



## Original article

Effects of an invasive grass on the demography of the Caribbean cactus *Harrisia portoricensis*: Implications for cacti conservationJulissa Rojas-Sandoval<sup>a,b,\*</sup>, Elvia Meléndez-Ackerman<sup>b,c</sup><sup>a</sup> Department of Biology, University of Puerto Rico, Río Piedras Campus, P.O. Box 23360, San Juan, PR 00931-3360, USA<sup>b</sup> Center for Applied Tropical Ecology and Conservation, University of Puerto Rico, P.O. Box 70377, San Juan, PR 00936-8377, USA<sup>c</sup> Department of Environmental Sciences, College of Natural Sciences, University of Puerto Rico, Río Piedras, P.O. Box 23341, San Juan, PR 00931-3341, USA

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## ABSTRACT

The impact of exotic species around the world is among the primary threats to the conservation and management of rare and endangered species. In this work we asked whether or not the presence of the African grass *Megathyrsus maximus* on Mona Island was associated with negative impacts on the demography of the endangered Caribbean cactus *Harrisia portoricensis*. To address this question we performed field observations where we compared demographic data collected at un-manipulated areas invaded by *Megathyrsus* with un-manipulated areas non-invaded by this exotic grass. Additionally, demographic data were also collected in areas in which we removed the exotic grass biomass using two alternative treatments: complete and partial grass removal. Results demonstrated that the presence of *Megathyrsus* has negative effects on demographic parameters of *Harrisia* at various stages throughout its life cycle. In general, the survival, growth, and reproduction of *Harrisia* plants were depressed under the presence of *Megathyrsus*. Growth and survival of seedlings and juveniles of *Harrisia* were more impacted by the presence of *Megathyrsus* than adult performance and seedling recruitment only occurred in areas with grass absence. Our combined results suggest that modifications of the micro-environment by the presence of *Megathyrsus* may add an additional level of vulnerability to the persistence of *Harrisia*, and as such this factor must be considered when designing conservation strategies for this endangered species. This study highlights the need for a greater emphasis on understanding the interactions between invasive grass species and native cacti, and the importance of such information in designing conservation strategies for cacti species elsewhere.

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## 1. Introduction

The Cactaceae is one of the most diverse plant families comprising more than 2000 species, most of which are native to dry and arid environments (Anderson, 2001; Nobel and Bobich, 2002). Within those environments, one of the primary threats to the conservation of native biodiversity is the invasion of exotic grasses (Chapin et al., 1996; Parker et al., 1999; Asner et al., 2004). The transformation of natural plant communities to areas dominated by exotic grasses can change key features of ecosystem function by altering fire regimes, hydrology cycles, biophysical dynamics, nutrients cycles, and community composition (D'Antonio et al.,

2000; Ehrenfeld, 2003; Mack and D'Antonio, 2003; Corbin and D'Antonio, 2004). For instance, grass invasions have been linked with increases in the frequency and intensity of fires in deserts of North America (Brooks et al., 2004) and are also the responsible for a threefold increase in the frequency of fires in Hawaiian dry forests (Hughes et al., 1991). The high densities attained by exotic grasses and the large amount of litter produced may reduce and even eliminate the occurrence of suitable sites for germination and establishment of other plants (Reynolds et al., 2001; Coleman and Levine, 2007). Also, exotic grasses often grow faster than native species and have a shallow root system which reduces the amount of light, nutrients, and water available for competitors and facilitates above-ground occupation (D'Antonio and Vitousek, 1992; Dyer and Rice, 1999; Brooks, 2000). Endemics and rare species should be particularly vulnerable to grass invasions because of their small population sizes, restricted geographic ranges, and in many cases poor competitiveness (Walck et al., 1999; Thomson, 2005).

Understanding how exotic grasses affect the demography of native and rare species and how these impacts interact with other

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limiting factors is essential to the design of successful management strategies for areas under the influence of grass invasions (Huenneke and Thomson, 1995; Thomson, 2005). Cacti are slow growing plants and have very low levels of natural recruitment (Sosa and Fleming, 2002). As such, the spread of exotic grasses into suitable habitats for native cacti may result in their displacement and extinction to the extent that grasses depress plant performance. At present, only two studies have addressed this possibility. In the columnar cactus *Pachycereus pecten-aboriginum*, the establishment of seedlings is inhibited on pasture areas dominated by the exotic buffelgrass (*Pennisetum ciliare*) in Sonora (Mexico) and consequently populations are dominated by adult plants (Morales-Romero and Molina-Freaner, 2008). In a follow up study authors suggest that the reduction in available tree cover and nurse plants due to the presence of buffelgrass, increase seedling mortality and restrict the regeneration of *P. pecten-aboriginum* at this site (Morales-Romero et al., 2012). Whether or not negative effects of exotic grasses on native cacti may extend to other demographic stages needs to be addressed to understand their full impact. This issue also needs to be addressed in more cacti species to formulate generalizations about the potential threats of exotic grasses to native cacti elsewhere.

*Harrisia portoricensis* (hereafter *Harrisia*) is a columnar cactus endemic to 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 (USFWS, 1990). The largest and most significant population of this species occurs on Mona Island where it is distributed primarily across the southeastern portion of the island (Rojas-Sandoval, 2010). *Harrisia* is currently listed as a threatened species under US Federal Regulation. This threatened status has been primarily attributed to habitat loss due to human activities and vegetation changes from feral goats and pigs (USFWS, 1990). Areas where *Harrisia* is most abundant on Mona Island have been invaded by the African grass *Megathyrsus maximus* (hereafter *Megathyrsus*). This facultative apomictic perennial grass produces herbaceous stems that can reach heights of up to 2-m and form new plants vegetatively when the stems bend and nodes touch the ground and root (Parsons, 1972). This grass was initially introduced in America as livestock forage, and eventually became invasive when it escaped from planted areas aided in part by the opening of native communities by fire and deforestation (Williams and Baruch, 2000). The time of arrival of this exotic grass to Mona Island is not well-defined. The first reported introduction of this grass on Mona Island was in 1888 (Wadsworth, 1973) and one study suggests was re-introduced around 1960's to support cattle activities (Cintrón and Rogers, 1991). Currently this grass occurs ubiquitously closer to the coastal areas and appears to be spreading across the island (Rojas-Sandoval, 2010). By 2008, Martinuzzi et al. (2008) reported that dry grasslands and pastures now cover 0.8% of the total area of Mona Island.

Prior data for Mona Island showed that when seedlings and juveniles of *Harrisia* grow under the cover of *Megathyrsus*, establishment and survival probabilities are lower than when they grow beneath the canopy of native shrubs (Rojas-Sandoval, 2010; Rojas-Sandoval and Meléndez-Ackerman, 2012). In the same study, open areas (i.e., areas without canopy completely exposed to sunlight) were even more unfavorable for germination and growth of *Harrisia* plants relative to sites where canopies were dominated by native shrub species or grasses. These results suggest that micro-climatic conditions may also play an important role for the establishment of *Harrisia* with the most favorable conditions occurring in areas beneath native shrubs and the least favorable conditions occurring in open areas (Rojas-Sandoval and Meléndez-Ackerman, 2012).

