Growth and Development of *Oenothera fruticosa* Is Influenced by Vernalization Duration, Photoperiod, Forcing Temperature, and Plant Growth Regulators

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ABSTRACT. Influences of vernalization duration, photoperiod, forcing temperature, and plant growth regulators (PGRs) on growth and development of *Oenothera fruticosa* L. ‘Youngii-lapsley’ (‘Youngii-lapsley’ sundrops) were determined. Young plants were vernalized at 5 °C for 0, 3, 6, 9, 12, or 15 weeks under a 9-hour photoperiod and subsequently forced in a 20 °C greenhouse under a 16-hour photoperiod. Only one plant in 2 years flowered without vernalization, while all plants flowered after receiving a vernalization treatment, regardless of its duration. Thus, *O. fruticosa* had a nearly obligate vernalization requirement. Time to visible bud and flower decreased by ≈1 week as vernalization duration increased from 3 to 15 weeks. All plants flowered under 10-, 12-, 13-, 14-, 16-, or 24-hour photoperiods or a 4-hour night interruption (NI) in a 20 °C greenhouse following 15-weeks vernalization at 5 °C. Time to flower decreased by ≈2 weeks, flower number decreased, and plant height increased as photoperiod increased from 10 to 16 hours. Days to flower, number of new nodes, and flower number under 24 hour and NI were similar to that of plants grown under a 16-hour photoperiod. In a separate study, plants were vernalized for 15 weeks and then forced under a 16-h photoperiod at 15.2, 18.2, 20.6, 23.8, 26.8, or 29.8 °C (average daily temperatures). Plants flowered 35 days faster at 29.8 °C but were 18 cm shorter than those grown at 15.2 °C. In addition, plants grown at 29.8 °C produced only one-sixth the number of flowers (with diameters that were 3.0 cm smaller) than plants grown at 15.2 °C. Days to visible bud and flowering were converted to rates, and base temperature (T_b) and thermal time to flowering (degree-days) were calculated as 4.4 °C and 606 °days, respectively. Effects of foliar applications of ancymidol (100 mg·L⁻¹), chlormequat (1500 mg·L⁻¹), paclobutrazol (30 mg·L⁻¹), daminozide (5000 mg·L⁻¹), and uniconazole (15 mg·L⁻¹) were determined on plants vernalized for 19 weeks and then forced at 20 °C under a 16-h photoperiod. Three spray applications of uniconazole reduced plant height at first flower by 31% compared with that of nontreated controls. All other PGRs did not affect plant growth. Chemical names used: α -cyclopropyl- α -(4-methoxyphenyl)-5-pyrimidinemethanol (ancymidol); (2-chloroethyl) trimethylammonium chloride (chlormequat); butanedioic acid mono-(2,2-dimethyl hydrazide) (daminozide); (2*R*,3*R*+2*S*,3*S*)-1-(4-chlorophenyl-4,4-dimethyl-2-[1,2,4-triazol-1-yl]) (paclobutrazol); (*E*)-(*S*)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1,2,4-triazol-1-yl)-pent-1-ene-3-ol (uniconazole).

Many species of *Oenothera* L. have been cultivated since the early 1800s when they were brought from North and South America to England, where they became popular garden plants (Wiesner, 1991). *Oenothera fruticosa*, or sundrops, is native to eastern North America and hardy in USDA zones 4 through 8. It typically flowers in June (Griffiths, 1994; Nau, 1996) and spreads by underground lateral shoots that appear shortly after flowering. In a preliminary screen, the vegetatively propagated ‘Youngii-lapsley’ showed great potential as a potted flowering plant, with its relatively long natural flowering time of up to 4 weeks and numerous large bright-yellow flowers (Frane, 1999). To our knowledge, *O. fruticosa* is not grown currently as a flowering potted plant and there is no published information on flower-induction requirements.

