

Isolation affects reproductive success in low-density but not high-density populations of two wind-pollinated *Thalictrum* species

Janet C. Steven · Donald M. Waller

Received: 3 March 2006 / Accepted: 5 July 2006 / Published online: 4 August 2006
© Springer Science+Business Media B.V. 2006

Abstract Since pollen usually travels limited distances in wind-pollinated plant species, plants growing at low density may become pollen limited. We examined how local pollen availability and population density affect reproductive success in two wind-pollinated, dioecious species, *Thalictrum fendleri* and *Thalictrum dioicum*. Distance to the nearest flowering male, the number of flowering males within 2 m, and flower number on those males served as measures of local pollen availability. Increased distance from pollen donors reduced seed set in the lowest-density population of each species, but seed set in high-density populations was not correlated with local pollen availability. For plants in high- and low-density populations at similar distances from pollen donors, this distance only affected seed set in low-density populations. To ensure that differences in resource availability were not causing spurious correlations between seed set and plant density, we constructed low-density artificial arrays in populations of *T. dioicum*. In these, seed

set decreased rapidly with increases in distance from pollen donors. Despite these effects, the density of males in a population was not correlated with average seed set in *T. dioicum*, and hand pollination in the *T. dioicum* populations also failed to increase seed set over natural levels. These results suggest that pollen receipt only limits seed set on isolated plants within low-density populations of *T. dioicum* and *T. fendleri*.

Keywords Dioecy · Pollen limitation · Seed set · *Thalictrum dioicum* · *Thalictrum fendleri* · Wind pollination

Introduction

Seed and fruit production in plants is frequently limited by the receipt of adequate pollen (Bierzychudek 1981; Burd 1994). Plants that cannot self-fertilize are dependent on pollen transfer from other plants in a population, and consequently decreasing densities of flowering plants in a population may decrease the likelihood of successful pollen transfer (Levin and Kerster 1974; Regal 1982; Whitehead 1983; Wilcock and Neiland 2002). An increase in the distance between flowering plants has been shown to decrease seed set by reducing the size and attractiveness of the floral display and increasing flight distances between plants in insect-pollinated *Brassica kaber* (Kunin 1993), *Lesquerella*

J. C. Steven · D. M. Waller
Department of Botany, University of Wisconsin at
Madison, Madison, WI, USA

Present Address:
J. C. Steven (✉)
Department of Biology, Sweet Briar College,
Sweet Briar, VA 24595, USA
e-mail: jsteven@sbc.edu

fendleri (Roll et al. 1997), and *Aconitum columbianum* (Bosch and Waser 2001). In wind-pollinated plants, decreased plant density also results in greater pollen loss between plants, potentially increasing pollen limitation (Regal 1982; Whitehead 1983). Levin and Kerster (1974) predicted that the reduced effectiveness of pollen transfer in low-density populations would be more severe in wind-pollinated plants than insect-pollinated plants because insects tend to compensate for lower densities by traveling farther between plants.

Studies of several wind-pollinated species have shown that most pollen is deposited near the source plant (reviewed in Levin and Kerster 1974; Tonsor 1985), suggesting that the distance between a plant and its nearby pollen donors and the quantity of pollen produced by those donors will strongly affect pollen receipt (Whitehead 1983). A fragmented and thinned population of *Quercus douglasii* studied by Knapp et al. (2001) did show a relationship between seed set and the number of pollen-producing neighbors, but other studies within populations of wind-pollinated trees and herbs have not supported this prediction. Russell et al. (1998) found no relationship between pollen load on stigmas and distance to the two nearest neighbors in a stand of *Cercocarpus ledifolius*. A stand of *Quercus macrocarpa* studied by Dow and Ashley (1998) also showed evidence of long-distance pollination, and nearby trees were no more likely to sire acorns than trees at greater distances. In the herb *Staberoha banksii*, the distance to the fourth nearest male was a better predictor of stigmatic pollen loads than the distance to the nearest male neighbor (Honig et al. 1992).

In contrast, studies of wind-pollinated herbs, shrubs and trees that have compared population densities and pollination success across multiple populations have consistently found a positive relationship between the two, suggesting that pollination is more effective at higher plant densities (Lemen 1980; Nilsson and Wästljung 1987; Berry and Calvo 1989; Allison 1990). This discrepancy between within- and among-population studies may be due to the importance of the overall size and density of a population to pollination success. In insect-pollinated plants, locally isolated plants that are part of a large population

tend to experience greater reproductive success than locally isolated plants in small populations (Ågren 1996; Groom 1998; Bosch and Waser 1999; Molano-Flores et al. 1999; Wilcock and Neiland 2002). In wind-pollinated species, flower production and pollen availability at the population level may also be more important than local isolation within populations (Wilcock and Neiland 2002).

