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Reproduction in an Orchid Can Be Resource-Limited over its Lifetime[1]

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ABSTRACT

Most orchids studied thus far show long-term resource adjustments to increases in fruit production within a flowering season, but none of these offers rewards to their potential pollinators. If nectar production is energetically expensive, then resources utilized to produce fruits and seeds may be even more limited in pollinator-rewarding orchids than in non-rewarding ones. Thus, resource adjustments may be more dramatic or entirely different in nectar producing plants. In this study, we performed artificial hand-pollinations for two consecutive flowering seasons in the nectar producing orchid *Comparettia falcata,* and tested whether or not fruit set, seed set, and seed viability were limited by the quantity of pollinations or by resources. In addition, we compared mechanisms of short-term (fruit abortion within seasons) and long-term consequences (percent change in leaf length and change in flower number per plant between seasons, probability of shoot and inflorescence production, and mortality) between hand- pollinated and unmanipulated plants. The relationships among plant traits related to vegetative size and reproduction also were examined. Hand-pollinations showed some negative effects. Fruit set was higher in hand-pollinated plants in the first season but was similar to the controls in the second. Seed set was significantly lower and abortions were higher than in unmanipulated plants. On the other hand, some of our measurements were unaffected by the hand-pollination treatment. Unexpectedly, there were no significant differences between groups in percent change in leaf length, change in flower number per plant between seasons, or the probability of shoot and inflorescence production. Although there was a strong correlation between leaf size and the number of flowers produced within a season, associations between leaf size and traits related to current or future reproduction were not consistent. Like other epiphytic orchids, pollination limitation occurred within a single season in *C. falcata,* but increases in fruit production also resulted in reduced lifetime fitness as estimated by a compounded fitness index. Contrary to all other epiphytic orchids studied, long-term adjustments to increased fruit production in *C. falcata* through reduction in future growth or flower and inflorescence production were either minor or lacking. Our results suggest that the nature of plant strategies associated with resource constraints during sexual reproduction may be dependent on whether or not plants have evolved traits that are costly.

RESUMEN

La mayoría de las orquídeas estudiadas hasta el presente presentan ajustes a aumentos en producción de frutos dentro de una temporada de floración pero ninguna de estas ofrece recompensas a sus polinizadores potenciales. Si la producción de nectar es energéticamente costosa, entonces los recursos utilizados para producir frutos y semillas podrían estar aún más limitados en las orquídeas que ofrecen recompensa que en las que no las ofrecen. Así, los ajustes de recursos podrían ser aún más dramáticos o totalmente diferentes. En este estudio realizamos polinizaciones artificiales por dos temporadas consecutivas en la orquídea productora de nectar *Comparettia falcata* y comprobamos si la producción de frutos y la producción y viabilidad de las semillas estaba limitada por la cantidad de polinizadores o de recursos. Además, comparamos las consecuencias a corto plazo (aborto de frutos dentro de una temporada) y a largo plazo (porciento de cambio en el largo de la hoja, cambio en el número de flores por planta entre temporadas, probabilidad de producción de tallo e inflorescencia y mortalidad) entre plantas polinizadas manualmente y plantas no manipuladas. La relación entre características de la planta relacionas con el tamaño vegetativo y la reproducción también fueron examinadas. Las polinizaciones manuales tuvieron effectos negativos. La producción de frutos fué mayor en las plantas polinizadas manualmente en la primera temporada pero fué similar en la segunda. La producción de semillas fué significativamente menor y el aborto de frutos fué significativamente mayor en plantas polinizadas manualmente. Por otro lado, algunas de nuestras medidas no pueron afectadas por el tratamiento de polinización. Inesperadamente, no hubo diferencias significativas en el porciento de cambio en tamaño de la hoja, en el cambio en

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número de flores por planta entre temporadas, en la probabilidad de produccion de frutos o inflorescencias, ni en mortalidad. Apesar de que hubo una fuerte correlación entre el tamaño de la hoja y el número de flores producidas dentro de una temporada, las asociaciones entre el tamaño de la hoja y características relacionadas con reproducción presente y futura no fueron consistentes. Al igual que otras orquídeas epífitas, la limitación por polinización ocurre dentro de una misma temporada en *C. falcata* pero aumentos en producción de frutos también resultaron en una disminución en la adecuación en el transcurso de la vida de la planta según un índice compuesto de adecuación estimado. Contrario a todas las demás orquídeas epífitas estudiadas, los ajustes a largo plazo en forma de reducción de crecimento futuro y reducción de flores e inflorecencias futuras fueron mínimos o estuvieron ausentes en *C. falcata.* Nuestro resultados sugieren que la naturaleza de las estrategias asociadas a limitación de recursos durante la reproducción sexual podrían depender de que las plantas hayan evolucionado o no características que son costosas.

