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FLORAL BIOLOGY AND REGULATION OF SEED SET AND SEED SIZE IN THE LILY, CLINTONIA BOREALIS[1]

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ABSTRACT

We studied the reproductive ecology of *Clintonia borealis*, a clonal understory species, in eastern Ontario. Flowers are protogynous and require insect pollination for outcrossing and maximum seed set. Most pollination is done by nectar-gathering bumble bees. We recorded pollen deposition and flowering patterns in 1983. Flowering lasted for about 10 days in mid-June. Stigmatic pollen loads were lowest at the onset of blooming, reflecting the scarcity of male-phase flowers. Pollination increased significantly by peak bloom and subsequently remained high. However, since bees fly mostly between neighboring stems, much of the pollen transferred may have been geitonogamous. In 1983, seed set per flower was not increased by supplementing pollination or by reducing the number of fruits competing for resources per stem. Rather, flowers set more seeds (14%) only if both treatments were performed simultaneously. Seed size was increased by 25% when competitive fruits were removed and by 5% more when pollen was added under the removal treatment. Further work in 1984 showed that pollination effects may be related to changes in pollen source. Selfed flowers set fewer and smaller seeds than outcrossed ones when screened from insects and hand pollinated. Outcrossing distance had little effect on seed set or seed size. Thus, in *C. borealis* seed number and seed size are limited by a balance between maternal resource availability and the amount of outcrossing provided by pollinators.

SEED PRODUCTION in flowering plants is constrained by two principle factors: 1) the amount of resources available for flower (Van Andel and Vera, 1977; Solbrig, 1981; Meagher and Antonovics, 1982), ovule (Snow, 1982; Wolfe, 1983), seed (Kawano, Hiratsuka and Hayashi, 1982; Lee and Bazzaz, 1982), and fruit production (Willson and Price, 1979; Stephenson, 1980, 1981; Udovic, 1981; Udovic and Aker, 1981); and 2) the amount and source of pollen that a plant's flowers receive (Willson, Miller and Rathcke, 1979; Primack and Lloyd, 1980; Schemske, 1980; Bierzychudek, 1981; Galen, 1985). The relative importance of resource and pollination levels to seed set not only varies among closely related species (Gross and Werner, 1983), but also within species, with flowering date (Schemske, 1977), habitat (Udovic, 1981), and floral attractiveness (Galen, 1985).

Seed size has been viewed as less responsive to environmental conditions than seed number (Harper, Lovell and Moore, 1970). However, recent studies (e.g., Thompson, 1984; Stanton, 1984a; Schaal, 1984) show that much phenotypic variation in seed size occurs in at least some plant species. Seed number and size are often negatively correlated at an interspecific level (Salisbury, 1942; Primack, 1978) as well as within populations of the same species (Primack, 1978; Janzen, 1982; Stanton, 1984a), indicating that intrinsic resource levels may limit investment in total seed mass of individual fruits. Little information is available on the importance of pollination levels to seed weight. High pollen receipt could reduce seed weight indirectly by augmenting seed number. Alternatively, excess pollination might allow maturation of selected, perhaps heavier, seeds in a manner analogous to selective fruit production (Bookman, 1984). If genes expressed in pollen tube growth are also active in embryo development, then competition among pollen tubes at high levels of pollen deposition could eliminate paternal genotypes that otherwise would yield small seeds. This prediction agrees with findings that male gametophytic competition can affect later stages of offspring development (Mulcahy, Mulcahy and Ottaviano, 1975; Ottaviano, Sari-Gorla and Mulcahy, 1980). Regardless of pollination intensity, pollen genotype influences seed weight in those

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plants that produce smaller seeds with selfing than outcrossing (Schemske and Pautler, 1984).

In this paper we examine temporal patterns of flowering and pollination and the regulation of seed set and seed size in the boreal forest lily, *Clintonia borealis* Ait. (Raf.). In so doing, we provide evidence that for this plant, seed set and seed size are not limited exclusively by either pollination or maternal resource levels, but rather, respond to the balance between these two environmental factors.

