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The effect of light environment, leaf area, and stored carbohydrates on inflorescence production by a rain forest understory palm

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Abstract Variation in flowering by long-lived plants may be correlated with current resource availability. If, however, there are trade-offs between current and future reproduction, or between reproduction and storage or growth, then understanding variation requires a whole-plant, longer-term perspective. Inflorescence production by *Calyptrogyne ghiesbreghtiana* Linden ex. H. Wendl., an understory palm, was studied over 3 years. Annual inflorescence production varied greatly and was correlated with variation in plant size and light environment. There was no trade-off between past inflorescence production and the frequency of future inflorescence production. On the contrary, individuals that produced more inflorescences than predicted from their size and light environment tended to continue to do so in subsequent years also. I manipulated the resource environment of a subset of plants by removal of leaves and/or reproductive spikes. Leaf removal suppressed inflorescence production for the following 2 years, but spike removal had no effect. One year after leaf removal stored reserves were, on average, back to pre-treatment levels. There was, however, a negative effect of recent inflorescence production on storage. Plants with higher levels of storage had higher inflorescence production in the next 75 days. In *C. ghiesbreghtiana* the resource cost of reproduction is apparent in short-term variation in stored reserves. In contrast, annual inflorescence production does not follow a trade-off pattern between successive years, but consistently reflects both plant size and the light environment.

Key words Allocation · *Calyptrogyne ghiesbreghtiana* · Carbohydrates · Flowering · Trade-offs

Introduction

Like many plants of the rain forest understory, *Calyptrogyne ghiesbreghtiana* Linden ex. H. Wendl. is long-lived and can flower at any time of year. There is, therefore, potential for great variation among individuals in reproductive effort. Why would individuals differ in flowering frequency? Natural selection should ensure that individuals invest resources in reproduction at a rate that maximizes lifetime reproductive success (Stearns 1976). Variation in flowering is typically assumed to reflect underlying variation in the resources that plants have available to commit to reproduction. Plants with more resources might increase fecundity by producing more flowers, either by flowering more often, or increasing flower number in each episode. This prediction is supported by studies that find that the quantity of flowers produced responds to variation in some important limiting resource, such as light (Chazdon 1984; Niesenbaum 1993) or water (Delph 1986; Herrera 1991). Other studies use plant size as a proxy for resource availability and find that bigger plants produce more flowers or flower more often (Aker 1982; Snow and Whigham 1989; Cipollini and Stiles 1991; Herrera 1991).

In addition to varying with plant size and light environment, a plant's current level of flower production may be influenced by its history of flower production. Reproductive tissues have an energetic cost, such that a high level of reproduction at one point in time might draw down reserves and consequently constrain future reproduction (Snow and Whigham 1989). Alternatively, the cost of reproduction may be manifest only in decreased vegetative growth or stored reserves (Chapin et al. 1990), which may, in turn, lead to an increased risk of mortality (Harper 1977; Law 1979; Janzen et al. 1980; Snow and Whigham 1989).

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The aim of this study is to characterize the strategy of reproductive investment by a long-lived understory plant. I have focused on three questions:

1. Does environmental variation lead to variation among individuals in flowering?
2. Does a conflict between flowering and growth or storage lead to detectable trade-offs between the past and the present?
3. How much variation in inflorescence production can be explained by variables measured in a limited time frame?

The focal species, *C. ghiesbreghtiana*, produces only one inflorescence in each flowering event. Variation in seed production per inflorescence is mostly determined by forces extrinsic to the plant, including floral herbivory (Cunningham 1995a), the number of flowers pollinated, effectiveness of pollen transfer (Cunningham 1996), and seed predation (Cunningham 1997). Consequently there are no resource-related effects on per-flowering episode seed production (Cunningham 1995b). Although there is variation among inflorescences in flower number, this variation explains very little of the variation among inflorescences in seed production (Cunningham 1995b). The control of reproductive investment in this species is therefore expected to be modulated by adjustments to the frequency of inflorescence production.

I consider the effect of plant size on the production of inflorescences and the number of flowers per inflorescence, and examine the effect of one potentially important resource, light. Light levels in the rain forest understory are typically extremely low (Chazdon and Fetcher 1984), and variation in the light environment has been shown to influence reproduction by understory palms (Chazdon 1984) and by other plants in tropical and temperate forests (Lubbers and Christensen 1986; Clark and Clark; 1987, Niesenbaum 1993). In contrast, water is unlikely to be limiting because *C. ghiesbreghtiana* occurs in depressions in a wet-tropical rain forest; similarly nutrients are unlikely to be limiting because this species grows in relatively rich volcanic and alluvial soils (Parker 1994). Experiments in nearby sites found nutrient enrichment had little effect on the growth of understory woody perennials (Denslow et al. 1987).