Here, we report how plant density affects reproductive success in multiple populations of two dioecious, wind-pollinated species of *Thalictrum* (Ranunculaceae). Because dioecy prevents self-fertilization and restricts pollen production to a subset of plants in a population, limited pollination success could occur in isolated females and/or at low population densities. To assess the relative importance of local isolation and overall population density to pollen limitation, we studied the relationship between local pollen availability and seed set both within and across populations.

Seed production and plant density may also be positively correlated among populations due to variation in the resource environment. Low light and nitrogen levels can limit establishment, survival, growth, and (in perennials) frequency of flowering as well as reduce the fraction of flowers that produce fruit and the number of seeds per fruit (Tilman 1982; Lubbers and Christensen 1986; McCall and Primack 1987; Niesenbaum 1993; Antos and Allen 1994, 1999; Kato and Hira 1999). Thus, populations in low-resource environments may have low plant density and low seed production, even if pollen quantities are sufficient (Kunin 1992; Roll et al. 1997; Bosch and Waser 1999, 2001). To ensure that variable resource levels did not confound our attempts to assess the effects of density on seed set, we complemented our observations in natural populations with experimental arrays of plants and experimental reductions in population density.

Methods

Study species

Thalictrum dioicum L. and *Thalictrum fendleri* Engelm. ex A. Gray are dioecious and wind-pollinated, and likely derived from a common hermaphroditic

insect-pollinated ancestor (Brunet and Liston 1999). Both species are polycarpic perennials between 30 cm and 80 cm in height. *Thalictrum dioicum* grows in mesic forests across eastern North America and did not grow clonally in the study sites. *Thalictrum fendleri* occurs in montane open forest and shrub habitats across western North America and northern Mexico and grew clonally at our study sites (Steven and Waller 2004). We treat ramets as individual plants here as they function independently in pollen release and capture. Since *Thalictrum* species have free, uniovulate carpels, we were able to easily assess both the number of ovules initially available and the number of seeds matured at fruiting.

Study sites

We studied four populations of *T. dioicum* in the Nicolet-Chequamegon National Forest, Wisconsin, USA and two populations of *T. fendleri* in the Bridger-Teton National Forest, Sublette County, Wyoming, USA (Table 1). All *T. dioicum* sites shared the same climate and grew on similar soils. However, the forest composition varied among sites. The *T. dioicum* County Road F site had a forest overstory dominated by *Pinus resinosa*. The Laona and Peshtigo River populations had an overstory composed mainly of *Acer saccharum* and *Pinus strobus*, and the Trestle Road site was under early-successional *Populus tremuloides*. Both *T. fendleri* populations were growing in *P. tremuloides* groves on mesic soils. Study areas within each population were selected to represent the typical densities and conditions at a site, and were limited in size by local topography (such as boulders or steep slopes); therefore the size of the sampled area varies somewhat among populations.

Flowering and seed set occurred between May 9 and June 22 in all *T. dioicum* sites during the 3 years of our study. We collected data at County Road F in 2000, 2001, and 2002, at Laona in 2000 and 2002. The Peshtigo River and Trestle Road sites were studied in 2002. We collected data in both *T. fendleri* sites in July of 2001.

Observations and experiments

To examine the relationship between plant density and reproductive success within populations, we

mapped locations of all plants within study areas in each population. We also tallied the number of flowers on each female, the distance of each female to its closest male neighbor, the number of flowers on that neighbor, the number of males within 2 m, and the total number of male flowers within 2 m. We measured seed set at maturity by dividing the number of mature carpels by the total number of carpels in ten randomly selected flowers. We experimentally reduced male flowering plant density for 3 years at one *T. dioicum* site, County Road F, to assess how local isolation affects seed set in an otherwise dense population. We clipped all male inflorescences off plants within a central $5 \times 5 \text{ m}^2$ patch of the $20 \times 17 \text{ m}^2$ study area before the anthers dehisced.

To test for pollen limitation among populations of different density, we hand-pollinated ten flowers when stigmas were receptive on each of 20 plants just outside of the mapped study area in all four *T. dioicum* populations in 2002. Male flowers with dehiscing anthers were collected from outside the study area, and pollen was shaken into a small plastic Petri dish. Stigmas were brushed gently against the pollen in the dish. We used a mix of pollen from at least three plants in the population and counted the fraction of carpels matured by each female at fruiting.

