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THE DISTRIBUTION AND REPRODUCTIVE PHENOLOGY OF THE MILKWEEDS

(ASCLEPIADACEAE: *ASCLEPIAS* AND *CYNANCHUM*) IN NEBRASKA

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The Asclepiadaceae are represented in Nebraska by seventeen native species of *Asclepias* and one of *Cynanchum*. Two species are here added to the State's flora: *Asclepias asperula* and *A. purpurascens*. Detailed county distribution maps are presented for all species based upon our extensive field and herbarium work, and numerous additions and corrections are made to the maps published in the *Atlas of the Flora of the Great Plains* in 1977. A map is presented showing the zone of hybridization of *A. speciosa* with *A. syriaca* in central Nebraska. Data are given on flowering and fruiting phenology for each species, and floral odors are described.

† † †

Seventeen of the 108 North American species of *Asclepias* occur in Nebraska, as does one of *Cynanchum*. Distribution maps of Nebraska's species were published in the *Atlas of the Flora of the Great Plains* (Great Plains Flora Association, 1977), and here we present numerous additions and corrections to those maps based upon our field and herbarium work since the *Atlas* was published. We also present information about floral fragrances as well as flowering and fruiting phenology in Nebraska.

MATERIALS AND METHODS

In our field work in Nebraska from 1985 through 1991 we made special efforts to supplement and correct distributional records for Nebraska as they appeared in the *Atlas*, some of which we knew were incomplete or incorrect. We also collected fruiting specimens because they are poorly represented in herbaria, and we recorded floral fragrances because they are seldom mentioned in the extensive taxonomic and ecological literature about the milk-

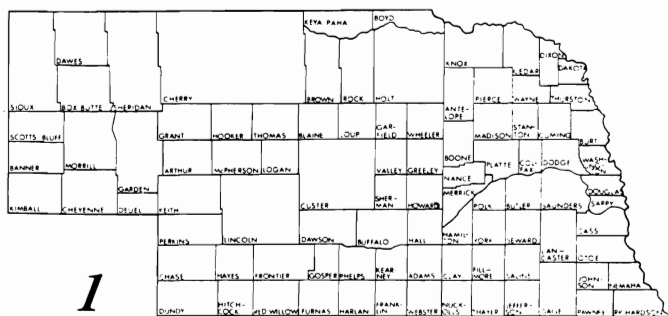
weeds. Voucher specimens from our collections are deposited in the Bessey Herbarium of the University of Nebraska–Lincoln (NEB).

We recorded distributional and phenological data in the field and from all Nebraska specimens in these herbaria (official herbarium acronyms of the International Association for Plant Taxonomy (Holmgren et al., 1981) are given where applicable): Cedar Point Biological Station in Keith County, Nebraska; Chadron State College (CSCN), Chadron, Nebraska; Doane College, Crete, Nebraska; Kansas State University (KSC), Manhattan; University of Kansas (KANU), Lawrence; University of Nebraska at Kearney; University of Nebraska–Lincoln (NEB); University of Nebraska at Omaha (OMA); and our personal collections. We also sought specimens of some species in the collection of the Missouri Botanical Garden (MO), St. Louis. We follow the nomenclature of Woodson's extensive monograph of North American *Asclepias* s.l. (Woodson, 1954a), which is also that used in the *Flora of the Great Plains* (Great Plains Flora Association, 1986), although we find acceptable the earlier recognition of *Acerates*, *Asclepias* s.s., and *Asclepiodora*. Those publications provide keys and detailed descriptions of the vegetative and floral morphology of our species. Synonyms are given for the following books that covered all or part of Nebraska: Peterson (1923), Rydberg (1932), Winter (1936), and Fernald (1950).

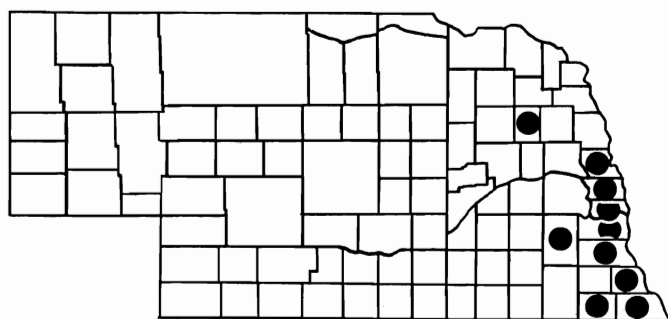
We scored each of the 1,157 herbarium specimens and our numerous field observations for one of six phenological categories: only buds present, buds and flowers present, only flowers present, only withered flowers present, immature fruits present,

and mature fruits present. Where a specimen had more than one of these stages, it was scored according to the most advanced stage present, e.g., a plant with flowers and immature fruits was scored as having immature fruits. We entered the data into a computer database and variously sorted it according to species, phenological status, county distribution, and regional distribution in Nebraska.

Our maps show with large black symbols (dots, diamonds) all the counties (which are named in Fig. 1) for which we have seen or collected voucher specimens; for most species, we have added numerous new records. Open circles on some maps show county records published in the *Atlas* that we reject for reasons given in the text. Records shown in the *Atlas* that we accept but for which we have not seen vouchers are indicated with a smaller black dot.



1



2 *Cynanchum laeve*

Figure 1, 2: 1. Map of Nebraska with counties named. 2. County distribution of *Cynanchum laeve*.

OBSERVATIONS

Cynanchum laeve (Michaux) Persoon, sandvine, honeyvine, climbing milkweed
Ampelamus albidus (Nuttall) Britton; *Gonolobus laevis* Michaux

The climbing habit is common in the Asclepiadaceae, but this is the only Nebraska species that climbs. The *Atlas* showed it to be in all six Missouri-riverside counties from Washington County southward; it was reported (Woodson, 1954a) and verified (Sutherland and Kaul, 1986) from Lancaster County, and we found it in Pawnee County (Fig. 2). We suspect it to be in Jefferson and Gage counties because it is known from adjacent counties in Kansas, but we have not yet found it there.

The plant is more common in cities than in the countryside. It is often seen twining on wire fences and clambering over shrubs and garden plants in Omaha, Bellevue, Plattsmouth, Nebraska City, and Lincoln. The large green follicles are prominent in fall and become tan and persist into winter, when they are especially obvious. The plant is a moderately troublesome weed, especially when it blankets ornamental shrubs and covers fences, and it occasionally rivals bindweed as a pest in crop fields in the Missouri River floodplain of our eastern counties. In Missouri, Steyermark (1967: 1210) noted that "... where it infests fields, it interferes with crop yields and is considered a more vicious pest than bindweed [*Convolvulus arvensis* L., another latex-bearing vine in a family close to Asclepiadaceae], and more difficult to get rid of."

The oldest Nebraska specimen we have seen was gathered in Richardson County in 1897, and only two specimens were gathered from then until 1972: Nemaha County in 1910 and Cass County in 1931. We are convinced that the species is native at least in Nebraska's Missouri-riverside counties.

Our field and herbarium observations show flowering from July 9 into October (Fig. 19). The flowers have a moderately strong but rather unpleasant sweet odor. Full-sized fruits are present after September 24, and dehiscence occurs in fall and winter; some follicles remain closed until the following March (Fig. 19).

