BIOTROPICA 28(1): 30–41 1996

Effects of Habitat, Plant Size, and Floral Display on Male and Female Reproductive Success of the Neotropical Orchid *Brassavola nodosa*[1]

Courtney J. Murren[2] and **Aaron M. Ellison**[3]

Department of Biological Sciences, Mount Holyoke College, Clapp Laboratory, South Hadley, Massachusetts, 01075-6418, U.S.A.

ABSTRACT

We examined correlatively the joint effects of light, supporting plant characteristics, plant size, and floral display on pollinia removal and fruit production of 103 individuals of the orchid *Brassavola nodosa* (L.) Lindl. at Peter Douglas Cay, Belize, Central America. This orchid is epiphytic on red mangroves (*Rhizophora mangle* L. [Rhizophoraceae]), and grows from 1–300 cm above ground. Light levels above each orchid, measured as direct site factor using hemispherical canopy photography, were 6–46 percent of potential direct sunlight. To characterize plant size, we counted the number of leaves of each plant and measured its longest leaf and the leaf subtending each inflorescence. The largest orchids were found in areas of high light availability, high above ground, and on large support structures. From June through early August 1993, and again in December 1993, orchids were surveyed every 3–4 days for reproductive status and success (removal of pollinia and/or fruit production). The 48 plants that flowered during these 7 months had more and longer leaves than the 55 plants that did not flower at any time in this time period. Plants flowered continuously throughout the summer; a complete reproductive cycle (bud appearance to fruit set) lasts 2–5 weeks. Pollinia were removed from 12 percent, and fruits were set by 30 percent, of the flowers produced in the summer. Because fruit set was much lower in the fall, the total proportion of fruit production relative to flower production over the 7-month study period was only 13 percent. Path analysis indicated that direct site factor, height above ground, and diameter of supporting structures significantly contributed to plant size and floral display area. In turn, floral display significantly affected both male and female reproductive success. We conclude that resources limit flower production and components of floral display, whereas pollinator availability likely limits reproductive success in *Brassavola nodosa.*

Key words: Brassavola nodosa; *epiphytes; mangroves; orchids; path analysis; pollination; resource limitation*; Rhizophora mangle.

Flower production and successful fruit-set in orchids are limited proximally by resources, pollinators, or both (*e.g.*, Montalvo & Ackerman 1987; Ackerman 1989; Calvo & Horvitz 1989; Snow & Whigham 1989; Zimmerman & Aide 1989; Ackerman & Montalvo 1990; Calvo 1990a, b). Differences in resource availability, which are reflected in microhabitat quality, may affect plant size and consequently, size of reproductive structures (*e.g.*, Cole & Firmage 1984; Samson & Werk 1986; Firmage & Cole 1988; Snow & Whigham 1989; Ackerman & Montalvo 1990; Robertson & Wyatt 1990). Beneath a forest canopy, for example, light quantity and quality varies over space and time (*e.g.*, Chazdon & Fetcher 1984; Niesenbaum 1993), and light availability has been correlated with changes in leaf size and shape, and flower size and number within an individual (*e.g.*, Givnish & Vermeij 1976; Givnish 1979; Samson & Werk 1986). Resource limitation may not be manifest in a single reproductive season, but data on successive reproductive cycles of orchids are uncommon (but see Montalvo & Ackerman 1987; Zimmerman & Aide 1989; Ackerman & Montalvo 1990; Calvo 1990a). Here we examine the relative contribution of light availability and host plant characteristics (diameter at point of epiphyte attachment, and height above ground) on reproductive success of *Brassavola nodosa* (L.) Lindl., a neotropical epiphytic orchid.

Production and size of flowers are components of reproductive effort, but are only correlates of overall reproductive success. The latter also includes pollen transfer (male reproductive success) and fruit-set (female reproductive success). Successful pollen removal and transfer as well as fruit-set depend on availability of vectors that are attracted to inflores-

---

[1] Received 15 June 1994; revision accepted 23 December 1994.

[2] Present address: Department of Ecology and Evolutionary Biology, University of Connecticut, U-43, Storrs, Connecticut, 06269-3043, U.S.A.

[3] Address all correspondence to A. M. Ellison at Mount Holyoke College.

cences (*e.g.*, Schemske 1980; Bierzychudek 1981; Ackerman 1989; Zimmerman and Aide 1989; Calvo & Horvitz 1990). Therefore, we also examined the relationship between floral display characteristics and successful pollinia removal and fruit-set in *B. nodosa*.

Specifically, we hypothesized that resources proximately limit flower production and flower size, while pollinators proximately limit fruit-set of *B. nodosa*. To address this hypothesis, we asked the following questions:

FLOWER PRODUCTION AND COMPONENTS OF FLORAL DISPLAY.—We ask the following questions. Is light availability related to plant size? Do other components of the epiphyte's immediate environment, specifically height above ground and diameter of support structure, contribute to flower production? Do larger plants produce more inflorescences, more flowers per inflorescence, and/or larger flowers?

FRUIT PRODUCTION AND POLLEN REMOVAL (REPRODUCTIVE SUCCESS).—We ask the following questions. How long does a flower remain open and receptive to pollinators? Do larger flowers or greater numbers of flowers per inflorescence increase male and female reproductive success? Are there differential effects of flower size and flower number on male and female reproductive success?

STUDY SITE

We studied *B. nodosa* during June, July, August, and December of 1993 at Peter Douglas Cay (17°43'N, 88°10'W), an ≈10 ha mangrove island, 12 km from the mainland, and within the lagoon complex of southern Belize, Central America (Stoddart *et al.* 1982). Two ≈0.1 ha sites were chosen for study, one on the northeast and one on the west side of the island. We chose these sites for their abundance of orchids, which are less dense elsewhere on the island, and which are otherwise rare throughout the Belizean cays (Fosberg *et al.* 1982). Edges of the two sites were 5–30 m from shore, and they were protected physically by a sand berm and surrounding fringing mangroves. The forest stand is primarily (78.8%) red mangrove (*Rhizophora mangle* L. [Rhizophoraceae]), with 8.3 percent black mangroves (*Avicennia germinans* [L.] Stearn [Avicenniaceae]) and 12.9 percent white mangroves (*Laguncularia racemosa* [L.] Gaertn.f. [Combretaceae]) (mangrove taxonomy follows Tomlinson 1986). Average canopy height at both sites was 8 m. Site I, the western, leeward site, had significantly larger trees (stem diameter at breast height [DBH] [$\bar{x}$ ± SD]: *Rhizophora*: 5.9 ± 3.98 cm; *Avicennia*: 10.0 ± 8.48 cm; *Laguncularia*: 13.8 ± 11.03 cm) than site II, the northeastern, windward site (DBH: *Rhizophora*: 4.9 ± 3.18 cm; *Avicennia*: 6.9 ± 6.98 cm; *Laguncularia*: 9.3 ± 7.02 cm; $P < 0.001$ for all three comparisons, t-tests on log-transformed data). However, there were no significant between-site differences in the DBH of trees hosting orchids (site I: 14.0 ± 11.75 cm; site II: 11.8 ± 8.36 cm; $P = 0.233$, t-test on log-transformed data).