Flowering of many herbaceous perennials is influenced by vernalization and photoperiod (Iversen and Weiler, 1994; Runkle et al., 1998; Whitman et al., 1996, 1997). Vernalization can be defined as the promotion of flower formation by a period of low temperatures, generally between –5 and 15 °C, with a broad optimum between 1 and 7 °C (Lang, 1965). In some species, a vernalization requirement can be linked to a subsequent photoperiod requirement (Vince-Prue, 1975). The role of vernalization and photoperiod in

flowering of various *Oenothera* species has been studied, and several different response types have been identified (Takimoto, 1985). Picard (1965) observed flowering of *O. biennis* var. *sulfurea* De Vries only after >10 weeks of treatment at 11 °C days/3 °C nights (D/N) followed by photoperiods ≥12 h. Many species of *Oenothera*, including *O. suaveolens* Pers., *O. longiflora* L., and *O. stricta* Lebed. ex Link, have facultative requirements for vernalization followed by an obligate requirement for long days (Chouard, 1960). *Oenothera rosea* L’Herit. ex Ait. is a facultative long-day plant with no response to vernalization (Chouard, 1960). In an initial screen, ‘Youngii-lapsley’ sundrops appeared to be a facultative long-day plant with an obligate vernalization requirement (Frane, 1999).

The effect of temperature on plant development rate is important to accurately time crop production, although to our knowledge there is no published timing information available for *O. fruticosa*. The relationship between temperature and rate of development toward flowering can be used to estimate the base temperature (T_b) and the number of units (degree-days) of thermal time above a base temperature required for flowering (Roberts and Summerfield, 1987).

Growing temperature can affect plant appearance as well as flower timing. For *Antirrhinum majus* L. ‘Jackpot’ (‘Jackpot’ snapdragon), there was a decrease in stem length, inflorescence length, and number of florets as temperature increased from 10 to 21 °C (Maginnes and Langhans, 1961). Flower size decreased with increasing temperature in *Galinsogaparviflora* Cavan., *Agrostemma githago* L. (Knapp, 1957); *Campanula carpatica* Jacq. ‘Blue Clips’ (Whitman et al., 1997), *Gaillardia × grandiflora* Van Houtte ‘Goblin’, *Leucanthemum × superbum* Bergman ex J. Ingram ‘Snowcap’ (‘Snowcap’ Shasta daisy), *Coreopsis grandiflora* Hogg ex Sweet

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‘Sunray’ (‘Sunray’ tickseed), and *Rudbeckia fulgida* Ait. ‘Goldsturm’ (Yuan et al., 1998).

A potential problem in growing *O. fruticosa* ‘Youngii-lapsley’ as a potted flowering plant is its relatively tall natural height (33 to 54 cm). Control of height by plant growth regulator (PGR) treatment may be required to produce high-quality potted plants. Although we have been unable to find any previous reports on the effect of PGRs on *O. fruticosa*, single applications of up to 3000 µg of chlormequat per pot to the root zone of chilled *O. biennis* plants reportedly had no effect on stem elongation or flowering (Pickard, 1967).

The objectives of this study were to determine and quantify the 1) vernalization and photoperiod requirements for growth and flowering, 2) effects of growing temperature on timing and flower quality, and 3) effect of five commercially available PGRs on plant height at first flower for *O. fruticosa* ‘Youngii-Lapsley’.

Materials and Methods

GENERAL. *Oenothera fruticosa* ‘Youngii-lapsley’ were received as rooted stem cuttings in 72-cell plug trays on 29 Oct. 1997 (Year 1) and 23 Sept. 1998 (Year 2) from the same commercial producer. Initial nodes were not counted in Year 1; in Year 2, the starting plants were uniform and averaged 18.0 ± 0.2 (SD) nodes. Plants were held in plug trays and exposed to natural day lengths (lat. 43 °N; ≈ 11 to 12 h) for 2 or 5 d (Year 1 or 2, respectively) until the experiments began. Vernalization treatments were provided to plants held in plug trays in controlled-environment coolers at 5 ± 0.2 °C with irradiation for 9 h·d⁻¹ from cool-white fluorescent lamps (F96T12/CW/VHO, Philips, Somerset, N.J.) at 10 to 20 µmol·m⁻²·s⁻¹ measured at canopy height using a quantum sensor (LI-189; LI-COR, Inc., Lincoln, Neb.). Plugs were watered as necessary (about two times per week) by using well water acidified to a pH of ≈ 6.0 with sulfuric acid (93% H₂SO₄).

