Research Reports

Environmental Control of Flowering in Pennsylvania Sedge

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SUMMARY. Pennsylvania sedge (*Carex pensylvanica*) is an upland forest sedge with restoration and horticultural potential as a low-maintenance groundcover for dry shade. For large landscape and restoration plantings, seed or achenes in this case are much preferred due to lower labor and material costs. However, pennsylvania sedge typically produces few achenes in its native habitat. As a first step in improving achene production, this research evaluated the effect of vernalization and photoperiod on floral initiation and development. We conclude that this sedge is an obligate short-day plant that does not require vernalization for flowering. Plants flowered when exposed to daylengths of 6 to 12 hours. Flowering was completely inhibited with 14-hour photoperiods. Pennsylvania sedge was florally determined after 4 weeks of 8-hour photoperiods. Inflorescence quantity and normal floral development varied by clone and by weeks of exposure to 8-hour photoperiods. For two of the clones, the largest number of normal monoecious inflorescences was produced with 8 to 10 weeks of 8-hour photoperiods while the other two clones only required 6 to 8 weeks of exposure to inductive photoperiods. Therefore, it is important to evaluate observable variation between clones when attempting to propagate pennsylvania sedge.

Pennsylvania sedge, a native of dry to mesic forests and savannas in the eastern half of Canada and the United States (Gleason and Cronquist, 1991), has both forest restoration and horticultural utility. This strongly rhizomatous species forms grass-like colonies (Curtis, 2006) that are suitable as a native groundcover (Meyer, 2004). Pennsylvania sedge is used for temperate forest restoration particularly in highly disturbed areas (Mottl et al., 2006). When planted densely in a managed landscape, it acts as a low-maintenance groundcover that thrives in dry shade where grasses do not usually flourish (McGinnis and Meyer, 2011) and tolerates mowing (Darke, 2004). Thus, this attractive sedge fills a much-needed niche for

shade-loving, grass-like plants. For large landscaping projects, it would be advantageous to directly sow cold-stratified or after-ripened achenes (McGinnis and Meyer, 2011) instead of using vegetative propagules. Pennsylvania sedge normally flowers in April in the northern United States (Hipp, 2008) but typically produces few achenes in its native habitat (Curtis, 2006) although it is reported to be self-compatible (Friedman and Barrett, 2009). As a first step in improving achene production, the environmental factors influencing floral initiation and development were studied.

The ability to manipulate flowering is a first step in developing commercial seed production protocols. Temperature and photoperiod are

two of the most important environmental factors in controlling flowering (Sung and Amasino, 2004). Vernalization is defined as the application of a cold treatment to a growing plant to promote flowering (Chouard, 1960; Taiz and Zeiger, 2006). By itself, vernalization does not result in floral initiation, but rather removes an impediment to flowering (Gendall and Simpson, 2006). The optimum vernalization temperature for a broad range of plants lies between 1 and 7 °C (Lang, 1965). In temperate zones, spring flowering, herbaceous perennials such as cushion spurge (*Euphorbia epithymoides*), evergreen candytuft (*Iberis sempervirens* 'Snowflake'), and columbine (*Aquilegia ×hybrida*) are more likely to require vernalization (Heins et al., 1997).

Many plants flower in response to a specific photoperiod (Garner and Allard, 1920). Photoperiods fall into five categories, but the first three are the most prevalent categories: short-day, long-day, day-neutral, intermediate-day, and amphiphotoperiodic-day plants (Thomas and Vince-Prue, 1997). Some plants require vernalization followed by long days to flower (Erwin, 2006).

