


Locations of seed abortion in response to defoliation differ with pollen source in a native perennial legume herb

Yuria J. Cardel | Suzanne Koptur 

Department of Biological Sciences, Institute of the Environment, International Center for Tropical Botany, Florida International University, University Park, Miami, FL 33199, USA

Correspondence

Suzanne Koptur, Department of Biological Sciences, International Center for Tropical Botany, Institute of the Environment, Florida International University, University Park, Miami, FL 33199 USA.
Email: kopturs@fiu.edu

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Abstract

Premise: In many flowering plants, flowers contain more ovules than fruits have seeds. What determines which ovules become seeds? When photosynthates are limited, as may happen when plants lose leaf area to herbivory, fewer fertilized ovules become seeds.

Methods: Greenhouse-grown ramets of distinct individuals of a perennial herbaceous legume were manually defoliated to various levels determined in the field, then self- or cross-pollinated. For each seed produced, we recorded its position in the fruit and its mass. From a subset of seeds from different treatments and positions in the fruits, we grew seedlings and measured their dry mass.

Results: Ovules were aborted more frequently in fruits from flowers that were self-pollinated and from those on plants with higher levels of defoliation. Ovules in the basal portion of the fruits were more likely to be aborted than those at the stigmatic end; this pattern was most pronounced for fruits after self-pollination with high levels of defoliation. Total number of seeds produced and seed mass per pod were greatest in cross-pollinated fruits after no or low levels of defoliation. Mean individual seed mass was greater for fruits with fewer seeds, indicating a trade-off between seed number and seed mass. Seedling dry mass (a measure of vigor) was greatest for seeds in the middle positions of fruit produced by cross-pollination after severe herbivory; no positional differences were seen for seeds from self-pollinated fruits.

Conclusions: Observed locations of seed abortion may have been selected not only by defoliation, but in part by propensity for dispersal, while positional differences in seedling vigor may be related to seed size and differential maternal allocation based on pollination treatment and leaf area lost.

KEYWORDS

Centrosema virginianum, defoliation, Fabaceae, fruit, legume, pollination, resource allocation, seed abortion, seed number, seed size, seedling performance

Genotypic characteristics of a pollen donor have an important impact on the fitness of offspring, affecting characteristics such as seed mass, germination, and survival (Marshall and Ellstrand, 1988; Bertin, 1989). In general, the number of fertilized ovules is usually higher than the number of seeds that plants produce, and variation in the number of ovules is lower than variation in seed number (Wyatt, 1981). These differences are indicative of the actions of complementary mechanisms: differential fertilization and post-fertilization maternal effects, such as seed abortion (Stephenson and Winsor, 1986; Travers and Mazer, 2001; Diaz et al., 2003). Seed abortion may be attributable to male–male competition in a post-pollination event, making maternal effects difficult to demonstrate (Cobb et al., 2002). However, mechanisms that regulate fruit set and

seed mass are clearly under maternal influence as well (Stephenson and Bertin, 1983; Lee and Bazzaz, 1986; Nakamura, 1986; Niesenbaum, 1999).

Under limitation of photosynthetic reserves, selective mating by maternal plants may be represented by abortion locations of fruits and seeds. If this selective abortion occurs, plants may be capable of increasing progeny fitness by adjusting reproductive allocation (Koptur et al., 1996; Marshall and Oliveras, 2001; Shaner and Marshall, 2003) and, in some cases, sex allocation (Avila-Sakar et al., 2001; Kudo et al., 2001; Narbona and Dirzo, 2010; Blake-Mahmud and Struwe, 2020).

Herbivory decreases energy available to plants by reducing photosynthetic tissue and presumably promoting shifts in resource allocation (Crawley, 1983). Herbivory in

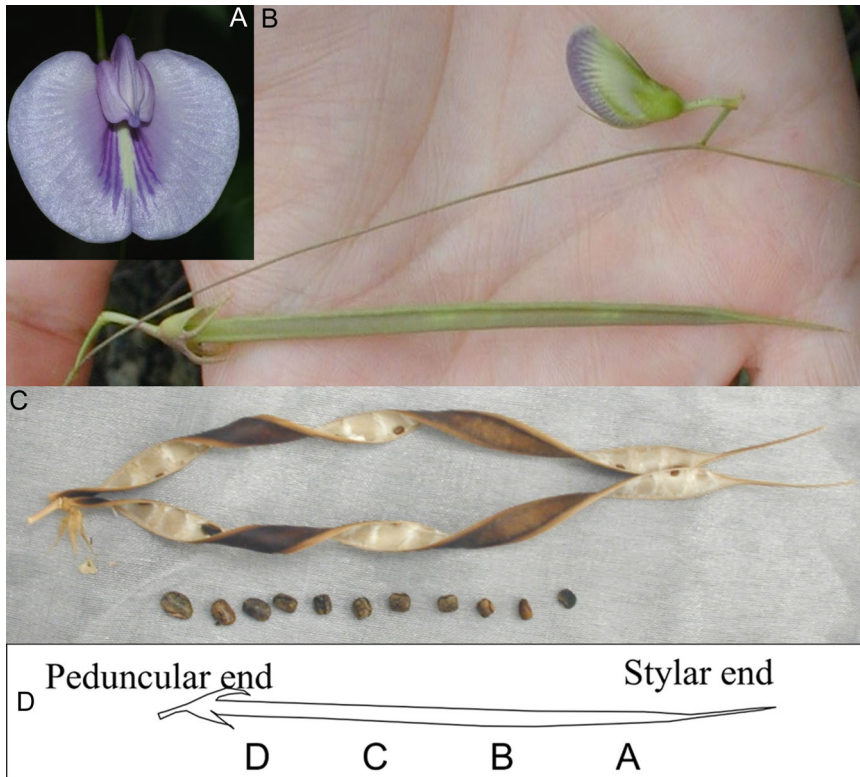


FIGURE 1 *Centrosema virginianum* (butterfly pea) flower, fruit, and seed. (A) Open flower; (B) stem with immature fruit and flower bud on palm of hand for scale; (C) mature, dehiscent fruit with aborted seeds still in capsule valves, and fully formed seeds below; (D) diagram of fruit with regions labeled A–D from distal stylar end to basal peduncular end.

maternal plants of wild radish grown in a greenhouse negatively affected components of progeny fitness, especially increasing seed abortion and vulnerability to virus in seeds produced (Agrawal, 2001), though effects on seed size/mass differed according to individual plants and families. Other studies of defoliation effects on legume reproduction showed that species of *Vicia* produced fewer seeds after defoliation (Brown et al., 1987; Nielsen, 1990; Koptur et al., 1996). If defoliation promotes abortion, it may also influence the degree of maternal plant selectivity, aborting certain seeds to optimize energy resources available.

