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Proximate and ultimate causes of low fruit production in Asclepias exaltata

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In *Asclepias exaltata* L., a hermaphroditic milkweed, fruit production is constrained primarily by the availability of nutrient resources, as shown by the increased survival of fruits after removal of competing fruits and after application of fertilizer. The results of other tests exclude genetic-developmental incompatibilities, fruit herbivory, and insufficient pollination as major causes of low fruit production.
Removal of half the flowers in each inflorescence had little effect on fruit production but decreased pollinarium removals by half, suggesting that one reason why few flowers mature fruits is that many flowers are produced primarily to enhance male reproduction. It also raises the possibility that fruit abortion is an adaptation that allows plants to invest resources more profitably in male reproduction, but tests of this hypothesis were inconclusive.

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У *Asclepias exaltata* ваточника с обоеполыми цветами продукция плодов исходно ограничена доступностью питательных веществ, что было показано на примере увеличения выживаемости плодов в случае удаления конкурирующих плодов или после внесения удобрений. Результаты других тестов исключают генетическую несовместимость, изъятие плодов фитофагами и неэффективность опыления, как основные причины низкой подукции плодов. Удаление части уветков в каждом соцветии оказывает небольшое влияние на продукцию плодов; но снижение изъятия поллинариев вдвое показывает, что одна из причин того, почему так мало цветов дают плоды состоит в том, что на многих цветках развиваются прежде всего мужские признаки. Это позволяет предполагать, что недоразвитие плодов - адаптация, позволяющая растениям более выгодно использовать ресурсы для репродукции мужских органов, но проверка этой гипотезы не дала убедительных результатов.

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1. Introduction

In many species of higher plants very few fruits mature relative to the number of fertile flowers (Stephenson 1981). Since fruit number is likely to be an important component of fitness, low fruit production raises two questions. First, what prevents more fruits from maturing, and second, if there are constraints keeping fruit production low, why are so many flowers produced? The relative numbers of flowers and fruits are important not only for the plant itself, but also for other members of its community, including competitors, pollinators, and seed predators.

There have been many studies of low fruit production (reviewed by Stephenson 1981) but relatively few that test more than one or two possible explanations from the available range of competing causal hypotheses. This paper reports the results of a study of the causes of low fruit to flower ratios in natural populations of the perennial, *Asclepias exaltata* L. (Asclepiadaceae). Although I do not examine physiological mechanisms, I do test a range of hypotheses for both proximate causes and ultimate, evolutionary functions.

It is convenient to separate the question into two components. First, why are there so few fruits? This is the proximate question of identifying the constraints keeping fruit production at its low, natural level. The hypotheses tested are a) insufficient pollination, b) genetic incompatibilities or abnormalities, c) fruit herbivory, and d) insufficient resources (e.g. light or nutrients). I am seeking the cause or causes actually controlling fruit numbers in the study populations. It is not sufficient, for example, to show that some flowers are not pollinated, because increased pollination still might not increase fruit numbers. Neither is it sufficient to show that fruiting decreases in deprivation experiments (e.g. excluding pollinators) unless it can be shown that similar deprivation occurs naturally.

The second half of the question is largely an ultimate, evolutionary one: why are there so many flowers? The hypotheses considered are that large flower numbers a) increase reproduction though the female function (seeds), or b) increase reproduction through the male function (pollen).

A. exaltata is suitable for studying the causes of low fruit to flower ratios because, as in other milkweeds (Woodson 1954), most flowers do not produce fruits and many young fruits are aborted. Plants produce an average of thirty flowers but fruits mature from fewer than one in twenty. Milkweeds are also suitable for studying the male component of fitness. Instead of having numerous, loose pollen grains, each flower has five pollinaria consisting of two connected pollen sacs or pollinia, each of which includes about 180 fused pollen grains. The number of pollinaria removed from a flower by pollinators is easily determined by inspection. Milkweed floral morphology and pollination is described by Bookman (1981).

2. Methods

I studied six populations of *A. exaltata,* designated A-F, in the forest understory of the E. S. George Reserve (see Cantrall 1953, Cooper 1958, Roller 1974) near Pinckney, Michigan. The "populations" were physically discrete groups, separated by 70 m or more, but not necessarily reproductively isolated.

