FACTORS INFLUENCING THE REPRODUCTIVE SUCCESS OF IPOMOEA PES-CAPRAE (CONVOLVULACEAE) AROUND THE GULF OF MEXICO[1]

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ABSTRACT

The reproductive biology of *Ipomoea pes-caprae,* a pantropical beach morning glory, was studied at five sites around the Gulf of Mexico. The primary pollinators were *Xylocopa* species (carpenter bees) which dispersed pollen up to 90 m. Exclusion experiments demonstrated that ants feeding on extrafloral nectaries increased seed set but did not protect seeds from predation by the bruchid beetle *Megacerus.* The water-dispersed seed and long-range dispersal of pollen may function to counter the sporophytic incompatability mechanism of the plant; populations exhibit a large neighborhood size. Key reproductive factors in the life cycle of *I. pes-caprae* are the long-range pollen flow and mass germination of water-dispersed seeds.

IPOMOEA PES-CAPRAE (L.) R. Br. (Convolvulaceae), a pantropical, perennial, trailing vine, often forms large mats just above the high tide line on coastal beaches and dunes throughout tropical and subtropical regions of the world (Fig. 1). It occurs on five continents and on most tropical islands (St. John, 1970). The species produces showy, bisexual, funnel-shaped flowers with copious nectar from a large circular nectary at the base of the flower and smaller amounts from glands on the sepals. Insect visitors are attracted to the flowers by the color and ultraviolet light patterns of the corolla; there is no notable floral odor. The plants are self-incompatible (Martin, 1970), producing water-dispersed seeds that remain viable for up to six months in sea water (Guppy, 1917). The plant's notched leaves (thus the common name—goat's foot) produce nectar from a pair of glands on each petiole near the point of blade attachment (Keeler and Kaul, 1979). Red nectaries on young leaves attract ants and various other visitors; black nectaries on older leaves do not attract insects.

The reproductive biology and population structure of *Ipomoea pes-caprae* present un-usual combinations of related life history at-tributes; the species lives in a narrow maritime-littoral habitat. The plant is a pioneer species with self-incompatibility mechanisms and water dispersed seeds; observations indicate abundant seed set despite high predation on seeds by bruchid beetles (*Megacerus*) (Wilson, 1977), and few seedlings occur in the popu-lations. To date, no studies have examined these aspects of the reproductive biology of *I. pes-caprae.*

In this study a series of experiments were designed to determine the importance of var-ious factors affecting the reproductive success of *I. pes-caprae* around the Gulf of Mexico. Important pollination vectors were identified and pollen flow quantitatively delimited. The amounts of seed predation by bruchid beetles on *I. pes-caprae* were contrasted with the ef-fects of ants feeding on extrafloral nectaries in relation to seed set and survival. Neighbor-hood size was calculated for two populations.

STUDY SITES AND METHODS—Four general as-pects of the reproductive biology of *I. pes-caprae* were investigated: floral biology, func-tion of petiolar nectaries, seed survivorship, and population structure (specific methods dis-cussed below).

We studied *I. pes-caprae* at five sites around the Gulf of Mexico from 1984 to 1987. The climate is subtropical to tropical at all sites. Study areas on the north shore of the Gulf were located on the beachfront at Grand Isle, LA (Devall, 1987a; lat 29°23′N, long 90°16′W), and South Padre Island, near Port Isabel, TX (lat 26°04′N, long 97°13′W). Study sites on the

Fig. 1. Habitat and plant of *Ipomoea pes-caprae* at San Bruno, Yucatán (× ¼).

south shore of the Gulf of Mexico were at Progreso, San Bruno, and Uaymitun, Yucatán, a few kilometers apart on the Gulf coast (lat 21°17′N, long 89°36′W). The population at San Bruno inhabits the beach just above the high tide line, whereas those at Uaymitun and Progreso occur at the back of the beach. *Ipomoea pes-caprae* populations generally vary in size from a few plants to large clumps covering several hundred square meters. The beachfront populations at Grand Isle and San Bruno, for example, were approximately 18 × 90 m in size; those at Uaymitun and Progreso, 90 × 180 m, and the South Padre Island population was 180 × 360 m.

At each study site we placed 15 1-m² quadrats five meters apart along a transect which paralleled the beach, beginning near the front left corner of the population (facing the beach). The exact location of the first quadrat was randomly chosen. Two other transects were located behind and parallel to the first, with five meters between each transect (45 quadrats total). Because *I. pes-caprae* stems root adventitiously at nodes, the extent of an individual plant cannot be easily determined. We there-fore counted stems longer than 30 cm in each quadrat to determine plant density. Within each quadrat we counted flowers, fruit, and seedlings.

