ECOLOGY OF MEAD'S MILKWEED (ASCLEPIAS MEADII TORREY)

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Abstract. Mead's milkweed (Asclepias meadii Torrey) is a plant of virgin prairies, whose pre-settlement range included much of the midwest. It is now a rare plant confined to prairie hay meadows, railroad rights-of-way, prairie preserves and pioneer cemeteries. Studies of approximately a hundred individual plants, producing hundreds of flowering and sterile stems, in the wild and in cultivation for seven years (1965-1971) indicated that it was a moderately-sized plant whose stems averaged 56 cm in height with sagittate sessile leaves with a herringbone arrangement of the veins. In late May to early June a mature stem produced a solitary, terminal, nodding umbel with an average of 12 flowers. Pollination was by digger bees (Anthophora spp.) and bumble bees (Bombus spp.). Approximately 6.4% of the flowering stems produced a long narrow pod averaging 12 cm in length and 1.3 cm in diameter with approximately 60 seeds per pod. Seed germination was relatively low (47.6%). Some plants in virgin prairies and in cultivation were over a quarter century old, and indications are they may live for a century or longer. In contrast to most milkweeds, the seedlings were difficult to grow. Four or more years were usually required to reach maturity. Like most milkweeds, a number of insects were associated with the plant. Most damaging were the larvae of the milkweed beetles (Tetraopes spp.) and milkweed weevils (Rhyssematus spp.) that fed on the roots and the adult weevils that girdled the peduncle causing the eventual collapse of the terminal umbel.

Key Words: Mead's milkweed, Asclepias meadii, prairie plant ecology, threatened species, tallgrass ecology, Illinois, Kansas, Missouri, Iowa

INTRODUCTION

Mead's milkweed (Asclepias meadii Torrey) was first collected by Dr. Samuel Barnum Mead, a physician-botanist, in western Illinois in 1843, as shown by herbarium specimens at the Chicago Natural History Museum. It was first reported in print in a list of plants of Hancock County published in the Prairie Farmer under the name of "Asclepias cordata non Walt?" (Mead 1846). A specimen of the plant was subsequently sent to John Torrey who recognized it as a new species and named it Asclepias meadii (Torrey 1856). This published description of the plant appeared in 1856 as a addendum to the second edition of Gray's Manual of Botany. However, from correspondence between Torrey and Mead and from the herbarium specimens at the Chicago Natural History Museum, it is probable that the plant was recognized as a new species and given the new name by Torrey sometime between 1846 and 1848.

In pre-settlement times Mead's milkweed appears to have had a wide distribution through the tallgrass region from northwestern Indiana (Deam 1940); southern Wisconsin (Greene 1880 and 1898), and northern Iowa (Fitzpatrick 1899, Greene 1907), to southern Illinois (Mead 1846, Lapham 1857, Patterson 1876, Brendel 1887, Huett 1897, McDonald 1899, Jones 1963), southern Missouri (Tracy 1886, Woodson 1954, Steyermark 1963), and northeastern Kansas (Carruth 1877, Gates 1940, McGregor 1948). With the plowing and cultivation of the prairies, the plant quickly disappeared. On December 15, 1871, Mead wrote to H. N. Patterson, a naturalist and plant collector from neighboring Henderson County: "My Asclepias Meadii is reduced very low. If possible will send at some other time with other plants which you may want. It grows 10-15 inches high, on high, rolling prairies, or did years ago. I have seen it in Missouri, and it has been found near Davenport, Iowa, ... but perhaps the plough has destroyed it". On April 1, 1872, Mead wrote: "Asclepias Meadii. This I have not met with for several years and my duplicates are reduced low, as many of my rare plants". In July 1879, Mead wrote: "Asclepias Meadii. I tried years ago to cultivate it. Rev. Green . . . ought to protect and preserve the plant for cultivation". The only specimen remaining in Hancock County at present, is a framed specimen hanging in the College Museum (Kibbe 1952).

Now, over a century after Mead wrote these letters, the species is extinct throughout a large part of its original range. It is still found in some of the prairie preserves and hay meadows and along a few railroad rights-of-way in western Missouri (8 counties) and northeastern Kansas (12 counties). Very small populations are found in two or three places in Iowa (2 counties) and Illinois (2 counties). Intensive field searches have failed to rediscover this plant in Indiana and Wisconsin. In September 1988, the United States Fish and Wildlife Service officially listed it as a Federally threatened species (Harrison 1988).

