to flower and average daily temperatures from date of forcing to average date of flowering of *Hosta* clones grown at various temperatures in 1998-1999.

Clone	Number of days to flower							Average air temperature (°C)					
	Temperature (°C)												
	14	17	20	23	26	29	Sign[z]	14	17	20	23	26	29
'Francee'	97	90	84	73	72	86	$L^{***}Q^{***}$	16.3	18.1	21.1	23.5	26.2	29.5
'Golden Scepter'	95	87	84	74	75	83	$L^{NS}Q^{NS}$	16.2	18.1	21.1	23.5	26.2	29.5
'Golden Tiara'	82	71	62	60	62	69	$L^{**}Q^{***}$	16.0	18.0	21.0	23.3	26.1	29.5
'Hyacinthina'	100	91	74	73	62	78	$L^{***}Q^{***}$	16.4	18.1	21.1	23.5	26.1	29.5
'Lancifolia'	113	105	92	88	82	100	$L^{***}Q^{***}$	16.8	18.3	21.1	23.6	26.2	29.4
montana	99	73	62	58	61	--[y]	$L^{***}Q^{***}$	16.4	18.1	21.0	23.3	26.1	--
plantaginea	--	114	96	99	85	97	Q^{**}	--	18.3	21.1	23.7	26.2	29.5
'Royal Standard'	120	122	103	106	108	106	$L^{NS}Q^{NS}$	17.0	18.4	21.1	23.8	26.4	29.4
'Tokudama' gold	82	67	56	55	56	58	$L^{***}Q^{***}$	16.0	17.8	21.0	23.3	26.1	29.6
'Tokudama' green	80	68	69	63	55	75	$L^{NS}Q^{NS}$	16.0	17.9	21.0	23.3	26.1	29.5
'Undulata'	84	75	78	72	66	85	$L^{NS}Q^{NS}$	16.1	18.1	21.1	23.5	26.1	29.5

[z] NS, *, **, ***Nonsignificant or significant linear (L) or quadratic (Q) at $P \leq 0.05$, 0.01, or 0.001, respectively.

[y] No plants flowered (--).

Table 3. Effect of forcing temperature on flowering percentage, plant height, and average leaf size of single-eye divsions of *Hosta* clones in 1997-1998.

Clone	Flowering %						Plant Height (cm)						Average leaf size (cm^2)					
	Temperature (°C)																	
	14	17	20	23	26	29	14	17	20	23	26	29	14	17	20	23	26	29
'Francee'	-[z]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
'Golden Scepter'	0	11	50	67	89	90	9	10	10	8	7	2	13	13	17	19	13	13
'Golden Tiara'	0	38	60	90	100	100	5	9	10	9	8	7	12	20	19	21	14	18
'Hyacinthina'	10	75	90	80	90	90	24	28	27	23	19	20	22	38	36	30	21	20
'Lancifolia'	0	22	78	80	60	56	12	10	10	9	9	10	16	18	18	29	14	15
montana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
plantaginea	0	0	0	10	10	20	19	26	26	22	19	15	89	98	96	82	70	50
'Royal Standard'	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
'Tokudama' gold	30	30	50	50	30	60	6	6	7	6	6	7	35	32	38	30	22	14
'Tokudama' green	30	22	33	0	10	10	7	7	8	7	6	7	26	25	32	24	20	13
'Undulata'	60	70	50	70	90	50	11	10	11	10	9	13	51	29	37	34	31	21

[z] No plants examined in 1997-1998.

Table 4. Effect of forcing temperature on flowering percentage, flower number, and inflorescence height of *Hosta* clones in 1998-1999.

Clone	Flowering %						Flower number							Inflorescence height (cm)						
	Temperature (°C)																			
	14	17	20	23	26	29	14	17	20	23	26	29	Sign[z]	14	17	20	23	26	29	Sign
'Francee'	80	90	100	100	100	90	14	11	13	10	10	9	$L^{**}Q^{NS}$	55	62	56	49	43	30	$L^{***}Q^{*}$
'Golden Scepter'	70	90	80	100	100	80	12	12	11	10	10	10	$L^{NS}Q^{NS}$	29	37	37	36	33	22	$L^{**}Q^{***}$
'Golden Tiara'	100	100	100	100	100	100	16	15	16	11	13	12	$L^{NS}Q^{NS}$	54	52	47	44	41	26	$L^{***}Q^{*}$
'Hyacinthina'	100	100	100	100	90	100	22	17	15	14	15	9	$L^{***}Q^{NS}$	59	64	59	60	61	35	$L^{***}Q^{***}$
'Lancifolia'	80	90	100	100	100	90	16	15	13	8	7	6	$L^{***}Q^{NS}$	55	57	48	46	49	28	$L^{***}Q^{*}$
montana	80	70	80	60	56	0	16	37	32	25	24	--[y]	$L^{NS}Q^{NS}$	52	69	70	65	63	--	$L^{NS}Q^{NS}$
plantaginea	0	60	56	78	100	50	--	16	11	10	11	8	Q^{NS}	--	50	44	40	39	28	Q^{NS}
'Royal Standard'	30	40	60	90	89	10	18	22	18	18	21	6	$L^{NS}Q^{NS}$	52	63	59	43	44	17	$L^{**}Q^{*}$
'Tokudama' gold	90	100	80	100	100	70	23	24	24	19	22	29	$L^{NS}Q^{NS}$	37	30	29	27	26	16	$L^{***}Q^{NS}$
'Tokudama' green	75	100	100	63	71	43	26	26	13	16	25	11	$L^{NS}Q^{NS}$	79	59	34	41	56	31	$L^{**}Q^{NS}$
'Undulata'	60	100	100	100	100	10	15	14	15	14	14	12	$L^{NS}Q^{NS}$	59	75	65	72	73	34	$L^{*}Q^{**}$

[z] ^{NS,*,**,***}Nonsignificant or significant linear (L) or quadratic (Q) at $P \leq 0.05$, 0.01, or 0.001, respectively.

[y] No plants flowered (--).

Table 5. Effect of forcing temperature on plant height, average leaf number, and average leaf size of *Hosta* clones in 1998-1999.

Clone	Plant Height (cm)							Average leaf number per shoot							Average leaf size (cm^2)						
	Temperature (°C)																				
	14	17	20	23	26	29	Sign[z]	14	17	20	23	26	29	Sign	14	17	20	23	26	29	Sign
'Francee'	27	25	20	21	18	19	$L^{***}Q^{*}$	6	6	6	7	8	8	$L^{NS}Q^{NS}$	57	52	43	42	33	41	$L^{**}Q^{NS}$
'Golden Scepter'	17	17	14	16	14	12	$L^{***}Q^{NS}$	8	8	10	9	8	9	$L^{NS}Q^{NS}$	19	19	17	20	17	16	$L^{NS}Q^{NS}$
'Golden Tiara'	19	16	16	13	16	16	$L^{NS}Q^{NS}$	9	8	8	9	9	9	$L^{NS}Q^{NS}$	32	26	29	27	24	17	$L^{**}Q^{NS}$
'Hyacinthina'	27	28	26	24	25	18	$L^{***}Q^{**}$	7	7	7	8	8	9	$L^{***}Q^{NS}$	61	72	57	63	52	29	$L^{***}Q^{**}$
'Lancifolia'	21	16	16	16	14	14	$L^{***}Q^{*}$	9	8	8	9	10	9	$L^{NS}Q^{NS}$	37	29	31	24	24	16	$L^{***}Q^{NS}$
montana	18	22	18	17	15	15	$L^{*}Q^{NS}$	6	6	4	9	6	5	$L^{NS}Q^{NS}$	79	105	96	65	70	33	$L^{***}Q^{NS}$
plantaginea	26	31	29	23	23	18	$L^{***}Q^{*}$	6	5	8	8	7	9	$L^{***}Q^{NS}$	64	123	97	79	85	67	$L^{NS}Q^{*}$
'Royal Standard'	26	24	24	21	22	13	$L^{***}Q^{*}$	6	7	6	7	8	9	$L^{**}Q^{NS}$	63	74	70	54	55	28	$L^{***}Q^{*}$
'Tokudama' gold	8	10	11	11	12	15	$L^{***}Q^{*}$	8	6	7	7	8	7	$L^{NS}Q^{NS}$	57	60	51	52	35	26	$L^{***}Q^{*}$
'Tokudama' green	18	11	11	13	16	14	$L^{NS}Q^{**}$	5	6	6	9	6	7	$L^{NS}Q^{NS}$	90	70	45	52	68	42	$L^{*}Q^{NS}$
'Undulata'	16	17	15	22	23	14	$L^{NS}Q^{**}$	8	7	10	9	9	10	$L^{**}Q^{NS}$	39	50	39	47	40	20	$L^{***}Q^{***}$

[z] ^{NS,*,**,***}Nonsignificant or significant linear (L) or quadratic (Q) at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 6. Effect of forcing temperature for the average number of days to emergence, days to visible bud, and days from visible bud to flower of *Hosta* clones in 1998-1999.

