



Effect of Male Pollen Donor and Female Seed Parent on Allocation of Resources to Developing Seeds and Fruit in *Chamaecrista fasciculata* (Leguminosae)

Charles B. Fenster

American Journal of Botany, Vol. 78, No. 1 (Jan., 1991), 13-23.

Stable URL:

<http://links.jstor.org/sici?sici=0002-9122%28199101%2978%3A1%3C13%3AEOMPDA%3E2.0.CO%3B2-V>

American Journal of Botany is currently published by Botanical Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/botsam.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

EFFECT OF MALE POLLEN DONOR AND FEMALE SEED PARENT ON ALLOCATION OF RESOURCES TO DEVELOPING SEEDS AND FRUIT IN *CHAMAECRISTA FASCICULATA* (LEGUMINOSAE)¹

CHARLES B. FENSTER²

The University of Chicago, Department of Biology, Barnes Laboratory,
5630 S. Ingleside Avenue, Chicago, Illinois 60647

In *Chamaecrista fasciculata*, fruit abortion levels are high and seed mass is highly variable, necessary preconditions for differential resource allocation of the female to seed and fruit sired by different males. This study investigated the relative role of pollen donor and seed parent on the allocation of resources to developing seed and fruit, and assessed the role of genetic relatedness in contributing to any observed paternal effect in *C. fasciculata*. In addition, pollen donor effects were contrasted to within-seed parent sources of variation in resource allocation due to pollination date and ovule position in the pod. Plants collected from the field were brought to a greenhouse where single-donor crosses were conducted controlling for pollen donor source and interplant distance, a measure of genetic relatedness. Seed mass, number of seed/fruit, fruit maturation time, and fruit abortion rate were measured as indicators of resource allocation to developing seed and fruit. Variation in resource allocation was largely determined by the seed parent. Pollen donor effects were limited to differences between self vs. non-self pollinations, suggesting that inbreeding depression following mating events between related individuals is the source of any variation among pollen donors on differential resource allocation to developing seed and fruit. Once the effect of inbreeding was removed, however, pollination date and ovule position played larger roles than pollen source. Since there was no detectable variation among male pollen donors in their ability to accrue resources from the female seed parent apart from inbreeding effects, it is concluded that the opportunity for postzygotic mate choice is limited in *C. fasciculata*.

A common phenomenon in hermaphroditic plants is the production of more flowers than can be matured to fruit (Stephenson, 1981; Sutherland and Delph, 1984). If fruit production is limited by resources then there may be an opportunity for mate choice, i.e., the differential allocation of resources to developing seed and fruit based on the expectation of higher progeny fitness in developing zygotes fa-

thered by "superior" males (Janzen, 1977; Charnov, 1979; Willson, 1979; Westoby and Rice, 1982; Stephenson and Bertin, 1983; Willson and Burley, 1983; Lee, 1984, 1988). The role of mate choice in the evolution of allocation patterns to developing seed and fruit depends on within-population variation in the ability of offspring of different male pollen donors to assimilate resources from the female seed parent (Lyons et al., 1989).

¹ Received for publication 18 December 1989; revision accepted 23 July 1990.

Discussions with C. Walter motivated this project. The author thanks M. Dudash for help in collecting the plants; the Illinois Department of Conservation and the Illinois Nature Preserves Commission; J. Nyhoff and S. Villalobos of Gooselake Prairie State Park; Sue Yamins, Betty McCarthy, and Wilbur Schroeder from The University of Chicago greenhouse; D. Schemske for continual advice and encouragement; D. Draper and D. Mertz for statistical advice; and D. Schemske, D. Charlesworth, R. Lande, E. Garber, J. Terri, M. Morgan, S. Barrett, M. Dudash, R. Scribailo, A. Winn, and T. Lee for comments on earlier versions of this manuscript. This research was supported in part by a grant from Sigma Xi, funds from an NIH Genetics Training Grant, The University of Chicago Hinds Fund, and The Biomedical Computation Facility at the University of Chicago.

² Current address: Department of Botany, The University of Maryland, College Park, MD 20742-5815.

Previous studies demonstrating evidence for mate choice in natural plant populations have not controlled for genetic relatedness between pollen donor and recipient as a source of variation in seed and fruit maturation patterns (Bertin, 1982; Bookman, 1984; Stephenson and Winsor, 1986; Casper, 1988). Variation among males in their ability to mature seed and fruit on females may be attributable to the interaction between male and female genotypes caused by genetic relatedness (Charlesworth, Schemske, and Sork, 1987; Lyons et al., 1989). Therefore, genetic relatedness between pollen donor and recipient with the consequent expression of inbreeding depression may explain the source of the male effect on seed and fruit set. Because gene flow is often limited in plants

(Ehrlich and Raven, 1969; Levin, 1981; but see Ellstrand and Marshall, 1985), populations are usually genetically subdivided so that interparent distance reflects the genetic relatedness between parents, i.e., there is a negative correlation between interplant distance and relatedness (Wright, 1978; Levin, 1984; Epperson and Clegg, 1986; Fenster 1988, 1991b). Although mate choice could include selection by the female based on genetic relatedness, mate choice is usually considered as an agent for sexual selection on male characters independent of selection to ensure outcrossing for the following reason: If the outcome of male-male competition is dependent on the genetic relatedness between parents, then the male genotype will be favored only in particular combinations of male and female genotypes. The successful male in one bout of competition on a female may be uncorrelated to the outcome of competitive interactions in other maternal environments. Thus, mating events across different levels of population subdivision may have significant genetic consequences for the offspring that are unrelated to mate choice in the context of sexual selection. Instead, the contribution of a male component to variation in resource allocation patterns may be a manifestation of different levels of inbreeding or outbreeding depression associated with the genetic relatedness of maternal and paternal parents (Charlesworth, Schemske, and Sork, 1987; Lyons et al., 1989; Waser and Price, 1989).

