

September 2007

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Claerbout, Ann E.; Coons, Janice M.; Owen, Henry R.; and Robertson, Kenneth R., "Floral Biology of *Physaria ludoviciana* (Brassicaceae), a Plant Rare to the Midwest" (2007). *Faculty Research & Creative Activity*. 133.
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Floral Biology of *Physaria ludoviciana* (Brassicaceae), a Plant Rare to the Midwest

Ann E. Claerbout, Janice M. Coons, Henry R. Owen and Kenneth R. Robertson

ABSTRACT

Physaria ludoviciana (Brassicaceae) is rare in Illinois, Minnesota, and Wisconsin. Environmental effects on floral development are unclear. Both self-compatibility and self-incompatibility occur within *Physaria* species. Objectives were to describe flowers, to determine how photoperiod affects flower development, and to predict whether flowers are self-compatible or self-incompatible. For photoperiods, greenhouse-grown plants were placed in either 16 or 8 hr photoperiods. Inflorescences and open flowers were counted weekly. For pollination, flowers were self-pollinated or cross-pollinated. Plants developed inflorescences after 20 and 28 d in long and short days, respectively. Inflorescences/plant increased for both photoperiods throughout the study. In short days, plants produced more inflorescences (10.8/plant) than in long days (7.1/plant). Anthesis started at 48 and 56 d for long and short days, respectively. Blooming peaked at 83 d (4.9 flowers/plant/day) for long days, and at 98 d (3.5 flowers/plant/day) for short days. Cross-pollinated flowers produced fruits, while self-pollinated ones did not.

INTRODUCTION

Physaria ludoviciana (Nuttall) O'Kane & Al-Shehbaz (silvery bladderpod; Brassicaceae), a sand prairie plant, is listed as endangered in both Illinois (Herkert and Ebinger 2002) and Minnesota (Minnesota Department of Natural Resources Non-game Wildlife 1996) and threatened in Wisconsin (Wisconsin Department of Natural Resources 2003). The plant was formerly of the genus *Lesquerella* (Al-Shehbaz and O'Kane 2002). In each of these three states, this species is reported in only one location. Recent studies have focused on the Illinois population, where the unique habitat of this plant was formed during the last glacial retreat, when sand was deposited throughout Illinois (Gleason 1910). The only natural population of *P. ludoviciana* in Illinois is at Henry Allan Gleason Nature Preserve (HAGNP) in Mason County (Herkert and Ebinger 2002). The Illinois population represents the eastern edge of its range within the United States where it extends west to Nevada, south to Arizona, and north to Montana and North Dakota (United States Department of Agriculture, Natural Resources Conservation Service 2002). In Illinois, *P. ludoviciana* grows in bowl-shaped sand blowouts that are naturally disturbed areas. Plants in HAGNP are aggregated and form three distinct colonies (Coons et al. 2000). Plants form a basal rosette of leaves, whose silvery appearance is due to a dense covering of fine, stellate trichomes. From the rosette, elongating inflorescences arise as racemes with yellow flowers. Previous studies show that the largest colony at HAGNP produced an average of 6.5, 3.2 and 6.2 inflorescences/plant in 1999, 2000

and 2002, respectively (Beach et al. 2001, Claerbout 2003, Coons et al. 2000). In June 2002, plants at the largest colony had an average of 0.6 flowers/inflorescence open on a given day, and these flowers were visited by insect species from at least five different orders (Claerbout 2003). Following natural pollination of flowers, 17.3, 14.4 and 23.7 fruits/inflorescence were produced in 1999, 2000 and 2002, respectively, with 2.4 and 3.4 seeds/fruit in 2000 and 2002, respectively (Beach et al. 2001, Claerbout 2003, Coons et al. 2000). Hence plants successfully produce fruits with seeds at HAGNP.

In Illinois, peak flowering of *P. ludoviciana* is in May with mature seed set in June (Beach et al. 2002). Flowers of many species that bloom in early spring are initiated by vernalization of plants during cold winter months (Hartmann et al. 1988) or by short days of autumn (Garner and Allard 1920, Lambers et al. 2000). When short days of autumn initiate the development of floral primordia, the low temperatures of winter stop development until temperatures increase in spring (Lambers et al. 2000). Floral initiation in *P. ludoviciana* also could be triggered when plants reach a certain developmental age. Studies investigating how vernalization, photoperiod or plant age influence flowering in *Physaria* species are not published. Another Brassicaceae species, *Arabidopsis thaliana*, was found to be a quantitative long day plant that would eventually flower under any photoperiod, although flowering was accelerated greatly by long days (Irish and Sussex 1990, Napp-Zinn 1985).