Clone	Number of Days to Emergence							Number of Days to Visible Bud							Number of Days from Visible bud to Flower						
	Temperature (°C)							Temperature (°C)							Temperature (°C)						
	14	17	20	23	26	29	Sign[z]	14	17	20	23	26	29	Sign	14	17	20	23	26	29	Sign
'Francee'	15	14	11	9	9	10	$L^{***}Q^{***}$	72	65	62	53	56	67	$L^{*}Q^{***}$	25	25	22	20	17	18	$L^{***}Q^{**}$
'Golden Scepter'	6	4	5	4	4	3	$L^{**}Q^{NS}$	64	56	59	51	54	64	$L^{NS}Q^{NS}$	31	31	25	23	20	18	$L^{*}Q^{*}$
'Golden Tiara'	7	7	7	6	7	8	$L^{NS}Q^{NS}$	48	40	38	37	43	52	$L^{NS}Q^{***}$	34	31	25	23	19	17	$L^{***}Q^{**}$
'Hyacinthina'	14	13	9	11	9	8	$L^{***}Q^{NS}$	75	67	54	54	46	60	$L^{***}Q^{***}$	25	23	20	19	15	16	$L^{***}Q^{NS}$
'Lancifolia'	5	7	5	4	5	5	$L^{*}Q^{NS}$	80	77	70	66	65	80	$L^{NS}Q^{***}$	33	27	21	21	17	18	$L^{***}Q^{***}$
montana	5	5	4	4	4	4	$L^{NS}Q^{NS}$	60	39	32	32	37	--[y]	$L^{NS}Q^{NS}$	39	34	30	26	25	--	$L^{***}Q^{*}$
plantaginea	5	4	4	4	3	4	$L^{NS}Q^{NS}$	--	87	76	80	67	74	Q^{*}	--	27	20	19	18	23	Q^{***}
'Royal Standard'	15	14	14	11	12	13	$L^{NS}Q^{NS}$	89	94	78	82	83	82	$L^{NS}Q^{NS}$	30	28	25	24	23	24	$L^{***}Q^{**}$
'Tokudama' gold	19	15	13	10	9	10	$L^{***}Q^{*}$	53	41	37	35	39	41	$L^{*}Q^{***}$	29	26	21	21	18	16	$L^{***}Q^{NS}$
'Tokudama' green	16	15	11	13	10	12	$L^{NS}Q^{NS}$	53	42	40	46	37	54	$L^{NS}Q^{NS}$	27	26	22	18	18	21	$L^{***}Q^{**}$
'Undulata'	9	7	7	7	5	6	$L^{***}Q^{NS}$	50	45	52	50	43	48	$L^{NS}Q^{NS}$	35	31	27	22	23	37	$L^{NS}Q^{***}$

[z] ^{NS,*,**,***}Nonsignificant or significant linear (L) or quadratic (Q) at $P \leq 0.05$, 0.01, or 0.001, respectively.

[y] No plants flowered (--).

Table 7. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud (VB), to flowering (FLW), and from VB to FLW for *Hosta* clones in 1998-1999. The base temperature (T_b) and degree days (°days) were calculated from the intercept and slope.

Clone	Developmental Stage (d)	Intercept (b_0) (1/d)	Slope (b_1) (1/d)/C	T_b(°C)	°days	r^2 [z]
'Francee'	Forcing to VB	2.50E-03 ± 2.70E-03	6.98E-04 ± 1.34E-04	-3.6	1433	0.44***
	VB to FLW	1.33E-02 ± 5.07E-03	1.58E-03 ± 2.52E-04	-8.4	635	0.53***
	Forcing to FLW	2.42E-03 ± 1.61E-03	4.78E-04 ± 7.96E-05	-5.1	2092	0.51***
'Golden Scepter'	Forcing to VB	7.06E-03 ± 5.09E-03	5.79E-04 ± 2.52E-04	-12.2	1727	0.14*
	VB to FLW	3.86E-04 ± 4.71E-03	1.88E-03 ± 2.33E-04	-0.2	533	0.67***
	Forcing to FLW	3.22E-03 ± 2.51E-03	4.56E-04 ± 1.24E-04	-7.1	2193	0.30**
'Golden Tiara'	Forcing to VB	9.60E-03 ± 5.25E-03	8.10E-04 ± 2.62E-04	-11.8	1235	0.22**
	VB to FLW	-3.71E-03 ± 3.69E-03	2.06E-03 ± 1.84E-04	1.8	487	0.79***
	Forcing to FLW	2.75E-03 ± 1.82E-03	6.17E-04 ± 9.09E-05	-4.5	1621	0.58***
'Hyacinthina'	Forcing to VB	1.61E-04 ± 1.49E-03	8.26E-04 ± 7.03E-05	-0.2	1211	0.62***
	VB to FLW	1.38E-02 ± 7.84E-03	1.68E-03 ± 3.93E-04	-8.2	596	0.32***
	Forcing to FLW	9.18E-04 ± 1.25E-03	5.67E-04 ± 6.25E-05	-1.6	1764	0.68***
'Lancifolia'	Forcing to VB	5.67E-03 ± 1.63E-03	4.08E-04 ± 8.02E-05	-13.9	2451	0.43***
	VB to FLW	-1.14E-02 ± 8.68E-03	2.62E-03 ± 4.27E-04	4.3	381	0.52***
	Forcing to FLW	2.57E-03 ± 7.48E-04	3.84E-04 ± 3.68E-05	-6.7	2604	0.76***

[z] NS, *, **, ***Nonsignificant or significant at P<0.05, 0.01, or 0.001, respectively

[y] Standard error

Table 7 (cont'd).

H. montana	Forcing to VB	-3.99E-02 ± 1.20E-02	3.53E-03 ± 6.46E-04	11.3	283	0.59***
	VB to FLW	-2.24E-03 ± 1.01E-02	1.74E-03 ± 5.43E-04	1.3	574	0.33**
	Forcing to FLW	-1.21E-02 ± 1.79E-03	1.38E-03 ± 2.57E-04	8.7	723	0.58***
H. plantaginea	Forcing to VB	4.38E-03 ± 1.89E-03	3.91E-04 ± 8.17E-05	-11.2	2558	0.47***
	VB to FLW	-2.06E-03 ± 9.39E-03	2.30E-03 ± 4.05E-04	0.9	435	0.55***
	Forcing to FLW	2.44E-03 ± 1.26E-03	3.52E-04 ± 5.43E-05	-6.9	2841	0.62***
'Royal Standard'	Forcing to VB	9.26E-03 ± 2.11E-03	1.26E-04 ± 9.33E-05	-73.5	7937	0.06NS
	VB to FLW	1.76E-02 ± 3.32E-03	1.02E-03 ± 1.47E-04	-17.3	979	0.64***
	Forcing to FLW	6.84E-03 ± 1.31E-03	1.07E-04 ± 5.74E-05	-63.9	9346	0.11NS
'Tokudama' gold	Forcing to VB	-7.11E-04 ± 3.38E-03	1.33E-03 ± 1.71E-04	0.5	754	0.61***
	VB to FLW	-1.31E-02 ± 1.61E-02	2.94E-03 ± 8.15E-04	4.5	340	0.27**
	Forcing to FLW	-3.17E-04 ± 1.51E-03	8.24E-04 ± 7.65E-05	0.4	1214	0.77***
'Tokudama' green	Forcing to VB	4.34E-03 ± 8.74E-03	1.03E-03 ± 4.67E-04	-4.2	970	0.29*
	VB to FLW	7.01E-03 ± 9.32E-03	1.80E-03 ± 4.98E-04	-3.9	554	0.52**
	Forcing to FLW	7.09E-03 ± 5.45E-03	3.94E-04 ± 2.89E-04	-18.0	2538	0.13NS
'Undulata'	Forcing to VB	2.03E-02 ± 5.38E-03	5.53E-05 ± 2.66E-04	-367.4	18070	0.0012NS
	VB to FLW	-9.09E-03 ± 8.01E-03	2.31E-03 ± 3.95E-04	3.9	433	0.5***
	Forcing to FLW	7.86E-03 ± 2.32E-03	2.73E-04 ± 1.15E-04	-28.8	3663	0.14*

[z] NS, *, **, ***Nonsignificant or significant at P<0.05, 0.01, or 0.001, respectively

[y] Standard error

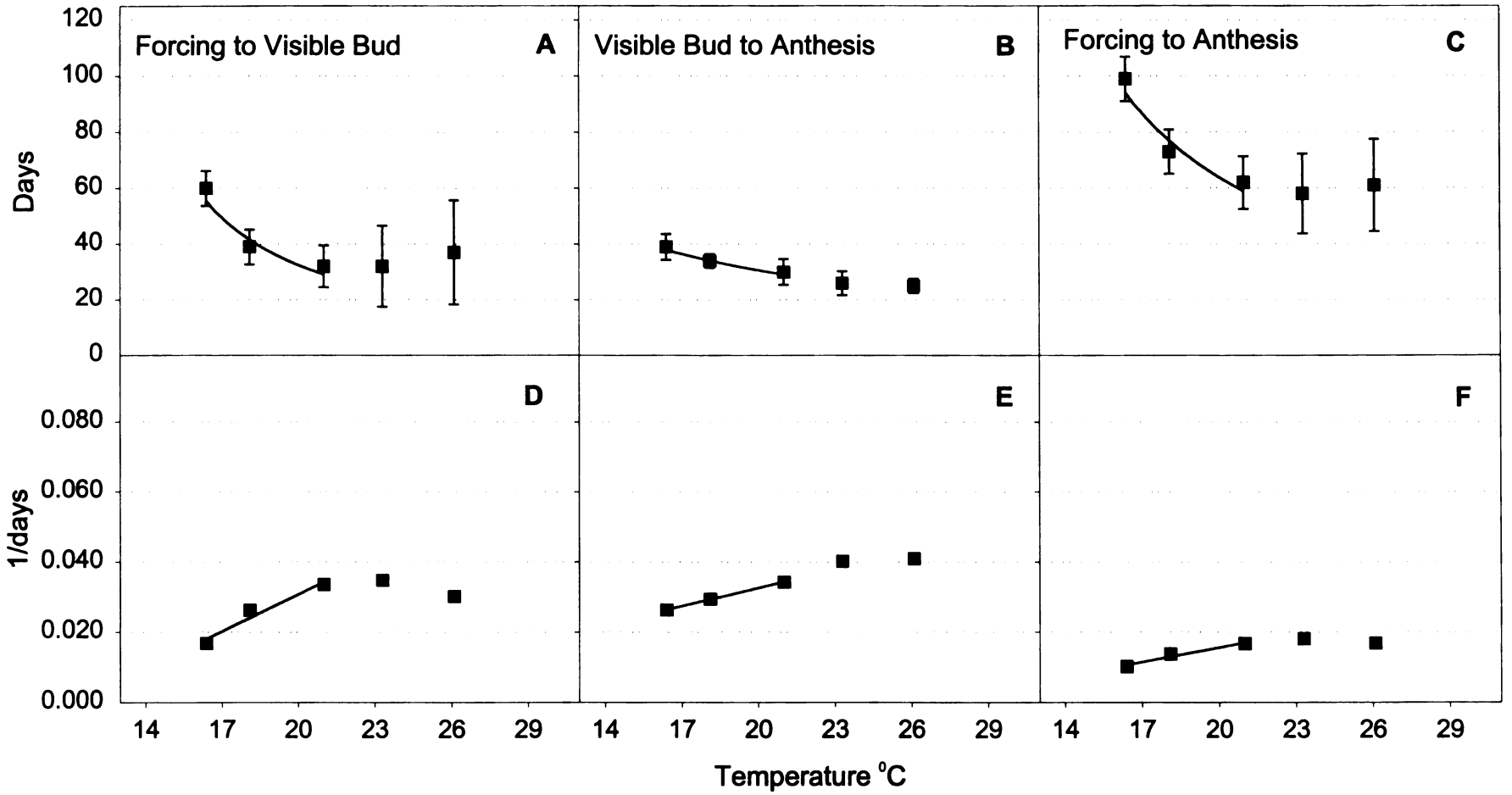


Figure 1. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta montana* in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

