Juvenility and Flowering Responses in

Chrysanthemum x *superbum* and *Coreopsis grandiflora* and *lanceolata*
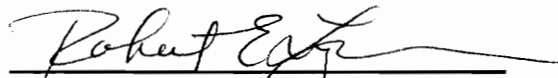
by

Margaret S. Damann

Thesis submitted to the Faculty of the

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in partial fulfillment of the requirements for the degree of
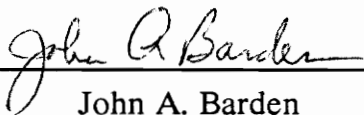
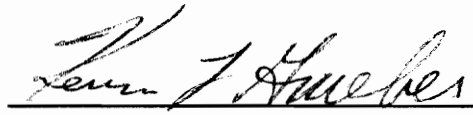Master of Science

in

Horticulture

APPROVED:

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Chrysanthemum x *superbum* and *Coreopsis grandiflora* and *lanceolata*

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(ABSTRACT)

Juvenility and flowering requirements were examined in *Coreopsis grandiflora* 'Sunray', *C. lanceolata* 'Early Sunrise', and *Chrysanthemum* x *superbum* 'G. Marconi' and 'Snow Lady'. *C. grandiflora* 'Sunray' and *C. lanceolata* 'Early Sunrise' grown from seed under continuous short days (SD) did not flower. 'Sunray' remained vegetative in long days (LD); however, LD induced flowering in 70 to 100% of the 'Early Sunrise' plants moved from SD to LD at true leaf stages beginning with 0 (cotyledons only) and progressing at 2 or 3 leaf increments to 24 leaves. The loss of juvenility in 'Early Sunrise' was gradual, with fastest flowering from onset of LD, 46 days, occurring when plants were transferred to LD at the 16 leaf stage. Plants moved to LD at six leaves flowered most rapidly from time of seeding, 84 days. Total leaf number at first flower increased as leaf number at transfer to LD increased. *Chrysanthemum* x *superbum* 'G. Marconi' was relatively unresponsive to LD, whereas all 'Snow Lady' plants flowered in LD treatments except the 24 leaf stage, which had 70% flowering. Although no 'G. Marconi' plants flowered under SD, 90% of the

'Snow Lady' plants flowered in continuous SD. In 'Snow Lady', transfer to LD at the cotyledon stage promoted fastest flowering from time of seeding, 75 days, and produced plants with the fewest number of leaves at first flower. Histological examination of apices of *C*. x *superbum* 'Snow Lady' revealed floral initiation in all 5 plants sampled following 3 weeks of LD. Initiation in SD started after the fifth week and was evident in all 5 plants sampled after the ninth week of SD.

The effects of chilling and a limited number of inductive photoperiods was examined in all 4 cultivars. Four months of natural outdoor chilling followed by at least 6 LD, promoted 40 to 100% flowering in *Coreopsis grandiflora* 'Sunray' and *Chrysanthemum* x *superbum* 'G. Marconi'. Chilling followed by SD increased flowering in each cultivar as compared to continuous SD with no chilling. The effects of limited inductive photoperiod (LIP) were evident in both *Coreopsis* cultivars, but not seen in either cultivar of *C*. x *superbum*. LIP inhibited stem elongation by approximately 10 cm in the chilled *Coreopsis* cultivars and also in *C. lanceolata* 'Early Sunrise' grown from seed with no chilling. LIP did not affect the scape length of either chilled or unchilled plants.

ACKNOWLEDGEMENTS

My sincere thanks to Dr. Robert Lyons for giving me the guidance and encouragement needed to accomplish the research and writing required for completion of this degree, for guiding and encouraging me in my teaching experiences, and for being a good neighbor (and not getting upset when I broke his lawn mower). Thanks also to Drs. John Barden and Kevin Grueber for providing their knowledge and support and for serving on my committee.

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Marilyn Echols, Donna Long, and Joyce Shelton have my respect and sincere thanks for all the assistance they offered in my battle against the computer!! Their friendship, patience, and willingness to answer my sometimes stupid questions was appreciated.

Very special thanks to Kathy Krentz for being such a super friend. Morning walks, softball games, good dinners, and her always positive attitude are memories I carry with me from Blacksburg. Thanks, also, to Dave Helmuth for lending a hand when I had tasks a little too big to handle by myself. These two are true blue friends, Midwestern Style.

And last, but certainly not least, my deepest thanks go to my fiancé Mike Compton. He stuck by me through it all, listened to my complaints and concerns, and managed to love me none the less. Thanks for not letting me give up, and for not giving up on me.

DEDICATION

This thesis, which has engulfed so much of my life the past two years, is dedicated in whole to my family. You have always been there to lend support and guidance and to "cheer me on" in everything I have attempted to do, even though you knew my endeavors would often take me far away from home. With you behind me, there was little doubt that I could accomplish the seemingly impossible. Thanks to Mom for the weekly packages and letters that sometimes made me laugh and other times brought tears to my eyes. I can only hope that I might someday possess just a fraction of your wisdom, patience and incredible loving ways. Dad, you kept my car running, kept gas in the tank, and were always there to offer guidance and some "Damann Humor" when I needed to laugh at myself and enjoy life a little bit more. Thanks also to Teresa, my older, "little" sister. You have encouraged me from my first day at UW-RF and have stuck by me through everything: weekends working at the Mermaid, the late night, long distance, stressed out phone calls, and the always too few, too fast vacations and visits. And Dennis... thanks for golfing on Tuesday nights, so Teresa had HOURS of uninterrupted phone time.

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Chapter I

Juvenility and Flowering Requirements in *Coreopsis
grandiflora* 'Sunray' and *Coreopsis lanceolata* 'Early Sunrise'

Abstract. To examine juvenility and the flowering requirements of *Coreopsis
grandiflora* 'Sunray' and *C. lanceolata* 'Early Sunrise', plants were grown under short
days (SD) and transferred to long days (LD) upon reaching true leaf stages beginning
with 0 (cotyledons only) and progressing at 2 leaf intervals to the 24 leaf stage.
Neither cultivar flowered in continuous SD, and 'Sunray' also remained vegetative in
LD. However, LD induced flowering in 70 to 100% of the 'Early Sunrise' plants in
each leaf number treatment. The loss of juvenility in 'Early Sunrise' was gradual,
with most rapid flowering from onset of LD, 46 days, occurring when plants were
transferred to LD at the 16 leaf stage. Plants moved to LD at 6 leaves flowered most
rapidly from time of seeding, 84 days. Total leaf number at first flower increased as
leaf number at transfer to LD increased. Stem length, scape length, and total height
at first flower followed no significant linear or quadratic regression with leaf number
at transfer to LD.

INTRODUCTION:

Plants cultivated within controlled environments for aesthetic value are the mainstay of the commercial floriculture industry. In 1987, these plants accounted for at least 2.15 billion dollars at the wholesale level in the U.S., including an 18 percent increase in the value of potted flowering plants over the previous year (Anon. 1988). Contrary to an expressed consumer desire for an expanded choice of plant material (Cathey, 1981; Herbert, 1977), fewer than 20 ornamental species make up the majority of cultivated floriculture offerings to the public (Anon., 1988). There appears to be room to expand the ornamental species selection available in the marketplace.

Currently, *Coreopsis* species are relatively insignificant commercially, but have market potential as evidenced by rising exposure in garden catalogs and perennial flower guides. *Coreopsis* plants possess attractive foliage, beautiful flowers in shades of yellow, and can tolerate diverse environmental conditions; they are also cold hardy at least through USDA zone 7. *Coreopsis*, or tickseed, is a genus generally reported to contain over 100 species (Everett, 1981; Giles et al., 1980; Bailey and Bailey, 1976; Bailey, 1949), although at least one source reports the species count to be about 50 (Gleason, 1974). *Coreopsis* is in the Asteraceae and most species are herbaceous annuals or perennials native to the Americas, Hawaiian Islands, and tropical Africa (Clausen and Ekstrom, 1989; Everett, 1981; Giles et al., 1980; Bailey and Bailey, 1976; Gleason, 1974; Bailey, 1949).

The best known cultivated perennial species in zone 7 are *C. lanceolata* and *C. grandiflora*. They have many similarities and their hybrids are frequently confused; this has also led to a debate over a definitive classification of these species as either annual or perennial (Clausen and Ekstrom, 1989; Thomas, 1982; Gleason, 1974). Leaf morphology, stem length, and flower head size and color are similar for both species but *C. lanceolata* has mostly basal foliage and a naked peduncle about as long as or longer than the leafy part of the stem. Conversely, *C. grandiflora* has branched stems, is leafy almost to the top, and has peduncles seldom half as long as the leafy part of the stem (Clausen and Ekstrom, 1989; Everett, 1981; Cronquist, 1980; Bailey and Bailey, 1976; Bailey, 1949). *C. lanceolata* is native to Michigan south to Florida, Western Ontario to Virginia, New Mexico, Louisiana, and Missouri (Clausen and Ekstrom, 1989; Everett, 1981; Giles et al., 1980; Bailey and Bailey, 1976; Gleason, 1974; Bailey, 1949). This species, in particular, is described as being well adapted for perennial and mixed flower borders, wildflower gardens, naturalized areas, and for use as cut flowers (Giles et al., 1980). The cultivar Early Sunrise, usually listed under *C. lanceolata*, is an important new introduction which flowers the same year after a spring sowing. In full sun its fully double, yellow flowers bloom 90-100 days from sowing and reach a height of 45 cm (18 inches).

C. grandiflora Nutt. is native to the Southern U.S. north to Missouri and Kansas (Clausen and Ekstrom, 1989; Bailey and Bailey, 1976; Gleason, 1974; Bailey, 1949). The cultivar Sunray is listed under this species, but not definitively (Clausen and Ekstrom, 1989). 'Sunray' grows to a height of 45 to 60 cm (1-1/2 to 2 feet), and

produces double, yellow flowers. Presently, there is some confusion about growth patterns and the flowering mechanism of *Coreopsis* species. With reference to *C. lanceolata*, Giles et al. (1980) reported that seeds sown in early spring in greenhouses or cold frames provide sparse flowering that season and heavier flowering the second season.

For *Coreopsis* species to become commercially marketable, potted ornamentals, research must elucidate their flowering mechanisms in order to facilitate control, manipulation, and scheduling of blooming. Investigations regarding photoperiodicity are an appropriate start due to the importance of this factor in many relatives of *Coreopsis*. Some plants are known to be sensitive to inductive photoperiods at a very early age. Several *Chenopodium* species show evidence of floral initiation in as few as 6 days after seed imbibition (Cumming, 1959) and seedlings of *Brassica campestris* are photoperiodically sensitive on the fourth day after germination (Friend, 1968). However, a period of juvenility, described as a physiologically-based time when a plant is insensitive to conditions later promoting floral initiation (Bernier et al., 1981), is common in plants. The duration of juvenility can be measured in years for most woody species but is often much shorter in herbaceous plants (Hackett, 1985). For many photoperiodic herbaceous species, the passage through juvenility can be gradual, characterized by a period of increased sensitivity to daylength rather than a total inability to flower (Bernier et al., 1981). Many attempts have been made to quantify the precise end of juvenility. In 1934, Purvis first postulated the concept of a required minimum leaf number needed before the apex was capable of initiating

floral organs. The transition from juvenility to maturity occurred when enough photosynthetic leaf area had been formed to sustain flowering and fruiting (Schwabe, 1976; Wareing and Frydman, 1976). However, it is questionable whether foliage plays the only role in floral induction. Systematic removal of leaves, even to the extreme of leaving only the rosette stem and shoot apex intact, did not alter the flowering response of *Eschscholtzia californica*, an indication that a specific node number may affect floral induction (Lyons and Booze-Daniels, 1986).

An early study classified *Coreopsis lanceolata grandiflora* as a long day (LD) plant when two-year-old field-grown plants flowered faster and more profusely with an extended natural daylength (Laurie and Poesch, 1932). Later, Ketellapper and Barbaro (1966) studied the role of photoperiod in flowering of *Coreopsis grandiflora*, which may have been the same species as studied earlier by Laurie and Poesch, given current taxonomic confusion. Plants remained vegetative in LD as well as short days (SD), but growth habits differed accordingly. Leaves on plants in SD remained small and prostrate while LD promoted elongated and erect foliage. Flowering occurred when given a LD-SD-LD regime. On this basis, Ketellapper and Barbaro determined *C. grandiflora* to be a short-long day (SLD) plant, however, the LD requirement was judged not to be absolute. *C. grandiflora* was also found to pass through a juvenile phase during which the plants exhibited little or no sensitivity to SD. The SLD flowering nature of *Coreopsis grandiflora* is occasionally still reported (Metzger, 1988).

Little published work concerning juvenility or flowering of *C. lanceolata* or *C. grandiflora* appeared after 1966, but it was not so for other plants. In working with

Eschscholtzia californica, Lyons and Neale (1983) identified a negative linear relationship between unfolded leaf stage and the rapidity of flowering, suggesting that as the plant aged, it became more responsive to the inductive LD photoperiod. This response was later confirmed; *E. californica* flowered most rapidly if 10 true leaves were present at the start of LD (Lyons and Booze-Daniels, 1986). Carter (1986) concluded that 8 to 10 LD were required for initiation of the terminal flower bud. If the LD stimulus was terminated prior to 8 cycles, anthesis would not occur. *Rudbeckia hirta* 'Marmalade' exhibits a similar response to LD with the onset of maturity, being most sensitive to LD if first grown in SD to 19 expanded leaves (Bourke, 1990). At this stage, plants would flower in 42 days, the most rapid flowering from onset of LD. *Gaillardia pulchella*, like *R. hirta* 'Marmalade' and *E. californica*, also appears to mature gradually (Bourke, 1990). *G. pulchella* plants possessing 20 leaves at the start of inductive LD flowered most rapidly.

The objectives of the present study were to quantify the end of juvenility in *Coreopsis* 'Early Sunrise' and 'Sunray', to compare flowering characteristics with earlier results from research on *Coreopsis grandiflora*, and to describe related vegetative characteristics.

MATERIALS AND METHODS:

Coreopsis lanceolata 'Early Sunrise' and *C. grandiflora* 'Sunray' seeds were sown on 13 June 1990 in a medium of 2 parts vermiculite: 1 part peatmoss (v/v) in cell packs and placed under intermittent mist. Treatments were assigned randomly at the time of sowing. Upon germination, misting ended and all packs were moved to SD. Plants were subsequently transplanted into 10 cm (4 inch) plastic pots using a mixture of 3 parts peatmoss: 1 part perlite: 1 part vermiculite (v/v/v). LD conditions were created by night interruption from 2200-0200 hr with 60W incandescent bulbs strung overhead to provide 3-4 μmol·m^{-2}·s^{-1} PPF at plant height. SD conditions were created by covering the plants from 1700-0800 hr with 100% light exclusion black sateen cloth. Ambient temperature for germination was 19-21°C day and night. Growing temperatures thereafter were 16-18°C nights. After transplanting, plants were fertilized weekly with 400 ppm N from 20N : 6.6P : 17.6K during irrigation.

Ten plants (reps) were transferred from SD to LD upon reaching the following true leaf stages: 0 (cotyledons only), 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24; a leaf was defined as possessing a fully expanded lamina. Ten plants of each cultivar remained in SD for the duration of the experiment as controls. Data taken at first flower included: number of days elapsed from both seeding and start of LD, number of expanded leaves along the main stem, stem length (from cotyledonary node to uppermost node possessing a visible, reproductive, axillary branch), non-

reproductive scape length (from last visible axillary branch to uppermost node possessing a leaf), and leafless scape length (from uppermost non-reproductive node to calyx attachment). First flower was defined as the date when ray florets had expanded perpendicular to the stem attachment. The experimental design was completely random; regression analysis and parabolic minimum point calculations (Rees and Sparks, 1969) were used to analyze the data.

RESULTS:

'Sunray' plants did not flower in any treatment group, including the SD control. 'Early Sunrise' plants also remained vegetative in SD but exhibited 70 to 90% flowering in LD treatments. Lack of 100% flowering was random and was not attributed to specific leaf number treatments. Regression analysis indicated a quadratic relationship between the number of days to flowering after the onset of LD and plant leaf number when first moved to LD (Figure 1.1). Plants transferred to LD at the cotyledon stage flowered in an average of 75 days while those introduced to LD at 24 leaves averaged 56 days. The calculated parabolic vertex (minimum point) occurred at 16 leaves and 46 days to flowering. There was also a quadratic relationship between plant leaf number at start of LD and the number of days from sowing to flowering (Figure 1.2). Plants transferred to LD at the cotyledon stage

flowered 91 days after sowing, while those introduced to LD at 24 leaves flowered after 125 days. The calculated parabolic minimum point showed that plants flowered most rapidly, 84 days after sowing, if they had 6 leaves when transferred to LD. Total leaf number at first flower also yielded a quadratic relationship (Figure 1.3); the cotyledon stage plants averaged 24 leaves while the 24 leaf stage plants averaged a total of 43 leaves.

Stem length, non-reproductive scape length, leafless scape length, and total height at first flower followed no significant linear or quadratic relationship with plant leaf number at the onset of LD. Their means were 13.4 cm, 1.5 cm, 21.0 cm, and 35.8 cm, respectively.

DISCUSSION:

Ketellapper and Barbaro (1966) found that *C. grandiflora* 'Single Mayfield Giant' plants remained vegetative when maintained in LD for 54 weeks or in 40 weeks of LD followed by 14 weeks of SD. Flowering occurred only when 8 additional weeks of LD followed the SD period, leading to the conclusion that this species was a SLD plant. When sample size was increased, 45% flowered after 40 weeks in only SD, however, there tended to be a single flower per plant, decreased stem elongation, and poor overall plant quality. Only 3% of plants grown under

continuous LD conditions flowered after 40 weeks. By contrast, *C. grandiflora* 'Sunray' plants held in SD for up to 10 weeks did not flower when transferred to LD, as might have been expected if they were indeed SLD plants (Metzger, 1988; Ketellapper and Barbaro, 1966). In *C. lanceolata* 'Early Sunrise', 70% of the plants flowered when placed in LD at the cotyledon stage, and all other treatment groups receiving LD had a minimum of 70% flowering, indicating a virtual absence of any reported absolute SD requirement (Ketellapper and Barbaro, 1966). Furthermore, continuous SD conditions did not elicit flowering in 'Early Sunrise' or 'Sunray', but it should be noted that the present research was terminated after 20 weeks, only half the time in which flowering was observed in continuous SD (Ketellapper and Barbaro, 1966). The duration of the research period has been a debatable factor in photoperiod studies. In fact, some believe that most obligate LD plants are actually facultative and will eventually flower, even in continuous SD (Evenari and Gutterman, 1966), which could account for the SD flowering of *Coreopsis* described previously (Ketellapper and Barbaro, 1966).

Ketellapper and Barbaro (1966) discussed a juvenile phase during which *Coreopsis* plants were less sensitive or insensitive to SD. Such a phenomenon characterized *C. lanceolata* 'Early Sunrise' but with respect to LD inductive conditions. Results from the present research indicated that this cultivar was most sensitive to LD at a calculated expanded leaf number of 16, when, theoretically, it would flower in 46 days. A more appropriate description of juvenility loss may be a leaf number range, based on the 95% confidence interval, rather than a single leaf

stage. In this case, *C. lanceolata* 'Early Sunrise' plants possessing 9-21 expanded leaves at the start of LD could be expected to flower most rapidly; this is compared to 15-24 leaves in *Rudbeckia*, 14-20 leaves in *Gaillardia pulchella* (Bourke, 1990), and 6-14 leaves in *Eschscholtzia californica* (Lyons and Booze-Daniels, 1986).

In determining a relationship between plant age and SD sensitivity, Ketellapper and Barbaro (1966) found that seedlings grown in LD for 9 weeks or less, then given 7 weeks of SD, did not flower upon return to LD conditions. However, after 15-20 weeks of initial LD growth, 7 weeks of SD were sufficient to promote 100% flowering upon return to LD. The 9 weeks of growth prior to inductive conditions corresponds to the treatment group of 20 leaves per plant at transfer to LD in the present experiment. Flowering occurred in 90% of the plants in this group. In breeding *C. lanceolata* 'Early Sunrise', the SD requirement appears to have been eliminated and the juvenility period greatly reduced. In contrast to the findings that *C. grandiflora* reached sensitivity to inductive photoperiods 15-20 weeks from planting (Ketellapper and Barbaro, 1966), in the present research 20 weeks was sufficient to bring 70 to 90% of plants in each leaf number treatment of 'Early Sunrise' to flower.

For comparison, it is also significant to point out that the original research by Ketellapper and Barbaro in 1966 utilized commercially available *C. grandiflora* 'Single Mayfield Giant' seed. However, due to large variability in response to environmental conditions, lines were then selected by those authors by collecting seeds from individual plants. Selection procedures were not reported, but it is possible that

selection for the SD flowering response occurred.

Coreopsis grandiflora 'Sunray' did not flower in SD or SLD conditions in the 20 weeks allowed for the present research. The duration of the experiment is a possible explanation for the differences in floral initiation responses between our research and previous work with *C. grandiflora* (Ketellapper and Barbaro, 1966). The use of available materials and methods and lack of scrutiny by statistical analysis could also alter the interpretation of the results of Ketellapper and Barbaro (1966). However, it is likely that the floral initiation requirements of 'Sunray' have been significantly altered through breeding and selection, to no longer resemble other cultivars within the species. This strongly suggests that flowering should not be characterized for an entire species, but is unique to cultivars within each species of *Coreopsis*, as indicated herein.