It is unknown whether *P. ludoviciana* is self compatible or self-incompatible. Self-incompatibility is widespread in the genus *Physaria*, but self-compatibility also occurs in some species of the genus (Rollins and Shaw 1973). *Physaria fendleri* and *P. gordonii*, southwestern relatives of *P. ludoviciana*, are self-incompatible (Delph 1986, Mitchell 1997).

Existing descriptions of the flowers of *P. ludoviciana* cover general details concerned with how to distinguish this species from other species in the genus or other similar species that belong to different genera of Brassicaceae (Fernald 1950, Mohlenbrock 1980, Payson 1922, Rollins 1993, Rollins and Shaw 1973). These descriptions do not focus on the floral biology of *P. ludoviciana*.

The overall goal of this study was to investigate the floral biology of *P. ludoviciana*. Specific objectives were to describe flowers, to determine how photoperiod affects flower development, and to predict whether flowers are self-compatible or self-incompatible.

MATERIALS AND METHODS

Floral Description

Complete detailed description of the flowers was made based on our own observations of herbarium specimens. Characters on each plant were measured using a stereo microscope, and photo macrographs were taken to illustrate

important morphological characters using Nikon Multiphot photomacrographic equipment. Representative voucher specimens for the morphological studies are: Colorado: Logan Co., Claerbout & Coons Al 0, 2002 (ILLS); Illinois: Mason Co., Evers 69432, 1961 (ILLS).

Plant Culture

Seeds of *Physaria ludoviciana* were hand collected from HAGNP in Mason County, Illinois during June 1999 in accordance with a Special Use Permit obtained from the Illinois Nature Preserves Commission. On October 23, 2000, seeds were planted in Cone-tainers™ (Stuewe & Sons, Inc., Corvallis, Oregon) that were 4 cm in diameter by 20 cm deep containing one of the following five soilless media (SunGro, Seneca, Illinois): SB100 Bedding Plant Mix, Germination Mix #3, SB500 High Porosity Mix, LC1 Sunshine Mix, or SB300 Universal Mix. These different growing media were chosen initially to determine the effects of different commercial growing media on seedling development of *P. ludoviciana*. No significant differences were found for media (unpubl. data).

Seedlings were transplanted on April 27, 2001 into square pots (11 cm by 11 cm by 35 cm deep) using 100% High Porosity Mix or 1:1 High Porosity Mix:coarse silica sand. Since this plant is native to sand prairies, these deep pots were used to accommodate the deep root system common to plants from these habitats. Plants were transplanted again on September 22, 2001 into round pots (22 cm in diameter by 37 cm deep) containing Universal Mix. Each time they were transplanted it was because they were beginning to deteriorate in appearance. When plants were removed from the pots during transplanting, the roots were distributed throughout the pots, but were not root bound. Plants remained in these round pots as they grew to maturity and throughout the duration of these experiments. Plants were watered three times a week in sunny weather and two times a week in cloudy weather. Average monthly greenhouse temperatures from October 2000 to April 2002 were 26°C (maximum) and 18°C (minimum). Plants were fertilized with 20-10-20 fertilizer at 250 mg/l N every other week. Older leaves were removed as they senesced.

Photoperiod

Fifteen cultivated plants of equivalent health and maturity (basal rosette stage) were selected for each photoperiod treatment in a greenhouse. The number of leaves in each rosette was counted at the beginning of the experiment for all plants selected for each photoperiod treatment. The photoperiod experiment began on October 19, 2001 when natural daylength was 11 hr (sunrise at 7:08 am and sunset at 6:07 pm). Long days (16 hr of light) were provided by supplemental lighting from 60-Watt incandescent lamps strung every 0.3 m along the bench, and one meter above the plants. Lamps were turned on at 5:30 am and off at 9:30 pm daily with an electric time clock. Short days (8 hr of light) were provided by pulling an opaque black shade cloth over the bench at 4:00 pm and removing it the following day at

