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Author(s): Douglas W. Schemske

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FLORAL CONVERGENCE AND POLLINATOR SHARING IN TWO BEE-POLLINATED TROPICAL HERBS¹

DOUGLAS W. SCHEMSKE

Department of Biology, University of Chicago, Chicago, Illinois 60637 USA

Abstract. The hypothesis that the understory herbs *Costus allenii* and *C. laevis* (Zingiberaceae) have converged in floral characteristics to use the same pollinator was investigated in central Panama. Observations and experiments indicated that these species (1) occupy the same habitats, (2) flower synchronously, (3) are identical in flower color, morphology, and nectar secretion patterns, (4) share the same pollinator, the bee *Euglossa imperialis*, (5) are self-compatible, but not autogamous, and (6) have strong barriers to hybridization. Both grow in low density along streamsides and produce a single flower per day for an extended period (up to 4 mo). Flower density is depressed through extensive predation by the weevil *Cholus cinctus*, which damaged 31% of all *C. allenii* and 60% of all *C. laevis* inflorescences. Direct observation of foraging bees indicated that individuals regularly visit both plant species. An experimental analysis of interspecific pollen transfer using powdered paint as a marker verified these results; 97% of the flowers checked had received heterospecific visits. The high probability of interspecific pollination did not affect fruiting success.

I suggest that low flower density, exaggerated by extreme floral predation, has selected for floral similarity and pollinator sharing in these species. Floral convergence increases effective flower density and nectar supplies, and probably increases the regularity and rate of pollinator visitation.

Key words: competition; convergence; *Costus*; *Euglossa*; flowering; mimicry; nectar production; Panama; phenology; pollination; predation; traplining; tropical forest.

INTRODUCTION

The tremendous diversity of floral displays observed in flowering plants is a result of selection exerted by pollinator foraging characteristics (Heinrich and Raven 1972) and intra- and interspecific competition for pollinator services. Intraspecific variation in pollination success as a function of floral display (Willson and Rathcke 1974, Willson and Price 1977, Schemske 1980a, b) illustrates the strong evolutionary influence of pollinators on reproductive characters. Interspecific competition for pollinators (see Holm 1966, Free 1968, 1970, Waser 1978) has led to the evolution of a diverse array of mechanisms that increase the specificity, predictability, and rate of pollinator visitation. Differences in flowering time (Robertson 1895, 1924, Mosquin 1971, Heithaus et al. 1975, Reader 1975, Heinrich 1976, Stiles 1977, Waser 1978), flower morphology (Grant and Grant 1964, Macior 1971, Stiles 1975, Inouye 1976, Schemske 1976), and flower color (Levin 1972, Jones 1978) among sympatric species are commonly attributed to selection for reducing competition for pollinators.

Although divergence in floral characteristics has received the most attention, Macior (1971) suggested that floral mimicry and pollinator sharing may be adaptive in species with restricted distributions. Two sorts of mimicry systems can be identified, based on pollinator rewards and plant abundance. In Batesian systems, a rare species that provides no food reward mimics the flowers of a more abundant "provider"

(see Macior 1968, 1971, Yeo 1968, Gentry 1974, Heinrich 1975, Wiens 1978, Brown and Brown 1979, Boyden 1980). In Müllerian systems, two or more species that offer food rewards converge in floral characters (Grant and Grant 1968, Macior 1971, Proctor and Yeo 1972, Brown and Brown 1979). Müllerian convergence (see Wiens 1978) increases the "effective" density of food rewards to pollinators and may increase pollination probabilities. With the exception of data collected by Brown and Brown (1979) on floral similarity and pollinator sharing in sympatric, hummingbird-pollinated species in Arizona (USA), most published reports of floral mimicry (references above) are poorly documented.

In this paper I present evidence for pollinator sharing in *Costus allenii* Maas and *C. laevis* Ruis and Pavon (Zingiberaceae), two bee-pollinated understory species of lowland tropical forest. Preliminary observations indicated that both are low-density species of similar habitats, with very similar flowers and broadly overlapping flowering times. To examine the hypothesis that these species are convergent, I quantified (1) flowering times, (2) nectar secretion patterns, (3) the extent of interspecific pollinator movement, and (4) the potential for interspecific hybridization. The evolutionary implications of pollinator sharing in this system are discussed with respect to the possible benefits of increased pollinator visitation.

COSTUS NATURAL HISTORY

Most neotropical *Costus* species are terrestrial understory herbs with leaves arranged in one to two spirals about the stem. Flowers are borne in terminal,

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TABLE 1. Floral characteristics and habitats of bee-pollinated *Costus* spp. in central Panama. Numbers in parentheses are SD and sample size, respectively.

