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The giant columnar cactus *Pachycereus pringlei* adaptively modifies its stem shape from the dry tropics into the arid mid-latitude deserts

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ABSTRACT

Because of the lack of leaves, the distributions of columnar cacti are limited by their capacity to trade off their photosynthetic chlorenchyma and their non-photosynthetic storage parenchyma. For species with wide latitudinal ranges, variations in stem surface area:volume ratios could play an adaptive role. Based on the fact that *Pachycereus pringlei* spans more than a 1000 km along the Baja California Peninsula, we used this species to analyze changes in stem allometry between populations. We selected six sites, from latitude 23°–31° N, ranging from 518 to 55 mm of annual rainfall. We used an allometric model to analyze the diameter-to-height relationship, estimating the parameters through linear modeling. The height of the main stem when the first branch emerges was estimated by regressing the height of the plant against the number of lateral shoots. The solar radiation intercepted by an unbranched 6-m-tall cardon was estimated using an irradiance model. The diameter of adult plants, the stem height when cardons begin to branch, and the surface area:volume ratio, were all associated to latitude and to latitude-related environmental variables such as rainfall. For any given height, the surface area:volume ratio decreases from the wetter tropics into the arid mid-latitude deserts.

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1. Introduction

Plant allometry, the differential scaling of the parts of a plant as it grows and develops, is intimately related to the plant's biomechanics, ecology, and evolution (Niklas et al., 2006). Plants may optimize their allometry according to the environment to which they are exposed. Competition for light or water can modify the allometry of a plant, and it is thus to be expected that allometric traits vary in a predictable manner along large-scale environmental gradients (Blanin et al., 2012). Because of their low surface area:volume ratio, cacti are frequently limited by their photosynthetic capacity, and therefore, the relationship between stem diameter and plant size is extremely important. Thinner stems have a lower amount of internal parenchyma to be sustained by a unit area of chlorenchyma than thicker stems, but they also have a lower water-storage ability that may represent a disadvantage in dry regions. Using biophysical simulations, Nobel (1980a, b) found that increases in stem diameter raised the minimum apical temperature

for the saguaro cactus *Carnegiea gigantea* and may help account for the greater extension of its range into higher latitudes compared to other, more slender species.

Allometric variations between populations of cacti along broad environmental gradients have been studied in three species of columnar cacti (1) *Pachycereus schottii* in Sonora, Mexico (27° 41′ N to 31° 53′ N; Felger and Lowe, 1967), (2) *Cephalocereus columna-trajani* in Tehuacán-Cuicatlán valley, Mexico (17° 20′ N to 18°53′ N; Valverde et al., 2007) and (3) *C. gigantea* in Arizona, USA (31° 53′ N to 33° 51′ N; Drezner, 2003). In the first two studies, dry tropical sites with more precipitation and higher mean temperatures showed the most slender individuals (higher surface area:volume ratio) and, as latitude increased, individuals became stouter and their surface area:volume ratio decreased. However, studying saguaros in the northernmost part of their distribution in Arizona, Drezner (2003) failed to find a correlation between stem diameter and latitude but found instead a correlation with spring precipitation. Although not strictly focusing on plant allometry, two other papers have described latitudinal patterns in plant architecture. Studying 25 species of North American columnar cacti whose ranged from 30° N latitude in southern Arizona to 15° N at the Isthmus of Tehuantepec, Oaxaca, Cornejo and Simpson (1997)

found that across each taxon cooler winter temperatures were associated with larger stem girths, and greater annual precipitation was associated with less frequent branching and taller branching heights. Studying the density and size structure of 26 populations of *Pachycereus pringlei* throughout its distribution range in the Sonoran Desert, Medel-Narváez et al. (2006) found that in the peninsular populations of Baja California the basal diameter of branched individuals tended to increase with latitude.

Vertical growth in columnar cacti allows them to maximize light interception in the morning and evening while minimizing the interception of solar radiation at noon when the sun is near the zenith, thus avoiding the risk of overheating during the hottest hours of the day (Zavala-Hurtado et al., 1998). Additionally, branching allows columnar cacti to increase their relative photosynthetic surface and water storage capacity (Drezner, 2014). For this reason, the height at which columnar cacti begin to branch is associated with a substantial change in the plant's photosynthetic and storage dynamics. The pattern of branching has also been associated with variations in environmental conditions. Saguaros, for example, branch when they reach 4.4—5.5 m high and variation in branching height is related to differences in precipitation, especially winter rainfall, within the distribution range of the species (Drezner, 2013).

The cardon cactus (*P. pringlei*) is a giant columnar cactus endemic to the Sonoran Desert and with a wide latitudinal distribution in the Peninsula of Baja California (23°—31° N). It may measure up to 20 m high and over 1 m in stem diameter (Turner et al., 1995) with stem-elongation rates of 3—23 cm per year (Delgado-Fernández et al., 2016), branching is mesotonous (Vázquez-Sánchez et al., 2012) and typically generates 2 to 11 branches (Medel-Narváez et al., 2006). Allometric variations in height, stem diameter, number of branches and branching patterns may have a strong influence on the plant's ability to (1) regulate the interception of photosynthetically active radiation (PAR); (2) minimize self-shading in branched plants (Geller and Nobel, 1986); (3) transport and store water (Drezner, 2003); (4) thermoregulate (Felger and Lowe, 1967), and (5) avoid damage from both the physical environment (drought, wind, freezing temperatures), and fungi and insects (Bashan et al., 1995).

