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REPRODUCTIVE STUDIES IN THE GENUS CALLIRHOE (MALVACEAE)

The University of Oklahoma

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THE UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

REPRODUCTIVE STUDIES IN THE GENUS CALLIRHOE (MALVACEAE)

A DISSERTATION
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
DOCTOR OF PHILOSOPHY

BY
BONNIE B. AMOS
Norman, Oklahoma

1981

REPRODUCTIVE STUDIES IN THE GENUS CALLIRHOE (MALVACEAE)

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PREFACE

This dissertation is prepared as three separate manuscripts with independent table and figure numeration in accordance with the format of refereed journals. The first article, "The Breeding System of Callirhoe involucrata (Malvaceae)", is in the format of Science, the other two are in that of American Journal of Botany. Citations to Amos (1981) refer to this dissertation.

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TABLE OF CONTENTS

	Page
LIST OF TABLES	vi
LIST OF FIGURES	vii
 Breeding System of <u>Callirhoe involucrata</u> (Malvaceae)	
ABSTRACT	2
TEXT	3
REFERENCES AND NOTES	9
TABLES	10
 Pollination Ecology of <u>Callirhoe involucrata</u> (Malvaceae)	
ABSTRACT	12
INTRODUCTION	13
BREEDING SYSTEM OF <u>CALLIRHOE INVOLUCRATA</u>	13
METHODS AND MATERIALS	14
RESULTS AND OBSERVATIONS	16
DISCUSSION	24
LITERATURE CITED	29
TABLES	32
FIGURES	37
 Reproductive Biology of <u>Callirhoe scabriuscula</u> (Malvaceae)	
ABSTRACT	42
INTRODUCTION	43

MATERIALS AND METHODS	43
OBSERVATIONS AND RESULTS	45
DISCUSSION	51
LITERATURE CITED	54
TABLES	56
FIGURES	61
APPENDICES	65

LIST OF TABLES

	Page
TABLE	
Breeding System of <u>Callirhoe involucrata</u> (Malvaceae)	
1. Comparison of Fruit Set of Autogamous and Geitonogamous Crosses	10
Pollination Ecology of <u>Callirhoe involucrata</u> (Malvaceae)	
1. Comparisons of Floral Phenologies	32
2. Distribution of Sexual Phases	33
3. Floral Visitors	34
Reproductive Biology of <u>Callirhoe scabriuscula</u> (Malvaceae)	
1. Fruit Set in Experimental Pollination	56
2. Community Composition	57
3. Floral Visitors	58

LIST OF FIGURES

FIGURE	Page
Pollination Ecology of <u>Callirhoe involucrata</u> (Malvaceae)	
1. Bee Colors of Claret Flowers	38
2. Bee Colors of White Flowers	40
Reproductive Biology of <u>Callirhoe scabriuscula</u> (Malvaceae)	
1. Bee Colors of Flowers	62
2. Pollen-Ovule Ratios	64

THE BREEDING SYSTEM OF CALLIRHOE INVOLUCRATA (MALVACEAE)

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ABSTRACT. Callirhoe involucrata (Torr.) Gray (Malvaceae) is protandrous; however, the temporal separation of the sexual phases is incomplete and the occurrence of a self pollination is possible. Unexpected results were obtained during a series of interplant and intraplant pollinations to determine the reproductive mode of this species: Cross pollinations between flowers on the same plant (geitonogamous crosses) resulted in fruit set while crosses involving the transfer of pollen within a flower (autogamous crosses) most often set less than 10% as many fruits. In a series of experiments to test this behavior, results were recorded as the presence or absence of fruit set for 342 crosses. Data were analyzed with chi-square based on (i) the type of cross by results, (ii) the type of cross by results by the age of the flower, and (iii) the type of cross by results by population. More geitonogamous crosses resulted in fruit set (50.7%) than autogamous crosses (8.3%). The number of successful autogamous crosses decreased with the age of the flower; however, the success of the geitonogamous crosses was not affected by floral age. In the study I recognized three distinctive breeding expressions (i) self-incompatible—neither the geitonogamous nor the autogamous crosses produced fruit, (ii) self-compatible—both types of crosses produced fruit, and (iii), what I call mixed compatible—geitonogamous crosses are favored. Responses among individuals varied in the expression of the mixed compatibility. Possible adaptative significance of the system is discussed in relation to pollen transfer.

Callirhoe (Malvaceae) is a North American genus comprised of approximately eight species with numerous varieties and forms (1). One of the most common members of this genus is the semi-weedy Callirhoe involucrata (Torr.) Gray, which occurs from Nebraska to northern Mexico, and is known by such common names as poppy mallow, cowboy rose, or winecup. This species is a decumbent perennial with numerous stems radiating from the crown. The flowers are large, 4-6.5 cm in diameter, actinomorphic, dish-shaped, and white or more commonly claret; the flowers occur on axillary and terminal elongated peduncles on long unbranched stems.

A protandrous pattern of floral development is characteristic of the Malvaceae. In C. involucrata, despite both temporal and spatial mechanisms which separate the sexual phases, dichogamy is incomplete. It is not uncommon to find much pollen remaining in the flower when the receptive stigma emerges. Therefore, the protandrous pattern does not eliminate the physical possibility of autogamy. In order to determine the mode of reproduction of this species, I conducted a series of breeding experiments. Biotic visitors were excluded and interplant and intrapant pollinations conducted. The latter experiments included both autogamous and geitonogamous transfer of pollen.

During these preliminary studies, an unusual phenomenon was observed. Geitonogamous crosses resulted in fruit set while autogamous crosses typically failed to set fruit (2). These results are surprising and problematic. The reasonable expectation is that autogamous and geitonogamous seed set should be comparable, because the two pollination modes are genetically equivalent. Therefore, I was highly skeptical: However, this type of relationship has been mentioned twice in the

literature, although only briefly and concerning other taxa (3). To determine whether this crossing phenomenon is real or an artifact, a more detailed study of the breeding system was conducted.

Based on the results from the preliminary studies, I designed a series of experiments employing both geitonogamous and autogamous crosses. To determine whether the stage of development of the anthers or stigma influenced the results, I categorized the staminate and pistillate phase of maturation each into three stages. The stages recognized for the staminate phase were based on level of anther dehiscence: stage one, approximately one-third of the anthers had dehisced; stage two, two-thirds had dehisced; and stage three, when all anthers had dehisced but the stigma lobes had not yet emerged. The pistillate phase was divided into categories based on the level of stigma lobe emergence: stage one, lobes erect; stage two, lobes expanded and reflexed, forming a crown; stage three, lobes lengthened and turned down into the staminal column. The stage was recorded for each flower involved in the cross. In addition, each plant and flower was distinctively labeled. Plants used in crosses were also identified by population to determine whether variation exists among populations. The experiments were conducted in the Department of Botany/Microbiology greenhouse at The University of Oklahoma with plants representing 17 populations collected from 1977 through 1979 (2).

Results were recorded as the presence or absence of fruit set for each of the 342 crosses. Fruit set was used rather than seed set because typically an abscission zone forms and the flower aborts in unsuccessful crosses. The data were compiled and analyzed by chi-square using the SPSS computer package with an IBM/370-158 computer at The University of Oklahoma. Two two-by-two contingency tables were generated with the chi-square based on the type of cross by

results. A third contingency table was based on the type of cross by results by stage of sexual maturation. Population variability was addressed through a chi-square analysis of the results of the geitonogamous and autogamous crosses by population.

None of the 67 flowers from which insects were excluded and without artificial self pollination set fruit. This indicates that the flowers are incapable of self-pollination; therefore, mechanical transfer of the pollen is necessary for fruit set. These 67 flowers were eliminated from subsequent data analyses.

The remaining 275 intraplant crosses formed the second contingency table. Only 11 of 133 autogamous crosses resulted in fruit set while approximately half, 72, of the 142 geitonogamous crosses resulted in fruit set ($\chi^2=56.7$, $P<0.00001$). The hypothesis that fruit set is independent of the type of cross must be rejected.

The values in Table 1 represent data obtained from chi-square analyses of the type of cross by the number of fruits set or not set by stage of sexual maturation for 227 crosses. Fruit was set in all of the stages for both types of crosses. Most important is the comparison of the results of the autogamous crosses with those of the geitonogamous crosses at the third stage of anther dehiscence. At the first stage of stigma emergence fruit set was approximately equal for both types of crosses. At the second and third stages of stigma emergence the number of successful autogamous crosses decreased with the age of the flower, thus by the time the stigmas come in contact with the self-pollen the probability of a successful cross is practically nil. However, the success of the geitonogamous crosses was not affected by the age of either the pollen or the stigma.

Responses were not necessarily absolute within a plant. This is illustrated with the ratio between the percentage of fruit set of the geitonogamous crosses and the percentage of fruit set in the autogamous crosses for plants that were involved

in both types of crosses. Thirteen plants did not set fruit in either the geitonogamous crosses or the autogamous crosses (0%:0%), these plants were apparently self-incompatible. There were three self-compatible plants (100%:100%), in the classical sense, and one plant in which half of the geitonogamous crosses and half of the autogamous crosses produced fruit (50%:50%). In 14 of the plants all of the geitonogamous crosses set fruit but none of the autogamous crosses produced fruit (100%:0%). In the remaining 15 plants more of the geitonogamous crosses resulted in fruit than the autogamous crosses (i.e. 50%:0%, 67%:0%, 33%:0%, 80%:25%). Thus it appears that the geitonogamous system is incomplete in about 35% of the plants but approximately 58% were either xenogamous or geitonogamous with less than 7% autogamous. From this, most plants (ca. 65%) seem to exhibit one of three breeding expressions: self-compatible, self-incompatible, and, what I call, mixed compatible. In the latter system geitonogamous crosses are favored over autogamous ones. Populations exhibit varying levels of these three systems (2). Thus, the breeding system is in a flux for the species or each population has adaptively or stochastically maintained an independent system.

Although the genetic or physiologic mechanism operating the mixed compatibility system is unknown, it is possible to reflect upon possible significance—Callirhoe involucrata exhibits temporal dioecism, that is, all flowers on a plant are typically in either the staminate phase or the pistillate phase (2,4). Because duration of the staminate phase is approximately 12 times as long as the pistillate phase in open field conditions (flowers close shortly after pollination, although autogamous crosses are typically delayed), the staminate phase predominates (2). This typically restricts geitonogamous and autogamous transfers (i.e. self-fertilization) and xenogamy (cross-fertilization) is maximized. Thus inbreeding would be

restricted in both the self-compatible and the mixed compatible system. However, when a flower is not pollinated the flower remains open and in the pistillate phase longer. Consequently, the duration of flowers in the pistillate phase on a plant and the proportion of pistillate flowers within the population increases, if inclement weather or other factors restrict pollen collection and pollination. These factors result in the breakdown of the temporal dioecism and thus increase the probability of the occurrence of geitonogamous and autogamous crosses. However, the described system restricts autogamy. It is under these conditions that the mixed compatibility system is operational.