Asclepias amplexicaulis Small, clasping-leaved or blunt-leaved milkweed

Collected from only four counties (Fig. 3): Cass (collected once), Cuming (once), Dodge (three

times), Sarpy (once); probably is (or was) in Gage, Johnson, Nemaha, Pawnee, and Richardson counties, judging from the distribution of the species nearby in Kansas (see *Atlas*), but we have not found it in those counties. Our oldest specimen is from Douglas County in 1904; most of our collections are from the 1970s and 1980s. Scattered individuals of this uncommon species occur in virgin prairies and other relatively undisturbed open places. Some of our specimens are from heavy loess soils and some are from sandy soil, which is often cited as the preferred substrate elsewhere, but the species is not in the Nebraska Sandhills. Flowering dates of the Nebraska specimens are June 1–17, and mature fruits are present by mid-July (Fig. 19).

***Asclepias arenaria* Torrey, sand milkweed**

Known from 50 counties (Fig. 4), 29 of which are new records from our field work since the *Atlas* was published in 1977. The *Atlas* record for Cheyenne County was based upon a 1924 specimen in NEB collected from Camp Clarke, which was near Bridgeport in what is now Morrill County but was then part of Cheyenne County. Restricted to deep, loose sand; abundant in the Sandhills, less so elsewhere but sometimes locally common in dry sand in river valleys and road cuts. Our oldest specimen was collected in Brown County in 1887.

Flowering in Nebraska is June 23–August 3, and full-sized fruits have been collected August 14–October 1 (Fig. 19). The plants are often prostrate or nearly so, especially at flowering time, but commonly become at least semi-erect as the fruits mature, although many plants are fruitless. The umbels of greenish flowers are thus on or near the ground and pollination is possibly effected by ground-dwelling insects or by the large black wasps that commonly visit the flowers, which have a moderately strong, slightly sweet but quite unpleasant chemical odor reminiscent of a pig-sty.

***Asclepias asperula* (Dcne.) Woodson var. *decumbens* (Nutt.) Shinnars, antelope horn, spider milkweed**

Asclepiodora decumbens (Nutt.) A. Gray

We have seen only one Nebraska specimen (*Churchill 5404*, Nuckolls County, May 25, 1975, NEB) of this species (Fig. 3), which is rather common from the Kansas-Nebraska border south to Texas (*Atlas*). The specimen was in the late bud stage. The species probably occurs in Franklin and Webster counties as well, judging from the distribu-

tion in adjacent Jewell and Smith counties in Kansas, as shown in the *Atlas*, but we have not found it there.

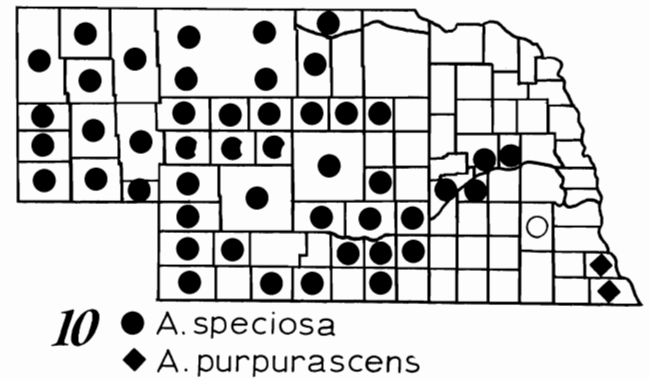
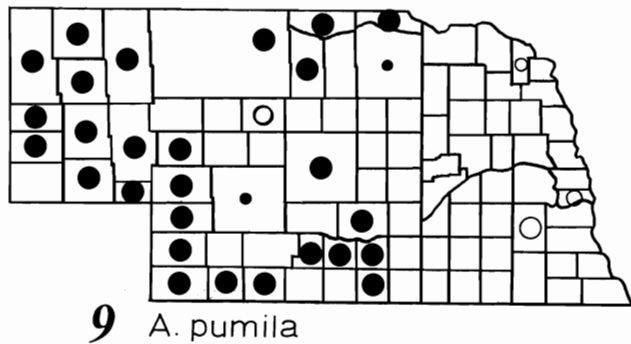
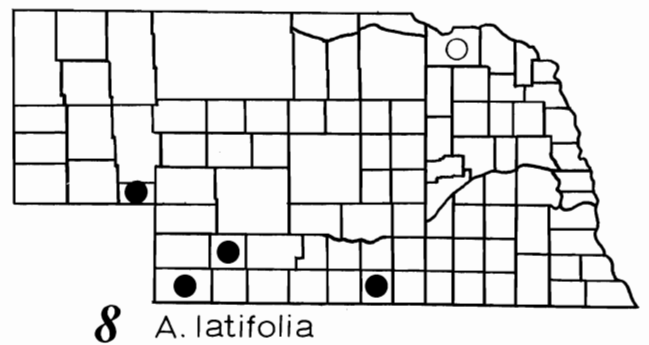
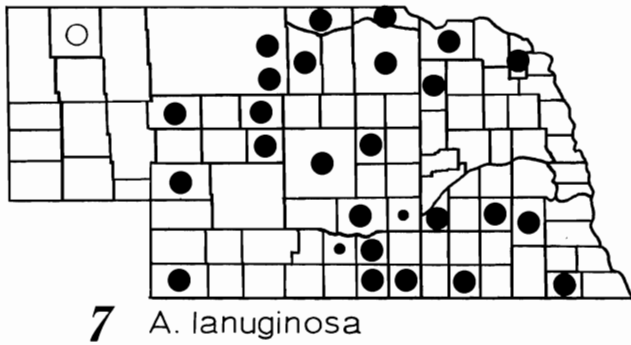
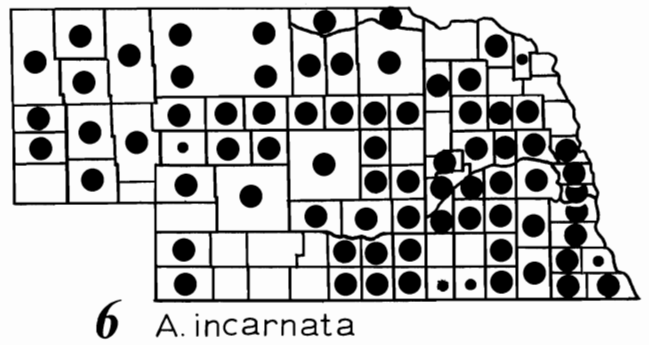
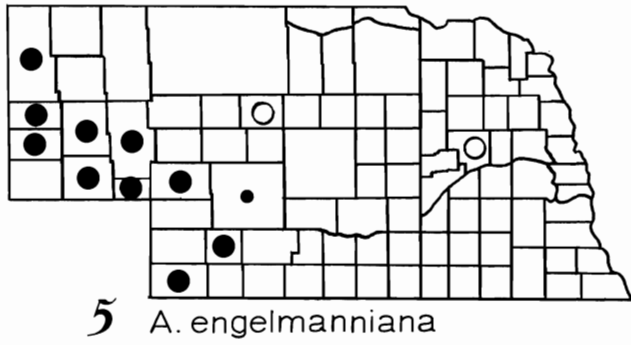
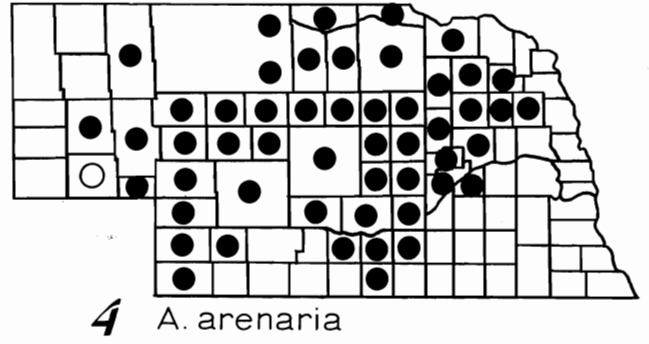
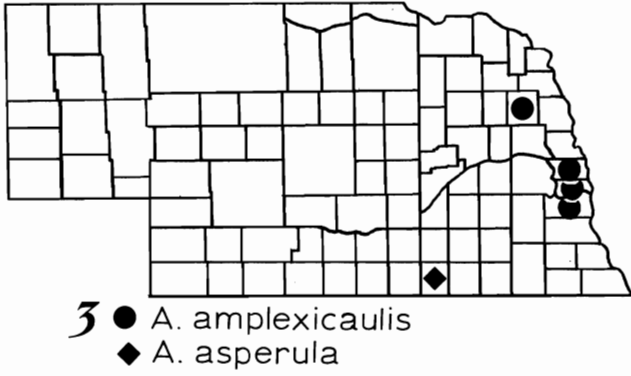
This species resembles *A. viridis*, which is sympatric in the western part of the latter's range in Nebraska and Kansas. Woodson (1954a), however, found no evidence of hybridization between them elsewhere.

