Patterns of abundance and population structure of *Pachycereus pringlei* (Cactaceae), a columnar cactus of the Sonoran Desert

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Abstract

Understanding the mechanisms that determine the distribution and abundance of plants is a major problem in ecology. However, very few studies have explored the factors controlling the abundance of columnar cacti throughout their range of distribution. In this paper, we describe the density and size structure of 26 populations of *Pachycereus pringlei* throughout its distribution range in the Sonoran Desert. Major differences in abundance were detected between island and mainland and peninsular areas, with islands sustaining significantly larger densities than mainland and peninsular populations. Within peninsular populations, the abundance was negatively associated with latitude and positively associated with annual and seasonal rainfall. In contrast, the abundance in mainland populations showed neither latitudinal trend nor an association with rainfall. In peninsular populations, mean height and basal diameter of branched plants showed a negative association with population density whereas mainland populations showed no significant association. None of the populations exhibited a population structure that fitted the log-normal distribution expected for young, growing populations with constant recruitment. Insular, peninsular and mainland populations showed a population structure with an uneven size distribution typical of populations experiencing regeneration pulses.

Introduction

Understanding what determines the distribution and abundance of organisms is a major problem in ecology as usually the factors that affect the distribution may also influence its abundance (Krebs 2002). Many factors, biotic and abiotic, operating at a range of spatial and temporal scales affects the abundance of plant populations (Harper 1977). Climate often plays a dominant role affecting a wide range of biological processes, and as a consequence, climate constrains the distribution of many plant species and affects global patterns of plant species diversity (Kleidon and Mooney 2000). At the local scale, however, biotic interactions often determine the abundance of plants (Harper 1977). Thus, the study of the factors affecting the distribution and abundance of particular plant species is an important ecological problem.

Columnar cacti exhibit great variation in their distribution range and abundance (Mourelle and

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Ezcurra 1997; Godinez-Alvarez et al. 2003). Low temperature often limits the latitudinal distribution (Nobel 1988), whereas factors such as rainfall level, soil properties, availability of nurse plants and livestock grazing often affect the local abundance (Godinez-Alvarez et al. 2003). Empirical studies have documented that the abundance of columnar cacti varies from a few to thousands of individuals per hectare (Steenberg and Lowe 1983; Valiente-Banuet and Ezcurra 1991). However, very few studies have explored the factors controlling the abundance at the regional scale or throughout the distribution range of a species.

Pachycereus pringlei (cardon) is the columnar cactus with the widest distribution in the Sonoran Desert (Turner et al. 1995). Its distribution includes almost the entire peninsula of Baja California, most islands of the Gulf of California and coastal areas in mainland Sonora, México (Figure 1). The abundance of cardon has been described in several locations along its distribution range (McAuliffe 1991; Turner et al. 1995; Valiente-Banuet et al. 1995; Silva 1996). Turner et al. (2003) have detected major differences in

abundance between islands and mainland sites in the Guaymas Bay area in Sonora. However, it is still unknown whether the differences in abundance detected in the Guaymas area are widespread and if major differences in abundance occur among insular, peninsular and mainland regions along the distribution range of this species (Figure 1).

The population structure and regeneration of cardon have been documented in Baja California (McAuliffe 1991; Silva 1996; Bullock et al. 2005). Using repeated photography, Bullock et al. (2005), were able to document that northern populations of the Peninsula are numerically stable or growing. The analysis of alluvial surfaces of different age allowed McAuliffe (1991) and Silva (1996) to infer that recruitment rates were greater in relatively younger soils. On the other hand, Bashan et al. (1995) have found an ailment, described as flat top decay that affect adult plants while Dubrovsky and Leon de la Luz (1996) described gall-like malformations in marginal peninsular populations. However, it is unknown how widespread are these ailments and
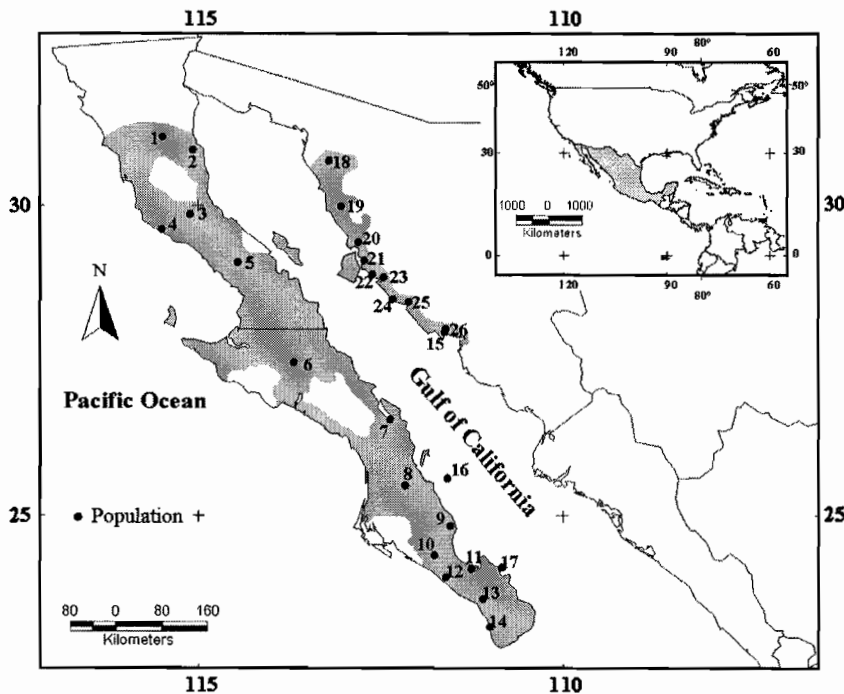

Figure 1. Map showing the geographical distribution of the 26 studied populations of *Pachycereus pringlei* along Sonora, Baja California, Baja California Sur, and Gulf of California Islands. The shaded area in northwestern México, represent the geographic distribution of *P. pringlei* (modified from Turner et al., 1995). See Table 1 for the exact location and name of each population.

whether they are affecting the regeneration and population structure of cardon along its distribution range. If these ailments are affecting regeneration, populations with a high frequency of flat top decay or gall-like malformations are expected to have low numbers of seedlings and juveniles (i.e. individuals <1 m in height). However, nothing is known about the effect of those ailments on the regeneration and the population structure along the distribution range of this species.

