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Foreword

The effects of climate change on the phenology and pollination of plants is expected to be a major factor in the problem of maintaining biodiversity as well as that of feeding a growing global population. Though ecologists and agricultural researchers have historically tried to stay out of each other's domains, climate change has dealt them a globe of shared problems that will not easily be teased apart. For example, the honey bees that agriculture depends upon to pollinate crops are not native to North America. Whether those introduced pollinators help or hinder native species is a complicated problem, but they are certainly a part of the environment that researchers are going to have to study more closely as the world's population grows. Many native species and human-produced cultivars have co-evolved to depend upon or compete with each other in ways that we haven't yet discovered. We are reaching back in time to pull out some phenology and pollination data that can be compared with current data to study changes in species genomes or gene activity that might be related to climate change.

Connie Taylor wrote "Pollination Ecology of *Sabatia campestris*" in 1972 based on data she collected while taking a summer course at the University of Oklahoma Biological Station at Lake Texoma. Written as a student research paper, its significance lies not in numerical data, but in her descriptions of pollination processes she observed in the field, which differed from those processes described from research done in green house environments.

Shang-Wen Liaw was a graduate student at the University of Central Oklahoma who studied under Gloria Caddell. His 1999 Master's thesis went unpublished as he took advantage of an opportunity to go directly into a Ph.D. program. We are proud to publish "The Structure of the Gynostegium, Breeding System, and Pollination Ecology of Spider Milkweed, *Asclepias viridis*."

If that requires more phenology and pollination terminology than you know, you can flip to the Critic's Choice essay in the back where we've reprinted Paul Buck's Botany Bay article from the Fall 2000 Gaillardia, "A Conversation with a Small Beetle." His explanation of pollination from the standpoint of the pollinator is both entertaining and educating.

You can take a break from pollination studies and read Amy Buthod's floristic inventory of Kessler Atmospheric and Ecological Field Station. This site holds great potential for future climate change comparisons using sophisticated environmental monitoring equipment that will enable a coupling of species inventories with climate change.

We also have an assessment of a five-year recovery from a burn at Wichita Mountains Wildlife Refuge by Oklahoma City University authors, Laura Jardine, Adam Ryburn, and Anthony Stancampiano. This is a great piece of local ecological research that can play an important role in predicting dynamics due to fires which may become more frequent due to climate change. Again this year, we have something for everyone.

If you do research in or about Oklahoma's native plant environments, please consider submitting your own manuscript next year. We want manuscripts based on the newest concepts in research as much as we want manuscripts based on historical data. We want manuscripts written by authors with years of experience, but our editorial staff is also ready to help first-time authors get the experience they need to develop science writing skills. The *Oklahoma Native Plant Record* is a professionally reviewed publication. Our abstracts are indexed in the "Centre for Agricultural Bioscience International" that is based in the U. K., and the *Record* is listed in the "Directory of Open Access Journals" https://doaj.org.

Sheila Strawn, Managing Editor

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POLLINATION ECOLOGY OF *SABATIA CAMPESTRIS* NUTT. (GENTIANACEAE)

Unpublished Report
University of Oklahoma Biological Station
Lake Texoma
1972

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Keywords: phenology, **Sabatia campestris***, autogamy, allogamy*

ABSTRACT

Flower timing studies in June and July (1972) on populations of *Sabatia campestris* Nutt. show this plant to be allogamous (out crossing) under natural field conditions. However, when environmental factors reduce populations of solitary bees or when flower populations are particularly extensive and dense, the uncollected pollen causes retention of anthers into the period of style opening and stigma presentation. Then autogamy (self-pollination) occurs. Pollinators observed were solitary bees in the genera *Calliopsis, Dialictus*, and infrequently *Augochlorella*. Pollen viability is generally excellent. A chromosomal count of n=12 indicated the presence of aneuploid races in this plant species. The lengthening of petals from anthesis to wilting and calyx from bud to fruit production indicates flower size cannot be used as a taxonomic character to separate species.

INTRODUCTION

Sabatia campestris Nutt. (Gentianaceae), prairie rose gentian, is a common prairie annual found from Illinois south through eastern Texas and east to Mississippi, with its greatest development in the prairie regions of the south central portion of the United States. The type specimen was collected from Oklahoma (Taylor and Taylor 1994) and its occurrence cited as "in the open prairies of Arkansas and Red River, common, flowering in June and July" (Nuttall 1836). The winged calyx that encloses the fruit is a unique species character. Perry (1971), studying cross fertilization between species, found *S. campestris* to be reproductively isolated from other species.

DESCRIPTION OF THE FLOWER

Flower timing studies in June and July (1972) on populations of *S. campestris* show this plant to be allogamous (out crossing) under natural field conditions. However, when environmental factors reduce populations of solitary bees or when flower populations are particularly extensive and dense, the uncollected pollen causes retention of anthers into the period of style opening and stigma presentation. Then autogamy (self-pollination) occurs.

The flowers are borne in a cymose inflorescence, the first flower terminal on a branch and subsequent flowers at the ends of opposite branches from below the first flower. The calyx is composed of five green

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sepals fused and winged at their lower edges, the lobes being 2–6 times longer than the calyx tube. The calyx continues to grow during flowering and during fruit maturation. The winged calyx tube lengthens to 8 mm, and the calyx lobes grow to 25 mm long. The corolla is composed of five petals fused at the base, rose to pink or rarely white. Petal lobes, like the calyx lobes, grow during flowering, reaching 23 mm long and 13 mm wide. The base of each petal lobe fades to white and has a rectangular yellow mark about the size and shape of the anther. This mark increases in length and intensity of yellow color during flowering. There are five anthers and one pistil with two branches, first green, then turning yellow with maturity. Fruit capsules and seeds are numerous.

METHODS

The floral aspect of reproduction and pollinator behavior studies were done under field conditions during the height of blooming. Two plots located at the northeast edge of Durant, Bryan County, Oklahoma, approximately 1.21 and 4.86 hectares [3 and 12 acres] in size, were intensively observed. Two plots in Marshall County, Oklahoma, one adjacent to the University of Oklahoma Biological Station (U.O.B.S.) on Lake Texoma and another along a roadside 4.82 km [3 mi] north of Willis were also observed. During the height of blooming in early June, flowers were marked by crewel yarns in the bud stage and checked three times daily, at a minimum, and during one night to determine floral presentation and movement of flower parts. Climatic conditions were also noted. Studies of pollinator presence were made by half-hour monitoring over several days, and behavior of bees were observed and recorded with a 35 mm single lens reflex camera. Autogamy (self-pollination) was confirmed by the use of pollinator exclusion bags. No seed set was obtained when styles were excised.

RESULTS

Observations

The following description of floral presentation is for a sunny summer day in the presence of pollinators—solitary bees. *S. campestris* is protandric (the anthers functioning first) with the opening bud displaying straight anthers; the green pistil with tightly twisted styles lies in a horizontal position when the flower is fully open. By 8:30 a.m. (CDST), the anthers will have recurved at the tip, splitting open to release pollen from the anther chamber (Figure 1). The timing of anther dehiscence is delayed by rain and cloudy weather, recurvation of anther tips and pollen presentation being delayed until as late as 11:30 a.m. under these conditions. The flower closes in the late evening, so no opening to floral parts is apparent. Closure is not as tight as in the bud. The first night is the only night full closing occurs.

On the second day, the anthers gradually curl further back and eventually tilt into a horizontal position. Anther presentation of pollen is usually for two days but may be extended for a third day. On the morning of the third day, the anthers fall to the center of the bowl shaped flower. Flowers presenting anthers for a third afternoon usually have anthers fall off the filaments in the evening. Anther presentation is greatly modified by pollinator absence, being considerably prolonged for another one or two days.

Presentation of the stigmatic surface typically begins with the falling of the anthers. While still in a horizontal position, the stigmatic surfaces begin to turn yellow. Staining with lactophenol aniline blue indicated receptivity is correlated with the appearance of the yellow color. The twined style branches begin untwisting gradually. Over 24 hours is required for the style to become erect and the stigmatic branches to completely untwist. Stigmatic presentation is from the third day after opening (Figure 2) until the flower wilts on the 6th or 7th day. Some blossoms showed stigmatic wilt prior to petal wilt. The sepals are retained until the fruit dehisces some months later.

Figure 1 Late day 2 showing curled dehiscence of anthers and unreceptive pistil with tightly twisted styles

Figure 2 Day 4 or 5 showing erect style with receptive untwisted style branches, no anthers, and mimic anther lines at base of petals

Pollination

Pollinators visiting *S. campestris* were solitary bees in the genera *Calliopsis* (Andrenidae), *Dialictus* (Halictidae), and *Augochlorella* (Halictidae). All species of solitary bees were shorter than the anther length. Visits were for pollen collection. Day and time of visitation and plot visited are summarized in Table 1. The flowers produced no nectar and seemed to hold little attraction for most other insects. Occasional visits by various crab spiders and insects from leaf hoppers to butterflies were noted, but they were scattered and infrequent. In the Durant plots, the size of the three principal pollinators diminished. The largest-sized species visited before June 10; the middle-sized species visited in mid-June; and toward the last few days of June and first two weeks of July, the smallest bee species was the pollinator.

The ecological interactions of bee and flower are pronounced. When flowers are open in the absence of pollinators, the anthers remain in an upright position for extended periods of time, and the total length of blooming is increased. Flowers in paper pollinator exclusion bags and screen wire cages had, by the 5th and 6th days, accumulated piles of pollen heaped on the anther and scattered in the bowl of the blossom. The presence of this accumulation of dehisced pollen excluded wind pollination as an effective pollination agent. The presence of anthers remaining in an upright position delayed stigma presentation for several days, as late as six or seven days after opening. Blooming time per flower was dramatically extended, one flower remaining unwilted for 14 days with the stigma still yellow and upright.

Collection of pollen was done in the same manner by all species of bees. After landing on the petal platform, they climbed up the anther, usually from the interior portion of the blossom. With the use of mouth parts, the pollen was collected and transferred by the front legs to the corbicula. After collecting for some minutes, the bee then packed the pollen into

Table 1 Times of bee visitation observed for plots

POLLINATOR	**VISITATION**		**LOCATION**
	DATE (1972)	TIME (CDST)	
Calliopsis sp.	before June 10	12:30–3:30	Durant
Dialictus sp. (black)	June	early morning	U.O.B.S.
Dialictus sp. (black)	late June	all afternoon	Durant
Dialictus sp. (metallic rust)	late June–early July	all afternoon	Durant
Augochlorella sp.	mid-June	noon	U.O.B.S. and N. of Willis

a firmer mass and was observed flying off for about one foot from the petal and then returning to the same blossom for further pollen. Anthers were usually worked in a counter-clockwise manner, taken one after another until pollen from all five were collected. A blossom was worked sometimes two or three more times around. The longest timed collection of pollen from one flower by one bee was seven minutes.

Bees seemed to be unable to discriminate between flowers presenting anthers and those presenting stigmatic surfaces until landing on the flower. A bee quickly realized the absence of collectable pollen and would fly immediately to another flower. No bee was observed on a flower without anthers for more than 15 s, unless the petal platform was used when packing pollen. As the bee climbed on the style branches in the same manner it did the stamens, the pollen of the corbicula brushed the stigmatic surface causing pollination. Quadrat sampling confirmed the hypotheses that pollen reward for bee visitation occurred in less than 40 percent of the blossoms open at any one time. Later in the bloom season, sampling showed flowers presenting pollen fell to 27 percent of the total open blossoms.

Pollen viability counts were made on material stained with either lactophenol analine blue or Snow's stain. Pollen viability was generally less than 1% non-viable pollen. Highest count of non-viable pollen was 41.7%. Lewis et al (1962) and Perry (1971) reported chromosome numbers of n=13. Collections of buds were made at three different times from the 1.21 ha [3 acre] Durant plot. All three counts were n=12. Chromosomal numbers for the genus as reported by Perry (1971) are n=13, 14, 16, 17, 18, 19, 32, and 38.

DISCUSSION

Perry (1971) reports the sequence of events in anthesis of *Sabatia* flowers for all species. His data for *S. campestris* are bud (day 1), petals expanding and anthers recurving (day 2), anthers dehiscent (day 3), pollen shed (days 7–8), and stigma uncoiling and receptivity (days 7–8). I assume floral timing is based on greenhouse plants, as he states his pollination and fruit set studies are done under these conditions. His data for floral timing is the same as the data I recorded under pollinator exclusion bags, indicating that this species is generally cross-pollinated. However, in the event of environmental influences which would hinder pollinator visits, the plants will set seed by self-pollination.

In the smaller plots, pollen collection was efficient throughout the blooming season. The 4.86 ha [12 acre] plot, densely populated by *S. campestris*, always had occasional blossoms from which pollen had not been collected. During observations, over a dozen flowers were observed with direct mechanical self-fertilization occurring by direct contact of the stigma surface with the anther. The only flowers not setting fruit were those which wilted during dry periods. All flowers in pollinator exclusion bags set fruit. In young plants with few blossoms, synchronization of flowers on the same plant was observed, all blossoms either presenting anthers or all presenting stigmas, but not presenting both on the same plant. Older plants with eight or more flowers usually lost this synchronization.

Each *S. campestris* blossom has a small eye or star located at the center of the flower. Each petal has a single yellow or green-yellow line notched at the apex, presented against a white background. The yellow line and white area enlarge and lines assume a bright yellow—at least to the human eye—as the stigmatic surfaces are presented. After anther shed, the yellow streaks and large yellow divergent style branches together provide a facsimile to the yellow flicker pattern of the presented anthers. The evolution of this pattern is often considered to be due to long and close bee pollinator association, with patterns on blossoms considered as nectar guides. This does not seem to be the case in *S. campestris*. The petals are pink, a color not generally associated with bee flowers. Various shadings were common in all plots, ranging from white, light pink, pink, to dark pink. Ultraviolet reflection did not occur on blossoms tested.

The floral whorls, both calyx and corolla, grow after anthesis. This extremely unusual growth pattern is responsible for the enlargement of the eye. The largest flower on any plant will be that blossom which has been open longest. Wilber (1955) noted that on some plants the central blossom was largest. Neither Wilbur (1955) nor Perry (1971) mention the continued growth of the blossom while in bloom. The calyx also continues growth after the petals wither. Length and width of the calyx and corolla have been used as taxonomic character to separate species. The phenomenon of continued growth also occurs in at least two other species. Examination of fresh flowers of a population of *S. angularis* (L.) Pursh, collected in June on the east side of the Glover River at Arkansas Crossing, McCurtain County, Oklahoma, showed the same size differentiation. The lengthening of petals from anthesis to wilting and calyx from bud to fruit production indicates flower size cannot be used as a taxonomic character to separate species. Differences of individual blossoms on a single plant varied from 5 to 9 mm as measured from petal tip to petal tip tangent to the fruit. Likewise, examination of specimens collected from a population of *S. arenicola* Green, collected in April from a littoral area behind the dunes 12.87 km [8 mi] west of Sabine Pass, Texas, showed size differences. Measurement of the petal lobes showed they increased between 2 and 3 mm from early blooming flowers to old blossoms beginning to wilt. Flowers in fruit had longer calyx lobes than those in flower. Continued growth of blossoms is suspected for other species from descriptions and discussions in the monograph (1955) of the genus.

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Thanks are due to Dr. J. R. Estes for direction in cytological work and to Dr. R. W. Thorp who identified the bees. Special recognition to Dick Carson, Stone Post Creations (rosecarson@juno.com), for the photographs of *Sabatia campestris*.

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THE STRUCTURE OF THE GYNOSTEGIUM, BREEDING SYSTEM, AND POLLINATION ECOLOGY OF SPIDER MILKWEED, *ASCLEPIAS VIRIDIS* WALTER (APOCYNACEAE)

Master's Thesis
University of Central Oklahoma
1999

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Keywords: phenology, reproduction, electron microscopy, self-incompatibility

ABSTRACT

Reproductive structures, flowering phenology, breeding system, and potential pollinators were described in two populations of *Asclepias viridis* Walter in Oklahoma in 1997 and 1998. Scanning electron microscopy was used to locate the stigmatic surfaces of the gynostegium, and a series of pollination treatments was performed including open-pollination, supplemental pollination, self-pollination, and within- and between-population cross-pollination. Flower visitors, their visitation rates, and numbers of pollinaria carried were recorded. Pollinia were inserted in four ways to determine which type of insertion results in pollen germination, and flowers were collected to determine how pollinia were inserted by insects. The stigmatic surfaces of *A. viridis* are located at the fusion point of the two styles at the base of the gynostegium. Self-pollinations produced no mature follicles, revealing self-incompatibility. In addition to genetic barriers, the low rate of natural fruit-set (1.87% in 1997 and 1.39% in 1998) is due to follicle abortion and predation of flowers and follicles. Supplemental pollination did not significantly increase fruit and seed set. Fruit-set from hand cross-pollinations at one site, but not the other, revealed a greater crossability between populations than within. *A. viridis* flowered from early May to late June, with a peak in late May. The mean number of flowers per inflorescence was 34.1, and the mean flowering span per inflorescence was 10.6 days. Over 20 families of insects, including those within the orders Hymenoptera, Lepidoptera, Coleoptera, and Hemiptera, visited flowers. Of the hymenopterans, solitary wasps, large carpenter bees, digger bees, and bumblebees carried pollinaria. Hymenopterans contributed the majority of visitations, and bumblebees (*Bombus* spp.; Apidae) were the most important pollinators based on numbers of pollinaria carried and frequency of visitation. The highest percentage of mature follicles was obtained when pollinia were inserted with the convex edge toward the stigmatic surface; natural pollinators almost always insert pollinia in this manner.

Editor's Note: Where nomenclature has been updated using ITIS–Integrated Taxonomic Information Service (http://www.itis.gov), the original name is in brackets [ ].

Shang-Wen Liaw
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INTRODUCTION

Asclepias (Apocynaceae) is a widespread genus with at least 108 species distributed in North America and the Antilles (Woodson 1954). Because of its floral complexity, it is considered a herkogamous genus, and pollination within natural populations is apparently dependent upon insect visits. The floral structure of *Asclepias* has been described in detail by several authors (Woodson 1947; Sparrow and Pearson 1948; Wyatt 1976; Sundell 1984; Morse 1987). Five antisepalous stamens are highly modified and fused with the stigmatic head to form a unique reproductive column called the gynostegium. A pair of coriaceous protruding flaps, or anther wings of two adjacent anthers, form a vertical slit along the gynostegium and open into a stigmatic chamber.

Five slits are arranged on the gynostegium. Each anther has two vertical pollen sacs (Woodson 1954), each of which contains a pollen mass called a pollinium. A pair of pollinia, from pollen sacs of two adjacent anthers, is joined by two ascending translator arms to a hollow, black, grooved body called the corpusculum located above the slit. The entire unit, which includes a pair of pollinia, a pair of translator arms, and the corpusculum, is called the pollinarium or the bipollinium (Newton 1984). The hoods or appendages of the five stamens join and surround the gynostegium, forming a corona. Each hood contains nectar and in some species contains an incurving structure called the horn. Two ovaries are located at the base of the flower above the calyx, and their two styles protrude and fuse to form a flat mass of tissue below the stigmatic head. According to Woodson (1947) and Wyatt (1976), however, the stigmatic surface is not at the flat top of the gynostegium but is actually shifted laterally and divided into five concave surfaces at the base of the five stigmatic chambers. This description appears to differ from Brongniart's illustration in 1832 (Sundell 1984), which indicates that the stigmatic surfaces may be located at the base of the gynostegium where the two styles are fused. According to Kevan et al. (1989), the nectaries of *Asclepias* are actually the walls of the stigmatic chambers, and concentration of nectar in the stigmatic chamber may either stimulate or inhibit pollen germination. Based on the similarities between constituents of nectar and stigmatic secretions (Kearns and Inouye 1993), staining may lead to a misinterpretation of the location of the stigmatic surface.

A depression or furrow is found on the flat top of the gynostegium in some *Asclepias* species; pollen tubes that enter stigmatic surfaces in three chambers on one side of the depression can reach one ovary, and pollen tubes reach the other ovary from the other two adjacent chambers (Broyles and Wyatt 1993). However, in some species, two follicles occasionally result from hand-pollination with a single pollinium (Kephart 1981; Morse 1993). Sage et al. (1990) assumed that the crossover may occur at the point at which the two styles are fused or during the growth of pollen tubes down the stylar canal. Consequently, to exactly locate the stigmatic surfaces and solve the mystery of the production of twin follicles, anatomical observation of the gynostegium is warranted.

Various vectors, mostly polytropic Hymenoptera and Lepidoptera (Macior 1965; Morse 1985), are presumably attracted by the abundant nectar secreted by *Asclepias* species (Willson and Bertin 1979; Willson et al. 1979). As insects forage on flowers, they remove pollinaria from the pollen sacs by hooking the corpusculum channel onto various body regions. Depending on the morphology of the various taxa of insects, pollinaria may attach to mouth parts, claws, pulvilli, tibiae, and tarsi. They often form complicated chains or masses as the corpusculum channel of one pollinarium hooks to a translator arm of another pollinarium (Frost 1965; Macior 1965). After a pollinarium is removed from a flower, the pollinia may dry in the air. The translator arms twist and rotate the pollinia 90 degrees so they can be easily inserted into the stigmatic chambers of other flowers (Kephart 1981). As insects move on flowers after landing, pollinia are precisely inserted into the stigmatic chambers. According to Wyatt (1976), who observed over 500 pollinia insertions of *A. tuberosa* L., insertion does not occur simply by chance but is more likely to be a specific process because, except rarely, all pollinia were inserted entirely inside the stigmatic chambers, and the convex surface of a pollinium was always brought into contact with the stigma. Whether all insect vectors show the same manner of pollinium insertion in other *Asclepias* species has never been reported. Therefore, the manner of pollinium insertion accomplished by insect vectors in relation to fruit-set of *Asclepias* within natural populations should be investigated further.

Because of the complex floral structure of *Asclepias*, many aspects of species in this genus have been investigated in past decades, including their breeding systems (e.g., Sparrow and Pearson 1948; Wyatt 1976; Kephart 1981; Broyles and Wyatt 1993; Shore 1993; Gold and Shore 1995); their floral biology, pollination ecology, and evolutionary ecology (e.g., Willson and Price 1977, 1980; Bookman 1983a, 1983b; Broyles and Wyatt 1991; Pleasants 1991; Fishbein and Venable 1996); and their reproductive biology in relation to the adaptations and behavior of insects (e.g., Frost 1965; Macior 1965; Willson and Rathcke 1974; Willson and Bertin 1979; Willson et al. 1979; Bertin and Willson 1980; Willson and Price 1980; Morse 1987; Jennersten and Morse 1991). In addition, aspects of their physiology, such as dormancy and germination of seeds, have also been studied (e.g., Oegema and Fletcher 1972; Baskin and Baskin 1977).

According to Wilber (1976), most species studied had a very low level of self-fertility as determined by the results of breeding system experiments. Sparrow and Pearson (1948) found that only two follicles developed from 1,354 hand self-pollinations in populations of *A. syriaca* L. However, they explained that one was certainly the result of the accidental introduction of foreign pollen by a bee, and the other was abnormal because most of its seeds were aborted and undersized. Wyatt (1976) self-pollinated 112 flowers in five different populations of *A. tuberosa*. Self-compatibility ranged from 0% to 9%, with a mean of 1.8%. Kephart (1981) reported the results of self-pollination treatments for three *Asclepias* species: none of 55 self-pollinated flowers from three populations of *A. verticillata* L. produced mature follicles; an average of 4.2% (3/73) of self-pollinated flowers produced follicles from two *A. syriaca* populations; and in seven populations of *A. incarnata* L., an average of 29.2% of self-pollinations produced follicles. Bookman (1984) found that only two *A. speciosa* Torr. ovaries fully matured into follicles among 240 hand self-pollinated flowers and concluded that *A. speciosa* populations have a few rare, self-compatible individuals. Broyles and Wyatt (1993) stated than none of 138 hand self-pollinated flowers in an *A. exaltata* L. population produced mature follicles. However, it is difficult to compare the degree of self-fertility among species because of the variation in techniques used by different researchers. For example, Bookman (1984) used pollinia inserted into the first, third, and fifth of the five stigmatic chambers per flower so that ovules of both ovaries could potentially be fertilized; whereas, Broyles and Wyatt (1993) used pollinia inserted into the fourth and fifth chambers so that ovules in only one of two ovaries could presumably be fertilized.

Many factors, such as light intensity, precipitation, temperature (Wyatt 1976; Waser 1983), leaf surface for photosynthesis and soil nutrients (Pleasants 1980), insufficient pollination (Wyatt 1976), and nectar concentration affecting pollen germination (Kevan et al. 1989) may influence the reproductive success of plant species. Woodson (1954) proposed that a relatively low rate of natural fruit-set, about 1%, occurs in almost all species of *Asclepias*. In a field study of follicle production in five populations of *A. speciosa*, Bookman (1984) found that only an average of 2.4% of all ovaries developed into mature follicles. Shannon and Wyatt (1986) found that an average of 2% fruit-set occurred in four populations of *A. exaltata*. Although spatial separation of anthers and stigmas and genetic self-incompatibility systems in angiosperms promote outcrossing, they may also be responsible for the low level of fruit-set in natural populations, especially in *Asclepias* (Broyles and Wyatt 1993). With such a high degree of spatial separation of pollen sacs and stigmas, *Asclepias* requires insects to accomplish pollination (Sparrow and Pearson 1948), and the efficiency of pollination often depends upon agreement of flower size and form with body form and behavior of insect pollinators (Macior 1965). Genetic self-incompatibility causes rejection of self-pollen (Broyles and Wyatt 1993), and a high rate of insect-mediated self-pollination has been suggested to contribute to the low natural fruit-set in *Asclepias* (Wyatt and Broyles 1994). Systems of self-incompatibility are generally classified as sporophytic and gametophytic (Kearns and Inouye 1993; Wyatt and Broyles 1994). However, a sporophytic incompatibility system seems unlikely to occur in *Asclepias* because its pollen grains are always able to germinate in the stigmatic chambers with the presence of favorable nectar concentration under natural conditions (Kevan et al. 1989). Consequently, a gametophytic incompatibility system, in which pollen tubes are usually arrested in the style, more likely occurs in *Asclepias*. Shore (1993) concluded that the rate of natural self-pollination in a population of *A. syriaca* was 66%.

Figure 1 The spider milkweed (*Asclepias viridis)*

A. viridis Walter, a herbaceous perennial commonly called spider or green milkweed (Figure 1), is distributed from Tennessee to Florida and westward to Nebraska and eastern Texas. In general, its inflorescence is a terminal and solitary compound umbel usually composed of 2–4 umbellets. Differing in some morphological aspects from many other *Asclepias* species, the flower of *A. viridis* has inflexed petals and no horn contained in the hood. Most of its populations are distributed within Kansas, Missouri, Oklahoma, Arkansas, and Texas (Woodson 1954). It is usually found along railroads, on roadsides, in abandoned fields, within disturbed prairies, and on dry hillsides in summer. It flowers from April to August.