Floral biology—Randomly chosen buds were covered with cotton bags during the afternoon before they opened. The next day we collected nectar from these flowers (a minimum of 7) hourly during the morning using hematocrit tubes. Nectar was measured and converted to volume; sugar concentration (mg solute/mg solution) was determined using a Bausch and Lomb refractometer. Nectar could not be collected from a flower more than once because the hematocrit tube damaged the nectary.

We observed *I. pes-caprae* flowers for insect foragers and flower robbers at various times of the day and night, recording insect visitation within a randomly chosen 1-m² area for 15 min out of each hour in 1984 and for each half-hour period during the morning and early afternoon in 1985 and 1986. Flowers in the population were also observed randomly. Insects visiting extrafloral nectaries were observed and collected, and were deposited at Tulane Uni-

versity; some duplicate specimens are at the USDA Laboratory, Beltsville, MD, and duplicates of bees are at the Snow Entomological Museum, Lawrence, KS.

To quantify pollination of *I. pes-caprae* by different insect groups (Schemske and Horvitz, 1984), we covered buds with cotton bags during the afternoon before anthesis. The bags were removed and flowers were available to insects throughout the morning. As soon as an insect visited, a flower was rebagged, tagged, and monitored for fruit set. Thus *only one insect* visited each flower. The total number of flowers visited by each insect species, and the number of visits that resulted in fruit set were used to calculate the percentage of visitation and pollination success of each species.

We estimated pollen flow by applying red, blue, or green fluorescent powder (white in visible light) to *I. pes-caprae* flowers at anthesis (Waser and Price, 1982), presuming that foragers do not visit these flowers differentially. A camel-hair brush was used to apply a small amount of powder to the anthers of five flowers in a 1-m circular quadrat. Five flowers within 2 m were covered with fine mesh bags to demonstrate that the dye was moved to other flowers by insects and not by the wind or other abiotic factors. In early afternoon, when insect activity had ceased, we collected flowers at measured distances from those marked with dye. Flowers within a 1 m circle of the quadrat were picked, then those 1–2 m from the quadrat, etc. Because the flowers were closed or partially closed by this time, the corolla protected the stigma. Each group of flowers was placed in a bag, carefully transported to the laboratory, and examined under a dissecting microscope using a longwave ultraviolet light source. Stigmas were scored for the presence of dye particles. The above experiments were conducted at each study area, though flight distance for bees was calculated only at the Progreso site.

Function of petiolar nectaries—To determine whether a mutualistic relationship existed between *I. pes-caprae* and ant visitors, we excluded ants from some *I. pes-caprae* stems by applying Tanglefoot, a sticky resin, to the bases of the stems. An equal number of stems, each with the same number of buds as an experimental stem, served as controls. Other vegetation was removed from around the experimental and control plants so that ants could not use it to gain access to the plants. We later collected mature fruits to compare seed production by experimental and control plants. Seeds were dissected and examined for pred-

ators. Resin was applied to 20 stems of potted plants without ants or beetles to ensure that Tanglefoot did not affect reproduction and an equal number of stems were tagged as controls. Flowers were hand-pollinated and the resulting seeds were collected and examined.

We examined flowers for missing stigmas and for herbivorous insects, and identified insects that most frequently damaged *I. pes-caprae* flowers and seeds, scoring the percentages of flowers and leaves eaten by herbivores. Seeds of *I. pes-caprae* were randomly collected from each study area at various times of the year, stored in plastic bags and checked for emergent beetle larvae (Janzen, 1980).

Seed survivorship—Seeds from each location were soaked in water for four days and then planted in pots containing a mixture of garden soil and sand. Other seeds were scarified with sandpaper, soaked in water until visibly swollen (not longer than four days) and planted in the same soil mixture.

Population structure—Genetic neighborhood size of *I. pes-caprae* at San Bruno was calculated using Wright's (1943, 1946) equation for neighborhood size of a population in a narrow habitat, such as one growing on a beach or along a river. Seed dispersal was not considered.

$$N = \frac{3.54}{2} dr \left(\sqrt{\frac{2p^2}{2n_p}} + \sqrt{\frac{2s^2}{n_s}} \right),$$

where d equals plant density; r equals the proportion of outcrossing; p equals pollen flow; s equals seed flow; and n_p and n_s equal the number of observed pollen flow distances and seed dispersal distances, respectively. Pollen dispersal distances were from the pollen flow experiment at San Bruno. *Ipomoea pes-caprae* is an obligate outcrosser, so the proportion of outcrossing equals 1. The density of plants in this one dimensional population, where all stems grow towards the water, is estimated to be 0.5. This is based on quadrat data, assuming that all stems originating in a 1-m² quadrat are part of the same plant. Neighborhood size was recalculated including a conservative estimate of seed dispersal. One hundred forty one pollinations should result in 242 seeds (Devall, 1987b). In this calculation, seed movement away from the parent due to fruits produced on long stems is ignored. We assume four seeds enter the Gulf and are dispersed 10 km down the beach, and we set the dispersal distance of the other 238 seeds to zero.