MATERIALS AND METHODS—*Plant and study area*—*Clintonia borealis* is an herbaceous plant that forms long-lived clones in the forest understory of the northeastern United States and Canada (Ashmun, Thomas and Pitelka, 1982). Seedling establishment is rare (Ashmun and Pitelka, 1985) and likely to be episodic, as in other perennial forest herbs (Van Andel and Rozema, 1974; Anderson and Beare, 1983). Ramets live for only one year and may or may not flower. Those that bloom have from one to six flowers; flower number is determinate with buds produced the preceding fall and maturing from the apex of the inflorescence downward. Nectar is produced throughout anthesis (Plowright, 1981). The showy yellow-green flowers are protogynous and set no seeds without entomophilous pollination (Thaler and Plowright, 1979). Although flowers are visited by many kinds of insects, bumble bees appear to be the most important pollinators. Thomson and Plowright (1980) observed that bumble bees deposit from 24–369 grains of pollen on visits to emasculated flowers of *C. borealis.* Seed production in populations of *C. borealis* correlates closely with bumble bee abundance suggesting that these insects not only play an important role as pollinators, but that their availability may limit seed numbers sustained by plants (Thaler and Plowright, 1979).

Experiments and observations reported in this paper were made during the summers of 1983 and 1984 in a population of *C. borealis* covering about 0.5 ha southeast of Bell Rapids, Hastings county, eastern Ontario. In this area, *C. borealis* forms dense flowering patches in clearings in the forest understory. We assumed that neighboring stems within each patch were probably ramets of the same clone.

Floral development—Following Plowright (1981) we recognized five flower age classes: 1) first opening (fo), the tepals beginning to relax and expose the stigma; 2) straight sided (ss), the tepals open to a diam of about 2.5–5.0 mm; 3) medium curled (mc), the corolla mouth expanded relative to the base; 4) bell (b), the tepals reflexed about 45° exposing the anthers; and 5) recurved (rc), the tepals curling backward from the corolla mouth. One to three flowers in each age class were collected from each of 10 separate patches (15–30 flowers total per age class). For every flower, the tube width, e.g., distance between opposite tepals at the corolla mouth, and the length of the floral tube formed by the tepals were measured. Anthers were scored as full, predehiscent; dehiscent; or dehisced, empty; and stigma receptivity was tested. We assayed receptivity by immediately staining stigmas of intact pistils with a mixture of freshly made benzidine solution (1% benzidine in 60% ethanol : hydrogen peroxide : water, 4:11:22 v/v/v) (King, 1960) after removal to the lab. This stain reacts with peroxidase enzymes present in receptive stigmas (Zeisler, 1938; Bredemeijer, 1982), changing the color of stigmatic tissue from white to blue in *C. borealis* and other lilies (C. Galen, pers. obs.). Stigmas were scored under a dissecting microscope as having no receptivity, no color change; low receptivity, blue color localized at the periphery of the stigma; or high receptivity, entire stigma staining blue. In each patch the duration of the flower age classes was recorded for three other flowers.

Phenology of flowering and pollen deposition—In 1983, the number of flowers of *C. borealis* in bloom in the study population was sampled at 3-day intervals over the entire flowering period (10 June–19 June). Observers counted flowers in each age class on perpendicular pairs of 10-m line transects walked from each of 10 randomly chosen points. On 10 June, 13 June, and 16 June, pistils were removed from flowers of four ramets on each transect and placed in glassine envelopes. In the lab, their stigmas were excised and immersed individually in drops of benzidine solution on microscope slides so that the total number of pollen grains deposited on each could be counted. Effects of flower age and sampling date on pollen deposition per stigma were determined by a two-way analysis of variance (anova) using the SAS general linear models (GLM) program. The interaction between sampling date and age class could not be tested for significance since no ss or mc flowers were collected on 16 June. The dependent variable, pollen grains per stigma, was log transformed prior to the anova to correct inequalities in variances among groups. Differences in pollen deposition between age classes on the three sampling dates were tested for significance after the anova using Tukey's test for unplanned