Key words: Comparettia falcata; *floral rewards; hummingbird pollination; nectar; orchid; pollen limitation; Puerto Rico; reproductive ecology; resource constraints.*

THE IMPORTANCE OF RESOURCE AND POLLEN AVAILABILITY FOR SEXUAL REPRODUCTION has been studied extensively in the Orchidaceae (Schemske 1980, Ackerman & Montero-Oliver 1985, Montalvo & Ackerman 1987, González-Díaz & Ackerman 1988, Zimmerman & Aide 1989, Ackerman 1989, Snow & Whigham 1989, Ackerman & Montalvo 1990, Calvo & Horvitz 1990, Primack & Hall 1990, Calvo 1993) in an effort to understand the mechanisms of trait evolution in what many consider the largest family of angiosperms. In most orchids studied thus far, paucity of pollinators and resource availability are the dominant constraints limiting sexual reproduction (Montalvo & Ackerman 1987, Ackerman 1989, Zimmerman & Aide 1989, Ackerman & Montalvo 1990; *c.f.* Schemske 1980, Calvo 1990). In these studies, pollen limitation was shown to occur within a single season, but increases in fruit production also resulted in long-term costs to the plants and possibly, lifetime fitness (*c.f.* Calvo & Horvitz 1990). All orchids studied thus far present a deception pollination strategy (no rewards are produced), which is a common pollination mechanism among terrestrial and epiphytic orchids (Ackerman 1986). We argue that to determine the prevalence of different limits to fruit production in the family, a wider spectrum of species with different life histories needs to be examined.

The orchid *Comparettia falcata* is a self-compatible orchid dependent on hummingbird pollination. Unlike many epiphytic orchids, it offers a nectar reward (Rodríguez-Robles *et al.* 1992). This reward, however, is small relative to most other plants pollinated by hummingbirds. Ackerman *et al.* (1994) did not support the hypothesis that directional selection on reduced nectar volumes in this orchid was occurring, but instead showed that the presence of nectar was needed for hummingbird visitation and fruit set. On the other hand, Salguero-Faría and Ackerman (1999) demonstrated that increases in nectar volumes in this orchid did not translate to increased fruit set or reduced plant fitness via inbreeding depression. They also proposed that the evolution of nectar reward in *C. falcata* was driven by a combination of pollination limitation and resource constraints.

We present observations on factors that limit sexual reproduction in the epiphytic orchid *C. falcata* within and between seasons. Nectar production can be energetically expensive (Southwick 1984, Koopowitz & Marchant 1998) so that resources utilized to produce fruits and seeds may be even more limited in rewarding orchids relative to non-rewarding ones. To test this hypothesis, we examined the relative importance of pollen and resource availability to sexual reproduction in this plant. We performed artificial hand-pollinations for two consecutive flowering seasons to test whether reproduction was limited by the quantity of pollinations or availability of resources. We also determined if fruit and seed set were correlated with plant size, age, and previous reproductive history. We then compared our results to similar studies with epiphytic orchids and also examined predictions about the evolutionary consequences of pollen and/or resource limitation in this plant.

METHODS

STUDY SITE.—This study was conducted between January 1989 and November 1991 at the Toro Negro Forest Reserve in Puerto Rico, which is classified as a Subtropical Lowland Montane Wet Forest according Holdridge's Life Zone System (Ewel & Whitmore 1973). Our site was near Lago El Guineo (18°09′30″N, 66°32′00″W; 1000 m elev.).

PLANT SYSTEM.—We studied a natural population of *C. falcata,* a perennial twig epiphyte that occurs in humid forests of middle to high elevation and is widespread but uncommon throughout the Neotropics (Ackerman 1995). The plant is caespitose and has small aggregated and cylindrical pseudobulbs (hereafter "shoots") with one, rarely two, coriaceous, oblong–elliptic, obtuse leaves (Ackerman 1995). Plants produce a single lateral inflorescence, usually an unbranched raceme of one to ten flowers. The deep rose-pink flowers open between February and May. The lateral sepals are fused, forming a curved spur that produces, on average, 3.7 μl of nectar with a mean sugar concentration of 14.0 g solute/100 g solution (Rodríguez-Robles *et al.* 1992). While no relationship has been shown between nectar variation and visitation frequency at Toro Negro (Rodríguez-Robles *et al.* 1992), nectar removal experiments have demonstrated that the presence of nectar is important for pollinator visitation (Ackerman *et al.* 1994) and that animal pollination is vital at this site (Rodríguez-Robles *et al.* 1992). In Toro Negro, *C. falcata* is pollinated by the traplining hummingbird *Chlorostilbon maugaeus* (Rodríguez-Robles *et al.* 1992).