We similarly calculated neighborhood size of a population growing on the back margin of the beach at Progreso with Wright's equation for a two-dimensional population,

$$N = 6.3dr \left(\frac{\sum p^2}{2n_p} + \frac{\sum s^2}{n_s} \right),$$

ignoring seed dispersal and based on a density of 0.5 plants/m². We used the results of the Progreso pollen flow experiment. We also calculated neighborhood size for a second back beach population at Progreso and a second beachfront population at San Bruno.

RESULTS—*Floral biology*—Peak flowering time for *I. pes-caprae* is July–September on the south Gulf coast and South Padre Island, TX, and July–August at Grand Isle, LA. Plants growing in protected spots commenced flowering in May on both the north and south Gulf coast. The mean number of flowers per 1-m² quadrat varied depending upon the time of the year. In peak periods, more than 3,000 flowers occurred daily in the large populations at the five study sites (ca. 1,600 m² or larger). At all sites *I. pes-caprae* flowers open at sunrise and close by early afternoon; flowers open later and close earlier on cloudy days. The corolla falls the following morning.

Ipomoea pes-caprae produces large, showy pink flowers with a lavender tint, with five darker pink stripes (Fig. 1). Five completely united petals comprise a funnel-shaped corolla 51–61 mm long and 59–69 mm wide ($N = 50$). The five green sepals, 12–14 mm long and 7–8 mm wide ($N = 50$), completely surround the flower base. The stamens are unequal, two of which usually exceed the stigma, one is of equal length, and two are shorter. They unite at their base with the corolla tube. The anthers dehisce extrorsely and produce spherical, spinulose pollen. Hairs at the filament base partially cover the ovary and the surrounding yellow nectary. The 2 mm ovary, which contains four ovules, bears a narrow style with a large capitate stigma. Shortly after anthesis, the stigma is receptive and the flowers begin producing nectar. Nectar is produced throughout the morning until noon, accumulating up to 5.7 μl of nectar. Though secretion continues until around 1 P.M., total accumulation generally decreases thereafter. One way analysis of variance revealed that the time of measurement significantly affected nectar secretion (Progreso, ems = 2.85, df = 227, df hr = 7, F = 25.82, P < 0.001). The mean sucrose equivalents (mg solute/mg solution) varied from 37 to 44.

Photographs revealed that the flowers of *I. pes-caprae* have an ultraviolet pattern. The limb of the corolla reflects ultraviolet light, appearing bright, while the inner part absorbs it. The stigma also reflects uv, so that a target pattern is formed. Observing the corolla by methods of Thien (1971), the flowers contrast vividly with the leaves and stems of the plant, which absorb ultraviolet and appear dark.

We collected 54 insect species from *I. pes-caprae* flowers, extrafloral nectaries and seeds (predators) on the south Gulf coast, and 31 species on the north coast. Only four species— *Megacerus leucospilus* (Bruchidae), *Campsomeris tolteca* (Scoliidae), *Solenopsis geminata* (Formicidae), and *Apis mellifera* (Apidae)— were collected on both north and south Gulf coasts, but congeneric ant and bee species were present around the Gulf of Mexico (Table 1).

During the entire flowering season, the first foragers to *I. pes-caprae* flowers at Progreso were large carpenter bees, *Xylocopa brasilianorum* and *X. strandi*. They left by 8 A.M., when a smaller bee, *Agapostemon nasutus*, began visiting the flowers. Most *A. nasutus* foraged between 8 and 9 A.M. Honey bees (*Apis mellifera*) were present during most of the morning, but visited most frequently around 11 A.M. Other bees, a beetle (*Megacerus leucospilus*; Bruchidae), ant species and several unmentioned insect species were occasional visitors. Few insects besides ants visited after midday. Ants entered the flowers even after they closed, and continued to visit during the night and the following day until the corollas fell. No insect was ever observed robbing nectar from *I. pes-caprae* flowers, and no robbing holes were observed.

Anthers and stigma press against the dorsi of large bees such as *X. brasilianorum* and *X. strandi*, as they crawl down the tube. Smaller bees (*Agapostemon nasutus*, *Ceratina* sp., and *Apis mellifera*) pick up pollen on their dorsi as they brush the stigma and anthers. The two *Xylocopa* species back out of the corolla tube, but smaller bees can turn in the flower base and exit head first. All bees pick up some pollen on the thorax while at the base of the flower.