There are no published reports on the reproductive biology and the pollination ecology of *A. viridis*. The purpose of this study is to describe the reproductive structures, flowering phenology, breeding system, and potential pollinators of *A. viridis*. Specifically, I asked the following questions: (1) Where are the stigmatic surfaces located within the gynostegium; (2) What is the flowering period of *A. viridis* in central Oklahoma; (3) What is the phenology of individual flowers and inflorescences; (4) Does *A. viridis* show a low level of self-compatibility as do other *Asclepias* species; (5) Does *A. viridis* demonstrate the low level of natural fruit-set exhibited by other *Asclepias* species, and if so, is it due to lack of pollination, lack of compatible pollen reaching stigmas, or lack of resources for follicle development; (6) Which insects visit frequently, carry pollinaria, and position themselves on the gynostegium so that they can be considered potential pollinators; (7) How are pollinia inserted into stigmatic chambers by natural pollinators; and (8) What type(s) of insertion can lead to pollen germination?

METHODS AND MATERIALS

Study Areas

Two populations of *A. viridis* were studied, the Arcadia Lake population (ALP) and the Bryant-Simmons population (BSP), separated by a distance of about 12.8 km [8 mi] (Figure 2). Most investigations were conducted at the ALP site (Figure 3). This study site (320 m [1050 ft] elevation) is a recovering grazed prairie on the shore of Lake Arcadia, 3.2 km [2 mi] east of I-35 on the south side of 15th Street (T13N R2W, Sec. 3), Edmond, Oklahoma County, Oklahoma. The western and northwestern sides of this area are both bounded by a crosstimber forest dominated by *Quercus stellata* Wangenh. and *Q. marilandica* Münchh. This research area slopes gradually from the center towards its southeastern boundary into Lake Arcadia. A residential area is adjacent to its northern boundary. It was heavily grazed by cattle until the early 1980s but is recovering towards a tallgrass prairie dominated in the fall by several native perennial species, such as *Schizachyrium scoparium* (Michx.) Nash [*Andropogon scoparius* Michx.], *Bothriochloa saccharoides* (Sw.) Rydb. [*A. saccharoides* Sw.], and *Sorghastrum nutans* (L.) Nash. On the other hand, many invaders, such as *Amphiachyrias dracunculoides* (DC.) Nutt. [*Gutierrezia dracunculoides* (DC.) S.F. Blake] and *Ambrosia* spp., still remain. In addition, the woody species *Juniperus virginiana* L. has invaded the site since the early 1980s. The BSP site (351 m [1150 ft] elevation), in contrast to the ALP site, is a relatively flat pasture and is privately owned (Figure 4). It is located at the northeast corner of Bryant Avenue and Simmons Road (T15N R2W, Sec. 30) in northern Edmond, Logan County, Oklahoma. This site was utilized only for the intra- and interpopulation cross-pollination study.

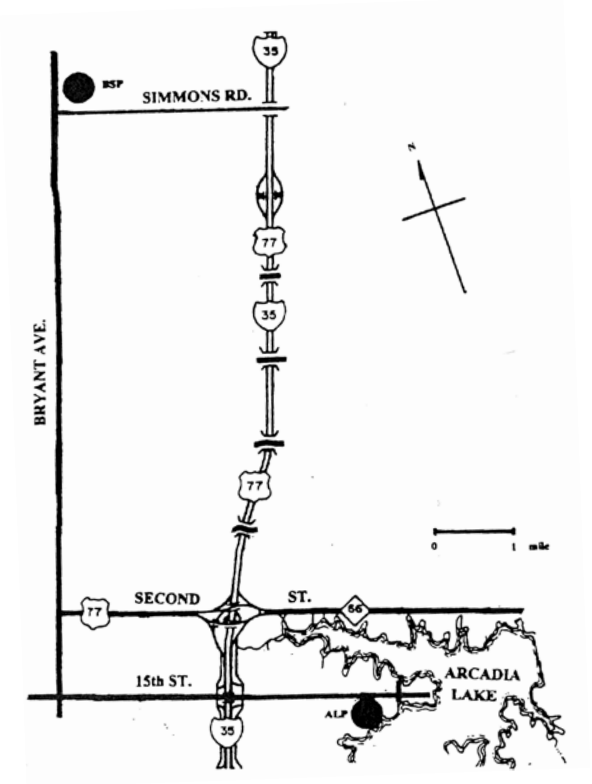


Figure 2 Locations of the UCO Lake Arcadia Research Area (ALP) and the Bryant Avenue-Simmons Road site (BSP).

Figure 3 The western edge of the UCO Lake Arcadia Research Area (ALP). It is bounded by *Quercus stellata* and *Q. marilandica*.

Figure 4 The Bryant-Simmons study site (BSP). This flat pasture is located at the northeast corner of Bryant Avenue and Simmons Road in northern Edmond, Logan County, Oklahoma.

Anatomical Structure of the Gynoecium

In order to locate the stigmatic surfaces, several flowers, some with insertions of pollinia, were collected from the ALP site. Flowers were dissected in several ways with a surgical razor blade to expose the entire gynoecium while they were still fresh. I used the method suggested by Ciampolini et al. (1990) but fixed specimens in 5% instead of 3% glutaraldehyde in 0.006 M cacodylate buffer at pH 7.2 and for 12 h instead of 3 h. Then the fixed specimens were dehydrated through an ethanol series (25% –1 h; 50%–1 h; 75%–1 h; 95%–1 h; and 100%–1 h). The specimens then were critical-point dried (SAMDRI-790A CPD, Tousimis Instrument, Rockville, Maryland) at 7391 kPa [1072 psi] and 31.1°C. Ethanol of 100% purity was used as an intermediate fluid, and liquid carbon dioxide was used as a transitional fluid during processes. After complete dehydration, specimens were mounted on metal specimen stubs by using silver paint as the adhesive and stored in a desiccator for 24 h. Finally, specimens were coated using a Hummer 10.2 Sputter Coater (Anatech, Ltd., Alexandria, Virginia) to achieve a 15 nm Au/Pd coating and examined under a LEO S420 scanning electron microscope (SEM, LEO, Inc., Cambridge, England).

Breeding System

The degree of stigma receptivity and pollen viability may vary with age of the flower and may differ among *Asclepias* species (Bookman 1983b; Morse 1987). To ensure pollen germination and stigma receptivity for hand-pollination treatments, several pollinia were collected from 1-, 2-, and 3-day-old flowers at the beginning of the 1998 flowering searson. Pollinia were incubated on agar plates consisting of 10% cane sugar and 2% agar (Kephart 1981) to check for pollen germination. After 4-hour incubation, the pollen tubes from 2-day-old flowers seemed to have longer pollen tubes. Therefore, I used pollinia from 2-day-old flowers for all hand-pollination treatments. Additionally, 1-, 2-, and 3-day-old flowers were collected, and 3% hydrogen peroxide was applied to check peroxidase activity of the stigma by the presence of a bubbling action (Kearns and Inouye 1993). Unfortunately, there was no apparent bubbling action on any flower. Therefore, I used 1- or 2-day-old flowers for all hand-pollinations, as the younger flowers have a higher stigma receptivity as suggested by Morse (1987).

Open pollination was observed and data were collected at the ALP site in 1997 and 1998 to estimate the level of natural fruit- and seed-set. To obtain an estimate of the overall percentage of fruit-set throughout the flowering season, the flowering season was divided into three periods: April 16–May 15, May 16–June 14, and June 15–July 14. At the beginning of each period, 20–30 stems with well-developed umbels were selected from the ALP site and tagged before flowers opened. No more than two stems per plant were sampled, and only one stem was sampled if a plant had fewer than six stems. Number of flowers on all sampled stems was counted and multiplied by 2 (# of ovaries/flower) for the computation of overall percentage of natural fruit-set. To compare percentage of fruit-set and number of seeds per mature follicle between natural pollination and other pollination treatments, three flowers on the umbel of each sampled stem were used, and one flower was tagged every other day after the first flower bud opened. After umbels were no longer attractive to pollinators, all sampled umbels were bagged with 15.4 cm × 20.3 cm [6 in × 8 in] hand-made pollination bags made of white nylon mesh to prevent destruction of developing follicles by phytophagous insects. The overall percentage of natural fruit-set was computed by the following formula:

$$\text{\% natural fruit-set} = \frac{\text{Total \# of fruits}}{\text{Total \# of flowers} \times \text{\# of ovaries per flower}}$$

Because *Asclepias* has two ovaries per flower, the percentage of natural fruit-set, therefore, was actually calculated as follows:

$$\text{\% natural fruit-set in } \textit{Asclepias} = \frac{\text{Total \# of fruits}}{\text{Total \# of flowers} \times 2}$$

Natural fruit-set indicates an overall percentage of fruits produced in nature as the result of open pollinations, but it does not indicate the total number of flowers pollinated or successfully fertilized. After flowers are visited by insect vectors, a successful fertilization may be detected by rapid expansion of the ovary and by recurving of the pedicel and an increase in its diameter. Developing follicles were closely monitored until they were mature, and size of aborted follicles was measured.

Supplemental pollination was performed to determine whether there is an increase in follicle production or in number of seeds per follicle after adding a cross pollinium into a stigmatic chamber. Five to 15 umbels, each from different plants, were sampled from the ALP site within each of the three blooming periods in 1998, and three flowers per umbel were used. One 2-day-old flower on each umbel was selected every other day after the first flower opened, and a 2-day-old pollinium collected from another plant some distance away was inserted into a single chamber. With curve-tipped pollination forceps, pollinia were carefully removed by hooking the tip of the forceps on the groove of the corpusculum. After pollinia were removed from flowers, they were placed onto a dry paper towel in a petri dish and were allowed to dry for several minutes to permit the 90 degree change in orientation of the translator arms. Insertions with the convex edge of pollinia toward the stigmatic surface were performed by using curve-tipped pollination forceps with the assistance of binocular headglasses (3.5 × magnification). To ensure that pollen tubes entered the same ovary on each flower, a cross pollinium was inserted into the stigmatic chamber adjacent to one on the same side of the furrow and into which a pollinium had been inserted by a pollinator. The sepals on both sides of the slit where a cross pollinium was inserted were marked with a black permanent marker. After insertions were performed, individual flowers were tagged but not bagged before follicles developed. Once follicles began to develop, they were bagged and then closely monitored until follicles matured. Later, mature follicles that developed on the side with the marked sepals were individually bagged with wax paper bags to prevent seed dispersal after dehiscence.

Intrapopulation and interpopulation cross-pollinations were performed at both the ALP and BSP sites in 1998 to compare the level of fruit-set within and between populations. Thirty plants, each with a single stem composed of a compound umbel, were sampled from each population. Fifteen plants were used for intrapopulation cross-pollination, and another fifteen were used for interpopulation cross-pollination. For interpopulation cross treatments, pollinia were transferred between the two populations. Umbels on sampled plants were bagged with 15.4 cm × 20.3 cm [6 in × 8 in] hand-made pollination bags of white nylon mesh and tagged while flowers were still in bud, to prevent visits from insects. Plants that died, due to predation or pathogens after insertions, were removed from the analysis. Three flowers per stem were used for the analysis. Two pollinia were separately inserted into the first and the fourth or the second and the fifth stigmatic chambers in order to ensure that both ovaries had an equal chance to be fertilized. I collected 2-day-old pollinia and inserted them, with the convex edge toward the stigmatic surface, into stigmatic chambers of 1- or 2-day-old flowers on different plants. One flower on each umbel was manipulated every other day. All treated flowers were tagged, and umbels were covered again as soon as insertions had been done. The percent fruit-set from intra- and interpopulation cross-pollination was computed separately by using the following formula:

$$\text{\% fruit-set from cross-pollination} = \frac{\text{Total \# of fruits}}{\text{Total \# of ovaries used for cross-pollination}}$$

Again, developing follicles were closely monitored, and number of fruits aborted was recorded until mature follicles were harvested.

The level of self-compatibility was estimated by performing self-pollinations at ALP in 1997. Fifteen umbels, each from different plants, were sampled, bagged, and tagged prior to flower opening. Three 1- or 2-day-old flowers on each umbel (one flower per umbellet) were selected, and two 2-day-old pollinia from different flowers on the same umbel were separately inserted into the first and the fourth or the second and the fifth stigmatic chambers of a flower. The level of self-compatibility was computed by using the following formula:

$$\text{\% fruit-set from self-pollination} = \frac{\text{Total \# of fruits}}{\text{Total \# of ovaries used for self-pollination}}$$

Flowers with the inserted pollinia were bagged again and monitored until flowers withered. If follicles developed, they were closely monitored until mature, then harvested and their seeds counted.

Flowering Phenology and Insect Visitation

Twenty-five randomly selected plots (2 m × 2 m) were established at the ALP site prior to the beginning of the flowering season in 1998 to study flowering phenology. The number of open flowers on all umbels within each plot was counted once a week in the late afternoon. Individual inflorescences or umbels sampled in 1997 and 1998 for open pollination treatment were used to determine the number of flowers per inflorescence and flowering span. Flowering of each inflorescence was monitored from the first flower opening to senescence of the last flower.

Insect visitations were observed once a week during the flowering season in 1998. Also, a camcorder was used to record insect activities in the field. Three unmanipulated plots (2 m × 2 m) with abundant open flowers were selected for each observation day. Each plot was observed 10 min per h from morning (0800) until evening (2000). The number of visitations to all three selected plots was totaled as the number of visitations for the entire day, and proportion of visits per insect taxon was also calculated. During the flowering season, 24 umbellets composed of 356 flowers were collected, and the numbers of pollinia inserted and removed were scored to detect pollinator activities.

Throughout the entire flowering season, insects were collected in the adjacent area to count the number of pollinia on the body parts of different insect genera and to determine which were potential pollinators. To maintain the size of insect populations, insects with no pollinaria carried were recorded and released. On the other hand, some insects with pollinaria were killed, and the parts of the body on which pollinaria were carried were observed under a dissecting microscope.

Insertions of Pollinia

To estimate whether seed-set resulting from a successful cross-pollination is directly related to the orientation of the inserted pollinium, four different types of pollinium insertion were performed at the ALP site in 1998: vertical insertion with the convex edge towards the stigmatic surface (VTS), vertical insertion with the convex edge opposite the stigmatic surface (VOS), horizontal insertion with the convex edge towards the ground (HTG), and horizontal insertion with the convex edge opposite the ground (HOG). For each type of insertion, 25 umbels, each from a different plant, were sampled, tagged, and bagged with 15.4 cm × 20.3 cm [6 in × 8 in] pollination bags prior to flower opening. All cross pollinia were collected from 2-day-old flowers, and one cross pollinium was inserted into the stigmatic chamber of a 1- or 2-day-old flower. Three flowers per umbel were manipulated. Two umbels for each type of insertion were used every other day. After pollinia were inserted, umbels were rebagged to prevent further pollination. All developing follicles were monitored until mature follicles were harvested, and the number of seeds per follicle was counted.

Statistical Analyses

The significance level for all statistical tests performed in this study was $\alpha = 0.05$. To compare percent fruit-set resulting from open-pollination with fruit set from supplemental pollination and to compare fruit-set from intrapopulation crosses with that from interpopulation crosses, a test for equality of two percentages (Sokal and Rohlf 1969) was used. Natural fruit-set between the 1997 and 1998 flowering seasons was also tested by equality of two percentages. A two tailed *t*-test (Zar 1984) was used to analyze whether a significant difference occurs between seed-set resulting from open-pollination with that from supplemental, hand cross-, and hand self-pollinations.

RESULTS AND DISCUSSION

The Structure of the Gynostegium

Like the anatomical structure of the gynoecium of several *Asclepias* species previously described (Woodson 1947, 1954; Wyatt and Broyles 1994), the gynoecium of *A. viridis* is composed of two separate, superior ovaries united by their styles and fused with the stamens to form the gynostegium (Figure 5). Five concave surfaces, generally known as stigmatic surfaces, are located within the stigmatic chambers. In this study, however, the results indicate that the stigmatic surfaces are not those five concave surfaces, nor are they located in each of the five stigmatic chambers. In fact, the pair of anther wings extending from two adjacent anthers are partially fused with the stigmatic head at the base of the stigmatic chambers (Figure 6). At the base of the stigmatic chambers, the filaments join together into a tube surrounding the ovaries and styles (Walters and Keil 1996; Figure 7).

My anatomical data provide evidence to argue that the stigmatic chambers are actually part of the androecium, not the gynoecium. In addition, numerous cuboidal cells line up in the concave surface of the stigmatic chamber to form a rather smooth wall (Figure 8) and function as nectaries. Therefore, the stigmatic chamber may position the inserted pollinium and either promote or inhibit germination of pollen tubes depending on the concentration of nectar (Kevan et al. 1989; Sage et al. 1990). In fact, the stigmatic surfaces appear to consist of numerous elongate epidermal cells located at the base of the gynostegium where the two styles unite (Figure 9). Furthermore, after pollen tubes germinate in the stigmatic chamber, they penetrate through the nectary tissue beneath the stigmatic chamber and then grow through a cylinder-like space between the stigmatic chambers and the stigmatic surfaces

(Figure 10) to reach the stigmatic surfaces from which they grow into one of the styles.

My findings are similar to A. T. Brongniart's illustration in 1832 of the reproductive structures of a typical milkweed flower (Sundell 1984). After combining the above findings with the orientation of the furrow on top of the gynostegium in relation to the position of the two styles, not only does the furrow divide the five chambers into two groups, but it also separates the two styles along the point of fusion of the two styles. Nevertheless, one of the stigmatic chambers could still possibly transmit pollen tubes into both styles (Figure 11). This discovery may explain why pollen tubes occasionally cross over at the point of fusion of the two styles (Sparrow and Pearson 1948; Morse 1993; Wyatt and Broyles 1994) to produce twin follicles after a pollinium is inserted into that particular chamber. According to my anatomical data, two adjacent chambers (1, 2) on one side of the furrow can transmit pollen tubes to one ovary, and two other adjacent chambers (4, 5) on the other side of the furrow can transmit pollen tubes to the other ovary (Figure 12). However, chamber 3, in line with the furrow, can potentially transmit pollen tubes to either or both ovaries to produce twin follicles (see Figure 12). In Morse's (1993) study of *A. syriaca*, 29% of all hand-pollinations produce mature follicles, and 1.86% of mature follicles were twin follicles. However, he did not specify which chamber was assigned to perform the insertions. If the chambers were randomly assigned, the probability of selecting the particular chamber is 0.2. Then it can be predicted that the maximum percent of twinning would be 5.8% in his study. In contrast, an increase in the number of twin follicles produced from hand pollination with a single insertion could be anticipated if the chamber in line with the furrow is specifically assigned. To avoid "crossing-over" and to enhance the probability that all pollen tubes of a single pollinium enter only one of the ovaries, the particular stigmatic chamber assigned for an insertion is an important consideration.

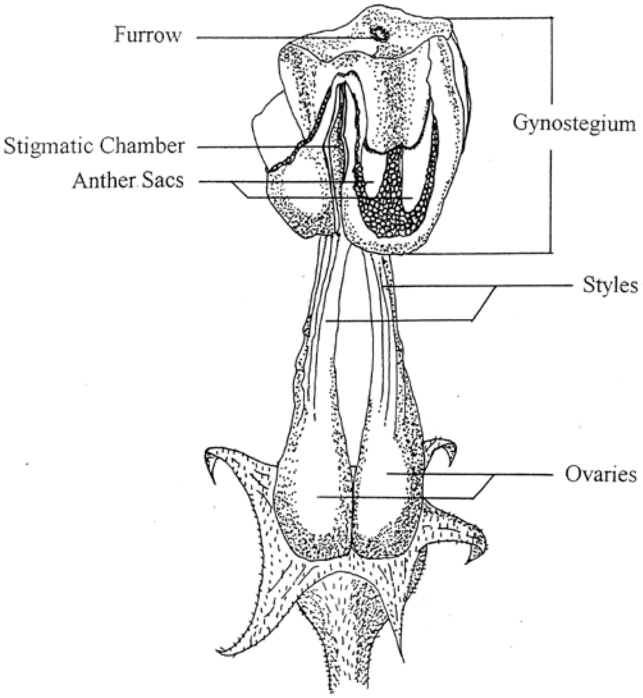


Figure 5 The reproductive structures of *Asclepias viridis*

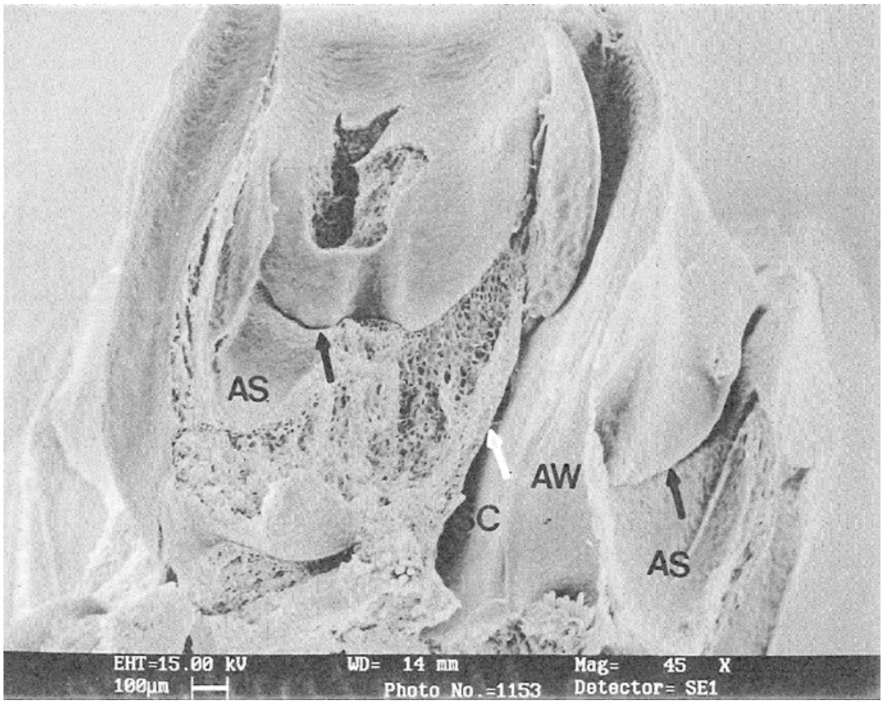


Figure 6 The relative position of the androecium and the gynoecium of the gynostegium of *Asclepias viridis*. The black arrows indicate the fusion between androecium and gynoecium and the white arrow indicates one of the anther wings (AW) removed to expose the stigmatic chamber (SC) to be part of the androecium. (Abbreviation: AS, anther sacs)

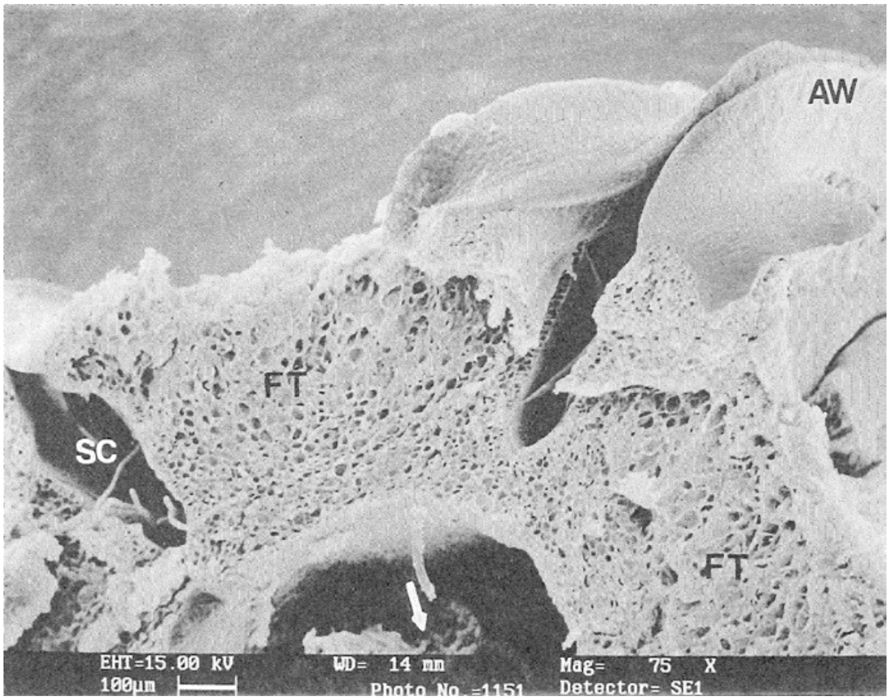


Figure 7 Filament tissue (FT) at the base of the androecium of the flower of *Asclepias viridis*. One of the styles is indicated by a white arrow. (Abbreviations: SC, stigmatic chamber; AW, anther wing)

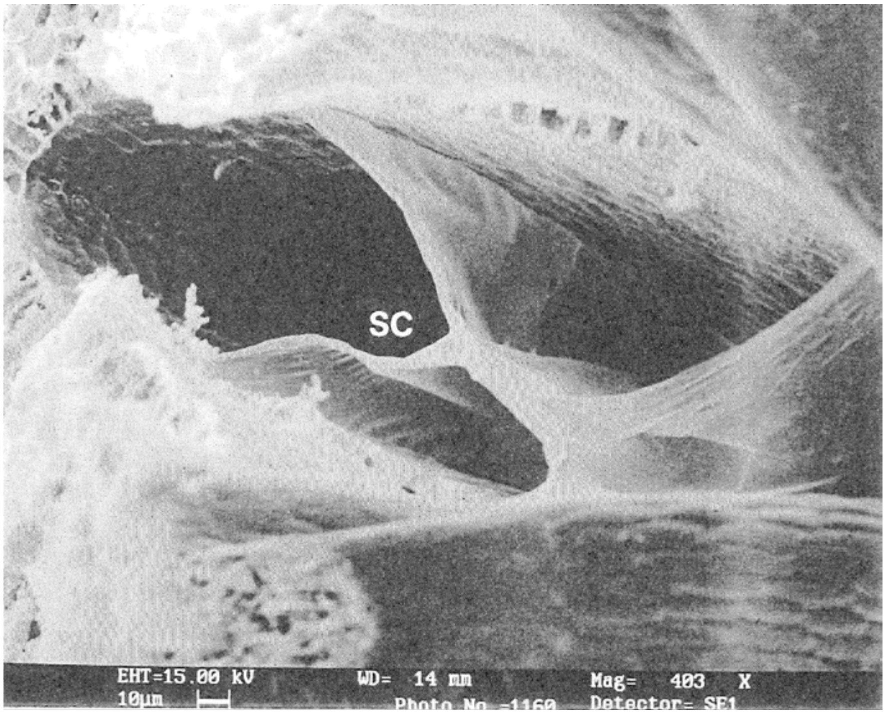


Figure 8 The stigmatic chamber (SC) and the nectaries of *Asclepias viridis* composed of numerous cuboidal cells

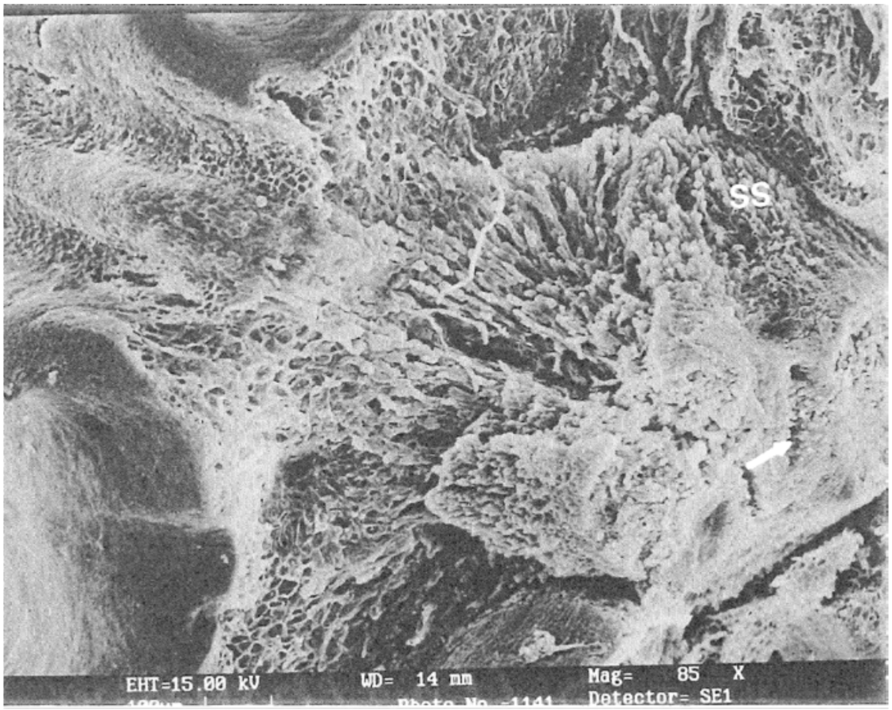


Figure 9 The stigmatic surface (SS) of flowers of *Asclepias viridis* at the base of the gynostegium. The white arrow in the lower right indicates the area of fusion of two styles.