Differences in the ability of seeds and fruit to assimilate resources, due to variation in the male pollen donors that sired them, must be heritable in order to have any evolutionary significance. The amount of resources available to an individual plant for developing seed and fruit may change dramatically through a season (Lloyd, 1980). Fruits may be selectively matured based on order of pollination (Stephenson, 1981). In addition, there may be differences among inflorescences (Janzen, 1971; Thompson, 1984) or among ovule positions within a fruit (Horovitz, Meiri, and Beiles, 1976; Schaal, 1980; Lee and Bazzaz, 1986) in their ability to assimilate and distribute resources to developing fruit and seed. Resource competition among developing seeds and fruit arising from environmental phenomena and strong maternal effects will reduce the heritability and diminish the rate of evolution of male traits in response to selection (Naylor, 1964; Lande and Arnold, 1983; Arnold and Wade, 1984).

Previously, no effect of pollen source on *in vivo* pollen tube growth was observed in *C. fasciculata* (Fenster and Sork, 1988), suggest-

ing that the role of gametophytic competition in prefertilization mate-choice is limited in this species. In addition, genetic relatedness is negatively correlated to interparent distance in this population of *C. fasciculata* (Fenster, 1988, 1991b). The goal of this study was to determine the opportunity for postfertilization mate-choice by examining the relative roles of pollen donor source and female seed parent on the allocation of resources to developing seed and fruit in *C. fasciculata*. The specific objectives were to 1) determine the role of inbreeding as a source of variation among pollen donor sources by varying interparent distance and 2) compare the effect of pollen source to two environmental sources of variation commonly influencing seed and fruit production in legumes: pollination date and ovule position. Seed mass, number of seed/fruit, fruit maturation time, and fruit abortion rate were measured as indicators of resource allocation to developing seed and fruit.

MATERIALS AND METHODS

Study organism and study site—*Chamaecrista fasciculata* Michx., partridge pea, formerly known as *Cassia fasciculata* (Irwin and Barneby, 1982), is a self-compatible, annual legume of old field, disturbed prairie, and savanna. In northern Illinois, *C. fasciculata* is exclusively bee-pollinated (Lee and Bazzaz, 1982a) and highly outcrossing (Fenster, 1988, 1991a). Seedlings emerge in late April and early May. Flowering begins in mid- to late July and continues until the first frost. From one to six flowers per inflorescence are produced in axillary racemes with each flower remaining open for only 1 day. The fruit is a typical legume pod, containing seven to 21 ovules arranged longitudinally. No endosperm is present in the mature seed.

The study population was located at Goose-lake Prairie Nature Preserve (GLP), Grundy Co., Illinois, a disturbed mesic prairie in the floodplain of the Illinois river. The population is naturally subdivided into subpopulations 50–200 m apart containing 100 to >1,000 adult flowering plants where the magnitude of gene flow is much greater within subpopulations compared to between subpopulations. Fourteen subpopulations were chosen using stratified random sampling.

Pollen donor source—*Effect of interparent distance*—To determine the average effect of interparent distance (a measure of genetic relatedness) on resource allocation to developing seed and fruit, field-collected plants were grown

in the greenhouse, and the fate of single male pollen-donor crosses was determined. Crosses were conducted between plants of known interparent distance. In late June 1983, juvenile plants were collected from 14 subpopulations at GLP. A 1.5 × 1.5-m quadrat was chosen randomly at one end of each subpopulation. From this quadrat two plants were chosen randomly to act as female parents (pollen recipients). Plants were 1) selfed, and crossed to pairs of male parents (pollen donors) chosen from 2) within the same quadrat as the female parents, 3) a 1.5-m quadrat, 2 m distant from the first, and 4) a 1.5-m quadrat at the opposite end of the subpopulations from the female parents, corresponding to interparent distances of ≤ 1.5 m, 3–5 m, and approximately 40 m, respectively. Pairs of males from single quadrats served as pollen donors for crosses between adjacent subpopulations (50–200 m, cross = 5), between intermediate distant subpopulations (400–800 m, cross = 6), and between far subpopulations (1,000–2,900 m, cross = 7). This sampling regime was replicated across the 14 subpopulations. Based on pollen and seed dispersal distances (Fenster, 1991a), the seven crosses corresponded to distances in terms of neighborhood units of self (cross 1), within a genetic neighborhood (cross 2), between adjacent neighborhoods (cross 3), between far neighborhoods in the same subpopulation (cross 4), and between neighborhoods in different subpopulations of increasing distance (crosses 5, 6, and 7).

Plants were grown in the greenhouse, where they were watered as needed and fertilized weekly (Peter's peat-lite 20-19-18). All seven classes of single-donor hand-pollinations were performed on 14 pairs of maternal plants (corresponding to the 14 chosen subpopulations). Pollen was collected by tapping a single male donor flower over a petri dish and was transferred to the recipient stigma with felt attached to a toothpick. Plants began flowering 3 August and continued through 14 September. All flowers on a plant were pollinated each day, but because of the time constraints of labeling each flower, only a randomly chosen subset was followed for each pollen donor source. If enough flowers were open on the maternal and paternal plants, all seven classes of pollinations were conducted in a single day, on randomly chosen flowers. If a particular cross was not possible on one day, it was conducted as soon as flowers on the pollen donor and recipient were available (usually the next day). Fruit were considered mature just prior to dehiscence when the entire pericarp had turned brown and when the seeds rattled when the fruit were touched. Fruit

were harvested from late August through October. On average, 11 flowers/plant cross-type and 5.5 flowers/plant/male were pollinated and followed.

The fate of each flower was determined as either nonaborted (fruit containing at least one viable seed, mass > 2 mg) or aborted. In non-aborted fruit the number of seeds per fruit were counted and mean individual seed mass/fruit was measured to the nearest 0.1 mg using a Mettler X80 scale. Maturation time was computed as the number of days between pollination and fruit harvest.