Before placement in the greenhouses, plugs were transplanted into 13-cm square plastic pots (1.1-L volume) with a soilless medium containing sphagnum peat, composted pine bark, vermiculite, and perlite (Strong-Lite High Porosity Mix, Strong-Lite, Pine Bluff, Ark.). Pots were spaced at 22 plants/m². Plants were fertilized at every irrigation with a nutrient solution of well water [electrical conductivity (EC) of 0.70 dS·m⁻¹ and 105, 35, and 23 (mg·L⁻¹) Ca, Mg, and S, respectively] acidified with H₂SO₄ to a titratable CaCO₃ alkalinity of 130 mg·L⁻¹. When supplemented with water-soluble fertilizers, this regime provided 125, 12, 125, and 13 mg·L⁻¹ N, P, K, and Ca, respectively, with 30% ammoniacal N and minor elements. The target ranges for EC and pH were 0.5 to 1.2 dS·m⁻¹ and 5.8 to 6.2, respectively, using a 2 water : 1 medium test procedure. The second year, it was necessary to drench all plants transplanted after 1 Jan. 1999 twice with a soluble fertilizer containing N at 750 mg·L⁻¹ and KHCO₃ at 7.2 g·L⁻¹ to raise the pH and EC to the desired ranges.

GREENHOUSE TEMPERATURE CONTROL AND DAILY LIGHT INTEGRAL COLLECTION. Air temperatures were monitored on all benches in each greenhouse with 36-gauge (0.127-mm-diameter) thermocouples connected to a datalogger (CR 10; Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 10 s and recorded the hourly average. Average daily air temperatures (ADTs) from transplant to average date of flowering were calculated for every treatment in each experiment and were used in all analyses. Temperatures in each greenhouse were controlled by an environmental computer (model CD750; Priva, De Lier, The Netherlands).

Light was measured at canopy level by using a quantum sensor (model LI-189) connected to the datalogger. The datalogger collected light data every 10 s and recorded the hourly average. Average daily light integrals (DLI) were calculated from planting to first flower. Light data were collected only in Year 2 for the vernalization experiment.

VERNALIZATION DURATION (EXPT. 1). Plants in plug trays were vernalized at 5 °C for 0, 3, 6, 9, 12, or 15 weeks. Experiments were initiated 31 Oct. 1997 (Year 1) and 28 Sept. 1998 (Year 2). Ten plants were removed from the cooler after each vernalization duration, transplanted, and grown in a greenhouse under a 16-h photoperiod. Measured average daily air temperatures (Years 1 and 2) and average DLI (Year 2 only) from the date of transplant to the average date of flowering are given in Table 1 for each vernalization duration. Photoperiodic and supplemental lighting were provided daily by 400-W high-pressure sodium lamps (HPS) between 0800 and 0000 HR. The HPS lamps delivered a photosynthetic photon flux (PPF) of 50 µmol·m⁻²·s⁻¹ at plant height. The lamps stayed on until the outside PPF exceeded 400 µmol·m⁻²·s⁻¹. If the outside PPF then dropped below 200 µmol·m⁻²·s⁻¹, lamps were again turned on until 2200 HR.

PHOTOPERIOD (EXPT. 2). Seven photoperiods [10, 12, 13, 14, 16, and 24 h and a 4-h night interruption (NI)] and two vernalization treatments (0 or 15 weeks) were tested. No plants flowered without vernalization, and only data from after vernalization are presented. Plants were vernalized in plug trays at 5 ± 0.2 °C as described above. Vernalized plants were transplanted on 18 Feb. 1998 (Year 1) and 12 Jan. 1999 (Year 2) and placed in a greenhouse under each of the seven photoperiod treatments. Photoperiods were assigned randomly each year to greenhouse benches. Actual average daily air temperatures from the date of transplant to the average date of flowering for both years are given in Table 2 for each photoperiod. Each year, there were 10 plants per photoperiod treatment.

Opaque blackcloth was pulled at 1700 HR and opened at 0800 HR every day on all benches so all plants under each photoperiodic treatment received a similar DLI. Starting at 1700 HR, photoperiods were delivered by day-extension lighting with incandescent lamps that were turned off after each photoperiod was completed. The 4-h NI was provided by incandescent lamps that were turned on at 2200 HR and off at 0200 HR. Day-extension and NI lighting with

Table 1. Average daily air temperatures and daily light integrals from date of transplant to average date of flowering for *Oenothera fruticosa* ‘Youngii-lapsley’ after each vernalization duration. Light data measurements were made only in 1998–99.

Year	Vernalization duration at 5 °C (weeks)					
	0	3	6	9	12	15
	Avg air temp during forcing (°C)					
1997–98	19.9	20.0	19.7	19.7	19.9	20.2
1998–99	---	21.1	20.9	20.1	20.3	20.8
	Avg daily light integral (mol·m ⁻² ·d ⁻¹)					
1998–99	---	12.6	11.2	10.6	10.6	11.6

---No plants flowered.