Pachycereus pringlei has one of longest latitudinal ranges of any columnar cactus, spanning more than a 1000 km along the Baja California Peninsula from the hot dry tropics of Baja's Cape Region (23° N), fed by the downpours of late-summer monsoons, to the drylands of the northern part of the Peninsula, where the Sonoran Desert meets the mediterranean ecosystems of the California Floristic Province (31° N) and a higher proportion of winter rains is received. Hypothesizing that such a broad range of conditions would in all likelihood be reflected in the plants' morphology and architecture, we studied this species along its entire latitudinal gradient to analyze variation between populations in (a) the cardon's height-to-stem diameter allometry and in (b) the plant's height when branching starts. In particular, we expected the stem diameter-to-height allometry to increase with latitude, as reported by the other studies, and hypothesized that allometric differences along the gradient could be of adaptive value for the plant.

2. Methods

2.1. Sampling sites

Six sites along the Baja California Peninsula were selected, from latitude 23.3°—30.8° N, encompassing the whole range of precipitation where the cardon is distributed, spanning from 55.3 to 517.9 mm of annual rainfall (1951—2010 historical records; CONAGUA, 2010). All sites are flat *bajadas* (slope < 4%) and located

on the Gulf of California divide of the peninsular ranges to minimize the effect of moisture derived from the mists of the Pacific Ocean (Fig. 1).

At each site, a 100 m × 100 m quadrat was randomly established within a larger area with cardon vegetation, less than 6 km from the nearest weather station. In October 2015 all individuals within the sample quadrat were counted, their height was recorded using a forester's hypsometer (Nikon Forestry 550, Nikon Vision Co. Tokyo, Japan), the stem perimeter at 1.3 m from ground level was recorded with a measuring tape and then converted to shoot diameter, and the number of branches was counted.

2.2. Height-diameter allometry

For the analysis of plant height vs. stem diameter we used the standard allometric equation, or power function, $y = k x^z$, where the parameter z is the allometric exponent that measures the curvature of the allometric curve, and k is a scaling coefficient. To estimate the allometric exponent z we used nonlinear regression as recommended by Zar (1968, see also Gould, 1979). The fit was done using the *nls* function in the statistical package R, which uses a Gauss-Newton search for the parameter values and the Delta method to estimate the standard errors of the fitted parameters (R Core Team, 2016). Once the allometric exponents were estimated for all sites, we tested them for significant differences between sites using pairwise *t*-tests for unequal variance and unequal sample sizes.

Because in our study the allometric exponents did not differ among sites, we maintained the null hypothesis that allometric relationships between height and diameter were similar in all sites, and following Gould (1979) we then tested whether the scaling parameter differed among populations in the different sites. For this purpose, we first transformed the height values into a new variable *w*, or "allometric height" such that $w = h^z$. The allometric model for the special case of *z* being constant for all sites was then fitted as a simple linear regression with zero intercept ($d = k . w$), and both the value and standard error of the *k*-parameter were obtained. Because this is now a simple linear regression, we used an ANCOVA design to include the fixed effect of the sites on the scaling coefficient *k*, and the estimated *k*-values were compared among sites using Bonferroni tests. The scaling coefficients *k* were correlated with a set of environmental variables describing each site (Table 1) to explore possible geographic trends in the value of the parameter. All analyses were done using the R package (R Core Team, 2016).

