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REPRODUCTIVE LIMITATIONS OF A LOCALLY RARE *ASCLEPIAS*

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ABSTRACT

Reproduction in populations of *Asclepias quadrifolia* and *A. syriaca* was examined at a western Vermont study site. While both field and forest populations of *A. syriaca* appeared to be heavily pollinated by *Apis* spp. and *Strymon* spp., observed pollinia insertion rates for the locally rare *A. quadrifolia* were among the lowest reported for the genus. Pollen and resource availability together are shown to closely account for the observed fruit production of <.007 fruits per *A. quadrifolia* flower. Comparisons of data for *A. quadrifolia* in Missouri, where the species is common, suggest that reproductive limitations may be an important factor contributing to the scarcity of *A. quadrifolia* in Vermont.

Key Words: reproductive limitations, *Asclepias,* rarity, biogeography, Vermont

INTRODUCTION

Biological rarity in plants has proven to be a highly subjective matter difficult to quantify and define (Drury, 1974, 1980; Harper, 1981; Krukeberg and Rabinowitz, 1985; Rabinowitz et al., 1986). Nevertheless, in recent times scientific interest in rarity has increased, perhaps partly because of the human-caused loss of biological diversity currently occurring on earth (Wilson, 1989). While globally rare species often are too endangered for rigorous scientific study, organisms which are locally rare provide an ethically more acceptable opportunity to investigate biological aspects of rarity.

One approach to understanding any form of rarity is to examine

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the process of reproduction and attempt to identify limiting factors. Reproductive comparisons of sympatric rare and common congeners may be a useful technique for gaining insight into the causes and consequences of biological rarity and commonness (Fiedler, 1987; Ornduff, 1989). Comparing data obtained at a location where a species is rare, with data where the species is common, may further enhance our understanding of rarity and the factors which limit reproduction (Ward, 1981).

Although reproductive ecology of *Asclepias* has been relatively well studied (reviewed by Shannon and Wyatt, 1986), there still is no consensus as to the relative importance of factors that determine levels of fruit initiation and maturation. *Asclepias syriaca* L. and *A. quadrifolia* Jacq. (Asclepiadaceae) are sympatric in the understory of a deciduous forest in western Vermont. While *A. syriaca* is commonly found in fields, roadsides, and newly created forest openings throughout North America, *A. quadrifolia* is the only *Asclepias* studied that grows in low-light forest understories throughout its range (Chaplin and Walker, 1982).

Only two studies of *Asclepias quadrifolia* have been published (Chaplin and Walker, 1982; Pleasants and Chaplin, 1983); both took place in Missouri, where this species is fairly common. Chaplin and Walker (1982) found for several populations of *A. quadrifolia* in Missouri that stem height was significantly correlated with total plant, root, and aboveground energy content (determined by bomb calorimetry). They also found that flower and fruit production in this species appeared to be limited by available energy reserves; plants under the threshold of 33–34 cm stem height (32–33 kilo joules total energy) are apparently unable to mature a seed pod successfully, likely due to the relatively high energetic cost (10.40 kj/pod).

The present study examines reproduction in *Asclepias quadrifolia* in Vermont, where this species approaches the northeastern edge of its range and is classified by the Vermont Nongame and Natural Heritage Program as "uncommon in the state" (Thompson, 1990). Energetic constraints and levels of pollination are assessed for their roles in limiting reproduction at the Vermont study site. In an effort to better understand why this species is locally rare, data from the Vermont populations of *A. quadrifolia* are also compared with data from sympatric populations of *A. syriaca* and Missouri populations of *A. quadrifolia* obtained from the two studies cited above.

MATERIALS AND METHODS

Species and Study Site

Asclepias is a widespread genus with 108 species and 9 subgenera distributed over three geographic regions: temperate to tropical North America, subtropical South America, and southern and eastern Africa (Woodson, 1954). *Asclepias syriaca* is a robust species often considered a "troublesome weed" in North America; underground rhizomes may form large clones of up to several thousand stems (Gleason, 1952). In contrast, *A. quadrifolia* is one of the smallest milkweeds (Woodson, 1954; Chaplin and Walker, 1982) and is incapable of asexual reproduction, with most plants producing a single stem from the rootcrown each spring (Chaplin and Walker, 1982; Cabin, pers. obs.). This species is typically found in low-light forest understories throughout the Appalachian and Ozark Mountains (Chaplin and Walker, 1982).