Ants are small relative to the flower and simply crawl down the corolla tube without touching the stigma. A few pollen grains sometimes adhere to an ant's body while it drinks nectar, and ants pull pollen grains from the stigma during the afternoon and carry them away. Large butterflies such as *Agraulis vanillae* (Nymphalidae) and *Phoebis sennae marcellina* (Pieridae) can insert their proboscises to the nectary without entering the corolla tube. Smaller Lepidopterans (*Polites vibex* (Hesper-

TABLE 1. *Hymenopteran visitors to flowers, extrafloral nectaries and seeds of* Ipomoea pes-caprae. *T = South Padre Island, L = Grand Isle, P = Progreso, U = Uaymitun, and S = San Bruno. F = flower, E = extrafloral nectary, D = seed; A = abundant, C = common, R = rare*

Species	Location	Plant part	Abundance
Bees			
Melissodes sp.	L, P, T	F	C, C, C
Agapostemon nasutus Smith	P, S, U	F	A, A, A
A. splendens (Lepeletier)	L	F	C
Centris decolorata Lepeletier	T	F	R
Centris sp.	P	F	C
Bombus pennsylvanicus (DeGeer)	T	F	C
Melitoma taurea (Say)	L	F	C
Apis mellifera L.	L, P, S, T, U	F	R, C, C, R, C
Xylocopa brasilianorum Linn.	P, S, U	F	C, C, C
Xylocopa strandi Dusmet & Alonso	P, S, U	F	C, C, C
X. micans Lepeletier	T	F	R
Augochlora sp.	P	F	C
Ceratina sp.	P, S, U	F	C, C, C
Eulaema tropica (Linnaeus)	P, S	F	R, R
Euglossa sp.	P	F	R
Eupelmus sp.	S	D	R
Wasps			
Campsomeris tolteca Saussure	P, S, T, U	F	C, C, R, C
Glenostictia sp.	T	F	R
Apanteles sp.	P, S, U	E	C, C, C
Ants			
Conomyrma insana (Buckley)	T	F, E	C
Conomyrma sp.	L, T	F, E	C, C
Iridomyrmex pruinosus (Roger)	L	F, E	C
Solenopsis geminata (F.)	P, S, T	F, E	A, A, C
Solenopsis invicta Buren	L	F, E	C
Pseudomyrmex sp.	S	F, E	C
Brachymyrmex sp.	P	F, E	C
Paratrechina longicornis (Latreille)	S	F, E	C
Camponotus planatus Roger	S	F, E	C
Monomorium carbonarium ebenium Forel	S	F, E	C
Cardiocondyla emeryi Forel	S	F, E	R

idae) *Pygarctia elegans* (Arctiidae) and others) fold their wings on entering a flower and do not touch reproductive parts. *Megacerus leucospilus* (Bruchidae) enter the flowers to drink nectar and eat pollen, picking up few pollen grains on their bodies, but more pollen is found on their comblike antennae.

The principal insect visitors—*Xylocopa brasilianorum, X. strandi, Agapostemon nasutus,* and *Apis mellifera*—differed significantly in their ability to pollinate *I. pes-caprae* (Table 2), demonstrated by the experiment carried out at Progreso ($\chi^2 = 21.6$, df = 3, $P < 0.001$) in which the pollination efficiency of various insects was tested. *Xylocopa brasilianorum* was the principal pollinator as 44 of its 72 visits resulted in fruit set, and the two species of *Xylocopa* carried out 49.5% of the pollination. *Agapostemon nasutus* pollinated 22.7% of the flowers. Although *A. mellifera* visited frequently, it had a low rate of pollination (12%). Other insects did not visit frequently enough to be included in the analysis. Ants and butterflies visited a few flowers, but fruit set never resulted. *Megacerus leucospilus* was found visiting only three flowers, but was successful 66.6% of the time.

Xylocopa brasilianorum flew farther between flowers (132 cm, SE = 28.9, $N = 10$) than the other three bee species for which we measured flight distance, *X. strandi,* 123 cm (SE = 20.8, $N = 10$); *Agapostemon nasutus,* 32 cm (SE = 4.9, $N = 10$); *Apis mellifera,* 17 cm (SE = 2.9, $N = 10$). A significant difference existed among flight distances of the four bees ($U = 28.8$, Kruskal-Wallis test, $P = 0.01$).

