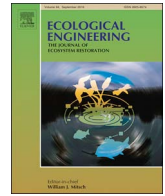




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Nurse species could facilitate the recruitment of mangrove seedlings after hydrological rehabilitation

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ABSTRACT

Changes in hydrology are one of the main causes of mangrove degradation; however, the reforestation of mangrove has been the main restoration activity and very little information on how pioneer species can facilitate the colonization and development of the mangrove species is available. After carrying out a water reconnection as the sole restoration action, secondary succession has occurred in the mangrove rehabilitation area of Celestun (Yucatan, SE Mexico). Two pioneer species, *Batis maritima* and *Salicornia virginica* were observed in plots with different coverage (0%, 20%, 100%) where the three natural mangrove species were established, with *Laguncularia racemosa* as the dominant species in density. The greatest interstitial mean salinity (79.9 g/kg) was recorded in the plots with 20% cover, while the lowest salinity (40.7 g/kg) was recorded in the plots with 100% of coverage. At the end of sampling period nutrient content (carbon, nitrogen and phosphorus) and organic matter in the sediment were greatest in the plots with 100% cover, whereas the lowest concentrations were observed in the site devoid of vegetation. The percentage cover of *S. virginica* and *B. maritima* changed over time; in the plot that started with 100% cover it decreased until it disappeared at the end of the study period, whereas it increased in the plots with 20% and 0% cover. This study shows that *B. maritima* and *S. virginica* has a function as “facilitator species” initially colonizing the bare soil and modifying its conditions (decreasing interstitial salinity and increasing nutrient), which favored colonization and growing of mangrove seedlings.

1. Introduction

Many mangrove ecosystems are affected by a variety of natural and anthropogenic disturbances, which vary in scale, intensity, and frequency (Sherman et al., 2000). The recovery of native vegetation after a large-scale disturbance is essential to prevent soil erosion and invasion of exotic species as well as for the recovery of the numerous functions and services provided by mangroves. However, it has been observed that the colonization and development of mangroves that have been disturbed can be slow and unpredictable, even more so if the seed source is scarce (McKee et al., 2007).

Changes in hydrology have been identified as one of the main causes of the degradation of mangrove areas, leading to great efforts being made in mangrove recovery by restoring their hydrological characteristics (hydrological rehabilitation) (Turner and Lewis, 1997). However, in most cases mangrove restoration has focused on planting propagules or mangrove seedlings (Proffitt and Devlin, 2005; Lewis, 2005). There

is very little information on how the first colonizing species (pioneers) favor the capture and establishment of seeds of mangrove species (McKee et al., 2007; Mckee and Rooth, 2008). In general, secondary succession in ecosystems where the environmental conditions have changed dramatically can be initiated through colonization by species that improve the physical conditions of the site and the availability of resources (Milbrandt and Tinsley, 2006). These pioneer herbaceous species once established lessen the effects of extreme environmental factors by acting as nurse plants (Nieting et al., 1963 in Padilla and Pugnaire, 2006). In areas where mangroves have been damaged, the early establishment of communities of non-woody vegetation has been observed, for example species of the genera *Salicornia*, *Batis*, *Borrhichia* and *Sesuvium* (Milbrandt and Tinsley, 2006; Lewis, 2011). Lewis et al. (1982) described how *Spartina alterniflora* acts as a “nurse-plant” that initially establishes on bare soil and facilitates succession to a community dominated by mangrove trees. It has also been observed that *Batis maritima* initially colonizes areas of dead mangroves, while in

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areas undergoing restoration it is a successful colonizer, contributing to the establishment of mangroves (Milbrandt and Tinsley, 2006). However, it has not been described how these species modify the environment conditions to favor the recovery of mangrove species. *B. maritima* is abundant in wetlands, demonstrates high tolerance to severe environmental conditions in which sediment salinity and temperature are high and is considered to be a pioneer species (Linnaeus et al., 2011; Pennings and Callaway, 2000).

The hydrological, geomorphological and soil characteristics of each site have a strong influence on the availability of mangrove seeds, the settlement percentage of seedlings, and their growth and mortality rates (Mckee, 1995; Dahdouh-Guebas et al., 1998; Cardona-Olarte, 2004). Among the factors regulating the establishment and development of the vegetation in mangroves are salinity, the frequency of flooding, light availability, physical disturbances, and herbivory (Duke, 2001; Cardona-Olarte, 2004), but the role of other pioneer species is not yet well understood.

In the case of mangroves associated with karstic environments, the sediment is poor in nutrients, particularly phosphorus, and it presents a close relationship with the groundwater hydrology of proximal ecosystems (coastal lagoons, coastal sea) (Feller, 1995; Feller et al., 2002; Feller et al., 2003, Feller et al., 2007). In these environments, there is a dependence on allochthonous input or efficient recycling of autochthonous nutrients (Koch, 1997), hence regeneration (establishment and –growth of the mangrove forest seeds and seedlings) may be limited by the availability of nutrients (Thom, 1982; Koch, 1997).

Despite the importance of regeneration in the structural development of mangrove trees and the role played by succession after a disturbance, few studies have focused on the processes that facilitate natural regeneration following hydrological rehabilitation, particularly the role played by pioneer plants such as *B. maritima* and *S. virginica* in the establishment of mangrove seedlings.