EXPERIMENTAL DESIGN.—On January 1989, we marked all the plants with developing inflorescences that we could find at the site. We selected a subset for this study and randomly assigned them to either experimental ($N = 25$) or control treatments ($N = 36$). We lost 7 inflorescences to herbivory and were left with 24 plants in the experimental group and 30 in the control. To determine the effect of pollination intensity on reproduction, we artificially cross-pollinated all the flowers on experimental plants (hereafter hand-pollinated) between February and April 1989. Control plants were left unmanipulated to allow natural pollination. Plants were monitored weekly for flower production, fruit initiation, fruit maturation, and fruit abortion. Aborted fruits were easily discernible as they gradually turned yellow and eventually fell from the plant. The experiment was repeated the following year (January–April 1990) using the same plants. In 1990, however, only a fraction of control and hand-pollinated plants produced inflorescences (37.9 and 25.0%, respectively).

For each plant in the experiment in 1989, we measured the following variables in the field: leaf size, number of live shoots, size of inflorescence stalk, and number of flowers. Retention of the leaf and inflorescence stalk from the previous years is very common in this orchid (E. J. Meléndez-Ackerman, pers. obs.), which also allowed us to measure the size of leaves and inflorescence stalks that were produced in 1988 on each plant. Leaf size was measured as the length of the longest axis on the leaf. Old shoots also are retained in *C. falcata*, and we thus used the total number of shoots as an estimate of plant age. Overall, plants had between 1 and 9 shoots, with an average of 4.1 shoots, and 89 percent of plants had between 1 to 6 shoots. This estimate is conservative because not all plants will produce shoots every year (Table 3). We checked for bias between the hand-pollinated and control groups in plant size, defined as number of live shoots, leaf size, and number of flowers. By all criteria, plant size was not different among treatments ($t < 1.07$, df $= 49$, $P > 0.28$).

EFFECT OF POLLINATION INTENSITY ON FRUIT AND SEED PRODUCTION.—An increase in reproductive success by hand-pollinated plants may indicate that reproduction is pollen limited, whereas uncoupling of pollination intensity from fruit or seed production could result from the lack of available resources for fruit maturation. If the latter is the case, pollen augmentation would neither cause a substantial increase in fruit or seed production nor result in increased fruit or seed abortion. To test for the occurrence of pollen or resource limitation, we examined differences in percent fruit set (no. fruits/no. flowers × 100) and percent fruit abortion (no. aborted fruits/no. initiated fruits × 100) among pollination treatments. Fruit set data were analyzed using a two-way ANOVA with season (1989, 1990) and pollination treatment (control vs. hand-pollination) as main effects. Data on fruit abortion were analyzed only for the 1989 season because abortion was rare in 1990 (see Results). Differences in fruit abortion were analyzed using a Student's *t*-test.

A reduction of seed crop or seed viability also would be consistent with the hypothesis of resource limitation. To test this, all mature fruits from control and hand- pollinated plants were collected and brought to the lab. For each fruit, we weighed the seed crop and used it as our estimate for the total number of seeds produced per fruit, because orchid seeds are tiny and numerous (>1000 seeds/fruit). We estimated the percent seed viability by viewing a sample of the minute transparent seeds under a microscope at 40× and counting the number of seeds without embryos from a total of 500 seeds viewed. We analyzed differences in seed crop (total seed weight/fruit) and seed viability (seeds with embryos/total seeds/fruit) between control and hand-pollinated plants using a Student's *t*-test. The analysis was performed only on data for the 1989 reproductive season since fruit production was meager in 1990 (see Results) and sample sizes were too small for that year.

EFFECT OF POLLINATION INTENSITY ON FUTURE GROWTH AND REPRODUCTION.—If lifetime reproduction is resource limited, then fruit augmentation in one year also may result in a decrease in future vegetative growth and reproduction. To examine this idea, for each plant, we calculated the percent change in leaf length [(leaf length second season − leaf length first season)/leaf length first season × 100] and the change in number of flowers between flowering seasons (1989–1990 and 1990–1991) and tested whether or not these variables were associated with pollination treatment. These data were analyzed using a two-way ANOVA with year and pollination treatment as main factors. We also determined if probabilities of producing a new shoot or a new inflorescence in subsequent flowering seasons were associated with pollination treatment by recording the frequency of control and hand-pollinated plants that produced new shoots and new inflorescences during 1990 and 1991 and those that did not. Frequency data were analyzed using a *G*-test analysis of independence (Sokal & Rohlf 1981).