STUDY SPECIES

Brassavola nodosa is an epiphytic and lithophytic orchid found in Mexico, southward through Central America into Venezuela and Peru, and on several islands in the West Indies (Urban 1964; Adams 1972; Jones 1973a, b, 1975; Liogier & Martorell 1982; Ames & Correll 1985). Jones (1973a, 1975) distinguishes three varieties of *B. nodosa*; following Jones (1973a, 1975), we studied *B. nodosa sensu stricto*. In coastal Belize, red, black, and white mangroves are the most common host trees. We have not seen *B. nodosa* growing naturally on the buttonwood mangrove, *Conocarpus erectus* L. (Combretaceae), although buttonwood is common in Belizean mangroves.

Brassavola nodosa grows sympodially. Each year, a single new shoot with a single leaf normally is produced. Occasionally, however, multiple shoots are produced from the previous year's growth. Consequently, clumps often form consisting of numerous, active shoots. Only the most recently produced shoots develop inflorescences (one per shoot), but because shoots remain connected, it is possible that older shoots contribute photosynthate to flowering shoots, and/or that flowering in previous years reduces the likelihood of a new shoot's flowering (due to resource limitation).

Brassavola nodosa flowers throughout the year in our study area. Each terminal raceme produces 1–7 synchronously-blooming, greenish-yellow flowers with white arrow-shaped lips (Fig. 1). The lips of flowers in our field population were 3.5 ± 0.52 cm wide and 5.9 ± 0.49 cm long (N = 268 flowers). The five slender, elongate tepals form a pentagonal display (Fig. 1). From dusk to dawn, the flowers emit a sweet fragrance, whose major component is 1,8-cineole (Hills *et al.* 1968, Williams 1981). Pollen is packaged in a single pollinarium composed of 8 pollinia, hidden beneath an anther cap. The flowers are self-compatible but not autogamous, and require a vector to effect polli-

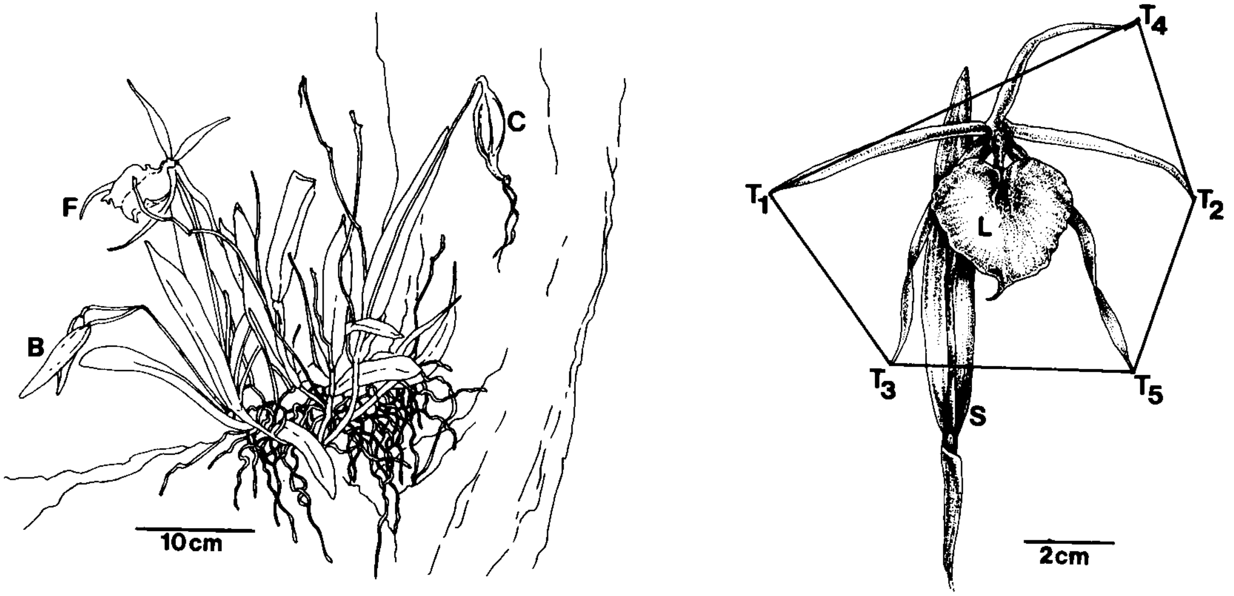

FIGURE 1. Illustrations of *B. nodosa*. Left: a reproductive plant with buds (B), flower (F) and fruit (C). Right: detail of a single flower, showing the flag leaf (S) subtending the raceme and our measures of flower size. Lip width was measured across the lip (L) at its widest point. Floral area was estimated as the area of pentagon $\overline{T_1T_2T_3T_4T_5}$, whose vertices are the five 'tepals' (petals: T_1 and T_2; sepals T_3, T_4, and T_5). Illustrations by Elizabeth J. Farnsworth.

nation (Schemske 1980; C. J. Murren, pers. obs.). Schemske (1980), citing a personal communication from R. L. Dressler, reported that *B. nodosa* is moth-pollinated. Van der Pijl and Dodson (1966) reported a sphingid moth as the pollinator of *B. nodosa*. Flower color, nocturnal fragrance, size, and morphology are all similar to other sphingid-pollinated species (Arditti 1992), but we have found no record of a specific pollinator for *B. nodosa*. Mean time from raceme appearance to anthesis was 22 d, and we observed that unpollinated flowers remain open 10–34 d ($\bar{x}$ = 20 d). Pollinarium removal was easily and non-destructively observed. Once pollinated, flowers senesced and fruit (capsule) production began immediately. Abortions occurred at all stages of floral development from raceme production through anthesis, but we did not observe fruit abortion.

