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The role of flower visitors in the explosive pollination of *Thalia geniculata* (Marantaceae), a Costa Rican marsh plant

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DAVIS, M. A. (Dept. Biol., Macalester Coll., St. Paul, MN 55105). The role of flower visitors in the explosive pollination of *Thalia geniculata* (Marantaceae), a Costa Rican marsh plant. Bull. Torrey Bot. Club 114:134–138. 1987.—Carpenter bees, hummingbirds, and butterflies are common flower visitors to a population of *Thalia geniculata* (Marantaceae), located in the Palo Verde Wildlife Refuge, Guanacaste Province, Costa Rica. In this study, the role of these pollinators in triggering the explosive pollination mechanism of *Thalia* was assessed and visitation rates were recorded in three successive years. Bees were found to trigger most flowers they visited, hummingbirds triggered approximately 50% of visited flowers, and butterflies did not trigger any. Visitation activity at flowers varied significantly in both space and time, and was influenced by flower height, a plant's proximity to other conspecifics, the strength of the wind (which varied daily) and possibly by the flowering state of other species growing nearby (which varied annually). *T. geniculata* was found to be able to produce seeds autogamously which prevents reduction in seed set in areas, or during periods, of low pollinator activity.

Key words: *Thalia geniculata*, explosive pollination, flower visitors, Marantaceae, Costa Rica.

Thalia geniculata, like other species in the Marantaceae, possesses a specialized pollination mechanism known as explosive secondary pollen presentation. Prior to anthesis, pollen is deposited in a stylar depression behind the stigma. When the flower opens, the style is hidden behind a cucullate (hooded) staminode, held in tension by a pressure sensitive spur. If a bill, proboscis, or steel probe is inserted into the corolla and strikes the spur with sufficient force, the style is catapulted around to the front of the flower, bringing the stigma in contact with the intruder, and simultaneously depositing pollen on the visitor (Kennedy 1978).

At the Palo Verde National Wildlife Refuge in Costa Rica, *T. geniculata* attracts a diverse group of flower visitors including female carpenter bees, *Xylocopa fimbriata* and *X. gualanensis*; hummingbirds, *Chlorostilbon canivetii* and *Amazilia tzacatl*; and skipper butterflies (Hesperiidae). The purpose of this study was to determine which visitors were most effective in triggering the pollinating mechanism in *T. geniculata.* In addition, since two other species in the genus, *T. dealbata* and *T. trichocalyx,* can produce seed autogamously (Kennedy personal communication), a second goal was to determine if *T. geniculata* is also capable of autogamous seed production or if it is dependent upon flower visitors for sexual reproduction.

The Plant. *Thalia geniculata* (Marantaceae) is a tropical herb which grows in dense populations along marsh edges. In northwestern Costa Rica, the species flowers at the beginning of the dry season, typically from late December through mid-January. Individual *T. geniculata* plants usually consist of multiple stems which can exceed 3 m in height. The small (1.5 cm diam) but showy light purple flowers are produced in pairs within a common bract and are borne on panicles from 0.5 to 3 m above the ground. Each flower is capable of producing a single arillate seed, although usually only one flower in a pair sets seed. The twin flowers open for a single day, and flowers on a

[1] Data for this study were gathered during the Dartmouth College Foreign Study Program in Biology 1978, 1979, and 1980. Students who were working on field problems that focused on the reproductive biology of *T. geniculata* collected some of the data. These persons were Bruce Maslock, Alexis Bond, Miguel Damien, Richard Aronson, Jayne Seymore, Scott Stoleson, Tom Gettinger, David Bachman, Diane Stewart, Cindy Berger, Sheila Cheston, Bruce Leighty, Bill Hunt, Jesse Pelton, Elizabeth Miller, and Bill Carlsen. I thank Jack Schultz for suggesting the project to me and Helen Kennedy for clarifying the precise nature of the pollinating mechanism.

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panicle open sequentially so that individual panicles exhibit an open pair of flowers on most days during the flowering season. Since plants may possess as many as 20 or more panicles, they always present a number of flowers to visitors. Seed development is very rapid in *T. geniculata,* and the swollen ovary containing a developing seed can be detected decisively 48 hr following anthesis. The aril remains attached to the panicle for 7 to 10 days before it dehisces.