Plant mortality also was followed but was too rare for data analysis. Only one plant in the control group died during the experiment.

While the effects of fruit production on different fitness components may not be obvious, the consequences of elevated fruit production may become apparent when the different fitness components are combined. For each plant group, we calculated a compounded fitness index using the following formula: C = [(mean fruit set/plant in 1989) × (mean seed crop/fruit/plant) × (average viability/crop/plant) + (mean fruit set/plant in 1990) × (mean seed crop/fruit/plant) × (estimated viability for 1990)] × (probability of producing inflorescence in 1991). The index includes the information on reproduction for three years. The term inside the brackets equals the total number of viable seeds per plant produced during two reproductive seasons. Only a small fraction of plants produced fruits in 1990 and most of these fruits dehisced before collection; thus data on seed crop were based only on a small fraction of fruits (average seed crop control: 0.313 g, $N = 4$; average seed crop experimental: 0.029 g; $N = 1$) and viability data were not gathered in that year. Since there were no significant differences between the average viabilities for controls and hand-pollinated plants in 1989 (Fig. 2), we used their average (0.97) as our estimated viability for 1990. The index was used to calculate the overall relative fitness of control versus hand-pollinated plants at the end of the study (relative fitness = C_i/C_{max}, where C_{max} = highest fitness value).

RELATIONSHIP BETWEEN PREVIOUS AND CURRENT GROWTH AND REPRODUCTION.—Associations between current plant size and reproduction, and between previous reproductive (or growth) history and reproductive success, also may result from resource constraints. First, we looked for correlations between parameters of plant size (*i.e.*, leaf length, number of live shoots, length of inflorescence stalk in 1989, and number of flowers in 1989) and traits related to previous growth and reproductive history (*i.e.*, leaf length in 1988, length of inflorescence stalk in 1988). Second, we tested if there were correlations between percent fruit set and percent fruit abortion in 1989 and the above traits. Correlation analyses for percent fruit set and percent fruit abortion were done separately for the control and hand-pollinated groups. We expected these correlations to be stronger in hand-pollinated plants if resources were a major constraint to fruit production and plants adjusted for future growth in response to increases in fruit production. To control for the probability of significant yields that could occur by chance due to multiple correlation tests, we also used a sequential Bonferroni technique (Rice 1989) that adjusted our selected α level (0.05) for the number of tests included on each correlation table (Tables 1 and 2).

OTHER CONSTRAINTS ON FRUIT PRODUCTION.—Other factors that could result in low fruit production are fruit and flower predation. If the frequency of these events were positively associated with increases in fruit initiation, then pollination increases may result in increases in fruit and seed predation, overriding the benefits of high pollination frequencies. During the 1989 and 1990 flowering seasons, we monitored inflorescence, and flower and fruit predation (weekly) in all plants until fruits matured. Herbivory and predation were too infrequent for data analyses. Of 66 fruits (controls: 14, hand-pollinated: 52) produced by all plants in 1989, 4 were damaged (probably by rats). Two of the eaten fruits were from control plants. In 1990, of 26 fruits produced, there was 1 fruit eaten from each plant group (controls: 16, hand- pollinated: 10). Inflorescence herbivory occurred in 2 of 11 inflorescences produced in the control group, while 1 of 6 inflorescences produced by the hand-pollinated

TABLE 1. *Correlation coefficients for percent fruit set and percent fruit abortion in 1989 versus plant traits related to size and reproduction. Separate analyses were done for control and hand-pollinated plants.*

Trait	Control plants		Hand-pollinated plants	
	Fruit set	Fruit abortion	Fruit set	Fruit abortion
Age	0.20	0.01	−0.11	−0.05
Leaf length (1988)	0.24	0.23	−0.07	0.02
Inflorescence length (1988)	−0.40	0.22	−0.31	0.27
Number of live shoots	0.16	0.34	−0.13	0.005
Leaf length (1989)	−0.03	−0.05	0.05	0.35
Inflorescence length (1989)	0.14	0.17	0.03	−0.48
Number of flowers (1989)	−0.02	0.32	0.09	0.70**

** Significant at the table-wide 0.001 level following a sequential Bonferroni analysis (Rice 1989).

group showed insect damage. Damaged inflorescences eventually withered and dried. These observations indicate that inflorescence and fruit herbivory were not associated with increases in fruit production.