The objective of the present study is to evaluate the effect of the establishment of *B. maritima* and *S. virginica* on interstitial water salinity and sediment nutrient content, and its role in facilitating the colonization and development of plants that are more characteristic of mangroves, including *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle*, after hydrological rehabilitation.

2. Material and methods

2.1. Study area

The study area is known as the “Rehabilitation area” of Ria (Lagoon) Celestun, located along the northwest coast of the Yucatan Peninsula (YP), Mexico, between coordinates 20°50' 58.7"N, 90° 23' 32.8"W, and 20° 50' 27.00"N and 90° 23' 18.97"W (Fig. 1). The causes of mangrove degradation in Celestun include changes in the flooding regime after the construction of roads on elevated dike bridges that cross the lagoon connecting the village of Celestun on the seashore to the continent. These reduced the surface water flow, leading to an increase in salt in the pore-water (over 100 g/kg) (Herrera-Silveira et al., 2012).

The study site is located within a total area of 50 ha adjacent to the lagoon. Hydrological restoration was performed by opening a main channel in 2008 and early 2009 (502 m length, 3 m width and 0.8 m deep) to restore the hydrological connectivity between the degraded area and the coastal lagoon (Ria Celestun, Herrera-Silveira et al., 2012).

The climate in the region is warm, semi-arid type BS1 (h) w (c) (García and Mosiño, 1992). During the year, there are three seasons: dry (March to May), rainy (June–October), and “nortes” (November–February), with a hurricane season from August to September (Herrera-Silveira, 1994). This pattern is presented in Fig. 2, which shows the monthly changes of temperature and rainfall from January 2009 until December 2011. The mean annual temperature is 28.5 °C, and it is highest in August and lowest in February. The average annual rainfall is 760 mm; the highest rainfall is in June (153 mm) and August (180 mm)

and the lowest between February (0 mm) and April (4 mm). The prevailing winds are of low intensity (0–15 km/hr), except for the months from November to February when there are storms characterized by heavy rain and strong winds (50–60 km/hr) associated with polar fronts known as “nortes” (Herrera-Silveira et al., 1998). The average evaporation rate for the region is 1400 mm/year. The tidal regime is mixed semi-diurnal with a mean range in water level variation of 0.6 m (Vega-Cendejas et al., 1997).

2.2. Experimental design

This study was carried out after the artificial channel was opened, allowing *B. maritima* and *S. virginica* to establish naturally. To determine the effect of the establishment of these two species on the colonization and development of mangrove seedlings after hydrological rehabilitation, 9 plots of 16 m² each (4 m × 4 m) were selected, in which different coverage of *B. maritima* and *S. virginica* was observed. These plots consisted of 3 with 100% cover, 3 with 20% cover, and 3 without vegetation (0%). The plots were located close to each other at a distance of one meter from the channel built as part of the hydrological rehabilitation actions (Fig. 1).

2.3. Determining the hydroperiod

An electronic water level recorder (Levellogger gold, model 3001) was used to determine the time, frequency and level of flooding and was programmed to take a reading every hour. The recorder was installed at one side of the experimental plots inside a PVC pipe 7.6 cm in diameter inserted into the sediment at a depth of 1 m, with a further 1.03 m exposed over the ground to prevent water from entering during high tide. The recorder was placed 0.85 m below the ground surface, and data were recorded between August 2009 and March 2012.

2.4. Sediment characterization

In each of the permanent plots 2 sediment samples were collected at the beginning (T1) and at the end (T2) (n = 12) of the study period (April 2009 and August 2012). The sediment samples were collected using a 40 cm long PVC corer with a diameter of 6 cm. Bulk density, organic matter and nutrient contents (total carbon, total nitrogen and total phosphorus) were measured from each sample. To determine the bulk density, the sediment samples were cut into 10 cm intervals, dried in an oven at 60 °C and the bulk density was calculated based on the ratio between the dry weight and volume. The organic matter content of the sediment was determined gravimetrically after each portion had been burned to ash in a muffle furnace at 550 °C for 4 h (Chen and Twilley, 1999). To determine total carbon and nitrogen, the samples were ground and homogenized; 20–30 mg was subsequently weighed in tin capsules in triplicate and these were analyzed with an automatic elemental analyzer, model FLASH-EA-1112 (Quest). Total phosphorus was measured by colorimetry following the methodology described by Aspila et al. (1976); Parsons et al. (1984).

In each of the plots three pore-water samples were taken at 40 cm depth using an acrylic tube and syringe. A multi-parameter YSI 30 probe (YSI, XYLEM, Inc., Ohio, USA) was used to measure salinity and temperature. These measurements were made every 4 months during three years in addition to the mangrove seedling sampling.