For the purposes of this study, individual plants are defined as all stems (up to 8, but usually 1 or 2) arising from a common rootstock. Excavations revealed occasional root connections between apparently distinct plants, but the rarity of such connections and the presence of consistent morphological differences between nearest neighbors suggest that vegetative spread is unusual.

In populations A (1979) and B (1980) I randomly assigned plants to one of several experimental treatments or to an untreated group, the latter serving both as controls and as a random sample for estimating reproductive measures in natural populations. The experimental treatments were designed primarily to test whether fruit survival would increase with a reduction in competition by other fruits. In pop. A the treatments were: 1) remove all umbels (= inflorescences) except the first to bloom on each stem, 2) remove all umbels but the last, 3) remove half the flowers from each umbel, and 4) enclose each umbel in a glassine bag for the first 4 d out of its 7–9 day anthesis period. In pop.B the treatments were: 1) remove all flowers, 2) remove half the flowers of each umbel, and 3) remove half the flowers of each umbel at the beginning of anthesis (all other removal treatments being performed at the end of anthesis).

I visited all plants at 2-d intervals during flowering. For each umbel I recorded flower number and the number of fruits initiated (hereafter simply "initiations"), detectable by swelling of the ovary and pedicel several days after abscission of the corona (the showy part of the flower). Cytological studies of *A. syriaca* have shown that swollen ovaries all have fertilized embryo sacs (Sparrow and Pearson 1948). For controls and some treatments, I also recorded the number of pollinaria removed from five randomly chosen flowers of each senescing umbel (flowering within an umbel is fairly synchronous; consecutive umbels on a stem usually bloom at 2–3 d intervals). I estimated the number of pollinaria removed from a plant by multiplying each umbel's rate per flower by the number of flowers in the umbel and then summing the umbel estimates. This measure can be used as an estimate of relative male fitness, though it necessarily neglects differences in post-removal success of pollinia.

After flowering I recorded the number of fruits remaining at 2–4 d intervals and, where possible, the cause of fruit death. In late September 1979, I counted the seeds of all fruits in pop.A. I made no seed counts in subsequent years since a) plant seed number was highly correlated with fruit number (Spearman's rank correlation, $r_s = 0.98$, $n = 111$), b) seed number per fruit was uncorrelated with other plant measures (initiations, fruits, flowers, initiations/flower, fruits/flower, fruits/initiation, date of flowering). Therefore I report fruit numbers as estimates of relative female fitness.

Much of the same data was collected for the same plants during a second season when no manipulations were performed, but this did not constitute a random sample of the plants flowering in the second year; only plants that had flowered in the previous year were included. Unless otherwise indicated, the data reported will be from the first study year of each population.

In populations E, C, and A (1981) I randomly assigned stems bearing at least two healthy, immature fruits (0.05 to 0.5 of mature length) to two groups. I left one group untreated and removed all but one randomly chosen fruit from each stem in the other group.

In pop.C (1980), I spread a single handful of 5-12-5 (N-P-K) fertilizer around the bases of plants assigned to one group. This was done on 1 July, when new flowers were no longer being produced. The next rain fell four days later. A control group was not treated. Group assignment was random except that any plant within 40 cm of a previously assigned plant was put into the same group in order to avoid neighbor effects.

In pop.F (1981), I removed one leaf of every pair from randomly chosen experimental plants and left a control group untreated. At the time, immature fruits had reached 0.05 to 0.5 of their mature length.

I conducted an experiment to see if slight fruit damage could induce abortion in pop.E (1981). On some randomly chosen stems, all immature fruits were pricked with an insect pin (about 0.3 mm diam.) at about 1/4 of the distance from base to tip, to a depth of half the fruit depth. Control stems were untreated.

I obtained data relevant to pollen flow by extracting a total of 40 pollinaria (from 10 plants) and recording the time taken for their twin pollinia to become oriented (by drying) at an angle of 45 degrees to each other. This orientation change is generally assumed to facilitate insertion of the pollinia into stigmatic chambers (Wyatt 1976, Kephart 1981, Bookman 1981). If the time required is long relative to the time pollinators remain on plants, self-pollination is probably rare (Chaplin and Walker 1981).

