LEAF PRODUCTION AND THE COST OF REPRODUCTION IN THE NEOTROPICAL RAIN FOREST CYCAD, *ZAMIA SKINNERI*

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SUMMARY

(1) Leaf production and reproductive output were followed over 6-6 years for 180 individuals of *Zamia skinneri*, a cycad of tropical rain forest understory. In this light-limited environment there were marked interactions between leaf production and cone (strobilus) production, indicating a significant 'cost of reproduction'.

(2) At the population level, leaf production peaked in May-July each year, causing an annual cycle in the number of leaves on individuals. On the average, plants produced a total of 8-8 leaves in four episodes over the 6-6 years.

(3) The median number of reproductive episodes for primary forest males and females was one over the 6-6-year period, but significantly more males produced cones two and three times.

(4) Both cone production and total leaf production were correlated with an index of canopy openness as well as with plant size.

(5) Reproductive individuals increased leaf number by an average of 28-41% one year prior to cone production. Very few reproductive individuals flushed new leaves in the year of reproduction, and female (but not male) leaf production was depressed for two years after cone production.

(6) The low rate of leaf and cone production, and the correlation of leaf production and reproductive output with canopy openness over a very small range of values, indicate that *Z. skinneri* is highly light-limited.

(7) The relation of leaf production to cone production and the depressing effect of reproduction on future cone production demonstrate a clear cost of reproduction, which in all aspects is higher for females than for males.

(8) Evaluation of the lifetime consequences to long-lived organisms of different patterns of allocation to reproductive and vegetative structures will require long-term observations on individuals in their natural habitat.

INTRODUCTION

The pattern of allocation of carbon and nutrients to primary plant functions is a critical determinant of the population biology of a species. Allocation patterns have been well studied in some crop species, but much less is known about plants in natural habitats (Ehleringer, Peary & Mooney 1986). One ecological approach to the study of allocation in natural populations has been the 'cost of reproduction' model with its central hypothesis that increased allocation to reproduction must be correlated with decreased allocation to other functions such as growth or future reproduction (Reznick 1985). A corollary of this hypothesis is that in dioecious species in which female reproductive investment exceeds male investment, the summed negative consequences of reproduction will be correspondingly higher in females than in males.

This report presents phenological data on leaf production and cone (strobilus) production over a 6-6-year period for *Zamia skinneri* Warc., a long-lived dioecious cycad.
of tropical lowland rain forest, documenting first the incidence, magnitude, and timing of leaf production, and then the consequences of different patterns of allocation to leaf and cone production. Temporal and environmental patterns of reproduction in *Z. skinneri* have been described elsewhere (Clark & Clark 1987a).

METHODS

*Zamia skinneri* is a single- or double-stemmed cycad occurring in wet tropical forest in Central America (Gómez 1982). Individuals have from one to thirty or more long-lived leaves. Reproduction is mainly from seed, although occasionally plants split into two when damaged by litterfall (personal observation). Males produce one to ten slender 7–15 cm tall cones which remain on the plant for about five months. Females usually produce a single much thicker 7–22 cm tall cone that matures in approximately eighteen months (Clark & Clark 1987a). Like all cycads, the species is strictly dioecious, and no reversals of sex were observed during the study.

Most small plants and some large ones are rosettes at ground level, while many large individuals develop an erect stem up to 1.5 m tall. Injury and stem breakage due to litterfall are common. Stem size is therefore not a satisfactory measure of plant age or size (i.e., plant biomass). This study used the maximum number of leaves observed on an individual as well as the number of leaflets on the largest leaf as indices of plant size. Due to the effects of catastrophic herbivory or physical injury these indices do not always increase monotonically with increasing age or total plant biomass; however, in this study and previous work (Clark & Clark 1987a) these measures of plant size were found to be strongly related to growth and reproductive performance.