Fertilization is nonrandom for many species of flowering plants (Stephenson and Winsor, 1986; Stephenson et al., 1988; Winsor et al., 2000; Avila-Sakar et al., 2001). Preferred regions of fertilization within fruit are related to higher vigor of seedlings, which in turn is related to higher fitness (Stephenson et al., 1988). If similar patterns apply to the mechanisms of selective seed abortion, detailed knowledge of (1) the frequency of abortion in different regions of the fruit and (2) the seed characteristics of those regions will be required to demonstrate that the quality of progeny has been selected to optimize the use of resources. If fertilization is position-dependent, position-dependent seed abortion within fruits strongly indicates allocation by maternal plants to favor certain offspring genotypes.

We conducted an experiment to test how defoliation influenced seed abortion between self-pollinated and cross-pollinated flowers in a self-compatible plant species. We analyzed post-fertilization patterns of seed abortion when maternal plants had different amounts of leaf area removed,

comparing how resource allocation in different regions within fruits changed under these artificial herbivory treatments. A change in the ability of the same pollen donors to sire seeds on damaged maternal plants compared with undamaged plants indicates that higher selectivity of abortion occurs when energy from photosynthesis is limited. We germinated seeds from different regions of fruits produced under the different defoliation and pollination treatments to see whether seedling size might differ because of these factors in combination.

Our aims were to (1) evaluate how defoliation (encompassing the range of levels observed in the field) affects seed production, comparing fruits from self-pollinated vs. cross-pollinated flowers, (2) compare post-fertilization positions of seed abortion in maternal plants when resources are limited by defoliation to three levels and in undefoliated controls, (3) detect any preferential resource allocation and seed development in different regions within fruits produced by two pollination (self- vs. cross-) and three defoliation treatments, and (4) compare seedling vigor from seeds produced in different regions of those fruits.

MATERIALS AND METHODS

The plant

Centrosema virginianum (L.) Bentham (Fabaceae: Papilionoideae), butterfly pea (Figure 1), is a perennial vine, native to the eastern United States, the West Indies, and Central

and South America (Gann et al., 2001–2022a; Isely, 1990). It occurs in the imperiled pine rockland habitat of southern Florida (Koptur, 2006), growing prostrate or climbing on other plants. It bears trifoliolate leaves and showy purple flowers that are pollinated by a variety of bees (Spears, 1987). Pods produce an average of 17 seeds when flowers are cross-pollinated and 8 seeds when self-pollinated (Cardel and Koptur, 2010). Seeds are ballistically projected from pods by sudden separation of the legume valves along both sutures.

This species provides several advantages for this study. (1) It is self-compatible, which allows comparisons of fertilization success between crossed and self-pollinated fruits (Spears, 1987; Cardel and Koptur, 2010); (2) flowers are not capable of automatic self-pollination, which facilitates controlled hand-pollination treatments (Spears, 1987; Cardel and Koptur, 2010); (3) it produces flowers year-round in the greenhouse and is easy to propagate from cuttings; (4) it produces pods in which early aborted seeds (or unfertilized ovules) and late aborted seeds are easy to distinguish.

Evaluation of foliar herbivory

We measured herbivory in three natural areas where *Centrosema virginianum* was abundant: Pine Shore Pineland Preserve (PS) and Rockdale Pineland Preserve (RD), both pine rockland fragments under the management of Miami-Dade County, Florida; and Long Pine Key (LPK) in Everglades National Park (ENP), Homestead, Florida, United States. The Pine Shore site (25.650°N, –80.374°W) is 32 ha and includes about 243 plant taxa. Rockdale (25.635°N, –80.340°W) is 154 ha with 316 plant taxa reported. Long Pine Key (25.313°N, –80.938°W), an area in the northeastern section of Everglades National Park, is surrounded by other natural habitats (sawgrass prairie and hardwood hammock) with 1129 plant taxa reported for all habitats combined (Gann et al., 2001–2022b).

To assess the amount of foliar herbivory, a total of 75 *Centrosema virginianum* plants were marked and mapped at each study site during the dry season of 1999–2000. To select individual plants, we haphazardly located and marked plants that had at least four nodes. Each plant selected was at least a meter from another *C. virginianum* individual. All the leaves of those plants were collected, cutting the leaf from the base of the petiole (to include petiolules whose leaflets were entirely consumed).

In the laboratory, we randomly selected nine leaflets per plant and assigned each leaflet to a damage class (0–5) according to the total percentage of herbivory (0: 0%; 1: 1–5%; 2: 6–12%; 3: 13–25%; 4: 26–50%; 5: 51–100%). Using the modified method of Dirzo and Dominguez (1995), we calculated the herbivory index (HI) for each individual of *C. virginianum* and used those values to compare damage at the three sites.

Though we did not systematically monitor plants and collect herbivores over time, several kinds of damage were

characteristic, and we observed several insects using the foliage for food and shelter. Insects encountered feeding on the plants in the field were collected and reared for identification.

