Promoting the Science of Ecology

POLLINATOR SHARING AND SEED SET OF
STELLARIA PUBERA: COMPETITION FOR POLLINATION[1]

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Abstract. I used field experiments to examine the effect of pollinator sharing on seed set in the understory herb *Stellaria pubera*. In piedmont North Carolina the solitary bee and fly pollinators of this species are also frequent visitors to *Claytonia virginica*. Removals of nearby flowers of *C. virginica* increased seed set of *S. pubera*. Examination of seed set in populations of potted plants indicated that the effect was due to the change in species composition rather than plant density. Variation in seed production was high, however, and even when flowers were provided with excess pollen through supplemental hand pollinations, only 20% of ovules produced seeds.

Competition for pollination appears to be one of several selective forces that act on blooming time of *S. pubera*. *Stellaria pubera* blooms slightly later than *C. virginica*. Whereas the seed set of early flowers was increased 13% by removal of *C. virginica* and 19% by hand pollination, seed set of late flowers was unaffected. Plants forced to bloom early also tended to be more pollinator-limited than control plants. Removal of *C. virginica* did not, however, increase the seed set of *S. pubera* plants forced to bloom early significantly more than that of control plants. Other forces are probably also involved in the maintenance of blooming time.

Key words: Claytonia virginica; *competition; field experiments; insects; phenology; pollinator-limitation; pollinators; reproduction; seeds;* Stellaria pubera.

INTRODUCTION

Competition has often been viewed as a prime force in evolution and as a determinant of population abundances. Competition between species typically involves a shortage of space, food, or some physical resource. Higher plants, however, may also compete interspecifically for pollination. Such competition occurs when plants of one species suffer a reduction in reproductive success as a result of sharing pollinators with other species. Reproductive success may be impaired either through a reduction in the number of visits made by pollinators, or through transfer, by animals or wind, of pollen from one species to flowers of another. Since 1895 when Robertson proposed the idea, numerous naturalists have argued that competition for pollination is a selective force responsible for much variation in floral characteristics (e.g., Grant 1949, Mosquin 1971, Heinrich 1975, Waser 1983). Pollinator sharing can mold floral attributes either through its effect on the female component of reproductive success, seed production, or on the male component, spread of pollen to conspecific stigmas (Charnov 1979, Willson 1979). Pollinator sharing may also contribute to the low seed sets in many natural populations (Kevan 1972, Reader 1975), and it could, under restricted conditions, lead to competitive exclusion of a plant species (Levin and Anderson 1970, Straw 1972, Waser 1978a). My main objectives are to investigate whether pollinator sharing indeed reduces seed set in a natural population and whether competition for pollination is a selective force on flowering time.

Although the last two decades have witnessed a surge of interest in pollination ecology, the evidence that species compete for pollination is still largely indirect. Competition for pollination is often inferred from apparently staggered flowering periods of species in the same community (Lewis 1961, Macior 1970, Frankie et al. 1974, Pojar 1974, Heinrich 1975, Reader 1975, Stiles 1977, Feinsinger 1978, Pleasants 1980, Lack 1982a). Other sorts of observational evidence of competition for pollination exist (e.g., Levin and Kerster 1967, Free 1968, Beattie 1969, Mosquin 1971, Levin and Berube 1972, Lack 1976, Howell 1977, Brown and Kodric-Brown 1979, Thomson 1980), but these data are also subject to alternative interpretations (reviewed in Waser 1983). Experimental studies of competition for pollination have been scarce (Waser 1978b, Kephart 1983). Only Waser has directly measured the effect of sharing pollinators, in this case hummingbirds, on a component of plant reproductive success.

In this paper I describe results from an experimental study of competition for pollination by nonsocial insects. I examine the effect of the presence of *Claytonia virginica* L. (Portulacaceae) on the seed set of *Stellaria pubera* Michaux (Caryophyllaceae), a vernal herb common in deciduous forests of eastern North America. These two plants, both visited by small bees and flies, partially overlap in blooming time, with *S. pubera* blooming slightly later than *C. virginica*. I ask two questions: (1) Does pollinator sharing with *C. virginica* reduce seed set in *S. pubera*? (2) Is competition for

pollination a selective force favoring later blooming in
S. pubera?

EXPERIMENTAL SYSTEM

Study sites

I conducted this study in mesic, lowland deciduous
forest in the piedmont region of North Carolina. One
study site (NA) was an alluvial area in the Oosting
Natural Area of Duke Forest, Orange County. The oth-
er main site (KD) was a rocky slope in the gate 24
access area of the Korstian Division of Duke Forest.
Stellaria pubera is equally abundant at the two sites.
At site NA, individual *S. pubera* plants are generally
isolated by clumps of *C. virginica,* so that their seed
set could be severely affected by pollinator sharing.
Claytonia virginica is extremely abundant over all of
site NA but is restricted to a narrow area along the
stream at site KD. In piedmont North Carolina this
species often forms dense stands with only scattered
individuals of other species interspersed. For this rea-
son, and because its seed set is usually not pollinator-
limited at these sites (Motten et al. 1981), pollinator
sharing probably has little effect on seed set. Other
common herbs at these sites that share pollinators and
overlap in blooming time with *S. pubera* are *Thalic-
trum thalictroides* and *Cardamine angustata.*

Floral biology

The floral biology of *Stellaria pubera* is similar to
that of *Claytonia virginica* in many respects (see Mot-
ten 1982*a*). Both species are self-compatible but not
self-pollinating and therefore require insect pollination
to produce seeds. Their protandrous flowers have white,
bowl-shaped corollas 1–2 cm in diameter and produce
pollen as well as similar amounts of nectar. Both species
are perennials.