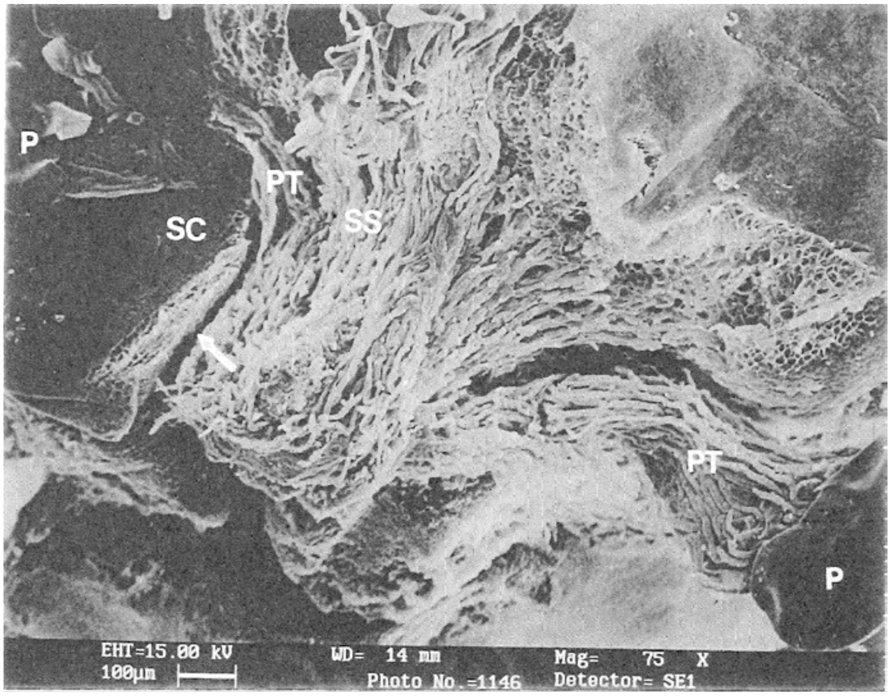


Figure 10 Pollen tubes (PT) of *Asclepias viridis* grow into the stigmatic surface (SS) after pollen grains germinate in the stigmatic chambers (SC). The cylinder-like space between the stigmatic chamber and the stigmatic surface is indicated by a white arrow. (Abbreviation: P, pollinium)

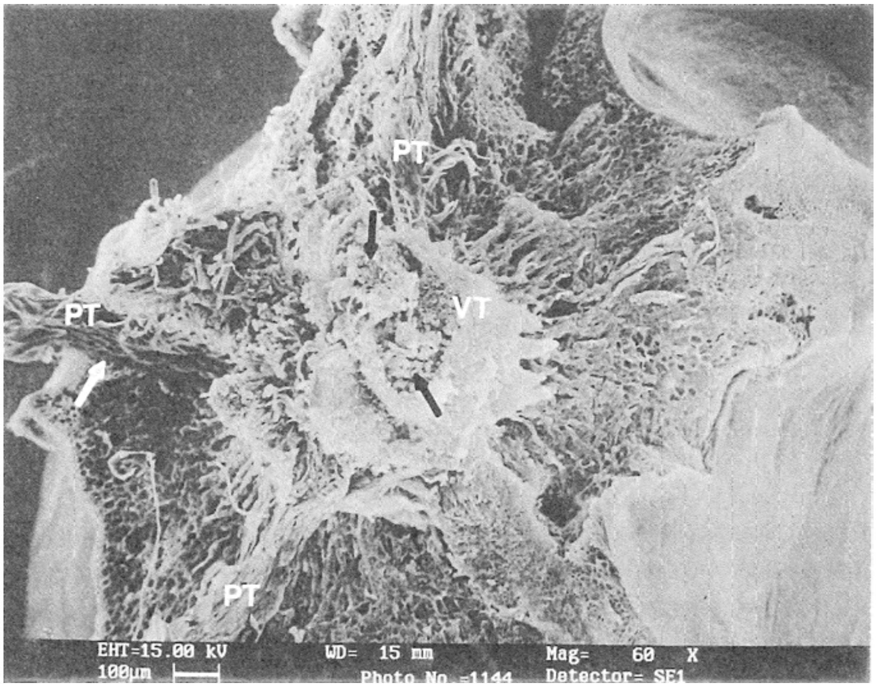


Figure 11 A view from the reverse side of the gynostegium of *Asclepias viridis* to show the relationship between the five stigmatic chambers and two styles. One of the chambers, indicated by a white arrow, can potentially transmit pollen tubes (PT) into both styles indicated by black arrows. (Abbreviation: VT, vascular tissue)

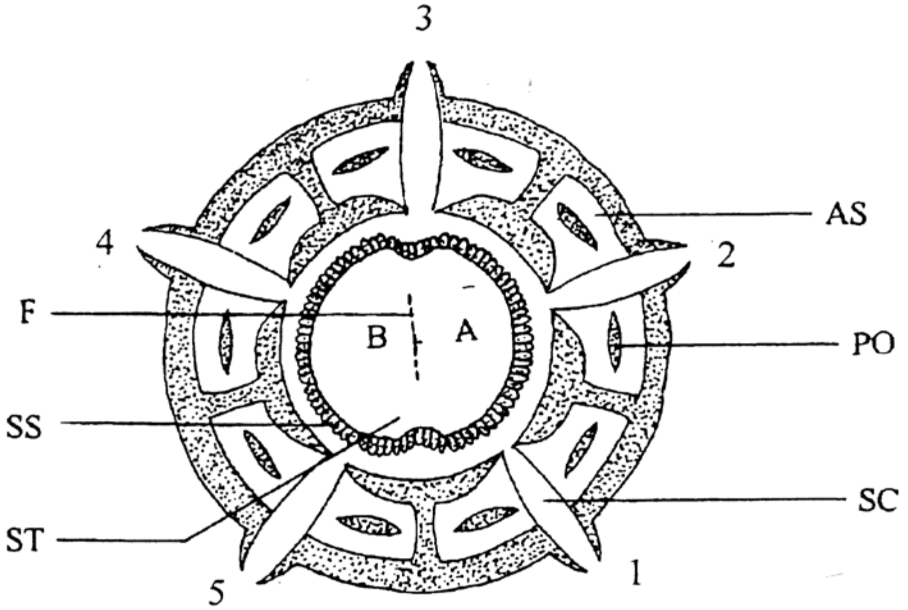


Figure 12 A transverse section of the gynostegium of *Asclepias viridis* shows the location of the stigmatic chambers (SC) relative to the styles (ST), the stigmatic surface (SS), and the furrow (F). Chambers 1 and 2 lead pollen tubes into style A, and chambers 4 and 5 lead pollen tubes into style B. Chamber 3 can possibly lead pollen tubes into styles A, B, or both ("cross-over"). (Abbreviations: AS, anther sac; P, pollinium)

Breeding System

Natural Fruit-Set, Predation, and Follicle Abortion

The overall percentage of natural fruit-set in the ALP population was 1.87% in 1997 and 1.39% in 1998 (Table 1). There was no statistically significant difference ($t = 1.786$, $P > 0.05$) in natural fruit-set between the two seasons. Similar results were also found on those tagged flowers for open pollination (see Table 1). A low level of young follicle production in my study may suggest that either a high level of self-pollen is deposited by pollinators, or insufficient pollination occurs in this population. After 24 umbellets composed of a total 356 flowers of different ages were examined for removal and insertion of pollinia (Figure 13), 87% of the pollinia, based on the lack of corpuscula on flowers, had been removed (9.2 ± 2.2 pollinia per flower; range 0–10), and 82% of sampled flowers had no corpuscula left. Ninety-one percent of flowers had been pollinated, and 58% of the slits were filled by at least one pollinium (2.9 ± 1.6 pollinia per flower; range 0–8) inserted by pollinators (see Figure 13). The natural insertion rate could be higher than these results indicate because some flowers on those umbels had not withered and could still attract pollinators. The results, however, suggest that pollinator limitation does not occur in this population because one cross pollinium is sufficient to initiate follicle production. Presumably, an insufficient number of pollen tubes germinating from compatible pollen and/or excessive self-pollination may be major causes of the failure of young follicles to be produced. In addition, my data show a

Table 1 Summary of breeding system of *Asclepias viridis*

Treatments	# of Infloescences	# of Ovaries	Flowers lost to predation	Very young follicle	Follicle abortion	Mature follicles*
Open 1997 Overall	70	4328	--	--	--	81 (1.87%)
1997 Tagged	70	420	--	--	--	8 (1.90%)
Open 1998 Overall	59	4320	359 (16.6%)	330 (7.6%)	243 (73.6%)	60 (1.39%)
1998 Tagged	59	354	--	--	--	5 (1.40%)
Supplemental 1998	25	150	--	--	--	5 (3.30%)
Selfed 1997	15	90	--	--	--	0
Crossed (at ALP)						
within population	15	90	3 (6.7%)	30 (35.7%)	21 (70.0%)	9 (10.7%)[a]
between population	15	90	3 (6.7%)	56 (66.7%)	34 (60.7%)	22 (26.2%)[a]
Crossed (at BSP)						
within population	15	90	9 (20.0%)	22 (30.6%)	16 (72.7%)	6 (8.3%)
between population	15	90	6 (13.3%)	54 (73.1%)	41 (75.9%)	13 (16.7%)

* Mature follicles were defined as follicles with fully developed seed when dehiscence occurred naturally.

-- No data were collected.

[a] Difference indicated is significant ($P < 0.05$) using the test for equality of percentages (Sokal and Rohlf, 1981).

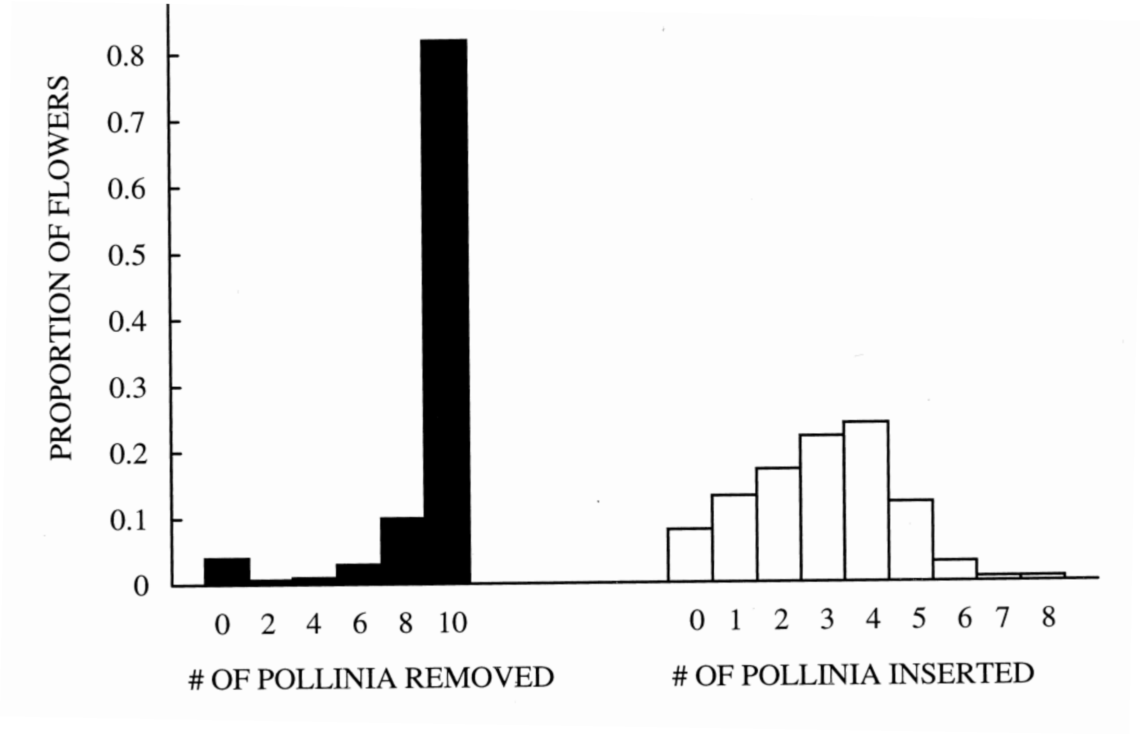


Figure 13 The proportion of flowers with different numbers of pollinia removed and inserted at the UCO Lake Arcadia Research Area. Removals of pollinia (0–10) were based on the numbers of missing corpuscula. Numbers of insertions from 0 to 8 (from left to right on insertions histogram) were based on the number of pollinia found in the stigmatic chambers. In some cases, more than two pollinia were counted in a single slit. A maximum of 8 inserted pollinia were scored. (N=356)

rather high level (about 17%) of flower and young follicle (about 8% of developing follicles) predation in this population. Particularly towards the end of the flowering season, phytophagous insects such as katydids (Tettigoniidae) severely attacked flowers, and over 27% of sampled flowers were consumed. Therefore, flower consumption by insects may also affect follicle production in natural populations.

In addition to low initiation of young follicles, the low level of fruit-set may result from a high level of follicle abortion in *Asclepias* populations. In my study, 73.6% of follicles from open pollination aborted at different sizes after initiated follicles became measurable (see Table 1). Abortion may be the major cause of failure of initiated follicles to mature, and two hypotheses, resource limitation and self-incompatibility, are often proposed to explain low fruit-set or low follicle survivorship (Shannon and Wyatt 1986; Wyatt and Broyles 1994).

The follicle survivorship curve for *A. viridis* (Figure 14) in my study shows that most mortality occurred before the follicles reached a length of about 4 cm (stage "d"). The effects of seed predators (*Oncopeltus* sp. and *Lygaeus* sp.) became detectable at later stages (stage "d" to maturity) of development. Particularly, clusters of *Lygaeus* sp. nymphs were often seen on mature follicles. However, they became common only later in the flowering season, so it is unlikely that they could be the primary cause of the decline of survivorship.

Therefore, I believe that mortality during the early stages of follicle development was caused by follicle abortion. Moreover, in my results from self-pollination and observations in the field, even though the pedicel of a self-pollinated flower showed a slight thickening in diameter, it never recurved over 90º from its original position on the peduncle before abscission occurred between the pedicel and peduncle. A cross-pollinated flower, in contrast, could be detected by a striking thickening and rapid recurving of the pedicel so that it became parallel with the peduncle and by continued development of the young follicle. Nevertheless, most developing follicles aborted before they were mature (2.14 cm ± 1.18 cm; mean ± SD; Figure 15). Unlike the self-pollinated young follicles, the aborted young follicles from cross-pollination generally remained on the stem with a "woody" pedicel. Flowers produced and cross-pollinated early in the flowering season seemed likely to develop into mature follicles successfully. On the other hand, follicles produced from the later cross-pollinated flowers on the same umbel generally aborted along the way before they reached maturity. This observation may suggest that competition for resources among developing follicles on a single plant of *A. viridis*, like in other studies (Willson and Price 1977; Queller 1985), may occur in my study population.

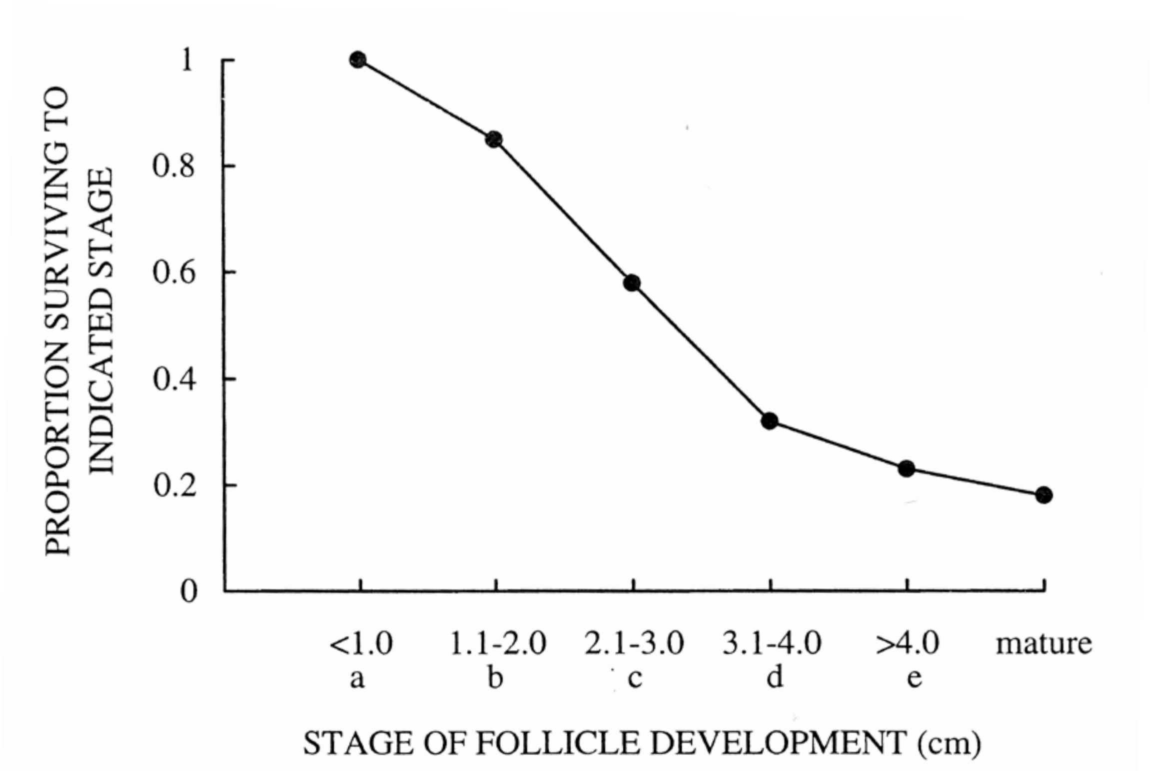


Figure 14 Survivorship curve of *Asclepias viridis* follicles at the UCO Lake Arcadia Research Area in 1998. The curve was based on aborted follicles which possibly resulted from cross-pollination in nature. (N=330)

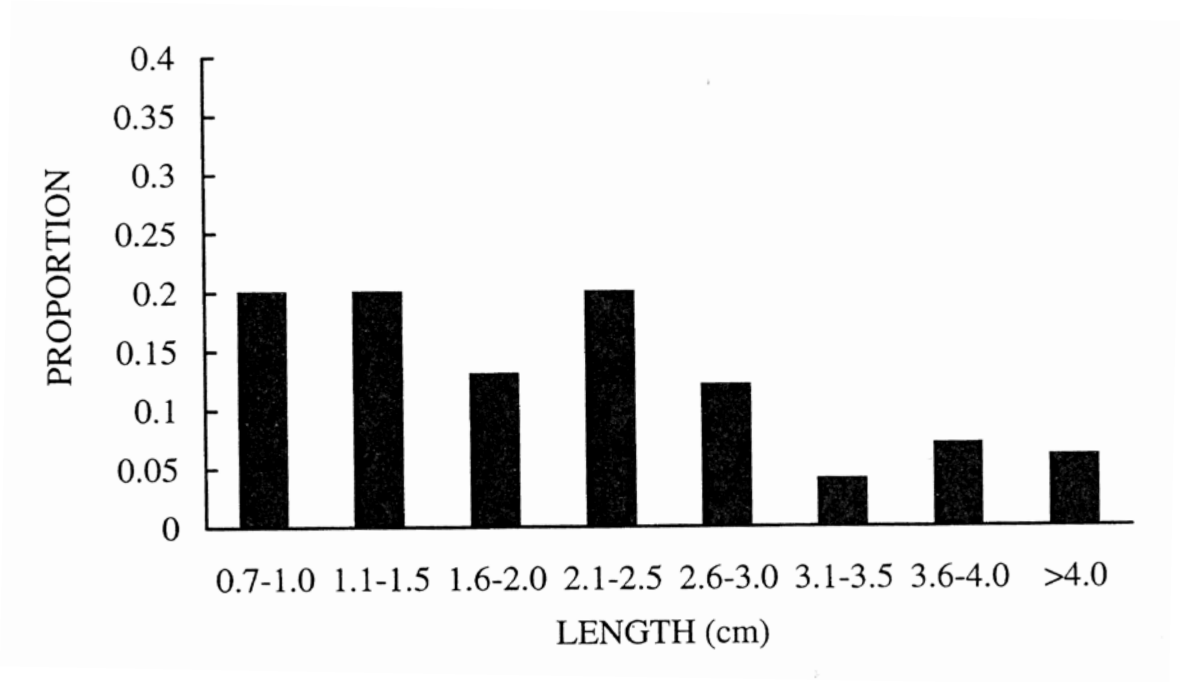
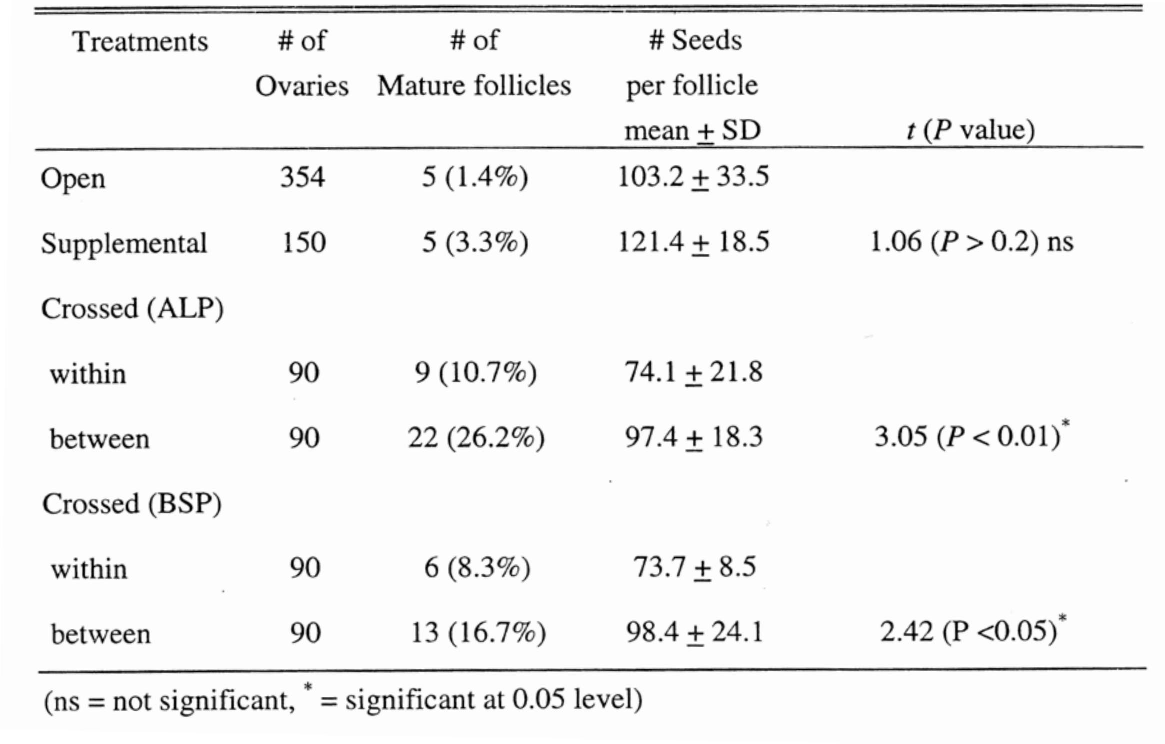


Figure 15 Proportion of aborted follicles of various lengths from open pollination of *Asclepias viridis* at the UCO Lake Arcadia Research Area in 1998 (mean ± SD = 2.14 cm ± 1.18 cm; N=138)

Table 2 Number of seeds in follicles resulting from pollination treatments and open pollination of *Asclepias viridis* during the 1998 flowering season



Treatments	# of Ovaries	# of Mature follicles	# Seeds per follicle mean ± SD	*t* (*P* value)
Open	354	5 (1.4%)	103.2 ± 33.5	
Supplemental	150	5 (3.3%)	121.4 ± 18.5	1.06 ($P > 0.2$) ns
Crossed (ALP)				
within	90	9 (10.7%)	74.1 ± 21.8	
between	90	22 (26.2%)	97.4 ± 18.3	3.05 ($P < 0.01$)*
Crossed (BSP)				
within	90	6 (8.3%)	73.7 ± 8.5	
between	90	13 (16.7%)	98.4 ± 24.1	2.42 (P <0.05)*

(ns = not significant, * = significant at 0.05 level)

Supplemental Pollination

Five out of 150 ovaries treated for supplemental pollination developed into mature follicles. The percent fruit-set (3.3%) for supplemental pollination was over twice that for open pollination for 1998 (see Table 1). However, this difference was not statistically significant ($t = 1.315$, $P > 0.1$). Moreover, although the number of apparently viable seeds per follicle was higher for supplemental pollination (121.4 ± 18.5) than for open pollination (103.2 ± 33.5; Table 2), there was not a statistically significant difference either ($t = 1.062$, $P > 0.2$). These results show that supplemental pollination of *A. viridis* is unable to increase fruit- and seed-set. The reason is perhaps pollen competition between self- and cross-pollen (Broyles and Wyatt 1993) in which self-pollen interferes with cross-pollen tubes and prevents them from penetrating the styles (Kahn and Morse 1991). As one properly inserted cross-pollinium is sufficient to initiate a young follicle which may reach maturity, subsequent pollinations in an *Asclepias* population seem only to play a minor role. Many studies (Ellstrand 1984; Schoen 1985; Brown et al. 1986) have shown that subsequent pollinations are successful in some species that disperse pollen grains individually, as evidence of multiple paternity was found among seeds within a fruit. However, multiple paternity occurs neither in *A. exaltata* (Broyles and Wyatt 1990) nor *A. syriaca* (Gold and Shore 1995) and may not occur among seeds within follicles of other *Asclepias* species.

Hand Cross-Pollination

At the ALP site, only nine follicles reached maturity from intrapopulation cross-pollinations; whereas, 22 mature follicles were harvested from interpopulation cross-pollinations. Six follicles were harvested from intrapopulation crosses and 13 follicles from interpopulation crosses from the BSP site. Follicle production at the ALP site was significantly different between the two treatments ($t = 2.65$, $P < 0.05$; see Table 1). Nevertheless, three developing follicles produced from the successful intrapopulation crosses were removed from the analysis due to seed predation. If these data were not excluded, follicle production would not be statistically different between the treatments at the ALP site ($t = 1.94$, $P > 0.05$). At the BSP site, follicle production between intra- and interpopulation crosses was not statistically different ($t = 1.58$, $P > 0.05$; see Table 1). However, follicles of interpopulation crosses produced higher seed-set than did follicles of intrapopulation crosses for both the ALP ($t = 3.05$, $P < 0.05$) and the BSP site ($t = 2.42$, $P < 0.05$; see Table 2).

