Scientific Electronic Archives
Issue ID: Sci. Elec. Arch. Vol. 13 (11)
November 2020
DOI: http://dx.doi.org/10.36560/131120201229
Article link
http://sea.ufr.edu.br/index.php?journal=SEA&page=article&op=view&path%5B%5D=1229&path%5B%5D=pdf
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ISSN 2316-9281

Carnauba demography: analysis of the spatial pattern

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Abstract. Studies of spatial patterns are important in the elaboration of hypotheses on the dynamics of plant populations. In this context, the research aimed to investigate the spatial pattern between different life stages (regenerating, young and adult) of the *Copernicia prunifera* an endemic palm from the Brazilian semiarid. The study was carried out on a plot present in a remaining area of the Caatinga biome. The second-order neighboring function (NDF) was used to determine the degree of aggregation (univariate analysis) and if there is an association between the life stages (bivariate analysis). The NDF spatial pattern analysis for all *C. prunifera* individuals showed significant levels of aggregation up to a radius of 6 m and random pattern at higher distances. The bivariate analysis resulted in aggregation with a radius of 8 m between regenerating individuals and reproductive adults, indicating spatial association. Factors such as limited seed dispersal around the maternal plant and intra-species competition in the early stages of *C. prunifera* life are possibly responsible for the changes observed in the spatial pattern between the life stages of the species.
Keywords: Arecaceae, native palm, population ecology

Introduction

The native Brazilian palm, *Copernicia prunifera* (Mill.) H.E.Moore (Arecaceae), is popularly known as carnauba and occurs mainly in the states of Piaui, Ceará and Rio Grande do Norte, where it is found in river valleys (SOUSA et al. 2015). The distribution in these areas, often flooded, indicates adaptations of the species to environments with low oxygen concentration, considering that the flooded soil does not affect the growth of the species (ARRUDA; CALBO, 2004).

C. prunifera is indicated for afforestation of streets and green areas. The adult individual can reach a height of more than 10 meters and produce between 45 and 60 annual leaves, which are used by extractive communities to obtain "carnauba wax" (GOMES et al., 2009; LACERDA et al. 2011). The fruits are 26.06 mm and 17.70 mm long and average diameter respectively, their seeds have a medium degree of humidity, and sowing is indicated right after the dispersion of the fruits (ARAÚJO et al., 2013). The flowers are hermaphrodite, and the species has a mixed reproduction system (SILVA et al., 2017).

Demographic aspects of plant populations have been commonly described through spatial correlations between ontogenetic stages or size classes (BAROT; GIGNOUX, 2003; FONSECA et al., 2017). The type of spatial distribution a species presents may be influenced by biotic factors such as dispersion and herbivory or by abiotic factors such as solar radiation, water, and soil type (BERNASOL; LIMA-RIBEIRO, 2010; COSTA et al., 2018).

Analysis of spatial patterns is important in the development of hypotheses on plant population dynamics (CONDIT et al., 2000; SOARES et al., 2019). In forest communities, plant populations have different biological characteristics. They are influenced by intra-species and interspecific relationships (ZHANG et al., 2020), and it is difficult to separate their effects on spatial distribution (ZHANG et al., 2016).

Knowledge about the distribution pattern of a species is an essential tool for management planning and execution of forestry treatments, whether the species is of interest for logging or not (COSTA et al., 2017; SALAKO et al., 2019; SILVA et al., 2019).

Investigating the spatial pattern of trees in different size classes, and according to their most abundant species, may provide evidence on the structure of the plant community (VIEIRA et al., 2010; WÉDJANGNON et al., 2020). From these data, it is also possible to indicate the existence of exploitation or population increase, as well as to indicate reproductive success, since understanding the form of aggregation of the species can provide indications of intervention in the population (PALUDO, 2011).

