

Reproductive Phenology of a Tropical Canopy Tree, *Spondias mombin*¹

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ABSTRACT

We studied the reproductive phenology of isolated populations of *Spondias mombin* to determine the degree of flowering and fruiting synchrony among populations and to examine spatial and temporal variability in fruit production. The study was conducted on six small islands (1.8–3.5 ha) in the Panama Canal. All individuals (10 cm in diameter at breast height (DBH)) were marked in 1991 and censused each year through 1994 to record recruits and deaths. All marked trees were censused monthly for flowering and fruiting activity from April 1992 through December 1995. *Spondias mombin* was seasonal and highly synchronous in flower and fruit production among islands and across years. Proportions of individuals fruiting varied among islands, years, and tree size classes. There was a positive relationship between probability of fruit production and tree size. Synchronous reproductive activity in *S. mombin* probably was due to responses to proximate environmental cues such as fluctuations in irradiance, but other factors must have been responsible for temporal and spatial variation in reproductive performance. We suggest that this variation may have been due partly to temporal and spatial differences in pollinator abundance.

Key words: flowering; fruiting; islands; Panama; phenology; reproduction; *Spondias mombin*.

TROPICAL FOREST PLANTS EXHIBIT A WIDE VARIETY OF reproductive phenologies. Flowering and fruiting activity often vary not only seasonally (Heideman 1989, van Schaik *et al.* 1993, Foster 1996) but also within and among populations (De Steven *et al.* 1987; Smith & Bronstein 1996). Seasonal variability generally reflects the influence of proximate environmental cues that initiate flowering and ultimate factors that select for particular reproductive phenologies. Proximate environmental cues include precipitation (Opler *et al.* 1980), water stress (Borchert 1980, Reich & Borchert 1982), and irradiance (Wright & van Schaik 1994), while ultimate factors include the necessity of outcrossing among individuals (Stiles 1977) and abundances of pollinators (Augsburger 1996), seed dispersers (Smythe 1970, Wheelwright 1985), and seed predators (Augsburger 1981). Spatial and long-term temporal variability in reproductive performance may reflect environmental variation and differences in pollinator abundance (Augsburger 1980). Identifying factors that influence reproductive phenologies is hampered by a lack of information on reproductive activity and performance of many tropical plants. A first step in studying reproductive performance, therefore, is to identify spatial and temporal patterns of reproductive activity. Such studies are important in laying the foundation for

identifying proximate cues and ultimate factors that underlie phenological patterns.

Spondias mombin L. (Anacardiaceae), a common canopy tree native to the lowlands of Mexico, Central America, and South America, shows distinctly seasonal vegetative and reproductive activity. In Panama, *S. mombin* is leafless for a short time at the beginning of the dry season before flowering, which is generally in April and May (Croat 1974a). Flowers are mostly bisexual in Panama, with some pistillate flowers. Fruits take approximately five months to mature and are generally ripe from July to October. A large tree may produce as many as 10,000 fruits in one crop. Individual *S. mombin* become sexually mature at a height of 5 to 30 m and *ca* 20 years of age. Average size of a mature individual is 60 cm in diameter at breast height (DBH). *Spondias mombin* is pollinated mostly by bees and other small insects and is partly dependent upon frugivorous birds and mammals for dispersal of seeds (Smythe 1970; Croat 1974a, b, 1978; Janzen 1985). Although *S. mombin* is found in both old and young forests, it is an early successional species that is intolerant of low light levels during recruitment (Nason & Hamrick 1997). Therefore, individuals are more common along forest edges and in secondary habitats (Stacy *et al.* 1996).

We investigated the flowering and fruiting phenologies of *S. mombin* populations isolated on six small islands in the Panama Canal with data collected over a four-year period. Our objective was

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to identify spatial and temporal patterns of *S. mombin* flowering and fruiting, thereby taking the first step in studying the reproductive success of this tree. We determined the degree of flowering and fruiting synchrony among populations and searched for spatial and temporal differences in fruiting activity. Small islands were ideal for this purpose because they were isolated and supported discrete stands of *S. mombin* in which all individuals could be studied.

