FLOWER, POD, AND SEED PRODUCTION IN EIGHTEEN SPECIES OF MILKWEEDS (*ASCLEPIAS*)

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Abstract. Over the course of three decades, studies were conducted on flower, pod, and seed production in 18 species of midwestern milkweeds. Eleven species were from northern Illinois and Indiana, and seven were from Wisconsin, Missouri, and Kansas. Flowers in more than 4,400 umbels, umbels and pods on more than 8,500 stems, and seeds in more than 1,600 pods were counted. *Asclepias meadii* had fewest of flowers per stem (mean 12.0), and *A. incarnata* had the most (mean 992.6). *Asclepias lanuginosa* bore the fewest pods per stem (mean 0.005), and *A. incarnata* had the most (mean 16.1). *Asclepias ovalifolia* produced the fewest seeds per pod (mean 22.7), and *A. syriaca* produced the most (mean 244.3). *Asclepias lanuginosa* and *A. stenophila* set the fewest seeds per stem (mean 2.0), and *A. syriaca* set the most (mean 1,119.6). A few species, *A. syriaca*, *A. incarnata*, and *A. verticillata*, appeared to produce seed sufficient to sustain healthy populations, but several species, *A. lanuginosa*, *A. meadii*, *A. ovalifolia*, and *A. quadrifolia*, appeared not to do so and may be facing declining populations and possible extinction. If the few remaining, widely scattered populations are self-incompatible, it would be difficult for effective pollination to occur. Further, today populations of native pollinators are low in numbers and in some cases may even be extinct locally.

INTRODUCTION

At a time when more-general, descriptive studies in ecology are being de-emphasized in favor of more-pecialized studies with a narrower focus, it is still important to collect baseline data, which serves a necessary role in modern ecological research. In 1961, with this in mind, a long-term study was undertaken to identify some of these baseline data relating to the reproductive capability of milkweeds.

Of the 18 species of midwestern milkweeds reported on in this paper, 16 are plants of prairies, marshes, savannas, and open woodlands (Table 1). The remaining two, common milkweed (*A. syriaca* L.) and whorled milkweed (*A. verticillata* L.), are common weeds of open fields and disturbed areas within prairies. Unfortunately, much of the literature on flower, pod, and seed production for milkweeds is limited to studies of these two weedy species and of swamp milkweed (*A. incarnata* L.), a plant of marshes (LaFuze and Greulach 1947, Sparrow and Pearson 1948, Stevens 1945, Wilson and Rathcke 1974, Wilson and Price 1977, 1980). Wyatt (1980, 1981) studied the reproductive biology of butterfly weed (*A. tuberosa* L.), and Shannon and Wyatt (1986) studied that of poke milkweed (*A. exaltata* L.). In addition to *A. exaltata* and *A. tuberosa*, Wilbur (1976) reported reproductive data for two other less common species, purple milkweed (*A. purpurascens* L.) and short green milkweed (*A. viridiflora* L.). The reproductive biology of the four-leaved milkweed (*A. quadrifolia* Jacq.) was reported on by Chaplin and Walker (1982) and Cabin et al. (1991). Betz (1989) studied the flower, pod, and seed production of Mead's milkweed (*A. meadii* Torr.). Some of these papers are based on limited sample sizes and localized populations.

Table 1. Habitats of *Asclepias*.

Species	*Habitat*
A. amplexicaulis	sandy prairies and barrens
A. exaltata	open woods and thickets
A. hirtella	wet-mesic to mesic prairies
A. incarnata	marshes and ditches
A. lanuginosa	eroding gravelly/sandy hill prairies
A. meadii	virgin mesic prairies and hay meadows
A. ovalifolia	sandy/silt loam savannas and prairies
A. perennis	southern marshes and swamps
A. purpurascens	mesic silt-loam savannas and thickets
A. quadrifolia	dry silt-loam savannas and thickets
A. stenophila	dry western prairies
A. sullivantii	moist silt-loam prairies
A. syriaca	waste places, weedy fields, roadsides
A. tuberosa	dry sand/silt loam prairies and roadsides
A. variegata	savannas and open woods
A. verticillata	weedy, calcareous fields, roadsides
A. viridiflora	dry sandy/gravelly prairies
A. viridis	sandy/calcareous pastures and prairies

