POLLINATION BIOLOGY OF A. SYRIACA L.   DUBAY, ROBERT CARR   MAY, 1977

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POLLINATION BIOLOGY OF *Asclepias syriaca* L.
(ASCLEPIADACEAE)

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Pollination Biology of Asclepias syriaca L. (Asclepiadaceae)

INTRODUCTION

The genus Asclepias is the most widely represented genus of the generally tropical to sub-tropical family Asclepiadaceae in the temperate areas of North America. Plants of the genus Asclepias, like most other members of the family Asclepiadaceae, have a highly modified floral structure with pollen in pollinia. Asclepias syriaca L. is a rhizomatous perennial herb 0.5-2 meters tall (see Table I), with a simple unbranched stem, milky sap, opposite elliptic to ovate-elliptic leaves which may be tomentose beneath but are glabrate above, and numerous flowers arranged in compact umbels. Asclepias syriaca is a successional weed that my inhabit roadsides, meadows, fields, and other such open areas in mountainous regions and in the piedmont. The plants thrive in a wide range of habitats which include a wide variety of soil types, nutrient levels, soil pH, organic composition, moisture level and water holding capacity, plant associations and degrees of sun intensities (see Table II). The species has been reported in most of the temperate regions and some central portions of eastern North America.

Asclepias syriaca appears to establish itself by means of its numerous seeds, each with a coma (a tuft of soft hairs), which are dispersed mainly by the wind. Once a plant is established, extensive asexual reproduction is possible by rhizomes, and rhizomatic cloning is suspected in many populations of A. syriaca. In later stages of succes-

TABLE I

$\bar{x}$ Plant Heights for Ten Populations of *Asclepias syriaca* L.

Population Number	$\bar{x}$ Plant Height (cm)	Range (cm)
All Populations	141	85-205
I	170	140-190
IIa	137	105-170
IIIa	134	100-175
IV	124	95-160
V	132	102-165
VI	128	100-166
VII	161	130-204
VIIIb	132	96-170
IX	162	121-189
X	146	105-196

TABLE II

Pop. No.	Plant Associates	Soil pH	Soil Moisture	Cover	Organic Matter
I	Deciduous trees, perennial and annual herbs	5.9	Very Moist	Closed canopy	5.3%
IIa	Composites, Graminoid species and shrubs	6.4	Dry	Open field	6.2%
III	Composites, few shrubs or trees Graminoids	6.2	Semi-dry to moist	Mostly open to partly shaded	4.0%
IV	*Rubus* spp., composite, shrubs and Graminoid	6.8	Semi-dry	Open thicket	4.4%
V	Mostly Graminoid, bordered by corn field	7.5	Dry	Open field	5.3%
VI	Graminoid spp., few shrubs	6.9	Dry	Open roadside area	4.9%
VII	Sm. trees, shrubs Graminoid and composite spp.	7.9	Dry to moist	Open to partially shaded	5.0%
VIII	Mostly Graminoid and composites previous agric. field	7.9	Dry to very dry	Open field early succession	2.0%
IX	Sm. shrubs, trees *Rubus* spp., Graminoid and composite	7.6	Semi-moist	Partial canopy	4.8%
X	Few trees, some shrubs, mostly composites, aquatic weeds and Graminoids	6.2	Wet to dry	Mostly open field with some shade	5.9%

sion, as the shade becomes too great, this plant dies out and is replaced by more shade tolerant species.

The time of blooming of A. syriaca varies considerably between and within populations of a given region, but generally extends from June to August, although a few plants may bloom as late as October. It has been suggested that differences in blooming time may depend on rhizome depth (C. Dubay, 1975) but there is no substantiating evidence.

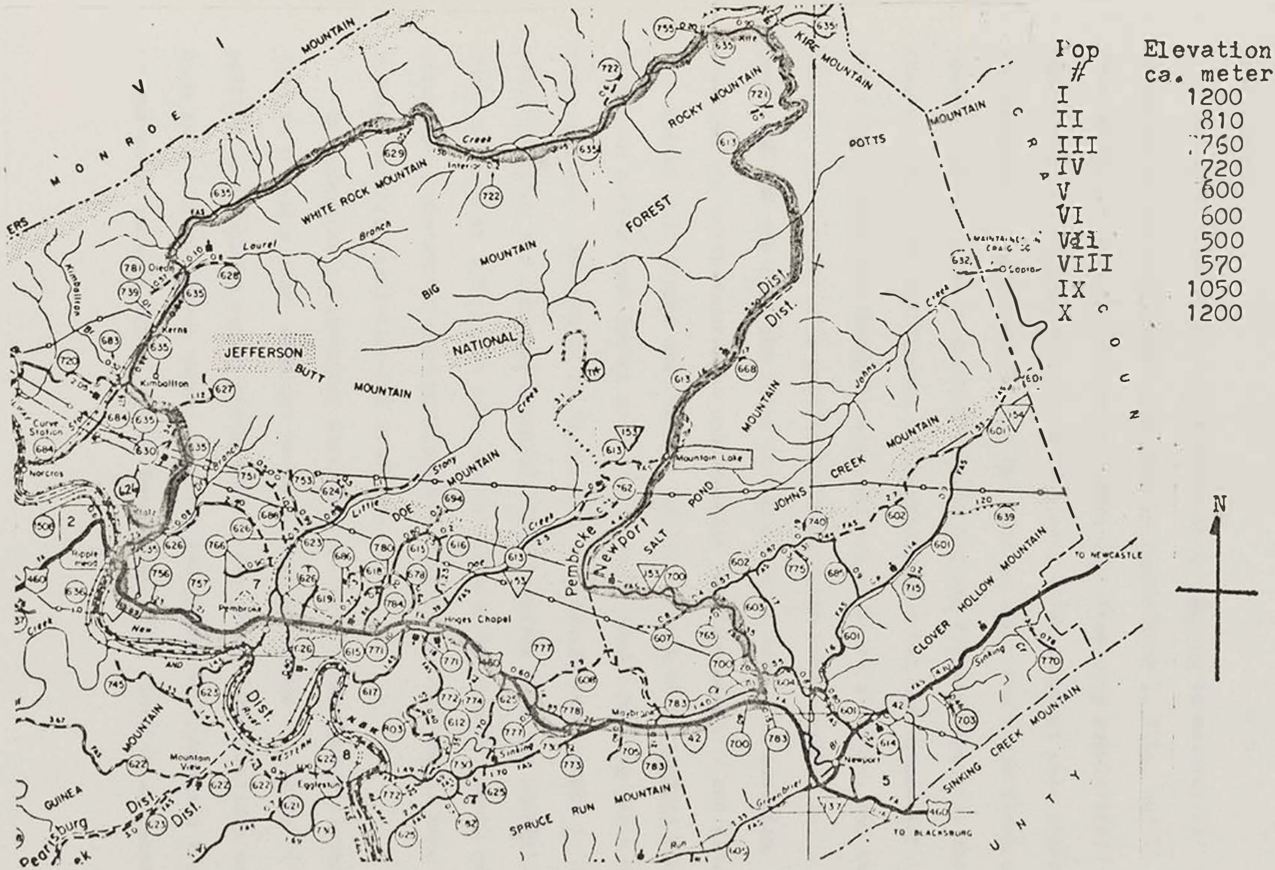
The main purpose of this research was to gather data to help explain and evaluate some aspects of the reproductive biology of Asclepias syriaca and closely related species. All collections and most experiments were done in natural field populations. Seed vernalization and germination were done in the laboratory.