My data from the ALP site are similar to Kephart's findings (1981) in which interpopulation cross-pollination yielded significantly higher fruit-set for both *A. incarnata* and *A. verticillata* but in contrast with Wyatt's findings (1976) for *A. tuberosa*. The "optimal outcrossing distance" has long been explained as the intermediate distances at which matings between individuals should produce the greatest fitness benefits (Waser and Price 1983; Kearns and Inouye 1993). It has been studied for some species (Price and Waser 1979; Sobrevila 1988) but has not yet been found for *Asclepias*. Kephart (1981) did not state the distance between the sampled populations in her study, but she explained that the different results for intra- and interpopulation cross-pollination was because of the lower similarity of S alleles between the individuals used for interpopulation crosses than for intrapopulation crosses. On the other hand, Wyatt (1976) suggested that crosses between highly dissimilar individuals from *A. tuberosa* populations 390 km apart might cause outbreeding depression leading to lower fruit-set. My results for both hand cross-pollination treatments at both sites suggest that neither an outbreeding depression nor an apparent inbreeding depression occurs between the two populations to lower the number of follicles produced from either intra- and interpopulation crosses. Nevertheless, results of seed production indicate that matings between individuals within these two isolated populations may affect seed-set in milkweed follicles. As suggested by Broyles and Wyatt (1991), mating between genetically similar individuals usually produced fruits with fewer viable seeds. Interestingly, 40% (20/50) of follicles produced from both hand cross-pollination treatments at both study sites were "twins." The percent of the twin follicles produced from double insertions is higher than in other studies (Sage, Broyles, and Wyatt 1990).

Self-Pollination

None of 90 self-pollinated ovaries successfully produced mature follicles at the ALP site in 1997 (see Table 1). This demonstrates that strong self-incompatibility occurs in *A. viridis*. In my study, 64 self-fertilized ovaries (71.1%) showed slight enlargement, pubescence, and usually remained green for 10–12 days, but no further development showed before they aborted. On the other hand, the rest of the self-pollinated ovaries that did not show these phenomena usually only remained for several days before abscission occurred. Recently, Wyatt and Broyles (1994) suggested that an ovarian self-incompatibility system, in which pollen tubes are rejected before or after penetrating ovules, typically occurs in *Asclepias*. Similarly, Kahn and Morse (1991) described a post fertilization incompatibility system, in which the embryo does not divide after self-pollenated tubes penetrate ovules in their *A. syriaca* population.

Flowering Phenology

In 1998, *A. viridis* began flowering in early May and reached its flowering peak in late May (Figure 16). Flowering densities declined from the third week (late May) after the beginning of flowering, and no flowers were observed in experimental plots in the seventh week. In general, the flowering period of *A. viridis* in my study area was seven weeks, even though a few open flowers were occasionally seen in late June. The mean number of flowers produced per inflorescence was 34.1 (SD = 10.2, range 14–69, N = 115; Figure 17). The mean flowering span (time from first flower opening to senescence of the last flower) per inflorescence was 10.6 d (SD = 0.99, range 7–13, N = 15).

Flower Visitors and Insect Visitation

Flower Visitors

Flowers of *A. viridis* were visited by at least 20 families of the orders Hymenoptera, Lepidoptera, Coleoptera, and Hemiptera. Occasional visits were recorded from other orders as well (Table 3). Overall, Hymenoptera are apparently the most frequent vectors, as 67% of captured Hymenoptera were carrying pollinaria (Table 4). This included 87% of captured Scoliidae (wasps), 98% of Apidae (bumblebees; *Bombus* spp.), and 68% of Anthophoridae (carpenter and digger bees). Among hymenopterans, *Bombus* spp. are the most active pollinators of *A. viridis*, based on the numbers of pollinaria carried (Figure 18). Of scored corpuscula, 94% were attached to their front legs (Figure 19). Bumblebees carried as many as 186 corpuscula on their front legs, with the corpusculum channel of one pollinarium hooked to a seta, and the other pollinaria linked together with the corpusculum channel of one pollinarium hooked to a translator arm of another pollinarium (Figure 20). During field observations, I noted that after bumblebees landed on flowers, they frequently brushed against the gynostegium rapidly with their front legs. This behavior might help to position their bodies on flowers while they take nectar, and it might enhance their efficiency in removing and inserting pollinia. In contrast, other hymenopterans, such as large carpenter bees (*Xylocopa*; Anthophoridae) and wasps, generally either sat on flowers or gently manipulated flowers for nectar. Consequently, their behavior may result in less contact with the gynostegium and result in removal of fewer pollinaria from flowers.

Even though halictid bees (Halictidae) and paper wasps (Vespidae) carry pollinaria of other *Asclepias* species (Macior 1965; Fishbein and Venable 1996), they did not carry pollinaria of *A. viridis*. Most of the time, halictid bees landed on one of the hoods to consume nectar and rarely contacted the gynostegium. Presumably, their small body size relative to the flower size and their behavior at the flowers restricted contact with the gynostegium. On the other hand, paper wasps landed just momentarily; this behavior and the reduced setae of their appendages may be factors contributing to the absence of pollinaria on their bodies.

Lepidoptera rarely carried the pollinaria of *A. viridis* in my study population, unlike observations for other *Asclepias* species (Willson et al. 1979; Fishbein and Venable 1996). Only one pollinarium, which was attached to a front leg, was found on the 43 captured individuals in the family Lycaenidae (see Table 4). No pollinaria were carried by 57 common skippers (Hesperiidae) captured in the field. Monarchs (Danaidae) and sulfur butterflies (Pieridae) were occasionally observed during the flowering season, but no visitations were recorded at plots.

One out of 109 captured soldier beetles (Cantharidae) carried a pollinarium on a mouth part. Soldier beetles visited flowers and chewed on the flower parts, mostly hoods, and fed on nectar. Due to the lack of sufficient field data, whether soldier beetles are able to function as pollinators in this population is still unknown. Families Lygaeidae and Pentatomidae of Hemiptera presumably only fed on vascular sap or nectar, due to their behavior at the flowers, and carried no pollinaria (see Table 4). Although flies (Diptera) also occasionally visited flowers of *A. viridis*, they were not collected. Therefore, their role in this plant population is uncertain.

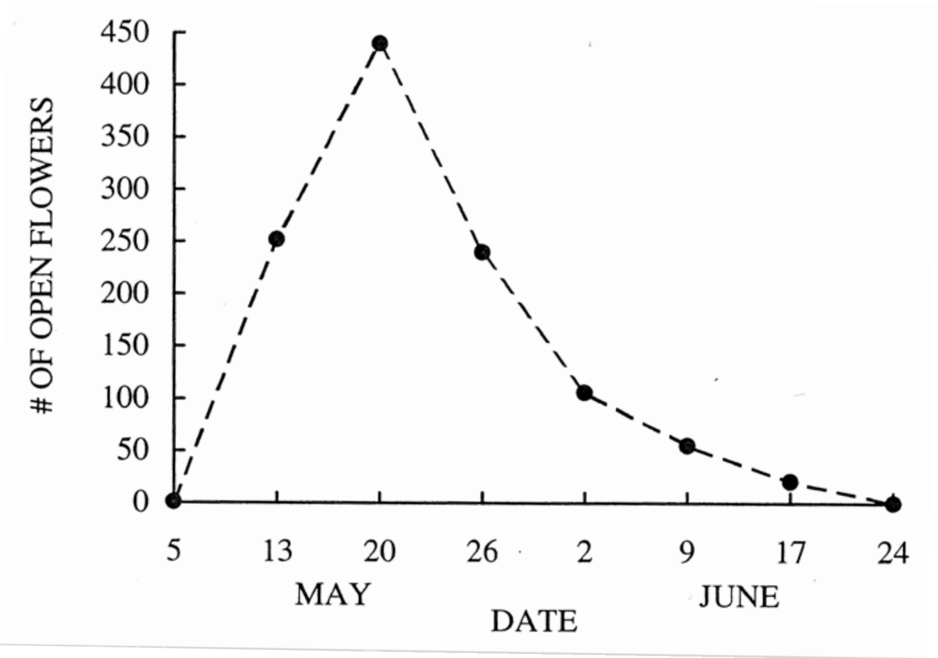


Figure 16 Flowering phenology of *Asclepias viridis* at the UCO Lake Arcadia Research Area in 1998. The flowering peak occurred in late May.

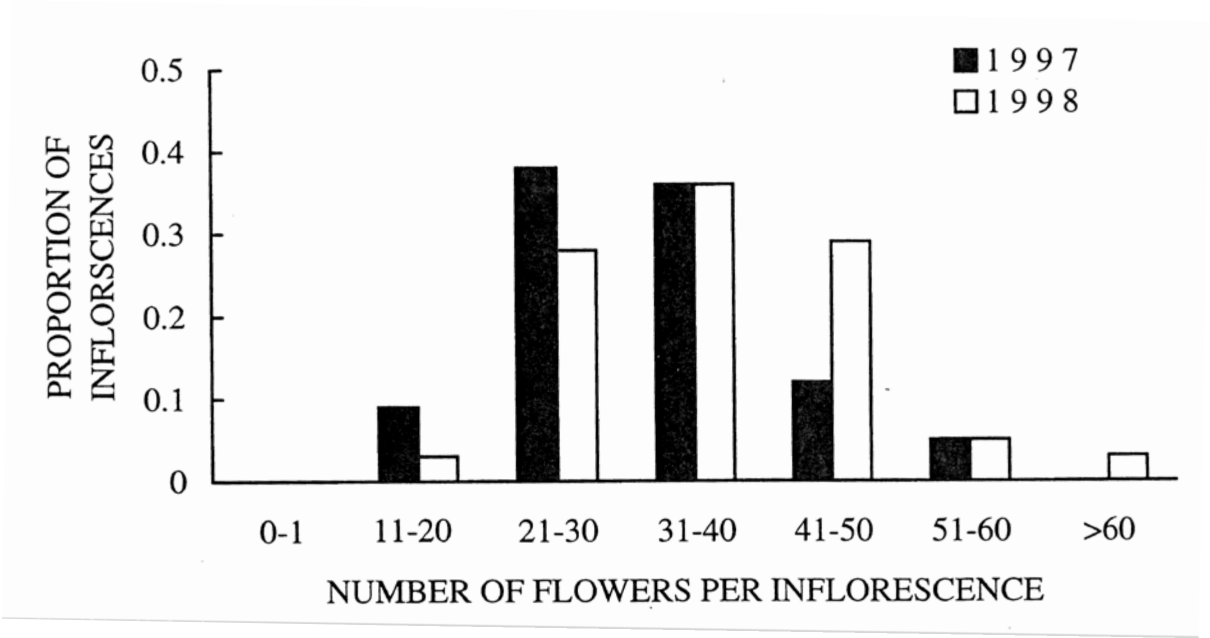


Figure 17 Proportion of *Asclepias viridis* inflorescences with different numbers of flowers at the UCO Lake Arcadia Research Area during the 1997 and 1998 seasons

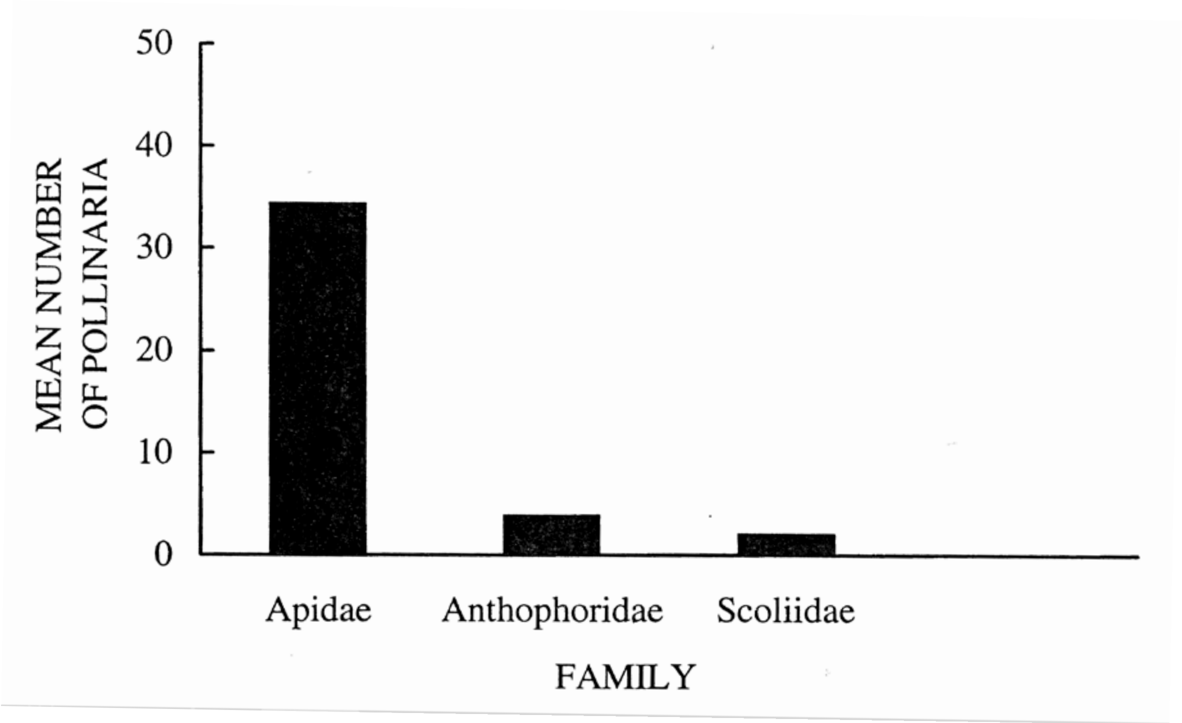
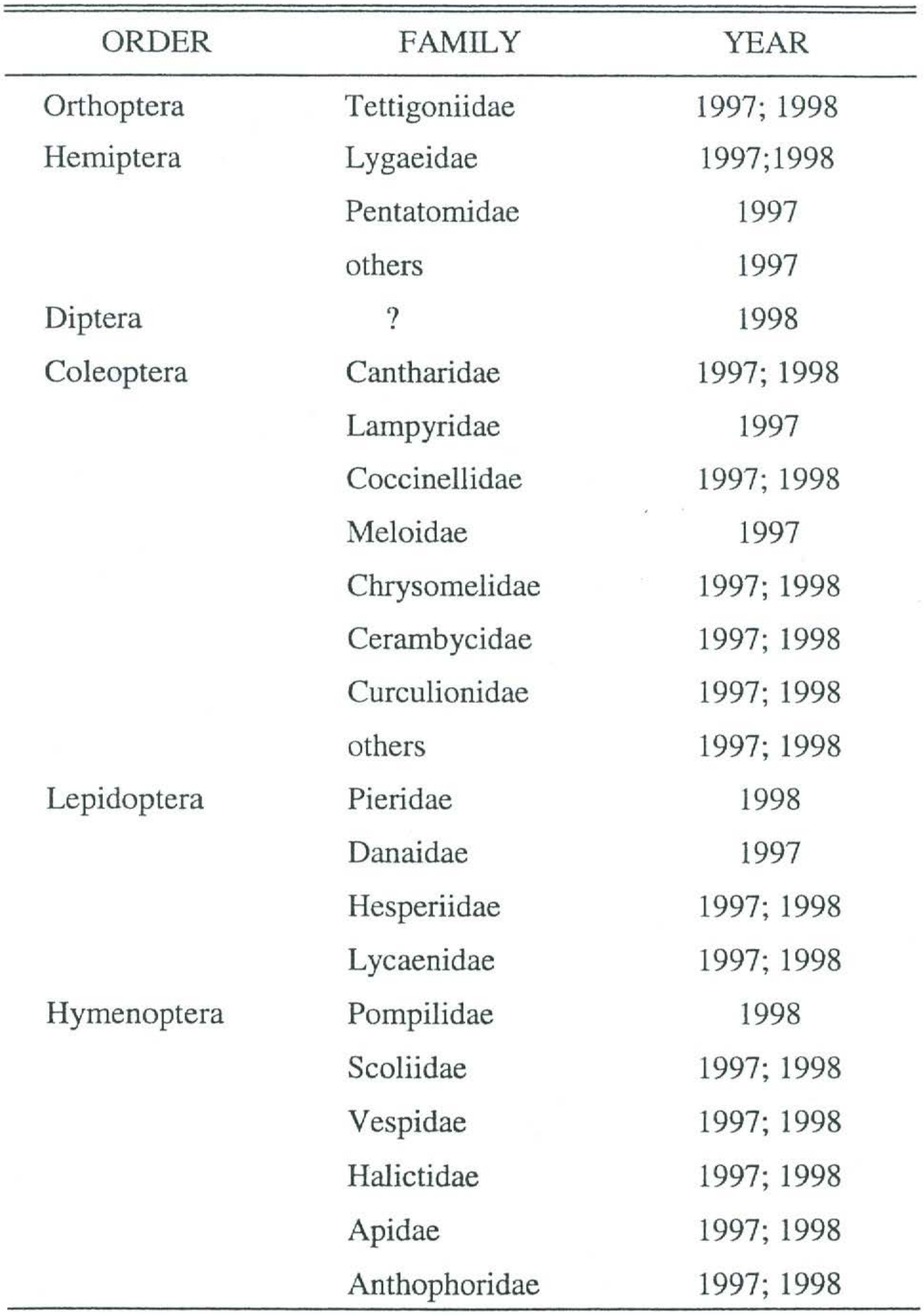


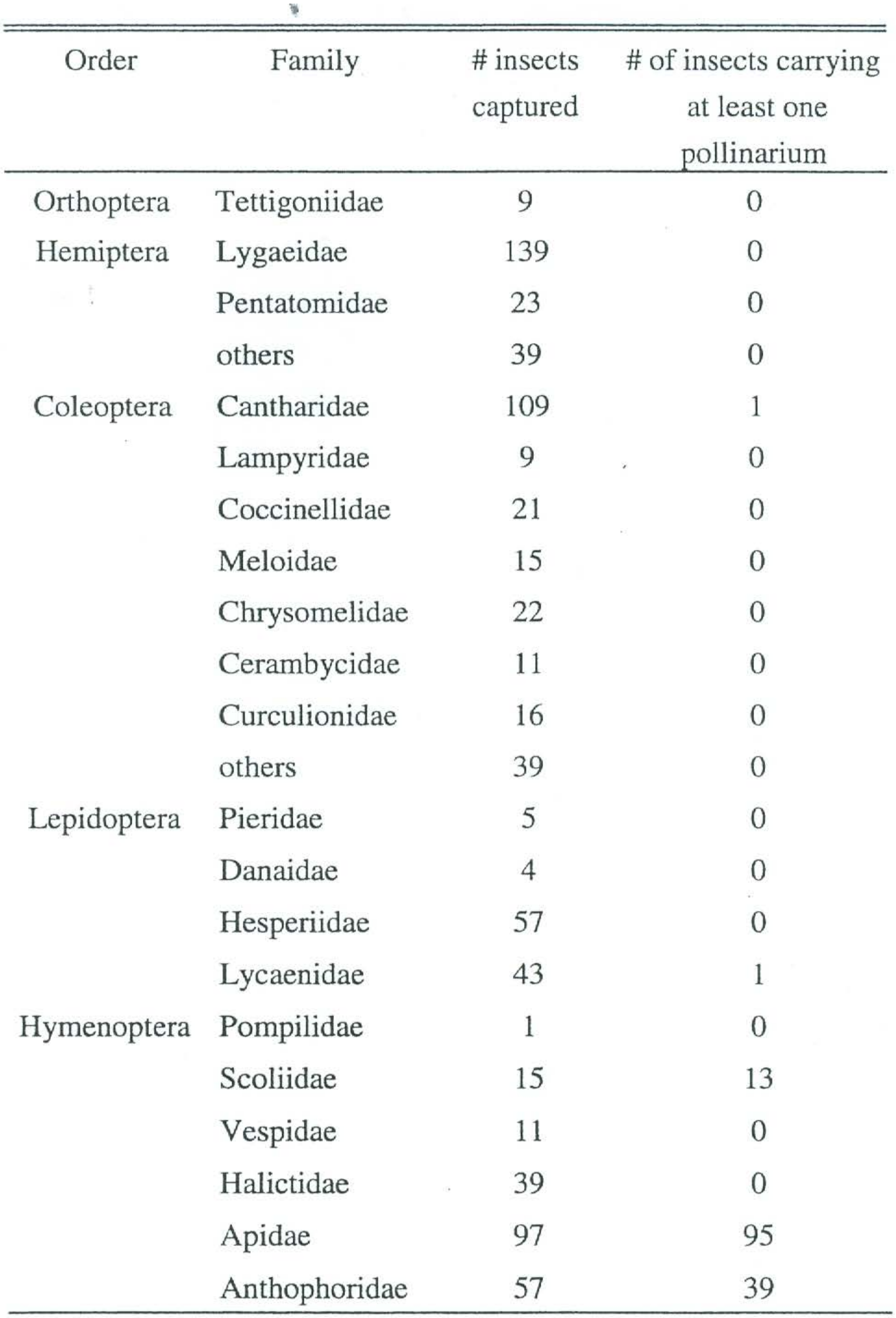
Figure 18 Average number of pollinaria scored from collected hymenopteran visitors to flowers of *Asclepias viridis* at the UCO Lake Arcadia Research Area in the 1997 and 1998 flowering seasons

Table 3 Orders and families of flower visitors to *Asclepias viridis* at the UCO Lake Arcadia Research Area during the 1997 and 1998 flowering seasons. Question mark (?) indicates that dipteran visitors were rarely observed landing on the flowers but were not collected.



ORDER	FAMILY	YEAR
Orthoptera	Tettigoniidae	1997; 1998
Hemiptera	Lygaeidae	1997;1998
	Pentatomidae	1997
	others	1997
Diptera	?	1998
Coleoptera	Cantharidae	1997; 1998
	Lampyridae	1997
	Coccinellidae	1997; 1998
	Meloidae	1997
	Chrysomelidae	1997; 1998
	Cerambycidae	1997; 1998
	Curculionidae	1997; 1998
	others	1997; 1998
Lepidoptera	Pieridae	1998
	Danaidae	1997
	Hesperiidae	1997; 1998
	Lycaenidae	1997; 1998
Hymenoptera	Pompilidae	1998
	Scoliidae	1997; 1998
	Vespidae	1997; 1998
	Halictidae	1997; 1998
	Apidae	1997; 1998
	Anthophoridae	1997; 1998

Table 4 Numbers of captured visitors from different families, and of those, numbers carrying at least one pollinarium. Data were collected during the flowering season of *Asclepias viridis* at the UCO Lake Arcadia Research Area in 1997 and 1998.



Order	Family	# insects captured	# of insects carrying at least one pollinarium
Orthoptera	Tettigoniidae	9	0
Hemiptera	Lygaeidae	139	0
	Pentatomidae	23	0
	others	39	0
Coleoptera	Cantharidae	109	1
	Lampyridae	9	0
	Coccinellidae	21	0
	Meloidae	15	0
	Chrysomelidae	22	0
	Cerambycidae	11	0
	Curculionidae	16	0
	others	39	0
Lepidoptera	Pieridae	5	0
	Danaidae	4	0
	Hesperiidae	57	0
	Lycaenidae	43	1
Hymenoptera	Pompilidae	1	0
	Scoliidae	15	13
	Vespidae	11	0
	Halictidae	39	0
	Apidae	97	95
	Anthophoridae	57	39

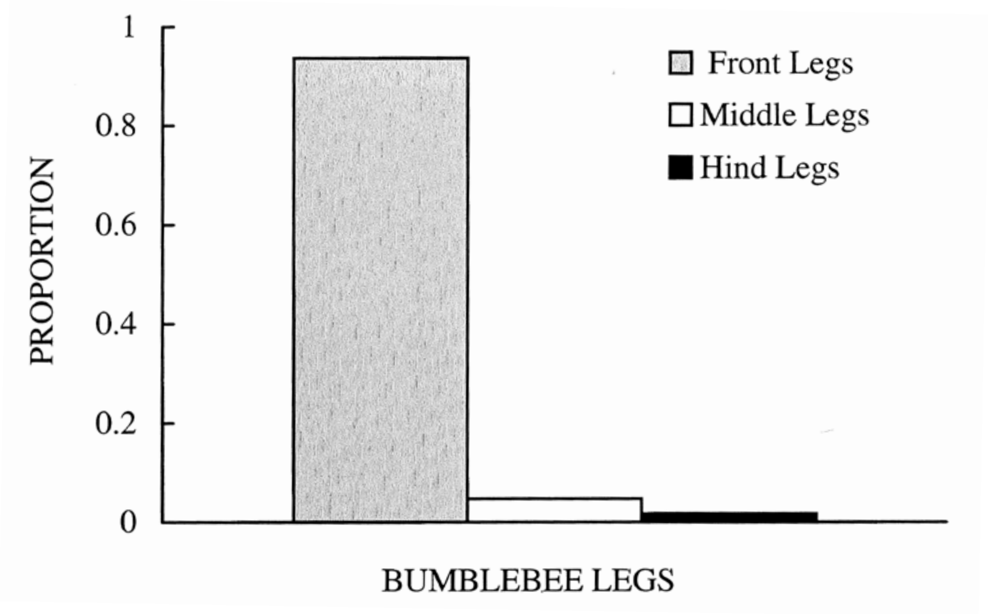


Figure 19 Proportion of pollinaria of *Asclepias viridis* on front, middle, and hind legs of bumblebees (*Bombus* spp.) collected at the UCO Lake Arcadia Research Area during the 1997 and 1998 flowering seasons

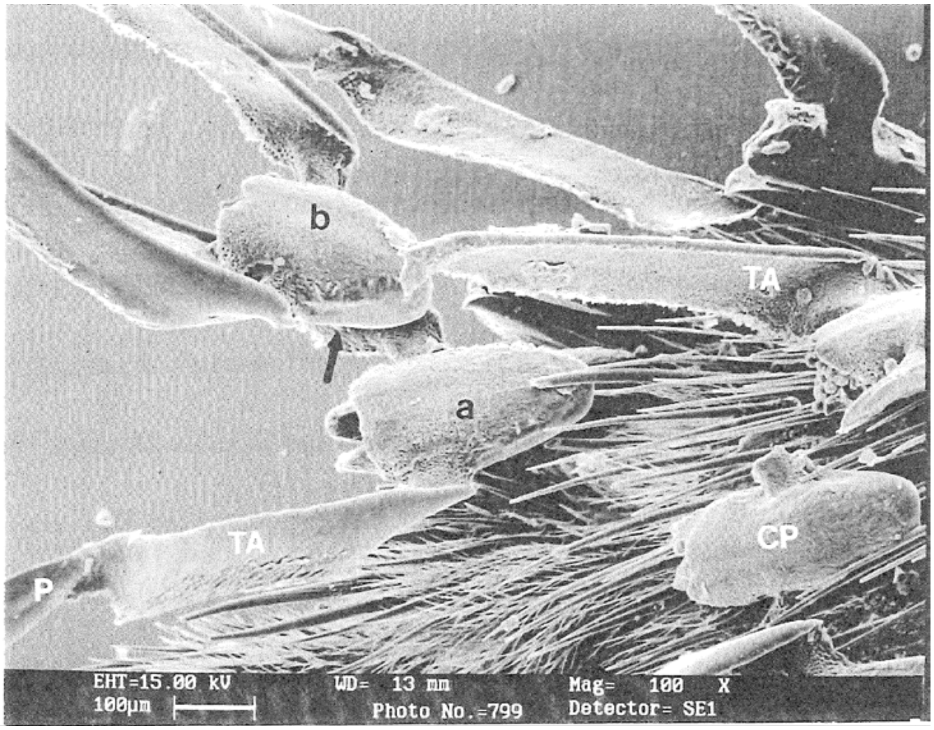


Figure 20 Several pollinaria of *Asclepias viridis* attached to a leg of a bumblebee (*Bombus* sp.). In this SEM picture, pollinarium "a" is directly attached on the leg by its corpusculum (CP). On the other hand, pollinarium "b" is attached to pollinarium "a" by clipping its corpusculum onto one of the translator arms (TA) of pollinarium "a", as indicated by a black arrow. (Abbreviation: P, pollinium) Photograph by D. Elmendorf.

