Natural Chilling and Limited Inductive Photoperiod Affect Flowering in Two Asteraceae Genera

M. Peggy Damann¹ and Robert E. Lyons²

Department of Horticulture, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0327

Additional index words. *Chrysanthemum* × *superbum*, *Coreopsis lanceolata*, *Coreopsis grandiflora*, long-day plant, shasta daisy, lance-leaf coreopsis, vernalization

Abstract. To examine the effects of chilling and a limited inductive photoperiod (LIP) on flowering of *Chrysanthemum* × *superbum* Bergmans ex J. Ingram ‘G. Marconi’ and ‘Snow Lady’, *Coreopsis grandiflora* Hogg ‘Sunray’, and *Coreopsis lanceolata* L. ‘Early Sunrise’, seeds were sown and plants were maintained in the greenhouse in short days (SDs) for 7 weeks, followed by 4 months of natural outdoor chilling for all plants except 10 of each cultivar, which remained in the greenhouse under SDs for the duration of the experiment. Upon return to greenhouse conditions, 10 plants of each cultivar were placed in SDs, all other chilled plants were placed in long-days (LDs) and subsequently transferred to SDs after receiving 6, 8, 10, 12, 14, 16, 18, 20, or 22 LD cycles. Ten chilled plants of each cultivar remained in LDs for the duration of the experiment. Continuous SDs without chilling resulted in 70%, 40%, 20%, and 10% flowering in ‘Snow Lady’, ‘Early Sunrise’, ‘Sunray’, and ‘G. Marconi’, respectively. Chilling, followed by a return to continuous SDs, improved flowering in all cultivars compared to SDs without chilling. The number of LD cycles required for 100% flowering varied with cultivar. Ninety percent of the chilled ‘Early Sunrise’ plants flowered with no LD cycles, and 100% flowering was produced by as few as six LD cycles. In ‘Snow Lady’, 100% flowering occurred in chilled plants with no LD cycles and those receiving at least 10 LD cycles. With only six or eight LD cycles, 90% and 80% of these plants, respectively, still flowered. The percentage of ‘G. Marconi’ and ‘Sunray’ plants flowering ranged from 40% to 100% in the chilled treatments, with a general trend for more flowering with an increase in the number of LD inductive cycles. Continuous LDs following chilling resulted in as high or higher percent flowering than any other treatments (100% for ‘G. Marconi’ and 90% for ‘Sunray’). The effects of LIP were evident in both *Coreopsis* cultivars but in neither *Chrysanthemum* × *superbum* cultivar. There was a linear relationship between the number of LDs received and stem length at first flower in ‘Sunray’ and ‘Early Sunrise’. In both cultivars, a reduction in stem elongation of about 10 cm occurred when plants received only 6 LDs compared to 22 LDs. The number of days from the start of LDs to first flower increased linearly as the number of LD cycles before the transfer back to SDs increased.

The concept of vernalization [the chilling of moistened or germinating seeds of winter strains of wheat (*Triticum aestivum* L.) and rye (*Secale cereale* L.)] originated from agronomic practices and observations in temperate climates. This concept has led to the practice of substituting artificial chilling for the natural exposure to winter to induce or hasten the ability to flower. Biennials, including *Daucus carota* (carrot), *Lunaria annua* (moneyplant), and *Hyoscyamus niger* (henbane), and many popular perennials, including *Chrysanthemum* species, require chilling for floral induction (Chouard, 1960; Hillman, 1969).

Even in photoperiod-sensitive plants, the flowering response often requires prior chilling. In biennial henbane and winter rye, a chilling treatment allowed plants to become responsive to long-days (LDs) and, in some cultivars of *Dendranthema grandiflora* (syn: *Chrysanthemum* × *morifolium*), a prior chilling period was necessary to stimulate short-day (SD) sensitivity. The chilling requirement, like photoperiodism, can be quantitative (plants from previously vernalized seed of ‘Petkus’ winter rye flowered after reaching six or seven leaves, whereas, in the absence of chilling, flowering occurred after reaching twenty-five leaves) or qualitative (the biennial strain of henbane is receptive to chilling only after 10 days as juvenile rosettes). Chilling can also modify or substitute for the LD requirement as in some strains of *Spinacia* (spinach) and *Trifolium* (clover) (Chouard, 1960; Hillman, 1969).

