

Flowering phenology and the evolution of fragmented prairie plant populations



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Introduction

The North American tallgrass prairie is one of the most fragmented ecosystems worldwide with less than 1% of the original habitat remaining. Remnant prairie plant populations exhibit spatial genetic structure and loss of genetic diversity (Wagenius *et al.* 2007). Fragmentation and isolation may lead to shifts in flowering time, either through local adaptation or drift. Such shifts may further increase temporal isolation and decrease gene flow among fragments.

We use *Echinacea angustifolia* as a model prairie species to study the genetic basis for temporal structuring in six remnant populations of varying size in western Minnesota using two common environment experiments. In the first experiment we investigate population differentiation in flowering phenology of plants originating from six nearby remnant populations. The second study evaluates how crossing types (inbred, random, and outbred) affect flowering phenology. Finally, we estimated flowering consistency among individuals between 2005 and 2006 and demonstrate how flowering phenology can influence reproductive fitness.

RESEARCH QUESTIONS

- 1) Do remnant prairie populations of *Echinacea* exhibit differentiation in flowering phenology?
- 2) Do inbreeding or outbreeding affect flowering phenology in remnant prairie populations?
- 3) How consistent is flowering phenology of individual *Echinacea* plants between flowering seasons?

Methods

STUDY SITE: 6400 ha in Western Minnesota Farmland with small remnant prairies.

MEASUREMENTS:

- Start date (first day the plant presented pollen)
- End date (last day the plant presented pollen)
- Duration (difference between end and start dates)

STUDY SPECIES: *Echinacea angustifolia* the narrow-leaved purple coneflower (fig. 1)

- Self-incompatible
- No specialized seed dispersal
- Takes 4-8 years before first flowering
- In the Asteraceae
- Generalist pollinators
- Long-lived (decades)
- Does not flower every season



Figure 1: *Echinacea angustifolia* flowering head.

EXPERIMENTAL DESIGNS

Population differentiation experiment

- Seeds were collected in 1995 and 1996 from six nearby remnant prairie populations (tbl. 1).
- Seeds were germinated and planted in an experimental common garden in 1996 (10-year-old plants) and 1997 (9-year-old plants) respectively.
- Daily flowering phenology was recorded in 2006 (219 plants).

Inbreeding and outbreeding experiment

- Plants from population differentiation experiment were hand pollinated in 1999 to produce progeny from three cross types:
 - ◊ **Outbred** – Parents chosen from different populations of origin.
 - ◊ **Random** – Parents chosen from the same population of origin.
 - ◊ **Inbred** – Parents related as half or full siblings.
- Daily flowering phenology was recorded in 2006 (88 plants).

Flowering consistency experiment

- Examined the consistency of flowering phenology in individual plants that flowered in both 2005 and 2006 (123 plants)

Data Analysis and Results

Selected generalized linear models with the response (start date, end date, or duration) modeled as poisson.

Population differentiation experiment:

- Population of origin and plant age interacted in their effect on start date and duration ($p \leq 0.05$).
- Population of origin in 9-year-old plants influenced start date, end date, and duration ($p \leq 0.02$; graphs 1 & 2).

Inbreeding and outbreeding experiment

- Cross type influenced start date, end date, and duration ($p \leq 0.05$; graphs 3 & 4).

Flowering consistency experiment

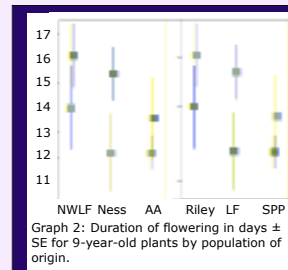
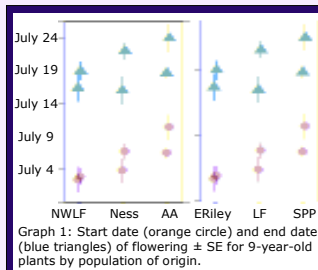
- Used the Kendall's tau rank correlation coefficient to test the correlation between flowering phenology measurements of individual plants between 2005 and 2006.
- All three phenological measurements were correlated between years:
 - ◊ Start date ($p = 0.02$)
 - ◊ End date ($p = 0.01$)
 - ◊ Duration ($p \approx 0.00$)

All data was analyzed using R 2.4.1 (The R Core Development Team 2006)

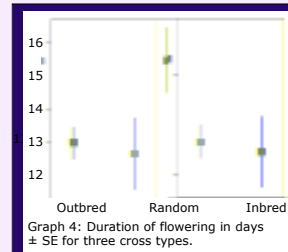
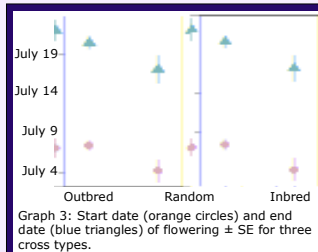
Population	Population size
SPP	5044 Estimated
LF	88
Eriley	46
AA	30
Ness	23
NWLF	11

Table 1: Number of flowering plants in each remnant population of origin in 1996.

Population differentiation experiment:



Inbreeding and outbreeding experiment:



Conclusions

Population differentiation experiment

- Flowering phenology of 9-year-old plants from six nearby remnant populations diverged in 2006.

Inbreeding and outcrossing experiment

- Inbred plants flowered on average almost a week earlier than random and outbred plants.
- Inbred and outbred plants flowered for a significantly shorter duration than random plants.

Flowering consistency experiment

- Between 2005 and 2006, flowering phenology measurements are correlated among individuals.



Discussion and Implications

- The largest population (SPP) flowered for a shorter duration than smaller remnant populations. This could be due to stabilizing selection in SPP while smaller populations may experience genetic drift. Another hypothesis is longer flowering duration is selected for in the small populations. Additional years of data are needed to determine the mechanisms affecting this trend.

- Inbred plants flowered earlier and for a shorter time than randomly mated plants. This limits the opportunity for successful pollination and can increase assortative mating between already inbred plants.

- Outbred plants flowered for a significantly shorter duration than randomly mated plants within a remnant population suggesting outbreeding depression. This indicates that even on a small scale (< 6km) these populations may be differentiated.

- Plants that were grown in a randomized common environment garden showed consistency in their flowering phenology between 2005 and 2005 suggesting a genetic basis for flowering.

- Flowering phenology is a very important fitness trait with direct consequences for reproductive success. Our study demonstrates that anthropogenic fragmentation can alter this trait in ways that may accelerate population isolation.



References and Acknowledgments

Wagenius, S., E. Lonsdorf, and C. Neuhäuser. 2007. Patch aging and the S-Allee effect: breeding system effects on the demographic response of plants to habitat fragmentation. In press, *The American Naturalist*.

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