

# Spatial and temporal variation in the fruiting phenology of palms in isolated stands

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## Abstract

**Fruiting phenologies of two species of palms, *Astrocaryum standleyanum* L. H. Bailey and *Attalea butyracea* (Mutis ex L. f) Wess. Boer, isolated on eight small (1.7–3.7 ha) forested islands in the Panama Canal were studied over a 33-month period. Individual palms were permanently marked with numbered aluminum tags and censused each month for the presence of ripe fruits. The dataset consisted of 1106 monthly observations of palms with ripe fruits among the 634 marked individuals. Mean densities of palms of reproductive size varied widely among islands, ranging from a low of 0.3 ha<sup>-1</sup> for *A. standleyanum* and 3.5 ha<sup>-1</sup> for *A. butyracea* to a high of 44.9 ha<sup>-1</sup> for *A. standleyanum* and 33.7 ha<sup>-1</sup> for *A. butyracea*. Both species showed distinctly seasonal periods of fruiting activity that varied in duration between the two species and among years. The timing of fruiting by *A. standleyanum* was highly synchronous among islands, whereas inter-island synchrony in *A. butyracea* was less pronounced. The percentages of marked individuals that fruited varied widely among islands and years. Results indicated that these palms responded to both spatially and temporally variable conditions that promoted fruit production. We suggest that pollinator abundances are a crucial factor affecting reproductive output. Conditions that favor successful reproduction and seed dispersal, such as pollinator activity and the attraction of dispersal agents, may be the ultimate factors that have influenced the reproductive phenologies of these two species of palms.**

*Keywords:* *Astrocaryum standleyanum*, *Attalea butyracea*, fruit production, palms, Panama, phenology.

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## Introduction

In tropical forests that experience a seasonal climate, many plants show distinct seasonal patterns in their vegetative and reproductive activities (e.g. Janzen 1967; Daubenmire 1972; Frankie *et al.* 1974; Foster 1982; Croat 1978). Seasonal reproduction depends on both proximate cues that trigger flowering and ultimate factors that influence the evolution of a plant's reproductive phenology (i.e. timing of flowering and fruit maturation; Foster 1982). Pollination by certain groups of insects, such as weevils, may select for highly synchronous flowering that takes advantage of periods of high pollinator abundance

(e.g. Henderson *et al.* 2000). However, when recruitment is dependent on animal seed dispersers, competition for such dispersers may select for variable levels of fruiting synchrony (Thies & Kalko 2004). Indeed, in Veracruz, Mexico, 11 species demonstrated highly synchronous flowering, with most species flowering during the dry season; however, species bore fruit almost year round (Ibarra-Manriquez 1992). Henderson *et al.* (2000) studied the flowering phenology of 27 species of palms in the central Amazon and found relationships between flowering synchrony, regularity and duration and the types of insects that pollinated the flowers. The importance of insect pollinators to fruit set may be seen in Scariot *et al.* (1991, 1995), who noted that individuals of *Acrocomia aculeata* (Jacq.) Lodd ex Mart. flowered from August to mid December, but that those individuals that flowered in

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October had the greatest fruit set. Similarly, DeSteven *et al.* (1987) noted that, although *Bactris major* Jacq. flowers all year round, only flowers appearing in the latter part of the rainy season produce ripe fruit. Thus, flowering performance of palms does not necessarily equate with overall fruit production and reproductive success (Adler *et al.* 1998), and individual reproductive success may vary considerably within populations (DeSteven *et al.* 1987).

Seasonal pollinator abundance is likely to be ultimately determined by broad-scale patterns, such as day length and rainfall. However, small-scale microclimatic patterns, such as exposure to rainy-season storms and dry-season trade winds may also influence local insect abundance and may lead to differences in reproductive output among spatially isolated stands. Thus, although stands within a region may experience the same ultimate reproductive cues, proximate cues that influence fruit set may vary and may have implications for stand dynamics and the maintenance of frugivore populations in fragmented forests.