Chrysanthemum × *superbum* (syn: *Chrysanthemum maximum*), commonly known as shasta daisy, was 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, *Chrysanthemum* × *superbum* was generally thought to require a chilling period for optimal flowering, but little research has addressed this possibility. The nonchilled ‘G. Marconi’ flowered sparsely under 14- and 18-h photoperiods at 18 and 24 °C minimum night temperatures (MNTs) (Shedron and Weiler, 1982). However, when 4.5 °C for 0, 4, 8, 12, or 16 weeks was followed by a 10-h photoperiod at 18 °C MNT, flowering was increased proportionately with 100% flowering after 16 weeks of chilling. The ineffectiveness of LDs in promoting flowering in nonchilled ‘G. Marconi’ plants was confirmed (Damann and Lyons, 1995); however, ‘Snow Lady’ flowered when grown in LDs from the cotyledon stage or in SDs followed by LDs.

The effects of chilling on flowering of *Coreopsis*, another LD species, have received limited research attention. Ketellapper and Barbaro (1966) grew plants from two genetic lines derived from *Coreopsis grandiflora* ‘Single Mayfield Giant’ under LDs for 12.5 weeks, followed by inductive conditions of 7 weeks of SDs at nonchilling temperatures or 7 weeks in continuous light at 3 °C, finally returning them to LDs. The 3 °C continuous light treatment produced almost 30% more flowering compared to plants grown at normal temperatures in SDs. When seedlings grown in LDs for 21 weeks were chilled at 3 °C in LDs for 42 days, 100% floral induction occurred (Ketellapper and Barbaro, 1966). With no chilling, *Coreopsis grandiflora* Hogg ‘Sunray’ failed to flower under LDs, but 70% to 90% of the *Coreopsis lanceolata* L. ‘Early Sunrise’ plants flowered when grown in continuous LD conditions or when transferred from SDs to LDs at various leaf stages. Neither cultivar flowered when

Received for publication 11 Aug. 1995. Accepted for publication 20 Feb. 1996. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Former graduate student.

²Professor. To whom correspondence should be addressed.

grown in continuous SDs (Damann and Lyons, 1993).

Limited inductive photoperiod (LIP), an expansion of Murneek's (1936) concept of photoperiodic inhibition, is a method whereby the plant is given the minimum number of inductive cycles to initiate flowering before transfer back to noninductive conditions. The LIP promotes flowering, but bolting-related stem elongation stops upon transfer back to SDs. LIP effectively controlled plant height in nonchilled *Coreopsis lanceolata* 'Early Sunrise' (Damann and Lyons, 1993) by inhibiting stem elongation without affecting scape length, resulting in plants that were better proportioned to the container than those that remained in LDs until anthesis.

The objective of this experiment was to examine the combined effects of natural chilling and LIP on flowering and stem length of *Chrysanthemum* $\times$ *superbum* 'G. Marconi' and 'Snow Lady', *Coreopsis grandiflora* 'Sunray', and *Coreopsis lanceolata* 'Early Sunrise'.

Fig. 1. The effects of a limited inductive photoperiod and chilling on flowering status of (A) *Chrysanthemum* $\times$ *superbum* 'G. Marconi' ($***\chi^2 = 54.3, P < 0.001$), (B) *Chrysanthemum* $\times$ *superbum* 'Snow Lady' ($*\chi^2 = 23.2, 0.1 < P < 0.01$), (C) *Coreopsis grandiflora* 'Sunray' ($*\chi^2 = 38.2, 0.1 < P < 0.01$), (D) *Coreopsis lanceolata* 'Early Sunrise' ($***\chi^2 = 64.5, P < 0.001$). SD, CH, and LD indicate continuous short days (SDs) with no chilling, chilled before return to continuous SDs, and continuous long days (LDs) following chilling, respectively. Treatment numbers indicate number of LDs before transfer to SDs. All LD treatments were chilled. Analysis conducted using actual data; percents presented for figure use only. solid bar = anthesis; shaded bar = aborted terminal flower bud; unshaded bar = vegetative.