A growing body of research in the area of population biology and related areas of Asclepiads (Willson and Rathcke, 1974; Wilbur, 1975; Wyatt, 1975; Galil and Zeroni, 1965; and other authors) provided the incentive and direction for this study.

METHODS AND MATERIALS

Initial research and collections were started in July, 1974 from three populations in Giles County in southwest Virginia. The first population was at the highest elevation (circa 1300 meters), in a mostly open field near the fire tower on Beanfield Mountain; the second was at medium elevation (circa 900 meters) on County Route 780 near Poverty Hollow; and the third population, now referred to as Population IIIa, was at the lowest altitude studied (circa 760 meters) at the junction of County Route 635 and 613 near Kire, Virginia. During the second year of study the high altitude population became inaccessable due to road construction and was consequently dropped from further study. The population at medium elevation, located near Poverty Hollow, Virginia, became infected during the blooming season by a plant pathogen, eliminating further study [of the reproductive biology] of the plants in that location during 1975. The low level population and nine new populations were studied during 1975. These populations were located along County Route 700 which cuts across the top of Salt Pond Mountain, along County Route 613 between Mountain Lake Biological Station and Kire, Virginia; along County Route 635 between Kire, Virginia, and U. S. Route 460 near Pembroke, Virginia; and along U. S. Route 460 near the base of Salt Pond Mountain (see population map and Table II).

The populations were selected along these routes in different habitats and at different elevations in order to obtain as much ecological diversity as possible. The majority of the populations were located in open or semi-open fields with the exception of Population I which was



Pop #	Elevation ca. meters
I	1200
II	810
III	760
IV	720
V	600
VI	600
VII	500
VIII	570
IX	1050
X	1200

under a dense tree canopy and Population IX which was under a broken tree canopy.

The time required for the flowers of A. syriaca to mature, to bloom and to set fruit was determined in Populations I, IIIa, and X. Five umbels on each of three plants were used from each population, for a total of fifteen umbels. Five stages of development were scored and recorded for each umbel: (1) the time at which the first flowers opened, (2) the time at which the umbel had all flowers open, (3) the time it took after all flowers of a particular umbel had opened for the first flowers to change from a red/pink color to a yellow, (4) the time for all flowers of a particular umbel to go from a yellow to brown and (5) the time the first fruits could be seen. In addition, the time for fruit maturation was recorded for Populations I and IIIa.

Winged pollinators and visitors to the flowers of A. syriaca were caught in a fine mesh insect net, placed in an insect killing jar and later mounted. Non-winged or flightless individuals were caught in an insect killing jar and then mounted. (Hummingbirds were not caught). Those animals of sufficient size and mobility to be able to remove and insert pollinia were termed pollinators. All other individuals were termed visitors, including all arachnids.

Experimental pollinations were done on caged newly opened flowers (one to two days after opening) so as to insure maximum viability of pollinia and maximum nectar production by the plant. Pollinations were done in the field on one umbel each from two plants of Population I and on one umbel each on six plants of Population IIIa. Each umbel received ten insertions, one each on different flowers, giving a total of 80 insertions. Flowers in Population I received pollinia from different plants of the same population (intra-population crosses). Some flowers of plants in Population IIIa received pollinia from flowers of another umbel of the same plant (self pollinations); two umbels in Population IIIa received pollinia from flowers of Population I (inter-population crosses); the flowers of the remaining two umbels of Population IIIa received pollinia from different plants of Population IIIa (intra-population crosses). Pollinia were removed by carefully pulling on the corpusculum that joins the two pollinia. A pollinium was then broken off of the translator arm with a pair of fine pointed tweezers. The pollinia were carefully inserted between the anther flaps or wings that cover the opening to the interstaminal slits in the gynostegium. In most cases the pollinia would easily fit between the anther flaps but in a few instances the wings had to be separated so as to allow for the insertion of the pollinia. Four plants, one from Population I and three from Population IIIa, had the convex surface of the pollinia inserted in the stigmatic chamber. The remaining insertions on the other four plants were done with the concave surface of the pollinium in contact with the stigmatic surface. The use of a head band magnifying device aided the pollinating operations.

Ten flowers from Population I and Population IIIa were sampled for a period of six days to determine the average hourly and total nectar flow per flower. Inflorescences were bagged to keep nectar-seeking insects away from the flowers, and nectar was collected from these bagged plants three times daily during daylight hours. Nectar was sucked from the five hoods of each flower with a 1 cc capacity syringe. The nectar was transferred to a vial, and later the amount was measured using a Pressure-Lok R 10 syringe (Precision Sampling Corporation, Baton Rouge, Louisiana). Samples for nectar sugar concentration were taken in a similar manner but were tested at the time of extraction to insure that evaporation did not affect the concentration. Concentrations of sugar in the nectar were determined by a hand refractometer (Type 1, Model Number 12855 and Type 2, Model Number 12899, National Instrument Company, Baltimore, Maryland).

Rhizomes were dug and followed to adjacent plants in Population IIIa to determine if the plants were actually cloning. Also, thirty plants were staked in the fall of 1974 to see if plants arise from the same location on the rhizome each year.

Seeds collected from plants during 1974 and 1975 were given a sixty to ninety day cold treatment to simulate conditions of nature. Vernalization temperatures ranged from 2° to 7°C. The seeds were then sorted according to size and weighed. After weighing, the seeds were planted approximately one centimeter deep in plastic planting trays filled with field soil. A total of five hundred seeds were planted.

The effect of experimental inflorescence size on the pollination of _A. syriaca_ was determined essentially by the methods used by Willson and Rathcke (1974). Experimental inflorescences were made by cutting off flower buds, thereby reducing the inflorescences to 1, 5, 10, 20, or 40 flowers. Controls were set up using unaltered inflorescences.