A mixed model partially hierarchical ANOVA (Brownlee, 1965) was used to examine the effect of interparent distance on mean individual seed mass/fruit, number of seeds produced/fruit and fruit maturation time with cross (model I), and subpopulation of maternal plant (model II) as the main effects. Female seed parent (model II) was nested within subpopulation. The random statement option in General Linear Models (GLM) (SAS, 1985) was used to determine the percentage of variation explained by each factor. The CATMOD procedure (SAS, 1985) was used to examine the effect of female seed parent and cross-type on fruit abortion. Mean seed mass/fruit, number of seed/fruit, and fruit maturation time were reciprocal square root, square root, and log transformed, respectively, to meet the assumptions of ANOVA (and for analyses listed below).

Variation among males—The effect of male identity on the allocation of resources to developing seed and fruit was examined using a nested ANOVA (NESTED, SAS, 1985) with male nested within female to determine the effect of male on mean individual seed mass/fruit, number of seed/fruit, and fruit maturation time. To simplify the analyses, female was elevated to a main effect by removing subpopulation from the analysis. Eliminating subpopulation from the analysis may inflate the amount of variation attributable to female effects but did not alter the interpretation of male effects (Brownlee, 1965). Male pollen donors, excluding self, across all distance classes were used in the analyses. Only males that were represented with two or more mature fruit on a female could be used for the ANOVA, resulting in an average of nine males nested within each female. The random statement option in GLM (SAS, 1985) was used to determine the percentage of variation explained by female and male.

Variation within a seed parent—Pollination date—In the ANOVA where cross-type was

TABLE 1. Mixed model, partial hierarchical ANOVA of mean individual seed mass/fruit, number of seeds/fruit, and fruit maturation time with cross (model I) and subpopulation (model II) as main effects^a

Source	Character								
	\bar{x} individual seed mass/fruit			No. seeds/fruit			Fruit maturation time		
	df	ms	F	df	ms	F	df	ms	F
Cross	6	0.0030	4.30*	6	1.0549	3.35**	6	0.00003	0.5
Subpopulation	13	0.0097	1.08	13	3.6676	2.88*	13	0.00014	0.6
Female (subpopulation)	14	0.0090	15.91**	14	1.2735	4.17***	14	0.00023	3.8***
Cross × subpopulation	78	0.0007	1.23	78	0.3148	1.03	78	0.00006	1.0
Cross × female (subpopulation)	83 ^b	0.0006	0.60	83 ^b	0.3055	1.06	83 ^b	0.00006	1.0
Error	373	0.0009		886	0.2817		1,013	0.00006	

^a * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

^b One plant was male sterile resulting in a loss of 1 df.

significant (Tables 1–3), the effect was due to differences between the self- and non-self pollination classes. Therefore, the self-pollination class was eliminated in all analyses to remove the effect of pollen source in the examination of within-seed parent sources of variation on seed and fruit development. Because of strong maternal effects, determination of the effect of date on seed and fruit yield, via regression analysis, would have necessitated separate regressions for each female. Differences among plants in phenology would have obscured any effect of date on seed and fruit yield if all plants were lumped into one regression analysis. Therefore, to simplify the analysis, date was converted from an ordinal to a class variable. The mean pollination date was calculated for each plant and then categorized into two classes, $< \bar{x}$ or $> \bar{x}$, on that plant. Grouping the data in this way may have minimized the effect of the independent variables, so that the results should be regarded as conservative. Each plant was considered a replicate in a Wilcoxon rank test of association to measure the effect of pollination date on fruit abortion. A two-way mixed model ANOVA was conducted with female (model II) and date (model I) as the main effects. The random statement option in GLM (SAS, 1985) was used to determine the percentage of variation explained by female and pollination date.

Ovule position—To determine if there was

TABLE 2. Effect of female and cross on fruit abortion rate determined by CATMOD^a

Source	df	Chi-square
Female	27	149.52 ^a
Cross	6	9.29
Female × cross	161 ^b	146.49

^a $P < 0.001$.

^b One plant was male sterile resulting in a loss of 1 df.

significant variation in the allocation of resources to developing seed within fruit, a random subsample of approximately one-third of the fruit was opened, and the presence or absence of mature viable seed as well as seed mass was determined for each ovule position. The ovule distal to the style was assigned position 1, and the ovule proximal to the style was assigned the last position. The mean and modal class of ovules/fruit of *C. fasciculata* at GLP was 13 with 1 SD = 3. The effect of ovule position on seed mass was examined in the modal ovule number class of fruit using Spearman rank correlation and a two-way mixed model ANOVA with female (model II) and ovule position (model I) as the main effects. Of the original 28 females, only 13 had two or more fruit with the modal number of ovules and were used in the ANOVA. The random statement option in GLM (SAS, 1985) was used to determine the percentage of variation explained by female and ovule position. The effect of ovule position on the probability of an ovule becoming a seed was examined for 13-ovule fruit using a Spearman rank test. The relationships between ovule position and 1) ovule abortion and 2) seed mass were also examined in ten- and 16-ovule fruit. Thus, the relationship between ovule position and the allocation of resources to developing seed was examined in the mean \pm 1 SD of the population of fruit.

RESULTS

Pollen donor source—Effect of interparent distance—Interparent distance had a significant effect on mean individual seed mass/fruit and number of seeds/fruit but not on fruit maturation time or fruit abortion rate (Tables 1, 2). Multiple comparison of means indicates that for those characters where cross-type was significant, the effect was strictly a self vs. non-

TABLE 3. Mean individual seed mass/fruit (mg), mean number of seed/fruit, mean fruit maturation time (days), and mean fruit abortion rate (%) of the seven pollination treatments, and the mean of 11 outcross classes combined. Means followed by same letter are not significantly different (seed mass, seed/fruit, fruit maturation time, Tukey's contrast of means, $P < 0.05$; fruit abortion rate CATMOD, SAS, $P < 0.05$)

Character	Cross type							All outcross Mean
	Self		Outcross (within subpopulation)		Outcross (between subpopulation)			
	1	2	3	4	5	6	7	
\bar{x} individual seed mass/fruit (mg)	6.2 A	6.5 B	6.9 B	6.8 B	6.6 B	6.6 B	6.6 B	6.7
\bar{x} no. seeds/fruit	9.4 A	10.9 B	11.4 B	10.9 B	11.2 B	11.3 B	10.6 B	11.1
\bar{x} fruit maturation time (days)	43.4 A	42.4 A	40.9 A	43.1 A	43.2 A	41.4 A	41.8 A	42.0
\bar{x} fruit abortion rate (%)	54.5 A	54.9 A	50.8 A	53.8 A	45.6 A	45.1 A	50.9 A	50.2

self phenomenon (Table 3). Selfing reduced mean seed mass by 8%, mean number of seed/fruit by 15%, and increased fruit maturation time by 3% and fruit abortion rate 9% compared to the mean of all outcross pollinations. Female had a significant effect on all characters in the models where cross-type was considered and was the only significant factor explaining variation in fruit maturation time (Table 1).