Floral initiation and development in sedges (*Carex* sp.) has been studied predominantly in northern European species. Twocolor sedge (*Carex bicolor*) was determined to flower under long days, while both smooth black sedge (*C. nigra*) and silvery sedge (*C. canescens*) required short days for floral initiation followed by long days for optimal floral development (Heide, 1997, 2002). In other species such as star sedge (*C. echinata*), twotipped sedge (*C. lachenalii*), yellow sedge (*C. flava*), brownish sedge (*C. brunnescens*), lesser blackscale sedge (*C. atrata*), norway sedge (*C. norvegica*), and little green sedge (*C. viridula* ssp. *viridula*), vernalization and short-day photoperiods were interchangeable in promoting floral initiation (Heide, 1997, 2002, 2004). The Arctic species, bigelow's sedge (*C. bigelowii*), required a more complex sequence of short days for floral initiation, a subsequent chilling treatment at 6 °C, and exposure to long days at 18 °C for optimum inflorescence heading and development (Heide, 1992). Pennsylvania sedge is a member of *Carex* section *Acrocystis*, which is a section composed of sedges native to dry forests (Crins and Rettig,

2003). This is the first known report of flowering regulation in *Acrocystis*.

The objective of this research was to identify the environmental factors that regulate flowering in pennsylvania sedge. We sought to determine whether this species requires vernalization, flowers in response to short- or long-day photoperiods, or requires a combination of vernalization and a specific photoperiod. In addition, we wanted to determine the critical photoperiod and the optimum number of weeks of inductive photoperiods for floral determination as well as to assess observable variation between clonal selections.

Materials and methods

VERNALIZATION AND PHOTOPERIOD REQUIREMENTS. On 2 July 2009, 20 plants were dug from a mixed seedling population (achene sources described in McGinnis and Meyer, 2011) maintained at the University of Minnesota Landscape Arboretum, Chaska, MN. Plants were not flowering and no floral primordia were observed upon close inspection of the crown. The plants were divided into 80 uniform divisions with ≈ 10 mature vegetative culms per division and the plants were randomized. Foliage was cut back to 6 cm and plants were transplanted into 16-fl oz square pots (4 inches diameter, 4 inches tall) containing Sunshine SB500 High Porosity Bark Mix (Sun Gro Horticulture, Seba Beach, AB, Canada). For 2 weeks, the plants were allowed to establish in a greenhouse with 22/18 °C (day/night) air temperature set-points and supplemental lighting from high-pressure sodium lamps was

provided to extend the photoperiod to 16-h days. Plants were moved to four growth chambers (Environmental Growth Chambers, Chagrin Falls, OH) for sequential vernalization and photoperiod treatments. In total, there were eight treatment combinations. Half of the plants were exposed to vernalizing temperatures of 5 °C for 12 weeks under either 16-h (long-day) or 8-h (short-day) photoperiods. The remainder of the plants was exposed to 12 weeks of nonvernalizing temperatures of 22 °C and either short-day or long-day photoperiods. After the initial 12-week treatment, plants were held for an additional 8 weeks under either short-day or long-day photoperiods at 22 °C (Table 1). In all growth chambers, plants were subjected to combined fluorescent (model F72T12/CW/VHO; Philips Lighting Co., Somerset, NJ) and incandescent lights (model 25A/IF, Philips Lighting Co.) at irradiance levels of 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height and with a combined red to far red ratio of $\approx 3:1$. The relative humidity (RH) was 50%. All plants were watered as necessary and fertilized with water-soluble 20N-4.4P-16.6K (Peters Professional Peat-Lite Special 20-10-20; Scotts-Sierra Horticultural Products Co., Marysville, OH) at the rate of 200 ppm nitrogen (N) every week throughout the experiment. Ten plants ($n = 10$) were randomly assigned to each of the eight treatment combinations. Three replications in total were conducted with start dates staggered at 2-week intervals for a total of 240 plants. Data from all replications were pooled for analysis. Percent flowering and days to first pollen shed were measured. Pennsylvania sedge produces multiple inflorescences per plant. Each inflorescence is monoecious and produces a terminal, male spike and one or more subordinate female spikes. Days to first pollen shed were recorded for the first flowering inflorescence on each plant. Plants were counted as having flowered if they produced one or more inflorescences.

CRITICAL PHOTOPERIOD FOR FLORAL INITIATION. Pennsylvania sedge cultivars were not available, so achenes were collected and germinated in 2010 from the above-described mixed seedling population maintained at the University of Minnesota Landscape Arboretum. Four seedlings were selected based on vigor and vegetatively propagated to serve as individual clones. The clonal selections were identified as MN101B, MN102O, MN103P, and MN104R and were grown as stock plants under a 16-h photoperiod with temperature setpoints as described above.

