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Morphology and Pollination Biology of an Intersectional Hybrid of *Costus* (Costaceae)

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ABSTRACT. An intersectional hybridization event between hummingbird-pollinated *Costus pulverulentus* (sect. *Ornithophilus*) and large bee-pollinated *C. guanaiensis* var. *macrostrobilus* (sect. *Costus*) in Belize, Central America, is documented by analyses of morphology and pollination biology. Morphologically the hybrid is intermediate between the parental species and retains floral characteristics adaptive to both hummingbird and bee pollination. Nectar secretion rate and sugar concentration but not sucrose:hexose ratio in the hybrid are intermediate between those of the parental species. The hybridization event probably arose by breakdown of strict hummingbird pollination in *Costus pulverulentus*.

Costus L. (Costaceae) occurs in moist habitats in the Neotropics, and is characterized by a spirally arranged phyllotaxy and showy terminal inflorescence. *Costus* is often found associated with species of *Calathea*, *Canna*, *Heliconia*, and *Renealmia* along the banks of rivers and streams and more disturbed habitats like forest trails, secondary forests, lightgaps, roadsides, and plantations.

In his earlier monograph of the Neotropical Costoideae, Maas (1972) divided the genus *Costus* into two subgenera: *Cadalvena*, represented by seven species restricted to South America; and *Costus*, consisting of 40 species ranging from northern Central America to South America. In a more recent treatment (Maas 1977), two presumably natural sections based on labellum characteristics are recognized in subg. *Costus*. Section *Costus* is characterized by bee-pollinated flowers; the labellum is white to yellow, and has a short broad tube and an open exposed limb or landing platform often striped with red or purple. Section *Ornithophilus* is characterized by hummingbird-pollinated flowers; the labellum is yellow, orange, or red, and has a narrow, thick-walled, fleshy tube barely exceeding the corolla. Several species, most notably *C. malortieanus* Wendl. and closely related *C. pictus* D. Don, appear to be intermediate in character between the two sections. According to F. G. Stiles (in Maas 1977), *C. malortieanus* represents a transition between bee-pollinated and hummingbird-pollinated species because it is visited and pollinated by both euglossine bees and hummingbirds.

Many species of *Costus* are sympatric and are visited by the same pollinators (Schemske 1981; pers. obs.). Hybridization has been described for species of *Costus* within each section (Maas 1972, 1977) but to date there are no records of hybridization between bee-pollinated and hummingbird-pollinated species (P. J. M. Maas pers. comm.). This study presents evidence for intersectional hybridization involving two *Costus* species, one adapted to bee-pollination and the other to hummingbird-pollination.

In 1976, a new *Costus* was discovered on the road to San Jose, 2.5 kilometers north of the junction with the San Antonio Road, Toledo District, Belize. A single population of nine plants was found growing at the road's edge for 50 meters. This site in moist tropical forest of the Mayan mountains at elevations of 200–250 meters is an area of active road construction and slash/burn agriculture.

The two suspected parental species occur within 100 meters of the putative hybrid population. *Costus guanaiensis* var. *macrostrobilus* (Schumann) Maas (sect. *Costus*), a robust species attaining heights over 3.5 meters, is found in more exposed and drier roadside habitats. *Costus pulverulentus* C. B. Presl (sect. *Ornithophilus*) is found in shaded and usually wetter roadside habitats than either *C. guanaiensis* var. *macro-*

TABLE 1. Morphological characters of *Costus guanaiensis, C. pulverulentus,* and the putative hybrid used in constructing Andersonian hybrid indices and Euclidean distance coefficients.

1. Sheath diameter (mm). 2. Ligule length (mm). 3. Petiole length (mm). 4. Leaf length (cm). 5. Leaf width (cm). 6. Inflorescence length (cm). 7. Inflorescence width (cm). 8. Plant height (cm). 9. Bract color. 10. Bract length (mm). 11. Bract width (mm). 12. Bract appendage length (mm). 13. Bract appendage width (mm). 14. Dilacerating bract fibers, presence or absence. 15. Bracteole length (mm). 16. Calyx length (mm). 17. Calyx width (mm). 18. Calyx lobe length (mm). 19. Corolla color. 20. Corolla tube length (mm). 21. Corolla tube diameter (mm). 22. Corolla lobe length (mm). 23. Corolla lobe width (mm). 24. Stamen length (mm). 25. Stamen width (mm). 26. Anther length (mm). 27. Style length (mm).

strobilus (hereafter simply referred to as *C. guanaiensis*) or the putative hybrid and forms large populations throughout the area. All three *Costus* populations flower during the rainy season from mid-June through late-November. *Costus scaber* Ruis & Pavon (sect. *Ornithophilus*) is the only other *Costus* species in the surrounding region, but it was not found in the hybrid zone. Based on floral and vegetative characteristics it was evident that *C. scaber* could not be a parental species of the putative hybrid.