Materials and Methods

Seeds of *Coreopsis lanceolata* 'Early Sunrise', *Coreopsis grandiflora* 'Sunray', and *Chrysanthemum* $\times$ *superbum* 'Snow Lady' and 'G. Marconi' were sown on 13 Aug. in a medium of 2 vermiculite : 1 peatmoss (by volume) in cell packs and placed under intermittent mist. Upon germination, misting ended and all cell packs were moved to SDs, which were created by covering the plants from 1700 to 0800 HR with 100% light-exclusion black sateen cloth. Plants were transplanted into 500-mL (10-cm) plastic pots on 19 Sept. using a mixture of 3 peatmoss : 1 perlite : 1 vermiculite (by volume) and fertilized weekly during irrigation with 400 ppm N from 20N-6.6P-17.6K. Greenhouse temperatures were set at 24/18 °C day/night. Treatments were assigned randomly at the time of transplanting.

Ten plants (replications) of each cultivar remained in the greenhouse under SDs (unchilled SD control), and all others were moved on 5 Oct. into a single-layer, polyethylene-covered, ventilated, and unheated Quonset structure. Shredded hardwood bark mulch was placed around and up to the pot rims, and shading compound was applied to the polyethylene covering. Plants were grown under prevailing air temperatures and natural lighting. Interior air temperature was recorded by a thermograph. Chilled plants were returned to the greenhouse (24/18 °C day/night) following 100 nights of temperatures reaching 4 °C (after about 4 months of chilling). Five plants of each cultivar were dissected and examined for apical floral initiation. Ten plants of each cultivar were placed under SDs (chilled SD control), and all others were

placed in LD conditions created by night interruption from 2200 to 0200 HR with 60-W incandescent bulbs strung overhead to provide 3 to 4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux at plant height. Ten plants of each cultivar were transferred from LDs to SDs after receiving LIP treatments of 6, 8, 10, 12, 14, 16, 18, 20, or 22 LD cycles. Ten chilled plants of each cultivar remained in LDs (LD control).

Data recorded at first flower (when ray florets had expanded perpendicular to the stem attachment) included number of days from the 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), plant height (stem plus scape), and the number of reproductive axillary branches at least 2 cm in length on the main stem. At the end of the experiment, reproductive status of each plant was recorded using three categories: vegetative only (no macroscopic evidence of flowers), reproductive but aborted, and reproductive to anthesis. Mean separation tests, chi-square, and regression analysis (SAS, 1988) with parabolic minimum-point calculations (Rees and Sparks, 1969) were used to analyze the data.

Results and Discussion

Chrysanthemum $\times$ *superbum* 'G. Marconi'. In this cultivar, flowering ranged from 50% to 100% in the chilled LD treatment groups (Fig.

1A). Only 10% of the unchilled SD control plants reached anthesis, while 50% of the chilled SD control plants flowered. Achieving reproductive status was highly dependent on chilling and LIP treatments; however, flower-bud abortion was sporadic and was not influenced by either of these factors. LD control plants flowered 31 and 51 days faster, respectively, than chilled and unchilled SD control plants (data not shown). The stems of LD control plants were nearly twice as long as those of any other group. Chilling followed by SDs or only a brief LD exposure inhibited axillary flower bud formation (data not shown). There was no significant linear or quadratic regression between LIP and any characteristics measured for this cultivar.

Although there is no universal direct relationship between chilling and a particular photoperiodic response, chilling confers a sensitivity to LDs in many plants, which subsequently promotes flowering (Hillman, 1969). This appears to be true in *Chrysanthemum ×superbum* 'G. Marconi', which failed to flower when grown without chilling in LDs (Shedron and Weiler, 1982), SDs followed by LDs, or continuous SDs (Damann and Lyons, 1995). In the present experiment, 4 months of natural chilling resulted in 50% to 100% flowering (Fig. 1A). However, the limited flowering in chilled plants maintained in continuous SDs or given only 6 LDs suggests that there is a minimum number of LDs that must follow the chilling period for maximum flowering to occur. Thus, the obligate chilling requirement reported earlier for 'G. Marconi' (Shedron and Weiler, 1982) is confirmed, but our data also indicates a need for a minimum of eight subsequent LD periods for maximum floral initiation.