Species	Flower color	Flower length (mm)	Length of nectar tube (mm)	Habitat
<i>C. allenii</i>	Yellow with red venation	70 (3.4, 25)	28 (2.4, 25)	Small gaps along streams in mature forest
<i>C. laevis</i>	Yellow with red venation	74 (2.8, 25)	31 (1.9, 25)	Small gaps along streams in mature forest
<i>C. guanaiensis</i>	Pink-red	82 (1.1, 10)	34 (1.2, 10)	Large treefalls and forest edge
<i>C. villosissimus</i>	Yellow	63 (3.1, 13)	24 (2.0, 13)	"Open," wet, disturbed sites in secondary vegetation

ovoid inflorescences that elongate markedly with age. Generally one flower is produced per day (rarely two) but flowering continues for an extended period (up to 4 mo). Flowers open in early morning and fall from the inflorescence by midafternoon. Each flower is subtended by a single, thick bract that encloses developing flowers and fruits. A vertical ridge on each bract secretes extrafloral nectar that attracts ants (see Schemske 1980c).

The tubular flowers are morphologically complex, with a three-part labellum the most conspicuous element (Maas 1972). The stamen is petaloid, and the tip is appressed to the labellum, thus closing the flower entrance. The anther is dithecic; the filiform style is enclosed between the thecae and the stigma is located at the top of the anther. In bee-pollinated *Costus*, pollinators push the petaloid stamen upwards to gain entrance to the tubular labellum and nectar-secreting tissues at the base of the flower.

Costus allenii and *C. laevis* are primarily restricted to moist streambanks in mature forest, and flower only in small treefall gaps or forest openings. Although they overlap broadly in habitat, *C. allenii* is somewhat more abundant than *C. laevis* in "closed," shaded sites. Flowers of the two species are virtually indistinguishable in color, with a yellowish corolla and red labellum with yellow venation. Ultraviolet color patterns, observed by the procedure of Eisner et al. (1969), are identical. Flower morphology is very similar, both in mean flower length (*C. allenii* = 70 mm; *C. laevis* = 74 mm) and mean length of the nectar tube (*C. allenii* = 28 mm; *C. laevis* = 31 mm) (Table 1). Both species are pollinated by euglossine bees.

Although floristically very similar, *C. allenii* and *C. laevis* have grossly different vegetative characteristics. The leaves of *C. allenii* are short, broad, and densely hairy, while those of *C. laevis* are slender and glabrous. Inflorescences of both species are terminal, on leafy stems, but inflorescences of *C. laevis* are borne higher above the ground than those of *C. allenii*, 2 m ($N = 61$, $SD = .68$) vs. 1.5 m ($N = 39$, $SD = .32$).

In the original description, based on a few dried

specimens, Maas (1972) indicated that *C. allenii* may be of hybrid origin, possibly with *C. laevis* as one of the parents. However, further work has indicated that *C. allenii* is certainly not a hybrid (Maas 1977). The geographic distribution of *Costus allenii* (Panama, Colombia, and Venezuela) is completely contained within, and broadly overlaps that of *C. laevis* (Guatemala to northern South America) (Maas 1972).

The marked similarity in floral characteristics between *C. allenii* and *C. laevis* is not observed in other sympatric *Costus* with similar pollination systems (Table 1). Two other bee-pollinated *Costus* are found in central Panama, *C. guanaiensis* Rugby and *C. villosissimus* Jacquin. The former is restricted to large treefall gaps in forest uplands and forest edge and has large (flower length = 82 mm), pinkish-red flowers, while the latter is never found in forest, occupies wet disturbed sites, and has smaller (mean flower length = 63 mm) yellow flowers (Table 1). Both species have a much wider entrance to the flower tube than *C. allenii* and *C. laevis*, and begin flowering later. Thus, *Costus allenii* and *C. laevis* are floristically and ecologically segregated from other bee-pollinated *Costus* (Table 1), although interspecific pollen exchange with *C. guanaiensis* probably occurs on rare occasions.

FLORAL PREDATION

Inflorescences of both *Costus allenii* and *C. laevis* are frequently attacked by the weevil *Cholus cinctus*. Weevils feed on mature, open flowers and chew through bracts to feed on flower buds. Flowers attacked after they open are quickly destroyed and rarely visited by pollinators. Flowers attacked in the bud stage almost never open. Damage caused by weevils drilling into developing floral tissues rarely kills the inflorescence but markedly influences the pattern of flowering. Predator-free inflorescences provide predictable nectar sources for pollinators, whereas inflorescences with weevil damage produce fewer flowers, at more irregular intervals. Thus, on the population level, predation by weevils decreases flower density,

and increases the spatial and temporal variation in flower production.