In Populations X and IIIb the flowers of the experimental inflorescences were collected, and the pollinia that had been removed and inserted were counted.

All pollinia inserted in the interstaminal slit, no matter how slightly, were counted. In Populations I through IX the experimental inflorescences were scored after three weeks to determine the initial fruit set, and again in two months to determine mature fruit set.

Plants from the 1974 population near Poverty Hollow, Virginia and plants from Population I were tested by the Plant Pathology Laboratory of the Virginia Polytechnic Institute and State University and by Dr. Meredith Blackwell, Professor of Mycology at Mountain Lake Biological Station during the summer of 1975, to determine the etiological agent that caused the rotting of the flowers of *A. syriaca.*

RESULTS

The pollinators of Asclepias syriaca that were captured were all insects (see Table III). In open sunny populations large showy moths and butterflies prevailed as the major pollinators. In shaded or partly shaded populations large flies were the main pollinators. Both shaded and sunny areas had approximately the same frequency of bee pollinators. Insect visitors too small to remove or insert the pollinia were small flies, small moths and butterflies and small bees. In addition to the visitors and pollinators many umbels had permanent or semi-permanent residents. These included ants, milkweed beetles, and spiders. Nidification by arachnids was a common occurrence. Milkweed beetles, quite commonly found on the plants' umbels or fruits, appear to be herbivorous rather than nectivorous. The spiders, as would be expected, were probably carnivorous on the large numbers and wide variety of insects visiting the milkweed. Occasionally larvae of the Monarch Butterfly, Danaus plexippus, were seen eating the leaves. In addition to the insects, hummingbirds were also frequent visitors to the milkweed plants. Despite their size it is doubted that they effected pollination due to their mode of gathering nectar and to the pollination system of A. syriaca (see Table III).

Nectar flow appears to start immediately after flowering begins and continues practically until the flowers turn brown and fall off the plant. However, nectar production appears to be maximum from day two of flowering until two or three days after the flowers turn yellow for a total of approximately thirteen days (see Tables IVa, b, c, and

TABLE III

Visitors and Pollinators of *Asclepias syriaca* L.

Family	Genus/species	Type
(Order-Coleoptera)		
Cantharidae	*Chauliognathus marginatus* Fabr.	V
Cerambycidae	*Anoploders* sp.	V
	Tetraopes tetrophthalmus (Foster)	H
Chrysomelidae	*Diabrotica undecimpuctata* Mann.	V
	Labidomera clivicollis (Kirby)	PP
	Undetermined	V
Coccinellidae	*Cycloneda sanguinea* (Linn.)	V
Mordellidae	*Anaspis rufa* Say	V
(Order-Diptera)		
Tachinidae	Undetermined	V
Anthomyiidae	Undetermined	V
Calliphoridae	*Calliphora vomitoria(Linnaeus)*	P
Dolichopdidae	*Condylostylus* sp.	V
Syrphidae	*Mylesia virginiensis*	P
	Undetermined	V
Tabanidae	*Tabanus calens* Linnaeus	P
(Order-Hemiptera)		
Lygaeidae	*Oncopeltus fasciatus* (Dallas)	P
Miridae	*Lygus lineolaris* (P. de B.)	V
Pentatomidae		
(Order-Hymenoptera)		
Apidae	*Apis mellifera*	P
Formicidae	*Camponotus castaneus americanus* Mayr	V(PP)
	Tapinoma sessil (Say)	V
Halictidae	*Lasioglossum* sp.	V
(Order-Mecoptera)		
Panorpidae	*Panorpa latipennis* Hine	V
(Order-Lepidoptera)		
Hesperiidae	*Epargyreus clarus*	P
Nymphalidae	*Speyeria cybele*	P
	Speyeria diana	P
Papillionidae	*Battus philenor*	P
	Papilio glaucus	P
	Papilio troilus	P
	Papilio cresphontes	P
	Papilio polyxenes	P
(Order-Araneae)		
Family-undetermined		C

V=visitor P=pollinator C=carnivore H=herbivore PP=possible pollinator

TABLE IVa

$\bar{x}$ Blooming Time for each Umbel of 3 plants

	Population X						
Umbel Number	1	2	3	4	5	6	7
Stage of Umbel							
1 Red buds to first flowers	---	---	4.0	6.5	6.5	10.0	7.0
2 First flowers to all flowers open	4.0	4.7	3.3	3.5	5.5	5.0	---
3 All flowers open to all flowers yellow	4.0	3.7	4.0	3.5	4.0	---	---
4 All flowers yellow to all flowers brown	4.3	5.3	2.5	4.0	---	---	---
5 All flowers brown to first fruits	2.0	---	---	---	---	---	---
Totals of 2, 3, 4	12.3	13.7	9.8	11.0			

TABLE IVb

$\bar{x}$ Blooming Time for each Umbel of 3 plants

	Population I						
Umbel Number	1	2	3	4	5	6	7
Stage of Umbel							
1 First flowers to all flowers open	4.2	5.3	3.2	4.0	---	---	5.1
2 All flowers open to all yellow	3.9	5.1	4.0	4.2	---	---	3.8
3 All yellow to all brown	4.5	4.0	5.2	3.9	---	---	4.0
Totals of 1, 2, 3	12.6	14.4	12.4				

TABLE IVc

$\bar{x}$ Blooming Time for each Umbel of 3 plants

	Population IIIa						
Umbel Number	1	2	3	4	5	6	7
Stage of Umbel							
1 First flowers to all flowers open	1.0	4.9	4.2	4.3	3.6	---	---
2 All flowers open to all yellow	---	4.0	4.5	4.1	4.5	---	---
3 All yellow to all brown	---	5.1	4.6	5.2	4.7	---	---
Totals of 1, 2, 3		14.0	13.3	13.6	12.8		

TABLE V

Nectar Flow

Population	Total Collected	Time Period (hours)	$\bar{x}$ per flower per hour
I (n=10)	158.3 ul	132	.04 ul
IIIa (n=10)	77.1 ul	144	.05 ul
X*	3.84.5 ul	515	.25 ul

* Figures from the data of C. Dubay and R. Robins, 1975

TABLE VI

% Sugar Concentration *A. syriaca* L. nectar

Population	Time of Day	x%	Range
I IIa IIIa	Entire day	17.86	5.0-45.8
	A.M.	16.31	5.0-27.0
	P.M.	23.90	12.0-45.8
X	Entire day	26.42	10.3-54.0
	A.M.	32.74	10.3-54.0
	P.M.	22.60	18.7-28.3
IIa IIIa IV	Entire day	17.94	5.0-45.8

Table V). The amount of flow varies greatly with the age of flowers. Mean nectar flow for Population I was .05 microliters per hour per flower; for Population IIIa, .04 microliters per hour per flower; and for Population X, .25 microliters per flower per hour. Differences in nectar flow between Populations I and IIIa and Population X could be explained by the differences in the age of the flowers. Nectar flow in Population X was calculated on flowers one to two days after opening but in Populations I and IIIa the flowers had been open for approximately six days. The study continued until the flowers yellowed.