Intermittently during the past thirty years, baseline data were collected on the reproductive productivity of the nine species mentioned above and on an additional nine midwestern species of *Asclepias*. These less common species were sand milkweed (*A. amplexicaulis* Sm.), tall green milkweed (*A. hirtella* (Pennell) Woodson), woolly milkweed (*A. lanuginosa* Nutt.), oval-leaved milkweed (*A. ovalifolia* Dcne.), thin-leaved milkweed (*A. perennis* Walt.), narrow-leaved milkweed (*A. stenophylla* A. Gray), prairie or Sullivant's milkweed (*A. sullivantii* Engelm.), white milkweed (*A. variegata* L.), and spider milkweed (*A. viridis* Walt.).

The scope of this study was quite broad and extended over many years. Large quantities of data were obtained, which lend themselves to statistical analysis. Such an analysis is projected and will be reported in a future publication.

The comparative data compiled in this study do shed some light on the ecological positions that the 18 *Asclepias* species held in presettlement plant communities of the Midwest. However, it is unfortunate that reproductive studies on milkweeds were not undertaken earlier, when native plant communities were still intact and available for more definitive studies. Today, having disappeared over much of their original ranges, many of these *Asclepias* species are difficult to locate. Thus, it is now much harder to obtain the adequate samples necessary to do a comprehensive study.

METHODS

Intensive collection of data on the reproductive biology of 18 species of milkweeds (*Asclepias*) was carried out over 11 growing seasons (1961-1971). Less extensive studies were continued during 1972-1990.

Most of the data recorded were for 11 species growing in northeastern Illinois and northwestern Indiana. These species were *A. amplexicaulis*, *A. exaltata*, *A. hirtella*, *A. incarnata*, *A. lanuginosa*, *A. purpurascens*, *A. sullivantii*, *A. syriaca*, *A. tuberosa*, *A. verticillata*, and *A. viridiflora*. The data for *A. meadii*, *A. quadrifolia*, *A. stenophila*, and *A. viridis* were collected in western Missouri and in northeastern Kansas; data for *A. ovalifolia* were obtained from populations in southern and central Wisconsin. For *A. perennis* and *A. variegata*, populations from southern Illinois and southeastern Missouri were used for the data collection. In addition, a few isolated plants of *A. meadii* from northeastern, central, and southern Illinois and a single plant of *A. ovalifolia* from northeastern Illinois were also used. While most of the data were obtained from wild populations, for 16 of the species, data were also taken from dozens of specimens grown from seed. The two species not grown were *A. stenophila* and *A. viridis*.

Although much of the data collected from year to year were from known individual plants and populations, new plants and populations were continually sought in order to diversify the population samples. The new individuals and populations, especially for the less common species, were found by searching natural communities where they could be expected to occur. Assistance in locating such areas was provided by knowledgeable local field ecologists and botanists. Other site information was obtained from herbarium specimens found at the Field Museum of Natural History, Chicago, and the Morton Arboretum, Lisle, Illinois. Fortuitous discoveries of individual plants or populations were made from time to time.

Some milkweeds typically produced a single flowering stem (genet) from the rootstock, while others produced multiple flowering stems (ramets). *Asclepias meadii* is an example of a species which usually produced only one flowering stem. On the other hand, rootstocks of *A. tuberosa* usually produced multiple flowering stems. In fact, a specimen of *A. tuberosa* which had been grown from seed, produced a bushy plant of 33 flowering stems (Betz, unpublished data). *Asclepias syriaca* and *A. verticillata* commonly produced large rhizomatous clones of flowering stems that extended over large areas and contained hundreds of stems. Because of this variability in stem production found among the 18 species, the unit of observation used for collecting data was the individual stem.