Chrysanthemum ×superbum 'Snow Lady'. In this cultivar,

Fig. 2. 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.

nearly 100% of the plants flowered, and achieving reproductive status was dependent upon chilling and LIP treatments (Fig. 1B). The unchilled SD control plants flowered fastest from the time of seeding and were taller than all other plants except those grown in continuous LDs following chilling (data not shown). There was no significant linear or quadratic regression between LIP exposure and any characteristics measured.

In previous research, 'Snow Lady' flowered profusely (70% to 100% of the plants) with no prior chilling exposure when grown in LDs from the cotyledon stage or if given SDs followed by LDs (Damann and Lyons, 1995). The most rapid flowering from seeding occurred if plants were transferred to LDs at the cotyledon stage; however, plants in continuous SDs also flowered eventually. In the present experiment, unchilled plants flowered faster from seeding than those that received 4 months of natural chilling, indicating the lack of a chilling requirement for floral induction of 'Snow Lady'. This is also supported by the observation that an estimated 15 to 18 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 previously reported by Damann and Lyons (1995).

Coreopsis grandiflora 'Sunray'. In this cultivar, flowering ranged from 40% to 90% across LD treatment groups and occurred in only 20% of the unchilled and 40% of the chilled SD control

Fig. 3. The effects of a limited inductive photoperiod and chilling received by *Coreopsis grandiflora* 'Sunray' on the number of days to flower from start of long days (LDs). $y = 138.0 - 8.64x + 0.229x^2$, $R^2 = 0.31^{**}$; parabolic minimum point is 18 LDs, 57 days to flowering; area bound by dashed lines indicates a 95% confidence interval.

Fig. 4. 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.

plants (Fig. 1C). Achieving reproductive status was dependent on chilling as was also seen in the *Chrysanthemum ×superbum* cultivars. Floral buds did not abort except on the LIP treated plants where the LD exposure was very brief and on the chilled plants held in continuous SDs. Stem length at first flower was linearly related to the number of LDs received (Fig. 2). Stems of plants given only 6 LDs averaged <1 cm, whereas stems of plants that received 22 LDs averaged 11.5 cm. There was a quadratic relationship between number of LDs received (LIP) and number of days from start of LDs to first flower (Fig. 3). Plants given 22 LDs before transfer back to SDs flowered about 36 days sooner than those receiving only six LD cycles. The calculated parabolic vertex (minimum point) occurred at 18 LDs where flowering occurred in only 57 days. LD control plants averaged 50 days from the end of chilling to first flower, which was more than twice as rapid as the response for unchilled or chilled SD control plants (data not shown). The stem length of LD control plants averaged 16.3 cm, whereas chilled and unchilled SD control plants had stems measuring <1.5 cm. LD control plants were about twice the height of unchilled and chilled SD control plants (data not shown). Scape length, plant height, and axillary flower bud number followed no significant regression relationship with LIP.

Despite the indications that *Coreopsis grandiflora* 'Sunray' will not flower in continuous LDs, SDs followed by LDs, or continuous SDs (Damann and Lyons, 1993), *Coreopsis grandiflora* has historically been characterized as a short-long-day (SLD) plant, requiring a period of SDs followed by LDs for floral initiation to occur (Ketellapper and Barbaro, 1966; Metzger,

Fig. 5. The effects of a limited inductive photoperiod and chilling received by *Coreopsis lanceolata* 'Early Sunrise' on the number of days to flower from start of long days (LDs). $y = 77.4 - 2.64x + 0.0629x^2$, $R^2 = 0.42^{**}$; parabolic minimum point is 20 LDs, 50 days to flowering; area bound by dashed lines indicates a 95% confidence interval.

