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Short communication

Shrubs promote nucleation in the Brazilian semi-arid region

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ABSTRACT

Anthropogenic environmental degradation transforms mature vegetation into sites in succession, and actions to restore these altered environments must be based on ecological theories. Nucleation, promoted by facilitation, is an ecological process that can be applied to the restoration of altered environments. The original vegetation of many semi-arid regions has been profoundly altered, and is difficult to recuperate due to rigorous climates. Observations of secondary succession sites raise the following question: do some semi-arid plant species promote nucleation processes and can they therefore be considered nurse species? To address this question, vegetation surveys were undertaken in different environments: under the canopy of the shrub *Combretum leprosum* and in adjacent open areas. Shrubs in different stages were classified by canopy size: small, intermediate and large. Diversity and number of seedlings increased as the size of the *C. leprosum* canopies increased. Some of the environmental variables examined supported the role of *C. leprosum* as a facilitator species, such as the improvement in soil conditions under its canopy. Thus *C. leprosum* could be of significant importance in restoring degraded areas of the semi-arid region where it is present, by allowing the establishment of other plant species.

1. Introduction

Successional theory explains the structure of many different plant communities, and the concepts governing succession are important in order to focus restoration efforts in degraded areas. One of the principal biological mechanisms involved in secondary succession is facilitation, which describes positive interactions resulting from changes in the abiotic environment or interference by other organisms (Callaway and Walker, 1997). An important model of succession is the so-called nucleation process (Yarranton and Morrison, 1974), in which the establishment of colonizing and facilitating species improves the conditions of the local environment for other species (Franks, 2003; Yarranton and Morrison, 1974) or provides perches for active dispersers (Duarte et al., 2006). In this way, the vegetation patch grows and succession proceeds outwards from the colonizing individuals (Franks, 2003). Although facilitation is of notable importance in the succession process, it is a widespread interaction, occurring in different stages of community development. It is an important interaction that continuously acts on vegetation diversity and function (Brooker et al., 2008). Competition also structures vegetation during succession, by contributing to species substitution: late successional species displace early successional species by competition (Tilman, 1987).

In arid and semi-arid environments, improving micro-environmental conditions will usually be a key process structuring the community (Fowler, 1986). In a meta-analysis of studies undertaken in the Mediterranean region, Gómez-Aparicio et al. (2004) concluded that pioneer shrub species facilitate the establishment of late succession woody species. Accordingly, facilitation by shrubs will have positive effects on the success of reforestation programs, mainly in ecosystems characterized by abiotic stress (Gómez-Aparicio et al., 2004). In fact, facilitation has already been successfully applied in vegetation restoration programs in highly degraded environments (Padilla and Pugnaire, 2006).

Environmental degradation is occurring over wide areas in the northeastern semi-arid region of Brazil, and it is estimated that 80% of the vegetation called caatinga has been severely altered. The few existing studies of vegetation composition demonstrate that in degraded areas of caatinga, *Combretum leprosum* Mart. has an aggregated distribution and can be one of (Costa et al., 2009) or the most abundant species (Moreira et al., 2007). In areas where *C. leprosum* is not so abundant, facilitation by other species requires investigation.

The dense foliage and rounded form of *C. leprosum*'s canopy lead to the question of whether *C. leprosum* is a facilitator species for other caatinga plants. Based on this question, the following hypothesis was raised: Shrubs of *C. leprosum* are active in the process

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of nucleation, facilitating the establishment of other woody species. In order to test this hypothesis, the following predictions were made: (1) as the canopy areas of *C. leprosum* individuals increase, the diversity of woody species growing under them should also increase; (2) the number of young woody plant species will be greater under the canopies of *C. leprosum* than in open areas, and their number will increase as the canopy areas increase; (3) soil nutrient content will be greater under *C. leprosum* canopies than in neighboring open areas, and will increase with increasing canopy area.

2. Materials and methods

The study areas were located on the extreme western edge of Crateús, in the state of Ceará, Brazil, at 368 m a.s.l. (05°07′03″S, 40°52′20″W). The region has high average annual temperatures (approx. 26.8 °C), and high solar radiation, with an average of approx. 2800 h/year. Rainfall levels have an average annual total of 645 mm, concentrated over three to four months (FUNCEME, 2012).

This study was undertaken in three areas of caatinga vegetation (*sensu stricto*, deciduous thorny savanna) that were undergoing secondary succession. Two of the study areas were within the "Reserva Natural Serra das Almas" (RPPN) while the third was in the same region but located on private land. The two RPPN areas were separated by 50 m, while the third study area was 1.5 km away.