8:00 am. Average irradiance for the short day bench ranged from 42 $\text{gmol s}^{-1} \text{m}^{-2}$ on a cloudy day (October 5, 2001) to 434 $\text{gmol s}^{-1} \text{m}^{-2}$ on a sunny day (November 16, 2001), and for the long day bench from 48 to 252 $\text{gmol s}^{-1} \text{m}^{-2}$ on the cloudy and sunny days, respectively. Average air temperatures during the photoperiod study were 25°C (maximum) and 23°C (minimum). The number of inflorescences, including pre-anthesis ones, and flowers at anthesis were counted weekly from their first appearance. The experiment ended after peak flowering had been reached for both treatments (107 d).

For statistical analyses, ANOVAs were ran in Microsoft Excel (Microsoft Corporation 2000) for leaf data and in SAS 8.2 (SAS Institute, Inc. 2001) for inflorescence and flower data. Means and standard errors were calculated.

Pollination

The pollination study began on February 11, 2002. Eight plants yielding 16 inflorescences with several flower buds each were selected from both the long day plants and the short day plants of the photoperiod experiment. Plants were combined on one bench with ambient light conditions. Inflorescences were assigned eight treatments randomly, yielding two replications of each treatment. The first pair of treatments was either cross-pollinated or self-pollinated. Other treatments included emasculation of anthers from flower buds and enclosure of inflorescence in translucent glassine paper bag 6.5 cm X 18.5 cm (Vincent 2006); however, these treatments interfered with successful floral development, and results from these treatments are not included. Emasculated buds became severely desiccated and bagged inflorescences became moldy. As a result, replication was limited by the available number of healthy inflorescences.

Open flowers were pollinated manually with "bee sticks" (Carolina Biological Supply Company, Burlington, North Carolina). Each inflorescence had a designated "bee stick" that was used for all of the pollinations on that inflorescence. The pollen source for each crossed inflorescence was from at least three open flowers on different plants. The pollen source for selfed inflorescences was from at least one other open flower on the same plant. An optical binocular magnifier (Optivisor, Donegan Optical Co., Lenexa, Kansas) magnifying 2.75 times at a focal length of 15 cm, was used to ensure that the pollen was collected on the "bee stick" and then deposited on the stigma. Flowers remained open for more than 1 d. Inflorescences were checked every 1 to 3 d for open flowers and treatments were applied to all open flowers on the inflorescence for 8 wk. Fertilization was considered successful if fruits with seeds developed. Two days after final pollinations, number of fruits/inflorescence, and number of pedicels/inflorescence were counted. Percentage of pedicels containing fruits was calculated using these numbers. Mature fruit with seeds was harvested from plants 39 d after final pollinations. These fruits and seeds were counted to calculate seeds/ fruit.

Statistical analysis tools in Microsoft Excel (Microsoft Corporation 2000) were used to calculate means and standard errors.

RESULTS

Floral Description

Following is the detailed description of the flowers of *Physaria ludoviciana* that we used in our studies of floral biology. Inflorescences compact, indeterminate racemes with ca. 10-70 flowers (Figure 1a), becoming elongate in fruit. Flowers, 6.2-6.8 mm long, 6.7-9.0 mm wide. Pedicels pubescent, 4.1-10.0 mm long, straight or recurved in a simple arch, especially in fruit. Sepals 4, erect, pubescent, lanceolate, keeled to cup shaped, 4.2-6.2 mm long, with acute apices and obtuse to truncate bases. Corolla with 4 distinct petals, diagonally disposed (cruciform) (Figure 1b). Petals yellow, 4.9-8.0 mm long, 1.2-2.6 mm wide, spatulate, with obtuse apices and truncate bases, recurving half way at anthesis. Stamens 6, tetradyncimous, the outer whorl with 1 shorter pair 2.3-3.7 mm long, and inner whorl with 2 longer inner pairs 3.5-7.0 mm long; anthers linear, dehiscent longitudinally, becoming forked at their base. Ovaries superior, pubescent, with stellate, spreading trichomes, 2-locular, the septum entire. Style linear, un branched, pubescent at the base, 2.0-2.7 mm long. Stigmas 2-lobed, not or only slightly expanded, with several glands (nectaries) subtending the ovary (Figure 1c).