TABLE 1. *Floral development in* Clintonia borealis. *Flower age classes: fo = first opening; ss = straight sided; mc = medium curled; b = bell; rc = recurved. Number of days in each age class was measured for 29 flowers*

Age class	Tube width (mm)	Tube length (mm)	Stigma receptivity			Anther condition			Days in age class
	$\bar{x}$ ± SE	$\bar{x}$ ± SE	Absent f (%)	Low f (%)	High f (%)	Full f (%)	Dehiscing f (%)	Empty f (%)	$\bar{x}$ ± SE
fo	1.4 ± 0.17	14.8 ± 0.35	1 (6)	12 (75)	3 (19)	16 (100)	0 (0)	0 (0)	0.1 ± 0.07
ss	3.4 ± 0.30	14.5 ± 0.22	0 (0)	12 (63)	7 (37)	19 (100)	0 (0)	0 (0)	0.1 ± 0.06
mc	11.4 ± 1.07	15.5 ± 0.29	0 (0)	5 (21)	19 (79)	24 (100)	0 (0)	0 (0)	0.6 ± 0.14
b	18.8 ± 0.68	15.9 ± 0.20	0 (0)	3 (9)	29 (91)	16 (50)	9 (28)	7 (22)	1.7 ± 0.25
rc	23.3 ± 0.49	15.2 ± 0.41	0 (0)	0 (0)	15 (100)	0 (0)	6 (33)	9 (67)	1.8 ± 0.24

pairwise contrasts at the 95% confidence level (Sokal and Rohlf, 1981).

Pollinator observations—In 1983 and 1984 bumble bees were seen on flowers of *C. borealis* throughout the flowering period. Since other studies (Thaler and Plowright, 1979; Thomson and Plowright, 1980) include details of bumble bee pollination in *C. borealis,* we limited present observations to the distances traveled by bees between inflorescences and the number of flowers visited on each inflorescence. Bumble bees of the species *Bombus vagans* and *B. perplexus* were followed during peak bloom (15 June), 1983.

Test of resource vs. pollination limitation of seed set and seed size—Prior to the onset of flowering in 1983, we selected 11 patches in which each of four neighboring ramets had four or more buds. In each patch, ramets were assigned at random to the following treatments: pollen addition, resource addition, pollen and resource addition, and control. In the pollen addition treatment, all flowers were left open to natural pollination and the lower, later blooming two to three flowers on each stem also received cross-pollination by hand. Each flower was pollinated on two consecutive days after reaching the bell age class to increase the likelihood that pollen addition would coincide with high stigma receptivity. Pollen was taken from a flower on a donor ramet in an isolated patch at least 10 m from the recipient to ensure outcrossing. Hand-pollination was accomplished by removing the donor anther with forceps and gently brushing it across the recipient stigma until the stigma surface was uniformly coated with pollen. In planning the resource addition treatment, we assumed that amounts of stored nutrients and photosynthates available per flower would be reduced by competition from other flowers and fruits on the same stem (Stephenson, 1981; Lee and Bazzaz, 1982). Accordingly, on inflorescences of the resource addition group, styles of upper flowers were clipped at first opening to prevent pollination and fruit set. The lower two to three flowers were left unmanipulated. This treatment therefore was expected to increase resources on a per flower basis to all unmanipulated flowers. In the pollen and resource addition treatment, stigmas were clipped in upper flowers and cross-pollinated in lower ones. Flowers on control stems were not manipulated, but only fruits of lower ones were collected. Following seed set (about mid-August) the proportion of ovules maturing into seeds was counted for each fruit. Seeds were weighed individually on a Mettler H16 analytical balance. The effects of treatments, flowering patch, and the treatment × patch interaction on seed set and seed weight were examined using anova (SAS GLM program). Proportions were angular transformed prior to the analysis to correct for non-normality. Separate anovas were run for seed set and seed weight. Average seed set and seed weight values of the four treatment groups were further compared following the anovas with Tukey's test at the 95% confidence level.