Columnar cacti usually exhibit two types of population structure (Godinez-Alvarez et al. 2003). Populations with an uneven distribution of individuals often suggest that recruitment occur in pulses whereas populations with large numbers of juveniles and pre-reproductive individuals and decreasing numbers of older size classes often reflects growing and expanding populations. Turner et al. (2003) have documented a recent increase (from 1903 to 1996) in the abundance of young individuals (established between 1930 and 1970), in insular populations whereas mainland populations have experienced episodic recruitment in the Guaymas area. Young populations with constant recruitment are expected to have a log-normal population structure (Silvertown and Lovett-Doust 1993; Solis-Montero et al. 2005). Thus, if insular populations have been experiencing constant recruitment, we expect to find a log-normal population structure. In contrast, if recruitment is episodic (pulse recruitment), we expect to find significant deviations from a log-normal population structure.

In this paper, we describe the abundance and population structure of 26 populations of *Pachycereus pringlei* covering the entire distribution range throughout the Sonoran Desert. First, we explore whether major differences in abundance occur between peninsular, insular and mainland populations. We then explore whether the abundance is associated with several environmental factors known to affect regeneration and growth of this species. We also describe how frequent is the flat top decay syndrome and explore its influence on regeneration. Finally, we describe the population structure in order to examine if populations fit the log-normal distribution expected under constant recruitment and whether insular and mainland or peninsular populations exhibit major differences in structure.

Methods

Study area

We sampled 26 populations of *Pachycereus pringlei* trying to cover its entire range of distribution in the Sonoran Desert. Fourteen populations were from the Baja California peninsular region, three from islands and nine from mainland Sonora (Figure 1, Table 1). Populations were selected on the basis of abundance, accessibility and being representative of the area. These areas are commonly known as "cardonales" in Mexican vegetation charts, and are usually found on alluvial plains.

Abundance

In each population, we established three one-hectare (100×100 m) plots, where we identified each individual of *P. pringlei*. In each plot we recorded the number of individuals of all size classes and obtained mean abundance per hectare as the average across plots and its standard deviation. In one location (Tio Ramon Island) we used three plots of $100 \, m^2$ (10×10 m) because the abundance was extremely high and it was impractical to record all the individuals found in one-hectare plots.

Population structure

In each plot we recorded height, number of branches, height of the first branch (i.e. trunk length), basal diameter and health status (i.e. whether apical meristems looked damaged and whether plants had many broken branches) of each plant. For each plant we recorded through visual inspection whether it had the symptoms described as flat top decay (Bashan et al. 1995). A graduated telescoping pole (15 m) was used to measure height, a vernier to measure basal diameter and a flexometer to measure the height of the first branch. Plants were assigned to 1-m height classes using a classification that has been used for other columnar cacti (Steenbergh and Lowe 1983; Kolberg and Lajtha 1997). The 0–1 m size class includes seedlings and juveniles whereas the 1–2 m class includes well established, pre-reproductive plants. The size class 2–3 m includes individuals

Table 1. Major attributes of populations and plants of *Pachycereus pringlei* sampled across its distribution range in the Sonoran Desert.