Photoperiod

With $p=0.02$ and $F=5.92$, the mean number of leaves per rosette was significantly higher for short day plants than for long day plants (Table 1). However, when number of leaves per rosette at the beginning of the experiment was plotted in a scatter plot against number of inflorescences at the end of the experiment for both long day and short day photoperiods, no patterns were apparent between number of leaves and number of inflorescences (Figure 2).

All plants (except one long day plant that died) developed inflorescences. In November, inflorescences were first observed in long day plants at 20 d ($0.1 : 0.4$ inflorescences/plant), and in short day plants at 28 d (2.5 ± 0.8 inflorescences/plant). With $p<0.001$ and $F=26.54$, plants in short days produced significantly more inflorescences per plant than long day plants (Table 1). The number of inflorescences produced per plant increased steadily for both photoperiods throughout the 107 d (Figure 3). In December, open flowers were first observed by day 48 in long day plants and by day 56 in short day plants (Figure 4). With $p=0.0057$ and $F=7.74$, mean number of open flowers per plant on a given day when plants were in bloom was significantly higher for long day plants than for short day plants (Table 1). In January, blooming peaked for long day plants with 4.9 flowers per plant per day at 83 d, and for short day plants with 3.5 flowers per plant per day at 98 d. Blooming continued until April 2002.



Figure 1. a. Inflorescence of *Physaria ludoviciana*, a compact, indeterminate raceme. b. Flowers of *Physaria ludoviciana* showing petals diagonally disposed (cruciform). c. Longitudinal section of *Physaria ludoviciana* flower. One sepal, one petal and two stamens were removed to show internal structure.

Pollination The pollination trial yielded 26.0 ± 16.1 fruits for cross-pollinated inflorescences on two separate plants. No fruit developed on the self-pollinated

inflorescences. Hence, this preliminary trial suggests that flowers are self-incompatible. At the end of the experiment, 63% of the total pedicels on the cross-pollinated inflorescences developed fruit. These fruit contained 2.3 +/- 0.2 seeds per fruit.

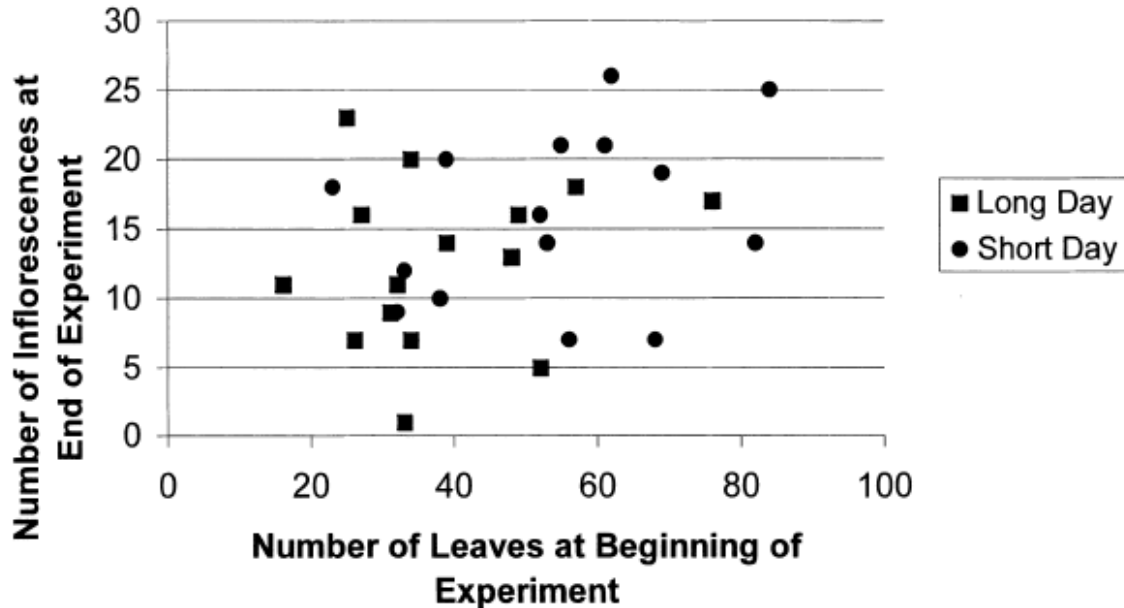


Figure 2. Scatter plot for number of leaves at the beginning of the experiment with number of inflorescences at the end of the experiment for *Physaria ludoviciana* plants in long day (16 hr) and short day (8 hr) photoperiods.