Since poor site quality could reduce both seed set and plant density, causing a spurious correlation between them, we established low-density experimental arrays of *T. dioicum* in areas lacking in *Thalictrum* adjacent to existing populations. We set up three arrays near Laona, two near Trestle Road, and one near County Road F. In each array, we used 20-cm fiberboard pots to transplant nine female plants and two to three male plants from the nearby population before flowering had begun. We selected large, healthy plants in an attempt to reduce the effect of resource limitation on seed set. Potted females were planted one to 50 m from the group of two to three males. Females were initially located at 1, 2, 3, 5, 8, 13, 21, 34, and 50 m; disturbance by wildlife at the County Road F site resulted in the loss of plants at the longest distances and the subsequent addition of plants at shorter distances. We assessed seed set on each female after fruits matured.

Table 1 Locations and characteristics of the *T. dioicum* and *T. fendleri* (Ranunculaceae) populations included in this study

Species	Site	Township/range site location	Year	Area sampled (m)	Fraction of mature carpels (mean \pm 1 SD)	Total flowering plant density (plants m ⁻²)	Density of flowering males (plants m ⁻²)	Density of flowering females (plants m ⁻²)	Percent of plants that are male	Number of flowers per female plant (mean \pm 1 SD)
<i>Thalictrum fendleri</i>	Kendall	T. 38 N. R. 110 W. S23 NE 1/4	2000	20 \times 19	0.523 \pm 0.269 a	0.62	0.36	0.27	57%	6.4 \pm 5.6
	Green River	T. 38 N. R. 110 W. S26 NE 1/4	2001	13 \times 13	0.275 \pm 0.226 b	0.34	0.17	0.17	49	7.7 \pm 6.5
<i>Thalictrum dioicum</i>	County Road F	T. 33 N. R. 17 E. S6 NE 1/4	2000	20 \times 17	0.653 \pm 0.136 bc	0.72	0.39	0.33	54	47.9 \pm 41.9
			2001	20 \times 17	0.656 \pm 0.192 bc	0.70	0.38	0.32	54	48.1 \pm 35.7
			2002	20 \times 17	0.653 \pm 0.259 bc	0.82	0.39	0.43	47	46.7 \pm 41.2
	Laona	T. 37 N. R. 15 E. S34 NE 1/4	2000	20 \times 12	0.512 \pm 0.235 a	0.68	0.35	0.33	52	33.4 \pm 60.7
	Trestle Road	T. 35 N. R. 15 E. S1 NE 1/4	2002	20 \times 12	0.647 \pm 0.341 abc	0.85	0.49	0.35	58	49.3 \pm 53.0
Peshigo River	T. 36 N. R. 16 E. S28 NW 1/4	2002	10 \times 10	0.756 \pm 0.143 c	0.91	0.28	0.63	31	30.9 \pm 24.8	
			2002	10 \times 10	0.535 \pm 0.232 ab	0.045	0.020	0.024	45	18.8 \pm 19.5

Thalictrum dioicum sites were located in northern Wisconsin, USA and *T. fendleri* sites were in Sublette County, Wyoming, USA. Densities reported for the County Road F site do not include males with buds removed before flowering. Means within species that share the same letter are not significantly different based on Tukey's method and $\alpha = 0.05$

Statistical analyses

The fraction of carpels matured was not a normally distributed variable in most populations, and we applied an arcsine square root transformation to this variable for all of the analyses within natural populations and for the pollen addition experiment. In the experimental arrays, the fraction of carpels matured was strongly skewed towards zero, and we analyzed these data with the nonparametric Spearman's Rho to determine how distance affects the fraction of carpels matured.

We treated data from different years within the same population as independent sets of observations, and in the County Road F sites, where male density was experimentally reduced, we based all calculations of site density on the plants left after clipping. We used an independent samples *t*-test in *T. fendleri* and analysis of variance in *T. dioicum* to compare between sites/years both the number of flowers per plant in females and the fraction of carpels matured. We used regression analysis to examine the relationship between site density and mean fraction of carpels matured in *T. dioicum*. Since sex ratio varied somewhat among sites in *T. dioicum*, we also conducted two additional regression analyses; one with male-only density as a predictor of seed set, and one with female-only density as a predictor of seed set. A positive relationship between female density and seed set suggests that site factors other than pollen availability, such as resource levels, are affecting the among-site patterns.

To compare pollen addition plants with control plants, we used an independent samples *t*-test for each site to compare fraction of carpels matured on hand-pollinated plants outside the mapped plots with unmanipulated plants within the mapped plots.