1988). In examining the flowering requirements of any reported SLD species, it is important to note that some SLD plants have interchangeable SD and chilling requirements (Chouard, 1960; Hillman, 1969). This was observed in seed-propagated *Coreopsis grandiflora* 'Single Mayfield Giant' (Ketellapper and Barbaro, 1966). A SLD photoperiod regime promoted only sparse flowering, but flowering was improved when SDs were replaced by chilling. In the present experiment, 4 months of natural chilling resulted in 40% to 90% flowering in 'Sunray' plants upon return to greenhouse conditions compared to 20% flowering in unchilled plants, thus confirming an obligate chilling requirement for this cultivar. However, unlike 'Single Mayfield Giant', SLDs failed to promote flowering in 'Sunray' (Damann and Lyons, 1993). Thus, 'Sunray' should more accurately be referred to as a chillable LD plant rather than a SLD plant. This also describes *Coreopsis grandiflora* 'Single Mayfield Giant' more accurately because flowering was enhanced when chilling replaced SDs (Ketellapper and Barbaro, 1966). The occurrence of flower-bud abortions (Fig. 1C) in 'Sunray' plants that received chilling followed by SDs or a brief LD exposure suggests that floral initiation occurred even when exposure to inductive conditions was <10 cycles; however, the stimulus needed to be continued for at least 10 cycles for anthesis to follow. It remains interesting to us, however, and presently unexplainable, why >10 LD cycles, in some cases, produced less flowering than 10 LD cycles (Fig. 1C). Although flower-bud abortion was not dependent on LIP in the other culti-

vars, it has been observed in the botanically unrelated *Eschscholzia californica* (Garrett, 1988).

Coreopsis lanceolata 'Early Sunrise'. All plants flowered when chilling was followed by LDs (Fig. 1D). Reproductive status was dependent on chilling and LIP treatments, with flower-bud abortions occurring only in plants that had never been chilled. A linear relationship was observed between LIP and stem length (Fig. 4), and a quadratic relationship between LIP and number of days to first flower from start of LDs (Fig. 5). Plants given 22 LDs flowered 14 days faster and had stems nearly 10 cm longer than plants that received only 6 LDs. The calculated parabolic minimum point indicated that plants given 20 LDs flowered fastest from start of LD treatments. There was no significant regression between LIP and scape length, plant height, or number of axillary flower buds. LD control plants averaged 44 days from chilling to first flower, whereas chilled and unchilled SD-control plants required about two and three times as many days to flower, respectively (data not shown). Chilled and unchilled SD control plants had shorter stems (1.7 and 1.9 cm, respectively) than plants that received 10 or more LD cycles before transfer back to SDs, whereas LD control plants had the longest stems (16.4 cm).

When propagated from seed, *Coreopsis lanceolata* 'Early Sunrise' differed from *Coreopsis grandiflora* 'Single Mayfield Giant' (Ketellapper and Barbaro, 1966) and 'Sunray' (Damann and Lyons, 1993) in that flowering was rapid and profuse (Fig. 1D) when grown under LDs. Damann and Lyons (1993) found that exposure to 8 LDs was sufficient to produce 100% flowering in unchilled 'Early Sunrise' plants. In the present experiment, chilling neither improved nor impeded flowering in this cultivar, but did affect flowering speed. In previous research, 'Early Sunrise' plants grown in SDs to maturity, then transferred to LD conditions, flowered about 91 days after onset of LDs (Damann and Lyons, 1993). In contrast, chilled plants maintained in continuous LDs flowered about 44 days after start of LDs in the present experiment.

The LD requirement for flowering in some *Spinacia* and *Trifolium* species can be modified or replaced by chilling (Chouard, 1960; Hillman, 1969). At first glance, this may appear to have happened in 'Sunray' and 'Early Sunrise' plants. Late, sporadic flowering occurred in unchilled and chilled SD controls. This delayed, sparse flowering in continuous SD conditions may have been a result of temperature rather than photoperiod. The obligate LD plant, *Rudbeckia hirta* L. (Murneek, 1940), flowered under artificially imposed SD conditions in response to excessive temperatures (32 to 38 °C). Occasional high temperatures (28 to 33 °C) in our greenhouses may have induced flowering among SD plants in this experiment as well.

Low temperatures can affect bolting and flowering separately. In *Scrofularia vernalis*, a cold treatment that was insufficient to stimulate bolting promoted flowering (Bernier et al., 1981). *Coreopsis grandiflora* 'Sunray' required chilling for flower initiation; however, stem elongation associated with flowering was controlled by the subsequent LDs, as evidenced by the effects of LIP. Allowing a plant only the minimum number of inductive LD cycles for floral initiation before transfer back to noninductive conditions inhibited plant height of *Eschscholzia californica* (Carter, 1986; Garrett, 1988), and *Rudbeckia hirta* (Orvos and Lyons, 1989). However, it had not been documented that LIP inhibits stem elongation of chilled plants. We observed that stems of chilled 'Early Sunrise' and 'Sunray' were about 10 cm shorter when given only 6 LDs compared to plants that received 22 LDs before being

transferred back to SDs. This is similar to the previously published reports for nonchilled 'Early Sunrise' (Damann and Lyons, 1993). However, the responsiveness of stem elongation to LIP was not universal even in chilled plants. Chilled *Chrysanthemum ×superbum* 'Snow Lady' and 'G. Marconi', although close relatives of *Coreopsis*, were not affected by LIP.