The vegetation in the study plots was seen to be segregated into two well-defined layers: a shrub and arboreal layer forming nuclei of different sizes, and a matrix of herbaceous plants. Beside the study plots the shrub and arboreal nuclei increase in area until they fuse into continuous vegetation cover. However, the plots chosen for this study did not include continuous forest, just patches of vegetation (nuclei 5–10 m apart from one another). The predominant species of the shrub and arboreal layer are: *C. leprosum* Mart. (which forms the nuclei), *Croton blanchetianus* Baill., *Caesalpinia bracteosa* Tul., and *Piptadenia communis* var. *stipulacea* Benth. The herbaceous layer is dominated by grasses, Leguminosae, and species of the family Lamiaceae, mainly *Hyptis umbrosa* Salz. In general, the herbaceous layer was 50–80 cm tall in the reserve area, and 20–30 cm tall on the private land. This variation in the herbaceous layer is the result of different management; the reserve area has been abandoned for about 10 years, whereas cattle (low density) graze on the private land.

A 100 m × 50 m rectangle was marked out in an area of homogeneous vegetation at each of the three sites, with the following sampling units selected within each rectangle: five young *C. leprosum* individuals; five intermediate sized individuals of the same species; and five large individuals (plus the respective areas around these plants). A total of 45 individuals (15 small, 15 medium and 15 large) were therefore evaluated. This classification into small, medium, and large plants was based on the area projected by their canopies onto the soil. We considered small individuals of *C. leprosum* as those plants with canopy areas between 1.44 and 6.76 m^2; intermediate plants had canopy areas between 15.00 and 25.60 m^2; and large plants had canopy areas between 28.00 and 64.28 m^2. Based on chronosequence studies in other semi-arid areas, the different sized shrubs were considered to represent different ages (Archer et al., 1988). Therefore, they could be considered as a rough estimation of the successional stage within each patch: initial → intermediate → more advanced stage; corresponding to small → intermediate → large size.

For diversity, all of the woody individuals >1 m (due to the difficulty in seedling identification) growing under the canopies of the shrubs were identified and counted. The density was obtained in one 1 m × 1 m quadrat under the shrub canopies and in adjacent open areas (3 m away from the edge of the canopy). In the quadrats, all woody plants (all plants <30 cm, due to the lack of plants >30 cm in the open area) were counted and density was calculated based on the numbers of seedlings and young plants per square meter. Thus, since the sampling effort was identical regardless of shrub size, no confounding effect of changing sampling effort depending on shrub size is expected in our results and conclusions.

Soil samples were collected under the canopies of the three shrub sizes and in the open area; three samples (from the top 20 cm of soil profile) composed of 10 sub-samples each were collected at each class of shrub sizes and in the open area. The ten sub-samples from each of the four microhabitats were homogenized and subsequently analyzed to determine N, organic matter (O.M.), C, P, K, Ca, Mg, S, AL + H, Al and pH. Briefly, pH was measured in water solution (1:2.5; v/v); C was obtained by organic matter oxidation with $K_2Cr_2O_7$ in sulfuric acidic and titration with Fe $(NH_4)_2(SO_4)_2 \cdot 6H_2O$; O.M. was calculated by O.M. = C × 1.724. N was obtained by the traditional Kjeldahl method. Al + H and Al were obtained by adding KCl to the sample and determined by titration with NaOH. Ca and Mg, by extraction with KCl and determination by titration; P was obtained by solubilization by H_2SO_4 and determined by spectrophotometry; S, by adding HCl and precipitation with $BaCl_2$, calcination of $BaSO_4$ and gravimetric determination of the precipitate; K, by extraction with HCl and determination by flame spectrophotometry (EMBRAPA, 1997).

Analyses of variance using randomization tests and orthogonal contrasts were employed to determine the effects of the presence and size of *C. leprosum* on the variables examined. The analyses compared the three classes of shrub with each other and likewise compared the areas under their canopies and in the open. Soil nutrients found under and outside of the canopy microhabitats of *C. leprosum* were also compared (pooling the data of the different canopy sizes). Analysis of variance was performed using Multi-vMinor v.2.3.17. Diversity levels were determined using the Shannon–Wiener index. Diversity and density data were plotted by grouping the data of equivalent size classes from each study site together.