MATERIALS AND METHODS

We tagged a total of 103 plants: 59 at site I and 44 at site II. These were all plants found during our initial survey of the two sites. Because it was difficult to distinguish between ramets (single sympodial shoots) and genets (clumps of connected shoots), we considered all apparently attached shoots to be part of a single clump (hereafter referred to as a plant), but we counted and measured leaves of individual shoots. For each plant, we recorded its height above ground, diameter of the host tree at the point of attachment, and host tree species. We noted whether the host tree was alive or dead, and on what part of the tree the orchid was growing. Light available to each orchid on an annual basis was estimated from hemispherical (fish-eye) photographs taken above each plant (Rich 1988, 1989; Rich *et al.* 1993). Photographs were taken with a levelled Nikon F3, 8 mm Nikon fish-eye lens, and Kodak T-Max film. Negatives were analyzed using the CANOPY analysis package (Rich 1989). This program estimates for a given latitude the amount of annual, available direct beam radiation (direct site factor [DSF]) as a percentage of total possible direct beam radiation. Rich *et al.* (1993) discussed in detail the use of DSF, and the high correlation between DSF and total available photosynthetically active radiation (PAR) measured with conventional quantum sensors.

Brassavola nodosa is an internationally listed endangered species and we therefore chose not to harvest plants to measure biomass. We counted the total number of leaves and measured the longest leaf (length and width ± 1 mm; thickness ± 0.1 mm) of each plant as indicators of plant size. We also measured the length, width, and thicknesses of all leaves on a random sample of 10 plants. These latter data supported the notion that leaf number and length of longest leaf were good indicators of plant size. Multiple linear regression showed that estimated total leaf area was well-predicted by the total number of leaves and the maximum leaf length ($r^2 = 0.91$, $P < 0.001$), and inclusion of leaf width and leaf thickness into the multiple regression model did not improve its fit.

Every 3–4 days for 54 days from 17 June to 8 August 1993, we monitored flower production and reproductive success of all plants at both sites. Racemes, buds, and flowers were all individually tagged with small plastic, numbered bands (National Band and Tag Co., Newport, Kentucky). To distinguish between the potential contribution of an individual shoot to reproductive effort and reproductive success and the potential contribution of the entire plant to reproduction, we focused attention on the leaf of a flowering shoot within the plant, which we refer to hereafter as a 'flag leaf' (Fig. 1). Length, width, and thickness of the flag leaf subtending each inflorescence were measured, as nearby leaves often contribute a disproportionate amount of photosynthate to associated reproductive structures (Evans & Rawson 1970, Lloyd 1980, Watson & Casper 1984, Blanke & Lenz 1989). In our statistical analyses of reproductive effort and reproductive success, we assessed shoot effects on reproductive success based on measurements of this flag leaf, and we assessed whole plant effects based on measurements of total number of leaves of the entire clump (flowering and nonflowering shoots). We also measured the length and width of the lip, and the lengths of all tepals of each flower when it was fully expanded. For our analysis of floral display, we used lip width as one measure of flower size. We also circumscribed a pentagon around each flower, using the ends of the five tepals as vertices of the pentagon (Fig. 1). Floral display area of a single flower was estimated as the area of this pentagon. Total floral display area per raceme was then computed as the sum of the pentagonal areas of all flowers on a single inflorescence.

Each time we monitored the plants, we noted presence or absence of the pollinarium (by presence or absence of the anther cap on the column), flower status (open, senescent, or aborted), and fruit production (visible swelling of the ovary). Plants were recensused when we returned to Belize on 29 December 1993. Racemes produced between August and December were easily counted, and intervening bud production assessed by counting abscission scars. Fruits, which persist for at least 6 mo, were also counted in December, but we could not estimate male reproductive success during the fall.

Data were analyzed using SYSTAT® (Wilkinson *et al.* 1992). We used EzPATH™ (Steiger 1989), an optional SYSTAT® module, for causal path analysis (see Mitchell 1993 for a recent summary, complete methodological description, and assumptions of path analysis). Data were transformed when necessary to meet assumptions of parametric analyses and path analysis. There were no significant differences in measured habitat or plant characteristics between the two sites, so results are discussed for the two sites pooled. We report sample means and standard deviations for all measured parameters.

RESULTS

FLOWER PRODUCTION AND COMPONENTS OF FLORAL DISPLAY.—In the mangrove understory at Peter Douglas Cay where *B. nodosa* grows, light quantity was variable. Direct site factor (DSF) reaching the censused plants ranged from 6 to 46 percent (16 ± 8.8%; Fig. 2). Plants grew 1–295 cm above the ground, with most (90%) occurring between 20 and 120 cm (91 ± 50.9 cm; Fig. 2). The vast majority (90.4%) of the plants were epiphytic on *Rhizophora*; 7.4 percent grew on *Laguncularia* and 2 percent grew on *Avicennia. Brassavola nodosa* occurred more frequently on *Rhizophora* than would be expected if it occurred on host trees in proportion to their abundance on the cay ($\chi^2 = 10.75$, df = 2, $P < 0.005$, G-test). Orchids growing on *Rhizophora* were found predominantly on boles, branches, and roots of living trees (82.4%), whereas those growing on *Laguncularia* mostly were on branches and boles of dead trees (85.7%). Of the two plants growing on *Avicennia,* one was on a live tree and one was on a dead tree. The diameter of the host tree at the point of attachment ranged from 1.5 to 82.7 cm (13.1 ± 10.49 cm; Fig. 2). Total number of leaves/plant ranged from 1 to ≈500, and the distribution was strongly right-skewed (cv = 211%). The joint relationship between these three measures of habitat and plant size is shown in Figure 2, where the symbol size is proportional to the *ln*(number of leaves). This figure illustrates that small orchids, growing low to the ground on small supports and receiving little light comprised the majority of the population and rarely flowered (open symbols). Number of leaves per plant (*ln*-transformed) was directly related to *ln*(diameter of its supporting branch) ($r = .46$, $P < 0.001$), and height above ground ($r = 0.42$, $P < 0.001$), but was not significantly correlated with *ln*(DSF) ($r = 0.17$, $P = 0.54$). Plants with more leaves also flowered more frequently (solid symbols).