Variation among males—Since there was no heterogeneity among the outcross classes of pollen donors in their ability to mature seed and fruit (Tables 1–3), an examination of the effect of individual male donor was not confounded by the factor of genetic relatedness between pollen donor and recipient. There were no significant effects of individual male pollen donor on mean seed mass/fruit, number of seed/fruit, and fruit maturation time, although female seed parent effects continued to be significant and large (Table 4).

Variation within a seed parent—*Pollination date*—The quality of the environment on the seed parent for developing seed and fruit varied temporally (Tables 5, 6). Mean individual seed mass/fruit and the number of seed produced/fruit were significantly lower in fruit derived from flowers in the second half vs. the first half of the flowering season (Table 6). Pollination date had no significant effect on fruit maturation time (Tables 5, 6).

Ovule position—Ovule position had a sig-

nificant effect on both the probability of an ovule becoming a mature seed (Fig. 1) and on eventual individual seed mass (Table 7; Fig. 1). Ovules distal to the style had a lower probability of becoming seed compared to ovules proximal to the style (Spearman rank correlation = 0.92, $P < 0.001$), and if the ovule did develop to a mature seed, the seed mass was lower (Spearman rank correlation = 0.67, $P < 0.02$). The relationship between increasing seed mass and ovule positions closer to the style was not uniform. Seeds maturing in the ovule position closest to the style had a significantly lower seed mass when compared with their nearest neighbors (Tukey's contrast, Fig. 1).

DISCUSSION

Pollen donor source—*Effect of interparent distance*—Interparent distance, an estimate of genetic relatedness among individuals, does not influence mean individual seed mass/fruit, number of seed/fruit, fruit maturation time, or fruit abortion rate beyond a self vs. non-self phenomenon. Selfing reduces seed mass and number of seeds/fruit, but there is no significant effect of selfing on fruit abortion rate or fruit maturation time. In some highly outcrossing species, maternal investment into seed and fruit resulting from self-pollinations is limited by early seed or fruit abortion (Squillace and Kraus, 1962; Sorensen, 1969; Owino and Zobel, 1977; Price and Waser, 1979; Schemske and Pautler, 1984; Levin, 1984; Waser and Price, 1989). The reduction in seed mass and

TABLE 4. ANOVA of effect of female and male nested within female on mean individual seed mass/fruit, number of seeds/fruit, and fruit maturation time

Source	Character								
	\bar{x} individual seed mass/fruit			No. seed/fruit			Fruit maturation time		
	df	ms	F	df	ms	F	df	ms	F
Female	27	0.0121	17.2 ^a	27	112.4	11.5 ^a	27	0.00019	2.7 ^a
Male (female)	208	0.0007	0.7	229	9.8	1.0	248	0.00006	1.0
Error	530	0.0010		612	9.7		712	0.00006	

^a $P < 0.001$.

TABLE 5. Two-way mixed model ANOVA's of effect of female (model II) and pollination date on mean individual seed mass/fruit, number of seeds/fruit, and fruit maturation time^a

Source	\bar{x} individual seed mass/fruit			No. seeds/fruit			Fruit maturation time		
	df	ms	F	df	ms	F	df	ms	F
Female	27	0.0076	10.9***	27	2.6120	10.0***	27	0.2832	2.9***
Pollination date	1	0.0083	8.3**	1	5.8810	10.4***	1	0.3593	1.8
Interaction	27	0.0010	1.4	27	0.5679	2.2**	27	0.1997	2.1**
Error	791	0.0007		870	0.2609		977	0.0961	

^a ** $P < 0.01$; *** $P < 0.001$.

number of seed/fruit following selfing probably reflects the expression of lethal and semilethal recessive genes in the developing zygotes (Wright, 1977). However, in *C. fasciculata* the reduction in resources allocated to selfed seed and fruit is small compared to the reduction in progeny fitness following selfing. In separate studies on *C. fasciculata* (Fenster, 1991b; Sork and Schemske, unpublished data), strong and significant inbreeding depression (greater than two-fold reduction in life time survivorship and reproduction of progeny) was expressed following selfing, and there was an association of inbreeding depression with population subdivision. Therefore, it appears that maternal plants of *C. fasciculata* are "unable to allocate" resources differentially to developing seed and fruit predicated on the expectation of future offspring quality.

It is important to emphasize that the variation in the allocation of resources to developing seed and fruit due to selfing vs. outcrossing was small in comparison to the variation due to maternal effects (subpopulation and female) and was comparable in some instances to variation within a seed parent (Table 8). The importance of female compared to cross-type in explaining variation in seed and fruit yield components is illustrated by the much greater variation observed among females than among cross-types. Fruit abortion rate varied from 54.5% following self-pollination to 45.1% (Table 3) for the "best" of the outcrossed pollination classes and from 16.7% to 73.3%

among all females. Similarly, mean seed mass, number of seeds/fruit, and fruit maturation time showed greater variation among females than among cross-types (Table 8).

Variation among males—When self pollen was removed from the pollen source, the role of male donor in determining variation of seed and fruit yield was essentially zero (Table 8), suggesting little opportunity for postzygotic mate-choice on male performance in *C. fasciculata*. The absence of a significant self vs. outcross effect on fruit abortion implies that the opportunity for a significant effect of male pollen donor on fruit abortion is also limited. If a female cannot differentiate between self and non-self, in terms of allocating resources to developing fruit, then it seems unlikely that a female could differentiate among pollen donors. No effect of male pollen donor was found, even though males were sampled across a broad level of population subdivision, from within the neighborhood or breeding unit of the female to far outside of it. The genetic representation of pollen donors on the female pollen recipients, and thus the opportunity for differences among males, far exceeded the range of pollen found in natural populations (Fenster, 1991a). Therefore, these results are a conservative estimate of the opportunity for mate choice to act on male performance in the maternal environment of *C. fasciculata*.