The two species differ in inflorescence structure and
plant size. In *S. pubera* the number of inflorescences
per plant ranges from 1 to 15 or more. The inflores-
cences branch repeatedly and dichotomously. Most in-
florescences bear 15 or fewer flowers (range = 1–35),
typically opening over a period of 3 wk. Each flower
remains staminate for 1–3 d while its erect anthers
dehisce. It then becomes receptive or pistillate as the
stamens spread outward to rest on the petals and the
stigma enlarges. Ovule number was usually between 9
and 21 at my sites. Although *S. pubera* produces rhi-
zomes, at my sites individual plants were usually widely
separated and could be easily distinguished.

A *C. virginica* plant has 1–5 inflorescences that arise
from a corm. Each inflorescence bears 6–15 flowers
that open 1–2 at a time.

METHODS AND RESULTS

Insect pollinators

I used two methods to quantify the extent to which
S. pubera shares floral visitors with *C. virginica.* First,

TABLE 1. Percentage of visits made by each insect type to
flowers in mixed-species plots. The percentages were av-
eraged over 62 observation intervals during which 1192
visits to *S. pubera* and 1552 to *C. virginica* were recorded.

Insect type	Percent of visits	
	S. pubera	*C. virginica*
Bombyliidae		
Bombylius major	65.1	54.1
Anthomyiidae		
Hylemya platura	0.4	1.7
Syrphidae	0.9	0.3
Tachinidae		
Gonia sp.	0.1	0.2
Anthophoridae		
Nomada spp.*	11.5	3.8
Andrenidae		
Andrena erigeniae	4.2	27.0
Other *Andrena*†	8.0	6.9
Halictidae		
Near *Dialictus abanei*	5.0	4.2
Megachilidae		
Osmia spp.	1.4	0.3
Hesperiidae	0.1	0.2
Lycaenidae		
Lycaenopsis argiolus	0.1	0.4
Pieridae		
Euchlo creusa lotta	0.1	0.4
Unknown	3.3	1.4

* Species could not always be distinguished in the field. See
Motten (1982*a*) for a list of species on *S. pubera* at sites NA
and KD.

† Mostly *A. nigrihirta.*

I recorded the number of visits to flowers in unma-
nipulated plots and the mixed-species plots used in
competition experiments (described below). For each
30-min observation period (total of 31 h) and each
flower species, I determined the percentage of all visits
made by each insect species. Second, I followed insects
at site NA and determined the percentage of individ-
uals visiting *S. pubera* that also visited *C. virginica* or
another species. Observations were made during the
periods of flowering overlap between *S. pubera* and *C.
virginica* in 1980–1982.

In order to find out whether shared visitors are the
actual pollinators of *S. pubera,* I measured the effec-
tiveness of its common visitors as pollinators. Plants
were enclosed in insect-proof cages except during pe-
riods of observation, when the number of visits by each
insect species to each receptive flower was noted. The
plants were then recaged until these flowers withered.
For each flower visited exactly once, I determined seed
set. As a control, I also measured seed set of those
flowers that received no visits.

Stellaria pubera clearly shares pollinators with *C.
virginica.* All insect species that visited *S. pubera* dur-
ing more than one observation period visited *C. vir-
ginica* as well (Table 1). The primary difference be-
tween visitors to these two species was that only *C.
virginica* received a substantial number of visits from
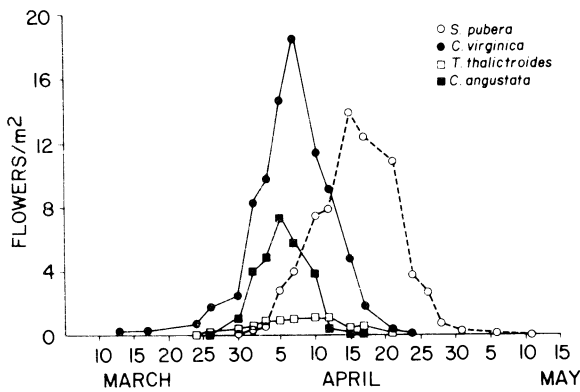the bee *Andrena erigeniae,* which depends on *Clay-*

FIG. 1. Flowering phenology at the Natural Area site during 1981. Starting with 24 March, each point represents the mean flower density for 9 2.0-m² and 18 1.0-m² plots. The other points are means for the larger plots only.