METHODS

Field Studies

Using information obtained from herbarium specimens at the Field Museum of Natural History, Chicago, searches were made to locate Mead's milkweed plants in virgin prairies along railroad rights-of-way in western Missouri-northeastern Kansas and in prairie hay meadows. With practice, the inconspicuous yellow-green umbels growing just below the tops of the grasses could be spotted within a six to ten meter radius of an observer. Additional help in locating the plant on large hay meadows was provided by female monarch butterflies searching for plants on which to lay their eggs. Once a female detected a plant (probably by scent) she would fly in an excited manner in decreasing circles till she was directly over the plant before she dropped down to lay her eggs. A close inspection of the area would reveal the blooming plant.

Because of the incomplete data that would have been obtained from plants annually mowed in mid-growth, a thorough search of prairie hay meadows and mowed prairie preserves for the plant was not undertaken. The few plants in hay meadows that were studied were protected by surrounding them with piles of brush marked with red flags mounted on top of the piles. This was done with the consent of the owner and prevented inadvertent mowing.

Plants were marked with a 30 cm luminescent orange stake placed a few centimeters from each specimen. Careful measurements were then taken of distances to the nearest telephone pole, fence post, etc., so that they could be found again. In prairie hay meadows a Brunton pocket transit-compass mounted on a tripod was used to get azimuths on two or three different distance landmarks (telephone poles, tree trunks, corners of barns, chimneys, etc.) to fix the positions of plants so they could be relocated again for further studies and to collect pods.

During seven years of field observations (1965-1971), stems were checked annually for height, number of nodes, attached leaves, and flowers. This was done from late May into early June. The stems were checked for the presence of pods in early August. Any pods observed were later collected in early September. Subsequently, the total number of seeds produced by all pods and their percentage of germination were determined. In addition, insect pollinators and associates of Mead's milkweed were collected and recorded during all of these three observational periods.

Cultivation Studies

The seeds collected from ripe pods of Mead's milkweed were stored in a cool room during the winter months. At the end of February the seeds were placed on wet filter paper in petri plates and put in a refrigerator set at 5 C. After ten weeks of this cold moist treatment, the seeds were planted individually, using blunt tongs, into pots filled with soil that was one-third sand and two-thirds loam. A well-drained soil was necessary to prevent the damping off of the seedlings.

Germination usually occurred within two weeks. The seedlings were difficult to raise because of their soft stems and of the presence of buds which were subject to injury from sucking insects. In the greenhouse they were attacked by thrips which caused spotting of leaves by destroying the chlorophyll-bearing cells. Outside the greenhouse, aphids injured and caused distorting of the terminal buds and leaves. To prevent this extensive thrip and aphid damage, it was necessary to clean the young seedlings each day with a wet camel's hair brush.

After the first killing frost, the seedlings were placed in a cold room kept at 5 C for the winter. When allowed to winter outdoors they were subject to winter kills which caused considerable losses.

During the second growing season, the young plants were stronger and could stand erect unsupported, but they still had to be cleaned and freed of insect pests. By the beginning of the third growing season, the seedlings were mature enough to be transplanted in the early spring into a prairie being restored at the Morton Arboretum, Lisle, Illinois. To insure their survival, they were not allowed to dry out during the first two weeks after transplanting.

In addition, 14 plants were grown in pots from seed to flowering stage, a process requiring from five to seven years. These potted plants: 1) facilitated the study of the rootstocks without harming the plants to any great extent, 2) allowed blooming plants to be placed in areas having high densities of potential pollinators, and 3) made flowers more accessible in efforts to hand-pollinate them.

RESULTS

Morphology

While a large portion of Mead's milkweed stems represent single isolated rockstocks, some rootstocks produce multiple stems. Because of this, the unit of observation used in these results is the stem rather than the plant. The data collected were on approximately 100 plants, producing hundreds of both flowering and sterile stems, over a period of seven years.

Height.

The heights of 604 blooming Mead's milkweed stems observed varied from 31 to 92 cm. The average height was 56 cm. In general, the plants found in unmowed railroad prairies were markedly taller and more robust than those found in hay meadows and subjected to annual mowing.

Nodes.

Three to seven nodes occurred on flowering stems, with an average of six. Usually the lower nodes were devoid of leaves.

Leaves.