Hand-pollinations were performed in the field, using watchmaker's forceps to insert a pollinium, convex margin first, into a stigmatic chamber. The number of hand pollinations per plant did not exceed natural pollination levels, and natural pollinators were excluded by use of glassine bags. Bagged flowers that had not been hand-pollinated never initiated fruits.

Data distributions were typically skewed to varying degrees and sometimes discrete, so I use non-parametric statistics. Unless otherwise indicated, pairwise comparisons are from one-tailed Mann-Whitney U tests (valid for continuous and discrete data; Conover 1980) and correlations are all Spearman's rank correlations (r_s).

Comparisons between treatments are on a per plant basis. Some per plant measures (e.g. pollinarium removals, initiations, fruits) tended to be correlated with flower number, but variances were not generally reduced by expressing data on a per flower, per plant basis. Therefore, I did not use any correction for flower number, except where it would be misleading not to do so, as in the one experiment in which plant flower number differed between treatments.

In order to minimize disturbance, the pollinator fauna was not sampled in the experimental populations. Field observations were supplemented by collections from window traps in a population (D) not used for other purposes.

3. Results

Each result is reported under the hypothesis to which it is most relevant. Results bearing on more than one hypothesis will be returned to in the discussion.

3.1. Is fruiting limited by fruit herbivory?

Three potential fruit herbivores were observed: *Labidomera clivicollis* (Coleoptera: Chrysomelidae), *Rhyssomatus* sp. (Coleoptera: Curculionidae), and larvae of *Danaus plexippus* (Lepidoptera: Danaidae). None is a fruit or seed specialist and only *Labidomera* was actually observed feeding on fruits.

Observed damage to fruits accounted for less than 10% of fruit mortality (Tab. 1). This fraction would be somewhat higher if fruits that disappeared for unknown reasons had been eaten, but the disappearances resembled aborted fruits (those that yellowed before abscission) in that they disappeared along with their pedicels. Stems whose fruits had been pricked with an insect pin matured fewer fruits than controls (0.89 ± 0.90 n = 35 stems, vs. 1.38 ± 1.02 n = 34, $p < 0.05$), showing that slight damage can increase abortion. However, due to the latex exuded from wounds, even damage on this

Tab. 1. Fates of fruits initiated on control plants.

	POP. A 1979	POP. B 1980
Matured	252	32
Eaten or aborted after herbivore damage	69	59
Aborted after storm damage	0	32
Aborted without previous fruit damage	499	437
Unknown	191	114
Total	1011	674

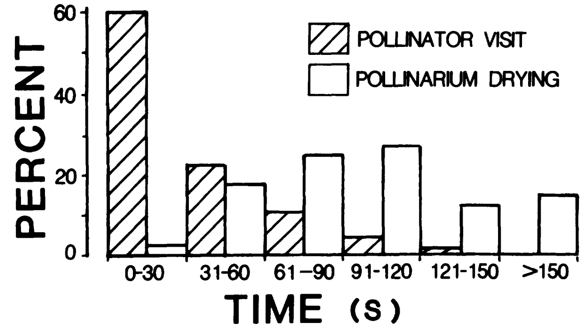

Fig. 1. Comparison of duration of pollinator visits to one plant with the time required after pollinarium extraction for the twin pollinia to orient at an angle of 45 degrees to each other. The change in orientation probably facilitates insertion of pollinia into stigmatic chambers (Wyatt 1976, Kephart 1981, Bookman 1981) and usually does not occur until after the pollinator has gone to another plant.

small scale would usually have been recorded as herbivory for the listing in Tab. 1.

3.2. Is fruiting limited by genetic incompatibilities or abnormalities?

Of 48 crossed hand pollinations, 22 (48%) initiated fruits, as did 26 of 39 (67%) selfed hand pollinations, which seems to rule out pre-fertilization self-incompatibility. Only one selfed fruit and four crossed fruits matured, but expected values were too low to permit a Chi-square test for higher survival of crossed fruits. The probability of an initiated fruit reaching 1 cm in length was greater for outcrossed fruits (11/22 vs 3/26, χ^2 = 8.53, $p < 0.005$) but the statistical test assumes independence of fruits which is not true for fruits on the same plant (see resource limitation section).