RESULTS

POLLINATION VS. RESOURCE CONSTRAINTS ON FRUIT AND SEED PRODUCTION.—The overall effects of year and pollination treatment on fruit set were not significant (year: $F_{1,64}$ = 3.84, P = 0.054; treatment: $F_{1,64}$ = 1.13, P = 0.29; Fig. 1); however, there was a significant year × treatment interaction in which hand-pollinated plants showed a significant increase in fruit set over naturally pollinated plants in 1989, but not in 1990 (year × treatment: $F_{1,64}$ = 4.64, P = 0.035). In 1989, the proportion of aborted fruits was higher among hand- pollinated plants (40.3%, N = 24) relative to the naturally pollinated (1.72%, N = 29; Mann-Whitney U = 896, P = 0.0001; Fig. 2); but overall, the number of aborted fruits was low in 1990 (controls: no abortions; hand-pollinated: one plant aborted all fruits). The seed crop per fruit of control plants was nearly twice that of the seed crop for hand-pollinated plants in 1989, but this tendency was marginally nonsignificant (t = 1.86, df = 25, P = 0.07; Fig. 2). There were no significant differences in seed viabilities between pollination treatments in 1989 (t = −0.12, df = 26, P = 0.91; Fig. 2).

CORRELATES BETWEEN VEGETATIVE AND REPRODUCTIVE TRAITS.—Our results showed no correlations among plant age, leaf, or inflorescence size. The number of live shoots also did not correlate with the above traits (Table 1). Similarly, past vegetative effort (indicated by leaf size in 1988) was not correlated with any reproductive or vegetative trait measured; however, there was a significant positive correlation between the number of flowers in 1989 and the size of the leaf in 1989 (Table 1).

Percent fruit set was not correlated with traits related to plant size or reproductive history for either pollination treatment (Table 2). A significant positive correlation between percent fruit abortion and the number of flowers per inflorescence was evident only in hand-pollinated plants (Table 2). No significant correlations were detected between percent fruit abortion and the remaining traits (Table 2).

EFFECTS OF POLLINATION INTENSITY ON FUTURE GROWTH AND REPRODUCTION.—There were no significant differences between pollination treatments

TABLE 2. *Correlation matrix for traits related to plant size and reproduction.*

	Age	Leaf length (1988)	Inflorescence length (1988)	No. live shoots	Leaf length (1989)	Inflorescence length (1989)	No. flowers (1989)
Age	—	0.37	−0.02	0.04	0.09	0.26	0.04
Leaf length (1988)		—	0.41	−0.02	0.43	0.28	0.27
Inflorescence length (1988)			—	0.11	0.14	−0.07	0.11
No. live shoots				—	−0.21	0.16	−0.06
Leaf length (1989)					—	0.24	0.58***
Inflorescence length (1989)						—	−0.14

*** Significant at the table-wide 0.001 level following a sequential Bonferroni analysis (Rice 1989).

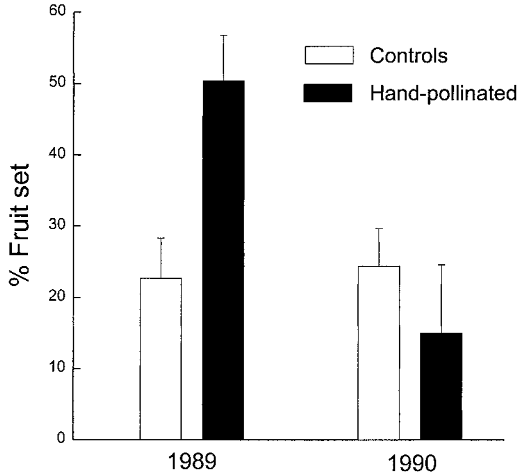

FIGURE 1. Differences in fruit set between control and experimental plants during the 1989 and 1990 reproductive seasons.