Insect Visitation

Hymenoptera accounted for 74% of overall visitation at the ALP site (Figure 21), of which Scoliidae, Anthophoridae, and Apidae accounted for 98% (Figure 22). *Bombus* spp. (Apidae) were the most frequent hymenopteran vectors, accounting for 73% of hymenopteran visitation and 53% of overall visitation. In general, hymenopterans visited flowers of *A. viridis* during all daily observation periods during the flowering season (Figure 23). Although bumblebees visited flowers from morning to evening, more visitations were recorded in the mid-afternoon to early evening (1400–2000) rather than in the morning to early afternoon (0800–1400). During the flowering season, carpenter bees were observed for the first three weeks and were rarely observed after the mid-flowering season (Figure 24). On the other hand, visitation by bumblebees to flowers gradually declined towards the mid-flowering season (mid-May to late-May) and increased towards the latter period of the flowering season (early-June to mid-June). This visitation pattern is perhaps related to flower density, which increased from mid-May to late-May and declined from late-May to mid-June. As flower density increased, this could have led to fewer visits per individual plant.

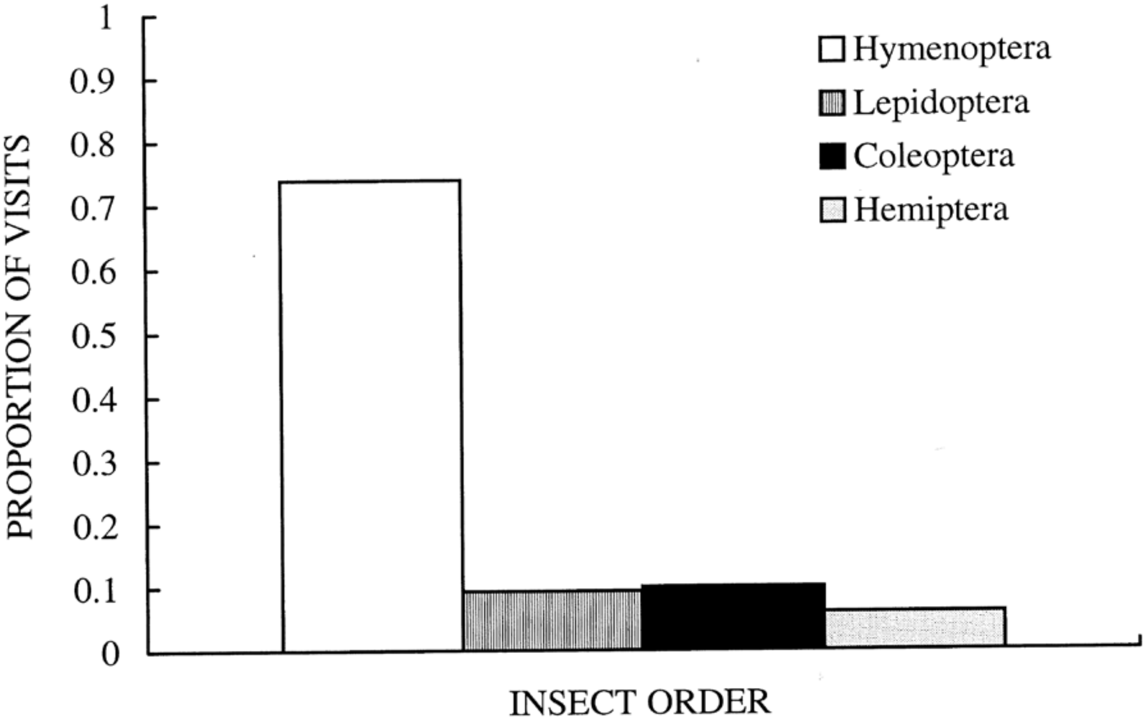


Figure 21 Proportion of visits by insect orders to flowers of *Asclepias viridis* at the UCO Lake Arcadia Research Area during the 1998 flowering season

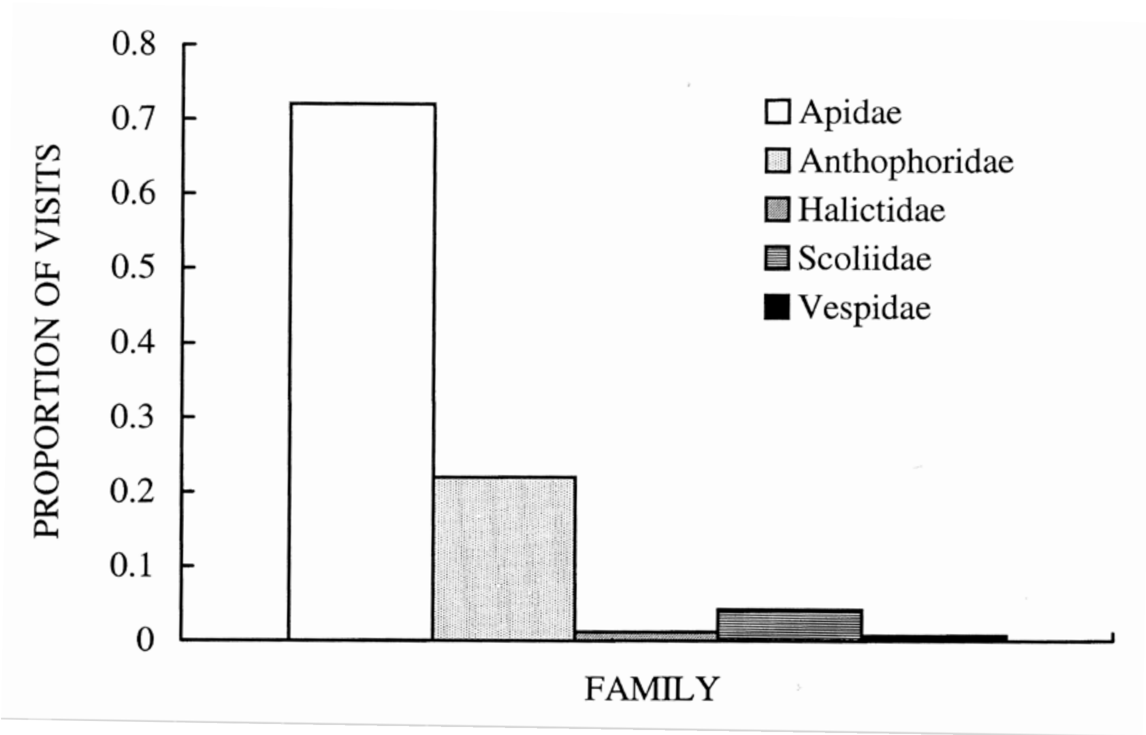


Figure 22 Proportion of visits by hymenopteran families to flowers of *Asclepias viridis* at the UCO Lake Arcadia Research Area during the 1998 flowering season

Pollinia Insertion

Eleven mature follicles were harvested from the VTS group (vertical insertion with the convex edge towards the stigmatic surface), and two mature follicles were harvested from the HOG group (horizontal insertion with the convex edge opposite the ground). Neither the VOS group (vertical insertion with the convex edge opposite the stigmatic surface) nor the HTG group (horizontal insertion with the convex edge towards the ground) produced mature follicles (Table 5). A statistical test was not performed due to insufficient data. Nevertheless, the percentage of mature follicles in the VTS group was apparently higher than in other groups, and pollinia are almost always inserted into the slits by insects in this manner in natural populations. Wyatt (1976) observed over 500 pollinia insertions of *A. tuberosa*, and all pollinia were inserted into the chambers with the convex edge brought into contact with the inner surfaces of the chambers. From my observation of 1035 pollinia insertions of *A. viridis*, almost all of them were inserted in this same manner. It is not surprising to obtain mature follicles from the HOG group. Although this type of insertion (HOG) was rare, a few were observed on flowers of collected umbels with the pollen tubes growing into the stigmatic chambers. However, this type of insertion perhaps occurs accidentally as flowers are visited by insects, such as when breakage occurs between the translator arms and the pollinium before the pollinium is oriented properly into a slit. A microscopic study of some flowers collected with the VOS and HTG types of insertions revealed that most pollen did not germinate, or pollen tubes were exposed outside of the slits and dried out in a few cases.

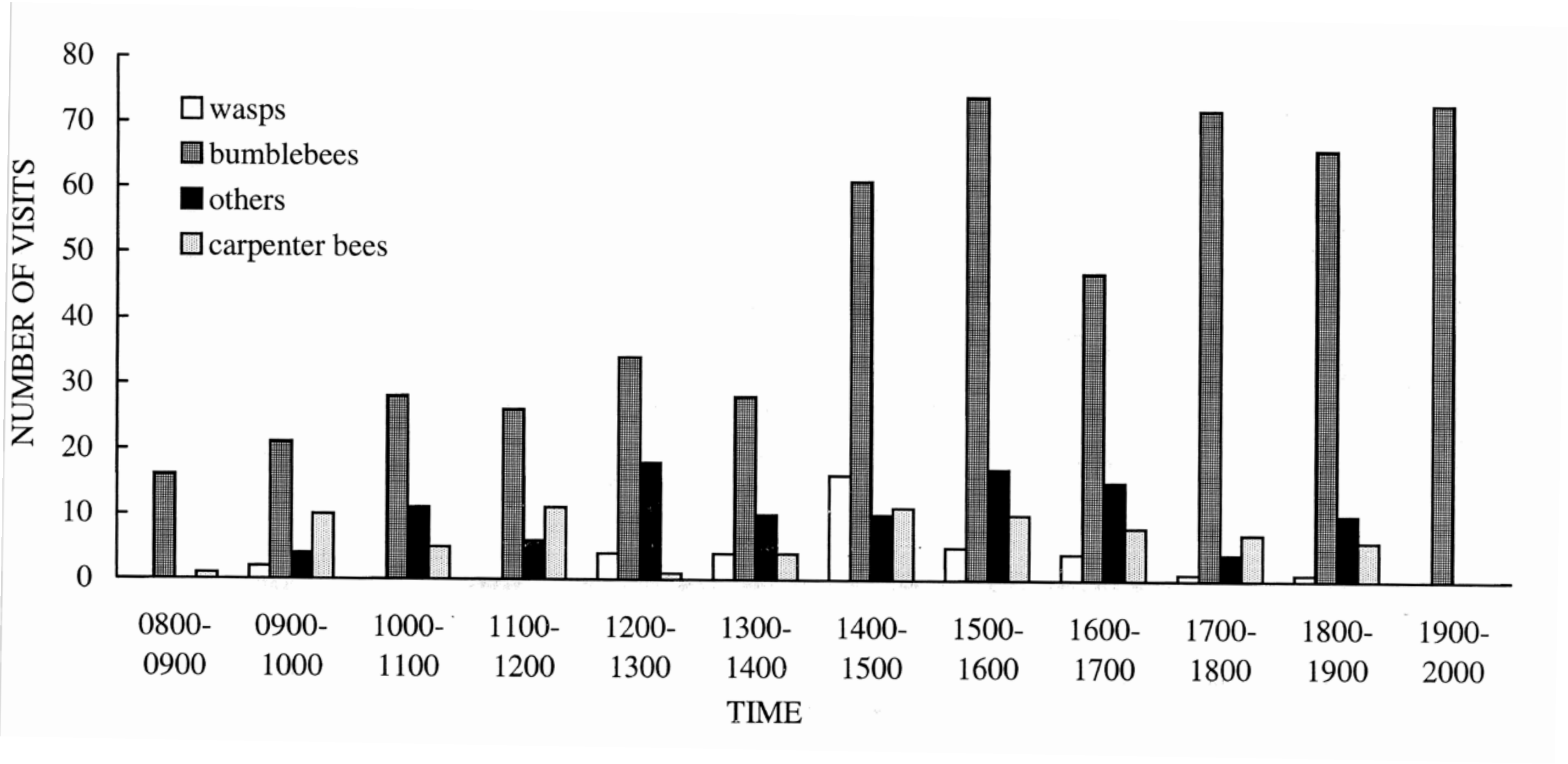


Figure 23 Number of visits by different hymenopterans to flowers of *Asclepias viridis* at the UCO Lake Arcadia Research Area during combined hourly observation periods in the 1998 flowering season. Insect visitation was observed once a week. Three plots (2 m × 2 m) were selected in the morning, and each was observed ten min per h.

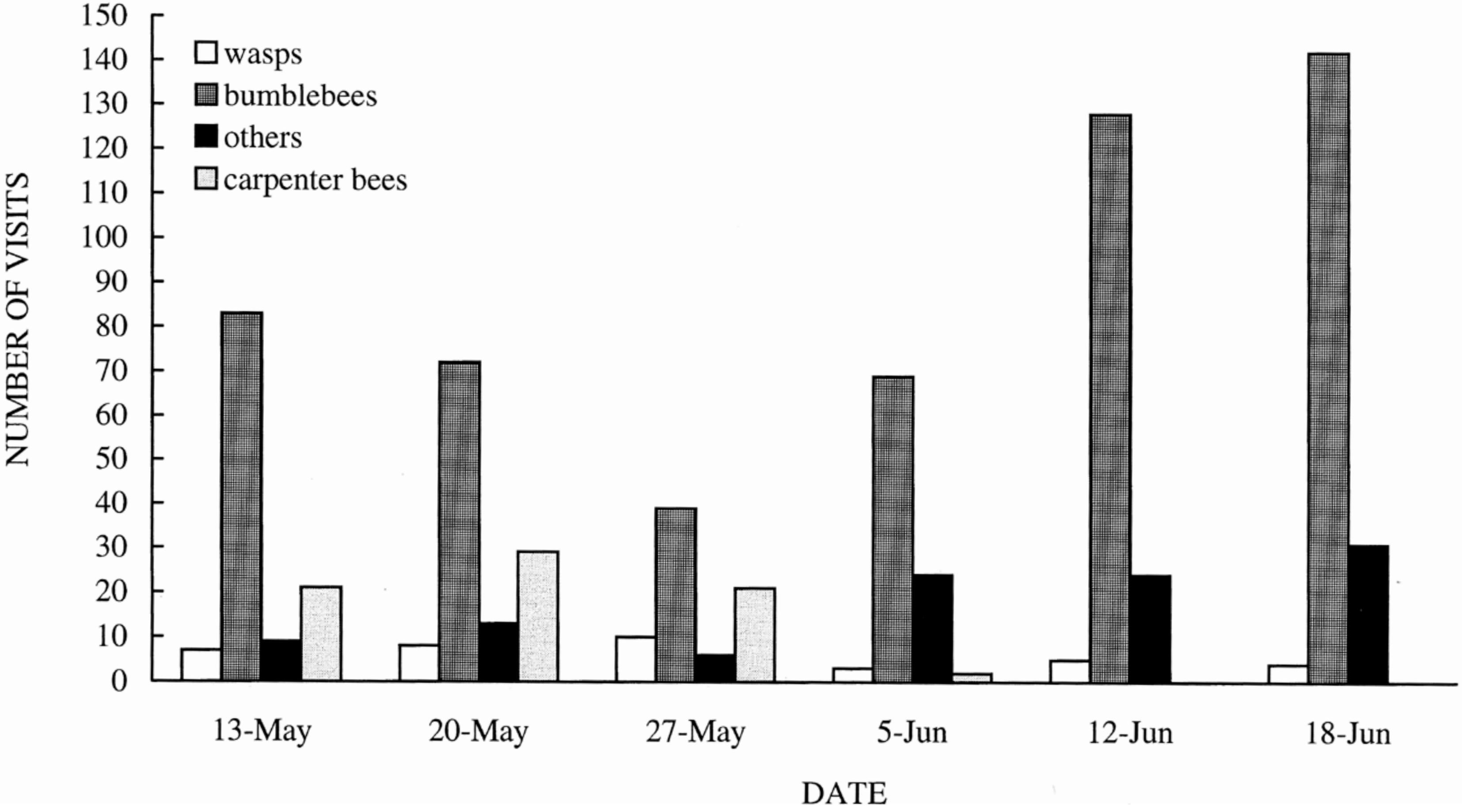


Figure 24 Number of visits by hymenopterans to flowers of *Asclepias viridis* at the UCO Lake Arcadia Research Area during the 1998 flowering season

Table 5 Fruit-set percentages for four different types of pollinium insertions for *Asclepias viridis*

Type of insertion	# attempted	# of mature follicles *	%
VTS	75	11	14.7
VOS	75	0	0.0
HTG	75	0	0.0
HOG	75	2	2.7

* Mature follicles were defined as follicles with fully developed seed when dehiscence occurs naturally.

Abbreviations: VTS, vertical insertion with the convex edge towards the stigmatic surface; VOS, vertical insertion with the convex edge opposite the stigmatic surface; HTG, horizontal insertion with the convex edge towards the ground; HOG, horizontal insertion with the convex edge opposite the ground.

CONCLUSIONS

The scanning electron microscope (SEM) study of the gynostegium provides the first three-dimensional observation of the spatial relationship between the gynoecium and androecium and also provides anatomical data to show that the most probable stigmatic surface is not within the stigmatic chambers but at the point of fusion of the two styles. The SEM pictures also show that pollen tubes from one chamber could enter either style. This may uncover the mystery of twinning in some *Asclepias* studied to date (Sparrow and Pearson 1948; Kephart 1981; Broyles and Wyatt 1990; Morse 1993) and suggest that chamber selection should be taken into account when pollinia are inserted if twinning is to be avoided.

Like some species of *Asclepias* investigated thus far (Wyatt and Broyles 1994), *A. viridis* appears to be entirely self-incompatible. Therefore, it is not surprising to obtain a low percent of natural fruit-set, an average of 1.6% in this study, even when pollinator insufficiency is excluded. Many of the pollinaria inserted into flowers may contain incompatible pollen. In addition, although resource limitation resulting in follicle abortion is another factor limiting follicle production in this natural population, other factors such as flower and follicle predation and plant diseases also contribute to the low natural fruit-set.

Lack of pollination does not appear to limit fruit-set in *A. viridis*. Of flowers collected, 91% had been pollinated, and supplemental pollination did not enhance fruit- or seed-set. Unlike other angiosperms that disperse pollen individually, several hundred pollen grains of *Asclepias* are dispersed and deposited in the stigmatic chambers as a unit by vectors. Not only is a single pollinium sufficient to produce a follicle, but it also can occasionally result in production of twin follicles. My anatomical observations of the gynostegium show that some pollen tubes grew on the stigmatic surface along the style instead of entering a stylar canal. This suggests that pollen tubes from a previously inserted pollinium may fully occupy the stylar canal. Consequently, pollen tubes from a second or a third inserted pollinium may be rejected and forced to grow along the styles. Nevertheless, further anatomical observations of the growth of pollen tubes into the styles are needed to support this viewpoint.

Many studies of hand-pollinations for *Asclepias* have been accomplished in greenhouses in which many environmental conditions, such as temperature, humidity, plant diseases, and predation, can be controlled to minimize the variables affecting results. The average success of intrapopulation crosses in this study was lower than in other published records for *Asclepias*. This may be due to intrinsic factors such as incompatibility of alleles and timing of nectar secretion or extrinsic factors such as humidty and temperature, which may dramatically affect the sugar concentration in nectar throughout a day and indirectly affect germination of pollen.

In agreement with other studies (Frost 1965; Macior 1965; Fishbein and Venable 1996), my data on flower-visiting taxa of *A. viridis*, including pollinaria carried by vectors and their visitation rates, indicate that hymenopterans are the most common pollinators associated with *Asclepias*. Among those, *Bombus* spp. are the most important because of their high visitation rate and ability to carry pollinaria. However, their pollination effectiveness in the population is still uncertain due to the lack of data on pollinia removal and insertion rates for this group alone. Large carpenter bees and some wasps also appear to function as pollinators. Many visitors of other families are suspected to be nectar robbers based on their visiting behavior such as idleness or long residence time on a single flower (small-sized lepidopterans and halictid bees), small body size mismatched to the flowers of *A. viridis* (halictid bees), and reduced tarsal hairs (paper wasps).

Many studies (Pleasants 1980; Gross and Werner 1983; Kephart 1983; Campbell 1985) suggest that insect visits to flowers are often associated with flowering phenology, and flowers within species or between species may, therefore, compete for pollinators when flower densities increase among species in a community. Combining my data on phenology and insect visitation, the visitation rate decreased as the flower density increased early in the flowering season, and the visitation rate of insect taxa increased as flower density decreased towards the late flowering season. Therefore, competition for pollination among individuals of *A. viridis* may occur.

In terms of the reproductive strategies of *A. viridis*, many factors, such as genetic barriers, timing of pollination, timing of nectar secretion, and resource limitation, appear to determine which pollinia result in mature follicles. Therefore, most flowers would play the role of pollen donor rather than pollen recipient. Furthermore, a successful cross-pollination of *Asclepias* may be primarily affected by the concentration of nectar. Whether genetic barriers or resource limitation play a major role in controlling fruit-set in a population of *Asclepias* is an interesting question to be studied in the future.

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A FLORISTIC INVENTORY OF THE UNIVERSITY OF OKLAHOMA'S KESSLER ATMOSPHERIC AND ECOLOGICAL FIELD STATION, MCCLAIN COUNTY, OKLAHOMA

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ABSTRACT

This paper reports the results of a vascular plant inventory at the University of Oklahoma's Kessler Atmospheric and Ecological Field Station in McClain County in the state of Oklahoma. A total of 388 taxa in 80 families were collected. Two hundred and fifty-seven genera, 361 species, and 27 infraspecific taxa were identified. The largest families were the Poaceae with 66 taxa and the Asteraceae with 55 taxa. Fifty-seven taxa were planted or non-native to the U.S. (14.7 % of the flora). Four taxa tracked by the Oklahoma Natural Heritage Inventory were found.

INTRODUCTION AND STUDY AREA

The Kessler Atmospheric and Ecological Field Station (KAEFS) at the University of Oklahoma was established on properties donated by Dr. Edwin Kessler from 1988 to 2011 (http://kaefs.ou.edu/). Located approximately 28 km southwest of the Norman campus, KAEFS promotes and facilitates collaborative research and learning. The station hosts both formal and informal courses, workshops, and numerous meteorological and biological experiments, including a long-term global warming experiment. The goal of this work was to compile a complete list of vascular plant taxa present at the site to assist current and future KAEFS researchers in species identification and documentation.

KAEFS occupies 146 ha in McClain County in central Oklahoma approximately 13 km from the town of Washington (Figure 1). Latitudinal extent ranges from 34°58'15.99"N to 34°59'10.61"N and longitudinal extent from 97°30'32.88"W to 97°31'42.63"W. Physiographically, the site is located within the Western Red-bed Plains geomorphic province, which consists of gently rolling hills of red sandstone and shale of Permian age (Curtis et al. 2008; Johnson 2008). Two soil associations predominate at KAEFS: the Nash-Lucent-Grant (deep to shallow, gently sloping to moderately steep loams over sandstone uplands) and the Port-Pulaski-Keokuk (deep, nearly level loamy soils on floodplains; Moebius and Sparwasser 1979). KAEFS is located within the subtropical humid (Cf) climate zone (Trewartha 1968), with a mean annual temperature of 16ºC. Low temperatures (to 3ºC) occur in January, while the warmest temperatures occur in July (to 28ºC; Oklahoma Climatological Survey 2016). The month of May is typically the wettest, with an average precipitation of 13.5 cm. Mean annual precipitation is

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96.7 cm (Oklahoma Climatological Survey 2016). Elevation ranges from 332 m to 343 m. The dominant potential vegetation type is tallgrass prairie (Duck and Fletcher 1943).

The KAEFS property has a long history of farming and livestock grazing. The first homestead was established in 1904, and crops such as cotton, sorghum, and wheat were grown on the property up until the early 1970s. The property has an equally long history of cattle grazing, and a small herd still roams the grasslands today (http://kaefs.ou.edu/). A population of the Mediterranean basin native *Carthamus lanatus* L. was discovered at the site in the mid-1970s and grew to approximately 3000 plants by 1989. It was eradicated in the early 1990s with a strict regime of hand-pulling (Kessler unpublished).

METHODS

Vouchers of vascular plant taxa encountered at KAEFS were made throughout the growing seasons (March through October) of 2013, 2014, and 2015. Vouchers for U.S. non-native or planted taxa were only collected from naturalized populations. Specimens were processed according to standard procedures. In addition to these vouchers, collections from an earlier, unpublished study were also examined to see if additional taxa had been collected. Manuals used for identification included Diggs et al. (1999) and Tyrl et al. (2015). Identifications were verified by comparison with specimens from the Robert Bebb Herbarium at the University of Oklahoma (OKL). Duration, growth habit, vegetation type, and nativity were determined using the PLANTS database (USDA-NRSC 2016) and Taylor and Taylor (1991). Classification and nomenclature follow Angiosperm Phylogeny Group III (Stevens 2001 onward) and the Integrated Taxonomic Information System (ITIS 2016). All specimens were deposited at OKL.

RESULTS AND DISCUSSION

A total of 388 taxa in 80 families were collected (Appendix). Two hundred and fifty-seven genera, 361 species, and 27 infraspecific taxa were identified. Two hundred and fifty-two taxa were perennials; there were 133 annuals and three biennials. The largest families were the Poaceae with 66 taxa and the Asteraceae with 55 taxa. Two-hundred and fifty-one taxa were forbs, and 91 were graminoids. There were 26 trees, 12 shrubs, and eight vines. Four taxa tracked by the Oklahoma Natural Heritage Inventory were found (Table 1). Three-hundred and seventy-nine of the 388 taxa were collected by the authors. Nine additional taxa were found during an earlier survey by former KAEFS researcher Becky Sherry.

Fifty-seven taxa were planted and naturalized or non-native to the U.S. (14.7 % of the flora). Fifty-six of these were non-native. This number is high when compared to surveys from other Oklahoma grassland-dominated sites (Table 2), but it is not surprising given the land use history at KAEFS. *Taxodium distichum*, which is native to southeastern Oklahoma, was also found but was planted by the former property owner and has since naturalized. The Poaceae had the greatest number of exotic taxa with 13. The Fabaceae followed with nine exotics. *Carthamus lanatus*, reported from the property as late as 1991, was not relocated (Kessler 1987; Hoagland et al. 2012; Kessler unpublished).