STUDY SITE

Most fieldwork was conducted in 1977 on Barro Colorado Island (BCI), Panama (formerly Canal Zone). BCI is $\approx 16 \text{ km}^2$, and was isolated from the mainland by formation of Gatun Lake during construction of the Panama Canal from 1911 to 1914 (Croat 1978). The vegetation is structurally mature, tropical moist forest, and the rugged terrain is dissected by numerous small streams. As in many tropical areas, forest structure is heterogeneous (Hallé et al. 1978), with an irregular upper canopy (25–40 m height) and frequent treefall gaps. The climate is seasonal; 92% of total precipitation (275 cm/yr) falls during the wet season (May to mid-December) (Croat 1978). Detailed descriptions of the vegetation, forest structure, and climate of BCI are given in Croat (1978), and Leigh et al. (*in press*).

The primary study area was a 1-km² section of old forest that encompassed most of the suitable habitats for *Costus allenii* and *C. laevis*, and included two major streams, Shannon and Balboa. No other understory plant species pollinated by euglossine bees were observed in habitats with flowering *C. allenii* or *C. laevis*.

Hand pollinations were made on plants growing along Pipeline Road, a section of structurally mature, lowland forest located 8 km northwest of Gamboa, Panama, and $\approx 15 \text{ km}$ east of BCI. The climate, vegetation, and structure of the forest are similar to that of BCI.

METHODS

To determine the extent of temporal overlap in flowering time, I censused all inflorescences of *C. allenii* and *C. laevis* in the study area every 10 d from April to December 1977. At each census, inflorescences were categorized as flowering or fruiting and checked for herbivore damage.

Nectar production was quantified by sampling "bagged" flowers with microcapillary tubes shortly after dawn (0630) and every 2.5 h thereafter until the flower fell from the inflorescence (1630). Flowers were bagged with fine-mesh cheesecloth to exclude pollinators. Sugar concentration of the nectar (in sucrose equivalents) was determined in the field with a temperature-compensated refractometer.

I used several methods to examine the extent of pollinator overlap between *C. allenii* and *C. laevis*. First, the taxonomic composition of the pollinator fauna was determined by collecting pollinators from both *Costus* species throughout the flowering season. Second, the extent of interspecific pollinator movement was assessed by direct observation of individual pollinators, and by marking flowers with powdered, fluorescent paint to track pollinator movements. Pollen

of *C. allenii* and *C. laevis* is morphologically very similar, so stigmatic pollen loads could not be used to examine interspecific pollen movement (see Brown and Brown 1979). Floral constancy of individual bees was quantified by monitoring visitation patterns to six *C. allenii* and eight *C. laevis* inflorescences along a 12-m section of Shannon stream. All *C. laevis* were in a large group (10 m²), with two *C. allenii* 1 m to the south, and four *C. allenii* 3–5 m to the north. Two observers followed the foraging paths of all bees entering the area. All observations were made in late morning, when pollinator visitation rates were highest. The second technique for assessing interspecific pollinator movement involved marking the anthers of all *C. allenii* in Shannon Ravine and all *C. laevis* in Balboa Ravine with powdered paint. Anthers were marked at dawn, and a different color was used in each ravine. In late afternoon of each day, stigmas were removed from all *C. laevis* in Shannon and *C. allenii* in Balboa, and inspected under a dissecting microscope. The presence of paint indicated interspecific pollinator movement and the potential for pollen transfer.

I quantified the distribution of both species to determine the potential for spatial partitioning of pollinators. For each inflorescence of *C. allenii* and *C. laevis*, I measured the distance to the nearest conspecific and to the nearest inflorescence of the other species. Only inflorescences that overlapped in flowering time by $\geq 5 \text{ d}$ were included as neighbors.

To examine the relationship between interspecific pollen flow and hybridization potential, I conducted a series of hand-pollinations of *Costus allenii*, *C. laevis*, and *C. guanaiensis* along Pipeline Road in mid-July 1977. For each species, I quantified seed production for selfed, outcrossed, and hybrid crosses, and examined the potential for autogamy (self-pollination). Intraspecific crosses (selfing, outcrossing) provide a baseline for assessing the results of hybrid crosses. Similarly, *C. guanaiensis* provides a base for comparing the results of crosses involving species that regularly exchange pollen (*C. allenii* \times *C. laevis*), and those that do not (*C. guanaiensis* \times *C. allenii*; *C. guanaiensis* \times *C. laevis*).

Flowers were hand-pollinated on nine inflorescences of *C. allenii* (four clones), 15 of *C. laevis* (six clones), and 11 of *C. guanaiensis* (seven clones). All inflorescences were bagged with fine-mesh cheesecloth to exclude pollinators. Pollen was transferred to the stigma during mid-morning with fine-tipped forceps. For outcrossing and hybrid crosses, pollen was obtained from a single clone per cross, with all clones equally represented as pollen parents during the course of the pollinations. Self pollen was obtained from the flower being pollinated. For hybrid crosses, each species served both as seed and pollen parents. Every several days, some bagged flowers of each species were not hand-pollinated to determine the po-

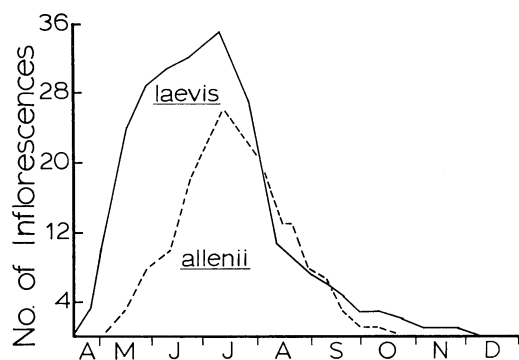


FIG. 1. Flowering phenology of *Costus allenii* (dashed line) and *C. laevis* (solid line) on Barro Colorado Island, Panama.

tential for autogamy. In all pollinations the number of pollen grains deposited per stigma far exceeded the number of ovules per ovary.