Many palms reproduce seasonally. Of the 13 species of palms studied by DeSteven *et al.* (1987) in central Panamá, nine species reproduced seasonally. *Astrocaryum standleyanum* L. H. Bailey and *Attalea butyracea* (Mutis ex L. F) Wess. Boer [*Scheelea zonensis* L. H. Bailey] are common and widely distributed neotropical palms that are particularly abundant in second-growth forests (Leigh 1999). Both species show extraordinarily high fruit production per unit area of crown (Hladik & Hladik 1969) and provide crucial resources for frugivores (e.g. Glanz *et al.* 1982; Adler 2000). *Astrocaryum standleyanum* is a monoecious subcanopy tree that is 7–15 m tall at reproductive height (DeSteven *et al.* 1987) and ranges from southeastern Costa Rica to the Pacific slope of Colombia and northern Ecuador (Henderson *et al.* 1995). *Attalea butyracea* is a monoecious canopy and subcanopy tree that is 6–15 m tall at reproductive height, with a maximum height of 30 m or more (DeSteven *et al.* 1987). This species ranges from southern Mexico southward into western Amazonia (Henderson *et al.* 1995). Flowering and fruiting by *A. standleyanum* are highly synchronous within populations on Barro Colorado Island (BCI) in central Panamá, whereas within-population reproduction by *A. butyracea* is only moderately synchronous (DeSteven *et al.* 1987). However, among-population reproductive synchrony and differences in reproductive success have not been examined for these two species, despite their abundance and importance for frugivores.

Our study focuses on the reproductive phenologies of both palm species in central Panamá. The 33-month study was conducted on eight small islands in Gatun Lake, where BCI is located centrally. Seasonal cues, such as day length and rainfall, were similar across the islands, but other factors that may have influenced reproductive

output, such as pollinator abundance, are likely to vary. In contrast to the study by DeSteven *et al.* (1987), which was conducted in one 15-km<sup>2</sup> contiguous forest, we studied spatially isolated stands of palms. Therefore, we addressed among-stand rather than within-stand phenological differences and we examined fruiting rather than flowering phenologies because fruiting is generally more synchronous than flowering in these species (DeSteven *et al.* 1987), and fruit production is a better indicator of reproductive success (DeSteven *et al.* 1987; Scariot *et al.* 1995; Adler *et al.* 1998). Our aims were to: (i) describe the distributions and densities of the two species of palms; (ii) examine the timing and duration of fruiting in each year; (iii) determine the degree of fruiting synchrony among the isolated palm stands; and (iv) compare reproductive output among those stands. If fruiting is constrained solely by broad-scale seasonal cues, such as rainfall and day length, then the timing and length of the fruiting seasons should be highly synchronous among even isolated palm stands. However, if small-scale microclimatic and habitat differences lead to differences in the pollinator communities among isolated stands, then reproductive output should vary among both islands and years. We conclude by discussing the observed spatial and temporal variation within the context of proximate cues and ultimate factors that may have shaped the observed phenologies.

## Materials and methods

### Study area

Over 200 islands occur within Gatun Lake (9°10'N, 79°50'W), which is an artificial impoundment that was created during the construction of the Panama Canal. We include in this study eight small islands ranging in size from 1.7 to 3.5 ha that are covered with tropical moist forest of varying ages and floristic compositions (designated as islands 4, 5, 8, 9, 12, 14, 51 and 52; described in detail by Adler 2000). These islands are located within a 40-km<sup>2</sup> area and experience the same major climatic patterns, such as rainfall seasonality and the occurrence of rainy-season storm systems and dry-season trade winds. However, microclimatic patterns, such as exposure to storm systems and trade winds, vary among the islands because some islands are better protected from such effects by neighboring land masses. The climate of the study area is highly seasonal with respect to precipitation; an 8-month rainy season is punctuated by a short but severe dry season that typically lasts from January through to April. Over 90% of the annual precipitation falls during the rainy-season months, and dry-season trade winds prevailing from the north-west have a pronounced drying effect. The mean annual rainfall on BCI is 2612 mm (Windsor 1990).

The only frugivorous mammals that maintained persistent populations on the islands throughout the study were spiny rats *Proechimys semispinosus* (Tomes) (Central American spiny rat; Adler 2000). Arboreal mammals such as *Sciurus granatensis* Humboldt (red-tailed squirrel) that could have removed fruits from the infructescences between monthly censuses were usually absent (Adler 1998). Other terrestrial mammals that may have preyed on palm seeds, such as *Dasyprocta punctata* Gray (Central American agouti) and *Cuniculus paca* (L) (lowland paca), were present on some islands, but only intermittently.