Region	Population	Latitude N	Longitude W	Total population				Branched individuals		
				Density Inds/ha	Regeneration index	Unbranched proportion (%)	Branched proportion (%)	Number of branches	Height (m)	Basal diameter (m)
P	1. San Pedro	31°05′ 43″	115°21′ 32″	31.0 (15.6)	28.7	43.5	56.5	10.7 (3.9)	6.7 (1.4)	0.45 (0.19)
	2. Punta Estrella	30°52′ 38″	115°52′ 48″	22.0 (8.5)	27.2	36.4	63.6	10.7 (1.5)	9.0 (0.3)	0.53 (0.09)
	3. Cataviña	29°50′ 27″	114°55′ 15″	51.7 (19.7)	13.9	58.1	41.9	5.7 (2.2)	7.6 (1.0)	0.50 (0.08)
	4. Puerto Canoas	29°36′ 38″	115°22′ 31″	23.5 (12.0)	27.9	38.3	61.7	6.7 (0.7)	8.3 (0.6)	0.53 (0.13)
	5. Punta Prieta	29°03′ 46″	114°09′ 10″	55.7 (24.5)	20.6	76.6	23.4	3.0 (0.4)	8.0 (0.5)	0.44 (0.04)
	6. San Francisco	27°26′ 54″	113°15′ 50″	78.7 (41.5)	14.7	67.8	32.2	4.0 (0.5)	6.1 (0.4)	0.38 (0.02)
	7. Bahia Concepcion	26°32′ 36″	111°42′ 43″	79.7 (17.4)	25.0	56.5	43.5	2.6 (0.5)	6.6 (0.4)	0.30 (0.01)
	8. Guatamote	25°28′ 55″	111°28′ 55″	129.7 (35.8)	38.0	70.7	29.3	4.5 (0.9)	6.8 (0.4)	0.3 (0.01)
	9. San Evaristo	24°49′ 01″	110°46′ 12″	554.0 (45.3)	2.2	62.4	38.1	2.4 (0.1)	3.9 (0.1)	0.3 (0.01)
	10. El Cien	24°20′ 43″	111°00′ 32″	206.3 (33.8)	22.7	71.2	28.8	4.3 (0.2)	5.5 (0.3)	0.3 (0.02)
	11. El Comitán	24°07′ 30″	110°25′ 30″	288.0 (57.9)	26.9	60.4	39.6	6.3 (0.7)	5.5 (0.2)	0.3 (0.01)
	12. La Conquista Agraria	24°00′ 00″	110°49′ 50″	126 (11.3)	24.6	73	27	4.7 (0.7)	4.6 (0.1)	0.37 (0.11)
	13. La Matanza	23°38′ 50″	110°15′ 16″	220.3 (72.8)	31	65.5	34.5	6.4 (0.3)	5.3 (0.1)	0.3 (0.09)
	14. Los Cabos	23°11′ 88″	110°07′ 30″	248.3 (45.7)	25.0	53.4	46.6	6.2 (0.1)	5.1 (0.1)	0.3 (0.02)
I	15. Tio Ramon Island	27°56′ 11″	110°51′ 11″	10250.0 (2050.6)	12.1	52.2	47.8	4.3 (0.5)	4.1 (0.4)	0.2 (0.01)
	16. Catalana Island	25°35′ 10″	110°48′ 25″	201.7 (56.6)	60.5	70.7	29.3	8.5 (0.2)	4.0 (0.6)	0.4 (0.03)
	17. Cerralvo Island	24°09′ 10″	109°55′ 30″	441.7 (54.4)	51.2	91.8	8.2	3.5 (0.04)	3.8 (0.3)	0.5 (0.39)
S	18. El Alamo	30°43′ 04″	112°41′ 22″	67.0 (4.2)	19.8	40.3	59.7	8.9 (1.0)	5.9 (0.01)	0.4 (0.01)
	19. Puerto Libertad	29°58′ 24″	112°29′ 35″	55.0 (3.6)	7.8	28.5	71.5	7.1 (0.6)	4.9 (0.1)	0.4 (0.01)
	20. San Gabriel	29°23′ 08″	112°13′ 10″	88.0 (8.5)	39.4	62.5	37.5	7.2 (1.2)	4.0 (2.0)	0.4 (0.01)
	21. El Sacrificio	29°05′ 44″	112°08′ 02″	50.5 (14.8)	18.6	37.6	62.4	10.7 (0.1)	5.8 (0.3)	0.4 (0.01)
	22. Bahia Kino	28°51′ 58″	111°59′ 46″	26.8 (9.1)	14.8	34.6	65.4	6.3 (0.9)	4.8 (0.3)	0.4 (0.01)
	23. San Nicolas	28°49′ 47″	111°48′ 22″	39.0 (5.4)	23.5	34.0	66.0	12.6 (2.4)	6.9 (0.9)	0.5 (0.08)
	24. El Cardonal	28°28′ 01″	111°40′ 02″	64.0 (11.3)	7.0	25.0	75.0	6.5 (0.6)	4.4 (0.3)	0.3 (0.04)
	25. Puerto Arturo	28°25′ 41″	111°25′ 00″	65.5 (7.8)	12.4	21.4	78.6	16.2 (0.1)	7.0 (0.3)	0.5 (0.0)
	26. El Sahuaral	27°59′ 27″	110°50′ 30″	76.0 (12.7)	26.2	25.7	74.3	27 (5.1)	7.7 (0.3)	0.6 (0.04)

Data are means, and standard deviations are shown in parenthesis. Regions: P, Peninsula of Baja California; I, Islands of the Gulf of California, and S, Mainland Sonora.

that start reproducing, while classes >2 m represent reproductive adults (Silva 1996). We used height in order to classify plants in size classes and to calculate the mean number and the standard deviation of plants per hectare and per size class. We used the proportion of young plants (<1 m in height) within populations as an index of regeneration as these individuals most likely represent recruits from the last 30–50 years (assuming a elongation rate of 2–3 cm/year, Steenbergh and Lowe 1977; Silva 1996). This index range from 0 to 1 and was used to explore if the flat top decay syndrome affects regeneration.

Data analysis

Nonparametric Kruskal–Wallis tests were used to evaluate whether significant differences exist among regions (peninsular, insular and mainland). Evaluated parameters included population density, mean height of branched plants, mean basal diameter and trunk height of branched individuals, regeneration index and mean number of branches. Dunn tests (Zar 1999) were used as a method of multiple comparisons between regional medians. We explored whether the abundance of *P. pringlei* showed an association with latitude through linear regression analysis. We also explored whether abundance showed any association with several climatological variables by regression analysis. Climatological variables included annual and seasonal rainfall, winter minimum temperature, mean number of freezing days and summer maximum temperature based on previous knowledge on their influence on regeneration and growth (Turner et al. 1995). Most variables were not correlated (data not shown) and thus we were able to use single regression analysis. Climatological data were obtained from stations located close (<20 km) to the sampled populations and available through the Eric II Data base (Quintas 2000). We also evaluated the influence of population density on several plant attributes through linear regression analysis. For each population we generated the expected log-normal size distribution using JMP software, based on the observed size distribution. Differences between the expected and the observed distribution were evaluated through the Kolmogorov-Smirnov test (Zar 1999). All statistical analyses used JMP version 4.0 (SAS Institute 2001).

Results

Abundance

The abundance of *P. pringlei* varied from 22 to 10,250 plants per hectare among populations through the distribution range. Within the peninsula, the abundance ranged from 22 to 554 plants/ha; within the mainland, density varied from 27 to 88 plants/ha, whereas the abundance on islands was much larger (202–10,250 plants/ha, see Table 1). The statistical analysis showed significant differences between regions ($H = 23.46$, $p < 0.0001$). Insular areas sustained significantly larger average densities than peninsular populations ($Q = 2.96$, $p < 0.01$), and peninsular sustained significantly larger average densities than mainland populations ($Q = 2.93$, $p < 0.05$).