Inflorescences were collected when seeds matured in early October, ≈ 2 mo after hand pollination, and all fruit from control and hand-pollinated flowers was checked. Mature, viable seeds were extremely hard, with a dark seed coat. Aborted seeds were pale, soft, and one-half to two-thirds the size of mature seeds.

RESULTS

Flowering phenology

Although *Costus laevis* began flowering earlier than *C. allenii*, the time of peak flowering was identical for both species, and flowering densities were very similar after the peak (Fig. 1). The mean flowering span (time from first to last flower) for inflorescences with more than one flower was 61.8 d for *C. laevis* (SD = 30.9, range 8–145, $N = 57$) and 33.2 d for *C. allenii* (SD = 17.3, range 6–93, $N = 52$). The mean number of flowers produced per inflorescence was 52.9 for *C. laevis* (SD = 28.6, range 4–115) and 24.9 for *C. allenii* (SD = 12.2, range 3–55). Both mean flowering span and flowers per inflorescence were significantly greater ($P < .001$, t test) for *C. laevis* than *C. allenii*.

Predation

Extensive weevil predation was observed for 31% of all *C. allenii* and 60% of all *C. laevis* inflorescences. The actual predation rate was probably higher, as weevils often destroyed mature floral tissues without drilling through flower bracts. Thus, for both species, the impact of weevils was sufficient to reduce flower density markedly and increase the variation in flower output per inflorescence. To determine if the probability of weevil predation increased with flowering span, I compared the frequency distribution of flowering span for inflorescences with weevil damage to that of inflorescences with no damage (Kolmogorov-Smirnov two-sample test; Siegel 1956). Flowering span was divided into 10-d intervals for *Costus allenii* and 20-d intervals

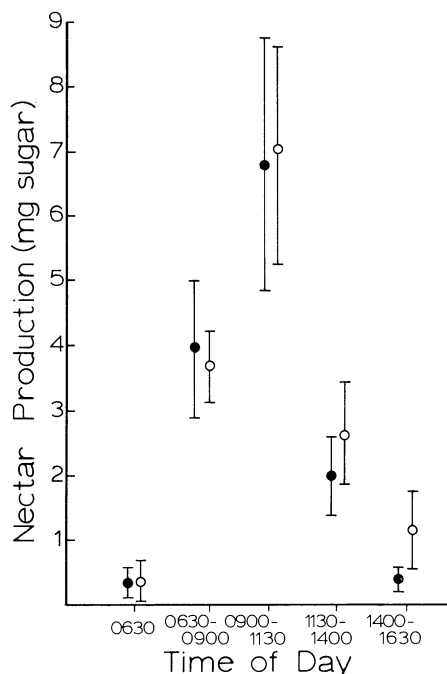


FIG. 2. Nectar production ($\bar{X} \pm 2$ SE) by bagged flowers of *Costus allenii* (O); and *C. laevis* (●) sampled at 0630 and every 2.5 h thereafter. $N = 17$ for *C. allenii*; $N = 19$ for *C. laevis*.

for *C. laevis*. There was no significant difference between distributions for *C. allenii* ($P > .10$) or *C. laevis* ($P > .30$). In addition, the probability of predation was independent of flowering time in both species. Inflorescences which produced the majority of their flowers during the period of peak flowering had the same predation probability as those which flowered primarily before or after the peak.

Nectar production

Nectar secretion patterns for *C. allenii* and *C. laevis* were identical, with maximum nectar output from mid- to late morning (Fig. 2). There was no significant difference between *C. allenii* and *C. laevis* in nectar concentration or nectar volume per flower. Nectar concentration, in sucrose equivalents, averaged 37%

TABLE 2. Foraging behavior of individual female *Euglossa imperialis* at a mixed patch of *Costus allenii* and *C. laevis*. The number of foraging bouts which were constant to *Costus allenii* or *C. laevis* or included both *Costus* species (=mixed), is given as a function of flowers visited per foraging bout.

	Flowers per bout						
	1	2	3	4	5	6	7
Number constant	41	34	20	6	3	1	0
Number mixed		5	21	20	8	5	5
Percent mixed		13	51	77	73	83	100

TABLE 3. Visitation patterns of the bee *Euglossa imperialis* (female) to *Costus allenii* and *C. laevis* growing in a mixed-species patch. The chi-square analysis compares the expected number of visits per species (in parentheses) to that observed. Expected values were calculated by multiplying the percent of flowers of each species available by the total flowers visited.