2.3. Plant height at first branching

Unlike other plants that start branching as saplings, many columnar cacti maintain an unbranched, monopodial growth form for many years and start branching after they reach a certain critical size (see Fig. S1 in Supplementary Material). To estimate in each site the mean size of the plants when branching begins, the number of branches in each sampled plant was plotted against the height of the main, or leading stem. The plant's height at the time when branching starts, which we will call "height-at-first-branching" was estimated at each site by regressing the height of the plants against the number of lateral shoots in branched individuals. The intersect of this line (i.e., the regression point when branches = 0) is an estimate of the height of the main shoot when the formation of branches starts. Using linear regression we estimated for each site the height-at-first-branching and its standard error, and then correlated its values against the set of environmental variables describing each site (Table 1 and Fig. 2).
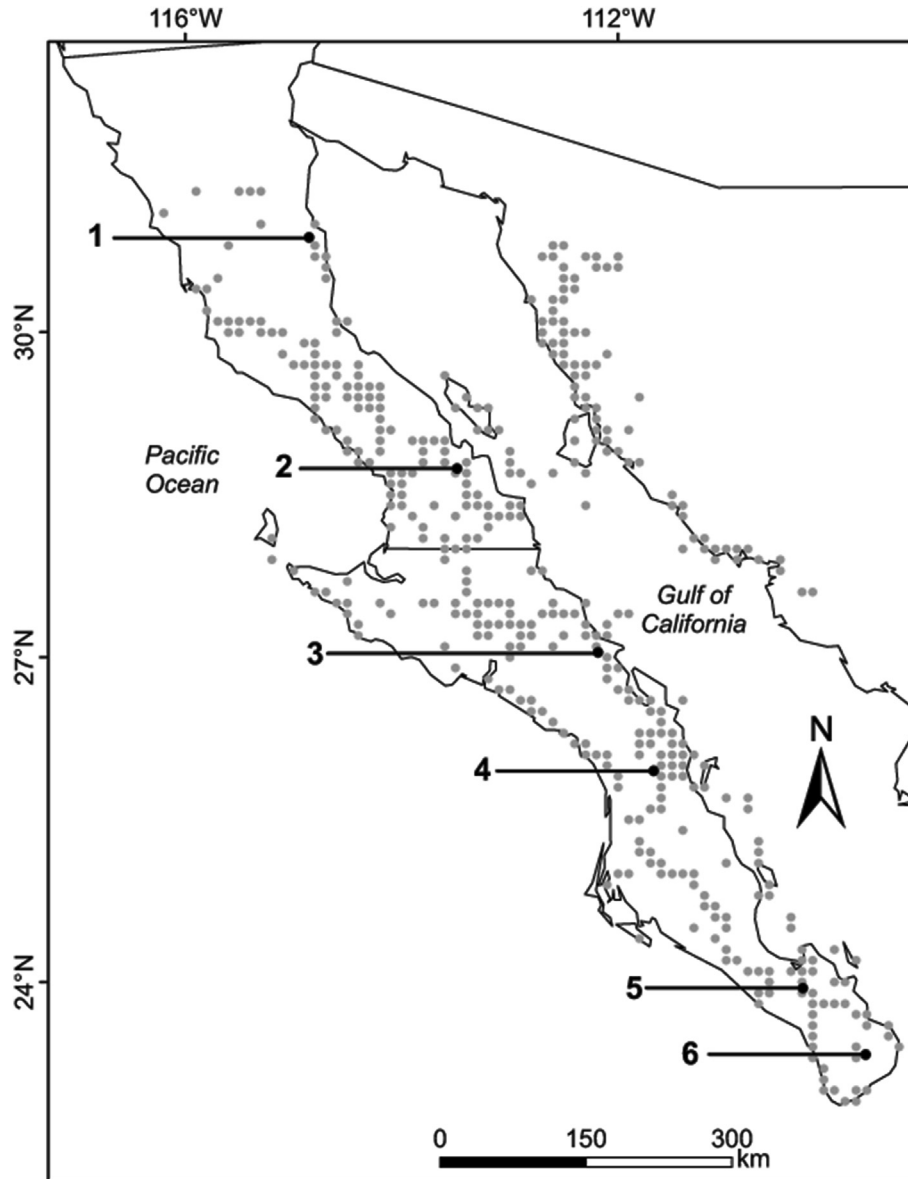
Fig. 1. Study sites and geographic range of cardon. Gray dots show cardon observations and collected specimens compiled by Turner et al. (1995); black dots show the study sites: (1) Percebú, (2) San Borja, (3) San José de Magdalena, (4) San Javier, (5) San Pedro, and (6) Mangle (coordinates in Table 1).

Table 1
Environmental variables at the study sites. Climatic data correspond to the 1951–2010 period (CONAGUA, 2010).