### Sampling design

All individual *A. standleyanum* and *A. butyracea* of reproductive size (DeSteven *et al.* 1987) were marked by affixing to the trunk with grafting tape a numbered aluminum tag, and their diameter was measured at breast height ([d.b.h.] 1.3 m above ground). All marked individuals were recensused each year thereafter through until 1994. All palms that died in each yearly interval were noted, and all palms that reached reproductive size in that interval were marked and included as recruits to the mature segment of each stand. From April 1992 through to December 1994, we conducted monthly phenological censuses of all marked *A. standleyanum* and *A. butyracea*. The numbers of ripe infructescences borne by each individual palm were recorded during the monthly censuses and constituted the dataset for this study. We included only those infructescences whose fruits matured and ripened because fruits were often aborted before reaching maturity. Furthermore, the time of fruit maturation had important implications for reproductive success because of the reliance of the two species on frugivorous mammals for seed dispersal (DeSteven *et al.* 1987; Smythe 1989; Hoch & Adler 1997; Adler & Kestell 1998; Leigh 1999) and predation on seeds by those same rodents (Adler 1995; Hoch & Adler 1997; Adler & Kestell 1998).

### Data analysis

We calculated yearly densities of all marked individuals of the two species of palms on each island, regardless of fruiting activity. We examined the timing and duration of fruiting by plotting, by island, the monthly densities of both palm species bearing ripe fruits over the 33-month study period. From these data, we determined the number of months in which the two species bore ripe fruits each year. To examine whether isolated stands of a species were synchronous in their fruiting activity, we used time series analyses to compute island-by-island cross-correlation functions of all possible pairwise combinations where sample sizes of fruiting individuals were sufficient.

Each time series, which consisted of monthly densities of individuals of a particular species bearing ripe fruit, was pre-whitened to achieve a stationary time series before calculating the cross-correlation functions. The critical value for a cross-correlation function was  $2.217/\sqrt{N}$  (Diggle 1990), where  $N$  was the number of monthly observations in the series. The effect of proximity of an island to other islands was examined by correlating the value of each cross-correlation function with distance between islands in a given island pairing.

We then calculated the percentages of marked individuals of the two species that produced ripe fruits each year, which served as an index of island-wide reproductive output. We used linear analysis of categorical data to search for differences in counts of individuals producing at least one infructescence with ripe fruits among islands and years. These models were appropriate for count rather than frequency data (Lindsey 1995) because the same individuals were censused each year. We constructed separate saturated models consisting of main effects (island and year) and an island  $\times$  year interaction for both species of palms. As counts of zero prohibited estimates of at least some parameters in a saturated model (Lindsey 1995), a zero was replaced with a one (Kleinbaum & Kupper 1978).

We also examined the numbers of infructescences with ripe fruits produced each year by individuals of the two species of palms, which served as an index of individual reproductive output. We used a non-parametric ANOVA to search for inter-island differences in this index. A separate model was constructed for a given species of palm each year. Only those islands that had at least 10 individuals of a given species that bore ripe fruit within a year were included in this analysis, and individuals that did not produce ripe fruit within a given year were excluded from analysis.

## Results

### Distributions and densities

We marked 625 individuals of reproductive size of the two palm species over the 33-month study period (Table 1). Both species of palms occurred on all eight islands, but densities of mature individuals varied widely (Table 1). Mean yearly densities of mature *A. standleyanum* varied from only 0.3 individuals  $\text{ha}^{-1}$  on island 51 to 44.9 individuals  $\text{ha}^{-1}$  on island 8. Densities of mature *A. butyracea* varied from 3.5 individuals  $\text{ha}^{-1}$  on island 5 to 33.7 individuals  $\text{ha}^{-1}$  on island 12. The mortality of marked palms over the study period was nearly equivalent to the recruitment, except on island 12 where seven individual *A. butyracea* died and none were recruited (Table 1).

