POPULATION STRUCTURE AND DISTRIBUTION OF *COCOS NUCIFERA* ALONG A STRETCH OF PACIFIC COAST, PARQUE NACIONAL CORCOVADO, COSTA RICA

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Abstract: The spatial distribution of a plant species can speak to conditions affecting growth, survival, and seed dispersal. The coconut palm, *Cocos nucifera*, is found along coastlines in tropical climates throughout the world. We studied a population of *C. nucifera* on a Pacific beach at Parque Nacional Corcovado, Costa Rica. We hypothesized that patchiness due to dispersal, and environmental limitations to establishment and growth, would influence the distribution of *C. nucifera* trees. Specifically, we predicted that (1) more *C. nucifera* would be found near reproducing adults than along the rest of the beach, (2) younger *C. nucifera* would be found farther from parent trees than older offspring, and (3) *C. nucifera* distribution would vary with shade and distance from water and would therefore be restricted to a zone of relatively constant width along the beach. Our results supported prediction 3 but failed to support predictions 1 and 2. Given the unique study system and the potential ease of experimental manipulations, we hope that our findings stimulate further research into the growth, survival, reproduction, and dispersal of *C. nucifera*.

Key Words: coconut, palm, population dynamics

INTRODUCTION

Habitat conditions, seed dispersal, competition, and predation determine the spatial distribution of plant species (Richardson and Bond 1991). Examining the distribution and size structure of a population can provide insights into the historical processes that may have shaped the establishment, survival, and growth rates of individuals in the population.

The coconut palm, *Cocos nucifera* (Arecaceae), has a pan-tropical coastal distribution. Once *C. nucifera* ovules are fertilized, the fruit (coconut) may take up to a year to mature to its full length of about 30 cm. When the fruit falls, it may be washed into the ocean and spend months traveling up to several thousand kilometers before being deposited on a beach (Zuchowski 2005). From personal observations, we noted that *C. nucifera* either occur in clusters, with one reproductive adult surrounded by immature offspring (henceforth called a "neighborhood"), or as solitary individuals.

Because the species is easy to recognize at all life stages, including the obvious, large seeds, and because it has a clearly defined coastal

distribution (apart from planting by humans), it may be well suited to a long-term study of its population dynamics. While we attempted to lay the foundation for such a long-term study, we focused on the following short-term questions: (1) How are different size classes of *C. nucifera* distributed along the beach, and (2) What factors might determine the species' spatial distribution? We hypothesized that the distribution of *C. nucifera* would be primarily determined by local dispersal from reproductive adults and by environmental factors that influence growth and survival following seed dispersal.

We made three short-term predictions, based on the assumption that size class and age are positively correlated. First, we expected to find more immature *C. nucifera* in neighborhoods than as solitary individuals, because we assumed input rates from a nearby parent plant would be higher than input rates from the ocean. Second, within each neighborhood we expected to find larger *C. nucifera* closer to the parent tree and smaller *C. nucifera* farther away, because individuals that establish close to the parent could competitively inhibit growth, and exclude later cohorts to more distant microsites. Third, we predicted that the distribution of *C. nucifera* would be consistent with shading limiting its landward range and wave action limiting its seaward range.

METHODS

We carried out our study on 4 and 5 February, 2007 at Parque Nacional Corcovado, Costa Rica. The park was partially cleared for agriculture until 1975 and is still recovering. Also, from c. 1975-1990, guards harvested almost all coconuts present in the study area, so seed input fell to near zero during that time.

We censused all of the *C. nucifera* that had germinated and survived along approximately 520 m of the beach (1114 steps at a mean of 46.9 cm/step), from the end of the airstrip at the Estación Biológica Sirena north to Rio Sirena. While one researcher paced the beach, others recorded location and relevant data for each *C. nucifera*. We placed each *C. nucifera* into one of five size classes: < 1 m tall, 1-3 m tall, > 3 m tall but non-woody, woody adult, and reproductive adult (tree with maturing coconuts). "Woody" refers to the emergence of the woody stem from the ground. Flowering adults without coconuts were placed in the "woody adult" category.