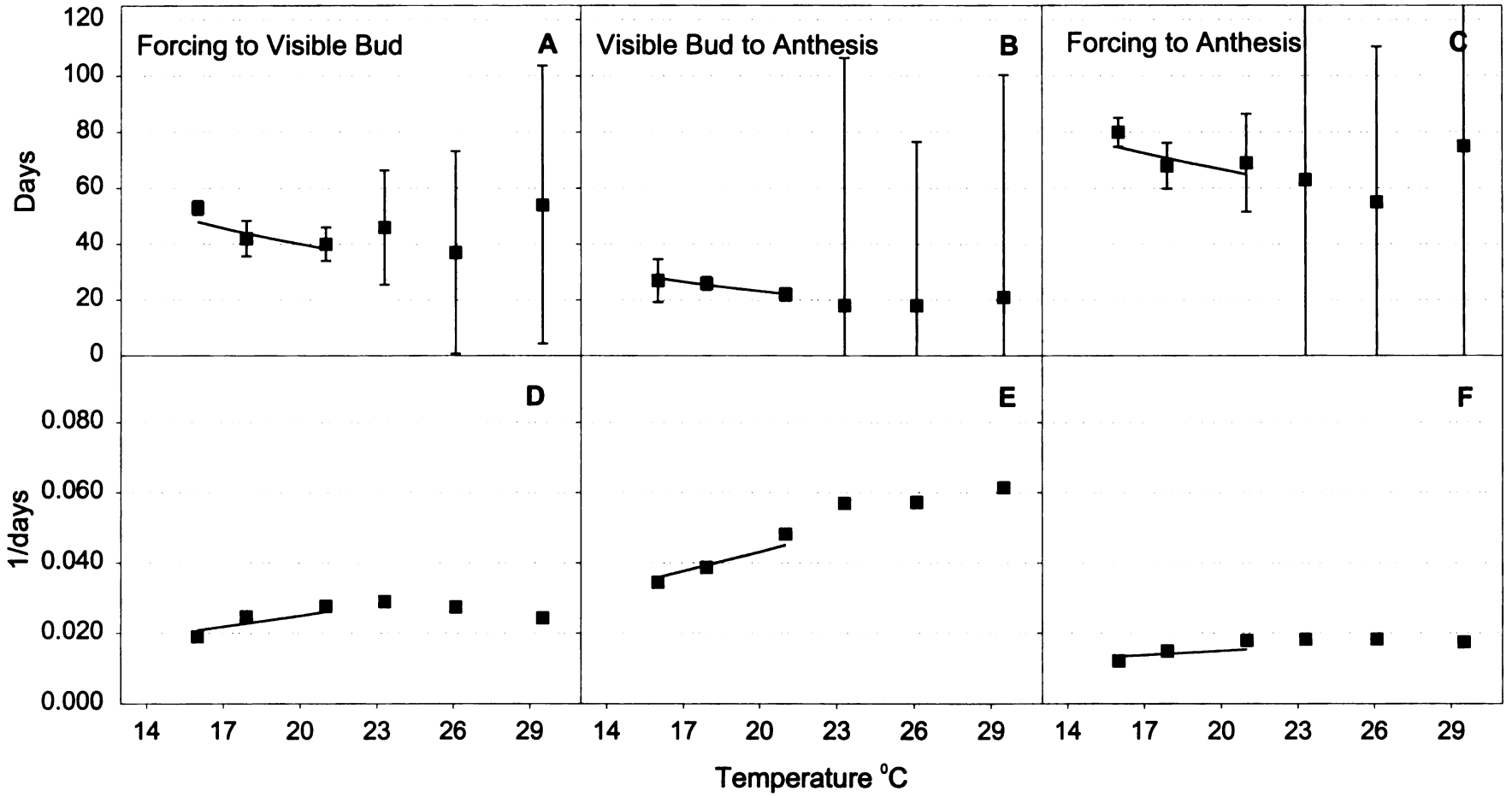


Figure 2. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta* 'Tokudama' green in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

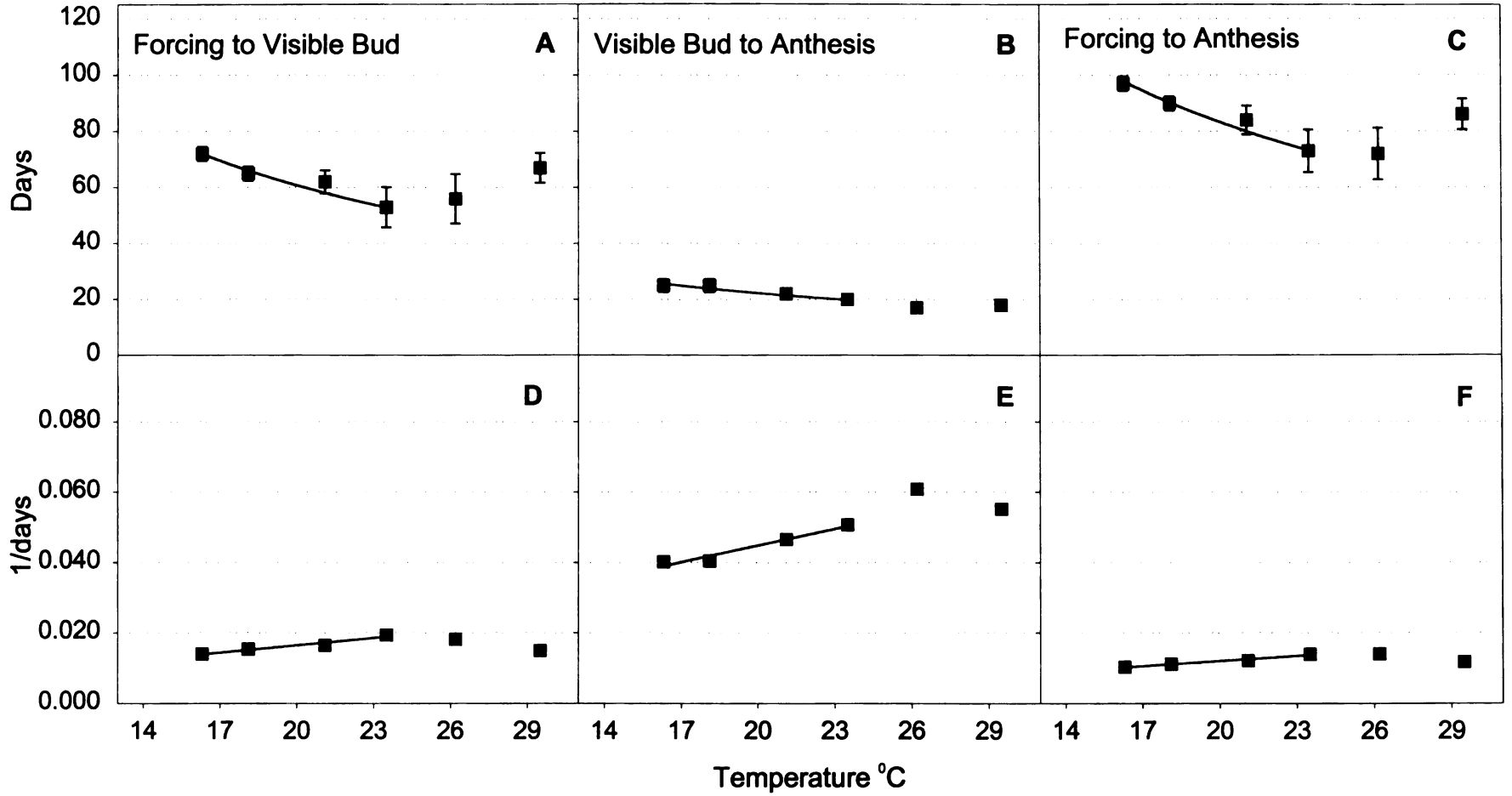


Figure 3. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta* 'Francee' in 1998-1999. The parameters of linear regression lines are presented in Table 7.
The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