Two weeks before the commencement of the experiment, stock plants were divided on 9 July 2010 to produce uniformly sized plants with ≈ 10 mature vegetative culms. Divisions were cut back to 6 cm and transplanted into 24-fl oz square pots (3.5 inches diameter, 5 inches tall) containing Sunshine SB500 High Porosity Bark Mix. Plants from each of the four clones were exposed to one of five photoperiods: 6-, 8-, 10-, 12-, or 14-h photoperiods for 10 weeks in five growth chambers with both fluorescent and incandescent lights as described above. Higher irradiance and fertilizer levels were used in this experiment and the subsequent one in an attempt to speed floral initiation. All plants were subjected to irradiance levels of 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, a temperature of 22 °C, and 50% RH. The irrigation and fertilizer schedule were as outlined previously except that plants were irrigated with 300 ppm N from water-soluble 20N-4.4P-16.6K (Peters Professional Peat-Lite Special 20-10-20).

Two plants ($n = 2$) from each of the four clones were randomly assigned to each of the five photoperiod treatments for a total of 40 plants per replication. The experiment was replicated three times at 2-week intervals for a total of 120 plants. Data from all replications were pooled for analysis. Data collected included days to visible bud, days to first pollen shed, and number of inflorescences per plant. Days to visible bud

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Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
29.5735	fl oz	mL	0.0338
2.54	inch(es)	cm	0.3937
1	ppm	mg·L ⁻¹	1
(°F - 32) ÷ 1.8	°F	°C	(°C × 1.8) + 32

Table 1. Temperature and photoperiod treatments affect flowering and average number of days to first flower in pennsylvania sedge. Back transformed confidence intervals are shown in parentheses.

Treatment combinations ^a	Avg flowering (%)	Avg time to first flower (d)
Non-vern LD-SD	0.0 b ^y	NA ^x
Non-vern LD-LD	0.0 b	NA
Non-vern SD-SD	86 (97, 70) a	92.7 (95.1, 90.4) a
Non-vern SD-LD	83 (96, 65) a	94.6 (96.7, 92.6) a
Vern LD-SD	1.1 (4.5, 0.0) b	140 (140, 140) b
Vern LD-LD	0.0 b	NA
Vern SD-SD	5.1 (19, 0.0) b	138 (160, 119) b
Vern SD-LD	0.0 b	NA
P value	$P < 0.001$	$P < 0.001$

^aDuring the first 12 weeks, plants were subjected to either non-vernalizing (non-vern) temperatures [22 °C (71.6 °F)] or vernalizing (vern) temperatures [5 °C (41.0 °F)]. All plants were exposed to 22 °C temperatures during the final 8-week treatment. SD denotes 8-h short-day photoperiods and LD denotes 16-h long-day photoperiods. Plants were exposed to the first listed photoperiod during the initial 12-week treatment and plants were exposed to the second listed photoperiod during the final 8-week treatment.

^yWithin column values followed by different letters are significantly different under Tukey's honestly significant difference test at $P < 0.05$ ($n = 10$ plants, three replications).

^xPlants marked with NA did not flower; therefore, average days to first flower could not be calculated.

and days to first pollen shed were recorded for the first inflorescence on each plant.

MINIMUM WEEKS OF INDUCTIVE TREATMENTS NECESSARY FOR FLORAL DETERMINATION. The four clones were divided and transplanted as described above beginning on 9 Dec. 2010. After allowing plants to establish in the greenhouse for 2 weeks under a 16-h photoperiod (temperature setpoints described above), all plants were placed in a growth chamber under an 8-h short-day photoperiod for 0, 2, 4, 6, 8, or 10 weeks. Irradiance, temperature, RH, and fertilizer levels were consistent with the previous experiment. After exposure to 0, 2, 4, 6, 8, or 10 weeks of short-day photoperiods, plants were transferred to a growth chamber programmed with a 16-h photoperiod (all other parameters being identical) for the remainder of the 10 weeks. After 10 weeks, all plants were returned to the greenhouse for an additional 4 weeks with a 16-h photoperiod. Three plants ($n = 3$) from each of the four clones were randomly assigned to each of the six photoperiod treatments for a total of 72 plants per replication. The experiment was replicated in time two additional times at 2-week intervals for a total of 216 plants. Data from all three replications were pooled for analysis. Data collected included days to visible bud, days to first pollen shed, and number of inflorescences at 14 weeks.