For each tree, we recorded its horizontal and vertical distances from that day's high tide mark, the amount of crowding vegetation at the level of the individual's leaves (low, medium, high), and the

amount of shading by the canopy above that individual (low, medium, high). At the beginning of our sampling, we reached consensus on levels of crowding and shading, which we assessed visually. High crowding was reserved for cases where the *C. nucifera* leaves were in close contact with surrounding vegetation, and high shading was reserved for cases where canopy cover above the individual approached the levels characteristic of the closed forest immediately inland from the study area. Vertical distances above high tide level were estimated by one researcher standing at the high tide mark, while another stood at the *C. nucifera* individual. They then estimated the vertical distance above high tide, in 0.5 m intervals, usually by approximating where a horizontal line from the eyes of one intersected the body of the other, accounting for height differences among researchers. Horizontal distances from the high tide mark were also estimated visually, after having paced several early samples. In spite of inherent measurement error in visual estimates (e.g., errors may be up to 0.25 m in vertical estimates, and up to 2 m in horizontal distances), we chose to maximize sample size and therefore sacrificed measurement precision for speed of sampling.

We characterized each neighborhood in the following manner. For each reproductive adult, we recorded the number of maturing coconuts present on the tree and whether or not a later cohort of younger, much smaller coconuts was developing above the maturing fruits. We also recorded the number of non-reproductive sprouted *C. nucifera* found in neighborhoods surrounding reproductive adults, and their distances from the central adult, estimated by pacing. Juveniles at successively greater distances from the reproductive adult were included in its neighborhood if they were within 5 m of that adult, or within 5 m of another juvenile that had already been included in that neighborhood. This criterion defined four neighborhoods around four reproductive adults.

We observed five very tall reproducing adults situated 15 m or more inland from the high tide mark, beyond the dense underbrush that covers the shoreline. We did not include these trees in our results because their size and location suggest they were likely planted by humans when this area was under cultivation and thus were not dispersed naturally. There was no evidence of offspring from these adults extending as "neighborhoods" into the shoreline habitat of our study area.

Combining all individuals from the four coconut palm neighborhoods, we tested for differences among size classes in mean distance to the nearest

reproductive adult with an ANOVA, using log-transformed data to achieve normality (N = 9 for < 1 m, N = 6 for 1-3 m, N = 8 for > 3 m, N = 2 for woody adult). We then repeated the analysis, excluding the woody adult category due to the small sample size. Next, we grouped our estimates of distances vertically and horizontally from the high tide mark into classes of low and high, and performed four 2-way contingency tests to evaluate correlations between two sets of categorical factors (shading and crowding vs. elevation above tide and distance from tide).

RESULTS

Within neighborhoods, the mean distance to the parent plant did not vary among age classes either with or without the woody adult category included in the analysis (With woody: $F_{3,20} = 0.93$, $P = 0.45$, Without woody: $F_{2,20} = 1.20$, $P = 0.32$, Table 1).

Table 1: Along a 520 m stretch of the Pacific coast at Parque Nacional Corcovado, Costa Rica, *Cocos nucifera* occurred as solitary individuals or within neighborhoods of offspring centered around a reproducing adult. We categorized all *C. nucifera* into size classes (as a proxy for age, which we could not determine). Within each neighborhood, we recorded the distance of each individual tree to the single reproducing adult.

Size Class	Mean distance to parent (m)	± 1 SE
< 1 m	1.37	0.21
1-3 m	1.36	0.25
> 3 m, non-woody	0.95	0.22
> 3 m, woody	1.61	0.62

Of the 72 individuals we censused, 39% occurred as members of a neighborhood, and 61% occurred as solitary individuals. Overall, the population of coconut trees on the stretch of beach we surveyed appeared skewed in favor of the youngest size class, with fewer individuals present in each successively larger size class (Fig. 1). This skew appeared stronger in the solitary trees than in the neighborhood trees (Fig. 1).

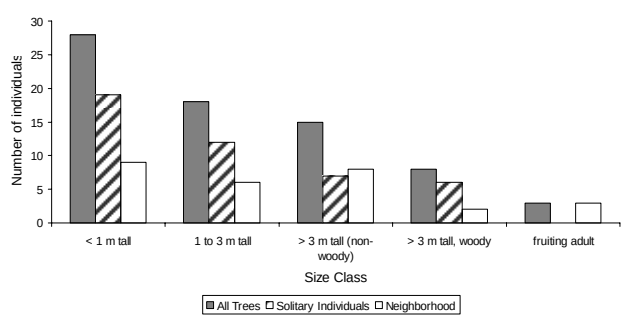

Figure 1: The population size distribution of *Cocos nucifera* individuals along a 520 m stretch of the Pacific coast at Parque Nacional Corcovado, Costa Rica consists of 44 solitary individuals and 28 trees in neighborhoods around reproductive adults.