Within sites, we used multiple regression to determine the effects of pollen availability on the fraction of carpels matured. We included the distance to the nearest potential pollen donor as a log-transformed independent variable because the distribution of pollen from a male plant is expected to decline rapidly. We also included three other measures to estimate pollen availability; the number of flowers on the nearest

potential pollen donor, the number of pollen donors less than 2 m away, and the total number of male flowers less than 2 m away. We used a combination of forwards and backwards elimination with a threshold of $\alpha = 0.10$ to identify significant independent variables and we report only results of significant models and factors.

Results

The dense *T. fendleri* site (Kendall) matured a greater fraction of carpels than the sparse site (Green River—Table 1; $t = 4.160$, $df = 86$, $P < 0.0001$). Comparisons among the *T. dioicum* populations showed a high variation among the populations/years in the fraction of carpels matured (Table 1; ANOVA: $F = 5.494$, $df = 6, 347$, $P < 0.0001$). However, density of all plants at a site was not a significant predictor of the fraction of carpels matured in *T. dioicum* ($r^2 = 0.45$, $F = 4.08$, $df = 6$, $P = 0.099$). When the two sexes were analyzed separately, density of males was not a predictor of the fraction of carpels matured ($r^2 = 0.14$, $F = 0.789$, $df = 6$, $P = 0.42$), but sites with a higher density of females had a greater fraction of matured carpels ($r^2 = 0.61$, $F = 7.81$, $df = 6$, $P = 0.038$). Adding pollen did not significantly increase the fraction of carpels matured in any of the *T. dioicum* populations (Fig. 1).

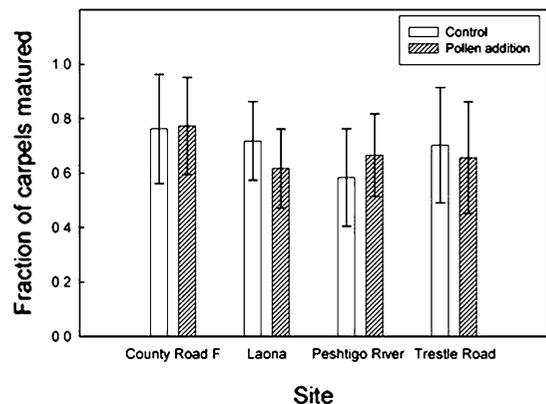


Fig. 1 Mean fraction of carpels matured in control and pollen addition treatments in four populations of *Thalictrum dioicum* (Ranunculaceae) in northern Wisconsin, USA in 2002. Error bars are ± 1 SE from the mean

Mean flower number per plant on females varied somewhat over sites in *T. dioicum* (ANOVA: $F = 2.186$, $df = 6, 354$, $P = 0.044$), and the lowest-density site (Peshtigo River) also had the lowest mean flower number. Flower number was not different between the two *T. fendleri* sites ($t = 0.980$, $df = 86$, $P = 0.330$).

In *T. fendleri*, none of our measures of pollen availability were significant predictors of seed set at Kendall, the high-density population, but decreasing distance to the nearest male and an increasing number of male flowers within 2 m increased seed set at Green River, the low-density population (Fig. 2, Table 2). Similarly, the distance to the nearest male was only a significant predictor of seed set at the lowest-density *T. dioicum* site (Peshtigo River—Table 2, Fig. 3). In a high-density *T. dioicum* population (Laona 2002), an increase in the total number of male flowers within 2 m increased seed set, and the density of males within 2 m had a marginally significant effect in the Laona 2000 population, a medium-density site (Table 2). Seed set in the highest density *T. dioicum* population (Trestle Road) was unrelated to any of the indexes of local pollen availability. In the County Road F population, none of the indexes were significant,

despite the local isolation of female plants through removal of male inflorescences (Fig. 3).

Only in the lowest-density *T. fendleri* and *T. dioicum* populations (Green River and Peshtigo River) did seed set decline with increasing distance to the nearest flowering male (Figs. 2, 3), and the amount of variation in seed set explained by the independent variables was also highest at these sites (Table 2). In the experimental arrays, seed set was sensitive to the proximity of males, and females more than 20 m from males rarely matured seeds (Fig. 4). While females at County Road F, Peshtigo River, and the artificial arrays experienced similar degrees of isolation from males, isolation did not affect seed set in the otherwise dense County Road F site, and had the strongest effect in the very low-density artificial arrays (Fig. 3).