2.5. Relative growth rate and survival of mangrove seedlings

The term seedling was given to the mangrove individuals already established in the sediment with a height of less than 50 cm. All the naturally established seedlings present in each of the plots were labeled, and their height from the ground to the apex was measured. Height measurements were performed and grouped per time period. The T1 measurements were from April 2009 to March 2010, while the T2

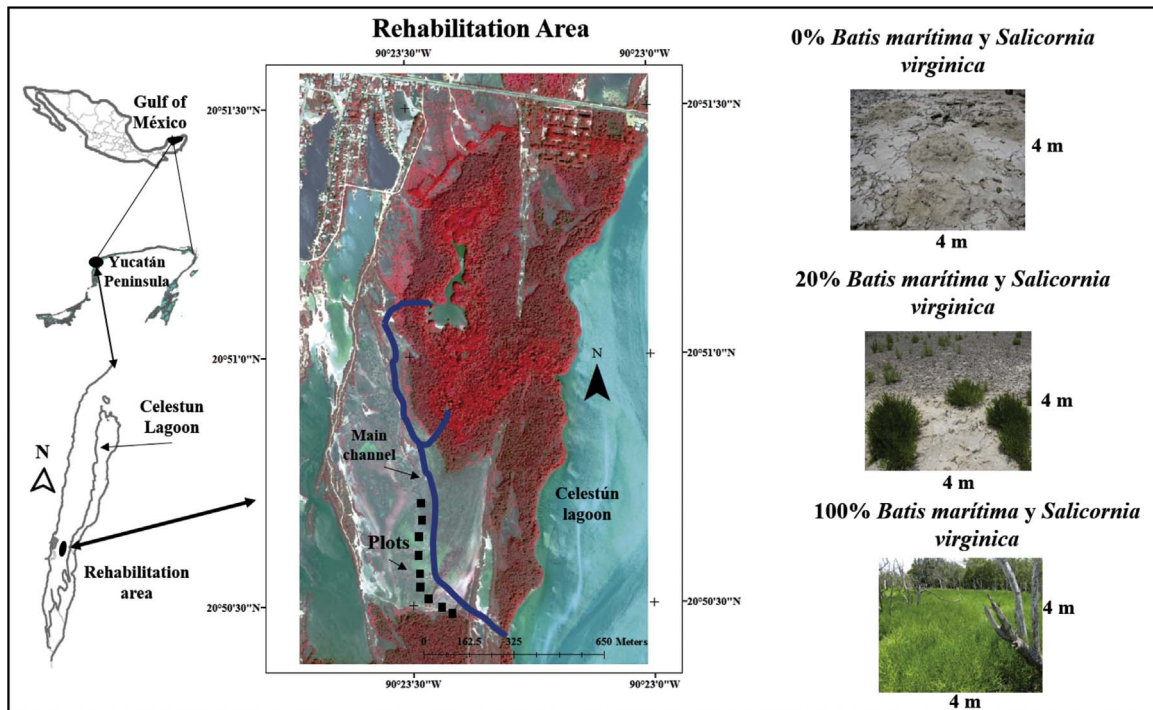


Fig. 1. Study area and location of the area rehabilitation in Celestun Yucatan, Mexico. Channel that restores the water connection between the degraded mangrove area and the lagoon is indicated.

measurements were from July 2010 to August 2012. The relative growth rate in height (RGH) was calculated by subtracting the previous height (T_{i-1}) from the height achieved at each time (T_i) and dividing it by the number of days elapsed (n). It should be noted that the original formula contains logarithms due to the sigmoid growth trend of plants. However, the initial stage of this growth curve is almost linear, hence the logarithms were excluded from the model: $(RGH = (T_i - T_{i-1})/n)$ (Ramírez and Rodríguez, 2004).

2.6. Determination of *B. maritima* and *S. virginica* cover

To record the cover of “pioneer-nurse” species in the plots, the Braun-Blanquet method was used (Fourqurean and Rutten, 2003). These measurements were performed at the same time as those of the mangrove seedlings.

2.7. Statistical analyses

To determine whether there are significant differences in pore-water salinity and temperature among the different plots and among the sampling periods of each plot, an analysis of variance was carried out for repeated measures (factorial ANOVA). The same analysis was also used to determine differences in total nutrient content in the sediment (carbon, nitrogen and phosphorus) among plots and years. Due to

violations in the sphericity assumption required for repeated measures, the Greenhouse-Geisser correction was used (Greenhouse and Geisser, 1959). Normality was assessed through probability plots, histograms, and Shapiro-Wilk tests (Legendre and Legendre, 1998). When significant differences were identified, pairwise comparisons were analyzed using “post-hoc Bonferroni” tests. A significance value of $p < 0.05$ was used for all the statistical analyses. Throughout the results, all values are related as the mean \pm standard error. The analyses were performed using the STATISTICA 7 program (StatSoft Inc., 2004).

3. Results

3.1. Hydroperiod

The mean water level in the rehabilitation area at the beginning of restoration (2009–2010) was 51.4 ± 6 cm, reaching values of up to 50 cm in 2009 and 69 cm in 2010. After these, the mean water level during 2011–2012 was down to 15 ± 2 cm (Table 1) with the highest value of 21 cm. The mean flooding duration at the beginning of the study period was 650 ± 15 h mo^{-1} registering values up to 700 h mo^{-1} , while after 18 months of the hydrological rehabilitation the flooding duration was down to 480 ± 5 h mo^{-1} . The mean frequency of inundation was lower during the first months of the restoration program with 2 ± 1 no. tides mo^{-1} , reaching 16 ± 3.8 no. tides

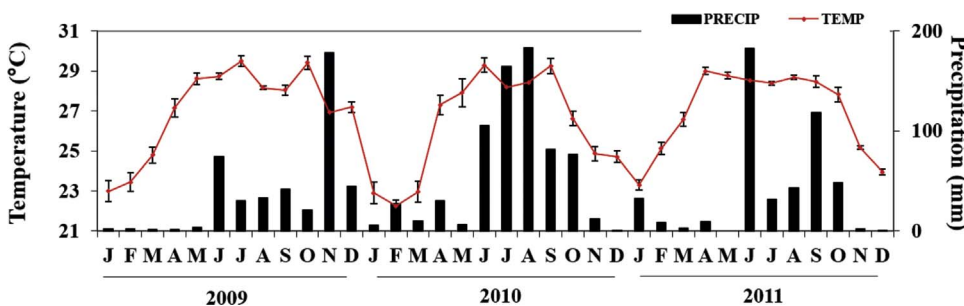


Fig. 2. Monthly variation in precipitation (mm) and temperature ($^{\circ}C$) during the study period (2009–2012), (Conagua.gob.mx).