METHODS

Morphology, pollen viability, chromosome number, and pollination biology were examined in the putative hybrid and suspected parental species to verify the occurrence of intersectional hybridization. Vegetative characteristics were obtained from dried specimens collected in the study area and surrounding region of Toledo District. Voucher specimens are deposited in WMU. Floral characteristics were obtained from material preserved in FAA. Twenty-seven morphological characters (table 1) were examined from seven individuals of the putative hybrid, nine individuals of *C. guanaiensis,* and 12 individuals of *C. pulverulentus.*

These characters were used to produce both Andersonian hybrid indices (Anderson 1936) and hybrid indices based on Euclidean distance coefficients (Wells 1980). The hybrid indices were standardized against the mean of character measurements from individuals of *Costus guanaiensis* var. *macrostrobilus* and *C. pulverulentus* located more than five kilometers from the study site. The corresponding mean measurements in the two reference populations were scaled between zero and one with zero representing the measurement of *C. guanaiensis* and one the measurement of *C. pulverulentus.* For each character, individuals of the putative hybrid and suspected parental populations were assigned the value of "0" if the character had a value on the reference scale less than 0.25, the value "0.5" if greater than or equal to 0.25 and less than or equal to 0.75, and the value "1.0" if greater than 0.75. The hybrid index for each individual was obtained by summing these values over all 27 characters.

The Euclidean distance diagram requires that two reference points be formed from character ranges *within* the populations hypothesized to be hybridizing. The reference point assigned to each putative parental population is composed of the set of 27 characters. The value of each character for a reference point is either the maximum or minimum value observed in the population. The maximum is used if the mean of the character is greater than the corresponding mean of the other parental population. The minimum is used if the mean of that particular character is less than the respective mean of the other parental population. The characters for each individual in the putative hybrid population, the suspected parental populations, as well as the two reference points, are then ranged between zero and one (see Wells 1980). The distance of each individual from the reference points is calculated using Euclidean distance equations (see Wells 1980) and plotted onto the distance diagram using a compass and ruler.

Pollen viability was assayed by the double staining technique of Owczaryak (1952). Viable pollen grains were easily identified by the combination of methyl green stained pollen exine and phloxine stained cytoplasm. The viable pollen grains expand and stain with both dyes whereas the aborted pollen grains remain shrunken and take only the methyl green exine stain. At least 500 pollen grains from each of at least four individuals per taxon were scored. Mitotic chromosome counts were made using young root tips pre-soaked in p-dichlo-

TABLE 2. Comparison of select morphological characters of *Costus guanaiensis*, the putative hybrid, and *C. pulverulentus* in Belize.

Character	*C. guanaiensis*	Putative hybrid	*C. pulverulentus*
Bract length/width (mm)	42–55/22–42	41–42/26–32	28–39/19–26
Bract appendage	Present	Present	Absent
Bract color	Green	Yellow-green	Orange-red
Dilacerating bract fibers	Absent	Present	Present
Bracteole length (mm)	25–40	22–27	13–21
Calyx length (mm)	11–17	9.5–16	7.5–10
Floral structure	Large, flaring labellum or "bee landing platform", opening 15–20 mm wide	Tubular labellum, short platform, opening 6–9 mm wide	Narrow tubular labellum, no platform, opening 2–3 mm wide
Floral color	White with pink-red stripes, yellowish white platform	Red, yellowish red platform	Orange-red to red
Floral texture	Thin, membranaceous	Thick, waxy	Thick, waxy
Corolla tube length (mm)	76–78	62–65	40–45
Labellum length (mm)	85–89	63–64	41–45