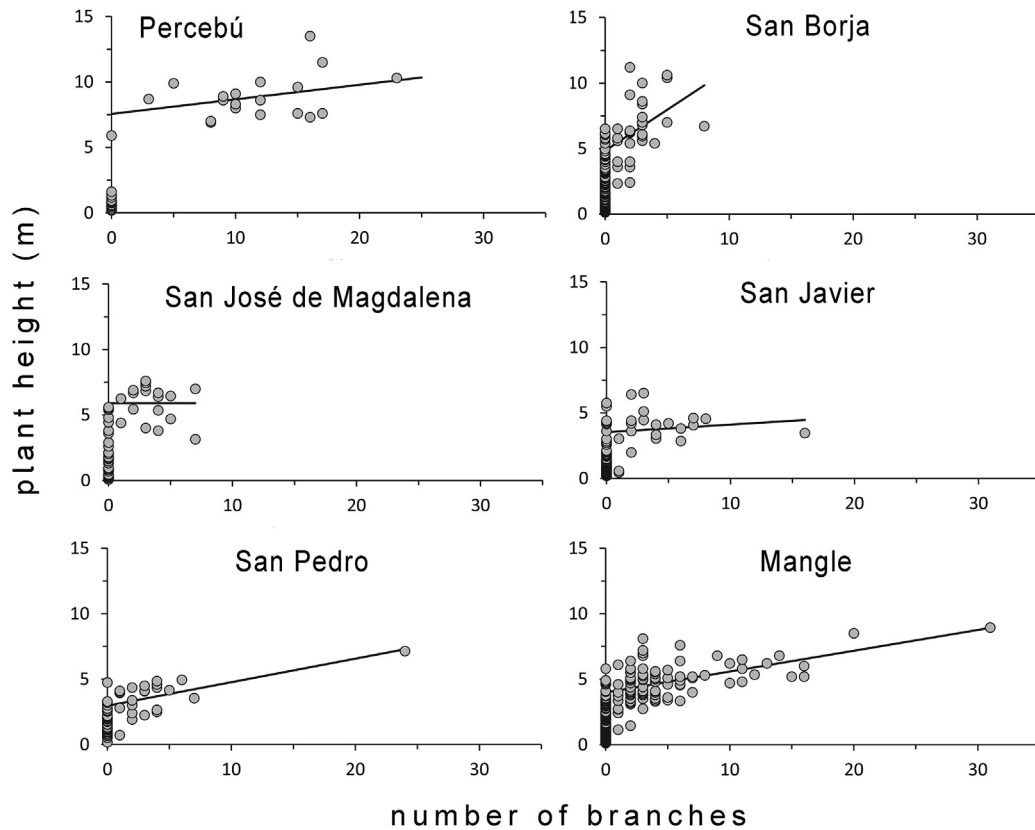|	1 Percebú	2 San Borja	3 San José de Magdalena	4 San Javier	5 San Pedro	6 Mangle
Average maximum temperature (°C)	28.0	27.8	30.8	28.1	31.8	32.9
Average minimum temperature (°C)	15.8	12.1	14.3	12.4	14.3	16.0
Average temperature (°C)	21.9	19.2	22.5	20.2	23.0	24.4
Maximum height of the cardons (m)	13.50	11.20	7.60	6.50	7.15	8.95
Density (cardons/ha)	39	187	50	157	57	255
Distance to the Pacific Ocean (km)	124	39	96	58	36	53
Distance to the Gulf of California (km)	5	28	8	19	29	21
Latitude	30.883	28.752	27.095	25.900	23.920	23.349
Longitude	−114.760	−113.767	−112.191	−111.548	−110.285	−109.644
Altitude (m)	35	419	144	459	171	289
Precipitation (mm)	55.3	114.0	180.0	297.1	335.1	517.9
Number of rainy days	5.3	12.5	10.5	12.6	25.2	23.5
Water per capita (m^3/individual)	1.41	0.60	3.60	1.89	5.87	2.03
Summer rainfall (June–October) (mm)	35.1	32.1	143.8	221.2	284.5	456.9
Winter rainfall (November–May) (mm)	20.2	82.0	36.2	75.9	50.6	61.0

Fig. 2. Estimation of plant height at first branching for the six sampled cardon populations along the Baja California Peninsula. Note that, despite the high variance of the data points the intercept of the regression lines decreases consistently from north (Percebú) to south (Mangle).

2.4. Surface area:volume ratio

Using the estimated allometric parameters, we calculated the mean surface area:volume ratio in each site for cardons of different heights. To do this, we calculated the surface and area of a cylinder of a given height and diameter. The area estimates were adjusted by a correction factor c for the plant ribs, estimated from four cardons of heights 4.1, 4.3, 5.0, and 5.5 m. In each plant, we measured the length of the rib-faceted perimeter and divided it by the overall perimeter measured with a tape. We then averaged the correction factor (c) for the four plants, to obtain a value of 1.28 ± 0.10 (i.e., the external area of the plant stem is 1.28 times higher than the area of a cylinder of similar diameter). Similarly, we corrected all estimates of plant volume by subtracting the mid-height of the ribs from the estimate of the stem diameter.

Thus, the surface area of a plant can be calculated as $s = c \, \pi \, d \, h$, where d is the stem's mean diameter, h is the height, and c is the correction factor for the added rib surface. Similarly, correcting for inter-rib space, the stem volume can be estimated as $v = \pi \, h \, (d^2 - 2d\varepsilon)/4$, where ε is the depth of each rib (see Supplementary Material, Supplement 3, for a proof). Simplifying the s/v quotient, the surface area:volume ratio becomes $s/v = 4 \, c/(d - 2\varepsilon)$. Recalling that $d = k \, h^z$, then the surface area:volume ratio can be expressed as $s/v = 4 \, c/(k \, h^z - 2\varepsilon)$, where k and z are the allometric parameters at each site and the mean rib elevation ε was taken as 1 cm (note that the final equation only uses height as a predictor of the surface area:volume ratio, a fact that minimizes potential errors induced by changing diameters).

2.5. Light interception model

The irradiance received by a cardon in Percebú and in Mangle, the northern and southernmost sites respectively, was estimated by decomposing an unbranched, 5-m-high adult cardon into 37 planes (the lowest 2 m of the plant were decomposed into 12 planes of varying azimuths, the upper 3 m into 12 additional planes, and the apical dome was decomposed into 13 small planes, see Zavala-Hurtado et al., 1998). The data for the construction of the figure were selected from adult cardons with a near height of 5 m growing in an unobstructed plain (Zavala-Hurtado et al., 1998). A computer program simulating direct solar radiation (Ezcurra et al., 1991) was supplied with data describing date and latitude for the site, as well as the azimuth, inclination, and area of the 37 light-intercepting planes to be simulated. Using standard astronomical equations (Meeus, 1988) the program calculates the apparent position of the sun from sunrise to sunset at 10-min intervals, and, using Gates (1980) method it integrates the daily direct solar radiation (in joules per square meter per day) for a whole year, using a value of 0.75 for atmospheric transmittance.