Insects carried *I. pes-caprae* pollen up to 90 m at the large populations at Progreso and San Bruno (Fig. 2). Flowers covered with tulle bags did not receive fluorescent pollen, demonstrating that abiotic factors do not disperse *I. pes-caprae* pollen. Similar results were obtained at Progreso, Uaymitun, and San Bruno, Yucatán, and at Grand Isle, LA. However, at South Padre

TABLE 2. *Efficacy of different insects at pollinating* Ipomoea pes-caprae *at Progreso, Yucatán. Efficiency refers to the percentage of flowers visited by a specific insect species that set fruit. Population efficiency refers to the percentage of all flower visits that resulted in fruit set*

Species	Visits	Fruit set	Efficiency	Population efficiency
Bees				
Xylocopa brasilianorum	72	44	61.1	45.4
Xylocopa strandi	8	4	50.0	4.1
Agapostemon nasutus females	55	18	32.7	18.6
Agapostemon nasutus males	21	4	19.1	4.1
Apis mellifera	41	12	29.3	12.4
Ceratina sp.	3	5	71.4	5.2
Eulaema tropica	5	5	83.3	5.2
Centris sp.	3	0	0.0	0.0
Euglossa sp.	3	0	0.0	0.0
Wasps				
Campsomeris tolteca	2	2	100.0	2.1
Beetles				
Megacerus leucospilus	3	2	66.7	2.1
unident. beetle	1	1	100.0	1.0
Ants				
Monomorium carbonarium e.	3	0	0.0	0.0
Solenopsis geminata	3	0	0.0	0.0
Unident. butterfly	2	0	0.0	0.0

Island, TX, insects did not carry pollen more than 5 m (Table 3). Pollen flow at South Padre Island differed significantly from that at other study areas (Kolmogorov-Smirnov test, $P = 0.01$).

Function of petiolar nectaries — Mostly flies and ants visited the petiolar extrafloral nectaries of *I. pes-caprae* at San Bruno. Forty-six percent of stems ($N = 263$) had one or more ants on or near an extrafloral nectary (not necessarily taking nectar). In the sampling period (290 min in periods of 10), individual ants were present 2.4 minutes on or near a petiolar extrafloral nectary (mean, SE = 0.1, $N = 25$). Ants rarely visited sepal nectaries but often entered flowers to forage for nectar and pollen.

Megacerus leucospilus, a bruchid beetle, lays eggs on developing fruits of *I. pes-caprae*; a larva burrows into a seed and kills the embryo (personal observation; Janzen, 1980) Only one larva develops per seed (Teran and Kingsolver, 1977) two months after which the mature beetle cuts a large round hole in the testa and exits. Populations of *I. pes-caprae* in Yucatán exhibited greater seed parasitism (up to 16.0%) than northern populations on the Gulf of Mexico (up to 3.6%) even though an additional species of bruchid, *M. coryphae*, was present.

Exclusion of ants from extrafloral nectaries of plants (use of Tanglefoot) resulted in lower seed set for all populations (Table 4). The experimental results were statistically significant in four of five experiments at our Yucatán sites, but not at our north coast sites. Seed predation by *Megacerus* was not significantly different for control and experimental plants (excluding ants from extrafloral nectaries) at any field location (Table 4). Twenty potted plants with tanglefoot produced slightly more seed than controls ($\bar{x} = 1.7$, SE = 0.4 and $\bar{x} = 1.6$, SE = 0.3, respectively).

Insects damaged less than 2% of the leaves in quadrats on the north shore of the Gulf, but damaged a higher percentage of leaves in the south (up to 32.3% at San Bruno, September 1986). Damage seldom consisted of more than a few small holes. Horses and donkeys in Yucatán did not eat *Ipomoea pes-caprae* leaves even when no other plants were within reach.

Beetles (*Phegonus rufipes* in Yucatán), grasshoppers (*Paraidemona mimica* and *Heliastus subroseus* in Texas), and unidentified caterpillars ate entire *I. pes-caprae* corollas and stigmas plus ovaries and developing seeds. Insects ate 6.3% of the corollas (Uaymitun, September 1985); 5.95% of flowers at the canal site in Yucatán lacked stigmas ($N = 222$) and 5.4% of the flowers contained caterpillars ($N = 222$). We did not find missing stigmas or caterpillars at Grand Isle ($N = 27$) or South Padre Island ($N = 91$).
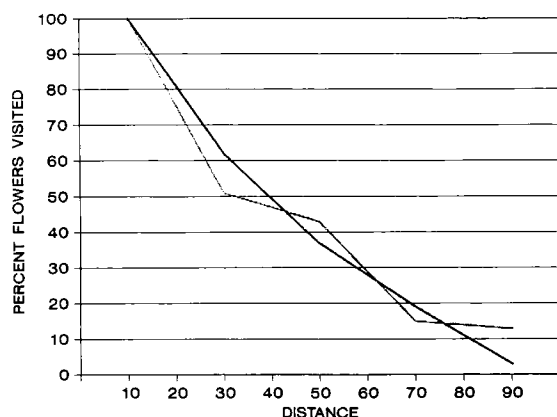
Fig. 2.   Pollen movement in two populations of *Ipomoea pes-caprae* on the coast of Yucatán, Mexico. Fluorescent powder was applied to the anthers of five flowers early in the morning (all within 1 m²); later in the day, flowers in the population were collected (in measured concentric circles from the point of application) and examined for dye. The dark and light lines represent populations at San Bruno and Progreso, respectively.