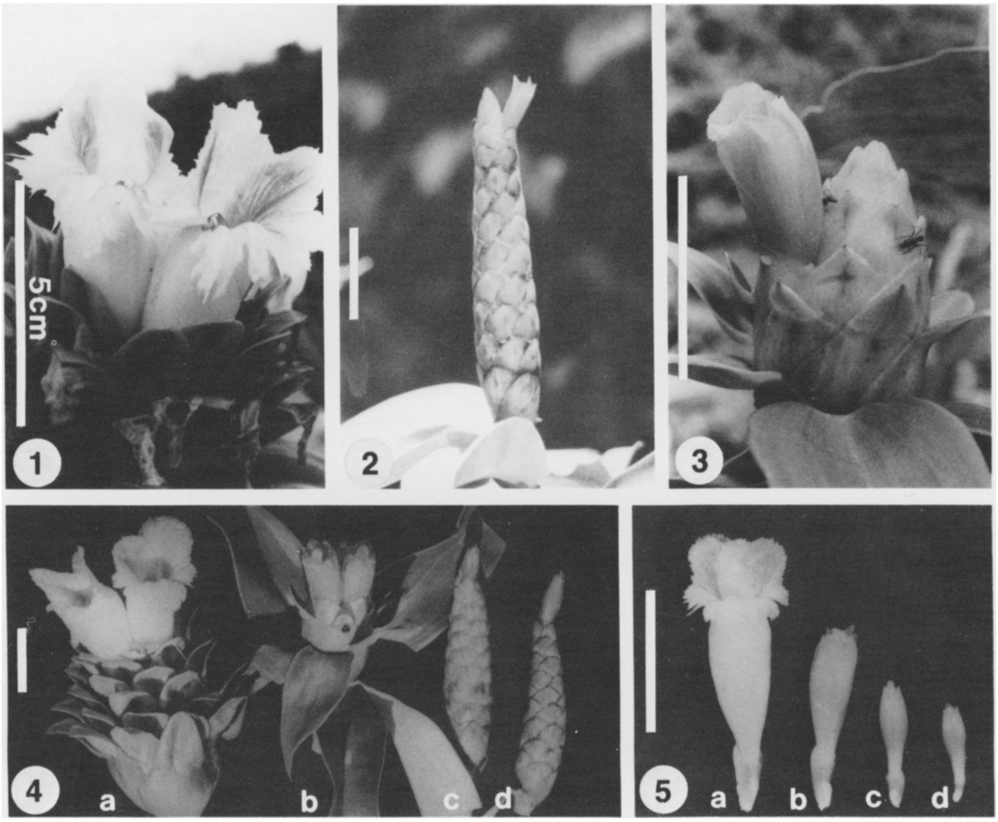
robenzene for nine hours, hydrolyzed in 10% HCl at 60°C for six minutes, and squashed in lacto-propionic orcein.

Nectar secretion patterns were quantified by repeatedly sampling bagged flowers with microcapillary tubes at hourly intervals from dawn (0600 hr) until the flowers either fell from the inflorescence or stopped producing measurable nectar (1500 hr). Nectar volume and nectar concentration (% sucrose equivalents on a weight/total weight basis) were recorded for each flower at each hour interval. Total sugar content (mg sucrose equivalents) was calculated from standard sucrose conversion values (Weast 1974). Records of visitors that used both pollen and nectar resources were made throughout an 8-hour period at each population. Nectar composition (sugars, amino acids, and other organic substances) was kindly determined by I. Baker, University of California, Berkeley, on four individuals of *Costus pulverulentus* and three each of *C. guanaiensis* and the putative hybrid following methods described (Baker and Baker 1976, 1979).

RESULTS

Morphology. Individuals of the new *Costus* population are consistently intermediate between individuals of *C. guanaiensis* and *C. pulverulentus* in both vegetative and floral characteristics (table 2). The putative hybrid has the large, ovoid, and leafy inflorescence and the reflexed bract appendages typical of *C. guanaiensis* and many other species in sect. *Costus* (figs. 1–2, 4–5). The floral structure and color of the putative hybrid, however, is more reminiscent of the red, narrow, and thick tubular flowers of *C. pulverulentus* and other members of hummingbird-pollinated sect. *Ornithophilus* (figs. 2–5). The presence of a wide floral opening and a small, yellowish "landing platform" (labellum lobe) indicate that the putative hybrid has retained some of the typical bee-pollination characters of sect. *Costus*, and *C. guanaiensis* in particular. The presence of dilacerating fibers on exposed bract margins of the putative hybrid, a trait found exclusively in *C. pulverulentus* (Maas 1972), further documents the parental influence of this species and excludes *C. scaber* of the same section from being considered one of the parental species.

Andersonian hybrid indices of individuals from the study area populations of *Costus guanaiensis*, *C. pulverulentus*, and the putative hybrid are depicted in figure 6. Based on the 27 characters used to generate the indices, the putative hybrid individuals are clearly intermediate between individuals of the two putative parental species. The sample mean of the indices for individuals of the putative hybrid population (10.1) is not significantly different from the expected mean (13.5) nor the actual mean (13.9) of the indices between the putative parental species (two-tailed *t*-test, $P > 0.05$ in both cases).