METHODS

The study was conducted on six islands (designated numbers 4, 8, 9, 12, 51, and 52 in Adler 1994) ranging in size from 1.8 to 3.5 ha and in isolation between 30 and 152 m from larger landmasses. All islands were located within a 40-km² area in the Panama Canal and within 3 km of Barro Colorado Island (BCI), which was located centrally in the

study area (Fig. 1). Islands were created upon damming of the Chagres River when building the Panama Canal. Hilltops subsequently were isolated as islands and are covered now with tropical moist forest. The study area experiences a severe dry season from mid-December through April and an eight-month rainy season. Within the last 50 years, mean annual rainfall has been *ca* 2600 mm, >90 percent of which falls during the rainy season (Windsor 1990).

We marked and determined DBH of all individual *S. mombin* ≥ 10 cm DBH on each study island in 1991. A serially numbered aluminum tag was affixed to each tree with grafting tape. We censused these trees each year through 1994. All individuals that reached 10 cm DBH between annual censuses were considered recruits and were marked and measured, and all individuals that died were recorded. Monthly censuses were conducted from April 1992 through December 1995 to determine

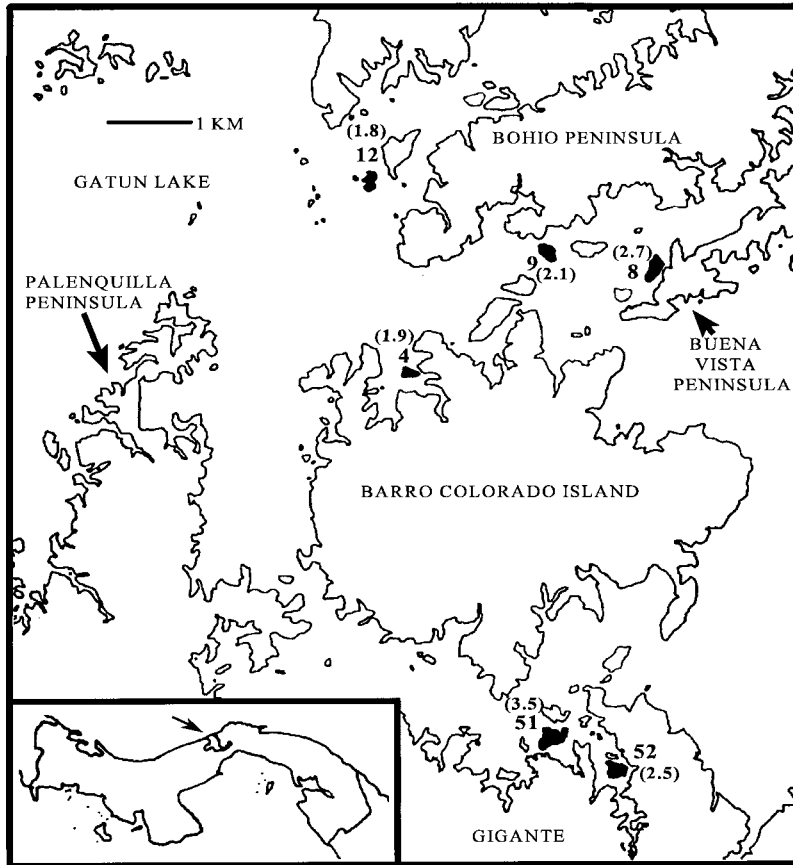


FIGURE 1. Locations of the six study islands in Gatun Lake, central Panama. Numbers in parentheses are island sizes (ha). Inset shows the location of the study area in central Panama.

if individuals produced flowers, unripe fruit, or ripe fruit. Because censuses of reproductive activity did not begin until April 1992, flowering data probably were incomplete for that year.

We constructed histograms for each island showing the numbers of individuals producing flowers, unripe fruit, and ripe fruit each month. We calculated cross-correlation functions (Diggle 1990) at a lag of zero for all possible paired combinations of islands to quantify the degree of reproductive synchrony among isolated populations. Separate functions were calculated for flowers, unripe fruit, and ripe fruit, with the numbers of individual trees in each reproductive mode representing the variable in each of the three sets of correlations. Flowering data in 1995 from islands 12, 51, and 52 could not be included in the analysis because no phenological censuses were conducted on those islands from January through April.