Several features of *Z. skinneri* make it ideal for long-term study of allocation to leaf production and reproduction. Reproductive structures are few and relatively long-lived. New leaves always originate in the centre of the rosette, and are produced in discrete flushes. Appearance of new leaves on an individual may be simultaneous or spread out over a period of up to three weeks. Development from crozier to fully expanded and hardened leaf takes about sixty-five days (D. A. Clark & D. B. Clark, unpublished data). After hardening, new leaves retain a distinctive light-green colour for several months. When a leaf dies, the base of the rachis often remains attached to the plant for many months; detached rachises also persist for months after falling from the plant. By counting several times a year the total number of leaves, as well as the number of new leaves and dead leaf rachises, it is possible to keep an exact record of leaf production without marking individual leaves.

The study was carried out at the La Selva Biological Station of the Organization for Tropical Studies, in the Atlantic lowlands of Costa Rica. The forest is classified as tropical wet (Hartshorn 1983), and has been described in detail by Holdridge *et al.* (1971) and Lieberman *et al.* (1985a,b). Rainfall averages 4 m annually (OTS, unpublished records).

In March 1980, 180 individuals of *Z. skinneri* were marked in primary and secondary forest at La Selva. The selection of plants was non-random (biased towards larger individuals), but was made without knowledge of the sex of the plant. All individuals were censused between three and five times per year until October 1986, a total of twenty-six censuses. For double-crowned individuals (*n* = 7) the total number of leaves on both crowns was recorded. In the first two censuses total leaf number, reproductive condition, and the presence and number of new, unhardened leaves were recorded. For the next twenty-four censuses the number and colour (green or brown) of dead leaf bases were also
Fig. 1. The rate of production of new leaves in *Zamia skinneri* (n = 180) at the La Selva Biological Station, Costa Rica (●—●—●). Rates were calculated as the total number of new leaves produced between censuses by the 180 individual plants, divided by the number of individuals, divided by the intercensus interval in days, times 100. Monthly rainfall totals in mm are shown on the upper curve (●—●—●).

noted. Episodes of leaf production (= 'flushes') were calculated as the number of censuses when new, unhardened leaves or hardened leaves produced between censuses, or both, were present on an individual.

In October 1982 and October 1985 canopy openness above all individuals in primary forest was measured using a spherical densiometer, a convex mirror with an engraved grid (Lemmon 1956). The two values were averaged for each individual to give an estimate of the average light environment of individuals during the study (n = 149 for these analyses; data for three individuals were lost).

RESULTS

*Phenology of leaf production*

Production of new leaves by *Zamia skinneri* is strongly seasonal (Fig. 1). From 1980 to 1986 maximum production of new leaves occurred in May–July, a period corresponding to the beginning of the rainy season. However, there were almost always some individuals with new leaves at each census; in only one of twenty-six censuses over 6-6 years were no new leaves encountered.

The concentration of new leaf flushing in a restricted interval caused an annual cycle in the number of leaves present on individuals (Fig. 2). From 1980 to 1986 an average of 92% of the individuals achieved their highest annual leaf number between May and July (n = 6 years, range 82–99%), after which leaf number remained stable or declined. The 1986 flush did not produce the increase in mean leaf number seen in the previous six years. This was caused not only by the lower rates of production of new leaves (Fig. 1 and Fig. 2, compare with 1981 and 1983), but also by increased leaf mortality.
Cycad phenology and reproduction cost

Fig. 2. Average number of leaves present on 180 Zamia skinneri at the La Selva Biological Station, Costa Rica, March 1980–October 1986.

Frequency of reproduction

Cone production by Z. skinneri at La Selva was restricted to the May–July period, which is the transition between the drier and wetter annual seasons. There were two major reproductive episodes during the study (1981 and 1985, Clark & Clark 1987a). Although the modal number of reproductive events over the 6·6 years was one for both males and females (Table 1), significantly more males than females reproduced more than once (Mann–Whitney U, one-tailed $P < 0·05$). Secondary forest plants which were larger and in better-lit sites, produced cones more frequently than primary forest plants (Table 1 and Clark & Clark 1987a). In primary forest, all nine marked females produced cones only once in 6·6 years.