Discussion

In low-density populations of both species, seed set is sensitive to the proximity of available pollen, but at greater population densities, variation in pollen availability seems to have very little impact on variation in seed set. In *T. dioicum*, we found that population-level seed set was

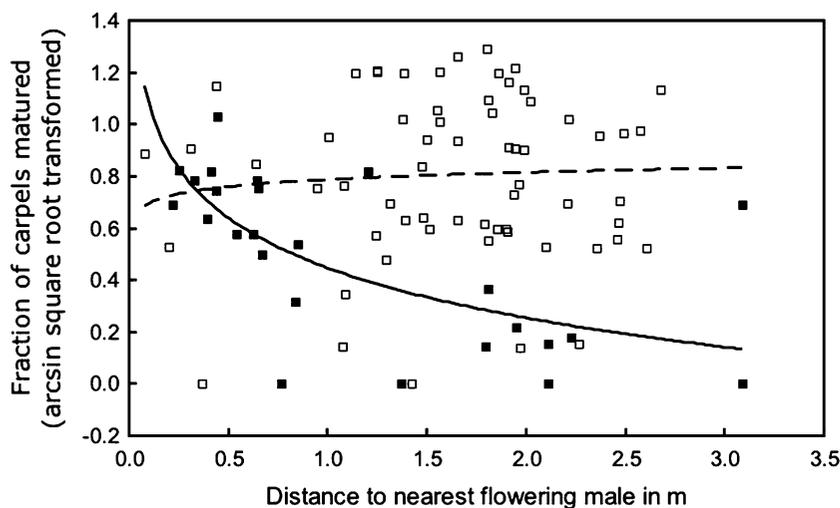


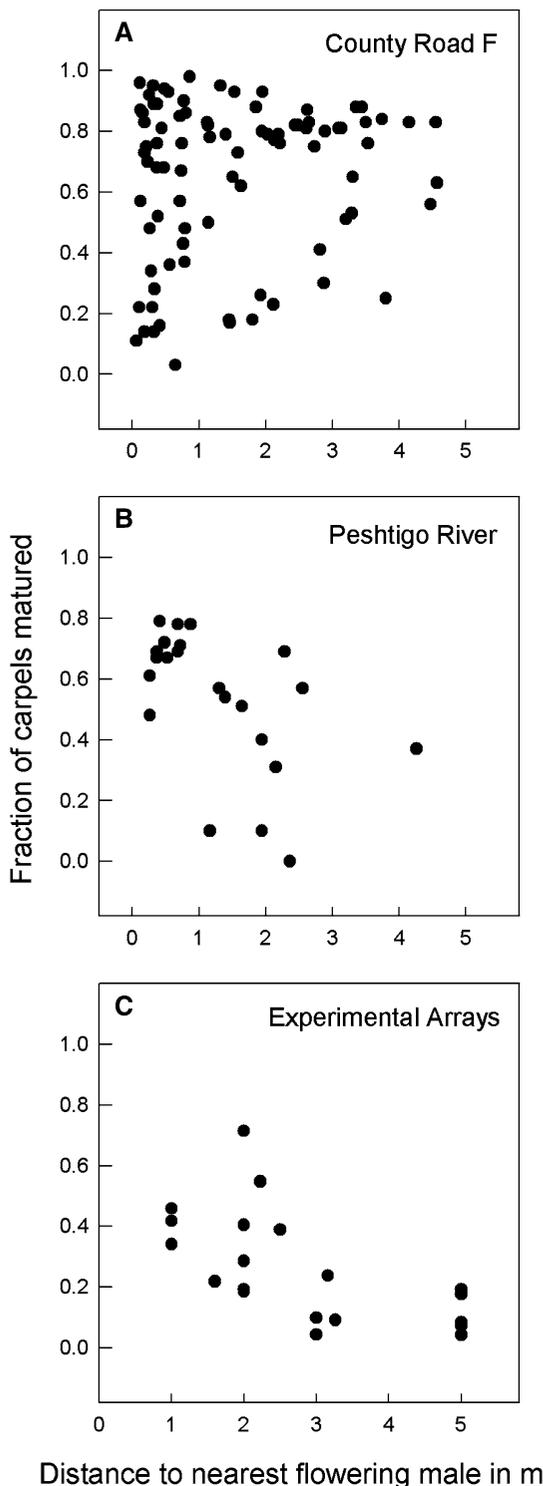
Fig. 2 Distance to the nearest flowering male in m as a predictor of the fraction of carpels matured on female plants in two *Thalictrum fendleri* (Ranunculaceae) sites in Sublette County, Wyoming, USA in 2001. A logarithmic best-fit line is shown for both populations, and distance is a

statistically significant predictor of seed set at Green River but not Kendall. The solid squares and solid line represent the Green River site and the open squares and dashed line represent the Kendall site