**Table 1** Total numbers of marked palms and the numbers recruiting and dying over the 33-month study period, mean yearly densities of marked palms, and numbers of monthly observations of marked palms producing infructescences with ripe fruits on the eight study islands

Island	Size (ha)	Isolation (m)	Individuals	Deaths	Recruits	Mean density (ha <sup>-1</sup> )	Fruiting observations
<i>Astrocaryum standleyanum</i>							
4	1.9	30	37	1	0	19.1	36
5	1.7	61	15	3	1	7.6	0
8	2.7	30	125	5	3	44.9	376
9	2.1	61	80	1	1	37.6	173
12	1.8	152	15	0	0	8.3	24
14	2.4	30	17	1	0	6.8	20
51	3.5	30	1	0	0	0.3	4
52	2.5	30	32	0	1	12.5	73
Total	18.6		322	11	6	17.1	680
<i>Attalea butyracea</i>							
4	1.9	30	22	1	0	11.4	36
5	1.7	61	6	0	0	3.5	2
8	2.7	30	67	3	1	24.3	92
9	2.1	61	59	1	0	27.9	139
12	1.8	152	64	7	0	33.7	43
14	2.4	30	14	0	0	5.8	15
51	3.5	30	14	0	0	4.0	25
52	2.5	30	57	2	2	22.1	74
Total	18.6		303	14	3	16.6	426

Isolation refers to the distance to the nearest larger body of land.

### Timing and duration of fruiting

We recorded 1106 monthly observations of marked palms with ripe fruits (Table 1). Both species showed distinctly seasonal periods of fruiting activity that varied in duration between the two species and among years (Fig. 1). The fruiting season of *A. standleyanum* varied from 0 months on island 4 in 1992 and on island 5 in all 3 years to 11 months on island 8 in 1994 (Table 2). In general, the greatest fruiting activity occurred at the end of the dry season (April) and through the first 2 months of the rainy season (May and June). However, this species showed two peak fruiting periods in both 1993 and 1994, and fruiting individuals were present throughout most of those 2 years. The fruiting season of *A. butyracea* varied from 0 months on island 5 in 1992 to 10 months on island 8 in 1994 (Table 2). *Attalea butyracea* generally fruited throughout most of each rainy season, with most fruiting activity occurring between May and November. The overall mean period of ripe fruit production was approximately 2 months longer each year for *A. butyracea* than for *A. standleyanum*, and the fruiting duration was greatest in 1994 (Table 2). It is important to note that the length of the fruiting period, particularly that of *A. standleyanum*, was underestimated in 1992 because censuses did not begin until April.

### Synchrony of fruiting

The density of fruiting *A. standleyanum* was highly synchronous among islands, with 9 of 10 pairwise cross-correlation functions being statistically significant (Table 3). Data from islands 4, 5 and 51 were omitted from analysis because of small numbers of individuals. Fruiting synchrony of *A. butyracea* among islands was not as pronounced, with only 5 of 21 cross-correlation functions being significant (Table 3). Data from island 5 were omitted from analysis. The degree of synchrony was not related to distance between islands in either species ( $r = 0.32$ ,  $P = 0.3701$  for *A. standleyanum*;  $r = 0.01$ ,  $P = 0.9573$  for *A. butyracea*).

### Reproductive output

The percentages of marked individuals that fruited varied spatially (Table 4). Percentages of fruiting *A. standleyanum* (island 51 was omitted from this analysis because only one individual occurred on that island) differed among islands ( $\chi^2 = 22.74$ , d.f. = 4,  $P = 0.0001$ ), but not among years ( $\chi^2 = 1.65$ , d.f. = 2,  $P = 0.4373$ ). The island  $\times$  year interaction was not significant ( $\chi^2 = 4.39$ , d.f. = 8,  $P = 0.8204$ ). *Astrocaryum standleyanum* on island 5 did not bear ripe fruit at any time throughout the entire study, and very few individuals fruited on island 4. By contrast,