Table 1. Number of leaves per rosette (n=15), inflorescences per plant (n=165), and open flowers per plant per day (n=165) for *Physaria ludoviciana* plants in long day (16 hr) and short day (8 hr) photoperiods

| Photoperiod | Leaves/Rosette | Inflorescences/Plant | Open Flowers/Plant/Day |
|-------------|-----------------------|----------------------|------------------------|
| Long day | 39 ± 4 b ^a | 7.1 ± 0.5 b | 2.4 ± 0.4 a |
| Short day | 53 ± 5 a | 10.8 ± 0.3 a | 1.0 ± 0.3 b |

^aMeans ± standard errors. Means within a column followed by a different letter are significantly different at 5% level.

DISCUSSION

These studies provide insight relative to factors that trigger floral initiation in *Physaria ludoviciana* including age, vernalization and photoperiod. Developmental age is one factor that can play a role in floral initiation. Plants were identical in age (one year old) when this experiment was initiated, and none had flowered prior to this study. During this study, plants in the greenhouse flowered from December 2001 to April 2002. In addition, since the study ended, these plants continued to flower during similar months of 2002-2003 and 2003-2004. Given that plants did not flower prior to this study, but continued to flower on a seasonal basis since this study, it suggests that plants need to reach a certain maturity before flowering. However, age is not the only factor involved with floral initiation, since flowering is seasonal. Another factor that can play a role in floral initiation is vernalization at temperatures between 0-10°C (Hartmann et al. 1988). Since plants flowered in

greenhouses where temperatures never dropped below 18°C, vernalization was not required for flower initiation of *P. ludoviciana*. A third factor that might initiate flowers is photoperiod. Since plants were in natural irradiance with ambient light conditions in the greenhouses prior to the photoperiod study, it is unknown if floral initiation was triggered already before the start of the experiment. When the photoperiod study began, natural day length was 11 hr, which exposed all plants to a short day photoperiod that could have initiated flowering. Further support that these plants require short days to initiate flowering comes from the observation that plants continued to bloom in December for two additional years after this study ended. So in green houses, short days of fall would initiate flowering with inflorescences appearing in November and blooming starting in December. This timing differs from native Illinois populations where inflorescences begin to emerge in March, and blooming starts in early May. If short days initiated flowering in native plants, development would stop in winter and start again with higher temperatures of spring (Lambers et al. 2000). Hence blooming would occur in early spring. However, in greenhouses with no low temperatures to stop development, flowers would continue to develop, and flowering would occur earlier than in the field. To summarize, plants must reach a certain developmental age to flower, and flower initiation does not require vernalization, but may be triggered by short days.