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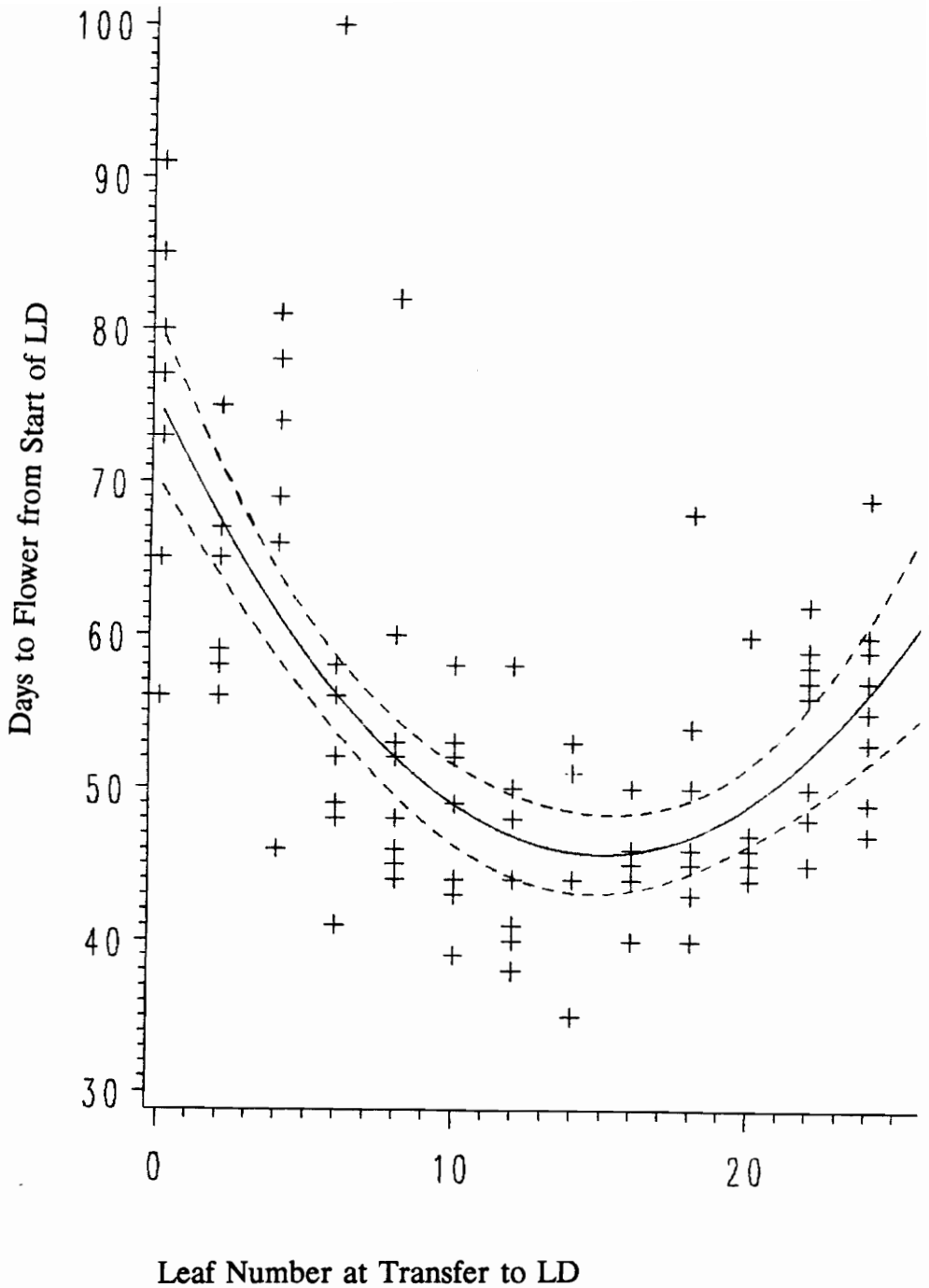
Figure 1.1 The effect of leaf number at transfer to long days (LD) on number of LD needed for flowering of *Coreopsis lanceolata* 'Early Sunrise'.
$y = 74.7 - 3.87x + 0.129x^2$, $R^2 = 0.44**$; parabolic minimum point is 16 leaves, 46 days to flowering; area bound by dashed lines indicates a 95% confidence interval.
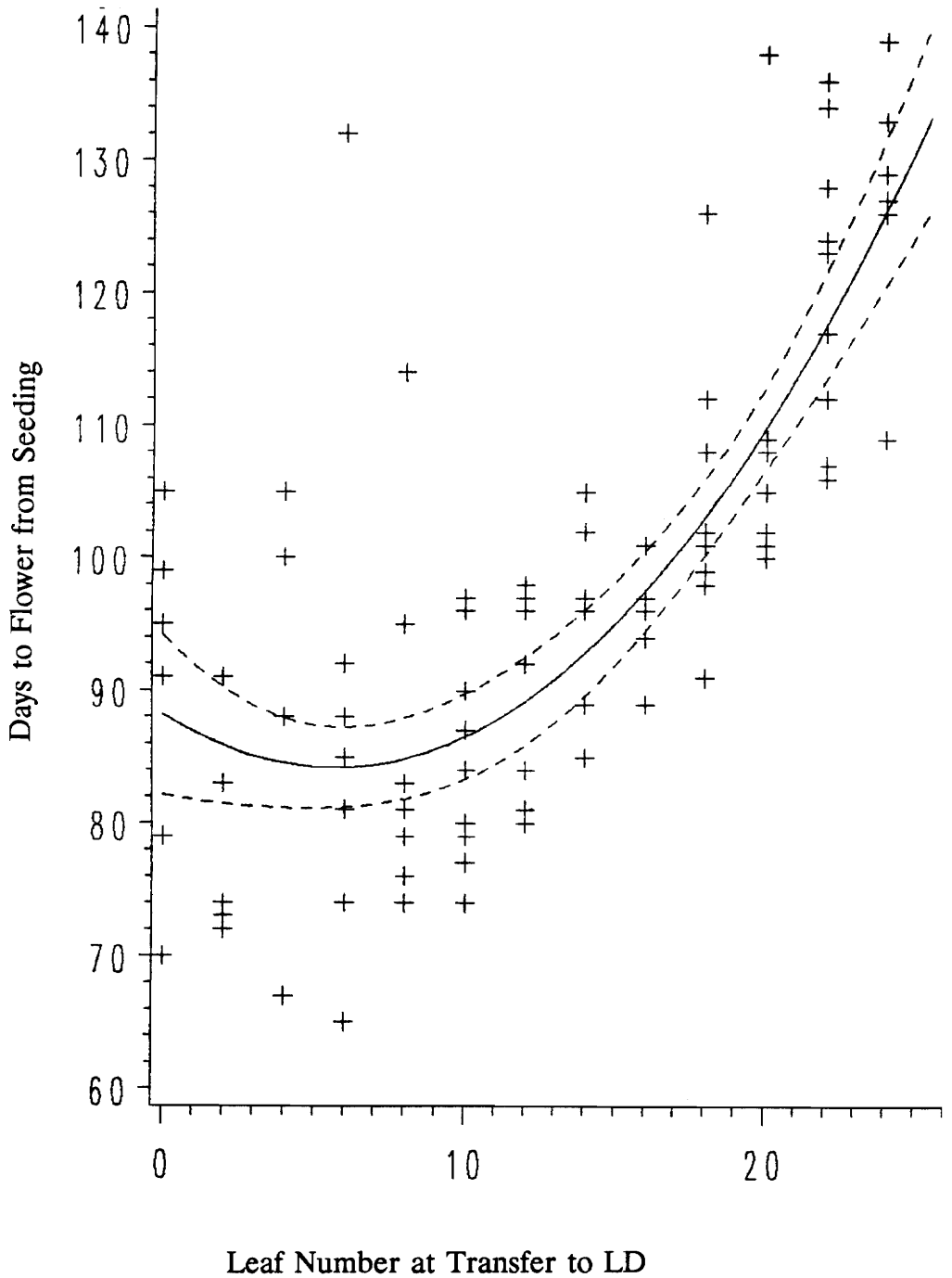
Figure 1.2 The effect of leaf number at transfer to long days (LD) on number of days from seeding to flower for *Coreopsis lanceolata* 'Early Sunrise'. $y = 88.2 - 1.41x + 0.125x^2$, $R^2 = 0.59**$; parabolic minimum point is 6 leaves, 84 days to flowering; area bound by dashed lines indicates 95% confidence interval.

Juvenility and flowering in *Coreopsis* species
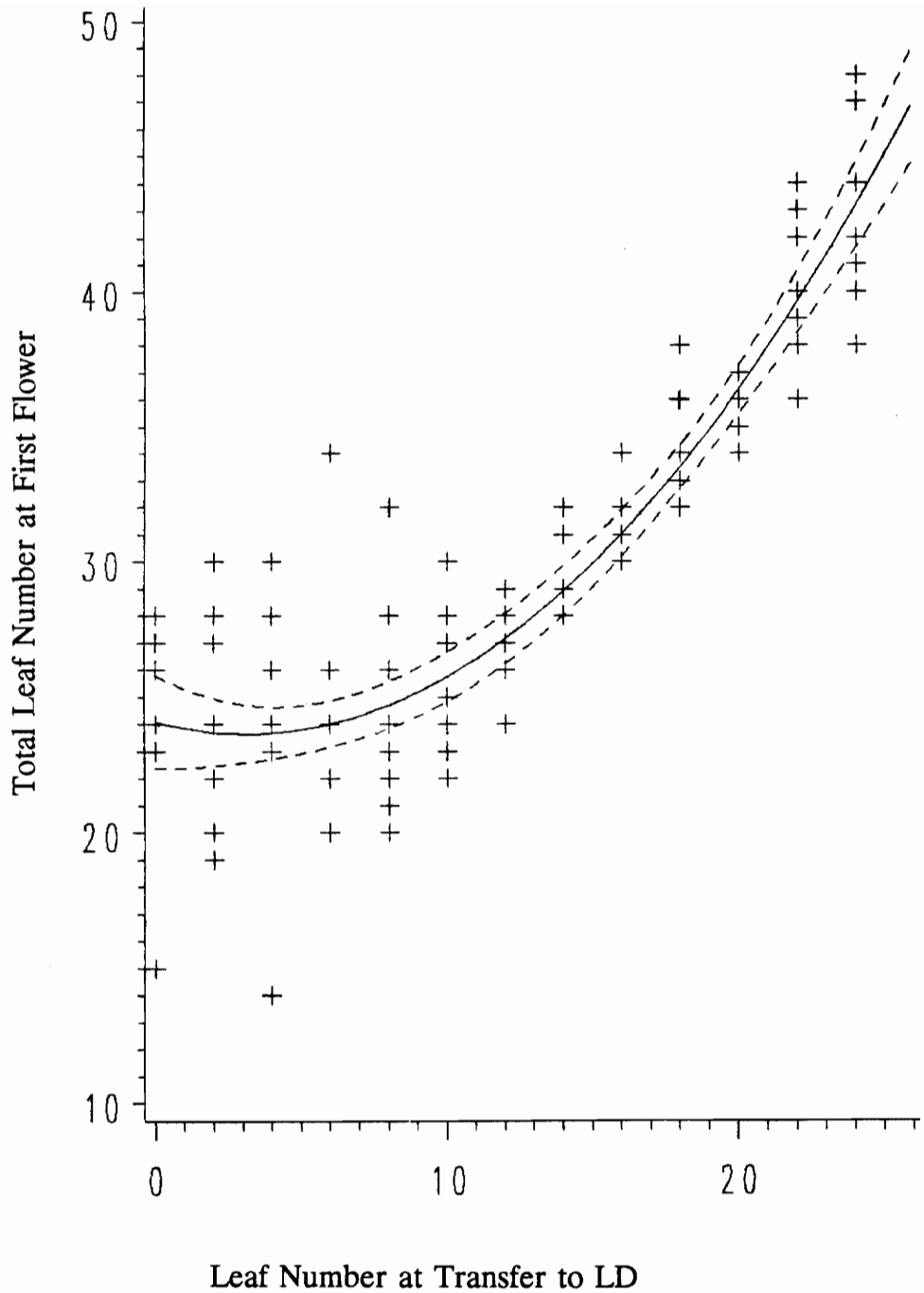
Figure 1.3 The effect of leaf number at transfer to long days (LD) on total leaf number at first flower for *Coreopsis lanceolata* 'Early Sunrise'. $y = 24.1 - 0.281x + 0.0448x^2$, $R^2 = 0.80$** ; area bound by dashed lines indicates a 95% confidence interval.

Chapter II

Juvenility and Flowering Requirements in
Chrysanthemum x *superbum* 'G. Marconi' and 'Snow Lady'

Abstract. Flowering requirements and juvenility were studied in *Chrysanthemum* x *superbum* 'G. Marconi', a standard cultivar, and 'Snow Lady', a dwarf cultivar. Seeds were sown and plants were maintained in short day (SD) conditions until transfer to long days (LD) at specific true leaf stages beginning with 0 (cotyledons only) and progressing at 3 leaf intervals to 24 leaves. 'G. Marconi' was relatively unresponsive to LD, whereas 100% flowering was observed in all 'Snow Lady' LD treatments except the 24 leaf stage, which had 70% flowering. Although all 'G. Marconi' plants remained vegetative under SD, 90% of the 'Snow Lady' plants flowered in continuous SD. In 'Snow Lady', transfer to LD at the cotyledon stage promoted most rapid flowering from time of seeding, 75 days, and produced plants with the fewest number of leaves at first flower. Fastest flowering from start of LD occurred when plants were maintained in SD to the 24 leaf stage. This can be attributed to floral initiation and development occurring while these plants were in SD, prior to reaching the transfer stage. Stem length, scape length, and total height followed no significant regression with leaf number at transfer to LD.

INTRODUCTION:

The genus *Chrysanthemum* is in the family Asteraceae and contains about 200 species, or fewer, depending on classification authority. It is a diverse genus of often aromatic annual and perennial herbs and subshrubs, native primarily to the Northern Hemisphere, particularly Asia and Europe (Jelitto and Schacht, 1990; Giles et al., 1980). Cultivars within the species *Chrysanthemum* x *superbum* Bergmans ex J. Ingram are often misclassified as *Chrysanthemum maximum*, which is thought to be one of the parental lines of this hybrid. According to Giles et al., (1980), plant breeder Luther Burbank is credited with interbreeding *C. maximum* (Pyrenes), *C. lacustre* (Portugal), *C. nipponicum* (Japan), and *C. leucanthemum* (United States), to produce *C.* x *superbum*, commonly known as shasta daisy.

Shasta daisy has strong stems which measure 30-90 cm (1-3 feet) high and are mostly unbranched or only sparingly so. Lower leaves are up to 30 cm (12 inches) long, including petiole; upper leaves are lanceolate and sessile. Solitary flower heads reach 10 cm (4 inches) or more across, have white ray florets and yellow disk florets, and are produced late spring to early fall, depending upon geographic location. The large-flowered cultivars are widely grown and are highly regarded cut flowers, as well as being used in garden borders and naturalized areas (Jelitto and Schacht, 1990; Bailey and Bailey, 1976).

C. x *superbum* generally requires overwintering for optimal flowering. However, Jelitto and Schacht (1990) stated that seeds sown in early spring will

produce flowers the first summer in USDA zone 5. 'G. Marconi' is a standard cultivar which produces large 12-15 cm (5-6 inch) double and semi-double blooms on stems up to 71 cm tall (28 inches). 'Snow Lady' is a highly floriferous, first-year-flowering cultivar, hardy enough to survive temperatures as low as -5°C. It is extra dwarf at 25 cm (10 inches), with a basal branching habit and a 30 cm (12 inch) canopy spread. The abundant flowers measure 6 cm (2-1/2 inches) across. 'Snow Lady' is recommended for annual bedding purposes and 4-inch pot culture, as well as being sold as a garden perennial.

Currently, *C. x superbum* cultivars are relatively insignificant to commercial floriculture, but they do have market potential as evidenced by rising exposure in garden catalogs and perennial flower guides. However, there is some confusion about the flowering requirements of individual cultivars, indicating a need to elucidate their flowering mechanisms and allow better manipulation and scheduling of blooming.

The role of photoperiod in flowering of *C. x superbum* has been studied periodically, with varying results. Flowering was hastened by increased daylength (Kofranek, 1952; Laurie and Poesch, 1932), and individual cultivars were found to be obligate long day (LD) plants (Griffin and Carpenter, 1964) or in need of a chilling period to induce flowering (Shedron and Weiler, 1982). The earliest report of a shasta daisy LD flowering requirement was by Laurie and Poesch (1932). Two-year-old field-grown plants of *Chrysanthemum maximum* (syn: *C. x superbum*) produced flowers earlier and more profusely when daylight periods were extended in the greenhouse, under Ohio conditions in January. Kofranek (1952) produced similar

results using a 4 hr night break (NB) illumination with the field grown cultivars Marconi, Majestic, and Esther Read, in Southern California. Flower diameter and stem length were slightly greater on control plants than on plants in the lighted plots. Plants subjected to NB produced open and elongated growth, whereas plants grown under normal daylength conditions were low and compact.

Flowering, stem elongation, growth habit and leaf size of shasta daisy 'T.E. Killian' and 'Esther Read' were daylength sensitive (Griffin and Carpenter, 1964). 'T.E. Killian' plants began flowering 2-1/2 months after the onset of 15 hr photoperiods but remained vegetative under shorter photoperiods. 'Esther Read' remained vegetative at 12 hrs while flowering at photoperiods of 13 hr and greater, with first flowers reaching anthesis 45-57 days after start of LD. Flower number per plant, stem length, and flower diameter increased as photoperiod was increased beyond the critical daylength. Plants exposed to the 12 hr photoperiod had short branches with leaves borne in a rosette pattern while 13 and 14 hr photoperiods encouraged a combination of elongated, horizontal development before bending upward. Stems grew upright and loose in a 15 hr photoperiod.

The flowering of *C.* x *superbum* 'G. Marconi' in response to photoperiod and temperature was examined by Shedron and Weiler (1982). Plants were grown for 11 weeks under short day (SD) conditions, then transferred to 10, 12, 14, 16, or 18 hr photoperiods at 18°C minimum night temperature (MNT). This experiment was terminated after 35 weeks, at which time no flowering was observed. In a second experiment, plants were grown under SD conditions for 11 weeks, then transferred

to 10, 12, 14, 18 hr photoperiods at 24°C MNT. This experiment was terminated after 25 weeks, with no flowering at the 2 shorter photoperiods, and only 10% and 20% flowering at the 14 and 18 hr photoperiods, respectively. Flowering was achieved in 100% of the plants with a 16 week chilling period at 4.5°C followed by a 10 hr photoperiod at 18°C MNT.

Although the relationship between flowering and photoperiod has been examined in shasta daisy, the influence of plant juvenility has been neglected. Some plants are known to be sensitive to inductive photoperiods at a very early age. Several *Chenopodium* species show evidence of floral initiation in as few as 6 days after seed imbibition (Cumming, 1959) and seedlings of *Brassica campestris* are photoperiodically sensitive 4 days after germination (Friend, 1968). However, a period of juvenility, described as a physiologically-based time when a plant is insensitive to conditions later promoting floral initiation (Bernier et al., 1981), is common in plants. The duration of juvenility can be measured in years for most woody species but is often much shorter in herbaceous plants (Hackett, 1985). For many photoperiodic herbaceous species, the passage through juvenility can be gradual, characterized by a period of increased sensitivity to daylength rather than a total inability to flower (Bernier et al., 1981). Many attempts have been made to quantify the precise end of juvenility. In 1934, Purvis first postulated the concept of a required minimum leaf number needed before the apex was capable of initiating floral organs. The transition from juvenility to maturity occurred when enough photosynthetic leaf area had been formed to sustain flowering and fruiting (Schwabe,

1976; Wareing and Frydman, 1976). However, it is questionable whether foliage plays the only role in floral induction in all plants. Systematic removal of leaves, even to the extreme of leaving only the rosette stem and shoot apex intact, did not alter the response of *Eschscholtzia californica* to LD induction, an indication that a specific node number may affect floral induction (Lyons and Booze-Daniels, 1986).

Despite the lack of attention given to the role of juvenility in flowering of *C. x superbum*, there are recent, documented works addressing this topic in other plants. In working with *Eschscholtzia californica*, Lyons and Neale (1983) identified a negative linear relationship between unfolded leaf stage and the rapidity of flowering, suggesting that as the plant aged, it became more responsive to the inductive LD. This response was later confirmed; as *E. californica* matured it would flower most rapidly if 10 expanded true leaves were present at the start of LD (Lyons and Booze-Daniels, 1986). Carter (1986) later concluded that 8 to 10 LD were required for initiation of the terminal flower bud. If the LD stimulus were terminated prior to 8 cycles, anthesis would not occur.

One can also turn to close relatives of *C. x superbum* for response comparisons. *Rudbeckia hirta* 'Marmalade' exhibits a similar response to LD with the onset of maturity, flowering most rapidly once placed in LD if first grown in SD to 19 expanded leaves (Bourke, 1990). At this stage, plants transferred to LD would flower in 42 days, the least amount of time of all treatments. *Gaillardia pulchella*, like *R. hirta* 'Marmalade' and *E. californica*, is not completely unresponsive to floral induction conditions, but appears to mature gradually. Plants possessing 20 leaves

at the start of inductive LD flowered most rapidly compared to plants placed in LD at lower leaf counts (Bourke, 1990).

The objectives of the present study were to quantify the end of juvenility in *Chrysanthemum* x *superbum* 'G. Marconi' and 'Snow Lady', to describe their individual and comparative responses to photoperiod, and to document related vegetative characteristics.

MATERIALS AND METHODS:

Chrysanthemum x *superbum* 'G. Marconi' and 'Snow Lady' seeds were sown on 5 June 1990 in a medium of 2 parts vermiculite: 1 part peatmoss (v/v) in cell packs and placed under intermittent mist. Treatments were assigned randomly at the time of sowing. Upon germination, misting ended and all packs were moved to SD. Plants were subsequently transplanted into 10 cm (4 inch) plastic pots using a mixture of 3 parts peatmoss: 1 part perlite: 1 part vermiculite (v/v/v). LD conditions were created by night interruption from 2200-0200 hr with 60W incandescent bulbs strung overhead to provide 3-4 μmol$\cdot$m^{-2}$\cdot$s^{-1} PPF at plant height. SD conditions were created by covering the plants from 1700-0800 hr with 100% light exclusion black sateen cloth. Ambient temperature for germination was 19-21°C day and night. Growing temperatures thereafter were 16-18°C nights. After transplanting, plants

were fertilized weekly during irrigation with 400 ppm N from 20N : 6.6P : 17.6K.

Ten plants (reps) were transferred from SD to LD upon reaching the following true leaf stages: 0 (cotyledons only), 3, 6, 9, 12, 15, 18, 21, 24; a leaf was defined as possessing a fully expanded lamina. Ten plants of each cultivar remained in SD for the duration of the experiment as controls. Data taken at first flower included: number of days elapsed from both seeding and start of LD, number of expanded leaves along the main stem, stem length (from cotyledonary node to uppermost node possessing a visible, reproductive, axillary branch), non-reproductive scape length (from last visible axillary branch to uppermost node possessing a leaf), and leafless scape length (from uppermost non-reproductive node to calyx attachment). First flower was defined as the date when ray florets had expanded perpendicular to the stem attachment. The experimental design was completely random; regression methods were used to compare leaf number treatment groups with plant characteristics of interest. A mean separation test was used to examine relationships between the SD-control group and leaf number treatment groups.

RESULTS:

The cultivar G. Marconi did not flower in SD and only 14 plants did so in LD. Flowering was random and could not be attributed to a specific leaf number

treatment. These plants exhibited wide variability in total height, ranging from 40-74 cm (data not presented).

There was 100% flowering of 'Snow Lady' plants in all treatments with the exception of the 24 leaf stage (70%) and the SD-control plants (90%). With SD-control plants deleted from the data set, regression analysis indicated a linear relationship between number of days from seeding to flower and leaf number at transfer to LD (Figure 2.1). Plants transferred at the cotyledon stage flowered fastest from seeding, 75 days, while those transferred to LD at 24 leaves flowered 123 days after seeding. There was also a linear relationship between the number of days to flower from the start of LD and leaf number at transfer to LD (Figure 2.2). The flowering response difference separating plants moved to LD at the 24 leaf stage and the cotyledon stage was approximately 26 days. There was a quadratic relationship between stem leaf number at first flower and leaf number at transfer to LD and a linear relationship between total leaf number at first flower and leaf number at transfer to LD (Figures 2.3 and 2.4). Stem leaf number ranged from 9 on plants grown in LD from the cotyledon stage to 28 leaves on plants moved to LD with 24 expanded leaves. The fewest number of total leaves at first flower, 15, occurred in plants grown in LD from the cotyledon stage. Plants held in SD until 24 expanded leaves had the most total leaves, 37.

There were no significant linear or quadratic relationships between number of expanded leaves when moved to LD and scape leaf number, stem length, scape length, or total height and their means were 19.5 leaves, 8.3 cm, 13.9 cm, and 22.2

cm. SD-control plants, having been excluded from the regression analysis, were compared to leaf number treatments via a means separation test. Control plants averaged 123 days from seeding to flower. They also had significantly more stem leaves, 25, and total leaves, 34, than the earliest treatments (0, 3, 6, 9 leaves), and had nearly twice as many scape leaves as plants transferred at 0, 9, 12, or 15 leaf stages. The scape length and total height of SD-control plants were almost 9 cm longer than 0 leaf stage plants.