Test of pollen quality effects on seed set and seed size—In 1983, pollen addition to naturally pollinated flowers increased two potentially limiting factors, total amount of pollen and proportion of outcross pollen deposited, concurrently. In 1984, we standardized the amount of pollen deposited per stigma and varied pollen source in order to determine whether pollen quality, per se, could affect seed set or seed size. The experiment was replicated in 15 flowering patches. In each patch, one ramet with four or more buds was selected at random prior to flowering and its inflorescence was enclosed in fine white nylon mesh bagging to exclude pollinators. The three lowermost flowers were randomly assigned to the following pollination treatments: selfing, near outcrossing, and far outcrossing. Older, unmanipulated flowers and flowers in the outcrossing groups were emasculated early in development (ss) to prevent accidental self-pollination or geitonogamy. Selfed flowers received pollen from their own

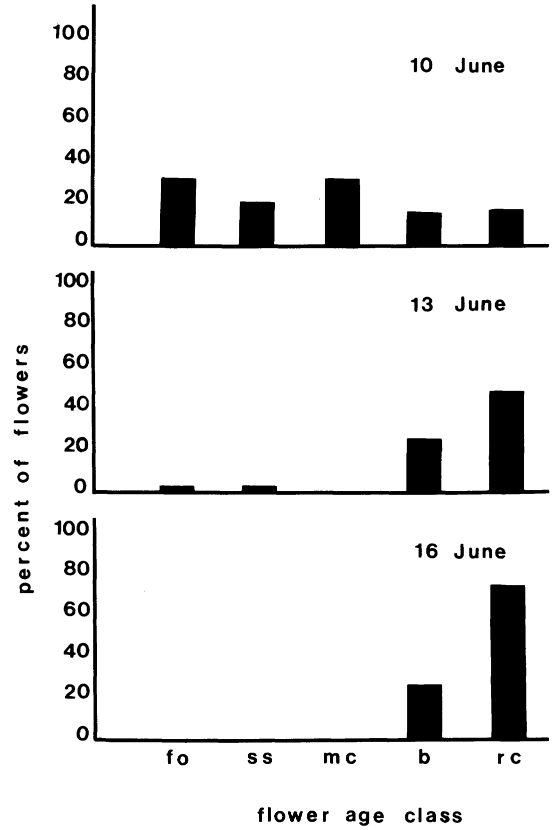

Fig. 1. Phenology of flower age classes in *Clintonia borealis* during 1983. Age classes: fo = first opening; ss = straight sided; mc = medium curled; b = bell; rc = recurved. Flowers are receptive to pollen from ss through rc age classes. Most anthers dehisce during the b age class.

anthers. After selfing was finished, anthers were removed to prevent additional pollination. Near outcross flowers were pollinated with pollen from isolated donor patches about 10 m from recipients. Far outcross flowers received pollen from plants growing about 200 m away. Pollinations were carried out as described above for the pollen addition treatment. We recorded the order of flowering in the inflorescence so that any effect due to pollination timing (Bookman, 1983) would be separable from that of pollination treatment. Bags were removed after styles abscissed from newly developing fruits, about 5 days after pollination. Ripened fruits were collected 4 wk later, and the proportion of ovules developing into seeds and individual seed weights in each were measured. Proportions were angular transformed and two analyses of covariance (ancova) were run, one for seed set and the other for seed weight, to examine the effects of pollination treatment. In both, flowering order was introduced as a covariate, and the effects of the interaction between pollination treatment and flowering order, and flowering patch from which each fruit was collected, were also assessed, using SAS GLM. Mean seed set per fruit and seed weight in different pollination groups were further compared after the ancovas using Tukey's test at the 95% confidence level.

TABLE 2. *Sums of squares table for analysis of variance in pollen deposition on stigmas in flowers of* Clintonia borealis. *Pollen grains per flower log transformed prior to anova*

Source of variation	df	Sums of squares	Mean square	*F*
Model	5	32.197	6.439	50.63****
Date	2	25.521	12.761	100.32****
Age class	3	6.676	2.225	17.49****
Error	67	8.522	0.127	
Total	72	40.719		

**** $P < 0.0001$.

RESULTS—*Flower development*—Flowers of *Clintonia borealis* pass rapidly through a juvenile age class (fo) of low stigma receptivity to the onset of female function (ss) (Table 1). Flowers in our study area retained stigma receptivity through the remainder of anthesis (mc–rc). Most pollen was shed during the (b) age class when anthers were entirely exposed by expansion of the corolla. Anthesis for flowers in the population lasted, on average, about 4.5 days (Table 1).