Table 1

Variation of hydroperiod characteristics and porewater salinity at before (T1) and after (T2), implementing hydrological rehabilitation (mean \pm SE).

	T1	T2
Water level (m)	0.51 \pm 0.06	0.15 \pm 0.02
Flooding duration (h mo ⁻¹)	650 \pm 15	480 \pm 5.7
Frequency of inundation (no. tides mo ⁻¹)	2 \pm 1	16 \pm 3.8
Salinity (gr/kg)	92.7 \pm 3.7	65.2 \pm 1.7
Temperature	28.8 \pm 0.31	29.4 \pm 0.10

mo⁻¹ toward the end of the study period (Table 1).

3.2. Physico-chemical variables of the sediment

Pore-water salinity showed significant differences ($F_{[2501]} = 553$; $p < 0.001$) among the three groups of plots, with the highest salinity recorded in the plots with 20% cover (80 \pm 15.9 g/kg), while the lowest salinity was recorded in the plot with 100% cover during all the study period (40.7 \pm 8.2 g/kg) (Fig. 3a). Similar differences in salinity were observed between years in the different plots ($F_{[3501]} = 45$; $p < 0.001$) with the lowest values in 2010 (10% lower than the maximum values). With regards to pore-water temperature, there were no differences among plots ($F_{[2501]} = 1.91$; $p > 0.14$) (Fig. 3b); significant differences among years were recorded ($F_{[3501]} = 41$; $p < 0.0001$), and the lowest temperature was recorded in 2010 (25 °C).

Bulk density presented significant differences among plots ($F_{[2122]} = 57$; $p < 0.0001$), showing the highest values in the plots with 0% and 20% cover in the two time periods with a mean of 0.82 \pm 0.02 g cm⁻³ in T1 and 0.71 \pm 0.02 g cm⁻³ in T2 (Table 2). The plot with 100% cover of *B. maritima* and *S. virginica* presented the greatest variation between years increasing to 0.72 \pm 0.02 g cm⁻³ between T1 and T2 (Table 1), while in the 20% cover plots the bulk density decreased slightly to 0.70 g cm⁻³ between time periods (Table 2).

The organic matter content of the sediment showed significant differences between plots ($F_{[2122]} = 134$; $p < 0.0001$) with the highest content in the plot with 100% cover (55.6 \pm 6.3%). Organic matter content only decreased from 2009 to 2012 in the plot with 100% cover, which showed significant differences between years ($F_{[1122]} = 74$; $p < 0.0001$) (Table 2).

Significant differences of carbon content were recorded among plots ($F_{[2122]} = 147$; $p < 0.0001$) with the highest content registered in the plot with 100% cover (25.04 \pm 0.95%, Bonferroni HSD test, $p < 0.0001$). Significant differences were observed between time periods only in the plot with 100% cover (Bonferroni HSD test, $p < 0.0001$), decreasing by 34% in T2 compared to T1 (Table 2).

Total nitrogen content showed significant differences among plots ($F_{[2122]} = 143$; $p < 0.0001$) (Table 2) with higher values in the plot with 100% cover (1.7 \pm 0.16%) than in the other plots. This total

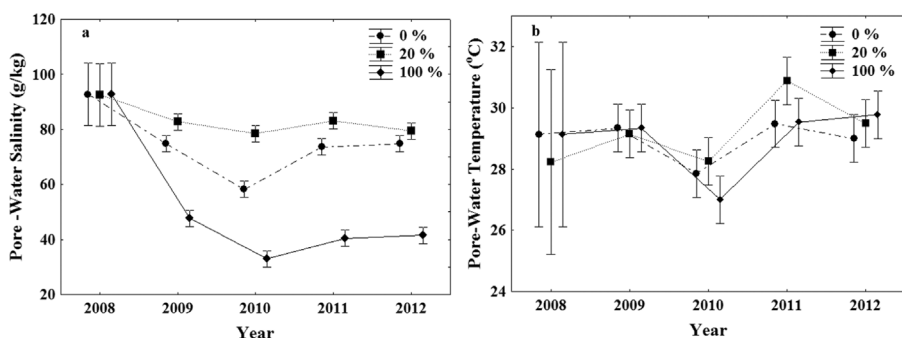


Fig. 3. Pore-water salinity (a) and temperature (b) trends (mean \pm SE) of the pore-water in each of the plots with coverage 100%, 20% and 0% of *S. virginica* y *B. maritima*.

Table 2

Comparison of the soil variables before (T1) and after (T2) implementing hydrological rehabilitation (mean \pm SE), in each of the coverage treatments (%) of the facilitating species.