Competition among fruits and seeds sired by different pollen donors should be most intense when resources are limited. Flowers opening in the second half of the flowering season have a lower probability of maturing to

TABLE 6. Effect of pollination date on mean individual seed mass/fruit, number of seeds/fruit, fruit maturation time, and fruit abortion rate. Means with the same letters are not significantly different, Tukey's contrast of means, $P < 0.05$, for mean individual seed mass/fruit, mean number of seed/fruit, and mean fruit maturation time; Wilcoxon Rank Test, $P < 0.05$, for fruit abortion rate

Pollination date	\bar{x} individual seed mass/fruit (mg)	\bar{x} number of seed/fruit	\bar{x} fruit maturation time (days)	\bar{x} fruit abortion rate (%)
Early	6.5 A	11.2 A	41.4 A	43 A
Late	6.3 B	9.9 B	42.1 A	57 B

TABLE 7. Two-way mixed model ANOVA of effect of female (model II) and ovule position (model I) on seed mass

Source	df	ms	F
Female	12	21.2107	8.3 ^a
Ovule position	12	5.6640	31.0 ^a
Female × ovule position	144	0.5553	0.8
Error	602	0.6854	

^a $P < 0.001$.

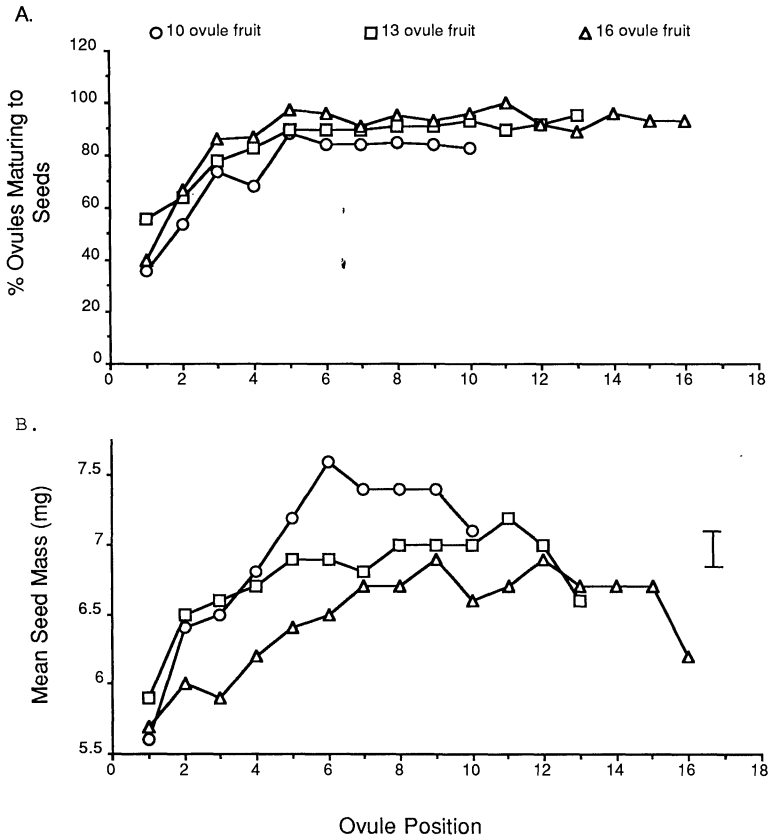


Fig. 1. Effect of ovule position on seed maturation (A) and seed mass (B). The first ovule position corresponds to the ovule closest to the peduncle, distal to the style. The modal class of 13 ovules/fruit (squares) is presented along with 16-ovule fruit, $\bar{x} + 1$ SD (triangles), and ten-ovule fruit, $\bar{x} - 1$ SD (circles). Sample sizes for each ovule position were 30, 87-94, and 30 fruit for the effect of ovule position on percent maturation on ten-, 13- and 16-ovule fruit, respectively. Sample sizes for each ovule position were 8-23, 52-84, and 12-23 seeds for the effect of ovule position on seed mass for ten-, 13- and 16-ovule fruit, respectively. Sample sizes varied among ovule positions for 13-ovule fruit because the location of several of the seed were unknown. The vertical bar (B) represents the minimum significant difference between means (Tukey's contrast, $P < 0.05$).

TABLE 8. Percentage of variation of mean individual seed mass/fruit, number of seed/fruit, and fruit maturation time explained by female seed parent, pollen donor (cross and male), pollination date, and ovule position

Model	Source	Character		
		Mean individual seed mass/fruit	Number of seeds/fruit	Fruit maturation time
1	Subpopulation	1.0	9.8	0
	Female (subpopulation)	23.1	7.9	4.3
	Cross	6.5	5.5	0
2	Female	29.6	25.4	5.2
	Male (female)	0	0.3	1.4
3	Female	25.9	18.9	2.4
	Pollination date	0.1	1.3	0
4	Female	35.0		
	Ovule position	0.9		

fruit and produce fruit with lower seed mass, indicating that resources are more limited. Lee and Bazzaz (1982a) demonstrated that removal of *C. fasciculata* fruit at advanced stages of development allowed later-initiated fruit that would normally have aborted to develop. Therefore, competition for resources among fruit pollinated by the different pollen donors was more intense for fruit derived from flowers opening during the second half of the flowering season. However, in this study there was no evidence of selective fruit abortion of self vs. outcrossed fruit nor were there any differences among the different distance classes or among individual male donors in mean individual seed mass/fruit, number of seed/fruit, and fruit maturation time when the analyses were confined to pollinations conducted in the second half of the phenology (Fenster, unpublished data).