Phenology of flowering and pollen deposition—*C. borealis* flowered at our study site for about 10 days in mid-June 1983, and earlier, from 30 May–15 June in 1984. Detailed records of flowering patterns during the first season are presented in Fig. 1. At the onset of bloom on 10 June, less than 20% of the open flowers sampled had begun to release pollen. However, by 13 June, about one-third of the flowers were in the hermaphroditic age class (b) and fewer than 5% of flowers were newly opening (fo). From 16 June until the end of blooming all flowers were in either hermaphroditic (b) or post-anther dehiscent, late female (rc) age classes. By 19 June, no open flowers were present in the study area.

Together, flower age and date of collection explained 79% of the variation in pollen deposition on stigmas of *C. borealis* during 1983 (Table 2). Pollen deposition patterns over the course of the flowering period are shown for each age class in Fig. 2. Early female phase flowers (ss and mc) received significantly fewer pollen grains on 10 June than 13 June, probably reflecting the scarcity of male phase flowers early in the blooming period. On both 10

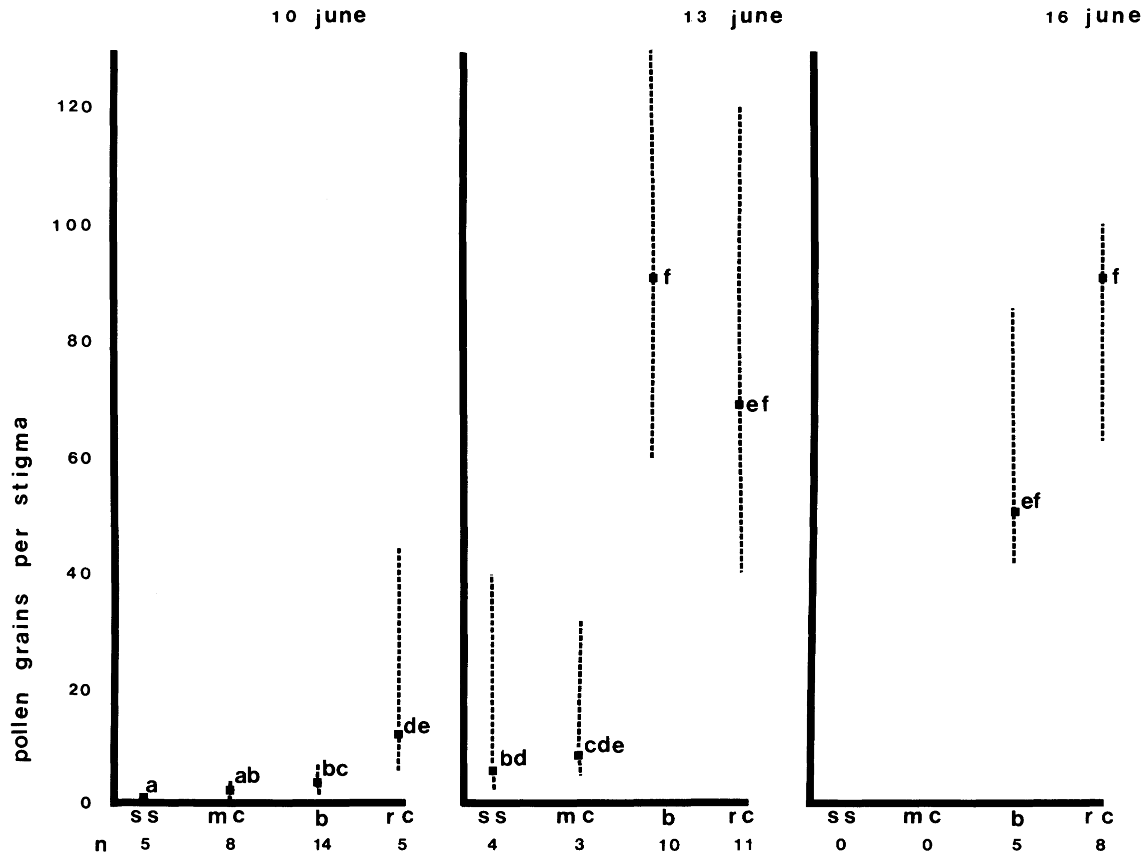

Fig. 2. Pollen deposition on stigmas at different flower ages in *Clintonia borealis*. Age classes: ss = straight sided; mc = medium curled; b = bell; rc = recurved. Stigmas are receptive from ss through rc and most pollen is released during b. Means and 95% confidence intervals are shown, as back transformed from log values. Means of groups sharing superscripts are not significantly different at 95% confidence level with Tukey's test for unplanned multiple contrasts.

June and 13 June, stigmas of flowers collected after anther dehiscence (rc) had about three times the amount of pollen found on stigmas of early female phase (mc) flowers. Total amounts of pollen accumulating on stigmas over the lifetimes of individual flowers were highly variable. Nonetheless, stigmas of (rc) flowers sampled on 16 June had received significantly higher pollen loads than those sampled on 10 June.

Pollinator observations—Bumble bees of the species *Bombus vagans* and *B. perplexus* visited flowers of *C. borealis* in the study area. Nearest neighbor flowering stems in the site were located 1.01 ± 0.19 m apart from each other. Bees usually flew between neighboring inflorescences and visited 40–50% of the flowers on each (Table 3).

