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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.

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)

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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).