In general, the abundance of *P. pringlei* throughout its distribution range showed no significant association with latitude ($F = 0.0001$, $p = 0.96$). However, clear regional differences were detected. Population density showed a significant negative association with latitude in the peninsula ($F = 10.47$, $r^2 = 0.47$, $p = 0.007$, see Figure 2a) but not in mainland ($F = 0.008$, $p = 0.93$, Figure 2a). Similarly, the abundance of *P. pringlei* showed no significant association with most environmental variables throughout the distribution range (see below). However, within the peninsula the abundance of *P. pringlei* showed a positive association with annual ($F = 36.61$, $r^2 = 0.75$, $p < 0.0001$, Figure 2b) and seasonal rainfall (July, August, September, October, and November; $F = 30.75$, $r^2 = 0.72$, $p = 0.0001$) but such association was not detected in mainland populations ($F = 1.25$, $p = 0.30$, for seasonal rainfall; and $F = 0.87$, $p = 0.38$, for total rainfall). In contrast with rainfall, the abundance of *P. pringlei* showed no significant association with the number of freezing days ($F = 1.59$, $p = 0.22$) or with summer maximum temperature ($F = 0.76$, $p = 0.40$) throughout the entire distribution range or for peninsular ($F = 1.4$, $p = 0.27$ for freezing days and $F = 0.15$, $p = 0.7$ for maximum temperature) or mainland populations ($F = 0.38$, $p = 0.56$ for freezing days and $F = 0.15$, $p = 0.15$ for maximum temperature). However, the abundance showed a marginal association with winter minimum temperature when analyzed throughout the entire range ($F = 2.21$, $p = 0.03$, Figure 2c) but such association
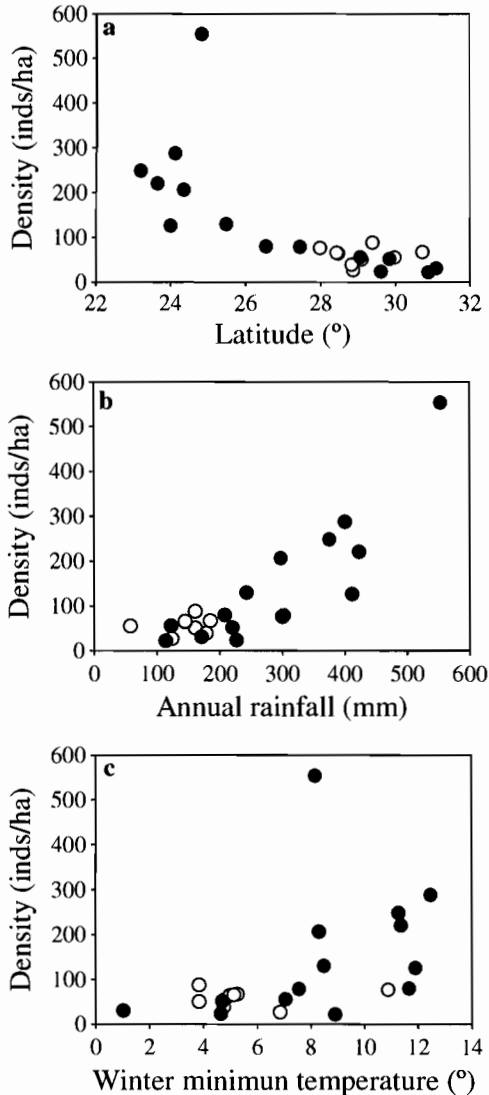
Figure 2. The abundance of *Pachycereus pringlei* (plants/ha) as a function of latitude (a), annual rainfall (b) and winter minimum temperature (c) along Peninsular (filled circles) and mainland (open circles) populations.

was not detected when analyzed just for peninsular ($F = 2.21$, $p = 0.16$) or for mainland populations ($F = 0.04$, $p = 0.84$).

In addition, some plant attributes showed an association with population abundance in some areas of the distribution range. For instance, in peninsular populations, mean height ($F = 19.57$, $r^2 = 0.62$, $p = 0.0008$) and basal diameter ($F = 13.13$, $r^2 = 0.52$, $p = 0.0035$) of branched individuals exhibited a negative association with mean density while the number of branches

($F = 2.19$, $p = 0.16$) and trunk height ($F = 0.0003$, $p = 0.98$) showed no significant relationship (Figure 3). In contrast, mainland populations showed no association between mean height and basal diameter with abundance ($F = 0.002$, $p = 0.97$ and $F = 0.16$, $p = 0.70$, respectively).

Regeneration

The index of regeneration (i.e. proportion of plants < 1 m within the population) ranged from 2 to 61% among populations (Table 1). Within the peninsula the index varied from 2 to 38%, from 7 to 39% in mainland, while islands showed the greatest range of variation from 12 to 61% (Table 1). The statistical analysis showed significant differences among regions ($H = 8.91$, $p = 0.01$). On the other hand, the proportion of adult plants showing the flat top decay syndrome throughout the distribution range of *P. pringlei* varied from 0 to 33.7% among populations. However, plants with this syndrome were
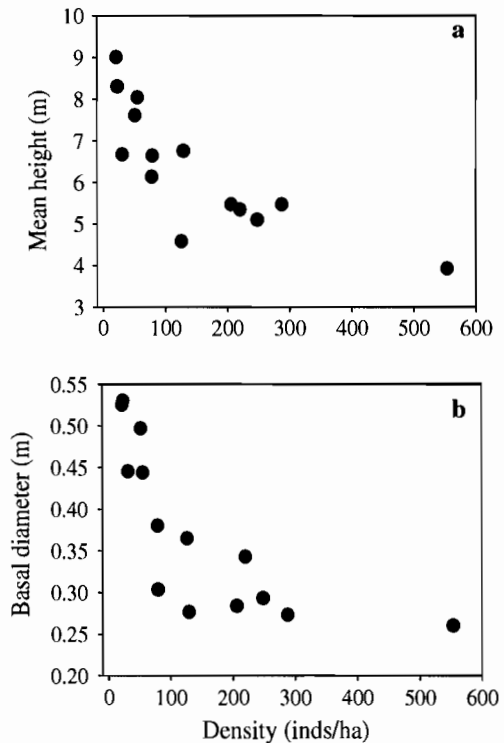

Figure 3. Relationship between plant height (a) and basal diameter (b) of adult plants as a function of population density in peninsular populations of *Pachycereus pringlei*.

restricted to one population (Bahia Concepcion) and affecting 33.7% of the adult plants (16% of the total). In this population, the proportion of young plants was 25% (Table 1). In contrast, very few individuals showed this syndrome throughout the distribution range. In consequence, the relationship between flat top decay and regeneration was not significant ($F = 0.45$, $p = 0.64$).