FIGS. 1–5. Flowers and inflorescences of *Costus* populations in and around the putative hybrid zone in Belize. 1. *C. guanaiensis.* 2. *C. pulverulentus.* 3. The putative hybrid. 4. Comparison of inflorescences. a. *C. guanaiensis.* b. The putative hybrid. c. *C. scaber.* d. *C. pulverulentus.* 5. Comparison of perianth. a. *C. guanaiensis.* b. The putative hybrid. c. *C. pulverulentus.* d. *C. scaber.*

Morphological intermediacy of the putative hybrid is shown in a Euclidean distance diagram (fig. 7). The central position of points representing individuals from the putative hybrid population without spreading between the putative parental positions suggest that the new *Costus* population is a simple F_1 hybrid.

A problem inherent in any morphological analysis of a presumed hybrid and its parental species is that morphological intermediacy is not a necessary outcome in the hybrid depending on the addictive effects of polygenic inheritance. A formal analysis of the morphological variation encountered in the putative hybrid and its parental species would require segregation tests and backcrosses.

Pollen viability. Pollen viability is 97% for *Costus pulverulentus* (number of individuals sampled $[N_{\mathrm{I}}] = 5$, total number of pollen grains examined $[N_{\mathrm{P}}] = 2017$). Pollen viability was 85% for *C. guanaiensis* ($N_{\mathrm{I}} = 6$, $N_{\mathrm{P}} = 2310$) and 86% for the putative hybrid ($N_{\mathrm{I}} = 4$, $N_{\mathrm{P}} = 4127$).

Chromosome number. Mitotic chromosome numbers for *Costus guanaiensis, C. pulverulentus,* and their putative hybrid are the same ($2n = 18$). These counts are the same as earlier mitotic counts of the two putative parental species (Maas 1972).

Pollination biology. The three *Costus* populations are visited by an array of fauna species (table 3). *Costus guanaiensis* is pollinated exclusively by large, pollen and nectar collecting female euglossine bees (*Eulaema* sp.). Pollen collecting was observed only in the early morning (0700–0900 hr) with nectar collecting the dominant activity when the available pollen was depleted. Visits by this species for the nectar reward were consistently observed at about 20-

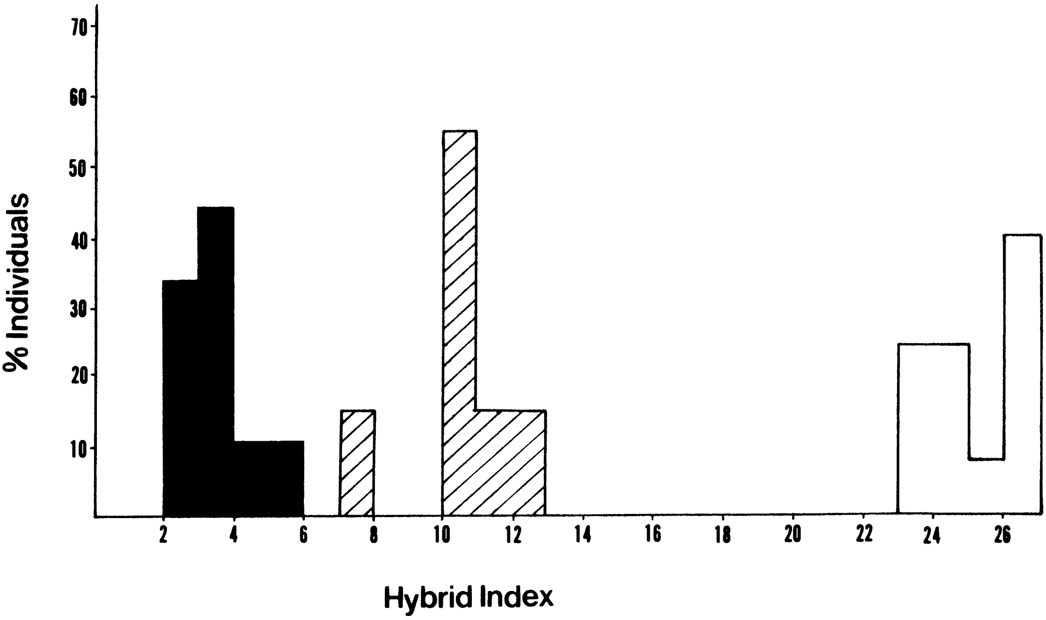


FIG. 6. Histogram of Andersonian hybrid indices for *Costus guanaiensis* (black, $N = 9$), the putative hybrid (striped, $N = 7$), and *C. pulverulentus* (white, $N = 12$) based on 27 morphological characters.

minute intervals. When entering the throat of the flower, the bees contact the single anther attached near the apex of the petaloid stamen and the stigma positioned just above the anther. Pollen deposition on the bee occurs on the dorsal surface of the abdomen and thorax. Individuals of small, brilliant green euglossine bees (*Euglossa* spp.) were also observed visiting *C. guanaiensis*. These euglossine bees are ineffective pollinators of *C. guanaiensis* because they do not contact either the anther or stigma when entering the throat of the flower.