Experimental design

We selected 15 genotypes collected from one site, the Rockdale Pineland, to serve as maternal plants and assigned a genotype number to each plant. We chose plants at least 5 m from one another to obtain distinct individuals. In early 2001, genets were propagated by cuttings made in the field to produce replicates of each genotype; multiple cuttings were made from each genotype/individual and rooted in wet soil in a cutting bench in a single pot. Five thriving cuttings were repotted and labeled with their genotype; four were used in the experiment, one served as a backup. Potted experimental plants were watered lightly every morning. In this way, we could apply the four defoliation treatments to one ramet of each genet, with both pollination treatments applied to each ramet; each genotype was simultaneously under the influence of all the experimental factors in a complete factorial experimental design. Once the ramets (plants) were fully established in the Florida International University (FIU) greenhouse in Miami, Florida, we applied four defoliation treatments to each genotype by partially clipping leaf tissue using sharp dissecting scissors to the assigned level on each ramet of that genotype. The treatments levels were chosen to cover the range of damage experienced by plants in natural situations: zero herbivory (control); ~33% herbivory (one third of each leaflet removed); 50% (half of each leaflet removed); ~66% (two thirds of each leaflet removed). Clipping treatments were applied throughout the experiment to every leaf produced after plants had acquired four nodes, after each leaf had fully expanded, and continued until the experiment was completed and all fruits were harvested.

Five unrelated plants were grown from seeds collected at the Pineshore site in the FIU greenhouse and used as pollen donors for xenogamous cross-pollinations. Pollen from at least three flowers from different plant donors was mixed and used to perform cross-pollinations; we did not follow individual pollen parents, but rather consolidated their pollen to be used as a uniform xenogamy treatment. Self-pollinations were performed using at least three flowers from the same maternal plant receiving the pollen. We used pollen from three flowers for each pollination to provide an excess of pollen so there would be no pollen limitation influencing fertilization. Pollinations were performed simply by inserting a small fingertip into the glassine envelope containing the anthers collected from donor flowers and bringing pollen to the stigma of the recipient flower. The first 15 fruits produced per cross per treatment on each ramet were collected as soon as they reached maturity (when the pod became dark in color, but not yet dehisced). At least one of each hand self- and cross-pollination was

performed every other day to space the treatments equally during plant development. Henceforth, fruits and seeds produced by self-pollination and cross-pollination may be referred as S-fruits or S-seeds and X-fruits or X-seeds, respectively.

Each fruit collected was visualized as divided in four sections. Each section contained ~25% of the total number of ovules, with “A” being the stylar end and “D” the peduncular end (similar to Stephenson et al., 1988). For each ovule position, we recorded whether a seed was present, and if not, whether it was aborted early (or not fertilized) or late (aborted after seed was initiated). We weighed all the seeds collected, then planted them in individual trays with 5 by 10 cells, tracking the identity of each seed. Before planting, seeds were scarified with 90% sulfuric acid for 5 min. If seeds did not germinate, we manually removed a small section of the seed coat with a scalpel. Subsequently, all these seeds germinated successfully. We did not compare germination rates among treatments because germination procedures were not uniform, but germination of scarified seeds was nearly 100%. We transferred germinated seeds to individual units in greenhouse trays, following the early growth of each one. After 30 days from emergence, we harvested a subsample of seedlings from seeds that germinated successfully; these were the first 15 seedlings of each treatment group that survived for 30 days. Seedlings were dried in an oven for 72 h at 80°C, then weighed.

Data analyses

Herbivory levels at the three field sites were compared using one-way ANOVA on the average of leaf scores for each of 75 individual plants at each site. We report not only the confidence intervals but range of values as those were used to justify the levels of artificial defoliation employed in the experiment.

Seed numbers, numbers of aborted ovules/seeds, total mass per fruit, and average seed mass per fruit were examined with split-plot ANOVA, using the MIXED procedure in SAS version 9.4 (SAS Institute, Cary, NC, USA). We used Tukey–Kramer adjusted *P*-values, model-based fixed effects to obtain SE, and obtained df using the Satterthwaite method. Post hoc tests (least significant difference [LSD], Student–Neuman–Keuls [SNK], and Dunnett C) were employed to clarify differences among treatments.

To evaluate the effects of defoliation and pollination treatment on the proportion of seeds aborted by region in fruits we used split-split-plot ANOVA on abortion of seeds in 60 fruits of each pollination × defoliation treatment in four locations within fruits. Herbivory treatment and pollination treatment were considered as fixed factors. The blocks were split by pollination treatment (self and cross) and split again by herbivory treatment, then by fruit region (A, B, C, D). Genotypes were used as replicates by plot

(random factor), and interactions with them were considered to evaluate genotype effect in the variance components. We employed the MIXED procedure for categorical variables, with the fixed effects method for standard errors and Satterthwaite method for degrees of freedom. The analysis was conducted using SAS using the proportion of arcsine-transformed seeds aborted to meet analysis assumptions. We used the same technique to examine the effects of defoliation and pollination treatment on the mass of individual seeds by region in fruits.

To test for compensation between the number of seeds produced and seed weight, we performed a partial correlation analysis between seed number and seed mass means for each defoliation treatment × pollination type × genotype combination. The number and mass of seeds were square-root-transformed to meet normality assumptions. We used the same technique to compare dry mass of seedlings produced by seeds from different regions of the fruits.

RESULTS

Evaluation of foliar herbivory

The three sites differed from one another in levels of foliar herbivory damage ($F_{2, 215} = 40.35$, $P < 0.0001$). The Everglades National Park plants had the lowest levels of damage, an average of 12% per plant, with a range from 1% to 19% leaf area lost; Rockdale was intermediate with an average of 18% damage, with a range from 0% to 45%; and Pine Shore plants had the most damage, 24% on average with a range of damage from 10% to 80%. Post hoc tests (LSD, SNK, and Dunnett C) all showed the three sites to be distinct from one another. These results informed the levels of defoliation we used in our greenhouse experiment, as individual plants in nature experienced levels of damage ranging from 0% to more than 60% leaf loss overall.