The main goal of this study was to evaluate whether or not the presence of *Megathyrsus* on Mona Island has negative effects on demographic parameters related to survival, growth, recruitment and reproduction of *Harrisia*. We addressed this question through field observations where we compared demographic data collected at un-manipulated areas invaded by *Megathyrsus* with un-manipulated areas non-invaded by this grass. Demographic data were also collected through field experiments where we removed the grass biomass using two alternative treatments: complete and partial grass removal. For both approaches we predicted that the presence of *Megathyrsus* would be associated with reductions in survival, growth, and reproduction of *Harrisia*. We used this information to discuss the potential effects of the presence of exotic grasses on the populations of this endemic species and the management implications for cacti communities under potential threats from grass invasions in arid environments.

## 2. Material and methods

### 2.1. Study site

All field work was conducted in the southeastern end of Mona Island Reserve from May 2007 to May 2009. The island is a 5517 ha raised platform of limestone rock located in the Caribbean Sea between Puerto Rico and Hispaniola (18°05'N, 67°54'W). Mona Island has a mean annual temperature of 26.8 °C, and a mean annual precipitation of 895.79 mm (Rojas-Sandoval and Meléndez-Ackerman, 2011). The dry season spans from December to April. Mona Island has no sources of fresh water. That combined with the excessive water percolation due to the dominant limestone bedrock and shallow soils provides a water-limited environment for plants and animals. Native vegetation in the study site has been classified as lowland dry limestone shrubland (Martinuzzi et al., 2008). This vegetation association is dominated by xerophytic shrubs, globular and columnar cacti, and trees with canopy heights between 1 and 3 m. Dry grassland community dominated by *Megathyrsus* has replaced 5.6% of the total area classified as lowland dry limestone shrubland and available data suggest that the grass expansion must have occurred somewhere between 1972 and 2004 (Cintrón and Rogers, 1991; Martinuzzi et al., 2008).

### 2.2. Study species

The genus *Harrisia* comprises 20 species, all of them endemic species with limited distributions. Fourteen of these species are restricted to the Caribbean region and six are restricted to the southeast of South America (Argentina, Bolivia, and Paraguay; Anderson, 2001). *Harrisia* is a slender columnar cactus which ramifies with age. Juvenile plants (<0.5 m height) are often unbranched whereas adults may reach heights of more than 2 m and are usually extensively branched (Rojas-Sandoval, 2010). This species is a night-flowering cactus with hermaphroditic flowers that open only for one night (Rojas-Sandoval and Meléndez-Ackerman, 2009). Plants are iteroparous and may produce flowers multiple times within a year (Rojas-Sandoval and Meléndez-Ackerman, 2011). Mature fruits are typically ornithochorous (yellow spineless berries) with a range of 1691–1703 seeds/fruits enclosed in a white pulp (Rojas-Sandoval and Meléndez-Ackerman, 2009).

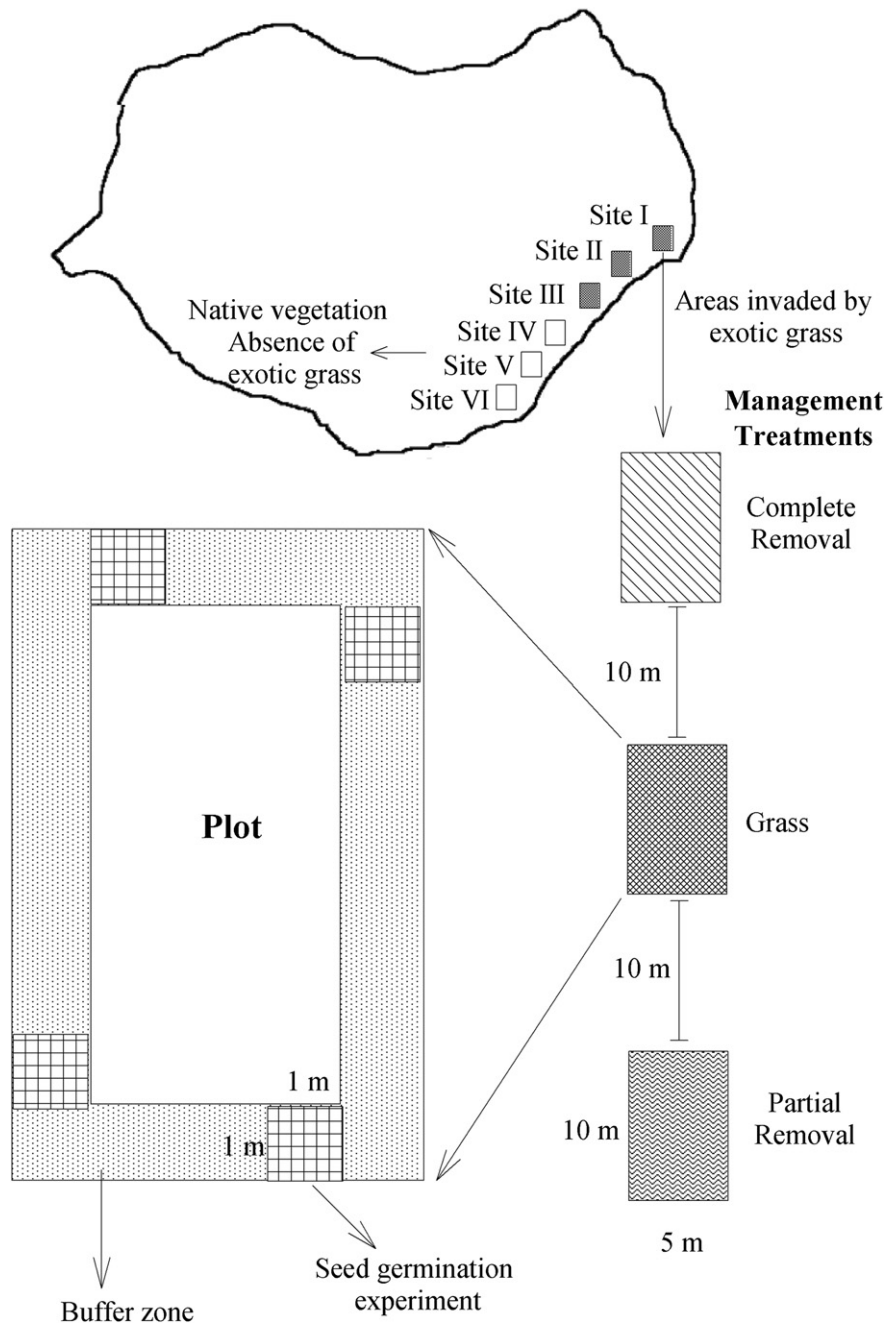
### 2.3. Experimental design

Twelve 5 × 10 m plots were established in May 2007 at six different sites separated by 100 m and with similar climate and topographic characteristics. All sites were characterized by exposed