In addition to examining natural levels of variation in inflorescence production I explore the effect of field manipulations. Leaves are a source of carbohydrates that may be expended on flowering, whereas reproductive structures may be significant resource sinks (Stephenson et al. 1988, Snow and Whigham 1989). I manipulated the resource balance of palms by removing leaves and/or reproductive spikes from some plants and examined the effect of these manipulations on the frequency of flowering in the subsequent 2 years. To determine the effect on allocation to storage I measured the amount of non-structural carbohydrates in the trunk of palms in the same population used for source/sink manipulations.

Materials and methods

Focal species and study sites

C. ghiesbreghtiana is an understory palm found in closed forests in Central America. Flowering phenology and pollination of this species is described by Cunningham (1995a). Populations of *C. ghiesbreghtiana* reach high densities in swamps within the rain forest of La Selva Biological Station, Costa Rica, where this study was conducted. Four study sites were selected in four separate swamps, which I refer to as Research, Saltito, Oriental, and Las Vegas.

Because reproductive spikes emerge from buds in leaf axils, the maximum rate of flowering is set by the rate of leaf production. Many palms flower less frequently than their potential by aborting axillary buds. Spikes last approximately 1 year on the plant before they decay (Cunningham 1995b), so the standing number of spikes provides an estimate of the number of inflorescences produced in the past year. Before anthesis flowers are enclosed in a peduncular bract that may contribute some photosynthate towards the cost of inflorescence production. After anthesis, however, there is very little green surface on reproductive spikes, except for the green of unripe fruit.

To determine leaf longevity and rate of production I tagged leaves on eight mature palms in May 1993, and surveyed the same plants again 9 months later. Three of the eight palms were damaged by tree falls before the second census, so estimates of leaf longevity are based on data from five plants. To estimate leaf longevity (L) I used the equation:

$$L = \{[(N_i + p)/f] - 1\}T,$$

where N_i is the number of leaves present at the beginning, and p and f respectively, the number produced and the number lost during the time interval T (Begon and Mortimer 1986).

C. ghiesbreghtiana has very little below-ground structure – the trunk typically extends no more than about 5 cm below the soil surface, and sometimes is wholly above-ground. The root system is adventitious and roots can emerge from any point along the length of the stem. These palms have no potential storage organs other than the trunk.

Variation in plant size, light environment, and flowering

Palms were surveyed in 1992, 1993 and 1994, and their trunk diameter, leaf area, light environment, and the number of reproductive spikes were recorded. To estimate leaf area I measured the length and width of the leaf blade for the three youngest fully expanded leaves. Treating these leaves as triangles, I estimated their area and multiplied the average area of these three leaves by total leaf number. Trunk diameter was measured at the base of the crown of leaves. To measure the light environment I took a photograph of the canopy above each plant with a hemispherical fisheye lens. The lens was positioned at approximately the average height of the palm's leaves, typically 1–2 m above the ground. Each photograph was digitized and then analyzed using SOLARCALC 6.0 (Chazdon and Field 1987). This program maps the course of the sun through the sky, as represented in the digitized image (I used five solar tracks, representing the full annual range of solar position) and estimates the amount of direct and diffuse radiation.

In 1992 I surveyed 131 plants at three sites (Research, Oriental, and Saltito). In 1993 measurements were repeated on these plants if they flowered during the research period, and new flowering plants were measured in each of these sites. A new site (Las Vegas) with 60 flowering plants was also surveyed (1993, $n = 248$). In 1994 I surveyed plants that had flowered in either of the previous two years, even if the plant currently had no reproductive spikes, and also included any new flowering individuals ($n = 282$). Three-quarters of the plants at the Las Vegas site were experimentally manipulated and so could not be included in measures of natural

variation. I counted the number of flowers on each inflorescence in 1992 and on 91 inflorescences in the Oriental and Saltito swamps in 1993. No data on flower number were collected in 1994.

Path analysis was used to analyze relationships between plant size, light environment, and flowering (Li 1975; Sokal and Rohlf 1981; Schemske and Horvitz 1988; Mitchell 1993). Path coefficients were calculated using the multiple regression and Pearson correlation functions in SYSTAT (Wilkinson 1992). To detect any deviations from linearity I inspected normal plots of residuals, and plotted residuals against estimates and against the other predictor variables in the model for all models used in path analyses and multiple regressions (Pedhazur 1982). Inspection of residuals for each model used indicated that linear regressions were appropriate.

Trade-offs in inflorescence production

If there is a direct trade-off between allocation to current inflorescence production and allocation to future inflorescence production, then one would predict that a period of frequent flowering should be followed by a period with relatively less flowering. To detect such a pattern, however, one must first account for other correlations with leaf area, trunk diameter, and light environment. The path analysis assesses these effects in 1993 and 1994. If there is a trade-off between years in reproductive investment this would be indicated by negative paths between last year's inflorescence production and the current year's inflorescence production.