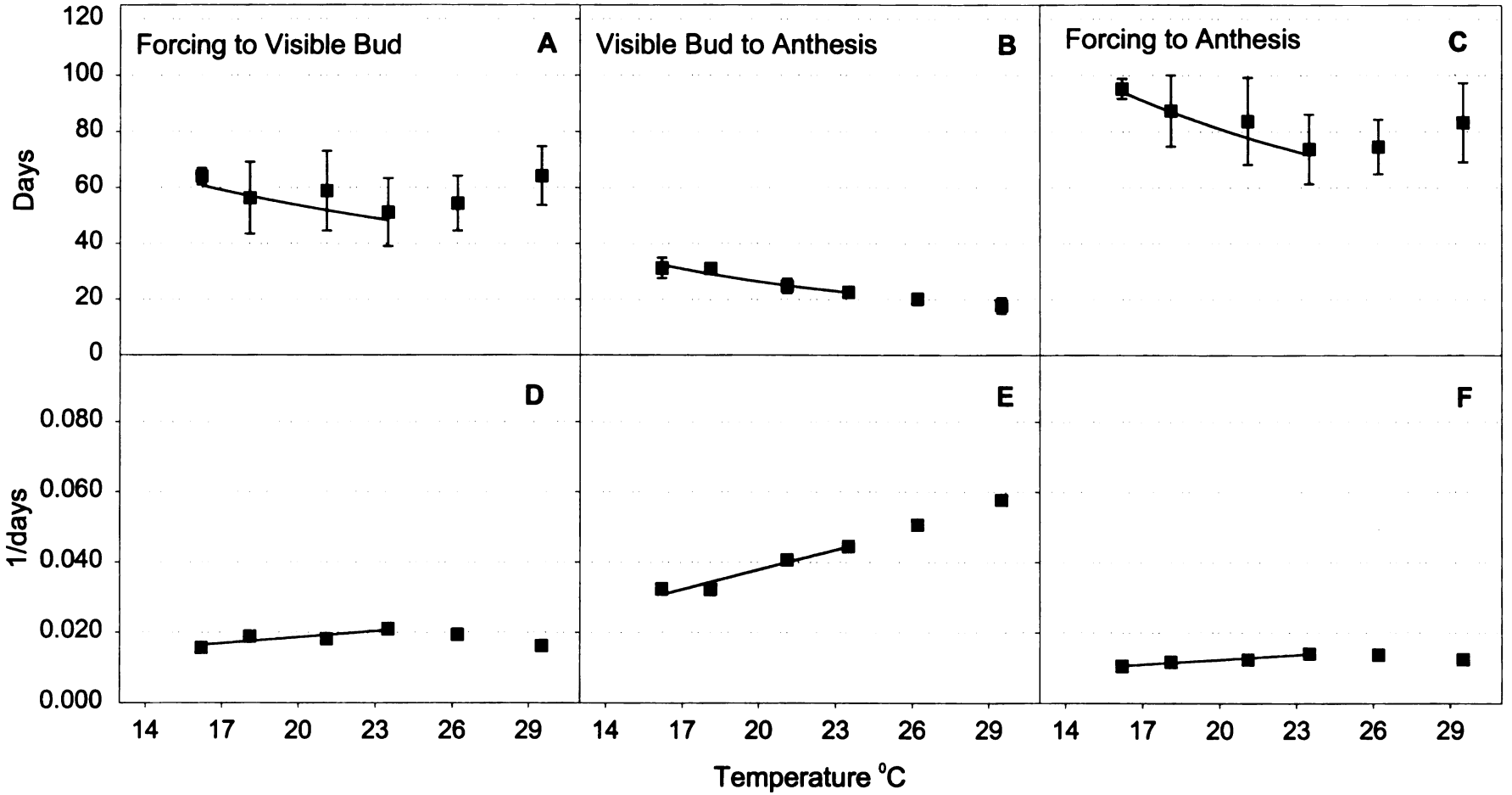


Figure 4. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta* 'Golden Scepter' in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

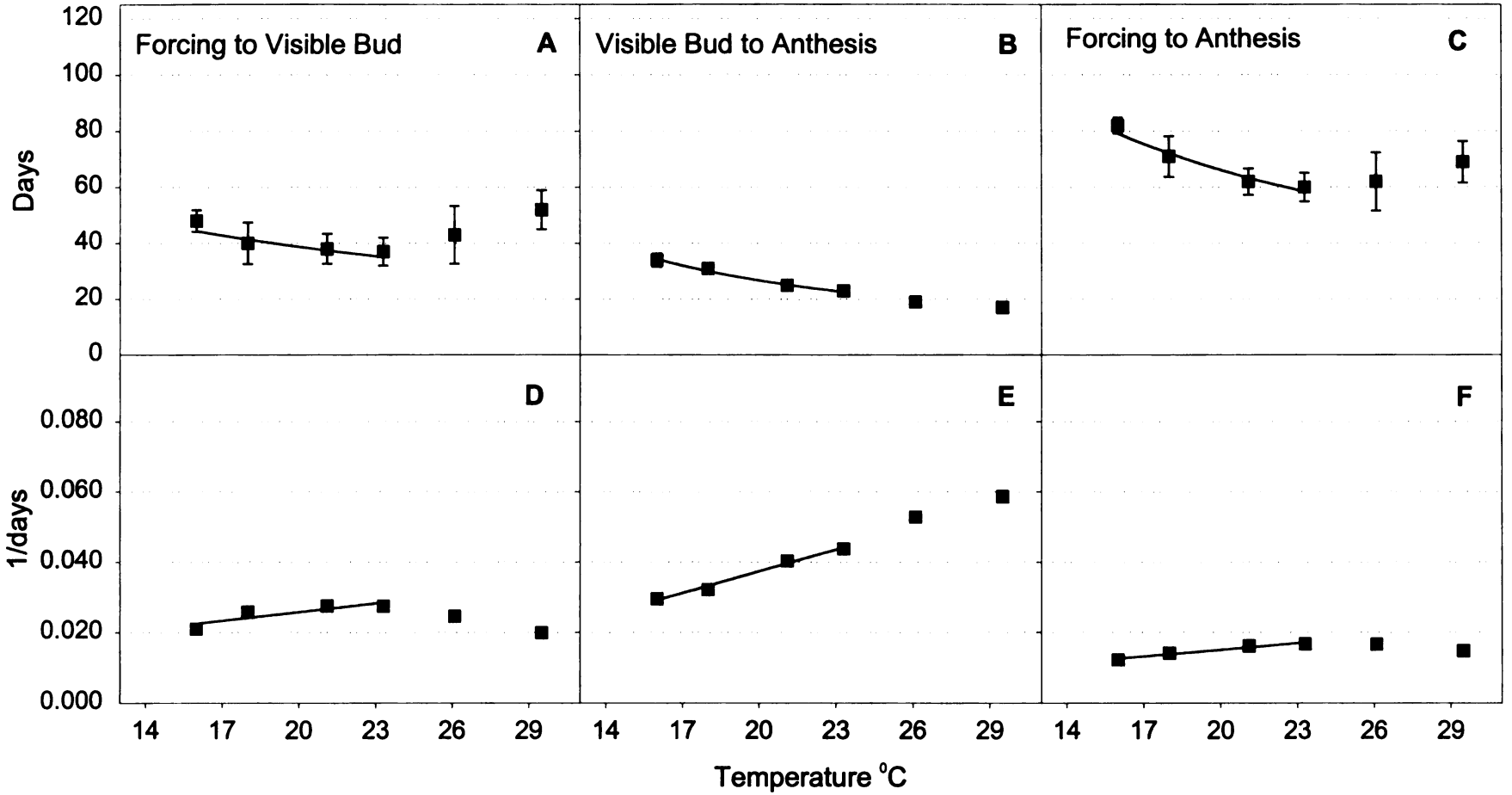


Figure 5. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta* 'Golden Tiara' in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

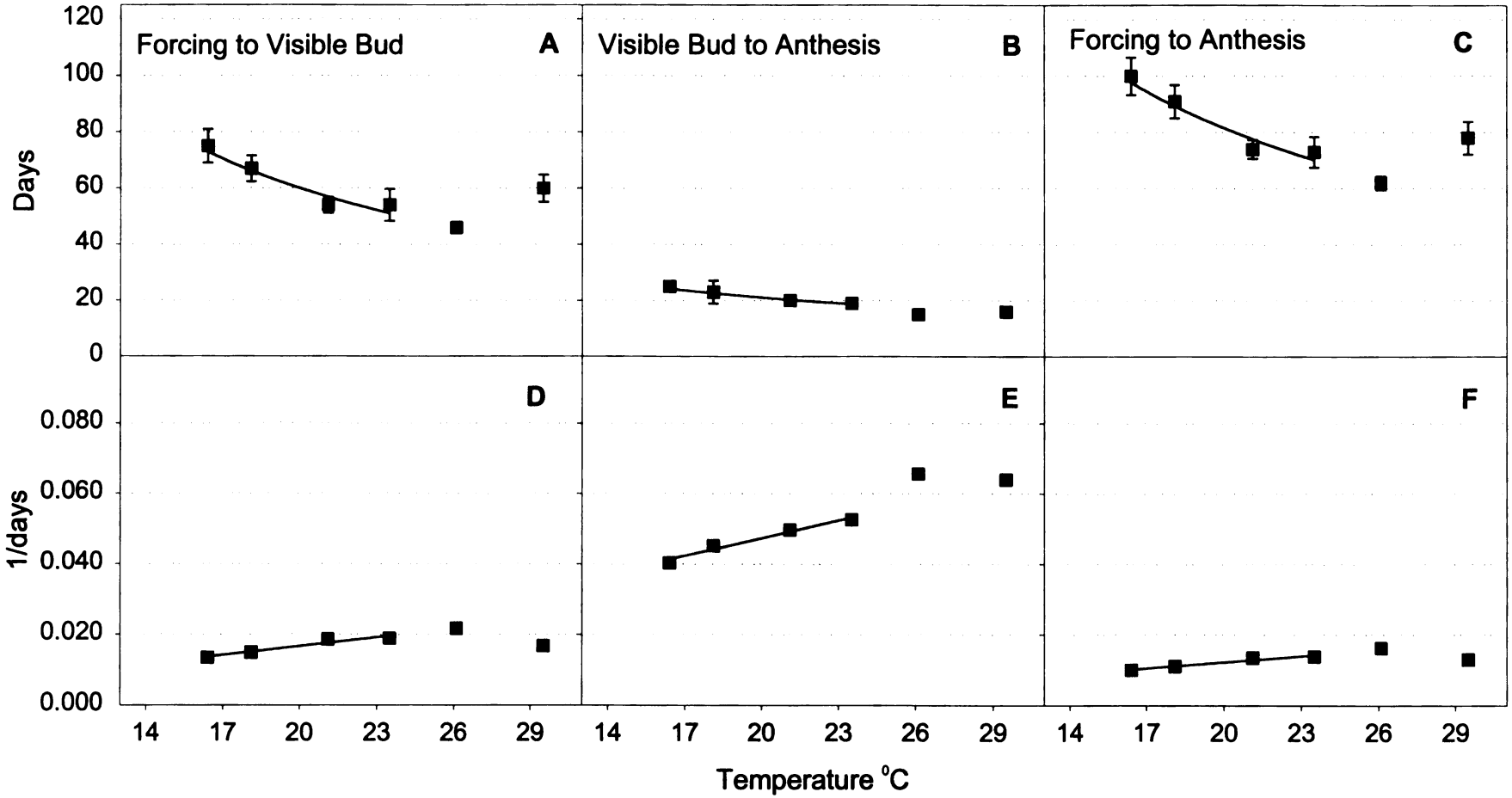
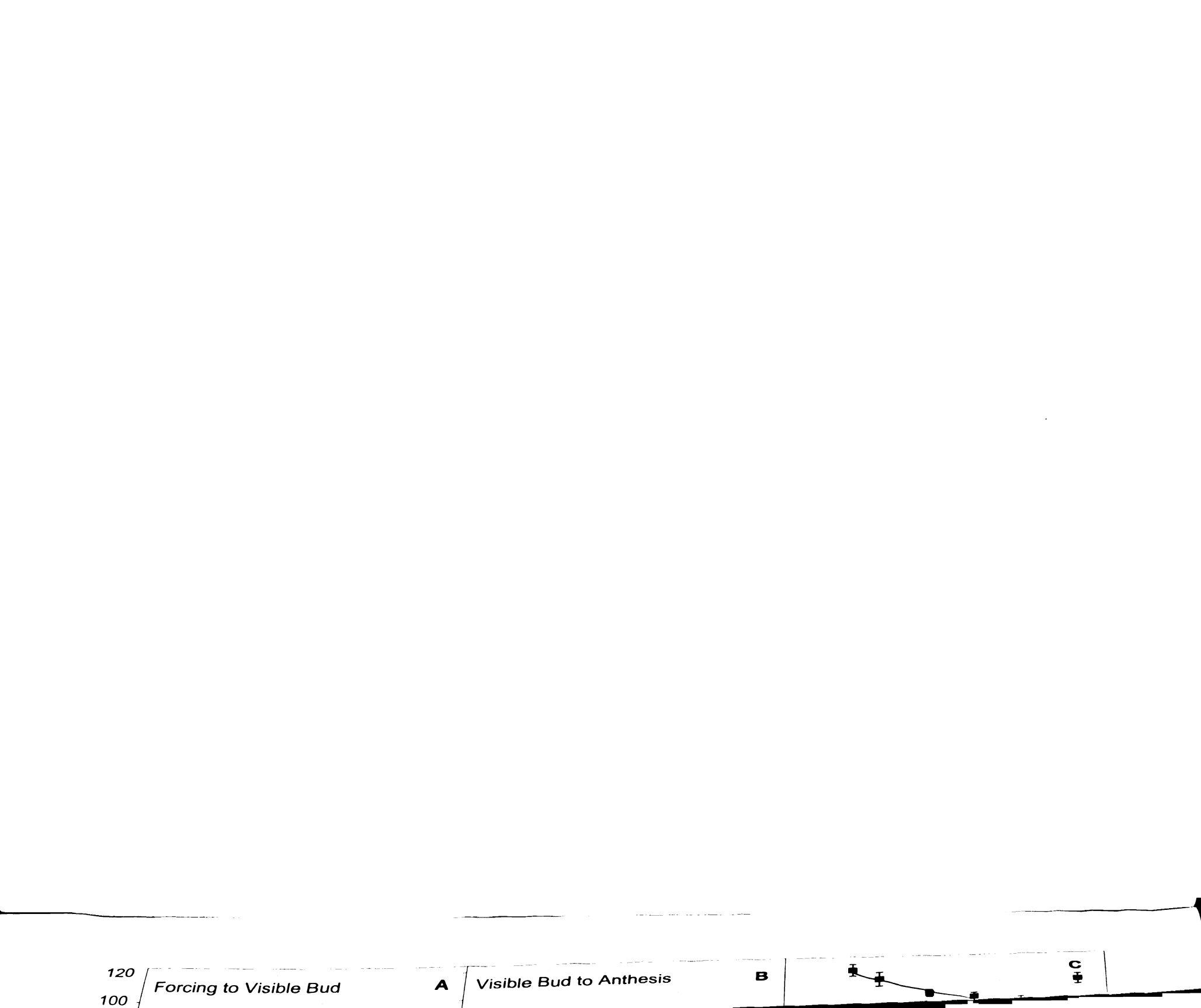