The sugar concentrations of the nectar of A. syriaca varied slightly between populations. On the whole Populations I, IIa, IIIa, IV, and IX had an overall nectar sugar concentration of 17.8%, a morning nectar sugar concentration of 16.33% and an afternoon and evening sugar concentration of 23.9%. Population X showed nectar sugar concentrations of 26.42%, 32.74%, and 22.60% for the entire day, morning and evening respectively. Shaded or partially shaded populations (Populations I and IX) had higher concentrations of nectar sugar (20.93%) than did open populations (Populations IIa, IIIa, and IV) which had an average sugar concentration of 17.94% (see Table VI).

Nectar concentrations greater than 2.5% sugar and less than 40% sugar are suitable for pollinia germination and enhance pollen tube growth. Ideally, nectar concentration between 10 and 20 percent are most suitable for pollinia germination and pollen tube growth. Plant latex, which may mix with the nectar of the plant during the possible injury to the plant caused during pollinia insertion, does not appear to retard pollinia germination (see Table VII, VIII, IX).

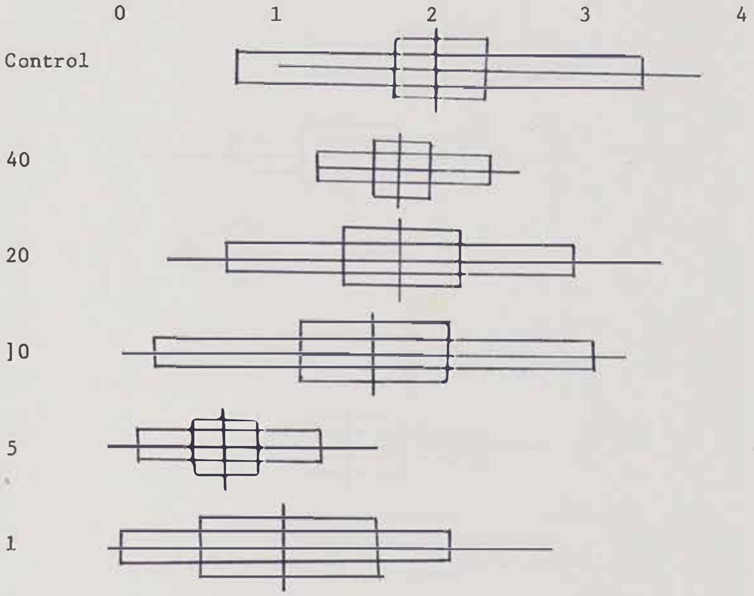
Inflorescences of 1, 5, 10, 20, and 40 flowers and control inflorescences did not have any great influence on the pollinia removal per flower. Greater variability was noted, however, in the range for the small inflorescences (≤5). The mean number of pollinia inserted per flower in the experimental inflorescences (1, 5, 10, 20, 40 and unmodified controls) gave a linear regression (slope=.2) for inflorescences with 10 or more flowers (see Chart I, II, III, and IV).

Inflorescences of A. syriaca with ten flowers appear adequate for pollination success. Inflorescences of less than ten flowers (5 and 1) had a mean initial fruit set per inflorescence of 2.00 and .60, respectively. Between 10 flowers per inflorescence and the control inflorescences (mean equals 49.5 flowers) initial mean fruit set ranged from a low of 3.71 fruits per inflorescence to a high for the controls of 5.78 (see Chart V and Table X). The success of these initial fruits reaching maturity (whole ripe pods) was 23.54%, 13.80%, 17.31%, 24.00%, 27.08%, and 21.62% for inflorescences with 1, 5, 10, 20, 40, and control flowers, respectively. The highest number of matured pods (mean=1.25 per inflorescence) was found on the larger control inflorescences. The fewest were found on the experimental inflorescences having only one flower (mean=.14 pods per inflorescence; see Chart V and Table XI). A mean mortality of 9.55 percent was noted for flowers of A. syriaca, mortality meaning that the flowers failed to mature and consequently did not open.

CHART I

Pollinia Inserted

Population X

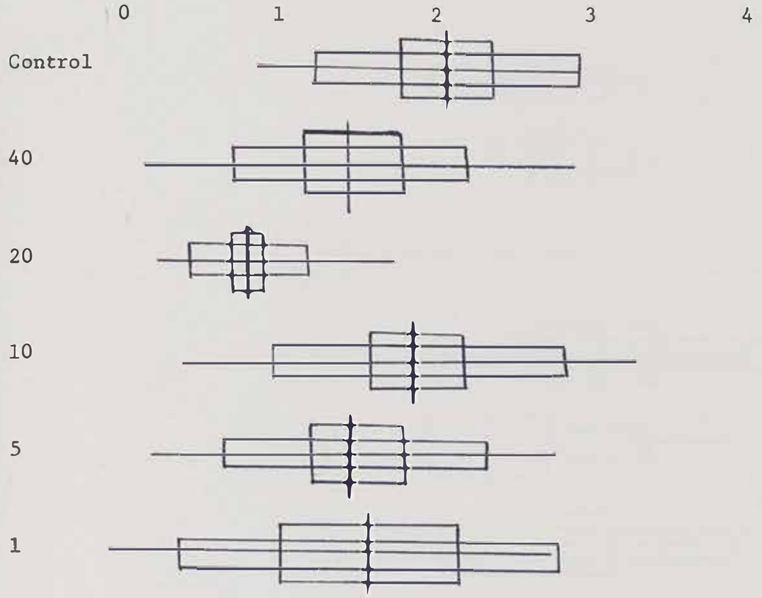


	$\bar{x}$	s	s.e.$\bar{x}$.	Range
Control	2.1	1.4	.3	1.0-3.9
40	1.9	0.6	.2	1.3-2.7
20	1.9	1.2	.4	.3-3.7
10	1.8	1.5	.5	.1-3.5
5	0.8	0.6	.2	.0-1.8
1	1.2	1.1	.6	.0-3.0

