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Sandra D. Buckner
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Thomas A. McGrath

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Vincent J. Voegeli

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THE POLLINATION BIOLOGY OF WOOLLY CORCHORUS, *CORCHORUS HIRSUTUS* (MALVACEAE / TILIACEAE), ON SAN SALVADOR AND INAGUA, BAHAMAS

Beverly J. Rathcke
Department of Ecology and Evolutionary Biology
University of Michigan
Ann Arbor, MI 48109-1048

Lee B. Kass
L.H. Bailey Hortorium
Department of Plant Biology
228 Plant Science
Cornell University
Ithaca, NY 14853-4301

Nancy B. Elliott
Department of Biology
Siena College
Loudonville, NY 12211-1462

ABSTRACT

Woolly Corchorus, (*Corchorus hirsutus*), is a common low shrub that grows in coppices and open fields throughout the Bahamas. We present the first description of its floral biology, breeding system, pollinators, and fruit set. Our pollination studies on San Salvador Island demonstrate that plants are self-incompatible and require outcross pollen and pollinators for fruit set. Flowers are unusual in having a short lifespan of less than five hours and in opening during mid-afternoon. Flowers are also unusual in not producing nectar so that pollen is the only pollinator reward. Bees, which forage for pollen, were the most frequent flower visitors and are probably the only effective pollinators. A sweat bee, (*Agapostemon columbi*: Halictidae), was observed visiting flowers on San Salvador and Inagua. Other frequent bee visitors on San Salvador were a leafcutter bee (*Megachile poeyi alleni*: Megachilidae) and a small, unidentified halictid bee. Floral traits closely match those described for a bee-pollination syndrome. Woolly Corchorus has a specialist hemipteran seed predator, *Ochrostomus pulchellus* (Lygaeidae), that may reduce fruit and seed set.

INTRODUCTION

The study of species on islands has provided insights into selection and evolution ever since Darwin's voyage to the Galapagos Islands. Islands typically have fewer and different pollinator species than mainland populations (Carlquist 1974, Feinsinger et al. 1982, Spears 1987, Elmqvist et al. 1992, Inoue 1993, Barrett 1996). Differences in pollinators can promote the evolution of different pollination syndromes (floral traits adapted to a pollinator type) and breeding systems (e.g., Carlquist 1974, Inoue 1993). The pollination biology and breeding systems of many plant species in the Bahamas have not been described, and data are not available for island-mainland comparisons. A goal of our research in the Bahamas has been to provide descriptions of the pollination and floral biology of common plant species (Rathcke 1998, Rathcke and Kass 2003a and 2003b, Rathcke et al. 1996, Rathcke et al. 2001b) and to record flower visitors (Rathcke et al. 2001a, Landry et al. *in press*).

Here we provide the first published description of the pollination biology of Woolly Corchorus (*Corchorus hirsutus* L.: Tiliaceae/Malvaceae). Literature searches using Biosis and the Web of Science revealed no recent

studies on the pollination biology of Woolly Corchorus. We describe floral traits, including phenology, morphology, and rewards, and present a description of the pollination syndrome. We did pollination experiments on San Salvador to determine the breeding system, and we recorded flower visitors (potential pollinators) on San Salvador and Inagua, Bahamas.

The genus, *Corchorus*, has traditionally been placed in the Tiliaceae (Correll and Correll 1982), but a recent study using sequence analysis of plastid genes has placed it in the Malvaceae (Bayer et al. 1999). Woolly Corchorus is a low shrub that grows in coppices, scrublands and open fields throughout the Bahamas and is also found in the West Indies, continental tropical America and northeast tropical Africa (Correll and Correll 1982, Wunderlin 1998). On San Salvador, Woolly Corchorus is a common shrub along roadsides and in disturbed areas of the Coastal Coppice Community (Smith 1993). The leaves are used in a medicinal tea on San Salvador (Smith 1993).

METHODS

Our studies on floral traits and pollination were done on Woolly Corchorus shrubs growing in a field southeast of the Gerace Research Center on San Salvador Island, Bahamas. We have permanently tagged 20 shrubs. In 2002 we estimated the size of each tagged plant as total length of major stems in meters; small twigs were not included. The total number of flowers open on each plant was monitored throughout the afternoon and evening on January 3, 2003. To plot flower opening, the percent of the total maximum flowers open (N = 491) was calculated for each time period and plotted against time. Stamens were counted for one flower for each of the 20 plants. One mature fruit (capsule) was collected from each of ten plants, length and width were measured and the number of seeds was counted.