Of the total population of 103 plants, two died

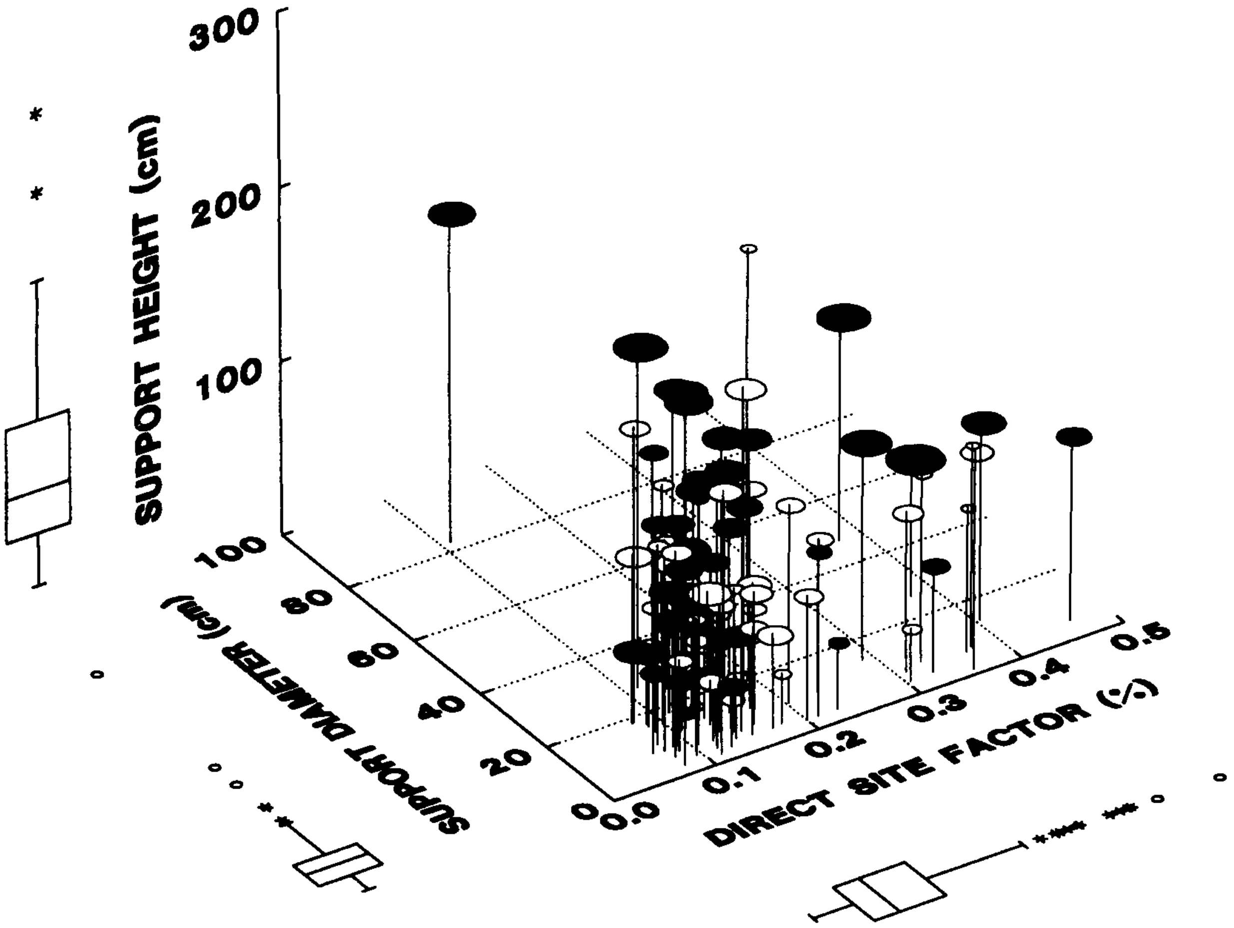

FIGURE 2. Relationship between three measures of habitat quality (DSF, height above ground, and diameter of host tree at point of attachment), plant size (number of leaves), and occurrence of at least one reproductive episode. Symbol size is proportional to the natural logarithm of the number of leaves. Open symbols indicate plants that never produced a raceme, and closed symbols indicate plants that produced at least one raceme between June and December 1993. Univariate distributions of DSF, height above ground, and support diameter are illustrated with box-plots (Tukey 1977) parallel to the corresponding axis. Box-plots indicate medians (vertical line within the rectangle), upper and lower quartiles (box edges), inner and outer fences (horizontal lines ending at the datum ≤ the median ± 1.5 times the difference between upper and lower quartile [=1.5 *hspreads*]), and extreme values (data points between 1.5 and 3 hspreads from the median are denoted by stars, and data points > 3 hspreads from the median are denoted by open circles).

between June and December, when their support structures rotted and fell into the mud. Fifty-five orchids did not produce any racemes between June and December (Table 1). Twenty-nine plants bloomed only in the summer months, 6 bloomed only in the fall, and 13 plants bloomed in both summer and fall. Mean leaf number and maximum leaf length were significantly larger for plants that flowered in either season than for plants that did not flower at all ($P < 0.001$, ANOVAs on *ln*[leaf number] and maximum leaf length), and those plants that bloomed in both the summer and the fall were the largest plants in the population (Table 1). Very little new vegetative growth (leaf production) occurred in the 7 months. We observed no significant differences in leaf number between August and December (paired t-tests on log-transformed data), whether the plant had flowered in either season (flowered only in summer: $t = 0.582$, df = 28, $P = 0.57$; flowered only in fall: $t = 1.9$, df = 5, $P = 0.1$; flowered in both summer and fall: $t = 1.943$, df = 12, $P = 0.08$), or had not flowered at all ($t = 0.487$, df = 54, $P = 0.63$).

We used discriminant function analysis (within the MGLH module of SYSTAT®) to determine if our measures of habitat variables (diameter of supporting structure, branch height, and DSF) and number of leaves (flowering + non-flowering shoots) were adequate to predict whether or not a plant flowered. We had complete habitat information for

TABLE 1. *Number of leaves and length of longest leaf ($\bar{x}$ ± SD) of orchids that did not produce racemes, produced racemens only in summer, produced racemes only in fall, or produced racemes in both summer and fall. Different superscripted letters indicate significant differences in number of leaves or length of longest leaf across the four categories* ($P < 0.05$, *Tukey's HSD test for multiple comparisons among means).*

	No racemes	Racemes in summer only	Racemes in fall only	Racemes in both summer and fall
Number of leaves	20 ± 18.7^{a}	52.3 ± 83.2^{b}	62.9 ± 47.1^{a,b}	96.5 ± 135.3^{b}
Length of longest leaf (cm)	10.9 ± 3.7^{a}	15.9 ± 2.6^{b}	17.7 ± 2.1^{b}	17.6 ± 4.9^{b}
N	55	29	6	13

94 plants, and we divided the plants into two groups: flowering (at any time between June and December) and not flowering. The discriminant analysis indicated a significant multivariate effect of the four variables (plant size and the three habitat measures) on likelihood of flowering ($F = 7.105$, df = 4, 89, $P < 0.001$, Hotelling's T^2-test). The standardized canonical coefficients (*ln*[DSF] = 0.139; *ln*[DBH] = −0.279; branch height = 0.184; *ln*[number of leaves] = −0.930) were used to construct a discriminant factor score for each plant that was used to predict from the four variables whether or not a plant flowered. The goodness-of-fit between the prediction from the discriminant analysis and actual plant flowering status was assessed using a *G*-test. The discriminant function analysis correctly predicted flowering status of 68 of the 94 plants (72%; $\chi^2 = 20.05$, $P < 0.001$).