In the summer of 1989, two plots of *Asclepias quadrifolia* and two populations of *A. syriaca* were studied. All plants are located within the Vermont Nature Conservancy's 110 ha Shaw Mountain Preserve, located near the southern tip of Lake Champlain, in the town of Benson, Rutland County, Vermont. The mountain consists of a limestone uplift which rises over 150 m from the surrounding land and hosts a variety of plants considered rare in Vermont (Vermont Nongame and Natural Heritage Database, 1990). On Shaw Mountain, *A. quadrifolia* is found primarily in grassy meadows in mature, mixed deciduous forests. At this site, *A. quadrifolia's* whitish to pinkish flowers are borne on no more than two umbels per stem, with most umbels containing 5–15 flowers. The majority of flowering stems on Shaw Mountain bloomed from about mid-June to the end of that month. As most *A. syriaca* stems in the study area did not bloom until early July, there was little overlap in the flowering phenology of these two *Asclepias* species. Individual stems of *A. syriaca* produced an average of four umbels, with each umbel containing about 40 flowers.

Asclepias quadrifolia

Two plots of *Asclepias quadrifolia* were established in the study area. The first plot was chosen to represent a typical stand of the species as it occurs on Shaw Mt. (scattered individuals growing at $\cong$ .2 stems/m^2). The plot measured 14 × 37 m and is dominated by scattered mid-size trees including *Acer saccharum* Marsh., *Carya ovata* (Mill.) K. Koch, *Pinus strobus* L., *Quercus alba* L. and *Ostrya virginiana* (Mill.) K. Koch, and contains low grasses and sedges in the understory. The second plot is about .5 km SE of the first and was chosen because it contained the highest density of flowering *A. quadrifolia* observed on Shaw Mountain ($\cong$ 4 stems/m^2); aside from this distinction the two plots were otherwise similar in habitat characteristics. In both plots the number of leaves per stem and height (ground to most distal leaf node) were measured for all *A. quadrifolia* stems. Each flowering stem was labeled and the number of umbels, flowers per umbel, and number of fruits was recorded at regular intervals. Due to the rarity of *A. quadrifolia* in Vermont, direct measurements of plant energy were not performed. Instead, plant energy was estimated using Chaplin and Walker's (1982) equation for converting stem height (in cm) to total plant energy (in kj) as follows: $\log_{10}$ total plant energy content = 0.014 (stem height) + 1.050 ($r = .75$, $P < .001$).

Asclepias syriaca

Two populations of *Asclepias syriaca* were studied on Shaw Mt. The first is located in an abandoned field about .5 km E from the first plot of *A. quadrifolia*; the second lies within the forest about 1 km S from the old field and is located in a substantial light gap created by recent logging. For the old field population, 20 flowering stems were randomly selected, labeled, and regularly monitored for fruit production; flowers from both populations were also examined for pollination levels (see below).

Pollination

In *Asclepias* flowers, pollen grains are enclosed in paired, waxy structures called pollinia; each pollinium generally contains enough pollen to fertilize an entire fruit (Bookman, 1984; Morse, 1985). Pairs of pollinia from adjacent anther-sacs of separate stamens are connected by translator arms to a common clip, the corpusculum. The entire structure of pollinia, translator arms, and corpusculum is called a pollinarium (plural pollinaria); each indi-

Table 1. Comparisons of flowering and nonflowering *Asclepias quadrifolia* stems on Shaw Mountain in Vermont with flowering ones in Missouri. Data for Missouri obtained from Chaplin and Walker (1982) and Pleasants and Chaplin (1983). Numbers are means ± 1 SE.

	Shaw Mt., VT		Columbia, MO Flowering
	Flowering (n = 65)	Nonflowering (n = 118)	
Stem Height (cm)**	30.5 ± 0.7	20.6 ± 0.6	≈40
# Leaves per Stem*	7.3 ± 0.2	6.1 ± 0.1	≈12
Energy per Stem (kj)	30.0[a]	21.8[a]	≈40.7
# Flowers per Stem	8.9 ± 0.8		29.6
# Umbels per Stem	1.2 ± 0.1		≈2

[a] Energy per stem calculated using Chaplin and Walker's (1982) equation for converting stem height (in cm) to kj (see text).
* $P < 0.01$, ** $P < 0.001$ (Vermont flowers only).

vidual flower contains two ovaries and five pairs of pollinia which straddle the five stigmatic chambers.