According to information on the demography of *C. prunifera*, individuals are known to occur in high density, characterizing *C. prunifera* is in monodominance (SILVA et al., 2014; PINHEIRO et al., 2017). In general, analyses of the spatial distribution pattern have revealed that most tropical tree species have varied aggregations in all diameter or height classes (CONDIT et al. 2000; HE et al., 1997; HUBBELL, 1979). Typically, this aggregation decreases with increasing age, as reported for *Cecropia obtusifolia* (EPPERSON et al. 1997), *Alsesis blackiana* and *Platypodium elegans* (HAMRICK et al., 1993), and *Shorea leprosula* (NG et al., 2004).

Given the context, this study aimed to investigate the spatial pattern of the *C. prunifera* palm in a remaining Caatinga biome population, as well as the spatial differences and associations between the size classes of the species, testing the following hypothesis: Does the species present an aggregated distribution pattern? Is there a spatial association between regenerating individuals and reproductive adults?

Methods

Study area and sampling

The research was conducted in an area belonging to the Specialized Agricultural Sciences Academic Unit of the Federal University of Rio Grande do Norte in the municipality of Macaíba, Brazil (Figure 1). The vegetational matrix is composed predominantly of Caatinga vegetation biome in different phytophysiognomies, among them: the Arboreal Caatinga, Shrubby Caatinga, and Anthropized Caatinga, and areas of the enclave and ecological tension with other vegetational domains, especially the Atlantic Forest.

According to the IBGE classification (1992), this is the Semideciduous Seasonal Lowland Forest, with a leaf shedding at the end of the drought period reaching more than 80% of a not very compact canopy. Some places in the study area are used for cattle grazing, especially during the dry season. The state of conservation, however, seems reasonable given the continuous tree cover in some stretches, without the marked dominance of a single species and the frequent presence of young trees in secondary vegetation.

The local climate is a transition between the As' and BSh' types of the Köppen classification, with high temperatures all year round and rainfall in autumn and winter (ALVARES et al., 2013). The average annual air temperature inferred for the area is around 26 °C, with an average annual rainfall of 1070.7 mm.

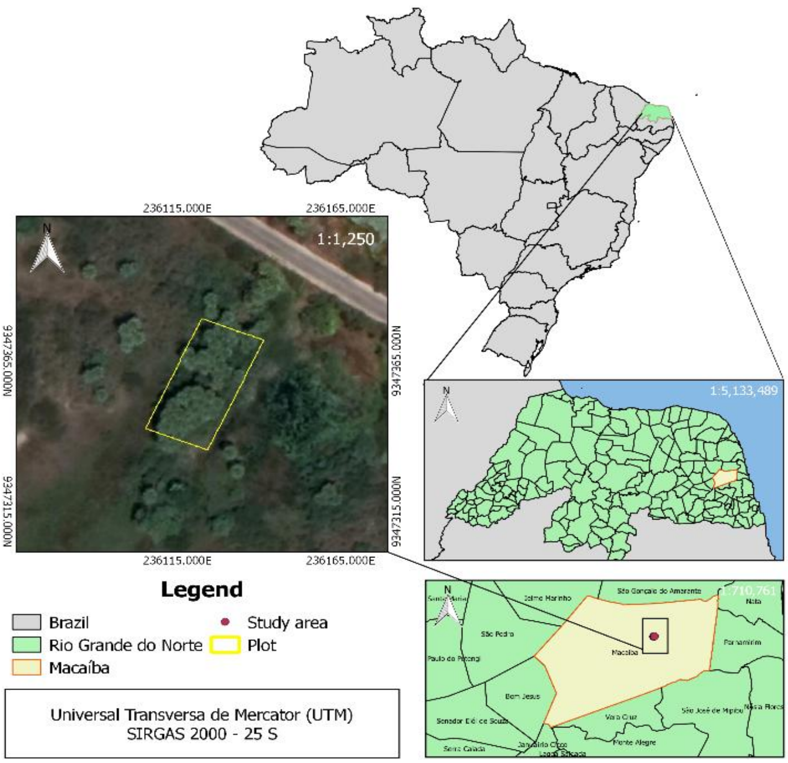

Figure 1. Location of the study area, municipality of Macaíba - Rio Grande do Norte, Brazil.