Branched plants

In general, branching started on individuals between 1.7 and 3.0 m in height in mainland populations, between 1.5 and 2.1 m in islands, and between 1.1 and 3.3 m in peninsular populations. The percentage of branched individuals ranged from 8 to 79% among populations (Table 1). No significant differences were detected in the proportion of branched plants among regions ($H = 4.98$, $p = 0.08$). However, the mean number of branches per adult plant varied significantly between regions ($H = 22.94$, $p < 0.0001$). Mainland ($Q = 4.7$, $p < 0.001$) and peninsular ($Q = 2.7$, $p < 0.05$) populations exhibited significantly greater number of branches than insular areas, whereas mainland and peninsular populations had equal number of branches ($Q = 0.35$, $p > 0.05$). The maximum number of branches recorded across the range was an individual at El Sahuaral with 132 branches. Mean height of branched plants ranged from 3.8 to 9.1 m among populations. Significant differences were detected for mean height among regions ($H = 19.08$, $p < 0.0001$). Branched individuals from mainland ($Q = 3.18$, $p < 0.002$) and peninsular ($Q = 4.35$, $p < 0.001$) populations were on average taller than insular, whereas peninsular and insular populations exhibit same height ($Q = 1.47$, $p > 0.05$). The tallest individual was recorded in Cataviña with 15.6 m. Trunk height ranged from 0.9 to 2.0 m among populations with mainland populations exhibiting longer trunks than insular ($Q = 2.76$, $p < 0.02$), whereas insular and peninsular ($Q = 2.22$, $p > 0.05$), and peninsular and mainland populations ($Q = 0.73$, $p > 0.05$) exhibit the same trunk height. The basal diameter of branched individuals ranged from 0.20 to 0.61 m and showed significant differences among regions ($H = 9.51$, $p = 0.009$). The basal diameter of peninsular ($Q = 2.46$, $p < 0.05$) and mainland populations

($Q = 2.69$, $p < 0.05$) were on average greater that insular areas, whereas peninsular and mainland populations exhibit the same diameter ($Q = 1.15$, $p > 0.05$). Regarding latitudinal patterns, only in peninsular populations, mean height ($F = 28.03$, $r^2 = 0.70$, $p = 0.0002$) and basal diameter ($F = 35.03$, $r^2 = 0.74$, $p < 0.0001$) of branched individuals showed a significant positive association with latitude.

Population structure

Height distribution among peninsular, mainland and island populations are shown in Figure 4, together with the expected log-normal distribution. In all populations, the Kolmogorov–Smirnoff test revealed significant differences between the observed and the expected distribution, indicating that none of the populations fitted the distribution expected for young, growing populations with constant recruitment. All populations exhibited an uneven distribution of size classes typical of populations with regeneration pulses (Figure 4).

Discussion

In this paper, we have shown that *P. pringlei* exhibit great variation in abundance throughout its distribution range. Islands sustained larger population densities than mainland and peninsular populations. Peninsular populations showed a latitudinal pattern of abundance that is closely associated with rainfall. In contrast, mainland populations showed no significant association with latitude and rainfall. None of the populations showed a size distribution that fitted the lognormal distribution that is expected for young growing populations under constant recruitment whereas all showed an uneven size distribution typical of populations with regeneration pulses.