Flower production alone does not predict fruit-set. Rather, if fruit-set is limited by pollinator availability, inflorescence display characteristics (*e.g.*, number of flowers, size of flowers) are thought to be subject to strong selection (*e.g.*, Schemske 1980). Total plant size significantly affected several components of floral display. Among the 48 flowering plants, there was a significant correlation between the total number of leaves and the total number of racemes produced ($r = 0.651$, df = 46, $P < 0.001$). Four racemes never developed buds and bud abortion was low (6.6%). There was a significant correlation between the number of racemes and the total number of flowers per plant ($r = 0.906$, df = 46, $P < 0.001$). Most racemes produced more than one flower (Table 2). Not surprisingly, as flower number increased, so did the total floral display area per raceme ($r = 0.981$, df = 16, $P < 0.001$). However, lip width per flower also increased significantly with increasing number of flowers ($r = 0.344$, df = 61, $P = 0.006$). This last result indicates that plants with more **total** flowers also had larger **individual** flowers, which may have been more attractive to pollinators. Among those 13 plants that flowered in both seasons, there was a significant positive relationship between the number of racemes produced in August and the number of racemes produced in December ($r^2 = 0.47$, $P = 0.007$, regression of December raceme production on August raceme production). The regression coefficient ($\beta_1 = 0.37$), indicated that plants that reproduced in both seasons produced just over one-third as many racemes in their second reproductive cycle.

We used path analysis to assess the joint effects of measured habitat parameters (Fig. 2) and plant vegetative characteristics on flower production and floral display area. The correlation matrix used as the input into the path analysis is given in Table

TABLE 2. *Number of racemes, flowers per raceme, and fruits produced by inflorescences with different numbers of flowers. Raw numbers are followed by percent of total numbers in the total population of racemes (120) and flowers (268). Percent of fruit production is based on the number of flowers in that category (flowers/raceme).*

	Number of flowers per raceme					
	1	2	3	4	5	6
Total racemes	33	50	19	13	4	1
(% of all racemes)	(27.5%)	(40.1%)	(15.8%)	(10.8%)	(3%)	(0.8%)
Total flowers	33	100	57	52	20	6
(% of all flowers)	(12%)	(37%)	(21%)	(19%)	(7%)	(2%)
Female success (fruit-set)	2	12	6	9	0	1
(% of flowers per category)	(6%)	(12%)	(11%)	(17%)		(17%)

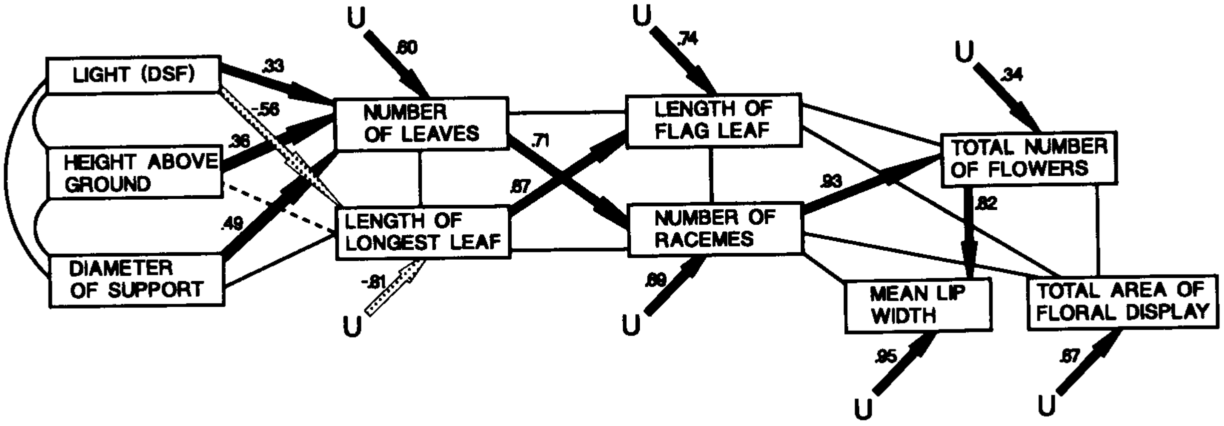

FIGURE 3. Path diagram illustrating joint relationships between measures of habitat quality, plant size, and flower production. Variables entered into the model are within boxes (DSF, support diameter, number of leaves, number of racemes, number of flowers, and total floral display area were *ln*-transformed prior to analysis). Significant path coefficients (coefficients ≠ 0; $P < 0.05$) are indicated by arrows; solid black arrows indicate positive path coefficients, dotted arrows indicate negative ones. The magnitude of each significant path coefficient is indicated adjacent to its arrow. Paths entered into the model, but whose coefficients were not significantly different from 0, are indicated by solid lines (positive coefficients) or dotted lines (negative coefficients). Unexplained variance for measures of plant size and flower production are indicated by U. Correlations between DSF, height above ground, and support diameter were entered as fixed terms into the path analysis prior to model evaluation (Steiger 1989); these values were taken from the matrix of correlation coefficients (Table 3).

3. This analysis was done only for those 26 plants whose flowers we had followed from bud through flowering in the summer. Plants that were already in flower when we began our censuses were excluded from this analysis because we could not be sure that we had identified accurately all racemes produced in that reproductive cycle. Plants which were still in bud in August, but which completed their reproductive cycle during the fall also were excluded because we did not have measures of their flower sizes. Thus, the results of our path analysis should be interpreted cautiously as a representation of how habitat and vegetative characteristics contribute to flower production.

The cascading effects of habitat on plant size, plant size on raceme production, and raceme production on flower production and flower size are illustrated in Figure 3. Direct site factor (DSF), height above ground, and support diameter had significant positive effects on total number of leaves, while DSF had a significant negative effect on the length of the longest leaf (*cf.* Givnish & Vermeij

TABLE 3. *Correlation matrix used as input for the path analysis illustrated in Figure 3. Variable abbreviations: BRANHT—Branch height; FLAGLEN—Length of flag leaf; LOGNLEAF—*ln*(number of leaves); MAXLFLEN—Length of longest leaf; LOGDSF—*ln*(DSF); LOGDBH—*ln*(DBH); LNTOTSPK—*ln*(total number of spikes); LNTOTFL—*ln*(total number of flowers); LNTAREA—*ln*(total floral display area); LPW—lip width.* N = *26 plants.*