For all trees observed, 49% experienced low crowding, 46% medium crowding, and 5% high crowding. For all trees observed, 47% experienced low canopy shading, 36% medium shading, and 17% high shading. Plants higher above the high tide mark experienced more shading ($\chi^2_{2,68}$ = 6.715, P = 0.0348). There was a similar tendency for greater shading with increasing distance from the high tide line that was marginally significant ($\chi^2_{2,68}$ = 4.959, P = 0.0838). In contrast to canopy shading, there was no tendency for crowding around coconut plants to vary with vertical height above, or horizontal distance from, the high tide mark ($\chi^2_{2,68}$ = 0.319, P = 0.8525; $\chi^2_{2,68}$ = 2.241, P = 0.3261). In relation to the height of the high tide line, *C. nucifera* ranged from -0.5 m to 1.0 m (mean ± 1 SE = 0.2 ± 0.05 m), in our estimates. Estimated horizontal distance from the high tide ranged from 0 m to 12 m, with a mean of 4.4 ± 0.3 m.

DISCUSSION

C. nucifera growing along the beach of Parque Nacional Corcovado are not distributed randomly. All but five of the observed *C. nucifera* were within 12 m (horizontally) from the high tide mark, reflecting the limitations of wave action as a dispersal vector. The degree of canopy shading may be a significant limitation to the landward range of *C. nucifera*. As expected, canopy cover was greater over coconut plants higher above high tide, reflecting a general increase in canopy cover from the beach to the well developed forest canopy inland. However, there was no corresponding trend in crowding by vegetation at the level of coconut foliage. Ground vegetation is well-developed just above high tide; this may be due in part to the sparse canopy cover which allows light to penetrate.

Both elevation above high tide and horizontal distance from high tide reflect limitations on oceanic transport of coconut seeds. Even waves of high amplitude cannot transport coconuts high above the tide level (except perhaps during storm events), and dense vegetation, even on a gently sloping shoreline, can physically restrict water-borne dispersal of coconuts inland.

The smallest size class contributed the highest proportion of individuals to the population, and the numbers of individuals per class declined with increasing size (Fig. 1). This size class distribution corresponds to the typical age structure found in tree populations that are either growing or stable. In contrast, the reverse trend (i.e., most individuals in large size classes), or an even size class distribution, would suggest that the population was in decline, since mortality occurs at each stage and larger size classes

are derived from smaller ones in the past. However the limitations of static data must be recognized explicitly. To infer dynamics, even from age structure data, one must assume constancy of seedling recruitment. If size class distributions are used in place of age distributions to infer population dynamics, interpretations must be made even more cautiously, in part because time intervals required to transition from one size class to the next may vary.

The unexpected finding that the majority of the *C. nucifera* occur as solitary individuals could be explained by the fact that after the high human harvesting of coconuts decreased in the late 1990's, larger cohorts of seedlings may have established. Before that time, human consumers may have removed coconuts that were near or on adult *C. nucifera* trees more frequently than solitary coconuts, because fruiting trees would be easier to find. Therefore, solitary coconuts may have had a greater per capita chance of germinating than would coconuts under their parent trees, resulting in the current high proportion of *C. nucifera* that exist as solitary individuals. We did not estimate the rate of input of coconut fruits from the ocean, and it is possible that some coconuts delivered outside the neighborhoods, by wave action, were derived originally from local adults.

A final goal of our study was to provide initial observations and hypotheses to help in the design of a future long-term study of the population dynamics of *C. nucifera* along the Pacific coast of Parque Nacional Corcovado. To that end, our dataset has been archived and will be available for future use. From our findings, we hypothesize that light, nutrient availability, water availability, wave action, and beach topography all contribute to the spatial distribution of *C. nucifera*. Mapping and permanently marking individuals (including ungerminated fruits), and monitoring survival, reproduction, and growth rates, would supply the information necessary to complete a life table and project *C. nucifera*'s population structure and growth rate. Experimental manipulations with coconut fruits would not be difficult, and may be used to test the effects of some of the hypothesized factors affecting the growth and survival of *C. nucifera.*

LITERATURE CITED

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