Leaves on a stem ranged in number from three to seven pairs, with an average of four pairs. The sagittate leaves were about 7.5 cm long and 3.3 cm wide, sessile, attached with a slightly upward slant and had a herringbone arrangement of the veins.

Roots.

The plant produced a white rootstock with a long fibrous emergent root penetrating downward into the soil. The rootstock may remain fixed in position for a few years; however, there was a tendency for it to shift in position. Thus, a plant may appear a short distance away from the place it was seen to grow the preceding year.

Umbel and flowers.

The stem produced a solitary, flat, disk-like umbel on an elongated peduncle. This peduncle had a characteristically hooked tip

that causes the umbel to nod downward. No other North American milkweed has this unusual characteristic. Unfortunately, this definitive feature has not been used in any of the taxonomic keys. Only 6.4% of the observed stems which flowered produced pods. Generally, one pod was produced per stem, but occasionally two were formed. The flowers were fragrant, and the corolla and lobes varied from green to yellow-green, turning to ivory in older flowers. The umbels had from 1 to 26 flowers, producing 12 on average (Table 1). Depending on latitude and weather conditions, blooming occurred in the period from the last week in May until the third or fourth week in June. The flowers lasted about five or six days.

Table 1. Umbel and flower production in Asclepias meadii (1965-1971).

Year	Stems observed	Stems with umbels	Total flowers	Average flowers/umbel			
	number						
1965	140	114	1520	13.3			
1966	131	106	1275	12.0			
1967	48	28	265	9.5			
1968	103	97	1176	12.1			
1969	127	92	1090	11.8			
1970	107	71	856	12.1			
1971	127	96	1082	11.3			
Total	783	604	7,264				
Average				12.0			

Pod and seed production.

The pod was long and narrow. It measured 11-12 cm in length and about 1.3 cm in diameter. The number of seeds per pod varied from 42 to 92, and had an average of 60 seeds per pod (Table 2). It took 100 to 110 days for the seeds to mature. If the flowers were pollinated during the first week of June, the pod was ripe by the second week of September.

Germination and Seedling Development

The viability of seed was relatively low; out of 2,429 seeds studied, only 1,156 germinated (47.6%) (Table 3). In germinating, the long petioles of the cotyledons appeared first above ground, followed by the emergence of the cotyledons themselves in a day or two. Within 48 hours after the appearance of the cotyledons, the epicotyl appeared above ground, which is unusual among members of the Asclepias, since more typically the epicotyl appears first, followed later by the cotyledons.

The seedlings were spindly and leaned over onto the ground and onto one another. The differed from mature plants in that they had linear leaves. If the terminal bud was injured, there was a tendency for the stem to produce a new shoot from an axillary bud. This was also true for mature plants. However, if the stem was cut off completely without leaving an axillary bud, the rootstock usually did not produce another stem that season.

Plant Associates

In remnant populations observed along railroad rights-of-ways and growing on deep silt loam soils, Mead's milkweed was found growing with approximately 60 species of prairie plants. Very common species of grass associated with the plant were prairie dropseed (Sporobolus heterolepis Gray), indiangrass [Sorghastrum nutans (L.) Nash], and big bluestem (Andropogon gerardii Vitman), growing in such abundance and age as to produce a comparatively low sward 60-90 cm high with few flowering culms. Prairie forbs commonly found with Mead's milkweed were white prairie clover [Petalostemum candidum (Willd.) Michx.], purple prairie clover [Petalostemum purpureum (Vent.) Rydb.], prairie gentian (Gentiana puberula Michx.), and prairie compass plant (Silphium laciniatum L.).

Table 2. Pod and seed production in Asclepias meadli (1965-1971).

Year	Total pods produced	Total seeds appearing viable	Total seeds appearing non-viable	Total seeds produced	Average pods/stem	Average seeds/pod
			num	iber	************	*********************
1965	16	949	44	993	0.14	62
1966	6	337	12	349	0.06	58
1967	1	10	45	55	0.04	55
1968	*****	V44AUV-				_
1969	4	204	43	247	0.04	62
1970	9	430	84	514	0.13	57
1971	4	233	38	271	0.04	68
Total	40	2,163	266	2,429		
Average					0.06	61

Table 3. Germination in Asclepias meadii (1965-1971).