To ensure that plants were visited at the proper time for observation of flowering and subsequent ripening of pods, a chart was constructed for the 18 species studied. Data for this chart were obtained primarily from field studies, but these were supplemented by data obtained from herbarium specimens at the Field Museum of Natural History, Chicago, and the Morton Arboretum, Lisle, Illinois.

Collection of data for most species was done by counting without damaging the plant part under observation. For certain species, determination of the number of flowers per stem was comparatively easy and thus could be carried out in the field. However, some of the more common, weedier species, such as A. syriaca, had so many flowers per umbel that field counting was not feasible. Instead, umbels were removed and taken separately in marked plastic bags into the laboratory for counting. If flowers had already fallen from an umbel, it was still possible to get an accurate count by observing scars left on the peduncle.

A similar difficulty held for *A. hirtella*, *A. stenophila*, and *A. verticillata*, in that they produced large numbers of lateral umbels. These species frequently had lost most or all of the flowers on the lower umbels of a stem and at the same time embryonic flowers were developing in the uppermost umbels. Such stems were cut at the base and carried into the laboratory for thorough study and counting. Frequently, a magnifying glass was required to count the tiny embryonic flowers in the uppermost umbels.

For other species, counting flowers per stem was sometimes difficult and time consuming. In *A. incarnata*, a stem typically produced so many flowers and umbels that a direct count of the flowers per stem was almost impossible. Because of this, a second method was developed: The mean number of flowers per umbel was multiplied by the mean number of umbels per stem to produce a mean number of flowers per stem. Comparing the results obtained by this method with those obtained by counting, showed that both methods were essentially equivalent (Table 4). For example, in *A. purpurascens*, the calculated mean number of flowers per stem was 73.0. Using the direct count method, the number was

Table 2. Flowers per umbel in Asclepias.

Species	*Range*	*Mean (S.D.)*[a]	*n*[b]
A. amplexicaulis	1-50	24.6 (9.5)	171
A. exaltata	1-44	13.6 (6.3)	216
A. hirtella	14-101	47.0 (18.8)	168
A. incarnata	11-51	28.2 (8.2)	154
A. lanuginosa	1-63	22.9 (9.2)	87
A. meadii	1-26	12.0 (3.3)	643
A. ovalifolia	1-25	9.3 (3.3)	237
A. perennis	1-38	14.1 (5.1)	115
A. purpurscens	1-75	30.4 (13.5)	292
A. quadrifolia	1-35	15.6 (6.3)	232
A. stenophila	3-29	17.0 (6.0)	86
A. sullivantii	1-40	29.2 (5.7)	223
A. syriaca	31-186	83.6 (27.7)	309
A. tuberosa	1-37	11.9 (4.9)	665
A. variegata	9 - 52	30.2 (10.0)	45
A. verticillata	3-25	11.7 (1.7)	453
A. viridiflora	18-108	50.5 (18.5)	133
A. viridis	1-23	7.2 (3.3)	246
Total			4,475

[a]S.D. = standard deviation.
[b]n = sample size.

Table 3. Umbels per stem in *Asclepias*.

Species	*Range*	*Mean (S.D.)*[a]	*n*[b]
A. amplexicaulis	1	1.0 (-)	171
A. exaltata	1-7	2.6 (1.4)	111
A. hirtella	1-27	8.7 (4.6)	450
A. incarnata	1-195	35.2 (35.5)	266
A. lanuginosa	1	1.0 (-)	87
A. meadii	1	1.0 (-)	643
A. ovalifolia	1-4	1.7 (1.8)	186
A. perennis	1-6	3.1 (1.5)	73
A. purpurascens	1-7	2.4 (1.1)	168
A. quadrifolia	1-4	1.7 (0.6)	103
A. stenophila	4-15	9.3 (2.5)	18
A. sullivantii	1-5	2.1 (0.8)	268
A. syriaca	1-9	4.3 (1.8)	319
A. tuberosa	1-25	7.4 (4.9)	458
A. variegata	1-5	2.3 (1.0)	19
A. verticillata	1-36	9.1 (7.1)	101
A. viridiflora	1-5	2.2 (1.0)	143
A. viridis	1-8	3.7 (1.6)	100
Total			3,714

[a]S.D. = standard deviation.
[b]n = sample size.