limestone rock and shallow soils with vegetation dominated by different cacti life-forms, xerophytic shrubs, and small trees with low canopy cover (<3 m height). Nine out of the 12 plots were located in sites (I, II, and III) where *Megathyrsus* had clearly invaded (average density: 9 ramets  $m^{-2}$ ) and where *Harrisia* exhibits high densities (Fig. 1). At each of these sites, we established three plots separated by a distance of 10 m. Plots were similar in the density of adult plants of *Harrisia*, containing a range of five to nine adult plants each. Plots at each site received one of the following grass management treatments: (1) *complete grass removal*: all above- and below-ground portions of *M. maximus* plants growing within the plot were hand-removed and grass litter were disposed of away from the plot, (2) *grass presence* (positive control): *Megathyrsus*

plants growing within the plot were left to grow and the plot was not manipulated, and (3) *partial grass removal*: all above-ground portions of *Megathyrsus* plants growing within the plot were trimmed at ground level using pruning scissors, removing grass litter from the plot and leaving grass roots intact. All treatments were represented at each site. A 1 m buffer zone was established around each plot performing the same grass management treatment as in the actual plot to minimize edge effects. Treatments in plots and buffer zones were maintained monthly for a period of two years (May 2007–May 2009).

In addition to these nine plots, we also established three  $5 \times 10$  m negative control plots (*grass absence*) also surrounded by a 1 m buffer zone at three different sites (IV, V, and VI) located as



**Fig. 1.** Experimental design set up on Mona Island in May 2007. Three sites were selected in areas invaded by *Megathyrsus maximus* (sites I, II, and III) and other three sites were selected in non-invaded areas (sites IV, V, and VI). At sites I, II, and III a cluster of three plots each one with a different grass management treatment (complete removal, grass presence, and partial removal) were established. At sites IV, V, and VI one negative control plot (grass absence) was established.

close as we could find them near the treatment sites (Fig. 1). All negative control plots lacked the exotic grass *Megathyrus*, were dominated by native shrubs and had densities of adult plants of *Harrisia* that were comparable to those subjected to the different grass management treatments. These negative control plots were also separated by 100 m between plots. In May 2007 all *Harrisia* plants located within the 12 plots were tagged and positioned with a GPS-72H (Garmin International Inc., Chicago, IL, USA). All 12 plots were used to monitor changes in survival, growth, and reproduction of established plants from different life-cycle stages (seedlings, juveniles, and adults) that were marked at the time of initial plot establishment and were followed thereafter.

#### 2.4. Microenvironmental conditions

To characterize the prevailing microenvironmental conditions under the different grass treatments, we placed a HOBO H21-002 Micro-station data logger (Onset Computer Corporation, Bourne, MA, USA) at the center of each of the 12 plots. The station monitored the following variables: air temperature ( $^{\circ}\text{C}$ ) and percentage of air relative humidity at 1 m from the ground, soil temperature at 5 cm depth ( $^{\circ}\text{C}$ ), soil water content at 20 cm depth ( $\text{m}^3 \text{m}^{-3}$ ), and photosynthetic active radiation ( $\text{PAR} = \mu\text{mol m}^{-2} \text{s}^{-1}$ ) at 1 m from the ground. Air temperature sensor was covered and isolated from direct sun radiation. Micro-stations were programmed to record each variable at 15 min intervals from December 2007 to May 2009. Using these values we calculated daily means for each variable that were in turn used to calculate monthly mean, maximum, and minimum values for all the variables except PAR. In the case of PAR, we estimated the monthly mean, maximum, and minimum values using daily data only from 0600 to 1800 h. Differences in micro-environmental variables were analyzed with repeated measures ANOVAs with treatments as main effect. For the analysis we first compared differences between the grass absence and the grass presence treatments and then we compared differences among grass management treatments (complete removal, partial removal, and grass presence).

#### 2.5. Treatment effects on plant survival and growth rate

For each tagged plant within the 12 plots, we measured total plant length in May 2007 to classify them into different demographic categories (see below). When plants were multi-branched, the length of each branch was measured from the tip to the point of attachment to the main stem and added that value to the length of the main central stem to obtain a measure of total plant length (Méndez et al., 2004). We used these measurements to classify all tagged plants into three size categories: (1) *seedlings*: individuals of all sizes between 0 and 10 cm, (2) *juveniles*: individuals of all sizes between 10 and 50 cm, and (3) *adults*: individuals greater than 50 cm. For all tagged *Harrisia* plants, we monitored the survival and changes in total plant length at 4-month intervals (May–September–January) from May 2007 until May 2009. We used this information to estimate survivorship and growth of plants in each size category. Survivorship was calculated as the number of individuals that survived at each census divided by the total number of individuals monitored. Growth was quantified as the increase in total plant length from one census to the next. Differences in survivorship attributed to the grass presence were analyzed using two different strategies. We first compared the grass absence (negative control) and the grass presence (positive control) treatments and we then compared the different grass management treatments (complete removal, partial removal, and grass presence). Survival was analyzed using the Kaplan-Meier method with statistical differences among the resulting survival

curves tested using the Log–Rank and Wilcoxon tests (Kleinbaum and Klein, 2005). Similar comparisons were made to analyze the growth rate of different demographic stages under different grass treatments. First we compared differences in plant growth between the grass absence and the grass presence treatments and then we compared differences among grass management treatments (complete removal, partial removal, and grass presence). Differences in plant growth were analyzed with repeated measures MANOVA with site and treatment as main effects.

#### 2.6. Treatment effects on reproduction

All tagged *Harrisia* plants within the 12 plots with total plant length values  $\geq 50$  cm were used to monitor reproductive output in response to different grass treatments. For each *Harrisia* plant greater than 50 cm we did monthly recordings of the number of buds (buds  $\leq 2$  cm), flowers (buds  $> 2$  cm), and fruits (fully developed fruits) from May 2007 to May 2009. For this species, the turnover of buds to flowers is less than four weeks. Buds larger than 2 cm grow into flowers in approximately 10 days later. Using these data we calculated the cumulative number of buds, flowers, and fruits produced per plant for each treatment throughout the study period. Repeated measures MANOVA was used first to test for differences in the mean cumulative number on buds, flowers, and fruits per plant between negative and positive controls. We then tested for differences in the means of these variables among grass management treatments (complete removal, partial removal, and grass presence) using repeated measures MANOVA with site and treatment as main effects. For this analysis, data was square-root transformed to fulfill assumptions.