CHART II

Pollinia Inserted

Population IIIb

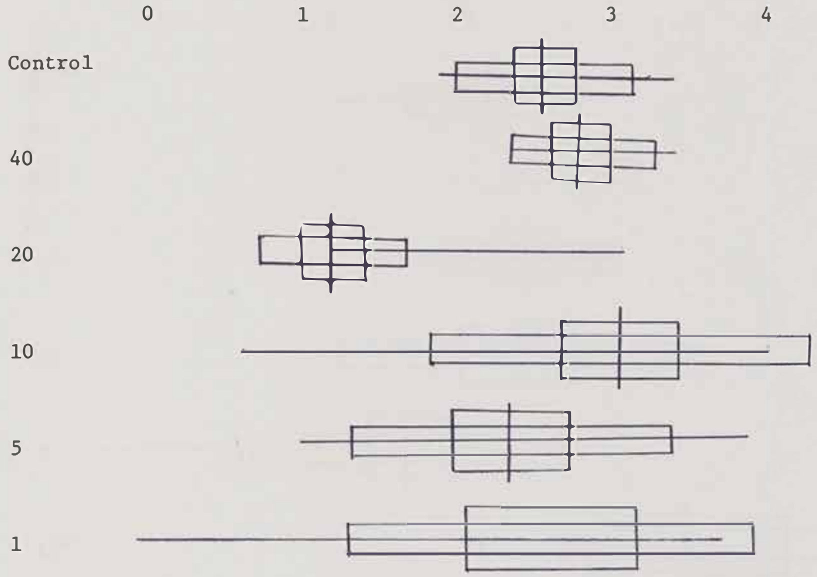


	$\bar{x}$	s	s.e.$\bar{x}$.	Range
Control	2.2	0.9	.3	.9-3.1
40	1.6	0.8	.3	.2-3.1
20	0.9	0.4	.1	.3-1.9
10	2.0	1.0	.3	.4-3.4
5	1.6	0.9	.3	.2-3.0
1	1.8	1.3	.6	.0-3.0

CHART III

Pollinia Removed

Population IIIb

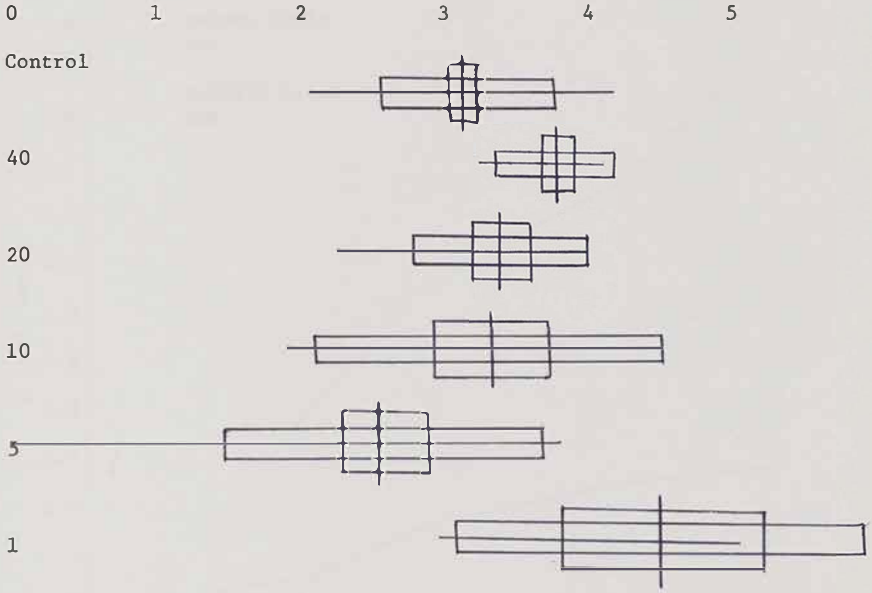


	$\bar{x}$	s	s.e.$\bar{x}$.	Range
Control	2.6	0.6	.2	1.9-3.5
40	2.9	0.5	.2	2.4-3.5
20	1.2	0.5	.2	1.2-3.2
10	3.2	1.3	.4	0.6-4.2
5	2.4	1.1	.4	1.0-4.0
1	2.8	1.4	.6	.0-4.0

CHART IV

Pollinia Removed

Population X



	$\bar{x}$	s	s.e.$\bar{x}$.	Range
Control	3.2	0.6	.1	2.1-4.2
40	3.8	0.4	.1	3.3-4.1
20	3.4	0.6	.2	2.3-4.0
10	3.3	1.2	.4	1.9-4.5
5	2.6	1.1	.3	.0-3.8
1	4.5	1.4	.7	3.0-5.0

CHART V

Initial and mature fruit set per inflorescence at different inflorescence sizes (All Populations)

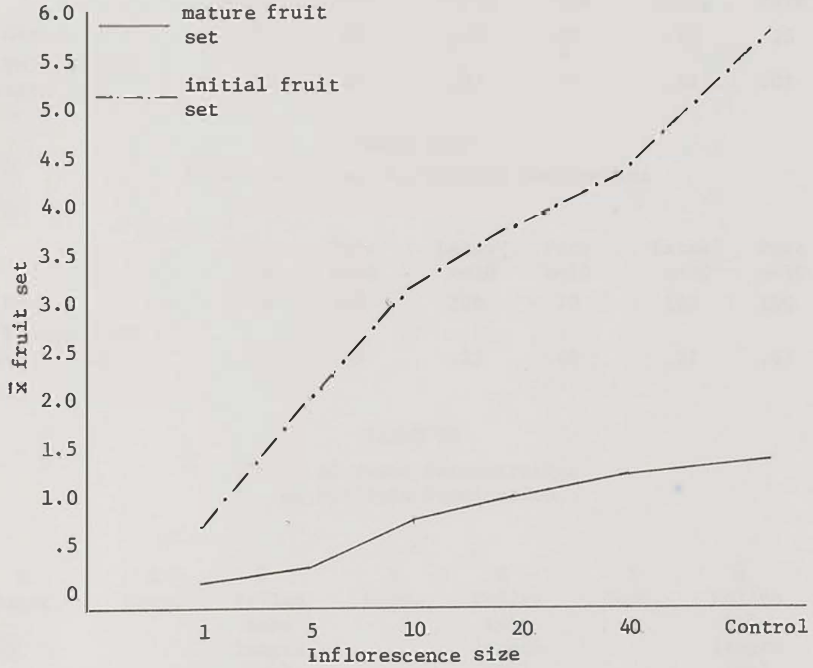


TABLE VII

Effect of Age of Flowers on Pollinia Germination

10% Nectar

	Buds prior to opening		New flowers (n=30)		Old flowers (n=10)	
	Borax	Pure	Borax	Pure	Borax	Pure
% Germ.	90	80	100	100	60	20
$\bar{x}$ Pollen Tube length (mm)	.22	.14	.37	.45	.04	.01