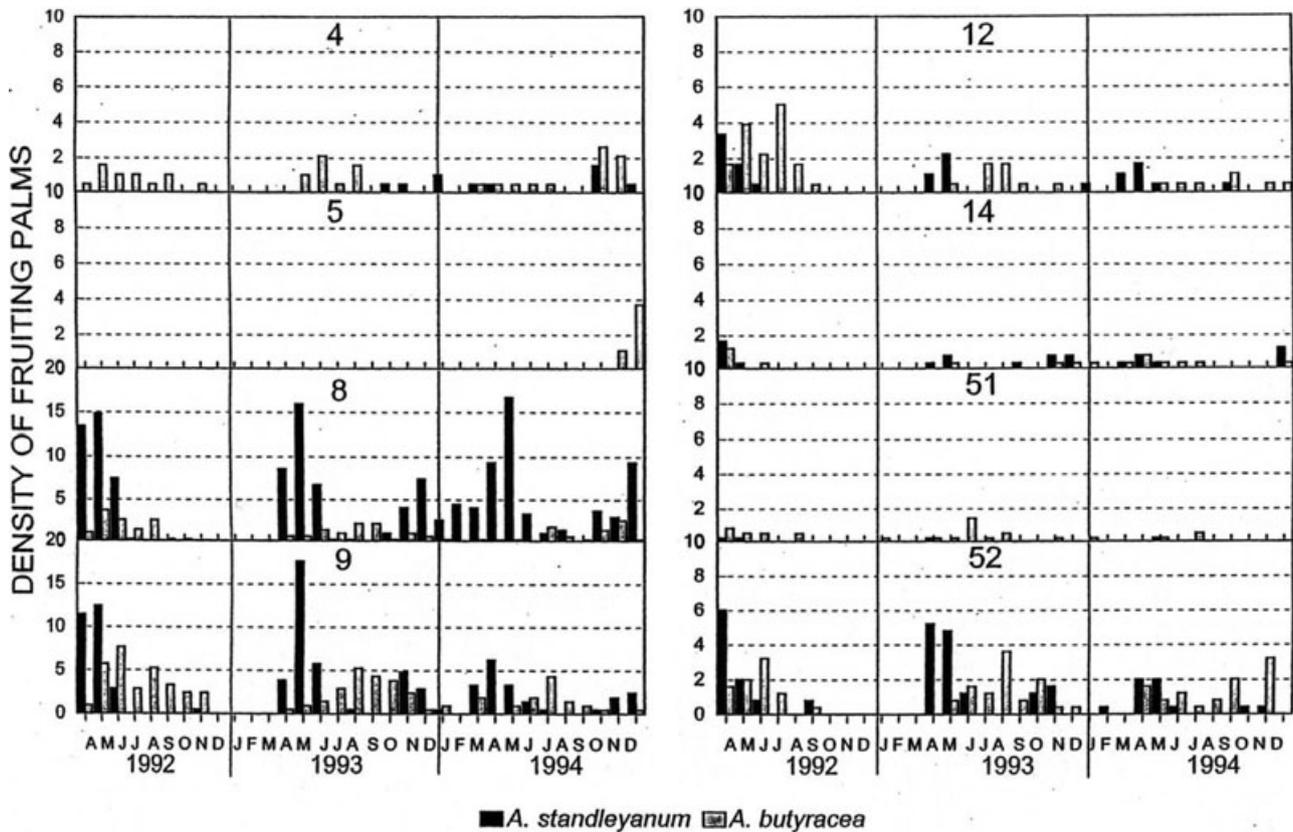


Fig. 1 Monthly densities of *Astrocaryum standleyanum* and *Attalea butyracea* bearing ripe fruits on the eight study islands (4, 5, 8, 9, 12, 14, 51 and 52).

Table 2 Numbers of months each year in which individual *Astrocaryum standleyanum* and *Attalea butyracea* palms bore ripe fruit

Island	<i>A. standleyanum</i>			<i>A. butyracea</i>		
	1992	1993	1994	1992	1993	1994
4	0	2	5	7	4	7
5	0	0	0	0	0	2
8	4	8	11	7	9	10
9	4	6	8	8	9	9
12	3	3	4	6	5	6
14	2	5	4	2	2	8
51	2	1	1	4	7	3
52	4	5	6	5	8	7
Mean	2.4	3.8	4.9	4.9	5.5	6.5

Censuses did not begin until April 1992.

much higher percentages of individuals fruited on islands 8, 9 and 52. Percentages of fruiting *A. butyracea* also differed among islands ( $\chi^2 = 35.62$ , d.f. = 5,  $P = 0.0001$ ), but not among years ( $\chi^2 = 4.06$ , d.f. = 2,  $P = 0.1316$ ). The island  $\times$  year interaction was not significant ( $\chi^2 = 9.75$ , d.f. = 10,  $P = 0.4626$ ). A greater percentage of individuals fruited on islands 4, 8, 9, 51 and 52.