STATISTICAL ANALYSIS. Data were evaluated using analysis of variance (R Development Core Team, 2011). In all experiments, the percent flowering

data were transformed using an arcsin, square root transformation because of the binomial distribution (Snedecor and Cochran, 1989). These data were then backtransformed and reported as percentages. Multiple mean comparisons were conducted using Tukey's honestly significant difference test. Means were considered significant at the $P < 0.05$ level.

Results and discussion

VERNALIZATION AND PHOTOPERIOD REQUIREMENTS. Vernalization and photoperiod treatments influenced pennsylvania sedge percent flowering [$P < 0.001$ (Table 1)]. Plants failed to flower after 12 weeks of vernalization at 5 °C, when followed by 8 weeks of long-day photoperiods at 22 °C. Of the four vernalization treatments, flowering percentages ranged from 0% to 5.1% (Table 1). In direct contrast to vernalization treatments, nonvernalized plants that were exposed to short-day conditions during the initial 12 weeks of the experiment flowered at the rate of 86% and 83% (Table 1). No plants flowered when exposed to 20 consecutive weeks of long-day photoperiods (Table 1) regardless of vernalization.

The average days to first flower were influenced by temperature and photoperiod treatments ($P < 0.001$, Table 1). For plants initially exposed to 12 weeks of short-day photoperiods and nonvernalizing temperatures, the average number of days to first flower was 92.7 and 94.6 d (Table 1). The photoperiod following 12 weeks of short days did not affect either

flowering percentage or average days to first flower because the plants were already florally determined during the initial 12 weeks. In contrast, the average number of days to first flower for vernalized plants that were subsequently exposed to short-day conditions was 138 to 140 d (Table 1).

It is likely that plants first exposed to either 12 weeks of vernalizing temperatures or long-day photoperiods would have subsequently flowered under short-day conditions if given sufficient time. However, the experiment ended at 20 weeks. Short days initiated flowering in pennsylvania sedge, but the plants required on average more than 90 d to flower at 22 °C under the conditions described in Expt. 1.

The failure of vernalization treatments to promote flowering within the 20-week experiment was unexpected. Many early spring flowering herbaceous plants require or benefit from vernalization (Padhye et al., 2006). Vernalization allowed other sedges such as brownish sedge, lesser black scale sedge, norway sedge, and little green sedge to flower under both long and short photoperiods (Heide, 1997). The shoot apical meristem in pennsylvania sedge apparently is competent to produce floral primordia and does not require vernalization to remove an impediment to floral initiation.

Based upon these results, we conclude pennsylvania sedge is an obligate short-day plant that will not flower under continuous long-day photoperiods. This photoperiodic requirement is similar to smooth black sedge and silvery sedge (Heide, 1997, 2002). In hindsight, it is not surprising that pennsylvania sedge is a short-day plant based upon the timing of flowering in the northern United States. In the wild, the plant flowers in April in the northern United States (Hipp, 2008). It is one of the earliest woodland plants to flower in spring and has earned the nickname, early sedge. Pennsylvania sedge most likely is initiated and florally determined in the fall similar to hairy sedge [*C. lacustris* (Bernard, 1974)] and then completes floral development in early spring when the snow melts.

Although pennsylvania sedge was shown to be an obligate short-day plant in this study, 14% to 17% of the plants failed to flower when exposed to 12 weeks of short-day

photoperiods, and we conclude that this is likely due to observable variation or poor vigor.