Costus pulverulentus is visited by several pollen vectors but most effectively by both hermit and non-hermit hummingbirds. Pollen deposition occurs on either the upper portions of the bill or on the facial feathers. Regular visits to these narrow-tubed flowers by the *Eulaema* sp. that visits *C. guanaiensis* were also observed. In one mixed patch of *C. pulverulentus* and *C. guanaiensis* outside the hybrid zone, individual bees visited both species on the same foraging bout. Non-hermit hummingbirds on the plants of *C. pulverulentus* routinely would chase away the intruding bees. The bees are too large to enter the narrow-tubed flowers of *C. pulverulentus* but would cling to the flower apex in the vertical position. The long-tongued *Eulaema* sp. apparently can reach the nectar at the base of the corolla because it can maintain this position for several seconds. Stamen contact occurs during these visits but pollen deposition is confined to the head region. Reciprocal pollen transfer by *Eulaema* sp. between *C. pulverulentus* and *C. guanaiensis* is possible but probably very rare in mixed populations.

The putative hybrid is visited by both the *Eulaema* sp. that regularly visit *Costus guanaiensis* and the hermit hummingbirds observed on *C. pulverulentus*. The floral tube of the putative hybrid flower is intermediate in size allowing for anther and stigma contact by both types of visitors.

Nectar secretion patterns in *Costus guanaiensis* and *C. pulverulentus* are somewhat similar with a mid-morning decline in nectar volume and a subsequent peak just prior to noon (fig. 8). *Costus guanaiensis*, however, produces larger hourly volumes ($\bar{x} = 16.6$ μl vs. $\bar{x} = 5.5$ μl) of more concentrated nectar ($\bar{x} = 26.5\%$ vs. $\bar{x} = 16.9\%$) than *C. pulverulentus*. The putative hybrid is intermediate in nectar secretion averaging 12.4 μl hr^{-1} of 19.7% nectar. Nectar concentration generally decreases during the day in all three

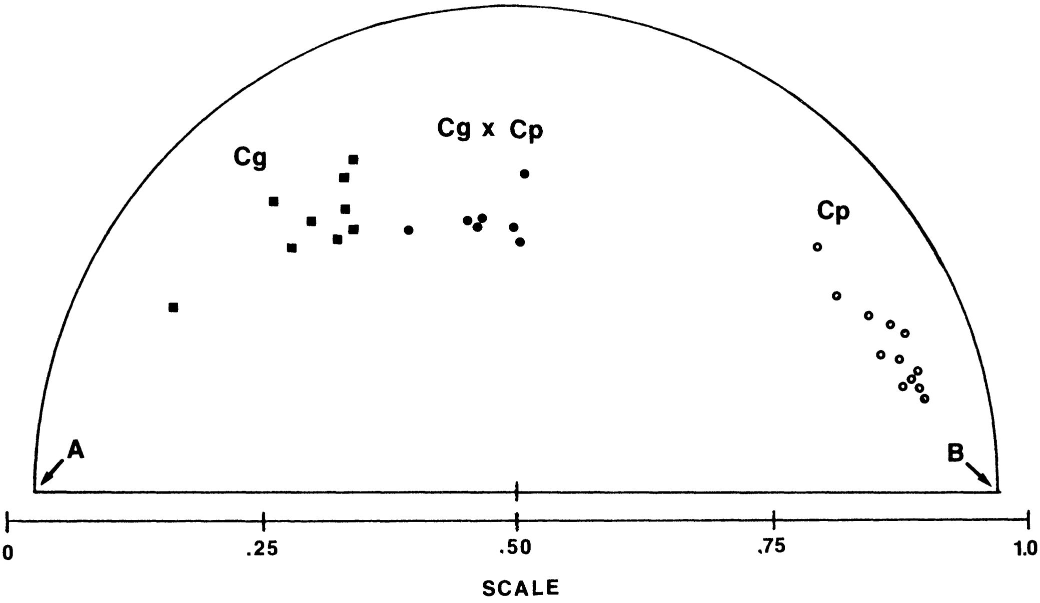


FIG. 7. Euclidean distance diagram of *Costus guanaiensis* (Cg, $N = 9$), the putative hybrid (Cg × Cp, $N = 7$), and *C. pulverulentus* (Cp, $N = 12$) based on 27 morphological characters. A and B are reference points for *C. guanaiensis* and *C. pulverulentus* generated by the algorithm.

populations. This decrease in nectar concentration observed is dramatic in *C. guanaiensis* and the putative hybrid because their flowers begin to abscise earlier in the afternoon.