FIG. 2. Layout of experimental populations. (a) Positions of the six *S. pubera* plants in each of the 24 plots of the 1982 removal experiment. (b) Design of each of the four blocks in the experiment involving synthetic populations of potted plants. The four treatments considered in this paper were among six assigned at random to plots at the vertices of a hexagon 5 m on a side. Area of the plot was kept constant. ○ *S. pubera* plant. ● *C. virginica* plant.

tonia pollen to feed its developing larvae (Davis and LaBerge 1975). The bee fly *Bombylius major* and bees in the genus *Nomada,* which together made 77% of the visits to *S. pubera,* were also responsible for more than half of the visits to *C. virginica.* Of 51 individuals that I followed for at least 10 floral visits and that went to *S. pubera,* all but 1 visited flowers of another species as well, and all but 6 visited *C. virginica.*

Bombylius major and *Nomada* spp. are not only common visitors to both plant species but also pollinate *S. pubera.* Thirty-eight of the 74 flowers visited once by *B. major* and all of the 11 flowers visited once by *Nomada* spp. produced a fruit. Both fruit sets were much higher than the fruit set of unvisited controls (3 of 16; $G^2 = 8.52, P < .005$ for *B. major; P < .0001* for *Nomada* spp.). Seeds/fruit averaged 2.59 for flowers visited by *B. major* and 2.72 for flowers visited by *Nomada* spp., but only 1.67 for controls.

Flowering phenology

To quantify the overlap in blooming time, the number of open flowers of each herb species was monitored in 27 permanent 1- or 2-m² quadrats at 2–3 d intervals during the spring of 1981. All quadrats were placed in areas of site NA where both *S. pubera* and *C. virginica* grew.

In both 1981 and 1982, *S pubera* initiated blooming 2–3 wk later than *C. virginica,* but flowering overlap between the two species was substantial. In 1981 *C. virginica* density fell below half of its peak value for the season on 11 April (Fig. 1). This date was used to divide the 1981 blooming season of *S. pubera* at site NA into early and late periods. Twenty-one percent of the area under the flowering curve of *S. pubera* fell in the early period (Fig. 1). Flowers of the other species visited by small bees and flies were relatively uncommon while *S. pubera* was in bloom (Fig. 1).

Competition experiments

Removal experiments. — I performed two removal experiments designed to measure directly the extent of seed-set reductions due to pollinator sharing at site NA. The 1981 removal experiment consisted of controls (C) and two removal treatments applied to square plots 1.41 m on a side. The first treatment (R1) effectively removed *C. virginica* as a competitor for pollination only; the second treatment eliminated competition for resources as well. In R1 plots, I placed an insect-proof cage over each *C. virginica* plant and hand-pollinated all caged flowers to ensure their continued use of normal levels of physical resources. Virtually all *Claytonia* flowers are normally pollinated at this site (Motten et al. 1981). Pollinating insects appeared to visit these plots at rates typical for areas without *C. virginica.* For the second treatment (R2), I completely removed each *C. virginica* plant within 25 cm of a *S. pubera* plant by gently scooping out the shallow corm, and clipped
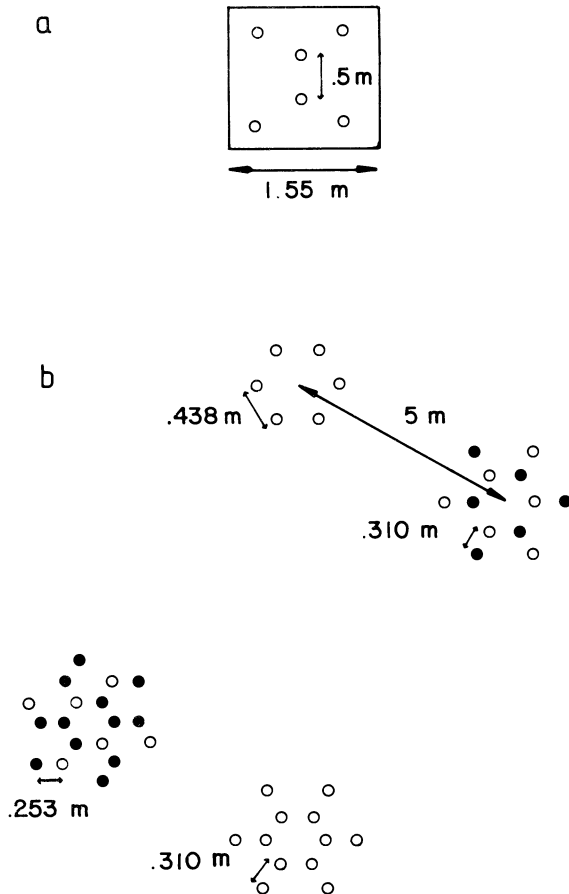
TABLE 2. The effect of removing *C. virginica* on mean seed set of *S. pubera* in 1981.

a) Mean seed set for plots subjected to three competitive regimes. The data are based on 1576 flowers.

Competitive regime	Mean early seed set	Mean late seed set	Number of plots
(C) Control	3.61	1.46	8
(R1) *C. virginica* caged and hand-pollinated	4.03	1.22	4
(R2) *C. virginica* completely removed	4.46	1.92	4

b) *P* values for comparisons of mean early seed set in a randomized block design with extra replication of the control treatment.

Null hypothesis	Alternative hypothesis	*P*
R1 = R2	R1 ≠ R2	.44
(½)(R1 + R2) = C	(½)(R1 + R2) > C	.07

TABLE 3. The effect of removing *C. virginica* on mean early seed set of *S. pubera*.

a) Seed set.