A linear model for categorical data was constructed to determine if proportions of individuals producing ripe fruit differed among islands and years. Linear models were appropriate for our repeated observations of the same observational units (*i.e.*, individual trees; Kleinbaum & Kupper 1978). We constructed a saturated model with both main effects (island and year) and the interaction term as independent variables, with numbers of individual trees producing or not producing ripe fruit representing the dependent variable. A separate linear model was constructed to determine if fruit production (numbers of trees producing or not producing ripe fruit) within tree size classes was similar among islands and years. We grouped trees into the following size classes: 10–19.9, 20–29.9, 30–39.9, and ≥ 40 cm DBH. A saturated model was constructed with three main effects (tree size, island, and year) and the interaction terms. We replaced observations of zero with 0.00001 because not all parameters in a saturated model could be estimated if there were zeros (Kleinbaum & Kupper 1978). Data collected from 1992 through 1994 were included in this analysis (trees were not measured in 1995). Logistic regression analysis was used to determine if there was a relationship between production of ripe fruit and tree size (DBH). Each tree represented a single observation, with presence or absence of ripe fruit as the dichotomous dependent variable and tree size as the independent variable. Data collected from 1992 through 1994 again were included in this analysis, and a separate model was constructed for each year.

RESULTS

We marked a total of 331 individual *S. mombin* during the 1991 tree census. From 1992 to 1994, there were 6 recruitments and 23 deaths, which changed the total number of individuals present on the islands each year. *Spondias mombin* already was flowering on all islands by the time phenological censuses began in April 1992 (Fig. 2). Flowering began as early as February in 1993 and 1994, and April in 1995. Peak flowering occurred in April and May for all islands and years and usually lasted for two months. Unripe fruit appeared as early as April on all islands and years, except in 1995, when unripe fruit did not appear until May. Fruit ripened as early as June in all years. Ripe fruit production peaked in August and September, although low frequencies of ripe fruit were produced into November from 1992 through 1994.

Cross-correlation functions indicated statistically synchronous flowering and unripe fruit production for all possible paired combinations of islands (Table 1). Similarly, ripe fruit production was statistically synchronous among all islands, with the exception of the comparison between islands 8 and 51. The proportions of individuals producing ripe fruit varied among islands ($\chi^2 = 80.49$, $df = 5$, $P < 0.0001$) and years ($\chi^2 = 31.20$, $df = 3$, $P < 0.0001$). The interaction term was also significant ($\chi^2 = 47.84$, $df = 15$, $P < 0.0001$), indicating that the proportions of individuals producing ripe fruit were not similar on a given island each year. Island 4, which had mostly large trees, also had the highest proportion of individuals producing ripe fruit (55%). Island 51, which had a high proportion of small trees, had only 16 percent of individuals producing ripe fruit over the four-year period. Ripe fruit production across all islands was highest in 1992 (53%) and lowest in 1994 (18%).

Fruit production varied among tree size classes ($\chi^2 = 452.38$, $df = 3$, $P < 0.0001$), islands ($\chi^2 = 37.72$, $df = 5$, $P < 0.0001$), and years ($\chi^2 = 6.25$, $df = 2$, $P < 0.01$; Table 2). The island \times size, size \times year, and island \times size \times year interactions were also significant ($\chi^2 = 48.44$, $df = 15$, $P < 0.0001$; $\chi^2 = 14.01$, $df = 6$, $P < 0.03$; $\chi^2 = 154.86$, $df = 29$, $P < 0.0001$, respectively), but the island \times year interaction was not significant ($\chi^2 = 12.83$, $df = 10$, $P > 0.05$). The smallest individual to produce ripe fruit was 11.6 cm DBH, although within the smallest size class, very few individuals produced ripe fruit (20%) over the three years in which trees were measured. In the largest size class, 84 percent of individuals produced ripe fruit over

