Factors affecting establishment success of the endangered Caribbean cactus *Harrisia portoricensis* (Cactaceae)

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Abstract: Early plant stages may be the most vulnerable within the life cycle of plants especially in arid ecosystems. Interference from exotic species may exacerbate this condition. We evaluated germination, seedling survival and growth in the endangered Caribbean cactus *Harrisia portoricensis,* as a function of sunlight exposure (i.e., growing under open and shaded areas), different shade providers (i.e., growing under two native shrubs and one exotic grass species), two levels of predation (i.e., exclusion and non-exclusion) and variable microenvironmental conditions (i.e., temperature, PAR, humidity). Field experiments demonstrated that suitable conditions for germination and establishment of *H. portoricensis* seedling are optimal in shaded areas beneath the canopy of established species, but experiments also demonstrated that the identity of the shade provider can have a significant influence on the outcome of these processes. *Harrisia portoricensis* seedlings had higher probabilities of survival and grew better (i.e., larger diameters) when they were transplanted beneath the canopy of native shrubs, than beneath the exotic grass species, where temperature and solar radiation values were on average much higher than those obtained under the canopies of native shrubs. We also detected that exclusion from potential predators did not increase seedling survival. Our combined results for *H. portoricensis* suggested that the modification of microenvironmental conditions by the exotic grass may lower the probability of recruitment and establishment of this endangered cactus species. Rev. Biol. Trop. 60 (2): 867-879. Epub 2012 June 01.

Key words: columnar cactus, *Harrisia portoricensis*, *Megathrysus maximus*, Mona Island, nurse plants, seed germination, seedling survival.

Germination, seedling establishment, and survival of young plants appear to be the most critical phase in the life cycle of cacti (Bowers 1997, Pimienta & Del Castillo 2002, Valiente *et al.* 2002, Godínez *et al.* 2003, Valverde *et al.* 2004). In arid and semi-arid environments, the combined effects of temperature, light, and water availability regulate germination, establishment, and survival of plants. Unpredictable rainfall, very high temperatures, and high solar radiation in those environments may influence these processes negatively leading to rare and sporadic germination and survival of early plant stages (Franco & Nobel 1989, Nolasco *et al.* 1997, Fleming & Valiente 2002, Nobel & Bobich 2002, De la Barrera & Nobel 2003, Suzán & Sosa 2006). Understanding, how abiotic factors ultimately influence plant recruitment processes is particularly important to endangered plant species where population persistence is at risk and development of plant management strategies is expected.

Cacti may be buffered from the harsh environmental conditions that characterize arid and semi-arid habitats when growing under the foliage of perennial plants functionally known

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as "nurse plants" (Steenbergh & Lowe 1977, Pierson & Turner 1998, Sosa & Fleming 2002, Godínez *et al.* 2003, Larrea & Soriano 2006). Trees, shrubs, grasses, agaves and other cacti may play the role of nurse plants. Evidence demonstrates that these nurse plants may protect early plant stages from intense sunlight, reduce soil temperatures, increase soil moisture, provide a shady microhabitat in which evapotranspiration is reduced, and protect seeds and seedlings from predation (Steenbergh & Lowe 1977, Jordan & Nobel 1981, Godínez & Valiente 1998, Valiente *et al.* 1991, Sosa & Fleming 2002, Valiente *et al.* 2002, Godínez *et al.* 2005). This phenomenon has been reported in about 36 cacti species representing different life-forms within the family (Steenbergh & Lowe 1977, Jordan & Nobel 1981, Valiente & Ezcurra 1991, Suzán *et al.* 1996, Sosa & Fleming 2002, Godínez *et al.* 2003).