Spike and leaf removal experiment

In 1993 I divided the 60 palms in the Las Vegas site into four groups of 15 plants, with an approximately similar distribution of leaf area, trunk diameter and spike number in each. These four groups were assigned to each of four treatments in a two-way design:

1. Removal of all but the three youngest leaves (counting unexpanded leaves)
2. Removal of all reproductive spikes (inflorescences and infructescences)
3. Removal of leaves and spikes
4. No manipulation

Treatments were set up over 2 days in early April 1993. In the following month I took canopy photographs above each palm. To assess the effect of spike and leaf removal I counted the number of still-living reproductive spikes on each palm (i.e., not including spikes that were past fruit maturation and withering) in February 1994, April 1994, and March 1995. Results of this experiment were analysed by two-way analysis of covariance. After accounting for covariance with trunk diameter and the previous year's light environment, residual variation in inflorescence number was approximately normal in both years, thereby permitting normal analysis.

Carbohydrate storage

I collected tissue samples from the 60 palms used in the spike and leaf removal experiment in early February 1994, 1 year after the experimental treatments. Samples were collected from the trunk at the base of the leaves using a tree corer (9 mm diameter) and the holes were plugged with cork stoppers. Because the apical meristem sits above the level of the leaf bases, I judged that removing tissue from the trunk below the leaf bases was unlikely to cause damage to the apical meristem. No plants showed any sign of decay or infection around the coring hole 1 year after removing the trunk samples.

Trunk tissue samples were freeze-dried within a few hours of collection. For analysis samples were ground, weighed, sonicated, and enzymatically digested with alpha-amylase then amylogluco-

sidase. Glucose concentration of the supernatant was determined colorimetrically using the phenol-sulfuric acid method (Dubois et al. 1956).

Results

Size, light, and flowering

In all three years of the study most plants produced two to five reproductive spikes. In 1992 the modal category was two, whereas in 1993 and 1994 the modal category was three. The greatest number of spikes counted on one palm was 11, in 1993. Only in 1994 did I collect data on the frequency with which plants failed to flower. I located almost all plants that I had found flowering in the previous 2 years, and 10% of these palms lacked reproductive spikes in 1994 (Fig. 1).

Plants produced on average 5.1 ± 1.2 (SD) new leaves per year. Leaf longevity was estimated to be 5.2 years; however, older leaves tended to accumulate epiphyllous growth and so may have ceased to be a net source of carbohydrates before 5 years had passed.

The number of flowers per inflorescence was less variable than the number of inflorescences per plant. The mean number of flowers per inflorescence was 234 ± 64.4 (SD) in 1992 ($n = 131$) and 250 ± 64.6 (SD) in 1993 ($n = 91$). Therefore the coefficient of variation in flowers per inflorescence was 26–27%, compared to 44–47% for number of inflorescences per plant (not including zeroes). Variation in plant size explained some of the variation in the number of flowers per inflorescence, whereas there was no significant effect of light environment (Table 1).

Mean photosynthetic photon flux density (PPFD) for all plants at all sites was $3.3 \text{ mol m}^{-2} \text{ day}^{-1}$ (SD = 1.5) in both 1992 ($n = 132$) and 1993 ($n = 248$). In 1994 the mean across all plants in all sites increased to $4.1 \text{ mol m}^{-2} \text{ day}^{-1}$ (SD = 2.4), consistent with some major tree

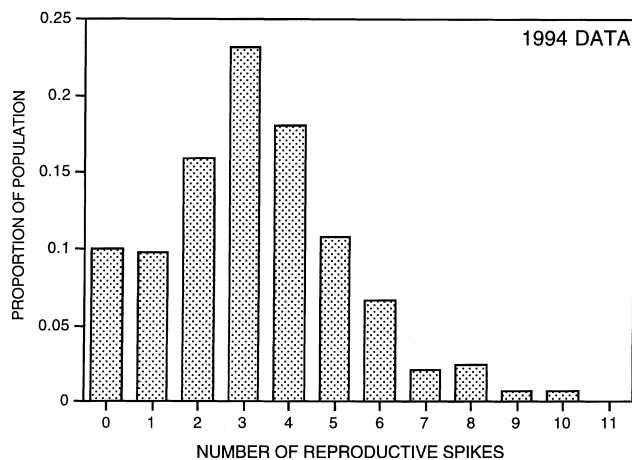


Fig. 1 Histogram of the number of reproductive spikes per plant in 1994 ($n = 289$). Histograms for 1992 and 1993 are similar, except that non-flowering palms were not counted

Table 1 Multiple regressions on number of flowers per inflorescence in 1992 and 1993, considering trunk diameter, leaf area and light availability (mean daily photosynthetic photon flux density, PPFD) in the same year