The predominant vegetation type encountered at KAEFS was the *Schizachyrium scoparium-Sorghastrum nutans* association, a herbaceous vegetation type found throughout Oklahoma on uplands with well-drained soils. Associated taxa included *Amorpha canescens*, *Dichanthelium oligosanthes* var. *oligosanthes*, *Panicum virgatum*, and *Symphotrichum ericoides* var. *ericoides* (Hoagland 2000).

We encountered three community types dominated by woody plants at KAEFS. The *Populus deltoides-Ulmus americana-Celtis laevigata* forest association was found on the bottomlands surrounding the property's larger order streams. This vegetation type is found frequently throughout the state (excluding the panhandle) on moist or wet soils along riparian corridors. Associated taxa found in this association included *Carya illinoinensis, Symphoricarpos orbiculatus,* and *Toxicodendron radicans* (Hoagland 2000). Small stands of *Quercus muehlenbergii* were encountered in mesic situations. Associated taxa included *Amphicarpaea bracteata, Desmodium glutinosum, Elephantopus carolinianus,* and *Phryma leptostachya.* Upland woodlands of the *Juniperus virginiana-Schizachyrium scoparium* association intergraded with the grasslands and the riparian zones of low order streams. This vegetation type is common throughout Oklahoma (excluding the panhandle) and is the product of fire suppression and land-use change. Associated taxa included *Andropogon virginicus, Cirsium altissimum, Quercus marilandica,* and *Smilax bona-nox* (Hoagland 2000).

Herbaceous wetland vegetation was restricted to ponds and creek channels. Plants found in this type included *Coleataenia anceps, Juncus torreyi, Lycopus americanus, Teucrium canadense,* and the invasive aquatic *Myriophyllum spicatum*. Disturbed areas included an area around a barn, the parking lots, and gravel roads. Plants in these areas included *Mollugo verticillata, Muhlenbergia paniculata, Polygonum ramosissimum,* and *Solanum rostratum*.

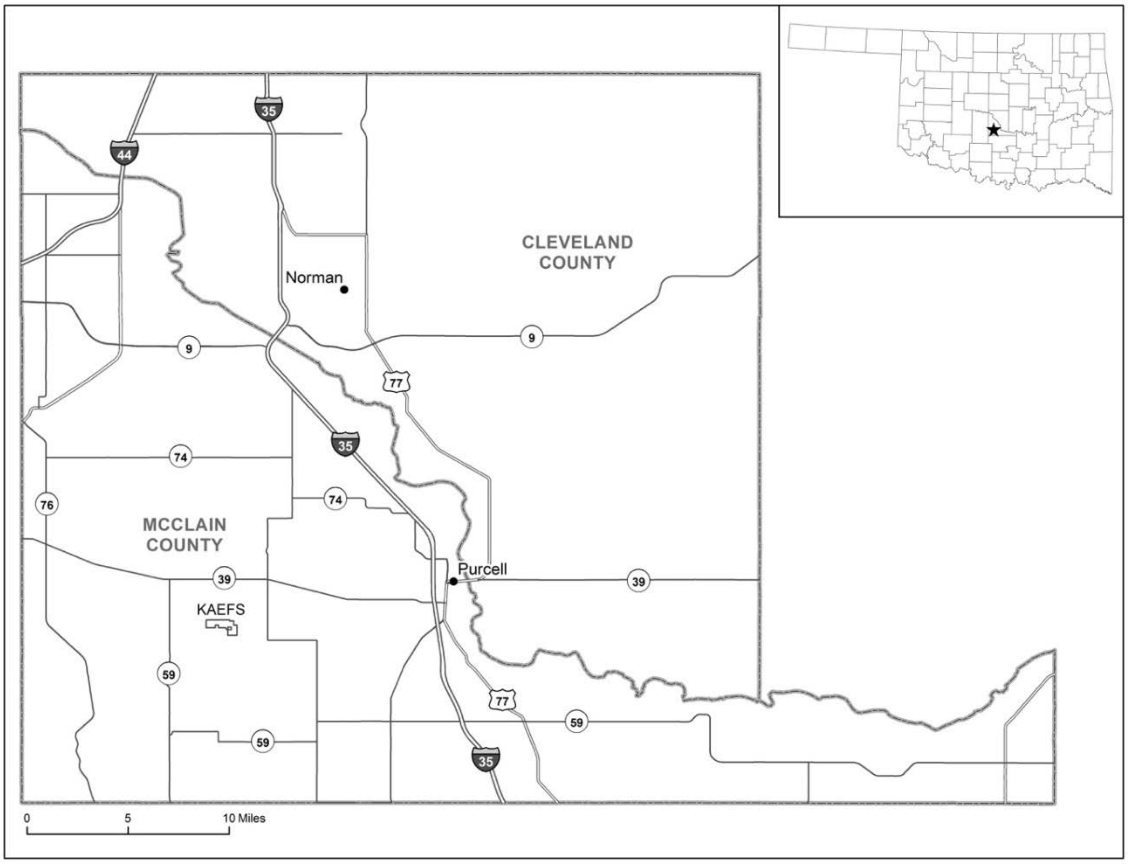

Figure 1 The Kessler Atmospheric and Ecological Field Station. Map by Todd Fagin, Oklahoma Biological Survey

Table 1 Taxa located during this study that are tracked by the Oklahoma Natural Heritage Inventory (Groves 1995; NatureServe Explorer 2016; Oklahoma Natural Heritage Inventory 2016). Status ranks are on a 1–5 scale, with a 1 indicating the taxon is critically imperiled. G ranks are at the global level, and S ranks are at the subnational or state level. Infraspecific taxa are assigned a T rank.

Family	**Taxon**	**Rank**
Convolvulaceae	*Ipomoea shumardiana* (Torr.) Shinners	S3G2G3
Cyperaceae	*Eleocharis geniculata* (L.) Roem. & Schult.	S2G5
Fabaceae	*Desmodium nuttalllii* (Schindl.) B.G. Schub.	S1G5
Plantaginaceae	*Plantago elongata* Pursh ssp. *elongata*	S3T3G4T4

Table 2 Comparison of exotic taxa from the KAEFS site with other Oklahoma grassland-dominated sites

Study site	**Reference**	**Size of site (ha)**	**Number of taxa found**	**Percentage of non-native taxa**
Kessler Atmospheric and Ecological Field Station, McClain County	This paper	146.0	388	14.7%
Pontotoc Ridge Nature Preserve, Johnston and Pontotoc Counties	Buthod et al., in preparation	848.2	616	8.8%
Tulsa Botanic Garden, Osage County	Hoagland and Buthod 2007	69.0	293	15.0%
Camp Kickapoo Boy Scout Camp, Canadian County	Hoagland and Buthod 2006	64.7	334	12.3%
Selman Living Laboratory, Woodward County	Buckallew and Caddell 2003	129.5	229	9.0%

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APPENDIX

List of Plant Taxa from the University of Oklahoma's Kessler Atmospheric and Ecological Field Station, McClain County, Oklahoma

Taxa list with duration, growth habit, vegetation type, and nativity. A=annual, B=biennial, P=perennial; F=forb, G=graminoid, S=shrub, T=tree, V=woody vine; DA=disturbed area, GL=*Schizachyrium scoparium-Sorghastrum nutans* grassland, HWV=herbaceous wetland vegetation, MF=*Quercus muehlenbergii* mesic forest, SBL=*Populus delotides-Ulmus americana-Celtis laevigata* stream bottomland, UWL=*Juniperus virginiana-Schizachyrium scoparium* upland woodland. An asterisk (*) indicates a taxon that is non-native to the United States. A tilde (~) indicates a taxon that is planted but native to Oklahoma. A dagger (†) indicates a tracked taxon. Duration and nativity were determined using the PLANTS Database (USDA-NRSC 2016); if the information from PLANTS was ambiguous, Taylor and Taylor (1991) was consulted. Common names were taken from PLANTS (USDA-NRSC 2016), and vegetation classifications were based on Hoagland (2000). All specimens were collected by the authors with the exception of those marked with the pound sign (#), which were collected by Becky Sherry. Specimens were assigned collection numbers with the prefix KES.

Acanthaceae

Ruellia humilis Nutt. (denseflowered waterwillow); P; F; GL; KES-327

Adoxaceae

Viburnum rufidulum Raf. (rusty blackhaw); P; S; UWL; KES-077

Amaranthaceae

**Chenopodium album* L. (lambsquarters); A; F; DA; KES-428
Chenopodium pratericola Rydb. (desert goosefoot); A; F; DA; KES-066
Iresine rhizomatosa Standl. (Juda's bush); P; F; SBL; KES-054

Amaryllidaceae

Allium canadense L. var. *fraseri* Ownbey (Fraser meadow garlic); P; F; GL; KES-152
Nothoscordum bivalve (L.) Britton (crow-poison); P; F; GL; KES-153

Anacardiaceae

Rhus copallinum L. (winged sumac); P; S; GL; KES-239
Rhus glabra L. (smooth sumac); P; S; GL; KES-052
Toxicodendron radicans (L.) Kuntze (eastern poison ivy); P; V; SBL; KES-051

Apiaceae

Ammoselinum butleri (Engelm. ex S. Watson) J.M. Coult. & Rose (Butler's sandparsley); A; F; GL; KES-050
#*Ammoselinum popei* Torr. & A. Gray (plains sandparsley); A; F; GL; KES-407
Chaerophyllum tainturieri Hook. var. *tainturieri* (hairyfruit wild chervil); A; F; SBL; KES-087
Daucus pusillus Michx. (American wild carrot); A; F; GL; KES-047
Sanicula canadensis L. (snakeroot); B; F; MF; KES-048
Spermolepis inermis (Nutt. ex DC.) Mathias & Constance (Red River scaleseed); A; F; GL; KES-049
**Torilis arvensis* (Huds.) Link (hedge parsley); A; F; DA; KES-227

Apocynaceae
Apocynum cannabinum L. (Indian hemp); P; F; GL; KES-046
Asclepias amplexicaulis Sm. (clasping milkweed); P; F; GL; KES-387
Asclepias stenophylla A. Gray (narrowleaf milkweed); P; F; GL; KES-041
Asclepias tuberosa L. (butterfly milkweed); P; F; GL; KES-040
Asclepias viridiflora Raf. (green comet milkweed); P; F; GL; KES-042
Asclepias viridis Walter (green milkweed); P; F; GL; KES-043
**Vinca major* L. (greater periwinkle); P; F; SBL; KES-045

Araliaceae
**Hedera helix* L. (English ivy); P; V; SBL; KES-044

Asparagaceae
Androstephium coeruleum (Scheele) Greene (blue funnel lily); P; F; GL; KES-154
Yucca glauca Nutt. (common yucca); P; S; GL; KES-393

Aspleniaceae
Asplenium platyneuron (L.) Britton, Sterns & Poggenb. (ebony spleenwort); P; F; UWL; KES-379

Asteraceae
Achillea millefolium L. (yarrow); P; F; GL; KES-030
Ambrosia psilostachya DC. (western ragweed); P; F; GL; KES-004
Ambrosia trifida L. (giant ragweed); A; F; GL; KES-006
Amphiachyris dracunculoides (DC.) Nutt. (broomweed); A; F; GL; KES-014
#*Antennaria parlinii* Fernald ssp. *fallax* (Greene) Bayer & Stebbins (Parlin's pussytoes); P; F; MF; KES-408
Artemisia ludoviciana Nutt. ssp. *mexicana* (Willd. ex Spreng.) D.D. Keck (white sagebrush); P; F; GL; KES-347
Berlandiera x betonicifolia (Hook.) Small (Texas greeneyes); P; F; GL; KES-008
Bidens bipinnata L. (Spanish needles); A; F; SBL; KES-012
Bradburia pilosa (Nutt.) Semple (golden aster); A; F; GL; KES-031
Cirsium altissimum (L.) Hill (tall thistle); B; F; UWL; KES-017
Cirsium undulatum (Nutt.) Spreng. (wavyleaf thistle); P; F; GL; KES-013
Conoclinium coelestinum (L.) DC. (mist flower); P; F; SBL; KES-019
Conyza canadensis (L.) Cronquist (horseweed); A; F; GL; KES-370
Conyza ramosissima Cronquist (dwarf horseweed); A; F; DA; KES-429
Diaperia verna (Raf.) Morefield (spring pygmycudweed); A; F; GL; KES-035
Echinacea angustifolia DC. (blacksamson); P; F; GL; KES-021
Eclipta prostrata (L.) L. (false daisy); A; F; HWV; KES-374
Elephantopus carolinianus Raeusch. (elephant's foot); P; F; MF; KES-376
Erechtites hieraciifolius (L.) Raf. ex DC. (American burnweed); A; F; GL; KES-423
Erigeron philadelphicus L.; (Philadelphia fleabane); P; F; SBL; KES-039
Erigeron strigosus Muhl. ex Willd. (prairie fleabane); A; F; GL; KES-003
Gaillardia aestivalis (Walter) H. Rock (summer gaillardia); P; F; GL; KES-027
Gamochaeta purpurea (L.) Cabrera (purple cudweed); P; F; GL; KES-313
Grindelia ciliata (Nutt.) Spreng. (wax goldenweed); A; F; GL; KES-011
Helianthus annuus L. (common sunflower); A; F; GL; KES-005
Helianthus maximiliani Schrad. (Maximilian sunflower); P; F; GL; KES-346

Helianthus mollis Lam. (ashy sunflower); P; F; GL; KES-015
Heterotheca subaxillaris (Lam.) Britt. & Rusby (camphorweed); A; F; GL; KES-344
Hieracium longipilum Torr. (longbeard hawkweed); P; F; GL; KES-001
Krigia caespitosa (Raf.) K.L. Chambers (common dwarf dandelion); A; F; GL; KES-395
Lactuca canadensis L. (Canada lettuce); A; F; SBL; KES-368
**Lactuca serriola* L. (prickly lettuce); A; F; DA; KES-022
Liatris pycnostachya Michx. (button snakeroot); P; F; GL; KES-363
Liatris squarrosa (L.) Michx. (gayfeather); P; F; GL; KES-010
Pseudognaphalium obtusifolium (L.) Hilliard & B.L. Burtt (rabbit-tobacco); A; F; GL; KES-009
Pyrrhopappus carolinianus (Walter) DC. (Carolina desert-chicory); A; F; GL; KES-294
Pyrrhopappus grandiflorus (Nutt.) Nutt. (false dandelion); P; F; GL; KES-026
Ratibida columnifera (Nutt.) Woot. & Standl. (yellow coneflower); P; F; GL; KES-033
Rudbeckia hirta L. (black-eyed Susan); P; F; GL; KES-028
Silphium asteriscus L. (starry rosinweed); P; F; GL; KES-430
Solidago missouriensis Nutt. (Missouri goldenrod); P; F; GL; KES-034
Solidago radula Nutt. (rough goldenrod); P; F; GL; KES-357
Solidago rigida L. (stiff prairie goldenrod); P; F; GL; KES-366
**Sonchus asper* (L.) Hill (spiny sowthistle); A; F; DA; KES-303
Symphyotrichum drummondii (Lindl.) G.L. Nesom var. *texanum* (E.S. Burgess) G.L. Nesom (blue wood aster); P; F; UWL; KES-356
Symphyotrichum ericoides (L.) G.L. Nesom var. *ericoides* (heath aster); P; F; GL; KES-353
Symphyotrichum patens (Aiton) G.L. Nesom var. *patens* (spreading aster); P; F; GL; KES-425
Symphyotrichum subulatum (Michx.) G.L. Nesom (salt marsh aster); P; F; HWV; KES-018
**Taraxacum erythrospermum* Andrz. ex Besser (rock dandelion); P; F; DA; KES-394
Tetraneuris linearifolia (Hook.) Greene (fineleaf fournerved daisy); A; F; GL; KES-037
#Thelesperma filifolium (Hook.) A. Gray (greenthread); P; F; GL; KES-411
**Tragopogon dubius* Scop. (yellow salsify); A; F; GL; KES-023
Verbesina virginica L. (Virginia crownbeard); P; F; SBL; KES-020
Vernonia baldwinii Torr. (western ironweed); P; F; GL; KES-007
Xanthium strumarium L. (cocklebur); A; F; HWV; KES-371

Boraginaceae

Lithospermum incisum Lehm. (narrowleaf puccoon); P; F; GL; KES-091

Brassicaceae

**Camelina microcarpa* DC. (littlepod false flax); A; F; GL; KES-079
**Capsella bursa-pastoris* (L.) Medik. (shepherd's purse); A; F; GL; KES-083
Cardamine pensylvanica Muhl. ex Willd. (Pennsylvania bittercress); A; F; SBL; KES-088
Descurainia pinnata (Walter) Britton (western tansymustard); A; F; GL; KES-089
Draba brachycarpa Nutt. ex Torr. & A. Gray (shortpod draba); A; F; GL; KES-080
Draba cuneifolia Nutt. ex Torr. & A. Gray (wedgeleaf draba); A; F; GL; KES-081
Lepidium austrinum Small (southern pepperweed); A; F; DA; KES-084
Lepidium oblongum Small (veiny pepperweed); A; F; GL; KES-082
Lepidium virginicum L. (Virginia peppergrass); A; F; GL; KES-078
Physaria ovalifolia (Rydb.) O'Kane & Al-Shehbaz ssp. *ovalifolia* (roundleaf bladderpod); P; F; GL; KES-086
Rorippa palustris (L.) Besser ssp. *palustris* (bog yellowcress); A; F; HWV; KES-297

Cactaceae
Escobaria missouriensis (Sweet) D.R. Hunt (Missouri foxtail cactus); P; F; GL; KES-250
Opuntia humifusa (Raf.) Raf. (devil's tongue); P; S; GL; KES-339

Campanulaceae
Triodanis perfoliata (L.) Nieuwl. ssp. *perfoliata* (clasping Venus' looking-glass); A; F; GL; KES-388

Cannabaceae
Celtis laevigata Willd. (sugarberry); P; T; SBL; KES-245

Caprifoliaceae
**Lonicera japonica* Thunb. (Japanese honeysuckle); P; V; SBL; KES-076
Symphoricarpos orbiculatus Moench (coralberry); P; S; SBL; KES-075

Caryophyllaceae
**Arenaria serpyllifolia* L. (thyme-leaved sandwort); A; F; GL; KES-072
**Cerastium pumilum* W. Curtis (European chickweed); A; F; GL; KES-073
**Dianthus armeria* L. (Deptford pink); A; F; GL; KES-068
Minuartia michauxii (Fenzl) Farw. (rock sandwort); P; F; GL; KES-382
Paronychia jamesii Torr. & A. Gray (James' nailwort); P; F; GL; KES-069
Sagina decumbens (Elliott) Torr. & A. Gray (beach pearlwort); A; F; GL; KES-071
Silene antirrhina L. (sleepy catchfly); A; F; GL; KES-067
**Stellaria media* (L.) Vill. (common chickweed); A; F; SBL; KES-074

Commelinaceae
Commelina erecta L. (whitemouth dayflower); P; F; SBL; KES-065
Tradescantia occidentalis (Britton) Smyth (prairie spiderwort); P; F; GL; KES-316

Convolvulaceae
Cuscuta cuspidata Engelm. (cusp dodder); P; F; GL; KES-055
Cuscuta pentagona Engelm. (fiveangled dodder); A; F; GL; KES-056
†*Ipomoea shumardiana* (Torr.) Shinners (narrowleaf morning-glory); P; F; GL; KES-064; S3G2G3

Cornaceae
Cornus drummondii C.A. Mey. (rough-leaf dogweed); P; T; SBL; KES-062

Cucurbitaceae
Cucurbita foetidissima Kunth (buffalo gourd); P; F; GL; KES-240
Melothria pendula L. (Guadeloupe cucumber); P; F; DA; KES-059

Cupressaceae
Juniperus virginiana L. (eastern red cedar); P; T; UWL; KES-057
~*Taxodium distichum* (L.) Rich. (bald cypress); P; T; SBL; KES-431

Cyperaceae
Carex aureolensis Steud. (goldenfruit sedge); P; G; HWV; KES-139
Carex blanda Dewey (eastern woodland sedge); P; G; UWL; KES-358

Carex brevior (Dewey) Mack. (shortbeak sedge); P; G; GL; KES-402
Carex cephalophora Muhl. ex Willd. (oval-leaf sedge); P; G; MF; KES-403
Carex gravida L.H. Bailey (heavy sedge); P; G; GL; KES-321
Cyperus acuminatus Torr. & Hook. ex Torr. (taperleaf flatsedge); P; G; HWV; KES-319
Cyperus echinatus (L.) Alph. Wood (globe flatsedge); P; G; GL; KES-138
*#*Cyperus esculentus* L. (chufa flatsedge); P; G; DA; KES-406
Cyperus lupulinus (Spreng.) Marcks (Great Plains flatsedge); P; G; GL; KES-134
Cyperus squarrosus L. (bearded flatsedge); A; G; HWV; KES-140
†*Eleocharis geniculata* (L.) Roem. & Schult. (Canada spikesedge); A; G; HWV; KES-335
Eleocharis montevidensis Kunth (sand spikesedge); P; G; HWV; KES-320
Eleocharis obtusa (Willd.) Schult. (blunt spikesedge); A; G; HWV; KES-382
Eleocharis palustris (L.) Roem. & Schult. (common spikerush); P; G; HWV; KES-137
Fimbristylis puberula (Michx.) Vahl var. *puberula* (hairy fimbry); P; G; GL; KES-336
Fuirena simplex Vahl var. *aristulata* (Torr.) Kral (umbrella sedge); P; G; HWV; KES-331
Lipocarpha drummondii (Nees) G.C. Tucker (Drummond's halfchaff sedge); A; G; HWV; KES-325
Schoenoplectus pungens (Vahl) Palla var. *longispicatus* (Britton) S.G. Sm. (common threesquare); P; G; HWV; KES-136
Scirpus atrovirens Willd. (darkgreen bulrush); P; G; HWV; KES-135
Scleria ciliata Nees (fringed nutrush); P; G; GL; KES-301

Ebenaceae

Diospyros virginiana L. (persimmon); P; T; SBL; KES-230

Elaeagnaceae

**Elaeagnus umbellata* Thunb. (oleaster); P; S; SBL; KES-169

Equisetaceae

Equisetum hyemale L. ssp. *affine* (Engelm.) Calder & Roy (scouring horsetail); P; F; SBL; KES-133

Euphorbiaceae

Acalypha ostryifolia Riddell (pineland threeseed mercury); A; F; SBL; KES-122
Acalypha virginica L. (Virginia threeseeded mercury); A; F; SBL; KES-131
Croton capitatus Michx. (wooly croton); A; F; GL; KES-123
Croton glandulosus L. (croton); A; F; GL; KES-121
Croton monanthogynus Michx. (one-seed croton); A; F; GL; KES-127
Euphorbia corollata L. (flowering spurge); P; F; GL; KES-124
Euphorbia dentata Michx. (toothed spurge); A; F; SBL; KES-120
Euphorbia maculata L. (spotted sandmat); A; F; GL; KES-129
Euphorbia marginata Pursh (snow on the mountain); A; F; GL; KES-125
Euphorbia nutans Lag. (eyebane); A; F; GL; KES-373
Euphorbia prostrata Aiton (prostrate sandmat); A; F; GL; KES-132
Stillingia sylvatica L. (queen's delight); P; F; GL; KES-126
Tragia betonicifolia Nutt. (betonyleaf noseburn); P; F; GL; KES-130

Fabaceae

Amorpha canescens Pursh (leadplant); P; F; GL; KES-098
Amorpha fruticosa L. (false indigo); P; S; HWV; KES-381

Amphicarpaea bracteata (L.) Fernald (hog peanut); A; F; MF; KES-112
Astragalus lotiflorus Hook. (lotus milkvetch); P; F; GL; KES-115
Baptisia australis (L.) R. Br. (blue wild indigo); P; F; GL; KES-390
Baptisia leucophaea Nutt. (plains wild indigo); P; F; GL; KES-118
Cercis canadensis L. (redbud); P; T; UWL; KES-119
Chamaecrista fasciculata (Michx.) Greene (partridge pea); A; F; GL; KES-097
Dalea aurea Nutt. ex Fraser (golden prairie clover); P; F; GL; KES-104
Dalea candida Michx. ex Willd. (white prairie clover); P; F; GL; KES-101
Dalea enneandra Nutt. ex Fraser (nine-anther prairie clover); P; F; GL; KES-092
Dalea purpurea Vent. (purple prairie clover); P; F; GL; KES-107
Desmanthus illinoensis (Michx.) MacMill. ex B.L. Rob. & Fernald (bundleflower); P; F; GL; KES-111
Desmodium glutinosum (Muhl. ex Willd.) Alph. Wood (large-flowered tickclover); P; F; MF; KES-249
†*Desmodium nuttallii* (Schindl.) B.G. Schub. (Nuttall's ticktrefoil); P; F; GL; KES-113; S1G5
Desmodium sessilifolium (Torr.) Torr. & A. Gray (sessile tickclover); P; F; GL; KES-105
Indigofera miniata Ortega (coastal indigo); P; F; GL; KES-110
**Kummerowia stipulacea* (Maxim.) Makino (Korean clover); A; F; GL; KES-305
**Lathyrus hirsutus* L. (Caley pea); A; F; GL; KES-306
Lespedeza capitata Michx. (bush clover); P; F; GL; KES-378
**Lespedeza cuneata* (Dum. Cours.) G. Don (sericea lespedeza); P; F; GL; KES-103
Lespedeza procumbens Michx. (trailing lespedeza); P; F; MF; KES-367
Lespedeza stuevei Nutt. (Stueve's lespedeza); P; F; UWL; KES-369
**Medicago minima* (L.) L. ex Bartal. (small medic); A; F; GL; KES-117
**Melilotus albus* Medik. (white sweetclover); A; F; GL; KES-432
**Melilotus officinalis* (L.) Lam. (yellow sweetclover); A; F; GL; KES-096
Mimosa nuttallii (DC. ex Britton & Rose) B.L. Turner (sensitive briar); P; F; GL; KES-094
Oxytropis lambertii Pursh (purple locoweed); P; F; GL; KES-386
Psoralidium tenuiflorum (Pursh) Rydb. (wild alfalfa); P; F; GL; KES-100
Robinia pseudoacacia L. (black locust); P; T; UWL; KES-114
**Securigera varia* (L.) Lassen (crownvetch); P; F; GL; KES-109
Strophostyles helvola (L.) Elliott (wild bean); A; F; GL; KES-106
Strophostyles leiosperma (Torr. & A. Gray) Piper (smoothseed wild bean); A; F; GL; KES-377
**Vicia sativa* L. (common vetch); A; F; GL; KES-116
**Vicia villosa* Roth (winter vetch); A; F; GL; KES-396

Fagaceae

Quercus macrocarpa Michx. (bur oak); P; T; MF; KES-235
Quercus marilandica Münchh. (blackjack oak); P; T; UWL; KES-231
Quercus muehlenbergii Engelm. (chinquapin oak); P; T; MF; KES-234

Gentianaceae

Eustoma exaltatum (L.) Salisb. ex G. Don ssp. *russellianum* (Hook.) Kartesz (showy prairie gentian); A; F; GL; KES-375
Sabatia campestris Nutt. (pink gentian); A; F; GL; KES-150

Geraniaceae

**Erodium cicutarium* (L.) L'Hér. ex Aiton (redstem stork's bill); A; F; DA; KES-149
Geranium texanum (Trel.) A. Heller (Texas geranium); A; F; GL; KES-148