DISCUSSION:

These results partially support the original conclusion that shasta daisy is a LD plant (Laurie and Poesch, 1932), however, considerable differences were apparent in the responses of 'G. Marconi' and 'Snow Lady'. The former remained completely vegetative in SD and showed only limited flowering under LD conditions for the five month duration of the experiment. This lack of response to LD is in direct contrast with the results of Laurie and Poesch (1932), Kofranek (1952), and Griffin and Carpenter (1964), who all reported earlier or enhanced flowering with the use of LD treatments. However, plant age can affect the LD flowering response of shasta daisy and therefore is a factor to consider. Plants which were field grown for 2 years were used by Laurie and Poesch (1932), and use of "rooted divisions" and plants obtained

from "clonal division" were used in the other studies (Griffin and Carpenter, 1964; Kofranek, 1952). The age and maturity of this plant material and the nature of overwintering conditions are left to speculation. The fact that most 'G. Marconi' plants in the present study remained vegetative under LD conditions confirms the most recent results of Shedron and Weiler (1982) who, like the present study, also utilized this cultivar as seed-produced experimental material.

'Snow Lady' plants flowered under both LD and SD, indicating a facultative rather than obligate LD requirement for floral initiation. Flowering was faster and more profuse in most LD treatments compared to SD-control plants, but the fact remains that flowers initiated under continuous SD as well. 'Snow Lady' plants transferred to LD at the cotyledon stage required 77 days from seeding to flower, while plants grown in continuous SD averaged 123 days. While it can be argued that most obligate LD plants will eventually flower if held in SD for an "extended period" of time (Evenari and Gutterman, 1966), taking less than twice the time to do so compared to the fastest plants in LD appears to simply indicate a facultative response which has not been previously reported for this species.

Since the 'Snow Lady' response is facultative and it is not known when exactly floral initiation takes place in SD, using the fastest flowering after onset of LD as an indication of end of juvenility is also inappropriate. Plants grown in SD to the 24 expanded leaf stage required only 34 LD to flower once transferred, compared to 43 LD if moved at the 21 leaf stage. This makes it appear as though the most rapid flowering from the onset of LD occurs if plants are transferred at later stages.

However, plants in this treatment group had actually bolted and possessed visible terminal buds before obtaining 24 expanded leaves and being moved to LD. For this treatment, and likely other younger groups as well, LD conditions served only for rapid development of the inflorescence, not initiation.

The length of time 'Snow Lady' plants remained in SD, before being transferred to LD, was reflected in other features of plant morphology and reinforced the conclusion of facultative LD flowering. Plants had more leaves at first flower if their prior exposure to SD was comparatively lengthy, indicating that SD favored vegetative growth but could not prolong it indefinitely. In contrast, plants possessing fewer leaves upon transfer to LD terminated vegetative growth and became reproductive earlier, thus resulting in fewer total leaves at first flower.

As with *Coreopsis lanceolata* (Chapter 1) and *Gaillardia pulchella* (Bourke, 1990), shasta daisy stem elongation was not significantly affected by leaf number at transfer to LD. Yet this lack of response is not pervasive in the family since *Rudbeckia hirta* exhibited maximum stem elongation when plants were transferred to LD at the 18 leaf stage (Bourke, 1990). The mean separation test identified a significant increase in scape length of SD-control plants when compared to those grown in LD from the cotyledon stage, also in contrast to previous results from other plants (Chapter 1; Bourke, 1990).

It is clear that 'Snow Lady' shasta daisy lacks the obligate flowering response and extended period of vegetative growth in non-inductive conditions which characterizes its related cultivars. It will flower in the range of 77 to 123 days from

seeding, regardless of daylength, although LD significantly enhances flowering. Therefore, this cultivar has remarkable marketing potential. It has an annual flowering habit not inhibited by LD or SD, and is also perennial.

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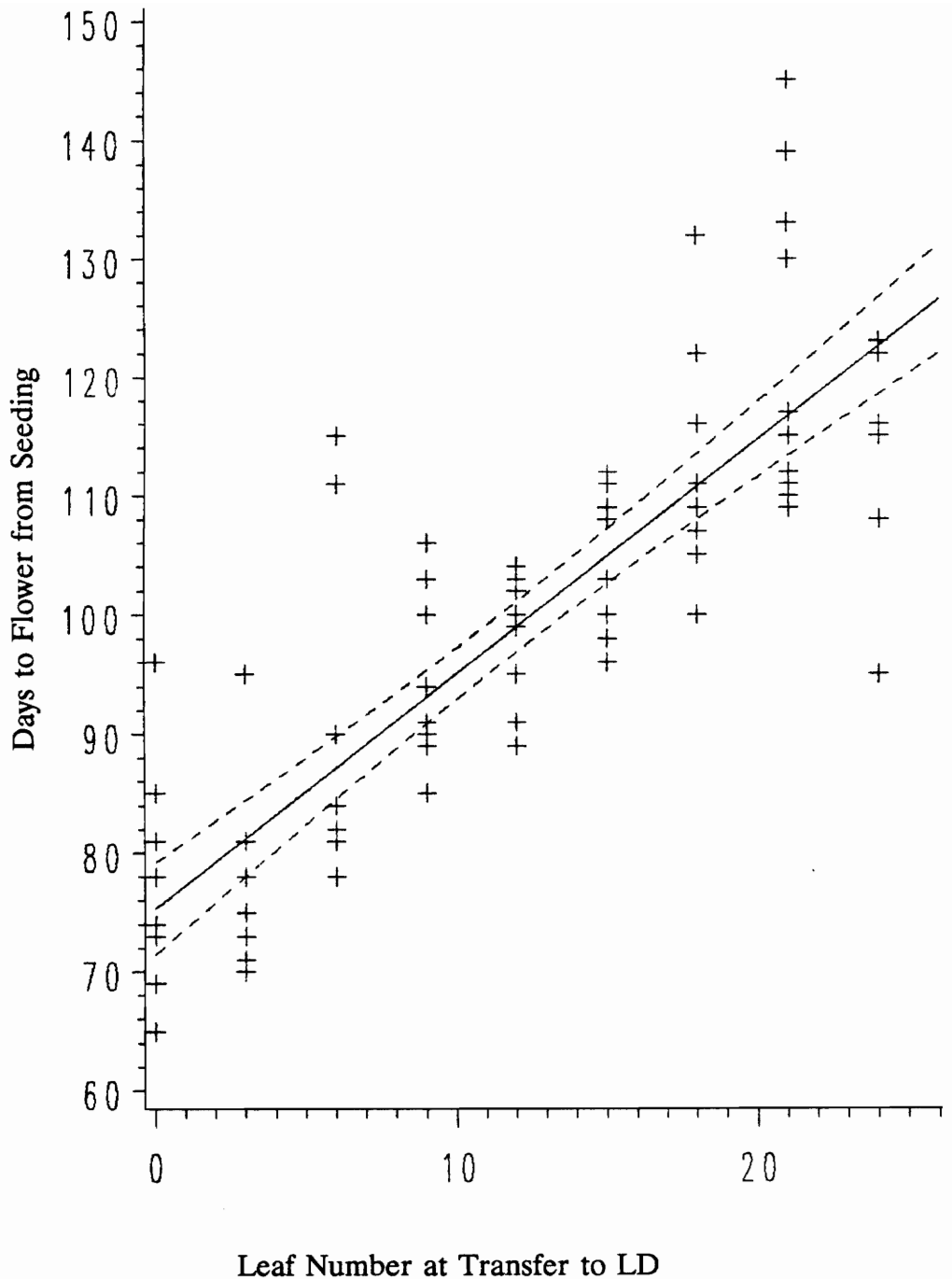
Figure 2.1   The effect of leaf number at transfer to long days (LD) on number of days from seeding to flower for *Chrysanthemum* x *superbum* 'Snow Lady'. $y = 75.4 + 1.97x$, $R^2 = 0.70^{**}$; area bound by dashed lines indicates a 95% confidence interval.
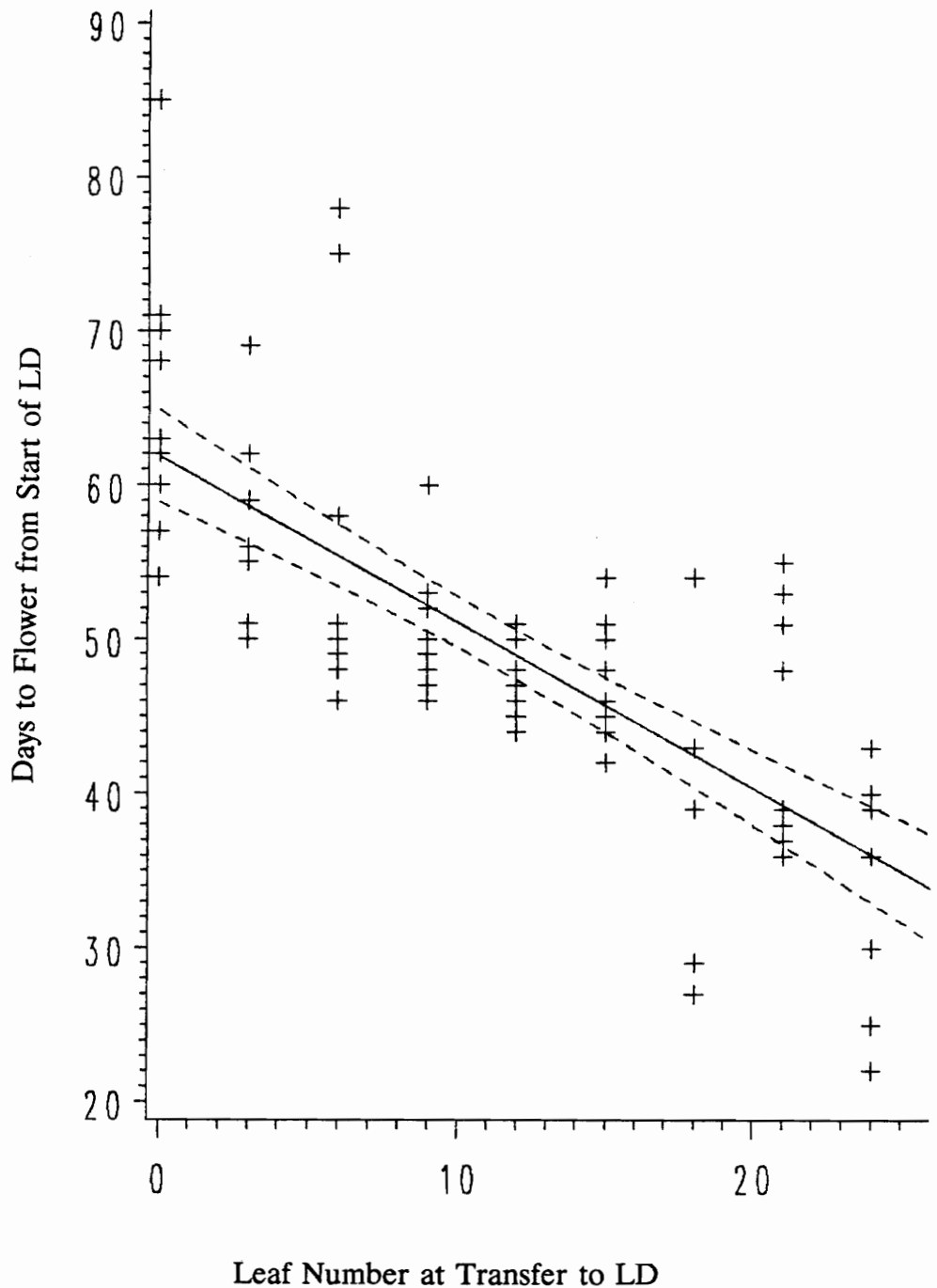
Figure 2.2   The effect of leaf number at transfer to long days (LD) on number of LD needed for flowering of *Chrysanthemum* x *superbum* 'Snow Lady'. $y = 61.9 - 1.07x$, $R^2 = 0.54$** ; area bound by dashed lines indicates a 95% confidence interval.
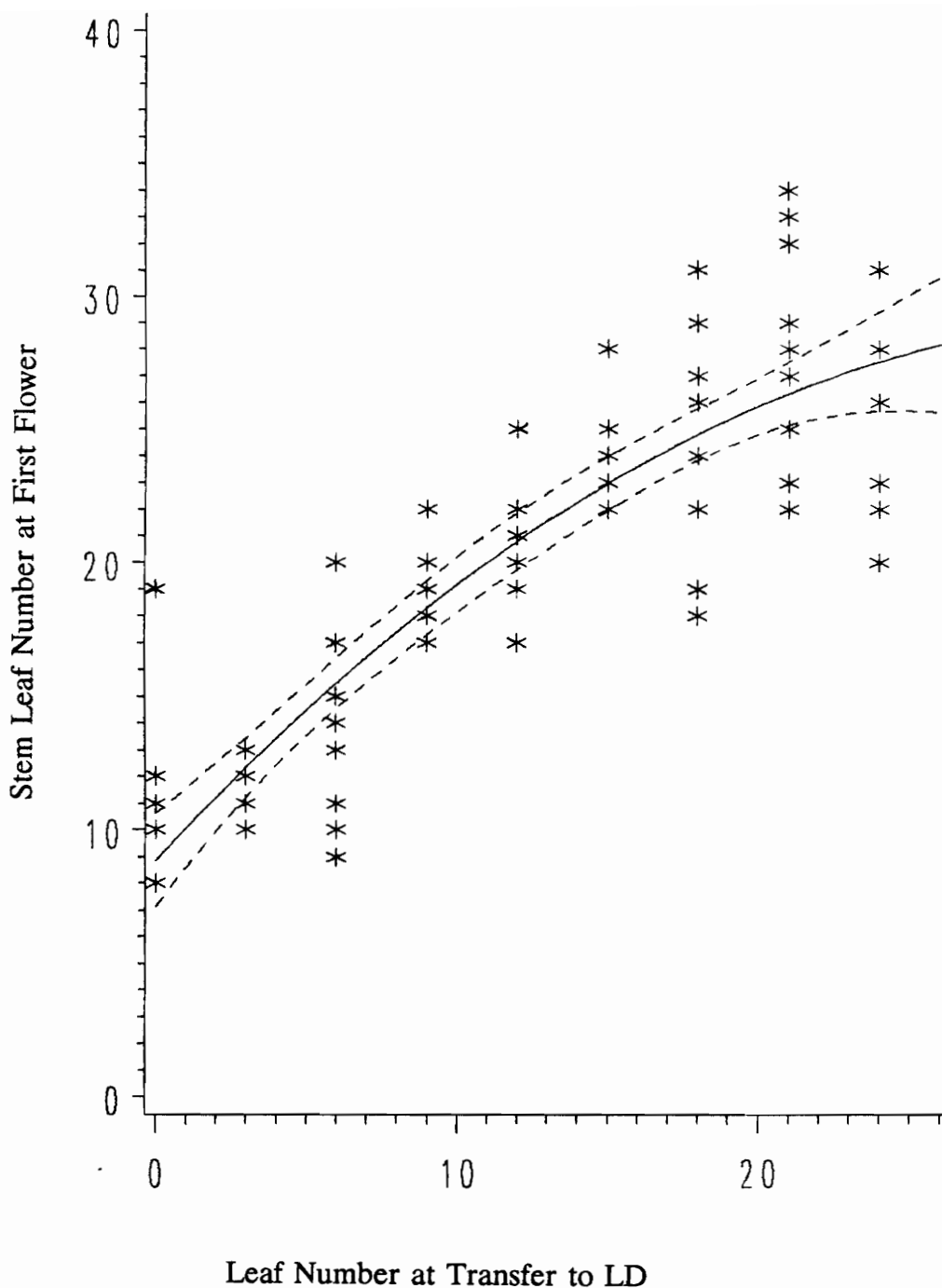
Figure 2.3   The effect of leaf number at transfer to long days (LD) on stem leaf
number at first flower for *Chrysanthemum* x *superbum* 'Snow Lady'.
$y = 8.87 + 1.21x - 0.0179x^2$, $R^2 = 0.77**$; area bound by dashed lines
indicates a 95% confidence interval.
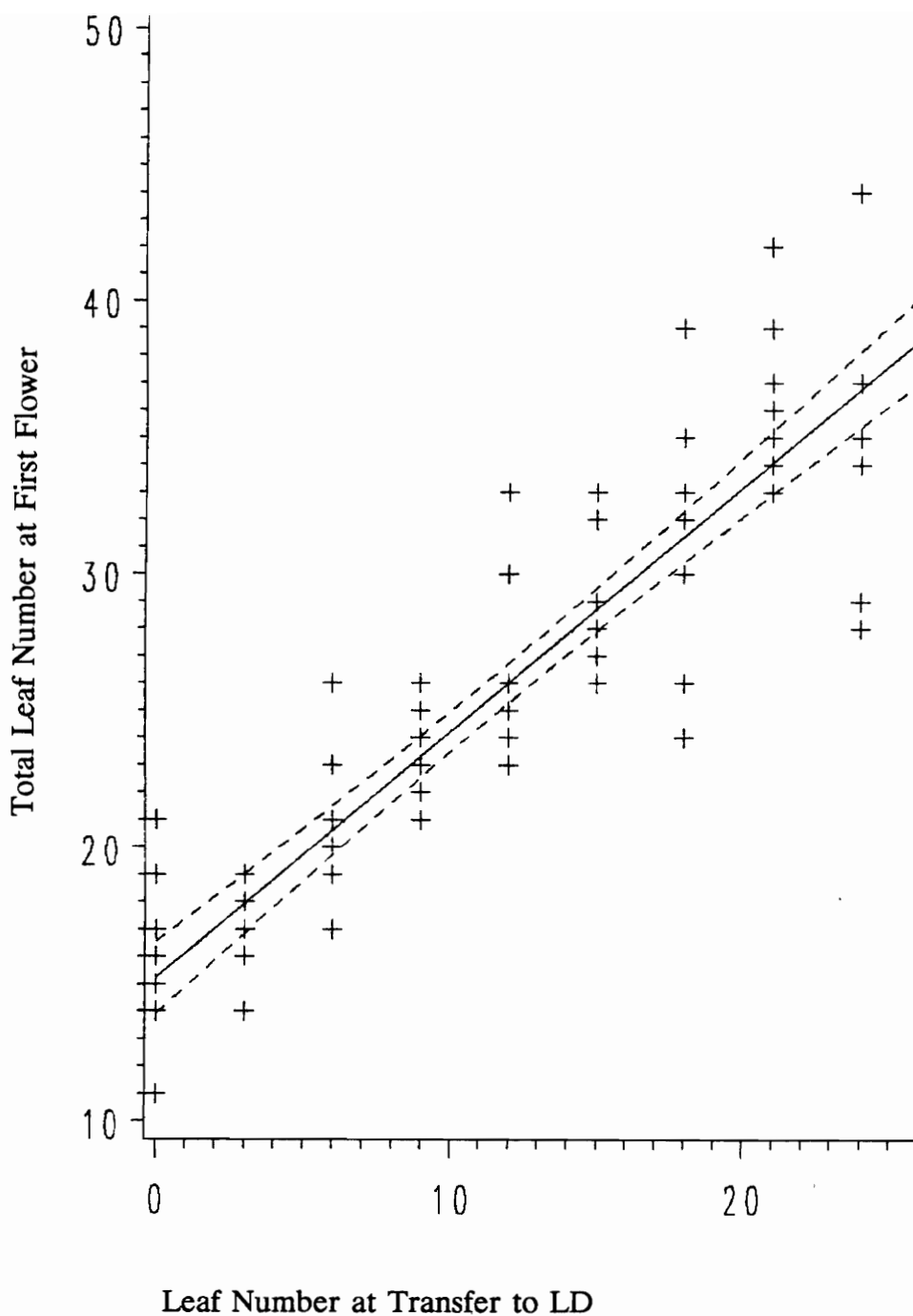
Figure 2.4 The effect of leaf number at start of long days (LD) on total leaf number at first flower for *Chrysanthemum* x *superbum* 'Snow Lady'. $y = 15.2 + 0.898x$, $R^2 = 0.81**$; area bound by dashed lines indicates a 95% confidence interval.

Chapter III

A Limited Number of Inductive Cycles Affects
Flowering of *Coreopsis lanceolata* 'Early Sunrise'

Abstract. Limited inductive photoperiod (LIP) inhibited stem elongation of *Coreopsis lanceolata* 'Early Sunrise' in all LD treatments and inhibited axillary flower bud development at 6 and 8 LD as compared to continuous LD but had no effects on scape length or total leaf number at first flower. Plants were grown in short days (SD) to 16 leaves, the theoretical end of juvenility, then transferred to long days (LD). Plants were moved back to SD after receiving 6, 8, 10, 12, 14, 16, 18, 20, or 22 LD cycles. Plant height at first flower was 17 cm if given only 6 LD compared to approximately 28 cm when allowed to remain in LD for 22 cycles. Inhibition of stem elongation by restricting the number of inductive cycles to as few as 10, effectively reduced overall plant height at first flower, with no significant loss of axillary flower buds. However, time of flowering was delayed with LIP, as indicated by a negative linear relationship between the number of LD received and the number of days to first flower from the onset of LD. Plants which received 22 LD before the switch back to SD flowered approximately 13 days sooner than those plants receiving only 6 LD.

INTRODUCTION:

Coreopsis, or tickseed, is in the family Asteraceae, and native to the Americas, Hawaiian Islands, and tropical Africa (Clausen and Ekstrom, 1989; Everett, 1981; Giles et al., 1980; Bailey and Bailey, 1976; Gleason, 1974; Bailey, 1949). *Coreopsis* possesses attractive foliage, beautiful flowers in shades of yellow, and the ability to tolerate diverse environmental conditions. Grown as herbaceous perennials in USDA zone 7, two of the most popular species are *C. lanceolata* and *C. grandiflora*. They have many similarities and their hybrids are frequently confused with one another, perpetuating conflicting reports of growth patterns and flowering mechanisms. They are most often described as perennials, but occasionally handled as annual plants (Thomas, 1982; Gleason, 1974) with the option that they be grown in greenhouses for late winter and early spring flowering (Everett, 1981). With reference to *C. lanceolata*, Giles et al. (1980) reported that seeds sown indoors in early spring or in cold frames yield sparse flowering that season and heavier flowering the next. Currently, *Coreopsis* are relatively insignificant commercial plants but are becoming more popular with consumers as evidenced by rising exposure in garden catalogs and perennial flower guides. It is clear that more research can better define the flowering characteristics of *Coreopsis* species and broaden their commercial appeal.

There is confusion in both botanical nomenclature and photoperiodic classification of these plants. *Coreopsis lanceolata grandiflora* was first classified as a long day (LD) plant when two-year-old field-grown plants flowered faster and more

profusely upon receiving an extended daylight period from 1800 to 2200 hr (Laurie and Poesch, 1932). Ketellapper and Barbaro (1966) also studied the photoperiodicity of *C. grandiflora*, most likely the same species as studied by Laurie and Poesch. Plants remained vegetative in both LD and short days (SD), but growth habits differed with daylength; in SD leaves remained small and prostrate while LD promoted elongated, erect foliage. Plants remained vegetative if given only LD or LD followed by SD, but flowered if given a LD-SD-LD regime. On this basis, the authors determined *C. grandiflora* to be a short-long day (SLD) plant. When a larger sample size was subsequently studied by Ketellapper and Barbaro, plants in continuous SD flowered, while nearly all plants given only LD remained vegetative. The requirement for LD was subsequently judged by the authors not to be absolute.

As recently as 1988, *C. grandiflora* remained classified as a SLD plant (Metzger, 1988). However, more recent results indicate that individual cultivars behave differently to photoperiod. In an attempt to clarify the flowering mechanisms and to quantify the end of juvenility (Chapter 1), *C. lanceolata* 'Early Sunrise' and *C. grandiflora* 'Sunray' plants were grown in SD to specific leaf numbers, then transferred to LD. 'Sunray' did not flower in any treatment group, including the SD control. 'Early Sunrise' exhibited 70 to 90% flowering in all LD treatments but the time to flowering was treatment dependent. Theoretical fastest flowering, 46 days from start of LD, occurred if plants were moved from SD to LD at 16 leaves; however, a range of 9-21 leaves was considered a more realistic end of juvenility based upon statistical analysis and confidence intervals. No 'Early Sunrise' plants

flowered in continuous SD.