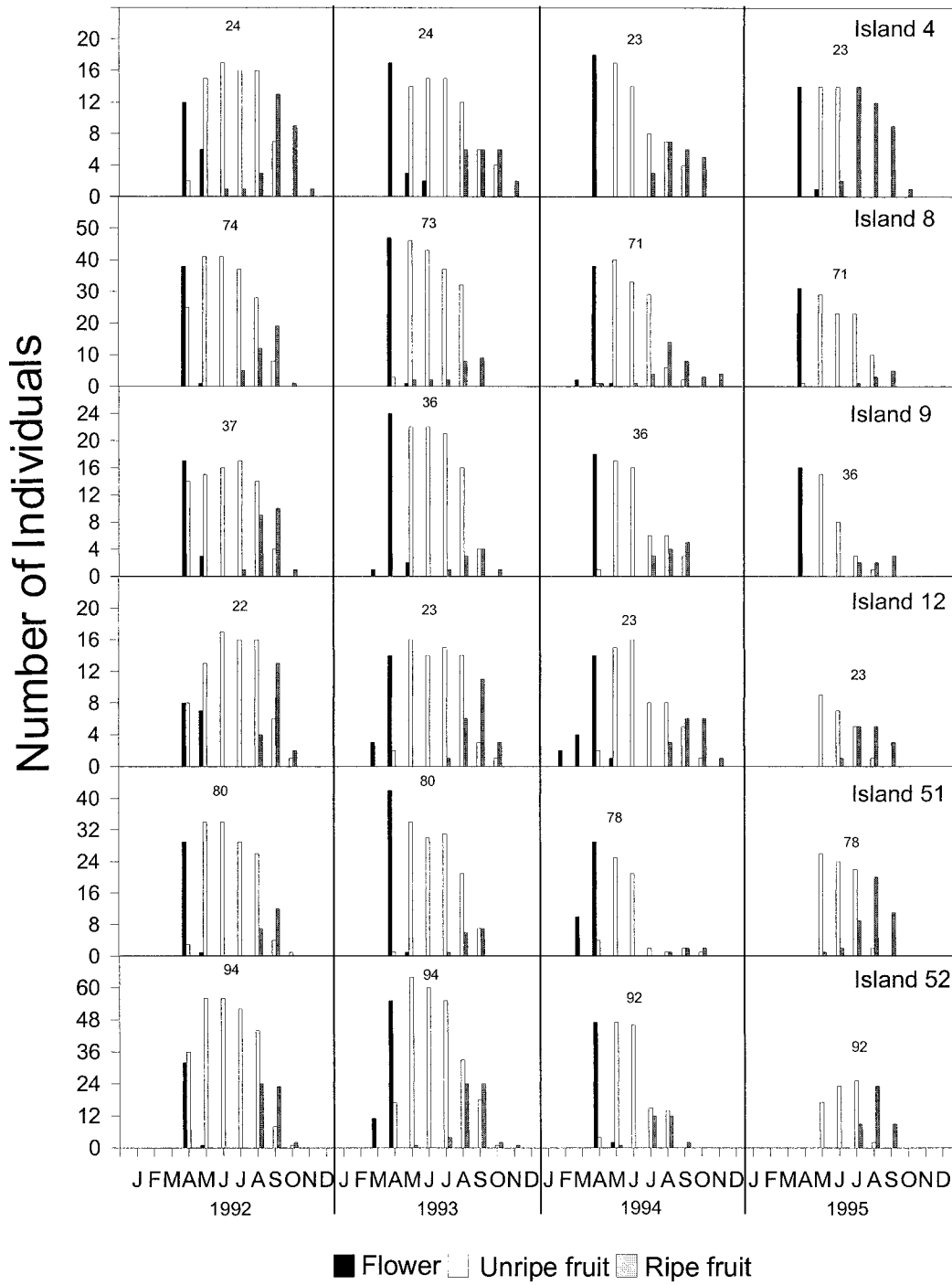


FIGURE 2. Histograms showing the numbers of individuals flowering and producing fruit on each island. Numbers above the histograms represent total numbers of marked individuals.

TABLE 1. Cross-correlation functions denoting the degree of synchrony of flowering, unripe fruit production, and ripe fruit production for each paired island cross. N = 45 time periods, functions ≥ 0.330 significant at $P < 0.05$; ^aN = 44 time periods, functions ≥ 0.334 significant at $P < 0.05$; NS = not significant.