	BRA NHT	FLAG LEN	LOGN LEAF	MAXL FLEN	LOG DSF	LOG DBH	LNTOT SPK	LNTO TFL	LNTA REA	LPW
BRANHT	1.000									
FLAGLEN	0.047	1.000								
LOGNLEAF	0.534	0.050	1.000							
MAXLFLEN	−0.117	0.670	0.071	1.000						
LOGDSF	0.154	−0.477	0.437	−0.431	1.000					
LOGDBH	0.256	0.082	0.619	0.257	0.103	1.000				
LNTOTSPK	0.305	0.152	0.714	0.141	0.336	0.357	1.000			
LNTOTFL	0.326	0.208	0.583	0.226	0.258	0.349	0.940	1.000		
LNTAREA	0.202	0.194	0.609	0.318	0.211	0.395	0.728	0.732	1.000	
LPW	0.108	−0.163	0.010	−0.050	0.100	0.155	0.133	0.221	0.060	1.000

TABLE 4. *Male and female flower success for flowers of different sizes. Flower size rank was determined based on the area of the pentagon circumscribing each flower (see Fig. 1). The largest flower on an inflorescence was assigned rank 1.*

Reproductive success	Flower size rank 1 (Largest)	2	3	4	5 (Smallest)
None	10 (35.7%)	13 (81.3%)	8 (57.1%)	5 (83.3%)	1 (50%)
Male (pollen removal)	7 (25%)	1 (6.3%)	1 (7.1%)	0	0
Female (fruit-set)	11 (39.3%)	2 (12.5%)	5 (35.7%)	1 (16.7%)	1 (50%)

1976). Total number of leaves per plant had a significant positive impact on number of racemes produced by the current year's shoots, which in turn was strongly correlated with the total number of flowers produced per plant. Significantly larger flowers were produced by plants which produced more flowers, and we illustrate in the next section that this increase in reproductive investment resulted in a concomitant increase in both male and female reproductive success. Contrary to one of our initial hypotheses, flag leaf size was not affected strongly by habitat (except through its influence on leaf length) nor did flag leaf size strongly affect any component of flower production or floral display. In other words, measures of total plant (genet) size were more useful in predicting reproductive effort than measures of the shoot (ramet) producing each inflorescence. The overall path analysis model fitted our data well ($\chi^2 = 29.0$, df = 23, $P = 0.18$, test for 'badness-of-fit'; Steiger 1989).

Reproductive success.—Flowers began to open within 3 days after buds were first observed. Fifty percent of buds were open after 10 days, and peak flowering was at 18–19 days. Flowers remained open without being pollinated from 12–37 days before beginning to senesce. Flowers senesced and fruit production began within 1 day of pollination, but no fruits were observed until 13 days after bud appearance and 10 days after the first flower was observed. We observed that within 1 week after a flower was pollinated, all other unpollinated flowers on that raceme aborted.

We were able to track the fates of 146 buds on 80 racemes from June through August. Only 21 (14.3%) fruits were produced from these buds. Eleven of these racemes produced one fruit and five racemes each produced two fruits. Of the additional 144 flowers that were already open when we arrived in Belize in June, only one produced a fruit. Forty additional racemes were produced between August and December, and nine of these yielded one fruit each. Pooled over both seasons, only 19 plants (18% of the population) accounted for all of the observed fruit production. Thirteen of these plants each had one fruit, three each had two, one had three, and two each matured four fruits.

Racemes produced 1–6 flowers (Table 2) and two-flowered inflorescences comprised the largest proportion (40.1%) of racemes. Overall, multiflowered racemes (≥2 flowers) accounted for 70.5 percent of the total, and 86 percent of all flowers occurred on these inflorescences (Table 2). Unlike the Panama population that Schemske (1980) studied, inflorescences in the Peter Douglas population with ≥3 flowers were abundant (30.8%). Two-flowered racemes were 6 times as likely to produce a fruit as single-flowered ones. Three- and four-flowered racemes were, respectively, three and four times as likely as single-flowered ones to produce a single fruit (Table 2). In the entire population pooled over both summer and winter, only 11 percent of the flowers ever set fruit.

For flowers that we could monitor regularly during the summer for pollinarium removal as well as fruit-set, estimates of male and female reproductive success were compared among flowers whose sizes were ranked within a raceme (Table 4). Only one flower had its pollinarium removed and also produced a fruit; to reduce the number of sparse cells in our tabulation, we scored this flower once in each reproductive success category. Note that since one pollinarium (composed of 8 pollinia) can successfully pollinate several flowers, the average male reproductive success reported in Table 4 is much lower than female reproductive success. Size rank was based on the area of the pentagon circumscribing the tepals of each flower (Fig. 1). For a multiflowered raceme, the flower with the largest pentagonal area was scored as rank 1, the second-largest flower was assigned rank 2, etc. Note that in this ranking system, a single-flowered inflorescence would have its flower assigned rank 1.

We observed that larger flowers tended to have a higher likelihood of both male and female reproductive success ($\chi^2 = 13.92$, df = 8, $P = 0.08$, *G*-test; Table 4). Because of the preponderance of sparse ($N < 5$) observations in Table 4, the *G*-test has a high probability of giving a Type I error (rejecting the null hypothesis of association when in fact it is true). Monte Carlo analysis of these data yielded identical results, however. For the five flower size categories in Table 4, the probability from the Monte Carlo analysis of obtaining the observed results by chance alone = 0.118. If the two smallest size categories were pooled, the probability of obtaining the observed results by chance alone was reduced to 0.065. Both Monte Carlo simulations, like the *G*-test, indicated that there was a (non-significant) trend towards association between flower size and reproductive success. Pollinarium removal was related most strongly to flower size rank, whereas fruit set was distributed more evenly among the three largest flower size categories. Forty percent of all inflorescences were two-flowered (Table 2), thus the failure rate among smaller flowers in this most common category was greatest (81.3%). Similar results were obtained when we used lip width as our measure of flower size (data not shown), but identical sizes of lip widths among some flowers on a single inflorescence resulted in assignment of identical size ranks and less statistical discrimination among flowers within an inflorescence.