Chrysanthemum ×superbum and *Coreopsis* cultivars have potential for potted plant culture and increased bedding plant sales. Determining chilling requirements will facilitate scheduling of blooming. Specific chilling requirements vary for 'G. Marconi' and 'Sunray', but 'Snow Lady' and 'Early Sunrise' will flower in response to photoperiod without need for chilling. Use of appropriate LIP treatments inhibits stem elongation, thereby decreasing plant height and increasing consumer appeal, but flowering may be delayed when the number of inductive cycles is limited.

Literature Cited

- Bernier, G., J. Kinet, and R.M. Sachs. 1981. The physiology of flowering. vol. 2. CRC Press, Boca Raton, Fla.
- Carter, K.F. 1986. Description and control of flowering in California poppy (*Eschscholzia californica* Cham.). MS thesis, Virginia Polytechnic Institute and State Univ., Blacksburg.
- Chouard, P. 1960. Vernalization and its relations to dormancy. Annu. Rev. Plant Physiol. 11:191–237.
- Damann, M.P. and R.E. Lyons. 1993. Juvenility, flowering and the effects of a limited inductive photoperiod in *Coreopsis grandiflora* and *C. lanceolata*. J. Amer. Soc. Hort. Sci. 118:513–518.
- Damann, M.P. and R.E. Lyons. 1995. Juvenility and photoperiodic flowering requirements of *Chrysanthemum ×superbum* 'G. Marconi' and 'Snow Lady' under short- and long-day conditions. J. Amer. Soc. Hort. Sci. 120:241–245.
- Garrett, E.B. 1988. Height control of *Eschscholzia californica* using ancymidol, cycocel, and limited inductive photoperiod. MS thesis, Virginia Polytechnic Institute and State Univ., Blacksburg.
- Griffin, C.W. and W.J. Carpenter. 1964. Photoperiodic response of shasta daisy clones Esther Read and T.E. Killian. Proc. Amer. Soc. Hort. Sci. 85:591–593.
- Hillman, W.S. 1969. Photoperiodism and vernalization, p. 557–601. In: M.B. Wilkins (ed.). The physiology of plant growth and development. McGraw-Hill, London.
- Ketellapper, H.J. and A. Barbaro. 1966. The role of photoperiod, vernalization, and gibberellic acid in floral induction, in *Coreopsis grandiflora* Nutt. Phytol. 23:33–41.
- Laurie, A. and G.H. Poesch. 1932. Photoperiodism. The value of supplementary illumination and reduction of light on flowering plants in the greenhouse. Ohio Agr. Expt. Sta. Bul. 512:1–42.
- Metzger, J.D. 1988. Hormones and reproductive development, p. 431–443. In: P.J. Davies (ed.). Plant hormones and their role in plant growth and development. Kluwer Academic Pub., Dordrecht, The Netherlands.
- Murneek, A.E. 1936. A separation of certain types of responses of plants to photoperiod. Proc. Amer. Soc. Hort. Sci. 34:507–509.
- Murneek, A.E. 1940. Length of day and temperature effects in *Rudbeckia*. Bot. Gaz. 102:269–279.
- Orvos, A.R. and R.E. Lyons. 1989. Photoperiodic inhibition of stem elongation and flowering in *Rudbeckia hirta* 'Marmalade'. J. Amer. Soc. Hort. Sci. 114:219–222.
- Rees, P.K. and F.W. Sparks. 1969. Calculus with analytic geometry. McGraw-Hill, New York.
- SAS Institute. SAS/STAT user's guide. 1988. Release 6.03. SAS Inst., Cary, N.C.
- Shedron, K.G. and T.C. Weiler. 1982. Regulation of growth and flowering in *Chrysanthemum ×superbum* Bergmans. J. Amer. Soc. Hort. Sci. 107:874–877.