Abundance

The range of variation in abundance recorded for *P. pringlei* is greater than the range that has been reported for other columnar cacti (Niering et al. 1963; Steenbergh and Lowe 1983; Valiente-Banuet and Ezcurra 1991; Esparza-Olguin et al. 2001;
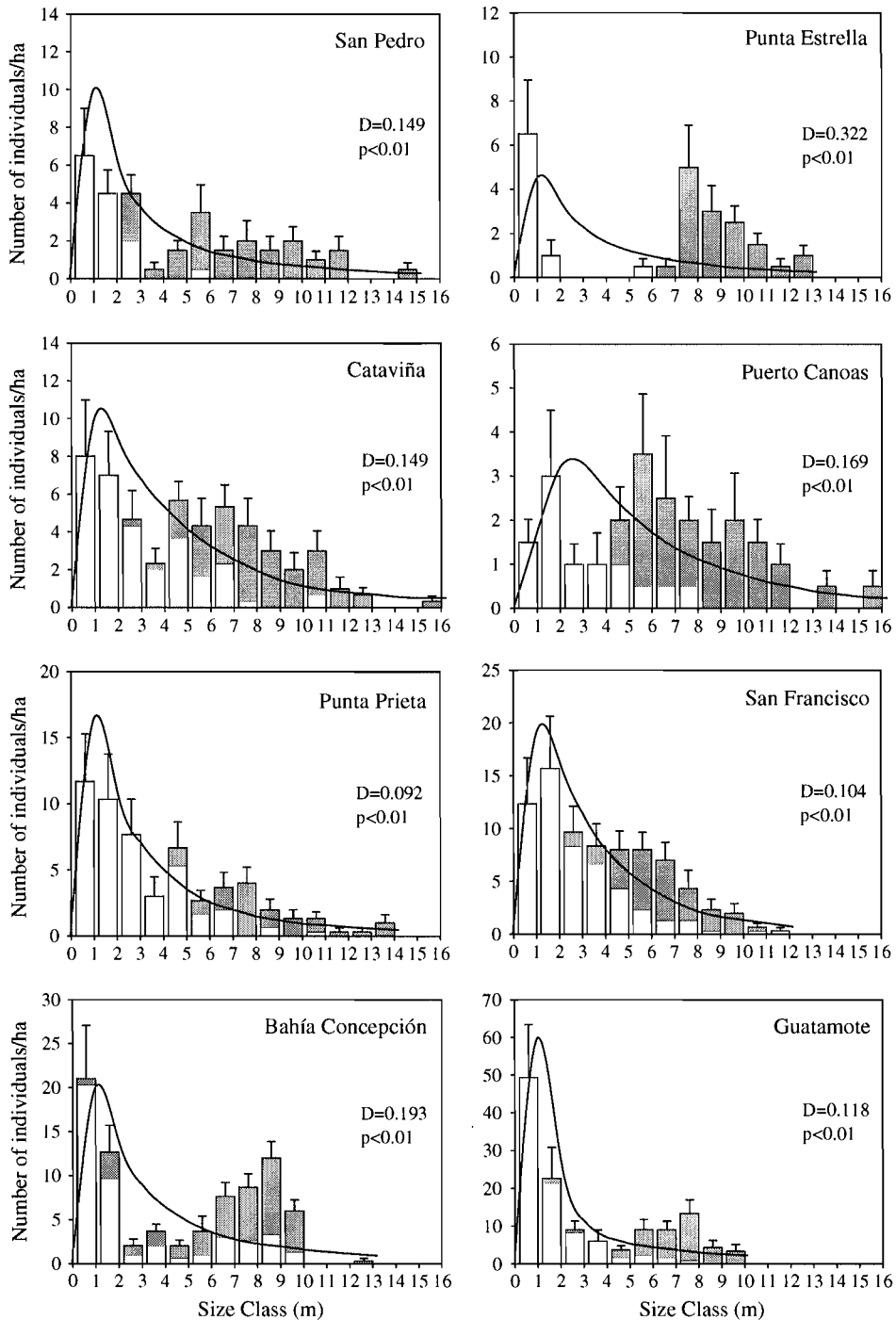
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Figure 4. Population structure of each of the 26 populations of *Pachycereus pringlei* studied along Sonoran Desert. Bars in each plot represent the mean number of individuals (+ 1 standard deviation) detected in 1 m height classes: white bars correspond to unbranched individuals; dark bars correspond to branched individuals. Lines in each plot represent the Log-normal expected distribution and D shows the results of the Kolmogorov–Smirnov goodness of fit test between the observed and expected distribution. Note that the *Y*-axis scale is not the same across populations in order to accommodate variation in abundance among sites.
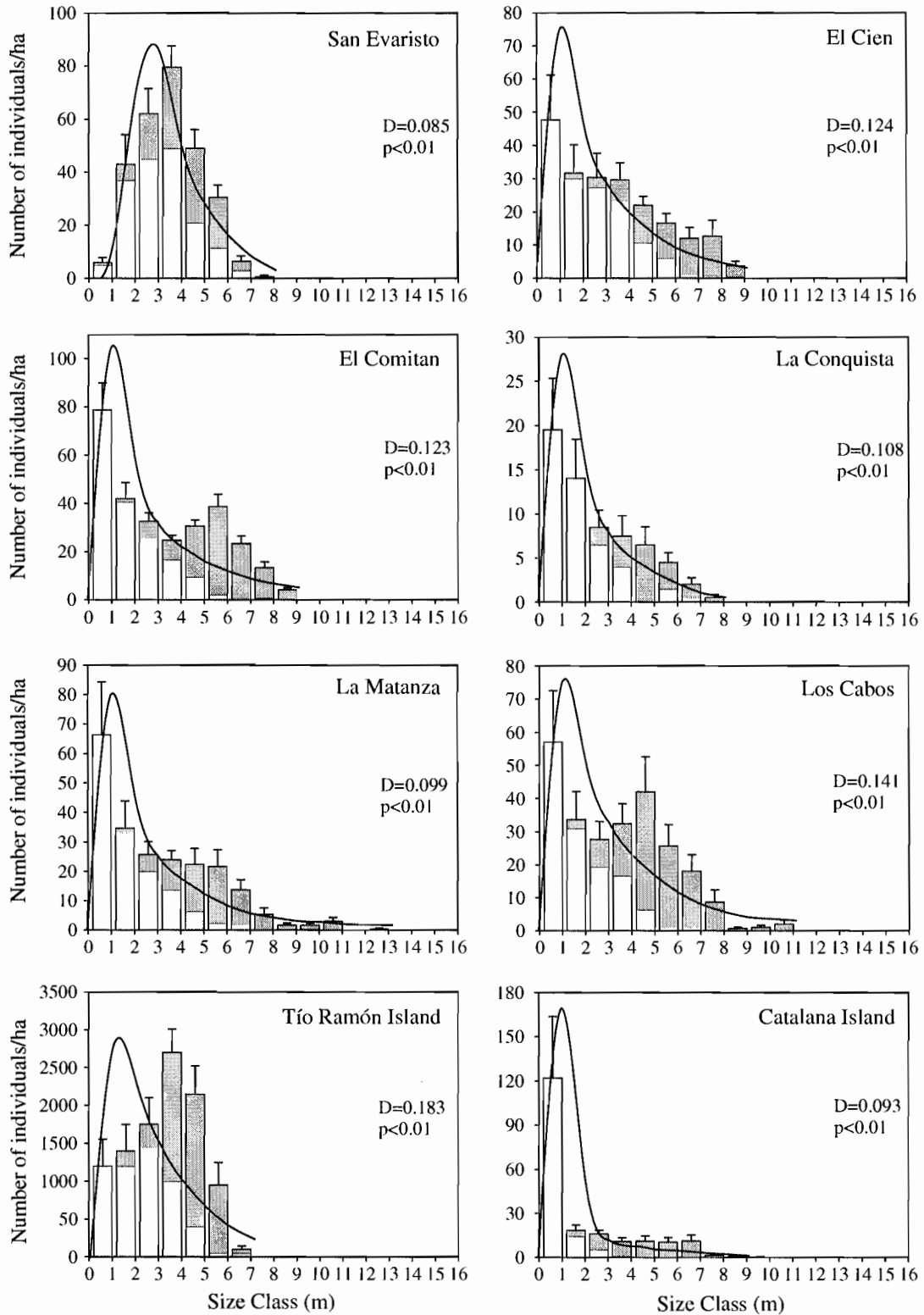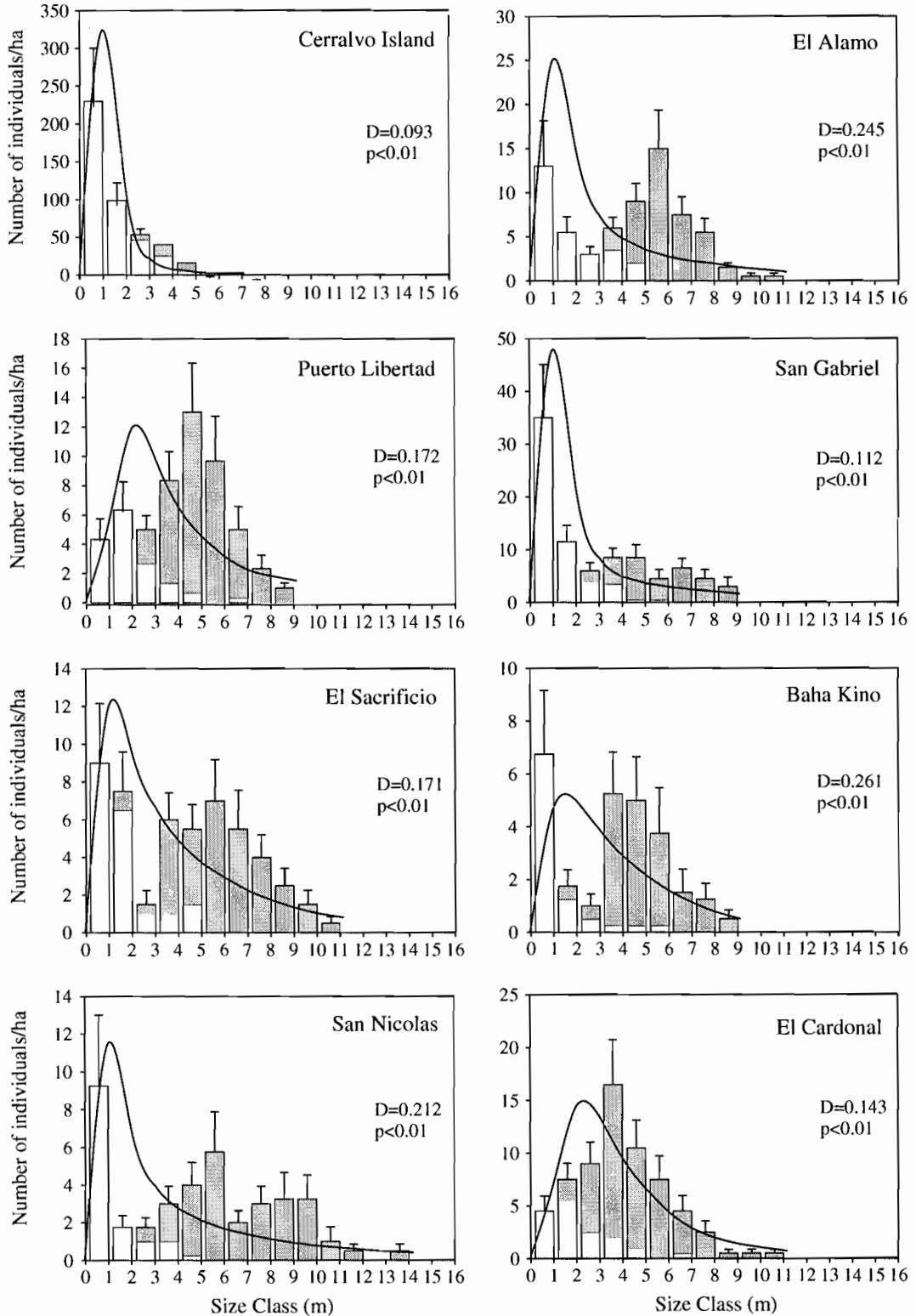
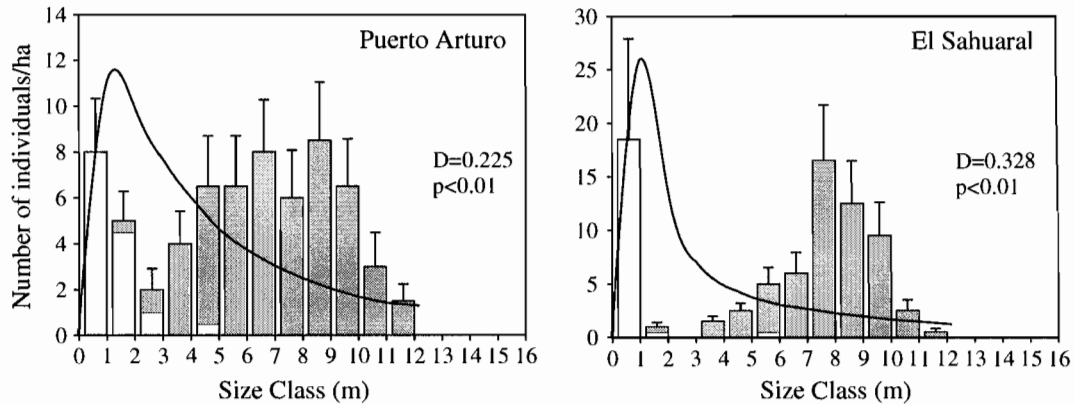*Figure 4.* Continued.