### 3. Results

#### 3.1. Microenvironmental conditions

The variation of microclimatic variables between grass absence and grass presence treatments was not significantly associated with site, time, or their interactions ( $F < 3.55$ ;  $P > 0.06$  in all cases). We only detected significant differences associated with the presence of grass in air temperature and soil water content (Table 1). Monthly mean maximum air temperatures were significantly higher in the grass presence treatment compared to the grass absence treatment ( $F_{1,17} = 17.64$ ;  $P < 0.001$ ). We also found that monthly mean ( $F_{1,17} = 19.74$ ;  $P < 0.001$ ), minimum ( $F_{1,17} = 7.24$ ;  $P = 0.008$ ), and maximum ( $F_{1,17} = 13.04$ ;  $P = 0.005$ ) soil water contents were significantly higher in the grass absence treatment than in the grass presence treatment. When we compared microclimatic variables among grass management treatments we did not detect differences associated with site, time, or their interactions ( $F < 2.80$ ;  $P > 0.08$  in all cases). Significant differences associated to grass management treatments were detected for air temperature, soil temperature, and soil water content (Table 1). Monthly mean maximum air temperatures were significantly different and on average  $2.7^{\circ}\text{C}$  higher in the grass presence treatment compared to the removal treatments ( $F_{2,17} = 18.97$ ;  $P < 0.001$ ). Differences among grass management treatments were also detected for monthly mean maximum soil temperatures ( $F_{2,17} = 10.28$ ;  $P < 0.001$ ). Complete and partial removal treatments had on average  $9.1^{\circ}\text{C}$  and  $8.5^{\circ}\text{C}$  higher mean maximum soil temperatures respectively than the grass presence treatment (Table 1). We also found that monthly mean ( $F_{2,17} = 3.85$ ;  $P = 0.02$ ) and minimum ( $F_{2,17} = 4.13$ ;  $P = 0.01$ ) soil water contents were significantly lower in the complete removal and the grass presence treatments than in the partial removal treatment. For percentages of relative humidity ( $F < 2.19$ ;  $P > 0.14$  in all cases) and for PAR ( $F < 1.92$ ;  $P > 0.20$  in all cases) we did not find differences



**Table 1**Microenvironmental variables recorded on Mona Island in plots with different grass treatments. Data are means  $\pm$  SE.  $n = 3$  replicates per treatment.

| Variables   | Complete removal    | Partial removal              | Grass presence                | Grass absence                 |
|---|---------------------|------------------------------|-------------------------------|-------------------------------|
| <b>Air temperature (<math>^{\circ}</math>C)</b>                   |                     |                              |                               |                               |
| Mean  | 29.96 $\pm$ 0.71    | 27.08 $\pm$ 0.66             | 27.22 $\pm$ 0.68              | 27.34 $\pm$ 0.67              |
| Maximum   | 35.78 $\pm$ 0.99    | 35.59 $\pm$ 0.80             | 38.43 $\pm$ 1.15 <sup>b</sup> | 35.81 $\pm$ 0.86 <sup>a</sup> |
| Minimum   | 20.25 $\pm$ 1.13    | 20.42 $\pm$ 1.06             | 20.17 $\pm$ 1.11              | 20.76 $\pm$ 0.97              |
| <b>Air relative humidity (%)</b>                                  |                     |                              |                               |                               |
| Mean  | 73.54 $\pm$ 2.21    | 74.39 $\pm$ 2.30             | 74.10 $\pm$ 2.31              | 74.68 $\pm$ 2.18              |
| Maximum   | 94.53 $\pm$ 0.75    | 94.82 $\pm$ 0.99             | 95.20 $\pm$ 0.87              | 94.87 $\pm$ 0.95              |
| Minimum   | 44.34 $\pm$ 4.37    | 46.97 $\pm$ 3.19             | 43.81 $\pm$ 3.57              | 47.15 $\pm$ 3.43              |
| <b>Soil temperature (<math>^{\circ}</math>C)</b>                  |                     |                              |                               |                               |
| Mean  | 30.28 $\pm$ 1.61    | 30.81 $\pm$ 2.24             | 29.67 $\pm$ 1.38              | 30.60 $\pm$ 1.56              |
| Maximum   | 54.71 $\pm$ 4.58    | 53.70 $\pm$ 4.40             | 45.12 $\pm$ 4.73 <sup>b</sup> | 46.63 $\pm$ 4.14              |
| Minimum   | 23.26 $\pm$ 0.86    | 23.29 $\pm$ 0.99             | 23.35 $\pm$ 0.94              | 23.46 $\pm$ 1.37              |
| <b>Soil water content (<math>\text{m}^3 \text{m}^{-3}</math>)</b> |                     |                              |                               |                               |
| Mean  | 0.06 $\pm$ 0.02     | 0.29 $\pm$ 0.17 <sup>b</sup> | 0.09 $\pm$ 0.05               | 0.27 $\pm$ 0.12 <sup>a</sup>  |
| Maximum   | 0.17 $\pm$ 0.07     | 0.26 $\pm$ 0.06              | 0.27 $\pm$ 0.08               | 0.40 $\pm$ 0.14 <sup>a</sup>  |
| Minimum   | 0.02 $\pm$ 0.01     | 0.11 $\pm$ 0.04 <sup>b</sup> | 0.02 $\pm$ 0.01               | 0.19 $\pm$ 0.04 <sup>a</sup>  |
| <b>PAR (<math>\mu\text{mol m}^{-2} \text{s}^{-1}</math>)</b>      |                     |                              |                               |                               |
| Mean  | 1004.82 $\pm$ 57.82 | 946.85 $\pm$ 96.05           | 910.60 $\pm$ 60.25            | 966.98 $\pm$ 62.78            |
| Maximum   | 1893.72 $\pm$ 75.61 | 1783.62 $\pm$ 88.10          | 1742.15 $\pm$ 93.38           | 1772.55 $\pm$ 63.12           |
| Minimum   | 26.45 $\pm$ 7.03    | 22.21 $\pm$ 7.58             | 25.10 $\pm$ 8.70              | 23.70 $\pm$ 6.52              |

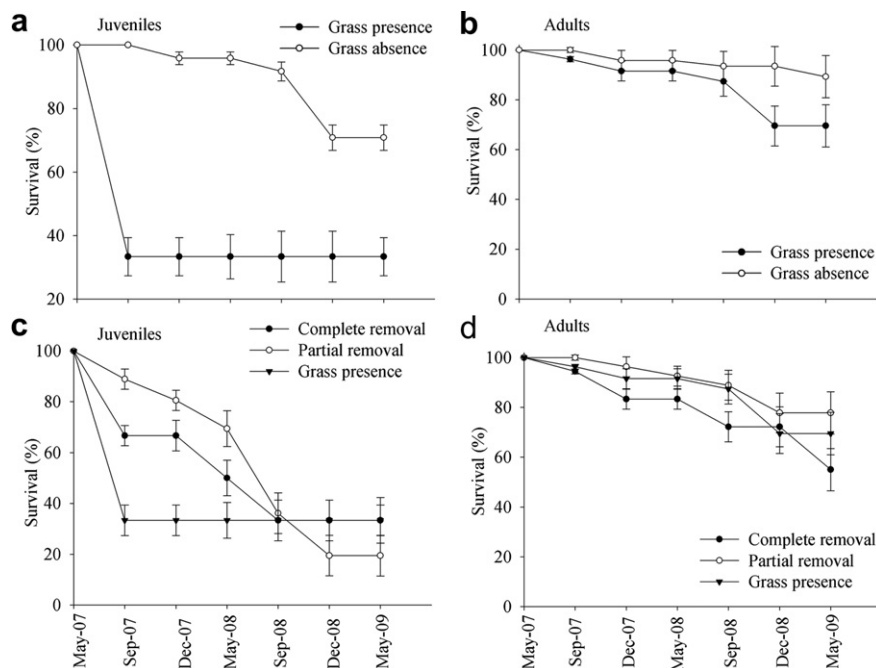
<sup>a</sup> Significant differences ( $P < 0.05$ ) between the grass absence and the grass presence treatments.<sup>b</sup> Significant differences ( $P < 0.05$ ) among grass management treatments.

neither between grass presence and grass absence treatments nor among grass management treatments.