S. pubera treatment	Mean early seed set		No. plots	Error MS	Error df
	Control	*C. virginica* removed			
In situ, 1981	3.61	4.25	16	0.59	10
Potted, 1982	3.98	4.46	12	0.76	10
Potted and forced-bloom, 1982	2.98	3.16	12	0.36	10

b) Combined statistical analysis (Cochran and Cox 1957).

Effect	df	Test statistic	*P*
Treatment of *S. pubera**	2,32	$F = 7.930$	<.01
Presence of *C. virginica**	32	$t = 1.938$	<.05†
Interaction	2,30	$F = 0.319$	>.70

* Main effects were tested after pooling the interaction and error mean squares.

† One-tailed comparison of removal and control plots.

off the inflorescences on each more distant *C. virginica* plant in the plot.

The experimental design consisted of four randomized blocks, each with two control plots and one plot for each of the removal treatments. Each plot contained 3–9 *S. pubera* plants. Flowers were assigned to the early and late blooming periods on the basis of their last day in the pistillate condition. For each plot, I determined mean seed set for each time period by first finding the mean for each plant and then taking the average of the means of all plants in the plot. Throughout this paper, mean seed set refers to a mean number of fully mature seeds per flower, including flowers that made no seeds.

In the 1982 removal experiment I manipulated the blooming time of *S. pubera* as well as the presence of *C. virginica*. An interaction between the effects of these two factors on seed set would indicate that competition for pollination acts as a selective force on blooming time. There were four treatments: early blooming *S. pubera* with *C. virginica* present (EC), early plants with *C. virginica* removed (ER), normal plants with *C. virginica* (NC), and normal plants with *C. virginica* removed (NR). Each treatment was applied to six plots 1.55 m on a side. I cut off the inflorescences of all naturally occuring *S. pubera* and substituted potted *S. pubera* plants. In this way I maintained the natural density of *S. pubera* while manipulating blooming time. Plants were dug up before flowering in 1981 and 1982 in the Korstian Division of Duke Forest. On 24 February 1982, half were moved to a greenhouse. On 9 March, by which time a few flowers had opened, six of these plants were placed in each EC and ER plot, and six control plants were placed in each NC and NR plot, as shown in Fig. 2a. All *C. virginica* inflorescences were cut off before flowering in the removal (ER and NR) plots. Every few days I counted the open flowers of each species in each plot.

Flowers were assigned to early and late blooming periods on the basis of their last day in the pistillate condition. The break point was 15 April, the day on which the density of *C. virginica* fell below half of its peak value for the 1982 season (Fig. 3). For each plot I determined the mean number of flowers per plant and the overall mean seed set as well as the mean seed set for each blooming period. In addition I determined the mean number of seeds per flower that were not attacked by predispersal seed predators.

Since each plot received only one treatment, statistical analyses employed the entire plot as the independent experimental unit. The 1981 removal experiment was analyzed as a randomized block design with extra replication of the control treatment. I partitioned the treatment effect into two orthogonal contrasts: R1 vs. R2, and C vs. R1 + R2. The 1982 experiment was analyzed with a 2 × 2 completely randomized ANOVA. The effect of removing *C. virginica* on mean early seed set was ascertained by means of a combined analysis of the series of results from all removal experiments (Cochran and Cox 1957). Throughout the paper, one-tailed probability levels were used in tests of null hypotheses for which the alternative hypothesis was unidirectional.

The hypothesis that pollinator sharing decreases seed production of *S. pubera* was evaluated primarily by analyzing the effect of removing *C. virginica* on mean early seed set. I used data from early flowers only, because it is on their seed set that I expected pollinator sharing to have its primary effect. Indeed, in both 1981 and 1982, removal of *C. virginica* flowers had no detectable effect on mean late seed set (both *P* > .50) or mean number of flowers per *S. pubera* plant (*P* > .25), indicating that a reduction in early seed set due to
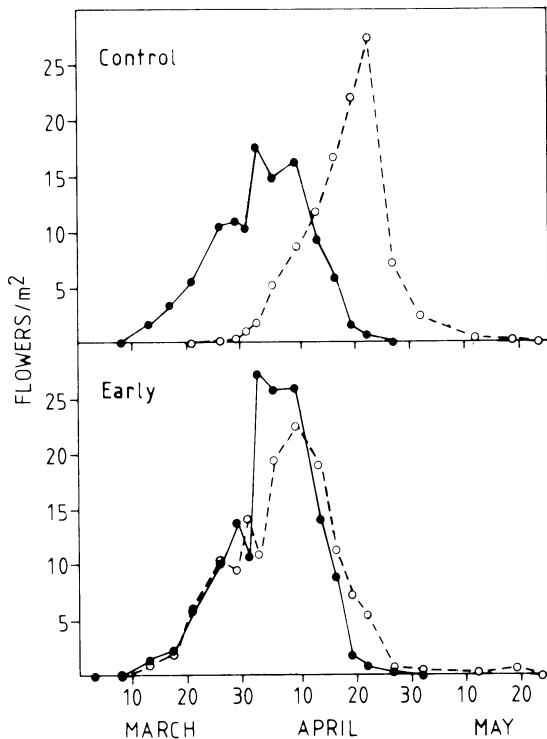
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FIG. 3. Flowering phenology during 1982 in control plots and in plots in which the *S. pubera* plants were forced to bloom early. Each point represents the mean flower density for six 2.4-m² plots. O *S. pubera*. ● *C. virginica*.