Figure 6. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta* 'Hyacinthina' in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.


120
100
Forcing to Visible Bud
A
Visible Bud to Anthesis
B
C

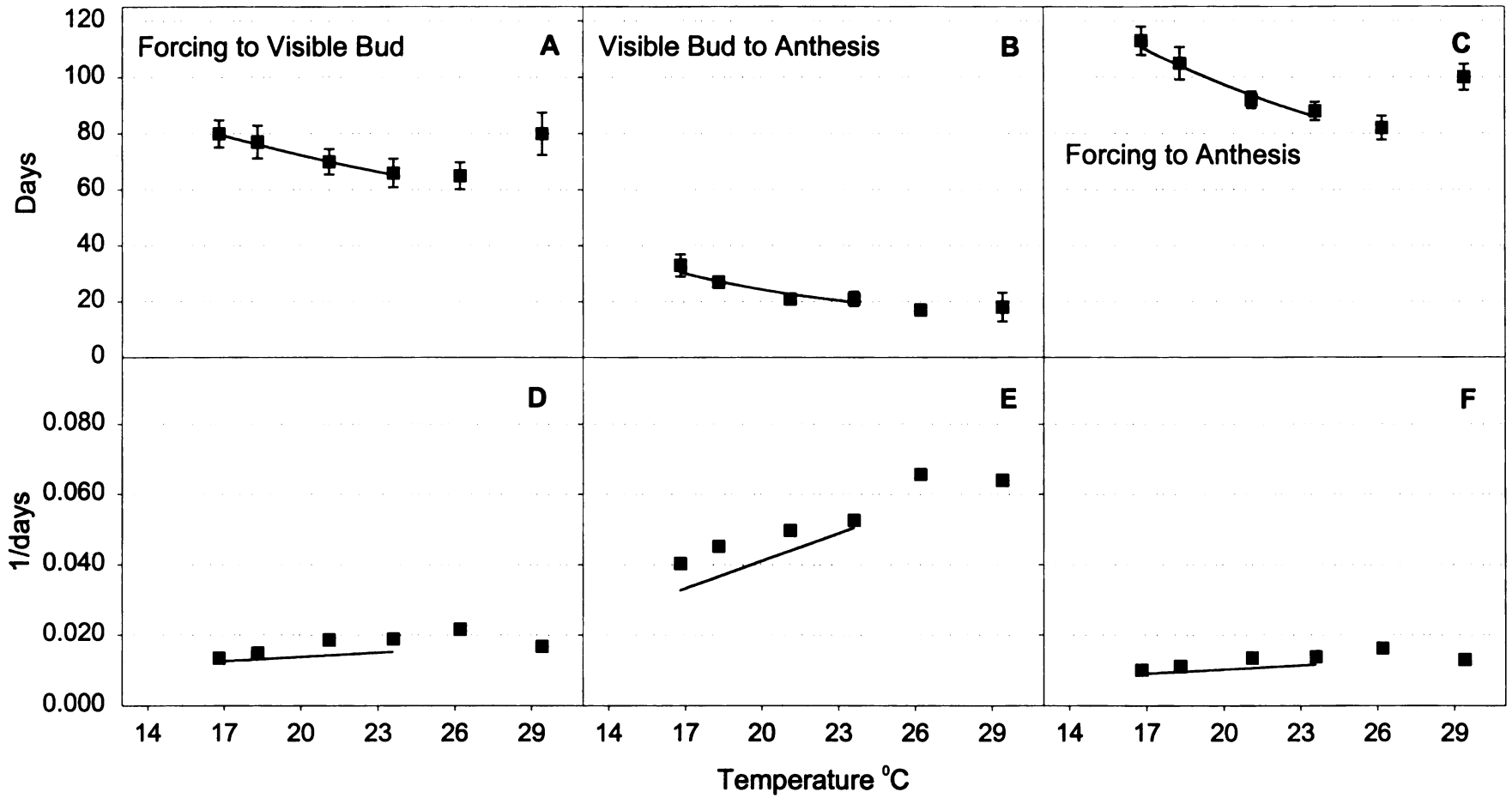


Figure 7. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta* 'Lancifolia' in 1998-1999. The parameters of linear regression lines are presented in Table 7.
The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