Date	Hours observed	Number of flowers available		Total foraging bouts	Number of flower visits		χ^2
		<i>C. allenii</i>	<i>C. laevis</i>		<i>C. allenii</i>	<i>C. laevis</i>	
24 Jun	2.5	4	9	22	23 (13)	18 (28)	11.3**
27 Jun	3.0	5	7	20	25 (18)	18 (25)	4.7*
28 Jun	3.0	7	10	22	31 (24)	27 (34)	3.5
29 Jun	2.2	6	6	13	20 (19)	18 (19)	0.1
2 Jul	3.0	7	5	36	88 (68)	29 (49)	14.0***
5 Jul	2.1	6	7	34	73 (49)	34 (58)	21.7***
6 Jul	2.7	7	5	22	47 (39)	20 (28)	3.9*

* $P < .05$; ** $P < .01$; *** $P < .001$.

for *C. allenii* (45 samples from 17 flowers), and 33% for *C. laevis* (46 samples from 19 flowers). The mean volume of nectar secreted per flower was 40.6 μ L for *C. allenii* (SD = 12.7, range 22–59, $N = 17$), and 42.4 μ L for *C. laevis* (SD = 13.4, range 26–72, $N = 19$).

Pollinator constancy

Females of the euglossine bee *Euglossa imperialis* Cockerell were the only visitors to flowers of *Costus allenii* and *C. laevis*. Direct observation of bees foraging in a mixed-species patch indicated that individuals were not constant to one or the other plant species (Table 2). Of the 128 foraging bouts with more than one flower visited, 50% were “mixed,” i.e., included both *C. allenii* and *C. laevis*. The frequency of mixed bouts increased steadily from 13% of all bouts with two flowers visited, to 100% of all bouts with seven flowers visited (Table 2). In only one of 128 bouts were more flowers visited than were available from the least abundant species, so mixed bouts were not due to low flower availability relative to flowers visited. In addition, nearest neighbors were always conspecifics at this site, so interspecific pollinator movements did not simply result from the lack of spatial segregation between plant species. Thus, the high proportion of mixed bouts clearly indicates nonspecific pollinator foraging.

General data concerning flower abundance and pollinator visitation in the observation patch are given in Table 3. The mean number of flowers available per day was seven (range 5–10) for *C. laevis*, and six (range 4–7) for *C. allenii* (Table 3). Total flower number in the patch ranged from 12 to 17. On five of the seven observation days, *C. allenii* received significantly more visits than expected, based on the relative abundance of *C. allenii* and *C. laevis* flowers (Table 3). However, the differential visitation to *C. allenii* was not extreme; the ratio of percent *C. allenii* flowers visited/percent *C. allenii* flowers available averaged only 1.4 (range 1.1–1.8).

The extensive interspecific pollen movement suggested from observations of individual pollinators (Table 2) was supported by results of the paint-movement experiment (Table 4). A total of 19 inflorescences of *Costus allenii* and 23 of *C. laevis* was used to monitor the pollinator-mediated transfer of paint during a 5-d period. The spatial distribution and abundance of these plants were virtually identical to those of the total population. Observation of foraging bees on paint-marked flowers indicated that paint and pollen were deposited on a dorsal plate of the thorax (scutum), and the pollen of both species is carried in exactly the same location. Of the 76 flowers of *C. allenii* and *C. laevis* checked during the study, 74 (97%) had

TABLE 4. Interspecific pollinator movements between *Costus allenii* and *C. laevis*, as indicated by the transfer of powdered paint from “marked” flowers of one species to unmarked flowers of the other. Numbers in parentheses give number of inflorescences.

Date	Shannon Ravine			Balboa Ravine		
	No. <i>C. allenii</i> marked	No. <i>C. laevis</i> checked	No. <i>C. laevis</i> with paint	No. <i>C. laevis</i> marked	No. <i>C. allenii</i> checked	No. <i>C. allenii</i> with paint
7 Jul	7	8	7	13	8 (7)	8 (7)
8 Jul	13 (12)	8 (7)	8 (7)	17 (15)	7	7
9 Jul	9	7	6	12	7	7
10 Jul	9	7	7	16 (15)	7 (6)	7 (6)
11 Jul	5	9 (8)	9 (8)	11	8 (7)	8 (7)
Totals	43 (42)	39 (37)	37 (35)	68 (66)	37 (34)	37 (34)
Percent interspecific transfer			95			100

TABLE 5. Spatial association between *Costus allenii* and *C. laevis* on Barro Colorado Island, Panama. $\chi^2_c = 46.2$, $P < .001$ (calculations follow Pielou 1974).