Test of resource vs. pollination limitation of seed set and seed size—Flowers of *C. borealis* contained 13.67 ± 0.30 (95% C.I.) ovules on average. The proportions of ovules developing into seeds and seed weights in flowers of control, resource addition, pollen addition, and pollen and resource addition groups varied significantly in 1983 (Table 4). About 25% of the variation in seed set and 20% of that in seed size was explained by genetic and/or environmental differences among maternal patches rather than by treatment effects. Additionally, mean seed weight was also affected by the interaction between patch and treatment. While both pollen and resource addition alone had slight positive effects on seed set, increases in the two factors simultaneously were necessary to cause a significant gain (14%) (Table 5). Seeds produced with extra resources available were about 1.3 times heavier than those set under natural conditions (Table 5). Pollen addition enhanced seed weight slightly but significantly in the presence of extra resources, but not at natural resource levels (Table 5).

TABLE 3. *Flower visitation by bumble bees collecting nectar from* Clintonia borealis

Species	N	Distance flown between stems (m) $\bar{x}$ 95% C.I.	Flowers visited per stem $\bar{x}$ 95% C.I.	% Flowers visited per stem $\bar{x}$ 95% C.I.
Bombus vagans	20	1.1 ± 0.7	1.5 ± 0.3	42 ± 10
B. perplexus	20	1.5 ± 0.7	1.7 ± 0.3	53 ± 12

Pollen quality effects on seed set and seed size—Pollen source significantly affected the percentage of ovules developing into seeds and the weight of individual seeds (Table 6). On average, selfed flowers set about one-third the amount of seeds set by flowers outcrossed with near or far pollen sources (Table 7). Seed weights following self-pollination were about 10% lower than those from the outcrossing treatments (Table 7). There were no significant differences in seed set or seed weight of near and far outcross groups (Table 7). As in 1983, seed set and seed weight varied significantly among maternal patches. Flowering order had no effect on seed set but was negatively related to seed weight ($\beta = -0.11$, $t = 2.58$, $P < 0.01$ for the least squares line of the pooled treatment groups). Seed weight decreased most sharply with blooming sequence in far outcross flowers, moderately in near outcross flowers, and most gradually in selfed flowers ($\beta = -0.21, -0.12,$ and -0.06, respectively for the three treatments; $F_{2,329} = 17.62$, $P < 0.001$ for differences between slopes; Table 6).