Fig. 1 shows the distribution of times required for twin pollinia to dry to a 45 degree orientation and the times that pollinators remain on a single plant. Most pollinia do not reach the state most suitable for insertion into a stigmatic chamber until after they have been carried away from the source plant. Return visits could lead to some selfing, but bees did not commonly return to a plant soon after leaving it.

Could genetic problems in outcrossed fruits be important in limiting fruit numbers? Two possibilities must be considered. First, fruit abortion could be simply the additive result of individual seed abortions; i.e. a fruit aborts when all its seeds fail. If this were so, there should also be considerable mortality of seeds within fruits that mature. This appears not to be true since the number of plump seeds in mature fruits (60.0 ± 16.0, n = 229) is not less than the number of ovules per carpel (55.1 ± 10.6, n = 15).

Alternatively, fruit numbers could be determined by abortion due to some collective property of all the seeds in a fruit, such as the number of viable seeds or their collective vigor. If this were so, then different fruits from the same genetic cross should usually share the same fate, because when there are many seeds per fruit, random sampling ensures that each fruit will contain very similar aggregates of genes. Tab. 2 shows the fates of fruits from 9 sets of hand-pollinations, each set with a single maternal parent and a single pollen parent. Two thirds of the sets produced both mature and aborted fruits (no evidence of mortality due to herbivores was seen).

3.3. Is fruiting limited by insufficient pollination?

The study plants were visited primarily by *Bombus* spp. and occasionally by *Apis mellifera*. The window traps in pop.D yielded a large sample of flying insects, including nocturnal ones, and no other important pollinium carriers were found. A single pollinarium was found on a cantharid beetle.

If pollination were limiting, fruit number per plant should be correlated with initiation number, and this was the case (pop.A, $r_s = 0.77$, $p < 0.0001$, n = 112; pop.B, $r_s = 0.33$, $p < 0.001$, n = 137). Since this could be an artifact of plant size (many-flowered plants get more pollinations and may also have more resources for fruit maturation), I also calculated the correlations between a plant's initiations per flower and its fruits per flower. These correlations were lower but still significant (pop.A, $r_s = 0.60$, $p < 0.0001$; pop.B, $r_s = 0.24$, $p < 0.01$).

The failure of initiated fruits to mature cannot be explained by insufficient pollination. In pop.A only 3 of 112 plants failed to initiate fruits and only 7 others matured all their fruits, leaving 91% with more pollinations than fruits. Of 137 plants in pop.B, 24 failed to initiate fruits and 3 matured all their initiations.

Pollination levels also fail to account for variation in fruit maturation between populations or between years. In the only year in which populations A and B were both studied (1980), pop.B had a much higher initiation rate, but maturation rates were nearly identical (see Tab. 3). For pop.A, initiation and maturation were both higher in 1979 than 1980, in accord with the pollination

Tab. 2. Survival of hand pollinated fruits with the same maternal and paternal parents.

Cross	Flowers pollinated	Fruits initiated	Fruits matured
1	12	10	2
2	12	9	2
3	8	7	4
4	8	7	0
5	8	6	3
6	8	5	1
7	8	3	0
8	8	3	0
9	4	3	3

Tab. 3. Reproductive measures per flower in populations A and B.

		1979		1980		1981	
		mean	no. flow.	mean	no. flow.	mean	no. flow.
Population A:	fruits matured	0.0475	(5261)	0.0092	(2403)		
	fruits initiated	0.192	(5261)	0.079	(2403)		
	pollinaria removed	0.700	(1764)	0.257	(844)		
Population B:	fruits matured			0.0098	(3271)	0.0315	(2191)
	fruits initiated			0.210	(3271)	no data	
	pollinaria removed			0.525	(773)	0.370	(646)

limitation hypothesis, but much of the difference is explained by higher fruit survival in 1979 (25% vs. 12%) rather than simply more pollinations. For pop.B a direct comparison is not possible since initiation data were not collected during the second year. But the higher pollinarium removal rate in that year suggests that pollination levels were also higher (pollinium removals and insertions are correlated in *A. tuberosa*; Wyatt 1980). Nevertheless, fruit maturation was lower than in the previous year.

