Table 1. Abundance of *P. amates* in different vegetation types during the day, compared between two sample types. Values are totals for 3 seine hauls and for 3 minnow traps (for 6 hrs) in each vegetation type.

Sample Type	Submerged Vegetation	Floating Vegetation
Seine Hauls	56	9
Minnow Traps	22	13

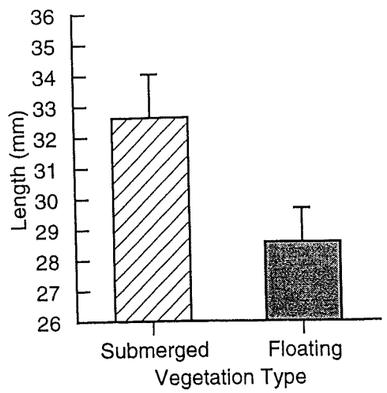

Fig. 1. Length of *P. amates* individuals caught during 6 hours of passive sampling at Rio Tempisque in Palo Verde, Costa Rica (mean ± 1 S.E.; submerged, n= 22; floating n = 13).

Discussion

As hypothesized, total abundance was higher in submerged than floating vegetation, suggesting that zooplankton density influences the spatial distribution of *P. amates*. However, contrary to our second hypothesis, *P. amates* under floating vegetation tended to be smaller than those under submerged vegetation during the day. This suggests that differences in predation pressure between the habitats, and differences in the vulnerability of small vs. large *P. amates*, may differ from our initial assumptions. *E. crassipes* forms a dense layer of surface vegetation that may provide shelter from wading birds that eat small fish. Also, larger *P. amates* may be more visible to predatory fish, and therefore more vulnerable to predation than juveniles; if so, larger *P. amates* would be expected in the complex submerged vegetation than in the floating vegetation.

Due to a large mesh size, the minnow traps were not as effective as seining for capturing juveniles. Also, larger fish are often able to escape seines (P. Pickhardt, *pers comm*). Thus, these two methods resulted in different size distributions sampled from the same population.

We were unable to catch fish at night to test our hypothesis that the abundance and size distribution of *P. amates* at night should be uniform across habitats. At night, *P. amates* may frequent parts of the marsh different from those that we sampled, or our sampling method may have been ineffective at catching them.

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Seed dispersal and colonization by seed predators in *Sterculia apetala* (Sterculiacea)

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Abstract. *Sterculia apetala* (Sterculiaceae), a tropical dry forest tree, experiences heavy seed predation by the hemipteran *Dysdercus bimaculatus* (Pyrrhocoridae). We predicted that *S. apetala* in our study area would employ synchronous phenology to satiate the predator and thus reduce seed predation. All trees examined fruited synchronously in January 1999. Seed density decreased exponentially with distance from the crown center. However, all dehisced fruits within 20 meters of the parent were colonized by *D. bimaculatus*. This species clearly depends on vertebrates to disperse seeds beyond 20 m for successful recruitment.

Keywords: Dysdercus bimaculatus, *seed shadow*, *Panama tree*

Introduction

Sterculia apetala (Sterculiaceae) is a biannually fruiting, monoecious tree in the dry forests of Central America (Croat, 1978). Fruits mature at the beginning of the dry season and typically abscise within a week of maturation. Each fruit is lined with irritating trichomes and usually contains 5 seeds. The cotton stainer bug, *Dysdercus bimaculatus* (Pyrrhocoridae), is believed to cause near-total mortality on *S. apetala* seeds under the parent tree (Croat, 1978). Janzen (1973) hypothesized that trees may employ a strategy of synchronous fruiting to satiate predators such as *D. bimaculatus*, thus allowing some seeds to escape predation.

We hypothesized that colonization by *D. bimaculatus* would decrease with increasing distance from the parent tree. This would occur if the seed predator is either attracted by the parent tree or aggregates in areas of highest fruit density. We also quantified the pattern of seed dispersal as a function of distance from the parent.