TABLE 4. The effects of manipulation of blooming time and removal of *C. virginica* flowers on overall seed set of *S. pubera* in 1982. A two-way ANOVA detected no significant effects on mean seed set.

	Mean seed set*			
	C. virginica present		C. virginica removed	
Blooming time	$\bar{x} \pm$ SE†	No. plots	$\bar{x} \pm$ SE†	No. plots
Early	2.80 ± 0.12	6	3.07 ± 0.31	6
Normal	2.62 ± 0.21	6	2.82 ± 0.18	6

* The data are based on all 5928 flowers, regardless of blooming time.

† Mean ±SE, over replicate plots, of mean seed set.

pollinator sharing would not be cancelled out by increases in other components of seed production (see also *Pollinator limitations*). Mean early seed set of *S. pubera* did not differ between plots from which *C. virginica* had been completely removed and those in which *C. virginica* had been removed as a competitor for pollination only (R2 vs. R1 in 1981 experiment; Table 2). Therefore, I do not distinguish between the different methods of removal in the combined analysis, but instead compare all removals with controls.

The combined analysis entailed the factors "presence of *C. virginica*" and "method of treating *S. pubera*." These methods were control (in 1981), potted (in 1982), and potted and forced to bloom early (in 1982). Removal of *C. virginica* increased the estimate of mean early seed set by 0.64 seeds per flower or 18% in 1981 (Table 2), and, averaging the results for early and normal blooming groups, by 0.33 seeds per flower or 9% in 1982 (Table 3). The analysis indicated that the effect of *C. virginica* was similar regardless of the treatment of *S. pubera* (Table 3). Overall, removal of *C. virginica* flowers significantly increased mean early seed set in *S. pubera* from 3.53 to 3.99, an increase of 13% ($P < .05$; Table 3).

In the 1982 removal experiment I not only manipulated the presence of *C. virginica* but also the blooming time of *S. pubera* (Fig. 3). Whereas only 32% of

the area under the flowering curve of *S. pubera* overlaps with the area under the curve of *C. virginica* in control plots, the overlap is 85% in plots with plants held in the greenhouse to induce early flowering.

Removal of nearby *C. virginica* flowers tended to increase overall seed set of potted *S. pubera* plants by somewhat more in plots with plants forced to bloom early than in control plots (Table 4), but the difference was not statistically significant (interaction effect, .50 > P > .40; Table 4).

Populations of potted plants.—A third competition experiment was designed to ascertain whether the effects of *C. virginica* on seed set were due merely to an increase in plant density or also to the change in species composition. There were four types of synthetic populations of potted plants: 6 *S. pubera* plants; 12 *S. pubera*; 6 *S. pubera* with 6 *C. virginica*; and 6 *S. pubera* with 12 *C. virginica*. I set the experiment up in 1981 in areas of the KD site where natural flowers of these species were sparse. The experimental design consisted of four blocks with treatments assigned at random to the four 1.5-m² plots within each block. Within a plot, plants were arranged in a hexagonal array to maximize interspecific mingling (Fig. 2b). The plants had been dug up in the Korstian Division before flowering in 1981, and each plant transplanted into its own pot. For each plot I determined mean early seed set, calculated as the average over all plants of the mean seed set per flower for flowers that finished blooming on or before 15 April.

The results show that the effect of *C. virginica* was not due to an increase in flower density, but rather to differences between its flowers and those of *S. pubera*. Seed set of these potted plants (Table 5) was similar to seed set in the removal experiment done that year with in situ plants (Table 2). The plots with 6 and those with 12 *S. pubera* plants produced similar numbers of seeds per flower (a priori comparison in a randomized block design, P > .80), indicating that conspecific density does not affect seed set. No difference could be detected between the effects of adding 6 and 12 *C. virginica* plants (P > .10). The two treatments with *C. virginica* did, however, average significantly fewer seeds per flower than the two treatments without (t = 1.92,

TABLE 5. Seed set of *S. pubera* in synthetic populations of potted plants. The mean over replicate plots of mean early seed set is provided for each of four treatments. S = *S. pubera* plant. C = *C. virginica* plant. Standard error of the treatment mean based on a randomized block design = 0.28.

Plant arrangement	Number of plots	Mean early seed set*	P	
12 S	4	4.07[a]	.87	
6 S	4	4.13[a]		.04*
6 S + 6 C	4	3.20[b]	.11	
6 S + 12 C	4	3.92[b]		

* The two means with superscript letter "a" are not significantly different ($P = .87$). The two means with superscript letter "b" are not significantly different ($P = .11$). The means lettered "a" are significantly larger than those lettered "b" (one-tailed $P = .04$). All of these are a priori comparisons.