Table 3 Cross-correlation functions of monthly densities of fruiting *Astrocaryum standleyanum* (above the diagonal) and *Attalea butyracea* (below the diagonal)

Island	Island						
	4	8	9	12	14	51	52
8	0.49*	—	0.34	0.39*	0.40*	NA	0.52*
9	0.19	0.59*	—	0.72*	0.61*	NA	0.50*
12	0.22	0.61*	0.07	—	0.78*	NA	0.81*
14	-0.11	-0.19	-0.15	-0.15	—	NA	0.76*
51	0.36	0.46*	0.28	-0.11	0.25	—	NA
52	0.40*	0.32	0.22	0.20	0.05	0.32	—

\*Indicates those cross-correlation functions that are statistically significant at  $P < 0.05$ . Data for *A. standleyanum* on islands 4, 5 and 51 and *A. butyracea* on island 5 were omitted from this analysis because too few individuals bore ripe fruit. NA, not available because of the small numbers of individuals bearing ripe fruits;  $n = 33$  months for each function.

The number of infructescences produced in a year by fruiting *A. standleyanum* ranged from one to nine, with most individuals producing only one. Islands 8 and 9 had the most individuals that produced multiple infructescences. For those islands where samples sizes were

**Table 4** Yearly percentages of palms bearing ripe fruits on the eight study islands in Panamá

Island	<i>Astrocaryum standleyanum</i>			<i>Attalea butyracea</i>		
	1992	1993	1994	1992	1993	1994
4	0.0 (37)	5.1 (36)	12.8 (36)	33.3 (22)	38.1 (22)	35.0 (21)
5	0.0 (14)	0.0 (13)	0.0 (12)	0.0 (6)	0.0 (6)	16.7 (6)
8	40.8 (122)	46.0 (122)	50.8 (120)	34.8 (66)	31.3 (67)	28.1 (64)
9	40.7 (79)	53.1 (79)	27.2 (79)	50.8 (59)	47.5 (59)	29.3 (58)
12	33.3 (15)	33.3 (15)	33.3 (15)	29.8 (64)	10.4 (61)	9.4 (57)
14	23.5 (17)	17.6 (16)	17.6 (16)	26.7 (14)	6.7 (14)	26.7 (14)
51	100.0 (1)	100.0 (1)	100.0 (1)	46.7 (14)	40.0 (14)	20.0 (14)
52	51.6 (31)	61.3 (31)	28.1 (32)	30.5 (55)	25.0 (56)	23.7 (55)

Numbers of marked individuals are in parentheses.

**Table 5** Mean numbers of infructescences with ripe fruits produced by individuals of the two species of palms on four of the study islands

Island	<i>Astrocaryum standleyanum</i>			<i>Attalea butyracea</i>		
	1992	1993	1994	1992	1993	1994
8	1.86 (51)	2.36 (58)	2.62 (63)	1.17 (23)	1.14 (21)	1.11 (18)
9	1.79 (33)	2.47 (43)	2.05 (22)	1.26 (30)	1.25 (28)	1.59 (17)
12	—	—	—	1.00 (20)	—	—
52	1.69 (33)	2.47 (43)	—	1.00 (18)	1.40 (15)	1.14 (14)
$\chi^2$ (d.f)	1.73 (2)	4.06 (2)	1.18 (1)	10.89 (3)*	4.02 (2)	7.79 (2)*

\*Indicates  $\chi^2$  values from the non-parametric ANOVA that are significant at  $P < 0.05$ . Means are calculated only for those islands and years that had at least 10 fruiting individuals. Numbers of fruiting individuals are in parentheses.

sufficient for comparison (islands 8, 9 and 52), the mean number of infructescences produced by individual *A. standleyanum* did not vary among islands (Table 5). Fruiting *A. butyracea* produced from one to four infructescences per year, with most individuals producing only one. The mean number of infructescences produced by *A. butyracea* varied among islands in both 1992 and 1994 on the islands where sample sizes were sufficient for this comparison (Table 5).