DISCUSSION

In the only other study of reproduction in *B. nodosa,* Schemske (1980) concluded that reproduction in this species is pollinator-limited based on increased fruit production following hand pollinations. He suggested that trade-offs between vegetative growth and sexual reproduction, along with increasing likelihood of mortality through time, would result in selection for early flowering by small plants and hence smaller or fewer-flowered inflorescences (see also Stearns 1976, 1992; Ackerman 1986). He hypothesized that multiflowered inflorescences would be selectively advantageous for *B. nodosa* because they would be more attractive to pollinators. The Panamanian population predominantly produced one- or two-flowered inflorescences and Schemske (1980) inferred that multiflowered inflorescences were in some way maladaptive, and therefore rare in nature. Schemske's (1980) data provided inferential support for this trade-off hypothesis, but he presented no information on plant size, resource availability, or mortality rates. In our study area multiflowered inflorescences were common, and both flower production and fruit-set of *B. nodosa* in Belize do appear to be influenced by habitat characteristics and pollinator activity, as has been found for other orchid species (*e.g.,* Zimmerman & Aide 1989, Ackerman & Montalvo 1990). Because the size of our study population was relatively small, we were unable both to gather reliable baseline demographic data (reported here) and simultaneously determine experimentally (through hand-pollinations) whether the orchids at Peter Douglas Cay were truly pollinator limited. The relatively high flower/fruit ratios (Table 2) strongly suggest pollinator limitation of fruit-set in our population.

We found that habitat components indeed reflected differences in plant size and flower production. *Brassavola nodosa* occurred most commonly on *Rhizophora,* and our data indicated some degree of host-preference at Peter Douglas Cay. We found that the largest plants occurred high above ground and on large diameter supports (Fig. 2). Higher attachment points allow plants to avoid flooding, salt spray, herbivory (two fruits, on a plant growing <30 cm above ground, were eaten by land crabs [*Ucides* or *Goneopsis* spp.]), or breakage during tropical storms. As fruit-set is ordinarily low, habitats where risk of fruit loss is minimized increase the possibility that seeds will mature successfully.

We expected that increased light availability would result in plants with more total leaves (flowering + non-flowering shoots) and hence more inflorescences, but DSF was not correlated significantly with total number of shoots and contributed only marginally to the overall discriminant factor score. Path analysis (Fig. 3) indicated that DSF positively affected leaf number, but negatively affected maximum leaf size (*cf.* Givnish & Vermeij 1976, Givnish 1979). Our other measures of habitat quality, support diameter and height above ground, also strongly affected leaf number, but not maximum leaf length (Fig. 3). The overall results of the path analysis suggest that plants with more total leaves produce more racemes, more flowers per raceme, and larger floral displays. Larger plants also were more likely to flower during both summer and fall. No significant vegetative growth occurred for any of the plants, reproductive or not, during our periods of observation. We conclude from these observations that larger plants allocate more of their stored resources to reproductive structures; *i.e.,* that non-flowering shoots can contribute resources to flowering shoots. Our finding that those plants which reproduced twice during these 7 months only produced one-third as many inflorescences in the second reproductive cycle indicates that there likely is some energetic cost to reproduction, at least in terms of future reproduction.

We also predicted that size of the leaf subtending each raceme would affect significantly flower number and size, but our results did not support this prediction. The limited role of the subtending leaf is supported further by our observation of a three-flowered raceme on a leafless shoot that nonetheless produced a fruit. This plant had 160 other non-flowering shoots (leaves). In contrast, a smaller plant bearing 36 leaves produced a four-flowered raceme, but when its flag leaf was eaten, all its flowers aborted immediately. The importance of the flag leaf in supplying resources to reproductive structures may vary with plant size and developmental stage of distal reproductive structures. Once ovary swelling begins, green carpel walls may supplement energy requirements for fruit maturation and structural maintenance, and dependence on nearby leaves may diminish (*e.g.,* Watson and Casper 1984, Blanke and Lenz 1989, Galen *et al.* 1993). After successful pollination of one (or occasionally two) flowers/raceme, other flowers on that raceme were observed to senesce quickly. This pattern suggests that resources are directed toward successful development of fruits, rather than maintenance of additional flowers, which would be expected in an environment where pollinator visits are rare.

Fruits were produced most frequently by large flowers on multiflowered racemes (Tables 2 and 3). Schemske (1980) also found significantly higher reproductive success of multiflowered racemes. Such racemes are common in Belize, but rare in Panama. Either the Panamanian population and the Belize population are taxonomically distinct or lower resource availability or quality at Schemske's site may have limited flower production.

Both Janzen *et al.* (1980) and Campbell (1987) warn that generalizations based on a single geographical location or reproductive season are suspect. Our study spanned two temporal seasons and several reproductive bouts, but vegetative growth may occur during the wetter winter and spring. Long-term observations would result in a better understanding of the effects of resources on flower production and subsequent reproductive success in *B. nodosa.* Hand-pollinations (Schemske 1980) and flower/fruit ratios (Schemske 1980; Table 2) suggest that reproductive success of *B. nodosa* is limited primarily by pollinators, not resources, although Snow and Whigham (1989) caution against the use of short-term, hand-pollination experiments as the only means of assessing pollinator limitation. Because pollinator availability appears to limit reproductive success for *B. nodosa,* it would be selectively advantageous for this orchid to produce greater numbers of flowers and larger display areas per flower, despite their potential energetic cost to the plant (see also Schemske 1980). However, until the pollinator(s) of *B. nodosa* is (are) identified positively, discussions of the role of pollinator limitation in reproductive success are inferential at best, and purely speculative at worst. Knowledge of the life history and behavior of the pollinator, and further systematic study of the genus *Brassavola* are needed before we can assess how pollinator limitation has affected the evolution of floral display of *B. nodosa* or other *Brassavola* species.

ACKNOWLEDGMENTS

We thank D. Chatterjea, M. Panuncio, K. Till, and H. Shannon for field assistance and E. J. Farnsworth for field assistance and for drawing Fig. 1. E. J. Farnsworth, E. R. Heithaus, R. L. Tremblay, K. Searcy, and an anonymous referee reviewed early versions of the manuscript and their helpful critiques resulted in a much-improved paper. R. L. Tremblay suggested the Monte Carlo analysis of the data presented in Table 4. This research was supported by NSF grant DEB 92-53743 to AME, and formed a portion of CJM's undergraduate senior honors thesis.

LITERATURE CITED

Ackerman, J. D. 1986. Coping with the epiphytic existence: pollination strategies. Selbyana 9: 2–60.

———. 1989. Limitations to sexual reproduction in *Encyclia krugii* (Orchidaceae). Syst. Bot. 14: 101–109.

———, and A. M. Montalvo. 1990. Short- and long- term limitations to fruit production in a tropical orchid. Ecology 71: 263–272.

Adams, C. D. 1972. Flowering plants of Jamaica. University of the West Indies, Mona, Jamaica.

Ames, O. A., and D. S. Correll. 1985. Orchids of Guatemala and Belize. Dover, New York, New York.

Arditti, J. 1992. Fundamentals of orchid biology. John Wiley and Sons, New York, New York.

Bierzychudek, P. 1981. Pollinator limitation of plant reproductive effort. Am. Nat. 117: 838–840.