3.4. Is fruiting limited by resources?

The between-year variation in fruit maturation (Tab. 3) can be explained by resource limitation. Both populations had lower fruiting success in 1980, a year in which two severe storms (16 and 29 July) damaged most plants. Some fruits were directly damaged by hail in the second storm, but most damage was in the form of bent stems and torn leaves, which could lower resource accrual or utilization. However, the treatment in which half the leaves were removed did not result in significantly fewer mature fruits than control plants (1.10 ± 0.77 vs. 1.49 ± 1.23, N = 39,40, $p = 0.10$).

If fruiting is resource-limited, a reduction in the number of competing fruits on a plant should increase survival of remaining fruits. When I removed all but one immature fruit from stems, the survival rate of remaining fruits did exceed the survival of fruits on untreated controls (0.591 ± 0.495 vs. 0.398 ± 0.308, $p < 0.05$, n = 66,68). However, the experimental stems also failed to mature any fruit more frequently than controls (0.409 vs. 0.221, $\chi^3 = 5.1$, $p < 0.05$) indicating that plants cannot always mature fruits, at least at this stage, even when resources are available.

Similar tests are provided by removing flowers at the end of anthesis, but here fruits are removed even before they are detectable as such. Bagging umbels for part of their anthesis period should reduce competition even earlier by preventing as much pollination from occurring. Results of these tests are given in Tab. 4. All treatments averaged fewer initiations than controls, but this caused a significant reduction in fruit number only in the most severe treatments ("leave first umbel" and "leave last umbel" which averaged 57% and 67% of flowers removed). Treatment plants typically had higher fruit survival (fruits per initiation), as predicted, but perhaps due to large variances, only one treatment was

Tab. 4. Per plant reproductive measures for experimental treatments designed to reduce fruit competition and their untreated controls. Treatments are: remove all but the first umbel on each stem, remove all but the last umbel on each stem, exclude pollinators by bagging umbels for 4 d, and remove half the flowers from each umbel (replicated). * $p<0.05$, ** $p<0.01$, *** $p<0.001$ (one-tailed Mann-Whitney U tests).

Treatment	Fruits matured			Fruits initiated			Fruits per initiation			Fruits per remaining flower		
	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Leave first umbel, pop.A	*1.50	1.00	20	***4.15	2.48	20	**0.382	0.227	19	*0.066	0.049	20
Leave last umbel, pop.A	**1.38	1.36	26	*6.15	4.73	26	0.260	0.233	24	*0.081	0.086	26
Controls w/>1 umbel, pop.A	2.51	2.31	91	10.22	9.69	91	0.280	0.218	90	0.033	0.041	91
Bagged four days, pop.A	1.67	1.34	33	*5.39	4.50	33	0.346	0.284	31	–	–	–
Remove half, pop.A	1.82	1.96	34	*7.00	8.04	34	0.370	0.328	31	*0.075	0.071	34
Controls, pop.A	2.23	2.19	112	9.02	9.19	112	0.300	0.252	109	0.053	0.048	112
Remove half, pop.B	0.174	0.489	46	**2.43	2.44	46	0.097	0.218	36	0.032	0.080	46
Controls, pop.B	0.234	0.489	137	5.01	5.48	137	0.064	0.176	113	0.017	0.088	137

Tab. 5. Effect of decreased fruiting on plant fruit and flower production the next year. The experimental treatments are: removing all but the first or the last umbel of each stem (which reduced fruiting – see Tab. 4), and removing all flowers (which prevents all fruiting). Plants were not treated in the second year. * $p<0.05$, † $p = 0.06$, one-tailed Mann-Whitney U test.