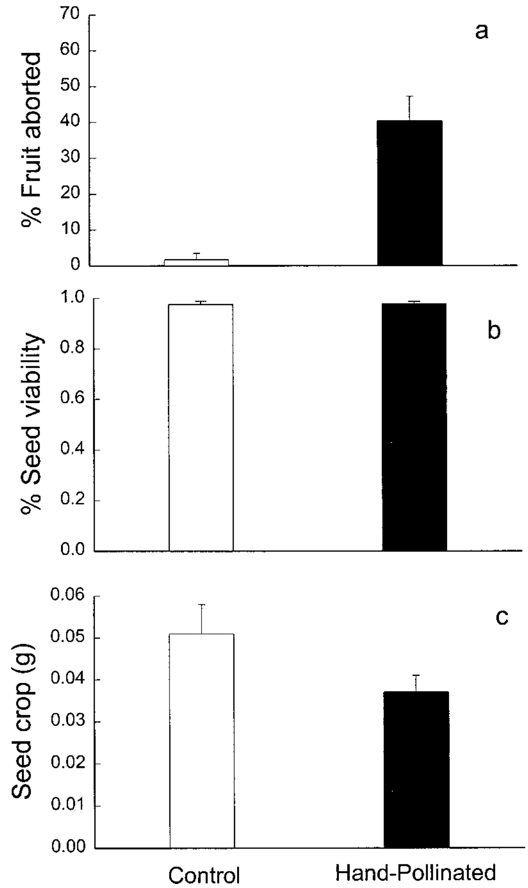

FIGURE 2. (a) Differences in percentage of aborted fruits. (b) Differences in total seed mass (seed crop). (c) Differences in the percentage of viable seeds per fruit. Error bars represent the standard errors around means. All data are for the 1989 reproductive season.

in percent change with respect to leaf length or change in the number of flowers produced between seasons, regardless of year (treatment: $F_{1,63} < 0.22$, $P > 0.64$; year × treatment: $F_{1,63} < 0.03$, $P > 0.86$; Fig. 3). Overall, mean leaf growth was positive and similar across years with a nonsignificant tendency for larger means in both plant groups (year: $F_{1,63} = 1.54$, $P > 0.21$). In contrast, both plant groups showed a significantly lower flower production in 1991 relative to 1990 (year: $F_{1,63} = 69.33$, $P < 0.0001$).

The probabilities of shoot or inflorescence production were not statistically associated with the intensity of pollination in 1990 or 1991 (Table 3); but in 1991, a larger fraction of plants failed to produce a shoot in the hand-pollinated group (66.6%) relative to the naturally pollinated control group (41.4%). Similar nonsignificant tendencies were observed for the frequency of plants that produced inflorescences in 1990 (controls: 37.9%, hand-pollinated: 25.0%) and 1991 (controls: 44.8%, hand-pollinated: 31.0%; Table 3).

Control plants had a compounded fitness index of 0.0125 with a total estimated 0.011 g of viable seeds per plant for the 1989 season and 0.017 g for the 1990 season. Hand-pollinated plants had an index of 0.007 and an estimated 0.018 g of viable seeds in the 1989 season, but only 0.0007 g of viable seeds in the 1990 season. The figures for the compound fitness give relative fitnesses of 1.00 and 0.56 for control and hand-pollinated plants, respectively. This result suggests that lifetime reproductive success is likely to be smaller in heavily pollinated plants relative to naturally pollinated plants, even when hand-pollinated plants produced more fruits and seeds initially.

DISCUSSION

EFFECT OF POLLINATION INTENSITY ON FRUIT AND SEED SET.—An increase in pollinations produced more fruits but fewer seeds per plant during the first reproductive season but not the second. Moreover, hand-pollinated plants showed a compounded fitness estimate about one-third that of control plants. These results suggest that sexual reproduction in this population is pollinator limited within a season but resource limited over the lifetime of the individuals. Such costs associated with fruit production when there is severe pollination limi-

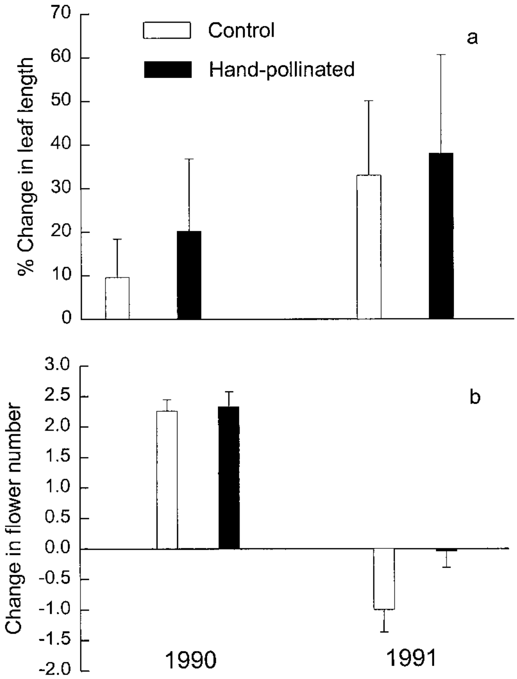

FIGURE 3. (a) Differences in the percentage change in leaf length between reproductive seasons. (b) Differences in the change in flower production per plant between reproductive seasons. Values for 1990 represent differences between 1989 and 1990. Values for 1991 represent differences between 1990 and 1991.

tation have been reported for most epiphytic orchids studied thus far (Montalvo & Ackerman 1987, Ackerman 1989, Zimmerman & Aide 1989, Ackerman & Montalvo 1990, Calvo 1993).