All individuals of *C. prunifera* were mapped in an area of 800 m², in a plot of 20 x 40 m, covering the occurrence of the species in the remaining population. The geographical positions of the individuals (x and y) were then recorded with GPS. The height of the plants was estimated with the use of steel metric strips or with the projection of a tree trimmer.

In all individuals present in the area, the presence and absence of reproductive structures, such as flower bud, flower, and fruit, was evaluated to characterize adult individuals. The population was divided in a representation by size class, being: 1) regenerating individuals (mean height. ± s.d. = 0.52 m ± 0.41 cm); 2) young individuals, without reproductive events (mean height. ± s.d. = 5.14 m ± 2.20 cm); and 3) adult individuals, with reproductive events (mean height. ± s.d. = 8.38 m ± 0.86 cm), totaling 120 plants (Table 1).

Data analysis

The neighbourhood density function (NDF), described by Condit et al. (2000), was used to evaluete the spatial pattern of individually cohorts (univariate analysis), and the spatial association between cohorts (bivariate analysis). Distance classes (t) between 1 and 20 m were used, where the limit t is approximately ½ of the longer plot length.

Through simulations, the distance classes in the correlograms were specified with intervals of 1 m to avoid the jagged plot effect of the observed NDF values (WIEGAND; MOLONEY, 2004). The correction of the edge effect was calculated, according to Goreaud and Pelissier (1999). Finally, correlograms were constructed with the NDF statistic values (t) as a function of the t-distance, compared to entirely randomized envelopes (upper and lower confidence intervals) obtained from 499 replications by the Monte Carlo test ($\alpha = 0.01$). The analyses were performed using the SpPack 1.38 program (PERRY, 2004).

Results and discussion

The density of *C. prunifera* individuals for each height class was of 0.09 ind.m-² for regenerating individuals (n = 69); 0.4 ind.m-² for young individuals, without reproductive events (n = 23); and 0.30 ind.m-² for adult individuals, with reproductive events (n = 28). The population structure of *C. prunifera* presented in the sample area shows the largest number of regenerating individuals in the early stages of development (Table 1).

Populations with higher numbers of individuals in the early stages of the establishment are common for several palm trees, such as *Euterpe globosa* C.F. Gaertn. (VAN VALEN, 1975), *Astrocaryum mexicanum* Liebm. ex Mart. (SARUKHÁN, 1980), *Iriartea deltoidea* Ruiz & Pav. (PINARD, 1993), *Phytelephas seemannii* O.F. Cook (BERNAL, 1998) and *Euterpe edulis* (REIS et al.., 1996; VIEIRA et al., 2010).

Table 1. Classes of *C. prunifera* individuals, population size (n), and proportion to the total sample (%).

Classes	Height ± stand. deviation	n	%
Regenerants	0.52 m ± 0.41 cm	69	57.5
Youth	5.14 m ± 2.20 cm	28	23.3
Adults	8.38 m ± 0.86 cm	23	19.2
Total		120	100

The spatial pattern of individuals in a population is dependent on the scale considered in the study. For plants, the spatial structure is the result of the spatial arrangement of parental plants, seed dispersal patterns, conditions for establishment, and intra-species and interspecific interactions (CONDIT et al., 2000). Specifically for palm trees, dispersion through regional scales has a more significant effect than environmental heterogeneity (VORMISTO et al., 2004).

In the case of phenology, the percentages of adult individuals with floral bud, flowering, and immature fruit were 15.4%, 11.5%, and 73.1% respectively. No individuals presenting mature fruits were observed due to the period in which the data collection was performed. The spatial position of the plants allowed the display of the aggregate pattern (Figure 2). Such characterization was corroborated by correlogram analyses. The NDF spatial pattern analysis for all individuals of *C. prunifera* (n = 120) showed significant levels of aggregation up to a radius of 6 m and random pattern at higher distances (Figure 3).