TABLE VIII

Effect of Latex on Pollinia Germination

	Latex n=30	Pure n=30	Latex n=10	Pure n=10	Latex n=20	Pure n=30
% Germ.	100	100	100	70	100	100
$\bar{x}$ Pollen Tube length (mm)	.25	.45	.13	.06	.21	.67

TABLE IX

Effect of Sugar Concentration on Pollinia Germination

% Sugar	% Germ.	$\bar{x}$ Pollen tube length (mm)	% Germ.	$\bar{x}$ Pollen tube length (mm)	% Germ.	$\bar{x}$ Pollen tube length (mm)
2.5	00	.00	100	.07	---	---
5.0	80	.07	100	.07	---	---
10.0	100	.45	100	.67	100	.72
20.0	98	.08	100	.36	100	.75
40.0	10	.01	100	.07	---	---

TABLE X

Initial Fruit Set

	$\bar{x}$	s	S.E.$\bar{x}$	Range
Control	5.78	4.19	.74	0-14
40	4.32	3.88	.53	0-18
20	3.75	3.55	.69	0-11
10	3.17	3.65	.69	0-11
5	2.00	1.94	.36	0-8
1	0.60	1.34	.25	0-7

TABLE XI

Mature Fruit Set

	$\bar{x}$	s	S.E.$\bar{x}$	Range
Control	1.25	1.34	.24	0-5
40	1.17	1.25	.17	0-4
20	.90	1.14	.18	0-5
10	.64	.86	.16	0-3
5	.28	.58	.11	0-2
1	.14	.52	.10	0-2

TABLE XII

Flowers and Inflorescences

	$\bar{x}$	s	S.E.$\bar{x}$	Range
# infls. per plant	4.60	1.93	.15	1-10
# flowers per plant	49.51	18.08	.96	3-124
Mortality	9.55	4.25	1.45	0-35

A mean of 4.60 inflorescences per stem was found in populations of *A. syriaca*, with a mean of 49.51 flowers per inflorescence. Inflorescences of the lower nodes generally had a higher number of flowers per inflorescence, as has been previously reported (Willson and Rathcke, 1974). Both the maximum number of inflorescences and the maximum number of flowers per inflorescence were lower for these ten populations in the Mountain Lake area than for the populations studied by Willson and Rathcke. Maximum number of inflorescences for the populations that I had under study was eleven with a maximum number of flowers per inflorescences of 124 (see Table XII). Willson and Rathcke (1974) reported a maximum of 12 inflorescences per stalk and a maximum of 180 flowers per inflorescence. However, maximum pod set per inflorescence was greater for the ten Virginia populations (5 pods) than it was for the populations studied by Willson and Rathcke (4 pods).

The mean number of seeds per pod was 203 with a range of 65 to 408 (n=200 pods). The average seed weight was .0041 grams (n=300 pods), with a range of .0005 grams to .0089 grams. Broken down by seed size, large, medium and small, the mean seed weights were 6.025 milligrams, 3.749 milligrams, and 2.382 milligrams, respectively (see Table XIII).

The mean germination of the milkweed seeds on the whole was 15.2%. A breakdown by size class showed the larger and heavier seeds with 22% germination, the medium size and weight seeds with 15% germination and the smallest and lightest seeds with only 2% germination, (above germination rates were from seeds of pods produced during 1974). Mixed groups of seeds (weight and size) from pods produced in 1975 at popula-

TABLE XIII

$\bar{x}$ seed weight of *Asclepias syriaca* L.

Seed Size	$\bar{x}$ Seed Weight (milligrams)	Range (milligrams)
Large n=100	6.025	3.6-8.9
Medium n=100	3.749	1.7-6.3
Small n=100	2.382	0.5-4.7
Grouped n=300	4.100	0.5-8.9

TABLE XIV

Seed Germination of *Asclepias syriaca* L.*

Seed Size	Seed Batch	Locale of Pop.	$\bar{x}$ Germ. Time (days)	Range of Germ. Time (days)	% Germ.
Large n=100	1974	Mtn.L.	17	10-25	22%
Medium n=100	1974	Mtn.L.	14	9-26	15%
Small n=100	1974	Mtn.L.	21	20-25	2%
Mixed n=100	1975	Mtn.L.	12	5-28	19%
Mixed n=100	1975	Amissville	15	14-27	18%

*Vernalization of seeds at 2°C-7°C for a period of 60-90 days.

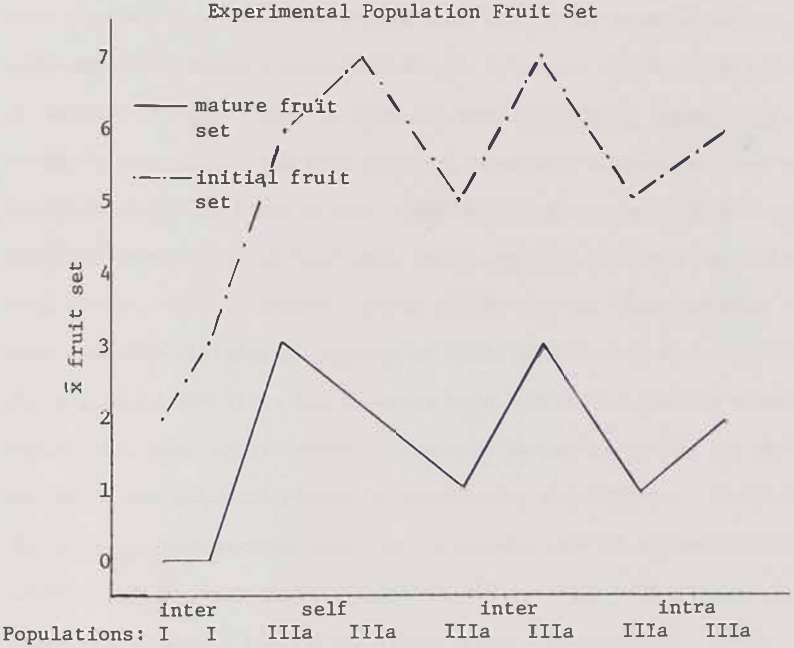
tions near Mountain Lake Biological Station gave a 19% germination rate and a population in the Piedmont of Virginia, located near Amissville, Virginia, gave a germination rate of 18%. One hundred seeds were tested in each group. Germination time ranged from a low of 5 days to a high of 28 days, after which time no further germination was observed (see Table XIV).