Table 2. Average daily air temperatures from date of transplant to average date of flowering for *Oenothera fruticosa* 'Youngii-lapsley' under each photoperiod. Temperature and light were monitored on each bench every 10 s during the growing period.

Year	Vernalization duration at 5 °C (weeks)	Photoperiod (h)						NI ²
		10	12	13	14	16	24	
		Avg air temp during forcing (°C)						
1997–98	15	21.1	20.8	20.6	21.9	21.8	21.1	21.1
1998–99	15	21.0	20.8	20.7	20.9	20.6	21.1	21.2

²9-h photoperiod plus 4-h night interruption (NI).

incandescent lamps provided 1 to 3 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at canopy level. Supplemental lighting was provided by HPS lamps that delivered $\approx 50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at canopy level between 0800 HR and 1700 HR.

FORCING TEMPERATURE (EXPT. 3). Starting 28 Sept. 1998, plants in plug trays were vernalized at 5 °C, as described above for 15 weeks until 12 Jan. 1999, when they were transplanted. At transplant, plants averaged 19.4 leaves. Ten plants were placed into each of six greenhouses set to 14, 17, 20, 23, 26, or 29 °C. Measured ADTs from transplant to visible bud and from visible bud to flower were similar and averaged 15.2, 18.2, 20.6, 23.6, 26.8, and 29.8 °C. Temperatures were carefully controlled; the greatest difference between ADT during days to visible bud and days from visible bud to flower at any temperature setting was 0.4 °C. From 0800 to 0000 HR each day, continual 16-h photoperiod was delivered by HPS lamps that provided $\approx 90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height.

PLANT GROWTH REGULATORS (EXPT. 4). Five commercially available plant growth regulators (PGRs) were tested for their ability to control plant height. The PGRs and rates tested included ancymidol at 100 $\text{mg}\cdot\text{L}^{-1}$ (Sepro, Carmel, Ind.), chlormequat at 1500 $\text{mg}\cdot\text{L}^{-1}$ (American Cyanamid Co., Wayne, N.J.), daminozide at 5000 $\text{mg}\cdot\text{L}^{-1}$ (Uniroyal, Middlebury, Conn.), paclobutrazol at 30 $\text{mg}\cdot\text{L}^{-1}$ (Uniroyal, Middlebury, Conn.), and uniconazole at 15 $\text{mg}\cdot\text{L}^{-1}$ (Valent, Walnut Creek, Calif.). Plants were given a 19-week vernalization treatment at 5 °C and on 6 Feb. 1999 were transplanted into 1.1-L containers and placed in a greenhouse set at 20 °C. A 16-h photoperiod was provided by HPS lamps, as described for Expt. 1. The actual daily average air temperature between transplant and average date of flowering was 20.6 °C, and the average daily light integral from transplant to first open flower was 14.9 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Plants were allowed to establish for 10 d before the first PGR spray. For each growth retardant, eight plants were sprayed until the solution dripped off the leaves ($\approx 3 \text{ mL}$ per plant). Following the first spray, plants were sprayed every 10 d until the first flower opened. In total, each PGR was applied to a plant three times. Eight plants were not sprayed with any chemical and served as the control.

DATA COLLECTION AND ANALYSIS. The data collected for all experiments included date of first visible flower bud (without dissection) and date of first open flower. Days to visible bud, days to flower, and days from visible bud to flower were calculated for each plant in all experiments. At first open flower, plant height (excluding the container) and number of visible flowers and buds were recorded. In Year 2, both the initial number of nodes and final number of nodes (counted to the last visible leaf) were recorded. The number of new nodes produced during forcing was calculated by subtracting the initial number of leaves from the final number of leaves. The number of lateral shoots and flowering lateral shoots was recorded for Expts. 1 and 2 in Year 2 only. Flower diameter was recorded for Expts. 3 and 4. For all experiments, plants that did not have visible buds after 15 weeks of forcing were considered nonflowering and were discarded. The few plants that died during

the experiment were discarded and not included in the results or calculations.