For regenerating individuals (n = 69), aggregation up to a radius of 6 m was observed (Figure 4A). Young individuals (n = 28) showed significant levels of aggregation up to a radius of 5 m, indicating an aggregated spatial pattern (Figure 4B). Similarly, for adult individuals (n = 23) significant levels of aggregation up to a radius of 5 m were observed and complete randomization at greater distances (Figure 4C).

The aggregate spatial distribution pattern may be influenced by the accumulation of large quantities of seeds in certain spatial portions (microsites). In contrast, other microsites would have low seed densities or zero density because of restricted seed dispersion. Thus, germination and recruitment rates are expected to be higher in spatial portions with seed accumulation relative to other environments, i.e. around the parental site. Therefore individuals would be aggregated in space (BARBOUR et al., 1987). This pattern of distribution is characteristic of plant species whose seeds are dispersed predominantly by autochory (barochory), in addition to the large quantities of seeds produced and long periods of fruiting (JANZEN, 1976). This seems to be the case for *C. prunifera*, as much of the fruit is naturally deposited close to the mother plant.

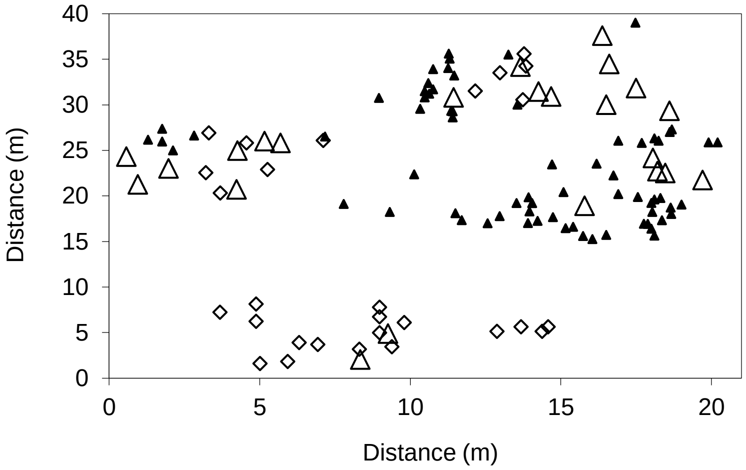

Figure 2. Spatial distribution of individuals in the remaining population of *C. prunifera*, where Δ indicates the reproductive adult individuals, ◊ indicates the young individuals and ▲ the regenerating individuals.

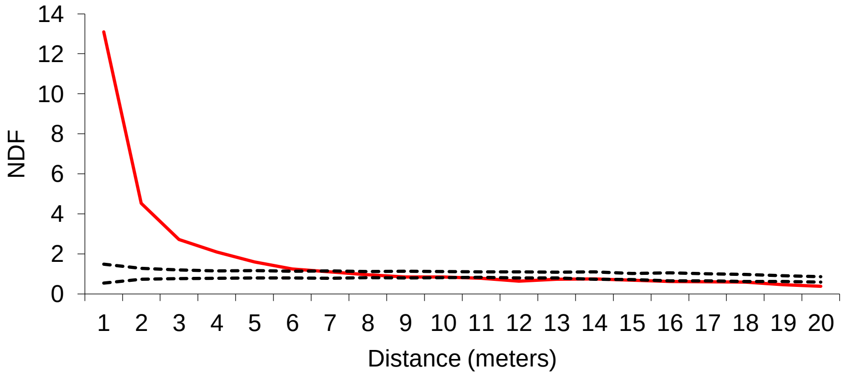

Figure 3. Correlogram present the analysis of the NDF spatial pattern of all *C. prunifera* individuals.