Year	Total seeds produced	Total seeds germinating	Percent germination
	number		070
1965	993	487	49.1
1966	349	162	46.4
1967	55	26	47.3
1968			-Mount
1969	247	95	38.5
1970	514	249	48.4
1971	271	137	50.6
Total	2,429	1,166	
Average			47.6

Insect Associates

Plant feeders.

Relatively few insects were collected on Mead's milkweed. The milkweed bug (Oncopeltus fasciatus Dallus) and the lesser milkweed bug (Lygaeus kalmii Stal) were occasionally found feeding in or on pods and appeared to do little harm to the plants. The same is true of the monarch butterfly (Danaus plexippus L.) whose caterpillars were only rarely found feeding on the leaves.

More damaging, however, was the cerambycid milkweed beetle (Tetraopes femoratus LeConte) which was occasionally found chewing on the flowers. Its larva is a borer in stems and roots of Asclepias species, and the appearance of the adult on Mead's milkweed would seem to indicate that it is also a borer in it. The common milkweed beetle (Tetraopes tetraophthalamus Forster) was never found on Mead's milkweed even though it was commonly found on plants of the common milkweed (Asclepias syriaca L.), growing in disturbed areas near Mead's milkweed plants.

Potentially damaging were the milkweed weevils (Rhyssematus annectans Casey and Rhyssematus lineaticollis Say), whose adults girdled the peduncle of flowering stems and caused the umbel to collapse and fall downward. Although it was reported in the literature that their larvae were found in the pods of milkweeds (Smith 1899, Blatchley and Leng 1916, Leonard 1928, Kissinger 1964), these have never been seen on or in the pods of any of the 18 species of Asclepias studied over a period of 25 years. However, the adults of Rhyssematus lineaticollis were seen emerging after dark from holes in the ground adjacent to the stems of Asclepias

plants. Like the milkweed beetle, the milkweed weevil larvae feeding on the roots of Mead's milkweed plants presumably could seriously injure and possible kill them.

Pollinators.

Few potential insect pollinators were observed on Mead's milkweed. However, two bumble bee queens were collected on it. The one queen, Bombus affinis Gresson, carried two pairs of pollinia on its right-front leg. The other, Bombus griseocollis (Degeer), had a pair of pollinia on the right-hind leg. In addition, two males and three female digger bees (Anthophora raui Rohwer) also were collected. Of these, one male had a pair of pollinia on its rightmiddle leg and a pair on its proboscis, and one female had a pair of pollinia on its right-front leg. It should be noted that the insects were still carrying intact pairs of pollinia. Thus, neither the Bombus queens nor the Anthophora bees had transferred pollinia to any stigmatic chambers. Nevertheless, it is possible that the Anthophora bees could be one of the most important pollinators of the species because of the larger populations of these bees found to be present at the time the plants are in flower. This is in contrast to the rather low populations of Bombus occurring at that time.

DISCUSSION

Mead's milkweed is a slow growing plant and requires at least four or more years after seed germination to reach flowering stage. Once established in a prairie, it can live for decades. Plants that were raised from seed in 1966 and planted in the restored prairie at the Morton Arboretum are still healthy and producing flowers in 1988. The same is true for fully mature plants first observed in 1965 on railroad prairies in western Missouri and northeastern Kansas.

Most rootstocks produced one stem, but others produced multiple stems, both flowering and sterile. Some formed clusters or clones with a flowering stem surrounded by a half-dozen sterile stems varying in size from those that equaled a flowering stem down to some that resembled two-year-old seedlings. A more uncommon clone was one in which three or four stems, both flowering and sterile, would be aligned in a row and separated from each other by a few centimeters. It would appear that these clones or small colonies were derived from the same rootstock.

In some cases stems suddenly wilted and died back in the middle of the growing season (12.5% in plants observed in 1965). In other instances, rootstocks produced flowering stems for a number of years and then stopped producing stems for a year or two before stems became evident again. During the years that stems were not readily seen where plants had previously been observed, a close examination usually disclosed a single small seedling-like stem or a few small stems. In both instances, it would appear that the

plants were being or had been attacked by borers (Tetraopes or Physemmatus) and had been stunted. If over a period of a few years a stem did not appear again, it was presumed that the rootstock was dead.