	0%	20%	100%
T1			
Bulk density (g/cm3)	0.82 \pm 0.03	0.82 \pm 0.01	0.16 \pm 0.01
Organic matter (%)	14.54 \pm 2.95	21.34 \pm 0.87	55.6 \pm 6.32
Total carbon (%)	10.96 \pm 0.13	10.17 \pm 0.14	25.04 \pm 0.95
Total nitrogen (%)	0.49 \pm 0.01	0.47 \pm 0.01	1.76 \pm 0.16
Total phosphorus (%)	0.06 \pm 0.001	0.06 \pm 0.002	0.09 \pm 0.002
T2			
Bulk density (g/cm3)	0.4 \pm 0.04	0.71 \pm 0.02	0.72 \pm 0.02
Organic matter (%)	13.85 \pm 2.75	20.16 \pm 1.28	27.08 \pm 4.96
Total carbon (%)	8.65 \pm 0.94	10.75 \pm 0.43	16.41 \pm 0.93
Total nitrogen (%)	0.37 \pm 0.05	0.51 \pm 0.03	1.03 \pm 0.10
Total phosphorus (%)	0.06 \pm 0.002	0.06 \pm 0.002	0.1 \pm 0.002

nitrogen content was significantly lower in T2 than in T1 (41% lower, Bonferroni HSD test, $p < 0.0001$).

With regard to total phosphorus, significant differences were observed among plots ($F_{[2122]} = 110$; $p < 0.0001$) (Table 2) with the highest content recorded in the plot with 100% cover (Table 1). No significant differences were observed between years ($F_{[2122]} = 110$; $p > 0.25$).

3.3. *B. maritima* and *S. virginica* cover

Different patterns of variation in cover of *B. maritima* and *S. virginica* took place in the three groups of plots during the study period. At the beginning of the sampling period (T1) in the plot with 100% cover both species were observed, but *S. virginica* dominated with average cover of 70%. However, as the experiment time elapsed, *S. virginica* and *B. maritima* coverage diminished until it disappeared (Fig. 4a). Although the cover of *B. maritima* remained constant approximately 30% throughout the sampling period, it also disappeared at the end, but remained until one sampling before.

In the plots with 20% initial cover, *S. virginica* was more abundant in both time periods but lower than in the 100% cover plots (Fig. 5a). However, as time progressed *B. maritima* took the lead growing faster than *S. virginica* for the rest of the period and finishing with cover of 40% and 30%, respectively (Fig. 4b).

In the case of the plots with 0% initial cover neither species was present at T1. *B. maritima* and *S. virginica* were recorded during sampling period T2 with similar coverage as 100% cover plots in T1 (Figs. 4a, c). After becoming colonized, the changes of coverage in these 0% cover plots through time were faster than in the 20% cover plots reaching 80% cover at the end of the sampling period, while *B. maritima* reached just half of this cover (Fig. 4c).

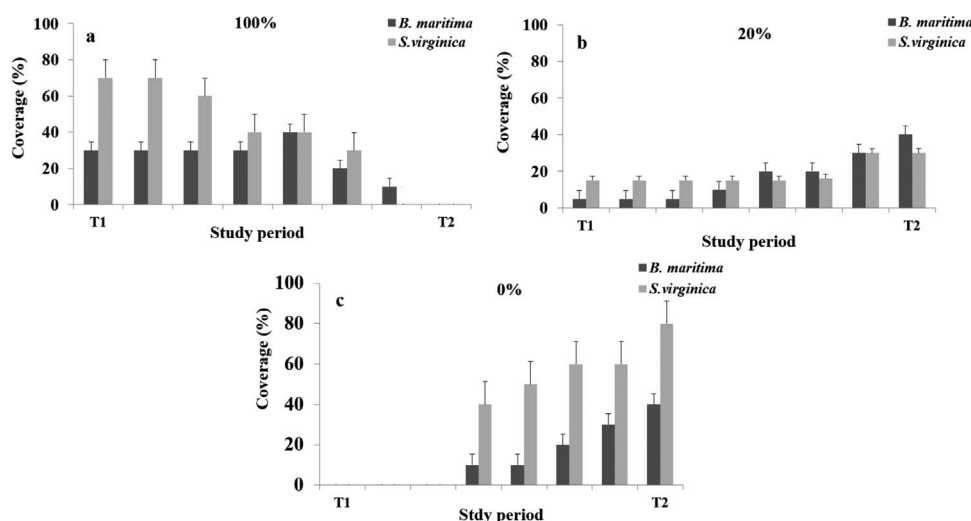


Fig. 4. Changes of the coverage (mean \pm SE) of *B. maritima* and *S. virginica* in the plots with coverage 100%, 20% and 0% through the monitoring time. Data were collected each four months, and T1 y T2 are indicated.

3.4. Mangrove seedling growth and survival

Mangrove seedlings were observed during all the experiment period only in plots with 100% cover of *B. maritima* and *S. virginica*. In the other plots, seedlings were observed less frequently. Seedlings of three species (*R. mangle*, *A. germinans* and *L. racemosa*) were observed. At T1 of the experiment the highest density was recorded in the 100% cover plot, being dominated by *L. racemosa*. At T2 the seedling density was lower in the 100% cover plots, but it increased in the 0% and 20% plots, however, these not reach the seedling numbers in 100% cover plots at any time during the experiment (Fig. 5a).