It appears that the advantage of the mixed compatibility system versus a self-compatibility system is not during fertilization or post fertilization stages, because autogamous and geitonogamous crosses are genetic equivalents; rather, the advantage must be prior to fertilization, that is to say, during pollination. Xenogamy is the primary mode of reproduction, obligately so in the self-incompatible plants and the pistillate plants in gynodioecious populations and facultatively in the mixed compatible and self-compatible plants, because of the temporal dioecism. Consequently, geitonogamous pollen transfer is relatively reduced. Geitonogamous transfer increases in plants having the mixed compatibility or the self-compatibility systems when pollination is delayed, that is, when few, or no, pollinators are active in the population or with poor pollinator efficiency such as visitation only by the non-specialist insects (2). Thus, the mixed compatibility system is not operational at all times, instead it represents a type of safety measure to insure seed set under circumstances when xenogamy is reduced. However, it remains problematic why a geitonogamous and not a geitonogamous-autogamous system would be advantageous as a fail-safe mechanism. It appears, based on

literature, that the most common fail-safe system occurs when the styles come in contact with the pollen mass of the same flower at the conclusion of anthesis. In Callirhoe involucrata, the styles do curve downward into the remnant pollen, yet fruit set via this process is nil, whereas pollen and styles of the same age in geitonogamous crosses yield fruit. It is possible that the system is a chance result of a shift in breeding systems and not directly under the process of selection. That is, if the system were in a state of flux from autogamy to xenogamy a newly derived physiological barrier to autogamy might not have affected geitonogamy. Conversely, evolution to autogamy may first have resulted in a breakdown of the inhibitors.

References and Notes

1. U. T. Waterfall, *Field and Laboratory* 19. 107 (1951).
2. B. B. Amos, dissertation, University of Oklahoma (1981). In the preliminary crosses, 63% of the geitonogamous crosses produced fruit while only 5% of the autogamous crosses resulted in fruit set. Populations involved in the crossing experiments are identified in the Appendix of the dissertation. Pollen collection and transfer was accomplished by first shaking pollen from the flower onto a paper tray and then placing the pollen onto all stigma lobes on the recipient stigma with either a paper spatula or by brushing the stigma lobes against the pollen in the tray. Because the pollen is large, it was possible to see if equal amounts of pollen were evenly distributed over the stigma lobes. Approximately equal amounts of pollen were used in both types of crosses. Pollinators for this species include two oligolectic bees, Diadasia afflicta and Melissodes intorta.
3. K. Faegri and L. van der Pijl. *The Principles of Pollination Ecology* (Pergamon Press, Oxford, 1971), pp. 166.
4. R. W. Cruden and S. M. Hermann-Parker. *Evolution* 31, 386 (1977). Temporal dioecism is defined as "a flower sequence which is synchronized so there is little or no overlap between staminate and pistillate phases of an individual plant." It is described for the flowering sequence in several protandrous and protogynous members of the Apiaceae.

TABLE 1. Comparison of percentage of fruit set for autogamous and geitonogamous crosses. Stages are defined in text.

		Autogamous Crosses	Geitonogamous Crosses		
♀	♂	Stage	Stage		
		1	1	2	3
1		26.7 ^a (N=15)	50.0 (N<10)	50.0 (N<10)	31.8 ^a (N=22)
2		19.2 ^b (N=26)	100.0 (N<10)	66.7 (N<10)	52.9 ^b (N=51)
3		2.2 ^c (N=45)	66.7 (N<10)	62.5 (N<10)	39.4 ^c (N=33)

^anot significant at 0.05 level

^b $\chi^2 = 8.06$, significance 0.005

^c $\chi^2 = 17.9$, significance 0.00001

THE POLLINATION ECOLOGY OF CALLIRHOE INVOLUCRATA (MALVACEAE)

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ABSTRACT—The breeding system of Callirhoe involucrata (Malvaceae) is heterogenous; three distinctive breeding expressions are recognized, (i) self-compatible—both geitonogamous and autogamous crosses produce fruit, (ii) self-incompatible—neither type of cross results in fruit set, and (iii) mixed compatible—more geitonogamous crosses produce fruit than the autogamous crosses. Although geitonogamy is favored in the latter breeding system, it is restricted in pollen transfer through temporal dioecism and pollinator flights. The flowers are protandrous; there is little overlap in the sexual phase of plants with more than one flower in anthesis (70.8% no overlap). Only 1.8% of 137 interfloral flights observed could result in geitonogamy. Therefore, the pollination system appears to have little impact on breeding dynamics. Copious amounts of pollen are produced, but nectar is the primary attractant; most floral visitors are nectar foragers. Pollen collection is essentially restricted to two species of oligolectic bees, Diadasia afflictata and Melissodes intorta. The frequency of both of these species is low and most pollinations are effected by generalist species while foraging for nectar.

(INTRODUCTION)

The evolutionary potential of a species is largely dependent on its reproductive biology. For an outcrossing species the reproductive biology is determined by two interactive components: the breeding system and the pollination system. There is ample evidence that an alteration in the mode of pollination, either change of pollinator or in pollinator densities may result in speciation or a change in the breeding system (Levin 1971, Straw 1955, Levin and Anderson 1970, Grant and Grant 1965, Eisikowitch 1973). The dependency of an obligate allogamous species on a pollen vector is one of the most vulnerable phases of the reproductive cycle. The breeding system of Callirhoe involucrata (Torr.) Gray (Malvaceae) is highly heterogenous (Amos 1981). This paper presents the results of a study of the floral biology, phenology, and pollination ecology of C. involucrata to investigate possible interactions of the breeding and pollination systems.

BREEDING SYSTEM OF CALLIRHOE INVOLUCRATA—In a series of intraplant crosses, more geitonogamous crosses resulted in fruit set (50.7%) than autogamous crosses (8.3%) ($P < 0.00001$) (Amos 1981). The number of successful autogamous crosses decreased with the age of flower; however, the success of geitonogamous crosses was unaffected by the stage of development of either the pollen or the stigma. In the study, I recognized three distinctive breeding expressions: (i) self-compatible—both types of crosses produced fruit, (ii) self-

incompatible—neither the geitonogamous nor the autogamous crosses produced fruit, and (iii) mixed compatible—geitonogamous crosses are favored. Responses among individuals varied in the expression of mixed compatibility.

METHODS AND MATERIALS—Study Sites—I studied Callirhoe involucrata at three Texas sites in Tom Green County near San Angelo and a fourth site in Menard County: (i) along Farm Road 584 near Mathis Field, (ii) in a small roadside park along South Concho Drive near Pecan Creek along the southern portion of Lake Nasworthy, (iii) the roadside along Ben Ficklin Road approximately $\frac{1}{4}$ mile north of Loop 306, and (iv) approximately $\frac{1}{4}$ mile west of Highway 83 along San Saba Avenue in Menard. All four populations were gynodioecious. The Mathis Field and Ben Ficklin Road populations were composed entirely of plants with claret-colored flowers. The Pecan Creek site had approximately equal numbers of white-flowered and claret-flowered plants; in addition, there were a few plants with lavender flowers, probable hybrids between white and claret forms. All plants at the Menard site had white flowers. Observations of phenology, pollinators, and insect behavior were made at these four sites during June of 1978 and 1979. In 1980, studies began in April and concluded in mid-July.

Floral morphology, phenology, and ecology—Phenological data were gathered through daily observations of tagged flowers between 0830 and 1800 hr CDT. Information gathered included: (i) time of flower opening, (ii) onset of anther dehiscence, (iii) the time of pollen presentation, (iv) the time of stigma emergence, (v) time of stigma receptivity, and (vi) duration of individual flowers. Seventy-five

flower buds were bagged with paper pollination bags (Central States "Slip-ezy" model 9235) to test the potential for self-pollination in the absence of floral visitors. Field observations were supported by observations of and experimentation with plants growing in the Department of Botany and Microbiology greenhouse at The University of Oklahoma.

On the first of May, 1980, at the Mathis Field location, estimates of vegetative areal cover and frequency and floral density were obtained with 40 0.5m^2 quadrats along a linear transect. From these data, the community was defined vegetatively by calculating Importance Percentage (relative frequency + relative cover/2). Flower density values were obtained for those species in flower. Floral values were not collected for plants considered to be non-entomophilous.

Reflectance spectrophotometry was used to estimate the spectral reflectance of the corolla. Photographs were taken with a single-lens reflex camera with Kodak Tri-X pan film using filters transmitting red (Soligor 25A), yellow (Vivitar 8K2), blue (Vivitar 80C), visible light (Tiffen UV haze), and ultraviolet (Tiffen 18A).

Plant phenological data were collected from 15 populations in central Texas (Amos 1981, Appendix III). A line transect was established through the population, and each plant encountered along this line was sampled. Information recorded included: the number of flowers per branch, the number of branches with flowers, and whether the flowers were in the staminate or pistillate phase. Flowers on pistillate plants were distinguished from perfect flowers in the pistillate phase. Comparisons of populations were based on the relative number of flowers in the staminate phase versus the pistillate phase. Data were analyzed by the chi-square test.

Floral foragers and pollinators—Insect visitors to C. involucrata flowers and other flowering members of the community were observed daily from 0800 to 1800 hr CDT. Special attention was given to the intrafloral behavior, the time per flower, and whether pollen or nectar was collected. Representatives of all insects observed visiting C. involucrata flowers were analyzed for the presence, body location, and identity of their pollen loads. Voucher specimens are deposited in the Bebb Herbarium at The University of Oklahoma.

Insects were tracked in the field to estimate the potential for xenogamy and geitonogamy. During this study the stage of floral phenology, either staminate or pistillate, was also noted.

Experiments to determine pollinator efficiency were conducted in the following manner: floral buds were bagged with paper pollination bags and tagged for subsequent identification. When the stigma had emerged, the bags were removed. After an insect visited the flower, the phenology of the flower based on the level of stigma emergence, the species of insect visitor, and comments on the foraging behavior were recorded. The flowers were rebagged and reexamined periodically until fruit set or abortion of the flower was evident.

Insect exclusion cages, which were constructed of fine mesh hardware cloth (opening ca. 1mm²), were placed over tagged floral buds on pistillate plants. After the tagged flowers had opened, the cage was removed. After an insect had foraged the flower, five stigma lobes were removed from the flower and the number of pollen grains counted. The species of insect, comments on its foraging behavior, and the average number of pollen grains were recorded.