Because environmental conditions inside and outside the flower can influence the trade-off between nectar concentration and volume (Corbet et al. 1979), the hourly nectar energy expenditures in mg sucrose equivalents (Bolten et al. 1979) were calculated for the three *Costus* populations (fig. 9). *Costus guanaiensis*, the putative hybrid, and *C. pulverulentus* expended 4.6, 2.5, and 0.9 mg sucrose equivalents per hour, respectively. Despite the wide fluctuations in nectar volume and concentration, individuals of all three *Costus* populations exhibit significantly linear cumulative energy expenditures in producing floral nectar, with the putative hybrid intermediate between the two putative parental species.

Sugars detected in the floral nectar include glucose and fructose (monosaccharides), sucrose (disaccharide), and melezitose (trisaccharide) (table 4). Nectar from each population was sucrose-dominant. The hummingbird-visited *Costus pulverulentus* has a lower disaccharide:monosaccharide ratio (2.2:1) than euglossine bee-visited *C. guanaiensis* (3.9:1). Surprisingly, the putative hybrid has the highest ratio (4.8:1). Proportional to this increase in the disaccharide:monosaccharide ratio is an in-

TABLE 3. Observed visitors to flowers of *Costus guanaiensis*, the putative hybrid, and *C. pulverulentus*. P+ indicates effective pollinator; P− indicates visitor ineffective in pollination.

Visitor	*C. guanaiensis*	*C. guanaiensis* × *C. pulverulentus*	*C. pulverulentus*
Amazilia tzacatl (rufous-tailed hummingbird)		P+	P+
A. candida (white bellied emerald)			P+
Phaethornis superciliosus (long-tailed hermit)		P+	P+
P. longuemareus (little hermit)			P+
Eulaema sp. (large euglossine bee)	P+	P+	P− (?)
Euglossa spp. (small, metallic euglossine bees)	P−		