66.7. For *A. sullivantii*, the comparative figures were 40.3 and 41.9, and for *A. verticillata*, these figures were 106.5 and 105.8.

This second method was also used in calculating mean numbers of seeds per stem. This was done by multiplying the mean number of seeds per pod by the mean number of pods per stem.

Also determined were the number of pods per stem, the number of seeds per pod, and thus the number of seeds per stem. If possible, recently ripened pods were used in counting seeds because it was more difficult to separate seeds from the comma in the dry state.

RESULTS

Flowers per Umbel

Counts were made of the number of flowers within individual umbels for all 18 species of milkweed (Table 2). This involved a total of 4,475 umbels. Ranges of flower numbers per umbel and mean number of flowers per umbel were determined for all species. The number of flowers per umbel ranged from 1 to 186. *Asclepias viridis* had the lowest mean number of flowers per umbel (7.2), while the highest mean number of flowers per umbel was exhibited by *A. syriaca* (83.6). For most milkweed species, the number of flowers per umbel gave normal distribution curves. However, there was a tendency for the curve to skew slightly toward the higher number of flowers.

Umbels per Stem

Umbels were counted for 3,714 stems of the 18 species to determine the number of umbels produced per stem (Table 3). *Asclepias incarnata* had the widest range in number of umbels per stem (1-195) and also produced the highest mean number of umbels per stem (35.2). In contrast, three species (*A. amplexicaulis*, *A. lanuginosa*, and *A. meadii*) produced only one umbel per stem. For most milkweed species, the number of umbels per stem gave normal distribution curves. Similar to the curves obtained for the flowers per umbel, there was a slight tendency for the curves of number of umbels per stem to skew toward the higher number of umbels. This was very pronounced for *A. incarnata*, which produced the most strongly skewed curve of all the species studied. While 77% of the stems in this species produced between 1 and 50 umbels, 23% of the stems produced 51 to 195 umbels.

Table 4. Flowers per stem in *Asclepias*.

Species	*Range*	*Mean (S.D.)*[a]	*n*[b]	*Mean**
A. amplexicaulis	1-50	24.6 (9.5)	171	24.6
A. exaltata	2-119	38.6 (26.8)	76	35.4
A. hirtella	197-631	369.4 (150.7)	10	408.9
A. incarnata	— - —	— —	—	992.6
A. lanuginosa	1-63	22.9 (9.2)	87	22.9
A. meadii	1-26	12.0 (3.3)	643	12.0
A. ovalifolia	2-39	15.8 (7.7)	109	15.8
A. perennis	12-112	42.8 (28.5)	33	43.7
A. purpurascens	3-195	66.7 (41.4)	85	73.0
A. quadrifolia	5-67	26.9 (13.8)	103	26.5
A. stenophila	— - —	— —	—	158.1
A. sullivantii	9 - 101	41.9 (19.2)	99	40.3
A. syriaca	200-858	474.7 (173.4)	33	359.5
A. tuberosa	7-226	89.5 (69.5)	61	88.1
A. variegata	9-143	70.3 (39.0)	19	69.5
A. verticillata	23-379	105.8 (88.9)	53	106.5
A. viridiflora	20-283	77.5 (55.5)	23	111.1
A. viridis	5-55	26.4 (12.1)	67	26.6
Total				1,672

[a] S.D.= standard deaviation.
[b] n = sample size.
* Calculated mean (numbers of flowers per umbel X numbers of umbels per stem).

Flowers per Stem

The mean number of flowers per stem was determined for 1,672 stems for 16 of the 18 species of milkweeds. This determination was made by direct counting and by calculating mean number of flowers per umbel multiplied by the mean number of umbels per stem (Table 4). Results obtained using the two methods were generally the same. For example, *A. quadrifolia* had a mean number of flowers per stem of 26.9 by direct counting and a mean of 26.5 by calculation. *Asclepias meadii* yielded the smallest mean number of flowers per stem (12.0). *Asclepias incarnata*, however, produced the highest mean number of flowers per stem (992.6), as determined by the indirect methods of calculation only.