Harrisia portoricensis Britton is a columnar cactus endemic to four Caribbean islands of the Puerto Rican bank. At present, this species is extinct on the island of Puerto Rico and is geographically restricted to the small islands of Mona, Monito and Desecheo (US Fish and Wildlife Service 1990, Liogier 1994). *Harrisia portoricensis* is listed as a threatened species under US Federal Regulation (US Fish and Wildlife Service 1990). This threatened status has been primarily attributed to habitat loss and vegetation changes from feral goats and pigs (US Fish and Wildlife Service 1990). The population on Mona Island is the largest remnant population of *H. portoricensis* to date and is distributed primarily across two vegetation types: lowland dry cactus shrubland and lowland dry limestone shrubland (Martinuzzi *et al.* 2008). At these sites, *Croton discolor* and *Reynosia uncinata* are xerophytic shrubs that dominate the landscape and are often found spatially associated with *H. portoricensis* (Rojas-Sandoval 2010). One hypothesis is that both species may serve as nurse plants of *H. portoricensis.* The grass *Megathyrsus maximus*, is a perennial African grass that was introduced on Mona Island to support prior cattle activities at this reserve (Cintrón & Rogers 1991) and seems to be spreading into prime *H. portoricensis* habitat (Rojas-Sandoval 2010). Literature suggests that grass invasions may have important negative effects on native biodiversity because they can compete effectively with native species (Hughes *et al.* 1991, D'Antonio & Vitousek 1992, Cabin *et al.* 2002, Levine *et al.* 2003, Seabloom *et al.* 2003). At present, no data exist on whether or not the presence of *M. maximus* has negative impacts on *H. portoricensis* populations. While *M. maximus* may compete for space and resources, positive effects on germination and establishment may also result if this species also functions as a nurse plant. Data on the role of native shrub species versus that of *M. maximus* on germination and establishment in *H. portoricensis* is one way to understand the potential interactions between this endemic cactus and the exotic grass that is invading its current habitat.

In this study we evaluated whether or not germination and seedlings survival of *H. portoricensis* was influenced by micro-environmental variation and by extension whether or not these processes were influenced by the type of species under which they were occurring (i.e., exotic grass: *M. maximus* or native shrubs: *C. discolor* and *R. uncinata*). We used this information to understand on how vulnerable are *H. portoricensis* populations to the potential effects of an exotic grass species, how important is the presence of shade providers for germination and establishment, and how susceptible are seedlings and young individuals to changes in micro-environmental factors. We hypothesized that germination, survival and growth of seedlings would be higher in shaded areas than in open areas as it occurs in many columnar cacti species. We also hypothesized that micro-environmental conditions (i.e., temperature, PAR, humidity) would be most favorable for *H. portoricensis* seedlings beneath the canopies of native shrubs than beneath the leaf cover of the exotic grass, and as a result seedling survival and growth would also be higher under native shrubs.

MATERIALS AND METHODS

Study species: *Harrisia portoricensis* Britton is a slender columnar cactus where juveniles are usually unbranched and adults may reach heights of more than 2m and present an extensive branching pattern (Liogier 1994). The density of *H. portoricensis* on Mona Island is 0.001plants/m^2 and a population size estimate of 59 857 (SE=1058) with a demographic profile that included plants in the adult (59%), juvenile (34%) and seedling stages (7%), indicating that at least some recruitment is occurring at this locality (Rojas-Sandoval 2010). This species is a night flowering cactus and plants produce flowers multiple times within a year (Rojas-Sandoval 2010). Reproductive plants produced large hermaphroditic flowers (mean length: 21.16±0.98cm; mean width: 5.25±0.27cm) that open only for one night. Flowers are nectariferous (mean volume 0.26±0.04mL/night) but visits by animals are highly infrequent, and pollination is mainly wind-facilitated with most of the fruit production resulting from self-pollination (Rojas-Sandoval & Meléndez-Ackerman 2009, 2011). Fruit production under natural conditions is high (88% fruit-set) and fruits mature in approximately 56 day. Fruits are typically ornithochorous with yellow, spineless and fleshy berries with more than 1 500 small black seeds enclosed in a white pulp (Rojas-Sandoval & Meléndez-Ackerman 2009). Propagation in *H. portoricensis* is mainly through seeds and spread by vegetative growth has not been detected (Rojas-Sandoval 2010).

Study site: The study was conducted at Mona Island Reserve, a semi-arid island located in the Caribbean Sea between Puerto Rico and Hispaniola (18°05' N - 67°54' W). The island itself is a raised platform of dolomite (magnesium-rich limestone rock) reaching up to 100m at its highest point (Frank *et al.* 1998, Cintrón 1991), and covering an area of 5 517ha. Mona has an annual mean temperature of 25°C, and receives an average annual rainfall of 810mm (Ewel & Whitmore 1973). The rainy season last from August to November with peaks in May and October, and the dry season run from December to April (Murphy & Lugo 1995). During the time of the experiments (May 2007-May 2009), annual mean rainfall was 986mm with peaks occurring always in May and between September-October. Mona is characterized by an irregular distribution of plants, exposed rocks, crevasses, cracks, and sinkholes with accumulated soil. Water availability is limited by an excessive water percolation through shallow soils and a limestone parent rock (Martinuzzi *et al.* 2008). The island's vegetation is classified as a subtropical dry forest. On the island, *H. portoriscensis* is most common at two plant communities: the lowland dry cactus shrubland and the lowland dry limestone shrubland (Martinuzzi *et al.* 2008). The lowland dry cactus shrubland is an area where exposed limestone rocks surround small shrubs and cactus species. The lowland dry limestone shrubland is an area impacted continuously by strong winds, salt spray and poor soil accumulation. The shrubs *Croton discolor* (Euphorbiaceae) and *Reynosia uncinata* (Rhamnaceae) are dominants species of both plant communities and frequently can be found in association with *H. portoricensis*. *Croton discolor* is a short semi-deciduous shrub (less than 1.5m) that only sheds its leaves under extreme drought conditions while *R. uncinata* is a taller (up to 4m) woody evergreen shrub that gradually replaces its leaves throughout the year. Approximately a 25% of both forests have been invaded by the African grass *Megathyrsus maximus* (Rojas-Sandoval 2010).