Leaf herbivores

We encountered larvae of the long-tailed skipper (*Urbanus proteus*, Lepidoptera: Hesperidae) between folded leaf surfaces of *C. virginianum* and skeletonized leaflets and folding suggestive of early and later instar caterpillars of this herbivore (or other skipper butterflies) on many plants. New leaves were favored by katydids and weevils (such as the citrus root weevil, *Pachnaeus litus*).

Seed production

There was a significant interaction between defoliation treatment and pollination type ($F_{3, 457} = 31.95$, $P < 0.0001$). X-fruits produced substantially more seeds than S-fruits at all levels of defoliation (Figure 2). For X-fruits, the number of seeds per fruit decreased significantly with each increased

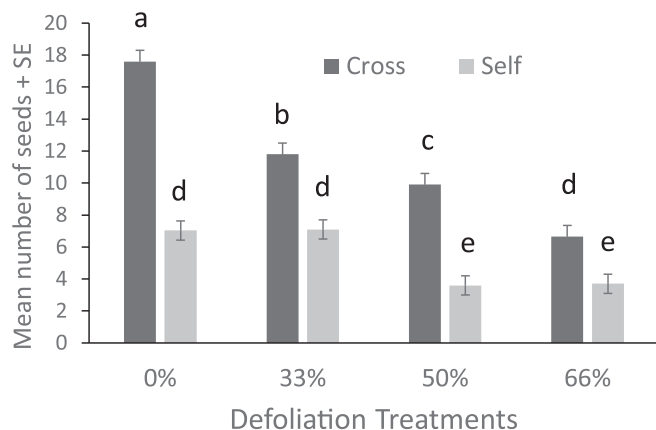


FIGURE 2 Mean number of seeds per fruit from flowers of *Centrosema virginianum* subject to different levels of defoliation and two pollination treatments (cross vs. self; X vs. S). Means with different letters are significantly different from one another ($P < 0.05$) as indicated by split-plot ANOVA.

level of defoliation. In S-fruits, the control and mild defoliation treatments did not differ from one another but produced substantially more seeds per fruit than the two higher levels of defoliation, which did not differ from one another (Figure 2).

Seed abortion

As for seed production, there was a significant interaction between defoliation level and pollination type ($F_{3, 457} = 17.10$, $P < 0.0001$). S-fruits had higher abortion rates than X-fruits throughout all defoliation treatments (Figure 3). Severely defoliated X-fruits had similar levels of abortion as control or little defoliated S-fruits. For both X- and S-fruits, the abortion levels of fruits from ramets experiencing control and light defoliation (0% and 33%) were not different from one another; neither did the abortion levels of fruits differ between those with moderate and higher levels of defoliation (50% and 66%).

Seed number vs. seed mass

There was a significant interaction between pollination type and defoliation treatment on total seed mass per fruit ($F_{3, 443} = 2.65$, $P = 0.0483$). Mean seed mass per fruit showed a much more significant interaction ($F_{3, 463} = 7.96$, $P < 0.0001$), and both pollination type and defoliation treatment had significant effects on this measure. Individual seeds from X-fruits were lighter than those from S-fruits (Figure 4) at all levels of defoliation, and mean seed mass increased with higher levels of defoliation. Individual seeds from S-fruits were significantly heavier with higher levels of defoliation (50% and 66%) than seeds produced on control or lightly defoliated plants (Figure 4).

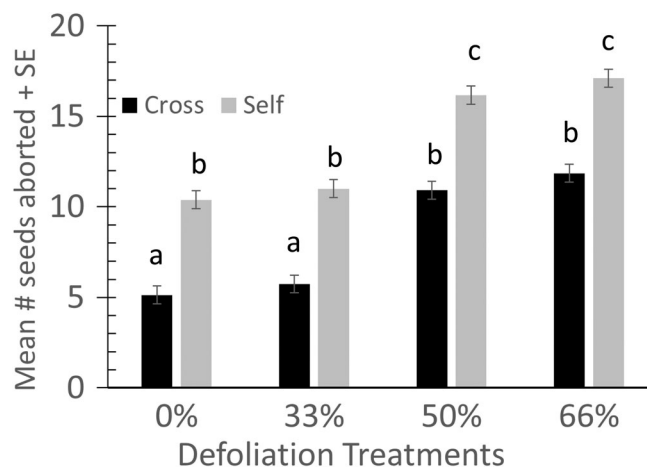


FIGURE 3 Mean number of ovules/seeds aborted per fruit from flowers of *Centrosema virginianum* subject to different levels of defoliation and two pollination treatments (cross vs. self; X vs. S). Means with different letters are significantly different from one another ($p < 0.05$) as indicated by split-plot ANOVA.

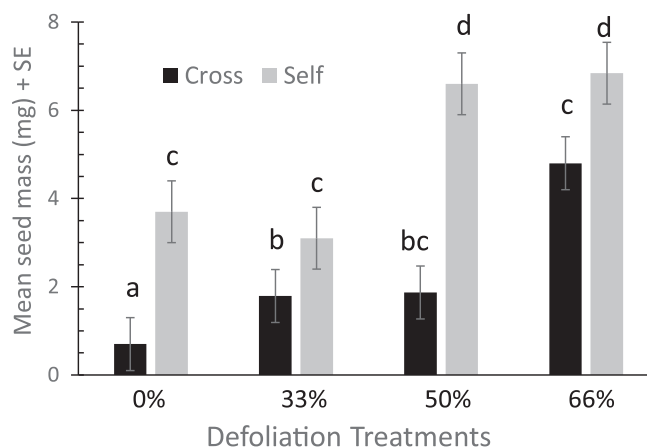


FIGURE 4 Mean seed mass of individual seeds per fruit from flowers of *Centrosema virginianum* subject to different levels of defoliation and two pollination treatments (cross vs. self; X vs. S). Means with different letters are significantly different from one another ($P < 0.05$) as indicated by split-plot ANOVA on log average seed weights.