Study Site. All observations and experiments were conducted at the Palo Verde National Wildlife Refuge (Refugio Rafael Lucas Rodriquez Caballero) in south-central Guanacaste Province in Costa Rica (10°20′N, 85°20′W). The study site lies in a region classified as a dry tropical forest (Holdridge's scheme). The plants were growing along the north edge of the large seasonal swamp which abuts the Rio Tempisque. The site was visited from January 5 to January 15, 1978; January 6 to January 15, 1979; and January 5 to January 12, 1980.

Materials and Methods. Observations were made by standing or sitting at the edge of a patch of *Thalia* and recording all flower visitors between 0800, when the flowers began to open, and 1800, when it became dark and the flowers began to close. On some days observations were made only in the morning or afternoon. Yearly totals for days of sampling, field hr of observation, and observer hr (field hr × no. observers) were: 1978—5 days, 36 field hr, 108 observer hr; 1979—5 days, 42 field hr, 98 observer hr; 1980—2 days, 18 field hr, 50 observer hr. Project totals were 12 sampling days, 96 field hr, and 266 observer hr.

Initial observations in 1978 suggested that flower visitors did not forage randomly, but

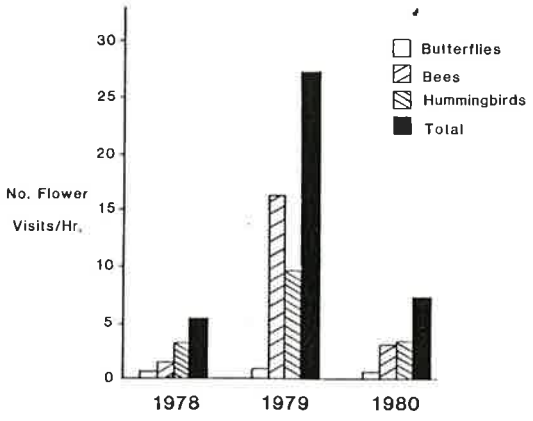


Fig. 1. The mean number of observed visits by the 3 types of flower visitors for each hr of observation in 1978 (108 hr), 1979 (98 hr) and 1980 (50 hr).

by inspecting flowers hourly between 0800 and 1800 hours during one day each year. On other days, additional flowers were checked once, at the end of the day (1800 hours). To test whether style tripping rates varied in space throughout the *Thalia* population, flowers in a central dense patch were inspected during one day in 1978 and one day in 1979, and the tripping rates compared with those from flowers on the periphery of the population.

To determine if *Thalia* is capable of selfing, 133 pairs of flowers were bagged with cheesecloth prior to opening, and the seed set was compared with unbagged flowers.

Results. A total of 3623 flower visits were recorded. Of these, 1946 (53.4%) were by bees, 1476 (40%) were by hummingbirds, and 201 (5.5%) were by butterflies.

Both the absolute and relative abundance of visitors varied markedly from year to year. The number of visits in 1979 was more than five times that in 1978 or 1980 (Fig. 1), due primarily to a 10-fold increase in

Table 1. Activity patterns of the three groups of flower visitors during a day of high visitation in 1979. Numbers indicated the proportion of total flowers visited during each of the different time periods.

	Morning (0800–1100)	Midday (1100–1430)	Late afternoon (1430–1730)
Bees (N = 783)	0.18	0.30	0.52
Hummingbirds (N = 144)	0.01	0.12	0.87
Butterflies (N = 62)	0.71	0.29	0

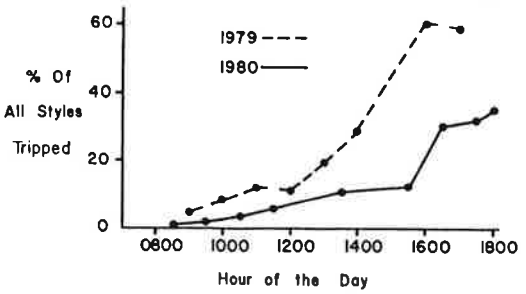
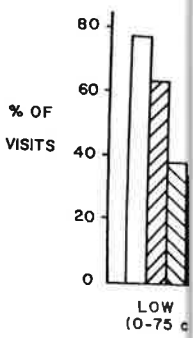


Fig. 2. The per cent of styles found to be tripped within flowers sampled at different times during the day. Both lines represent data collected during one day: N = 600 styles (300 flower pairs) in 1979 and 526 styles (263 flower pairs) in 1980. In 1979 flowers were sampled randomly at each time period; in 1980 the same 263 flower pairs were checked throughout the day.