Seeds collection: Fifteen mature fruits of *H. portoricensis* were randomly collected from plants growing in the study site in August 2007. Each fruit was collected from a different plant and their seeds were extracted and washed with tap and distilled water to remove the pulp. Seeds were dried using absorbent paper, pooled and placed in paper bags for storage at room temperature until required. These seeds were used to perform seedlings survival and seedlings performance field experiments. In August

2008, we repeated the same procedure and collected 15 mature fruits from 15 different plants to obtain a new pool of seeds that were later used in the germination experiment.

Seed germination experiment: To estimate the rate of seed germination under natural and laboratory conditions, and to identify conditions required for seed germination, we performed a germination experiment in September 2008 that included the following treatments: (1) open treatment: seeds were germinated in open areas receiving direct sunlight at any time during the day, (2) shade treatment: seeds were germinated in shaded areas beneath the canopy of *Croton discolor*, the most common shrub species in the study site, and (3) control treatment: seeds were germinated in the laboratory under controlled conditions of light (15h light: 9h dark), humidity (90% relative humidity) and temperature (minimum 24ºC: maximum 30ºC) (Sosa & Fleming 2002). For open and shade treatments, 100 seeds were sown in the field and placed directly on the soil in a 25×25cm plot subdivided into 25 grids (four seeds were placed each 5cm). These plots were located in areas fully exposed to the sun (open treatment) and in areas fully shaded in which shade was provided by the surrounding canopy of *C. discolor* and seedlings received no direct sunlight at any time during the day even with changes in sun direction (shade treatment). Ten replicates were performed per treatment for a total of 1 000 seeds per treatment. For the control treatment, 1 000 seeds were sown among ten 12×22cm plastic-trays (100 seeds per trays) filled with non-sterilized soil collected from the study site. For all treatments, the proportion of germinated seeds was recorded for 120 days. The criterion used to determine seed germination was radical emergence. Differences in seed germination among treatments were compared using Kruskal-Wallis because data did not fulfill assumptions to carry out parametric analysis.

Seedling survival experiment: To estimate the survival and growth of *H. portoricensis* seedlings under natural conditions, we

designed an experiment that evaluated two contrasting sunlight exposure conditions, and ruled out the potential effects of natural predators on the outcomes by performing the experiments under conditions of exclusion and non-exclusion of potential predators. Five hundred seeds from 15 different fruits were sown in November 2007 in plastic nursery traits with multiple cavities filled with soil collected from the study site. We sowed one seed per cavity under greenhouse conditions on Mona Island. In February 2008, one month after seedling emergence, we randomly selected and transplanted 80 seedlings to the field. Forty seedlings were transplanted to 20 different open sites (two seedlings per site) with direct sunlight at any time during the day, and another 40 seedlings were transplanted to 20 shaded sites (two seedlings per site) under the canopy of *Croton discolor*. Open and shaded sites were distributed on Mona Island across an area of approximately 10ha that included the two vegetation types where *H. portoricensis* is most common: lowland dry cactus shrubland and lowland dry limestone shrubland. At each site, half of the seedlings were covered with a cage (7×7×7cm) made of 2mm metal screen mesh to exclude potential predators. Once in the field, seedlings were not watered artificially. The height and diameter of each seedling at the moment that they were placed on the field were measured with a caliper. Seedlings were checked for survival and measured for growth (height and diameter) monthly for one year. Differences in seedling survivorship at the end of the experiment were analyzed following the Kaplan-Meier method and statistical differences among the survival curves of each treatment were tested with Log-Rank and Wilcoxon tests (Pepe & Fleming 1989, Kleinbaum & Klein 2005). Seedling growth parameters for each treatment were analyzed separately because all seedlings transplanted to open sites had died before the third month.