***Asclepias engelmanniana* Woodson, narrow-leaved milkweed**

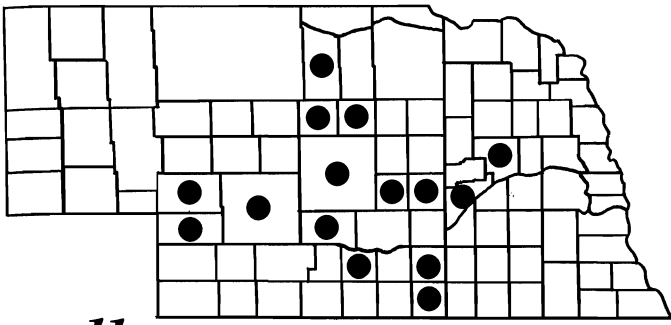
Acerates auriculata Engelm.; *Asclepias auriculata* (Engelm.) Holzinger; *Acerates floridana* (Lam.) A.S. Hitchc., misapplied in Peterson (1923)

We have seen or collected specimens of this species from ten counties in Panhandle and southwestern counties (Fig. 5), six more than shown in the *Atlas*. Woodson (1954a) listed it for Lincoln County, a likely locale, and we accept that record although we have not seen a voucher. Although it probably once occurred in Chase and Perkins counties, we have not found it there and we suspect it to be extirpated by the extensive agrarian activities in those counties. A record was shown in the *Atlas* for Thomas County, based upon a correctly-identified specimen in NEB (*Pool & Williams s.n.*, 1911) that Woodson listed, but we reject it because the specimen is part of a collection of dubious provenance, the species is unknown in other Sandhills counties, and Thomas County probably lacks suitable habitat for it. Woodson (1954a: 184) cited it for Platte County, which is far removed from the main range of the species. We cannot trace the source of Woodson's attribution because neither our surveyed herbaria nor the Missouri Botanical Garden (MO), where he worked, have a voucher from Platte County; we have not seen the species there and we doubt its presence. However, Novacek et al. (1985) reported it even farther east—from Harrison and Pottawattamie counties, Iowa, across the Missouri River from Nebraska.

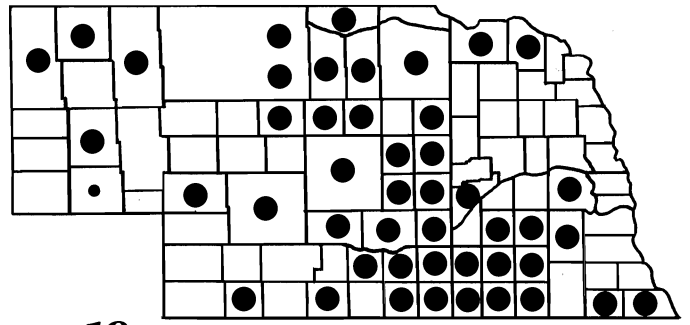
Our oldest specimens are from Garden County in 1890 and Dundy County in 1893; collectively, our surveyed herbaria have only about a dozen specimens. However, our field experience shows that the species is much more common than these meager collections suggest, but individuals are scattered and rather easy to overlook, although they are often very tall (to 1.5 m). They are found on sandy, rocky slopes and sandy, level uplands, but the species is unknown from the deep, loose sand of the Sandhills.



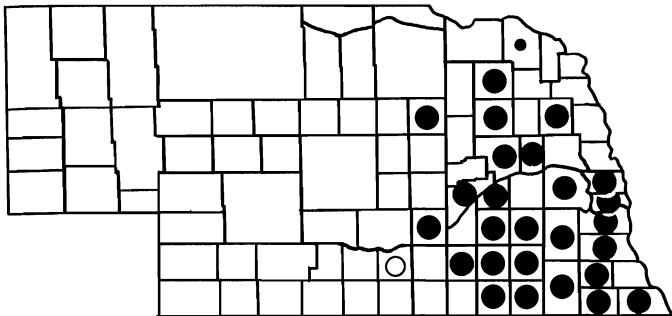
Figures 3–18. Distribution by county of all Nebraska *Asclepias*. Large black dots and diamonds indicate that we have collected or seen at least one herbarium specimen from that county. Small black dots indicate records shown in the Atlas that we accept, but we have not seen voucher specimens. Open circles indicate records published in the Atlas that we reject for reasons given in the text.