3. Results

3.1. Height-stem diameter allometry

The allometric exponent z estimated by nonlinear modeling was quite uniform in all sites (ca. 0.5) with the exception of Percebú, the northernmost site, where its value was 0.64 (se $\pm$ 0.08). The height

distribution of the population at Percebú is strongly bimodal: there is a cluster of small plants lower than 1.6 m, and a second cluster of larger plants taller than 6 m, with no intermediate individuals (Fig. 3). The lack of a continuous size distribution might explain the relatively high values of z in this site, and specially its significantly higher standard error compared to the z-exponent in other sites (see Table S1 in Supplementary Material). However, when multiple comparisons were applied, the difference was found to be not significant. Thus, we calculated a pooled value of z for the whole dataset ($z = 0.52 \pm 0.01$) by averaging the estimated exponents at all sites.

In contrast, the scaling coefficient k (estimated in all sites for a fixed value of $z = 0.52$) clearly increased with latitude at all sites ($r = 0.95$, $P = 0.004$; Fig. 4a). In strong agreement with this result, the mean diameter of adult plants, taken as all plants in each site with heights between 4 and 10 m (we did not take into account plants taller than 10 m because they occur only in the two northernmost sites, Percebú and San Borja), also showed a clear trend along the N—S geographic gradient (correlation for site means $r = 0.92$, $n = 6$, $P = 0.009$; correlation for all individual plants $r = 0.74$, $n = 176$, $P < 0.0001$; Fig. 4b). Environmental estimates of moisture availability patterns, such as number of rainy days, and total and summer rainfall, which are themselves associated with the latitudinal gradient where the species is distributed, showed also significant correlations with diametric scaling estimates (Table 2).

3.2. Plant height at first branching

The threshold height at which the cardons end monopodial

growth and begin to branch ranged from 7.55 (± 1.01) m in Percebú, to the north, to 2.96 (± 0.51) m in San Pedro, to the south (Figs. 2 and 4c). The plants at Percebú, which on average maintain a monopodial growth habit until surpassing 7 m in height, generate, once branching starts, a greater number of branches than at any other site. Despite the relatively large standard error of the regression intercepts in Fig. 2, between-sites differences in branching height were significant (Fig. 4c). The plant height when cardons begin to branch is also positively correlated with latitude ($r = 0.85$, $P = 0.03$; Fig. 4c), and therefore with other latitude-related variables such as the number of rainy days and total precipitation (Table 2).

3.3. Surface area:volume ratio

The calculated, size specific surface area:volume ratio decreases with increasing cardon height, as should be allometrically expected (Fig. 5a). More importantly, the simulation showed three distinct groups of sites: (a) The two most southern sites, San Pedro and Mangle, located in the tropical Cape Region, had consistently higher s/v values than the rest. (b) The three sites located in the central part of the peninsula (San Borja, San José de Magdalena, and San Javier) showed similar s/v curves. (c) Finally, the northernmost sampling station, Percebú, showed the lowest s/v values.

3.4. Light interception model

The estimation of direct solar radiation received by a 5 m high cardon in Percebú and another in Mangle over one year (Fig. 5b) showed that cardons in Percebú receive less solar radiation when compared with those of Mangle from October to February, when
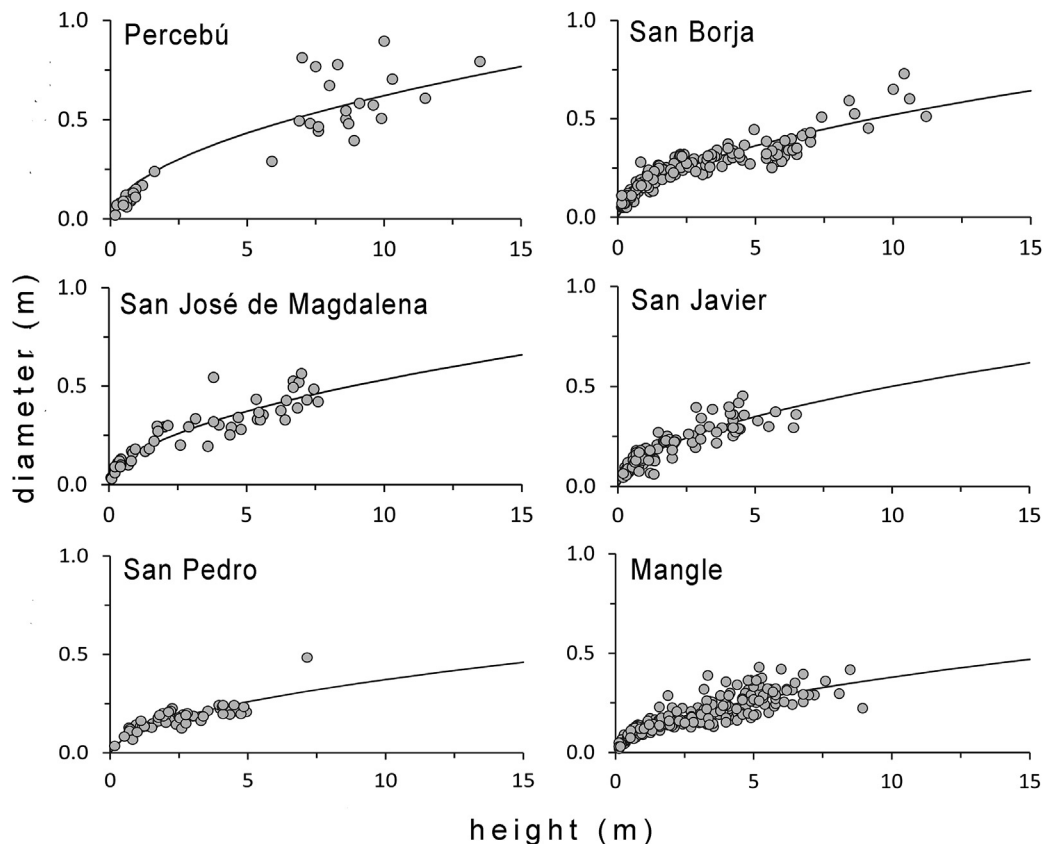