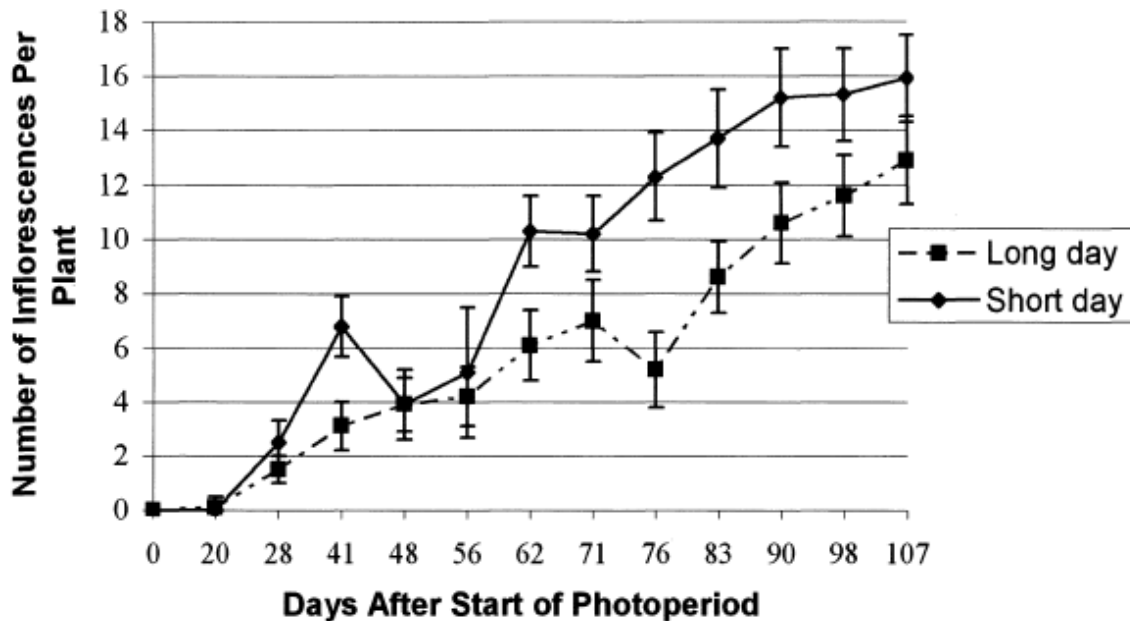


Figure 3. Number of inflorescences per plant produced over time for *Physaria ludoviciana* plants in long day (16 hr) and short day (8 hr) photoperiods. Means \pm standard errors.

At the beginning of the experiment, the number of leaves on the basal rosettes of plants was significantly higher for short day plants than for long day plants even though all plants were the same age. A scatter plot (Figure 2) showing number of leaves versus number of inflorescences shows no apparent pattern between leaf number and number of inflorescences for long day and short day plants. Therefore,

the fact that short day plants produced significantly more inflorescences was not linked to leaf number.

Photoperiod was not an absolute requirement for development of *P. ludoviciana* flowers, since both long day and short day plants developed flowers. Short day plants developed more inflorescences, whereas long day plants developed flowers earlier and had more flowers open on a given day. Studies on another member of Brassicaceae, *Arabidopsis thaliana*, also flowered with both long and short days, while long day conditions accelerated flowering (Irish and Sussex 1990, Napp-Zinn 1985). In *P. ludoviciana*, long day plants put their energy into producing more flowers/inflorescence and short day plants tended to produce more inflorescences with fewer open flowers/day.

Although replication was limited to only two inflorescences on two plants, the preliminary experiment showed fruit production on cross pollinated flowers and none on self-pollinated flowers, suggesting that plants are self-incompatible. This result is supported by the known self-incompatibility of other southwestern relatives of *P. ludoviciana* (Delph 1986, Mitchell 1997) and contradicted by other self-compatible species of the genus (Rollins and Shaw 1973). In the event that flowering plants are again available for greenhouse experiments, this study should be repeated with a larger replication of treatments.

In greenhouses, the average number of reproductive structures produced by 30 plants was greater or equal to numbers of reproductive structures produced by plants in the largest colony of the native Illinois population at HAGNP. Plants in the native colony produced a maximum of 6.5 and a minimum of 3.2 inflorescences/plant (Beach et al. 2001, Claerbout 2003, Coons et al. 2000), while greenhouse plants produced a range of 12.9 to 15.9 inflorescences/plant for long day plants and short day plants, respectively. Hence, more inflorescences/plant were produced in greenhouse plants than in the native colony. In June 2002, plants in the native colony had an average of 4 open flowers/plant on a single day (Claerbout 2003), while flowering plants in greenhouses with long days and short days had 4.9 and 3.5 open flowers per plant, respectively, on their peak flowering day. Thus, open flowers on a given day were comparable in field and greenhouse plants. In the field, flowering peaks in May and lasts approximately six weeks whereas in the greenhouse, flowering peaked in January and lasted approximately four months. The native colony produced a maximum of 23.7 fruits/inflorescence in 2002 and a minimum of 14.4 fruits/inflorescence in 2000 (Beach et al. 2001, Claerbout 2003, Coons et al. 2000), which indicated the 26 fruits/inflorescence developed on cross-pollinated greenhouse plants were close to the maximum number produced by the native colony. Plants in the native colony produced 2.4 to 3.4 seeds/fruit depending on year (Claerbout 2003, Coons et al. 2000) compared to 2.3 seeds/fruit in greenhouse plants. Thus, production of seeds/fruits for greenhouse plants was close to the minimum number produced by the native colony. The greater number of inflorescences, and maximum fruit production in greenhouse plants relative to native plants may be due to increased water and

nutrient availability provided in greenhouses. Thus, the overall reproductive capacity of plants in greenhouses was equivalent to or better than those of the native Illinois colony.