High RGR values in the 100% cover plots were recorded in both time periods T1 and T2, while lower RGR values were observed in the 20% and 0% plots in both time periods (Fig. 5b).

Low RGR was registered in the 20% and 0% cover plots in both time periods. The lowest RGR of the whole study period corresponded to *A. germinans*, *R. mangle* ($0.10\text{--}0.16\text{ cm day}^{-1}$), in contrast with the RGR of *L. racemosa* ($0.14\text{--}0.21\text{ cm day}^{-1}$) which was doubled those of the two other species during almost all the whole study period.

With respect to percentage survival, the highest value was recorded by *L. racemosa* during the entire study period with final survival of 77%, followed by *R. mangle* which maintained final survival of 68%, and the specie with the lowest survival throughout the sampling period was *A. germinans* (60%) (Fig. 5c).

4. Discussion

The results of this study show that with re-establishing a water connection with a coastal lagoon as the unique rehabilitation measure

in a degraded mangrove area, the hydrological and sediment conditions change, and the process of secondary succession and mangrove recovery was favored. As a first phase of biological recovery, the colonization and progress of two pioneer halophyte species, *B. maritima* and *S. virginica*, was registered followed by natural reestablishment and growth of mangrove seedlings.

Mangrove restoration through hydrologic rehabilitation (re-connecting mangrove and coastal waters) has been successful at restoring environmental conditions in degraded areas (Brockmeyer et al., 1997). The input of water to the restored mangroves in the study site led to changes in hydroperiod and soil parameters. The effect of water connection reestablishment between the natural system and restored area changed the hydroperiod through time in the experimental plots. Water levels dropped ($0.35 \pm 0.1\text{ m}$) as well as the flooding inundation ($170 \pm 4.72\text{ h}$) (Table 1). These conditions favored the establishment of *B. maritima* and *S. virginica* followed by seeds and seedlings of mangroves. The nursery plants need lower water level conditions and less flood time, while seedling roots of mangroves under these hydroperiod conditions could reach the sediment and decrease the time they remain floating, remaining viable for their germination and growth because their reserves as seeds or seedlings is are limited to a few weeks (Mckee, 1995).

The initial pore-water salinity decreased from $> 100\text{ gr/kg}$ to < 85 in 0% and 30% cover plots and $< 35\text{ gr/kg}$ in 100% cover plots (Fig. 3a). In addition to the salt washing from the hydrological rehabilitation in the restored mangrove area, *B. maritima* and *S. virginica* are recognized as plant species that extract salt from sediment helping its desalination (Ungar, 1998; Yensen, 2006). Pore-water temperature was not reduced with hydrological rehabilitation, but its variability

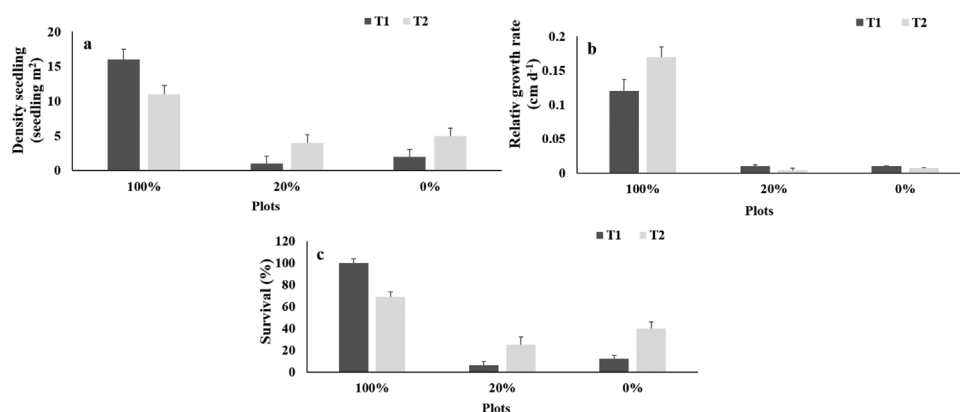


Fig. 5. Changes of the seedling density (a), relative growth rate (b) and survival (c) (mean \pm SE) in the plots with coverage 100%, 20% and 0% of *B. maritima* and *S. virginica*.

decreased significantly (Fig. 3b). Large temperature changes mean large energy costs for plants to keep their metabolism stable (Feller et al., 2010). Milbrandt and Tinsley (2006) mentioned that the temperature recorded in areas covered by *B. maritima* is significantly lower ($< 35^{\circ}\text{C}$) than in areas devoid of vegetation (43°C), which could facilitate the establishment of mangrove seeds and seedlings. Salinity and temperature were lower in 2010 probably because it was a year with high total precipitation (731 mm) in the study period (Figs. 2 and 4), suggesting connectivity between the local climate condition and environmental factors, a feature that should be considered in the long term if climate change forecasts are correct.