Fruits with fewer seeds had heavier seeds than did fruits with more seeds. Correlation of mean seed number per fruit and mean seed mass (controlled for pollination type, defoliation treatment, and genotype; $n = 102$, $df = 97$) was -0.362 , evidence of a trade-off between seed number and seed mass over all treatments (Figure 5).

Defoliation effects on selective seed abortion

The proportion of seeds aborted differed within fruits with pollination and defoliation treatments (Table 1). These results, and the consistency of patterns among defoliation

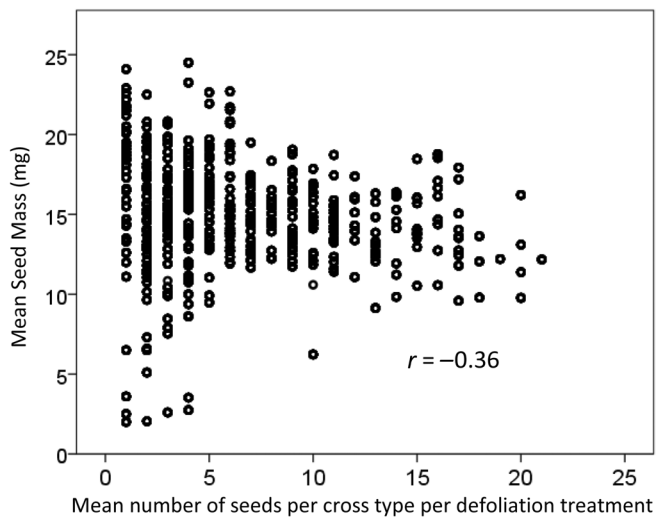


FIGURE 5 Mean number of seeds per fruit from flowers of *Centrosema virginianum* over all pollination \times defoliation combinations versus mean seed mass. Correlation between mean seed number and mean seed mass indicated by r -value.

TABLE 1 Split-split-plot ANOVA on abortion of seeds in four locations within fruits of *Centrosema virginiana* individuals subject to two pollination treatments (cross vs. self; X vs. S) and four levels of defoliation (0, 33, 50, and 66%) over their growing period. Each defoliation level \times pollination treatment is represented by 60 fruits. Mixed procedure for categorical variables, fixed effects standard error method, degrees of freedom Satterthwaite method. Convergence criteria met when using arcsine-square-root values of the proportions. Type 3 tests of fixed effects. Num df, degrees of freedom of the numerator; Den df, degrees of freedom of the denominator. For example, for defoliation level, $F_{3, 42} = 135.34$, $P < 0.0001$.

Effect	Num df	Den df	F	$P > F$
Defoliation level (Defol)	3	42	135.34	< 0.0001
Pollination treatment (Poll)	1	56	561.64	<0.0001
Defol \times Poll	3	56	42.2	<0.0001
Location (Loc)	3	336	37.51	<0.0001
Defol \times Loc	9	336	0.97	0.4667
Poll \times Loc	3	336	8.86	<0.0001
Defol \times Poll \times Loc	9	336	0.80	0.6132

treatments, suggested that aborted seeds were not randomly located. Visual inspection of the abortion locations showed that control plants and plants with low levels of leaf damage did not differ in the proportion of X-seed abortion along the fruit regions, but severely damaged plants did (Figure 6). In these plants, abortion was lower in the fruit middle regions B and C (Figure 6). It was only for the ~33% defoliation treatment in X-fruits that region D (the peduncular, basal region) showed the highest proportion of seed abortion. Seed abortion in S-fruits was highest in region D for all defoliation treatments (Figure 6).

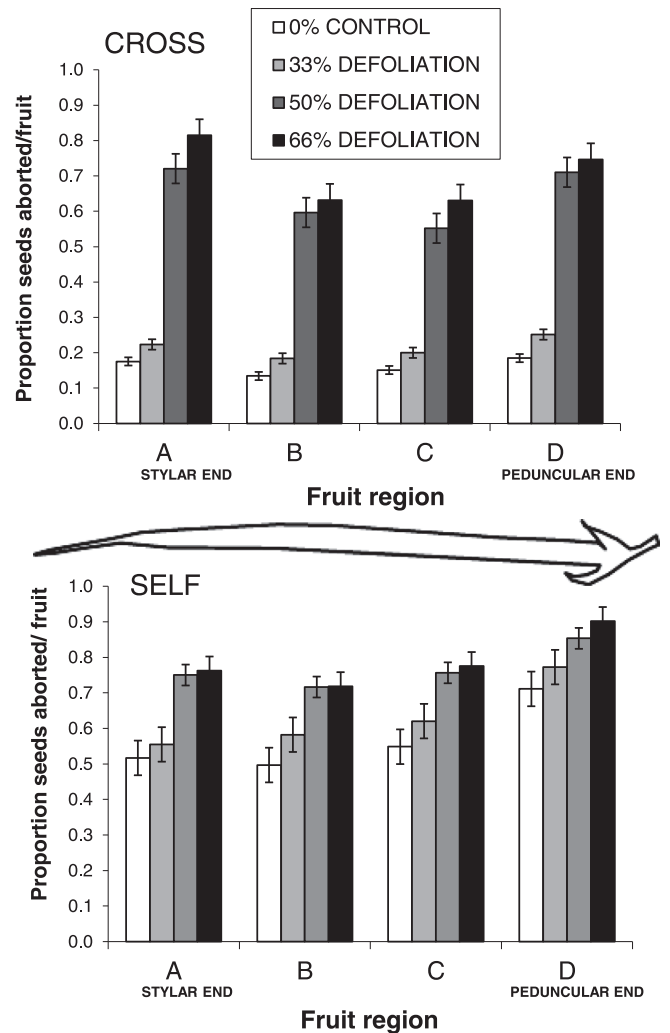


FIGURE 6 Proportion of seeds/ovules aborted in different regions of fruits of *Centrosema virginianum* subject to different levels of defoliation and two pollination treatments (cross vs. self; X vs. S). Top: fruits from cross-pollinated flowers; bottom: fruits from self-pollinated flowers. See Table 1.