For *A. syriaca*, there was a notable difference in the mean number of flowers per stem obtained by the method of direct counting (474.7) in contrast to that obtained by the method of calculation (359.5). This is probably due, in part, to the population sample used for the direct count being too small (33); also, partially due to the fact that the direct count involved only a few clones with limited diversity. The mean number of flowers per umbel determined for the small sample of 33 stems by count (84.7) was approximately the same as that determined for the larger more diverse population by calculation (83.6). However, there was a difference found in the mean numbers of umbels per stem, using the two methods. The counted population had a mean number of 5.6 umbels per stem in contrast to the mean number of 4.3 umbels per stem calculated for the other population. The counted sample had on average 1.3 more umbels per stem, and thus each stem had a theoretical capacity of 110.1 more flowers per stem. The actual number obtained by counting was 115.2. Thus, the discrepancy shown between the mean number of flowers per stem, when comparing the results obtained from direct counting (474.7) with the results obtained from calculating (359.5), can be explained by the larger mean number of umbels per stem in the relatively small population sample used for direct counting. Lesser differences in the mean number of flowers per stem observed in two other species (*A. hirtella* and *A. viridiflora*) also seem to be due to the small samples used in the direct count (Table 4).

Pods and Pods per Stem

Marked variation in pod production also occurred for the 18 species studied. The number of pods produced on 4,794 stems observed ranged from 0 (1) to 75 (Table 5). The high of 75 was found for *A. incarnata*. The mean number of pods per stem varied from a low of 0.005 in *A. lanuginosa* to a high of 16.1 in *A. incarnata*.

Milkweed flowers possess two separate ovaries, each with the potential to produce a mature pod. These twin pods share the same pedicel. In one study of *A. syriaca*, 5.4% of the pods were double or twins (Sparrow and Pearson 1948), and in another study on the same species, the percentages ranged from 9.5 to 24.5% (Moore 1947). In the present study, 3.7% of the pods produced by *A. syriaca* were twin or double pods. The figure for *A. amplexicaulis* was 0.83%; for *A. sullivantii*, 2.3%; and for *A. verticillata*, 1.9%.

Milkweed pods (follicles) varied greatly in size, shape, and the manner of attachment of pedicels to the peduncle (Table 6.). In general, the larger, coarser milkweeds, such as, *A. amplexicaulis*, *A. purpurascens*, *A. sullivantii*, *A. syriaca*, and *A. viridis* had the largest pods, and the smaller less robust species, such as *A. quadrifolia* and *A. lanuginosa*, had the smallest ones. *Asclepias meadii* had long,

Table 5. Pods per stem in *Asclepias*.

Species	*Range*	*Mean*	*n*[a]
A. amplexicaulis	0-5	1.3	136
A. exaltata	0-6	0.7	73
A. hirtella	0-15	2.9	387
A. incarnata	0-75	16.1	184
A. lanuginosa	0-1	0.005	437
A. meadii	0-2	0.06	643
A. ovalifolia	0-3	0.15	71
A. perennis	0-2	1.4	5
A. purpurascens	0-5	1.2	46
A. quadrifolia	0-2	0.06	103
A. stenophila	0-1	0.18	11
A. sullivantii	0-5	1.5	329
A. syriaca	0-42	4.6	645
A. tuberosa	0-9	1.8	671
A. variegata	0-1	0.24	17
A. verticillata	0-20	2.6	931
A. viridiflora	0-8	2.0	55
A. viridis	0-5	1.9	50
Total			4,794

[a]n = sample size.