Year 1 treatment	Year 2 flowers		Year 2 fruits	
	mean	s.d.	mean	s.d.
Leave first umbel, n=19	8.4	11.6	0.0	0.0
Leave last umbel, n=23	21.1	25.2	†0.304	0.589
Controls, n=86	16.9	25.6	0.186	0.564
Flowers removed, n=32	*27.3	23.4	0.875	1.314
Controls, n=114	19.4	18.6	0.614	0.847

significantly higher than its controls. However, flowers remaining after treatment had a significantly higher probability than control flowers of maturing fruit in 3 of the 4 flower removal treatments.

If resources are limiting, an enforced saving of resources in one year (by reducing fruiting) could result in higher fruit or flower production in the following year. The two partial flower removal experiments that reduced fruit production (reported above) did not result in increased fruit or flower production the following year, though one change approached significance (Tab. 5). The experimental group in which I prevented all fruiting by removing all flowers did produce significantly more flowers than controls the next year, but not significantly more fruits.

The analysis of the fertilization treatment (Tab. 6) is complicated by the fact that, despite random assignment to treatments, fertilized plants averaged fewer flowers and therefore fewer initiations than controls. This introduces a bias since both of these measures are correlated with fruit number within treatment groups (for flowers and fruits, $r_s = 0.36$ and 0.37, both $p < 0.05$; for initiations and fruits, $r_s = 0.65$ and 0.54, both $p < 0.001$). This bias may explain why fertilized plants did not raise significantly more fruits than controls. Fertilized plants did raise a higher proportion of fruits initiated, suggesting that N, P, or K does play a role in limiting fruit production.

3.5. Why so many flowers?

Large flower numbers could function in male success (through pollen), female success (through seeds), or some combination of both. Plant flower number is correlated with both pollinarium removals (pop.A $r_s = 0.77$, pop.B $r_s = 0.71$, both $p < 0.0001$) and fruit numbers (pop.A, $r_s = 0.50$, $p < 0.0001$; pop.B, $r_s = 0.20$, $p < 0.05$) but the latter could be due to large plants having more resources for both flowers and fruits rather than to a direct effect of flower number on fruit number.

The possibility of such a plant size effect is eliminated in the experiment in which half the flowers of each umbel are removed prior to anthesis. Plants treated in this way expose half as many flowers to pollinators as controls, but due to random group assignment, should not differ in size or in the resources available to them. Tab. 7 shows that this treatment significantly reduced the number of pollinaria removed but, despite a nearly significant decline in initiations ($p = 0.06$), there was no effect on mature fruit number. Two facts suggest that the lack of difference in fruiting cannot be attributed to

Tab. 6. Per plant effects of nutrient enrichment with N-P-K fertilizer.

Treatment	Fruits matured			Flowers			Fruits initiated			Fruits per initiation		
	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Fertilized	0.735	0.995	49	**23.4	20.6	49	*3.71	5.04	49	*0.252	0.293	37
Not fertilized	0.547	0.695	53	28.7	17.5	53	4.96	5.13	53	0.134	0.203	46

* $p<0.05$, ** $p<0.01$; One tailed Mann-Whitney U test.

Tab. 7. Effects of removing half the flowers of each umbel on per plant measures of male and female reproduction. Smaller displays reduce male, but not female, success. (See text).

Treatment	Pollinaria extracted			Initiated fruits			18-day-old fruits			Matured fruits		
	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Half removed	*6.35	7.11	50	3.44	3.58	50	1.14	1.21	50	0.320	0.683	50
Controls	12.45	15.28	89	5.01	5.48	137	1.15	1.19	137	0.234	0.489	137

* $p < 0.05$, one-tailed Mann-Whitney U test.

the unusual storm damage in the year of the experiment. First, there was no difference in the numbers of 18-d-old fruits, the average age when the second, more serious, storm struck (Tab. 7). The 18-d-old fruit numbers probably provide a close approximation to the numbers that would have been matured since in the previous year, without storm damage, 91% of fruit mortality had occurred by this age. Second, a similar treatment in the previous year (though with flowers removed at the end of anthesis) also caused no significant reduction in fruiting (Tab. 4).