## Discussion

### *Distributions and densities*

*Astrocaryum standleyanum* and *A. butyracea* occurred at variable, but often high densities on the study islands. On BCI, densities of individuals of reproductive size are also variable and are highest in young forest, where *A. standleyanum* reaches densities of 40 ha<sup>-1</sup>, and *A. butyracea* reaches densities of 20 ha<sup>-1</sup> (Leigh 1999). *Attalea butyracea* belongs to a subset of common second-growth tree species, including *Protium panamense* (Rose) I. M. Johnston and *Swartzia simplex* (Sw.) Spreng., that occur at higher densities on small islands than on the adjacent mainland. This subset of trees, which may also include *A. standleyanum*, has been favored on small islands pre-

sumably because of reduced abundances of mammalian seed predators and resistance to the drying effects of dry-season trade winds (Leigh *et al.* 1993).

### *Timing and duration of fruiting*

Both species of palms in our study showed distinctly seasonal fruiting periods. The number of months within a year in which individuals bore ripe fruits varied from zero to 11 in our study, with an overall mean of 3.7 months. DeSteven *et al.* (1987) found that *A. standleyanum* on BCI bore ripe fruits for 4–6 months, with a mean of 4.8 months. *Attalea butyracea* generally showed only one peak in fruiting activity, which usually fell between the two *A. standleyanum* peaks. The number of months in which individuals within a stand bore ripe fruits varied from zero to 10 months, with an overall mean of 5.6 months. DeSteven *et al.* (1987) found that *A. butyracea* bore ripe fruits on BCI for 4–7 months, with a 4-year mean of 5.3 months. Thus, there was considerable variability in fruiting seasons among the isolated stands of both species in our study and between the island stands and those on BCI.

### *Synchrony of fruiting*

We found a high degree of fruiting synchrony of *A. standleyanum* among the isolated stands, a finding consistent

with that of DeSteven *et al.* (1987) for within-population synchrony. The moderate among-stand fruiting synchrony of *A. butyracea* was similar to that found by DeSteven *et al.* (1987) for within-population reproductive activity. The lesser synchrony among isolated *A. butyracea* stands relative to *A. standleyanum* may result, at least in part, from the longer fruiting period of the former species and the greater amount of time required for its fruits to reach maturity. Maturation time is approximately 10 months for *A. standleyanum* (fruits from the previous year's flowers generally are absent by the time flowering begins again), whereas maturation time is greater than 1 year for *A. butyracea* (flowering begins while mature fruits are still present; Croat 1978). A longer maturation period for fruits may lead to greater variability in fruiting duration and, therefore, to lesser among-stand synchrony. The degree of synchrony in fruiting activity between pairs of islands was not related in either species to the proximity of the islands to each other. Thus, random factors or factors that varied across individual islands rather than major climatic patterns must have been responsible for differences in the synchrony of fruiting activity among islands.

#### *Reproductive output*

Reproductive output (measured as the percentage of individuals producing ripe fruit) varied widely among the *A. standleyanum* stands. Output was greatest on islands 8, 9 and 52, where approximately half of all individuals produced ripe fruit each year. This output was poorer than that observed by DeSteven *et al.* (1987) on BCI, where 69% of mature individuals fruited. Individual reproductive output (measured as the number of ripe infructescences produced by an individual) showed little variation among the three islands (8, 9 and 52) where at least 10 individuals bore mature fruits. The overall mean of 2.1 ripe infructescences in those three stands was similar to the stands on BCI studied by DeSteven *et al.* (1987), where individuals produced a mean of 2.8 infructescences. The maximum individual reproductive output of nine infructescences was greater than the maximum of six infructescences reported by DeSteven *et al.* (1987). Leigh (1999) noted that fruit crops of this palm were poor on BCI in 1994, but we did not find a consistent decline in reproductive output across the islands in that year.