RESULTS AND OBSERVATIONS— Floral morphology, phenology, and ecology— Callirhoe involucrata is a decumbent, prostrate plant from a napiform root.

The unbranched stems are procumbent, sometimes ascending, and extend in all directions from the center. Flowers occur singly on axillary and terminal elongated peduncles. The actinomorphic dish-shaped corolla, 4-6.5 cm in diameter, is composed of five obovate, truncate, claret, lavender, or white petals. The petals in the purple flowers are white on the basal portion forming a white ring in the center of the blossom. The flowers have a faint sweet odor. The anthers are numerous (20 to 40), and the filaments are fused around the pistil. In gynodioecious populations, the pistillate plants may exhibit a marked reduction in anther number. Copious amounts of spiny, yellow pollen, approximately 150μ in diameter, are produced. The style branches are fimbriate and are the same in number as the cells of the ovary; they are stigmatic along the inner surface. The fruits are carpellate, one-seeded, arranged in a circle and as many in number as the stigmas (16-20). The five nectaries are at the base of the calyx and alternate with the petals. They produce small amounts of nectar, 0.1-0.3 μ l, throughout the life of the flower.

The purple flowers exhibit three basic coloration patterns revealed in the reflectance spectrophotometry study (Fig. 1). The distal portion of the blossom, which comprises approximately two-thirds of each petal, varies in all three from bee blue-green to bee yellow-green.¹⁾ The staminal column, anthers and pollen are bee yellow. A ring of bee white encircles the staminal column in each of the three patterns; this is not differentiated to the human eye. In the first and second patterns the basal portion of each petal is bee yellow. In flowers exhibiting the second pattern, there is an additional narrow band of bee white between the distal and basal portion of each petal. The third coloration pattern exhibits these three

¹⁾The colors designated are based on studies and interpretations of honeybee vision (Frisch 1950, 1954, Kevan 1978, Proctor and Yeo 1972).

bands but the color differs towards the center of the flower. The narrow second band is bee yellow and the basal portion, which forms the third band, is bee black. All three color forms were observed in both perfect and pistillate flowers.

The white color form also exhibited three patterns (Fig. 2). In each of these the bee white ring at the base of the staminal column was present. In the first pattern the petals were uniformly bee yellow; the staminal column, anthers and pollen were also bee yellow. In the second and third patterns the distal portions of the petals were bee yellow and the basal portion a darker bee yellow. This also was the coloration in the third pattern, but there again was an additional narrow band of bee white between these. To the human eye the petals are uniformly white in all flowers.

Anther dehiscence begins with those anthers at the apex of the staminal column and proceeds downward over a 16 hr period. About 20 hr after cessation of dehiscence, the stigma lobes emerge from the staminal column. They remain erect for about 5 hr and then gradually begin to elongate and recurve, eventually curving into the column in the old flower. Flowers open at approximately 0830 hr and close each evening shortly before sunset. The flowers continue to open each morning for as long as eight days. They close 30-90 minutes after pollination; however, autogamous crosses are typically delayed. During inclement weather the petals do not fully open. Despite both temporal and spatial mechanisms to separate the sexual phases, the dichogamy is incomplete; pollen is typically abundant when the receptive stigma emerges.

Crosses conducted in the greenhouse and supportive field crosses indicate the Mathis Field population is comprised of plants that exhibit self-incompatibility and partial mixed compatibility, in which approximately half of the geitonogamous crosses within a plant produced fruit, and none, or very few, of the autogamous

crosses resulted in fruit set. None of the 75 flowers bagged with insect exclusion bags in the field produced fruit; therefore, a pollen vector is necessary for fruit set.

Callirhoe involucrata was most abundant at the Mathis Field site in a shallow roadside ditch along Highway 584; the transect for sampling the composition of the community was established in this area. Members of the Poaceae formed the dominant vegetative category; Engelmannia pinnatifida, Callirhoe involucrata, and Medicago minima were important secondary species (Amos 1981, Appendix IV). The species having the highest floral density in this area was Engelmannia pinnatifida; C. involucrata was third following Teucrium laciniatum (Amos 1981, Appendix V). Other species in flower were present along the road margins and in a large mesquite flat southeast of the study site; therefore, these represent only the potential nectar and pollen sources within the immediate area. The three other study sites were dominated by C. involucrata. There were few other plant species in flower in the immediate area.

A high percentage of plants in each population had only one flower per branch ($\bar{x} = 96.7\%$) and many of the plants had only one flower in anthesis at a time ($\bar{x} = 32.7\%$) (Table 1). Of the total flowers sampled in each population, in most populations (73%) there were more flowers in the staminate phase than in the pistillate phase. There was little overlap in the sexual phase of those plants that had more than one flower in anthesis (70.8% no overlap). In plants with overlap, again the staminate phase was dominant in regard to the number of flowers (64% in the staminate phase) (Table 2).

Floral foragers and pollinators—Flowers of Callirhoe provide three attractants for anthophilous visitors: nectar, pollen, and shelter (Table 3). Nectar is the

primary attractant, although many of the species observed visiting the flowers for nectar typically do not pollinate the flowers because of their size or their behavior in the flowers.

Class I—The smaller insects (Table 3) land on a petal and crawl into the flower along the petal. They forage for nectar at the base of the staminal column and exit the flower from a petal. These insects rarely come in contact with the stigma lobes. None of these insects were observed collecting pollen, but because of the abundance of pollen, which is often in large deposits around the nectaries at the base of the staminal column, Callirhoe pollen was commonly found in the hairs of the small hymenopterans. However, only sporadic pollen grains were in the corbiculae or pollen baskets. The soldier fly, Labostigmina texasiana, is large enough to brush against the stigma lobes when the lobes are reflexed, but the efficiency of this insect as a pollinator is minimal because it typically remains in a single flower for 1-3 hrs. The male of this species uses the flower as shelter during the night; several were observed in blossoms early in the morning before the petals had unfurled. Class I insects therefore most often remove nectar from the system without effecting pollination.

Class II—The larger nectar-foraging insects (Table 3) often come in contact with the stigma lobes during nectar foraging. Many of these were frequent floral visitors. Two subclasses were recognized based on floral behavior. Apis mellifera and Agapostemon texanus fly to the flower, grasp a petal with the fore legs, and then either pull back the apex of the petal or crawl-fly over the petal, entering the flower between the entry petal and the staminal column. Foragers of these two species visit all five nectaries head down with the dorsum of the abdomen against the petals. Exit from the flower is from a petal. An average visitation period for the honey bee is 9 sec (range 1-39, N = 85).

This behavior is different than that of the large solitary bees in this class. These bees fly directly into the center of the flower, often landing with considerable impact on the top of the staminal column. Foraging is with the head down and the dorsum of the abdomen against the staminal column. The staminal column is used as a "take-off" platform from the flower. The average time for solitary bees in a flower is 6 sec (range 1-30, N = 120).

Two species of scarab beetles were occasional floral visitors; they were particularly common at the two sites with white-flowered C. involucrata. These insects forage for nectar similarly to the solitary bees. They circle the staminal column head down with the dorsum of their elytra against the staminal column. Both species typically remain in a flower for several minutes. They appear to be constant visitors of Callirhoe in that they were observed to fly directly to another Callirhoe flower.

None of the insects in Class II were observed collecting pollen but again because of the abundance of pollen and the manner in which the insects enter the flower and forage for nectar, there was often abundant pollen on the head, abdomen, and legs. The bees in this group, with the exception of Agapostemon texanus, are hairy; much pollen is caught in the hairs. All of the bees were observed cleaning Callirhoe pollen from their bodies, although not after each floral visit. The solitary bees remain in the flower while grooming. Agapostemon texanus usually rests against the petals near the floor of the corolla while grooming. The other solitary bees perch atop the staminal column while grooming the pollen from their head and thorax with their front legs prior to leaving the flower. Honeybees typically flew from the flower to rest on the ground or on vegetation for grooming. Although the grooming period was often extensive (3-6 min), the insects were unable to remove

all of the pollen from their bodies. All of the insects in Class II are capable of pollinating the flowers.

Class III—Only five species of bees were observed collecting pollen or found to have packed Callirhoe pollen in their corbiculae (Table 3). Two polylectic species of bees, Halictus ligatus and Lasioglossum sp., were only rarely observed collecting pollen. However, they were common nectar foragers on Callirhoe. Other pollen collectors were Diadasia afflicta and two species of Melissodes. Diadasia afflicta and Melissodes intorta are oligolectic on Callirhoe (Schlising 1972, Linsley and MacSwain 1958, LaBerge 1956). These species also visit the flowers for nectar and the males of D. afflicta and M. intorta use the flower for shelter during inclement weather and at night. Notes accompanying specimens of Diadasia afflicta at the Dallas Natural Museum of History reveal that Lloyd Shinnars (unpubl.) also observed this species in flowers during cool, overcast days. The oligolectic bees collected pollen in a similar manner; they crawled rapidly around the staminal column one to three times brushing the pollen from the anthers onto their pollen baskets. Nectar was not collected during pollen forays. Observations of any species collecting pollen were rare at anytime during daily studies; therefore, it was difficult to detect diurnal patterns in pollen collections.

Forager flight patterns—The foraging flight of the honeybee typically followed a "drunkard's walk" from flower to nearby flower. Flight times between flowers for this species ranged from 2-7 sec with an average of 5 sec. The intra- and interfloral behavior of the honeybee was constant and regular, consequently flights could be tracked some distance.

Several of the solitary bees were alike in size and coloration; this, coupled with their rapid movements and similar foraging behavior, made field identification

to species for each observation very difficult. Therefore, remarks apply to groups of species rather than an individual species; the group includes Diadasia afflicta, Melissodes spp., Diadasia rinconis, Megachile amica, and Lithurgus littoralis. Periods of flight between flowers ranged from 2-3 sec; short bursts of erratic circling above a cluster of flowers for 4-6 sec were not uncommon. Bees typically visited a few flowers in an area and then flew a meter or more away before beginning another short foraging series, hence these bees were much more difficult to track.

Flights were tracked until the bee was lost; in the case of the honeybee this typically was when the bee was observed leaving the study area. The solitary bees were most often lost between foraging series. In nine honeybee flights, the honeybees visited a total of 122 flowers, ($\bar{x}$ = 13.6 flowers per flight) 18 of which were in the pistillate phase, including both perfect and pistillate flowers. Of the 113 interfloral flights, 79.6% were sequentially between flowers on different plants. Only 1.8% of the flights between flowers on the same plant were from a flower in the staminate phase to one in the pistillate phase.