		Nearest neighbor		Total
		<i>C. allenii</i>	<i>C. laevis</i>	
Base plant	<i>C. allenii</i>	41	11	52
	<i>C. laevis</i>	7	50	57
	Total	48	61	109

paint deposited on their stigmas, indicating consistent interspecific pollinator movement (Table 4). These data clearly indicate that *Costus allenii* and *C. laevis* regularly exchange pollen. Despite the proximity of the two study ravines (≈ 400 m), no paint was moved between sites.

Spatial distribution

Flowering stems of *Costus allenii* and *C. laevis* were significantly segregated ($P < .001$), as determined by calculating an adjusted chi-square, χ^2_c (Pielou 1974), on a 2×2 table of nearest-neighbor identities (Table 5). For *C. allenii*, 27% of the nearest flowering inflorescences were *C. laevis*, but only 14% of the nearest neighbors to *C. laevis* were *C. allenii*. The frequency distributions of conspecific distances for *C. allenii* and *C. laevis* were very similar, with 62% of all *C. allenii* and 58% of all *C. laevis* within 2 m of a conspecific (Fig. 3). In contrast, only 5% of all interspecific distances fall within this range. Despite the spatial segregation between species (Table 5), 65% of all interspecific distances ($N = 109$) were ≤ 30 m (Fig. 3). Thus, the segregation of *C. allenii* and *C. laevis* is on a relatively small scale, far smaller than the foraging range of female euglossine bees (D. Schemske, *personal observation*).

Fruit production

The mean percent of flowers producing fruit per inflorescence was 75 for *Costus allenii* and 58 for *C.*

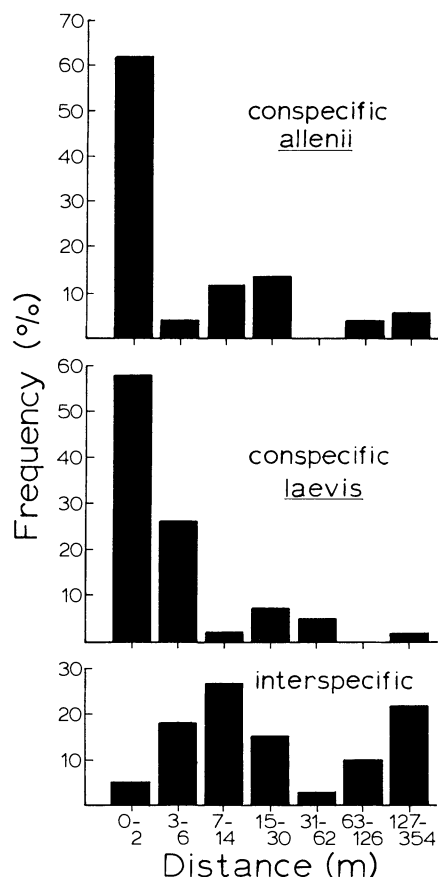


FIG. 3. Frequency distribution of minimum distance between conspecific inflorescences for *Costus allenii* (top, $N = 52$ inflorescences), and *C. laevis* (middle, $N = 57$ inflorescences), and the minimum interspecific distance between all *C. allenii* and *C. laevis* (bottom, $N = 109$ inflorescences).

laevis. There was no seasonal variation in the fruiting success of either species, despite the fact that late-flowering inflorescences of *C. laevis* overlapped broadly with the main flowering period of *C. allenii*, while early flowering *C. laevis* did not (Fig. 1). Thus,

TABLE 6. Seed production per fruit by selfing, outcrossing, and hybridization in *Costus allenii*, *C. laevis*, and *C. guanaiensis*. The first number in parentheses gives the mean number of abortions per fruit, the second number gives sample size, i.e., number of flowers pollinated.

Crosses	Seed parents		
	<i>C. allenii</i> $\bar{X} \pm 2$ SE	<i>C. laevis</i> $\bar{X} \pm 2$ SE	<i>C. guanaiensis</i> $\bar{X} \pm 2$ SE
Intraspecific			
Selfed	34.3 \pm 3.2 (16.2, 42)	36.1 \pm 7.4 (0.3, 43)	66.8 \pm 19.5 (0.8, 24)
Outcrossed	50.4 \pm 5.4 (0.3, 39)	53.4 \pm 4.4 (0.1, 48)	109.8 \pm 12.4 (1.7, 29)
Hybrid			
Pollen parents			
<i>C. allenii</i>	...	0.8 \pm 0.6 (0.0, 53)	35.3 \pm 11.3 (0.6, 33)
<i>C. laevis</i>	2.9 \pm 1.9 (1.1, 40)	...	55.3 \pm 10.2 (1.2, 31)
<i>C. guanaiensis</i>	26.6 \pm 4.7 (1.2, 38)	2.4 \pm 1.9 (0.0, 29)	...

the lower fruiting success of *C. laevis* (see above) is not a direct result of interactions with *C. allenii*, e.g., competition for pollinators. Although weevils caused most fruiting failures in both species, inflorescences with no apparent weevil damage often had some flowers that failed to produce fruit. Because abortion was rarely observed, this suggests that fruiting is occasionally pollinator limited, but the high rate of weevil predation prevented experimental pollinations to test this hypothesis. Because the ovaries of weevil-free, unpollinated flowers appeared identical to those of weevil-destroyed flowers (with no damage to bracts), I could not determine the frequency of fruiting failure due to lack of pollination.