Table 2 Within-site regression of fraction of matured carpels (arcsine square root transformed) on local pollen availability characteristics in populations of *T. dioicum* (Ranunculaceae) in northern Wisconsin, USA and *T. fendleri* (Ranunculaceae) in Sublette County, Wyoming, USA

Species	Site	Year	Total flowering plant density (plants m ⁻²)	Regression analysis				Coefficient	T	P-value of factor	
				r ²	df	F	P-value				Factor
<i>Thalictrum fendleri</i>	Kendall Green River	2001	0.62	–	–	–	–	–	–	–	
		2001	0.34	0.589	24	13.94	<0.0001	Male flowers <2 m	2.30 × 10 ⁻³	2.15	0.043
<i>Thalictrum dioicum</i>	County Road F	2000	0.72	–	–	–	–	–	–	–	
		2001	0.70	–	–	–	–	–	–	–	
		2002	0.82	–	–	–	–	–	–	–	
	Laona	2000	0.68	0.053	58	3.169	0.080	Males <2 m	1.58 × 10 ⁻²	1.78	0.080
		2002	0.85	0.070	63	4.670	0.035	Male flowers <2 m	2.51 × 10 ⁻⁴	2.16	0.035
	Trestle Road	2002	0.91	–	–	–	–	–	–	–	
Peshtigo River	2002	0.045	0.27	21	7.47	0.013	Distance to nearest male	-0.180	-2.73	0.013	

Sites were tested with the following four factors: log distance to nearest male (distance to nearest male), number of flowers on the nearest male, total number of male flowers within 2 m (male flowers <2 m), and total number of males within 2 m (males <2 m). Only models with factors remaining after backwards elimination multiple regression with a threshold of $\alpha = 0.10$ are reported. All male inflorescences were removed from a 5 × 5 m² patch in the center of the County Road F site in all the 3 years to artificially lower density, and the clipped plants are not included in the regression or density calculation



correlated with female density but not male density, and hand pollinations did not significantly increase seed set. It appears that variation

Fig. 3 Fraction of carpels matured as a function of distance to nearest male for *Thalictrum dioicum* (Ranunculaceae) plants at three sites in northern Wisconsin, USA; (a) County Road F in 2000, a high-density population where density was reduced by clipping male plants before anthesis, (b) Peshtigo River in 2002, and (c) the experimental arrays located at three sites in 2002 (only females 5 m or less from a male are included in the figure)

in seed set among sites in *T. dioicum*, and much of the variation within sites, is likely due to factors other than the general availability of pollen. We also found a similar trend in *T. fendleri*, in which the more dense population showed no relationship between pollen availability and seed set.

Population-level seed set in *T. dioicum* was not significantly related to total population density or the density of males in the population. However, sites with a higher density of females also had higher levels of seed set. These results are consistent with resource limitation of seed set, rather than pollen limitation. *Thalictrum dioicum* plants in sites with more resources available for female survival, growth, and flowering could also have more resources to invest in seed set (McCall and Primack 1987). The lack of a relationship between male density and seed set suggests that increasing population-level densities of pollen are not significantly impacting population-level seed set in *T. dioicum*.

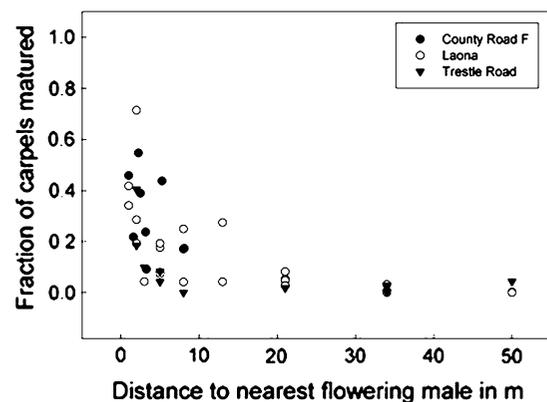


Fig. 4 Fraction of carpels matured as a function of distance to nearest male in m in experimental arrays of *Thalictrum dioicum* (Ranunculaceae) plants at three sites in northern Wisconsin, USA in 2002. Distance was significantly negatively correlated with the fraction of carpels matured ($r = -0.572$, Spearman's Rho = -0.7813 , $P < 0.0001$)

At the plant level, local pollen availability was not a significant predictor of seed set in high-density *T. dioicum* and *T. fendleri* populations. Even when *T. dioicum* females in the otherwise high-density County Road F population experienced levels of local isolation similar to females in the low-density population, seed set was not related to the distance to the nearest flowering male. Although pollen dispersal from individual plants is typically leptokurtic (Levin and Kerster 1974), pollen from many plants may produce a pollen cloud adequate to pollinate flowers even on locally isolated females. Thermal turbulence in the forest understory during warm spring days may keep pollen airborne and close to the ground, increasing the chance of pollination (Dowding 1987; Jackson and Lyford 1999).