Haloragaceae
Myriophyllum spicatum L. (Eurasian water-milfoil); P; F; HWV; KES-341

Heliotropiaceae
Heliotropium tenellum (Nutt.) Torr. (pasture heliotrope); A; F; GL; KES-090

Hydrocharitaceae
Najas guadalupensis (Spreng.) Magnus (southern waternymph); A; F; HWV; KES-311

Hypericaceae
Hypericum drummondii (Grev. & Hook.) Torr. & A. Gray (nits-and-lice); A; F; GL; KES-380

Iridaceae
**Iris germanica* L. (German iris); P; F; SBL; KES-439
Sisyrinchium angustifolium Mill. (blue-eyed grass); P; F; GL; KES-146

Juglandaceae
Carya illinoinensis (Wangenh.) K. Koch; (pecan); P; T; SBL; KES-323

Juncaceae
Juncus brachyphyllus Wiegand (tuftedstem rush); P; G; HWV; KES-145
Juncus dudleyi Wiegand (Dudley's rush); P; G; GL; KES-398
Juncus interior Wiegand (inland rush); P; G; GL; KES-397
Juncus marginatus Rostk. (grassleaf rush); P; G; HWV; KES-144
Juncus torreyi Coville (Torrey's rush); P; G; HWV; KES-143

Krameriaceae
Krameria lanceolata Torr. (trailing ratany); P; F; GL; KES-164

Lamiaceae
Hedeoma drummondii Benth. (false pennyroyal); P; F; GL; KES-161
Hedeoma hispida Pursh (rough pennyroyal); A; F; GL; KES-159
**Lamium amplexicaule* L. (henbit deadnettle); A; F; GL; KES-162
**Lamium purpureum* L. (purple deadnettle); A; F; SBL; KES-163
Lycopus americanus Muhl. ex W.P.C. Bartram (American bugleweed); P; F; HWV; KES-158
Monarda clinopodioides A. Gray (basil beebalm); A; F; GL; KES-160
Monarda fistulosa L. (wild bergamot); P; F; GL; KES-156
Salvia azurea Michx. ex Lam. (blue sage); P; F; GL; KE-157
Teucrium canadense L. (American germander); P; F; HWV; KES-155

Linaceae
Linum sulcatum Riddell (grooved flax); A; F; GL; KES-151

Lythraceae
Ammannia coccinea Rottb. (valley redstem); A; F; HWV; KES-364

Malvaceae
Callirhoe involucrata (Torr. & A. Gray) A. Gray (winecup); P; F; GL; KES-168

Menispermaceae
Cocculus carolinus (L.) DC. (Carolina snailseed); P; F; UWL; KES-233

Molluginaceae
Mollugo verticillata L. (green carpetweed); A; F; DA; KES-167

Montiaceae
Claytonia virginica L. (springbeauty); P; F; GL; KES-282
Phemeranthus parviflorus (Nutt.) Kiger (sunbright); P; F; GL; KES-317

Moraceae
Maclura pomifera (Raf.) C.K. Schneid. (bois d'arc); P; T; SBL; KES-248
**Morus alba* L. (white mulberry); P; T; DA; KES-166
Morus rubra L. (red mulberry); P; T; SBL; KES-165

Nyctaginaceae
Mirabilis albida (Walter) Heimerl (white four o'clock); P; F; GL; KES-361
Mirabilis linearis (Pursh) Heimerl (narrowleaf four o'clock); P; F; GL; KES-383

Oleaceae
Fraxinus pennsylvanica Marsh. (green ash); P; T; SBL; KES-379

Onagraceae
Oenothera berlandieri (Spach) Steud. ssp. *berlandieri* (Spach) Steud. (Berlandier's sundrops); P; F; GL; KES-218
Oenothera curtiflora W.L. Wagner & Hoch (velvety gaura); A; F; GL; KES-217
Oenothera glaucifolia W.L. Wagner & Hoch (false gaura); P; F; GL; KES-221
Oenothera laciniata Hill (cut-leaf evening primrose); P; F; GL; KES-220
Oenothera macrocarpa Nutt. (large-fruited evening primrose); P; F; GL; KES-219
Oenothera rhombipetala Nutt. ex Torr. & A. Gray (fourpoint evening primrose); P; F; GL; KES-222
Oenothera sinuosa W.L. Wagner & Hoch (wavyleaf gaura); P; F; GL; KES-223
Oenothera triangulata (Buckley) W.L. Wagner & Hoch (prairie beeblossom); A; F; GL; KES-391

Ophioglossaceae
Ophioglossum engelmannii Prantl (limestone adder's tongue); P; F; GL; KES-216

Orchidaceae
Spiranthes cernua (L.) Rich. (nodding lady's tresses); P; F; GL; KES-385

Orobanchaceae
Agalinis heterophylla (Nutt.) Small (prairie false foxglove); A; F; GL; KES-381
Buchnera americana L. (American blue hearts); P; F; GL; KES-266
Castilleja indivisa Engelm. (Indian paintbrush); A; F; GL; KES-267

Oxalidaceae
Oxalis corniculata L. (yellow wood-sorrel); P; F; GL; KES-215
Oxalis violacea L. (violet wood-sorrel); P; F; GL; KES-384

Penthoraceae
Penthorum sedoides L. (ditch stonecrop); P; F; HWV; KES-061

Phyrmaceae
Phryma leptostachya L. (American lopseed); P; F; MF; KES-293

Phytolaccaceae
Phytolacca americana L. (pokeweed); P; F; DA; KES-334

Plantaginaceae
Leucospora multifida (Michx.) Nutt. (narrowleaf paleseed); A; F; HWV; KES-265
Nuttallanthus texanus (Scheele) D.A. Sutton (Texas toadflax); B; F; GL; KES-392
Penstemon cobaea Nutt. (large beardtongue); P; F; GL; KES-385
Plantago aristata Michx. (bottlebrush plantain); A; F; GL; KES-289
†*Plantago elongata* Pursh ssp. *elongata* (prairie plantain); A; F; GL; KES-290; S3T3G4T4
Plantago patagonica Jacq. (wooly plantain); A; F; GL; KES-309
Plantago rhodosperma Decne. (redseed plantain); A; F; GL; KES-291
Plantago rugelii Decne. (blackseed plantain); P; F; SBL; KES-433
**Veronica arvensis* L. (common speedwell); A; F; GL; KES-268
*#*Veronica peregrina* L. (purslane speedwell); A; F; GL; KES-410

Platanaceae
Platanus occidentalis L. (American sycamore); P; T; SBL; KES-389

Poaceae
**Aegilops cylindrica* Host (jointed goatgrass); A; G; GL; KES-170
Agrostis hyemalis (Walter) Britton, Sterns & Poggenb. (ticklegrass); P; G; GL; KES-214
Andropogon gerardii Vitman (big bluestem); P; G; GL; KES-213
Andropogon ternarius Michx. (splitbeard bluestem); P; G; GL; KES-351
Andropogon virginicus L. (broomsedge); P; G; GL; KES-424
Aristida longespica Poir. (slimspike threeawn); A; G; GL; KES-178
Aristida purpurea Nutt. var. *longiseta* (Steud.) Vasey (Fendler threeawn); P; G; GL; KES-211
Aristida purpurea Nutt var. *purpurea* (purple threeawn); P; G; GL; KES-175
**Bothriochloa ischaemum* (L.) Keng (yellow bluestem); P; G; GL; KES-210
Bothriochloa laguroides (DC.) Herter var. *torreyana* (Steud.) M. Marchi & Longhi-Wagner (silver beardgrass); P; G; GL; KES-209
Bouteloua curtipendula (Michx.) Torr. (sideoats grama); P; G; GL; KES-208
Bouteloua dactyloides (Nutt.) Columbus (buffalo grass); P; G; GL; KES-376
Bouteloua gracilis (Kunth) Lag. ex Griffiths (blue grama); P; G; GL; KES-207
Bouteloua hirsuta Lag. (hairy grama); P; G; GL; KES-206
Bouteloua rigidiseta (Steud.) Hitchc. (Texas grama); P; G; GL; KES-205
**Bromus arvensis* L. (field brome); A; G; GL; KES-204
**Bromus catharticus* Vahl (rescue grass); A; G; GL; KES-173

Bromus pubescens Muhl. ex Willd. (Canada brome); P; G; UWL; KES-203
**Bromus tectorum* L. (cheatgrass); A; G; GL; KES-174
Cenchrus spinifex Cav. (coastal sandbur); P; G; GL; KES-383
Chasmanthium latifolium (Michx.) H.O. Yates (inland sea oats); P; G; SBL; KES-202
Chloris verticillata Nutt. (windmill grass); P; G; GL; KES-201
Chloris virgata Sw. (feather fingergrass); A; G; GL; KES-434
Coleataenia anceps (Michx.) Soreng (beaked panicgrass); P; G; HWV; KES-187
**Cynodon dactylon* (L.) Pers. (Bermuda grass); P; G; GL; KES-228
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *lindheimeri* (Nash) Gould & C.A. Clark (Lindheimer panicgrass); P; G; GL; KES-296
Dichanthelium malacophyllum (Nash) Gould (softleaf rosette grass); P; G; UWL; KES-194
Dichanthelium oligosanthes (Schult.) Gould var. *oligosanthes* (Heller's rosette grass); P; G; GL; KES-193
Dichanthelium sphaerocarpon (Elliott) Gould (roundseed panicgrass); P; G; GL; KES-426
Digitaria ciliaris (Retz.) Pers. (southern crabgrass); A; G; GL; KES-435
Digitaria cognata (Schult.) Pilg. (fall witchgrass); P; G; GL; KES-198
Distichlis spicata (L.) Greene (saltgrass); P; G; GL; KES-378
Echinochloa muricata (P. Beauv.) Fernald (rough barnyard grass); A; G; HWV; KES-298
Elymus canadensis L. (Canada wildrye); P; G; GL; KES-197
Elymus virginicus L. (Virginia wild rye); P; G; UWL; KES-196
**Eragrostis cilianensis* (Bellardi) Vignolo ex Janch. (stinkgrass); A; G; GL; KES-384
Eragrostis curtipedicellata Buckley (gummy lovegrass); P; G; GL; KES-192
**Eragrostis curvula* (Schrad.) Nees (weeping lovegrass); P; G; GL; KES-329
Eragrostis hirsuta (Michx.) Nees (bigtop lovegrass); P; G; GL; KES-191
Eragrostis secundiflora J. Presl ssp. *oxylepis* (Torr.) S.D. Koch (red lovegrass); P; G; GL; KES-190
Eragrostis sessilispica Buckley (tumble lovegrass); P; G; GL; KES-200
#*Eragrostis trichodes* (Nutt.) Alph. Wood (sand lovegrass); P; G; GL; KES-412
Hordeum pusillum Nutt. (little barley); A; G; GL; KES-377
Leersia virginica Willd. (whitegrass); P; G; HWV; KES-189
**Lolium perenne* L. (perennial ryegrass); P; G; GL; KES-188
Mnesithea cylindrica (Michx.) de Koning & Sosef (mousetail); P; G; GL; KES-199
#*Muhlenbergia capillaris* (Lam.) Trin. (hairawn muhly); P; G; GL; KES-199
Muhlenbergia paniculata (Nutt.) Columbus (tumblegrass); P; G; DA; KES-330
Panicum capillare L. (witchgrass); A; G; GL; KES-186
Panicum philadelphicum Bernh. ex Trin. (Philadelphia witchgrass); A; G; GL; KES-345
Panicum virgatum L. (switchgrass); P; G; GL; KES-185
**Paspalum dilatatum* Poir. (Dallis grass); P; G; GL; KES-184
Paspalum distichum Houtt. (knotgrass); P; G; GL; KES-183
Paspalum setaceum Michx. (thin paspalum); P; G; GL; KES-182
Phalaris caroliniana Walter (maygrass); A; G; GL; KES-386
**Poa annua* L. (annual bluegrass); A; G; GL; KES-172
Schizachyrium scoparium (Michx.) Nash (little bluestem); P; G; GL; KES-181
Setaria parviflora (Poir.) Kerguélen (knotroot foxtail); P; G; GL; KES-326
**Setaria viridis* (L.) P. Beauv. (green bristlegrass); A; G; GL; KES-315
Sorghastrum nutans (L.) Nash (Indian grass); P; G; GL; KES-372
**Sorghum halepense* (L.) Pers. (Johnson grass); P; G; GL; KES-180
Sphenopholis obtusata (Michx.) Scribn. (prairie wedgescale); P; G; HWV; KES-176
Sporobolus cryptandrus (Torr.) A. Gray (sand dropseed); P; G; GL; KES-314

Sporobolus pyramidatus (Lam.) Hitchc. (Madagascar dropseed); P; G; GL; KES-179
Tridens flavus (L.) Hitchc. (purpletop); P; G; GL; KES-177
Vulpia octoflora (Walter) Rydb. (poverty grass); A; G; GL; KES-171

Polygalaceae

Polygala alba Nutt. (white milkwort); P; F; GL; KES-288
Polygala incarnata L. (pink milkwort); A; F; GL; KES-287
Polygala verticillata L. (whorled milkwort); A; F; GL; KES-286

Polygonaceae

Eriogonum annuum Nutt. (annual buckwheat); A; F; GL; KES-355
Eriogonum longifolium Nutt. (longleaf buckwheat); P; F; GL; KES-284
**Fallopia convolvulus* (L.) Á. Löve (black bindweed); A; F; GL; KES-312
Persicaria lapathifolia (L.) Gray (pale smartweed); A; F; HWV; KES-229
Persicaria punctata (Elliott) Small (dotted smartweed); A; F; HWV; KES-285
Polygonum ramosissimum Michx. (bushy knotweed); A; F; DA; KES-360
**Rumex crispus* L. (curly dock); P; F; HWV; KES-283
#*Rumex hastatulus* Baldwin (heartwing sorrel); P; F; GL; KES-409

Potamogetonaceae

Potamogeton nodosus Poir. (longleaf pondweed); P; F; HWV; KES-322

Primulaceae

Samolus valerandi L. (smallflower brookweed); P; F; HWV; KES-295

Ranunculaceae

Anemone berlandieri Pritz. (ten-petal windflower); P; F; GL; KES-281
Delphinium carolinianum Walter ssp. *virescens* (Nutt.) R.E. Brooks (Carolina larkspur); P; F; GL; KES-391

Rosaceae

Geum canadense Jacq. (white avens); P; F; MF; KES-304
**Potentilla recta* L. (erect cinquefoil); P; F; GL; KES-280
Prunus angustifolia Marshall (Chickasaw plum); P; S; GL; KES-226
Prunus mexicana S. Watson (Mexican plum); P; T; GL; KES-241
**Pyrus calleryana* Decne. (Callery pear); P; T; UWL; KES-278
Rosa foliolosa Nutt. ex Torr. & A. Gray (prairie rose); P; F; GL; KES-224
**Rosa multiflora* Thunb. (mulitflora rose); P; V; SBL; KES-277
Rubus pensilvanicus Poir. (Oklahoma blackberry); P; S; GL; KES-436

Rubiaceae

Cephalanthus occidentalis L. (buttonbush); P; S; HWV; KES-337
**Cruciata pedemontana* (Bellardi) Ehrend. (piedmont bedstraw); A; F; GL; KES-275
Diodella teres (Walter) Small (poor-joe); A; F; GL; KES-272
Galium aparine L. (catchweed bedstraw); A; F; GL; KES-276
Galium virgatum Nutt. (southwest bedstraw); A; F; GL; KES-271
Houstonia pusilla Schoepf (prairie bluets); A; F; GL; KES-274
Stenaria nigricans (Lam.) Terrell var. *nigricans* (diamond flowers); P; F; GL; KES-273

Salicaceae
Populus deltoides W. Bartram ex Marshall (cottonwood); P; T; SBL; KES-236
Salix exigua Nutt. (narrowleaf willow); P; T; HWV; KES-270
Salix nigra Marshall (black willow); P; T; HWV; KES-269

Sapindaceae
Acer negundo L. (boxelder); P; T; SBL; KES-247
Sapindus saponaria L. var. *drummondii* (Hook. & Arn.) L.D. Benson (western soapberry); P; T; UWL; KES-246

Sapotaceae
Sideroxylon lanuginosum Michx. (chittamwood); P; T; UWL; KES-237

Smilacaceae
Smilax bona-nox L. (greenbrier); P; F; UWL; KES-264
Smilax rotundifolia L. (roundleaf greenbrier); P; F; UWL; KES-300
Smilax tamnoides L. (bristly greenbrier); P; F; UWL; KES-350

Solanaceae
*#*Lycium barbarum* L. (common matrimonyvine); P; S; unknown habitat; KES-427
Physalis cinerascens (Dunal) Hitchc. (smallflower groundcherry); P; F; GL; KES-260
Solanum dimidiatum Raf. (horsenettle); P; F; GL; KES-262
Solanum elaeagnifolium Cav. (silverleaf nightshade); P; F; GL; KES-263
Solanum rostratum Dunal (buffalo bur); A; F; DA; KES-225

Ulmaceae
Ulmus americana L. (American elm); P; T; SBL; KES-238
**Ulmus pumila* (Siberian elm); P; T; DA; KES-437
Ulmus rubra Muhl. (slippery elm); P; T; SBL; KES-387

Urticaceae
Parietaria pensylvanica Muhl. ex Willd. (Pennsylvania pellitory); A; F; SBL; KES-243

Valerianaceae
Valerianella amarella (Lindh. ex Engelm.) Krok (hairy cornsalad); A; F; GL; KES-257
Valerianella radiata (L.) Dufr. (beaked cornsalad); A; F; GL; KES-258

Verbenaceae
Glandularia pumila (Rydb.) Umber (pink mock vervain); A; F; GL; KES-256
Phyla lanceolata (Michx.) Greene (lanceleaf fogfruit); P; F; HWV; KES-254
Verbena bracteata Cav. ex Lag. & Rodr. (bigbract verbena); A; F; GL; KES-232
Verbena halei Small (slender verbena); P; F; GL; KES-255

Violaceae
Viola bicolor Pursh (Johnny jump-up); A; F; GL; KES-253
Viola sororia Willd. var. *missouriensis* (Greene) L.E. McKinney (common blue violet); P; F; MF; KES-252

Vitaceae

Ampelopsis cordata Michx. (heartleaf peppervine); P; V; SBL; KES-388
Parthenocissus quinquefolia (L.) Planch. (Virginia creeper); P; V; SBL; KES-244
Vitis cinerea (Engelm.) Engelm. ex Millard (graybark grape); P; V; SBL; KES-251
Vitis vulpina L. (frost grape); P; V; SBL; KES-302

Xanthorrhoeaceae

**Hemerocallis fulva* (L.) L. (orange daylily); P; F; SBL; KES-440

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EFFECTS OF FIRE SEVERITY ON HABITAT RECOVERY IN A MIXED GRASS PRAIRIE ECOSYSTEM

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ABSTRACT

We assessed the recovery and current status of three mixed grass prairie sites 5 yr post burn in the Wichita Mountains Wildlife Refuge, Indiahoma, Oklahoma. These sites represent three burn histories: moderate burn, severe burn, and unburned. We used a modified point-intercept method to sample 38 habitat variables at 280 points along three transects at each site. These data were subjected to principal components analysis to assess trends in habitat structure among the sites. The first three components explained 66.6% of the variation in the dataset. Component I represents a gradient from short forbs, lichen covered rocks, and minimal disturbance to areas of tall grasses and ungulate disturbance. Component II represents a gradient from tall forbs and water disturbance to areas with woody shrubs, short herbaceous litter, and graminoid and moss ground cover. Component III represents a gradient from areas with mid-level forbs, fecal matter and herbaceous litter ground cover to areas with tall grasses and bare ground. Projections of the burn treatment sites onto principal components I–III indicate that the moderate and unburned sites cluster closely on component I but are distinct along components II and III. We interpret our results as supporting a relationship between high severity fire and more complete nutrient cycling from accumulated litter, leading initially post fire to dense grass cover followed by increasing forb cover. This increase in forage density potentially alters the grazing patterns of large herbivores, which inflicts higher levels of disturbance. Conversely, the unburned and moderate burn sites had a greater diversity of herbaceous species at lower coverage densities, perhaps resulting from reestablshiment from surviving shoots and seeds.

INTRODUCTION

Prairie ecosystems are maintained primarily through disturbance, herbivory, and competition. Fire is the principal disturbance type and can be manipulated and controlled by humans, or it can have a completely uncontrolled influence on the landscape. Historically, fire has been perceived in a negative context as having a detrimental effect on livestock, timber, and other human-desired resources, and has subsequently been suppressed (Bland et al. 1973; Archer 1989; Allen and Palmer 2011). This attitude has softened somewhat in recent years, and fire is commonly used as a range management tool in an attempt to maximize forage quality, remove non-palatable tissues, and to control encroachment of woody species (Archer 1994; Raynor et al. 2015; Collins 2016). Controlled burns are typically undertaken

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when winds are low and humidity is high. Perimeters are established, and, if conducted properly, specific areas are evenly burned in terms of both areal extent and fire severity (Gibson and Hulbert 1987; Rideout-Hanzak et al. 2011; Gill et al. 2013; Winter 2013). These types of fires allow researchers to conduct before and after studies regarding a variety of ecological effects (Collins and Calabrese 2012; Winter et al. 2013; Larson 2014). Studies such as these produce valuable information due, in part, to the ability of researchers to replicate them. However, there are limits imposed on the various treatments involved by the fact that they must be controlled. This includes variables such as areal extent, fire intensity, burned patch shapes, and nonrandom site selection. Wildfires, on the other hand, whether human caused or natural, more closely represent the environmental pressures under which communities have evolved. All human controls are lost, and fires take their natural course as determined by climatic conditions (e.g. drought), wind direction, wind speed, fuel volume and quality, time since last burn, and topography (Gibson and Hulbert 1987). For example, spring fires generally tend to increase above ground biomass production by a few dominant grass species. This results in low species richness and diversity of forbs as competition for light increases (Gibson and Hulbert 1987; Collins and Calabrese 2011; Winter et al. 2013). Lowland areas support increased grass biomass and lower species diversity than upland prairie. These lower areas tend to have more available nutrients and soil moisture. Upland areas tend to have lower quality soils and therefore less dense vegetation. This combination of biotic (fuel volume and quality) and abiotic (elevation and moisture) factors, in addition to other physical factors such as wind speed and direction, determine fire characteristics. Because studies following these natural events are initiated after the fact and as such cannot be replicated, sampling cannot be entirely randomized. Additionally, there are no pre-established controls available for before and after comparison (Wiens and Parker 1995).

In this study, we compared the recovery of plant communities, assessed by sampling horizontal and vertical habitat structure, subjected to different burn treatments five years after a wildfire (Ferguson fire) in the Special Use Area (SUA) of the Wichita Mountains Wildlife Refuge (WMWR) in Indiahoma, Oklahoma. The objective of this paper is to describe the broad gradients of variation in the physical structure of these mixed grass prairie communities.

METHODS AND MATERIALS

The Wichita Mountains Wildlife Refuge is located in Comanche County, Oklahoma (Figure 1). It covers 23,885 ha of the Central Great Plains ecoregion (Woods et al. 2005). The SUA covers 14,136 ha on roughly the northern 2/3 of the refuge. It consists of low, rounded granite mountains permeated by mixed grass prairie. Mesophytic forests border streams and xeric forests consisting mostly of blackjack oak (*Quercus marilandica* Münchh.), post oak (*Q. stellata* Wangenh.), and eastern red cedar (*Juniperus virginiana* L.) and occur on lower granite hills. The Ferguson fire started on 1 September 2011, approximately 900 m east of the WMWR Visitor Center. Southerly winds rapidly pushed the fire northward into the SUA where the landscape was subjected to an incinerating burn that resulted in no remaining living vegetation. As the fire moved northward, it completely jumped small pockets of the landscape leaving them unburned. After burning through the refuge and exiting the north boundary, a northerly wind shift occurred pushing the fire southwest and back onto the refuge. This wind-shifted leg of the fire was less intense than the initial blaze due to light precipitation and light winds resulting in a moderately burned

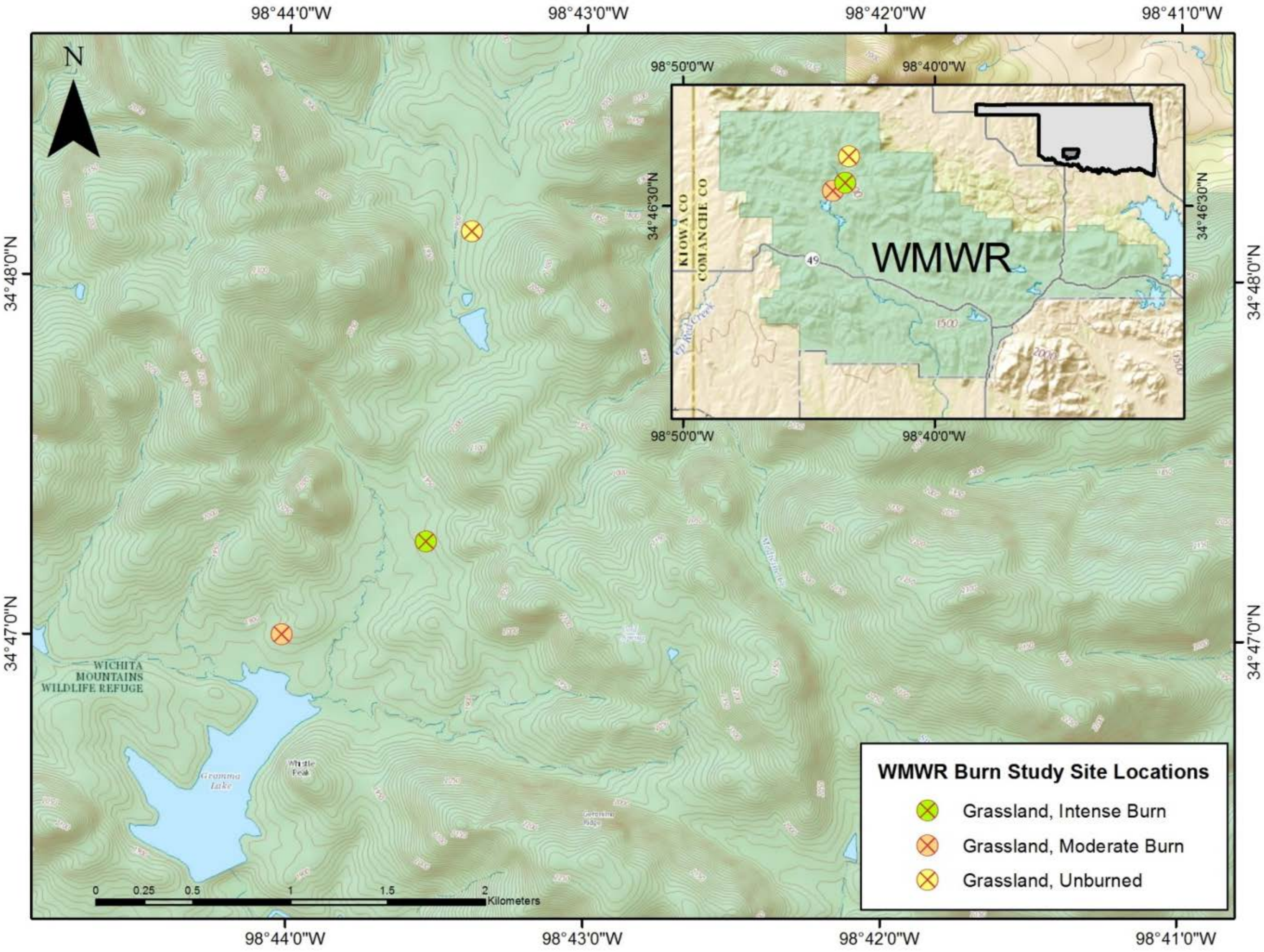

Figure 1 Location of the Wichita Mountains Wildlife Refuge, Comanche County, Oklahoma (inset) and three study sites