Seed size variation within fruits

The ANOVA showed no significant interactions among pollination type, defoliation level, and position of seeds in fruits on mass of individual seeds (Table 2). There was a marginally significant effect of pollination type and position in fruit on individual seed mass ($P = 0.056$ in both cases). Over all positions, only the basal (D) region had seeds with substantially lower mass than those from the other regions (Figure 7), with seed mass slightly heavier from S-fruits than X-fruits.

Progeny and their position along the fruit

We found a contrast in the performance of progeny produced in X-fruits from regions B, C, and D compared

TABLE 2 Split-split-plot ANOVA on individual seed mass in four locations within fruits of *Centrosema virginiana* individuals subject to two pollination treatments (cross vs. self; X vs. S) and four levels of defoliation (0, 33, 50, and 66%) over their growing period.

Effect	Num df	Den Df	F	P > F
Genotype	1	2614	35.027	<0.0001
Defoliation level (Defol)	3	9.4	1.672	0.239
Pollination treatment (Poll)	1	3.34	8.232	0.056
Defol × Poll	3	9.747	2.801	0.096
Location (Loc)	3	1.895	19.053	0.056
Defol × Loc	9	9.005	0.940	0.536
Poll × Loc	3	9.175	1.198	0.364
Defol × Poll × Loc	9	2614	0.795	0.621

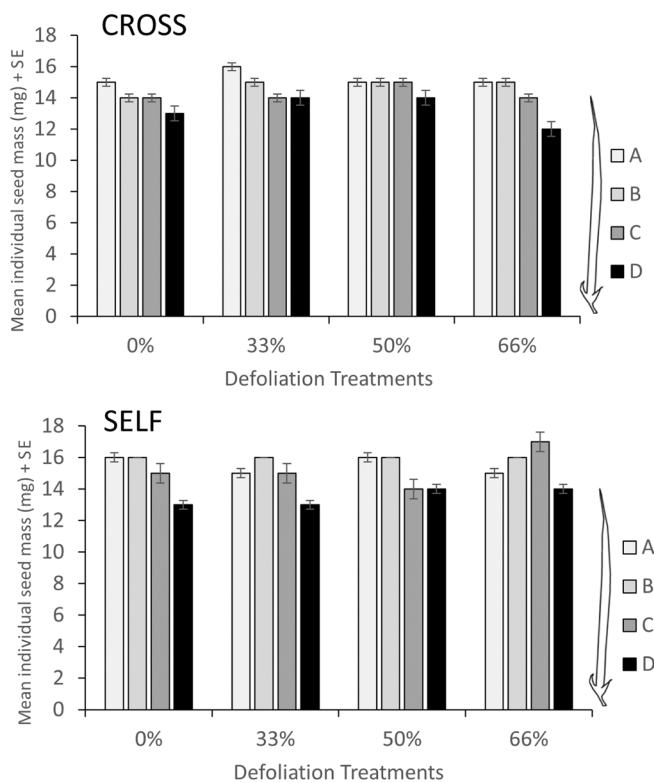


FIGURE 7 Mean individual seed mass from different regions of fruits of *Centrosema virginianum* subject to different levels of defoliation and two pollination treatments (cross vs. self; X vs. S). Top: seeds from fruits from cross-pollinated flowers; bottom: seeds from fruits from self-pollinated flowers. See Table 2.

with A: seedlings produced from seeds at the stylar end of the fruit were lighter than the others (Figure 8) in terms of seedling dry mass at 30 days. In S-fruits, seedlings grown from seeds at the base of the fruit (region D) were considerably lighter in three of the four defoliation treatments, the reverse of the pattern in X-fruits (Figure 8).

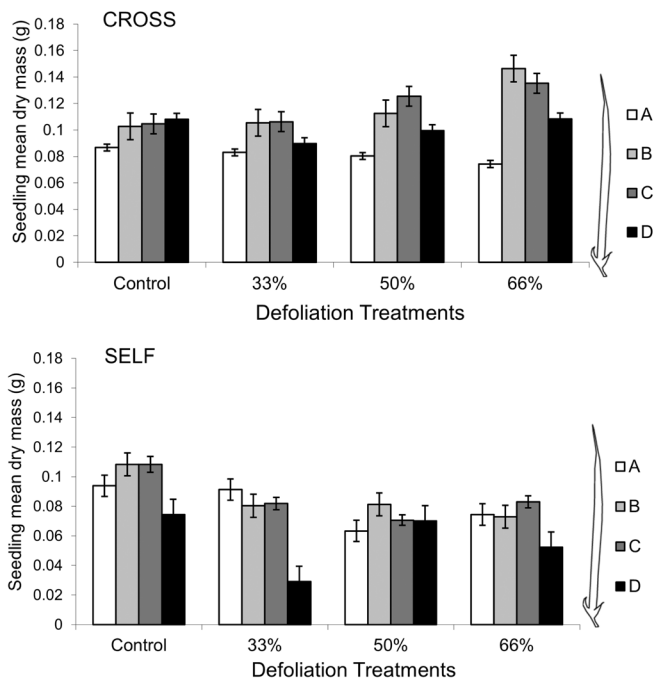


FIGURE 8 Mean seedling dry mass + SE of seeds from different regions of fruits of *Centrosema virginianum* subject to different levels of defoliation and two pollination treatments (cross vs. self; X vs. S). Top: seedlings from fruits from cross-pollinated flowers; bottom: seedlings from fruits from self-pollinated flowers. A, B, C, D indicate regions of the fruit from stylar end to peduncular end.