Table 6. Size of pods in Asclepias

Species	*Length (cm) (Range)*	*Length (cm) (mean)*	*Diameter (cm) (mean)*	*n*[a]
A. amplexicaulis	8.3 - 15.5	12.6	1.9	86
A. exaltata	7.8 - 12.8	10.5	1.2	128
A. hirtella	7.0 - 11.8	9.8	1.5	167
A. incarnata	5.9 - 8.5	7.4	0.8	54
A. lanuginosa	— - —	7.6	1.2	1
A. meadii	6.9 - 15.8	11.8	1.1	40
A. ovalifolia	4.8 - 6.6	6.4	1.8	11
A. perennis	3.9 - 6.8	5.6	1.0	16
A. purpurascens	9.0 - 15.0	11.8	1.4	59
A. quadrifolia	8.8 - 10.4	9.6	0.5	12
A. stenophila	9.2 - 10.1	9.6	0.7	2
A. sullivantii	8.2 - 13.6	10.4	2.3	150
A. syriaca	6.5 - 13.6	10.0	2.9	112
A. tuberosa	8.4 - 15.5	11.8	1.3	151
A. variegata	10.5 - 15.7	12.7	1.0	3
A. verticillata	4.7 - 10.2	7.2	0.5	160
A. viridiflora	6.5 - 14.5	9.6	1.5	103
A. viridis	— - —	—	—	—
Total				1,255

[a]n = sample size.

narrow pods, while *A. perennis* had short, globular ones. Three species (*A. incarnata*, *A. quadrifolia*, and *A. verticillata*) had erect pods on erect pedicels. *Asclepias perennis* had pendulous pods (hanging down) on recurved or slightly deflexed pedicels. All of the other 14 species of *Asclepias* had erect pods on deflexed pedicels.

Seeds and Seeds per Pod

A total of 127,220 seeds were counted in 1,672 pods for the 18 species of *Asclepias* studied (Table 7). The numbers of seeds per pod ranged from a low of 11 in *A. meadii* to a high of 309 in *A. syriaca*. The mean number of seeds per pod varied from a low of 22.7 in *A. ovalifolia* to a high of 244.3 in *A. syriaca*. The larger, coarser species of milkweeds produced the highest mean number of seeds per pod. These were *A. amplexicaulis* (117.8), *A. purpurascens* (180.7), *A. sullivantii* (182.2), and *A. syriaca* (244.3). On the other hand, the smaller, less robust species usually had the smallest pods with the lowest mean number of seeds in them. These were *A. lanuginosa* (39.0) and *A. quadrifolia* (27.6). A few species produced pods with inflated endocarps; these pods were moderately large, but contained relatively few seeds. Two such species were *A. hirtella* (51.2) and *A. ovalifolia* (22.7).

While the seeds of all *Asclepias* species are similar, there were some morphological differences among them. For example, the seeds of *A. sullivantii* were larger and lighter brown than seeds of *A. syriaca*. *Asclepias hirtella* produced seeds which had larger margins and had a darker brown color than most of the other milkweed species. The seeds of *A. lanuginosa* were smaller and darker than many of the other species. *Asclepias perennis* seeds do not bear a tuft of silky hairs (coma) at the hilum like all of the other species.

A variable number of seeds for the species studied appeared to lack embryos and/or sufficient amounts of food reserves for normal germination (0.2 to 4.8%). Species that had higher percentages of these apparently undeveloped seeds were *A. meadii* (14.0%), *A. lanuginosa* (60.1%), and *A. ovalifolia* (78.0%). Two species, *A. ovalifolia* and *A. quadrifolia*, produced one pod each that was normal in size but contained only visibily undeveloped seeds. Two other species, *A. lanuginosa* and *A. meadii*, produced one pod each that was of normal size but completely empty and without any seeds.

Seeds per Stem

The mean seeds per stem for the 18 species were obtained by multiplying the mean number of seeds per pod by the mean number of pods per stem. *A. lanuginosa* produced the lowest mean number of seeds per stem (0.2), while *A. syriaca* had the highest (1,123.8). The mean seeds per stem for the other 16 species of *Asclepias* were as follows: *A. amplexicaulis* (153.1), *A. exaltata* (59.6), *A. hirtella* (148.5), *A. incarnata* (872.2), *A. meadii* (3.6), *A. ovalifolia* (3.4), *A. perennis* (58.1), *A. purpurascens* (216.8), *A. quadrifolia* (1.7), *A. stenophila* (8.0), *A. sullivantii* (273.3), *A. tuberosa* (132.8), *A. variegata* (25.9), *A. verticillata* (118.8), *A. viridiflora* (170.8), and *A. viridis* (209.6).

