DENSITY-DEPENDENT GROWTH OF THE COLUMNAR CACTUS, *LEMAIREOCEREUS ARAGONII*

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Abstract: Intraspecific competition for resources often results in density-dependent growth. The columnar cactus *Lemaireocereus aragonii* has waxy rings that can be used to determine annual growth rate. We examined the effects of plant density on cactus growth rates. Cactus growth rate decreased with increasing cactus density in the presence of woody plants but was unrelated to cactus density when woody plants were absent. Elevation was unrelated to cactus growth rate. Further studies are needed to understand how density-dependence of growth translates into demographic effects on fecundity and survival.

Key words: Palo Verde, waxy growth rings

INTRODUCTION

Density-dependent growth in plants occurs when resources are limited. At high densities, individuals must share resources, and thus a smaller amount of a given resource is available to each individual. Competition for resources may affect growth rate, development, and reproduction (Begon et al. 1990). In this study we investigated the effects of varying conspecific and woody plant densities on the growth rate of the columnar cactus *Lemaireocereus aragonii.*

L. aragonii grows in the deciduous dry forests of Costa Rica, usually on steep limestone cliffs and outcroppings. *L. aragonii* grows primarily during the dry season when light availability is high, using internally stored water from the wet season. A waxy coating is deposited at the plant's meristem during the wet season, forming rings that can be used to measure annual extension growth of the cacti over time (Buskirk and Otis 1994).

These cacti and other woody plants growing on rocky outcroppings might compete for limited resources such as space, nutrients, and water. If so, the growth of *L. aragonii* would be negatively related to the neighborhood density of competitors, including conspecifics and woody plants.

METHODS

On 13 - 14 January 2004, we collected data on *L. aragonii* near the OTS field station in Palo Verde National Park, Guanacaste, Costa Rica. We sampled five discrete populations of cacti that were each located on different limestone outcroppings (about 5 - 250 m^2 each). Sample sites were located at the north end of the Sendero Mapache, as well as along the trail to the Mirador Guayacan west of the Sendero El Cactus.

For each cactus plant, we measured the number, height, and diameter of cactus stalks, the distance between each of the five most recent growth rings, altitude, the categorical presence or absence of woody plants (> 1 cm in diameter) within a 1 m radius, and the number of other cacti growing within a 1 m radius. We calculated the annual growth rate over the last five years by averaging the height of the five most recent growth rings. Because the condition of growth rings varied from cactus to cactus (the oldest having faded beyond recognition), we collected growth data only from cacti that had the five most recent rings visible enough to measure accurately. We measured cacti < 3 m in height that had at least five rings visible. Cacti with > 10% surface area damaged (i.e. brown, mottled, rotten, or scarred sections) were ex-

cluded from our study.

We log-transformed average annual growth to improve normality and homoscedasticity, and then used linear regression to model the relationship between cactus growth rate and cactus density in the presence and absence of woody plants. We also evaluated all possible regression models that included elevation.

RESULTS

Cactus growth rate decreased with increasing cactus density in the presence of woody plants ($F_{1, 24} = 6.33$, $P = 0.02$), but was unrelated to cactus density when woody plants were absent ($F_{1, 31} = 0.00$, $P = 0.96$; Fig. 1). Elevation was unrelated to cactus growth rate (or the residuals of cactus growth rate as a function of cactus density) in the presence or absence of woody plants ($P > 0.40$ for effects of elevation in all possible regression models).

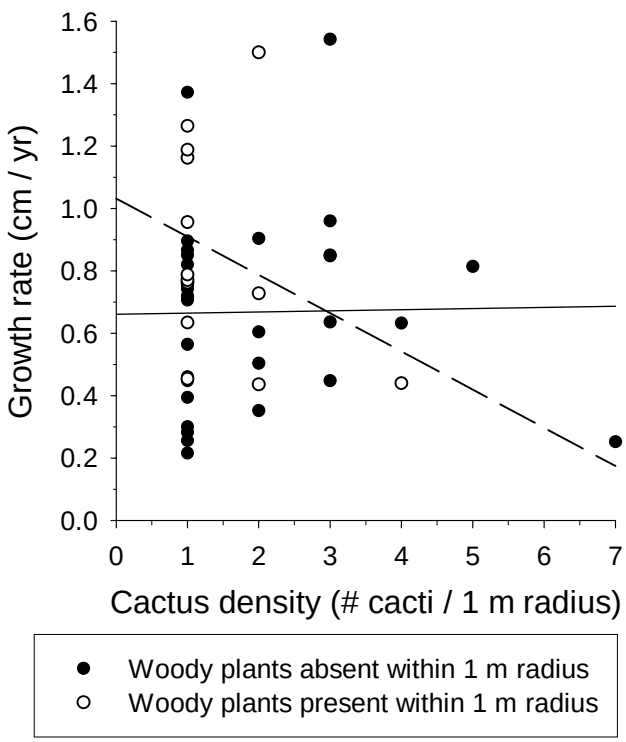

Figure 1. Relationship between cactus density and growth rate in the presence and absence of woody plants. Solid line = regression with woody plants absent; dashed line = regression with woody plants present. Cactus growth rate decreased with increasing density of conspecifics in the presence of woody plants ($y = 1.03 - 0.12x$, $r^2 = 0.10$) but not in the absence of woody plants.

DISCUSSION

Cactus growth rate was negatively density-dependent as predicted if there is resource limitation, but only in the presence of woody plants. In the absence of trees, cactus density may not be high enough for density dependent growth to occur. Although we did not quantify dispersion, the cacti appeared to be uniformly dispersed, so perhaps this spacing is sufficient to preclude resource limitation. The fact that density-dependence only emerged in the presence of woody plants suggests that woody plants are depleting one or more of the resources that can be limiting for cacti (perhaps water, nitrogen, or phosphorus).

Although we measured growth rate of *L. aragonii* as an indicator of density dependence, the ultimate effects of competition are on fecundity and survivorship (Begon, et al. 1990). There may be additional effects of density on cacti that are not apparent through our study. Long-term demographic studies could look at the fecundity and survivorship of cacti to further test for density-dependent effects on *L. aragonii*.

LITERATURE CITED

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