The ten observed visitation patterns of the solitary bees were much shorter ($\bar{x}$ = 2.5 flowers per flight), which reflects both my difficulty in following them and the bees' behavior and the distance between forays. Of the 26 flowers observed during visitation flights, only 4 were in the pistillate phase. Approximately 60% of the flights were sequentially between flowers on different plants. None of the flights between flowers on the same plant were from staminate phase to pistillate phase.

The experiments conducted to test pollinator efficiency and to estimate the average number of pollen grains deposited on the stigma during nectar foraging

were originally intended for comparison of the different species of insect visitors. Honeybees were much more frequent floral visitors than the solitary bees and honeybees were, by far, the most common visitors to the flowers during the experiments, despite attempts to dissuade them. Therefore, the data reflect only this species' activity. Few flowers (9.1%) produced fruit when bees visited flowers with erect stigma lobes in the early stage of stigma emergence (Amos 1981, Appendix VI). As the flowers aged and the stigma lobes first elongated and then reflexed the percentage of visited flowers resulting in fruit set increased, to 65.2% and 77.8% respectively.

The average number of pollen grains deposited on the stigma lobes by the honeybee was 17 grains per lobe (N = 35). Greenhouse studies show that less than 17 grains per lobe are sufficient for fertilization.

DISCUSSION—The flowers of Callirhoe involucrata form an open dish-shaped blossom, which excludes few, if any, types of insects (Faegri and van der Pijl 1971). The bee colors in the flower form a target-type pattern of concentric circles (Figs. 1 and 2).

Although pollen is present in copious amounts, essentially throughout the life of the flower, it does not appear to represent an important insect attractant. Pollen collection is limited to a few species of specialized bees that were infrequent floral visitors. The two oligolectic bees, Diadasia afflicta and Melissodes intorta, are reported to collect pollen only from Callirhoe, and in the study area C. involucrata pollen is collected essentially only by these two species. Insect specialists are assumed to be more efficient at using their preferred resource than are generalists (Strickler 1979, Stebbins 1970). Oligolectic bees may be the most

efficient or the only pollinator for the host plant species, as is the case of Hemihalictus lustrans on Pyrrhopappus carolinianus (Estes and Thorp 1975). Because of their foraging behavior, D. afflictata and M. intorta undoubtedly pollinate flowers which are in the pistillate phase when they visit, but because their frequency is low, they were not important pollinators at the study sites.

Other insects, inadvertently dusted with pollen during nectar foraging, attempt to clean it from their bodies. Much pollen is lost in the grooming activities and there are often large deposits of pollen on the corolla floor shortly before the flowers close. Apparently this reaction is not uncommon in the mallows (Stephen et al. 1969). In spite of this behavior, this group formed the most important pollinators in the study area. Honeybees are included in this group although, because of the difference in orientation to the staminal column during foraging, they are more effective one-visit pollinators when the stigma lobes are reflexed, that is in older flowers.

Pollen dispersal in C. involucrata, despite the specialized pollen collectors, is therefore indiscriminate, at least in the areas studied. A high ratio of pollen to ovules or seeds has been related to inefficient pollen transfer (Baker and Hurd 1968, Cruden 1977, Solbrig 1970).

In addition, there appears to be, functionally at least, a shift away from pollen as an attractant. Populations thus far observed have a high proportion of pistillate plants. Pistillate plants typically produce more flowers, albeit smaller, than the perfect plants. The pistillate flowers provide nectar and increase the nectar supply in the population without contributing pollen. Of particular note is the bee white ring at the base of the staminal column immediately above the nectaries in each of the color forms, perhaps serving as a nectar guide.

Because of the centrifugal pattern of growth, first produced flowers are toward the center and more recent flowers at the periphery of a branch. The basal flower on a branch has, most often, been pollinated and is closed before the next produced flower on that branch opens. Therefore, the nearest open flowers on a plant are on separate branches. In addition, because the long unbranched stems radiate from the central stalk, the flowers on a plant are often some distance apart.

Callirhoe involucrata exhibits temporal dioecism; all flowers on a plant are typically in either the staminate phase or the pistillate phase. Because duration of the staminate phase is approximately 12 times as long as the pistillate phase in open field conditions, the staminate phase predominates. Cruden and Hermann-Parker (1977) defined this term and reported a similar pattern of flower sequence in several protandrous and protogynous members of the Apiaceae, most of which were self-compatible. In their study, they inferred that temporal dioecism was maximizing fitness by minimizing geitonogamy (i.e., self-fertilization) and maximizing xenogamy (i.e., cross fertilization). The system apparently functions in the same fashion in C. involucrata, even though a high percentage of plants are self-incompatible. However, when a flower is not pollinated it remains open and in the pistillate phase longer. Consequently, the duration of flowers in the pistillate phase on a plant and the proportion of pistillate plants within the population increases when inclement weather or other factors result in the breakdown of the temporal dioecism. This increases the probability of the occurrence of geitonogamous and autogamous crosses. It is only under these conditions that the mixed compatibility system is operative.

However, observations of insect flights indicate that geitonogamous pollen transfer is still restricted. Few of the flights of either the honeybees or the solitary

bees were intraplant flights, fewer still were from staminate phase to pistillate phase. The mixed compatibility system seems to have little impact on breeding dynamics and may be a by-product of the shift from self-incompatibility to self-compatibility.

Even though the relationship between the oligoleges and C. involucrata appears to be relatively unimportant for reproduction of the plant, the reliability of the oligoleges may be important when the frequency of the generalists is reduced. This occurs most often when competition for pollinators is at its height. Bees typically are more constant in their pollen resources than in nectar resources (Macior 1974, Strickler 1979, Stebbins 1970). The distribution of activity, selection of species, and constancy among species depends on the attractiveness of floral signals and the availability of pollen and nectar (Levin and Anderson 1970). As food densities and plant community compositions change, a generalist or nectar forager is apt to change food preference (Levin and Anderson 1970). It is conceivable that under these conditions, bees in Class II might no longer be constant floral visitors to C. involucrata but some seed set would be assured because of the dependency of the oligolectic bees on Callirhoe pollen. For instance, honeybees were not observed on C. involucrata at the Mathis Field site from 0830 hrs to 1030-1200 hrs for approximately a three-week period during the study because during this time the bees were working the flowers of Engelmannia pinnatifida. Only after the flowers of E. pinnatifida wilted each morning did honeybees begin visiting the flowers of C. involucrata.

In summary, the reproductive biology of Callirhoe involucrata is flexible in both the breeding system and in the mode of pollination. The breeding system is normally considered to reflect the predictability of pollinators in the habitat

(Cruden 1976), in C. involucrata the primary pollinators are generalists and their activities may change with ecological conditions. With a decrease in pollinator activity or pollinator reliability, there is an obvious advantage in self-compatibility (Cruden 1976). In this species under these conditions there is a shift toward self-fertilization, albeit still dependent on insect vectors, with the mixed compatibility system.

Literature Cited

- Amos, B. B. 1981. Reproductive studies in the genus Callirhoe (Malvaceae). Ph.D. dissertation, University of Oklahoma, Norman, Oklahoma.
- Baker, H. G. and P. D. Hurd, Jr. 1968. Intrafloral ecology. *Ann. Rev. Entomol.* 13: 385-414.
- Cruden, R. W. 1976. Intraspecific variation in pollen-ovule ratios and nectar secretion - preliminary evidence of ecotypic adaptation. *Ann. Mo. Bot. Gard.* 63: 277-289.
- _____. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32-46.
- _____ and S. M. Hermann-Parker. 1977. Temporal dioecism: an alternative to dioecism? *Evolution* 31: 863-866.
- Eisikowitch, D. 1973. Mode of pollination as a consequence of ecological factors, p. 283-288. In (ed.) V. H. Heywood, *Taxonomy and Ecology*. Academic Press, New York.
- Estes, J. R. and R. W. Thorp. 1975. Pollination ecology of Pyrrhopappus carolinianus (Compositae). *Amer. J. Bot.* 62: 148-159.
- Faegri, K. and L. van der Pijl. 1971. *The Principles of Pollination Ecology*. Pergamon Press, New York.
- Grant, V. and K. Grant. 1965. *Flower Pollination in the Phlox Family*. Columbia Univ. Press, New York.

- Kevan, P. G. 1978. Floral coloration, its colorimetric analysis and significance in anthecology, p. 51-78. In (ed.) A. J. Richards, The Pollination of Flowers by Insects. Linnean Society Symposium Series No. 6.
- LaBerge, W. E. 1956. A revision of the bees of the genus Melissodes in North and Central America, part II (Hymenoptera, Apidae). Univ. Kansas Sci. Bull. 38: 533-578.
- Levin, D. A. 1971. The origin of reproductive isolating mechanisms in flowering plants. Taxon 20: 91-113.
- _____ and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. Amer. Nat. 104: 455-467.
- Linsley, E. G. and J. W. MacSwain. 1958. The significance of floral constancy among bees of the genus Diadasia (Hymenoptera, Anthophoridae). Evolution 12: 219-223.
- Macior, L. W. 1974. Behavioral aspects of coadaptations between flowers and insect pollinators. Ann. Mo. Bot. Gard. 61: 760-769.
- Proctor, M. and P. Yeo. 1972. The Pollination of Flowers. Taplinger Publishing Co., New York.
- Schlising, R. A. 1972. Foraging and nest provisioning behavior of the oligolectic bee, Diadasia bituberculata. Pan-Pacific Entomol. 48: 175-188.
- Solbrig, O. T. 1970. Principles and Methods of Plant Biosystematics. MacMillan Co., London.
- Stebbins, G. L. 1970. Adaptive radiation of reproductive characteristics in angiosperms I. Pollination mechanisms. Ann. Rev. Ecol. Syst. 1: 307-326.

- Stephen, W. P., G. E. Bohart, and P. F. Torchio. 1969. The Biology and External Morphology of Bees. Agricultural Experiment Station, Oregon State Univ., Corvallis, Oregon.
- Straw, R. M. 1955. Hybridization, homogamy, and sympatric speciation. *Evolution* 9: 441-444.
- Strickler, K. 1979. Specialization and foraging efficiency of solitary bees. *Ecology* 60: 998-1009.

TABLE 1. Comparisons of floral phenology for 15 populations in central Texas.

Population	Percentage of plants with one flower per branch	Percentage of flowers in the staminate phase	Percentage of flowers in the pistillate phase
1	96	71	16
2	100	69	26
3	100	68	39
4	98	79	16
5	90	76	16
6	96	80	16
7	99	71	39
8	98	68	60
9	100	48	36
10	98	45	18
11	98	72	47
12	89	27	42
13	95	37	46
14	94	66	26
15	99	72	48

TABLE 2. Distribution of sexual phases. Number of plants = 1,125, number of flowers = 3,112.