3. Results

Diversity indices were high under large *C. leprosum* shrubs, medium under intermediate sized shrubs, and smaller under small individuals (Fig. 1; ANOVA; $F_{[2,42]} = 27.4$, $P = 0.001$). The densities of seedlings and young plants of other woody species (Fig. 2) were greater under intermediate and large shrubs (ANOVA; $F_{[2,39]} = 6.74$, $P = 0.02$) and did not significantly differ from each other (ANOVA;

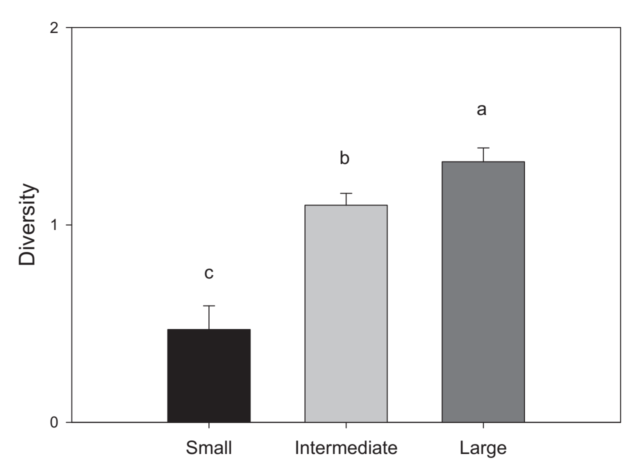

Fig. 1. Diversity (Shannon–Wiener diversity index) under the canopy of *C. leprosum* shrubs of different sizes. Data are mean values ± 1 SE; $n = 15$. Bars with different letters are significantly different (ANOVA by randomization tests, orthogonal contrasts for analysis of variance, $P <= 0.05$).

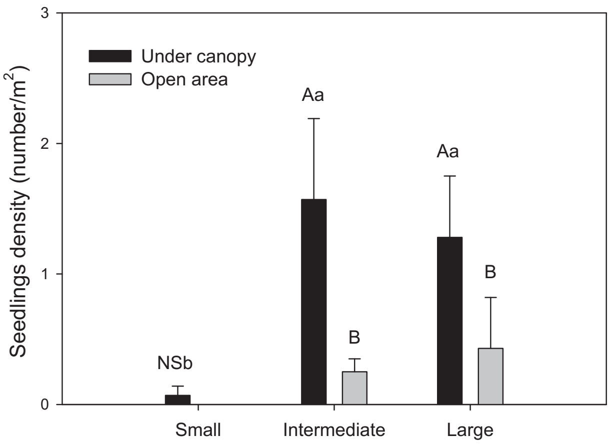

Fig. 2. Number of seedlings and young plants of woody species growing under and outside the canopies of *C. leprosum* shrubs of different size classes (mean ± 1 SE; $n = 15$). Lower case letters indicate significant differences among shrub sizes. Upper case letters indicate significant differences among microhabitats (either under or outside of the canopy perimeter) for each shrub size class (ANOVA by randomization tests, orthogonal contrasts for analysis of variance, $P <= 0.05$).

$F_{[2,39]} = 1.01$, $P = 0.27$), these parameters were smaller under small individuals (differing significantly from both those with intermediate [ANOVA; $F_{[2,39]} = 6.64$, $P = 0.001$] and large [ANOVA; $F_{[2,39]} = 2.46$, $P = 0.03$] canopies). Comparing the densities under the *C. leprosum* canopies and in the open, the differences were significant for the intermediate (ANOVA; $F_{[2,39]} = 9.79$, $P = 0.007$) and large (ANOVA; $F_{[2,39]} = 4.98$, $P = 0.01$) individuals, although not for small ones (ANOVA; $F_{[2,39]} = 0.01$, $P = 1.00$). The species found associated with *C. leprosum* were: *Amburana cearensis* (Allemão) A. C. Smith, *Bauhinia* sp., *C. bracteosa* Tul., *Cochlospermum vitifolium* (Willdenow) Sprengel, *Cordia oncocalix* Allemão, *Croton adenocalyx* Baill, *Lantana camara* L., *Licania rígida* Benth., *Mimosa caesalpiniifolia* Benth., *Piptadenia stipulacea* Benth., *Senna* sp. and *Allamanda blanchetti* A. DC.

The N, O.M. and C contents of the soil were higher beneath the canopy than in open (ANOVA; $F_{[1,9]} = 1.22$, $P = 0.03$; $F_{[1,9]} = 3.39$, $P = 0.02$; $F_{[1,9]} = 1.13$, $P = 0.02$, respectively; Table 1). The other nutrient contents did not show significant differences between the two microhabitats.

4. Discussion

Our results demonstrate that species diversity and the establishment of woody species in recuperating semi-arid sites are higher under the canopy of *C. leprosum* than in open areas. Also, as the canopies increase in volume, the areas they shade increase too, allowing greater numbers of plants to colonize the sites. These observations confirm that *C. leprosum* acts as a facilitator plant during succession in the Brazilian caatinga vegetation. The species facilitated by *C. leprosum* would probably not be able to independently colonize the environments available at the initial succession stages, although this needs to be further explored. As nucleation processes are related to facilitation and dispersal, it could be interesting to separate the facilitative effect from the perch effect, i.e. the process in which trees are used as perches by frugivorous birds (Debussche et al., 1982). In the caatinga vegetation 40% of species are vertebrate-dispersed (Tabarelli et al., 2003). However, among the 12 species found growing under the shrub canopy in this study, 7 were autochorous, 3 anemochorous and 2 zoochorous, indicating that for most species there is no increased tendency to be dispersed underneath the shrub. Hence, facilitatory mechanisms should be the main process driving co-occurrence among *C. leprosum* and its understory species.