Hand-pollinations: selfing, outcrossing, and hybridization

Interspecific pollinations between *Costus allenii* and *C. laevis* produced 2.9 and 0.8 seeds per fruit, with *C. allenii* as seed and pollen parent, respectively, while both species produced ≈ 35 seeds per fruit when selfed and 50 seeds per fruit when outcrossed (Table 6). For *Costus allenii* \times *C. laevis* crosses, the ratio of hybrid/selfed seeds per fruit was $< .08$. In contrast, with *Costus guanaiensis* as the seed parent, the ratio of hybrid:selfed seeds per fruit was 0.53 for crosses with *C. allenii* and 0.83 for crosses with *C. laevis*. Thus, there are strong barriers to interspecific hybridization between *C. allenii* and *C. laevis*, but *C. guanaiensis* produces abundant hybrid seed when hand-pollinated (Table 6).

Interspecific incompatibility in *Costus allenii* was highly specific. Although this species rejected *C. laevis* pollen (less than three seeds per fruit), it produced abundant seed (27 seeds per fruit) when pollinated by *C. guanaiensis* (Table 6). Conversely, *Costus laevis* rejected *C. allenii* and *C. guanaiensis* pollen, with less than three seeds per fruit in hybrid crosses (Table 6). In all hybrid crosses, less than two seeds were aborted per fruit.

For all three species tested, mean seed production per fruit by outcrossing was significantly greater ($P < .001$; t test) than that from selfing (Table 6). The ratio of selfed:outcrossed seeds per fruit was very constant across species, 0.68 for *C. allenii* and *C. laevis*, and 0.61 for *C. guanaiensis*. Control flowers without hand-pollination produced no seed ($N = 43$ for *C. allenii*, 36 for *C. laevis*, and 37 for *C. guanaiensis*); thus all species are self-compatible but not self-pollinating. The lower seed production through selfing is apparently due to abortion of selfed ovules in *C. allenii*, but not in *C. laevis* or *C. guanaiensis* (Table 6).

DISCUSSION

Costus allenii and *C. laevis* are remarkably similar in habitat, floral morphology, flowering time, and nectar production, and use the same nonselective polli-

nator. However, the high probability of interspecific pollination that results from floral similarity does not influence pollination effectiveness: fruiting failure was primarily a result of weevil predation, and both species have strong barriers to hybridization. In contrast to these observations, it is commonly concluded that competition for pollinators lowers reproductive success and selects for plant characteristics that reduce the extent of pollinator sharing (Levin and Anderson 1970). The alternate view, that floral similarity and pollinator sharing may be adaptive in some circumstances, has received little attention. Brown and Brown (1979) suggest that coexisting, hummingbird-pollinated plants in Arizona have converged in floral characteristics to share nonselective hummingbirds. Similarly, I suggest that pollinator sharing in *Costus allenii* and *C. laevis* is advantageous. In support of the convergence hypothesis, I first reject the hypothesis that these species partition pollinators, then discuss the evolutionary implications of pollinator sharing in this system.

Rejection of the partitioning hypotheses

Flowering time.—The high overlap in flowering time between *Costus allenii* and *C. laevis* (Fig. 1) does not support the hypothesis that these plant species partition pollinators by temporal segregation of flowering, as suggested for other plant communities (Pojar 1974, Frankie 1975, Stiles 1977, Waser 1978). In addition, the marked similarity in nectar production patterns (Fig. 2) does not provide an opportunity for diurnal partitioning of pollinators, as observed for sympatric, butterfly-pollinated *Anguria* (Gilbert 1975). On the average, *C. laevis* inflorescences flower $1.9\times$ longer than *C. allenii* but begin flowering earlier. The flowering densities of *C. allenii* and *C. laevis* were very different early in the season but virtually identical in the latter half (Fig. 1). Heinrich (1975) observed a similar flowering pattern in a model-mimicry system, where a late-flowering, nectarless species mimics the flowers of an early-flowering, nectar-producing species. Because *C. allenii* and *C. laevis* secrete the same amount of nectar, at virtually the same rate (Fig. 2), both species may function as Müllerian mimics with respect to food rewards.