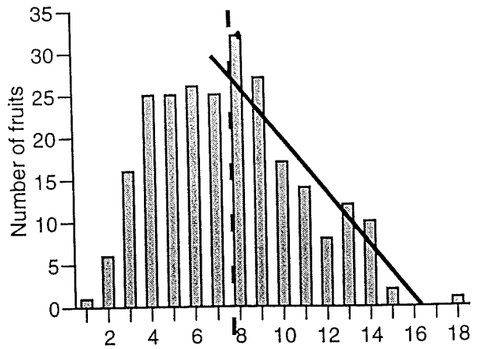
Methods

Observations of *S. apetala* were made on 14 and 15 January, 1999, 1 km north of the OTS biological station at Palo Verde National Park, Costa Rica. We searched 4 hectares of primary forest centered on the Cerros Calizos trail for *S. apetala* adults (>30 cm dbh) and recorded their reproductive status. We chose three "focal" trees at least 40m away from conspecific adults for detailed study. Around each focal tree, fruits were counted in three sectors, each 10 degrees wide and 20 m long. Fruits were classified as empty of seeds; dehisced with *D. bimaculatus* present; dehisced without *D. bimaculatus* present; or closed. Sectors originated at the center of the crown, estimated as the point on the ground beneath the center of the canopy. Fruit distances from the crown center were recorded in 1 m classes.

Experiments were done to test colonization rates by *D. bimaculatus* at varying distances from the parent tree. From the three focal trees, we selected two with similar numbers of fallen fruits. Seven transects were used, four under one tree and three under the other. Fruits that were closed and therefore had no prior colonization by *D. bimaculatus* were opened and placed on each transect at 1, 5, 10, and 15 m from the center of the crown. Fruits with seeds that were dried or moldy (6 out of 28) were excluded from the analysis. The levels of colonization for each fruit were assessed 0.5, 2, 5, and 24 hr after placement. Colonization levels were ranked from 0 (no *D. bimaculatus* present); 1 (1- 20 *D. bimaculatus*); 2 (20-50 *D. bimaculatus*); or 3 (fruit completely covered by *D. bimaculatus*). For each distance and time, a colonization index was calculated across the 7 transects as the mean colonization rank for the samples.

Results

All 9 *S. apetala* individuals observed fruited synchronously in January 1999. Beyond the crown radius (ca. 8 m), the number of fruits in 1 m annuli decreased with distance (Fig. 1). The number of fallen fruits per unit area decreased exponentially with distance from crown center (Fig. 2).



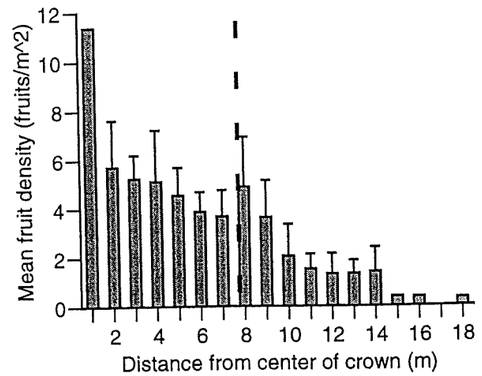


Fig 1. Number of fallen fruits within 1 m annuli as a function of distance from the center of crown of *Sterculia apetala* trees at Palo Verde National Park, Costa Rica (means ±1 SE). Dashed line represents approximate margin of crown. Fruit abundance decreases with distance beyond 8 m (R^2=0.84, df=10, P<0.001).

Fig 2. Mean fruit density as a function of distance from the center of the crown of *S. apetala*. Density of fruit/m^2 decreases exponentially from center of crown (linear regression of log-transformed data, R^2=0.39, df=69, P<0.0001).

Mean density of fruits beneath the crown was 5.5/m^2, while mean density from 15 to 20 m was 0.2/m^2. In every fallen fruit within the 9 sectors (except those that were closed or contained dried seeds), the seeds were absent or colonized by *D. bimaculatus* (Fig. 3).