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Although butterflies confined most of their activity to the morning, most flower visits occurred during the afternoon, particularly between 1400 and 1600 hours, when bees and hummingbirds were most active (Table 1). The increase in visitation rates during the afternoon corresponds to a similar increase in the proportion of styles that are tripped at this time (Fig. 2). The proportion of styles tripped at the end of the day varied significantly from year to year in a way which also corresponded to the level of visitor activity. In 1978 and 1980, years of relatively low activity, 54.9% (N = 408, data pooled from 3 days) and 35.0% (N = 526, data from a single day) of the styles were tripped at 1800 hours, while in 1979 64.3% (N = 866, data pooled from 4 days) were tripped ($P < 0.01$, variance test for the homogeneity of the binomial distribution: Snedecor and Cochran 1967). Tripping rates among low, medium, and high flowers also varied significantly, and again the pattern of style tripping corresponds to the pattern of pollinator activity (Table 2).

A census (N = 389) of flowers in 1979 revealed that 34% were less than 75 cm from the ground, 46% between 75 and 150 cm from the ground, and 20% higher than 150 cm. The flower visitors showed a preference for the lower flowers ($P < 0.001$, chi-squared), although the preference was far more pronounced among the butterflies and hummingbirds (Fig. 3).

In addition to annual variation, there was significant day to day variation in visitation rates. On many days during the study, the majority of flowers under observation were never visited, and on some days, particularly windy days, visitation sometimes dropped to zero. Even during peak visitation days during 1979, many flowers were never visited. A comparison of hummingbird foraging on January 12, 1978, when there was little wind, with that two days later when it was very windy, showed that the birds that were still foraging on the windy day concentrated their activity on lower flowers (Table 3).

On days of low visitation, many flowers still exhibited tripped styles by the end of the afternoon. By tripping the flowers manually during the day, it was clear that the tripping mechanism becomes more and more sensitive as the day progresses, which suggested that the styles may be capable of tripping spontaneously. This was verified by covering 23 pairs of flowers with cheesecloth prior to anthesis and checking them at 1700 hours. Eight exhibited at least 1 tripped style even though none had been visited. In 1978, 50 flowers were checked by flashlight at 2100 hours, and all had

Table 2. Visitation frequency for flowers growing at different heights, compared with the proportion of styles found to be tripped in each height level at the end of the day. Both sets of data were obtained from the same patch of *Thalia* during one day in 1979.

	Low (<75 cm)	Medium (75–150 cm)	High (>150 cm)
All flower visitations (N = 989)	0.38	0.45	0.17
Tripped styles (N = 600)	0.63	0.74	0.40

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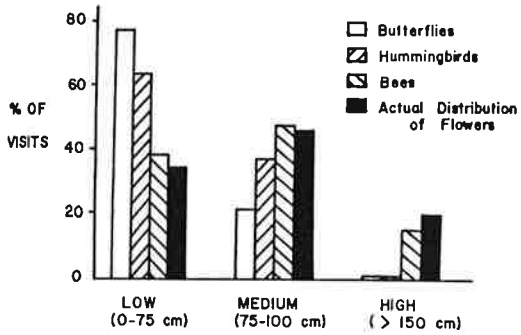

Fig. 3. The proportion of flower visits made at 3 different height levels by butterflies (N = 62), bees (N = 1297), and hummingbirds (N = 821) in 1979. The data are pooled from 5 days of observation. The actual distribution of flowers, percentage in each height class, is shown by the solid black bars.

closed, or were closing. All but 5 exhibited at least one tripped style.

Of 133 pairs of flowers bagged with cheesecloth, 66 (49.6%) produced a fruit, compared to 73 of 127 (57.5%) for the unbagged flowers ($z = 1.28$, $P > 0.2$, normal approximation for the difference between two proportions; Snedecor and Cochran 1967); thus unvisited flowers can set seed.

When the style tripping rates of central and peripheral plants were compared, it was found that the tripping rate was significantly higher in the central part of the patch. By the end of the day, 80% of the styles (N = 250) from central plants had been tripped compared to 51% (N = 250) from peripheral plants ($P < 0.001$, data from the two years combined).