Seedling performance experiment: To compare the performance of *H. portoricensis*, we used a field experiment where seedlings were placed beneath the canopies of

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three shade provider species: *Croton discolor*, *Reynosia uncinata* and *Megathyrsus maximus*. Ten focal plants were randomly selected in February 2008 for each shade provider species, and two one-month-old seedlings were transplanted directly on soil beneath the canopy of each plant. Following the same methodology that we described in the previous experiment, seedling survival and growth parameters (height and diameter) were recorded monthly from February 2008 until May 2009 (15 months). Differences in seedling growth and survivorship at the end of the experiments were compared among the three shade provider species using one-way ANOVA and the Kaplan-Meir method respectively. All analyses were performed using JMP 7.0 (SAS Institute Inc. 2007). We recorded temperature and relative humidity beneath the focal plants and in nearby open sites with direct sunlight exposure with HOBO® Prov2 data-loggers. Additionally, in March 28, 2008 (dry season) and September 30, 2008 (rainy season) at 0 700, 1 300 and 1 700hr we quantified photosynthetic active radiation (PAR) at the projected shade beneath the canopy of different types of focal plants using a Ceptometer-AccuPAR LP80 (Decagon Devices, USA). Specifically we measured PAR at five plants for each shade provider species and for each focal plant there was an adjacent open site with direct sunlight where PAR was recorded as well. The combined information on temperature, relative humidity and PAR was used to characterize the 'typical' microenvironmental conditions beneath each shade provider species as well as in open sites.

RESULTS

Seed germination experiment: The number of seeds germinated after 120 days differed among treatments (Kruskal-Wallis χ^2=24.34, df=2, p<0.001, Fig. 1). The proportion of germinated seeds under laboratory conditions was 4.3 times higher than the proportion of germinated seeds placed in field shade treatments in the field. None of the seeds sown in open sites with direct sunlight exposure germinated

(Fig. 1). On average, seeds began to germinate 54 days after sowing for both the laboratory and the field shade treatments (Fig. 2). The end of the experiment obtained the highest germination percentage under laboratory conditions with 31.4% of germination. In the shade treatment the percentage of germinated seeds was much lower and scarcely reached values of 7.2%. Seed germination halted for both treatments after 90 days (Fig. 2).
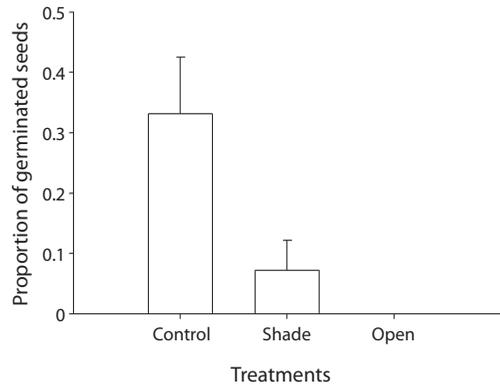
Fig. 1. Proportion of germinated seeds for *Harrisia portoricensis* under laboratory conditions (control treatment), in the field beneath the canopy of *Croton discolor* (shade treatment), and in areas with direct sunlight exposure (open treatment). Data are means±SE.
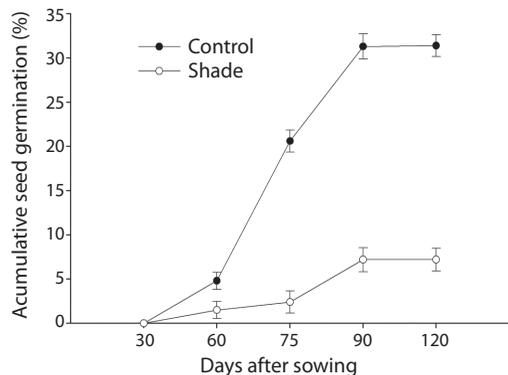
Fig. 2. Cumulative seed germination for *Harrisia portoricensis* after 120 days under laboratory conditions (control treatment), and in the field beneath the canopy of *Croton discolor* (shade treatment). No germination occurred in open treatment. Each data point represents means±SE.

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Seedling survival experiment: The survival of transplanted seedlings was low and upon completion of the experiment only seven individuals were alive at shaded sites in the field (Table 1). Analyses of the survivorship curves indicated significant differences among experimental treatments (Log-Rank test: $\chi^2=34.2$, p<0.0001, Wilcoxon test: $\chi^2=30.4$, p<0.0001, Fig. 3). All seedlings transplanted to open sites died by the second month and only seedlings that were placed at shaded sites survived after one year in the field. Contrary to our expectations, seedling survival in shaded sites was not higher when seedlings were excluded from potential predators (G test=3.06, df=1, p=0.2, Fig. 3). Finally, for the two growth parameters analyzed, surviving seedlings growing under

exclusion and non-exclusion conditions did not differ neither in height (t=-0.69, df=5, p=0.52) nor in diameter (t=0.73, df=5, p=0.49) by the end of the experiment (Table 1).