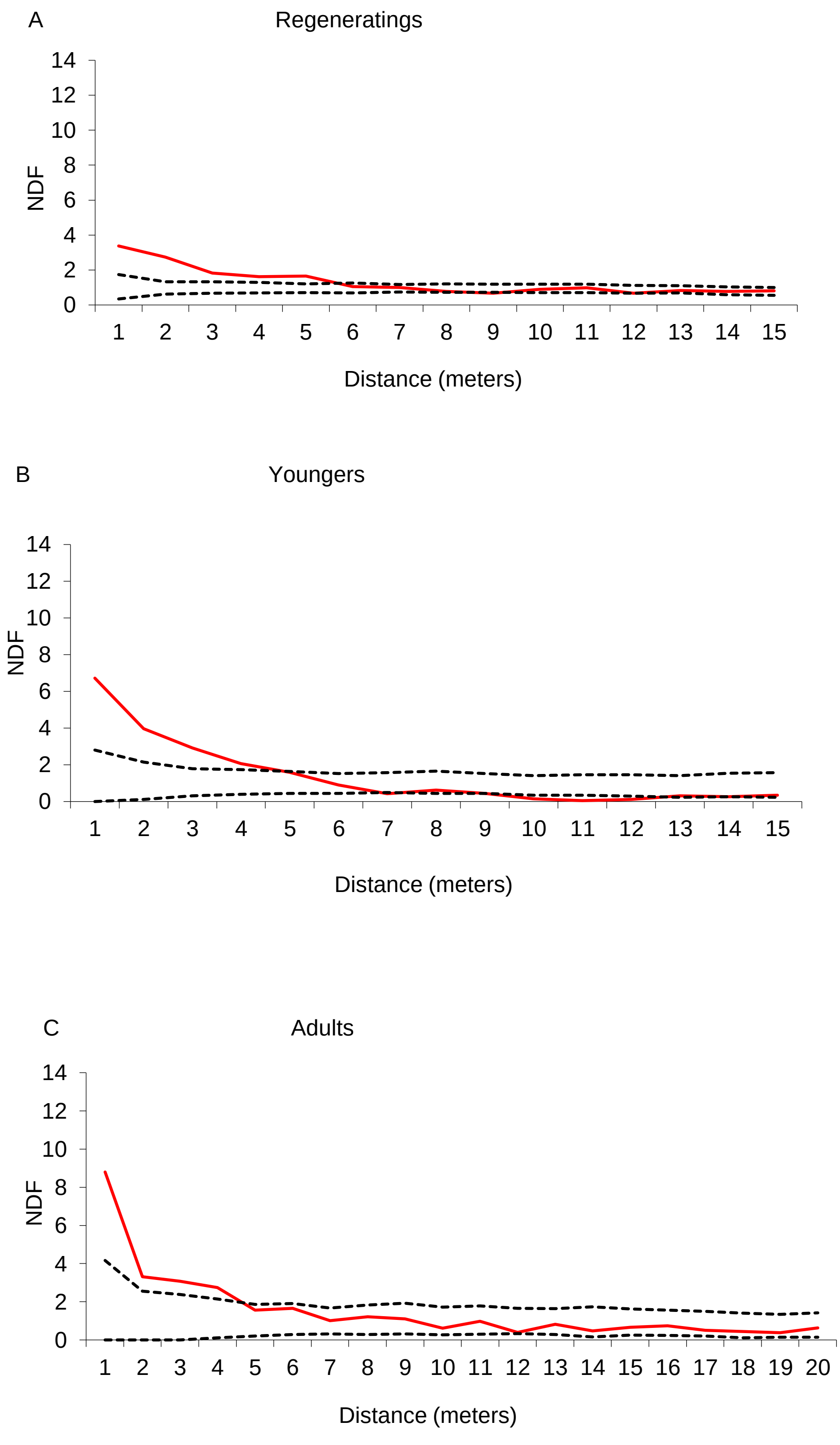

Figure 4. The correlograms present the analysis of the NDF spatial pattern of *C. prunifera* regenerating individuals (A), young individuals (B) and adults (C).

A similar pattern to the present study was found in a natural population of *C. prunifera*, in the municipality of Lagoa de Pedras, RN (SILVA et al., 2014). However, not necessarily, the distribution pattern of palm trees is aggregated in the first distance classes, as observed in different populations of *Syagrus oleracea* (SOARES et al., 2019).