### 3.2. Treatment effects on plant survival and growth rate

Most individuals tagged ( $n = 128$  plants) and monitored within plots were adult (75–85%) and juveniles (13–20%), with seedlings detected in very low frequencies (1–3%). Seedlings were only detected in the grass absence treatment, whereas adults and

juveniles were detected in all treatments. Over the course of the experiment, new recruitments were also highly infrequent and only detected in the grass absence treatment. When we compared survivorship curves for grass presence and grass absence treatments (positive and negative controls), the absence of the exotic grass significantly increased the survival probability of juveniles (Log–Rank test,  $\chi^2 = 6.07$ ,  $P = 0.01$ ; Wilcoxon test,  $\chi^2 = 16.2$ ,  $P < 0.001$ ; Fig. 2a) and adults of *Harrisia* (Log–Rank test,  $\chi^2 = 4.8$ ,  $P = 0.04$ ; Wilcoxon test,  $\chi^2 = 6.5$ ,  $P = 0.03$ ; Fig. 2b). By the end of the



**Fig. 2.** Survivorship of juvenile (a, c) and adult plants (b, d) of *Harrisia portoricensis* in plots with different grass management treatments. Plants were monitored at 4-month intervals from May 2007 to May 2009. Data are means  $\pm$  SE.

experiment the highest percentages of juveniles (70%) and adults (93%) that survived were found in the grass absence treatment (Fig. 2a, b). In contrast, survivorship curves were not significantly different among grass management treatments (complete removal, partial removal, and grass presence) for juveniles (Log–Rank test,  $\chi^2 = 5.76$ ,  $P = 0.06$ ; Wilcoxon test,  $\chi^2 = 0.03$ ,  $P = 0.98$ ; Fig. 2c) and adults (Log–Rank test,  $\chi^2 = 4.19$ ,  $P = 0.12$ ; Wilcoxon test,  $\chi^2 = 3.58$ ,  $P = 0.16$ ; Fig. 2d). Overall, juvenile survivorship was low ranging from 19% to 33% (Fig. 2b). Adults in general had higher survivorships than juveniles, with values ranging from 50% to 77% (Fig. 2d).

Growth rates for juvenile and adult of *Harrisia* in the grass absence treatment were higher than for plants in the grass presence treatment (Juveniles,  $F = 2.83$ ,  $P = 0.02$ ; Adults,  $F = 1.49$ ,  $P = 0.03$ ; Fig. 3a, b). We did not detect significant effects attributed to site, treatment, time nor their interactions on plant growth rates for juveniles ( $F < 1.96$ ;  $P > 0.19$  in all cases; Fig. 3c) and adults ( $F < 3.89$ ;  $P > 0.17$  in all cases; Fig. 3d) when considering the three grass management treatments. Overall, growth rates for juvenile and adult plants exhibited similar behaviors through time regardless of treatments with peaks of growth rates occurring in January 2008 and January 2009.

3.3. Treatment effects on reproduction

Plants growing in the grass absence treatment produced significantly more buds, flowers, and fruits than plants growing in the grass presence treatment ( $F > 2.74$ ;  $P < 0.02$  in all cases; Fig. 4). The cumulative number of buds, flowers, and fruits produced for plants in the grass absence treatment were twice than the cumulative values for plants in the grass presence treatment (Fig. 4). We did not detect significant effects attributed to site, treatment, time nor their interactions on reproductive behavior related to the production of buds, flowers, and fruits when comparing grass management treatments ( $F < 1.74$ ;  $P > 0.16$  in all cases; Fig. 5). For these treatments, the cumulative number of buds, flowers, and fruits produced for *Harrisia* plants during the study period were very similar (Fig. 5).

4. Discussion

The combined results of this study suggest that the presence of the exotic grass *Megathyrsus* has the potential to negatively impact the demographic dynamics of *Harrisia* by affecting various stages throughout its life cycle. Overall, plant survival, growth, and reproduction were depressed at un-manipulated areas under the presence of *Megathyrsus* compared to un-manipulated areas with grass absence. Under those conditions our data also demonstrated that early plant stages may be more vulnerable to the presence of *Megathyrsus* than adult stages. Natural seedling recruitment only occurred in plots with grass absence treatment. We also detected that juveniles displayed higher survival probabilities than seedlings and lower survival probabilities relative to adults and that these probabilities were even lower at un-manipulated areas under the presence of *Megathyrsus* relative to areas where it was absent. Likewise, growth activity for juveniles and adults, plant reproductive output (bud and flower production) and plant reproductive success (fruit production) were also depressed by the presence of this exotic grass when compared to un-manipulated areas where the grass was absent.

Despite these observed patterns, different grass removal treatments fail to show enhanced survival, growth, and reproduction for *Harrisia* plants. The lack of positive responses to experimental grass removal treatments could have resulted from a number of factors that are not necessarily mutually exclusive. For example, removing the grass biomass partially or completely increased soil maximum temperatures (above 54 °C) in plots to levels close to the inhibition threshold for most physiological processes (Smith et al., 1984, 1997; Nobel and Bobich, 2002). Additionally, values recorded for soil water content were very low in plots with complete grass removal as well as in plots with grass cover. Thus, the combination of unfavorable microclimates in the complete and partial grass removal treatments (i.e., very high soil temperatures in both and low water content under complete grass removal) probably rendered them as sites that were as unfavorable as the positive controls.