All experiments were completely randomized designs. Data were analyzed by using the general linear models procedure (SAS Inst., Cary, N.C.) for analysis of variance and linear regression procedure for regression models. Duncan's multiple range test was used to analyze the PGR experiment (Expt. 4) because of the discontinuous nature of the treatments. The vernalization duration and photoperiod experiments (Expts. 1 and 2, respectively) were replicated in time and the years were used as replications.

Results and Discussion

VERNALIZATION DURATION (EXPT. 1). Horticulturally, *O. fruticosa* 'Youngii-lapsley' had an obligate vernalization requirement. Without a vernalization treatment, only one out of 10 plants flowered in Year 1 and no plants flowered in Year 2 (Fig. 1A). This single plant was the only one that flowered without vernalization in any of our experiments (one out of 180 plants tested without vernalization), and its flowering behavior was quite different from that of all other plants examined. It flowered 42 to 54 d slower (Fig. 1B), produced 47 to 55 more nodes (data not shown), was 23 to 34 cm shorter (Fig. 1D), and produced $\approx 25\%$ the number of flowers that other plants did for Year 1 (Fig. 1A). When grown outdoors, lateral shoots of *O. fruticosa* 'Youngii-lapsley' occasionally formed flowers in August in large plantings (personal observations). Thus, botanically, the vernalization requirement is nearly but not completely obligate.

Three weeks was adequate to fulfill the vernalization requirement for *O. fruticosa* 'Youngii-lapsley'. As vernalization duration increased from 3 to 15 weeks, there was only a half-day decrease in time to visible bud and flower for every subsequent week of vernalization (Fig. 1B). It took 19 d to go from visible bud to open flower, and this time was not affected by the vernalization duration (Fig. 1B). The number of new nodes produced during forcing decreased linearly at less than one node per week with increasing vernalization duration (Fig. 1C). This result correlated with the small decrease in time to flower ($r^2 = 0.37$; $P \leq 0.01$). Plant height increased with vernalization durations up to 9 weeks but decreased after longer vernalization durations (Fig. 1D). Plants in Year 2 were 11 cm shorter than those grown in Year 1 over all vernalization durations. All vernalized plants, independent of duration, produced ≈ 10 lateral branches, and 65% of these lateral branches formed flowers. The number of flowers and buds counted at first open flower increased linearly with vernalization duration, with about six more flowers for every additional week of vernalization (Fig. 1E).

PHOTOPERIOD (EXPT. 2). *Oenothera fruticosa* 'Youngii-Lapsley' can be classified as a facultative long-day plant. After a 15-week vernalization period, all plants flowered under all photoperiods. Days to flower and to visible bud decreased linearly as photoperiod increased from 10 to 16 h, but there was no further change as

Fig. 1. Regrowth and flowering of *Oenothera fruticosa* 'Youngii-lapsley' in response to increasing vernalization duration at 5 °C (Expt. 1). Squares and triangles represent data from Year 1 and Year 2, respectively. In B, open symbols denote days to flower (DTF); closed symbols, days to visible bud (DTVB). Data presented in C, D, and E were collected when the first flower opened on each plant. Except for 0 weeks vernalization, each symbol is based on 10 observations. Vertical bars represent 95% confidence intervals, and, when smaller than symbols, are not shown. Regression analysis did not include data from 0 weeks vernalization. Q^* = quadratic trend significant at $P \leq 0.05$.

Fig. 2. Regrowth and flowering of *Oenothera fruticosa* 'Youngii-lapsley' to various photoperiods after 15 weeks of vernalization at 5 °C (Expt. 2). Squares and triangles represent data from Year 1 and Year 2, respectively. In A, upper graph is days to flower (DTF); lower graph is days to visible bud (DTVB). Solid circles in E are the average of Year 1 and Year 2. Continual photoperiod treatments consisted of 9-h natural days extended with light from incandescent lamps. NI = 4-h night interruption. Data presented in B, C, D, and E were collected when the first flower opened on each plant. Each symbol is based on 10 observations. Vertical bars represent 95% confidence intervals, and, when smaller than symbols, are not shown. Q^{***} = quadratic trend significant at $P \leq 0.001$.