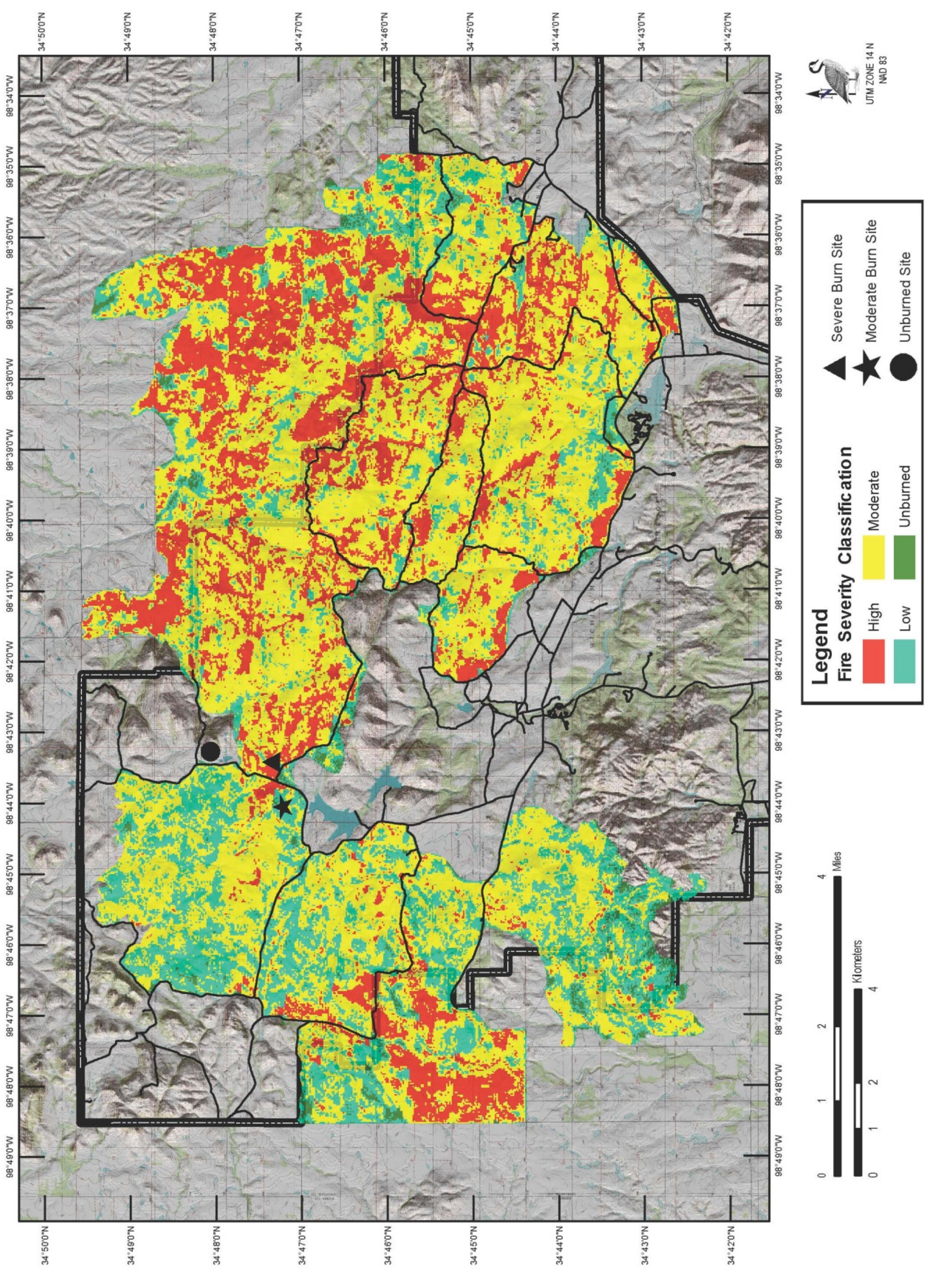

Figure 2 Fire severity in the Wichita Mountains Wildlife Refuge, Comanche County, Oklahoma

landscape where not all vegetation was destroyed. A total of 11,270 ha was burned on the WMWR. The Ferguson fire followed the hottest summer on record in Oklahoma since 1895 and moderate to extreme drought conditions in Comanche County since May 2010 (NOAA 2010).

We established three survey sites on 7 May 2016, one for each burn treatment (severe, moderate, and unburned), in mixed grass prairie of the SUA. Each site consisted of three 90 m transect arms extending from a center node (c-node) with one arm oriented in a north-south direction (0 to 180°). The other two arms extended from the c-node to the southeast (135°) and southwest (225°) for a linear total of 270 m/site. The maximum distance between sites was 2,351 m (unburned to moderate burn), and the minimum distance was 935 m (moderate to severe burn). The distance from the unburned to the severe burn site was 1,605 m (see Figure 1). Site elevations were within a 6.7 m range with the severe burn at 589.5 m, moderate burn at 582.8 m, and the unburned site at 585.5 m. We sampled the physical structure at each site from 5–11 June 2016.

We assigned fire impact as unburned, moderate burn, and severe burn as determined by Stambaugh et al. (2015) (Figure 2). These classifications were derived through a combination of remote sensing, ground truthing, and modelling. Unburned indicates that the area after the fire was indistinguishable from pre-fire conditions. The moderate burn class represents a mixture of effects on the dominant vegetation with some patches of above ground cover completely removed while others show little or no change and low mortality of the dominant vegetation. High severity burn indicates complete consumption of the canopy (Stambaugh et al. 2015).

We used a modified point-intercept method to sample 38 habitat variables along each transect at each site. These variables included measures of ground disturbance, ground cover, and vertical cover (Table 1). To determine ground disturbance and cover, we passed a 3 mm x 1 m rod vertically through the vegetation and onto the substrate at 0.5 m horizontal intervals along each transect. We recorded the ground disturbance and cover type at the point of contact. Ground disturbance type was determined by obvious alteration of ground cover, if any. At the same time, we determined vertical structure in decimeter intervals (1–10) by recording the interval at which any vertical cover contacted the rod. We sampled a total of 270 points at each site (Figure 3).

We used these data in a principal-components analysis (PCA) to assess patterns in habitat structure 5 yr post fire. PCA is an unconstrained ordination method that is useful for visualizing broad patterns of covariation in a multivariate data set (Anderson and Willis 2003). All calculations were performed using NT-SYS (Rohlf 1998). We mean-centered the raw data and calculated correlations among the variables. We then projected the standardized data onto eigenvectors projected from the correlation matrix.

Table 1 Categories and description of variable codes used in point-intercept sampling of three burn treatments in the WMWR. Vertical cover (VC) is measured in decimeter categories.

Category	**Variable No.**	**Variable Code**	**Habitat Variable Description**
Disturbance (Dist)	1	N	None
	2	UN	Ungulate
	3	W	Water
	4	H	Human
Ground Cover (GC)	5	CG	Crown Graminoid
	6	CF	Crown Forb
	7	L	Lichen
	8	M	Moss
	9	AC	Algae/Cyanobacteria
	10	LH	Litter Herbaceous
	11	GR	Gravel <7.5cm
	12	CO	Cobble >7.5-25cm
	13	BO	Boulder >25cm
	14	WA	Water
	15	BG	Bare Ground
	16	FM	Fecal Matter
Vertical Cover (VC)	17-20	LHV	Herbaceous Litter Vertical Hits
	21-28	FCG	Graminoid Foliage Cover Vertical Hits
	29-34	FCF	Forb Foliage Cover Vertical Hits
	35-38	FCS	Shrub Foliage Cover Vertical Hits

Figure 3 Author Laura Jardine sampling vertical structure at intense burn site in Wichita Mountains Wildlife Refuge

We surveyed the flora at each site by recording the presence of each species encountered (Table 2). Plant species identification followed the *Flora of Oklahoma: Keys and Description* (Tyrl et al. 2015).

RESULTS

Principal components analysis of 38 habitat variables produced three axes that accounted for 66.6% of the variation. Principal component I (PC I) explained 32.8%, PC II 19.5%, and PCIII 14.3% of the variation. Component I represents a gradient from short forbs, lichen covered cobble and boulders, and low disturbance to areas of tall grasses and ungulate disturbance (Table 3). Component II represents a gradient from tall forbs and water disturbance to areas with woody shrubs, herbaceous litter near the surface, and graminoid and moss ground cover. Component III represents a gradient from areas with mid-level forbs, fecal matter, and herbaceous litter ground cover to areas with tall grasses and bare ground cover. Projections of the burn treatment sites onto PC I, PC II, and PC III indicate that the moderate and unburned sites cluster closely on PC I but are distinct along PC II and PC III (Figure 4). The severe burn has the highest positive loadings along PC I and is intermediate with respect to PC II (see Figure 4). The three transects for unburned and moderate burn sites cluster tightly within sites along PC III, but the two sites themselves are separated. The transects in the severe burn are widely separated along PC III.

The plant species composition of the three sites is as follows: unburned – 40 species of 20 families; moderate burn – 40 species of 23 families; and severe burn – 28 species of 13 families (see Table 2).

DISCUSSION

There have been few studies that inventory the flora of the Wichita Mountains (Eskew 1938; Osborn and Allan 1949; Buck 1977; Collins and Barber 1986; Carter et al. 2008). Other studies associate mixed grass prairie floristic components of the WMWR with specific mammal assemblages (Osborn and Allan 1949; Stancampiano and Caire 1995). Stancampiano and Schnell (2004) assessed small mammal distributions across nearby Fort Sill using, among others, vertical structure of vegetation. It appears that no studies have been published of the vertical structure or cover types on the WMWR prior to this study. Floristic composition across all sites is consistent with unpublished seasonal checklists and published floras of the area (Buck 1977;

Table 2 Plant community composition of three burn treatments in the Wichita Mountains Wildlife Refuge

Species	**Common name**	**Family**	**Moderate Burn**	**Severe Burn**	**No Burn**
Allium canadense	Canada garlic	Amaryllidaceae	X	X	X
Daucus carota	Wild carrot	Apiaceae	X		X
Ptilimnium nuttallii	Nuttall's mockbishopweed	Apiaceae			X
Asclepias viridis	Green antelope horn	Apocynaceae	X	X	X
Yucca glauca	Small soapweed	Asparagaceae	X		
Achillea millefolium	Yarrow	Asteraceae	X	X	X
Ambrosia psilostachya	Western ragweed	Asteraceae	X	X	X
Artemisia ludoviciana	Louisiana sagewort	Asteraceae	X	X	
Chaetopappa asteroides	Least daisy	Asteraceae	X	X	X
Cirsium undulatum	Wavyleaf thistle	Asteraceae	X		X
Coreopsis lanceolata	Lanceleaf coreopsis	Asteraceae	X		X
Echinacea angustifolia	Black sampson	Asteraceae	X		X
Gaillardia pulchella	Indian blanket	Asteraceae	X	X	X
Helenium amarum	Bitter sneezeweed	Asteraceae	X		X
Thelesperma filifolium	Plains greenthread	Asteraceae			X
Vernonia baldwinii	Baldwin ironweed	Asteraceae	X	X	
Lepidium virginicum	Virginia pepperwort	Brassicaceae	X	X	X
Paysonia auriculata	Earleaf bladderpod	Brassicaceae			X
Echinocereus reichenbachii	Lace hedgehog cactus	Cactaceae	X		
Opuntia humifusa var. *humifusa*	Prickly pear	Cactaceae	X		X
Triodanis perfoliata ssp. *biflora*	Small venus looking-glass	Campanulaceae			X
Symphoricarpos orbiculatus	Buckberry	Caprifoliaceae	X	X	X
Valerianella radiata	Cornsalad	Caprifoliaceae		X	
Tradescantia ohiensis	Smoothstalk spiderwort	Commelinaceae	X	X	X
Cuscuta cuspidata	Cusp dodder	Convolvulaceae	X		
Sedum nuttallii	Yellow stonecrop	Crassulaceae	X		X
Juniperus virginiana	Eastern red cedar	Cupressaceae			X
Carex sp.	Sedge	Cyperaceae		X	X
Eleocharis montevidensis	Sand spikesedge	Cyperaceae		X	X
Amorpha canescens	Leadplant	Fabaceae	X	X	
Baptisia australis	Blue wild indigo	Fabaceae	X	X	X
Lespedeza virginica	Slender lespedeza	Fabaceae			X

Table 2 (continued)

Species	**Common name**	**Family**	**Moderate Burn**	**Severe Burn**	**No Burn**
Mimosa nuttallii	Catclaw sensitive brier	Fabaceae	X		X
Quercus marilandica	Blackjack oak	Fagaceae			X
Quercus stellata	Post oak	Fagaceae			X
Geranium carolinianum	Carolina geranium	Geraniaceae	X	X	
Juncus sp.	Rush	Juncaceae			X
Callirhoe involucrata	Low poppymallow, winecup	Malvaceae	X		
Oenothera glaucifolia	False guara	Onagraceae	X	X	X
Oenothera suffrutescens	Scarlet beeblossom	Onagraceae	X	X	X
Castilleja purpurea var. *citrina*	Citron paintbrush	Orobanchaceae	X		
Oxalis stricta	Sheep sorrel	Oxalidaceae			X
Nuttallanthus texanus	Texas toadflax	Plantaginaceae	X		X
Plantago aristata	Bottlebrush plantain	Plantaginaceae	X		X
Plantago virginica	Paleseed plantain	Plantaginaceae		X	
Alopecurus carolinianus	Carolina foxtail	Poaceae			X
Bromus japonicus	Japanese brome	Poaceae		X	
Bromus tectorum	Cheatgrass	Poaceae	X	X	X
Dichanthelium oligosanthes	Scribner's panicum	Poaceae		X	X
Elymus repens	Quackgrass	Poaceae	X		
Hordeum pusillum	Little barley	Poaceae		X	X
Mnesithea cylindrica	Carolina jointtail grass	Poaceae		X	
Panicum virgatum	Switch grass	Poaceae	X	X	
Schizachyrium scoparium	Little bluestem	Poaceae		X	X
Geum canadense	White avens	Rosaceae	X		
Prunus angustifolia	Chickasaw plum (sand plum)	Rosaceae	X	X	
Stenaria nigricans var. *nigricans*	Narrowleaf bluet	Rubiaceae	X		
Selaginella peruviana	Sheldon selaginella	Selaginellacea	X		
Solanum carolinense	Carolina groundcherry	Solanaceae	X	X	
Glandularia canadensis	Rose verbena	Verbenaceae	X		X

Table 3 Summary of principal components analysis of 38 habitat variables for nine burn treatment sites

Variable	PCI	PCII	PCIII
VC-LHV 1	0.3276	0.5352	0.4793
VC-FCG 1	-0.7487	-0.4238	0.0202
VC-FCF 1	-0.8446	0.1512	-0.0202
VC-LHV 2	-0.0607	0.3614	0.3851
VC-FCG 2	-0.5746	-0.3075	0.1936
VC-FCF 2	-0.2223	-0.0764	-0.5285
VC-LHV 3	-0.2355	0.3395	-0.3065
VC-FCG 3	0.9065	0.3400	-0.1269
VC-FCF 3	0.0143	-0.0071	-0.7783
VC-LHV 4	-0.4187	0.4370	0.0380
VC-FCG 4	0.8107	0.3034	0.2569
VC-FCF 4	0.5395	-0.5924	-0.1209
VC-FCS 4	-0.3047	0.7298	-0.1569
VC-FCG 5	0.9105	0.0613	0.1999
VC-FCF 5	0.2135	-0.5646	-0.1058
VC-FCS 5	-0.3047	0.7298	-0.1569
VC-FCG 6	0.4988	0.6896	0.4904
VC-FCF 6	0.6083	-0.3815	-0.2211
VC-FCS 6	-0.3047	0.7298	-0.1569
VC-FCG 7	0.8268	0.1727	0.5080
VC-FCS 7	-0.3047	0.7298	-0.1569
VC-FCG 9	0.5711	0.3764	0.6516

Table 3 (continued)

Variable	**PCI**	**PCII**	**PCIII**
Dist-N	-0.9067	0.2242	0.0895
Dist-UN	0.9394	-0.1228	-0.0914
Dist-W	-0.6050	-0.5713	0.4695
Dist-H	0.6083	-0.3815	-0.2211
GC-CG	0.1550	0.8001	0.0796
GC-CF	-0.5041	-0.1689	0.0406
GC-L	-0.8289	-0.0900	0.3338
GC-M	-0.3086	0.8362	-0.1531
GC-AC	-0.2352	0.3120	-0.3838
GC-LH	0.5002	-0.2972	-0.7984
GC-GR	-0.2206	0.2877	-0.4824
GC-CO	-0.8596	0.0177	0.2127
GC-BO	-0.8100	-0.2332	0.4047
GC-WA	-0.6050	-0.5713	0.4695
GC-BG	0.3922	-0.1612	0.7967
GC-FM	0.2043	-0.0715	-0.5141
% total variance	32.77	19.54	14.28
Cumulative %	32.77	52.31	66.58

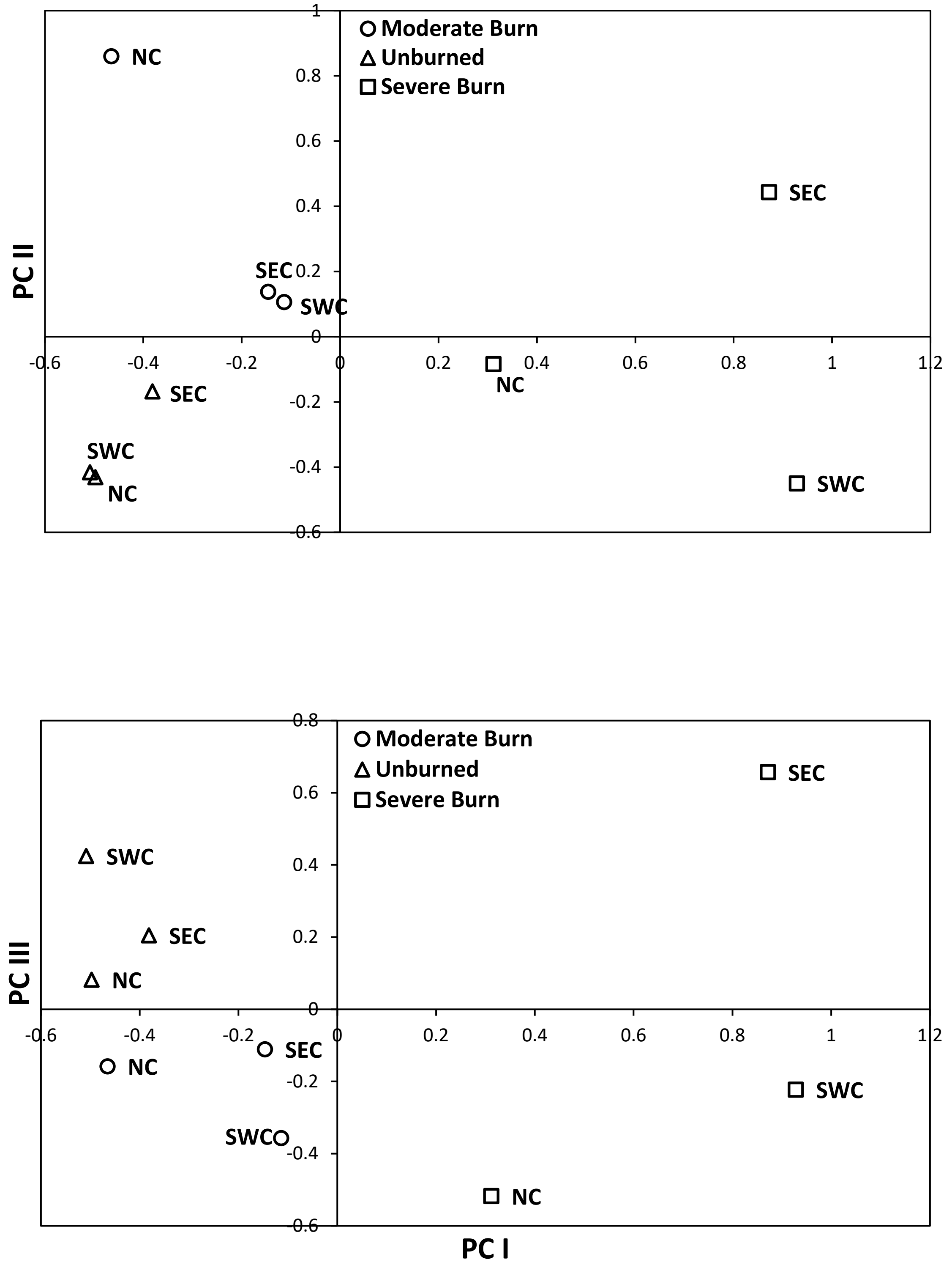

Figure 4 Projections of 3 study plots (NC=North to Central node; SEC=Southeast to Central node; SWC=Southwest to Central node) based on 38 variables onto principal components I, II, and III in the Special Use Area of the Wichita Mountains Wildlife Area

Carter et al. 2008). The unburned and moderate burn sites had higher spring species composition and cover of forbs when compared to the severe burn site which had higher cover of grasses.

The gradients produced by the PCA are consistent with other prairie fire studies with regard to plant species richness and the physical structure of the plant community (Gibson and Hulbert 1987; Collins and Calabrese 2012; Winter et al. 2013). Our study involved three study sites located within 2.5 km of each other, which reflects similar abiotic and biotic conditions.

Many studies measure differences in post fire prairie communities based on frequency of fires (Gibson and Hulbert 1987; Collins and Calabrese 2012; Winter et al. 2013). Using controlled fires in the tallgrass Konza Prairie, Gibson and Hulbert (1987) concluded that time since the last fire was the greatest determinant of prairie species composition. They also found that cover of grasses decreased over time, while cover of forbs and woody species increased. As in most controlled burns, fire severity was not taken into account. Their study took place prior to the reintroduction of bison to the Konza Prairie; therefore, there was no effect on vegetation from grazing. We made the assumption, a priori, that grazing by large herbivores (bison, elk, and longhorn cattle) was equal across all three burn treatments, post fire. Our analysis infers that large herbivores do indeed prefer the severe burn site forage at this point in recovery. We did, however, observe these large herbivores at all three sites. As indicated in studies of tallgrass ecosystems (Fuhlendorf and Engle 2004; Allred et al. 2011), it is possible that fire and grazing interact in landscapes to increase heterogeneity, as fire concentrates grazing activity to certain burned patches thereby reducing grazing in others. Our study supports the findings of many others in that fire severity also affects the recovery of vegetation, including not only composition but also its vertical and horizontal structure (Gibson and Hulbert 1987; Collins and Calabrese 2012; Winter et al. 2013). This follows the pattern of allogenic change due to fire fostering an increased probability of autogenic change (e.g., grazing) and its subsequent effects across the landscape.

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Critic's Choice Essay

A CONVERSATION WITH A SMALL BEETLE

Reprinted from *Gaillardia*, Fall 2000

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Today we find our lives filled with technological innovations such as personal computers, the internet and email, supersonic aircraft, space probes, interspecies gene transfers, and on and on. Yet, you think *we* lead an unusual life! Let me tell you what happened recently to an insect acquaintance. She related her tale of woe as I sat out back watching the tall phlox Pat Folley gave me grow taller.

First, a number of gardeners in the neighborhood grow *Arum italicum* Mill., an arum lily, for its large, attractive, light veined leaves and clusters of beautiful, bright red berries which appear late in the growing season. Introduced to North America, the species is native to southern Europe and in some areas of Italy is considered a common weed.

In Oklahoma, flowering takes place in May, and in arum the reproductive structure is actually not the typical flower but an inflorescence surrounded by a large leaf. On our Oklahoma Native Plant Society field trips we have seen numerous Jack-in-the-Pulpit plants, and the floral system is quite similar. The erect flowering stalk (spadix) is enclosed in an enveloping bract (spathe). The flowers are unisexual with the pistillate (female) at the base of the spadix and the staminate (male) above. Over those two sets of fertile flowers is a whorl of sterile flowers which, when inflated, form a barrier between the floral chamber within the spathe and the open area above.

My friend, a small, dark beetle, said her recent experience started one warm afternoon while foraging when she sensed what she felt was the aroma of food (you and I would probably say it smelled like a combination of carrion and urine).

She followed her "nose" to a large plant (we later identified it as *Arum italicum*) and landed on the open throat of the spathe. A large number of beetles, gnats, and blowflies had already gathered.

She sensed the aroma was welling up from the tubular spathe and, again following her "nose," walked to the opening. She reported slipping at the edge on tiny oil droplets and falling through some bristles into the depths of the chamber. There she found the stigmas of the pistillate flowers covered with a sweet, slimy fluid. She noted the inflated bristles that so readily permitted her fall were keeping large insects out. They were forced to fly off, seeking food elsewhere.

Once at the bottom of the pit, her first thought was of escape. However, she discovered the walls of the lower chamber were just as slippery as the upper spathe surface, and climbing out was impossible until she realized she could climb over the lower female flowers. As she did, she noticed others with pollen on their backs losing those grains to the sticky surfaces of the female flowers as

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they labored upward. Unfortunately when the group reached the base of the bristles, they encountered downward pointing hairs which prevented further progress.

She lamented, "What to do?", but only briefly. The chamber was warm and out of the rain, abundant food was being produced by the flowers, and about half the crowd was male. There was but one thing to do — PARTY!

With the setting of the sun, my friend and the others settled down. I do not know if it was the darkness, full bellies and party fatigue, or simply bedtime for little beetles. However, during the night the staminate flowers matured and rained pollen from above.

With dawn and the rising sun, everyone awoke to find themselves coated with pollen adhering to the sticky exudate from the stigmas. Once again, how to escape? Lo and behold, the downward pointing hairs had wilted along with the bristles, and it was possible to climb up and over their wrinkled surfaces to the throat of the spathe and freedom.

Interestingly, the upper portion of the spathe (appendix) had lost the carrion aroma, and my friend with her pollen-laden companions, previously prisoners of the night, flew away. However, the escaping insects picked up the aroma of another arum inflorescence and agreed to drop by for a visit, only to be trapped in a new prison chamber. This time, one where the pollen on their backs would be transferred to the flowers, and pollination would take place. When I last saw my friend, she was joining a group headed toward yet another arum plant.

There is an additional feature of arum I would like to mention before closing. The terminal portion of the spadix, the appendix, is the source of the aroma, unpleasant to you and me but attractive to my beetle friend. While the chemical producing the aroma is being released, the appendix tissue generates heat to the point that it may be as much as 36 degrees warmer than the surrounding air. Research suggests the temperature elevation serves to volatilize the smelly compound, increasing the speed with which it is spread into the atmosphere. For most of us, that is an interesting aspect of the overall process, and we quickly see the reason behind it. For you chemists, it raises another question. What metabolic pathways are utilized by the plant to produce such significant energy release? How do the plants do it?

What an interesting story and introduction to pollination ecology right in the back yard. You see there is a benefit to taking a few minutes to chat with a small beetle.

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