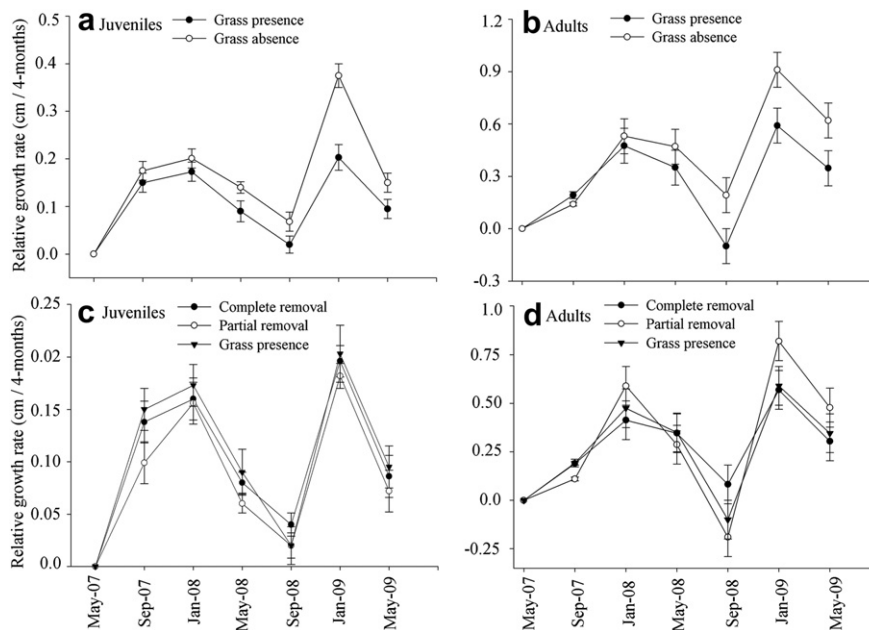
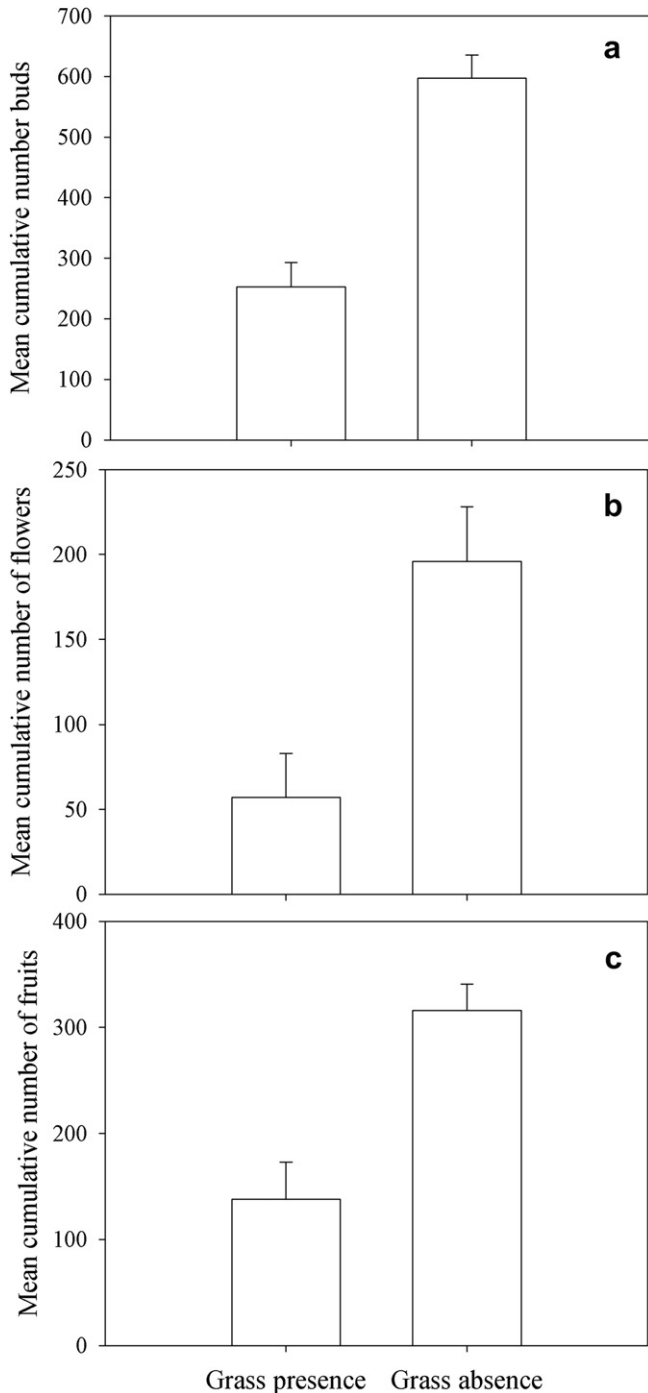
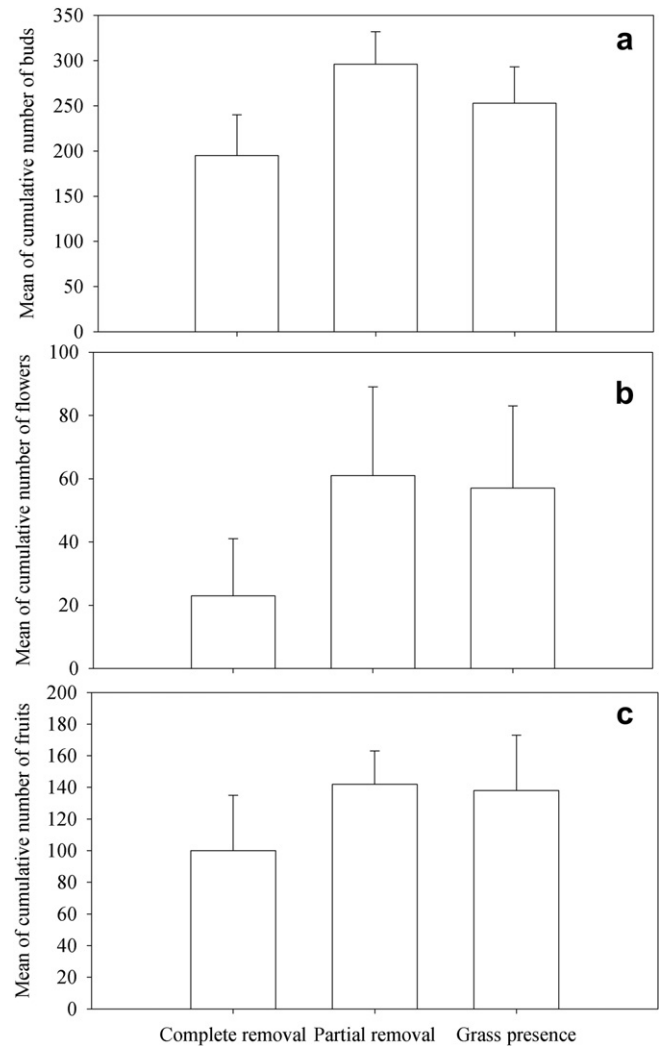


Fig. 3. Growth rates for juvenile (a, c) and adult plants (b, d) of *Harrisia portoricensis* in plots with different grass management treatments. Plants were monitored at 4-month intervals from May 2007 to May 2009. Data are means ± SE.



**Fig. 4.** Mean cumulative number of buds (a), flowers (b), and fruits (c) produced for *Harrisia portocensis* plants growing in plots with grass presence and grass absence treatments.  $N = 52$  plants. Note that y-axis have different scales.