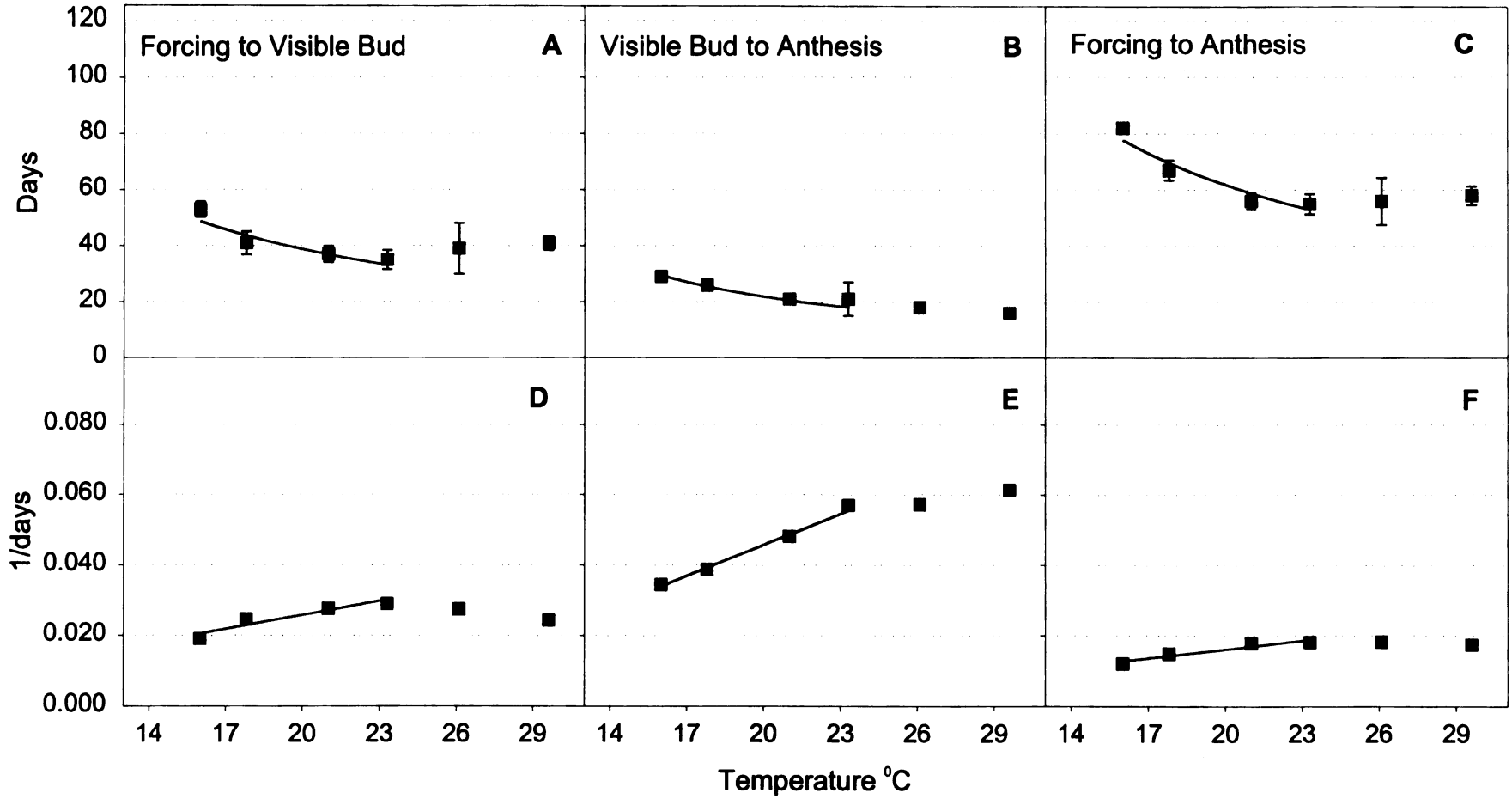


Figure 8. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for Hosta 'Tokudama' gold in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.


120
100
Forcing to Visible Bud
A
Visible Bud to Anthesis
B
Forcing to Anthesis
C

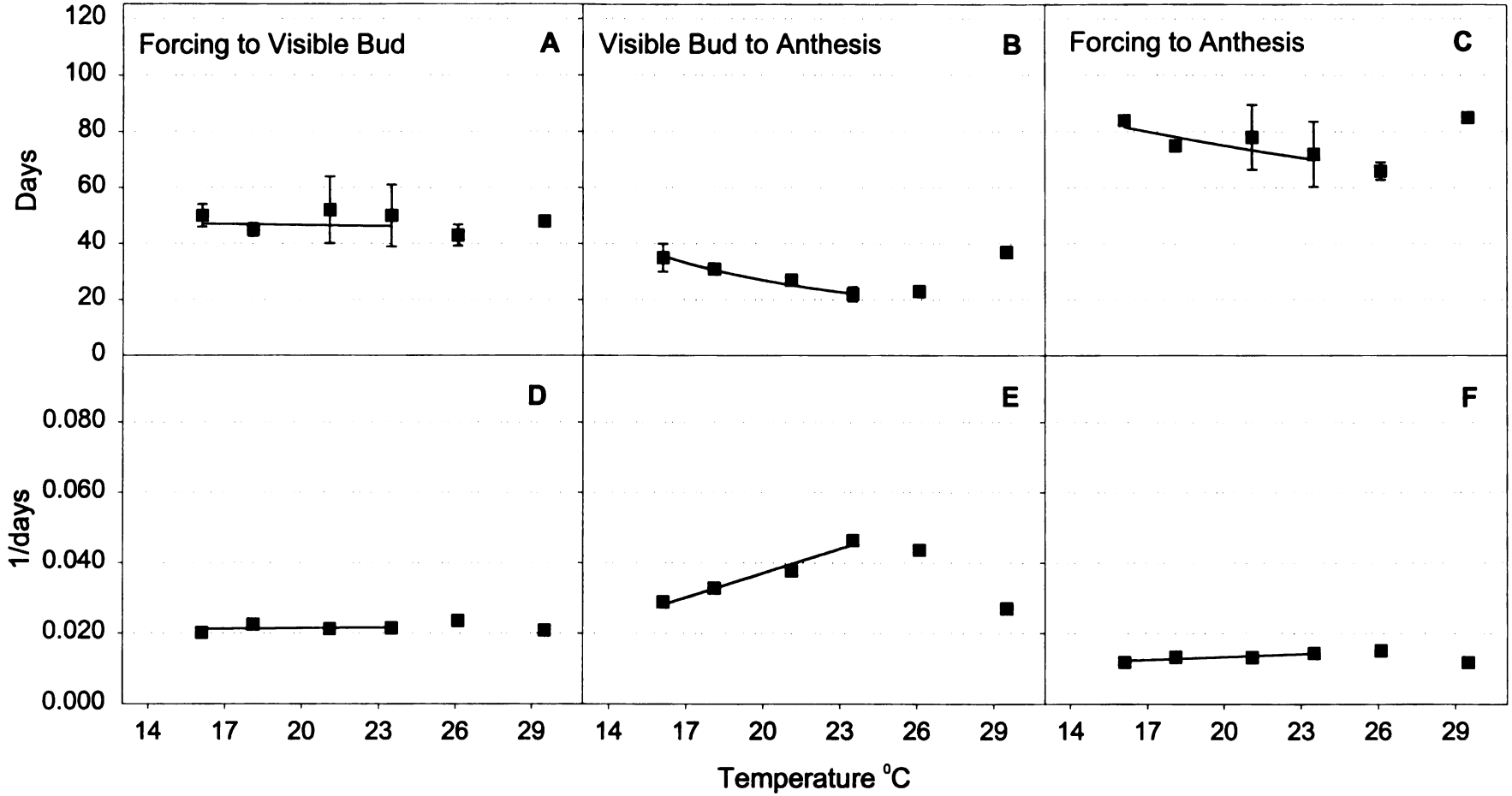


Figure 9. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta* 'Undulata' in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

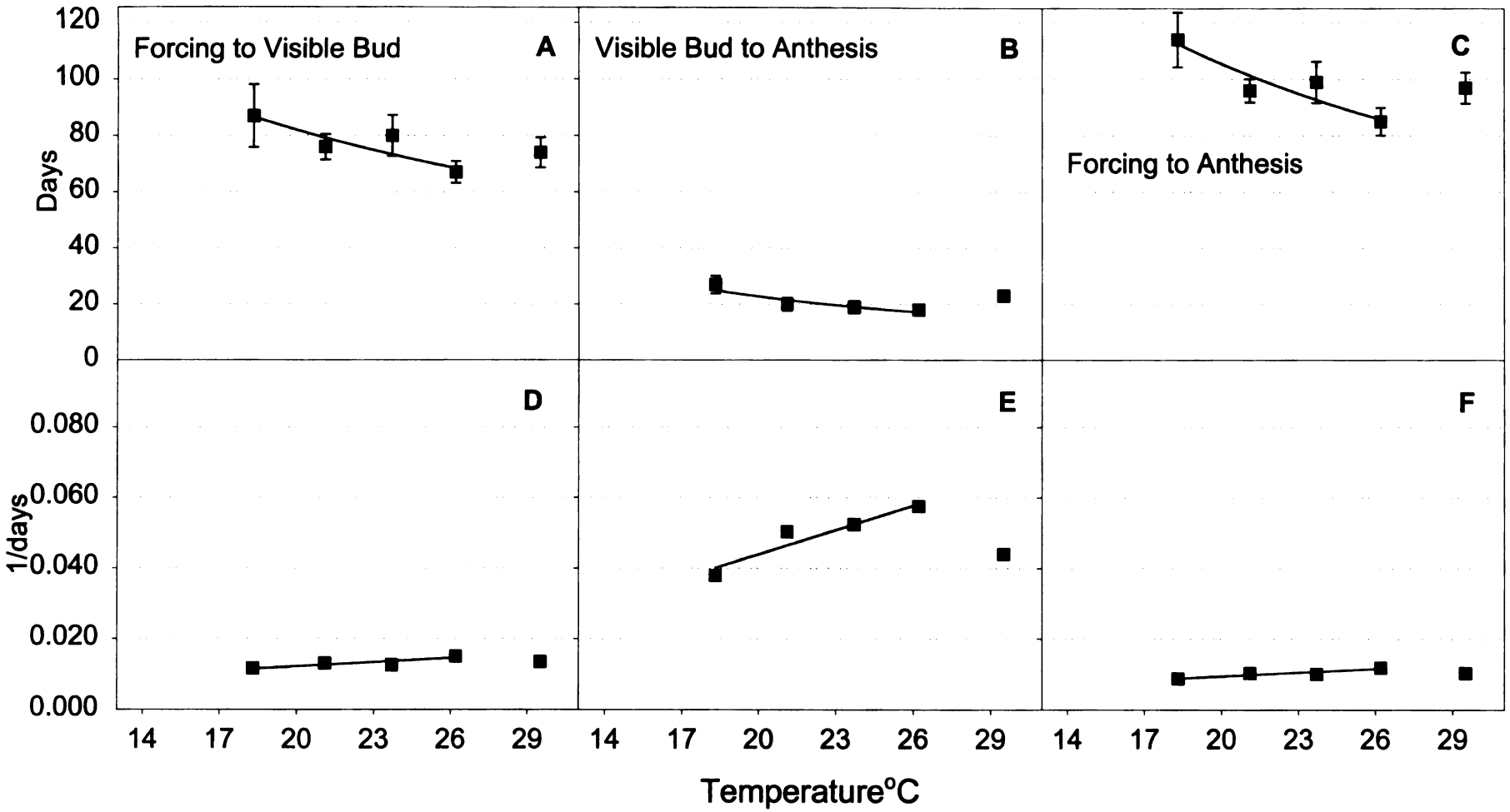


Figure 10. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta plantaginea* in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