TABLE 3.   Percent of Ipomoea pes-caprae *flowers receiving pollen from marked donor flowers 0–5 and 5–10 m distant at five study sites*

Location	0–5 m from experimental flowers		5–10 m from experimental flowers	
	Flowers visited	No. of flowers	Flowers visited	No. of flowers
Progreso	100.0	47	100.0	33
San Bruno	100.0	18	100.0	27
Uaymitun	100.0	21	100.0	20
Grand Isle	100.0	21	100.0	4
South Padre Island	8.3	24	0.0	15

Seed survivorship — The globose, 4-valved *Ipomoea pes-caprae* fruit produces four villous seeds and bears nectaries at the base of the sepals. Fruits mature in two months. The San Bruno population produced the most fruits per quadrat, 21.5 (mean, SE = 5.3, N = 28), in September 1985. In spite of abundant fruit production, very few seedlings resulted (Table 5). The largest number of seedlings recorded was a mean of 1.14 (SE = 0.7) at Grand Isle, LA, in September 1985, after a severe storm in the Gulf in August. A mean of 1.1 (SE = 0.8) was recorded at San Bruno in September 1986, also after a storm.

Results from the germination experiment utilizing unscarified seed from the five sites (N = 30) were as follows: 0% for Uaymitun, Grand Isle, and South Padre Island; 2.8%, Progreso; and 5.6%, San Bruno. In contrast, 85% germination occurred in the five groups of scarified seed. The three groups of seed with no germination were obviously different from the scarified seed. Scarified seed from all locations germinated significantly better than the unscarified seed from Progreso and San Bruno (Kolmogorov-Smirnov test, $P = 0.01$).

Population structure — Ignoring seed dispersal, neighborhood size of the beachfront *I. pes-caprae* population at San Bruno was calculated to be 14 individuals. When neighborhood size was recalculated including a conservative estimate of seed dispersal, the resulting neighborhood size of the population was over 1,000.

Neighborhood size of the population on the back margin of the beach at Progreso was 932 plants, ignoring seed dispersal. We similarly calculated neighborhood size for a second back beach population at Progreso and another beachfront population at San Bruno; neighborhood sizes were 12,000 and 1,172 individuals, respectively.

DISCUSSION — *Floral biology* — The primary pollinators of *Ipomoea pes-caprae* around the Gulf of Mexico were bees. The ultraviolet pattern should make the flowers more visible to bees, who see in the ultraviolet range. Large *Xylocopa* bees were the most successful pollinators in Yucatán, as determined by observation and experiment (Table 2). They are probably important pollinators of *I. pes-caprae* in other parts of the world as well, i.e., *X. micans* was collected in *I. pes-caprae* flowers in Texas, *X. confusa* was observed visiting *I. pes-caprae* in Java (Docters van Leeuwen, 1927) and other *Xylocopa* species were collected and observed in Martinique and St. Martin in the Caribbean (Devall, 1987b). *Agapostemon* species frequently visited *I. pes-caprae* flowers as well and compensated for lack of efficiency as pollinators by large numbers of flower visits (22.7% of the pollination). Other bee species visited infrequently, but pollinated *I. pes-caprae* flowers. It is interesting to note that the seed predator, *Megacerus leucospilus* was also an efficient pollinator of *I. pes-caprae* although it had a low frequency of visits. This suggests coevolution between the two species may have occurred. Ants and butterflies were not successful pollinators, no doubt because they could obtain nectar without touching the flower's reproductive parts.

The distance insects carried *I. pes-caprae* pollen is comparable to the distance recorded

TABLE 4. *Comparison of seed production by* Ipomoea pes-caprae *plants from which ants were excluded. Letters indicate location: PROG = Progreso, UAY1, UAY2 = Uaymitun, SB1, SB2 = San Bruno, GI = Grand Isle, SPI = South Padre Island. Seed and bad seed data are means, SE in parentheses. Bad seed = seed with* Megacerus *larvae*

	PROG	UAY1	UAY2	SB1	SB2	GI	SPI
Date	6/85	9/85	7/86	6/85	9/85	8/86	5/86
Experimental							
No. stems	7	28	38	15	31	13	53
Seed	1.1 (0.7)	0.5 (0.2)	0.7 (0.3)	0.8 (0.4)	1.5 (0.4)	4.5 (1.4)	2.4 (0.5)
Bad seed	0	0.3 (0.1)	0.4 (0.2)	0.3 (0.3)	0.4 (0.1)	0.1 (0.1)	0
Control							
No. stems	11	30	37	9	29	13	49
Seed	3.6 (0.7)	1.4 (0.4)	0.7 (0.3)	4.3 (1.4)	3.0 (0.4)	6.3 (1.6)	3.2 (0.5)
Bad seed	0	0.3 (0.1)	0.2 (0.1)	0.1 (0.1)	0.5 (0.1)	0.1 (0.0)	0
t_s							
Seed	1.97*	2.08*	0.04	2.12*	2.58*	1.07	1.53
Bad seed		0.01	1.17	1.62	0.54	0.63	