The vegetative growth habit of both cultivars held in SD was a tight rosette of small prostrate leaves. Rosette plants, including these species of *Coreopsis,* usually bolt prior to flowering. The bolting process, comprised of stem and scape elongation, has been studied extensively as a single response, but less so as a pair of independent mechanisms. Murneek (1936) grew *Rudbeckia* plants under natural daylengths (10 to 13 hr) then transferred them to SD (7 hr) or LD (14 to 15 hr). Plants moved to LD were tall with normal flowers. Those transferred to SD persisted as vegetative rosettes, formed flowers within the rosette, or produced a rosette with "vegetative flowers" bearing a few normally colored petals with the remainder being green. Thus, a certain number of days was needed to fully induce the initiation and subsequent growth of flowers, suggesting that an accumulation of certain substances may have been needed to induce full development of reproductive organs. This was viewed as evidence that photoperiod affects stem elongation and flowering (i.e. bolting) separately. The curtailment of stem elongation by a photoperiod unfavorable for flowering was designated as "photoperiodic inhibition" (Murneek, 1936).

Murneek (1940) continued his studies using *Rudbeckia bicolor* 'Superba' (syn: *R. hirta*), a close relative of *Coreopsis*. Plants grown under LD for 20, 25, 30, 35, or 40 days were then moved back to SD. Leaves of plants receiving only 20 and 25 LD reverted to a more horizontal position after only 2 days back in SD conditions, while those given more LD did not exhibit this growth change in SD. The short photoperiod inhibited stem elongation, regardless of prior LD exposure, but

additional leaves were produced in abundance. Murneek's shortest LD treatments, 20 and 25 cycles, resulted in strictly vegetative rosettes or incomplete floral induction characterized by the previously described "vegetative flowers." Sexual reproduction was said to be induced by a certain number of LD and would continue even if switched to non-inductive conditions. However, stem elongation was not induced, but rather maintained and fostered under inductive conditions, and therefore ceased when inductive conditions were discontinued.

Once again using *R. bicolor*, the interaction between temperature and photoperiod was also examined (Murneek, 1940). Plants held continuously under 7 hr photoperiods produced a single, normally developed flower at 90-100°F. The scapes were unusually short, however, with very few elongated enough to elevate the inflorescence above the vegetative rosette. There was no stem elongation and the leaves were arched, again illustrating the separate effects of photoperiod on floral initiation and stem elongation, with the suggestion that the high night temperature could substitute for the LD required for *Rudbeckia* floral induction.

Greulach (1942) examined 6 composite species to study further the residual effects of photoperiod, as had been first characterized by Garner and Allard (1923). The SD plant *Cosmos bipinnatus* required 5 to 11 SD cycles to achieve limited flowering, and 12 or more SD produced abundant flowering. However, *Cosmos sulphureus*, another SD plant, flowered sparsely after just a single inductive cycle with increased flowering evident as the number of SD increased. The LD plants *Rudbeckia hirta*, *Matricaria parthenoides*, *Centaurea cyanus*, and *Coreopsis tinctoria*

were found to require 17, 10, 10 and 18 LD cycles, respectively, for sparse flowering. Photoperiodic inhibition of stem elongation with simultaneous flowering occurred exclusively in *R. hirta* when switched back to SD; flowering in the other LD species occurred only with concurrent stem elongation.

Almost 65 years after the initial research, the separation of the bolting response was again examined in *Rudbeckia hirta* 'Marmalade' (Orvos and Lyons, 1989). Flowering occurred in SD following only 4 LD cycles but plants averaged only 23.5 cm tall, compared to 52.9 cm after 50 LD. In fact, the lack of stem elongation attributable to any limited LD exposure up to and including 24 cycles was superior to a 50 ppm ancymidol application, the most effective ancymidol level tested in that study. Flowering speed was also enhanced by extended periods of LD.

Genetically based evidence also exists to support stem elongation and flowering as separate processes (Zeevart, 1976). First, genetic analysis of *Silene armeria* demonstrated that GA-induced stem elongation and flower formation are determined by two separate genes. Secondly, growth retardants were found partly or fully to suppress growth while allowing flower formation to continue normally.

The bolting process with regard to the individual contributions of the scape and stem, and the effects of a limited number of inductive photoperiods on elongation of each of these structures has been examined in recent literature. Limited inductive photoperiod (LIP), an expansion of Murneek's 1936 original concept of "photoperiodic inhibition," is a method whereby the plant is given the minimum number of inductive cycles to initiate flowering, then is transferred back to

non-inductive conditions. LIP promotes flowering, but stem elongation associated with bolting in LD plants stops upon transfer back to SD. Carter (1986) first described the relationship between stem and peduncle length and the effectiveness of LIP as a height control mechanism in *Eschscholtzia californica*. Varying the number of LD cycles before transfer back to SD had no effect on peduncle length, however, stem elongation was greatly reduced. This resulted in plants which were shorter and better proportioned to the container than those which remained in LD until anthesis. Garrett (1988) subsequently showed that the stem length of *E. californica* increased with additional LD exposure. Most recently, a significant relationship was found between LIP exposure and both stem length and total height in *E. californica* (Damann, unpublished). Stem length of plants in continuous LD averaged 17.6 cm, while those transferred to SD after 10 and 15 LD averaged 3.2 cm and 7.4 cm, respectively. There was no significant relationship between LIP and scape length.

The objectives of the present study were to determine the minimum number of LD cycles required for induction and initiation of flowering and to examine the effects of LIP on stem and scape elongation in *Coreopsis lanceolata* 'Early Sunrise'.

MATERIALS AND METHODS:

Coreopsis lanceolata 'Early Sunrise' seeds were sown on 8 Jan 1991 in a medium of 2 parts vermiculite: 1 part peatmoss (v/v) in cell packs and placed under intermittent mist. Upon germination, misting ended and all packs were moved to SD. Plants were subsequently transplanted into 10 cm (4 inch) plastic pots using a mixture of 1 part peatmoss: 1 part perlite: 1 part vermiculite (v/v/v). Treatments were assigned randomly at the time of transplanting. SD were created by covering the plants from 1700-0800 hr with 100% light exclusion black sateen cloth. Ambient temperature for germination was 19-21°C day and night. After transplanting, plants were fertilized weekly during irrigation with 400 ppm N from 20N : 6.6P : 17.6K.

Plants were grown under SD conditions through the end of juvenility, 16 leaves per plant (Chapter 1), at which time all were moved to LD conditions, except ten plants (reps) which remained in SD as controls. LD conditions were created by night interruption from 2200-0200 hr with 60W incandescent bulbs strung overhead to provide 3-4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF at plant height. Plants were then transferred back to SD conditions in groups of ten, following 6, 8, 10, 12, 14, 16, 18, 20, 22 LD cycles, with ten plants remaining in LD for the duration of the experiment.

Data taken at first flower included: number of days elapsed from start of LD, stem length (from cotyledonary node to uppermost node possessing a visible, reproductive, axillary branch), scape length (from last visible axillary branch to calyx attachment), total leaf number, and number of axillary floral buds (at least 2 cm in

length). First flower was defined as the date when ray florets had expanded perpendicular to the stem axis. At the termination of the experiment, 21 weeks after seeding, reproductive status of each plant was recorded using three categories: vegetative only (no macroscopic evidence of flowers), reproductive but aborted, and reproductive to anthesis. Statistical analysis included chi-square to determine the independence of LIP treatments from reproductive status, regression analysis to determine relationships between LIP treatment groups and all plant characteristics measured and a mean separation test to compare the SD and LD controls with the LIP treatments.

RESULTS:

Flowering ranged from 80-100% across treatments and chi-square analysis indicated that no relationship existed between those plants which did not flower and the LIP treatments.

With SD and LD control plants deleted from the data set, regression analysis indicated a quadratic relationship between the number of LD received and total height at first flower (Figure 3.1a), averaging 17.0 cm if given 6 LD and 27.9 cm when given 22 LD before transfer back to SD (Figure 3.1b). A quadratic regression also characterized the relationship between the number of LD received and stem

length at first flower (Figure 3.2a). Stem length of plants receiving only 6 LD averaged 2.3 cm, while those receiving 22 LD averaged 13.5 cm (Figure 3.2b). A linear relationship between number of LD received and number of days to first flower indicated that plants given 22 LD before the switch back to SD would flower approximately 92 days from start of LD, while those given only 6 LD would require 105 days to flower after onset of LD (Figure 3.3).

Scape length, number of axillary flower buds, and total leaf number at first flower followed no significant linear or quadratic relationship with number of LD received before transfer back to SD. Control groups, having been excluded from the regression analysis, were compared to the other treatments via mean separation tests. Scape length, stem length, and plant height of LD-controls were significantly longer than those of any other treatment group (Table 3.1). There were more axillary flower buds on LD-control plants than on SD-control plants or on plants which received 6, 8, and 14 LD (Table 3.2).

SD-control plants required nearly 20 additional days to flower and had approximately 8 more leaves at first flower than plants having received LD. They also averaged less than one axillary flower bud per plant, more than 2 buds fewer than plants which received only 6 LD (Table 3.2).

All correlation coefficients (r) between number of days to flower, stem length, scape length, total height, number of axillary flower buds, and total leaf number were significant at the 5% level (Table 3.3). The strongest correlations were between total height and stem length ($r = .91$) and total height and scape length ($r = .82$).

DISCUSSION:

The minimum number of LD cycles required for floral initiation in *Coreopsis lanceolata* 'Early Sunrise' is comparatively few; 80% of the plants flowered after receiving only 6 LD cycles. In contrast, Greulach (1942) reported 18 LD cycles were needed for sparse flowering of *Coreopsis tinctoria* and 10 to 17 inductive cycles were required for flowering of other selected members of the Asteraceae. 'Early Sunrise' *Coreopsis* never produced the "vegetative", or abnormal, flowers which *Rudbeckia hirta* produced when given a limited number of inductive cycles (Beckwith, 1991; Greulach, 1942; Murneek, 1940; Murneek, 1936).

The LIP-based, delayed flowering observed in *C. lanceolata* 'Early Sunrise' is reinforced by the negative correlation between stem length and number of days to flower and the positive correlation between stem length and plant height (Table 3.3). The plants which received relatively fewer LD cycles were slower to flower, had greater stem inhibition, and thus were shorter plants. Although similar results were reported in *Rudbeckia hirta* (Orvos and Lyons, 1989), this is not a universal response. *Eschscholtzia californica*, a botanically primitive plant, flowered approximately 33 days after start of LD, totally unaffected by LIP (Garrett, 1988).

Coreopsis species have historically been reported to be obligate LD plants (Laurie and Poesch, 1932), although occasionally as SLD plants (Metzger, 1988; Ketellapper and Barbaro, 1966). Even though *C. lanceolata* 'Early Sunrise' flowered under continuous SD, this does not necessarily contradict its reported LD flowering

nature. The obligate LD plant *Rudbeckia bicolor* (syn: *R. hirta*), flowered under SD when given constant 90°F temperatures (Murneek, 1940), and late, sporadic flowering was also seen in *R. hirta* 'Marmalade' when temperatures occasionally reached 25°C under the SD cloth for short periods of time (Orvos and Lyons, 1989). In the present study LD treatments began on February 1, and flowering was completed by mid-June. During March and April, despite cooling systems, greenhouse temperatures were recorded as frequently reaching highs of 28 to 33°C (82 to 92°F). Afternoon heat build-up would have been compounded by the pulling of SD cloths over benches at 1700 hr.

Flowering and bolting have been shown to be related, but separable, processes (Orvos and Lyons, 1989; Bernier et al., 1981; Zeevart, 1976; Greulach, 1942; Murneek, 1940; Murneek, 1936). However, we can now go one step further and better separate bolting into its two component parts: the elongation of the stem and the scape. In *C. lanceolata* 'Early Sunrise', a terminal flowering plant, this bolting is clearly two distinct processes with separate control mechanisms. Plant height can be manipulated by LD cycle number, as previously seen in *R. hirta* (Orvos and Lyons, 1989), yet any height reduction is solely attributable to the inhibition of stem elongation, leaving scape length unaltered by LIP, as is also the case with *E. californica* (Garrett, 1988; Damann, unpublished). It is apparent that if floral initiation and development have begun in *C. lanceolata* 'Early Sunrise', the scape will elongate unaltered despite a return to non-inductive conditions. Murneek (1940) postulated several possible explanations for the occurrence of flowering without stem

elongation. Production of a substance under inductive conditions, which then becomes in short supply when the plant is switched back to SD, or the production of an inhibitor in SD, are two of the possibilities. Now, these would need to be expanded; there is a relationship between LD exposure and stem elongation, but this relationship does not exist for scape elongation.

This study also confirms that axillary flower bud number is not sacrificed in *Coreopsis lanceolata* 'Early Sunrise' when LIP is employed as a height control mechanism. Just limiting the number of LD to 22, versus continuous LD exposure, can inhibit stem length and total height, with virtually no loss of axillary bud potential. Axillary flower bud number remains the same once the plant has received at least 10 LD, at which point plant height has been inhibited by nearly 20 cm. It appears as if LIP could be used effectively to produce a *C. lanceolata* 'Early Sunrise' specimen feasible for potted plant culture without the use of chemical growth retardants.

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Table 3.1 The effect of a limited number of inductive long day (LD) cycles received by *Coreopsis lanceolata* 'Early Sunrise' on stem length, scape length, and total height at first flower.

No. of LD	Stem length (cm)		Scape length (cm)		Total height (cm)	
LD[z]	17.0	a[y]	22.1	a	39.2	a
22	13.4	b	14.1	b	27.5	b
20	11.2	c	15.1	b	26.3	b
18	9.3	c	14.6	b	23.8	bc
16	7.2	d	13.3	b	20.3	cd
14	5.1	e	14.7	b	19.7	cd
12	4.0	e	14.5	b	18.6	de
10	3.7	e	14.5	b	18.2	de
8	2.6	e	14.6	b	17.2	de
6	2.2	e	14.1	b	16.3	de
SD[x]	2.1	e	11.9	b	14.1	e

[z]Continuous long day controls
[y]Means separation within columns, Student-Newman-Keuls test, $p = 0.05$.
[x]Continuous short day controls

Table 3.2   The effect of a limited number of inductive long day (LD) cycles received by *Coreopsis lanceolata* 'Early Sunrise' on number of days to flower from start of LD, number of axillary flower buds, and total leaf number at first flower.

No. of LD	No. of days to flower from start of LD		No. of buds		Total leaf number	
LD[z]	91	c[y]	6.1	a	26	b
22	91	c	5.5	abc	27	b
20	95	c	5.2	abc	27	b
18	93	c	5.9	ab	27	b
16	99	bc	5.7	ab	26	b
14	100	bc	3.3	bcd	27	b
12	103	b	4.7	abcd	26	b
10	103	b	3.7	abcd	25	b
8	104	b	3.0	cd	26	b
6	105	b	2.5	d	28	b
SD[x]	125	a	0.1	e	36	a

[z]Continuous long day controls
[y]Means separation within columns, Student-Newman-Keuls test, p = 0.05.
[x]Continuous short day controls

Table 3.3 Correlation coefficients (r) for number of days to flower, stem length, scape length, total height, number of axillary flower buds, and total leaf number for *Coreopsis lanceolata* 'Early Sunrise'.

	Stem length (cm)	Scape length (cm)	Total height (cm)	No. of flower buds	Total leaf no.
No. of days to flower	-0.69[z]	-0.52	-0.71	-0.71	0.62
Stem length		0.49	0.91	0.59	-0.22
Scape length			0.82	0.41	-0.22
Total height				0.61	-0.26
No. of flower buds					-0.47

[z]All correlation are significant at p = 0.05.

Figure 3.1a The effect of a limited number of inductive long day (LD) cycles received by *Coreopsis lanceolata* 'Early Sunrise' on plant height at first flower. $y = 18.2 - 0.443x + 0.0403x^2$, $R^2 = 0.48**$; area bound by dashed lines indicates a 95% confidence interval.

Figure 3.1b The effect of a limited number of inductive long day (LD) cycles received by *Coreopsis lanceolata* 'Early Sunrise' on plant height at first flower. Numbers refer to the number of LD cycles received before transfer back to SD (22, 20, 18, 16 above; 14, 12, 10, 8, 6 below); LD-C indicates a continuous LD plant.
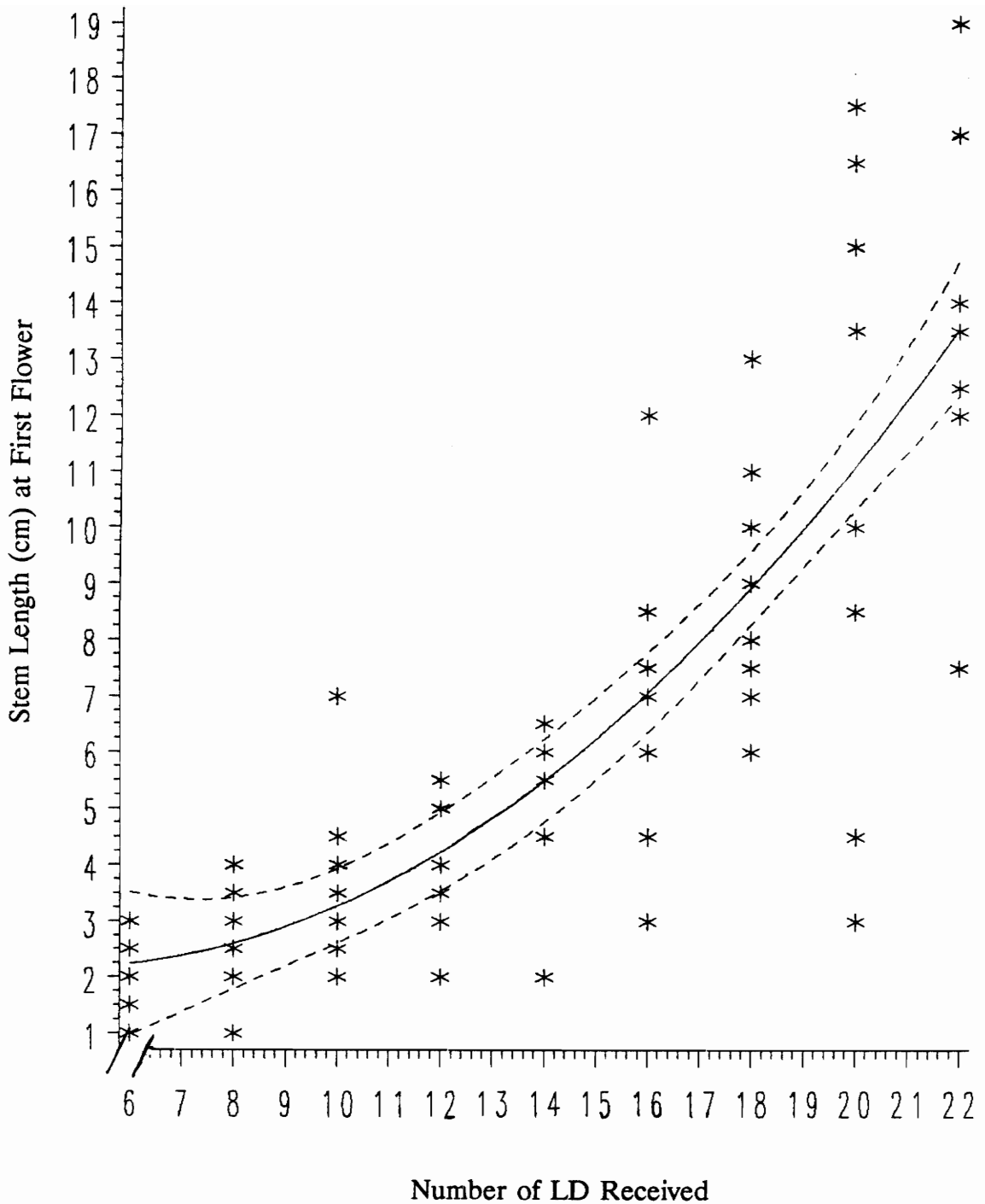
Figure 3.2a The effect of a limited number of inductive long day (LD) cycles received by *Coreopsis lanceolata* 'Early Sunrise' on stem length at first flower. $y = 3.10 - 0.353x + 0.0376x^2$, $R^2 = 0.72**$; area bound by dashed lines indicates a 95% confidence interval.
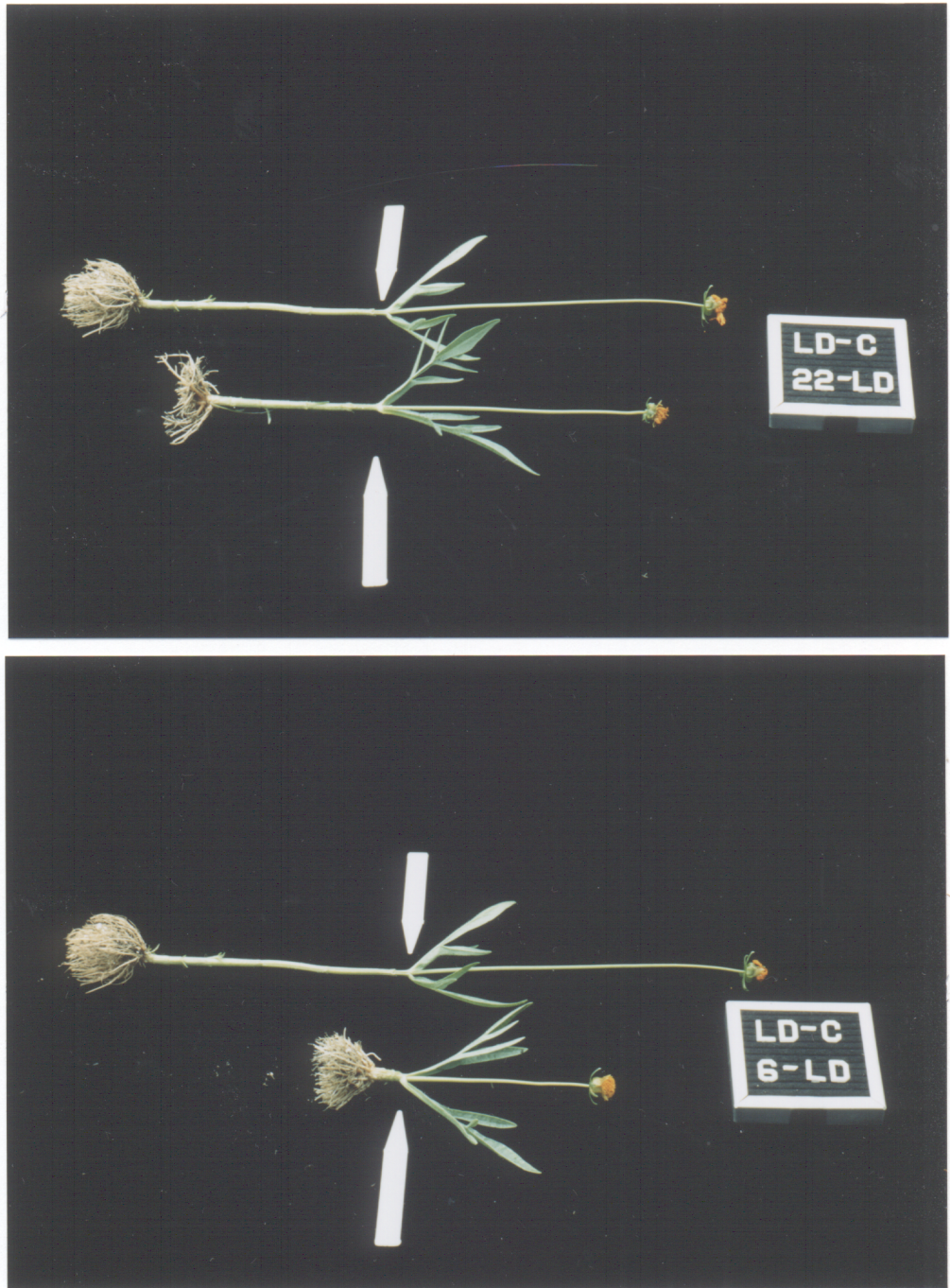
Figure 3.2b The effect of a limited number of inductive long day (LD) cycles received by *Coreopsis lanceolata* 'Early Sunrise' on stem and scape elongation. Numbers refer to the number of LD cycles received before transfer back to SD; LD-C indicates a continuous LD plant; pointer marks junction of stem and scape.