Fig. 3. Allometric relationship between height and diameter of cardon individuals at each studied population, plotted on an arithmetic scale. Trend lines (site-specific power functions) show how mean diameter varies depending on plant height assuming an equal allometric coefficient (z) of value 0.52 for all populations.
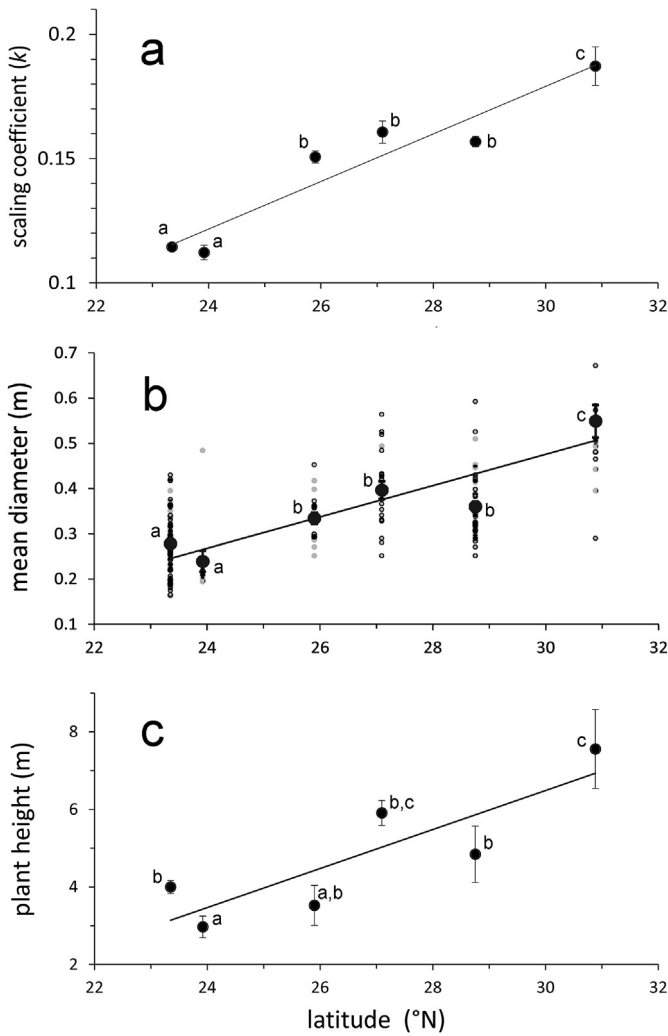
Fig. 4. Correlations between latitude and (a) the scaling coefficient *k* among sites, (b) diameter of adult cardons (small gray points) and site-specific mean diameters (large black points), and (c) plant height at first branching, showing that plants in the northern edge of the distribution are thicker and start branching when they reach ca. 6—7 m in height, while plants in the tropical boundary are thinner and start branching when they reach 3—4 m (in height in all graphs, the confidence intervals indicate ± 1 st. error; points within a graph labeled with similar letters do not differ significantly from each other).
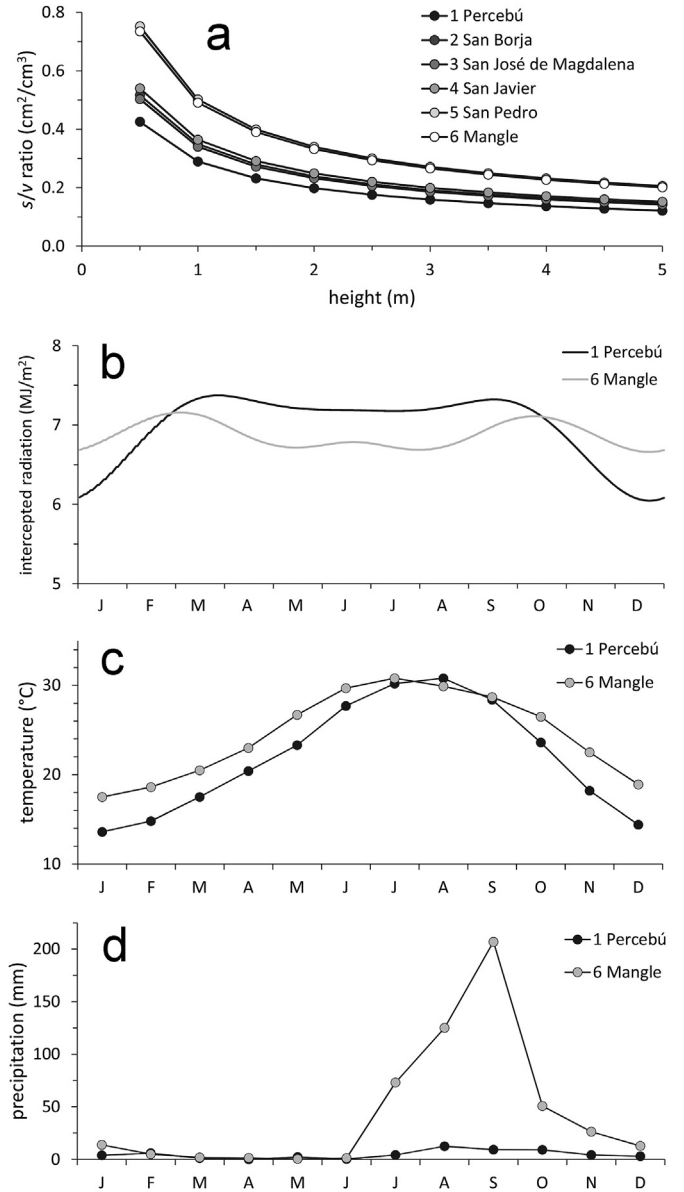
Fig. 5. (a) Variation of the surface area:volume ratio in monopodial cardons as a function of stem height in the six studied populations. (b) Daily direct solar radiation intercepted throughout the year by an unbranched, 6-m-tall cardon for the northernmost site (Percebú, 31° N) and southernmost site (Mangle, 23° N). (c) Mean monthly temperatures and (d) mean monthly rainfall in Percebú and Mangle (CONAGUA, 2010).

