# Factors affecting the distribution of columnar cactus (*Stenocereus aragonii*) in a tropical dry forest

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*Abstract:* Several plant families have evolved Crassulacean acid metabolism (CAM) as a strategy for avoiding dessication and improving water use efficiency. This physiological pathway enables CAM plants to thrive in high light, low moisture environments. We tested the hypothesis that the distribution of *Stenocereus aragonii*, a CAM species in tropical dry forests, would depend upon light availability and soil moisture. We found that *S. aragonii* was located preferentially in dry, open areas with rocky soil. We attribute this distribution largely to the cacti's use of the CAM pathway, which enables it to survive in otherwise uninhabitable sites. In this way, the CAM pathway contributes to overall diversity in tropical forests.

*Key Words: Cactaceae, CAM,* Lemaireocereus aragonii

## Introduction

In tropical dry forests, there is constant competition among plants for resources, especially water. Several plant species have evolved metabolic adaptations to avoid desiccation and improve water use efficiency. One of these adaptations is the Crassulacean acid metabolism (CAM) pathway, which enables plants to fix carbon during the night to an intermediate form and transform this compound to glucose during the day. By opening stomata only at night when temperatures are lower, CAM plants minimize their water loss to evapotranspiration. However, with this adaptation comes tradeoffs: CAM plants are inefficient photosynthesizers at low light levels due to their high light compensation point (Begon et al. 1990). The ability of CAM plants to conserve water, together with their high light requirement, should make them particularly well suited to open areas within tropical dry forests.

*Stenocereus aragonii* (formerly *Lemaireocereus aragonii*), a member of the Cactaceae family, utilizes the CAM pathway (Hopkins 1995). Therefore, we hypothesized that its distribution would be dependent upon microhabitat light and moisture conditions. We predicted that this species would be more common in areas of low soil moisture and high light intensity. We further predicted that cacti would occur where water availability and vegetation density are low, such as along rocky ridges.

## Methods

The research was conducted 11 - 12 January 2002 in Palo Verde National Park, Guanacaste Province, Costa Rica. We used the Guayacan Trail near the OTS field station as a transect and surveyed all cacti within 25 m on either side of the trail. For each individual, we recorded height, canopy cover, substrate type, soil moisture and basal area of trees in the immediate vicinity. A spherical densiometer was used to estimate the percent canopy cover directly over each cactus. Substrate type was classified as rock, thin layer of soil over rock (<10 cm) or deep soil (>10 cm) and moisture was measured with a soil moisture meter for the latter two categories as a percent of saturation. The basal area of trees in the immediate vicinity of cacti was estimated using an English BAF 10X prism at several points around the perimeter of each cacti patch and the mean value was assigned to all individual cacti within that patch.

We compared sites where cacti occurred to 32 sites not occupied by cacti along the same trail. For the latter, we stopped every 50 m along the transect and walked a random distance 0 - 25 m perpendicular to the trail. At each of these points, we measured canopy cover, basal area of surrounding trees, substrate type and soil moisture. These unoccupied sites are hereafter referred to as control sites.

Differences in substrate type between cacti and control were tested with chi-square. We evaluated correlations among the factors we hypothesized would affect cactus distribution: soil moisture, canopy cover and basal area, using data from all sites. We then developed one-, two- and three-parameter logistic regression models predicting cactus presence with the factors soil moisture, canopy cover and basal area.

## Results

Cacti were found more frequently than random on thin soil covering rock and on bare rock and less frequently than random on deeper soil ($\chi^2 = 76.3$, df = 2, $P < 0.001$). Positive correlations were found among soil moisture, canopy cover and basal area at all sites sampled (Table 1). Among the logistic regression models we developed (Table 2), the best one-parameter model was soil moisture ($r^2 = 0.37$). The two-parameter regressions incorporating soil moisture and either canopy cover ($r^2 = 0.42$) or basal area ($r^2 = 0.41$) explained more variation and both parameters were significant. Adding a third parameter explained only slightly more variation ($r^2 = 0.44$) and basal area was only marginally significant in the model. Therefore, we concluded that the two-parameter models incorporating soil moisture and either canopy cover or basal area were superior to the other models as the best and most parsimonious predictors of cactus presence.

## Discussion

As predicted, the distribution of

TABLE 1. Correlation matrix among environmental variables hypothesized to affect cactus distribution.

| | Soil Moisture | Canopy Cover | Basal Area |
|---|---|---|---|
| Soil moisture | -- | 0.45 | 0.41 |
| Canopy cover | -- | -- | 0.34 |
| Basal area | -- | -- | -- |

TABLE 2. Logistic regression models predicting cactus presence and incorporating one, two, or three parameters. P values indicate whether each parameter had a significant effect in the model.

| Model parameters | $r^2$ | $X^2$ | P value soil moisture | P value canopy cover | P value basal area |
|---|---|---|---|---|---|
| Soil moisture | 0.37 | 58.68 | 0.01 | -- | -- |
| Canopy cover | 0.23 | 36.85 | -- | < 0.0001 | -- |
| Basal area | 0.15 | 23.19 | -- | -- | 0.0001 |
| Soil moisture & canopy cover | 0.42 | 66.25 | 0.03 | 0.009 | -- |
| Soil moisture & basal area | 0.41 | 64.11 | 0.01 | -- | 0.02 |
| Basal area & canopy cover | 0.30 | 47.72 | -- | < 0.0001 | 0.003 |
| Soil moisture, canopy cover & basal area | 0.44 | 69.62 | 0.03 | 0.02 | 0.07 |

*Stenocereus aragonii* was significantly related to substrate type, soil moisture, canopy cover and the basal area of surrounding trees. Sites where *S. aragonii* was found were rockier, drier, more open and had fewer and/or smaller surrounding trees than control sites along our transect.

The distribution of *S. aragonii*, however, did not seem to be dependent on any individual site characteristic, but rather on a suite of related characteristics. The two models that best predicted cactus presence were those including (1) soil moisture - canopy cover and (2) soil moisture - basal area. Based on this result we might expect that basal area of surrounding trees and canopy cover would be highly correlated, but this is not the case ($r = 0.34$). Also, in the three-parameter model, canopy cover was significant and basal area was marginally significant. It appears that these two parameters are measuring slightly different aspects of a site and are both valuable for predicting cactus presence. Canopy cover is a more direct indicator of sunlight reaching the cactus, which could explain its higher significance level over basal area.

The non-random distribution of *S. aragonii* that we observed supports a theoretical distribution based on the benefits and limitations of the CAM pathway. *S. aragonii*, owing to adaptations that include its specialized metabolism, is able to grow in areas that seem to be relatively uninhabitable by most other plants (pers. obs.). Physiological specializations in plants allow for increased habitat partitioning and help to explain the high diversity of plant species in Neotropical forests.

## Literature Cited

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