To determine the breeding system, we did experimental pollinations on the San Salvador population. In December 2002 we tagged and studied 20 shrubs. To determine if flowers can self-pollinate and self-fertilize, buds were bagged with bridal-veil netting and left unmanipulated (Bagged, No Hand-pollination Treatment). To determine if plants are self-compatible (can self-fertilize), buds were bagged and self-pollen was added to stigmas by rubbing dehisced anthers over the stigma within the flower (Bagged, Self-pollen added). To quantify fruit set under natural pollination, flowers were left exposed to visitors (Open, Natural Pollination) umbels were examined every day and new flowers were recorded and hand-pollinated depending on the treatment. Each treatment flower was tagged with a thread tied loosely around the pedicel and was monitored for subsequent fruit set. In December 2000, we did only two pollination treatments on five shrubs: Bagged, No hand-pollination and Open, Natural pollination.

Fruit set is calculated as % Fruit set = 100 (fruits/flowers). Fruit set was based on the development and expansion of the ovary. This initial fruit development more closely reflects successful fertilization than later fruit set which may be determined by abortion due to low resources or damage. Fruit set was measured 7-11 days after being exposed to pollination treatments. By this time, it was clear whether the ovaries would develop or not. Often undeveloped ovaries had abscised. Seed set was not measured for the treatment flowers because ovaries were small and ovules were difficult to count.

All flower visitors on San Salvador and on Inagua were recorded. On San Salvador, we (LBK and BJR) recorded flower visitors during December 2000, December 2002 and June 2003, and on Inagua, N. Elliot recorded flower visitors in January 2003. Nomenclature for insect visitors is based on Roberts (1972), Elliott (1993), Smith et al. (1994), and Janjic and Packer (2003).

Statistics were done using SPSS Version 10.0. For fruit set, significant differences were tested using non-parametric Mann-Whitney U-tests because percentage data were not normally distributed and variances were unequal.

RESULTS

Flowering Phenology

Our observations on San Salvador show Woolly Corchorus flowering in December 1994,

1999, 2000 and 2002, in April-May 2000, and June 1985 and 2003. All plants had buds, flowers, developing fruit, and mature fruit during these observation periods. Woolly Corchorus was flowering in January 2003 on Inagua. The species is described as flowering throughout the year (Correll and Correll 1982, Kass 1991).

Flower and Fruit Biology

Figure. 1. The flower of Woolly Corchorus, Corchorus hirsutus (Malvaceae/Tiliaceae)*, being visited by a leaf-cutter bee,* Megachile poeyi alleni (Megachilidae)*, on San Salvador Island, Bahamas.*

Woolly Corchorus flowers are bright yellow and have four or five petals (see Correll and Correll 1982, Kass 1991) (Figure 1). In our study population, the proportion of flowers having five petals (vs. four petals) was 0.44 (S.D. 0.22, N = 15 plants, 150 flowers), and the range was 0 to 0.80. All but one plant had a mixture of both four- and five-petaled flowers with both morphs often occurring in the same umbel. The average number of stamens per flower in the study population was 122.2 (S.D. = 28.1, N = 19 plants), and stamen number ranged from 80 to 194. Stamens were 4-6 mm long (N = 10 plants, 10 flowers). Pollen is bright yellow and very visible on flower visitors. The sepals are woolly, as are the leaves.

Flowers are displayed in small umbels (Figure 1). In our study population, umbels had an average of 8.0 buds (SD = 0.76, range = 5-10, N = 7 plants). Most umbels (86%) had only one open flower during any one day, 12% had two flowers open, and 1.4% had 3 flowers open; none had more than 3 flowers open on any one day (N=20 plants, 282 umbels). For the 20 tagged plants, total flowers open on the entire plant on one day ranged from 2 to 153. The number of flowers open on one day increased with plant size (stem length in meters) (regression; flowers = -6.9 + 3.7 size; $r = 0.73$, $P < 0.0001$).