The results of this study are in accord with

Antonovics and Schmitt (1986), Mitchell-Olds (1986), and Mazer (1987) who found strong seed parent effects but no genetic variation among male donors for seed yield components in *Anthoxanthum odoratum*, *Impatiens pallida*, and *Raphanus raphanistrum*, respectively. Lee and Bazzaz (1982a, b) also observed no differential abortion between self and outcross pollen donors, nor between single vs. mixed outcrossed pollen loads in similar experiments with *C. fasciculata*. Many studies have demonstrated large variation among seed parents in their ability to mature seed (Casper, 1984; Guth and Weller, 1986).

Other studies documenting significant male donor effects in natural populations on fruit abortion and seed number/fruit were conducted with males taken from outside the population, beyond the range of pollen dispersal (Bookman, 1984; Vander Kloet and Tosh, 1984). In the latter study, plants were collected as male pollen donors and female pollen recipients along a transect from Florida to North Carolina. Therefore, variation among pollen donors in these instances may not reflect opportunities for female choice but may be manifestations of heterosis between unrelated individuals. Much of the variation among pollen donors of *Campsis radicans* in their ability to produce fruit (Bertin, 1982) is attributable to male-female interactions (Robbins and Travis, 1986). No one male is superior, but specific pollen donor-recipient combinations suffered from incompatibility or inbreeding depression. Experimentally removing fruit or ovules and observing offspring of lower quality compared with naturally aborted fruit or ovules (Stephenson and Winsor, 1986; Casper, 1988) may be confounded with differential abortion of fruit or seed following selfing or mating events between related individuals.

Marshall and Ellstrand (1986) observed significant variation among male pollen donors in seed production in a population of self-incompatible *Raphanus sativus*. However, it is not clear to what extent genetic similarity may have contributed to the variation among males because they did not control for genetic relatedness, and the male effect was much smaller than the female effect on seed mass and number of seed/fruit. Their study differed from the present study in that they pollinated flowers with pollen from several males at once. Competition among males may be more intense in their study due to within-fruit competition. In *C. fasciculata* there is considerable pollen carry-over (Fenster, 1991a) so that multiply-sired fruit are probably the rule rather than the exception. However, Sork and Schemske (un-

published data) demonstrate that fertilization and the allocation of resources to developing seed and fruit in *C. fasciculata* are random with respect to pollen source in multiply-sired fruit. Thus, the opportunity for mate choice was probably not biased downward in this study by confining comparisons among males in their ability to accrue resources at the fruit level.

Variation within a seed parent—Pollination date—Within-plant variation in seed mass, number of seeds/fruit, fruit maturation time, and fruit abortion rate strongly suggest that resources are not evenly distributed within the plant to developing seed and fruit in *C. fasciculata*. A negative correlation between pollination date and seed mass, number of seeds/fruit, and fruit abortion rate has been observed in a number of studies (Salisbury, 1942; Cavers and Steel, 1984; Lee and Bazzaz, 1982a, b; Thompson, 1984; Mazer, 1987). Fruit fertilized later in the season are unable to compete with more developed fruit as resource sinks (Olufajo, Daniels, and Scarisbrick, 1982). Plants consist of physiological subunits which may function autonomously in their acquisition and distribution of resources (Watson and Casper, 1984). The inflorescence and its subtending leaf is an important level for resource competition (Janzen, 1971; Harper, 1977; Willson and Price, 1977; Stephenson, 1980; Wyatt, 1982). Garrish and Lee (1989) have demonstrated by inflorescence and defoliation experiments that competition for resources occurs both at the inflorescence and whole plant level in *C. fasciculata*. Resource competition due to these position effects may determine the extent of ovule abortion following selfing (Martin and Lee, unpublished data).

Ovule position—Within the fruit, peduncular ovules had a lower probability of maturing seeds and had a lower eventual mature seed mass compared to ovules proximal to the style (see also Lee and Bazzaz, 1986), and have been observed in other legumes (Schaal, 1980). In *C. fasciculata* the ovule position effect was observed in the absence of selfing. In contrast, Nakamura (1988) found that lower seed mass associated with the peduncular position in *Phaseolus vulgaris* only occurred following selfing, implicating an inbreeding component to the position effect.

The lower probability of ovules maturing to seed in the peduncular end may reflect the basipetal growth of pollen tubes resulting in a lower fertilization rate of the peduncular ovules (Lee and Bazzaz, 1986). The peduncular ovules that are fertilized may suffer delayed fertiliza-

tion and thus may lag behind in their ability to act as efficient resource sinks (Lee and Bazzaz, 1986). The lower seed mass of the most extreme stylar ovule may reflect a tendency for pollen tubes to miss this ovule (Hossaert and Valero, 1988). Consequently, it suffers delayed fertilization and may not assimilate resources as well as its neighboring ovules.

The differential allocation of resources among the ovule positions probably does not reflect an opportunity for gametophytic competition among male pollen donors. In another study on *C. fasciculata*, Fenster and Sork (1988) found no variation among pollen donor sources (self vs. outcrossed and among individual male donors) for in vivo pollen tube growth rate. Therefore, there appears to be little opportunity for selection to act on males via their ability to fertilize "preferred" ovules at the stylar end of the fruit.

Morphological constraints (Watson and Casper, 1984) may also play a role in the lowered success of the most peduncular ovule. In *C. fasciculata* the valves of the fruit at the peduncular end meet at an acute angle resulting in a constrained environment for the peduncular ovule. When the peduncular ovule does mature to a seed it is often misshapen.

Evolutionary implications of seed parent effects—In this greenhouse study, there was approximately 50% fruit abortion and 25% seed abortion. Although there was no effect of pollen donor source beyond inbreeding, the effect of seed parent on seed and fruit yield was always significant and strong. In contrast to the role of pollen donor source, pollination date and ovule position in the pod played strong roles in the allocation of resources to developing fruit and ovules. These strong maternal and within-plant environmental effects could retard the evolutionary response to selection for pollen donor-mediated allocation of resources to developing ovules and fruit (Naylor, 1964).