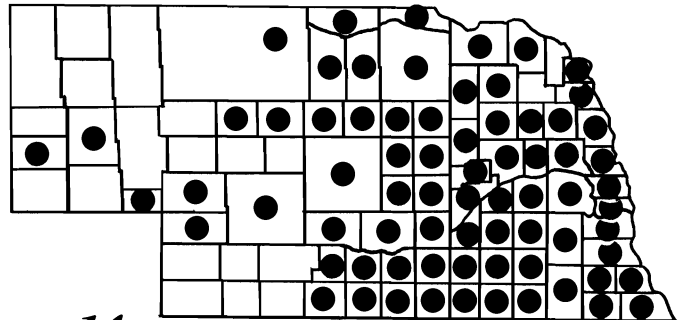
11 *A. speciosa* X *A. syriaca*



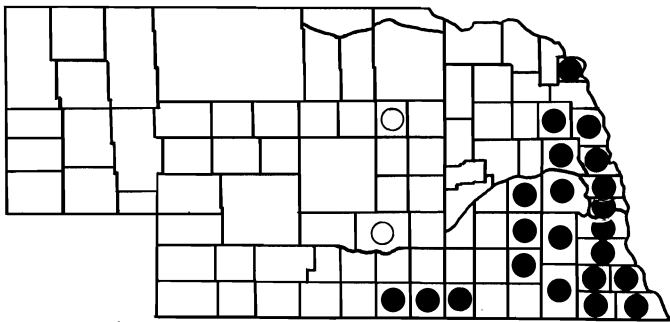
12 *A. stenophylla*



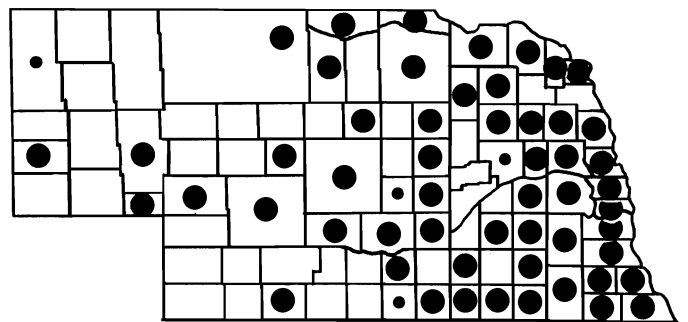
13 *A. sullivantii*



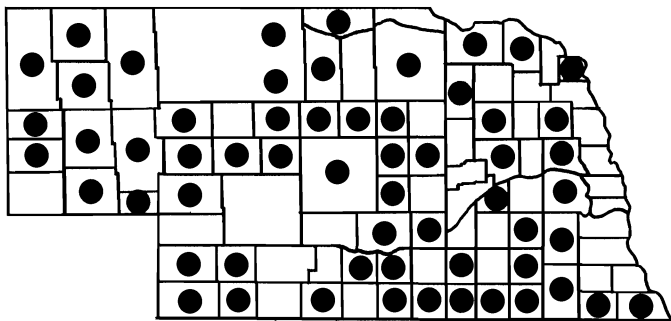
14 *A. syriaca*



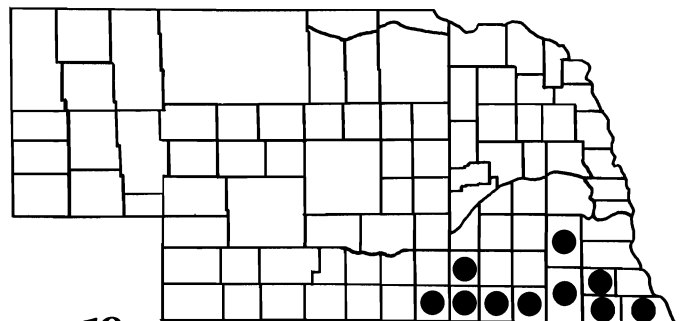
15 *A. tuberosa*



16 *A. verticillata*



17 *A. viridiflora*



18 *A. viridis*

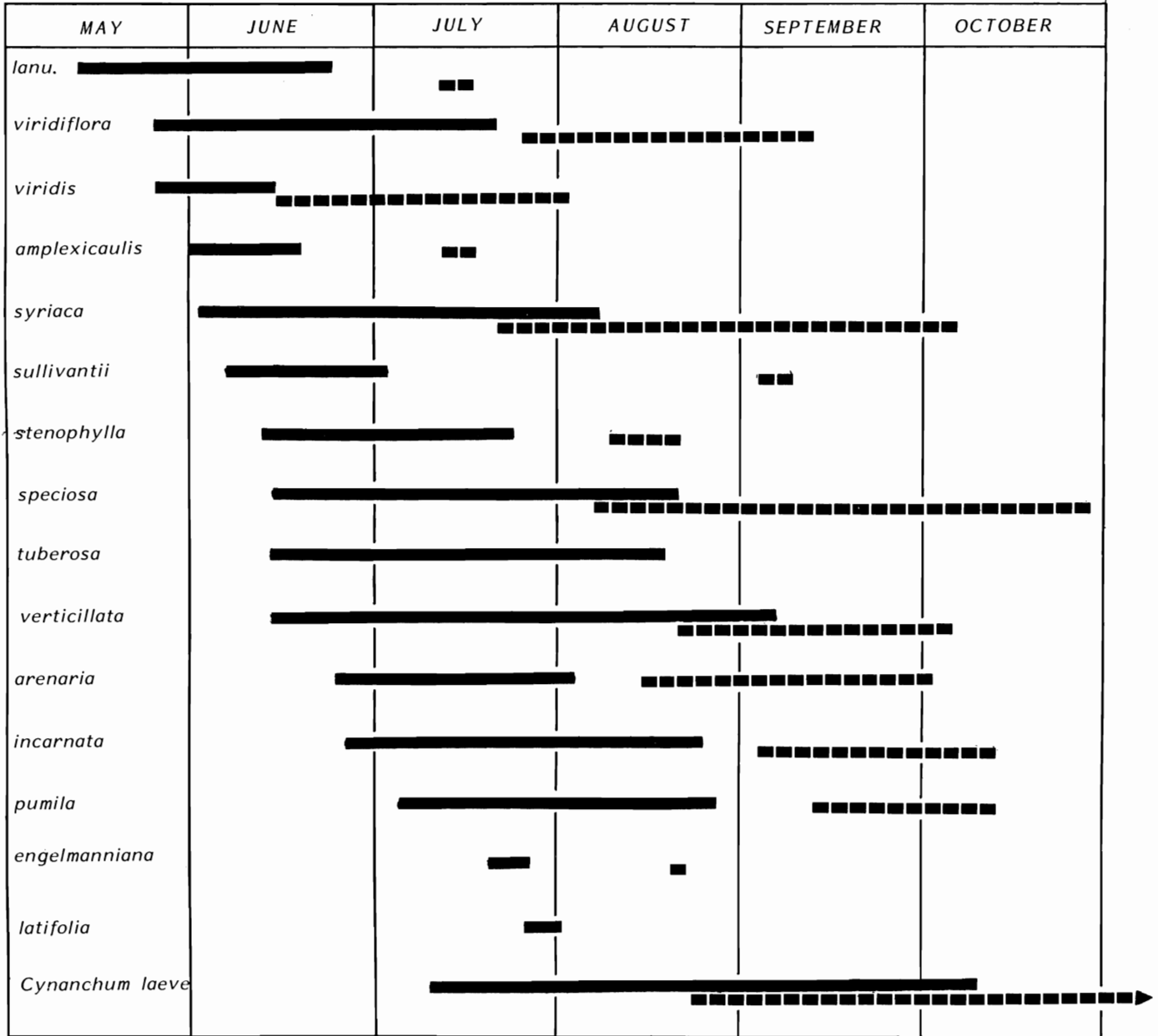


Figure 19. Flowering and fruiting phenology of fifteen species of *Asclepias* and one of *Cynanchum* in Nebraska, as determined from field work and herbarium specimens, all years combined. Flowering data (solid lines) are very complete for all species except *A. engelmanniana* and *A. latifolia*, which are poorly collected but common in their range. Data on fruiting (dashed lines) are sketchy for most species because fruits are seldom collected. Full-sized but immature fruits are usually present for long periods, with maturity and dehiscence occurring later in the season. Two milkweeds, *A. asperula* and *A. purpurascens* are each represented in Nebraska by only a single voucher specimen and thus their phenology cannot be plotted.