The pollinaria of *Asclepias* facilitate accurate quantification of both male (pollinium removal) and female (pollinium insertion) reproductive functions. To estimate pollinial movement on Shaw Mountain, flower samples of both milkweed species were collected throughout the flowering period and examined under a dissecting microscope for pollinaria removals and pollinia insertions. Flowers of *A. quadrifolia* were obtained at 2-day intervals from randomly selected plants occurring in the general vicinity of the two established plots. In addition, some sampling of the flowers within plot 2 was conducted to determine whether this unusually dense stand was differentially attracting pollinators. Flower samples of *A. syriaca* were collected from randomly-selected individuals in the old field population at 2-day intervals; flowers from the forest population were collected only once.

RESULTS

Data from the two *Asclepias quadrifolia* plots on Shaw Mountain (combined in Table 1) show that flowering stems were significantly taller and produced more leaves than nonflowering stems ($P < .001$ and .01, respectively). Compared to data reported by Chaplin and Walker (1982) in Missouri, the flowering stems ob-

Table 2. Comparative pollination of *Asclepias quadrifolia* in Vermont and Missouri with *A. syriaca* in Vermont. The pollinaria removal and insertion data for Missouri are taken from Pleasants and Chaplin (1983). Numbers are means ± 1 SE.

	A. syriaca flowers (Shaw Mt.)		*A. quadrifolia* flowers	
	Field (n = 155)	Forest (n = 40)	Shaw Mt., VT (n = 234)	Columbia, MO (n = 27)
Pollinaria Removed (per flower)	2.48 ± 0.21	2.08	0.64 ± 0.11	2.23 ± 0.18
Pollinia Inserted (per flower)	0.81 ± 0.15	0.82	0.02 ± 0.01	1.28 ± 0.18
Insertions/Removals (%)	32.7%	39.4%	3.8%	57.4%

served on Shaw Mountain were smaller in size and produced a much more modest floral display.

Table 2 compares pollination levels between populations of *Asclepias quadrifolia* and *A. syriaca* on Shaw Mountain with Pleasants and Chaplin's (1983) populations of *A. quadrifolia* in Missouri. Despite the differences in density, the insertion and removal rates of the two plots of *A. quadrifolia* on Shaw Mountain were not significantly different and thus are combined in Table 2. The observed insertion rate per *A. quadrifolia* flower on Shaw Mountain (.02) is among the lowest reported for the genus. In addition, the number of observed pollinia insertions for this species is less than 4% of the observed pollinaria removals, while in Missouri this same percentage exceeds 55%. These results suggest that *A. quadrifolia* flowers studied on Shaw Mountain are pollinated with much lower frequency and efficiency (i.e., more pollen is wasted by vectors removing but not inserting pollinia) than in the Missouri populations. Despite repeated observations, potential pollinators for *A. quadrifolia* were never observed. In contrast, both field and forest populations of *A. syriaca* were often covered with insect visitors, most frequently *Apis* spp. and *Strymon* spp.

Fruit initiation and maturation comparisons between *Asclepias quadrifolia* and *A. syriaca* on Shaw Mountain show that fruit production was much greater in *A. syriaca,* even when the comparison is made on a per flower basis (Table 3). While *A. syriaca* showed considerable fruit abortion on Shaw Mountain (> 65%

Table 3. Comparisons of fruit set between flowering stems of *Asclepias* species on Shaw Mountain, Vermont, shown with ± 1 SE. There are no significant differences between the two plots of *A. quadrifolia*.

	A. quadrifolia		*A. syriaca*
	Plot 1 ($n = 28$)	Plot 2 ($n = 37$)	Field only ($n = 20$)
Total Fruit Initiated	5	2	132
Mean Fruit Initiated (per stem)	0.179 ± 0.116	0.054 ± 0.038	6.6 ± 5.540
Mean Fruit Initiated (per flower)	0.009 ± 0.006	0.006 ± 0.005	0.05 ± 0.006
Total Fruit Matured (as of Aug. 12)	4	2	46
Mean Fruit Matured (per stem)	0.143 ± 0.112	0.054 ± 0.038	2.3 ± 0.250
Mean Fruit Matured (per flower)	0.007 ± 0.005	0.006 ± 0.005	0.023 ± 0.004

as of Aug. 12), only one initiated *A. quadrifolia* fruit in the two plots failed to mature, and this failure was due to herbivory rather than abortion.

