

Spatial Relationships and Competition in a Chilean Desert Cactus

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Summary. In the Atacama Desert of northern Chile, cacti of the genus *Copiapoa* occur in extensive, relatively dense, monospecific stands. The spatial distribution patterns within several stands of *Copiapoa cinerea* v. *columna-alba* were analyzed for evidence of competitive interactions among individuals. There was no indication that competition was affecting stand density. Mean annual precipitation is only 25 mm/yr, but estimates of maximum possible water use within a stand were much lower. It was shown that the time between rainstorms is long compared to the water storage capacity of the plant stems, especially in the case of small individuals. We conclude that population densities in *Copiapoa* are limited by the difficulty of establishment, not by competition.

Introduction

Plant distribution patterns in desert communities have been examined in several studies that attempted to demonstrate a relationship between regular spacing and competition for water among individuals (early work reviewed in Anderson, 1971; additional studies by Waisel, 1971; Moore and Bhadresa, 1978). Anderson questioned the evidence that such spacing was at all common and had anything to do with competition.

Yeaton and Cody (1976) analyzed competitive interactions within and among three succulent species in the Mohave Desert, using a method described by Pielou (1960) that is independent of the degree of randomness in the distribution pattern. Fonteyn and Mahall (1978) used an experimental water relations approach to demonstrate competition between two Mohave Desert shrub species.

In the world's driest deserts, plant communities of one or two species are typical. The evidence that water competition gives rise to regular spacing comes from such communities. Further, plants in these areas are typically widely spaced, regardless of pattern, and the factor or factors that limit stand density have yet to be demonstrated.

The Atacama Desert of northern Chile provided a unique opportunity to examine these questions. There, species of cactus in the genus *Copiapoa* occur extensively as pure stands of apparently uniform density (Fig. 1). Individuals are clearly discrete, and sizes of the cylindrical single or double stems could be readily measured. Rainfall in this region averages 25mm/yr, and rainless periods of several years' duration are common. Lack of water clearly constitutes the primary limit to plant growth.

In this study we used several models to examine the distribution patterns in stands of *Copiapoa cinerea* (Phil.) Br. & R. v. *columna-alba* (Ritt.) Backbg for evidence that competition among individuals for a finite resource was limiting the densities of these stands.

Materials and Methods

The study area was located at Pan de Azucar, latitude 26°15'S, about 1.5 km from the coast. Three stands were analyzed by staking a plot in each stand (Plots 1, 2, 3). The plots were 56, 49, and 49 m², respectively. Height and distance to nearest neighbor were recorded for every plant in the plot. Plants were divided into three height classes; where the nearest neighbor was of a lower ranking height class, distances to successive neighbors were measured until a neighbor of the same height class was noted. This enabled us to examine patterns obtained by eliminating smaller individuals from the sample. In Plot 1 dead individuals were also noted when they occurred as nearest neighbors.

A fourth stand (called Stand 4) was sampled by throwing 1 m² quadrats at 4 m intervals and counting all live and dead individuals. Heights and diameters of live plants were recorded.

The roots of 9 plants of different sizes were excavated and mapped to determine the relationship between plant size and the horizontal extent of root area.

Results

Patterning

Plant-to-neighbor distances in Plots 1, 2 and 3 were analyzed according to a method described in Pielou (1960) (see also Morisita, 1954). In a randomly distributed population, the frequency distribution of the plant-to-neighbor distances, r , is defined by the function $2\lambda re^{-\lambda r^2}$, where λ is the mean number of plants per circle of unit radius. The plant-to-neighbor distances measured are divided into distance classes, and the above function is integrated to determine the expected frequency of neighbor pairs in each class. The actual frequencies are then tested against a chi square distribution. An excess of very short and very long plant-to-neighbor distances indicates a clumped distribution, and an excess of middle distances indicates overdispersion.

The first analyses were based on all the plants in each of the three plots. Subsequent analyses excluded first the smallest height class and then the smallest and middle height classes (Ta-

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Fig. 1. A typical stand of *Copiapoa* at Pan de Azucar

Table 1. Degree of dispersion of plants of different size classes in three stands of *Copiapoa*

Plot	All plants	Plants > 4 cm	Plants > 10 cm
1	Random	Random	Random
2	Clumped ($P < 0.005$)	Random	Clumped ($P < 0.025$)
3	Clumped ($P < 0.01$)	Random	Random

ble 1). There was no indication of overdispersion in any of the plots or among the larger individuals. Some of the distributions were clumped, but there was no tendency for distributions to become less clumped when smaller (presumably younger) plants were excluded from the data.

Even in a clumped or random distribution, very short plant-to-neighbor distances may be precluded by the potential for competition between such closely spaced individuals. To determine whether competition was preventing the occurrence of very close neighbors in *Copiapoa* stands, Plots 1 and 3 were analyzed using truncated distributions of plant-to-neighbor distances as described by Pielou (1962). In this method, only the shorter interplant distances are tallied and compared to an expected truncated distribution generated from the mean of the squares of plant-to-neighbor distances. A paucity of very short distances indicates that plants separated by less than some minimum distance cannot persist.

In Plot 1, interplant distances over 35 cm were eliminated, and in Plot 3 the upper bound was 30 cm. In neither case did the truncated distributions differ from the expected distributions. That is, the number of individuals 10 to 20 cm apart was no less than expected, given the population densities.