Interpopulation experimental crosses showed an average initial pod set of 2.5 pods and 6.0 pods per ten flowers, for Population I and IIIa, respectively. No pods matured in Population I and an average of 2 pods per ten flowers matured in Population IIIa (n=40). Intrapopulation crosses showed an average initial fruit set of 5.5 pods, for ten flowers, (Population IIIa) with an average mature pod set of 1.5 pods per ten flowers (n=20). Selfed plants of Population IIIa showed, on the average, 6.5 pods initially set, per ten flowers, and an average mature pod set of 2.5 pods per ten flowers (n=20). Only one pollinium was inserted in each flower (see Chart VI).

Plants separated by less than 1 to 2 meters appear to be connected to each other by rhizomes. Plants spatially separated by more than 3 to 5 meters appear not to be connected by rhizomes and such plants are probably from a different initial seed. In several cases stalks were found to arise from the same point on the rhizome in successive years. One stalk, in fact, was seen to be encased by the dead stalk of the previous year. Most stalks, however, appear to arise from different points on the rhizome each year.

CHART VI

Experimental Population Fruit Set



Population I $\bar{x}$ fruit set (initial and mature pods)
$\bar{x}$ inter initial = .25
$\bar{x}$ inter mature = .00

Population IIIa $\bar{x}$ self initial = .65
$\bar{x}$ self mature = .25
$\bar{x}$ inter initial = .60
$\bar{x}$ inter mature = .20
$\bar{x}$ intra initial = .55
$\bar{x}$ intra mature = .15

		initial	mature
Total population I and IIIa	=	.51	.15
Total population I	=	.25	.00
Total population IIIa	=	.60	.20

DISCUSSION

There is probably very little transfer of pollen between milkweed populations separated by more than one to two hundred meters since most pollinators cannot or do not span this distance in search of nectar. Interestingly enough, the moth _Halysidota tessellaris,_ a very strong flier, has been shown to span very large distances and has been caught in light traps. Examination of these insects caught in light traps revealed that many had _A. syriaca_ pollinia on their legs (Frost, 1958). However, Frost (1958) had not observed this moth actually visiting _A. syriaca_ or other milkweed plants. Recent field studies (1974) in the Mountain Lake Biological Station region showed this moth to be common in the area but again it was not observed on the milkweed plants in neighboring populations. Presumably the moth escaped daytime detection on populations of milkweeds because it gathers its nectar at night. Collections of nocturnal insects from milkweed plants may reveal other pollinators.

Nearly all _Asclepias_ populations under observation were plagued by the herbivorous activities of the common milkweed beetle. This insect would eat immature and opened flowers and maturing and matured pods and is probably in part responsible for the flower mortality, abortion rate and low seed set of the milkweeds. Natural controls for this beetle are probably the nidifying arachnids commonly found on _A. syriaca_ and other asclepiads. No plants were seen to have milkweed beetles present if spiders were present. Spiders, by their carnivorous nature, probably also consumed many nectar seeking visitors and pollinators of A. syriaca.

Based on pollinia removal, there is no substantial difference in pollinator activities between inflorescences bearing 1, 5, 10, 20, 40, or higher number of flowers. However, insertion rates for pollinia tend to favor inflorescences with ten or more flowers in respect to pollinations, especially in Population X. This is in contradiction to the previously held theory that inflorescence sizes of twenty or more flowers were most successful in reference to energy input, pollinator attractiveness and pod set. A closer correlation is found between the insertion rate of pollinia and initial fruit set than there is between pollinia removal and pollinia insertion or pollinia removal and initial fruit set. It would appear that the more accurate indicator of mature fruit set would be that of pollinia insertion. In further dealing with inflorescence sizes of A. syriaca and their relationship to pollinator attractiveness one should take into account flower mortality, in this study 9.55%, prior to opening, but this mortality rate appears to be highly variable.

In agreement with Wyatt (1975), I must discount the previously held view that asclepiads are an undesirable subject for breeding experiments (Woodson, 1963). On the contrary, A. syriaca was easily pollinated in the field without the aid of such elaborate equipment as was used by Wyatt working on a closely related species. Further, knowing that the flowers under study were inserted with pollinia from the desired flowers insured the validity of experiments on selfing, crossing within populations and crossing between populations. Initial fruit sets were nearly the same for flowers that were selfed (65%), outcrossed with pollinia from the same populations (55%), and outcrossed with pollinia from different populations (60%). The same type of relationship was seen between mode of crossing and mature fruit set. The higher abortion rate of these experimental plants may be a result of higher humidity caused by the bagging procedures. Future studies should include the unbagging of the plants at the end of flowering to allow for more natural conditions.

The orientation of the pollinia at the time of insertion appears unimportant. Previous studies have indicated that the pollinium's convex surface must be inserted at a certain angle so as to insure that the convex surface of the pollinium comes into contact with the stigmatic surface of the flower (Wyatt, 1975; Galil and Zeroni, 1969). The present study indicates no such necessity for "proper" orientation of the pollinium within the stigmatic chamber so long as the pollinium comes into contact with the abundant nectar of the plant, which soon covers the entire pollinium and initiates pollen tube growth. Once pollen tube growth is initiated, the direction and extent of growth is controlled, most likely, by chemical substances produced by gynecial parts of the plant. Such a response, a chemotropism, has been demonstrated in hundreds of plants. Recent research indicates that calcium ions may be producing this chemotropism (Salisbury and Ross, 1969).

Asclepias syriaca does not appear to have any reproductive isolating mechanism within the species. Reports that such exists (Moore, 1946; Sparrow and Pearson, 1948; Woodson, 1954) should be reconsidered in the view of current research (Dubay, R. 1975; Wyatt, 1975). Based on the random movement of pollinators from flower to flower, inflorescence to inflorescence and plant to plant it could be assumed that intrapopulation crosses occur more than do selfings but the latter are likely to be common.

Although A. syriaca is capable of cloning and possibly does clone frequently, a population or even a small clump of plants of this species should not be considered a clone without physical investigation of the rhizomes of the plants or stalks in question. The populations dealt with in this study should best be considered, based on this research, interbreeding populations or group of plants closely grouped together. I am sure that certain populations contained clones within them and it is possible that the entire population may be a clone, as may be the case in Populations I and IV, but further studies are necessary to ascertain the degree of cloning within populations.

In plants with wind despersed seeds, like A. syriaca, there is a high probability that more than one seed will land and germinate on suitably disturbed land and grow into mature plants. These plants, will through vegetative and sexual means produce a population of A. syriaca. This perennial plant's rhizomes will continually send up stalks, year after year, even despite plowing. Population VIIIb was, in fact, located in a recently plowed field, the owner of which stated that A. syriaca would come up year after year in continually plowed fields. I believe that the so-called "new" populations that spring up along roadsides of newly disturbed areas are not, in fact, new populations but shoots sent up by existing rhizomes of *A. syriaca* that are present in the soil. As is the case of many perennial plants, *A. syriaca* may not produce flowers in the first season of growth from seeds. Current research (R. Dubay) is investigating this aspect of the species.