Plant size, reproductive history, and leaf production

The number of leaves produced over the study increased with plant size, defined either as the maximum number of leaves observed on a plant over this period or as the number of leaflets on the largest leaf (Table 2). Because reproductive plants were larger than non-

<table>
<thead>
<tr>
<th>Number of reproductive events</th>
<th>Proportion of plants</th>
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<tbody>
<tr>
<td></td>
<td>PF</td>
<td>SF</td>
<td>PF</td>
<td>SF</td>
</tr>
<tr>
<td>1</td>
<td>0·62</td>
<td>0·14</td>
<td>1·00</td>
<td>0·50</td>
</tr>
<tr>
<td>2</td>
<td>0·32</td>
<td>0·43</td>
<td>0·00</td>
<td>0·33</td>
</tr>
<tr>
<td>3</td>
<td>0·05</td>
<td>0·36</td>
<td>0·00</td>
<td>0·17</td>
</tr>
<tr>
<td>4</td>
<td>0·00</td>
<td>0·07</td>
<td>0·00</td>
<td>0·00</td>
</tr>
</tbody>
</table>

$n = (37) (14) (9) (6)$

Table 1. Number of episodes of cone production by Zamia skinneri at the La Selva Biological Station, Costa Rica, from March 1980 until October 1986. PF = Primary forest, SF = secondary forest.
Table 2. Mean number of new leaves per plant (n in parentheses) produced by 180 *Zamia skinneri* from March 1980 until October 1986 at the La Selva Biological Station, Costa Rica. Plants are classified according to their reproductive performance over this period, and by the maximum number of leaves or maximum number of leaflets per leaf observed during the study. Size-class divisions were chosen to separate the sample into terciles as nearly as possible. Probability values are the probability of a difference in production of new leaves among reproductive categories at each size class, computed by Kruskal–Wallis non-parametric ANOVA.

<table>
<thead>
<tr>
<th>Plant size</th>
<th>Mean leaf production 1980–86</th>
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</thead>
<tbody>
<tr>
<td>Maximum number of leaves observed</td>
<td>Non-reproductives</td>
</tr>
<tr>
<td>≤5</td>
<td>4.9 (53)</td>
</tr>
<tr>
<td>6–7</td>
<td>7.8 (40)</td>
</tr>
<tr>
<td>&gt;7</td>
<td>11.8 (21)</td>
</tr>
<tr>
<td>Number of leaflets on largest leaf</td>
<td></td>
</tr>
<tr>
<td>≤11</td>
<td>5.1 (36)</td>
</tr>
<tr>
<td>12–13</td>
<td>6.6 (45)</td>
</tr>
<tr>
<td>&gt;13</td>
<td>10.3 (33)</td>
</tr>
</tbody>
</table>

reproductive ones, mean leaf production by reproducitives was higher than that of non-reproducitives. When equal-sized plants were compared, however, there were no statistically significant interactions between reproductive performance and leaf production (Table 2).

The total number of leaves produced during the 6.6 years ranged from one on two small non-reproductive individuals to forty-five on a large double-crowned female (x̄ = 8.8). Almost half of the plants produced less than one leaf per year on average (eighty-three of 180 plants produced six or fewer new leaves in 6.6 years). The number of leaves produced per flush per plant ranged from one to twelve (x̄ = 2.2, n = 720 flushes).