Our specimens show that flowering in Nebraska is July 18–24, with buds visible as early as July 7 and withering flowers present until August 3 (Fig. 19). The flowers have a rather strong odor of lilac and cinnamon. Our few fruiting specimens were collected in late August.

***Asclepias incarnata* Linnaeus subspecies *incarnata*, swamp milkweed**

We have records of this common plant from most counties in Nebraska (Fig. 6), although we cannot find it in six southwestern counties despite intensive searching. Our oldest specimens are

from Lancaster County (1873), Brown and Polk counties (1878), Brown and Sarpy counties (1887), Cherry County (1889) and Cherry, Dixon, Douglas, Dundy, Garden, and Lancaster counties in the 1890s. The species is our only milkweed of wet soils and sometimes grows at the water's edge.

The specimens we saw indicate flowering in Nebraska from June 24 to August 24, with withered flowers present until September 7 (Fig. 19). We have not detected a floral fragrance, but Brotherton (1984) noted "a flat sugary fragrance...infrequently." Full-sized fruits have been collected in Nebraska from September 3 to October 10 (Fig. 19), and dehiscence is mostly in October.

Although the reproductive biology of many milkweed species has been studied elsewhere, only that of *A. incarnata* has been researched in detail in Nebraska. Brotherton (1984) studied populations in Douglas and Sarpy counties, Nebraska, and in nearby Harrison County, Iowa. He found some evidence of self-fertility and autogamy in bagged inflorescences, but the plants were mostly outcrossing. He analyzed the insect visitors and found five orders and 25 families represented. Beetles and the larvae of monarch butterflies (*Danaus plexippus* L.) damaged the leaves, and a sphinx moth (*Hyles lineata* (Fabricius)) and the painted-lady butterfly (*Vanessa cardui* L.) were nectar thieves. The most abundant pollinators were hymenopterans, including the introduced honeybee, *Apis mellifera* L.; the bumblebees *Pyrobombus griseocollis* (DeGeer) in early summer and *Megabombus pennsylvanicus* (DeGeer) later in summer; and some solitary wasps, especially *Sphex ichneumoneus* L., the great golden digger wasp. Lepidopteran pollinators were less important: the tiger swallowtail (*Papilio glaucus* L.), the silver-spotted skipper (*Epargyreus clarus* (Cromer)), and occasionally the monarch butterfly.

Asclepias lanuginosa Nuttall, woolly milkweed
Acerates lanuginosa (Nutt.) Dcne. Woodson (1954a) used *Asclepias nuttalliana* Torr. but corrected that (1954b) to *A. lanuginosa* Nutt., which has priority; the species he (1954a) called *A. lanuginosa* HBK is *A. otarioides* Fourn. (Woodson, 1954b), which does not occur in Nebraska.

Our surveyed herbaria show this uncommon plant to be in 24 counties (Fig. 7), but probably it is in many more. The *Atlas* shows it for Dawes County, but none of our surveyed herbaria has a specimen from that part of the State, including the herbarium (CSCN) in Dawes County, and Woodson (1954a) did not cite it from there, and so we reject that record. The species is unknown in most Missouri-riverside

counties in Iowa (except for Woodbury County: Woodson, 1954a; Nicolson and Russell, 1955) or Nebraska (except Dixon and Knox counties).

Our oldest specimen is from Lancaster County, 1890; we have seen specimens from Dixon and Thomas counties in 1893, from Buffalo County in 1898, Holt County in 1899, Custer County in 1902, and Valley County in 1910, but the next specimens were not collected until 1947. *Asclepias lanuginosa* occurs as scattered individuals in dry, often sandy prairies but is found on loess and glacial till too, and it is known from the loose, fine sand of the Sandhills. The specimens we saw show that flowering in Nebraska is from May 10 to June 26, and withered flowers are present until July 14, when immature fruits are present (Fig. 19). The flowers are odorless. Our few fruiting specimens were collected in July (Fig. 19).

Asclepias latifolia Rafinesque, broad-leaved milkweed

We have seen or gathered specimens from Deuel, Dundy, Hayes, and Franklin counties, all in southwestern Nebraska (Fig. 8), where we have found it to be locally abundant. It doubtless occurs in other counties in the southern tier. A station for Knox County was published by Woodson (1954a) and incorporated into the *Atlas*, but we have neither collected nor seen specimens from that county, and there are none at the Missouri Botanical Garden (MO), where Woodson worked, and so we reject that record, which is well beyond the range of the species.

Flowering in Nebraska is from July 25 to August 1 according to our field observations and the few specimens we found in herbaria (Fig. 19); specimens from Kansas show flowering from July 18 to August 16, a span probably typical for the species in Nebraska. The floral fragrance of rather strong cinnamon and lilac resembles that of *A. speciosa*, which sometimes grows with it, and of *A. engelmanniana*, which often grows nearby. We have seen no fruiting specimens in the field or herbaria.

Asclepias pumila (A. Gray) Vail, dwarf milkweed

We have seen specimens from 27 counties, all west of 98°W longitude (Fig. 9), and we accept the *Atlas* records for Custer, Holt, and Kearney counties, which were based upon Woodson (1954a). The dwarf milkweed is locally common in dry, sometimes hard soils, but it is known from the Sandhills in Arthur and Brown counties; we do not accept a specimen in NEB (*Pool, s.n.*, 1912) supposedly from

Thomas County in the Sandhills because it is part of a large collection of dubious provenance. The record in the *Atlas* for Sarpy County, far east of the main range of the species, is based upon a specimen in NEB collected in 1873 that is part of another collection of dubious origin; the species has not been collected there (an intensively-collected and quite unlikely county for this species) again and so we reject that record too. The *Atlas*, following Woodson (1954a), showed it for Lancaster County, another unlikely station, but we have not seen the species there despite intensive collecting, or can we find a voucher specimen; thus we reject that record. The *Atlas* record for Dixon County was based upon a specimen in NEB from Boyd County whose label was originally misinterpreted.

Our oldest specimens are from Cheyenne County in 1880 and Box Butte and Garden counties in 1890, and the species has been collected irregularly since then, with few specimens gathered between the 1910s and the 1960s. Flowering in Nebraska is from July 5 to August 28 (Fig. 19), and the floral fragrance is sweet and light. Full-sized fruits have been collected between August 14 and October 17; dehiscence is in late September and October.

***Asclepias purpurascens* Linnaeus, purple milkweed**

This species is known in Nebraska only from Richardson and Nemaha counties (Fig. 10), where we collected the first Nebraska specimens in 1989 and 1990. Wyatt and Hunt (1991) found evidence that it hybridizes with *A. syriaca* in Virginia, raising the possibility that such hybrids might be found in Nebraska where the two species are sympatric.