Seedling performance experiment: In the field, all three shade provider species had a fraction of surviving *H. portoricensis* seedlings underneath them 15 months after seedlings were transplanted. However, analysis of the survivorship curves indicated significant differences among shade providers (Log-Rank test: $\chi^2=31.2$, p<0.0001, Wilcoxon test: $\chi^2=48.2$, p<0.0001, Fig. 4). By the end of the experiment, a higher percentage of seedlings survived beneath the canopy of *R. uncinata* (40%) and *C. discolor* (30%) than beneath the shade of *M. maximus* (15%). For the two growth parameters analyzed, we detected differences among shade providers in seedling diameter ($F_{2,14}=3.21$, p=0.04, Fig. 5A) but not in seedling height ($F_{2,14}=1.87$, p=0.17, Fig. 5B). At the end of the experiment, the average diameters of seedlings growing under *C. discolor* and *R. uncinata* were twice the average diameter of seedlings growing under *M. maximus* (Fig. 5A).

Monthly mean temperatures were significantly higher in open sites than beneath the canopies of the shade providers ($F_{3,61}=3.32$, p=0.02, Table 2), but contrary to our expectations did not differ among shade provider species (Table 2). During the experiment, mean temperatures varying from 29.09°C in open sites to 27.62°C under shade providers (Table 2). In contrast, monthly mean
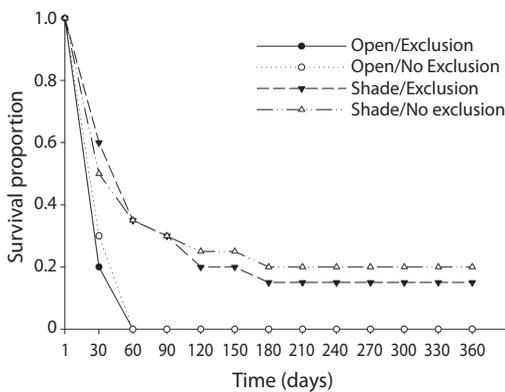
Fig. 3. Survival of *Harrisia portoricensis* seedlings transplanted under four experimental treatments after one year of monitoring. N initial=20 seedlings/treatment.

TABLE 1

Survivorship and growth parameters after one year in the field for *Harrisia portoricensis* seedlings transplanted under four experimental treatments

Treatments	n	Number of seedlings survival after one year	Seedling survivorship (percentage)	Mean height (mm±SE)	Mean diameter (mm±SE)
Open/Exclusion	20	0	0	-	-
Open/No exclusion	20	0	0	-	-
Shade/Exclusion	20	3	15%	8.39±0.10	3.88±0.13
Shade/No exclusion	20	4	20%	8.47±0.13	3.72±0.15

n = number of transplanted seedlings to the field.
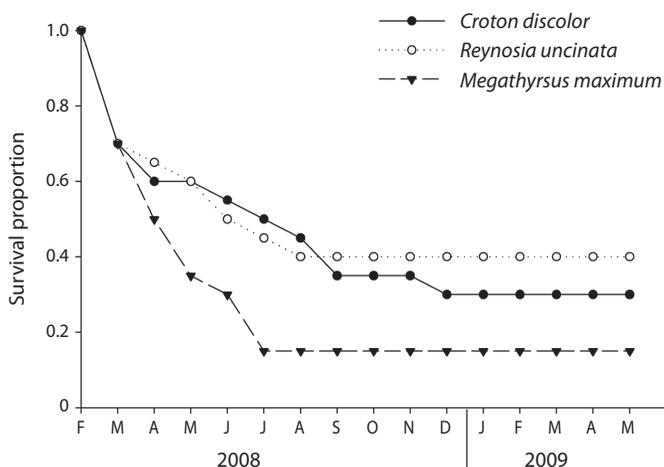
Fig. 4. Survival of *Harrisia portoricensis* seedlings under three different shade provider: the native shrubs *Croton discolor* and *Reynosia uncinata* and the exotic grass *Megathyrsus maximus.* N initial=20 seedlings/treatment.