DISCUSSION

For most milkweeds, all the flowers in a given umbel open within a day or two of each other (Betz, unpublished data). These are thus capable of being pollinated for a period of about five or six days (Morse 1987, Betz, unpublished data). In order for pollination to be effective, the pollinating insect, usually a hymenopteran (Betz, unpublished data), must insert the pollinia into the stigmatic chamber of the flower with the convex side of the pollinia entering first. Within a few days following pollination, the pedicels of the flowers that have been successfully pollinated will begin to thicken and, in most species, deflex downward, followed by the development of a small pod.

Transfer of a pollinium into a stigmatic chamber of a flower does not necessarily mean that a pod will form. If the pollinium is

Table 7. Seeds per pod in *Asclepias*.

Species	*Range*	*Mean (S.D.)*[a]	*n*[b]
A. amplexicaulis	60-186	117.8 (20.4)	86
A. exaltata	24-121	84.1 (18.9)	128
A. hirtella	31-70	51.2 (7.2)	197
A. incarnata	16-113	54.2 (14.1)	189
A. lanuginosa	38-40	39.0 (1.0)	2
A. meadii	11-112	59.6 (22.9)	45
A. ovalifolia	15-37	22.7 (8.9)	6
A. perennis	26-51	41.5 (6.3)	22
A. purpurascens	91-245	180.7 (31.5)	59
A. quadrifolia	19-33	27.6 (4.4)	14
A. stenophila	40-49	44.5 (5.0)	2
A. sullivantii	116-253	182.2 (24.8)	148
A. syriaca	164-309	244.3 (31.2)	182
A. tuberosa	47-92	73.8 (14.7)	151
A. variegata	88-116	108.0 (14.0)	4
A. verticillata	17-66	45.7 (9.5)	297
A. viridiflora	20-129	85.4 (19.3)	130
A. viridis	85-154	110.3 (24.8)	10
Total			1,672

[a] S.D. = standard deviation.
[b] n = sample size.

inserted in reverse into the stigmatic chamber, the pollen may germinate, but the pollen tube may never reach the ovary to fertilize the ovules (Galil and Zeroni 1969). In other instances, pods may be initiated, but will abort because the flower has been pollinated with a pollinium from the same or genetically closely related plant (Sparrow and Pearson 1948, Kephart 1981). A pod may also abort due to competition among the developing pods for limited nutrients from the parent plant. Eleven plants of *A. meadii*, grown from seed in pots and flowering in their third year of growth, were placed in a virgin prairie (Markham Prairie, Markham, Illinois) to be pollinated by resident bumble bees. Within one week 21 pedicels began to enlarge and twist downward, indicating that pollinia had been inserted into stigmatic chambers and that pods were beginning to form. Eventually most of these initiated pods fell off, leaving only three pods to mature. Pod abortion has been reported by others (Sparrow and Pearson 1948, Wilson and Price 1974).

Abortion of developing pods was also observed for a potted plant of *A. meadii* grown from seed which had been hand-pollinated with pollinia taken from an isolated non-seed setting plant of *A. meadii* from southern Illinois. This plant initiated two pods which eventually became unequal in size. For a time both pods grew at the same rate, and it appeared that both would mature. However, one began to outgrow the other. Gradually, the smaller one stopped growing, began to decrease in size, regressed, and finally degenerated into a tiny vestigal appendage adjacent to the mature pod. It appeared that the larger pod was using nutrients derived from the smaller one.