However, not all the restored area responded to the hydrologic rehabilitation at the same speed because the initial conditions were quite different among the experimental plots. Although the experimental plots were close to each other, differences among them in sediment characteristics such as bulk density and organic matter at T1 (Table 2) could be responsible for the initial establishment of *B. maritima* and *S. virginica*. In the 100% plots, lower bulk density ($0.16 \pm 0.01 \text{ g cm}^{-3}$) means that sediment is less compact and the fine roots of *B. maritima* and *S. virginica* can penetrate the sediment and spread vegetatively faster (Elexander and Dunton, 2002). During the T2 sampling in the 0% experimental plots the bulk density was down (0.4 ± 0.04), and *B. maritima* and *S. virginica* were registered (Fig. 4b). As frequency of inundation increased ($16 \text{ no. tides mo}^{-1}$), these could have favored decompaction of the sediment toward the end of the experiment and bulk density reduction (Table 1), registering nursery plants in the 0% cover plots in T2 at similar coverage as the 100% cover plots in T1 (Fig. 4c). Differences in environmental characteristics at small spatial scales could explain the spatial heterogeneity of the vegetation structure of restored mangroves and the variability of mangrove landscapes subjected to environmental gradients. Small-scale spatial differences of variables such as topography, physicochemical pore-water and sediment characteristics at the beginning of the development of mangrove forests as observed in the experimental plots, are probably maintained over time, with some of the factors responsible for the spatial variability of the community structure and mangrove landscapes (Simenstad et al., 2006).

McKee et al. (2007) in Belize described that the presence of herbaceous plants such as *Distichlis spicata* and *Sesuvium portulacastrum* favors the recruitment and survival of mangrove seedlings. Lewis et al. (2005) planted cordgrass and observed that these herbaceous plants caught seeds from adjacent forests at high tide and thus allowed rapid secondary succession. After 5 years, they noted that the density of individuals decreased as the mangrove canopy was growing, and the cordgrass appeared out of this. However, these reports did not measure changes in the environmental conditions of pore-water and sediments, which helps to explain the mechanism that favors the establishment of mangroves, as was done in this work.

The colonization of restored mangrove areas by species such as *B. maritima* and *S. virginica* generates changes in abiotic conditions such as pore-water salinity, bulk density, and organic matter among others (Fig. 4; Table 2), favoring the germination of other species in a previously intolerable habitat; Connell and Slatyer (1977) call these “facilitator species”. In our study site, pore-water salinity was lower in the plots where *B. maritima* and *S. virginica* cover was 100% during the study period. In contrast, in the sites devoid of vegetation and with low cover, pore-water salinity was higher ($> 80 \text{ g/kg}$) at levels considered stressful for mangroves (Feller et al., 2010).

These halophyte species are characterized by the accumulation of salt sequestered in cellular vacuoles as a mechanism of osmoregulation (Yensen, 2006), modifying the soil chemistry (Ungar, 1998). McKee et al. (2007) in mangroves from Belize recorded interstitial salinity $> 45 \text{ g/kg}$ in sites devoid of vegetation, while in patches where *D. spicata* was present, these values were $< 40 \text{ g/kg}$. In our study, a 33–55% decrease in pore-water salinity was observed in plots with 100% cover of *B. maritima* and *S. virginica* with respect to plots with 20 and 0% cover,

suggesting that these species are capable of changing soil conditions.

In addition to salinity, other environmental factors including the availability of nutrients affect the composition, distribution, growth, and abundance of mangrove seedlings (McKee, 1995; Koch, 1997). In our study, total nutrient content (carbon, TC; nitrogen, TN and phosphorus, TP) and organic matter in the sediment were higher in the plots with 100% cover of *B. maritima* and *S. virginica*, while lower concentrations were observed in the other plots with low cover and devoid of vegetation (Table 2). The decrease in concentration of both TC and TN and in organic matter in the sediment between 2009 and 2012 in the plots with 100% cover may be due to fragmentation of the dead organic matter of herbaceous species (mainly *S. virginica*) by detritivores (crabs were more abundant in the area with 100% cover, personal observation). This fragmentation of detritus would favor its decomposition and subsequent loss during the flow-ebb of the water that enters the channel and floods the experimental plots. The lack of differences between years in the TP content of the sediment is probably because the loss of TP is lower because of the sediment's calcareous nature, allowing the accumulation of precipitated P with Ca. So far there have been no studies in the literature, as far as we know, that quantified the changes in nutrient content in sites where *B. maritima* and *S. virginica*, or some type of herbaceous plant, are present following restoration. Furthermore, we do not know of long-term studies on restored mangroves where the effect of this process of secondary succession can be compared to the characteristics of the soil.

It has been observed that *S. virginica* competes with *B. maritima* and *Salicornia bigelovii* in disturbed habitats where sediment salinity is high. However, the cover of *S. virginica* is limited by competition with *B. maritima* or *S. bigelovii* under flood conditions and a reduction of sediment salinity (King et al., 1990 in Lineaus et al., 2011). The response of *B. maritima* to changes in hydrological conditions may vary according to the environmental setting. In hypersaline coastal wetlands in Texas that presented a salinity range of 10.5–115.4 gr/kg, *B. maritima* cover extended following freshwater flooding, while in Baja California (Mexico), an increase in *B. maritima* was due to the water entrance being obstructed, which led to an increase in the pore-water salinity up to 102 g/kg (Whigham et al., 2009). Ibarra and Tapia (1991) also described that the growth of *B. maritima* decreases at salinity values higher than 50‰ of the value of seawater; these suggest that *B. maritima* requires relatively high salinity but not as high as *S. virginica*. In our study, the percentage cover of *S. virginica* changed over time: in the plots that started with 100% cover, where the lowest interstitial salinity was observed, it gradually decreased until it disappeared at the end of the study period, whereas in the plots with 20% and 0% cover, characterized by greater salinity, it increased. Similar behavior by *B. maritima* has been observed, although the change in cover is not as drastic as that observed in *S. virginica*.