The aggregate pattern found for adult individuals may indicate little influence of abiotic factors (environmental heterogeneity, such as availability of space, light, or water) and influence of biotic factors (such as intra-species and interspecific competition or herbivory) on the distribution of individuals. Additionally, the aggregate pattern, as observed in this paper, is typical in tropical forests, where smaller individuals have high aggregation, changing the demographic pattern as they grow because of competition (CAPRETZ et al., 2012).

Although the young individuals showed a greater tendency to a group in the first distance classes (LARA-ROMERO et al., 2016), the same pattern was verified in all ontogenetic stages. This fact can be explained by the monodominance of the carnauba (SILVA et al., 2014). The number of young individuals was also higher than the adult individuals of *C. prunifera*, in a natural population, in the municipality of São Miguel do Gostoso, RN (PINHEIRO et al., 2017), which favors the regeneration of populations and their persistence in the long term. According to Silva Júnior (2004), the "J-inverted" pattern indicates a positive balance between recruitment and mortality, being characteristic of self-regenerative populations, since such pattern only occurs when smaller individuals successively replace adult individuals in the population.

Although the conservation status of the area seems reasonable given the frequent presence of regenerants, it can be observed that the site is used for grazing cattle, especially during the rainy season. The intensification of alternative land use, causing a change in the landscape, may reduce the occurrence of smaller individuals of *C. prunifera*, as observed in populations of the *Hyphaene thebaica* Mart palm (IDOHOU et al., 2016). Thus, the low connection between population viability and demographic responses indicates a higher probability of local extinctions of populations due to anthropic pressure (SELWOOD et al., 2014).

Bivariate analysis (NDF) showed significant levels of aggregation up to a radius of 8 m between regenerating individuals and reproductive adults, indicating a spatial association and restricted dispersion around the parental (Figure 5). This is further corroborated by the absence of spatial association between young individuals (without reproductive events) and adult individuals (reproductive), which may also indicate random or density-dependent mortality.

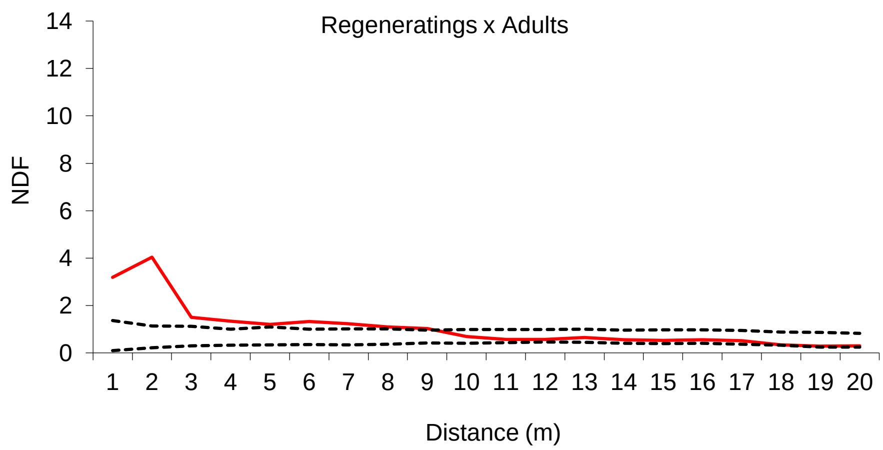

Figure 5. The correlograms present the analysis of bivariate analysis between the regenerating and adult reproductive individuals (F), with a 95% confidence interval (C.I.).

This absence of spatial association may indicate possible past disturbances, natural or human-made, such as selective logging, fires, deforestation, and herbivory. Such facts may lead to the loss of essential dispersants of the species, considerably altering the spatial pattern of individuals, with implications for population demography (BAGCHI et al., 2018).

Conclusions

C. prunifera has an aggregated spatial pattern up to a radius of 5 to 6 m in all life stages. Bivariate analysis showed significant levels of aggregation up to a radius of 8 m between regenerating individuals and reproductive adults, indicating a spatial association and restricted dispersion around the parental. Thus, factors such as restricted seed dispersal around the maternal plant and intra-species competition in the early stages of *C. prunifera* life are possibly responsible for the changes observed in the spatial pattern between the life stages of the species.

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