In their floral development, milkweeds have evolved two different strategies. The first strategy, exhibited by *A. amplexicaulis*, *A. lanuginosa*, and *A. meadii*, involves the production of a terminal umbel with all flowers opening within a day or two of one another. The species showing this strategy appear to rely on one or two dependable pollinators (Betz 1989). The second strategy, exhibited by the species, *A. hirtella*, *A. incarnata*, *A. stenophila*, and *A. syriaca*, involves the successive production of a number of umbels having flowers in bloom over a longer period of time. Individual plants of *A. hirtella* have been observed to have ripened pods, open and shedding seeds at the base of the plant, while at the upper end of the stem, umbels with flowers were being visited by various pollinators. The milkweed species exhibiting this strategy have a larger number of different insects to pollinate their flowers as compared to the first group (Betz, unpublished data). Because of possible unfavorable pollinating conditions during a short blooming period—inclement weather, etc.—species with a terminal umbel would be less likely to produce a pod than would the second group of species with a succession of blooming umbels.

The range and mean number of flowers and umbels per stem produced by most milkweeds today are undoubtedly the same as in presettlement times. However, it is possible and highly probable that the numbers of pods per stem produced by some milkweed species today are less than those which would have been produced in presettlement times. It is difficult to conceive that *A. meadii* and *A. quadrifolia*, both with a mean pod per stem ratio of 0.06, and *A. lanuginosa*, with a ratio of 0.005, could have sustained adequate populations over long periods of time in the presettlement prairies and savannas with such low pod production (Table 5). There is also the possibility that in presettlement times, as today, the number of pods produced per stem varied in an irregular manner about a mean. When large populations are considered over relatively extended periods, mean number of pods per stem may have been related to the mean number of umbels per stem that a species produced. For four species, this relationship may have further involved the production of a mean number of about one pod per umbel for their populations generally. This is suggested by the following data: *A. amplexicaulis* produced a mean of 1.3 pods per umbel, *A. syriaca* had 1.1, *A. viridiflora* (0.9), and *A. sullivantii* (0.7). This relationship did not appear to hold for the other 14 species of milkweeds under present day conditions. However, in the past with higher populations of both milkweeds and pollinators this relationship may have existed.

Further, it should be noted that in presettlement times there were large expanses of prairies, savannas, open and closed forests, marshes, and intervening ecotones. These plant communities in turn supported high populations of insect species, including the pollinators of the various milkweeds. This helped to assure an ample supply of seeds (and seedlings) to maintain adequate population levels necessary for survival.

The ecological communities of today are much altered. They are fragmented and degraded, and there is heavy competition from non-native plants. Populations for all insects, including the pollinators of milkweeds, are probably low in number, in part, due to the lack of suitable habitats and food sources and to the widespread use of insectides. While there is little experimental evidence to document this decrease in insect populations, there is some historical evidence. During the 1930s, when lower speeds were prevalent, the radiators, windshields, and bumpers of automobiles had to be cleaned of hundreds of insects killed after driving only a few miles through the countryside (Betz, personal observation). Again during the 1930s, hundreds of thousands of monarch butterflies (*Danaus plexippus* L.) passed through the inner city of Chicago each fall on their migrations southward (Betz, personal observation). These observations of insect abundance are things of the past. Insect populations may have been even greater during presettlement times.

The weedy species *A. syriaca* is apparently maintaining adequate population levels today, just as it did in presettlement times. In part, this is the result of the availability of large areas of disturbed ground as well as the production of relatively large numbers of flowers, pods, and seeds. Moreover, the formation of large clones, sometimes containing hundreds of flowering stems, has also helped. The success of this species in maintaining adequate populations may also be due, in part, to the fact that their flowers are pollinated by a higher proportion of exotic species, including the Eurasian honey bee (*Apis mellifer* L.) (Betz, unpublished data).

On the other hand, many of the other milkweed species are undergoing population declines because of the degradation and fragmentation of their habitats and the consequent loss of their insect pollinators. It would appear that many milkweeds, especially the smaller ones with narrower ecological tolerances and few flowers and seeds per stem, may have difficulty in surviving under present ecological conditions. A few species, such as *A. meadii*, *A. lanuginosa*, and *A. ovalifolia*, are now included on threatened or endangered species lists.

Finally, many of the milkweed populations observed for this study over the past 30 years have disappeared, and few new populations have appeared to take their place (Betz, personal observation). Thus, this study would be difficult to replicate today.

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