DISCUSSION—Flowering in *C. borealis* was highly synchronized at our study area, lasting about 10 days in 1983 and 2 wk in 1984. Since flowers are protogynous, little pollen may be available for early opening flowers before their own anthers dehisce. Such pollen deficits could have contributed to the significantly lower pollen deposition per stigma at the earliest census date compared to deposition at later dates. These results suggest that early flowering plants in this population may be more strongly pollen limited than later flowering ones. Evidence for changes in pollination availability over the course of the flowering season has been found in other systems as well (Schemske, 1977; Motten, 1982; Gross and Werner, 1983).

Outcrossing among plants at our study site may have been limited, at least in 1983. Bumble bees were observed flying mostly between neighboring inflorescences and visiting about two flowers or half of those available on each. Although Thomson and Plowright (1980) showed that a bee load of pollen may be deposited over up to seven sequential flower visits, actual pollen carryover from any particular flower is likely to be lower than this, because bee loads are accumulated from several pollen sources. Thus, in light of the short average flight distances found in the present study and the clonal growth habit of *C. borealis,* much of the pollen transfer occurring in this population appears likely to be geitonogamous. Evidence that bees provide some cross-pollination is suggested by the moderate level of seed set of open-pollinated flowers relative to that of completely selfed or outcrossed flowers. Outcross pollination was on average 2.8 times as effective as

TABLE 4. *Sums of squares table for (a) the proportion of ovules developing into seeds and (b) seed weight in* Clintonia borealis *following test of resource vs. pollination limitation. Seed set proportions angular transformed prior to anova*

Source of variation	df	Sums of squares	Mean square	F
(a) Model	36	4.243	0.118	3.15**
Treatment	3	0.342	0.114	3.05*
Patch	10	2.371	0.237	6.34****
Treatment × patch	23	1.529	0.066	1.78
Error	28	5.289	0.037	
Total	64	9.532		
(b) Model	37	598.360	16.172	47.40****
Treatment	3	137.838	5.947	134.68****
Patch	10	205.570	20.557	60.26****
Treatment × patch	24	254.954	10.623	31.14****
Error	1,076	367.072	0.341	
Total	1,113	965.432		

* $P < 0.05$; ** $P < 0.01$; **** $P < 0.0001$.

TABLE 5. *Results of test for resource vs. pollination limitation of the proportion of ovules developing into seeds and seed weight in flowers of* Clintonia borealis. *Means and 95% confidence intervals (C.I.) for proportions are back transformed from angular values. Groups sharing superscript in columns do not differ significantly at* $\alpha = 0.05$ *level with respect to the variate listed. Significance assigned with Tukey's test for unplanned pairwise contrasts*

Pollination level	Resource level	N (flowers)	Seed set %		N (seeds)	Seed weight (mg)	
			$\bar{x}$	95% C.I.		$\bar{x}$	95% C.I.
Natural	Natural	16	79^{a}	65–90	159	2.8^{a}	2.67–2.93
	Increased	27	85^{ab}	74–93	282	3.7^{b}	3.62–3.78
Increased	Natural	22	80^{ab}	73–86	234	2.7^{a}	2.59–2.81
	Increased	20	91^{b}	84–96	207	3.9^{c}	3.74–4.06

self-pollination and 1.2 times as effective as open pollination.

Pollination and resource levels together had significant effects on seed set and seed size in 1983. By supplementing both factors simultaneously, average seed set was increased by 14% and seed weight by 29%. In contrast with results from other systems (Willson and Schemske, 1980; Bierzychudek, 1981; Stephenson, 1981; Udovic, 1981; Lee and Bazzaz, 1982; Galen, 1985) neither pollen nor resource levels alone limited seed set. Our results suggest that for *C. borealis,* seed set is finely tuned to a balance of resource and pollination conditions rather than to large variation in either, per se. It should be noted, however, that given a larger sample size (e.g., comparable to that for individual seed weight), the 6% increase in seed set with resource addition only might become significant. Seed weight was strongly and significantly influenced by resource availability. Removal of fruits or flowers, by reducing competition for shared maternal resources, has also led to gains in seed weight of remaining fruits in other species (Hodgson and Blackman, 1957; Van Steveninck, 1957; Maun and Cavers, 1971). Evidence that fruits compete for shared maternal resources in *C. borealis* is also provided by the negative relationship between flowering order and seed weight in 1984 pollination treatments. Interestingly, the strength of this interaction depended on pollen quality. Outcrossing treatments were characterized by sharper declines in seed weight with blooming sequence than selfing. Pollen addition in the presence of extra resources had a slight but significant positive effect on seed weight. Similar findings are mentioned by Stanton (1984a). High pollination intensity, by fostering conditions in which pollen tubes compete rigorously for available ovules, could select for larger seed size if pollen tube growth rate and seed size are genetically correlated (Ter Avanesian, 1978). Alternatively, as comparison of seed size between selfed vs. outcrossed groups suggests, pollen quality in *C. borealis* could limit seed size under conditions where only low or moderate numbers