	<u>No Overlap</u>			Equal	Staminate Dominant	Pistillate Dominant
<u>Number Plants</u>	502	106	189	108	169	51
<u>Number Flowers</u>						
Staminate Phase	1004	-	-	141	771	70
Pistillate Phase	-	131	-	141	263	148
(Perfect Flowers)						
Pistillate Flowers	-	-	443	-	-	-

TABLE 3. Insect visitors of Callirhoe involucrata in relation to floral attractant and foraging behavior. Class I is composed of nectar foragers that are not pollinators because of their size and/or intrafloral behavior. Class II includes larger nectar foragers capable of pollinating the flowers; Class III includes pollen collecting bees.

Species	Attractants		
	Nectar	Pollen	Shelter
CLASS I			
Hymenoptera			
<u>Anthidium palmarum</u> Cockerell ^a	•		
<u>Colletes scopiventer</u> Swenk ^a	•		
<u>Dialictus pruinosisiformis</u> Crawford ^b	•		
<u>Halictus tripartitus</u> Cockerell ^b	•		
<u>Perdita texana texana</u> Cockerell ^a	•		
<u>Pseudomasaris texanus</u> Cresson ^c	○		
<u>Pterosarus</u> undescribed species ^a	○		
Lepidoptera ^d			
<u>Mimoschinia rufofascialis novalis</u> Grote	•		
<u>Thyris maculata</u> Harris	•		
Stratiomyidae			
<u>Labostigmina texasiana</u> Johnson ^e	•		•
<u>Nemotelus</u> sp. ^f	•		

TABLE 3. Continued

Species	Attractants		
	Nectar	Pollen	Shelter
CLASS II			
Hymenoptera			
<u>Agapostemon texanus</u> Cresson ^h	•		
<u>Apis mellifera</u> Linnaeus	•		
<u>Diadasia rinconis</u> Cockerell ^g	•		
<u>Lithurgus littoralis</u> Cockerell ^a	•		
<u>Megachile amica</u> Cresson ^h	•		
Coleoptera ⁱ			
<u>Euphoria kerni</u> Haldeman	•		
<u>Trichiotinus texanus</u> Horn	•		
CLASS III			
Hymenoptera			
<u>Diadasia afflicta</u> Cresson ^{a,g}	•	•	•
<u>Halictus ligatus</u> Say ^h	•	○	
<u>Lasioglossum</u> sp. ^a	•	○	
<u>Melissodes intorta</u> Cresson ^g	•	•	•
<u>Melissodes tristis</u> Cockerell ^g	•	?	○

^adetermined by R. W. Brooks, University of Kansas

^bdetermined by G. C. Eickwort, Cornell University

^cdetermined by R. M. Bohart, University of California at Davis

^ddetermined by D. A. Ferguson, USDA Beltsville Agricultural Research Center

TABLE 3. Continued

^edetermined by W. J. Hanson, Utah State University

^fdetermined by W. W. Wirth, USDA Beltsville Agricultural Research Center

^gdetermined by W. E. LaBerge, Illinois Natural History Survey

^hdetermined by R. W. Thorp, University of California at Davis

ⁱdetermined by W. J. Gibson, Stephen F. Austin State University

^oobserved only rarely.

Figure 1. Bee colors of Callirhoe involucrata claret flowers.

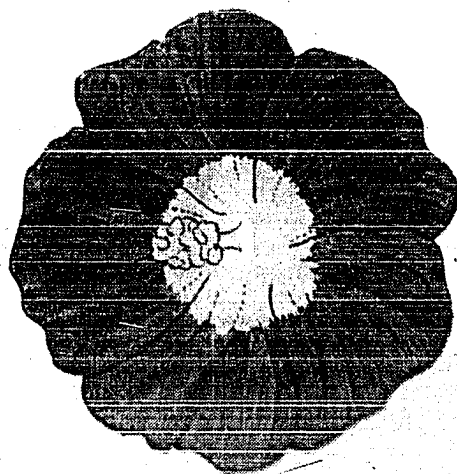
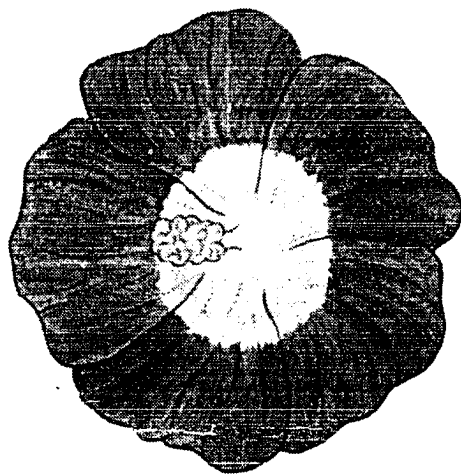
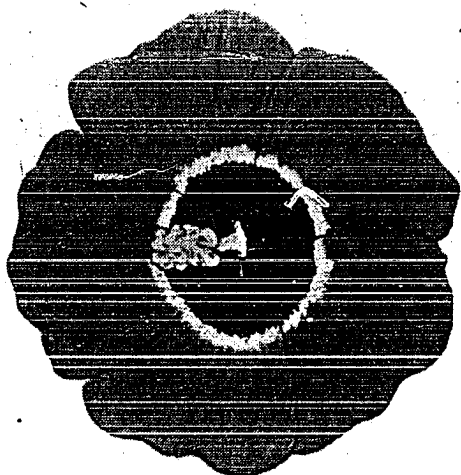
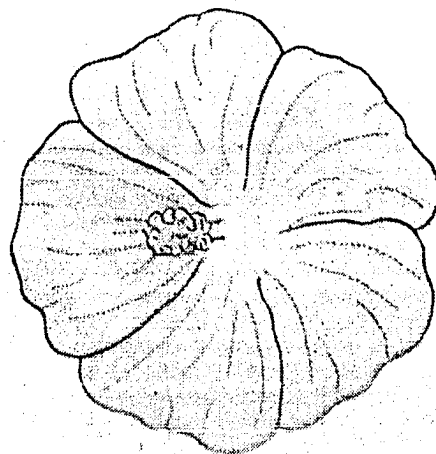
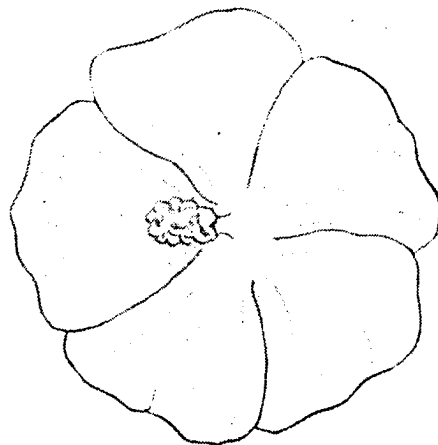
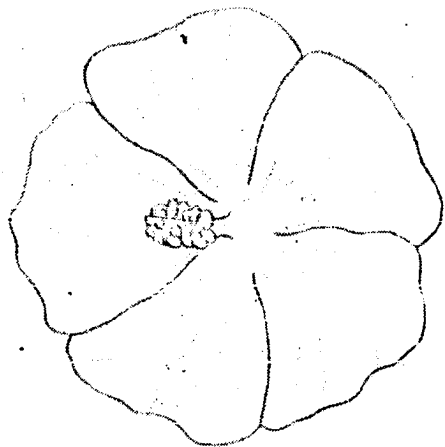


Figure 2. Bee colors of Callirhoe involucrata white flowers.



THE REPRODUCTIVE BIOLOGY OF CALLIRHOE SCABRIUSCULA (MALVACEAE)

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ABSTRACT—The reproductive biology of Callirhoe scabriuscula (Malvaceae) was studied during the spring of 1978, 1979, and 1980, and comparisons of the pollination system of this species were made with dominant species in the community. Callirhoe scabriuscula is an obligate allogamous species; an insect vector is necessary for fruit set. More geitonogamous crosses resulted in fruit set (88.5%) than autogamous crosses (12.5%). This type of breeding system has been reported in Callirhoe involucrata and is referred to as mixed compatibility. Although geitonogamy is favored in the breeding system, it is restricted in pollen transfer because of temporal dioecism. The flowers are protandrous; there is little overlap in the sexual phases of plants with more than one flower in anthesis. The C. scabriuscula habitat supports a high diversity of species in flower during the early spring. Dominants were defined quantitatively; C. scabriuscula is neither a vegetative nor a floral dominant in the community. Based on bagging experiments and estimates of pollen-ovule ratios, the dominants in the community are out-crossing species. There appears to be little competition for pollinators among species. Two factors appear to be decreasing competition: (i) diurnal differences in presentation of floral rewards, and (ii) differences in insect visitors. Callirhoe scabriuscula acts as an opportunist as the flowers are open for long periods of the day and generalist species visit C. scabriuscula for nectar in the absence of preferred resources. Pollen collection is restricted to two species of oligolectic bees, Diadasia afflicta and Melissodes intorta. Five species of bees were observed using the blossoms for shelter.

(INTRODUCTION)

Callirhoe scabriuscula Robins. (Malvaceae) is a narrow endemic of central Texas that has recently been given endangered species status by the U. S. Fish and Wildlife Service (U. S. Fish and Wildlife Service 1980). The species' range is restricted to a 160 hectare pocket of deep loose sand. The habitat itself is unusual for the region and was formed by a combination of alluvial and eolian action (Amos 1979). The sands were carried to the area by a major river and then deposited above the floodplain by the wind, apparently only during storm events since the deposit of sand is in opposition to the direction of the prevailing winds. The habitat supports a high diversity and density of flowering plants in the early spring. Because of the rarity and unusual habitat of C. scabriuscula, a study of the reproductive biology of this species was initiated to determine possible interactions with other flowering taxa in the community.

MATERIALS AND METHODS—Field observations were conducted during May of 1978 and May through June in 1979 and 1980.¹⁾

Floral morphology and phenology—Floral phenology and morphology were observed and related to the pollination and reproductive systems of the species.

¹⁾The precarious position of this species necessitates omitting study site locations.

Data collected include: time of flower opening, mode of presentation of pollen, receptivity of the stigma, and duration of individual flowers. Plant phenological data collected included: number of flowering branches, number of flowers in anthesis per branch, and the staminate or pistillate phase of flowers.

Reflectance spectrophotometry was used to estimate the spectral reflectance of the corolla. Photographs were taken with a single-lens reflex camera with Kodak Tri-X pan film using filters transmitting red (Soligor 25A), yellow (Vivitar No. 8K2), blue (Vivitar 80C), visible light (Tiffen UV haze), and ultraviolet (Tiffen 18A).