4. Discussion

The results indicate that low fruit to flower ratios in *A. exaltata* are due to a combination of a proximate lack of resources and selection that has produced "excess" flowers for male competition. The possibility that other factors might be important in other populations, or might have been important in the past, cannot be excluded, but they appear to be relatively unimportant in the study populations.

Fruit herbivory is important in some milkweeds (Wilbur 1976, Hartman 1977, Price and Willson 1979) but seems not to be in *A. exaltata*. Herbivory on other tissues could, of course, reduce fruiting, but I have subsumed this possibility under resource limitation.

Self-fertilization is not an absolute barrier to fruit production and is probably rare anyway, as suggested by the slow conformational change of pollinaria (Fig. 1), by the hit-or-miss nature of the pollination mechanism, and by Morse's (1981, 1982) studies showing that *A. syriaca* pollinia remain on bumblebees for an average of several hours. The hypothesis that fruit abortion results from the summed inviabilities of seeds does not fit with the low incidence of seed inviability within fruits that do mature. The collective genetic vigor of seeds within a fruit might influence which fruits survive, but two facts show that it does not determine the number that survive. First, fruits from the same genetic cross often fare differently (Tab. 2), showing that considerable variation in abortion remains to be explained even when genetic differences are small. Second, the increased survival of fruits after removal of competing fruits shows that fruits that would have been aborted are genetically capable of maturation.

Some insufficiency of pollination could be indicated by the fact that initiation numbers are correlated with fruit numbers, even when corrected for flower number. However, if this correlation were causal, it should be more pronounced in population B since its pollination level was lower than population A's, and the opposite is true. Insufficient pollination can be at most a partial cause of low fruiting because it cannot account for the many fruits that are aborted.

Resource limitation is supported by the fruit reduction experiments. Of the six reduction treatments, five showed increased fruit survival, though the difference was significant in only two. Two possible biases may have mitigated against a stronger result. First, removal of flowers or fruits causes some damage to experimental plants that is not experienced by controls. Second, a measurement bias is suggested by the treatment in pop.A in which half the flowers of each umbel were removed. This treatment should have reduced initiations by 50% rather than the 14% recorded (Tab. 4). This is explicable if some abortion occurs during the several days before initiation can be detected and if, as in later stages, a fruit is more likely to be aborted if it has many competitors. Since controls have more young fruits, their initiation rates would be underestimated, and therefore their fruit survival overestimated. Against this interpretation, the 50% flower removal experiment in pop.B did yield the expected 50% reduction in initiations, but then the overall initiation rate was lower in pop.B (Tab. 3) so any measurement bias due to fruit competition would be expected to diminish. Since the recorded initiation rate might be biased, Tab. 4 also reports the number of fruits matured per remaining flower, which is significantly higher for all three removal treatments in pop.A (Tab. 4).

Resource limitation also best accounts for the between-season variation in fruiting success, assuming that storm damage reduces resource utilization. The plausibility of this assumption is reduced by the lack of significant reduction in fruits when half of the leaves were removed (though the mean was 26% lower). However, leaf removal mimics only one aspect of storm damage. Leaf removal does reduce fruiting in some milkweeds of open habitat (Willson and Price 1980). *A. exaltata* matures its fruits under a forest canopy and may rely more on stored photosynthate.

As in some other milkweeds (Willson and Price 1980), application of fertilizer increased fruit survival, suggesting limitation by N, P, or K.

By excluding alternative hypotheses, the results of these tests add strength to the general consensus (Willson and Price 1980, Chaplin and Walker 1982, Bookman 1983) that milkweed fruiting is resource limited. There are two principal dissents from this view. Beare and Perkins (1982) claim that many *A. tuberosa* plants do not fruit because the openings to the stigmatic chambers are too narrow to admit pollinia, but their sample sizes are very small. Such a barrier is not present in *A. exaltata* since most plants do initiate fruits. Wyatt (1976, 1980, 1981) argues that in *A. tuberosa* both resource limitation and extrinsic factors such as insufficient pollination are important. However, the fact that many or most flowers do not get pollinated does not necessarily implicate insufficient pollination, as he seems to suggest. Lack of pollination will certainly prevent individual flowers from setting fruit, but may have no effect on total fruit production if there are sufficient pollinations to use up the available nutrient resources.