TABLE 6. *Sums of squares table for (a) the proportion of ovules developing into seeds and (b) seed weight in* Clintonia borealis *following pollination treatments with self, near outcross, and far outcross pollen sources. Seed set proportions angular transformed prior to the ancova*

Source of variation	df	Sums of squares	Mean square	F
(a) Model	19	8.555	0.450	3.45***
Treatment	2	2.411	1.205	9.25***
Order[a]	1	0.062	0.062	0.47
Treatment × order	2	0.283	0.142	1.09
Patch	14	5.800	0.414	3.18**
Error	22	2.867	0.130	
Total	41	11.422		
(b) Model	19	261.550	13.765	42.66****
Treatment	2	11.308	5.654	17.52****
Order	1	10.054	10.054	31.15****
Treatment × order	2	11.375	5.688	17.62****
Patch	14	228.815	16.343	50.65****
Error	329	106.180	0.3227	
Total	348	367.73		

[a] Order refers to order in which treated flower opened on an inflorescence.

** $P < 0.01$; *** $P < 0.005$; **** $P < 0.001$.

TABLE 7. *Seed set (percent of ovules per fruit developing into seeds) and seed weight in* Clintonia borealis *following pollination with pollen from self, near outcross, and far outcross donors. Treatments were replicated in 15 flowering patches. Sample sizes are 14 flowers per treatment due to damage of one fruit in each group. Means and 95% confidence intervals (C.I.) for seed set are back transformed from angular values. Means sharing superscripts in columns are not significantly different at the $\alpha = 0.05$ level with Tukey's test for unplanned pairwise contrasts*

Pollen source	Seed set (%)		N (seeds)	Seed weight (mg)	
	$\bar{x}$	95% C.I.		$\bar{x}$	95% C.I.
Self	32	10–62	72	4.1^a	3.8–4.4
Near outcross	91^b	61–100	136	4.4^b	4.3–4.6
Far outcross	92^b	64–100	142	4.6^b	4.4–4.7

of pollen grains are available. Self-pollination produced comparable seed weight reductions in *Costus allenii* (Zingiberaceae) (Schemske and Pautler, 1984). Contrary to other recent studies (Waser and Price, 1983), we found no relationship between reproductive success and distance over which outcrossing was performed.

Differences between patches or maternal clones accounted for large proportions of the variance in both seed set in 1983 and seed weight in 1983 and 1984. Additionally, seed weight varied markedly between the two years, presumably due to changes in resource levels during fruit development. Within-year effects could be due to either environmental or genetic differences. In related work, we have found that subtle changes in light availability (e.g., 20% shading of the green fruits only) can have significant effects on fruit and seed size (Galen, unpubl. data). Currently, we are investigating potential effects of genetic variation among clones on the number and size of seeds that each produces.

Seed production and size are likely to be important in the life history of *C. borealis,* as demographic studies have indicated that mortality may be heaviest at the time of genet initiation (Ashmun and Pitelka, 1985). Seed size is correlated with germination and seedling survival under competitive conditions in several systems (e.g., Schaal, 1980; Stanton, 1984b; Gross, 1984). Though the relationship between these attributes is as yet unknown for *C. borealis,* we hope in future studies to address this topic, exploring the consequences of pollination conditions and resource availability during seed set to actual patterns of establishment in natural populations.

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