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Godinez-Alvarez and Valiente-Banuet 2004). The major difference in abundance detected in this study between island and mainland populations was previously noted by Hastings and Turner (1965a) and Turner et al. (1995, 2003) for the Guaymas Bay. Turner et al. (2003) recorded densities of nearly 8000 plants/ha in two nearby islands (Mellizas) of the Guaymas Bay and noted that populations were increasing in numbers during the 20th century that contrasted to nearby mainland populations (Turner et al. 1995, 2003). The contrast in abundance between Tio Ramon Island and El Sahuaral (see Table 1) is typical of the Guaymas area. We currently do not know what mechanism may be generating such great differences in abundance between island and mainland populations. Geological or soil differences are unlikely as in the Guaymas area both island and mainland sites have similar geological origin (INEGI 1982). However, it is likely that the contrast in abundance is due to differences in biotic factors associated with seedling establishment. It is well known that rodents and lagomorphs play an important role during the establishment phase of columnar cacti (Turner et al. 1969; Steenbergh and Lowe 1983). It is also known that small islands in the Gulf of California posses lower species diversity for rodents and lagomorphs than adjacent mainland or peninsular areas (Lawlor et al. 2002). Thus, it is possible that differences in abundance reflect great differences in seed predation and/or seedling herbivory due to rodents and lagomorphs between areas. Studies using seeds and seedlings transplanted under different experimental treatments in adjacent island and mainland areas could reveal the mechanism underlying such differences in abundance.