When fruits were placed around 2 focal *S. apetala* trees, colonization levels increased over the first 5 hours. After 30 minutes, *D. bimaculatus* had discovered all fruits <10 m from the center of the crown, and after 5 hours, all

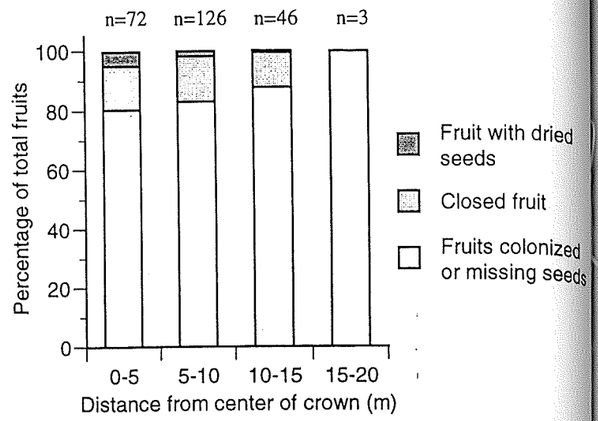


Fig 3. Status of fallen *S. apetela* fruits at Palo Verde National Park, Costa Rica. There was no trend in the percentage of fruit damaged with increasing distance from the center of the crown (Kruskal-Wallis: X^2 =5.26, df=3, P=0.15).

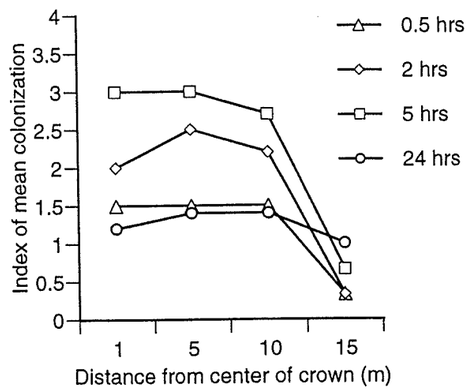


Fig 4. Colonization index (see methods) over time of *D. bimaculatus* on *S. apetala* fruits at 1, 5, 10, and 15 m from the center of the crown, Palo Verde National Park, Costa Rica (0.5 hrs: G=9.816, p=0.13; 2 hrs: G=18.643, p=0.03; 5 hrs:G=13.823, p=0.03; 24 hrs: G=15.669, p=0.07. Statistics compiled from colonization levels taken at each distance).

fruits at 1 m and 5 m were completely covered by the seed predators (Fig. 4).

By 24 hrs, the pattern of colonization had changed. On fruits close to the parent, the density of predators actually declined, while on those 15 m away, colonization levels continued to increase (Fig. 4). We did not test this changing pattern statistically, however.

At both 2 and 5 hours, there was a significant decrease in colonization levels with distance from the center of the crown (Fig. 4). Nonetheless, all fruits in our experiment,

including those at 15 m were found by *D. bimaculatus*.

Discussion

Because all *S. apetala* fruits within 20m of crown center, whether placed or naturally dehisced, were discovered by *D. bimaculatus*, it seems unlikely that recruitment can occur within this distance of the parent. Janzen (1972) similarly found that all seeds within 30 m of the parent were discovered by seed predators in the genus *Dysdercus*; only seeds placed 90 m away escaped. This implies that *S. apetala* relies on vertebrates to distribute fruits far from the parent to escape seed predation. The slower increase in colonization levels farther from the parent do suggest that search time increases with distance, or with decreasing fruit density. At a great enough distance, seeds may not be discovered before germination. We observed white-faced monkeys and variegated squirrels taking *S. apetala* fruits. These vectors may be responsible for the long distance dispersal that appears to be essential for successful recruitment in *S. apetala*.

Although all *S. apetala* trees in our sample fruited synchronously, consistent with masting theory, there was no evidence of escape from seed predation due to predator satiation. It remains possible, however, that masting on a 2 yr cycle reduces predator populations sufficiently that seeds dispersed far from the parent by vertebrates may escape predation.

One important detail remains unresolved. The mechanism by which *D. bimaculatus* destroys seeds needs to be determined; seeds covered with *D. bimaculatus* for 24 hrs showed no visible signs of damage.

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