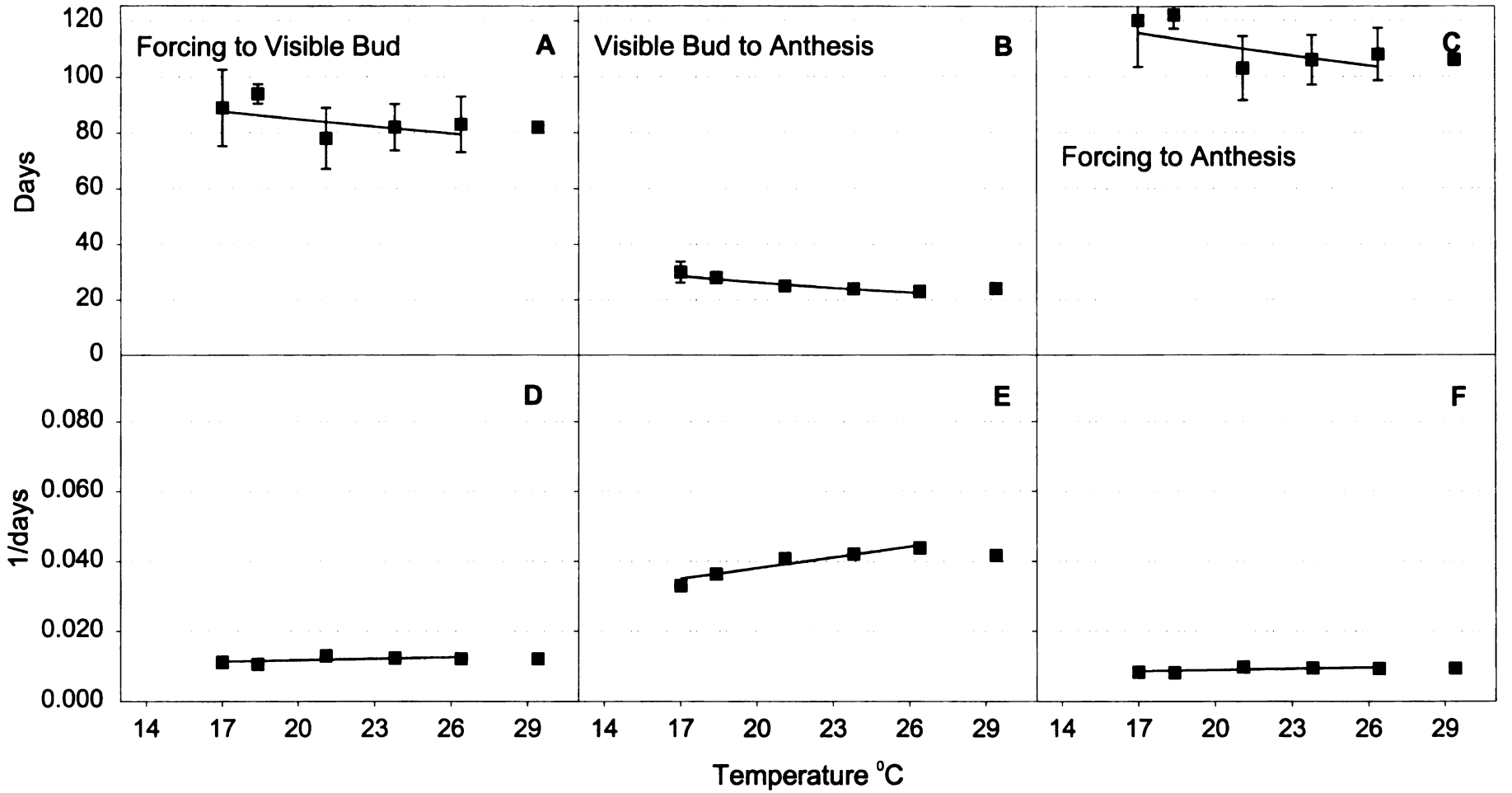


Figure 11. The effects of temperature on time and the rate of progress from forcing to visible bud (A, D), from visible bud to anthesis (B, E), and from forcing to anthesis (C, F) for *Hosta* 'Royal Standard' in 1998-1999. The parameters of linear regression lines are presented in Table 7. The regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F. Error bars represent 95% confidence intervals.

APPENDIX A

Development of *Hosta* 'Halcyon' Lateral Buds

Objective: To determine the influence photoperiod, benzyladenine, and plant orientation have on development of *Hosta* 'Halcyon' lateral buds.

Plant Material and Culture. Field-grown *Hosta* 'Hacyon' plants were received from Twixwood Nursery (Berrien Springs, Michigan) on August 18, 1997. The foliage and flower stalks had been cut 10 cm above each crown, and all visible lateral buds had been removed. Eighty uniform plants were potted upright into 13-cm (1.1 L) square containers filled with a commercial soilless medium composed of composted pine bark, vermiculite, Canadian sphagnum peat, and coarse perlite with a wetting agent, lime, and starter fertilizer charge (High Porosity Mix, Strong-Lite Products, Pine Bluff, AR). Plants were fertilized at every irrigation with a nutrient solution made from well water (EC of 0.70 $mScm^{-1}$ and 105, 35, and 23 mgL^{-1} Ca, Mg and S respectively) acidified with H_2SO_4 to a titratable alkalinity of approximately 130 mgL^{-1} $CaCO_3$ and water soluble fertilizer providing 125-12-125-13 N-P-K-Ca mgL^{-1} (30% ammonical N) plus 1.0-0.5-0.5-0.5-0.1-0.1 (Fe, Mn, Zn, Cu, B, Mo) mgL^{-1} (MSU Special, Greencare Fertilizers, Chicago, IL).

Treatments. Zero or five ml of a 50-ppm benzyladenine (BA) (Accell, Abbott Laboratories, Chicago, IL) solution were poured onto each hosta crown planted in an upright position. Twenty-four hours after BA application, plants were tilted horizontally or remained upright. Plants were placed under long days (LD) or 9-hour short days (SD) on August 19, 1997, and remained under these conditions for five weeks. Photoperiods were established by covering plants with opaque black cloth from 1700 to 0800 to provide 9-hr of natural light. Sixty-watt incandescent lights delivered 3 to 5 $\mu mol\ m^{-2}s^{-1}$ from 2200 to 0200 to simulate long days. Four-hundred-watt high-pressure sodium (HPS) lamps provided a photosynthetic photon flux (PPF) of 100 $\mu mol \cdot m^{-2}\ s^{-1}$ starting at 0800 and continuing until the outside PPF exceeded 400 $\mu mol \cdot m^{-2}\ s^{-1}$.

If the outside PPF then dropped below 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ lamps were again turned on until 1700.

Data Collection and Analysis. Lateral shoot number, lateral bud number, and bud length were evaluated five weeks after treatment. A lateral bud was recorded when the bud measured at least 2 mm in length. Buds were measured and placed in categories to less than 1 cm, equal to 1 cm, or greater than 1 cm in length. A lateral shoot was recorded when at least one leaf had unfolded following emergence from a lateral bud. The total number of available buds per plant was calculated by summing the number of shoots and the number of visible buds present five weeks after treatment. The percentage of available buds developing into a shoot and those measuring greater than 1 cm, equal to 1 cm, and less than 1 cm was determined for each treatment. Data were arcsin transformed then analyzed using analysis of variance (ANOVA). Results are presented in Table 1.

Results and Discussion. Benzyladenine is a cytokinin that promotes lateral bud development in many plants, including *Hosta* (Garner et al, 1997; Garner et al, 1998; Keever, 1994). Generally, short days (SD) induce dormancy of *Hosta* lateral buds and promote lateral bud development, while long days (LD) promote vegetative growth (Finical et al, 1997).

Benzyladenine had no effect on average bud number or on the percentage of buds that formed shoots or measured less than, equal to, or greater than 1 cm in length. A low application rate and reduced volume may account for *Hosta* 'Halcyon's lack of response to BA. However, BA has been shown to markedly affect the number of lateral shoots produced on a single plant (Garner et al, 1997); therefore, higher rates of BA at greater volumes might increase the number of *Hosta* 'Halcyon' lateral shoots produced.

Photoperiod did not affect total bud number for each treatment; yet, photoperiod did affect the percentage of buds that developed into shoots and the length of remaining buds. Short

photoperiods promoted lateral bud enlargement but not shoot development. Long photoperiods promoted shoot development from lateral buds.

Plant orientation affected the percentage of total buds that developed into a lateral shoot with horizontally-oriented plants producing more shoots than vertically-oriented plants. Photoperiod, benzyladenine, and plant orientation interacted to affect the percentage of buds that developed into a shoot. A greater percentage of buds on horizontally-oriented plants with or without BA application and vertically-oriented plants with a BA application developed into shoots than other treatments.

Average lateral bud number was unaffected by benzyladenine, plant orientation, or photoperiod. It is assumed that a predetermined number of latent buds were present on plants prior to experimentation, therefore total bud number would not be affected by treatment. However, commercial hosta producers can expect a greater number of shoots to emerge from plants grown under LD conditions as few shoots developed from the lateral buds of plants grown under SD conditions despite BA application or plant orientation. A horizontal orientation also encouraged vegetative growth from lateral buds, and plants placed on their side are expected to develop more shoots than those planted upright. BA application has been shown to induce growth from lateral buds, yet the volume and concentration used in this experiment were insufficient to significantly affect lateral bud development and shoot growth.

Table 1. Effect of benzyladenine, plant orientation, and photoperiod on development of *Hosta* 'Halcyon' lateral buds. Plants used in this experiment were dug in mid-August, 1997, foliage removed to 10 cm above the crown, and all lateral buds ≥ 5 mm in length removed.

Photoperiod[a]	Orientation	BA (ppm)	Average number of buds	Bud Developmental Stage			
				< 1 cm	= 1 cm	>1 cm	Shoots
				(% of total buds)			
SD	Horizontal	0	1.7	29	12	41	18
		50	1.4	14	0	57	29
	Vertical	0	2.0	25	0	65	10
		50	1.7	47	18	35	0
LD	Horizontal	0	1.6	0	0	6	94
		50	1.7	12	0	35	53
	Vertical	0	1.2	33	8	8	50
		50	1.4	7	7	14	71
ANOVA[b]							
	BA		NS	NS	NS	NS	NS
	Photoperiod		NS	NS	NS	*	*
	BA*Photo		NS	NS	NS	NS	NS
	Orientation		NS	NS	NS	NS	*
	BA*Orien		NS	NS	NS	NS	NS
	Photo*Orien		NS	NS	NS	NS	NS
	BA*Photo*Orien		NS	NS	NS	NS	*

[a] SD: 9-hr photoperiod; LD: 9-hr photoperiod plus 4-hr night interruption.
[b] NS, Not sigificant; *, significant at $P<0.05$.