$df = 9$, one-tailed $P < .05$). In this case, removal of *C. virginica* appeared to increase seed production by 13%, a value similar to that obtained in the other competition experiments. The consistency of the seed-set reductions in all three experiments provides strong evidence that pollinator sharing reduces seed set in *S. pubera* (combined analysis comparing treatments with and without *C. virginica*, $t = 2.53$, $df = 39$, one-tailed $P < .01$).

Pollinator limitations

As a supplement to these direct experiments, I examined a prediction of the hypothesis that pollinator sharing reduces seed set in *S. pubera*. If this hypothesis is true, then the seed set of *S. pubera* plants which bloom early, when *C. virginica* flowers are abundant, will be restricted by a low level of pollen transfer. All else being equal, early-blooming plants will be more pollinator-limited than late-blooming ones. Although allocation of resources within a plant can complicate this pattern, it will usually hold for flowers as well as plants. I investigated the prediction by comparing the effect of hand pollination on seed set of early and late flowers of *S. pubera* plants at site NA, and by comparing the overall effect on these plants to that on plants forced to bloom early.

In 1981 I chose 16 pairs of *S. pubera* plants growing within 1 m of each other and randomly assigned one member in each pair to receive hand pollinations while the other served as a control. Only the earliest blooming inflorescence on each plant was used. In 1982 I used 23 single plants rather than pairs, and hand pollinated flowers on one of the two earliest inflorescences on each plant while leaving the other as a control. All plants were adjacent to dense stands of *C. virginica*. Every day pollen was applied to stigmas of all pistillate flowers on the designated inflorescences; each flower received pollen from conspecific flowers several metres away. The flowers on each inflorescence were assigned to the early and late blooming periods (the breakpoints

were 11 April in 1981 and 15 April in 1982) on the basis of their last day pistillate. Both number of seeds and the percentage of ovules that matured into seeds were determined. For each inflorescence I then calculated mean seed sets and mean percent seed sets for early flowers only, late flowers only, and all flowers.

For separate tests of the effect of hand pollination on single variables, I used paired-comparison t tests supplemented by Bonferroni simultaneous confidence intervals. The multivariate technique of profile analysis for a randomized block design (Timm 1975) was employed to test the null hypothesis that hand pollination has the same effect on mean seed set of early flowers as on mean seed set of late flowers on the same plants.

I also measured the degree of pollinator limitation experienced by *S. pubera* plants forced to bloom early. On 24 February 1982 I moved nine plants potted the previous year into a greenhouse. Thirteen days later I placed the plants 0.63 m apart in two rows at site NA. One inflorescence on each plant was randomly chosen to receive hand pollinations while another served as a control. Initially, pollen was obtained from two other plants forced to bloom early, and later from other plants at the site. Mean seed sets for various blooming periods were determined for each inflorescence.

The seed production of *S. pubera* flowers that bloomed early when *C. virginica* flowers were dense was restricted by a low level of pollen transfer, whereas later flowers were not pollinator-limited. This pattern holds for both mean seed set and mean percent seed set. I discuss below the analyses of mean seed set. Profile analysis confirmed that hand pollination increased mean seed set of early flowers more than that of late flowers ($P < .05$). Separate analyses for the two blooming periods showed that hand pollination significantly increased the mean seed set for early flowers ($P < .05$) but had no effect on mean late seed set ($P > .90$; Table 6). During the early period, the supplemental pollen increased mean seed set by 19%. Most of this effect was due to the increase from 82 to 95% in the percentage of flowers that made a fruit, rather than to an increase in mean seeds per fruit. Inclusion of "year" (1981 or 1982) as a factor in the analysis does not alter the results. Even though 68% of the flowers bloomed during the late period, mean seed set based on all flowers regardless of blooming date was significantly increased by hand pollination (one-tailed $P < .05$). Since number of flowers per inflorescence was unaffected by the treatment (Wilcoxon signed-ranks test, $T = 316$, $df = 38$, $P > .25$), total seed production was increased similarly.

Hand-pollinated inflorescences on plants forced to bloom early also averaged more seeds per flower than control inflorescences on the same plants. Since the sample size is small, I have not analyzed these data statistically. Instead, I simply describe trends. Mean seed set for flowers that bloomed before natural plants

TABLE 6. The effect of hand pollination on mean seed set of naturally blooming *S. pubera* inflorescences.

a) Mean values

Treatment	Mean early seed set	Mean late seed set
Hand-pollinated	3.77	1.56
Control	3.16	1.54

b) Statistical analysis

Variable	SE difference	df	t	Univariate P
Mean early seed set	0.294	38	2.074	.023*
Mean late seed set	0.249	38	0.068	.946

* One-tailed. $P < .05$ when adjusted for multiple comparisons by the Bonferroni method.

initiated blooming was 1.50 for control and 1.70 for hand-pollinated inflorescences. Mean seed set after this period was 2.29 for control and 2.93 for hand-pollinated inflorescences. In contrast to the situation in natural plants, pollinator-limitation in these forced-bloom plants was apparently not restricted to the first flowers produced. Whereas the difference between mean seed set of hand-pollinated and control flowers produced at level 4 or higher (the eighth and later flowers on each inflorescence) was very small (0.18) for natural plants, it was substantial (0.62) for forced-bloom plants. Although the procedural differences between the two experiments preclude a definitive inference, my estimate for the increase in seed set due to hand pollination appears greater for early plants than for plants allowed to bloom naturally (0.58 vs. 0.21 seeds per flower).