DISCUSSION

Leaf loss to herbivory or artificial defoliation reduces photosynthate resources available to plants and may negatively affect reproduction either directly or indirectly (Mothershead and Marquis, 2000): directly in terms of fruit and seed set, and/or indirectly in terms of flower size, attractiveness to pollinators, and subsequent pollen receipt. Additionally, increased chemical defense in response to herbivory may negatively affect floral visitors (Jacobsen and Raguso, 2018). The greenhouse experiment we described here addresses only the direct effects of reduced energy on fruit and seed production. A subsequent greenhouse experiment showed that mean corolla diameter of moderately defoliated plants was substantially smaller than that in control plants, but significantly larger than that of severely defoliated plants (Y. J. Cardel, unpublished data). The effects of flower size on pollinator attraction and pollen receipt in the field were not measured, however.

In many flowering plants, entire fruits may be aborted in response to defoliation because limited energy is available for only some to mature (Wise and Cummins, 2006), favoring those with more desirable parentage (i.e., products of outcrossing rather than self-fertilization) because they will produce seeds less closely related to the maternal parent, which promotes larger seeds, better germination,

and more vigorous progeny (Baskin and Baskin, 2019). Not only aboveground damage, but also root herbivory influences flower production and fruit and seed abortion (Barber et al., 2015; Ghyselen et al., 2015).

We have demonstrated that defoliation strongly increases abortion of seeds in *Centrosema virginianum* plants grown in the greenhouse. The data suggest that seeds were also aborted on undamaged plants and more frequently in fruits that were self-pollinated. Selective abortion likely occurs because plants allocate more energy resources to cross-pollinated fruits. Plants under extreme defoliation also maintained this pattern.

The difference in seeds produced may be the result of both the reduction of energy availability and embryo quality. Abortion of unfertilized ovules was not attributed to pollen limitation because large loads of pollen were deposited on the receptive surface of the stigma. Because abortion rates were similar, and of similar patterns, among all control plants (see below), we attribute the variation in seed abortion to maternal effects. Because both types of hand pollination were done on the same ramet of an individual, and at the same time, preference of X-seeds over S-seed likely explains the higher levels of X-seeds aborted.

We found a negative relationship between seed size and number, and through visual inspection, we can see that plants with low numbers of seeds have high average seed mass, especially in the higher defoliation treatments. Apparently, compensation has occurred to maximize production of a few good seeds. Because changes in seed number per fruit were not compensated by changes in individual seed mass of X-fruits, both seed number and mean individual seed mass can be considered indicators of allocation per fruit in maternal plants under extreme resource limitation. For S-fruits, neither variable is a complete indicator of resource allocation, and both can be considered jointly as total seed mass per fruit (Marshall and Ellstrand, 1988).

Resource allocation in *Centrosema virginianum* shifted in response to defoliation. Seed number was compensated by seed mass on undamaged plants and on plants with low levels of defoliation in fruits resulting from cross-pollination. Similar patterns were also found among fruits resulting from self-pollination on defoliated plants: heavily damaged plants produced fewer but heavier seeds.

These results are different from findings in annual legumes. *Vicia sativa*, an annual legume with autogamous fruit production, produced fewer and smaller seeds at higher levels of defoliation plants (Koptur et al., 1996). It is likely that perennial plants like *C. virginianum* invest more resources in high quality progeny, sacrificing number of seeds when resources are scarce, because they have opportunity for future reproduction, while annuals have only one opportunity to reproduce. However, these results are also in contrast to those of experiments with *Lotus corniculatus* (Stephenson, 1984) where partially defoliated plants aborted flowers but matured the same number of fruits and seeds and seeds of similar mass to control plants.

In our experiment, *Centrosema* plants continually produced flowers regardless of defoliation treatments.

Differential donor success can occur at any stage in the reproductive cycle (Stephenson and Bertin, 1983). In this experiment, we did not distinguish among pollen parents because we combined several each time for cross-pollinations, comparing only cross- versus self-pollen donors. In *C. virginianum*, maternal effects showed a great influence on both post-pollination and post-fertilization processes, in contrast to some other legumes (e.g., Fenster, 1991). First, a high frequency of early abortion in specific regions of the fruit indicates a strong influence of pollen competition in the ovary. According to theory, when resources are scarce, plants should abort some fruits and seeds, and selectively mature only those of high quality (Janzen, 1977), resulting in offspring with greater vigor (Niesenbaum, 1996; Baskin and Baskin, 2019). Second, increased abortion with defoliation treatments in X-fruits, as well as higher rates of abortion in S-fruits, demonstrate that maternal effects also direct offspring quality. Genotyping seeds has revealed that seeds produced with self-pollen, and also those produced with pollen from close relatives, are more frequently aborted than those resulting from pollination by unrelated individuals (Collevatti et al., 2009).

The progeny-vigor results concurred with studies of nonrandom fertilization within fruits of zucchini, where more seeds were sired in specific regions of the zucchini and high-vigor progeny resulted from those seeds (Stephenson et al., 1988). Seeds of *C. virginianum* from middle regions of X-fruits in severe defoliation treatments produced more vigorous seedlings. Although S-seedlings in the A region weighed less than seedlings from other fruit regions, seedling vigor did not vary among the other fruit regions, suggesting a more random allocation of resources with S-pollination. This less-selective process may have been a position-dependent resource effect rather than a selection for better genotypes. Another aspect of seedling vigor is speed of germination, as earlier produced seedlings may subsequently grow larger and gain a competitive advantage over those that start their lives later. We were not able to make that comparison in this study, but that may play an important role as well as seedling size attained after 30 days.