Breeding system—The potentials for autogamy and geitonogamy were tested by covering flowers in late bud stage with paper pollination bags (Central States "Slip-ezy" No. 9235). Those being tested for self-pollination were allowed to develop under the bags. In the remaining tests, the bags were removed after anthesis and pollen was transferred to the stigma lobes within a flower for artificial autogamous transfer and between flowers on the same plant for geitonogamous transfers. The phenology of flowers involved in crosses was noted by recording the degree of anther dehiscence and stigma emergence. Experiments were repeated using unbagged flowers with plants growing in the absence of pollen vectors in the greenhouse at The University of Oklahoma. Seed set from open pollination was estimated by fruit-set, the number of seeds per fruit, and the number of aborted flowers per plant.

Community ecology and breeding systems—The community was defined vegetatively with an Importance Percentage (relative frequency + relative areal cover/ 2). These were obtained with 40 0.5 m^2 quadrats established along a linear

transect through the largest study site. Early in June, 1980, floral attributes of the community were described with an Importance Percentage (relative density + relative frequency + relative cover/ 3). Data were collected using 80 0.1 m² quadrats. As an indication of the breeding system of the community, mature flower buds of several cohabiting species were collected, fixed in 95% ethanol and from these, pollen-ovule ratios were estimated. The results were compared with breeding classes as described by Cruden (1977). In addition, inflorescences of the four floral dominants of the community were bagged to exclude insects in order to determine the potentials for seed-set in the absence of pollinators.

Diurnal changes in insect activity on other species in flower within the community were also noted. Comparisons were made among species in regard to frequency and times of insect visitation.

Floral foragers and pollinators—Insect visitors to C. scabriuscula were observed daily from 0830 to 1800 hr. During observation, notations were made concerning intrafloral behavior, length of visitation, and whether pollen or nectar was collected. In addition to these observations, a linear transect comprised of 50-100 tagged flowers was established through the population. This transect was walked at approximately half hour intervals and the number of insects per flower recorded. Representatives of each species observed visiting the flower were collected and the location, identities, and amounts of pollen on their bodies analyzed.

OBSERVATIONS AND RESULTS— Floral morphology and phenology—Callirhoe scabriuscula is an erect, 2-5 dm, simple or basally branched perennial

herb. The five petals, $\bar{x} = 3.5$ cm long and $\bar{x} = 2.1$ cm wide, form an erect bowl-shaped blossom, approximately 3.5 cm in diameter, with a dark maroon center ring.

Based on spectral reflectance, the distal portion of the petals appear bee-bluegreen, the basal portion bee-black, the staminal column bee-green and pollen bee-orange (Fig. 1).²⁾

Copious amounts, $\bar{x} = 26,701$ grains per flower, of spiny pollen approximately 150μ in diameter are produced. Small amounts of nectar, $0.1-0.3 \mu$ l, are produced throughout anthesis from each of the five nectaries, which are opposite the sepals.

Anther dehiscence commences at the apex of the staminal column and proceeds basipetally over approximately a 16 hr period. About 20 hr after cessation of dehiscence, the stigma lobes emerge from the staminal column. They remain erect for about 5 hr and then gradually begin to elongate and curve downward, eventually curving into the staminal column. The flowers open each morning 2-3 hr after sunrise and close shortly before sunset each evening. Within 30-90 min after pollination, the flowers close permanently; however, closing in autogamous crosses is typically delayed. If not pollinated, flowers continue to open each morning for 6-8 days. Callirhoe scabriuscula exhibits temporal dioecism with little or no overlap in the sexual phases of flowers on a plant (Amos 1981 Appendix VII). Because duration of the staminate phase is approximately 12 times as long as the pistillate phase in open field conditions, the staminate phase predominates. Based on data collected in 1980, 70% of the flowers in the population were in the staminate phase

²⁾The colors designated are based on studies and interpretations of honeybee vision (Kevan 1978, Frisch 1950, 1954, Proctor and Yeo 1972).

(Amos 1981 Appendix VIII). Approximately 82% of the flowering branches had only one flower in anthesis at a time. The plants produce several branches per plant and may produce as many as 159 flowers in one season (Amos 1981 Appendix VIII). The data collected in 1979 reflect an unusually cool wet spring; the growing season was extended into the first part of July.

None of the flowers that were enclosed produced fruit (Table 1). More geitonogamous crosses set fruit than the autogamous crosses while nearly all of the xenogamous crosses produced fruit. These results were also obtained in a study of the breeding system of Callirhoe involucrata (Amos 1981). In Callirhoe involucrata, the number of successful autogamous crosses decreased with the age of the flower; however, the success of geitonogamous crosses was unaffected by the stage of development of either the pollen or the stigma. Preliminary data indicate this is also the case with C. scabriuscula. This type of response, in which geitonogamous crosses are favored, was referred to as a mixed compatibility system. Approximately 85% of the 359 flowers on 15 plants produced fruit under field conditions.

The species in Table 2 represent plants in the immediate vicinity of the C. scabriuscula study site; the sandy habitat was heterogeneous in areas of disturbance or on swales, and species composition differed. Therefore, this list presents only some of the nectar and pollen resources available in the area. From these data, Callirhoe scabriuscula is neither a vegetative nor a floral dominant of the community.

None of the inflorescences of the four species— Gaillardia pulchella, Hymenopappus flavescens, Schrankia nuttallii, and Tradescantia occidentalis—which were enclosed produced seeds and I infer that all are allogamous. Figure 2 represents the logarithmic values of the pollen-ovule ratios for 13 species, including

these four species, in relation to the five categories proposed by Cruden (1977). Seven of the 13 species fall upon or beyond the last outcrossing index, xenogamy. The value for C. scabriuscula, along with those for Monarda punctata and Cnidoscolus texanus, is between the classes of xenogamy and facultative xenogamy. Eriogonum multiflorum and Schrankia nuttallii are within the range of values associated with facultative xenogamy. The value for the remaining species, Oenothera rhombipetala, is between the classes of obligate autogamy and facultative autogamy. The P/O value for Cnidoscolus texanus is in concurrence with the results of a pollination study indicating primary pollen transfer is allogamous (Perkins et al. 1975). Interestingly, the P/O value for Oenothera rhombipetala does not agree with the report of its allogamous phalenophilous mode of pollination (Carpenter 1977). Low P/O values have been reported for other species in the Onagraceae; these are considered to reflect a highly efficient pollination system mediated by viscin threads (Cruden and Jensen 1979).

Floral resources changed throughout the day. The flowers of Tradescantia occidentalis and Schrankia nuttallii were open during the morning, approximately 0800-1100 hr and 0900-1100 hr respectively; the heads of Aphanostephus skirrhobasis unfurled shortly after noon. Although some flowers of Oenothera rhombipetala and Cnidoscolus texanus were open during the day, more flowers opened in the evening, between 1830-2200 hr, and insect visitors were more common during evening hours. The heads of Gaillardia pulchella and Hymenopappus flavescens were open throughout the day but more insects visited these flowers during particular times of the day, 1030-1800 hr for G. pulchella and 1200-1300 hr, 1730-1900 hr for H. flavescens. The flowers of Opuntia macrorhiza and C. scabriuscula opened in early morning, about 0830 hr, and closed in the evening shortly before sunset.

Floral foragers and pollinators—There was also a difference in types of insect visitors among these species. Honeybees and small halictid bees were common on the flowers of Tradescantia occidentalis and Schrankia nuttallii in the morning and were frequently observed on the inflorescences of Gaillardia pulchella in the afternoon. Interestingly, honeybees were never observed visiting the flowers of C. scabriuscula although they were frequent visitors to Callirhoe involucrata (Amos 1981). There was little or no overlap among insect visitors for several species. As an example, Diptera were the most common insects observed on the flowers of Hymenopappus flavescens; these insects were rarely observed on the flowers of other species.

Many of the insects observed in C. scabriuscula flowers were ineffectual pollinators because of their size and/or behavior (Table 3). Dialictus pruinosisiformis, a small bee, enters and exits the flower by a petal during nectar foraging and rarely comes in contact with the stigma lobes. Mimoschinia rufofascialis novalis was an infrequent nectar forager; this moth typically remained in a single flower for long periods of time. Taxa of the genus Nemotelus were abundant in the flowers throughout the latter part of May. These insects foraged for nectar, remained in a single flower for most of a day, and entered and exited the flower by a petal. Labostigmina texasiana and Euphoria kerni were infrequent nectar foragers. Both of these insects are large enough to brush against the stigma lobes during nectar foraging activities.

Agapostemon radiatus and Agapostemon texanus were common floral nectar foragers. Agapostemon texanus typically had pollen on its body from several species, mostly composites, and was observed taking nectar from C. scabriuscula and then flying directly to Gaillardia pulchella for pollen. Agapostemon radiatus

was more constant in its visitations to Callirhoe. Individuals of this species were often observed having difficulty in leaving the flower. In particular, one individual was observed attempting to get out of a Callirhoe flower for 47 min. The insect tried repeatedly to fly out of the flower from the floor of the corolla; the bowl-shaped blossom appeared to impede exit in this manner. Both of these species may pollinate the flowers but are not as effective as the other large solitary bees because of the lack of hair on their bodies and the fact that they rarely use the staminal column.

Diadasia afflicta and Melissodes intorta were observed collecting both nectar and pollen; both of these species have been reported as oligolectic on Callirhoe (Schlising 1972, Linsley and MacSwain 1958, LaBerge 1956). In addition, D. afflicta uses the flower as shelter during inclement weather. These bees and the remaining bees, with the exception of Hesperapis, were difficult to distinguish to species for each observation because they are similar in coloration and move rapidly. Therefore, remarks are directed toward these species as a group (Table 3). These bees land atop of the staminal column when entering the blossom, forage for nectar with the dorsum of the abdomen against the column, and use it for a "take-off" platform upon leaving. Approximately one fourth of the observations of these bees made during transect counts (Table 3) were of individuals that were not foraging, rather, they were clinging to the staminal column. Bees often remain in a single flower in this position for 2-3 hr. Four species, in addition to D. afflicta, use the flowers as shelter during inclement weather (windy, cool, or overcast) and at night (Table 3). Megachile mucorosa and Diadasia enavata were collected from the flowers early in the morning before the petals had opened. It is not known if these species visit Callirhoe flowers during the day. Hesperapis comes to the flowers

between 1800-2000 hr covered with bright orange composite pollen, probably Gaillardia pulchella. They emerge in the morning shortly after the flowers open; these bees were not observed visiting Callirhoe scabriuscula for either pollen or nectar. Diadasia diminuta was not seen foraging on Callirhoe flowers although on several occasions, individuals were observed clinging to the staminal column. Each bee was observed in the same flower for 4-5 hr. In two instances, during the period of observation, the flower, having been pollinated, closed and the petals curled tightly around the insect. The bee remained in the flower for about 2 hr after the flower had closed.