Another possibility for the lack of positive responses to experimental grass removal could be that plants are responding to one or more environmental factors that may have been modified by the grass presence but that perhaps cannot be changed readily back to a pre-invasion condition just by removing the exotic grass (Corbin and D'Antonio, 2004). Soil water content may be such a factor. In this study, grass invaded sites had very low soil water content relative to non-invaded sites. Grasses are known to have high evapotranspiration rates (Melgoza et al., 1990; Williams and Baruch, 2000) and can turn deplete the soil's water making it



**Fig. 5.** Mean cumulative number of buds (a), flowers (b), and fruits (c) produced for *Harrisia portocensis* plants growing in plots with complete grass removal, partial grass removal, and grass presence treatments.  $N = 65$  plants. Note that y-axis have different scales.

unavailable to other plants. This may be the case for *Megathyrsus* which, like other African grasses, has an extensive shallow root system that facilitates rapid water and nutrient uptake (Williams and Baruch, 2002). Links between reduced soil water content induced by exotic grasses and depressed reproductive activity and growth in native plants has been reported for the exotic grass *Bromus tectorum*, in Nevada (USA) (Melgoza et al., 1990). The hypothesis of high evapotranspiration rates as the mechanism responsible for depleting soil water content in areas dominated by *Megathyrsus* is supported by the fact that the partial removal treatment which lacks photosynthetic grass leaves but has an under-ground organic root system and an above-ground dead organic layer (although minute) had on average a significantly higher mean soil water content relative to the grass presence treatment and comparable to those recorded at the negative controls. These latter sites, dominated by native species, also had significantly higher soil water contents than any other treatment, suggesting that native species at this site may be less efficient at removing water from the soils and may promote more humid soil environments.

Literature on plant invasions suggests that reductions in demographic parameters of native plants by invasive species often

result from complex interactions between plants and their modified environments (Gould and Gorcho, 2000; Levine et al., 2003; Seabloom et al., 2003). The suppression of native plants by exotic grasses is often attributed to competition for light, water, and nutrients (Vitousek, 1986; D'Antonio and Vitousek, 1992). In the case of *Harrisia*, our data suggest that responses to grass presence are unlikely driven by differences in light environments, air temperatures or relative humidity changes. Indeed, our results suggest that light is unlikely to be the factor regulating these responses in *Harrisia* mainly because light environments tend to be more or less equivalent among the different canopy types. Additionally, given the high mean PAR values (averages  $> 957.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) recorded at sites with different treatments, we consider that light is unlikely to be a limiting factor for this cactus species at the study sites on Mona Island. Air temperature and relative humidity values were also equivalent among treatments. These results are not surprising given that the study area (which is very close to the ocean) lacks tall canopies (less than 1 m tall; Cintrón and Rogers, 1991) and receives very strong winds all year long (Martinuzzi et al., 2008). The combined effects of these factors may lead to well-lighted sites across all treatments and to the homogenization of air temperatures and relative humidity despite their apparent local structural differences. Based on our combined results and on studies that have looked at the responses of cacti to water availability, negative responses of *Harrisia* in the presence of *Megathyrsus* are likely to be at least partly related to differences in soil water content. Changes in water availability and soil moisture are known to have major effects on ecosystem structure and function in water stressed environments (Noy-Meir, 1973; Kemp, 1983; Pavón and Briones, 2001).

Beyond the evident exotic grass effects, our results provided important information on the vulnerability and behavior of different demographic stages of *Harrisia* under natural conditions. For this cactus species, seedling recruitment is low, erratic, and seems to be enhanced when the vegetation community is dominated by native species and the exotic grass is not present. Even when the literature evidence shows that adult cacti have extraordinary adaptations to low water availability, the high surface area to volume ratio estimated for cactus seedlings combined with the seedlings low water use efficiency due to  $C_3$  metabolism during the early stages are factors that limit their successful establishment to a few suitable years (Steenbergh and Lowe, 1977; Nobel and Bobich, 2002). Studies on seedling establishment of columnar cactus species under natural conditions have demonstrated that recruitment events are often associated with irregular pulses of precipitation and to the presence of nurse plants which essentially serve as environmental buffers (Steenbergh and Lowe, 1977; Jordan and Nobel, 1981; Valiente-Banuet et al., 1991, 2002; Valiente-Banuet and Ezcurra, 1991; Sosa and Fleming, 2002). We know from a previous study that early life stages of *Harrisia* grow optimally and have higher survival probabilities when they grow under the canopy of native shrubs, but have high mortality probabilities and reduced growth rates when they grow beneath *Megathyrsus* (Rojas-Sandoval and Meléndez-Ackerman, 2012). Similar results were detected for the columnar cacti *P. pecten-aboriginum* in which seedlings establishment is reduced and seedling mortality increased in buffelgrass pasture areas (Morales-Romero and Molina-Freaner, 2008; Morales-Romero et al., 2012).

## 5. Conclusions

On the whole, our data suggest that modifications of the natural environment of Mona Island by the presence of the exotic grass *Megathyrsus* may add an additional level of vulnerability to populations of *Harrisia*. Variation in demographic parameters

measured in this study seems to be related to changes in micro-environmental conditions. Long-term studies considering the impact of this exotic grass species on population dynamics of *Harrisia* would be needed to develop comprehensive monitoring strategies for this endangered species. Despite the negative effects associated with the presence of the grass, the interplay between plant responses and microenvironmental conditions is such that management strategies would not only need to consider the removal of the exotic grass but also take into account correlated negative changes in environmental conditions that may follow grass removal. Finally, a combined use of experimental strategies like those presented here, would be helpful to detect unwanted results following potential management strategies. These results may be important to the management of plant species in dry and arid ecosystems where grass invasions seem to be common and where management strategies may need to be considered to protect native species and most importantly threatened and endangered species. For cacti species under the threat of invasive grasses a management strategy that combines grass removal and manipulations that create favorable conditions for germination and establishment may be the most appropriate.

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## References

- Anderson, E.F., 2001. The Cactus Family. Timber Press Inc., Portland, Oregon, USA.
- Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E., Harris, T., 2004. Grazing systems, ecosystem responses, and global change. *Annu. Rev. Environ. Resour.* 28, 261–299.
- Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. *Am. Midland. Nat.* 144, 92–108.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D.A., 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54, 677–688.
- Chapin, F.S., Reynolds, H., D'Antonio, C.M., Eckhart, V., 1996. The functional role of species in terrestrial ecosystems. In: Walker, B., Steffen, W. (Eds.), *Global Change in Terrestrial Ecosystems*. Cambridge University Press, Cambridge, UK, pp. 403–428.
- Cintrón, B., Rogers, L., 1991. Plant communities of Mona Island. *Acta Científica* 5, 10–64.
- Coleman, H.M., Levine, J.M., 2007. Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow. *Biol. Invasions* 9, 65–71.
- Corbin, J.D., D'Antonio, C.M., 2004. Competition between native perennial and exotic annual grasses, implications for an historical invasion. *Ecology* 85, 1273–1283.
- D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87.
- D'Antonio, C.M., Tunison, J.T., Loh, R.K., 2000. Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral. Ecol.* 25, 507–522.
- Dryer, A.R., Rice, K.J., 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80, 2697–2710.
- Ehrenfeld, J.G., 2003. Effects of exotic plant invasions on soil nutrients cycling processes. *Ecosystems* 6, 503–523.
- Gould, M.A., Gorcho, D.L., 2000. Effect of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species native annuals. *Am. Midland. Nat.* 144, 36–50.
- Huenneke, L.F., Thomson, J.K., 1995. Potential interference between a threatened endemic thistle and an invasive nonnative plant. *Conserv. Biol.* 9, 416–425.
- Hughes, F., Vitousek, P.M., Tunison, T., 1991. Alien grass invasion and fire in the seasonal submontane zone in Hawaii. *Ecology* 72, 743–746.