In contrast, Chaplin and Walker (1982) reported that 80–90% of the initiated *Asclepias quadrifolia* pods in their Missouri populations were lost within 3 weeks of the end of flowering, nearly all due to fruit abortion. Nevertheless, 50% of their pod-producing plants not damaged by herbivores successfully matured at least 1 pod (Pleasants and Chaplin, 1983).

Despite the size and, presumably, energy differences between *Asclepias quadrifolia* from Missouri and Vermont, all the pod-producing stems on Shaw Mountain are above the height and energy thresholds found in Missouri. By assuming that each pollinium inserted into a flower on a stem taller than 33 cm (i.e., a stem with sufficient energy to mature a pod) resulted in the initiation of 1 fruit, actual fruit production in the two *A. quadrifolia* plots on Shaw Mountain can be predicted with remarkable accuracy (Table 4). The two plots on Shaw Mountain contained a combined 183 stems, of which 65 produced at least one flower. Of these 65 stems, 22 were at or above the minimum size of 33–34 cm stem height apparently needed for pod maturation. Multiplying these 22 plants by their own mean number of flowers per

Table 4. Comparisons of actual fruit set with predicted fruit set of *Asclepias quadrifolia*. Predictions calculated by assuming that each pollinium inserted into the stigmatic chamber of a flower on a mature plant (i.e., a plant with sufficient stored energy to mature a seed pod; see text) resulted in the initiation of one fruit.

	A. quadrifolia in Vermont		
	Plot 1	Plot 2	Total
Flowering Stems	28	37	65
No. stems > 33 cm	8	14	22
Mean no. Flowers (per stem)	13.88	10.79	11.9
Mean no. Insertions (per flower)	0.03	0.02	0.024
Predicted Fruit (insertions × no. flowers × no. stems)	3.33	2.56	6.29
Actual Fruit (as of Aug. 12)	4	2	6

stem (11.9) times the mean insertion rate per flower (.024) (the average of plot 2 and random flower samples), equals a total of 6.29 insertions for these 22 stems; the actual number of total fruits as of August 12 was six.

DISCUSSION

The results of this study suggest that both energetic constraints and low rate of pollination limited reproductive output in *Asclepias quadrifolia* on Shaw Mountain in 1989. Of the plants studied, only about 10% were apparently large enough to mature pods; low pollinia insertion rates appeared to further restrict fecundity. The observation that pollination levels were not significantly different for the most dense stand of *A. quadrifolia* found at Shaw Mountain suggest that the pollinators of this species may not be responsive to local floral density.

Their larger size and increased levels of pollination apparently enabled sympatric *Asclepias syriaca* stems to initiate many more fruits per flower than *A. quadrifolia*. Even though about two-thirds of the initiated *A. syriaca* pods failed to mature, primarily as a result of fruit abortion, pod maturation per *A. syriaca* flower still was an order of magnitude greater than that observed for *A. quadrifolia*. If asclepiads are capable of selective fruit abortion (Bookman, 1984), it is conceivable that the low fruit initiation and apparent lack of fruit abortion observed for *A. quadrifolia* in this study may result in seeds of lower quality than those matured by nearby *A. syriaca* stems or by *A. quadrifolia* in Missouri, where fruit abortion rates can reach 80–90% (Chaplin and Walker, 1982). Whether there is any general pattern of seed quality and pollination intensity gradually decreasing as populations of *A. quadrifolia* and/or other species approach the edges of their geographical distributions was not investigated.

Suitable habitat patches of open, sparse forest understories may further limit the distribution and abundance of *Asclepias quadrifolia* on Shaw Mountain and perhaps in northern New England as well. At other sites in Vermont known to have harbored populations of *A. quadrifolia,* one of us (R.C.) found that recent forest succession often invaded large sections of what had been grassy, clear patches where *A. quadrifolia* once grew. In many areas of Vermont it thus appears likely that forest succession may eliminate suitable habitat for this species before a given *A. quadrifolia* seed can germinate and store enough energy to flower and set seed (if and when the flower is pollinated). Future studies are needed to clarify what creates and maintains these types of habitats, and why this particular habitat is more common in the southern Appalachian and Ozark Mountains. Additional work on Shaw Mountain and other sites in Vermont could also help determine if the low levels of pollination and pod production for *A. quadrifolia* found in this study accurately reflect larger spatial and temporal patterns for this species in northern New England.

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