Reproductive output of *A. butyracea* also varied widely among isolated stands and was greatest on islands 4, 8, 9, 51 and 52, where approximately one-third of all individuals bore ripe fruit. This output was considerably poorer than that on BCI, where 81% of adults fruited (DeSteven *et al.* 1987). Individual reproductive output also varied and was poorer than on BCI. On the four islands (8, 9, 12 and 52) where at least 10 individuals bore ripe fruit within

a year, individuals produced an overall mean of 1.2 and a maximum of four infructescences. By contrast, DeSteven *et al.* (1987) found a mean of 3.7 and a maximum of seven infructescences per individual on BCI.

Variation in reproductive output among isolated stands indicates that random factors or factors that vary on a small spatial scale must underlie this variation in output, as with fruiting synchrony. Proximate cues for flowering, such as responses to climatic seasonality or photoperiod, may be eliminated as factors that determine spatial variation in individual reproductive output. The simplest explanation is that of random or unpredictable factors that differentially affect individuals on islands. As both species are probably pollinated by insects (DeSteven *et al.* 1987), we suggest that a likely alternative explanation for such variation lies in differences in the distribution and abundance of pollinators among the islands. Islands differ widely in their exposure to dry-season trade winds and rainy-season storms that could affect pollinator populations. Island 5, which has extremely poor reproductive output by those two species of palms, is particularly exposed to wind and storms. The forest on that island has a low canopy and frequently experiences major treefalls (Adler 2000). Wind and storms could also affect reproductive success directly by influencing soil moisture regimes and by damaging reproductive structures. The higher reproductive output of palms on BCI also supports this conclusion because the larger land mass would likely support larger populations and more diverse communities of insect pollinators. A study of pollinator abundance and microclimatic variation in relation to flowering phenology of these palms should further elucidate the causes of variation in reproductive output.

#### *Proximate cues and ultimate factors*

*Astrocaryum standleyanum* typically flowers in the rainy season in July and August on BCI (DeSteven 1987), and fruits mature during the following dry and rainy seasons. *Attalea butyracea* also flowers during the rainy season (DeSteven 1987), and the fruits mature the following rainy season. DeSteven *et al.* (1987) suggested that the proximate cue for flowering in *A. standleyanum* may be photoperiod and for *A. butyracea* it may be increased rainfall at the beginning of the rainy season. Leigh (1999) suggested that *A. standleyanum* may flower in delayed response to the onset of the rainy season. Although no studies have identified the proximate cues that initiate flowering in these two species, our results indicate that this cue must be similar across the study area because of the moderate to high degree of among-stand fruiting synchrony. Photoperiod and rainfall, therefore, remain as plausible proximate cues. Flowering by these two species may be timed to coincide with greater activity of potential insect pollina-

tors during the rainy season, which could be a likely ultimate factor for flowering (DeSteven 1987).

Both species of palms fruit throughout the period of greatest community-wide fruit production on the islands (Adler 1998). Seeds of both species are heavily preyed on by rodents (Smythe 1989; Adler 1995; Hoch & Adler 1997; Adler & Kestell 1998) and bruchid beetles (Wright 1983; Forget *et al.* 1994; Harms & Dalling 2000) and largely require scatter hoarding rodents, such as agoutis and spiny rats, to disperse the seeds for successful germination (Smythe 1989; Hoch & Adler 1997; Adler & Kestell 1998). Spiny rats may be particularly important as seed dispersers and predators on the islands because they are the only rodents that maintain persistent populations (Adler 1998). As the two palms produce fruit when many other large-seeded species also fruit, competition for seed dispersers in central Panama may be intense. The long fruiting seasons for both species may enhance the probability of successful seed dispersal and germination. Furthermore, the periods of greatest fruit production by these two palms do not coincide, thereby reducing competition for shared seed dispersers. We suggest that conditions that favor successful pollination (i.e. high pollinator abundance) and seed dispersal (i.e. reduced competition for dispersal agents) are the ultimate factors that have influenced the reproductive phenologies of these two species of palms. Thus, the ultimate factors that have influenced the evolution of the timing of flowering and fruit maturation are no doubt different.

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