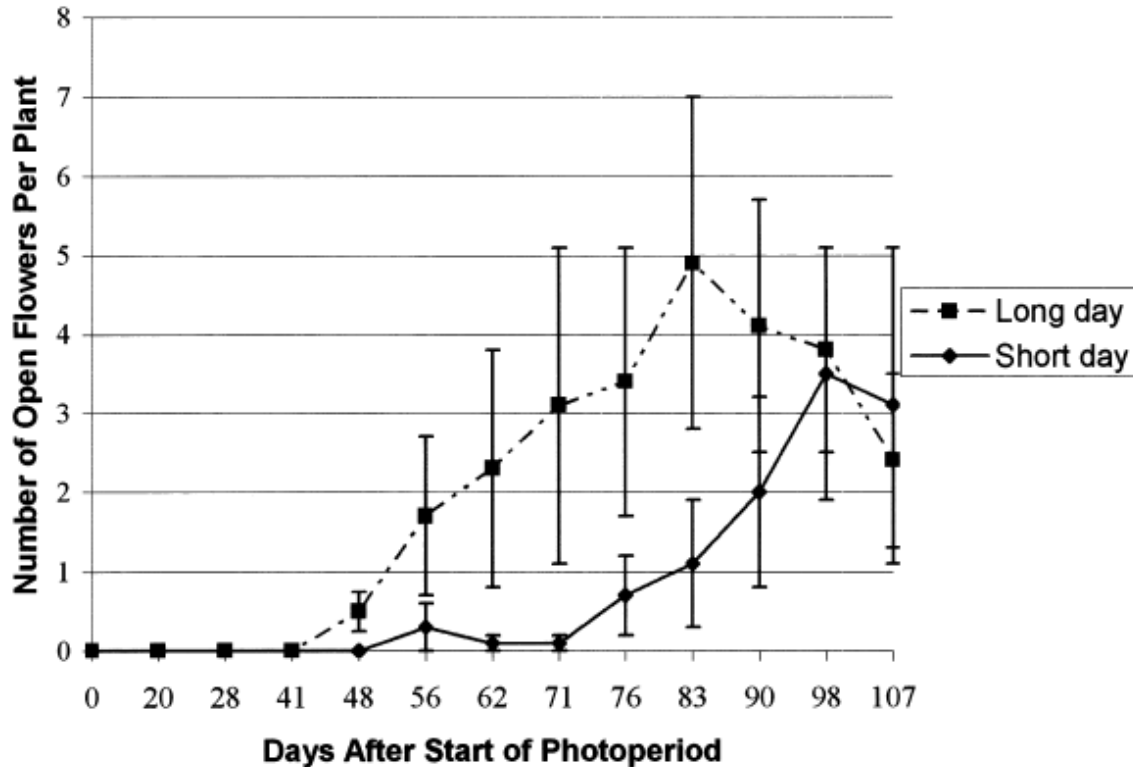


Figure 4. Number of open flowers per plant produced with time for *Physaria ludoviciana* plants in long day (16 hr) and short day (8 hr) photoperiods. Means \pm standard errors.

ACKNOWLEDGMENTS

The authors acknowledge the Illinois Nature Preserves Commission for granting the permit to collect seeds. We also thank Ms. Jennifer L. Franklin and Dr. John E. Ebinger for their assistance with seed collection as well as Mr. Christian Deters for starting the seedlings. Thanks also to the Plant Care Facility Staff with the University of Illinois at Urbana-Champaign for their care of plants.

LITERATURE CITED

- Al-Shehbaz, I.A. and S.L. O'Kane. 2002. *Lesquerella* is united within *Physaria* (Brassicaceae). *Novon* 12:319-329.
- Beach, S.E., J.M. Coons, H.R. Owen, B.L. Todd, and M.A.L. Smith. 2001. Comparison of seed production and germination in three distinct colonies of *Lesquerella ludoviciana*. *Proceedings of Botanical Society of America Meetings at Albuquerque, New Mexico in August, 2001*, p. 46. Abstract.