Table 2

Summary statistics for linear regression for the scaling coefficient *k*, mean diameter of adult plants, and mean plant height when the first branch is produced against environmental variables. Correlations significant at the 5% level are marked in italics, while correlations significant at the 1% level are marked in bold type.

	k	Mean diameter of adult plants	Plant height at first branching
Average maximum temperature (°C)	−0.79	−0.63	−0.42
Average minimum temperature (°C)	−0.10	0.22	0.37
Average temperature (°C)	−0.53	−0.26	−0.08
Maximum height of the cardons (m)	0.61	0.74	0.76
Density (cardons/ha)	−0.44	−0.46	−0.45
Distance to the Pacific Ocean (km)	0.77	*0.89*	*0.90*
Distance to the Gulf of California (km)	−0.72	*−0.81*	*−0.83*
Latitude	***0.95***	***0.92***	***0.85***
Precipitation (mm)	−0.89	−0.79	−0.73
Number of rainy days	***−0.99***	***−0.91***	*−0.82*
Water per capita (m³/individual)	−0.55	−0.50	−0.43
Summer rainfall (June to October) (mm)	*−0.86*	−0.74	−0.66
Winter rainfall (November to May) (mm)	−0.40	−0.61	−0.69

low temperatures predominate, but receive more radiation during the remaining months (March to September) characterized by higher temperatures (Fig. 5c). Cardons in the Cape Region have less variation in the amount of intercepted solar radiation throughout the year by being within the tropics and also face less variation in temperature along the year while receiving more precipitation, especially during summer (Fig. 5d).

4. Discussion

The diameter of adult plants, the height of plants when branching is triggered, and their surface area:volume ratio are all strongly associated to environmental variables that vary with latitude (precipitation, number of rainy days, or summer precipitation). The latitudinal trend in the diameter-to-height allometry in *P. pringlei* is similar to that reported for *Pachycereus schottii* and *Cephalocereus columna-trajani*: plants in tropical sites with higher precipitation and temperature are relatively slender compared to those found in higher latitudes with less precipitation and lower temperatures (Felger and Lowe, 1967; Valverde et al., 2007).

The Colorado Desert in the northernmost range of *P. pringlei* has a much higher variation in its temperature than the tropical dry-lands of the Cape Region. It is a hyper-arid, harsh environment with little nurse-plant shade, and where cactus establishment needs anomalously high rainfall, a fact that might explain the large gap in the distribution of plant heights. In winter it can reach freezing temperatures at dawn, while in summer it can reach 48 °C during the day. But because of their extratropical location of cardons near its northern limit, the columnar architecture intercepts less solar radiation in winter, compared to the tropical populations of the south, at a time when warming the plant's tissues would be advantageous. The results of our solar radiation model confirm those of Nobel's (1980a, b) biophysical simulations for saguaro, which indicated that an increase in stem diameter could raise the minimum apical temperature more than 3 °C by enhancing the stem's thermal inertia, and also support the tenets of Felger and Lowe (1967) who concluded that in the Sonoran Desert "the greater nocturnal thermal lag associated with the larger stem mass provides a decided low temperature selective advantage" for giant columnar cacti like the saguaro.