Fig. 3. Effects of growing temperature on (A) time from transplant to visible bud, (B) visible bud to flower, and (C) transplant to flower, and (D) rate of progress toward visible bud, (E) visible bud to flower, and (F) to flower in *Oenothera fruticosa* 'Youngii-lapsley' (Expt. 3). Each symbol is based on 10 observations. Vertical bars represent 95% confidence intervals, and, when smaller than symbols, are not shown. Parameters of linear regression lines are presented in Table 3. The quadratic regression lines in A, B, and C are the reciprocals of correlated linear regression lines in D, E, and F.

photoperiod increased from 16 to 24 h (Fig. 2A). Days to flower was 40 under NI, a duration similar to that of plants grown under 16-h photoperiods. The time from visible bud to flower was 18 to 20 d and was unaffected by photoperiod. The number of new nodes produced during forcing decreased linearly from 42 to 27 as photoperiod increased from 10 to 16 h (Fig. 2B) and was closely correlated with the observed decrease in time to flower ($P = 0.003$).

The number of flowers and buds at first flower decreased markedly as photoperiod increased from 10 to 16 h (Fig. 2C). There were no difference between number of flowers and buds at 16 h and 24 h. Plants grown under 10-h photoperiods had over 100 flowers per plant. Under 4-h NI, there were ≈ 50 flowers per plant, a number similar to that of plants grown under 16-h photoperiods.

The number of total lateral shoots decreased with increasing photoperiod (Fig. 2D). About 60% of the lateral shoots flowered independent of photoperiod (data not shown). The change in the number of lateral shoots under the different photoperiods had a marked effect on plant appearance. Plants grown under photoperiods ≤ 14 h were leafy and had abundant flowers, while those grown under photoperiods ≥ 14 h were spindly and had sparse flowers.

Table 3. Parameters of linear regression analysis relating forcing temperature to rate of progress from transplant to visible bud (VB), visible bud to flowering (VB to FLW), and transplant to flowering (FLW) for *Oenothera fruticosa* 'Youngii-lapsley'; intercept and slope were used to calculate base temperature (T_b) and degree-days.

Developmental stage (d)	Intercept (b_0) 1/d	Slope (b_1) (1/d)/°C	T_b (°C)	Degree-days	r^2
Transplant to VB	$-3.56E-3 \pm 7.99E-3^2$	$2.45E-3 \pm 3.49E-4$	1.5	408	0.91**
VB to FLW	$-3.42E-2 \pm 1.56E-3$	$4.72E-3 \pm 6.77E-5$	7.3	211	0.99***
Transplant to FLW	$-7.21E-3 \pm 2.75E-3$	$1.65E-3 \pm 1.20E-4$	4.4	606	0.97***

²Standard error.

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

Measured at first open flower, plants were consistently tallest at 14-h, 24-h, and NI (Fig. 2E), though the absolute differences in height were small. Under NI, height was generally similar to that of plants grown under 14- and 24-h photoperiods. There was no correlation between the number of new nodes and plant height (Fig. 2B and E).

FORCING TEMPERATURE (EXPT. 3). Days to visible bud, days from visible bud to flower, and days to flower decreased as ADT increased (Fig. 3A–C). The plants flowered uniformly and variability for time to visible bud and to flower was fewer than 4 d at each temperature. An increase from 15.2 to 20.6 °C accelerated flowering more than an increase from 20.6 to 29.8 °C. For example, time to flower decreased by 24 d (from 60 to 36 d) as temperature increased 5.4 °C (from 15.2 to 20.6 °C), but only by 11 d (from 36 to 25) when temperature increased 9.2 °C (from

20.6 to 29.8 °C).

The rate of progress toward visible bud, from visible bud to flowering, and to flowering was highly correlated with temperature (Table 3; Fig. 3D–F). Base temperatures for each developmental stage ranged from 1.5 to 7.3 °C (Table 3). *Oenothera fruticosa* required 606 degree-days to flower. The days required to complete a developmental stage can be calculated as degree-days/($T_a - T_b$). Differences between predicted and observed time for any developmental stage and temperature were no greater than 5 d (data not shown).

The number of flowers and buds per plant decreased linearly from over 170 to fewer than 30 as temperature increased from 15.2 to 29.8 °C, an average reduction of nine flowers for every 1 °C increase (Fig. 4A). Flower diameter decreased from 7 to 4 cm as temperature increased (Fig. 4B), a threefold difference in flower area (assuming that flower shape is circular). Taken together, there was a ≈ 20 -fold reduction in flower area per plant when growing temperature was increased from 15.2 to 29.8 °C. Increasing temperature resulted in reduced flower size of *Coreopsis grandiflora* Hogg ex Sweet. 'Sunray', *Leucanthemum x superbum* Bergman ex J. Ingram 'Snowcap', *Rudbeckia fulgida* Ait. 'Goldsturm' (Yuan et al., 1998), *Campanula carpatica* 'Blue Clips' (Whitman et al., 1997), *Coreopsis verticillata* L. 'Moonbeam', *Campanula* 'Birch Hybrid', and other herbaceous perennials (Frane, 1999).