It may be argued that studying the consequences of increased resource use over two years in *C. falcata* does not give a good estimate of lifetime effects because these plants may live several years. In long-lived plants, several years may be needed to regain lost resources without a decrease in lifetime fitness. We believe that this is not the case for *C. falcata* due to various reasons. First, while these plants are perennial, they may not live very long relative to other long-lived plants. Our estimates of plant age suggest that these plants probably live less than a decade (see Methods), thereby limiting the opportunities for recovery. Second, during recovery periods (*i.e.*, 1990 reproductive season), the estimated advantage in the number of viable seeds of control over hand-pollinated plants is 24 to 1, a much larger difference than the observed advantage of hand-pollinated over controls (1.6 to 1) when initial resources were presumably equal (*i.e.*, 1989 reproductive season). This suggests that the fitness advantage for the hand-pollinated plants in the first season would be too small to offset their long-term fitness losses, even with the capacity to recover lost resources.

Previous studies have shown various mechanisms by which epiphytic orchids compensate for increases in fruit production (Montalvo & Ackerman 1987, Ackerman 1989, Zimmerman & Aide 1989, Ackerman & Montalvo 1990, Calvo 1993). Most commonly, these mechanisms involve a reduction in vegetative (*i.e.*, leaf size) and reproductive (*i.e.*, flower number, number of inflorescences) growth in future reproductive seasons. In contrast, our results indicate that mainly there are major short-term adjustments to increases in fruit set in *C. falcata* (increased fruit abortion or reduced seed mass per fruit). Unlike other orchids studied before, *C. falcata* is a nectar-producing orchid. In this context, nectar may be adding a cost to orchid reproduction that results in reduced seed production as a response to increases in pollinations.

Previously, compensation through fruit abortions have been shown only for the orchids *Ionopsis utricularioides* and *Encyclia krugii* (Montalvo & Ackerman 1987, Ackerman 1989); however, in

TABLE 3. *Number of individuals that produced new shoots and new inflorescences in 1990 and 1991.*

	1990		1991	
	Yes	No	Yes	No
Production of new shoots				
Control	22	7	17	12
Hand-pollinated	21	3	8	16
	G = 1.14, df = 1, $P > 0.05$		G = 3.34, df = 1, $P > 0.05$	
Production of new inflorescence				
Control	11	18	13	16
Hand-pollinated	6	18	9	15
	G = 1.02, df = 1, $P > 0.05$		G = 0.29, df = 1, $P > 0.05$	

these orchids, future growth and reproduction were reduced dramatically in response to increases in fruit production, which does not occur in *C. falcata.* Unlike *C. falcata, I. utricularioides* and *E. krugii* grow in drier forests (perhaps more nutrient or water limited), which may explain their need for long-term compensation in response to increased fruit set.

Resource limitations to the quality of fruits (*i.e.*, smaller fruits) also have been reported in the orchid *Aspasia principisa*, which unlike *C. falcata*, may reach up to 0.47 m in size (Zimmerman & Aide 1989). This is surprising, given that plants with longer leaves have a larger photosynthetic surface, and presumably have a higher capacity for storing photosynthates and allocating energy to reproduction (Stephenson 1981). Perhaps, decisions to allocate resources to seed production in *C. falcata* and *A. principisa* are more dependent on the current resource environment (*e.g.*, current rainfall) than on accumulated resources. Some of our results would seem to agree. For example, fruit production in one season did not correlate with size-related characteristics (*i.e.*, leaf size and the number of live shoots; Table 2). In addition, associations between size-related traits and traits related to previous size or reproduction were either lacking or inconsistent (Tables 1 and 2).

Salguero-Faría and Ackerman (1999) showed a lack of selection in favor of higher nectar rewards in *C. falcata.* They suggested that small quantities of nectar in *C. falcata* were maintained by stabilizing selection in which plant reproductive success is limited by a combination of pollinator and resource constraints. Our results corroborate that fruit and seed production in this orchid indeed are constrained by the combination of these factors. Selection in favor of intermediate nectar rewards in this species is likely to occur through two mechanisms. First, further increases in visitation as a result of higher nectar production would not translate into increases in fruit and seed production over the lifetime of these plants because of the cost associated with the production of a large number of fruits. Second, nectar production most likely entails a cost and when resource constraints are severe, a decrease in energy allocation to nectar production may occur (Southwick 1984, Pyke 1991, Koopowitz & Marchant 1998).