***Asclepias speciosa* Torrey, showy milkweed**

We have seen specimens of this locally common species from most counties west of 98°W (Fig. 10), and undoubtedly it occurs in all such counties. Its range extends eastward in the low, sandy soils of the Platte Valley to Colfax County. The *Atlas* shows it to be in Lancaster County, but we do not accept that record, which is based upon a single specimen of dubious identity, because the species has not been seen or collected there or in nearby counties again, despite intensive field work; furthermore, those counties lack the sandy soils favored by the species.

Asclepias speciosa grows mostly in low places such as floodplains and roadside ditches in somewhat to very sandy soils; in the deep, loose sand of the Sandhills it is most abundant in the interdunal

sands. It is very common in the Panhandle counties and is almost always in sight along the roadways. It is sometimes rather weedy, invading cropland and other disturbed soils, and it also thrives in sod of smooth brome. The plants are solitary or in loose colonies or, especially in the Panhandle counties, form rather tight clumps of stiffly erect stems.

The oldest specimens we saw are from Garden, Keith, and Sheridan counties in 1884 and Phelps County in 1890. Flowering in Nebraska is from June 10 to August 19 (Fig. 19). However, our extensive observations in the field show that most flowering is over by August 1, and some full-sized but unripened fruits are present then. Roadside plants that have been mowed usually re-sprout and re-bloom into August, the flowering season thus being artificially extended. Plants in fertile, irrigated soils near croplands also produce flowers well into August, and they grow very tall (to 2 m) in those conditions. The strong floral fragrance is rather like lilac, but sweeter and much heavier. Flower color varies from intense dark pink to pale rose and occasionally to white. Fruiting specimens have been collected in Nebraska between August 4 and October 28 (Fig. 19), and dehiscence is mostly in September and October.

This species hybridizes with *A. syriaca* in Nebraska (see below). Both species are being grown commercially in several counties scattered across the State, and the coma of the harvested seeds is used as an insulator in bedding.

Asclepias speciosa* X *A. syriaca

We have seen or collected specimens of this hybrid from 15 counties (Fig. 11), where it is fairly common. It probably occurs wherever the parental species are sympatric. We have found the parental species and nearly every possible intermediate in floral structure in some sites (e.g., in Kearney, Lincoln, and Perkins counties), and we presume introgression is occurring. The hybrid is known in Kansas, the Dakotas, and western Minnesota—all areas of sympatry of the parental species. Stevens synthesized it in North Dakota (Woodson, 1954a).

Adams, Tomb, and Price (1987) used chemical data from alkanes, fatty acids, and triterpenoids that showed hybridization and backcrossing between the two species in Kansas and Nebraska. Their data from isozymes showed the parental species to be almost identical. Although the species usually show some differences in soil preferences, those authors suggested further work to outline in-

traspecific variation before definitive statements are made about whether *A. speciosa* and *A. syriaca* should be retained as species or treated as subspecies of a single species.

Asclepias stenophylla A. Gray, narrow-leaved milkweed

Acerates angustifolia (Nutt.) Dcne.

We have seen specimens from many counties across the State, but the species is apparently absent from most Missouri-riverside counties of easternmost Nebraska (Fig. 12). However, Novacek et al. (1985) reported it from Plymouth County, Iowa, across the Missouri River from Dakota County, Nebraska, and Roosa et al. (1991) reported it from Sioux and Guthrie counties, Iowa.

The species is sometimes rather common as scattered individuals in remnant virgin prairies. A few specimens are from the soft sand of the Sandhills, but the species is not common there. Our oldest specimens are from Clay County in 1885, Cherry County in 1889, and Kearney, Lancaster, and Sheridan counties in the 1890s; few were gathered from the 1910s through the 1940s, but many were gathered in the 1970s and 1980s.

Flowering in Nebraska is from June 10 to July 20 (Fig. 19), according to our field notes and specimens in the herbaria we surveyed. We cannot detect a floral odor. The few fruiting specimens collected in Nebraska were gathered between August 10 and August 20 (Fig. 19), but dehiscence is probably much later than that.

Asclepias sullivantii Engelm. ex A. Gray, smooth milkweed

Known from most counties in southeastern Nebraska and from Colfax, Cuming, Merrick, Pierce, Platte, and Wheeler counties north of the Platte River (Fig. 13). It probably occurs (or once occurred) in most counties east of 98°W longitude, but we have been unable to find it now in some of those counties, and there are no earlier collections from them. It is a plant mostly of low, moist (but not permanently saturated) prairies and it grows on floodplains and in level roadside ditches, sometimes with *A. syriaca* and *A. verticillata*, but not in sandy soils. We seldom find it on slopes, and then only in southern-tier counties. It is locally common, e.g., between U.S. Highway 6 and the parallel railroad from Ashland (Saunders County) west to Fairmont (Fillmore County), where it suddenly disappears; along Nebraska Highway 4 in Jefferson County;

and in several low meadows bordering the Platte River. The species was no doubt once more abundant because so many of the low prairies it favors have been converted to cropland and pastureland. It seems to be relatively intolerant of disturbance. We reject the *Atlas* record for Kearney County because we have not seen a voucher in our surveyed herbaria, including the herbarium in adjacent Buffalo County; a recently-published floristic list (Nagel and Kolstad, 1987) for the Platte River meadows adjacent to Kearney County—prime habitat for the species—does not include it; and Woodson (1954a) does not attribute it to that county.

Our oldest specimens were gathered from Lancaster County in 1887 and Sarpy County in 1891; we have seen no specimens collected between 1911 and 1944, and most were obtained in the 1960s–1980s.

Asclepias sullivantii has been collected flowering in Nebraska between June 8 and July 2 (Fig. 19), but withered flowers have been collected as late as August 10. The floral odor is faint and slightly sweet. Specimens with full-sized fruits have been collected August 2–23 in Nebraska, and with mature fruits September 3–7 (Fig. 19); dehiscence is in mid- to late September.

Asclepias syriaca Linnaeus, common milkweed

This familiar plant is abundant in the eastern two-thirds of the State (Fig. 14), but westward it is largely replaced by *A. speciosa* (Fig. 10), with which it hybridizes (Fig. 11). The western limits of the natural range are unclear, but the species has probably moved westward as a weed with agrarian development in the western counties. Curiously, the species is unreported in recent treatments of the floras of Colorado (Weber, 1990) and Wyoming (Dorn, 1988), but we have found it to be locally abundant in Perkins county, bordering Colorado, and it is reported from Banner and Scotts Bluff counties (on the Wyoming border) in the *Atlas* (we cannot locate voucher specimens for those two counties, however). Our oldest specimens are from Saline County in 1881. Although the species is common and even weedy in crop fields and roadsides, there is a curious gap in our records, the herbaria we surveyed having no Nebraska specimens collected between 1907 and 1961; most of the specimens were collected in the 1960s–1980s.

Unlike the closely-related *A. speciosa*, it inhabits most soil types in the State, from deep loose sand to dry and heavy loess, and it occasionally grows in saline soils and in marshes. It tolerates consider-

able disturbance but also thrives in undisturbed, virgin prairies.

The species is markedly variable in stature, leaf size, flower color, and fruit shape and ornamentation. The tallest plants we found were in forest borders, thickets, and edges of irrigated and fertilized croplands, where they can be 2 m tall. Flower color ranges from dark to pale rose and can approach sordid white, especially in shadier habitats, where the leaves are often more strongly acute. The genetic and environmental factors causing such variability have not been studied in Nebraska.