Besides the shrub effect on woody species, herbaceous plants growing in semi-arid and arid environments may also benefit from the protection shrubs provide from direct insolation, over-heating and an increase in water and nutrient content (Pugnaire et al., 1996). We know that by only including part of the community (woody plants) our results could be biased, since we only cover part of the interactions that act in structuring the community. Some findings should be interpreted with caution, and further investigated in future studies.

According to Hastwell and Facelli (2003), facilitation in arid environments occurs mainly through shading (but see Holmgren et al., 1997). As the semi-arid caatinga environment is subject to high levels of solar radiation, the microclimate provided by *C. leprosum* may be a primary factor facilitating the establishment of woody species that are less tolerant to rigorous environmental conditions. Increases in seedling and young plant densities were only seen under intermediate and large shrubs, as the young, smaller shrubs have only modest canopies and have microclimates similar to open areas. Young individuals initially have more vertically aligned canopies, but as they grow older their canopies increase in height and diameter and their branches can extend to the ground. Evidence for the importance of leaf cover in facilitation was reported by Reisman-Berman (2007), who noted that plant densities under shrub canopies in a semi-arid region responded in a unimodal manner to canopy size; with the highest plant densities being associated with canopies of low to medium leaf cover (providing 71 and 82% shade respectively), and very low densities associated with open areas or canopies with very high leaf cover (93% shade).

In light of the observation that species diversity and the numbers of seedlings and young plants are greater under the canopies of *C. leprosum* shrubs than in open areas, the question arises as to what mechanisms are involved in this phenomenon? The present work was able to at least partially respond to this question, but in order to better understand the mechanisms leading to facilitation by *C. leprosum* it will be necessary to directly measure the changes in environmental conditions conferred by its shade, and the accompanying responses of the facilitated species to the sheltered microclimate. Among the different environmental factors altered by the nurse plant, we evaluated the nutrient levels of the soil. Additionally, we measured air temperature and humidity and photosynthetically active radiation (PAR) in five shrubs and five adjacent open area points at another semi-arid site in Pentecostes, Ceará State. Temperature was 2 °C lower under the canopy and PAR was 80% lower under the canopy, but humidity was 2.20% higher in the open area. These results provide additional evidence that shrubs have a facilitator effect. However, a more accurate evaluation

Table 1
Soil nutrient contents outside and under the canopy perimeter of *C. leprosum* shrubs (mean ± 1 SE; $n = 3$). Values for soils under shrubs of different class sizes were pooled together. Significant differences among microhabitats are indicated with an asterisk; ns – no significant differences ($P <= 0.05$).

Soil chemistry	Microhabitats	
	Open area	Under shrub canopy
pH (H_2O)	5.03 ± 0.06 ns	5.15 ± 0.13
O.M. (%)	8.20 ± 0.28 *	13.22 ± 1.05
$Al^{3+} + H^{+}$ ($cmol_c$/kg)	2.04 ± 0.14 ns	2.48 ± 0.11
C/N	10.0 ± 0.57 ns	10.11 ± 0.29
C (g/kg)	4.76 ± 0.16 *	7.67 ± 0.61
N (g/kg)	0.48 ± 0.03 *	0.76 ± 0.06
K^{+} ($cmol_c$/kg)	0.23 ± 0.01 ns	0.24 ± 0.02
Ca^{2+} ($cmol_c$/kg)	0.93 ± 0.06 ns	1.59 ± 0.21
Mg^{2+} ($cmol_c$/kg)	0.93 ± 0.03 ns	1.32 ± 0.20
S ($cmol_c$/kg)	2.33 ± 0.06 ns	3.41 ± 0.42
Al^{3+} ($cmol_c$/kg)	0.55 ± 0.05 ns	0.42 ± 0.05

of the microhabitat variables and seedling responses must be made in future studies.

Soil nutrients (O.M., C, and N) were found in greater concentrations under the canopy of *C. leprosum* than outside its projection area. However we did not find a difference between the shrub sizes (data not shown). The increased concentrations of nutrients in the canopy projection zone may result from an accumulation of leaf-litter there, as well as fecal deposition or food-spillage by birds, mammals, reptiles and even invertebrates.

The improvements in soil conditions and the other benefits provided by *C. leprosum* for the successful establishment of other species may aid practical human efforts in restoring degraded areas in the semi-arid region of Brazil, and presents a case for conducting further studies concerning the mechanisms involved in facilitation.

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