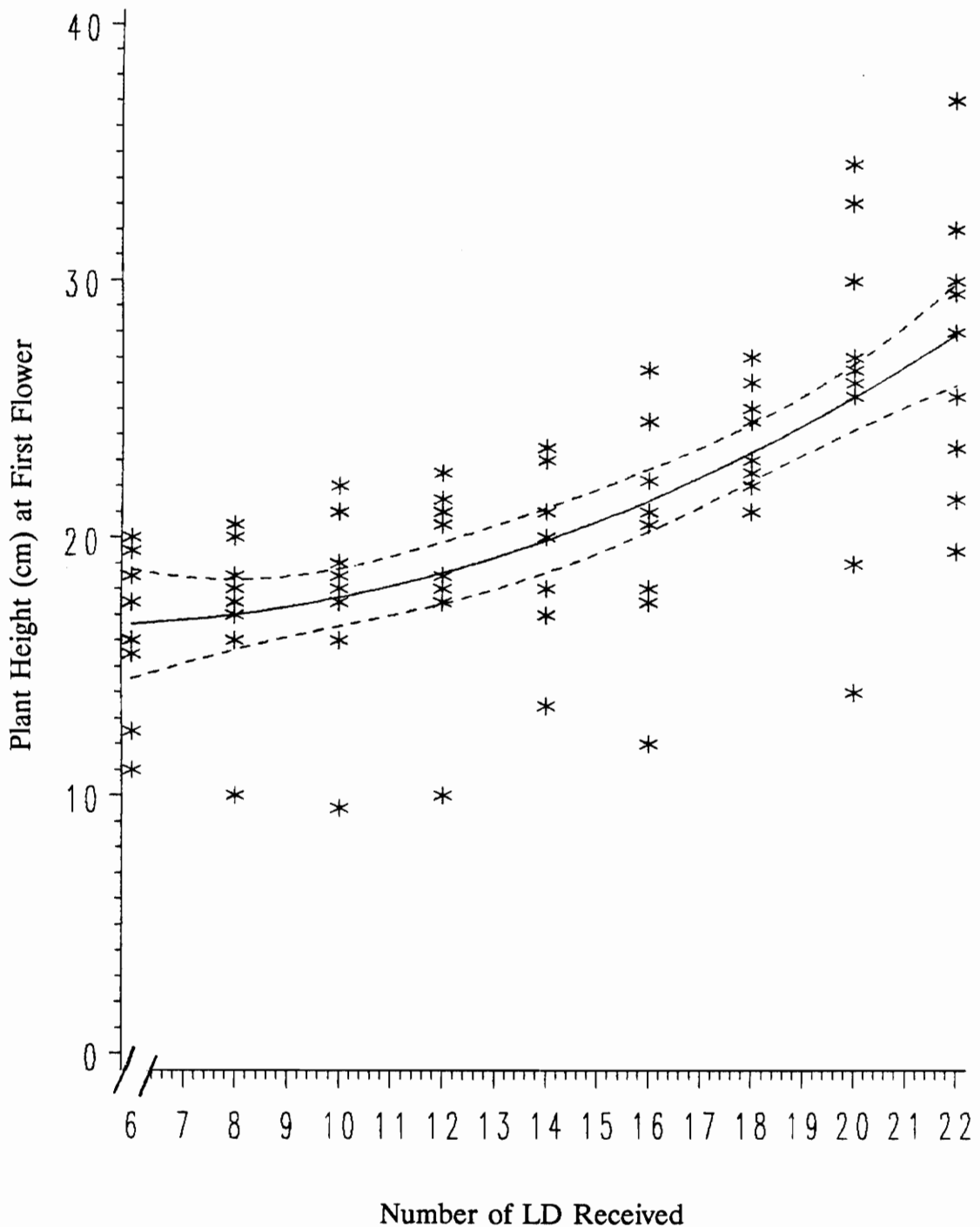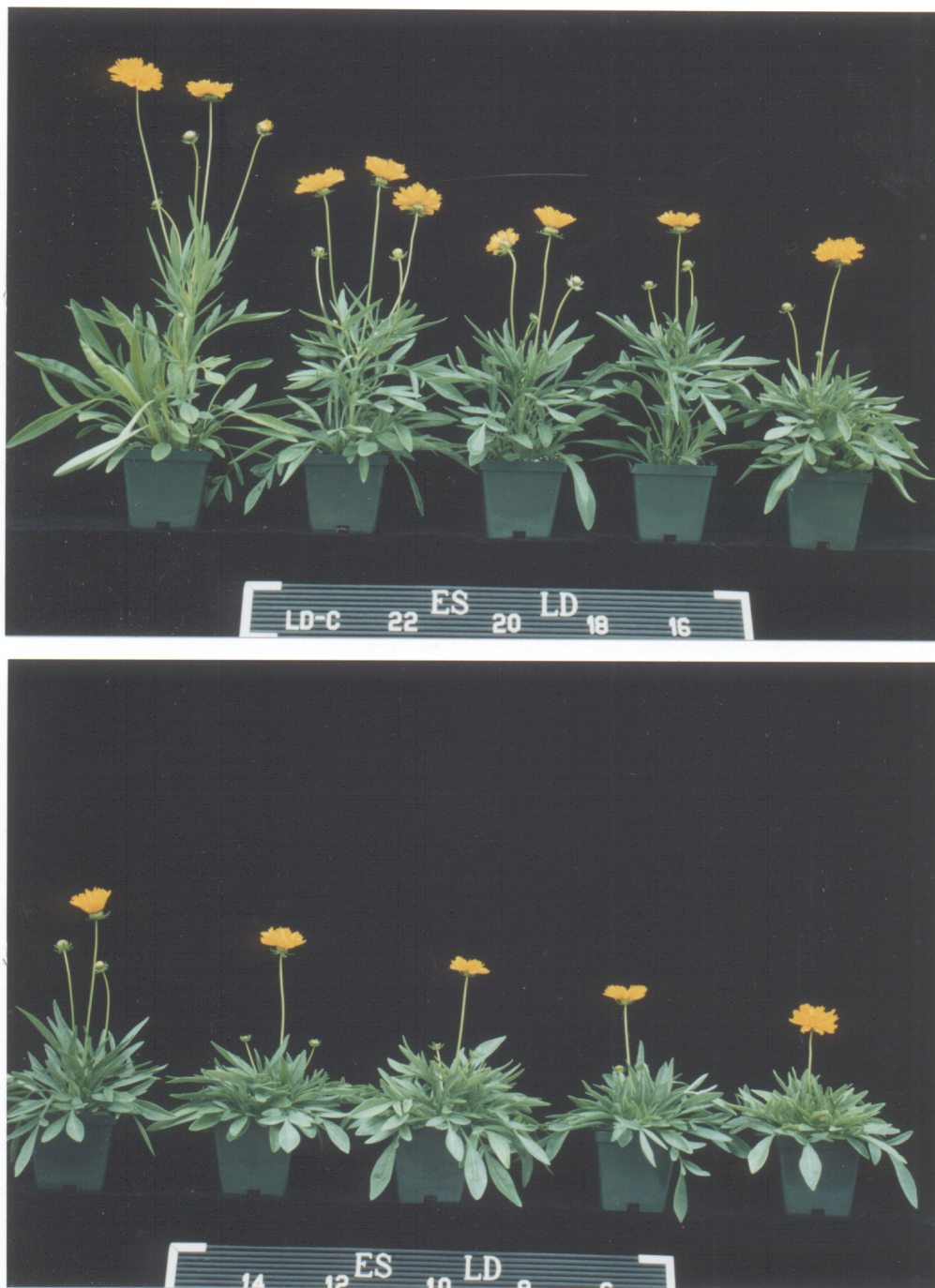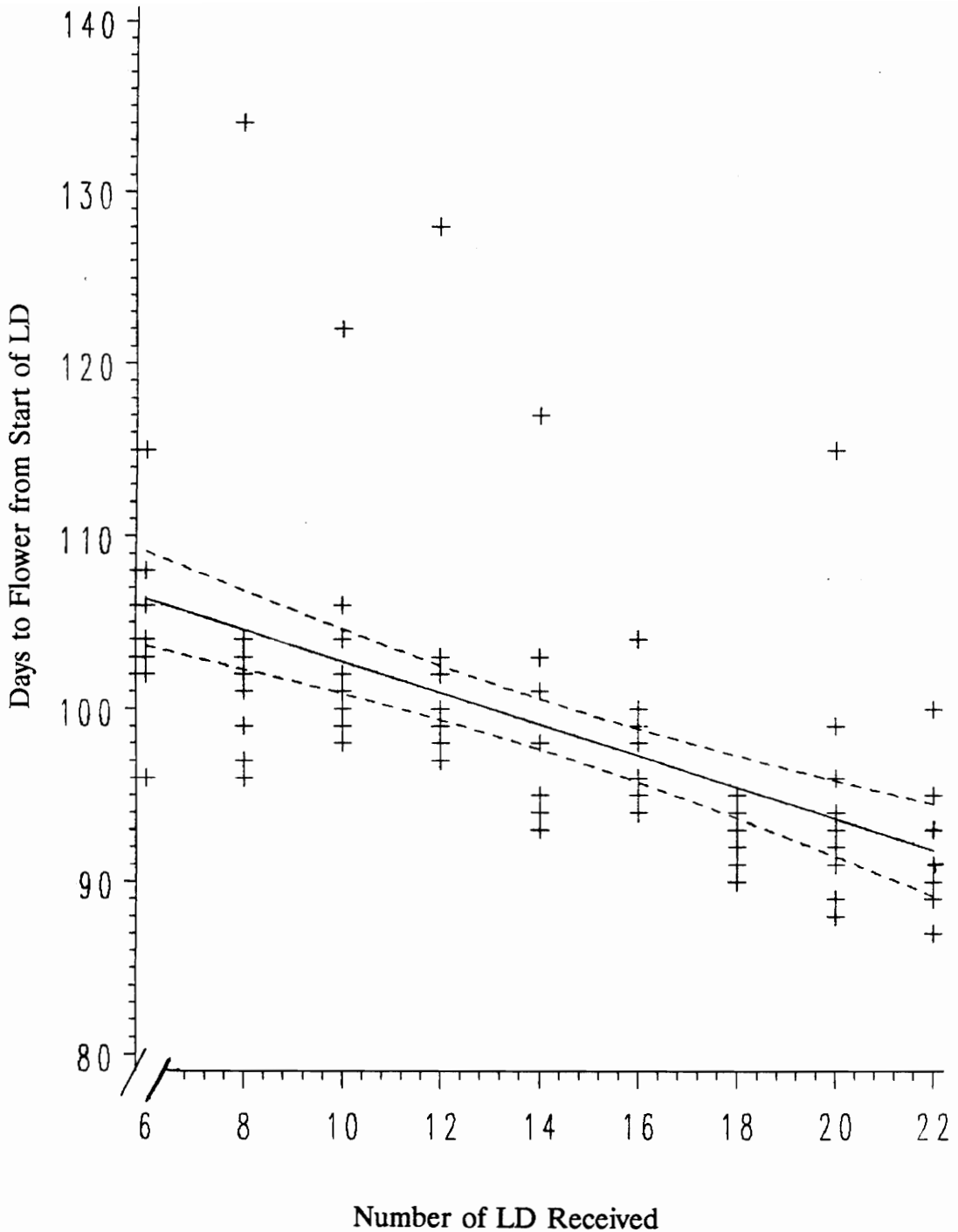Figure 3.3   The effect of a limited number of inductive long day (LD) cycles received by *Coreopsis lanceolata* 'Early Sunrise' on number of days to flower from start of LD. y = 110.0 - 0.829x, R^2 = 0.34** ; area bound by dashed lines indicates a 95% confidence interval.

Chapter IV

Natural Chilling and a Limited Number of Inductive
Photoperiods Affect Flowering in Two Genera of the Asteraceae

Abstract. To examine the effects of chilling and a limited inductive photoperiod (LIP) on flowering of *Chrysanthemum x superbum* cultivars G. Marconi and Snow Lady, *Coreopsis grandiflora* 'Sunray' and *C. lanceolata* 'Early Sunrise', seeds were sown and plants maintained in the greenhouse in short days (SD) for 7 weeks, prior to 4 months of natural outdoor chilling. Upon return to greenhouse conditions, plants were placed in long days (LD) and subsequently transferred from LD to SD after receiving 6, 8, 10, 12, 14, 16, 18, 20 or 22 LD cycles. Continuous SD without chilling for the duration of the experiment promoted 70, 40, 20 and 10% flowering in 'Snow Lady', 'Early Sunrise', 'Sunray,' and 'G. Marconi', respectively. Chilling, followed by a return to continuous SD, increased flowering in each cultivar compared to SD with no chilling. Flowering in 'G. Marconi' and 'Sunray' was sporadic in LD treatments, ranging from 40 to 100%. However, 10 LD cycles promoted 100% flowering in 'Snow Lady' and there was 100% flowering in all 'Early Sunrise' LD treatments. The effects of LIP were evident in both *Coreopsis* cultivars, but not seen in either cultivar of *Chrysanthemum x superbum*. Regression analysis indicated a linear relationship between the number of LD received and stem length at first flower in 'Sunray' and 'Early Sunrise'. In both cultivars, a reduction in stem elongation of approximately

10 cm was observed in plants which received only 6 LD, compared to those given 22 LD. The number of days from start of LD to first flower was also affected by the number of LD received; faster flowering occurred with an increased number of LD cycles before the transfer back to SD.

INTRODUCTION:

The concept of vernalization originated from agronomic practices and observations in temperate countries. Winter cereals needed to be planted before the end of winter for flowering to occur within 12 months, whereas spring types would flower soon after the spring sowing (Chouard, 1960). The term "vernalization" has had a variety of meanings; originally it was used to describe the substitution of artificial chilling for the natural exposure to winter usually necessary for flower initiation. Although, in the strictest sense, vernalization was the chilling of moistened or germinating seeds of winter strains of wheat and rye, near identical flowering can be produced on seedlings and fully developed plants when subjected to chilling (Hillman, 1969; Chouard, 1960). Vernalization should appropriately be used to describe the consequence of chilling which induces or hastens the capacity for flowering; bud break induced by cold temperatures or flowering induced by high temperatures is not correctly referred to as vernalization (Chouard, 1960). Biennials requiring vernalization include *Daucus* (carrot), *Lunaria* (money-plant), and *Hyoscyamus* (henbane). Many popular perennials, including *Chrysanthemum* species also require vernalization (Hillman, 1969).

The vernalization requirement, like photoperiodism, can be quantitative or qualitative. Previously vernalized seed from the winter rye 'Petkus' will flower upon reaching 6 or 7 leaves, just like the annual type rye. In the absence of vernalization, the plant will not flower until reaching 25 leaves and is said to be quantitative. In

contrast, the biennial strain of henbane has an absolute chilling requirement. Fully vernalized, it responds as the annual strain does, but without vernalization it will not flower. Henbane plants are "juvenile" until the rosettes are 10 days old, at which time they can perceive the vernalization treatment. The sensitivity to vernalization increases from age 10 to 30 days, then remains constant. Increasing the length of the vernalization period (up to 4 or more weeks) will decrease time to flowering once plants are removed from chilling (Hillman, 1969; Chouard, 1960).

Vernalization can also be related to photoperiodicity. In both biennial henbane and winter rye, vernalization allows the plant to become responsive to long days (LD) and in some cultivars of *Chrysanthemum morifolium* a preparatory chilling period is necessary to stimulate short day (SD) sensitivity. However, in some strains of *Spinacia* (spinach) and *Trifolium* (clover) vernalization can modify or substitute for the LD requirement. In *Campanula medium* and *Lolium perenne*, SD treatments can replace the cold requirement, thereby making a vernalizable LD plant behave like a short-long day (SLD) plant (Hillman, 1969; Chouard, 1960).

Chrysanthemum x *superbum* (syn: *C. maximum*), commonly known as shasta daisy, is historically reported to be a LD plant (Laurie and Poesch, 1932) with variable LD requirements for individual cultivars (Griffin and Carpenter, 1964). Due to its perennial nature, *C.* x *superbum* is generally thought to require chilling for optimal flowering but little research has addressed this possibility. The cultivar G. Marconi flowered only sparsely under both 14 and 18 hr photoperiods at 18 and 24°C minimum night temperatures (Shedron and Weiler, 1982). Subsequently,

exposure to vernalization at 4.5° C for 0, 4, 8, 12, and 16 weeks followed by a 10 hr photoperiod at 18° C minimum night temperature increased flowering proportionately with length of vernalization; 100% flowering occurred after 16 weeks of chilling. The inability of LD to substitute for chilling and thereby promote flowering, was recently confirmed in sexually propagated 'G. Marconi' plants. In contrast, the cultivar Snow Lady flowered in LD when either grown in LD from the cotyledon stage or if given LD preceded by SD. 'Snow Lady' also flowered under continuous SD conditions (Chapter 2).

The effects of vernalization on *Coreopsis* species have also been given only limited research attention. Two selected genetic lines of *Coreopsis grandiflora* 'Single Mayfield Giant' seedlings were grown under LD conditions for 12-1/2 weeks, then vernalized for 7 weeks at 3°C in continuous light. Vernalization produced almost 30% more flowering in each line compared to plants in SD. When 21 week old plants were used, 42 days at 3°C under LD produced 100% floral induction (Ketellapper and Barbaro, 1966). Recently, an attempt was made to determine the flowering requirements of *Coreopsis grandiflora* 'Sunray' and *C. lanceolata* 'Early Sunrise'. With no prior chilling, 'Sunray' did not flower with LD, but 70 to 90% of the 'Early Sunrise' plants flowered when grown in continuous LD or transferred from SD to LD at various leaf stages. Neither cultivar flowered when grown in continuous SD (Chapter 1).

The objective of this experiment was to examine the effects of natural chilling and a limited inductive photoperiod on flowering of *Chrysanthemum* x *superbum* 'G.

Marconi' and 'Snow Lady', *Coreopsis grandiflora* 'Sunray' and *Coreopsis lanceolata* 'Early Sunrise'.

MATERIALS AND METHODS:

Coreopsis lanceolata 'Early Sunrise', *C. grandiflora* 'Sunray' and *Chrysanthemum x superbum* 'Snow Lady' and 'G. Marconi' seeds were sown on 13 Aug 1990 in a medium of 2 parts vermiculite: 1 part peatmoss (v/v) in cell packs and placed under intermittent mist. Upon germination, misting ended and all packs were moved to SD. Plants were subsequently transplanted into 10 cm (4 inch) plastic pots on 19 Sept 1990, using a mixture of 3 parts peatmoss: 1 part perlite: 1 part vermiculite (v/v/v). Treatments were assigned randomly at the time of transplanting. SD conditions were created by covering the plants from 1700-0800 hr with 100% light exclusion black sateen cloth. After transplanting, plants were fertilized weekly during irrigation with 400 ppm N from 20N : 6.6P : 17.6K.

Ten plants (reps) of each cultivar remained in the greenhouse under SD; all others were moved outdoors on 5 Oct 1990 into a single layer, poly-covered, ventilated, unheated Quonset structure. Shredded bark mulch was placed around the pots for insulation, and shading compound was applied to the poly covering to decrease heat build up on sunny days. Interior temperature was recorded by a

thermograph. All plants were moved indoors on 1 Feb 1991, by which time approximately 100 nights of 4°C or below had accumulated. Five plants of each cultivar were immediately dissected and examined for apical floral initiation. Ten plants of each cultivar were placed under SD, all others were placed in LD conditions created by night interruption from 2200-0200 hr with 60W incandescent bulbs strung overhead to provide 3-4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF at plant height. From those returned to LD, 10 of each cultivar were transferred back to SD after receiving a limited inductive photoperiod (LIP) of 6, 8, 10, 12, 14, 16, 18, 20, or 22 LD cycles, and 10 chilled plants of each cultivar remained in LD. Data taken at first flower included: number of days elapsed from end of chilling to first flower, stem length (from cotyledonary node to uppermost node possessing a visible, reproductive, axillary branch), scape length (from last visible axillary branch to calyx attachment) and the number of reproductive axillary branches at least 2 cm in length on the main stem. First flower was defined as the date when ray florets had expanded perpendicular to the stem attachment. The number of chilled and unchilled SD control plants which flowered, and the number of chilled plants in each LD treatment which flowered were also recorded. The experimental design was completely random; chi-square was used to determine the independence of chilling and LIP treatments from reproductive status; a mean separation test and regression analysis with parabolic minimum point calculations (Rees and Sparks, 1969) were used to determine relationships between LIP and growth characteristics.

RESULTS:

Flowering in *Chrysanthemum* x *superbum* 'G. Marconi' ranged from 50 to 100% in the chilled-LD treatment groups (Table 4.1). Only 1 of the unchilled-SD-control plants reached anthesis whereas prior chilling elevated this response to 50%. Reproductive status was highly dependent on chilling and LIP treatments, yet flower bud abortion was not. LD-control plants flowered 31 and 51 days faster, respectively, from start of indoor treatments than chilled-SD-control and unchilled-SD-control plants (Table 4.2). The stems of LD-control plants were longer than those of any other group and chilling followed by SD or only a brief LD exposure inhibited axillary flower bud formation. With control groups deleted, there was no significant linear or quadratic regression between LIP and any characteristics measured.

Nearly 100% of the *C.* x *superbum* 'Snow Lady' plants flowered and reproductive status was dependent upon chilling and LIP treatments (Table 4.3). The unchilled SD-control plants flowered faster from the time of seeding than all other plants and were taller than all other plants except those in the LD-control group (Table 4.4). With control groups deleted, there was no significant linear or quadratic regression between LIP exposure and any characteristics measured. Although no evidence of floral primordia was seen during microscopic examination of 5 plants of each cultivar, inspection of all plants immediately following chilling, revealed definite signs of floral initiation on several 'Snow Lady' plants.

Flowering in *Coreopsis grandiflora* 'Sunray' ranged from 40 to 90% across LD

treatment groups and occurred in only 20% of the unchilled and 40% of the chilled-SD-control plants (Table 4.5). Reproductive status was dependent on chilling and LIP treatments with floral bud abortions restricted to chilled plants held in SD or only briefly exposed to LD. With control groups deleted, regression analysis indicated a linear relationship between number of LD received and stem length at first flower (Figure 4.1); plants receiving 6 LD had stems averaging less than 1 cm, while stems on those plants receiving 22 LD averaged 11.5 cm. There was a weak quadratic relationship between LIP and number of days from start of LD to first flower (Figure 4.2). Plants given 22 LD before the transfer back to SD flowered approximately 36 days sooner than those receiving only 6 LD cycles. The calculated parabolic vertex (minimum point) occurred at 18 LD and 57 days to flowering. Scape length, plant height, and axillary flower bud number followed no significant regression relationship with LIP and averaged 16.7 cm, 23.7 cm, and 2 buds, respectively.