* $P < 0.05$; Wilcoxon 2-sample test.

by Linhart (1973) for hummingbird pollination of *Heliconia* (most visits were within 20 m of the last flower visited). *Ipomoea pes-caprae* pollen disperses much farther than that measured for many other species: 1.4 m, 0.8 m, and 1.7 m for three colonies of *Phlox* pollinated by butterflies (Levin and Kerster, 1968); Schmitt (1980) recorded flight distances for bumblebees and butterflies visiting *Senecio* of 0.3–1.1 m and 2.3–12.4 m, respectively; Schaal (1980) reported 1.8 m pollen flow distance for bees pollinating *Lupinus texanus*; Waddington (1981) 0.3 m flight distance for bumblebees visiting *Delphinium virescens*; Handel (1976) 1 m for wind-dispersed pollen of *Carex plantaginus* and *C. platyphylla.*

The long between-flower distances of *Xylocopa* species (as demonstrated by *X. brasilianorum*) would promote cross-pollination in a self-incompatible species such as *I. pes-caprae,* in a narrow, long habitat (the beach) because one plant may form large mats or all the plants in one area may be clones. The Yucatán *Xylocopa* species hover high in the air after visiting a number of flowers, appear to choose flowers deliberately, and do not enter flowers recently visited by themselves or other foragers (personal observation). Van der Pijl (1954) also observed this and suggested that *Xylocopa* bees sense the odor of insects that first enter the flower.

Function of petiolar nectaries — The presence of ants on extrafloral nectaries and in flowers of *I. pes-caprae* was of limited importance in populations around the Gulf of Mexico. Seed destruction by *Megacerus* was not significantly different between control and experimental plants. Indeed, the percentage of seeds para-

sitized at all study areas around the Gulf of Mexico (highest 6.0%) was low in comparison to 47.2% of seeds destroyed by *M. leucospilus* in Hawaii (Devall, 1987b) and 15–85% of seeds in Costa Rica (Wilson, 1977). This also contrasts with the findings of Keeler (1980) in which ants reduced seed predation by bruchid beetles in *I. leptophylla* by 10.8%.

Although ants had little effect on seed predation by bruchid beetles, seed production was significantly lower for experimental plants without ants on extrafloral nectaries in Yucatán (four out of five experiments), but not for northern populations.

The observations of nectaries demonstrated that the petiolar extrafloral nectaries of *Ipomoea pes-caprae* attract ants, but the leaves are otherwise protected from herbivores by the indole alkaloid ergotamine (Jirawongse, Pharadai, and Tantivatana, 1979) and by the milky latex, as Keeler (1980) suggested for *I. leptophylla.* Seeds are also protected from most insects by ergotamine (Jirawongse et al., 1979), but bruchids have apparently evolved the ability to eat seeds containing alkaloids (Teran and Kingsolver, 1977). Flower parts are apparently not protected by chemicals or latex, because they are eaten by caterpillars, beetles and grasshoppers.

Unlike visitors to some other species that have been studied, including *Ipomoea* species (Keeler, 1977, 1980, 1981; Baker, Opler, and Baker, 1978; Bentley, 1977), ants visiting *I. pes-caprae* foraged in flowers as well as in extrafloral nectaries. The lack of separation of floral and extrafloral nectary visitors suggests that there may be fewer differences between floral and extrafloral nectar of *I. pes-caprae* than have been found in other species (Keeler, 1977). The

TABLE 5. *Mean stem, fruit, and seedling density and incidence of herbivory for* Ipomoea pes-caprae *around the Gulf of Mexico, collected from 45 m² quadrats (each location) during July 1986. Grand Isle data were collected in August 1986. Standard deviations in parentheses*

Location	Stem density	Fruit density	Seedling density	Percentage of insect damaged leaves
Progreso	5.80 (3.63)	3.47 (8.07)	0.02 (0.15)	5.28 (11.58)
South Padre Island	3.60 (4.14)	0.30 (0.53)	0.00 (0.00)	1.03 (5.47)
Grand Isle	0.60 (1.37)	1.64 (5.10)	0.00 (0.00)	0.00 (0.00)
Uaymitun	6.04 (5.71)	0.00 (0.00)	0.00 (0.00)	0.94 (2.40)
San Bruno	5.36 (4.54)	0.00 (0.00)	0.00 (0.00)	12.53 (16.23)

petiolar nectaries function before and during flowering and perhaps accustom the ants to patrol the plant before the appearance of flowers (Keeler, 1980). The floral and extrafloral nectaries may offer the ants greater incentive to remain on the plant during flowering. Sepal nectaries probably do not play a large role in defense of *I. pes-caprae,* since they were ignored by ants.