Independent variable	Dependent variable Flowers per inflorescence 1992 ($n = 131$, $R^2 = 0.218$)		Dependent variable Flowers per inflorescence 1993 ($n = 91$, $R^2 = 0.284$)	
	Standardized coefficient	P	Standardized coefficient	P
Trunk diameter	0.194	0.077	0.457	0.002
Leaf area	0.326	0.002	0.162	0.263
PPFD	0.023	0.777	-0.102	0.306

falls opening the canopy in two sites that year. Thus there is a strong correlation between mean PPFD in 1992 and 1993, but reduced correlation between PPFD in either of these years and PPFD in 1994 (Fig. 3).

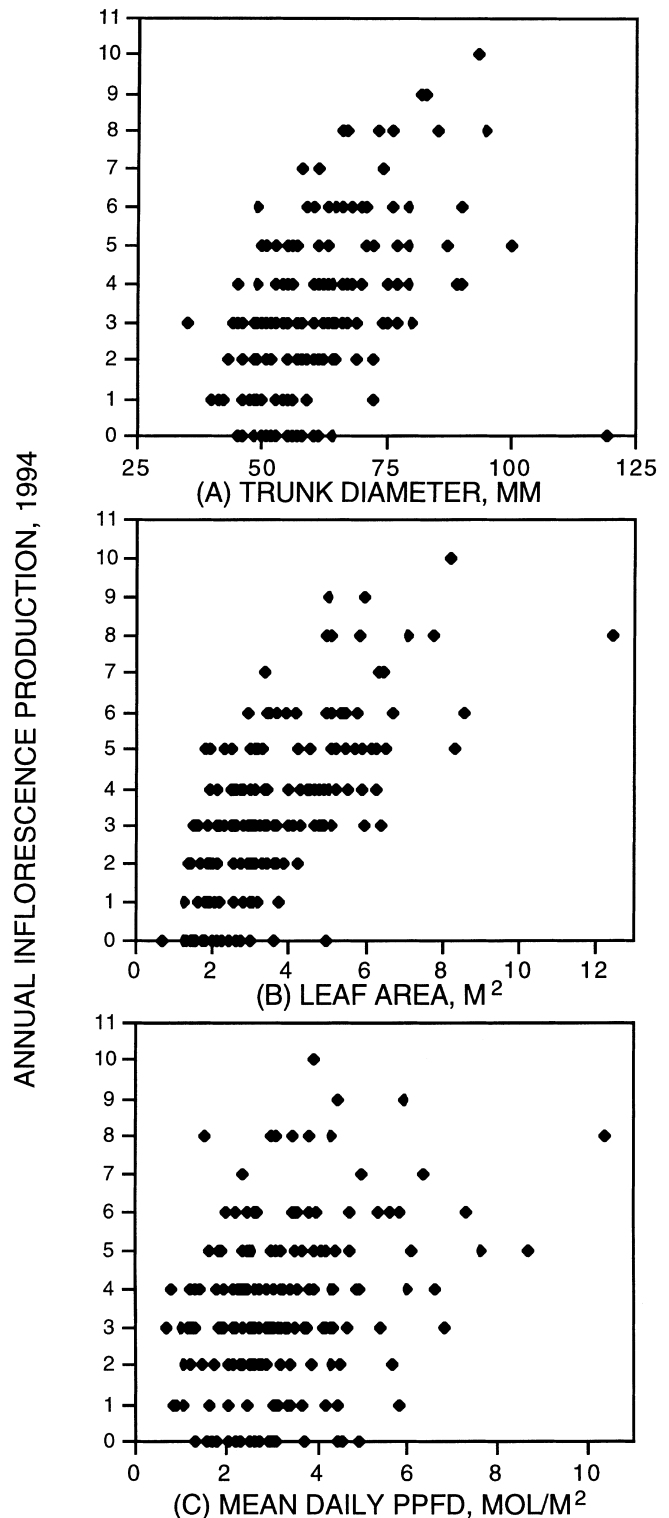
In all three years there were positive correlations between inflorescence production and trunk diameter, leaf area, and light availability (e.g., Fig. 2). There were also correlations among these independent variables. The model used for path analysis includes these effects, but in addition includes effects of light environment, plant size and inflorescence production in the previous year on plant size and inflorescence production on 1993 and 1994. Data for the previous year were not available in 1992, so all paths are within the year.

In 1992 there was a strong positive effect of trunk diameter on leaf area. As expected, significant paths link trunk diameter in one year to trunk diameter in the next, and similarly for leaf area. In addition, however, there were significant paths from leaf area to trunk diameter in the subsequent year, suggesting a measurable effect of leaf area on future vegetative growth. In summary, plants with big trunks supported more leaf area, which led to growth in trunk diameter in the following year.