TABLE 2

Micro-environmental conditions recorded beneath the canopies of three different shade providers and in open sites at Mona Island Reserve from February 2008 to May 2009

Variables	Under *Croton discolor*	Under *Reynosia uncinata*	Under *Megathyrsus maximum*	Open Sites
Temperature (ºC)				
Mean	27.74±0.32	27.62±0.34	27.96±0.38	29.09±0.39[*]
Maximum	38.52±0.23	38.31±0.12	39.72±0.35[*]	42.20±1.73[*]
Minimum	20.48±0.42	20.52±0.31	20.46±0.43	20.31±0.44
Air Relative humidity (%)				
Mean	74.22±1.17	74.88±1.21	74.10±1.32	73.96±1.35
Maximum	94.70±1.42	94.83±1.38	94.63±1.56	94.67±1.59
Minimum	45.83±1.15	45.93±1.11	45.77±1.30	45.74±1.48
PAR ($\mu mol/m^2s$)				
March 2008				
0700 h	96.9±2.6	93.8±5.2	156.2±12.1[*]	243.3±11.8[*]
1300 h	438.2±18.5	426.5±15.9	1462.6±27.8[*]	2071.8±10.6[*]
1700 h	171.4±14.1	169.1±9.56	562.6±19.5[*]	823.3±16.7[*]
September 2008				
0700 h	34.9±2.5	30.7±2.8	77.5±6.1[*]	210.4±6.9[*]
1300 h	311.2±8.3	307.1±7.5	1028.3±15.8[*]	1749.7±15.2[*]
1700 h	36.5±5.4	36.7±5.6	141.8±9.6[*]	562.1±9.6[*]

Data are means ± SE. Values in the same row with asterisks (*) are statistically different (Tukey test at p<0.05).

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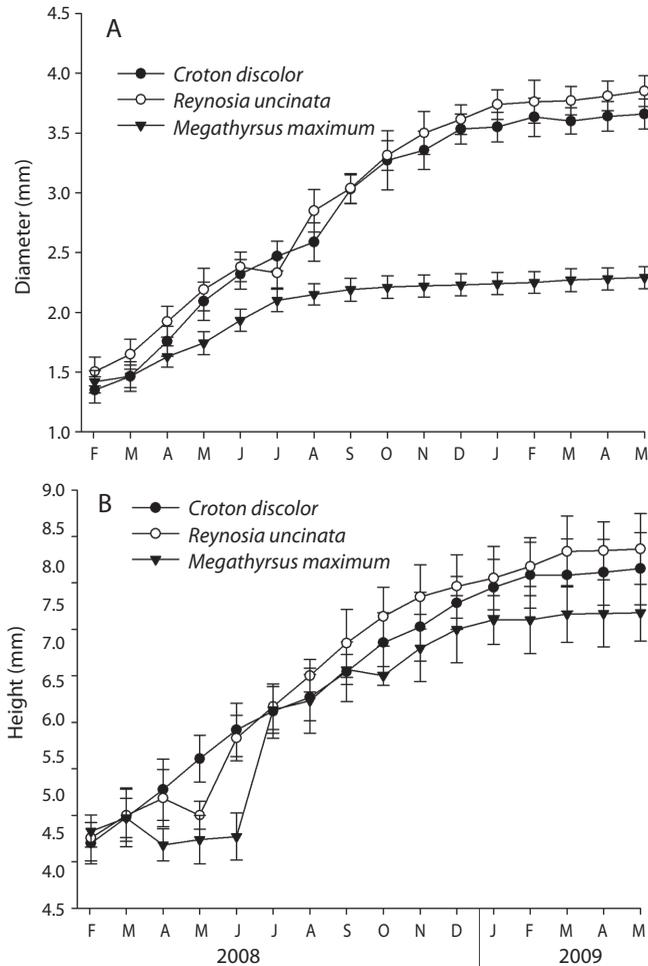
Fig. 5. Growth parameters recorded for *Harrisia portoricensis* seedlings transplanted under different shade providers. (**A**) Diameter. (**B**) Height. Data are means±SE. N initial=20 seedlings/treatment.

maximum temperatures were significantly different among shade providers ($F_{3,61}$=4.33, p=0.03, Table 2). We found that maximum temperatures in open areas and beneath *M. maximus* were significantly higher than beneath the canopies of the native shrubs. Maximum temperatures were beneath the canopy of *M. maximus* and in open areas were 1.4°C and 3.8°C respectively, and higher than under the canopies of native shrubs (Table 2). We did not find differences in the percentages of relative humidity recorded beneath the shade providers and in open sites over the length of the experiment ($F_{3,61}$=0.07, p=0.92, Table 2). As we expected, PAR values were significantly higher in open sites than underneath the shade providers, but they were also highest beneath *M. maximus* foliage than under the canopies of *C. discolor* and *R. uncinata* in March and September (p<0.0001 in all cases, Table 2). On average PAR values were 2.8 times higher beneath the leaf cover of *M. maximus* than beneath the canopy of the native shrubs (Table 2).