The plant's height when branching begins increases with latitude. Drezner (2014) reported that, for saguaros in Arizona branching not only increases the plant's photosynthetic surface but also its reproductive potential, because new branches offer more reproductive meristems in the branches' areoles for flowering. Under this assumption, the northern populations of *P. pringlei* seem to invest energy resources into the vegetative structure of the trunk rather than into reproduction for a longer part of the plant's life history compared to southern populations. In our study we only estimated the height of the main shoot at the point when plants begin to branch, that is, the ontogenetic triggering of branch development, but we did not quantify the height of the lateral areoles from where branches are produced from the main shoot. This aspect of cactus development, however, has been well studied by Cornejo and Simpson (1997), and by Cody (1984, 2002). Although branching patterns are at least in part phyletically determined, their studies report that, as a general rule, in hot tropical environments such as thorn forests, branching is acrotonous, that is, it tends to occur in the upper part of the stems giving the plants a tree-like appearance, while in the drier, middle-latitude deserts branching tends to be mesotonous or even basitonous, i.e., branches tend to develop from the lower parts of the stem giving the plants a shrub-like appearance. Although we did not measure the height of branch insertion, the pattern described by these authors was clearly visible along our latitudinal gradient: cardons in the northern part of the distribution branch from the lower part of the stem, while those in the south branch from the center or even the upper part of the stem (Fig. 6).

Finally, it is interesting to note that the height-to-diameter pattern we report in this study seems also to occur in other groups. In a recent revision of the worldwide occurrence of sarcocaulescence (i.e., dryland plants with giant fleshy stems) Ávila-Lovera and Ezcurra (2016) report a trend of increasing diversity of fleshy-stemmed trees in Baja California from the tropical thorn forests of the Cape Region into the sarcocaulescent scrubs of the central and northern deserts of the peninsula. Similarly, Felger and
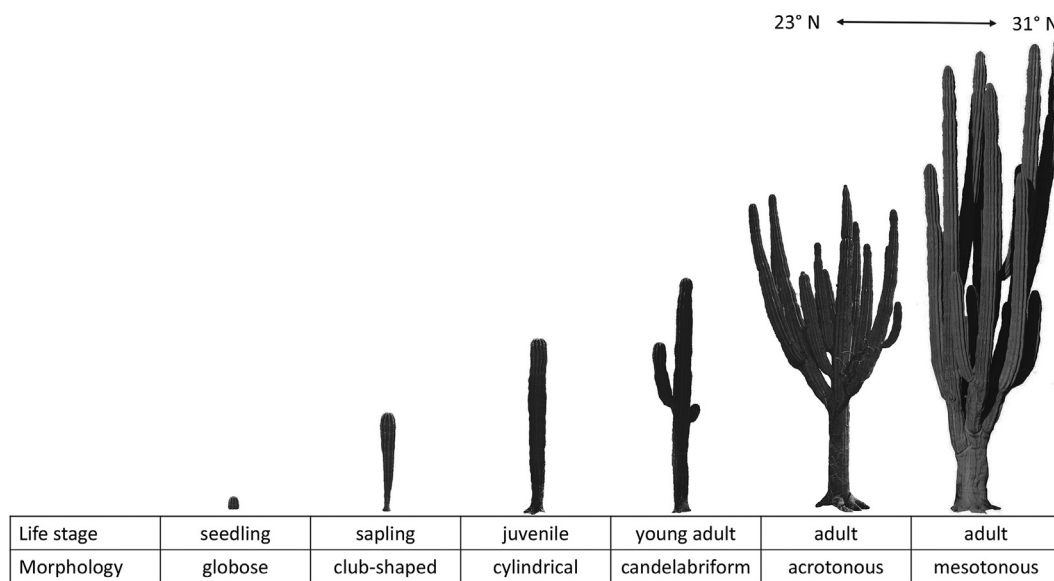

Life stage	seedling	sapling	juvenile	young adult	adult	adult
Morphology	globose	club-shaped	cylindrical	candelabriform	acrotonous	mesotonous

Fig. 6. Morphologies of cardon along the plant's life stages. Morphologies during the first four stages are roughly similar throughout the latitudinal gradient. In large adults, however, differences imposed by latitude become apparent: Cardon plants in the tropical dry forests of Mangle (23° N) have thinner stems (ca. 35 cm in diameter) and an acrotonous branching pattern, while plants in the hyper-arid Lower Colorado Desert at Percebú (31° N) show robust stems (ca. 50 cm diameter) and mesotonous branching.

Joyal (1999) note that palms in Baja California show a similar trend: the northernmost species *Brahea armata* and *Washingtonia filifera* have stout, thicker trunks and dull-colored leaves compared to their southern Baja California congeners *Brahea brandegii* and *Washingtonia robusta*, which have more slender trunks and greener leaf blades, and suggest that the pattern is an adaptation to aridity and/or winter freezing. An attractive next step in the understanding of morphological traits in columnar cacti along large-scale biogeographic gradients is to study variation in color of the cardon along the latitudinal gradient where it is distributed and see whether it follows the same pattern described for palms.

We conclude that as cardon cacti shift from the dry tropics into the extremely arid mid-latitude deserts of the Baja California peninsula the plants become substantially more robust and delay branching maintaining thick monopodial stems until they reach 6 m or more in height. The surface area:volume ratio at any plant size decreases from the wetter tropics into the arid mid-latitude deserts. Massive trunks and low area:volume ratios give the plants a high thermal inertia, which seems to play a crucial role in cactus survival at the northern edge of their distribution.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2017.07.004.

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