Bigger plants produce more inflorescences. There are positive effects of trunk diameter and leaf area on spike number in 1992 and 1993. In 1994 there is a strong effect of leaf area on spike number, and a weak negative path from trunk diameter to spike number. Plants that produce more inflorescences than predicted by their size and light environment tend to do the same in subsequent years. This effect is illustrated by significant positive paths linking inflorescence production in 1993 and 1994 to the previous year's inflorescence production.

There were significant positive effects of light environment on plant size and inflorescence production. In 1992 the current light environment had positive effects on trunk diameter and inflorescence production. In 1993 and 1994 the effects of the previous year's light environment were stronger than the current light environment. Previous year's light had a positive effect on leaf area in 1993, and on inflorescence production in 1994.

Fig. 2A–C Scatter plots of three resource variables on annual inflorescence production in 1994 ($n = 183$). **A** Trunk diameter in 1994, **B** leaf area in 1994, **C** mean daily photosynthetic photon flux density (PPFD) in 1993. Multiple regression showed that these three variables together explained 47.5% of the variance in inflorescence production



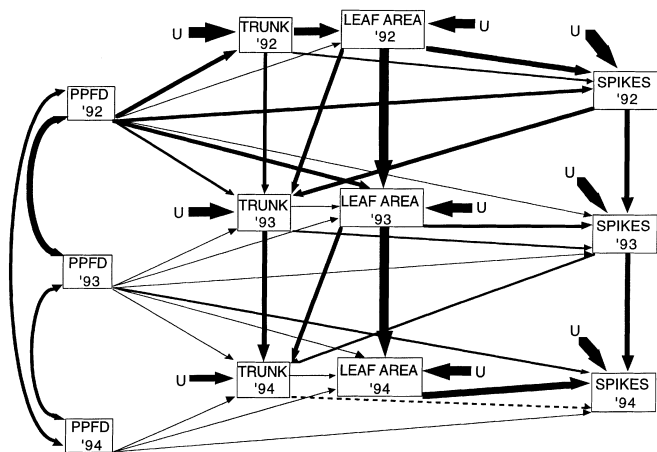


Fig. 3 Path analysis for number of reproductive spikes per plant, in 1992, 1993 and 1994. Arrow thickness is approximately proportional to the size of the path coefficient (from Table 2). Dashed lines denote significant negative paths. Double-headed arrows denote correlation between predictor variables. U denotes total unexplained variation [square root of (1-R²)]

Spike and leaf removal experiment

Analysis of covariance indicates a significant effect of leaf removal on inflorescence production one year after the manipulation (Table 3). Two years after leaf removal the effect is weak, but on the margin of significance (Table 3). Spike removal had no significant effect, and there was no significant interaction between treatments (Table 3). The effect of leaf removal is apparent comparing the distributions of the two sub-populations – those that had leaves removed, and those that did not (Fig. 4). Because leaf lifespan is ~5.2 years, palms in the removal treatment still had fewer leaves 2 years after the manipulation (11 ± 1.8, compared to 17 ± 4.6 in palms that did not have leaves removed, *t*-test with unequal variances, *P* < 0.001).