Height at first flower was 35% shorter as temperature increased from 15.2 to 23.8 °C (Fig. 4C). As forcing temperature increased from 23.8 to 29.8 °C, there was almost no further change in plant height.

PLANT GROWTH REGULATORS (EXPT. 4). Uniconazole reduced plant height at flower by 31% compared to the nontreated controls. No other PGR reduced plant height in these experiments. Days to visible bud, days to flower, number of new leaves, or number of flowers was not affected by plant growth regulator application (data not shown). However, flower diameter on plants sprayed with uniconazole was 36% smaller than that of the controls, which resulted in a 58% flower area reduction. Although daminozide and chlormequat did not reduce plant height, plants sprayed with these PGRs as well as uniconazole had shorter lateral stems compared with that of control plants. The shorter stems changed the plants' natural conical shape to a cylindrical one. Further studies using different rates and application strategy of uniconazole and perhaps other PGRs individually or in combination are needed to identify PGRs and rates that effectively control height without such a drastic reduction in flower size and change in plant shape.

Flower production was influenced strongly by relatively small increases in light levels. For example, plants vernalized for 15 weeks and grown under natural light with a 16-h photoperiod and supplemental light provided by HPS lamps (Expt. 1) produced 97 flowers, while those in Expt. 2, also vernalized for 15 weeks and provided a 16-h photoperiod with day extension from incandescent lamps, produced only 47 flowers (Year 2). Plants received an estimated 9.0 or 11.6 mol·m⁻²·d⁻¹ of total PAR when given day extension with incandescent lamps or HPS lamps, respectively. Increasing irradiance increased flower number in a number of herbaceous perennial

species (Cameron et al., unpublished). For *Dendranthema ×grandiflorum* Kitam. 'Resilience' ('Resilience' chrysanthemum) grown under a 12-h day, flower number increased from 7.2 to 19.0 as daily light integral increased from 10.4 to 29.9 mol·m⁻²·d⁻¹ (Warrington and Norton, 1991). Total flower area per plant was found to increase also for *D. ×grandiflorum* 'Bright Golden Anne' as PPF increased (Karlsson and Heins, 1986).

Oenothera fruticosa 'Youngii-lapsley' performed well indoors in preliminary postharvest trials, and floral display was acceptable for 20 d. Although each flower lasted only 2 to 3 d, new flowers opened even under low interior light. After interior evaluation, the same plants were planted outdoors in a trial garden and have overwintered with no losses and flowered well (data not shown).

In summary, *Oenothera fruticosa* 'Youngii-lapsley' has great potential as a potted flowering ornamental plant. Horticulturally, it is a facultative long-day plant with an obligate vernalization requirement, the only *Oenothera* reported to have this combination of requirements. Flowering occurred consistently after a minimum 3-week vernalization treatment, delivered to 18-node plants in plugs trays followed by any photoperiod ≥10 h. *Oenothera fruticosa* 'Youngii-lapsley' flowered under all tested photoperiods, but flowering was accelerated by ≈2 weeks under the longer photoperiods. Though slower to flower, plants were most attractive and better suited as potted plants when grown under photoperiods ≤14 h with ample light because of the higher numbers of vegetative and flowering lateral shoots. For forcing plants, an ADT between 17 and 20 °C is probably optimal to reduce production time with a minimal in quality reduction. Plants will be ready to market in 50 to 60 d by using these production conditions. Uniconazole at 15 mg·L⁻¹ can be used to reduce plant height ≈30% but also will decrease flower diameter by 36%. A production protocol has been developed for *O. fruticosa* 'Youngii-lapsley' based largely on the results of this study (Clough et al., 1999).

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Fig. 4. Effects of forcing temperature on (A) number of flowers and buds, (B) flower diameter, and (C) plant height in *Oenothera fruticosa* 'Youngii-lapsley' (Expt. 3). All parameters were measured when the first flower opened. Each symbol is based on 10 observations. Vertical bars represent 95% confidence intervals, and, when smaller than symbols, are not shown. Q*** = quadratic trend significant at 0.001.