Individuals within populations of *A. syriaca* are produced asexually be means of rhizomes and sexually from seeds. The ratio of sexually to asexually produced individuals appears to vary from population to population. This is difficult to quantify since the extent of individual clones within a population is often difficult to determine. The establishment of new populations, however, appears to be far more likely from seeds than from chance rhizomatic propagation. In addition sexual reproduction offers an opportunity of recombination and better adaptation for varied habitats.

The computation of asexual biological potential seems unrealistic since the life span and growth rate of the rhizomes are so difficult to measure. However, a rough measurement of the relative sexual reproductive potential of a population might be obtained from the following (or some similar) computation:

$$\begin{array}{c}\bar{x}\ \text{no. of infls.}\\ \text{per flowering}\\ \text{stalk}\end{array} \quad \begin{array}{c}\bar{x}\ \text{mature}\\ \text{pods per}\\ \text{infls.}\end{array} \quad \begin{array}{c}\text{no. seeds}\\ \text{per pod}\end{array} \times \begin{array}{c}\text{germ.}\\ \text{rate}\end{array} \quad \begin{array}{c}\text{no. of flowering}\\ \text{stalks per pop.}\end{array}$$

Such an equation might give highly variable answers with strong fluctuation in the intensity of the effect of certain biotic factors (predation by milkweed beetle and larval stage of the monarch butterfly and infection by Alternaria sp.), environmental factors, plant variations and edaphic factors, the latter seemingly being least important in most cases. Furthermore, the previously proposed view that full seeds should be considered equally viable (Willson and Rathcke, 1974) should be discounted in light of the present germination data.

Nectar flow in A. syriaca, although highly variable within and between populations, appears more than adequate to attract pollinators and to supply visitors not engaged in pollination with sufficient amounts of nectar. Substantiation of this statement can be made by observing the high degree of pollinator and visitor activity within any milkweed population during the flowering period of the plants (June-September). The nectar sugar concentrations maintained by A. syriaca are within the optimal range for pollinia germination and pollen tube growth. Variations in sugar concentrations and rate of nectar production may be directly linked with the photosynthetic activity of the plant. It is doubted that evaporation plays much more than a minor role in variations of sugar concentrations or nectar flow.

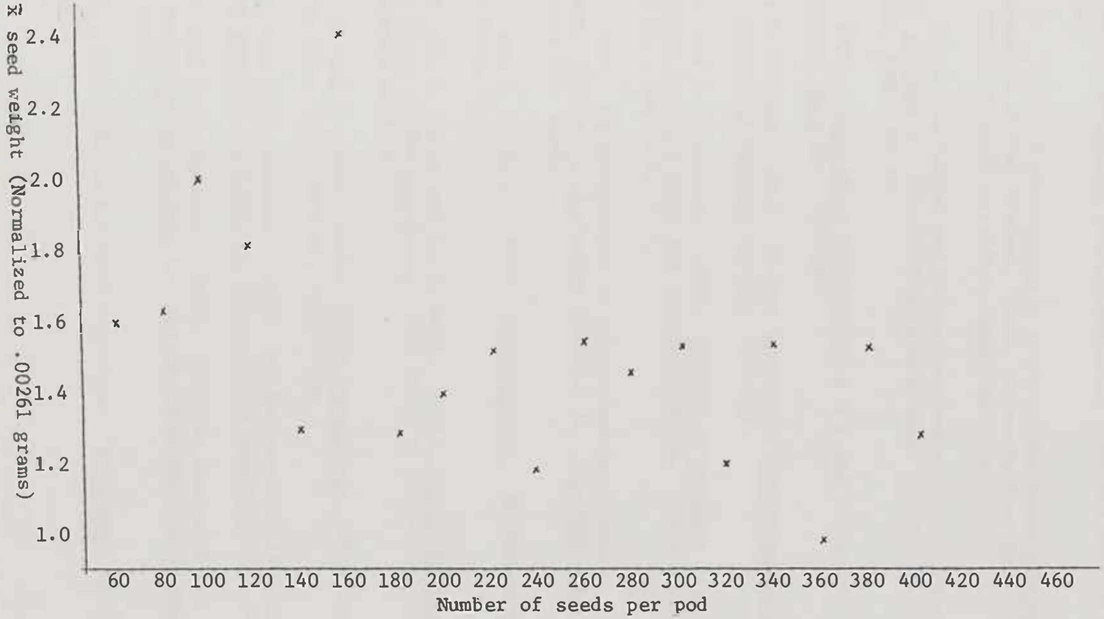
The results of this study do not support Stevens' (1945) proposal that seed weight is inversely related to the number of seeds per pod (see Chart VII). However, as is often the case, the larger seeds produce larger and more healthy seedlings, with a larger germination rate, which would have a larger survival rate. Further research in this area should prove valuable in formulating a working equation for determining the biological potential of the species.

Asclepias syriaca thrives and competes successfully with herbaceous as well as small woody plants, in open dry to moist fields. In shaded areas, where circulation of air is limited and relative humidity is high, the plant competes unsuccessfully with more shade tolerant understory plants and soon is excluded because it grows so tall that it is easily knocked over by the wind or rain. This horizontal position makes the plant unable to compete for necessary light, and stored food of the roots is gradually used up. The plant eventually dies back due to lack of nourishment. This tall growth of *A. syriaca* in the stalk is not unique to the species but holds true for most plants, that are genetically capable, that are subjected to low light intensities. In addition to being vegetatively "outcompeted" in damp, shady areas, *A. syriaca* is subject to a fungus, probably by *Alternaria* sp., which thrives under damp conditions and not only destroys flowers but also can cause the abortion of fertilized ovules thereby reducing pod production and consequent seed production. This was the case for two such populations under study.

Soil chemistry, pH, percent organic matter, nutrients present, water holding capacity and amount of precipitation seem unimportant, at least in the ranges exhibited by the populations under study, in regard to the welfare of the plants, their inflorescence number, pod production and seed production. It has been suggested that the total number of flowers and inflorescences may be influenced by the nutrient budget of the plant (Willson and Rathcke, 1974). This does not appear to be the case since the plant variations in such areas (inflorescence number and number of flowers) seems totally unrelated to the nutrient level of the plant.

CHART VII

Weight of seeds/ Number of seeds per pod



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