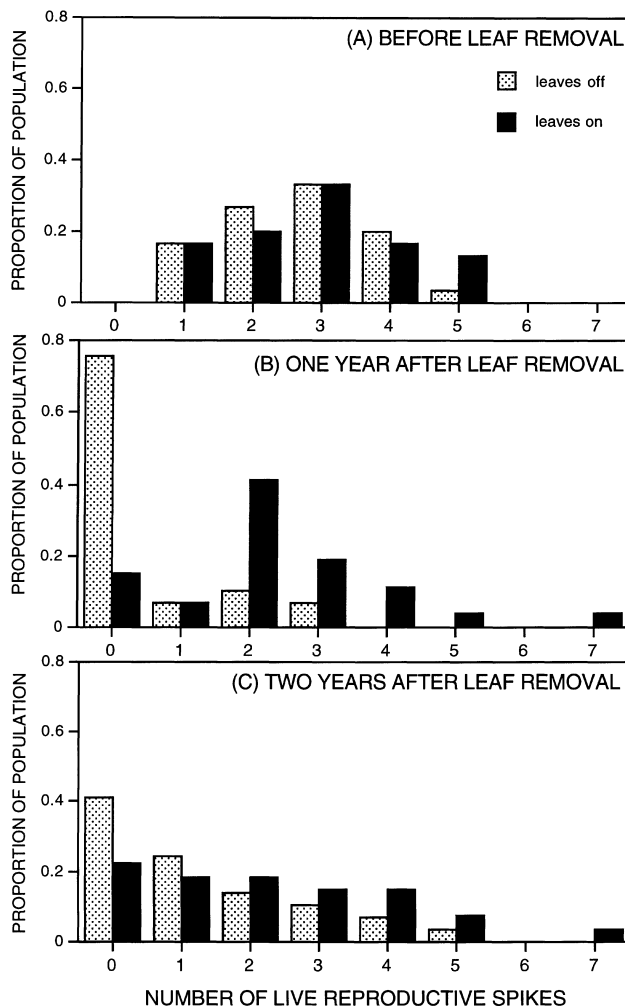


Fig. 4A–C Frequency histograms of the number of live reproductive spikes on each palm in source/sink manipulation experiment. **A** In February 1993, before the leaf removal experiment, comparing the population selected to lose leaves (stippled, *n* = 30) to those selected to retain leaves (solid, *n* = 30). **B** In April 1994, 13 months after leaf removal treatment: leaves removed (stippled, *n* = 29), leaves not removed (solid, *n* = 27). **C** In March 1995, 24 months after leaf removal treatment: leaves removed (stippled, *n* = 29), leaves not removed (solid, *n* = 27)

Table 2 Path coefficients (for Fig. 3) and variance explained (R²) from multiple regressions. For dependent variables in 1993 and 1994 effects include variables from the previous year

Dependent variable	Independent variables Same year			Previous year				<i>n</i>	R ²
	PPFD	Trunk diameter		PPFD	Trunk diameter		Spikes		
		Leaf area	Leaf area		Leaf area	Spikes			
Trunk '92	0.302*							131	0.09
Leaf area '92	-0.023	0.685*						131	0.45
Spiques '92	0.218*	0.11	0.486*					131	0.41
Trunk '93	0.066			0.188	0.261	0.263	0.206	43	0.52
Leaf area '93	-0.023	-0.041		0.279*		0.800*		43	0.76
Spiques '93	0.029	0.139	0.291*	0.066			0.448*	43	0.63
Trunk '94	0.007			0.086	0.441*	0.349*	0.117*	182	0.67
Leaf area '94	-0.038	0.055		-0.003		0.854*		181	0.79
Spiques '94	-0.041	-0.156*	0.561*	0.139*			0.409*	181	0.59

**P* ≤ 0.05

Table 3 Analysis of covariance in production of reproductive spikes after leaf and spike removal treatments in April 1993 (two-way design). Overall degrees of freedom declined in 1995 because three plants were destroyed by tree falls. Residual variation in number of living spikes, after regression with trunk diameter and light environment, was approximately normal, suggesting that normal analysis was appropriate

Source of variation	Dependent variable			Dependent variable		
	Living spikes, April 1994			Living spikes, March 1995		
	<i>df</i>	MS	<i>P</i>	<i>df</i>	MS	<i>P</i>
Leaf removal treatment	1	9.13	0.004	1	9.15	0.057
Spike removal treatment	1	1.98	0.166	1	1.28	0.469
Leaf × Spike interaction	1	0.29	0.595	1	1.68	0.406
Trunk diameter 1994 (co-var.)	1	7.52	0.008	1	11.31	0.035
Previous year's light (co-var.)	1	0.14	0.711	1	20.52	0.005
Error	51	1.41		48	2.40	

Table 4 Path coefficients (for Fig. 5) and variance explained (R^2) from multiple regressions on number of living spikes and stored carbohydrates after leaf removal experiment. The number of living spikes was counted in February 1994 (10 months after leaf removal

treatment) and again 75 days later, in April 1994. Stored carbohydrates and trunk diameter were measured in February, light environment (PPFD) and leaf area were measured before leaf removal treatment in February 1993

Dependent variable	Independent variables							R^2
	Trunk 1994	Leaf area 1993	Leaf treatment	PPFD 1993	Living spikes Feb. '94	Storage Feb. '94	<i>n</i>	
Living spikes, Feb. '94	0.207	0.145	-0.350*	0.010			57	0.25
Storage, Feb. '94	-0.110	0.290	-0.106	0.150	-0.326*		57	0.13
Living spikes April '94	0.240*	-0.131	-0.377*	0.035	0.636*	0.271*	56	0.76

* $P \leq 0.05$

Stored carbohydrates

Tissue samples from trunks of the 60 palms in the source/sink manipulation experiment contained, on average, 6.9% (SD = 3.1%) total non-structural carbohydrates by weight. A two-way analysis of covariance (including plant size traits and light environment) found no significant effect of leaf or reproductive spike removal on the level of stored carbohydrates in the subsequent

year. Significant variation in stored carbohydrates is, however, apparent in a path analysis that includes inflorescence production in addition to treatment effect, plant size, and light environment (Fig. 5). As was apparent in the non-manipulated population followed for 3 years (Fig. 3), plants that flower more than predicted given their size and environment tend to continue to do so in the future, hence there is a strong direct effect of the number of living spikes in February 1994 on the number of living spikes in April 1994 (Fig. 5). There is, however, a second path via the level of stored carbohydrates. The number of living spikes in February has a negative effect on the current level of stored reserves, and the level of stored reserves has a positive effect on the number of living spikes in April (Fig. 5, Table 4).