Control groups, having been deleted from the regression analysis, were compared to other treatment groups via a means separation test. LD-control plants averaged 50 days from the end of chilling to first flower; this was more than twice as rapid as unchilled or chilled-SD-control plants which flowered in 100 and 121 days after the termination of chilling, respectively. The stem length of LD-control plants averaged 16.3 cm, while chilled and unchilled-SD-control plants both had stems measuring less than 1.5 cm. LD-control plants were also approximately twice as tall as unchilled and chilled-SD-control plants (Table 4.6).

All *Coreopsis lanceolata* 'Early Sunrise' plants flowered when chilling was

followed by LD (Table 4.7). Reproductive status was dependent on chilling and LIP treatments with flower bud abortions occurring only in plants that had never been chilled. With control groups deleted, there was a linear relationship between LIP and stem length (Figure 4.3) and a quadratic relationship between LIP and number of days to first flower from start of LD (Figure 4.4). Plants given 22 LD flowered 14 days faster and had stems nearly 10 cm longer than the plants which received only 6 LD. The calculated parabolic minimum point indicated that plants which received 20 LD flowered fastest, 50 days, from start of LD treatments. There was no significant regression between LIP and scape length, plant height, or number of axillary flower buds and their means were 15.2 cm, 23.2 cm, and 3 buds, respectively.

Control groups, having been deleted form the regression analysis, were compared to LD treatments via a means separation test. Unchilled-SD-control plants required 115 days from the end of chilling to first flower, more than any other treatment group. Chilled-SD-control plants required 85 days from the end of chilling to first flower, more than any LD treatment group. LD-control plants averaged 44 days from chilling to first flower. The average stem length of unchilled and chilled-SD-control plants (1.9 and 1.7 cm, respectively) was less than stems of plants receiving 10 LD or more before transfer back to SD. The stems of LD-control plants averaged 16.4 cm; this is longer than plants in any other treatment group. Scape length, and height of plants in the LD-control group were significantly greater than those of any other treatment groups (Table 4.8).

DISCUSSION:

In previous research, *Chrysanthemum* x *superbum* 'Snow Lady' flowered profusely with no prior chilling exposure when grown in LD from the cotyledon stage or if given SD followed by LD. The most rapid flowering from seeding occurred if plants were transferred to LD at the cotyledon stage, however, plants in continuous SD flowered much later (Chapter 2). In the present experiment, unchilled plants flowered faster from seeding than those which received 4 months of natural chilling, indicating the lack of any requirement for vernalization in this cultivar. This is also supported by the observation that an estimated 15 to 18 *C.* x *superbum* 'Snow Lady' plants possessed small, necrotic, terminal flower buds immediately upon removal from chilling. These traces of floral initiation which must have occurred under the SD conditions of late October, support the facultative LD flowering nature of this cultivar as reported previously (Chapter 2).

Although there is no universal direct relationship between vernalization and a particular photoperiodic response, vernalization can confer a sensitivity to LD in many plants, which subsequently promotes flowering (Hillman, 1969). This certainly appears to be true in *Chrysanthemum* x *superbum* 'G Marconi' and *Coreopsis grandiflora* 'Sunray'. *C.* x *superbum* 'G. Marconi' did not flower when grown in LD (Shedron and Weiler, 1982), SD followed by LD, or continuous SD (Chapter 2). In the present experiment, 4 months of natural chilling promoted flowering in 50 to 100% of the plants. However, the limited flowering in chilled plants maintained in

continuous SD or given only 6 LD suggests that there is a minimum number of LD which must follow the chilling period for maximum flowering to occur. This not only confirms the obligate vernalization requirement reported earlier for 'G. Marconi' (Shedron and Weiler, 1982), but also indicates a further need for LD to succeed chilling for maximum floral initiation.

Despite recent research indicating that *Coreopsis grandiflora* 'Sunray' will not flower in continuous LD, SD followed by LD, or continuous SD (Chapter 1), *C. grandiflora* has historically been characterized as a SLD plant (Metzger, 1988; Ketellapper and Barbaro, 1966). In examining the flowering requirements of SLD species, it is important to note that in some SLD plants the SD requirement and a chilling period are interchangeable (Hillman, 1969; Chouard, 1960). This phenomenon was observed in seed-produced *C. grandiflora* 'Single Mayfield Giant' (Ketellapper and Barbaro, 1966). A SLD photoperiod regime promoted only sparse flowering, but when SD was replaced by chilling, flowering was increased. In the present experiment, 4 months of natural chilling promoted flowering in 40 to 90% of 'Sunray' plants upon return to greenhouse conditions; thus confirming an obligate vernalization requirement for this cultivar. However, unlike 'Single Mayfield Giant', SLD did not promote flowering in 'Sunray' (Chapter 1). Thus, the cultivar Sunray should more descriptively be referred to as a vernalizable LD plant, rather than a SLD plant. This characterization also describes *C. grandiflora* 'Single Mayfield Giant' more accurately since flowering was enhanced when chilling replaced SD (Ketellapper and Barbaro, 1966). The occurrence of flower bud abortions in 'Sunray' plants

receiving chilling followed by SD or a brief LD exposure suggests that floral initiation will occur under limited exposure to inductive conditions, however, the stimulus needs to be continued for at least 10 cycles for anthesis to follow. Although flower bud abortion was not dependent on LIP in the other cultivars in the present experiment, it occurred in *Eschscholtzia californica* (Garrett, 1988).

Coreopsis lanceolata 'Early Sunrise' also differs from both *C. grandiflora* 'Single Mayfield Giant' (Ketellapper and Barbaro, 1966) and 'Sunray' (Chapter 1) by flowering quickly and profusely when produced from seed and grown under LD. A minimum exposure to 8 LD was sufficient to produce 100% flowering in 'Early Sunrise' (Chapter 3) whereas vernalization neither improved nor impeded flowering in this cultivar, but did affect flowering speed. 'Early Sunrise' plants which were grown in SD to maturity, then transferred to LD conditions, flowered approximately 91 days after onset of LD (Chapter 3), in contrast to vernalized plants maintained in continuous LD which flowered approximately 44 days after start of LD.

The LD requirement for flowering in some *Spinacia* and *Trifolium* species can be modified or replaced by vernalization (Hillman, 1969; Chouard, 1960). At first glance, this may appear to have happened in 'Sunray' and 'Early Sunrise' plants. Late, sporadic flowering occurred in both unchilled and chilled SD controls. This delayed, sparse flowering in continuous SD conditions is more likely a result of temperature than photoperiod. The obligate LD plant *Rudbeckia hirta* (Murneek, 1940; Orvos and Lyons, 1989) flowered under artificially imposed SD conditions, in response to excessive temperatures. *Coreopsis lanceolata* 'Early Sunrise' has also been

reported to flower in SD when greenhouse temperatures exceeded 25°C (Chapter 3). High temperatures are a reasonable explanation for the flowering observed in SD in this experiment as well. Greenhouse temperatures frequently reached a maximum of 28 to 33°C.

Low temperatures can affect bolting and flowering separately; in *Scrofularia vernalis* a cold treatment that is insufficient to stimulate bolting, can promote flowering (Bernier et al., 1981). *Coreopsis grandiflora* 'Sunray' requires vernalization for flower initiation, however, the stem elongation associated with flowering is controlled by the subsequent LD, as evidenced by the effects of LIP. Allowing a plant only the minimum number of inductive LD cycles for floral initiation, prior to transfer back to non-inductive conditions, has been shown to inhibit plant height of *Eschscholtzia californica* (Garrett, 1988; Carter, 1986), and *Rudbeckia hirta* (Orvos and Lyons, 1989) another member of the Asteraceae. However, it was not known if LIP would inhibit stem elongation of vernalized plants as well. In vernalized 'Early Sunrise' plants there was approximately a 10 cm decrease in stem elongation when given only 6 LD, as compared to those receiving 22 LD before being transferred back to SD. This is similar to results of non-vernalized 'Early Sunrise' plants in which stems averaged 2.3 cm in the 6 LD treatment, and 13.5 cm when given 22 LD cycles (Chapter 3). The cultivar Sunray responded in a similar manner, with approximately a 10 cm reduction in stem elongation when LD were limited to 6 rather than 22. However, the responsiveness to LIP, despite previous chilling, is not universal. Vernalized *Chrysanthemum* x *superbum* 'Snow Lady' and 'G. Marconi', although close

relatives of *Coreopsis*, were affected very little by LIP.

Although stem elongation can be inhibited by LIP, one drawback is the delayed flowering observed when the number of inductive cycles is very limited. It is not surprising that this was apparent in the vernalized 'Early Sunrise' and 'Sunray' plants; it has also been reported in non-vernalized 'Early Sunrise' plants (Chapter 3) and *Rudbeckia hirta* (Orvos and Lyons, 1989). However, flowering in *Eschscholtzia californica*, a botanically primitive plant, will proceed at the same pace, unaltered by LIP.

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Table 4.1   The effects of a limited inductive photoperiod and chilling on flowering status of *Chrysanthemum* x *superbum* 'G. Marconi'.

Treatment***	Anthesis (%)	Aborted buds (%)	Vegetative (%)
SD^z	10	20	70
ch SD^y	50	0	50
6 LD^x	50	0	50
8 LD	80	0	20
10 LD	80	10	10
12 LD	90	0	10
14 LD	90	0	10
16 LD	100	0	0
18 LD	90	0	10
20 LD	90	0	10
22 LD	90	10	0
LD^w	100	0	0

^{z}Plants were held in continuous SD with no chilling.
^{y}Plants were chilled prior to return to continuous SD.
^{x}Number of LD before transfer to SD; all LD treatments were chilled.
^{w}Plants were grown in continuous LD following chilling.
*** χ^2 = 54.3, p < 0.001. Analysis conducted using actual data; percents presented for table use only.

Table 4.2 The effects of a limited inductive photoperiod and chilling on *Chrysanthemum x superbum* 'G. Marconi' number of days to flower, stem length, scape length, plant height, and axillary flower bud number.

Treatment	No. of days to flower[z]	Stem length (cm)	Scape length (cm)	Plant height (cm)	No. of buds
SD[y]	110 a[x]	9.0 b	23.0 ab	32.0 a	3.0 a
ch SD[w]	90 b	6.0 b	25.9 ab	29.9 a	0.4 b
6 LD[v]	83 bc	5.3 b	25.7 ab	31.0 a	0.6 b
8 LD	90 b	4.4 b	30.8 a	35.1 a	0.5 b
10 LD	72 bcd	7.7 b	21.1 ab	28.1 a	1.5 ab
12 LD	72 bcd	7.0 b	22.3 ab	29.3 a	1.2 ab
14 LD	71 bcd	6.9 b	18.6 b	25.6 a	1.7 ab
16 LD	74 bcd	8.0 b	20.5 ab	28.4 a	1.3 ab
18 LD	72 bcd	9.4 b	17.2 b	26.6 a	1.7 ab
20 LD	64 cd	8.6 b	16.2 b	24.8 a	1.7 ab
22 LD	70 bcd	8.9 b	20.1 ab	29.0 a	2.3 ab
LD[u]	59 d	15.8 a	20.6 ab	36.4 a	2.2 ab

[z]Number of days from the end of chilling to first flower.
[y]Plants were held in continuous SD with no chilling.
[x]Means separation within columns, Student-Newman-Keuls test, $p = 0.05$.
[w]Plants were chilled prior to return to continuous SD.
[v]Number of LD before transfer to SD; all LD treatments were chilled.
[u]Plants were grown in continuous LD following chilling.

Table 4.3 The effects of a limited inductive photoperiod and chilling on flowering status of *Chrysanthemum* x *superbum* 'Snow Lady'.

Treatment*	Anthesis (%)	Aborted buds (%)	Vegetative (%)
SD^z	70	0	30
ch SD^y	100	0	0
6 LD^x	90	0	10
8 LD	80	0	20
10 LD	100	0	0
12 LD	100	0	0
14 LD	100	0	0
16 LD	100	0	0
18 LD	100	0	0
20 LD	100	0	0
22 LD	100	0	0
LD^w	100	0	0

^{z}Plants were held in continuous SD with no chilling.
^{y}Plants were chilled prior to return to continuous SD.
^{x}Number of LD before transfer to SD; all LD treatments were chilled.
^{w}Plants were grown in continuous LD following chilling.
* χ^2 = 23.2, $0.1 < p < 0.01$. Analysis conducted using actual data. Percents presented for table use only.

Table 4.4 The effects of a limited inductive photoperiod and chilling on *Chrysanthemum x superbum* 'Snow Lady' number of days to flower, stem length, scape length, plant height, and axillary flower bud number.

Treatment	No. of days to flower[z]	Stem length (cm)	Scape length (cm)	Plant height (cm)	No. of buds
SD[y]	208 b[x]	7.1 a	14.6 a	21.7 a	2.3 a
ch SD[w]	256 a	2.6 b	14.3 a	16.8 bc	4.1 a
6 LD[v]	248 a	2.6 b	13.3 a	15.9 bc	4.2 a
8 LD	246 a	3.3 b	11.9 a	15.3 bc	4.8 a
10 LD	249 a	3.4 b	10.0 a	13.3 c	4.1 a
12 LD	239 a	4.5 ab	10.8 a	15.2 bc	4.0 a
14 LD	238 a	3.0 b	10.9 a	13.9 c	3.9 a
16 LD	237 a	5.0 ab	11.6 a	16.6 bc	4.7 a
18 LD	233 a	3.3 b	11.3 a	14.6 bc	4.3 a
20 LD	238 a	4.8 ab	10.0 a	14.8 bc	4.0 a
22 LD	235 a	4.8 ab	11.5 a	15.2 bc	4.4 a
LD[u]	233 a	5.3 ab	13.7 a	19.0 ab	4.9 a

[z]Number of days from date of sowing to first flower.
[y]Plants were held in continuous SD with no chilling.
[x]Means separation within columns, Student-Newman-Keuls test, p = 0.05.
[w]Plants were chilled prior to return to continuous SD.
[v]Number of LD before transfer to SD; all LD treatments were chilled.
[u]Plants were grown in continuous LD following chilling.

Table 4.5 The effects of a limited inductive photoperiod and chilling on flowering status of *Coreopsis grandiflora* 'Sunray'.

Treatment*	Anthesis (%)	Aborted buds (%)	Vegetative (%)
SD^z	20	0	80
ch SD^y	40	20	40
6 LD^x	60	10	30
8 LD	60	20	20
10 LD	70	10	20
12 LD	40	0	60
14 LD	90	0	10
16 LD	60	0	40
18 LD	60	0	40
20 LD	70	0	30
22 LD	90	0	10
LD^w	90	0	10

^{z}Plants were held in continuous SD with no chilling.
^{y}Plants were chilled prior to return to continuous SD.
^{x}Number of LD before transfer to SD; all LD treatments were chilled.
^{w}Plants were grown in continuous LD following chilling.
* $\chi^2 = 38.2$, $0.1 < p < 0.01$. Analysis conducted using actual data. Percents presented for table use only.

Table 4.6 The effects of a limited inductive photoperiod and chilling on *Coreopsis grandiflora* 'Sunray' scape length, plant height, and axillary flower bud number.

Treatment	Scape length (cm)		Plant height (cm)		No. of buds	
SD^z	17.8	ab^y	19.0	bc	1.0	a
ch SD^x	16.6	ab	18.0	bc	1.0	a
6 LD^w	16.7	ab	18.1	bc	1.9	a
8 LD	15.5	ab	17.0	c	0.3	a
10 LD	20.1	ab	22.8	bc	2.3	a
12 LD	14.9	ab	18.9	bc	2.3	a
14 LD	17.4	ab	22.5	bc	2.3	a
16 LD	15.0	ab	24.3	bc	2.2	a
18 LD	13.1	b	18.2	bc	1.3	a
20 LD	16.4	ab	29.9	ab	3.3	a
22 LD	14.0	ab	23.9	bc	1.5	a
LD^v	21.0	a	37.3	a	2.6	a

^{z}Plants were held in continuous SD with no chilling.
^{y}Means separation within columns, Student-Newman-Keuls test, $p = 0.05$.
^{x}Plants were chilled prior to return to continuous SD.
^{w}Number of LD before transfer to SD; all LD treatments were chilled.
^{v}Plants were grown in continuous LD following chilling.

Table 4.7 The effects of a limited inductive photoperiod and chilling on flowering status of *Coreopsis lanceolata* 'Early Sunrise'.

Treatment***	Anthesis (%)	Aborted buds (%)	Vegetative (%)
SD^z	40	40	20
ch SD^y	90	0	10
6 LD^x	100	0	0
8 LD	100	0	0
10 LD	100	0	0
12 LD	100	0	0
14 LD	100	0	0
16 LD	100	0	0
18 LD	100	0	0
20 LD	100	0	0
22 LD	100	0	0
LD^w	100	0	0

^{z}Plants were held in continuous SD with no chilling.
^{y}Plants were chilled prior to return to continuous SD.
^{x}Number of LD before transfer to SD; all LD treatments were chilled.
^{w}Plants were grown in continuous LD following chilling.
*** χ^2 = 64.5, p < 0.001. Analysis conducted using actual data. Percents presented for table use only.

Table 4.8 The effects of a limited inductive photoperiod and chilling on *Coreopsis lanceolata* 'Early Sunrise' scape length, plant height, and axillary flower bud number.

Treatment	Scape length (cm)		Plant height (cm)		No. of buds	
SD[z]	12.7	b[y]	14.6	e	0.0	d
ch SD[x]	13.8	b	15.5	e	0.8	cd
6 LD[w]	15.8	b	19.3	d	2.8	bc
8 LD	15.9	b	20.2	d	3.9	ab
10 LD	16.6	b	21.4	cd	3.8	ab
12 LD	14.7	b	21.0	cd	3.6	ab
14 LD	14.2	b	23.8	bcd	3.1	bc
16 LD	14.6	b	23.5	bcd	4.9	ab
18 LD	14.8	b	25.3	bc	4.0	ab
20 LD	13.4	b	23.6	bcd	2.8	bc
22 LD	13.4	b	26.5	b	3.0	bc
LD[v]	21.4	a	37.8	a	5.8	a

[z]Plants were held in continuous SD with no chilling.
[y]Means separation within columns, Student-Newman-Keuls test, p = 0.05.
[x]Plants were chilled prior to return to continuous SD.
[w]Number of LD before transfer to SD; all LD treatments were chilled.
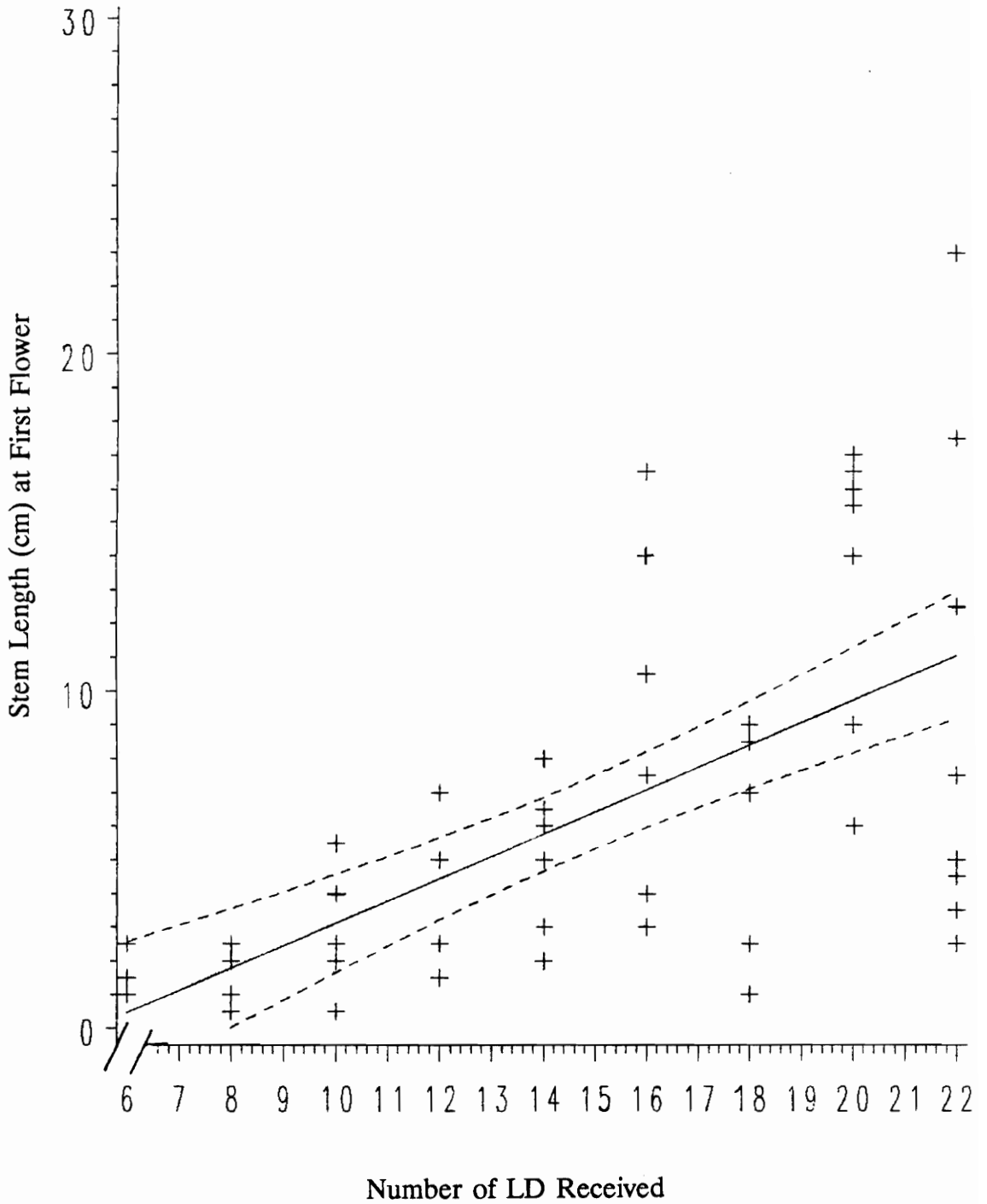[v]Plants were grown in continuous LD following chilling.