In natural populations there are other environmental interactions, controlled in this greenhouse study, that might further diminish any pollen donor source effect (Garwood and Horvitz, 1985; Weller, 1985; Winn and Werner, 1987). Variation in water availability has a large effect on seed and fruit abortion (Lee and Bazzaz, 1982a), and temporal and spatial variation in seed predation on *C. fasciculata* is also large (Lee and Bazzaz, 1982a). In natural populations the opportunity for differential resource allocation to progeny of different paternity may be further limited by these environmental constraints.

Since no variation among male pollen donor

sources in their ability to obtain resources for developing seed and fruit was observed, the opportunity for mate choice to act on postfertilization male performance on the seed parent is limited. However, the overproduction of flowers in *C. fasciculata* may still be associated with male reproductive fitness through pollen production and dispersal. In the highly selfing autogamous congener, *C. nictitans*, flower abortion rate is much lower (Lee, 1989; Fenster, unpublished data), suggesting that over-initiation of flowers in outcrossing *C. fasciculata* may be due to a combination of bet-hedging against an unpredictable environment (Lee, 1988) and selection for increased male fitness.

LITERATURE CITED

- ANTONOVICS, J., AND J. SCHMITT. 1986. Paternal and maternal effects on propagule size in *Anthoxanthum odoratum*. *Oecologia* 69: 277-282.
- ARNOLD, S. J., AND M. J. WADE. 1984. On the measurement of natural and sexual selection: theory. *Evolution* 38: 709-719.
- BERTIN, R. I. 1982. Paternity and fruit production in trumpet creeper (*Campis radicans*). *American Naturalist* 119: 694-709.
- BOOKMAN, S. S. 1984. Evidence for selective fruit production in *Asclepias*. *Evolution* 38: 72-86.
- BROWNLEE, K. A. 1965. Statistical theory and methodology in science and engineering. John Wiley and Sons, New York.
- CASPER, B. B. 1984. On the evolution of embryo abortion in the herbaceous perennial *Cryptantha flava*. *Evolution* 38: 1337-1349.
- . 1988. Evidence for selective embryo abortion in *Cryptantha flava*. *American Naturalist* 132: 318-326.
- CAVERS, P. B., AND M. G. STEEL. 1984. Patterns of change in seed weight over time on individual plants. *American Naturalist* 124: 324-335.
- CHARLESWORTH, D., D. W. SCHEMSKE, AND V. L. SORK. 1987. The evolution of plant reproductive characters: sexual versus natural selection. In S. Stearns [ed.], *The evolution of sex*. Birkhauser-Verlag, Basel.
- CHARNOV, E. L. 1979. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences* 76: 2480-2484.
- EHRlich, P. R., AND P. H. RAVEN. 1969. Differentiation of populations. *Science* 165: 1228-1232.
- ELLSTRAND, N. C., AND D. L. MARSHALL. 1985. Interpopulation gene flow by pollen in wild radish, *Raphanus sativus*. *American Naturalist* 26: 606-616.
- EPPELSON, B. K., AND M. T. CLEGG. 1986. Spatial-auto correlation analysis of flower color polymorphisms within substructured populations of morning glory (*Ipomoea purpurea*). *American Naturalist* 128: 840-858.
- FENSTER, C. B. 1988. Gene flow and population differentiation in *Chamaecrista fasciculata* (Leguminosae). Ph.D. dissertation, The University of Chicago. Chicago, IL.
- . 1991a. Gene flow in *Chamaecrista fasciculata* I. Gene dispersal. *Evolution*. In press.
- . 1991b. Gene flow in *Chamaecrista fasciculata* II. Gene establishment. *Evolution*. In press.