However, the abundance of local pollen did impact seed set within a few populations of *T. dioicum*, and distance to the nearest flowering male explained 27% of the variation in seed set at the lowest-density population. In addition, seed set declined rapidly with increasing distance from males in the low-density experimental arrays of *T. dioicum*. While the number of arrays we used was small, all arrays showed a similar strong relationship, and they were designed to ensure that the density effects we measured were not an artifact of resource limitations to both plant density and seed set. Thus, the decrease in pollen receipt due to isolation appears to limit seed set in isolated plants in already low-density populations independent of resource availability. However, the number of plants experiencing this level of isolation is likely to be low. Plants in small, marginal populations and plants at the edges of larger populations are the most likely to experience pollen limitation.

Our pollen addition experiment showed little evidence for pollen limitation in the study populations of *T. dioicum*. Although hand pollinations did increase seed set slightly at Peshtigo River (the lowest density *T. dioicum* site), hand pollinations at Laona resulted in a slight decrease in seed set, and neither trend was significant. Therefore, while pollen limitation does potentially occur at very low densities in natural populations, it does not appear to be a widespread phenomenon within populations of *T. dioicum*.

The two *T. fendleri* populations we studied were similar to *T. dioicum* in their relationship among overall population density, local isolation, and seed set. For Kendall, the high-density *T. fendleri* site, none of the measures of local pollen availability affected seed set, and a hand pollination experiment at this site in 2002 (Steven and Waller 2004) did not significantly increase seed set. However, local pollen availability appears to be influencing reproductive success at Green River, the low-density population of *T. fendleri*. The measures of pollen availability included in the multiple regression analysis for this site explained 59% of the observed variability in seed set, and the mean seed set was about half that of the high-density *T. fendleri* population. While plants in both populations show similar levels of seed set in plants close to a pollen donor, increasing isolation only reduces seed set in the low-density population.

Local pollen availability appears to affect seed set more in *T. fendleri* than in *T. dioicum*. Although the Peshtigo River site, the lowest-density *T. dioicum* population, was much less dense than the Green River site, measures of local pollen availability at Peshtigo River only explained 27% of the variation in seed set, and average seed set at the site was not the lowest observed in *T. dioicum*. This difference could potentially be due to greater pollen production in *T. dioicum*; it produces three times as many pollen grains per ovule than *T. fendleri*, and also produces more flowers per plant (Steven and Waller 2004).

Dioecious wind-pollinated plants like *T. fendleri* and *T. dioicum* may be particularly susceptible to pollen limitation as they cannot self-fertilize and only some plants produce pollen. However, we only found evidence for pollen limitation in isolated plants in low-density populations. While seed set can be sensitive to pollen production in some environments, most of the populations we studied seem to be effectively avoiding pollen limitation. The production of high numbers of pollen grains as observed in these dioecious species (Steven and Waller 2004) and other out-crossed wind-pollinated plants (Cruden 1977) appears to ensure pollination in most moderate- to high-density populations even in locally isolated plants. Thus, the same characters that make these

species vulnerable to pollen limitation may have provided selection pressure to increase pollen production to levels that now generally assure reproductive success.

Acknowledgements We thank Murray Clayton, Thomas Givnish, Thomas Sharkey, Linda Graham, and four anonymous reviewers for helpful comments and discussion on earlier drafts of this manuscript. Brian Anacker, Jeanne Sheahan, Timothy Lisko and Josh Ladwig provided assistance in the field. This study constitutes part of JS's dissertation research at the University of Wisconsin-Madison, and is based upon work supported under a National Science Foundation Graduate Fellowship to JS and grants from the Beta Chapter of SDE-Graduate Women in Science and the J. J. Davis fund of the Botany Department at UW-Madison.