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DISCUSSION

We predicted that germination, survival and growth of *H. portoricensis* seedlings on Mona Island would be higher in shaded areas than in open areas due to more benign microclimatic conditions. In general, our results for field and laboratory experiments support this hypothesis and demonstrate the importance of "shaded" environments for the early life cycle stages of this cactus species. Our results also suggest that temperature and solar radiation are abiotic factors that could influence the occurrence of recruitments events into the populations of *H. portoricensis*. Studies have shown that shade created by perennial nurse plants can decrease solar radiation, temperatures, and water evaporation, and as a result enhance the germination, growth and establishment of young cacti beneath their canopies (Jordan & Nobel 1981, Valiente & Ezcurra 1991, Valiente *et al.* 1991, Nolasco *et al.* 1997, Leira & Parra 1999, Sosa & Fleming 2002). For many species of cacti, in addition to nurse plants, rocks and other surface irregularities such as holes and cracks may act as potential facilitators of germination and seedling establishment (Godínez *et al.*, 2003, Mungía & Sosa 2007, Peters *et al.* 2008). However, for *H. portoricensis* in the study site we have not observed nurse rock syndrome, but we do not rule out the existence of this phenomenon.

Our combined results for *H. portoricensis* also demonstrated that suitable conditions for germination and seedling establishment are tied to type of shade provided by the different species in our study. Although the number of seedlings used in the experiments were low, our data showed that *H. portoricensis* seedlings on Mona Island have higher probabilities of survival and grew better (i.e., higher diameters) if they were transplanted beneath the canopies of two native shrubs species *C. discolor* and *R. uncinata* than beneath the exotic grass *M. maximus*. It is likely that these differences are related to differences in microclimatic conditions under the different shade providers because both temperature and incident solar radiation were much higher underneath this exotic grass than underneath the native shrubs. Results strongly suggest that the exotic grass does not provide the same degree of environmental shelter that native shrubs do.

Seedling survival and seedling growth were higher under the canopy of *C. discolor* and *R. uncinata* which in contrast to *M. maximus* do not suffer from leaf loss during the dry season and thus provide a more consistent foliage cover and less solar radiation underneath their canopies throughout the year (Rojas-Sandoval 2010). Areas with high solar radiation can lead to high temperatures, high evapotranspiration and low soil moisture availability, and as a result lower the probability of survival and growth for cactus seedlings (Godínez & Valiente 1998, Valiente & Ezcurra 1991, Nolasco *et al.* 1997, Suzán & Sosa 2006). Another alternative explanation, although not mutually exclusive, for the observed lower seedling survival and performance under *M. maximus* canopies relative to the native shrub species is that this grass is indeed a better competitor for water and/or nutrients than *H. portoricensis* seedlings (Williams & Baruch 2000, Rojas-Sandoval 2010). When they become invasive, alien grasses have been shown to influence soil's hydrology, rates of mineralization, litter structure and may compete more efficiently for water and nutrients than native plant species (Hughes *et al.* 1991, D'Antonio & Vitousek 1992, Cabin *et al.* 2002, Levine *et al.* 2003, Seabloom *et al.* 2003). A recent study reports that regeneration of the columnar cactus species *Pachycereus pecten-aboriginum* is inhibited at areas dominated by buffelgrass (*Pennisetum ciliare*) in the Sonoran Desert. For those areas, the authors suggest that interference with buffelgrass and the extraction of water from the upper soil surface by this grass may be responsible for the high levels of mortality in this cactus species (Morales-Romero & Molina-Freaner 2008).

Our results indicated that the percentages of seeds germinated and the probabilities of seedling survival for *H. portoricensis* under natural conditions were very low. For field experiments, seed germination was nil in open