Table 3. Relationships between leaf production, plant size, and canopy openness for *Zamia skinneri* in primary forest (n = 149) at the La Selva Biological Station, Costa Rica. Total = total leaf production over 6.6 years; open = average canopy openness above individuals (see Methods); maxleaflet = number of leaflets on the largest leaf; maxleaf = maximum number of leaves observed on an individual during the study; r = parametric correlation coefficient, r_s = Spearman’s non-parametric correlation coefficient, r_p = parametric partial correlation coefficient (Sokal & Rohl 1981).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Statistic</th>
<th>P</th>
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</thead>
<tbody>
<tr>
<td>TOTLVS × OPEN</td>
<td>r = 0.38</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>r_s = 0.41</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>TOTLVS × MAXLEAFLET</td>
<td>r = 0.59</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>r_s = 0.56</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>TOTLVS × MAXLEAF</td>
<td>r = 0.76</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>r_s = 0.70</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>OPEN × MAXLEAFLET</td>
<td>r = 0.38</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>r_s = 0.37</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>OPEN × MAXLEAF</td>
<td>r = 0.37</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>r_s = 0.39</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>OPEN × TOTLVS (MAXLEAF controlled)</td>
<td>r_p = 0.17</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>(MAXLEAFLET controlled)</td>
<td>r_p = 0.21</td>
<td>&lt; 0.01</td>
</tr>
</tbody>
</table>
Fig. 3. Average number of leaves present per plant for *Zamia skinneri* at La Selva Biological Station, Costa Rica, which were active females (▲, n = 8), males (●, n = 35), or non-reproductives (■, n = 137) in 1981. Vertical arrow represents first appearance of strobili; pollination occurs c. 2–3 months later.

Fig. 4. Average number of leaves present per plant in *Zamia skinneri* at La Selva Biological Station, Costa Rica, which were active females (▲, n = 7), males (●, n = 20), or non-reproductives (■, n = 153) in 1985. Vertical arrow represents first appearance of strobili; pollination occurs c. 2–3 months later.
Table 4. Relationship between timing of leaf production and reproduction in *Zamia skinneri*, at La Selva Biological Station, Costa Rica. The year periods are calculated beginning in May, which is the beginning of the yearly peak in leaf production and reproduction (see Fig. 1). The 1986 data end in October 1986, but include the main leaf production period for 1986.

<table>
<thead>
<tr>
<th></th>
<th>1 year before cone production</th>
<th>Year of cone production</th>
<th>1 year after cone production</th>
<th>2 years after cone production</th>
<th>(n)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1981 reproduction</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-reproductives</td>
<td>68.6</td>
<td>54.7</td>
<td>48.2</td>
<td>49.6</td>
<td>137</td>
</tr>
<tr>
<td>Males</td>
<td>82.9</td>
<td>17.1</td>
<td>80.0</td>
<td>48.6</td>
<td>35</td>
</tr>
<tr>
<td>Females</td>
<td>87.5</td>
<td>12.5</td>
<td>25.0</td>
<td>37.5</td>
<td>8</td>
</tr>
<tr>
<td><strong>1985 reproduction</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-reproductives</td>
<td>54.9</td>
<td>52.9</td>
<td>38.6</td>
<td>—</td>
<td>153</td>
</tr>
<tr>
<td>Males</td>
<td>85.0</td>
<td>10.0</td>
<td>40.0</td>
<td>—</td>
<td>20</td>
</tr>
<tr>
<td>Females</td>
<td>100.0</td>
<td>14.3</td>
<td>0.0</td>
<td>—</td>
<td>7</td>
</tr>
</tbody>
</table>

Individuals produced new leaves between one and eleven times during the study ($\bar{x} = 4.0$ flushes, $n = 180$ plants). In only 16% of the sample was there one or more episode of leaf production per year. Frequency of new leaf flushing was correlated with plant size (Spearman’s $r_s = 0.21$ with maximum number of leaflets, $P < 0.01$; $r_s = 0.29$ with maximum number of leaves, $P < 0.005$), as well as with the total number of leaves produced over the study ($r_s = 0.66$, $P < 0.005$). When plants were grouped by size and reproductive class (as in Table 2), there were no significant differences in frequency of leaf production among reproductive categories in any size-class.