DISCUSSION

Pollinator sharing and seed set

Seed production of *Stellaria pubera* was decreased by the presence of *Claytonia virginica* flowers. The experimental designs employed allow me to attribute this effect to pollinator sharing rather than to competition for physical resources. One experiment used a removal method that made the competitor unavailable to pollinators, presumably without affecting its uptake of physical resources. In the other competition experiments plants were individually potted and were not shaded by other herbs. My experiments indicate that *S. pubera* competes interspecifically, but not intraspecifically, for pollination.

My removal experiments measured the effects of pollinator sharing on seed set directly without imposing an artificial spatial pattern on the flowers. Although the experimental areas were not randomly chosen, their plant spatial patterns were not at all unusual for site NA and other alluvial areas in Duke Forest. In other habitats, for example the rocky slopes typical of site KD, *C. virginica* is absent, and there control of seed production and selective pressures on floral characteristics must be different. Models based on the mecha-

nism of competition indicate that my experimental plots were large enough to detect most of the effect of pollinator sharing on seed set of the central plants (Campbell 1983). Although Waser (1978b) also demonstrated seed set reductions in synthetic populations of potted plants, probably through transfer of pollen between species by hummingbirds, it is unclear to what extent the same phenomenon takes place in natural populations where the two plant species are less intermingled and fewer pollinator flights are interspecific.

Removal of *C. virginica* probably increases the lifetime seed production of *S. pubera* plants. Although in some other perennials increases in fruit set are compensated for by abnormally low fruit set the subsequent year (Stephenson 1981, Chaplin and Walker 1982), I observed no such cost to reproduction in *S. pubera*. Potted plants that spent the 1981 season in plots without *C. virginica* and those in plots with *C. virginica* produced similar numbers of flowers (48 vs. 59; ANOVA, $F = 0.31$, df = 1, 41, $P > .50$) and seeds per flower (2.77 vs. 2.74; $F = 0.003$, $P > .90$) at site NA in 1982.

The use of hand pollinations allowed me to estimate the extent to which seed set of *S. pubera* inflorescences is restricted by a low level of pollen transfer. Are plants equally pollinator-limited? My measurements of pollinator-limitation take into account nonindependence of flowers on the same inflorescence, but they ignore the possibility that resources used by hand-pollinated inflorescences to make extra seeds were obtained at the expense of low seed set in adjacent inflorescences. Extensive postpollination movement of resources in *S. pubera* seems, however, unlikely. Not only does each inflorescence have its own set of leaves, but there is no compensation within an inflorescence; mean seed set of untreated flowers did not differ between those on inflorescences with mostly hand-pollinated flowers and those on control inflorescences (paired-comparison $t = 0.84$, df = 20, $P > .25$).

Pollinator sharing with *C. virginica* appears to account for about two-thirds of the total pollinator-limitation experienced by *S. pubera*. Although the confidence limits for these estimates are wide, removal of *C. virginica* increased seed set of early flowers by 13%, whereas excess pollination increased it by 19%. The remainder of the pollinator-limitation may have been due to extended periods of rain or temperatures below 14°C which prevent the pollinators from flying at all. During the longest interval of such inclement weather in the spring of 1982, 5–8 April, hand-pollinated inflorescences averaged 1.38 more seeds per flower than control inflorescences. In contrast, the increase in seed set was only 0.40 before this period (1–4 April) and 0.55 between it and the end of the overlap period (9–15 April; Fig. 4d).

Seed set was pollinator-limited even though fruit set was fairly high in the natural population (82% during the overlap period) and provision of excess pollen had

little effect on seeds per fruit. In contrast to fruit set, seed set was quite low; in 1981 and 1982 mean early seed set was 26% and mean late seed set was 15%. Overall, inflorescences matured 18% of their ovules. Even with full pollination, only 20% of the ovules matured into seeds. The poor seed production despite availability of excess pollen may be due to low resource availability. Combinations of inadequate pollinator service and limited physical resources have also been suggested for *Asimina triloba* (Willson and Schemske 1980) and *Passiflora vitifolia* (Snow 1982).

The high variance in seed set unrelated to pollination level or to the time of the season also suggests that restricted pollination is not the only factor responsible for low seed set. Differences among plants accounted for the most variance (40% in a nested ANOVA of number of seeds produced by early flowers in control plots of the 1981 removal experiment). Block (representing areas of 10–100 m²), plot, and inflorescence together accounted for only 20%. In addition, even though the locations of potted plants were re-randomized between 1981 and 1982, there was a high correlation ($r^2 = .61$, $P < .0001$) between years in mean early seed set of these plants.

In experiencing pollinator-limitation *S. pubera* may be exceptional among the spring understory herbs pollinated by small bees and flies in piedmont North Carolina. Motten (1982a) suggests that the seed productions of these plants are in general not restricted by insufficient pollination. Despite the absence of effects on current seed production in most of these species, competition for pollination may, however, have produced or be maintaining floral characteristics through differential effects on the reproductive success of alternative phenotypes (Motten 1982b).