The specimens indicate that flowering in Nebraska is between June 2 and August 22 (Fig. 19) but is mostly in June and July. Reblooming occurs after midsummer mowing, and plants in fertile and well-watered soils produce flowers far into August. The floral fragrance is sweet and heavy, but not quite as strong as that of *A. speciosa*. Older flowers are usually odorless. Full-sized (but not necessarily ripe) fruits have been collected between July 18 and October 5 (Fig. 19); dehiscence and seed-dispersal is mostly in late summer and fall. Many plants are fruitless, but those in rich habitats can produce as many as 40 follicles on a stem, although the average is far less than that.

Asclepias syriaca hybridizes with *A. speciosa* in Nebraska (see discussions above). Elsewhere, it is known to hybridize with *A. exaltata* L. (Kephart et al., 1988; Wyatt and Hunt, 1991), an eastern species not known in Nebraska. Although it resembles and often occurs with *A. sullivantii*, we have seen no evidence of hybridization, and Woodson (1954a) noted the absence of such hybrids in the specimens he saw.

***Asclepias tuberosa* Linnaeus subspecies interior**
Woodson, butterfly milkweed, pleurisy root

Collected from 22 counties, all southeast of a line from Dakota to Webster counties (Fig. 15); undoubtedly it is in all such counties. It grows in virgin prairies as well as roadcuts and pastures but is not abundant in Nebraska. Most of our collections are from loess and glacial till. From Minnesota to Indiana the species often occurs in sand plains and sand dunes, but in Nebraska it is absent from the Sandhills, although it is known from sandy soil in Cuming County. The *Atlas* dot for Garfield County, which is mostly in the Sandhills, was based upon Bates's Webster County specimen in NEB, collected in 1912; the label data were misinterpreted during preparation of the *Atlas*. We cannot find a voucher specimen for the *Atlas* record for Buffalo County,

whose flora is well-collected; none of the herbaria we surveyed has a specimen, including the herbarium in that county, and Woodson (1954a) doesn't indicate it there so we reject that record.

Flowering specimens have been collected in Nebraska from June 9 until August 17 (Fig. 19). We have not detected a floral odor. Our surveyed herbaria had no fruiting specimens, but we have seen green but full-sized fruits in the field on August 15; fruits of cultivated specimens dehisce in September.

Asclepias tuberosa is sometimes grown as an ornamental in Nebraska gardens, but many of those plants are purchased from sources beyond our range and sometimes have yellow and orange bicolored or entirely yellow flowers, which are common in wild populations north and south of the State (Woodson, 1964). Nebraska plants have entirely red-orange flowers, occasionally with a touch of yellow.

***Asclepias verticillata* Linnaeus, whorled milkweed**

We have seen specimens of this rather common species from most counties (Fig. 16), especially those east of the Panhandle, and while it probably occurs throughout the State, it is more abundant eastward. Often in remnant virgin prairies, it is also tolerant of disturbance and so is sometimes abundant and even weedy in cropland and roadside ditches. It is rather broad in its tolerance of soil types, growing in the loose sand of the Sandhills as well as in the heavy loess of the eastern counties. And while it is often found in dry prairies with such species as *A. tuberosa* and *A. viridis*, it is not uncommon in moister roadside ditches with *A. sullivantii*, *A. speciosa*, or *A. syriaca*.

Our oldest specimen is from Lancaster County in 1875, and we have seen many specimens taken from that date to the close of the Nineteenth Century, after which time collecting intensity decreased until the 1960s–1980s. The specimens we examined and our field observations show that this species has the longest flowering season of our species: June 12–September 8 (Fig. 19). The flowers have a weak to somewhat strong and rather chemical odor suggestive of commercial disinfectants used in public lavatories. The flowers swarm with butterflies, moths, and beetles. Full-sized but immature fruits have been found from June 25 to September 12, and mature fruits from August 20 to October 5 (Fig. 19); dehiscence is mostly in September, often when the plants' leaves are falling or afterwards.

***Asclepias viridiflora* Rafinesque, green milkweed**
Acerates viridiflora (Raf.) Eat.

Occurs across the State in sandy or heavy soils (Fig. 17). Rather common but never abundant, occurring as scattered individuals in virgin or somewhat disturbed prairies and on road cuts, often on rather sandy soil. Woodson (1954a) reports that it spreads to abandoned cropland but we have not seen it in such places, which are uncommon in Nebraska. The variable leaf shapes show no obvious correlation with habitat and, in fact, plants with different leaf forms often coexist at a site. Woodson (1954a) was unable to detect any consistent pattern of foliar shapes.

The specimens we have seen show that the species was first collected in Nebraska from Lancaster County in 1875 and it has been collected more or less regularly since then. Flowering in Nebraska is from May 23 to July 18 (Fig. 19), and the flowers are odorless. Full-sized fruits have been collected in Nebraska from July 22 to September 8 (Fig. 19), and dehiscence occurs in August and September.

***Asclepias viridis* Walter, antelope horn, spider milkweed**
Asclepiodora viridis (Walt.) A. Gray

This milkweed was poorly collected in Nebraska until the 1980s, when we searched intensively for it because we knew it to be more abundant and widespread than our few herbarium specimens suggested. The *Atlas* showed it to be in five southeastern and southern-tier counties; we have since found it in five others (Fig. 18) and are certain that it will be found in still others nearby. We found it to be locally abundant in southern Gage and Jefferson counties, where it occurs on roadsides and in overgrazed pastures, apparently increasing in the latter conditions, even in sod of smooth brome. It occurs scattered in remnant virgin prairies and abandoned cropland. In Lancaster County, at the very north edge of the species' range, it flowers and fruits abundantly and sheds copious seeds

The oldest Nebraska specimen we have seen was collected in Webster County in 1908, and we did not see any specimens collected between then and 1952, when it was taken from Clay County; most of the specimens were gathered in the 1970s and 1980s. Our specimens and field observations show that it flowers in Nebraska from May 24 to June 12 (Fig. 19). The flowers have a weak and somewhat sweet

odor. We have seen full-sized fruits collected between June 13 and July 31 (Fig. 19), and we have seen dehiscence in the third week of July, at which time many of the plants begin to yellow and wither.

Excluded and expected species

Rydberg (1932) indicated *Asclepias ovalifolia* Dene. in Nebraska but we have seen no specimens and later works have not included it. It is known in South Dakota and northern Iowa and might eventually be discovered in northeastern Nebraska. The rare *A. meadii* Torrey is known from Brown County, Kansas, adjacent to Richardson County, Nebraska, and from southwestern Iowa; it possibly grows in extreme southeastern Nebraska.