Leaf production and light

Mean canopy openness (see Methods) over individuals in primary forest ranged from < 1% to 3%. The total number of leaves produced over 6.6 years was highly significantly correlated with canopy openness (Table 3). Plant size was also correlated with canopy openness. Total leaf production was still significantly correlated with mean canopy openness when plant size was controlled for by partial correlation analysis (Sokal & Rohlf 1981) (Table 3). Although the variables in this analysis do not all meet the assumptions of parametric partial correlation analysis (including the normality requirement), non-parametric correlations were very similar to parametric values (Table 3).

Timing of leaf production in relation to reproduction

The timing and patterns of leaf production were similar in both major reproductive episodes (1981 and 1985). Cone production was preceded by a large flush of new leaves on reproductive individuals one year prior to reproduction (Fig. 3 and Fig. 4). Females flushed more leaves than did males, and both produced many more than did the non-reproductives. Mean number of leaves declined steadily up to the time of cone production, and for males and females continued to decline for at least one additional year. In contrast to the reproductive individuals, most non-reproductive plants produced new leaves in the years of reproductive episodes (Table 4). One year after cone production the incidence of male leaf production rose substantially, but the incidence of female leaf production remained severely depressed (Table 4).
DISCUSSION

_Life in the slow-lane: light-limitation in the understory_

_Zamia skinneri_ inhabits a world where light is in short supply. In the dimly lit understory of tropical rain forest, the biological style of _Z. skinneri_ can be summarized in one word: _slow_. The average reproductive individual reproduced only once in 6–6 years. Mean annual leaf production was only 1·3 leaves per individual. In half of the plants there were on average fewer leaves in the last thirteen censuses than in the first thirteen. Even in individuals which were ‘growing’ (higher average leaf number in last thirteen censuses than in the first thirteen) there were on average only 1·3 additional leaves during the second half of the study. Age at first reproduction is currently unknown; judging from the slow increase in leaf number, leaflet number, and leaf size in known-age seedlings, several decades are required to reach maturity in primary forest.

_Z. skinneri_ is notable for the large size, small number, high cost and longevity of its vegetative and reproductive structures. For example, of 329 leaves marked in 1980, more than half survived four years, and 15% were alive after six years (D. B. Clark & D. A. Clark, unpublished data). _Z. skinneri_ can produce its relatively expensive leaves and reproductive structures only at the stem apex. The advantages of the ‘big, few, long-lived, and expensive’ morphology over one which is ‘small, numerous, ephemeral, and cheap’ are not apparent. A morphology with numerous smaller leaves and many meristems would appear to be better adapted for rapid adjustment to short-term favourable or unfavourable conditions. Perhaps the scale of change in rain forest understory microconditions is so slow that such flexibility is not important. The large-module approach of _Z. skinneri_ may be more efficient for surviving with at least low photosynthesis between fairly infrequent light-increasing events.

The driving force in allocation to growth and reproduction for _Zamia skinneri_ in primary rain forest is light availability. Both the frequency of reproduction and total leaf production are positively correlated with increasing canopy openness (Table 3). These effects were detected within a very small range of canopy openness values (<1–3%), values which coincide with the very low light intensities (1–2% of full sun) reported by Chazdon & Fetscher (1984) for shaded understory conditions at La Selva. At these levels of irradiance, an increase of 1% of full sun can represent a 100% increase in photosynthetically active radiation (PAR). The effects of such small differences in irradiance are likely to be physiologically important, since the photosynthetic response curve of _Z. skinneri_ is linear with a steep slope at understory light intensities (S. F. Oberbauer, unpublished data).

Reproduction in _Z. skinneri_ is preceded by a major flush of new leaves in the year prior to cone production; at this time, leaf number on the future reproductive plants increases by 28–41%. It is not known if the resources for this flush and the subsequent cone production are acquired slowly over a period of years, or more quickly, e.g. in response to a light-increasing event such as a tree or branch-fall. It is clear from the phenological and reproductive patterns, however, that the replacement of these resources occurs on the scale of one to several years.