Several studies have shown that flower number per umbel in milkweeds is a trait that is adjusted by selection primarily to increase male success (Willson and Rathcke 1974, Willson and Price 1977, Chaplin and Walker 1982). This study points to a similar conclusion for the total number of flowers on plants. The measure of relative male success, pollinaria removals, does not take into account post-removal differences in success, but this does not affect the conclusion unless post-removal success is correlated with flower number, such that pollinia removed from plants with many flowers are either consistently more or consistently less successful than pollinia removed from plants with few flowers. Such a correlation could exist if pollinators stay on many-flowered plants long enough that a considerably higher fraction of their extracted pollinia are wasted in self-pollination, but the evidence against self-pollination cited above suggests that this is not the case.

Bateman (1948), basing his reasoning on *Drosophila* studies, noted that increasing the number of matings will usually be more important for male fitness because females quickly obtain sufficient matings to fertilize all the eggs they can afford to produce. Similar reasoning applies to hermaphrodites, provided the female function is resource limited (Charnov 1979), so it is not surprising to find that pollination displays are fine-tuned primarily to increase male success (see Queller 1983 for other examples in *A. exaltata*).

I have not empirically excluded the possibility that increased flower numbers are selected because, by providing more initiations, they allow the plant a better chance to choose good fruits. Non-random maturation of fruits does occur (Bertin 1982, Lee and Bazzaz 1982, Bookman 1984), but there are several reasons to believe that any advantage due to increased choice is not as important as male success in selecting for large flower numbers.

First, *A. exaltata* does not seem to choose fruits on the basis of seed number, as shown by the absence of any correlation between seed number per fruit and any measure of the amount of choice a plant has (initiations, initiations/flower, or treatment vs. controls when initiations are reduced artificially). Second, there is evidence against the importance of choice in selection for another "male" character, the temporal distribution of flowers (Queller 1983).

Third, if there is an advantage to choice, it is likely to show diminishing returns. If a plant can afford 'm' fruits and already has 'n' initiations, the probability that the next initiation will be among the m best is m/(n + 1), which declines with increasing n. If plants are imperfect at choosing the best fruits there is even less advantage (though choice might nevertheless have value if the variance in fruit quality were very high). In contrast, if pollinia are carried far enough to avoid saturation of immediate neighbors, as the data suggest (Fig. 1 and Morse 1981, 1982), then returns on pollinia removals do not diminish markedly.

Finally, the greater importance of male success in selecting for large flower numbers is supported by the observation that males in dioecious species often have more flowers than females (Lloyd and Webb 1977).

The fact that andromonoecy (some female-sterile flowers on hermaphrodite plants) has not evolved in *Asclepias* suggests that there may be some female advantage to having many flowers. However, excess fruits can be aborted at little cost (Bookman 1983) so there is little to be gained from andromonoecy and even a very small female advantage, whether through choice or occasionally insufficient pollination, should suffice to maintain female fertility.

I have been unable to demonstrate that fruit abortion is an adaptation to allow resources to be spent more profitably om male success. The evidence for a trade-off between fruit and flower production is equivocal, at least between seasons (Tab. 5), although it is well-established for another woodland milkweed, *A. quadrifolia* (Chaplin and Walker 1982). Where there are such trade-offs, relative investments in male and female reproduction can, in principle, be predicted by sex allocation theory (Charlesworth and Charlesworth 1981, Charnov 1982), though the input variables are often difficult to measure. One prediction that is testable is that individuals who are particularly efficient in one sexual function should invest relatively more in that function (see Trivers and Willard 1973 for an equivalent prediction for separate sexes). In milkweeds, this could mean that the plants most efficient as males (e.g. highest pollinarium removal per flower) should abort more fruits in order to invest more in their efficient flowers. Unfortunately, this prediction could not be made for *A. exaltata* because a plant's pollinarium removal rate was not correlated from one year to the next (pop.A, r_s = 0.01, n = 104; pop.B, r_s = 0.03, n = 74), so that an efficient male could not gain by aborting fruits in order to produce more flowers the next year.

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