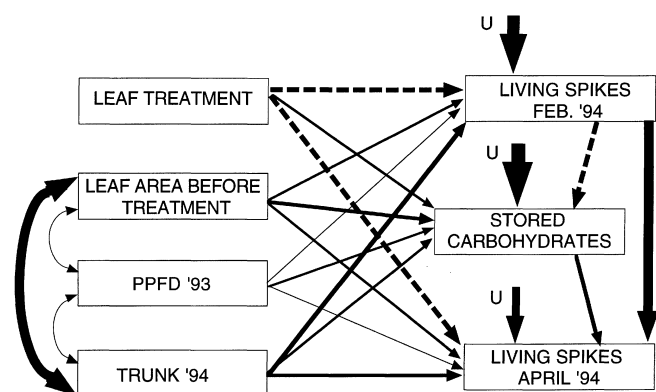


Fig. 5 Path diagram for number of reproductive spikes per plant ($n = 56$) early in 1994 (1 year after leaf removal treatment), stored reserves measured at the same time, and the number of new inflorescences 75 days later. Arrow thickness is approximately proportional to the size of the path coefficient (from Table 4). Dashed lines denote significant negative paths. Double-headed arrows denote correlation between predictor variables. *U* denotes total unexplained variation [square root of $(1-R^2)$]

Discussion

Variation in inflorescence production

There is great variation in annual inflorescence production by *C. ghiesbreghtiana*. Approximately 10% of reproductively mature individuals failed to flower at all, while other palms produced up to 11 inflorescences. This disparity establishes the potential for great differences among individuals in long term seed production, due solely to variation in flowering frequency.

Inflorescence production was correlated with trunk diameter and leaf area of palms. A large leaf area and

thick trunk may help a plant harvest light and store carbohydrates, but carbohydrate production depends on the availability of light. The estimated PPFD at the plant's microsite 1 year previous explains additional variance in inflorescence production not explained by plant size (Table 2, Fig. 3). The fact that light environment in past years explained more variance in inflorescence production than the current light environment should not be surprising, considering that inflorescence production is being assessed for the past year. A recent change in light environment is unlikely to be reflected in the standing number of inflorescences. The importance of the past year's light environment to flowering has also been noted for the shrub *Lindera benzoin*, growing under the canopy of temperate forests (Niesenbaum 1993).

Because inflorescences emerge from leaf axils, the upper limit of production is linked to the rate of leaf production. On average, about five new leaves were produced each year, and two to three spikes emerged. Therefore inflorescence production is not normally at the maximum level set by availability of inflorescence buds.

Plant size and light environment measures were estimates based on observation at only one point in time for each plant, in each year of data collection. Leaf area was not measured precisely, but extrapolated from the area of three leaves on each plant – the estimate does not account for different age or condition of leaves. Light environment was estimated from photographs of the canopy above plants, and cannot account for the constantly changing nature of the canopy through time, as canopy and sub-canopy plants grow or fall. Given these limitations of the data, it is striking that they can explain more than 40% of the variation in inflorescence production, even without including the correlation with the previous year's inflorescence production (Fig. 2, Table 2). These results suggest that inflorescence production is closely linked to these parameters. If one could know the photosynthetically active leaf area and light environment precisely, and how these variables have changed through time, it is likely that one could predict inflorescence production with great accuracy. This might not be particularly surprising for a species with a predictable, short flowering season, but is remarkable for a long-lived species with such varied inflorescence production as *C. ghiesbreghtiana*.

Although much variation in inflorescence production can be explained by trunk diameter, leaf area and light environment, path analysis suggests that other important effects have not been measured. The positive paths connecting current inflorescence production to the previous year's inflorescence production indicate that some plants are consistent over-performers, presumably due to unmeasured sources of environmental or genetic variation. This pattern is apparent in the unmanipulated population, comparing one year to the next, and in the experimentally manipulated population, comparing the number of living spikes before and after a 75-day interval.

The cost of reproduction

It is often supposed that there is a cost to reproduction that will be reflected in resource trade-offs, such that a period of abundant flowering would be followed by a period of poor flowering. Studying a temperate orchid, Snow and Whigham (1989) clearly demonstrated reduced growth and flowering following a reproductive event. If such trade-offs occurred in *C. ghiesbreghtiana* then the disparity among plants in inflorescence production in one year would be diminished by compensating performance in the future. Furthermore, the existence of trade-offs would limit our ability to predict inflorescence production on the basis of plant size and light environment, because the past record of flowering would be an important variable in any predictive model. But such resource trade-offs did not emerge from the data analyzed on the one or two year time scale. In fact, palms that produced more inflorescences than expected (for their size and light environment) were likely to do so in subsequent years also.

