Factors influencing growth of *Lemaireocereus aragonii (Cactaceae)* in a deciduous dry forest

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Abstract. We compared vertical extension growth of *Lemaireocereus aragonii* from 1989-1998 to annual climatic data for Palo Verde National Park, Costa Rica. We hypothesized that annual rainfall would correlate positively with growth. We also predicted that cacti in deeper soils, and with higher light exposure, would have greater extension growth. However, we found no significant relationship between growth and annual rainfall. Low light resulted in decreased growth. Cacti on bare rock reached maximum growth rates at intermediate light availability, possibly due to water limitation on limestone substrate in high light. In contrast, plants rooted in soil reached maximum growth at high light levels.

Key Words: extension growth, cactus, Palo Verde

INTRODUCTION

Lemaireocereus aragonii, a columnar cactus in the deciduous dry forests of Palo Verde, is found mostly on steep limestone cliffs with poor soils, in high light. *L. aragonii* has CAM photosynthesis, which allows it to grow better in conditions of lower water availability than C_3 plants, provided light availability is high. This cactus stores water during the wet season, growing almost exclusively during the dry season when exposure to sunlight is high because of a lack of canopy cover. During the wet season, when *L. aragonii* grows little, each stem deposits a waxy coating at the meristem, which accumulates as annual rings around the stem. These waxy growth bands can be used to measure annual extension growth (Buskirk and Otis, 1994).

We hypothesized that growth rate would increase with annual precipitation. We also predicted that growth rates would be higher for cacti in areas of high light availability and those rooted in soil, which retains more moisture than bare rock.

METHODS

Sites were ca. 1 km north of the OTS field station at Palo Verde, Costa Rica. We measured annual extension growth on all *L. aragonii* individuals within 100 m of the Mirador Guyacan and on the limestone outcroppings within 200 m of the Sendero Mapache trail, that met the following criteria. 1) 0.5-2.75 meters in total height with a clearly dominant leader (i.e., the main stem was more than 5 times the length of any of the secondary branches), 2) stem damage (i.e., browning, scarring, and/or deep constrictions on the stem) was <10%.

Annual extension growth for the period 1989-1998 was measured as the distance between successive waxy annual bands. For each individual, we summed the extension growth for all 10 years, and calculated the percentage of this total for each year. This percent growth was used in the data analysis in order to group cacti for mean comparisons. We recorded total height and minimum age, measured as the total number of distinct intervals between bands. Substrate type was classified as either bare rock, or rock with a thin layer of soil. Light availability was classified as "full" (exposure throughout the day), "intermediate" due to shading from rock and vegetation (excluding foliage because trees ae deciduous during the cactius growing season), or "low" (complete shading for at least a third of the day). We compared these data with climatic data from Estacion La Guinea, Filadelfia, approximately 25 km west of the field station.

RESULTS

Although there appeared to be an inverse relationship between the total annual precipitation in the Guanacaste region and the annual mean percent growth of the *L. aragonii* individuals (Fig. 1), the trend was not significant (r^2=0.24, df=5, P=0.33).

Mean growth over the entire 10-year period increased significantly with light availability (Fig. 2, ANOVA, F=7.88, df=2,37, P=0.001). Substrate differences had no significant effect (ANOVA, F=2.94, df=1,37, P=0.094). However, the interaction between light availability and substrate did affect cactus growth (Fig. 2,

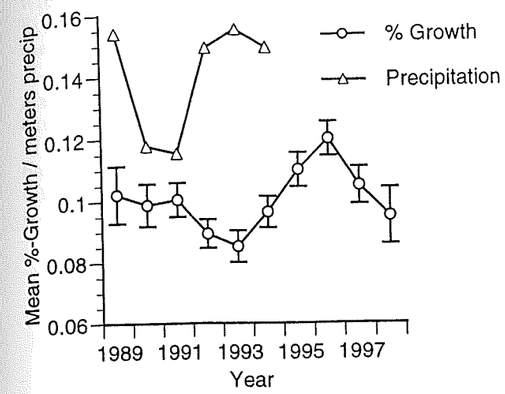

Fig. 1. A comparison of annual mean percent growth of *L. aragonii* at Palo Verde, Costa Rica with annual precipitation data (Mean ± SE) for a nearby weather station (see text). For each individual, we summed the extension growth for all 10 years, and calculated the percentage of this total for each year. No climate data were available for 1995-1998.

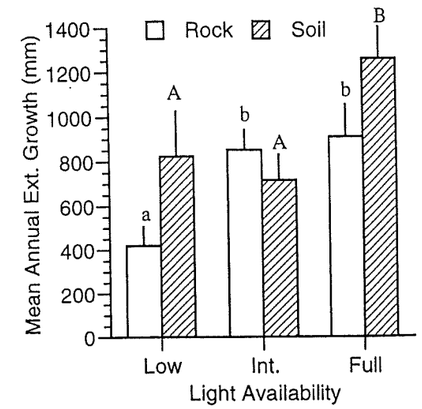

Fig. 2. Mean annual extension growths for 1989-1998 in *L. aragonii* as a function of light availability for two substrate types at Palo Verde, Costa Rica. Different letters indicate significant differences within substrate (rock or soil).

ANOVA, F=3.31, df=2,37, P=0.047). Growth rates for cacti on rock were lowest at low light levels, but growth at intermediate and high light levels were similar. Individuals in soil had similar growth rates at low and intermediate light levels, but the rates increased at high light levels.

DISCUSSION

In contrast to expectations, there was no correspondence between the precipitation data and *L. aragonii* growth. Total rainfall may not be the main factor determining yearly cactus growth. A longer period of climate data could reveal a pattern, but other factors, such as dry season length, may be more important than precipitation.

As hypothesized, individuals had significantly higher growth over 10 years in locations of higher light availability. CAM photosynthetic plants have a high light compensation point, being inefficient at lower light levels (Begon *et al.*, 1990). Contrary to our hypothesis, cacti in soil did not have a significantly higher growth rate than those growing on bare rock, (although the means did differ in the predicted direction, P=.094). Cacti in soil probably have higher water availability, tending to increase growth, but they may also experience increased competition, due to greater plant biomass on soil than on bare rock.

Growth rates for cacti on rock may level out at intermediate light levels because low water and nutrient availability in rocky habitats limit growth, even with high light exposure. These limitations may not be as severe in soil substrates, allowing growth rates to increase up to the highest light levels.

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