Flowers usually open in late afternoon (Kass 1991). In the San Salvador population of 20 plants, the first flowers opened at 2:30 PM and all were open by 4:30-5:00 PM on January 3, 2003 (Figure 2). Flowers started closing after dark about 7:00 PM and nearly all were closed by 7:30 PM. Flowers senesce after this, so flower lifespan is only 3-5 hours. On Inagua, flowers opened by 2:00 PM in January 2003. Flower opening appears to be sensitive to light levels; on cloudy days, flowers may open earlier, even in the morning. One plant that was growing near an outside yard light had many flowers still open at 8:00 PM.

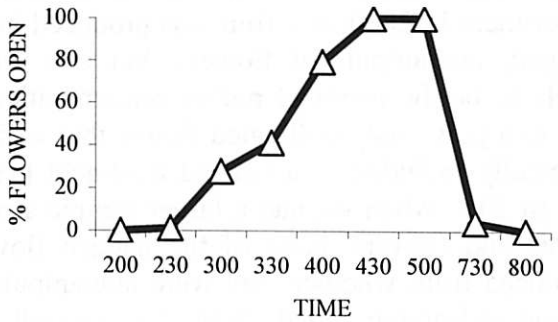

Figure 2. The timing of flower opening during one day for Woolly Corchorus, Corchorus hirsutus *on San Salvador, January 3, 2003. The percent of the maximum number of flowers open for 20 tagged plants are shown for different times during the afternoon and evening.*

Flowers do not secrete nectar. No nectar could be collected and no glistening was observed in the flowers. The floral diagram in Correll and

Correll (1982, p. 910) does not show any glandular tissue in the flower. Pollen appears to be the only pollinator reward. The numerous stamens supply abundant pollen. Flowers had no detectable odor, even when placed into glass vials to concentrate any volatiles. Bioassays were made with several researchers.

Fruits are woolly, oblong capsules and contain 4-5 celled ovaries (Correll and Correll 1982, Smith 1993) (Figure 1). In the study population average fruit width was 6.7 mm (S.D. = 0.87, N = 9 plants) and length was 14 mm (S.D. = 15, N = 9 plants). The average number of seeds per fruit was 31.7 (S.D. = 15.0, N = 9 plants) and ranged from 9 to 60 in healthy fruits. Two fruits had been eaten and had only 2 and 4 seeds. Fruit length (mm) significantly predicted seed number (regression; seeds = -25.2 + 4.0 length mm; r = 0.33; P = 0.04). Seeds are black and 1.4-2 mm long (Correll and Correll 1982, personal observations), but seeds were larger (2.8 mm) in fruits that had only 2-4 seeds.

Breeding System

Flowers are hermaphroditic (i.e. perfect), having both male and female parts (Figure 1). The stigma is 1-2 mm above the anthers, which may reduce self-pollination. In our pollination experiment in 2000, one fruit was produced in the bagged, unmanipulated flowers, but this seems likely to be the result of pollen contamination or due to a previously pollinated flower that was accidentally included in a bagged treatment (Table 1). In 2002 when we had a larger sample size of plants and flowers, none of the bagged flowers produced fruit, whether they were unmanipulated or had self-pollen added (Table 1). Overall, our results suggest that plants are self-incompatible and that flowers require pollinator and outcross pollen for fruit set.

Table 1. Breeding system of Woolly Corchorus, Corchorus hirsutus, *on San Salvador, Bahamas as determined by pollination experiments during two years. % Fruit set = 100 (fruit/flowers). Means and Standard Deviations are shown. N = number. Fruit sets of bagged flowers (pollinators excluded) and open flowers (natural pollination) are significantly different (Mann-Whitney U test, N = 5 plants, **P = 0.008). The single fruit set in 2001 is probably due to contamination (see text). For the 2003 data, tests cannot be done with zero values.*

TREATMENT	N plants	N flowers	% Fruit set
January 2001			
Bagged, No hand-pollination	5	54	1.8 ± 4.02
Open, Natural pollination	5	75	42.8± 20.24**
January 2003			
Bagged, No hand-pollination	20	39	0
Bagged, self-pollen added	20	46	0
Open, natural pollination	20	46	84.8±30.92