- Jordan, P.W., Nobel, P.S., 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. *Ecology* 62, 901–906.
- Kemp, P.R., 1983. Phenological patterns on Chihuahuan desert plants in relation to the timing of water availability. *J. Ecol.* 71, 427–436.
- Kleinbaum, D.G., Klein, M., 2005. *Survival Analysis, A Self-learning Text*. Springer + Science Business Media Inc., New York, USA.
- Levine, J.L., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impact of the exotic plant invasions. *Proc. R. Soc. Lond. B* 270, 775–781.
- Mack, M.C., D'Antonio, C.M., 2003. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecol. Appl.* 13, 154–166.
- Martinuzzi, S., Gould, W.A., Ramos, O.M., Martínez, A., Calle, P., Pérez-Buitrago, N., Fumero-Cabán, J.J., 2008. Mapping tropical dry forest habitats integrating: Landsat NDVI, Ikonos imagery, and topographic information in the Caribbean Island of Mona. *Rev. Biol. Trop.* 56, 625–639.
- Melgoza, G., Nowak, R.S., Taush, R.J., 1990. Soil water exploitation after fire, competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83, 7–13.
- Méndez, M., Durán, R., Olmsted, I., Oyama, K., 2004. Population dynamics of *Pterocereus gaumeri*, a rare and endemic columnar cactus of Mexico. *Biotropica* 36, 492–504.
- Morales-Romero, D., Molina-Freaner, F., 2008. Influence of buffelgrass pasture conversion on the regeneration and reproduction of the columnar cactus *Pachycereus pecten-aboriginum* in the northwestern Mexico. *J. Arid Environ.* 72, 228–237.
- Morales-Romero, D., Godínez-Alvarez, H., Campos-Alves, J., Molina-Freaner, F., 2012. Effects of land conversion on the regeneration of *Pachycereus pecten-aboriginum* and its consequences on the population dynamics in northwestern Mexico. *J. Arid Environ.* 77, 123–129.
- Nobel, P.S., Bobich, E.G., 2002. *Environmental biology*. In: Nobel, P.S. (Ed.), *Cacti: Biology and Uses*. University of California Press, Berkeley, CA, USA, pp. 57–74.
- Noy-Meir, I., 1973. Desert ecosystem: environment and producers. *Annu. Rev. Ecol. Syst.* 4, 25–52.
- Parsons, J.J., 1972. Spread of African grasses to the American tropics. *J. Range Manag.* 25, 12–17.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions* 1, 3–19.
- Pavón, N.P., Briones, O., 2001. Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. *J. Arid Environ.* 49, 265–277.
- Reynolds, S.A., Corbin, J.D., D'Antonio, C.M., 2001. The effects of litter and temperature on the germination of native and exotic grasses in a coastal California grassland. *Madroño* 48, 230–235.
- Rojas-Sandoval, J., 2010. Identification and evaluation of vulnerability factors affecting the Caribbean cactus species *Harrisia portoricensis*. PhD. dissertation, University of Puerto Rico, Puerto Rico.
- Rojas-Sandoval, J., Meléndez-Ackerman, E., 2009. Pollination biology of *Harrisia portoricensis* (Cactaceae), an endangered Caribbean species. *Am. J. Bot.* 96, 2270–2278.
- Rojas-Sandoval, J., Meléndez-Ackerman, E., 2011. Reproductive phenology of the Caribbean cactus *Harrisia portoricensis*: rainfall and temperature associations. *Botany* 89, 861–871.
- Rojas-Sandoval, J., Meléndez-Ackerman, E., 2012. Factors affecting establishment success of the endangered Caribbean cactus *Harrisia portoricensis*. *Rev. Biol. Trop.* 60, 1–13.
- Seabloom, E.W., Harpole, W.S., Reichman, O.J., Tilman, D., 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci.* 100, 13384–13389.
- Smith, S.D., Dinnen-Zophy, B., Nobel, P.S., 1984. High temperature responses of North American cacti. *Ecology* 65, 643–651.
- Smith, S.D., Monson, R.K., Anderson, J.E., 1997. *Physiological Ecology of North America Desert Plants*. Springer-Verlag, Berlin, Germany.
- Steenbergh, W.F., Lowe, C.H., 1977. *Ecology of the Saguaro: II. Reproduction, Germination, Establishment, Growth, and Survival of the Young Plants*. National Park Service, Washington DC, USA.
- Sosa, V.J., Fleming, T.H., 2002. Why are columnar cacti associated with nurse plants? In: Fleming, T.H., Valiente-Banuet, A. (Eds.), *Columnar Cacti and Their Mutualists*. The University of Arizona Press, Tucson, Arizona, USA, pp. 306–323.
- Thomson, D., 2005. Measuring the effects of invasive species on the demography of a rare endemic plant. *Biol. Invasions* 7, 615–624.
- US Fish and Wildlife Service (USFWS), 1990. *Endangered and threatened wildlife and plant, Rules and Regulations*, US Fish and Wildlife Service Report 50 CRF, pp. 32252–32255.
- Valiente-Banuet, A., Bolongaro-Crevena, A., Briones, O., Ezcurra, E., Rosas, M., Nuñez, H., Barnard, G., Vázquez, E., 1991. Spatial relationship between cacti and nurse shrubs in a semiarid environment in Central Mexico. *J. Veg. Sci.* 2, 15–20.
- Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *J. Ecol.* 79, 961–971.
- Valiente-Banuet, A., Arizmendi, M., Rojas-Martínez, A., Casas, A., Godínez-Alvarez, H., Silva, C., Dávila-Aranda, P., 2002. Biotic interactions and population dynamics of columnar cacti. In: Fleming, T.H., Valiente-Banuet, A. (Eds.), *Columnar Cacti and Their Mutualists*. The University of Arizona Press, Tucson, Arizona, USA, pp. 225–240.
- Vitousek, P.M., 1986. Biological invasions and ecosystem properties, can species make a difference? In: Mooney, H.A., Drake, J. (Eds.), *Biological Invasions of North America and Hawaii*. Springer, USA, pp. 163–176.
- Wadsworth, F.W., 1973. *The historical resources of Mona Island, Appendix N*. In: *Ambiental, Junta de Calidad* (Ed.), *Las Islas de Mona y Monito: Una evaluación de sus recursos naturales e históricos*, pp. N1–N37. San Juan, Puerto Rico.
- Walck, J.L., Baskin, J.M., Baskin, C.C., 1999. Effects of competition from introduced plants on establishment, survival, growth, and reproduction of the rare plant *Solidago shortii* (Asteraceae). *Biol. Conserv.* 88, 213–219.
- Williams, D.G., Baruch, Z., 2000. African grass invasion in the Americas, ecosystem consequences and the role of ecophysiology. *Biol. Invasions* 2, 123–140.