Competition for pollination and blooming time

In *S. pubera*, competition for pollination appears to favor selectively a relatively late blooming time. Removal of *C. virginica* increased the seed set of early-blooming flowers but not late flowers (Fig. 4). Early flowers also suffered greater pollinator-limitation. These patterns could reflect merely an artificially high drain on resources by early fruits which leaves little for late ones, rather than a true difference in pollinator-limitation over the season. My work suggests, however, that this is not the case; plants forced to bloom early appeared to experience greater overall pollinator-limitation than unmanipulated ones. If *S. pubera* exhibits heritable variation in flowering time, as a wide variety of other plant species do (Allard and Hansche 1964), these results suggest that pollinator sharing may influence the evolution or maintenance of blooming time.

Although in general my work supports the selection hypothesis, removal of the competitor did not have a significantly greater effect on plants forced to bloom early than on naturally blooming plants. It should be noted that this experiment tested a more subtle effect
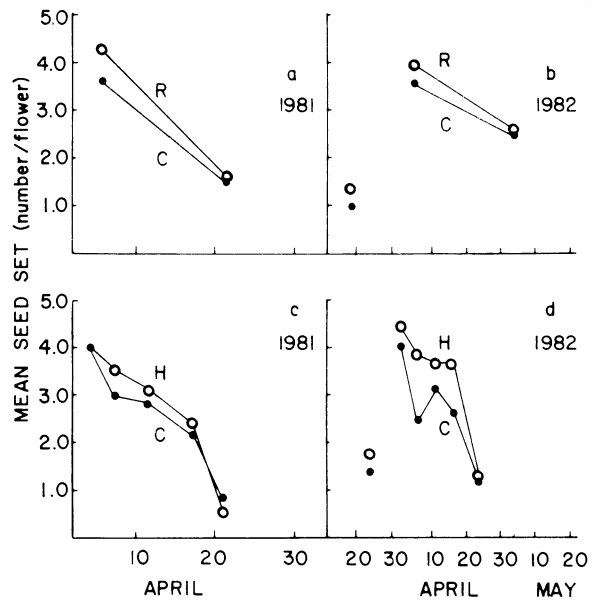

FIG. 4. Seasonal patterns in components of female reproductive success in *S. pubera*. (a) Mean seeds per flower in removal (R) and control (C) plots during 1981. (b) Same as (a) but during 1982. (c) Mean seeds per flower for hand-pollinated (H) and control (C) inflorescences in 1981. (d) Same as (c) but during 1982. Symbols not connected by lines represent data for greenhouse-forced flowers that finished blooming before 28 March, the day unmanipulated plants initiated blooming. All symbols are graphed at the midpoints of the sampling intervals.

than the others. By 16 April plants kept in the greenhouse produced 74% and control plants 20% of their blossoms. Assuming that removal of *C. virginica* increases seed set of early flowers by 13% but that of late flowers not at all, removal is expected to increase total seed production by 10% in the greenhouse plants and 3% in the control plants. My experiment lacked sufficient statistical power to detect such a small difference.

Not surprisingly, other selective forces appear to act on blooming time of *S. pubera*. The earliest flowers on plants forced to bloom early produced few seeds compared to flowers that bloomed during the normal overlap period, even when hand pollinated (Fig. 4d). Cold weather early in the season could be responsible and may favor late blooming. Other selective forces may act in the opposite direction. Late flowers mature only about half as many seeds as early flowers, even when excess pollen is supplied (comparison among dates in MANOVA, $P < .01$; Table 6). This decline in seed set is correlated with canopy development. Schemske (1977) has suggested that similar drops in seed set of other vernal understory herbs are due to falling light levels. If so, light availability would favor early blooming. I also have some evidence (D. Campbell, *personal observation*) that predispersal seed predation by *Coleophora coenosipenella* (Lepidoptera: Coleophoridae)

acts as a selective force on blooming time. It is likely that all the factors together result in balancing selection that maintains blooming time. Mean seeds per flower matured and not attacked by predators was lower in plots with plants forced to bloom early than in plots with control plants in 1982 (ANOVA, $F = 5.16$, df = 1, 10, $P < .05$).

There is a growing body of mostly indirect evidence that competition for pollination selects for divergence in flowering time, as well as divergence in morphology or color, especially among plants pollinated by social hymenopterans (e.g., Heinrich 1975, Pleasants 1980, Gross and Werner 1983, Kephart 1983) and hummingbirds (e.g., Waser 1978b). Convergence in floral characteristics, due to an increase in pollinator visits in the presence of another plant species, and absence of interaction have, however, been suggested as well (Brown and Kodric-Brown 1979, Parrish and Bazzaz 1979, Poole and Rathcke 1979, Rabinowitz et al. 1981, Schemske 1981, Lack 1982b, Thomson 1982). It is by no means clear, in the absence of any other information, what kind of interaction is most likely to occur between plant species visited by the same pollinators. Experimental studies that combine flower removals with variation of plant characteristics will provide strong evidence bearing on pollinator sharing as a selective force, especially if they measure male as well as female reproductive success.

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