- , AND V. L. SORK. 1988. Effect of crossing distance and male parent on in vivo pollen tube growth in *Chamaecrista fasciculata*. *American Journal of Botany* 75: 1898–1903.
- GARRISH, R. S., AND T. D. LEE. 1989. Physiological integration in *Cassia fasciculata*: inflorescence removal and defoliation experiments. *Oecologia* 81: 279–284.
- GARWOOD, N. C., AND C. C. HORVITZ. 1985. Factors limiting fruit and seed production of a temperate shrub *Staphylea trifolia* L. (Staphuleaceae). *American Journal of Botany* 72: 453–466.
- GUTH, C. J., AND S. G. WELLER. 1986. Pollination, fertilization and ovule abortion in *Oxalis magnifica*. *American Journal of Botany* 73: 246–253.
- HARPER, J. L. 1977. Population biology of plants. Academic Press, London.
- HOROVITZ, A., L. MEIRI, AND A. BEILES. 1976. Effects of ovule positions in fabaceous flowers on seed set and outcrossing rates. *Botanical Gazette* 137: 250–254.
- HOSSAERT, M., AND M. VALERO. 1988. Effect of ovule position in the pod on patterns of seed formation in two species of *Lathyrus* (Leguminosae and Papilionidae). *American Journal of Botany* 75: 1714–1731.
- IRWIN, H. W., AND R. C. BARNEY. 1982. The American Cassiinae. A synoptical revision of Leguminosae tribe Cassiinae subtribe Cassiinae in the New World. Memoirs of the New York Botanical Garden, vol. 35, p. 2. The New York Botanical Garden, New York.
- JANZEN, D. H. 1971. Escape of *Cassia grandis* L. beans from predators in time and space. *Ecology* 52: 964–979.
- . 1977. A note on optimal mate selection by plants. *American Naturalist* 111: 365–371.
- LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- LEE, T. D. 1984. Patterns of fruit maturation: a gametophyte competition hypothesis. *American Naturalist* 123: 427–432.
- . 1988. Patterns of fruit and seed production. In J. L. Doust and L. L. Doust [eds.], Plant reproductive ecology. Oxford University Press, New York.
- . 1989. Patterns of fruit and seed production in a Vermont population of *Cassia nictitans* L. (Caesalpinieae). *Bulletin of the Torrey Botanical Club* 116: 15–21.
- , AND F. A. BAZZAZ. 1982a. Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. *Ecology* 63: 1361–1373.
- , AND ———. 1982b. Regulation of fruit maturation pattern in an annual legume, *Cassia fasciculata*. *Ecology* 63: 1374–1388.
- , AND ———. 1986. Maternal regulation of fecundity: non-random ovule abortion in *Cassia fasciculata* Michx. *Oecologia* 68: 439–465.
- LEVIN, D. A. 1981. Dispersal versus gene flow in plants. *Annals of the Missouri Botanical Garden* 68: 233–253.
- . 1984. Inbreeding depression and proximity dependent crossing success in *Phlox drummondii*. *Evolution* 38: 116–127.
- LLOYD, D. G. 1980. Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive season. *New Phytologist* 86: 69–79.
- LYONS, E. E., N. M. WASER, M. V. PRICE, J. ANTONOVICS, AND A. F. MOTTEN. 1989. Sources of variation in plant reproductive success and implications for concepts of sexual selection. *American Naturalist* 134: 409–433.
- MARSHALL, D. L., AND N. C. ELLSTRAND. 1986. Sexual selection in *Raphanus sativus*, experimental data on non-random fertilization, maternal choice and consequences of multiple paternity. *American Naturalist* 127: 446–461.
- MAZER, S. J. 1987. Parental effects on seed development and seed yield in *Raphanus raphanistrum*: implications for natural and sexual selection. *Evolution* 41: 355–371.
- MITCHELL-OLDS, T. 1986. Quantitative genetics of survival and growth in *Impatiens capensis*. *Evolution* 40: 107–116.
- NAKAMURA, R. R. 1988. Seed abortion and seed size variation within fruits of *Phaseolus vulgaris*: pollen donor and resource limitation effects. *American Journal of Botany* 75: 1003–1010.
- NAYLOR, A. 1964. Natural selection through maternal influence. *Heredity* 19: 509–511.
- OLUFAJO, O. O., R. W. DANIELS, AND D. H. SCARISBRICK. 1982. The effect of pod removal on the translocation of carbon 14 photosynthate from leaves of *Phaseolus vulgaris* L. cv. Lochness. *Journal of the Horticultural Society* 57: 333–338.
- OWINO, F., AND B. ZOBEL. 1977. Genotype \times environment interaction and genotypic stability in Loblolly pine III. Heterosis and heterosis \times environment interaction. *Silvae Genetica* 26: 2–3.
- PRICE, M. V., AND N. M. WASER. 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *Nature* 277: 294–297.
- ROBBINS, L., AND J. TRAVIS. 1986. Examining the relationship between functional gender and gender specialization in hermaphroditic plants. *American Naturalist* 128: 406–415.
- SALISBURY, E. J. 1942. The reproductive capacity of plants. Bell Press, London.
- SAS INSTITUTE, INC. 1985. SAS user's guide: statistics, version 5 ed. SAS Institute, Inc., Cary, NC.
- SCHAAL, B. A. 1980. Reproductive capacity and seed size in *Lupinus texensis*. *American Journal of Botany* 67: 701–709.
- SCHEMSKE, D. W., AND L. P. PAUTLER. 1984. The effects of pollen composition on fitness components in a neotropical herb. *Oecologia* 62: 31–46.
- SORENSEN, F. 1969. Embryonic genetic load in coastal Douglas fir *Pseudotsuga menziesii* var. *menziesii*. *American Naturalist* 103: 389–398.
- SQUILLACE, A. E., AND J. F. KRAUS. 1962. Effects of inbreeding on seed yield, germination, rate of germination, and seedling growth in slash pine. In Forest genetics workshop, Macon, GA, 1962.
- STEPHENSON, A. G. 1980. Fruit set, herbivory, fruit reduction and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). *Ecology* 61: 57–64.
- . 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12: 253–279.
- , AND R. I. BERTIN. 1983. Male competition, female choice, and sexual selection in plants. In L. Real [ed.], Pollination biology, 109–149. Academic Press, New York.
- , AND J. A. WINSOR. 1986. *Lotus corniculatus* regulates offspring quality through selective fruit abortion. *Evolution* 40: 453–458.
- SUTHERLAND, S., AND L. F. DELPH. 1984. On the importance of male fitness in plants: patterns of fruit set. *Ecology* 65: 1093–1104.
- THOMPSON, J. N. 1984. Variation among individual seed masses in *Lomatium grayi* (umbelliferae) under con-

- trolled conditions: magnitude and partitioning of the variance. *Ecology* 65: 626–631.
- VANDER KLOET, S. P., AND D. TOSH. 1984. Effects of pollen donors on seed production, seed weight, germination, and seedling vigor in *Vaccinium corymbosum* L. *American Midland Naturalist* 112: 392–396.
- WASER, N. M., AND M. V. PRICE. 1989. Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. *Evolution* 43: 1097–1109.
- WATSON, M. A., AND B. B. CASPER. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics* 15: 233–258.
- WELLER, S. G. 1985. The life-history of *Lithospermum caroliniense*, a long-lived herbaceous sand dune species. *Ecological Monographs* 55: 49–67.
- WESTOBY, M., AND B. RICE. 1982. Evolution of the seed plants and inclusive fitness of plant tissues. *Evolution* 36: 713–724.
- WILLSON, M. F. 1979. Sexual selection and dicliny in angiosperms. *American Naturalist* 119: 579–583.
- , AND N. BURLEY. 1983. Mate choice in plants: mechanisms and consequences. Princeton Biological Monographs, Princeton, NJ.
- , AND P. W. PRICE. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution* 31: 495–511.
- WINN, A. A., AND P. A. WERNER. 1987. Regulation of seed yield within and among populations of *Prunella vulgaris*. *Ecology* 68: 1224–1233.
- WRIGHT, S. 1977. Evolution and the genetics of population, vol. 3. Experimental results and evolutionary deductions. University of Chicago Press, Chicago.
- . 1978. Evolution and the genetics of populations, vol. 4. Variability within and among natural populations. University of Chicago Press, Chicago.
- WYATT, R. 1982. Inflorescence architecture: how flower number, arrangement, and phenology affect pollination and fruit set. *American Journal of Botany* 69: 585–594.