This and other studies have demonstrated that an interplay between pollinator and resource limitation affects lifetime reproductive success in animal pollinated epiphytic orchids (*e.g.*, Zimmerman *et al.* 1989). This may have general implications for the evolution of floral traits in these systems. For example, floral traits other than rewards also may be under stabilizing selection in these systems. Our data show that in hand-pollinated plants, the percentage of aborted fruits was positively correlated with the number of flowers produced. Similarly, variation in flower production of *C. falcata* has been linked to variation in the probability of pollinations and pollinaria removals (Rodríguez-Robles *et al.* 1992), but not to variation in fruit set following natural pollination (this study) or the frequency of self-pollination (Salguero-Faría & Ackerman 1999). This suggests that, like nectar production, evolution of flower number in *C. falcata* also may be the result of trade-offs between frequency of pollination and resource limitation. The combined results of these studies suggest two non-mutually exclusive mechanisms for the evolution of flower number. First, a large number of flowers may be favored through increases in the male component of fitness (pollinaria removals). Second, excess flowers may be advantageous when resources are abundant due to year-to-year variation in rainfall or environmental heterogeneity in resource availability. A test of these selective mechanisms would require long-term studies that link the probability of pollinia removal with measurements of male fitness, as well as studies that examine the effect of hand-pollinations and nutrient addition on long-term male and female fitness.

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LITERATURE CITED

ACKERMAN, J. D. 1986. Mechanisms and evolution of food-deceptive pollination systems in orchids. Lindleyana 1: 108–113.

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

———. 1995. An orchid flora of Puerto Rico and the Virgin Islands. Mem. N.Y. Bot. Gard. 73: 1–203.

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

———, AND J. C. MONTERO-OLIVER. 1985. Reproductive biology of *Oncidium variegatum*: moon phases, pollination, and fruit set. Am. Orchid Soc. Bull. 54: 326–329.

———, J. A. RODRÍGUEZ-ROBLES, AND E. J. MELÉNDEZ-ACKERMAN. 1994. A meager nectar offering by an epiphytic orchid is better than nothing. Biotropica 26: 44–49.

ARNOLD, R. M. 1982. Pollination, predation and seed set in *Linaria vulgaris* (Scrophulariaceae). Amer. Midl. Nat. 107: 360–369.

CALVO, R. N. 1990. Four-year growth and reproduction of *Cyclopogon cranichioides* (Orchidaceae) in south Florida. Am. J. Bot. 77: 736–741.

———. 1993. Orchid pollination intensity and frequency and the cost of fruiting. Ecology 74: 1033–1042.

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

EWEL, J. J., AND J. L. WHITMORE. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA For. Serv. Res. Pap. ITF-18. Institute of Tropical Forestry, Rio Piedras, Puerto Rico.

GONZÁLEZ-DÍAZ, N., AND J. D. ACKERMAN. 1988. Pollination, fruit set, and seed production in the orchid *Oeceoclades maculata.* Lindleyana 3: 150–155.

KOOPOWITZ, H., AND T. A. MARCHANT. 1998. Postpollination nectar reabsorption in the African epiphyte *Aerangis verdickii* (Orchidaceae). Am. J. Bot. 85: 508–512.

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

PRIMACK, R., AND P. HALL. 1990. Costs of reproduction in the pink lady's slipper orchid: a four-year experimental study. Am. Nat. 136: 638–656.

PYKE, G. H. 1991. What does it cost a plant to produce floral nectar? Nature 350: 58–59.

RICE, W. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

RODRÍGUEZ-ROBLES, J. A., E. J. MELÉNDEZ, AND J. D. ACKERMAN. 1992. Effects of display size, flowering phenology, and nectar availability on effective visitation frequency in *Comparettia falcata* (Orchidaceae). Am. J. Bot. 79: 1009–1017.

SALGUERO-FARÍA J. A., AND J. D. ACKERMAN. 1999. A nectar reward: is more better? Biotropica 31: 303–311

SCHEMSKE, D. W. 1980. Evolution of 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.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd edition. W. H. Freeman, New York, New York.

SOUTHWICK, E. E. 1984. Photosynthate allocation to floral nectar: a neglected energy investment. Ecology 65: 1775–1779.

STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annu. Rev. Ecol. Syst. 12: 253–279.

ZIMMERMAN, J. K., AND T. M. AIDE. 1989. Patterns of fruit production in a Neotropical orchid: pollinator vs. resource limitation. Am. J. Bot. 76: 67–73

———, D. W. ROUBIK, AND J. D. ACKERMAN. 1989. Asynchronous phenologies of a Neotropical orchid and its euglossine bee pollinator. Ecology 70: 1192–1195.