The exclusion experiments indicate that ants visiting extrafloral and floral nectaries significantly increased seed set at four sites in Yucatán (except for the repeat experiment at Uaymitun: Table 4). Ants presumably affect reproductive success by driving away caterpillars, beetles and grasshoppers that consume flower parts. Because ants continue visiting flowers until the corollas fall the day after blooming, they can protect flowers against caterpillars, which visit both closed and open flowers. Barton (1986) also found variation in the effectiveness of extrafloral nectaries at one site, which was ascribed to fluctuations in insect numbers. Greenhouse plants treated with Tanglefoot produced slightly more seeds than control plants, demonstrating that toxicity of tanglefoot did not reduce seed set of experimental plants in the field.

Ant visitors benefit *I. pes-caprae* populations less on the northern coast of the Gulf of Mexico, where there are fewer herbivores, as evidenced by less herbivory on stigmas and fewer caterpillars in flowers. Herbivore damage to a plant probably has to be moderately high before ants can noticeably affect reproduction. Our results are similar to those of Barton (1986), who found that abundance of herbivores had to be high before ants could influence reproductive success. Also, ant species differ at the various sites and some ant species reduce herbivore damage more than others (Elias and Gelband, 1975; Bentley, 1977; Schemske, 1980; Beckmann and Stucky, 1981).

Seed survivorship—Pioneer species and colonizers of disturbed habitats are often self-compatible (Baker, 1955); thus, the problem of one pioneer at a new location being unable to set seed is avoided. It is suggested that apparent germination of many buried seeds after storms may negate the effect of incompatibility mechanisms for this colonizing species. Usually few seedlings occur in *I. pes-caprae* populations and, as evidenced by the germination experiment, seed scarification is helpful in germination. It is suggested that a severe storm or hurricane brings fresh water from rain, wears away the testa of accumulated seed on the beach or perhaps uncovers buried seed. Thus more than one seed would germinate at the same time. The seed experiments and quadrat data supported this, since very few seed germinated without scarification and soaking in water, and numerous seedlings were observed at Grand Isle and at San Bruno following a storm. A possible influx of nutrients brought by a storm would help new seedlings become established.

Population structure—Just as the pollen flow distance of *I. pes-caprae* is large, the neighborhood size is also large. Pollinator foraging behavior affects pollen dispersal of plants, and therefore neighborhood structure (Schmitt, 1980). *Ipomoea pes-caprae* seeds are water-dispersed and can float for long periods (Ridley, 1930); however, the extensive pollen dispersal is also an effective force in gene flow. Wright (1946) stated that populations of 1,000 or more achieve panmixia. Thus, both populations of *I. pes-caprae* growing on the beachfront at the high tide line where water dispersal may easily occur and those on the back margin of the beach where seeds usually are not able to enter the water, but populations are two dimensional, should be subject to little differentiation through genetic drift. These calculations demonstrate that pollen dispersal is much more important to gene flow in populations growing away from the beach front, where long distance water dispersal is seldom possible. However, seeds travel small distances from the parent because they are produced on

long stems (Ridley, 1930) and may be transported in sand used for construction of roads and buildings.

As noted, *I. pes-caprae* is distributed throughout the subtropical and tropical regions of the world. Quite possibly, seed set is low within some areas of its range because of lack of long-distance pollinators; secondary pollinators may cause limited seed set. For example, the low pollen flow in the South Padre Island population may be due to the absence of *Xylocopa* bees. Yet these areas maintain robust populations of *I. pes-caprae,* possibly because of long range seed dispersal.

In conclusion, plants of *I. pes-caprae* around the Gulf of Mexico exhibited large pink flowers, sporophytic incompatibility mechanisms, long range dispersal of pollen, low seed predation, water-dispersed seeds, and low seedling production except after storms. Neighborhood size of populations was estimated to be large and approaching that of certain insects.

This study demonstrates that the reproductive biology of *I. pes-caprae* is explicable when its chief pollinators and tropical strand habitat are taken into account. The key factors in the reproductive success of populations around the Gulf of Mexico appear to be the long range dispersal of pollen by *Xylocopa* bees and the water-dispersed seeds. The behavior of the *Xylocopa* bees to enter only flowers without previous insect visitors enforces the long flight characteristics to disperse pollen long distances to overcome incompatibility mechanisms in genets. The result is high seed set.

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