Horvitz and Schemske (1988) also looked for resource trade-offs as a consequence of reproductive effort in a tropical perennial, but one with a herbaceous habit. They removed inflorescences from some individuals and increased fruit production using hand pollination on other individuals, then looked for effects on growth, survival and reproduction in the subsequent year. No significant effects emerged. In discussing their results they imply that the absence of any measurable cost to reproduction may be typical of long-lived perennial plants.

Although this study, and that of Horvitz and Schemske (1988), did not detect any effect of reproductive effort in one year on reproductive effort in the subsequent year, considering natural and artificially induced variation, it is indisputable that reproduction entails some energetic cost. Experimentally defoliated palms had a reduced rate of inflorescence production, still detectable 2 years later. These palms were not able to harvest as much light until leaves were replaced, and this reduced resource availability was expressed in reduced reproduction. I also detected effects on stored carbohydrates. Recent flowering had a negative effect on stored reserves, while the level of storage had a positive effect on the amount of flowering in the next few months (Fig. 5) indicating that carbohydrates stored in the trunk are being used as a short-term buffer for the cost of reproduction.

The negative path from trunk diameter to spike number in 1994 may indicate that palms that invest more in trunk growth can suffer reduced inflorescence production. Evidence for this is, however, equivocal given that the effect was weak (though significant) in 1994, and not apparent in the previous year, when the path from trunk diameter to inflorescence production was positive (though non-significant).

There is, therefore, a measurable cost to reproduction, but this cost is not expressed as a between-year

trade-off in inflorescence production. If there is a trade-off in inflorescence production it is occurring over a time scale of less than 1 or greater than 2 years, or is too subtle to be detectable against the background of individual variation from other sources.

Because inflorescences of *C. ghiesbreghtiana* vary in the number of fruit that they mature, the actual cost of each reproductive spike is probably variable (Snow and Whigham 1989). Unfortunately, it was impossible to determine how many fruit (if any) developed on every inflorescence produced through the year on each palm. If these data were known it is possible that some more substantial reproductive cost would be detectable. However, such a cost must be relatively rarely incurred in the field population because the pattern of inflorescence production is contrary to that expected in a trade-off model.

Stored carbohydrates

Although leaf removal affected flowering frequency for at least 2 years, there was no effect of leaf removal on the level of stored carbohydrate in the trunk in the subsequent year. The positive effect of leaf area before the removal experiment, and the negative effect of recent flowering only explained 10% of variation in storage (Table 4). Together these patterns suggest that palms allocate to storage first and flowering second, so that 1 year after defoliation, storage levels are, on average, close to a normal level, while inflorescence production remains suppressed. Variation in the level of stored carbohydrates did respond to variation in inflorescence production, with recent flowering drawing down reserves, and higher reserves leading to more flowering in the next few months. This pattern is consistent with a strategy in which the expansion of another inflorescence is cued when storage exceeds a threshold and suppressed when storage is below the threshold, thus maintaining a relatively stable level of storage.

Other researchers that have experimentally defoliated palms have recorded little or no effects on survivorship, and at some levels even positive effects on growth or reproduction (Mendoza et al. 1987; Oyama and Mendoza 1990; Chazdon 1991; Ratsirarson 1993). These results have been interpreted as evidence that these palms were able to mobilize stored reserves, although storage was not measured in these studies. Although resilient to defoliation, *Astrocaryum mexicanum*, *Geonoma congesta*, and *Neodypsis decaryi* showed suppressed reproduction after some levels of leaf or ramet removal (Mendoza et al. 1987; Chazdon 1991; Ratsirarson 1993) as was also observed in *C. ghiesbreghtiana*. These species may be using a similar strategy to *C. ghiesbreghtiana*, using stored reserves to survive periods of low resource availability and buffer the cost of reproduction, but allocating to storage in preference to reproduction after periods of resource stress.

Conclusions

There is great variation in annual inflorescence production among individuals of *C. ghiesbreghtiana*, which may lead to substantial differences in reproductive success over the long term. Much of the variation in flower production is correlated with variation in plant size and the recent history of the light environment. These patterns, and the significant effect of defoliation on inflorescence production, make it clear that variation in flowering is largely controlled by variation in resource supply. In addition, there is a measurable cost of reproduction in terms of allocation to storage. This trade-off is subtle, and most apparent on the time scale of a few months. On a one to two year time scale there is no detectable effect of past flowering on the frequency of future flowering. On the contrary, some plants consistently produce more inflorescences than predicted by their size and light environment.

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