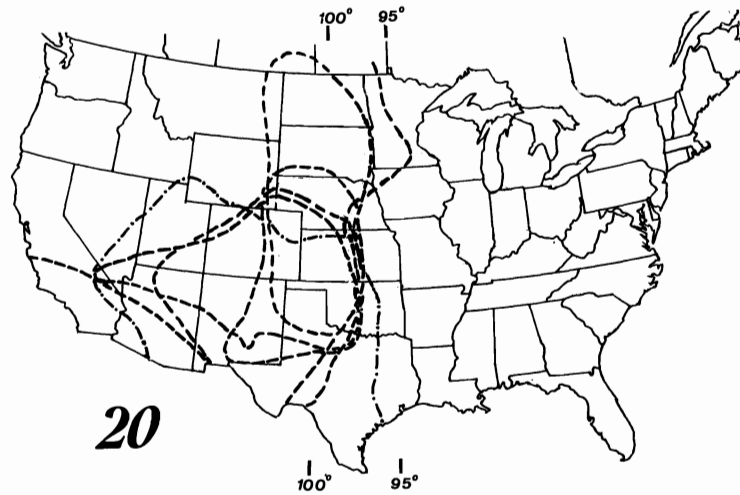
A specimen in NEB (*Kramer 87*, July 1926) of *Asclepias subverticillata* (A. Gray) Vail (*vide* Woodson) is from Sioux County. The species has not been collected in Nebraska since then, and the nearest station is Carbon County in south-central Wyoming (Dorn, 1988); we prefer to reserve judgment until we have seen more specimens.

A specimen in NEB of *Asclepias exaltata* L. (*vide* Woodson) collected by Engberg has a note obviously added later and not in Engberg's hand, "supposedly found near Fremont, Dodge County, Nebraska, July, 1893", a location so far out of range that we reject the record (as we do so many other Engberg specimens that apparently were attributed at a later date to Dodge County—Engberg's home—by someone else); furthermore, the species has not since been discovered in Nebraska.

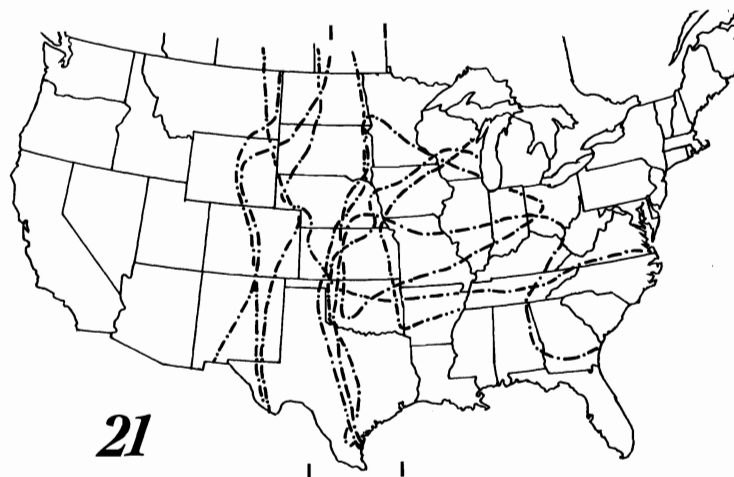
PHYTOGEOGRAPHY

Nine of the eighteen species of Asclepiadaceae native to Nebraska reach western distributional limits in the State (Figs. 20–21). One, *Asclepias speciosa*, extends to the west coast. Eight species range far east of Nebraska, seven to the Atlantic coast. Six reach their eastern limits in Nebraska, and five also reach their northern limits here.

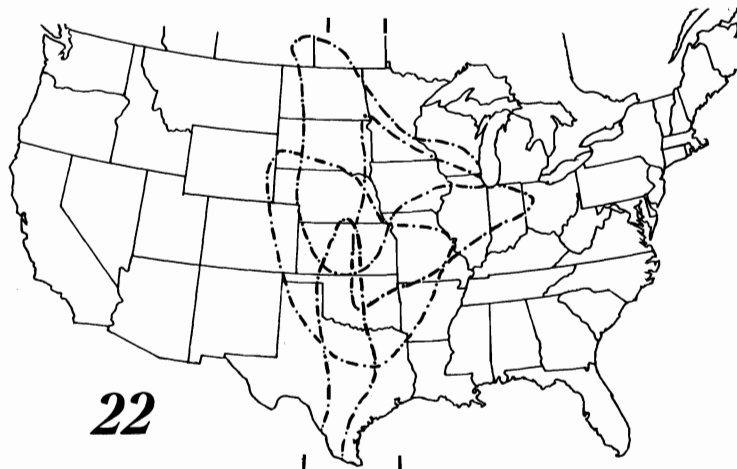
When the distributions of all Nebraska species are examined (Figs. 20–22) it is evident that twelve of our species reach their eastern or western limit at about the 98th meridian in Nebraska, Kansas, and Oklahoma, a familiar biogeographic pattern known many groups of plants and animals. Küchler (1970) called this north-south boundary the Tatschl Line, based upon Tatschl's (1970) dissertation, which identified the line for several species of *Psoralea*.



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Figures 20–22: 20. Distribution of Nebraska's species of *Asclepias* that have western and southwestern affinities. They share a common eastern boundary near the 98th meridian from Nebraska to Texas, but their western boundaries are diverse. 21. Distribution of Nebraska's species of *Asclepias* that have eastern affinity, with one species (*A. sullivanii*) of central affinity. Some species share a western boundary near the 98th meridian. 22. Distribution of four Nebraska species of *Asclepias* of the central part of the continent. Two species share an eastern-western boundary near the 98th meridian.

Likewise, the two southwestern species that reach their northeastern limits in the State are also part of a common pattern, as are the the northwestern limit of two others. Thus the Asclepiadaceae in Nebraska show phytogeographic patterns found in so many other plant groups. Woodson (1954a) presented a composite distribution map of all North American species of *Asclepias* and from it inferred six centers of concentration of species. Four of those centers contain Nebraska taxa: Appalachian (7 of our species), Ozarkian (2), Floridian (2), and Mexican (4) (some species occur in more than one center); only the Californian and Antillean centers are not represented in Nebraska's flora. Thus Nebraska's milkweeds are of various phytogeographic affinities, as is true for so much of the grassland flora of interior North America.

Current status of the species in Nebraska

The past century of agrarian development in the State has undoubtedly altered the abundance of all our milkweeds, increasing a few but decreasing most. Like most of Nebraska's native flora, most of our milkweeds are much reduced in abundance by past plowing of the virgin prairie and now by excessive roadside mowing and uninhibited application of herbicides there and elsewhere. It is too late to find some species in some counties whose native flora is virtually extirpated (e.g., Polk, York, and Clay counties), even though they surely once occurred there as evidenced by their presence in surrounding counties. The loss of native prairies surely has decreased the abundance of many species intolerant of disturbance, such as *A. amplexicaulis* and *A. lanuginosa*, but no species is known to have been extirpated from the State. Species confined to escarpments or to agriculturally-marginal soils have probably fared somewhat better—*A. engelmanniana*, *A. latifolia*, and *A. pumila*, for example. The two newly-discovered species in the State, *A. asperula* and *A. purpurascens*, are known only from a few Nebraska specimens, but they are common in adjacent states and their apparent rarity in Nebraska is an artifact of their ranges barely entering the State. The weedier species—*Asclepias speciosa*, *A. syriaca*, *A. verticillata*, *Cynanchum laeve*—are probably as common or even more common than they were before agricultural disturbance.

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