References

- Allison TD (1990) Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. *Ecology* 71:516–522
- Antos JA, Allen GA (1994) Biomass allocation among reproductive structures in the dioecious shrub *Oemleria cerasiformis* – a functional interpretation. *J Ecol* 82:21–29
- Antos JA, Allen GA (1999) Patterns of reproductive effort in male and female shrubs of *Oemleria cerasiformis*: a 6-year study. *J Ecol* 87:77–84
- Ågren J (1996) Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* 77:1779–1790
- Berry PE, Calvo RN (1989) Wind pollination, self-incompatibility and altitudinal shifts in pollination systems in the High Andean genus *Espeletia* (Asteraceae). *Am J Bot* 76:1602–1614
- Bierzychudek P (1981) Pollinator limitation of plant reproductive effort. *Am Nat* 117:838–840
- Bosch M, Waser NM (1999) Effects of local density on pollination and reproduction in *Delphinium nuttalianum* and *Aconitum columbianum* (Ranunculaceae). *Am J Bot* 86:871–879
- Bosch M, Waser NM (2001) Experimental manipulation of plant density and its effect on pollination and reproduction of two congeneric montane herbs. *Oecologia* 126:76–83
- Brunet J, Liston A (1999) The evolution of dioecy in the genus *Thalictrum* (meadow rue) (Ranunculaceae). International Botanical Congress, St. Louis, MO, USA
- Burd M (1994) Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Bot Rev* 60:83–139
- Cruden RW (1977) Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31:32–46
- Dow BD, Ashley MV (1998) High levels of gene flow in bur oak revealed by paternity analysis using microsatellites. *J Hered* 89:62–70
- Dowding P (1987) Wind pollination mechanisms and aerobiology. *Int Rev Cytol* 107:421–437
- Groom MJ (1998) Allee effects limit population viability of an annual plant. *Am Nat* 151:487–496
- Honig MA, Linder HP, Bond WJ (1992) Efficacy of wind pollination: pollen load size and natural microgametophyte populations in wind-pollinated *Staberoha banksii* (Restionaceae). *Am J Bot* 79:443–448
- Jackson ST, Lyford ME (1999) Pollen dispersal models in Quaternary plant ecology: assumptions, parameters, and prescriptions. *Bot Rev* 65:39–75
- Kato E, Hiura T (1999) Fruit set in *Styrax obassia* (Styracaceae): the effect of light availability, display size, and local floral density. *Am J Bot* 86:495–501
- Knapp EE, Goedde MA, Rice KJ (2001) Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* 128:48–55
- Kunin WE (1992) Density and reproductive success in wild populations of *Diploaxis eruroides* (Brassicaceae). *Oecologia* 91:129–133
- Kunin WE (1993) Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology* 74:2145–2160
- Lemen C (1980) Allocation of reproductive effort to the male and female strategies in wind-pollinated plants. *Oecologia* 45:156–159
- Levin DA, Kerster HW (1974) Gene flow in seed plants. *Evol Biol* 7:139–220
- Lubbers AE, Christensen NL (1986) Intraseasonal variation in seed production among flowers and plants of *Thalictrum thalictroides* (Ranunculaceae). *Am J Bot* 73:190–203
- McCall C, Primack RB (1987) Resources limit the fecundity of three woodland herbs. *Oecologia* 71:431–435
- Molano-Flores B, Hendrix SD, Heard SB (1999) The effect of population size on stigma pollen load, fruit set, and seed set in *Allium stellatum* Ker. (Liliaceae). *Int J Plant Sci* 160:753–757
- Niesenbaum RA (1993) Light or pollen- seasonal limitations on female reproductive success in the understory shrub *Lindera benzoin*. *J Ecol* 81:315–323
- Nilsson SG, Wästljung U (1987) Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* 68:260–265
- Regal PJ (1982) Pollination by wind and animals: ecology of geographic patterns. *Annu Rev Ecol Syst* 13:497–524
- Roll J, Mitchell RJ, Cabin RJ, Marshall DL (1997) Reproductive success increases with local density of conspecifics in a desert mustard (*Lesquerella fendleri*). *Conserv Biol* 11:738–746
- Russell SK, Schupp EW, Tepedino VJ (1998) Reproductive biology of curleaf mountain mahogany, *Cercocarpus ledifolius* (Rosaceae): self-compatibility, pollen limitation, and wind pollination. *Plant Species Biol* 13:7–12

- Steven JC, Waller DM (2004) Reproductive alternatives to insect pollination in four species of *Thalictrum* (Ranunculaceae). *Plant Species Biol* 19:73–80
- Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, NJ
- Tonsor SJ (1985) Leptokurtic pollen-flow, non-leptokurtic gene-flow in a wind-pollinated herb, *Plantago lanceolata* L. *Oecologia* 67:442–446
- Whitehead DR (1983) Wind pollination: some ecological and evolutionary perspectives. In: Real L (ed), *Pollination biology*. Academic Press, Inc., New York, pp 97–109
- Wilcock C, Neiland R (2002) Pollination failure in plants: why it happens and when it matters. *Trends Plant Sci* 7:270–277