In our field experiment, even though the hydrological rehabilitation improved the pore-water and sediment conditions of the mangrove restoration area, natural small-scale spatial variability favored *B. maritima* and *S. virginica* coverage differences among the experimental plots; thus, the next step in secondary succession processes corresponding to the colonization with mangrove plants was different too.

At T1, mangrove seedling density was higher in the plots with 100% cover of *B. maritima* and *S. virginica* ($16 \pm 2 \text{ seedling m}^{-2}$) with respect to the 20% and 0% cover plot ($3 \pm 1 \text{ seedling m}^{-2}$). Although in our study area three mangrove species established naturally (*L. racemosa*, *R. mangle* and *A. germinans*), *L. racemosa* was the dominant species, followed by *R. mangle* and *A. germinans* at lower density (Fig. 5a).

These findings suggest that the establishment of these herbaceous plants favored the recruitment of mangrove seedlings, and they acted as nursery species. Lema et al. (2003) observed that *B. maritima* favors the anchorage of propagules and mangrove seeds, acting as retention structures. It has been observed that the successful recovery of mangrove restoration sites can be facilitated by the establishment of *B. maritima* and *S. perennis* when natural sources of propagules are

available, or by planting mangrove seedlings in existing stands of halophytes where restoration areas are propagule-limited (Donnelly and Walters, 2014).

Regarding seedling mangrove species, the dominance of *L. racemosa* should be because this specie is characterized by naturally establishing in areas after a disturbance; it can grow on sites with a wide range of salinity from freshwater to seawater (Sobrado, 2005). In our study, *L. racemosa* showed the highest growth rate (0.20 cm d^{-1}) at the beginning of the sampling period in comparison with *A. germinans* (0.16 cm d^{-1}) and *R. mangle* (0.17 cm d^{-1}), suggesting that *L. racemosa* also behaves as a pioneer species in our rehabilitation area.

Milbrandt and Tinsley (2006) observed a growth rate of 0.07 cm day^{-1} for *A. germinans*, however in our study we recorded a higher growth rate (0.16 cm day^{-1}). Several authors (Suarez et al., 1998) have described that, despite tolerating large fluctuations in salinity and having greater resistance to hypersaline conditions, the seedling development and subsequent growth of *A. germinans* is limited under these conditions. In Belize, McKee et al. (2007) noted that in patches of herbaceous plants such as *Sesuvium* and *Distichlis* as well as in areas devoid of vegetation, *R. mangle*, *A. germinans* and *L. racemosa* establish naturally.

Restored sites initially planted with *R. mangle* have been observed to become naturally colonized by *L. racemosa* and *A. germinans* (McKee and Faulkner, 2000). On the other hand, Rovai et al. (2012) registered that after a decade of planting with *R. mangle*, the environmental conditions changed and natural regeneration occurred favoring *L. racemosa*, which is recognized as a specie that dominates disturbed mangrove environments. Our results and those of McKee et al. (2007) agree with the adaptive differences recorded among mangrove species and the various herbaceous species that are prone to colonizing different sites depending on the specific characteristics of each habitat. Therefore, local and small spatial scale information is needed to evaluate each site before and after rehabilitation actions; in our case hydroperiod, pore-water and sediment information was the most relevant.

After three years of hydrological rehabilitation acted on the environmental conditions of the restored area, changes in the biological characteristics were registered at the T2 sampling time. The nursery plants that had occupied the plots with 100% coverage disappeared completely (Fig. 4a). This may be because the individual mangroves increased in height and shady conditions were created, inhibiting the growth of *B. maritima*. In these experimental plots the mangrove plants reached a mean height of 3 m, and this results in overshadowing. *B. maritima* and *S. virginica* have been reported to require open space and high incident light for growth (Ungar, 1998; Whigham et al., 2009).

The results of this study indicate that hydrological rehabilitation of heavily degraded mangrove areas (without cover of mangrove species) triggers a process of succession starting with improving hydroperiod variables, followed by improving pore-water and sediment conditions, which favored succession wherein *B. maritima* and *S. virginica* were first established modifying the soil conditions for the arrival of mangrove seedlings. The cover of these pioneering herbaceous species decreased with increasing height of mangrove individuals, probably due to overshadowing and competition for available sediment nutrients and space.

This research showed that *B. maritima* and *S. virginica* function as “biological facilitators”, initially colonizing the bare soil and continuing with modifications of the sediment that were initiated by the hydrological rehabilitation (decreasing interstitial salinity and increasing nutrient concentrations in the soil), at the end favoring colonization by mangrove seedlings and their subsequent growth.

This research shows that in a subtropical karstic environment recovery of a characteristic mangrove forest community is possible, at least in its early stages, through hydrological rehabilitation of heavily degraded areas. These results also indicate that hydrological rehabilitation, mainly the hydroperiod variables, can promote the process of succession in heavily degraded mangrove areas and can be an

effective alternative restoration action for mangrove ecosystems instead of directly replanting mangrove seedlings. However, environmental differences at small spatial scales could be drivers of the recovery trajectory in mangrove areas subjected to restoration processes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2017.07.030>.

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