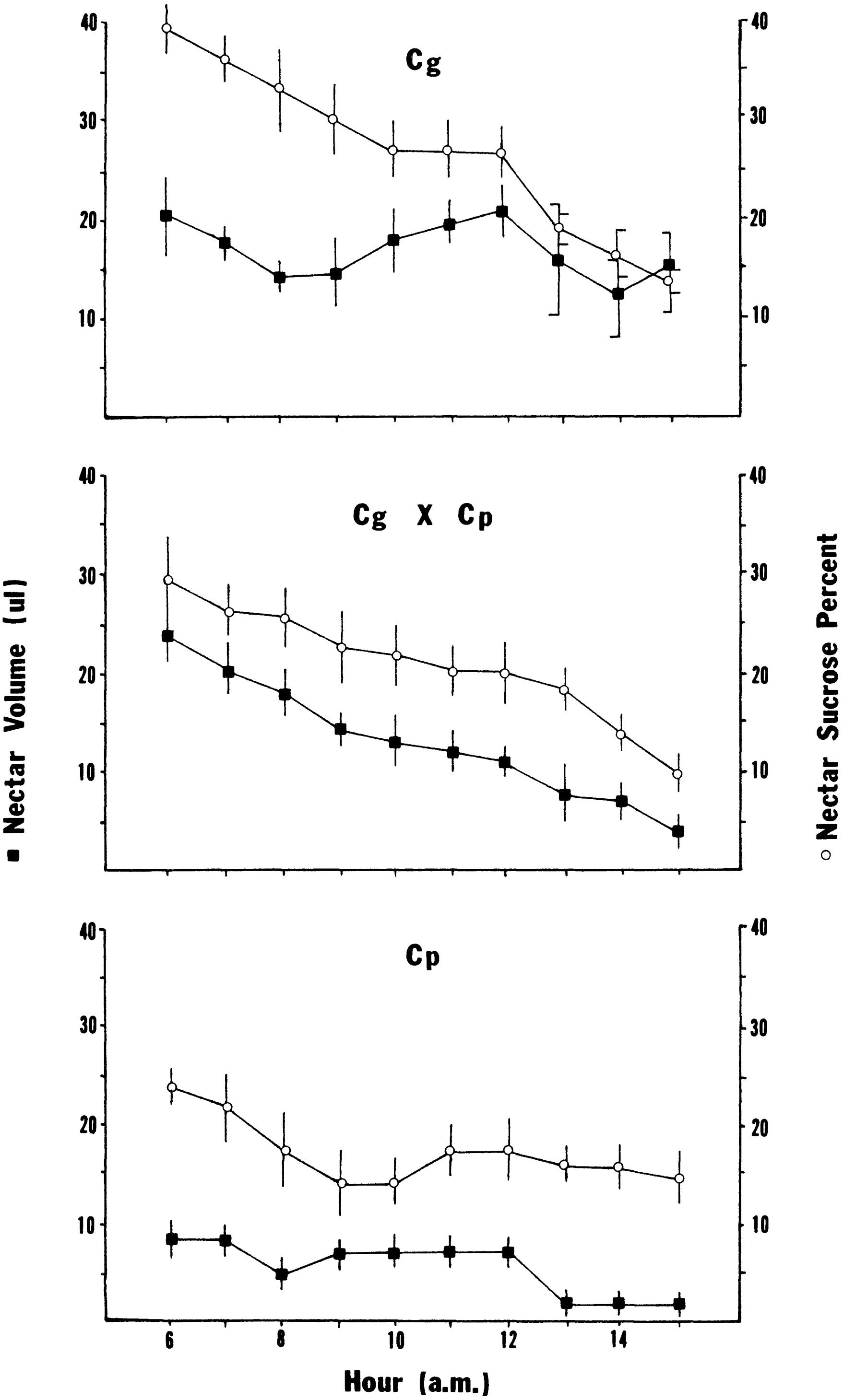


FIG. 8. Average hourly nectar production in *Costus guanaiensis* (Cg, $N = 4$), the putative hybrid (Cg × Cp, $N = 4$), and *C. pulverulentus* (Cp, $N = 6$). Bars represent 1 standard error.

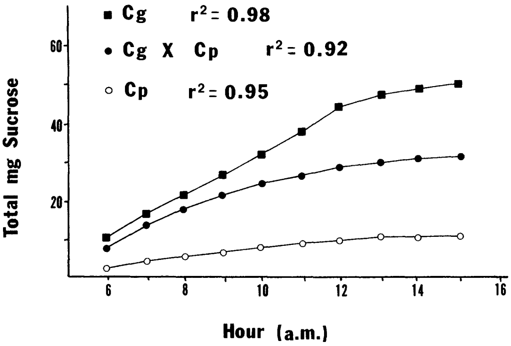


FIG. 9. Cumulative production of hourly sucrose equivalents in floral nectar of *Costus guanaiensis* (Cg, *N* = 4), the putative hybrid (Cg × Cp, *N* = 4), and *C. pulverulentus* (Cp, *N* = 6).

crease in the presence of the trisaccharide melezitose.

Amino acid composition of floral nectar was similar in *Costus guanaiensis, C. pulverulentus,* and the putative hybrid. Trace amounts of alanine, glutamine, glycine, isoleucine, leucine, proline, and valine were present in the nectars. Serine was the most abundant amino acid present with values of 3–4 on a scale of 1 to 5 with 5 representing the largest value. Proteins, phenols, alkaloids, and lipids were all absent from the nectar.

DISCUSSION

Interspecific competition for pollinators and the subsequent selection for reducing this competition have often been cited as evolutionary forces leading to the diversification of flowering times (Gentry 1974; Stiles 1977), flowering morphologies (Schemske 1976; Stiles 1975), and flower color (Jones 1978) among congeneric and sympatric species in the Neotropics. The diversity of floral morphologies and colors in both the bee- (sect. *Costus*) and hummingbird-pollinated (sect. *Ornithophilus*) species indicates that floral evolution has been important in the diversification of *Costus* (Maas 1972, 1977; Schemske 1981).

Whether this diversification within *Costus* has been accompanied by the formation of internal genetic reproductive barriers is poorly known. The more than occasional occurrence of natural intrasectional hybrids (Maas 1972, 1977) might suggest that post-pollination barriers within each section are weak. The only known instance where strong hybridization barriers have been shown to be important within a section of *Costus* is between *C. allenii* Maas and *C. laevis* Ruiz & Pavón (both of sect. *Costus*) (Schemske 1981). These two unrelated species apparently have converged in floral characteristics to share the same pollinator, with selection operating in the formation or strengthening of internal barriers to prevent hybridization (Schemske 1981). *Costus guanaiensis* of the same section, however, has high seed set when pollinated by either of these species. Despite the occurrence of intrasectional hybrids, hybridization in *Costus* must be considered rare when the frequency of associations and transfer of pollen between sympatric species is taken into account.