Discussion. The likelihood that a flower visitor will trigger the explosive pollination mechanism in *T. geniculata* is dependent upon foraging behavior and time of day. Owing to their size and foraging behavior (they force their heads into the flower), the bees trip most of the flowers they visit, irrespective of time of day. With their thin bills and long tongues, hummingbirds often extract nectar without tripping the flower. However hummingbirds do frequently trip the styles, particularly in the afternoon when the trigger is most sensitive. The skipper butterflies fail to trip the styles for two likely reasons: (1) they feed by alighting on the flower and inserting their long thin proboscis into the corolla and may often not even strike the pressure sensitive spur; and (2) they are not heavy enough to activate the tripping mechanism were they to strike it, which is compounded by the fact that they do most of the foraging early in the morning when the trigger is least sensitive.

Table 3. Height distribution of flowers visited by hummingbirds on a calm and a windy day during 1978. The two distributions are significantly different from one another ($\chi^2 = 16.11$, $P < 0.001$).

	Jan 12 (calm)	Jan 14 (windy)
Low flowers	42	80
Middle flowers	84	59
High flowers	18	25

An unanticipated finding of this study was that visitation rates varied greatly in both space and time. The year to year variation in bee activity might be due to opportunistic foraging behavior of the polylectic bees. Hurd (1978) reported 31 species visited by *X. fimbriata* for pollen and nectar, including *T. geniculata*, and more than 20 host species have been recorded for *X. gualanensis* (Sage 1968). In 1978, although most *Thalia* plants in the population were flowering and the bees were common, they primarily visited *Parkinsonia aculeata*, a small leguminous tree which at Palo Verde is abundant in the habitat of *T. geniculata*. During the study period in 1979, *P. aculeata* had very few flowers and visitations to *Thalia* were much higher. In 1980, the low number of visits could be due to the fact that by the second week in January most *T. geniculata* plants had completed flowering. *Xylocopa* bees were present in the area, but foraged primarily in a nearby tree, *Glirisidia sepium* (Fabaceae), a species heavily visited by *Xylocopa* bees in Guanacaste Province (Janzen 1983).

Within years, visitation rates were affected by wind speed. Although the relationship between wind speed and visitation rates was not specifically studied, it was apparent that visitation declined markedly as wind speed increased. On certain very windy days, observations actually were discontinued because flowers were not being visited at all.

The preference for low flowers is also likely related to wind. *Thalia* plants are tall and willowy, and the upper panicles are blown about more than those on the lower stems. Moreover, the lower flowers derive some wind protection from the marsh sedge. The

butterflies are unable to alight on a *Thalia* flower even in a light breeze, which explains not only their strong preference for low flowers, but also their absence in the afternoon, when a breeze usually develops. Although the hummingbirds are very mobile and acrobatic in flight, they still must maintain their position at a flower by hovering, and thus any flower motion makes feeding difficult. The bees are least affected by the wind; once they have secured themselves on a flower, even a very strong gust of wind seldom dislodges them. However, a strong wind will hinder and often prevent the initial landing.

The higher tripping rates found in central patches of the population are consistent with a study by Hartgerink *et al.* (1978), who found that the tripping rates of clumped *T. geniculata* were significantly higher than those for dispersed plants. The higher frequency of tripped styles among more centrally located plants may be explained by a resource concentration effect (Root 1973) in which the flower visitors are more likely to find a dense stand, or by assuming foraging efficiency (Pyke 1978) in which flower visitors prefer to forage in areas where they can expend less energy moving between the flowers.

More data are needed to establish conclusively the reasons behind the spatial and temporal variation in visitation rates. In any case, the fact that visitation rates do vary markedly in space and time, and that flowers are open for only a single day, means that for any given flower there is considerable uncertainty as to whether it will get visited at all. Even on days of high visitation, not all flowers are visited. Bierzychudek (1981) pointed out that in certain plants reproductive effort might be pollinator limited. However, during times of low pollinator abundance plants may be able to prevent reduction in seed set through autogamous production of seed (Kaur *et al.* 1978; Schemske 1977; Pellmyr 1985). It is possible that the seeds produced autogamously by *T. geniculata* are of lower quality than those produced through outcrossing. Nevertheless, by possessing a backup method of producing seeds autogamously, *T. geniculata* is less vulnerable to periods of low pollinator activity.

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