| Island pairs | Flowers | Unripe fruits | Ripe fruits |
|--------------|----------------------|---------------|-------------|
| 4 × 8 | 0.96250 | 0.90431 | 0.57890 |
| 4 × 9 | 0.96897 | 0.92014 | 0.63417 |
| 4 × 12 | 0.87243 ^a | 0.94873 | 0.56017 |
| 4 × 51 | 0.85886 ^a | 0.90920 | 0.82537 |
| 4 × 52 | 0.87422 ^a | 0.88571 | 0.70400 |
| 8 × 9 | 0.99175 | 0.95527 | 0.91504 |
| 8 × 12 | 0.85122 ^a | 0.94800 | 0.77892 |
| 8 × 51 | 0.92450 ^a | 0.65895 | NS |
| 8 × 52 | 0.91668 ^a | 0.95045 | 0.79891 |
| 9 × 12 | 0.84801 ^a | 0.95939 | 0.77553 |
| 9 × 51 | 0.90534 ^a | 0.90882 | 0.35619 |
| 9 × 52 | 0.90070 ^a | 0.95330 | 0.84012 |
| 12 × 51 | 0.91789 ^a | 0.90453 | 0.57415 |
| 12 × 52 | 0.92938 ^a | 0.94847 | 0.83659 |
| 51 × 52 | 0.96413 ^a | 0.92571 | 0.61901 |

the three-year study period. There was a significant positive relationship between the production of ripe fruit and tree size in all three years included in the analysis (Table 3). Thus, larger trees had a higher probability of producing ripe fruit.

DISCUSSION

Isolated populations of *S. mombin* displayed highly seasonal and synchronous patterns in flowering and fruiting phenologies. Peak flowering occurred from April to May at the end of the dry season and beginning of the rainy season. Synchronous flowering of *S. mombin* was consistent with Foster's (1996) observation that tree species flowering early in the rainy season on BCI were synchronous. Ripe fruit production was highly synchronous among islands and peaked from August to October. Although we have no concurrent data from adjacent mainland populations of *S. mombin*, Croat (1974b, 1978) had noted similar flowering and fruiting activity, and Smythe (1970) acknowledged a similar period of ripe fruit production on BCI. In contrast, Frankie *et al.* (1974) had stated that *S. mombin* best exemplified a set of tree species that lacked synchrony in flowering activity in a tropical wet forest of Costa Rica. We can offer no explanation for this difference in synchrony, particularly since the forest in Costa Rica also experienced a prolonged dry season. *Spondias mombin*, however, displays variable reproductive traits throughout its vast

TABLE 2. Percentages of individuals producing ripe fruit within size classes on each island each year, with number of trees in parentheses.

| Island | 10–19.9 m | 20–29.9 cm | 30–39.9 cm | ≥ 40 cm |
|--------|-----------|------------|------------|--------------|
| 1992 | | | | |
| 4 | 0 (1) | 63 (8) | 100 (1) | 100 (14) |
| 8 | 50 (20) | 79 (29) | 67 (18) | 71 (7) |
| 9 | 0 (10) | 45 (11) | 100 (4) | 83 (12) |
| 12 | 17 (6) | 100 (3) | 100 (2) | 91 (11) |
| 51 | 14 (36) | 69 (13) | 73 (15) | 88 (16) |
| 52 | 39 (36) | 81 (32) | 100 (15) | 82 (11) |
| 1993 | | | | |
| 4 | 0 (1) | 45 (7) | 66 (3) | 92 (13) |
| 8 | 45 (20) | 73 (26) | 75 (20) | 57 (7) |
| 9 | 12 (8) | 60 (10) | 100 (6) | 83 (12) |
| 12 | 14 (7) | 100 (4) | 100 (1) | 100 (11) |
| 51 | 0 (36) | 64 (14) | 75 (12) | 89 (18) |
| 52 | 29 (31) | 84 (33) | 0 (1) | 83 (12) |
| 1994 | | | | |
| 4 | 100 (1) | 33 (6) | 67 (3) | 92 (13) |
| 8 | 30 (20) | 64 (25) | 68 (18) | 71 (7) |
| 9 | 0 (8) | 44 (9) | 43 (7) | 83 (12) |
| 12 | 0 (6) | 75 (4) | 100 (2) | 91 (11) |
| 51 | 3 (34) | 36 (14) | 73 (11) | 63 (19) |
| 52 | 7 (28) | 55 (31) | 78 (18) | 87 (15) |

range, reportedly being monoecious in Costa Rica (Bawa & Opler 1975), dioecious in Mexico (Pennington & Sarukhan 1968), and having bisexual flowers in Panama (Croat 1978). Therefore, it may not be surprising to find populations with different phenological patterns.