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APPENDIX B

Fall-Induced Dormancy of *Hosta* 'Royal Standard'

Objective: To determine temperature, photoperiod, and foliage removal effects on dormancy of *Hosta* 'Royal Standard'.

Plant Material and Culture. Container-grown *Hosta* 'Royal Standard' plants were received from Twixwood Nursery (Berrien Springs, Michigan) on August 18, 1997. Plants were fertilized at every irrigation with a nutrient solution made from well water (EC of 0.70 $mScm^{-1}$ and 105, 35, and 23 mgL^{-1} Ca, Mg and S respectively) acidified with H_2SO_4 to a titratable alkalinity of approximately 130 mgL^{-1} $CaCO_3$ and water soluble fertilizer providing 125-12-125-13 N-P-K-Ca mgL^{-1} (30% ammonical N) plus 1.0-0.5-0.5-0.5-0.1-0.1 (Fe, Mn, Zn, Cu, B, Mo) mgL^{-1} (MSU Special, Greencare Fertilizers, Chicago, IL).

Treatments. Plants were initially placed in a 20°C greenhouse or moved outside and exposed to natural temperatures (Figure 1). Plants received natural photoperiods (ND), long photoperiods (LD), or short photoperiods (SD) for six weeks beginning August 22, 1997. SD and LD photoperiods were established by covering plants with opaque black cloth from 1700 to 0800 so plants received 9-hr of natural light. Long days were simulated with 60-W incandescent bulbs delivering 3 to 5 $\mu mol\ m^{-2}\ s^{-1}$ from 2200 to 0200. Plants receiving natural photoperiods were exposed to 13 hours 36 minutes of light in August declining to 11 hours 55 minutes of light in October as determined by sunrise and sunset. Four-hundred-watt high-pressure sodium (HPS) lamps provided supplemental lighting with a photosynthetic photon flux (PPF) of 100 $\mu mol \cdot m^{-2}\ s^{-1}$ starting at 0800 and continuing until the outside PPF exceeded 400 $\mu mol \cdot m^{-2}\ s^{-1}$. If the outside PPF then dropped below 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ lamps were again turned on until 1700. Foliage was removed 10 cm above the crown 2, 4, or 6 weeks after the start of photoperiod treatments, and plants were transferred to a 20°C greenhouse with LD night-interruption lighting to ensure continued growth of nondormant plants. Foliage was not removed from control plants.

Data Collection and Analysis. Shoot emergence, shoot number, lateral bud number, and bud weight were recorded five weeks after foliage removal for half the plants. Data on the remaining plants were recorded eleven weeks after foliage removal. Preliminary analyses revealed no significant differences between collection timings, and data were combined. Data were analyzed using analysis of covariance (ANCOVA) and treatment means are presented in Table 1. Shoot number, bud number, and bud weight treatment means were adjusted to a covariate, whether the plant flowered prior to photoperiod treatments (flowering shoot). Treatment means were adjusted using the linear model $y_{ij} = \mu_i + \beta(x_{ij} - x_{..}) + e_{ij}$ where μ_i is the treatment mean, β is the slope for the linear regression, x_{ij} is the covariate for the jth plant in the ith treatment, $x_{..}$ is the average covariate value, and e_{ij} is the experimental error. Statistical analysis is presented in Table 2.

Results and Discussion. *Hosta* 'Royal Standard' shoot number, lateral bud number, and lateral bud weight were dependent on whether the plant was reproductive before photoperiod treatments. Reproductive plants produced 1.3 more shoots, 1.3 more lateral buds, and buds that weighed 0.7 more grams than those of nonreproductive plants. In *Hosta*, flowering releases apical dominance of lateral buds that have the potential to develop into new shoots under favorable environmental conditions.

The hosta leaf appears to be an additional source of growth inhibition with foliage removal releasing the correlative inhibition of lateral buds by the leaves. The time of foliage removal after photoperiod treatment affected *Hosta* 'Royal Standard' shoot number, lateral bud number, and lateral bud weight. Lateral bud outgrowth was suppressed in control plants with intact leaves compared to plants where leaves were removed. Consequently, the average bud number and bud weight of control plants and plants with foliage removal after six weeks was greater than two or four week treatments since buds did not develop into shoots. The average bud weight was also greater for control plants than for those cut back after six weeks. The inhibition of lateral bud

outgrowth resulted in control plants developing larger buds over the duration of the experiment with a smaller proportion of those buds developing into lateral shoots.

Clearly, the presence of leaves greatly inhibits the outgrowth of lateral buds into shoots. It is unclear from this experiment at what point *Hosta* species and cultivars enter dormancy in the fall, and if the dormant state can be reversed by photoperiod or temperature. *Hosta* 'Royal Standard' plants in this experiment did not show signs of dormancy after six weeks of controlled photoperiods and declining temeperatures. *Hosta* 'Royal Standard' is a hybrid cross of *Hosta plantaginea* and *Hosta sieboldiana* (Schmid, 1991). *Hosta plantaginea* and 'Royal Standard' do not require cold temperatures to break dormancy (Fausey, 1999). If the plants were entering a dormant state from experimental treatments, the subsequent long day photoperiod or greenhouse temperatures were sufficient stimuli to promote growth. However, cultivars that require cold to overcome dormancy would be expected to show true signs of dormancy, namely few lateral shoots emerging from buds upon transfer from natural to greenhouse conditions.

References

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Schmid, W. G. 1991. The Genus Hosta -- Giboshi Zoku. Timber Press, Portland, OR.

Table 1. Fall-induced dormancy of *Hosta* 'Royal Standard'. Plants were grown outdoors and in a 20°C greenhouse and were exposed to SD, ND, or LD photoperiods beginning August 22, 1997 for six weeks. Foliage was removed from plants at two-week intervals from the start of the experiment, and plants were transferred to a 20°C greenhouse with LD lighting for six weeks. The number of shoots and buds, and the weight of the buds were determined for each plant.

Time of foliage removal (wk)	Photoperiod[a]	Temperature[b]	Shoots[c]	Buds[c]	Bud weight[c] (g)
2	SD	Natural	1.5	3.0	0.5
		20	1.7	1.8	0.2
	ND	Natural	1.8	2.9	0.4
		20	1.8	1.9	0.3
	LD	Natural	3.0	2.5	0.4
		20	2.0	2.3	0.3
4	SD	Natural	2.1	3.7	0.6
		20	1.7	2.8	0.5
	ND	Natural	2.2	3.1	0.4
		20	2.4	2.2	0.3
	LD	Natural	1.5	3.2	0.8
		20	1.7	2.2	0.5
6	SD	Natural	2.4	3.4	0.8
		20	1.7	3.7	1.1
	ND	Natural	2.5	5.7	1.2
		20	1.7	3.5	0.9
	LD	Natural	3.1	3.2	0.9
		20	1.9	3.3	0.7
Control	SD	Natural	1.7	4.4	1.9
		20	2.0	4.3	1.6
	ND	Natural	1.8	5.0	1.8
		20	0.6	5.4	3.0
	LD	Natural	1.6	3.1	1.2
		20	0.6	4.1	2.3

[a] SD: 9-hr photoperiod; ND: natural photoperiod from 08/97 to 10/97; LD: 9-h plus 4-h night interruption from 2200 to 0200.
[b] Natural: outdoor temperature from 08/97 to 10/97; 20°C: greenhouse temperature.
[c] Least squares means adjusted for a covariate, flowering shoot.
[d] NS, Not significant; *, significant at $P<0.05$.

Table 1 (cont'd).

Significance[d]				
	Temperature	*	*	NS
	Photoperiod	NS	*	NS
	Temp*Photo	NS	*	NS
	Time	*	*	*
	Temp*Time	NS	*	*
	Photo*Time	*	NS	NS
	Temp*Photo* Time	NS	NS	*
	Flower shoot	*	*	*
Contrasts	Natural vs 20°C	*	*	NS
	LD vs SD	NS	NS	NS
	LD vs ND	NS	*	NS
	ND vs SD	NS	NS	NS
	2 week vs 4 week	NS	*	NS
	2 week vs 6 week	NS	*	*
	2 week vs Control	*	*	*
	4 week vs 6 week	NS	*	*
	4 week vs Control	*	*	*
	6 week vs Control	*	NS	*

[a] SD: 9-hr photoperiod; ND: natural photoperiod from 08/97 to 10/97; LD: 9-h plus 4-h night interruption from 2200 to 0200.

[b] Natural: outdoor temperature from 08/97 to 10/97; 20°C: greenhouse temperature.

[c] Least squares means adjusted for a covariate, flowering shoot.

[d] NS, Not significant; *, significant at $P<0.05$.

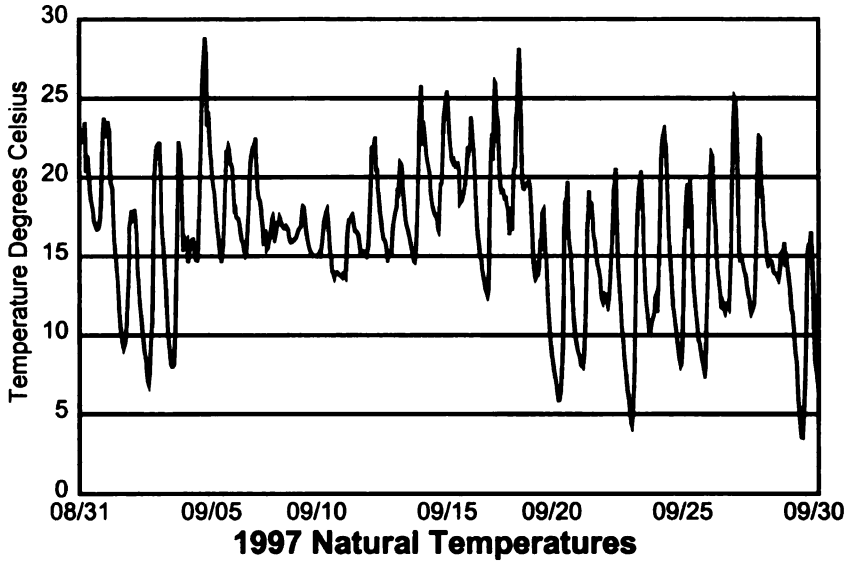

Figure 1. Natural air temperatures from 08/31/97 to 09/30/97, East Lansing, MI.