Blanke, M. M., and F. Lenz. 1989. Fruit photosynthesis. Plant Cell Envir. 12: 31–46.

Campbell, D. R. 1987. Interpopulation variation in fruit production: the role of pollination-limitation in the Olympic Mountains. Am. J. Bot. 74: 269–273.

Chazdon, R., and D. Fletcher. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. J. Ecol. 72: 553–564.

Calvo, R. N. 1990a. Four-year growth and reproduction of *Cyclopogon cranichoides* (Orchidaceae) in South Florida. Am. J. Bot. 77: 736–741.

———. 1990b. Inflorescence size and fruit distribution among individuals in three orchid species. Am. J. Bot. 77: 1378–1381.

———, and C. C. Horvitz. 1990. Pollinator limitation, cost of reproduction and fitness in plants: a transition-matrix demographic approach. Am. Nat. 136: 499–516.

Cohen, D. 1971. Maximizing yield when growth is limited by time or limiting resources. J. Theor. Biol. 33: 299–307.

Cole, F. R., and D. H. Firmage. 1984. The floral ecology of *Platanthera blephariglottis*. Am. J. Bot. 71: 700–710.

Evans, L. T., and H. M. Rawson. 1970. Photosynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. Aust. J. Biol. Sci. 23: 245–254.

Firmage, D. H., and F. R. Cole. 1988. Reproductive success and inflorescence size of *Calopogon tuberosus* (Orchidaceae). Am. J. Bot. 75: 1371–1377.

Fosberg, F. R., D. R. Stoddart, M.-H. Sachet, and D. L. Spellman. 1982. Plants of the Belize cays. Atoll Res. Bull. 258: 1–77.

Galen, C., T. E. Dawson, and M. L. Stanton. 1993. Carpels as leaves: meeting the carbon cost of reproduction in an alpine buttercup. Oecologia (Berl.) 95: 187–193.

Givnish, T. J. 1979. On the adaptive significance of leaf form. *In* O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven (Eds.). Topics in plant population biology, pp. 375–407. Columbia University Press, New York, New York.

———, and G. J. Vermeij. 1976. Sizes and shapes of liana leaves. Am. Nat. 110: 743–778.

Hills, H. G., N. H. Williams, and C. H. Dodson. 1968. Identification of some orchid fragrance components. Am. Orchid Soc. Bull. 37: 967–971.

Janzen, D. H., P. DeVries, D. E. Gladstone, M. L. Higgins, and T. M. Lewinsohn. 1980. Self- and cross-pollination of *Encyclia cordigera* (Orchidaceae) in Santa Rosa National Park, Costa Rica. Biotropica 12: 72–74.

Jones, H. G. 1973a. Synopsis of Middle American *Brassavola*. Am. Midl. Nat. 89: 499–503.

———. 1973b. The genus *Brassavola* as an example of infrageneric evolution in the Orchidaceae. Adansonia 13: 235–239.

———. 1975. Nomenclatural revision of the genus *Brassavola* R. Br. of the Orchidaceae. Ann. Naturhist. Mus. in Wien Bot. 79: 9–22.

Liogier, H. A. and L. F. Martorell. 1982. Flora of Puerto Rico and adjacent islands: a systematic synopsis. Editorial de la Universidad de Puerto Rico, San Juan, Puerto Rico.

Lloyd, D. G. 1980. Sexual strategies in plants I. An hypothesis of serial adjustment of maternal investment during one reproductive session. New Phytol. 86: 69–79.

Mitchell, R. J. 1993. Path analysis: pollination. *In* S. M. Scheiner and J. Gurevitch (Eds.) Design and analysis of ecological experiments, pp. 211–231. Chapman and Hall, New York, New York.

Montalvo, A. M., and J. D. Ackerman. 1987. Limitations to fruit production in *Ionopsis utricularioides* (Orchidaceae). Biotropica 19: 24–31.

Niesenbaum, R. A. 1993. Light or pollen—seasonal limitations on female reproductive success in the understory shrub *Lindera benzoin*. J. Ecol. 81: 315–323.

Rich, P. M. 1988. Video image analysis of hemispherical canopy photography. *In* P. W. Mausel (Ed.), First special workshop on videography, pp. 84–95. Terre Haute, Indiana.

———. 1989. A manual for analysis of hemispherical canopy photography. Los Alamos Technical Manual LA-11733-M, Los Alamos National Laboratory, Los Alamos, New Mexico.

———, D. A. Clark, D. B. Clark, and S. F. Oberbauer. 1993. Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. Ag. For. Meteor. 65: 107–127.

Robertson, J. L., and R. Wyatt. 1990. Reproductive biology of the yellow-fringed orchid, *Platanthera ciliaris*. Am. J. Bot. 77: 388–398.

Samson, D. A., and K. S. Werk. 1986. Size dependent effects in the analysis of reproductive effort in plants. Am. Nat. 127: 667–680.

Schemske, D. W. 1980. Evolution of the floral display in the orchid *Brassavola nodosa*. Evolution 34: 489–493.

Snow, A. A., and D. F. Whigham. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). Ecology 70: 1286–1293.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Q. Rev. Biol. 51: 3–47.

———. 1992. The evolution of life histories. Oxford University Press, New York, New York.

Steiger, J. H. 1989. EzPATH: A supplementary module for SYSTAT and SYGRAPH. SYSTAT, Inc., Evanston, Illinois.

Stoddart, D. R., F. R. Fosberg, and D. L. Spellman. 1982. Cays of the Belize barrier reef and lagoon. Atoll Res. Bull. 256: 1–76.

Tomlinson, P. B. 1986. The botany of mangroves. Cambridge University Press, Cambridge, England.

Tukey, J. W. 1977. Exploratory data analysis. Addison-Wesley, Reading, Massachusetts.

Urban, I. (Ed.) 1964. Symbolae Antillanae seu Fundementa Florae Indiae Occidentalis, Volume IV. Asher and Co., Amsterdam.

Van der Pijl, L., and C. H. Dodson. 1966. Orchid flowers: their pollinators and evolution. University of Miami Press, Coral Gables, Florida.

Watson, M. A., and B. B. Casper. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. Ann. Rev. Ecol. Syst. 15: 233–258.

Wilkinson, L., M. Hill, J. P. Welna, and G. K. Birkenbeuel. 1992. SYSTAT for Windows, Version 5. SYSTAT, Inc., Evanston, Illinois.

Williams, N. H. 1981. Floral fragrance components of *Brassavola* (Orchidaceae: Laeliinae). Selbyana 5: 279–285.

Zimmerman, J. K., and T. M. Aide. 1989. Patterns of capsule production in a neotropical orchid: pollinator vs. resource limitation. Am. J. Bot. 76:63–73.