Seasonal and synchronous reproductive phenologies can provide adaptive advantages. For example, synchronous flowering can attract pollinators (Marquis 1988) and may be particularly important for *S. mombin* because populations in Panama are outcrossed (Stacy *et al.* 1996, Nason & Hamrick 1997). Outcrossing increases dependence on pollinators such

TABLE 3. Results of logistic regression analysis for all islands each year to determine the relationship between fruit production (presence or absence of ripe fruit) and tree size (DBH).

| Variable | β | χ^2 | P |
|-----------|---------|----------|--------|
| 1992 | | | |
| Intercept | -2.223 | 38.402 | 0.0001 |
| DBH | 0.105 | 54.272 | 0.0001 |
| 1993 | | | |
| Intercept | -2.655 | 48.041 | 0.0001 |
| DBH | 0.116 | 61.032 | 0.0001 |
| 1994 | | | |
| Intercept | -2.628 | 56.736 | 0.0001 |
| DBH | 0.089 | 58.474 | 0.0001 |

as insects for cross-pollination, and in the case of isolated populations, pollen from outside sources (Nason & Hamrick 1997). Similarly, synchronous fruit production may satiate seed predators (Janzen 1971) and attract frugivores needed for seed dispersal (Smythe 1970). The proximate cue for initiating flowering near the end of the dry season may be seasonal variation in irradiance (Wright & Cornejo 1990, Wright & van Schaik 1994). Although an extended dry period may be employed by many plants to initiate flowering, this cue seems unlikely to be used by *S. mombin* because many individuals in our study were located at the edge of the islands and had their roots largely submerged in water year-round. Thus, pollinators or seed dispersers and predators presumably are ultimate factors that select for synchronous reproductive activity, with environmental conditions such as seasonal changes in irradiance serving as the proximate cue to initiate and synchronize flowering.

The proportion of individuals producing ripe fruit was not consistent across islands or years. Differences in fruit production among islands was due partly to differences in the distribution of trees among size classes. For example, islands 4 and 12 had few trees in the smaller size classes (which fruit less frequently), while islands 8, 51, and 52 had more individuals in these smaller classes. Temporal differences in fruit production is consistent with studies of many Neotropical canopy trees. In Costa Rica, if a small proportion of *S. mombin* individuals suddenly flowered, they often failed to produce fruit (Frankie *et al.* 1974). Although fruiting activity was highly seasonal in *Tetragastris panamensis*, another canopy tree in central Panama, fruit production varied among years, with some complete failures of fruit production (Howe 1980). Furthermore, if the preceding dry season was too wet, many tree species flowered but failed to produce fruit (Foster 1996). In this study, production of ripe fruit was dependent upon tree size, which also was noted by Nason and Hamrick (1997) in isolated populations of *S. mombin*. Fruit production by *S. mombin*, however, was lower on smaller islands than in continuous forest when adjusted for tree size (Nason & Hamrick 1997). Lower fruit production on smaller islands may have been associated with low pollinator abundances, and the temporal and spatial variability in fruit production

by *S. mombin* reported here also may have been due partly to variation in pollinator abundances.

Reproductive success of trees depends not only on the quantity of seeds produced but also on successful seed dispersal and germination. In large tracts of forest, many vertebrate frugivores may act as seed predators and dispersers, and insects (*e.g.*, bruchid beetles) also may prey upon seeds. On the study islands, the main vertebrate seed predator and disperser is probably *Proechimys semispinosus*, a frugivorous and granivorous rodent that is known to consume *S. mombin* seeds (Adler 1995) and to scatterhoard seeds (Adler & Kestell 1998). This species is the only mammal that maintains persistent populations on the study islands (Adler 1996). Although the mesocarp is consumed by many frugivores, seeds of *S. mombin* are protected by a tough endocarp, and therefore are of no interest to most vertebrates except rodents such as *P. semispinosus* that are able to gnaw through the endocarp to consume the seeds (Adler 1995). Therefore, predation and dispersal by *P. semispinosus* may influence germination of *S. mombin* seeds on these islands (Smythe 1970, Hammond 1995), thereby influencing the ultimate reproductive success of individual trees.

Although small isolated populations of tropical trees may not be representative of reproductive processes in larger tracts of forest (Hall *et al.* 1996), our results showed that even isolated populations of *S. mombin* have highly seasonal and synchronous flowering and fruiting phenologies. The numbers of individuals that produce ripe fruit, however, were not consistent over space or time. Future studies should examine pollinator populations, proximate cues, and ultimate factors influencing reproductive patterns of *S. mombin*, and investigate the importance of rodents as seed predators and dispersers.

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