A major unknown factor in all tropical rain forests is the scale (frequency and magnitude) of environmental change around understory plants. Although forest turnover rates have been estimated (e.g. Hartshorn 1978; Brokaw 1985; Lieberman _et al_ 1985a), there are no data on temporal changes in microenvironments around understory individuals. Smith (1987) suggested that rain forest herbs may survive mainly as
suppressed, declining individuals awaiting reproduction in the next light gap. In this study a high percentage of the individuals did show a decrease in leaf number over time, consistent with Smith’s hypothesis. Cone production in Z. skinneri, however, was not restricted to gaps, and in fact the great majority of reproductive individuals occurred in deeply-shaded understorey sites. Nevertheless, the correlations of leaf production and reproduction with very small increases in light suggest that light-increasing events are critical to overall performance. This study suggests that Z. skinneri is a shade specialist, an opportunist taking advantage of small increases in PAR. These increases are likely to be caused not just by overhead canopy gaps penetrating to the forest floor, but also by gaps to the side opening up lateral shafts of light, broken branches and fallen palm leaves, and seasonally deciduous trees (cf. Clark & Clark 1987b).

Cost of reproduction

The general inverse relation between reproduction in plants and vegetative growth is well established (Harper 1977; Kramer & Kozlowski 1979; Willson 1983; Bazzaz et al. 1987). In dioecious species the cost of reproduction has generally been shown to be higher in females than in males. Males flower more frequently (Bullock & Bawa 1981; Bullock, Beach & Bawa, 1983; Meagher & Antonovics 1982), and show fewer or no effects of reproduction on growth (Linhart & Mitton 1985; Meagher & Antonovics 1982; Herrera 1984; but see Sakai & Burris 1985 for a counter-example).

In Zamia skinneri no difference was found in total leaf production or in frequency of leaf flushing when equal-sized reproductive and non-reproductive individuals were compared over the 6-6 year period. Nevertheless, costs of reproduction were clearly evident in many phenological and reproductive patterns within this period. In most individuals at least a two-year non-reproductive period preceded reproduction. This was undoubtedly related to the need for a major investment in new leaves in the year prior to cone production. Cone production in turn resulted in at least a four-year period of non-reproduction in most plants in primary forest. Most reproductive plants produce no new leaves in the year they produce cones, and show lower leaf number for up to six years afterwards. On the scale of several years, resource allocation to leaf production and reproduction determines future phenology and growth potentials.

 Females allocated more time and energy to reproduction than did males. Not surprisingly, therefore, the costs of reproduction observed in this study were higher for females than for males. Females supported cones for eighteen months, while the smaller male cones lasted only five or six (Clark & Clark 1987a). Prior to both major reproductive events, females produced more leaves, both proportionately and absolutely, than did males. The depressing effect of reproduction on subsequent production of new leaves was stronger in females than in males, and females reproduced significantly less frequently than males.

Several studies have shown or postulated a long-term trade-off between reproduction and longevity (Meagher & Antonovics 1982; Piñero, Sarukhán & Alberdi, 1982; Smith & Young 1982; Law 1979; Savage & Ashton 1983). For Zamia skinneri, the decrease in size (decline in total leaf number) which follows cone production could have long-term effects on the fitness of the plant. For both sexes, larger individuals (with more leaves) produce larger cones and can produce cones at more frequent intervals; larger male plants also produce more cones in a given episode (Clark & Clark 1987a). Reproduction at small sizes, then, could be strongly disadvantageous because it delays growth to the more fecund sizes.
The present study, although of 6-6 years duration, was too brief to evaluate the eventual effects of reproduction and leaf production on individuals that appear to survive for at least one and perhaps several centuries (D. A. Clark & D. B. Clark, unpublished data). Long-term observations on organisms in their natural habitat are critical for evaluating on a per-individual basis the lifetime consequences of differing allocations to growth and reproduction.

ACKNOWLEDGMENTS

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REFERENCES


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