DISCUSSION—Observations of insects actively collecting pollen were rare, although because of the abundance of pollen in the flowers, all observed insects were liberally dusted with it. Therefore, all of the larger solitary insects are capable of pollinating the flowers because of their intrafloral behavior. Most of the species utilizing the flowers as shelter are not effective pollinators since they typically visit only one flower, although the potential for autogamous transfer is not entirely eliminated. With the presence of the temporal dioecism, xenogamy appears to be the primary mode of pollen transfer; geitonogamy is more significant than autogamy because of the mixed compatibility system.

The diversity and density of flowering plants in the spring is high; many of these species, including C. scabriuscula, are allogamous and are dependent on insects for pollination. Few of the dominants appear to compete for services of a specific element of the pollinator fauna at the same time. Competition for pollinators has been considered to be a major factor in the evolution of the floral phenology within plant communities (Heithaus 1974). The timing of the presentation

of floral attractants is interesting. In this community, insect activity was highest on those species whose flowers were open only briefly (i.e., Tradescantia occidentalis, Schrankia nuttallii); conversely, the floral rewards of C. scabriuscula are present the entire time the flowers are open, the flowers are open from early morning to late evening, and pollinator frequency is low. Generalists, such as Agapostemon texanus, A. radiatus, and Megachile amica, were often observed on flowers of other plant species, particularly Gaillardia pulchella. Preference by pollinators for one plant species over another is well documented (Levin and Anderson 1970).

As new resources appear and then dissipate with the short-term flowers, the insects are apt to shift foraging patterns around these changes. The adaptive significance of a constant, although perhaps not as alluring, resource would be for insect activity during the absence or or in the interim between the presentations of the more attractive rewards. Callirhoe scabriuscula appears to be an opportunist.

With the exception of the generalists, which comprise only a portion of the pollinators to C. scabriuscula, there is little sharing of C. scabriuscula pollinators with other floral constituents in the community. The specialists, Diadasia afflicta and Melissodes intorta, were not observed foraging on other species. Greater specialization or utilization of a smaller proportion of the total resources has been reported to occur as the number of species in the community increases (Heithaus 1974). Also, Moldenke (1971) noted the proportion of oligolectic bees increased as plant species diversity increased.

Pollinators can be divided into two major groups: (i) a generalist group of nectar foragers including flies, moths, bees, and beetles, and, (ii) a small group of specialized bees that visit the flowers for nectar, pollen, and shelter. The latter

group is most important. Their constancy adds a measure of reliability to the pollination system (Levin and Anderson 1970).

Even though pollinator frequency is low and there are many other pollinator resources available in the community, Callirhoe scabriuscula flowers set large numbers of fruit and seed because of the length of time a flower is open and the dependency of the oligolectic bees on C. scabriuscula pollen.

Literature Cited

- Amos, B. 1979. Determination of Callirhoe scabriuscula as an Endangered Species. Technical Report prepared for the U. S. Fish and Wildlife Service.
- Amos, B. 1981. Reproductive studies in the genus Callirhoe (Malvaceae). Ph.D. dissertation, University of Oklahoma, Norman, Oklahoma.
- Carpenter, C. S. 1977. Pollination ecology of Oenothera rhombipetala. Unpublished manuscript.
- Cruden, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32-46.
- _____ and K. G. Jensen. 1979. Viscin threads, pollination efficiency and low pollen-ovule ratios. *Amer. J. Bot.* 66: 875-879.
- Frisch, K. von. 1950. Bees, their Vision, Chemical Senses and Language. Cornell Univ. Press, Ithaca, NY.
- Frisch, K. von. 1954. The Dancing Bees. Methuen, London.
- Heithaus, E. R. 1974. The role of plant-pollinator interactions in determining community structure. *Ann. Mo. Bot. Gard.* 61: 675-691.
- Kevan, P. G. 1978. Floral coloration, its colorimetric analysis and significance in anthecology, p. 51-78. *In* (ed.) A. J. Richards, *The Pollination of Flowers by Insects*, Linnean Society.
- LaBerge, W. E. 1956. A revision of the bees of the genus Melissodes in North and Central America, part II (Hymenoptera, Apidae). *Univ. Kansas Sci. Bull.* 38: 533-578.

- Levin, D. A. and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *Amer. Nat.* 104: 455-467.
- Linsley, E. G. and J. W. MacSwain. 1958. The significance of floral constancy among bees of the genus Diadasia (Hymenoptera, Anthophoridae). *Evolution* 12: 219-223.
- Moldenke, A. R. 1971. Studies of the species diversity of California plant communities. Ph.D. Thesis in Biological Sciences, Stanford University.
- Perkins, G., J. R. Estes, and R. W. Thorp. 1975. Pollination of Cnidoscolus texanus (Euphorbiaceae) in southwestern Oklahoma. *Southwest. Nat.* 20: 391-396.
- Proctor, M. and P. Yeo. 1972. *The Pollination of Flowers*. Taplinger Publishing Co., New York.
- Schlising, R. A. 1972. Foraging and nest provisioning behavior of the oligolectic bee, Diadasia bituberculata. *Pan-Pacific Entomol.* 48: 175-188.
- U. S. Fish and Wildlife Service. 1980. Endangered and threatened wildlife and plants: Review of plant taxa for listing as endangered or threatened species. *Federal Register* 42: 82480-82569.

TABLE 1. Percentage of fruit set in experimental pollinations.

Treatment	Percentage of Fruit Set	N
Insects Excluded, Non-manipulated	0	35
Artificial Autogamous Crosses	12.5	16
Geitonogamous Crosses	88.5	26
Xenogamous Crosses	96.7	30
Open Pollination	84.7	359

TABLE 2. Species composition of Callirhoe scabriuscula community.

Species	Importance Percentage	
	Vegetative	Floral
<u>Tradescantia occidentalis</u> (Britt.) Smyth.	7.5	46.5
<u>Gaillardia pulchella</u> Foug.	7.4	32.3
<u>Cnidoscolus texanus</u> (Muell. Arg.) Small	6.8	8.7
<u>Schrankia nuttallii</u> (DC.) Standl.	6.6	17.9
<u>Eriogonum multiflorum</u> Benth.	6.1	0.2
<u>Hymenopappus flavescens</u> Gray	5.8	6.6
<u>Heterotheca latifolia</u> Buckl.	5.1	---
<u>Cenchrus incertus</u> M.A. Curtis	5.0	---
<u>Sporobolus cryptandrus</u> (Torr.) Gray	3.5	---
<u>Euphorbia missurica</u> Raf.	3.4	6.4
<u>Opuntia macrorhiza</u> Engelm.	3.0	---
<u>Aphanostephus skirrhobasis</u> (DC.) Trel.	2.4	6.0
<u>Solanum citrullifolium</u> A. Br.	2.4	2.0
<u>Helianthus annuus</u> L.	1.4	---
<u>Callirhoe scabriuscula</u> Robins.	1.2	3.9
<u>Monarda punctata</u> L.	1.1	2.8
<u>Oenothera rhombipetala</u> T. & G.	1.0	0.7

TABLE 3. Insect visitors to Callirhoe scabriuscula in relation to attraction, common times of foraging, and frequency. Frequency is based on 3,600 observations, (--) indicates specific time was not apparent.

<u>Species</u>	<u>Attractants</u>			<u>Observation</u>	<u>Frequency</u>
	<u>Nectar</u>	<u>Pollen</u>	<u>Shelter</u>	<u>Times</u>	
COLEOPTERA					
<u>Euphoria kerni</u> Hald ^h	•			--	0
DIPTERA					
Bombyliidae ^d	?			--	13
<u>Labostigmina texasiana</u> Johnson ^f	•			--	2
<u>Nemotelus</u> sp. ^g	•			--	582
HYMENOPTERA					
<u>Agapostemon radiatus</u> Say ^a	•			--	42
<u>Agapostemon texanus</u> Cresson ^a	•			1200-1400	18
<u>Diadasia afflictata</u> Cresson ^{b,c}	•	•	•	0930-1700	127*
<u>Diadasia diminuta</u> Cresson ^c			•	--	8
<u>Diadasia enavata</u> Cresson ^a			•	1700-0800	0

TABLE 3. Continued

<u>Species</u>	<u>Attractants</u>			<u>Observation</u>	<u>Frequency</u>
	<u>Nectar</u>	<u>Pollen</u>	<u>Shelter</u>	<u>Times</u>	
<u>Dialictus prunosiformis</u> Crawford ^d	•			1200-1400	8
<u>Hesperapis</u> undescribed species ^b			•	1800-0800	12
<u>Megachile amica</u> Cresson ^c	•			---	*
<u>Megachile mucorosa</u> Cresson ^c			•	---	*
<u>Melissodes intorta</u> Cresson ^c	•	•		---	*
<u>Melissodes tepaneca</u> Cresson ^c		•		---	*
LEPIDOPTERA					
<u>Mimoschinia rufofascialis novalis</u> Grote ^e	•			---	4