Figure 4.1 The effects of a limited inductive photoperiod and chilling received by *Coreopsis grandiflora* 'Sunray' on stem length at first flower. $y = 0.704x - 3.97$, $R^2 = 0.44^{**}$; area bound by dashed lines indicates a 95% confidence interval.
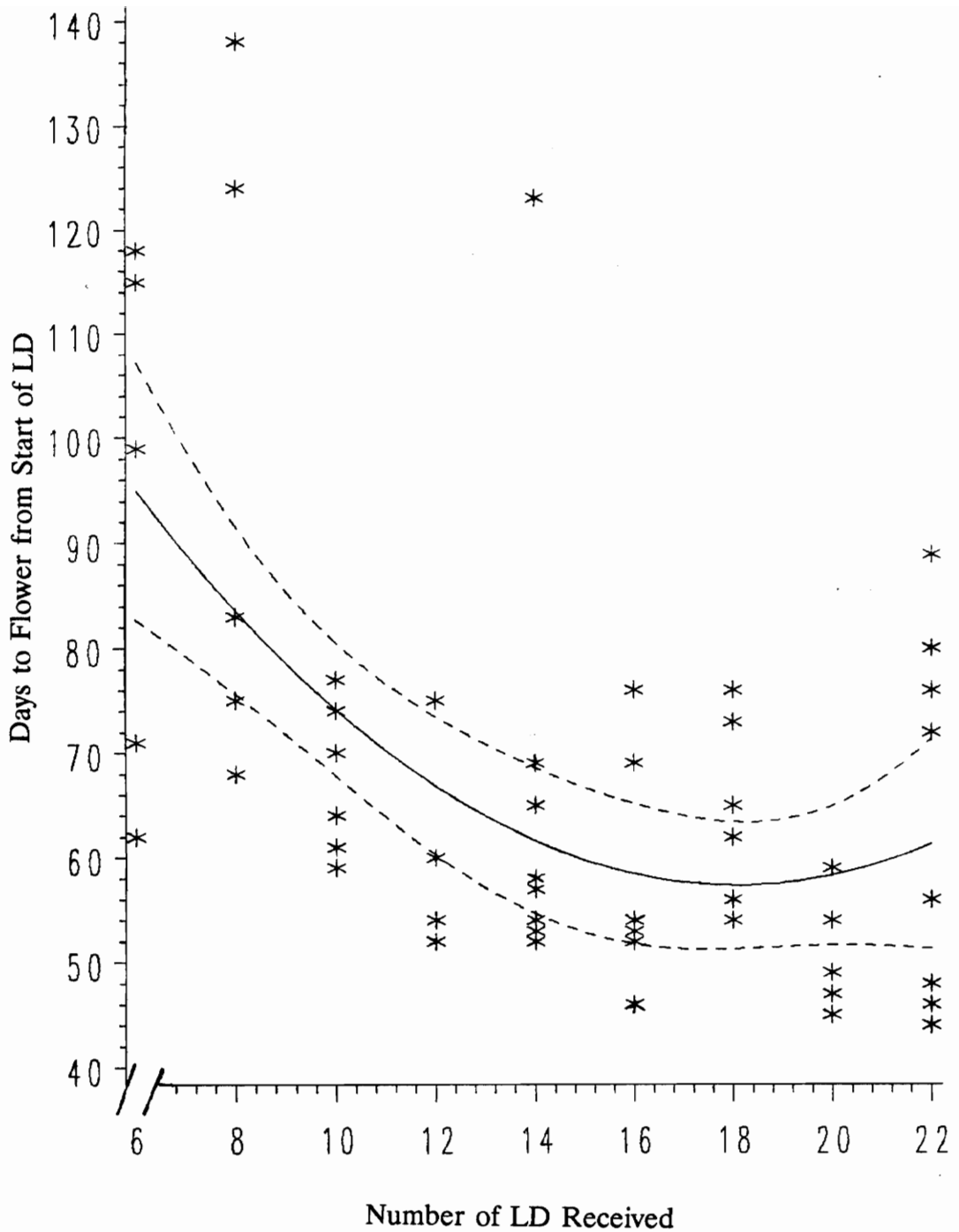
Figure 4.2 The effects of a limited inductive photoperiod and chilling received by *Coreopsis grandiflora* 'Sunray' number of days to flower from start of LD. $y = 138.0 - 8.64x + 0.229x^2$, $R^2 = 0.31$**; parabolic minimum point is 18 LD, 57 days to flowering; area bound by dashed lines indicates a 95% confidence interval.
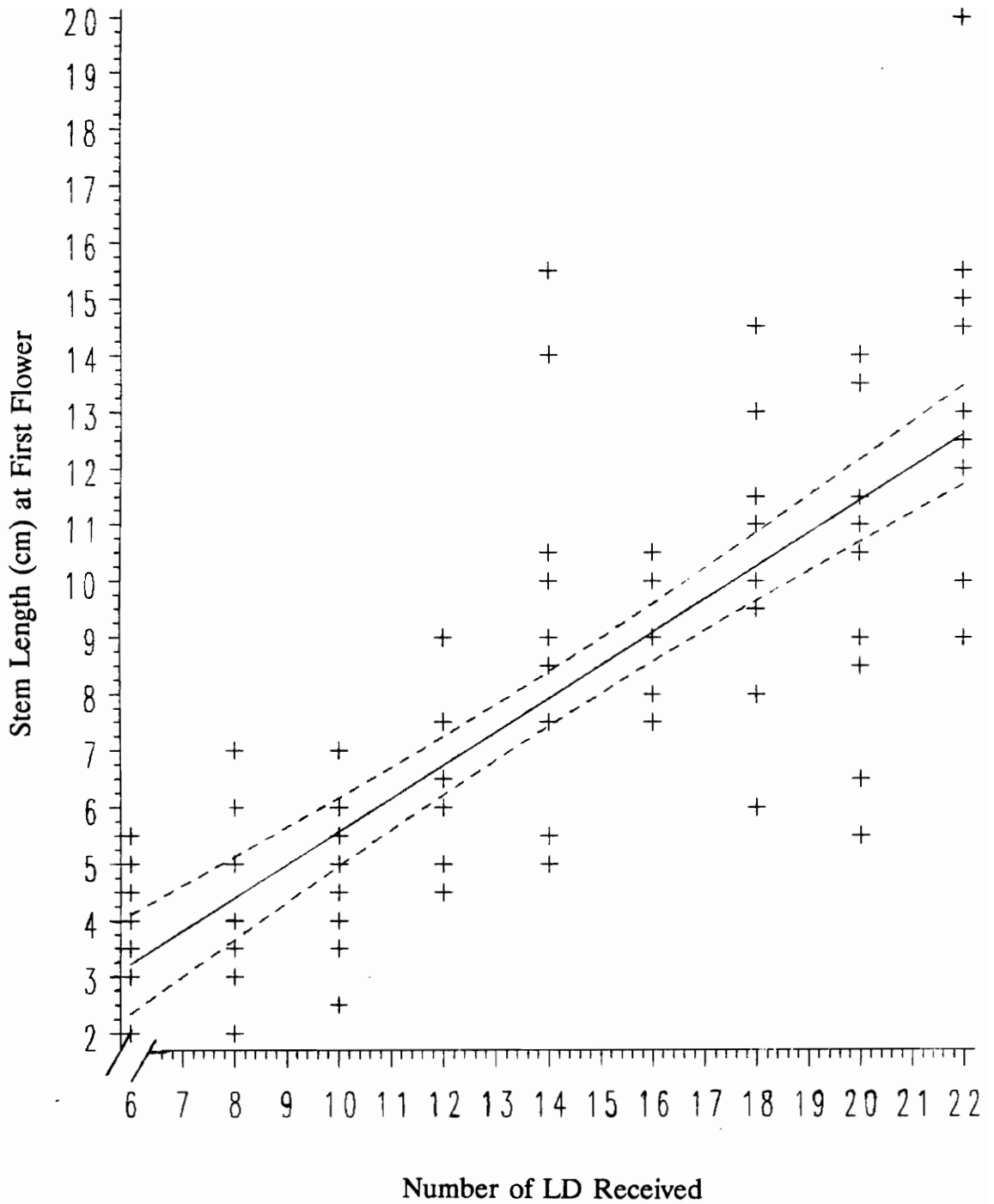
Figure 4.3 The effects of a limited inductive photoperiod and chilling received by *Coreopsis lanceolata* 'Early Sunrise' on stem length at first flower. $y = 0.586x - 0.291$, $R^2 = 0.64**$; area bound by dashed lines indicates a 95% confidence interval.
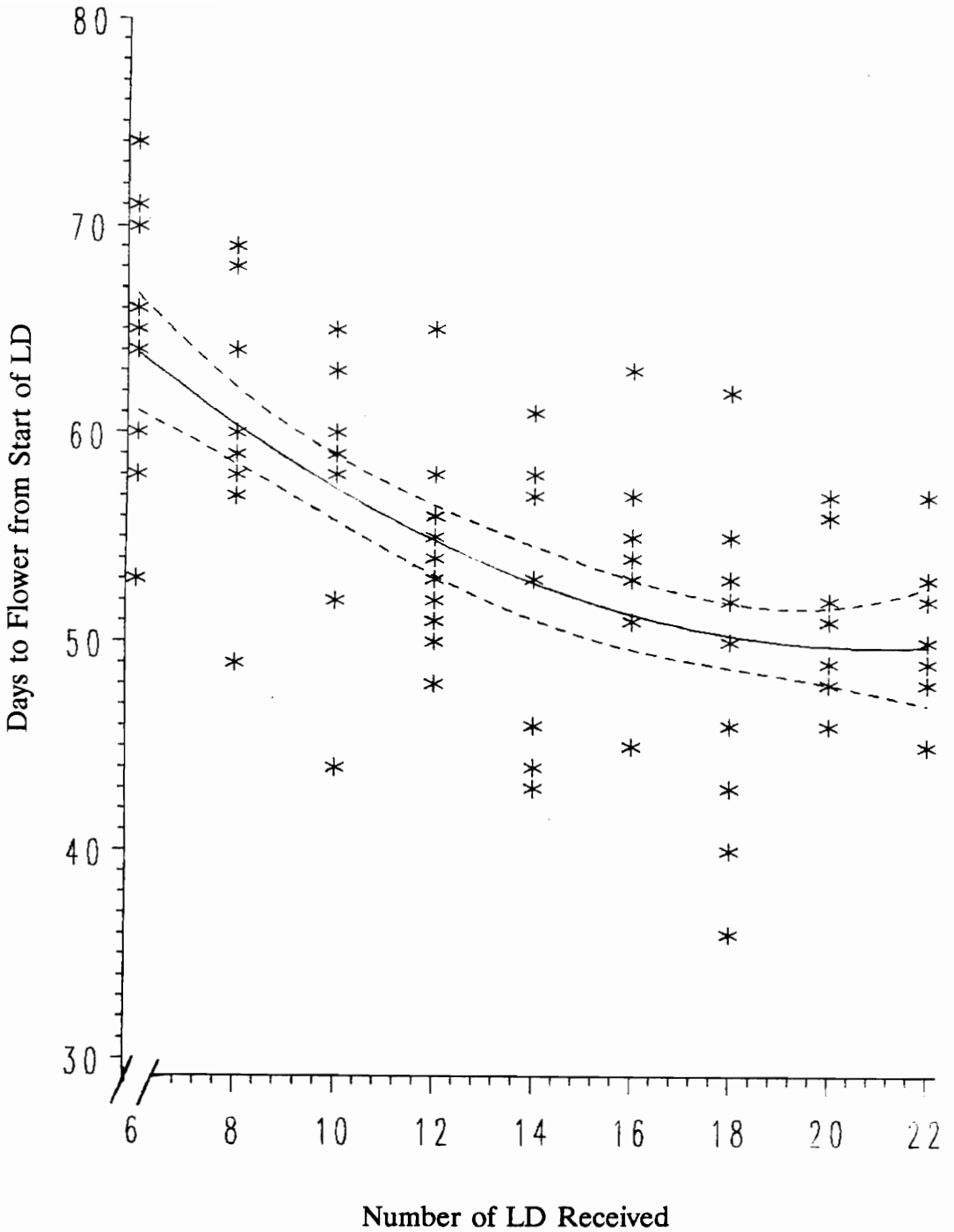
Figure 4.4 The effects of a limited inductive photoperiod and chilling received by *Coreopsis lanceolata* 'Early Sunrise' on number of days to flower from start of LD. $y = 77.4 - 2.64x + 0.0629 \, x^2$, $R^2 = 0.42**$; parabolic minimum point is 20 LD, 50 days to flowering; area bound by dashed lines indicates a 95% confidence interval.

Chapter V

Histological Examination of *Chrysanthemum* x *superbum*
'Snow Lady' Grown under SD and LD Conditions.

Abstract. This research compared floral initiation in *Chrysanthemum* x *superbum* 'Snow Lady' in short days (SD) and long days (LD). Following germination, plants were maintained under SD conditions until approximately 4 leaves per plant, at which time one half of the plants were moved to LD. Five plants were sampled each week from both LD and SD and prepared for histological examination of the shoot apices. Under LD, all plants were in floral initiation stages after the third week. Plants grown in SD began showing signs of floral initiation following the fifth week, however, initiation was variable and sporadic. Complete initiation occurred after the ninth week in SD.

INTRODUCTION:

Garner and Allard (1923) originally described the regulatory action of daylength in floral initiation or inhibition in plants. Further research elaborated on this concept and classified plants as LD which flower when the daylength exceeds or equals a critical length, and SD when daylengths are equal to or less than a critical length. Today, even though it is known that plants flower in response to the relative length of the dark period, the categories SD plants and LD plants are retained. A photoperiodic requirement can be obligate (absolute, qualitative), or facultative (quantitative), in which case the plant will eventually flower under unfavorable conditions (Metzger, 1988).

Flowering status might seem to be a very simple, judgmental determination at first glance; a plant is either flowering or it is not. However, several more factors need to be considered. For instance, a plant may be induced to flower by two different treatments, flowering profusely under one treatment, while only sparsely in the other. The rate of reproductive development is also important and can be affected by different photoperiods. Due to the complexity of quantifying flowering, several techniques have been used. The percentage of plants flowering, the number of buds, flowers or flower nodes per plant, the rate of development as measured by the increase in leaf number from the beginning of a treatment until flowering occurs, or the microscopic examination of apical development are all possibilities (Metzger, 1988).

The characteristics of a vegetative meristem and how it changes prior to and during floral initiation have been described in great detail (Bernier et al., 1981). In most vegetative meristems a complex zonation can be recognized. This typically includes the "central zone" composed of the centrally located cells of the tunica and corpus, a ring-shaped "peripheral zone" which surrounds the central zone and includes the tunica and corpus cells located in the flanks of the meristem, and the "pith-rib meristem" which lies directly below the central zone and is composed of large, flattened, vacuolated cells. In the transition from a vegetative state to flowering in Asteraceae species, the apical shoot elongates and is followed by the formation of an enlarged capitulum. The tunica and corpus cells exhibit enhanced cell division, the cells of the pith-rib meristem become vacuolated and elongated, and the characteristic zonation typical of a vegetative meristem begins to disappear. Meristem doming at this stage is due to cell expansion in the pith-rib meristem and the basal corpus. Involucral bracts are formed very low on the flanks by periclinal divisions of the second tunica layer. In later stages of floral initiation, the central parenchymatous core increases in size and meristematic cells expand over the entire surface of this core to create a uniform mantle several cells deep. Finally, periclinal divisions in the first corpus layer produce floret primordia (Bernier et al., 1981).

Similar apical responses to inductive LD have been documented for several LD species. Mature *Eschscholtzia californica* plants exhibit apical doming after 6 LD cycles, elongation of primordia internodes occurred after 7 LD, and the tunica-corpus cell layers became disorganized by 8 LD (Carter, 1986). In *Rudbeckia hirta* (syn: *R.*

bicolor), a close relative of *Chrysanthemum* x *superbum*, mitotic activity rises in the central zone after 2 to 4 LD cycles; however, this induction period is insufficient for promotion of flowering in 2 to 3 month old plants. After 6 to 8 LD, activity in the central zone continues to rise and the beginning of flower primordia formation marks the transition to the reproductive phase (Kochankov and Chailakhyan, 1986). The transition to flowering in *Gaillardia pulchella* (Bourke, 1990), also in the Asteraceae, was marked by an increased apical height and width, an increased number of tunica cell layers, and an enlarged area of organized corpus cells beneath the tunica.

Chrysanthemum x *superbum* (syn: *C. maximum*) flowers in response to LD (Griffin and Carpenter, 1964; Kofranek, 1952; Laurie and Poesch, 1932) or after chilling (Shedron and Weiler, 1982). However, 'Snow Lady' is a recent introduction marketed for its ability to flower the first year after a spring seeding. In an attempt to quantify the juvenile phase and describe its response to photoperiod (Chapter 2), 'Snow Lady' responded as a facultative LD flowering plant in contrast to the previously reported obligate LD nature of other cultivars within this species.

The objectives of this experiment were to describe and compare the apical events during floral initiation in *Chrysanthemum* x *superbum* 'Snow Lady' grown in continuous SD and continuous LD conditions in light of its facultative LD flowering nature.

MATERIALS AND METHODS:

Chrysanthemum x *superbum* 'Snow Lady' seeds were sown on 8 Jan 1991 in a medium of 2 parts vermiculite: 1 part peatmoss (v/v) in cell packs and placed under intermittent mist. Upon germination, misting ended and all packs were moved to SD. At approximately 4 leaves per plant, all plants were transplanted into 10 cm (4 inch) plastic pots using a mixture of 1 part peatmoss: 1 part perlite: 1 part vermiculite (v/v/v). Plants were randomly selected and evenly distributed between SD and LD at the time of transplanting. SD conditions were created by covering the plants from 1700-0800 hr with 100% light exclusion black sateen cloth. LD conditions were created by night interruption from 2200-0200 hr with 60W incandescent bulbs strung overhead to provide 3-4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF. Ambient temperature for germination was 19-21°C day and night. After transplanting, plants were fertilized weekly during irrigation with 400 ppm N from 20N : 6.6P : 17.6K.

Five plants (reps) were sampled weekly from both LD and SD, beginning 1 week after transplanting. Sampling consisted of separating the shoot from the roots, then removing all expanded leaves. The shoot apex and smallest leaves were fixed in formalin-acetic acid-alcohol (FAA). The number of expanded leaves per plant was recorded. Sampling continued for 12 weeks in SD and in LD until all 5 reps of a single treatment possessed visible terminal flower buds.

Tissue samples were dehydrated automatically according to the protocol in Table 5.1. Paraffin-infiltrated tissue was then embedded in paraffin blocks and

sequentially and longitudinally sectioned at 8 μm until reaching the approximate center of the apex. Tissue was mounted, stained with Mayers Hemalum, and counter stained with Erythrosin (Table 5.2). Slides were examined via light microscopy for indications of floral initiation.

RESULTS:

Leaf unfolding occurred more quickly on plants grown in LD than in SD (Table 5.3). Floral initiation had begun in the 5 plants sampled after 1 week in LD as evidenced by slight doming of the apices and primordial internode elongation (Figure 5.1). By the end of the second week in LD, the apical doming was nearly hemispherical, internode elongation was much more pronounced and cells of the pith-rib meristem were arranged in a columnar pattern (Figure 5.2). After 3 weeks in LD, involucral bracts were present and a uniform mantle of cells had expanded over the entire surface of the central parenchymatous core (Figure 5.3). Although apical floral initiation was complete after 3 weeks in LD, sampling continued through the fifth week at which time all 5 plants had visible terminal flower buds.

Apical examination after 5 weeks in SD revealed vegetative meristems typified by a relatively flat apex (Figure 5.4), as well as slight apical doming on some plants (Figure 5.5). Sampling after 6 weeks in SD showed apical doming in 4 of 5 plants.

Following 7 weeks in SD, apices were domed and nearly hemispherical, primordial internode elongation and columnarization were evident, and vacuolation and elongation of the pith-rib meristem had occurred (Figure 5.6). Stages of floral initiation were similar following the eighth week in SD, with enhanced apical doming and internode elongation. Floral initiation was evident in plants in all 5 reps following the ninth week of sampling. Two plants possessed visible terminal buds at the time of sampling (Figure 5.7), while histological examination of the remaining 3 plant meristems revealed apical doming, primordial internode elongation and columnarization of the pith-rib meristem. Sampling continued through the twelfth week; each week 2 plants were in visible bud at sampling and histological examination revealed various stages of floral initiation (Figure 5.8) in the other plants from each treatment.

DISCUSSION:

During recent examination of photoperiodicity and the flowering nature of *Chrysanthemum* x *superbum* 'Snow Lady' (Chapter 2), floral initiation occurred under both SD and LD. Plants were grown in SD to specific leaf numbers, beginning with 0 (cotyledons only) and progressing at 3 leaf intervals to 24 leaves, at which time plants were transferred to LD. Defying an anticipated obligate LD requirement for

floral initiation, plants in the 21 and 24 leaf stage treatments possessed visible terminal flower buds before reaching the designated transfer stage. In the present experiment, the average leaf number of plants sampled at weeks 7, 8, and 9 was 17.0, 19.2, and 22.8, respectively. Therefore, noting the sporadic flowering which occurred at the microscopic level at these sample stages, floral initiation in SD prior to 24 leaves (Chapter 2) is not surprising.

Earlier research with *Eschscholtzia californica* and *Rudbeckia hirta* indicated the first signs of floral initiation to occur following 6 LD cycles (Carter, 1986) and 6 to 8 LD (Kochankov and Chailakhyan, 1986), respectively. However, the number of inductive cycles required for floral initiation can be affected by several factors, including the length of the photoperiod, the criterion for transition to flowering, the duration of the observations, and plant age. Although 6 to 8 LD were required for complete floral initiation in 3 month old *R. hirta* plants, as few as 3 LD induced seven-month old plants (Kochankov and Chailakhyan, 1986). An attempt to compare results from the present experiment, in which plants were grown for only 1 month (approximately 4 leaves) prior to start of LD treatments, to previous documentation of the number of inductive cycles needed for floral initiation, is invalid. Although 3 weeks of LD were needed for complete initiation in *C. x superbum* 'Snow Lady', under these conditions, plants of different ages could not be expected to respond to inductive conditions similarly.

The growth rate of plants in SD, measured by an increase in expanded leaf number each week, was slower than the rate of growth in LD plants (Figure 5.9).

However, the time required for apical floral initiation in all 5 plants within the treatment, 3 weeks in LD compared to 9 weeks in SD, reflects not only this slower development of leaves, but also the fact that plants grown in SD produce more leaves per plant before initiation occurs. Plants sampled after 3 weeks in LD had fewer than half as many leaves per plant compared to those grown in SD for 9 weeks. Therefore, delayed flowering cannot solely be a growth rate issue under less favorable SD, but can also be attributed to a delay in actual floral initiation. Although there is not a common leaf number per plant for floral initiation in LD and SD, the 2 photoperiods can be compared to determine the number of LD or SD cycles needed to reach a particular floral initiation stage. Apical floral initiation after 2 weeks in LD (Figure 5.2) is nearly identical to the initiation stage found after 7 weeks in SD (Figure 5.6). Theoretically, 1 LD equals 3.5 SD, or, considering the time required for floral initiation to occur in all plants within each treatment, 3 weeks of LD are equivalent to 9 weeks of SD. Thus, the previously proposed facultative LD flowering nature of *C.* x *superbum* 'Snow Lady' (Chapter 2) is not only confirmed, but also quantified. Flowering will occur in both LD and SD, however, initiation is faster and more uniform in LD and plants grown in SD will possess more leaves at anthesis.

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Table 5.1 Tissue dehydration series.

Treatment		Time
Ethanol	80%	10 minutes
"	95%	10
"	95%	10
"	100%	25
"	100%	10
"	100%	20
Xylene		20
Xylene		25
Paraffin		20
Paraffin		30
Paraffin		30

Table 5.2 Tissue stain sequence for Mayers Hemalum and Erythrosin.

Treatment	Time
Xylene	5 minutes
Ethanol (100%)	5
Ethanol (100%)	5
Ethanol (95%)	5
Distilled water	2
Hemalum	6
Distilled water	1
Distilled water	1
Tap water	1
Ethanol (30%)	5
Ethanol (80%)	5
Ethanol (95%)	5
Erythrosin	15 seconds
Ethanol (100%)	5
Ethanol (100%)	5
Xylene with clove oil	5 minutes
Xylene (100%)	5
Xylene (100%)	5

Table 5.3 Number of expanded *Chrysanthemum* x *superbum* 'Snow Lady' leaves per plant at the time of sampling.