Flower Visitors

On San Salvador, the only flower visitors that we observed on Woolly Corchorus were three species of bees. During December 2000-January 2001, the only flower visitor we observed was a leafcutter bee, *Megachile* (*Pseudocentron*) *poeyi alleni* Mitchell (Hymenoptera: Megachilidae) (Figure 1). These bees never probed the flowers for nectar. Instead, they rubbed their abdomens over the stamens of the flowers as they moved quickly around the top of each flower. Their abdomens were usually bright yellow with pollen and these bees commonly moved between plants and were probably effective pollinators. During December 2002-January 2003, *M poeyi alleni* was the most frequent flower visitor, but two other occasional visitors were a sweat bee, *Agapostemon columbi* Roberts (Hymenoptera: Halictidae) and a small black bee (4-5 mm long), possibly *Dialictus* (Halictidae). During June-July 2003, all three species were seen visiting flowers, but the most frequent visitor was the small black Halictid. These small bees often foraged for pollen without touching the stigma and may frequently act as pollen thieves, rather than pollinators. The larger sweat bee, *A. columbi*, was typically seen visiting

a single flower on a plant and flying out of the local area rather than to a nearby plant.

On San Salvador, we never observed butterflies visiting flowers of Woolly Corchorus, although many species were frequently seen flying in the area and visiting other co-flowering species. We commonly saw Thrips (Order: Thysanoptera) in the flowers, but these small insects are unlikely to be significant cross-pollinators as they probably seldom move between plants. Thrips feed on plant juices or nectar and are probably herbivores, rather than pollinators.

On Inagua in January 2003, diverse species were observed visiting flowers of Woolly Corchorus including bees, butterflies, and flies. The most frequent visitor was a sweat bee, tentatively identified as *Agapostemon columbi* Roberts (Hymenoptera: Halictidae) by Dr. B. Dan forth. This species was also a visitor on San Salvador. Females of A. *columbi* visited flowers and males hovered around, possibly waiting to mate. The other visitors were infrequent and included two butterfly species (*Wallengrenia drury* Lattreille (Hesperiidae) and *Strymon martialis* (Herrich-Schaffer) (Lycaenidae). Two fly species (one Bombycid species and one species unidentified to family) were also observed on flowers. The butterflies and flies may have been "accidental" visitors because they typically forage for nectar which is not available. They may have been deceived or may use the flowers as a resting platform. These visitors could transfer pollen, but because they are probably infrequent and inconstant visitors, it seems unlikely that they are significant pollinators.

If the identification of the bee, *A. columbi*, on Inagua is confirmed by further examination and comparisons, this would be a new distributional record. *Agapostemon columbi* has only been reported for San Salvador (Watling's Island) in the Bahamas (Roberts 1972, Janjic and Packer 2003). Based on a parsimony analysis of morphological characters, Janjic and Packer (2003) place this species in *columbi-ochromops* clade of eight species that all occur on islands in the Bahamas or the Caribbean.

Pollination Syndrome

Woolly Corchorus appears to be specialized for bee pollination. The floral traits are similar to those described as being characteristic of a bee-pollination syndrome (Howe and Westley 1988) (Table 2). The lack of nectar is unusual, but nectar is not a necessary reward to attract bees that also collect pollen. The many anthers per flower provide an ample pollen reward. The variation in petal number (4-5) is relatively unusual for plants but is common in the Tiliaceae (Correll and Correll 1982).

Table 2. The pollination syndrome of Woolly Corchorus, Corchorus hirsutus *(Malvaceae/Tiliaceae), on San Salvador, Bahamas compared to the floral traits characteristic of a bee pollination syndrome (based on Howe and Westley 1988; see also text for discussion.) *indicates a difference between Woolly Corchorus and the bee pollination syndrome or an unusual floral trait... A thesis = flower opening.*

TRAITS	WOOLLY CORCHORUS	BEE
COLOR	bright yellow	variable but not red
ODOR	not detectable	sweet
SHAPE	radial symmetry	radial or bilateral
	*No tube; no nectar	flat or broad tube
	*petals are 4 or 5	
ANTHESIS	afternoon/evening	day/night
NECTAR	*none	moderate amounts
POLLEN	abundant	abundant

Fruit/Seed Predators

We frequently observed the hemipteran seed predator, *Ochrostomus pulchellus* (Hemiptera: Lygaeidae) (formerly *Craspeduchus bilimeki*) on Woolly Corchorus plants, usually on the developing fruits. Often adults and young nymphs were aggregated on umbels; we saw several adults mating on plants. Some fruits had few seeds, probably caused by feeding by this species. This species has only been observed feeding on Woolly Corchorus on San Salvador and may be

specialized (Elliott 1987). Elliott also collected this species on Woolly Corchorus on Inagua in January 2003.