Even less is known about reproductive barriers between the two sections in *Costus.* To date no intersectional hybrids have been reported. This comparative study of the morphology and pollination biology of the new *Costus* population in Belize with two sympatric species strongly supports the intersectional hybrid origin of the new *Costus* population. The intersectional origin of the hybrid is best seen in features of the inflorescence and flower. The hybrid has acquired the squat, appendaged inflorescence of *C. guanaiensis* but the yellowish white and shortly appendaged bracts approach those of *C. pulverulentus.* The flower of the hybrid has the red tubular corolla of hummingbird-pollinated *C. pulverulentus* but the yellowish "landing platform" and large diameter opening of bee-pollinated *C. guanaiensis.*

The average hourly volume (16.6 μl) and average concentration (26.5%) of *Costus guanaiensis* nectar is within the range of nectar production for flowers pollinated by long-tongued bees (Baker and Baker 1975); the smaller hourly volume (5.5 μl) of less concentrated (16.9%) nectar in *C. pulverulentus* is within the range of nectar production for flowers pollinated by hummingbirds (Baker 1975; Bolten and Feinsinger 1978). It is not surprising that both hummingbirds and large bees visit the hybrid flower because it is structurally intermediate between the classical bee and hummingbird flowers and exhibits an intermediacy in nectar production.

The sucrose-dominant nectar of the hybrid and parental *Costus* populations is concordant with results from previous surveys (Baker and Baker 1982, 1983) and pollinator preference

TABLE 4. Sugar composition in floral nectar of *Costus guanaiensis*, the putative hybrid, and *C. pulverulentus*.

Taxon	*N*	Percentage (based on weight)				Ratio of sucrose : glucose + fructose
		Glucose	Fructose	Sucrose	Melezitose	
C. guanaiensis	3	0.081	0.121	0.794	0.004	3.9:1
C. guanaiensis × *C. pulverulentus*	3	0.095	0.075	0.823	0.007	4.8:1
C. pulverulentus	4	0.155	0.156	0.688	0.001	2.2:1

(Stiles 1976) of hummingbird and long-tongued bee-visited flowers. It is interesting that the nectar available to the large *Eulaema* sp. bees is more sucrose-dominant (3.9:1, sucrose : hexose) than that available to hummingbirds (2.2:1). The hybrid flower nectar has a higher sucrose : hexose ratio (4.8:1) than either parental species and suggests that the inheritance of nectar composition is more complex than usually believed. A lack of qualitative variation in amino acid complements of floral nectar between the parental species prevented verification of the hybrid origin of the newly found population of *Costus* by comparison of amino acids (see Baker and Baker 1976).

The breakdown of strictly hummingbird pollination in *Costus pulverulentus*, as seen in mixed *Costus* patches, is most likely responsible for the formation of the hybrid. It is unclear if the hybrid individuals represent the F_1 products of a single hybridization event or if subsequent introgression with either parental species has occurred. Transfer of pollen from the hybrid to either parental species is highly likely due to the intermediate pollination syndrome of the hybrid. Unfortunately, attempts with water-soluble dyes to observe pollen movement by both hummingbird and bee vectors among the hybrid and parental individuals have proven unsuccessful. The unusually high pollen viability of the hybrid, greater than that of *Costus guanaiensis*, would allow for backcrossing if no post-pollination compatibility barriers exist. Because plants obtained from the three populations in the hybrid zone have not yet flowered in synchrony, crosses among the three populations have not been made. Further support for the hybrid origin of the new *Costus* population and clarification of its status as either an F_1 or an introgressed hybrid population might emerge from analysis of endonuclease restriction site variation in nuclear ribosomal DNA (rDNA) and chloroplast DNA of the three populations. For the few restriction enzymes examined, rDNA from the hybrid appears to be similar to that of *C. guanaiensis* and not to that of *C. pulverulentus* (Sytsma unpubl. data).

The occurrence of an intersectional hybrid in *Costus* between two species with divergent modes of pollination raises several questions about reproductive barriers in *Costus*. Has little genetic incompatibility arisen within each section of *Costus* or even between sections during diversification of the genus? Is species integrity in *Costus* maintained by mechanical barriers to interspecific pollen movement or by pollinator specificity? Has hybridization and subsequent gene flow between species played an important role within and between the two sections of *Costus*? In *Heliconia* (Heliconiaceae), another Neotropical monocot genus exhibiting extensive floral differentiation, progamic (post-pollination but pre-fertilization) barriers to hybridization are well developed, although hybrids, as in *Costus*, are known but relatively rare (Kress 1983). Answers to these questions concerning the biosystematics of *Costus* are being sought by a survey of post-pollination barriers to hybridization and a DNA-based phylogenetic analysis of the subgenus *Costus*.

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