The abundance of peninsular populations exhibited a clear latitudinal pattern that was strongly associated with rainfall. Summer rains tend to be more important in southern Baja California than in northern Baja (Hastings and Turner 1965b). Tropical Hurricanes are also known to bring significant amounts of rainfall to southern Baja (Hasting and Turner 1965b). It is also well known that *P. pringlei* disperse its seeds before the summer rains and seedling establishment is associated with summer rains (Turner et al. 1995). Thus, it is not surprising that the abundance of *P. pringlei* along the peninsula is associated with annual as well as summer and fall rainfall as this is the critical season for seedling establishment (Turner 1990). In contrast with peninsular populations, mainland populations showed no association with latitude or rainfall. In Sonora, *P. pringlei* occupy a narrow coastal band with little variation in annual rainfall along its limited latitudinal distribution. In this region, although there is some latitudinal variation, the major axis of variation in rainfall is longitudinal (west to east, Ives 1949; Wiseman 1980). Thus, in this area of the range of *P. pringlei*, the variation in abundance does not appear to be associated with rainfall. Unfortunately, the number of island populations included in this study was limited and thus we were unable to explore the relationship between abundance and climate in this area of the distribution range. However, it is likely that given the contrast in the latitudinal range among peninsular, insular and mainland populations, peninsular populations

are subject to greater environmental variation and thus show a clear response in abundance. Our data also showed evidence that winter minimum temperature affects the overall abundance of *P. pringlei* throughout the distribution range. Thus, in addition to constraining the northern latitudinal limits (Nobel 1988), minimum temperature also affects the abundance of *P. pringlei*.

It is interesting that two plant attributes (height and basal diameter) showed a negative association with plant density in peninsular but not in mainland populations. Regional differences in the range of variation in abundance may explain why the association was detected just in peninsular populations. Density dependence is seldom detected in desert plants where water is considered as the major limiting factor (Miller and Huenneke 2000). However, it is known that the root system of *P. pringlei* is quite extensive (Niklas et al. 2002) and it is likely that at high densities, plant interference may occur. Dense populations of *P. pringlei* may respond by a reduction in water uptake and storage, apical growth and reproductive potential as has been reported for *Carnegiea gigantea* (McAuliffe and Janzen 1986). Thus future studies should explore the mechanisms by which height and basal diameter are affected by plant density in *P. pringlei*.

Regeneration and flat top decay

Most populations had significant numbers of juveniles (<1 m, see Table 1), suggesting that recruitment has not ceased in recent years and that most populations are not facing major regeneration problems. Bashan et al. (1995) detected an ailment (flat top decay) that affected populations of *P. pringlei* from Baja California Sur. Our study revealed that this syndrome was restricted to the south-central peninsular region as we did not detected significant numbers of adult plants with this ailment throughout the distribution range. We detected just one population (Bahia Concepcion) where a significant proportion of adult plants (33.7%) had the flat top decay syndrome, a value similar to the one reported by Bashan et al. (1995). Elsewhere, the proportion of young plants affected by this syndrome was very low (0.05%) and most plants were not affected. Thus, judging by the proportion of young plants (<1 m) at Bahia Concepcion (25%) and the fact that there is no

relationship between the frequency of flat top decay and regeneration, the available evidence suggests that this syndrome is not having a significant effect on regeneration.

Population structure

Our data showed that none of the populations fitted the log-normal size distribution expected for young, growing populations with constant recruitment (Silvertown and Lovett-Doust 1993; Solis-Montero et al. 2005). Our data on population structure are more consistent with a distribution subject to pulse recruitment. Even on islands where the abundance was greater and the distribution looked like a left uni-modal distribution (see Figure 4), the statistical analysis revealed that these populations did not fit the log-normal distribution. These populations have an uneven distribution, as in populations experiencing episodic pulses of regeneration. The size distributions observed throughout the range of distribution of *P. pringlei* is similar to the observed for other columnar cacti from the Tehuacán Valley (Ezparza-Olguin et al. 2001; Godinez-Alvarez and Valiente-Banuet 2004) and the Sonoran Desert (Steenbergh and Lowe 1983; Kolberg and Lajtha 1997). On those populations seedling recruitment may occur at irregular time intervals when favorable environmental conditions (i.e. heavy rainfall) favor seedling survivorship.

Finally we would like to comment on the conservation status of *P. pringlei* throughout the Sonoran Desert. In general, our data reveal that most populations of *P. pringlei* are not facing regeneration problems throughout its distribution range. Our observations suggest that most populations have episodic recruitment events that provide sufficient numbers of juveniles for population maintenance. We have observed, however, disturbance of populations near human settlements whose long-term effects are unknown. Future studies should estimate population growth rates near human settlements and in areas being developed for tourism in order to evaluate the ecological impact of these activities. A formal demographic study on selected islands and some peninsular and mainland populations would provide critical information on the current

status (i.e. whether populations are numerically stable, decreasing or increasing) of this columnar cactus.

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