Pollinators.—Both *Costus allenii* and *C. laevis* were visited exclusively by females of the bee *Euglossa imperialis*. Direct observation of individual bees in mixed-species patches indicated a very high rate of interspecific pollinations (Table 2). These results were supported by an experimental analysis of pollinator constancy, which demonstrated extensive interspecific pollen transfer (Table 4). Because anther position is identical in each species, there is no spatial segregation of pollen loads on individual pollinators, as observed in other systems (Macior 1971, Brown and Brown 1979). These data clearly indicate that *Costus*

allenii and *C. laevis* do not partition pollinators by attracting different pollinator species or by flower constancy of individual pollinators.

Floral convergence and pollinator sharing

For nectar-producing plants, floral convergence increases "effective" flower density and nectar supplies. Pollinator sharing by convergent species probably increases the probability and/or rate of pollinator visitation. I suggest that convergence may be particularly important in plant species that flower at low densities, such that nectar rewards at the population and individual levels are insufficient to attract and sustain an adequate pollinator pool.

Costus allenii and *C. laevis* are clearly low-density species. On the 1-km² study area, I observed a total of only 52 *C. allenii* and 57 *C. laevis* inflorescences. The greatest density was reached in mid-July, when 26 *C. allenii* and 35 *C. laevis* inflorescences were in flower (Fig. 1). Because each inflorescence produces only a single flower per day (rarely two), flower density is always low. Although 60% of the nearest conspecific distances were ≤ 2 m for both species (Fig. 3), nearest neighbors were usually from the same clone, and clones rarely produced more than three inflorescences. The small clone size and irregular distribution of conspecifics in suitable habitats result in very few local "patches" of increased density. Flowering *Costus allenii* and *C. laevis* were equally abundant after the time of peak flowering (Fig. 1), thus floral convergence doubled effective flower density at this time. Convergence in flowering time may also serve to satiate floral predators but there was no evidence that the timing of flower production influenced the probability of predation in these species.

Weevil predation of *Costus allenii* and *C. laevis* further reduces flower density and dramatically increases the temporal variation in flower production per inflorescence. I suggest that predator-mediated depression of flower density may decrease the regularity of visitation by the bee *Euglossa imperialis*, the pollinator of both *Costus* species. The foraging behavior of female *E. imperialis*, a member of the tribe Euglossini (subfamily Bombinae), may render it particularly sensitive to short-term changes in flower density. Euglossine bees often forage along a consistent route, visiting the same plants on a day-to-day basis (D. Schemske, *personal observation*). This "traplining" behavior (Janzen 1971) is commonly observed in pollination systems where low-density plant species like *Costus* produce few flowers per day for an extended period. Interplant distances are often large in traplined plant species, thus pollinators may delete nonproductive plants or habitats from their traplines to decrease foraging costs. The high rate of weevil predation on *Costus* inflorescences (31% of *C. allenii*; 60% of *C. laevis*) probably exerts strong selection on these species to

increase "effective" flower density, thus reducing the tendency for pollinators to alter trapline composition. In this context, floral convergence between *C. allenii* and *C. laevis*, and pollinator sharing, may maintain pollinator traplines despite periodic flowering failure.

Hybridization.—The high rate of interspecific pollen transfer between these two sympatric congeners may select for strong barriers to hybridization. Results from extensive hand-pollinations of *Costus allenii* and *C. laevis* support this hypothesis (Table 6). In contrast to the hybridization barriers observed between these two species, *C. guanaiensis*, a species of treefalls and forest edge, produces abundant seed from interspecific crosses (Table 6). These data suggest that hybridization barriers may be influenced by the frequency of interspecific pollinations (Grant 1966). If hybrids have reduced fitness, those species that regularly exchange pollen will be under stronger selective pressure to develop hybridization barriers than those that do not. *C. guanaiensis* is ecologically segregated from *C. allenii* and *C. laevis*, thus interspecific pollinations with *C. guanaiensis* are rare. In contrast, *C. allenii* and *C. laevis* regularly exchange pollen, and have strong barriers to hybridization.

Evolutionary relationships.—The hypothesis that the floral similarity of *Costus allenii* and *C. laevis* is an evolutionary response to selection for pollinator sharing, rather than a consequence of common ancestry, can be supported on several levels. First, the tremendous diversity of floral colors and morphologies in the genus *Costus*, including both hummingbird- and bee-pollinated species (Maas 1972), indicates that the evolutionary history of the group is characterized by divergence in floral characters. Thus, there has been considerable floristic evolution. Second, although phylogenetic histories are unknown, it is unlikely that the unusual similarity between *Costus allenii* and *C. laevis* follows from recent sympatry. This explanation would require convergent evolution of floral characters during isolation and insufficient time and/or weak selection for floral divergence. The marked differences in leaf size, shape, and pubescence between *Costus allenii* and *C. laevis* indicate that there has been evolution of vegetative characters, so time is probably not a factor. We expect that floral characters could change as well, particularly given the marked floristic evolution in the genus, as noted above. The close floristic similarity of *Costus allenii* and *C. laevis* suggests that selection for floral similarity and pollinator sharing has been a major evolutionary force.

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