Pod production in Mead's milkweed was extremely low, and the pods contained relatively large numbers of aborted seed (11.1%). The germination of seed was also comparatively low (47.6%). This low production both of pods and viable seed would appear to be due in part to: 1) the low populations of insect pollinators, 2) the low populations of Mead's milkweed available to attract potential pollinators and thus enhance cross-pollination which is necessary to set viable seed (Woodson 1947), and 3) the incompatibility between the closely related plants found within the isolated clones and colonies.

In pre-settlement prairies, Mead's milkweed presumably had healthy reproducing populations with many plants producing pods. Since the species lived in a relatively stable plant community and was long-lived, it could produce small numbers of flowers and pods with relatively few seeds and still survive. During pre-settlement times, there were large numbers of pollinating bees on the virgin prairies utilizing a large diversity of prairie forbs blooming in a continuous spectrum throughout the growing season. This assured that Mead's milkweed flowers had adequate numbers of pollinators available to them. The occasional loss of individual plants to borers and other disease organisms would easily be offset by the production of new seedlings from seeds which were continually being produced.

However, with the coming of the settlers all of this changed. The populations of Mead's milkweed on the silt-loam prairies of Illinois, Iowa, and northern Missouri were plowed under along with the rest of the other prairie plants. The populations of the plant in western Missouri and northeastern Kansas fared much better since they were growing on poorer soils which were never immediately cultivated. Some of these were eventually turned into hay meadows. Mead's milkweed plants, still found in these hay meadows and in the prairie preserves derived from hay meadows probably represent survivors of larger populations originally found on those areas of the prairie which became hay meadows over a century ago. Annual mowing has prevented these plants surviving in the hay meadows from reproducing and maturing seed. Inasmuch as prairies originally surrounding the hay meadows were destroyed by plowing, no new seeds of Mead's milkweed are now available from the outside to increase their numbers within these old hay meadow populations. With a continuing loss of individual plants to borers, disease organisms and mowing stress, it is probable that the populations in the hay meadows will continue to decline and eventually become extinct.

Even unmowed railroad prairies have declining populations of Mead's milkweed because of constant herbicide application, shading of encroaching woody plants which are spreading due to lack of fires and digging and trenching done in laying television and telephone cables. The laying of cable along the Missouri Pacific Railroad west of Sedalia, Missouri, in the early 1980s resulted in the destruction of more than 70 Mead's milkweed plants growing in prairies along that right-of-way.

Because of the slow continuing destruction of the hay meadows by plowing and of the elimination of the railroad prairies by spraying, shading, and trenching, Mead's milkweed eventually will survive mainly in prairie preserves. In order to enhance survival of this plant in these sanctuaries, it is imperative to manage the prairie preserves so that they can be returned as closely as possible to their pre-settlement condition. This means the discontinuance of mowing as a management tool. Mowing stresses the plants, not only by preventing the production of ripened pods, but also by weakening them through shortening their growing season. The low level of food reserves in plants that have been mowed the previous season is reflected in the reduced viable seed production the following season. Even seeds which do germinate often produce seedlings that are weak and fail to survive. Mowing probably also has a detrimental effect on populations of potential pollinators.

Along with the cessation of mowing, prescribed burns should be a part of management of the preserves in order to envigorate the growth and reproduction of Mead's milkweed.

To increase the genetic variability of the present small populations in these preserves, both seeds and seedlings should be introduced from neighboring preserves. In addition, seedlings derived from plants growing in the northern remnant prairies (Illinois and Iowa) should be grown in greenhouses for reintroducing Mead's milkweed into prairie preserves in Iowa, Illinois, Indiana, southern Wisconsin, and northern Missouri where this species has been eliminated.

However, cultivating and establishing Mead's milkweed in preserves is a difficult task. More than 800 two-year old seedlings were grown and transplanted into a restored prairie (600 seedlings). a virgin sandy-loam prairie (50 seedlings) and an old settler cemetery without prairie vegetation but having a deep prairie soil (150 seedlings). Only 2 plants were ever established. A major reason for this failure may have been genetic; the plants were grown from seed collected in western Missouri-northeastern Kansas and may not have had the ability to withstand the winter conditions of northern Illinois. For that reason, the remnant populations in Iowa and Illinois are very important in being reservoirs of an ecotype(s) adapted to a more northerly climatic regimen which could be very important in the re-establishment of Mead's milkweed in the northern prairie preserves. If these measures are undertaken, there is reason to believe that Mead's milkweed could again become a self-sustaining member of the tallgrass prairie ecosystem and remain so for centuries to come.

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