Sampling date (week)	LD[z] leaves per plant			SD[y] leaves per plant		
	mean	min.	max.	mean	min.	max.
1	5.4	5	6	5.4	5	6
2	7.0	6	8	6.0	5	7
3	8.8	7	10	9.0	8	10
4	12.4	10	14	10.4	9	13
5	18.4	16	23	12.6	12	13
6				14.8	14	16
7				17.0	15	18
8				19.2	17	23
9				22.8	18	30
10				26.8	21	37
11				25.2	23	30
12				29.0	21	46

[z]All 5 plants sampled after week 5 possessed visible terminal flower buds at the time of sampling.
[y]Two of the 5 plants sampled after 9, 10, 11, and 12 weeks possessed visible terminal flower buds at the time of sampling.
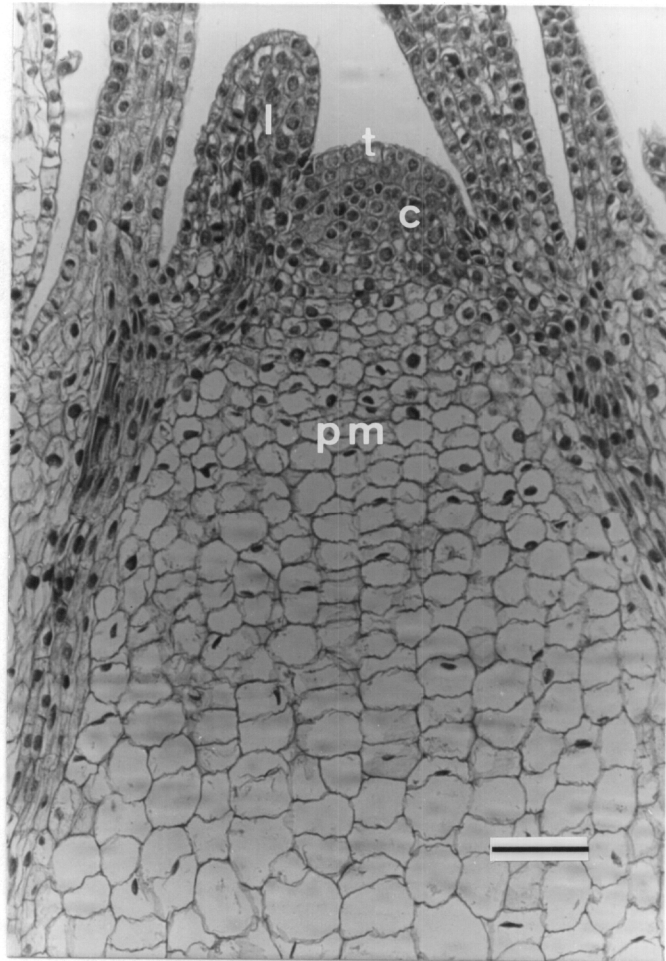
Figure 5.1   The vegetative apex of *Chrysanthemum* x *superbum* 'Snow Lady' sampled
after 1 week of LD. t: tunica; c: corpus; l: leaf primordia; pm: pith-rib
meristem.   Bar = 100 μm.
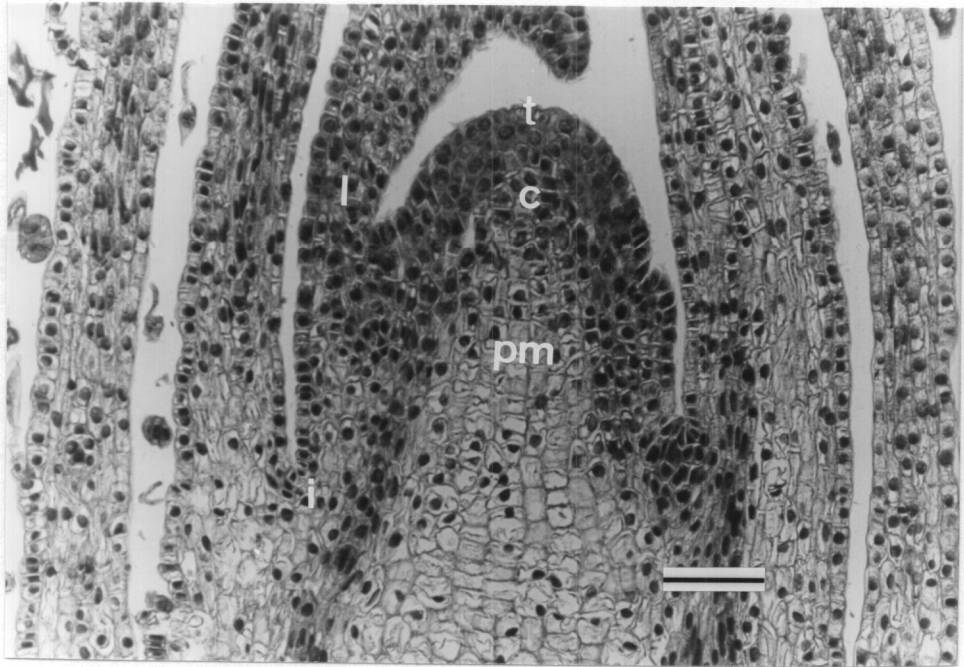
Figure 5.2 Floral initiation in *Chrysanthemum* x *superbum* 'Snow Lady' following the second week of LD. Note the large nuclei in the corpus cells (c), elongation of the pith-rib meristem (pm) and elongation of primordial internodes (i). t: tunica; l: leaf primordia. Bar = 100 μm.
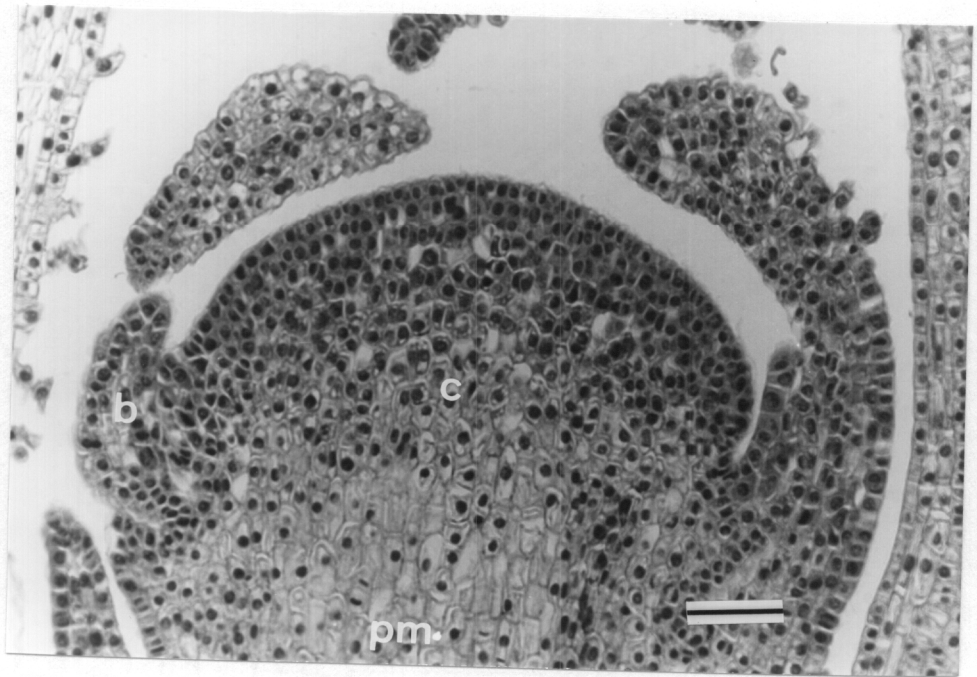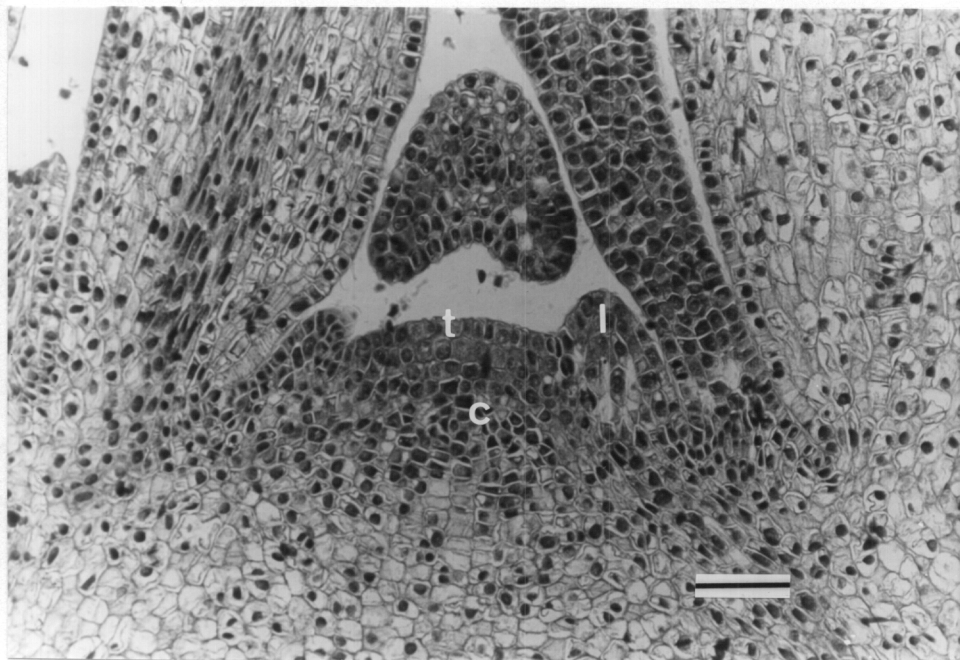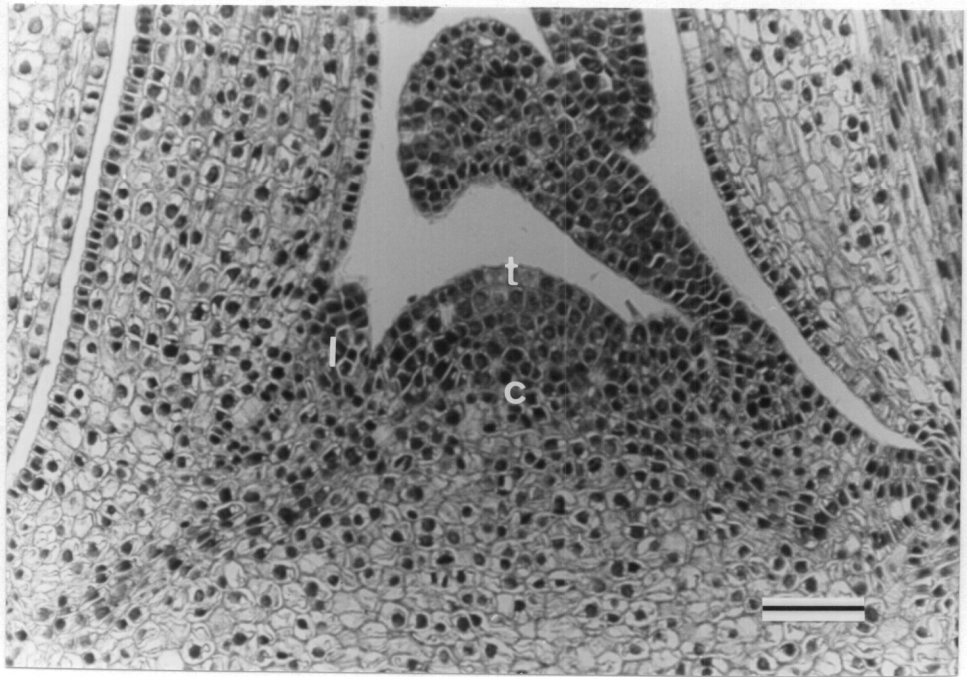
Figure 5.3   *Chrysanthemum* x *superbum* 'Snow Lady' sampled after 3 weeks in LD.
Note vacuolation and elongation of the basal corpus (c) and the pith-rib
meristem (pm) and formation of involucral bracts (b).   Bar = 100 μm.

Figure 5.4   The vegetative apex of *Chrysanthemum* x *superbum* 'Snow Lady' sampled
after 5 weeks in SD.   t: tunica; c: corpus; l: leaf primordia.   Bar =
100 μm.

Figure 5.5   Apical doming in *Chrysanthemum* x *superbum* 'Snow Lady' sampled after 5 weeks in SD. t: tunica; c: corpus; l: leaf primordia. Bar = 100 μm.
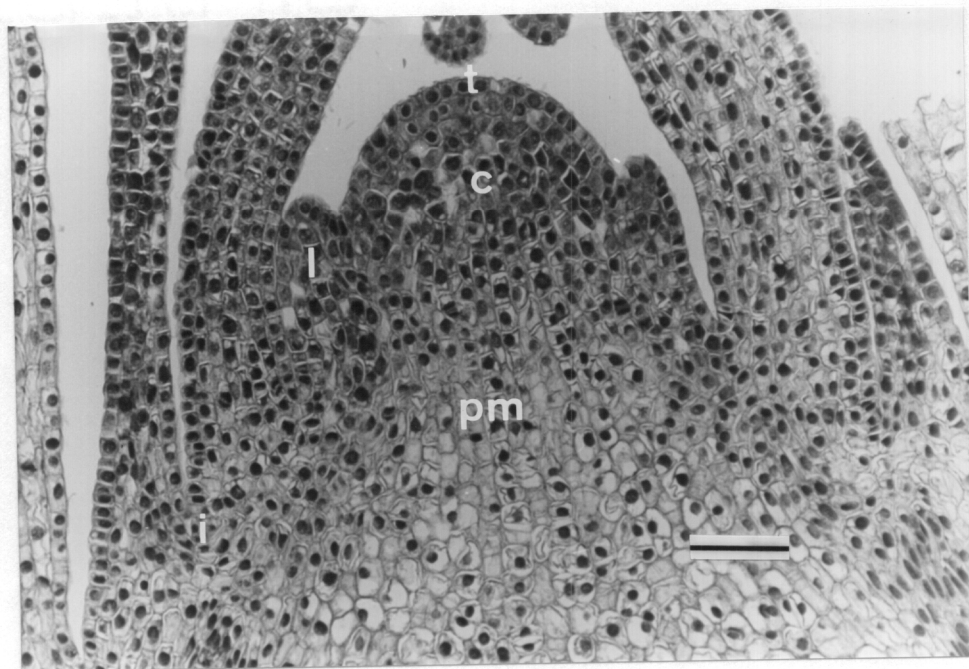
Figure 5.6   Elongation of the pith-rib meristem (pm) and elongation of primordial internodes (i) in *Chrysanthemum* x *superbum* 'Snow Lady' following 7 weeks in SD. t: tunica; c: corpus; l: leaf primordia. Bar = 100 μm.
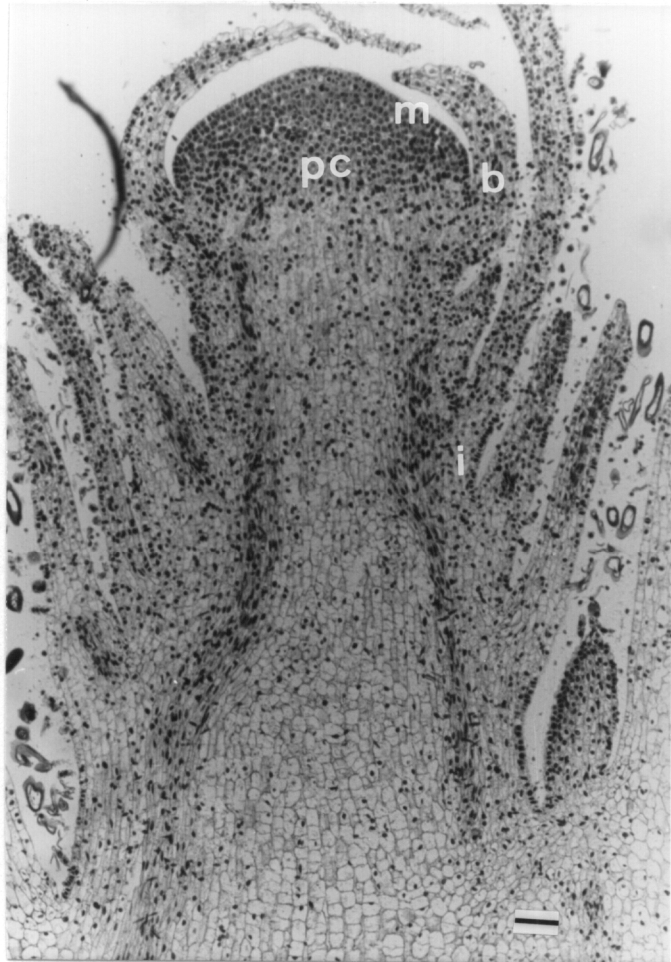
Figure 5.7 *Chrysanthemum* x *superbum* 'Snow Lady' following 9 weeks of SD. Note primordial internode elongation (i), involucral bract formation (b) and the meristematic mantle of cells (m) spread over the parenchymatous core (pc). Bar = 100 μm.
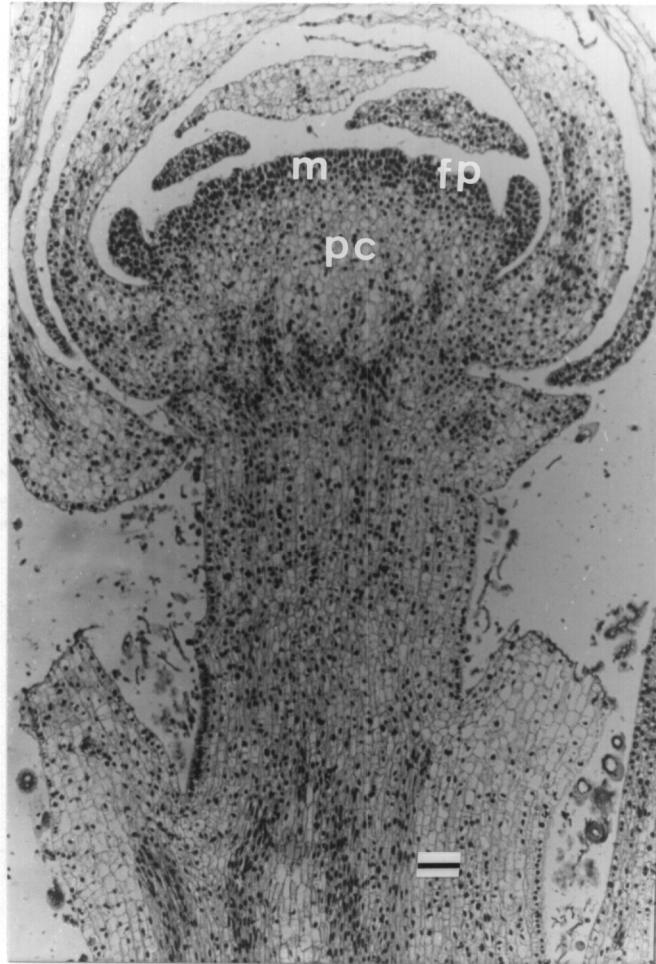
Figure 5.8   The advanced stages of floral initiation in a *Chrysanthemum* x *superbum* 'Snow Lady' apex from SD week 10. Note meristematic mantle of cells (m) covering the parenchymatous core (pc) and floret primordia (fp) forming acropetally on both flanks of the meristem. Bar = 100 μm.
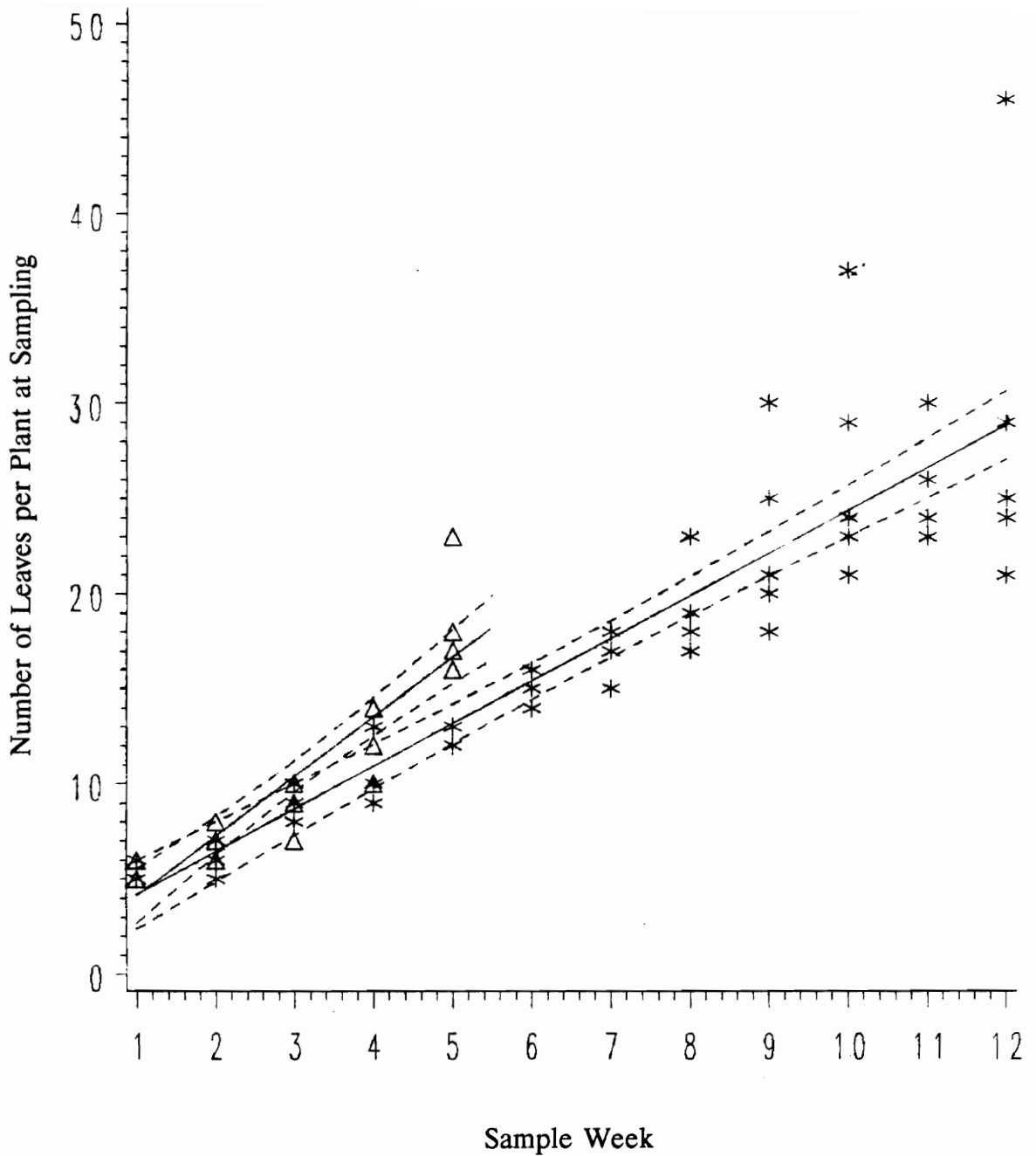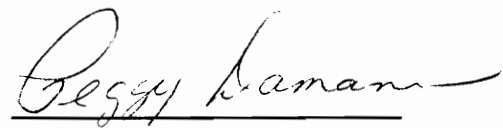
Figure 5.9   Rate of *Chrysanthemum* x *superbum* leaf unfolding in LD and SD. Triangles represent LD treatments, y = 0.980 + 3.14x ; stars represent SD treatments, y = 3.04 + 1.88x.

VITA

Margaret S. Damann was born to Donald and Bernadine Damann on September 15, 1965, in Savage, Minnesota, and was given the nickname "Peggy" soon after birth. She grew up in east-central Minnesota, attended Braham High School and graduated in May, 1984. She earned a Bachelor's of Science in Horticulture from the University of Wisconsin at River Falls (UW-RF) in 1989 and a Master's of Science in Horticulture, with a specialty in floriculture, from Virginia Polytechnic Institute and State University (VPI and SU) in 1991. Initiated into Pi Alpha Xi, national honorary society for floriculture and ornamental horticulture in 1988, Damann was elected Vice president of the alpha-zeta chapter, UW-RF, that same year and served as President of the Kappa chapter, VPI and SU, during 1990-91. She has also been a member of the American Society for Horticultural Science (ASHS) since 1989.

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