We initially expected that the basal regions in the ovary have a spatial nutritional advantage because of their proximity to the sources of photosynthesis (Stephenson et al., 1988), but appreciate that ovules in the distal position may have had a temporal advantage. In *Pongamia*, a legume with two ovules that regularly matures only one seed, the peduncular (basal) seed is deprived of resources in the presence of the stigmatic seed (Arathi et al., 1999). Seed abortion is often the result of competition for maternal resources (Lee and Bazzaz, 1986; Ganeshiah and Uma Shaanker, 1988; Uma Shaanker et al., 1988), with the differential capacity of developing seeds to draw resources for themselves related to their time of fertilization (Carney et al., 1996). Earlier-fertilized ovules may begin development sooner and provide a greater sink for nutrients, depriving ovules fertilized later of energy needed for

seed development. Legume fruits have seeds in a linear sequence, and those closest to the stigmatic end of the fruit are likely to be fertilized first. Other species with linearly arranged ovules (legumes: Bawa and Webb, 1984; Hossaert and Valero, 1988; Lee and Bazzaz, 1986; Nakamura, 1988; Rocha and Stephenson, 1990; Tyberk, 1993; Webb and Bawa, 1985; Mena-Ali and Rocha, 2005a; Arathi, 2011; Susko, 2006; Vasudeva and Sareen, 2011; Valtueña et al., 2012; Calviño, 2014; non-legumes: Guth and Weller, 1986; Carney et al., 1996; Susko and Lovett-Doust, 1998; Susko and Clubb, 2008) show higher frequencies of fruits with more seeds toward the stigmatic end and fewer at the base. In some species, the pattern of abortion differs between S-fruits and X-fruits. For example, in *Alliaria petiolata* (Susko and Lovett-Doust, 1998) and *Hesperis matronalis* (Susko and Clubb, 2008), more seeds are aborted at the stylar end with self-pollinations, but the opposite is true in cross-pollinated fruits. Seeds produced toward the stylar end tend to be heavier, and seedling performance may correlate with ovule position and seed size in fruits with many seeds (Rocha and Stephenson, 1990). Experimental selective destruction of ovules in distal positions has been shown to increase the rate of maturation of basal ovules into seeds, but seeds in basal fruit positions have lower vigor (lower germination rates, subsequent growth, and flowering) than those in stylar positions (Rocha and Stephenson, 1991; Mena-Ali and Rocha, 2005b).

In our study, we found larger seeds at the stylar end and in the center regions of the fruits. The pattern of seed abortion and seed size may be influenced not only by maternal provisioning, but selection for dispersal, as in the wind-dispersed legume trees *Butea monosperma* (Ganeshaiyah and Uma Shaanker, 1991) and *Dalbergia sissoo* (Vasudeva and Sareen, 2011). A study of ballistic seed projection in *Vicia sativa* and *Croton capitatus* demonstrated that more seeds were projected from the upper rather than the lower half of the plants, and the number of fruits and seeds produced were position-dependent (Garrison et al., 2000). We did not test for differences in seed abortion at different heights on the plant, but if position along the plant is important for seed dispersal, position within fruits could be also important in plants with explosively dehiscent fruits. It is reasonable to predict that seeds at the base of a dehiscing legume will not move as far from the plant as those in the middle, and seeds at the tip will likely be projected the farthest when the fruit dehisces, if they are not stuck in the edges. This phenomenon should be further investigated.

Artificial defoliation (Mothershead and Marquis, 2000), large herbivores (Guy et al., 2021; Cutter et al., 2022), insects (Nihranz et al., 2020), and pathogens (Van Dijk et al., 2021) can have large influences on plants and pollinators. Artificial damage to flowers and florivory can deter visitation, pollination, and subsequent fruit set (Vega-Polanco et al., 2020). A recent meta-analysis concluded that real herbivores have substantial negative effects on floral traits, plant attractiveness to pollinators, and plant reproductive success; however, artificial damage did not always replicate the effects of actual herbivory (Moreira et al., 2019).

CONCLUSIONS

In this study, we analyzed selectivity of abortion through a variety of factors present in a hermaphroditic, self-compatible, perennial species. We demonstrated that defoliation increases abortion of seeds in all fruits, more severely in selfed than in outcrossed flowers. Early processes of reproduction, such as fertilization, especially interactions within the maternal plants, need to be further studied to understand in which stages maternal plants that are affected by defoliation modify resources allocation strategies. While we defoliated ramets of 15 genotypes grown in a greenhouse, a similar experiment in the field might reveal more complex patterns in plants that are subjected to environmental variability in biotic and physical challenges. Metanalysis has shown that some plants may compensate for leaf area lost to herbivory if resources are abundant (e.g., herbaceous monocots) or scarce (e.g., broadleaf perennials), or even overcompensate in those conditions (Hawkes and Sullivan, 2001). The fitness costs of resistance to herbivores will also play a role as to which genotypes prevail in the real world (Strauss et al., 2002), depending on the type of resources and particular plants in question (Wise and Abrahamson, 2007).

Plant responses to herbivory and floral development share an unexpectedly large number of genes, suggesting that they may share a common molecular mechanism and likely coevolved in nature (Ke et al., 2021). Much remains to be learned about the dual effects of herbivory and pollination on flowering plants, including the importance of plant density (Underwood et al., 2020). It has been demonstrated experimentally that herbivory and plant defense have a stronger influence than pollination in *Trifolium repens* (Santangelo et al., 2018), contrasting with results showing that pollination has a stronger selective influence on fitness of wild strawberries than does herbivory (Egan et al., 2021). It is clearly important to consider the three-way interaction of herbivores, plants, and pollinators as drivers of evolutionary change to get the whole picture.

AUTHOR CONTRIBUTIONS

Both authors conceived and designed the project; Y.C. conducted the experiments; both authors analyzed and interpreted the data. Both authors drafted and revised the manuscript and have given permission for its submission to *AJB*. Both authors are accountable for all aspects of the project, its presentation, and integrity.

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DATA AVAILABILITY STATEMENT

Data are archived in the Florida International University Dataverse at <https://doi.org/10.34703/gzx1-9v95/FGWQBF> where it will be publicly available along with its metadata.

ORCID

Suzanne Koptur  <http://orcid.org/0000-0002-6617-0171>

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