CRITICAL PHOTOPERIOD FOR FLORAL INITIATION. This experiment identified the critical photoperiod for flowering. Photoperiod influenced the percentage of pennsylvania sedge flowering ($P < 0.001$), but clonal origin did not. All plants exposed to 6-, 8-, 10-, and 12-h photoperiods flowered (data not shown). No plants flowered under the 14-h photoperiod. Therefore, the critical photoperiod is less than 14 h. Pennsylvania sedge is considered a short-day plant, even though floral initiation took place with a 12-h photoperiod, because the plants only flower when exposed to fewer hours than the critical photoperiod (Thomas and Vince-Prue, 1997).

The average days to first flower were impacted by both photoperiod ($P < 0.01$) and clonal origin ($P < 0.001$). On average, the MN104R clone (6-h photoperiod) required 68 d to flower. In contrast, MN101B (8-, 10-, and 12-h photoperiods), MN102O (6-, 8-, and 10-h photoperiods), and MN103P (8-, 10-, and 12-h photoperiods) flowered on average in fewer than 60 d (Fig. 1). Within clones, there was no significant difference in average days to flower among photoperiods except a minor difference within MN103P (Fig. 1).

Photoperiod ($P < 0.001$) and clonal origin ($P < 0.001$) also affected

the average number of inflorescences. When MN104R was exposed to 6-, 10-, and 12-h photoperiods, this clone produced on average fewer than seven inflorescences per plant (Fig. 1), significantly fewer than the two highest flowering photoperiod treatments for MN101B (8-h and 12-h photoperiods) and the three highest for MN102O (8-h, 10-h, and 12-h photoperiods). The latter five treatment combinations produced in excess of 30 inflorescences per plant (Fig. 1). Within clones, there was no significant difference in the number of inflorescences produced across the range of photoperiods (Fig. 1).

Although not statistically significant, the 8-h photoperiod produced the most consistent time to flower of all photoperiods. Average days to first flower under the 8-h photoperiod were less than 60 d for all four clones and had a range of 54.2 to 59.8 d (Fig. 1). Furthermore, MN101B, MN102O, and MN103P produced more than 25 inflorescences per plant and MN104R averaged 14 inflorescences under the 8-h photoperiod (Fig. 1). Based upon consistent results, the 8-h photoperiod was selected as the standard photoperiod for the final experiment.

MINIMUM WEEKS OF INDUCTIVE TREATMENTS NECESSARY FOR FLORAL DETERMINATION. The minimum number of weeks needed to induce flowering were clearly delineated among treatments. The number of weeks of

8-h short-day inductive photoperiodic treatments influenced the percent of pennsylvania sedge flowering ($P < 0.001$), while clonal origin had no significant effect. Plants exposed to 0 or 2 weeks of short-day photoperiods failed to flower by the end of the 14-week experiment. In contrast, 99% of plants flowered when exposed to 4 or 6 weeks of short days and 100% of plants flowered when exposed to 8 or 10 weeks of short days (data not shown). Number of weeks of short-day photoperiods did not affect average days to first flower. We conclude that pennsylvania sedge plants are florally determined after exposure to 4 weeks of 8-h inductive treatments.

With respect to the average number of inflorescences produced per plant, an interaction occurred between the number of weeks of photoperiodic treatments and clonal origin (Table 2). Overall, MN104R produced fewer inflorescences than MN101B and MN102O when exposed to 6, 8, or 10 weeks of short-day photoperiods (Table 2).

In this experiment, MN102O and MN103P produced abnormal inflorescences when they received fewer than 8 weeks of short-day photoperiods. At just 4 weeks of short-day photoperiods, MN103P regularly produced pseudoviviparous growth emanating from where the staminate and pistillate spikes should be (Fig. 2B). Pseudoviviparous growth is defined as the substitution of asexual propagules (plantlets) in place of sexual reproductive structures such as seeds (Elmqvist and Cox, 1996). When plants received 6 weeks of exposure to short days, pseudoviviparous growth replaced only the pistillate spikes in both MN102O and MN103P (Fig. 2C). While this is qualitative evidence, it does support exposing clones like MN103P and MN102O to a minimum of 8 weeks of short-day photoperiods to ensure normal inflorescence development. In comparison, MN101B and MN104R showed an increase in male function when the plants received 10 weeks of short-day photoperiods (Fig. 2D). Normally, the pistillate and staminate spikes are separate in this monoecious plant (Gleason and Cronquist, 1991). However, MN101B and MN104R regularly produced a tiny staminate spike on the tip of what should have

Fig. 1. Average number of days to first flower and average number of inflorescences by photoperiod and by clone (MN101B, MN102O, MN103P, and MN104R) in pennsylvania sedge plants. Standard error of the means is indicated by error bars. Bars labeled with different letters were significantly different according to Tukey's honestly significant difference test at $P < 0.05$ ($n = 2$, three replications). Average number of days to flower was analyzed independently of average number of inflorescences.