DISCUSSION

Woolly Corchorus appears to be specialized for bee pollination. Although the flowers look generalized because they are dish-shaped and the anthers and stigma are exposed, the flowers produce no nectar and therefore are infrequently visited by insects other than bees. Bees foraged for pollen, and bees were the most frequent flower visitors on San Salvador and Inagua. On San Salvador, three bee species were observed visiting Woolly Corchorus. On Inagua, only one species was observed and this species, *Agapostemon columbi* Roberts: Halictidae, was also seen on San Salvador.

The different bee species probably vary in their effectiveness as pollinators of Woolly Corchorus. On San Salvador, a leafcutter bee, *Megachile poeyi alleni* (Megachilidae), was the most frequent visitor and may be the most effective pollinator because bees typically rubbed their pollen-covered abdomens over the stigma, and individuals moved between plants during a foraging bout. The two other bee species may be less effective pollinators. On San Salvador the sweat bee, *A. columbi*, was an infrequent visitor and was seldom observed moving between plants, although it was a frequent visitor on Inagua. On San Salvador, a small black halictid, possibly *Dialictus*, was rare except during June-July 2003 when it was the most frequent flower visitor. However, these small bees were probably pollen thieves, rather than pollinators, because individual bees seldom touched the stigma as they foraged for pollen.

In general, bees are relatively infrequent visitors to flowers on San Salvador, but they were abundant visitors to Woolly Corchorus. We have seldom observed bee species visiting flowers (Rathcke et al. 2001a, Rathcke, *personal observations*), although a number of species are present on the island (Elliott 1993). Although carpenter bees (*Xylocopa cubaecola*: Anthophoridae) were frequent visitors of some nearby shrubs on San Salvador during this period, we never observed them visiting Woolly Corchorus (Rathcke et al. unpublished data). Syrphid flies (mostly *Palpada* spp) are common visitors to other species, such as White Mangrove (Rathcke et al. 2001, Rathcke et al. this Symposium), but we have never observed them visiting Woolly Corchorus on San Salvador

The flowers of Woolly Corchorus are unusual in having a very short lifespan of three-five hours and opening in the afternoon. Most plant species have floral longevities of 2-4 days, although many tropical species do have floral lifespans of one day (Primack, 1985). On San Salvador, many species have floral lifespans of one day (*personal observations*). Such short floral longevity can indicate that pollination is predictable and reliable (Primack 1985, Ashmann and Schoen 1994, Rathcke 2003). Alternatively, the short longevity of tropical flowers is often attributed to predation or disease that prevents longer floral life (Primack 1985). We saw no evidence of floral predation for this species, or other species in general. However, the hemipteran seed predator, *Ochrostomus pulchellus* (Lygaeidae) (formerly *Craspeduchus bilimeki)*, was commonly observed on plants; the nymphs and adults pierce the fruit capsules and feed on developing ovaries (Elliott 1987) and could reduce fruit and seed set.

Because Woolly Corchorus is specialized for bee pollination, is self-incompatible, and has an unusually short flower lifespan of 3-4 hours, the reproduction of this species may be especially vulnerable to habitat and species changes (see Rathcke and Jules 1993, Rathcke 1998, Eshbaugh and Wilson 1996).

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tion of the bee, *Agapostemon columbi*. The identification of *Ochrostomus* (Lygaeidae) was checked with specimens at the American Museum of Natural History. Insect identifications were also checked using voucher specimens in the insect collection at the Gerace Research Center and in the Bahamian National Entomological Collection in the Department of Agriculture's Conservation Unit Building at the Botanic Garden in Nassau.

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