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areas but even under the shade only 7.2% seeds germinated. Because temperature and soil moisture are often inversely related in the field (as temperature increases soil moisture decreases), one possibility is that in open areas direct solar radiation warms the soil and reduces soil moisture to levels below those required for germination (Valiente & Ezcurra 1991, Laksmi *et al.* 2003). On Mona Island, soil temperatures can reach 70ºC in open areas (Rojas-Sandoval 2010), and these elevated temperatures may also directly inhibit germination or damage seeds placed in the field. Nevertheless, experiments that control air temperatures independent from surface moisture are needed to decide on the mechanisms by which temperature influences seed germination on this species. On the other hand, even under the most optimal conditions, germination dynamics for *H. portoricensis* were noticeably different than what is reported for other cactus species. Literature on seed germination shows that for most cactus species, seeds germinate within a week (Rojas & Vázquez 2000). For *H. portoricensis,* seed germination, on average, occurred after 54 days. It is possible that germination may require ample hydration periods as a way to keep germination from occurring until environmental conditions are suitable. Dudrovsky (1996) demonstrated that seeds for five cacti species in the Sonoran Desert have a hydration memory which can allow them to tolerate dehydration and hydration events and germinate in accordance with the previous hydration experience. An alternative is that this species are naturally animal dispersed and may need scarification to trigger germination. This possibility has not been shown in columnar cacti like *H. portoricensis* but has been shown for cacti in the subfamily Opuntiodeae, in which germination may take few months if seeds do not pass by digestive tract of birds (Rojas & Vázquez 2000). Further studies evaluating seed longevity, dormancy capacity, and the specific conditions (i.e., light, temperature and scarification) necessary to enhance germination rates are essential for the management and conservation of this species.

Surprisingly, we found that predator exclusions did not improve the probability of *H. portoricensis* seedling survival but our study only evaluated this possibility at one point in time. Previous studies comparing predation on seedlings have indicated that predation intensity may vary depending on environmental conditions, intensity of the drought, latitude, and predator abundance (Valiente & Ezcurra 1991, Sosa & Fleming 2002). In addition, predation intensity on columnar cactus seedlings could also vary depending upon whether seedlings are located beneath shrubs species or in open areas (Sosa & Fleming 2002). Temporal studies that look at potential cactus-predator interactions at times where environmental conditions are more benign might be required to determine whether or not predation can be ruled out completely as a factor limiting the survivorship and growth of *H. portoricensis* at Mona Island.

Overall, our data suggested that for *H. portoricensis,* microenvironmental conditions provided by native shrubs species from the understory may play a primary role in the germination, establishments, and growth of this cactus species. During the study period rainfall was above the average annual rainfall value reported for Mona Island, thus water limitation appears not to be a factor affecting the establishment and survivorship of *H. portoricensis* seedlings. The presence and expansion of *M. maximus* may diminish the availability of environmental conditions that are optimal (i.e., mild temperatures and low solar radiation) for germination and establishment in this species (Rojas-Sandoval & Meléndez-Ackerman in preparation). African grasses are often fire-adapted and are able to thrive under conditions of low water availability (Williams & Baruch 2000). The observed trends for temperature increases and the expected reductions in rainfall events for the Caribbean region as a result of the climate change (Singh 1997, Neelin *et al.* 2006) may be conditions that could facilitate further spread and invasion of *M. maximus.* Further spread of this African grass may reduce the amount of optimal environments for germination and establishment of *H. portoricensis* and

if so present and added vulnerability beyond those listed thus far to this native endemic and threaten cactus. From a management perspective, efforts to protect *H. portoricensis* would also need to consider increasing *in situ* management of this exotic grass and the use of native shrub species as a way to enhance germination and seedling establishment.

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RESUMEN

Las etapas iniciales de las plantas parecen ser las más vulnerables de su ciclo de vida, especialmente en ecosistemas áridos. Interferencias de especies exóticas pueden exacerbar esta condición. Evaluamos la germinación, supervivencia y crecimiento de plántulas del cactus en peligro de extinción *Harrisia portoricensis*, en función de la exposición a la luz solar, diferentes proveedores de sombra, exclusión de potenciales depredadores y condiciones micro-ambientales variables. Los experimentos demostraron que las condiciones adecuadas para la germinación y el establecimiento de plántulas de *H. portoricensis* son óptimas en áreas de sombra, bajo el dosel de especies establecidas, pero también demostraron que la identidad de los proveedores de sombra puede tener una influencia significativa sobre los resultados de estos procesos y que la exclusión de depredadores no aumentó la probabilidad de supervivencia de las plántulas. Las plántulas de *H. portoricensis* tuvieron mayores probabilidades de supervivencia y crecieron mejor cuando fueron transplantadas bajo la sombra de los arbustos nativos que bajo la sombra del pasto exótico, donde la temperatura y la radiación solar fueron en promedio mucho mayores que las obtenidas bajo la sombra de los arbustos nativos. Nuestros resultados sugieren que las modificaciones de las condiciones micro-ambientales por este pasto exótico pueden disminuir la probabilidad de reclutamiento y establecimiento de esta especie en peligro.

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