^adetermined by R. W. Thorp, University of California at Davis

^bdetermined by R. W. Brooks, University of Kansas

^cdetermined by W. E. LaBerge, Illinois Natural History Survey

^ddetermined by G. C. Eickwort, Cornell University

^edetermined by D. A. Ferguson, USDA Beltsville Agricultural Research Center

^fdetermined by W. J. Hanson, Utah State University

^gdetermined by W. W. Wirth, USDA Beltsville Agricultural Research Center

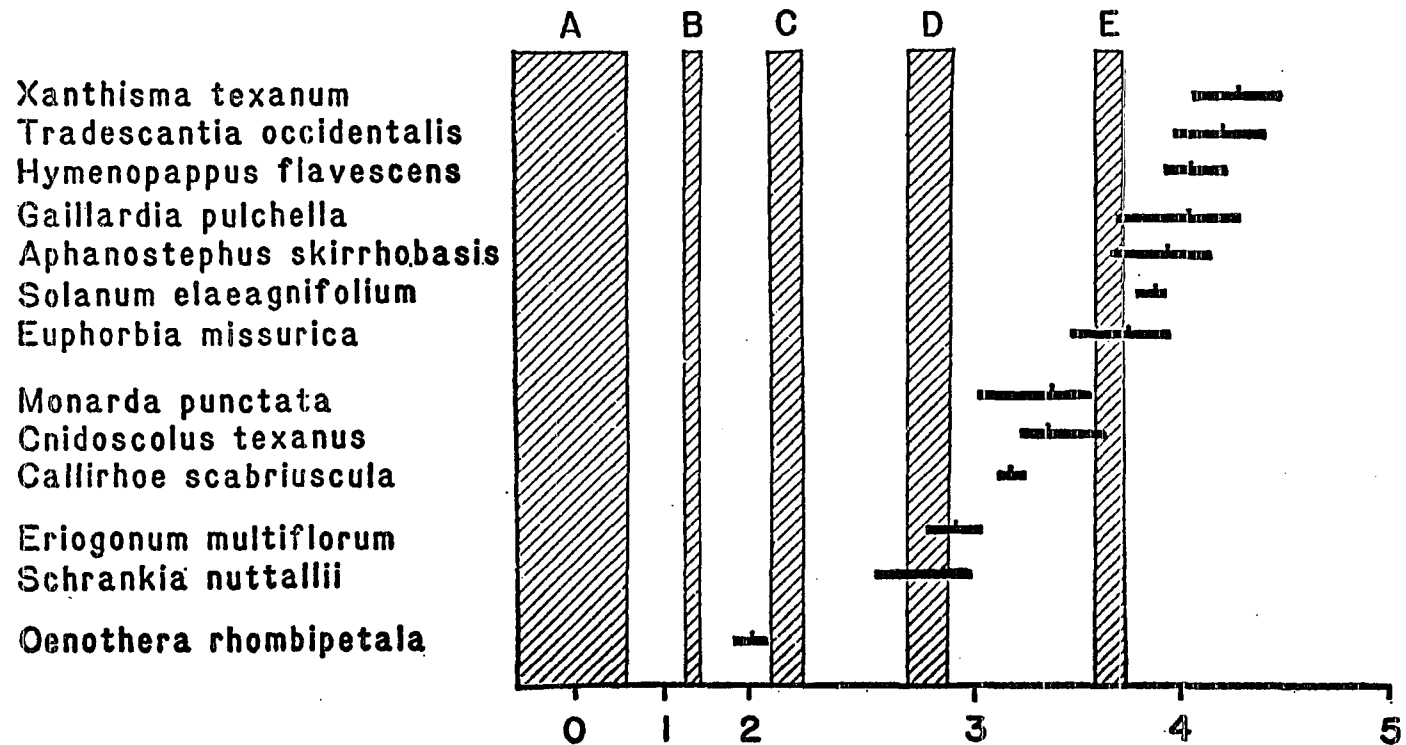
^hdetermined by W. J. Gibson, Stephen F. Austin State University

*The value of 127 pertains to these species as a group.

Figure 1. Bee colors of Callirhoe scabriuscula.



Figure 2. Logarithmic values for average (black vertical mark) and range (black horizontal bar) of pollen-ovule ratios for thirteen species in C. scabriuscula community. Vertical bars indicate the five outcrossing indices as defined by Cruden (1977), A = Cleistogamy B = Obligate autogamy, C = Facultative autogamy, D = Facultative xenogamy, and E = Xenogamy.



APPENDIX I. Populations used in the crossing experiments. All counties are in Texas.

Number	Location
1	Tom Green, Head-of-the-River Ranch, approx. 3½ miles south of Christoval, white flowered.
2	Tom Green, Christoval, roadside park south of town along highway 277, white flowered.
3	Williamson, Round Rock, white flowered.
4	Kenedy (I), 1.7 miles south of Sarita along highway 77.
5	Kenedy (II), 2.5 miles south of Sarita along highway 77.
6	Brooks (II), 5 miles west of Falfurrias along highway 285.
7	Brooks (I), west edge of Falfurrias along highway 285.
8	Jim Hogg, 5 miles east of Hebbronville along highway 285.
9	San Patricio (I), 2½ miles southwest of Mathis along highway 259.
10	Tom Green, Mathis Airport, San Angelo.
11	Webb (II), 6 miles west Encinal along highway 44 in culvert.
12	Webb (I), 2 miles west of Encinal along highway 44.
13	Wilson, approx. 6½ miles south of Nixon in oak thicket in roadside park along highway 80.
14	San Patricio (II), north side of bridge on Nueces River on highway 357, approx. 3 miles south of Mathis.
15	Gonzales (II), approx. 2 miles north of Belmont on the roadside along highway 85.
16	Gonzales (I), approx. 2 miles south of Belmont on the roadside along highway 80 in an oak thicket.

- 17 Val Verde, Juno.
- 18 Menard, San Saba Avenue in Menard Approx. $\frac{1}{2}$ mile west of highway 83.

APPENDIX II. Comparison of breeding systems.

Population	Percentage of Fruit Set		N	Probability
	Autogamous	Geitonogamous		
4 Kenedy Co.	11.1	75.0	9,8	0.013*
8 Jim Hogg Co.	23.1	66.7	13,15	0.02'
11 Webb Co.	3.2	55.0	31,20	0.00001'
18 Menard Co.	0	85.7	6,7	0.004*
5 Kenedy Co.	0	9.1	9,11	0.55*
9 San Patricio Co.	12.5	35.7	8,14	0.24'
14 San Patricio Co.	7.7	33.3	13,18	0.09'

* Fisher's Exact Test level of significance = 0.025

' Chi-square level of significance = 0.05

APPENDIX III. Identification and location of populations involved in
plant phenology studies. All counties are in Texas.

Population	Location
1	Tom Green Co., San Angelo, Mathis Field Airport, along Farm Road 584, April 23, 1980, purple-flowered plants.
2	Tom Green Co., San Angelo, Mathis Field Airport, along Farm Road 584, April 21, 1980.
3	Tom Green Co., San Angelo, along Ben Ficklin Road approx. $\frac{1}{2}$ mile north of intersection with Loop 306, April 24, 1980, purple-flowered plants.
4	Tom Green Co., San Angelo, lawn at 612 E. 24th Street, May 12, 1980, purple-flowered plants.
5	Tom Green Co., San Angelo, roadside near intersection of 24th Street and Marx Street, May 12, 1980, purple-flowered plants.
6	Tom Green Co., San Angelo, lawn at 2308 Armstrong, May 12 1980, purple-flowered plants.
7	Tom Green Co., San Angelo, along Ben Ficklin Road approx. $\frac{1}{2}$ mile north of intersection with Loop 306, April 26, 1980.
8	Tom Green Co., 8.9 miles west from intersection of Highway 2288 and Highway 853 on 853, May 12, 1980, purple-flowered plants.
9	Tom Green Co., 4.6 miles south, southeast from intersection of Highway 67 and Farm Road 2335 on 2335, intersection near Tankersly, May 17, 1980, purple-flowered plants.

- 10 Tom Green Co., along South Concho Drive near Pecan Creek
along the southern portion of Lake Nasworthy, May 17, 1980,
purple, lavender, and white-flowered plants.
- 11 Menard Co., Menard, between Motel 83 and train depot
in ditch along Highway 83, May 20, 1980, white-flowered
plants.
- 12 Tom Green Co., roadside 2.9 miles north of intersection
of Highway 2335 and 277 on 277, May 18, 1980, white-
flowered plants.
- 13 Tom Green Co., roadside park south of Christoval, along
Highway 277, May 18, 1980, white-flowered plants.
- 14 Menard Co., Menard, approx. 3/4 mile west of intersection
of Highway 83 and San Saba Avenue, May 18, 1980, white-
flowered plants.
- 15 Menard Co., Menard, vacant lot east of West Texas Utilities
near intersection of Highway 83 and San Saba Avenue on
San Saba Avenue, May 18, 1980, white-flowered plants.

APPENDIX IV. Vegetative values for Mathis Field community, importance percentage represents an average of relative frequency and relative cover.

Species	Relative Frequency	Relative Cover	Importance Percentage
Poaceae	15.3	31.4	23.3
<u>Engelmannia pinnatifida</u> Nutt.	14.5	13.1	13.8
<u>Callirhoe involucrata</u> (Torr.) Gray	11.9	14.8	13.3
<u>Medicago minima</u> (L.) L.	11.4	13.4	12.4
<u>Ambrosia artemisiifolia</u> L.	8.9	5.4	7.2
<u>Ruellia metzae</u> Tharp	7.9	6.0	7.0
Seedlings	9.6	3.7	6.7
<u>Teucrium laciniatum</u> Torr.	5.8	5.4	5.6
<u>Ratibida columnaris</u> (Sims) D. Don.	3.8	1.2	2.5
<u>Gaura</u> sp.	2.3	2.0	2.1
<u>Siphonoglossa pilosella</u> (Nees) Torr.	2.3	1.4	1.9
<u>Croton</u> sp.	1.8	0.6	1.2
<u>Abutilon</u> sp.	1.2	0.3	0.8
<u>Verbena bipinnatifida</u> Nutt.	0.8	0.3	0.5
<u>Tradescantia occidentalis</u> (Britt.) Smyth.	0.8	0.2	0.5
<u>Oxalis dillenii</u> Jacq.	0.8	0.1	0.4
<u>Hymenopappus tenuifolius</u> Pursh	0.3	0.2	0.3
<u>Clematis</u> sp.	0.3	0.2	0.3
<u>Verbena hastata</u> L.	0.3	0.1	0.2

APPENDIX V. Floral density values for plants in flower in the Callirhoe involucrata community at the Mathis Field site. Density values for members of the Asteraceae are based on the number of heads. Ruellia metzae was in flower at the time of sampling but this is primarily a nocturnal, crepuscular species and corollas fall off during early morning.

Species	Relative Density
<u>Engelmannia pinnatifida</u>	50.7
<u>Teucrium laciniatum</u>	18.4
<u>Callirhoe involucrata</u>	16.1
<u>Siphonoglossa pilosella</u>	8.0
<u>Verbena bipinnatifida</u>	4.1
<u>Gaura</u> sp.	0.7
<u>Hymenopappus tenuifolius</u>	0.7
<u>Verbena hastata</u>	0.7
<u>Abutilon</u> sp.	0.2
<u>Oxalis dilleni</u>	0.2
<u>Tradescantia occidentalis</u>	0.2

APPENDIX VI. Fruit set in one floral visitation by Apis mellifera in
relation to flower age.

Level of Stigma Emergence	Percentage of Fruit Set	N
1. Lobes erect	9.1	11
2. Lobes reflected, forming a crown	65.2	23
3. Lobes elongated and turned downward into the staminal column	77.8	9

APPENDIX VII. Comparisons of sexual distributions for Callirhoe
scabriuscula.

	No Overlap		Equal	Staminate Dominant	Pistillate Dominant
Number of Plants	27	7	6	6	1
Number of Flowers					
Staminate Phase	30	-	6	17	2
Pistillate Phase	-	8	6	6	4

APPENDIX VIII. Floral phenological data for Ellirhoe scabriuscula, per plant basis.

Year	$\bar{x}$ # Flowers	$\bar{x}$ # Branches in Flower	$\bar{x}$ # Flower Abortions	$\bar{x}$ # Flowers at One Time
1979	41.4 range 4-156	3.5 range 1-22	4.0	5.0
1980	26.1 range 4-39	1.5 range 1-7	2.2	1.6