Table 2. Average number of pennsylvania sedge inflorescences produced per plant by clone and by duration of exposure to 8-h photoperiodic inductive treatments.

Clone	Avg inflorescences [mean $\pm$ SE (no.)]			
	4 wk	6 wk	8 wk	10 wk
MN101B	30 $\pm$ 5 efg ^z	54 $\pm$ 5 bcd	72 $\pm$ 8 ab	59 $\pm$ 5 bc
MN102O	13 $\pm$ 4 gh	46 $\pm$ 5 cde	61 $\pm$ 6 abc	79 $\pm$ 6 a
MN103P	12 $\pm$ 4 gh	37 $\pm$ 9 de	36 $\pm$ 4 de	59 $\pm$ 11 bc
MN104R	9 $\pm$ 3 h	15 $\pm$ 4 fgh	33 $\pm$ 4 ef	36 $\pm$ 8 de
Significance	<i>P</i> value			
Clone $\times$ Weeks	0.00422			

^zAverage values within the table labeled with different lowercase letters were significantly different according to Tukey's honestly significant difference test at *P* < 0.05 (*n* = three plants, three replications).

Fig. 2. Normal and abnormal inflorescences in pennsylvania sedge. (A) Normal inflorescence with intact staminate spike (S) and subordinate pistillate spikes (P) with perigynia and dried stigmas. (B) Note the pseudoviviparous growth that is originating from the terminal staminate spike (S) and subordinate pistillate spikes (P) in a plant from clone MN103P that was exposed to 4 weeks of 8 h photoperiods. (C) The pseudoviviparous growth originating from the pistillate spikes (P) in a plant from clone MN103P that was exposed to 6 weeks of 8-h photoperiods. (D) An abnormal inflorescence from clone MN101B that has received 10 weeks of 8-h photoperiods. Note the staminate spikes (S) arising from what should purely be a pistillate spike.

been a purely pistillate spike when exposed to 10 weeks of 8-h photoperiods (Fig. 2D). Therefore, determining the optimum number of weeks of inductive photoperiods for each clone is imperative for producing a normal reproductive spike.

In all three experiments, all plants displayed a change in floral dichogamy or sequence. Pennsylvania sedge, a monoecious species, usually exhibits protogynous flowering that is defined as when the stigmas appear first and become receptive before the

stamens reach anthesis (Friedman and Barrett, 2009). However, all plants in these experiments showed protandry; pollen shed preceded stigmatic presentation (data not shown). This observation can be beneficial in a commercial application if outcrossing is desired. If pollen shed completely precedes stigmatic presentation on an individual inflorescence culm, then pollination of the pistillate flowers using diverse pollen sources can be used to increase outcrossing rates in the inflorescence culms without emasculation. Pennsylvania sedge sets fewer seeds when it is self-pollinated vs. artificially pollinated with pollen from other sources (Friedman and Barrett, 2009).

Conclusion

Pennsylvania sedge is an obligate short-day plant and vernalization does not promote or accelerate flowering. Plants initiated flowers with photoperiods from 6 to 12 h. An 8-h photoperiod produced consistently high inflorescence production across four clones with an average of fewer than 60 d to first flower. All four clones used in this study required a minimum of 4 weeks of an 8-h photoperiod to be florally determined. However, depending upon clonal origin, 6 to 10 weeks of short-day inductive conditions appear to be required for the production of normal monoecious inflorescence culms. Based on the observable variation in this experiment, it is critical to select a clone capable of producing a large number of normal inflorescences when attempting to propagate pennsylvania sedge.

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