Beach, S.E., J.M. Coons, H.R. Owen, B.L. Todd, and M.A.L. Smith. 2002. Seed vigor of *Lesquerella ludoviciana* as affected by colony and maturity. *Trans. Illinois State Acad. Sci.* 95:99. Abstract.

Claerbout, A.E. 2003. Survival strategies of two Illinois endangered plants: *Lesquerella ludoviciana* (Silvery Bladderpod) and *Stylisma pickeringii* var. *pattersonii* (Patterson Bindweed). M.S. thesis, University of Illinois, Urbana, Illinois.

Coons, J.M., H.R. Owen, J.L. Franklin, and J.E. Ebinger. 2000. Reproductive potential of silvery bladderpod (*Lesquerella ludoviciana*). *Amer. J. Bot.* 87:41. Abstract.

Delph, L.F. 1986. Factors regulating fruit and seed production in the desert annual *Lesquerella gordonii*. *Oecologia* 69:471-476.

Fernald, M.L. 1950. *Gray's manual of botany*, 8th ed. American Book Company, New York, New York.

Garner, W. and H. Allard. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction of plants. *J. Agric. Res.* 18:553-607.

Gleason, H.A. 1910. The vegetation of the inland sand deposits of Illinois. *Bull. Illinois State Lab. Nat. Hist.* 9:23-174.

Hartmann, H., A. Kofranek, V. Rubatzky, and W. Flocker. 1988. *Plant science: growth, development, and utilization of cultivated plants*. Prentice Hall, Englewood Cliffs, New Jersey.

Herkert, J.R. and J.E. Ebinger. 2002. *Endangered and threatened species of Illinois: status and distribution. Volume 1. Plants*. Illinois Endangered Species Protection Board, Springfield, Illinois.

Irish, V.F. and I.M. Sussex. 1990. Function of the *ap2* gene during *Arabidopsis* floral development. *The Plant Cell* 2:741-753.

Lambers, H., F.S. Chapin, III, and T.L. Pons. 2000. *Plant physiological ecology*. Springer Verlag, New York, New York. Microsoft Corporation. 2000.

Microsoft Excel. Redmond, Washington.

Minnesota Department of Natural Resources Non-game Wildlife. 1996. *Alphabetical index by scientific name of endangered, threatened, and special concern species*. St. Paul, Minnesota.

Mitchell, R.J. 1997. Effects of pollen quantity on progeny vigor: evidence from the desert mustard *Lesquerella fendleri*. *Evolution* 51:1679-1684.

Mohlenbrock, R.H. 1980. The illustrated flora of Illinois, flowering plants, willows to mustards. Southern Illinois University Press, Carbondale and Edwardsville, Illinois.

Napp-Zinn, K. 1985. *Arabidopsis thaliana*. p. 492-503. In: Haley, H.A. (ed.). CRC Handbook of Flowering. Volume 1. CRC Press, Boca Raton, Florida.

Payson, E.B. 1922. A monograph of the genus *Lesquerella*. Ann. Missouri Bot. Gard. 8:103-236.

Rollins, R.C. 1993. The Cruciferae of continental North America. Stanford University Press, Stanford, California.

Rollins, R.C. and E.A. Shaw. 1973. The genus *Lesquerella* (Cruciferae) in North America. Harvard University Press, Cambridge, Massachusetts.

SAS Institute, Inc. 2001. SAS 8.2 system for Windows, 8th ed. Cary, North Carolina.

United States Department of Agriculture, Natural Resources Conservation Service. 2002. The PLANTS Database, Version 3.5 (<http://plants.usda.gov>). National Plants Data Center, Baton Rouge, Louisiana, Data accessed: February 2003.

Vincent, L. 2006. Controlled pollination of maize, Maize Mapping Project (http://www.maizegdb.org/IMP/WEB/pollen.htm#four_three). University of Missouri-Columbia, Missouri, Data accessed: November 2006.

Wisconsin Department of Natural Resources. 2003. Endangered and threatened species factsheet-plants. <http://www.dnr.state.wi.us/org/lands/er/factsheets/plants.htm>. Data accessed: April 2003.