A third method of assessing the presence of competition among individuals using distance sampling is based on the assumption that plants growing close together have less of the resources available to each, such that the sum of the sizes of neighboring plants

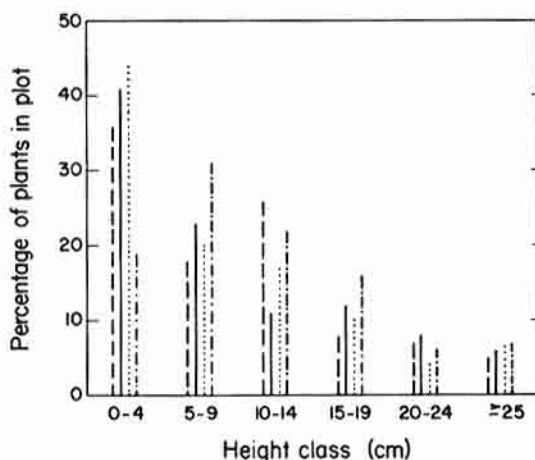


Fig. 2. Height class distributions of individuals in the four stands sampled. Plot 1 (---); Plot 2 (—); Plot 3 (···), Stand 4 (-·-)

should be inversely correlated to the distance between them (Pielou, 1960; Yeaton and Cody, 1976; Yeaton, 1978). Using the sum of the heights of nearest neighbors, we computed the correlation with distance between them for Plots 1, 2, and 3. In all cases, the correlation coefficients were very close to zero (< 0.05), indicating no competition effect on height growth. In Plots 2 and 3 we repeated these computations, using only nearest neighbors closer than 40 cm and 30 cm, respectively, on the assumption that far apart individuals were not contributing to competitive interactions. Again, the correlation coefficients were close to zero.

If competition was limiting stand density, smaller individuals would be expected to have suffered most severely. Even if death was random among individuals, mortality in smaller plants should be discernible, since these were most common in the stand (cf. Fig. 2). In Plot 1, 14 of 100 nearest neighbors were dead plants. In Stand 4, 135 individuals were counted, of which 34 were dead. In all cases these were large, not small, stems.

In the second part of the study, we evaluated water use on a per area basis by all plants within the plot boundaries. This represented maximal resource use by the population, since plots were located in areas of high plant density.

The distributions of individual heights were similar in the three plots and the quadrat-sampled stand (Fig. 2). There was a preponderance of small individuals, and frequencies declined as height increased. The first two of six height classes included over 50% of the plants, and one third were less than 4 cm tall.

The horizontal root extension of individual plants was determined by excavating and mapping the roots of nine plants of different sizes (Fig. 3). *Copiapoa* is a typically shallow-rooted stem succulent; none of the roots exceeded 8 cm in depth. To compute total root area we used the maximum radius of root extension in each compass quadrant to determine the root area of that quadrant and then summed the four quadrant areas. Horizontal root area was approximately linearly related to plant height (Fig. 4).

Using the above plant height-to-root-area relationship and the plant densities weighted by the height class distributions, we calculated the horizontal root area per unit of ground surface area for each of the sampled stands (Table 2). This ratio was near to or greater than 1 in all cases, indicating that the soil area at shallow depth was potentially completely exploited.

To compute maximum potential water use within a plot we used the stem heights and diameters recorded from Stand 4 to specify a stem height-to-diameter relationship (Fig. 5). Using this function, the cactus densities weighted by height class distributions, and the fact that the growth form of *Copiapoa* is closely approximated by a cylinder, we computed cactus stem surface area and volume per unit area of ground surface.

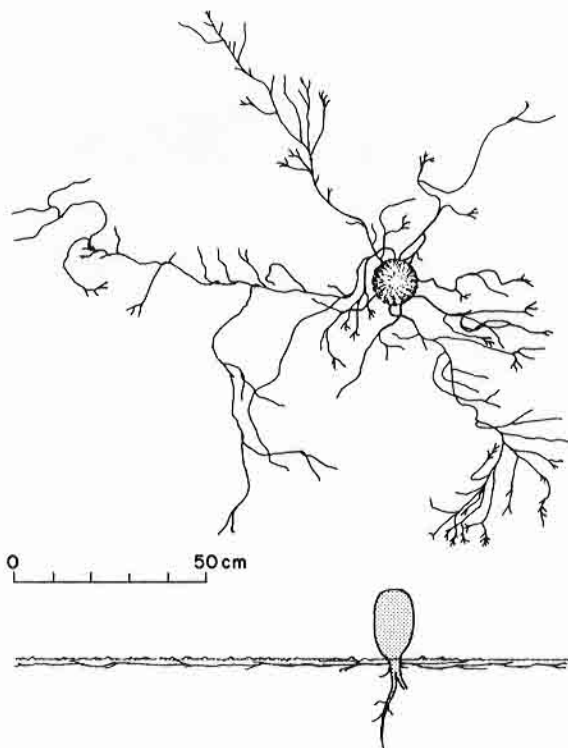


Fig. 3. Scaled drawing of the root system of a *Copiapoa*. The roots of this individual were within 3 cm of the surface

In the ensuing series of calculations, only Plot 1 is presented, since all the plots had similar densities and size class distributions. In Plot 1 there were 0.0459 m² of stem surface and 1.04 l of stem volume per m² ground surface. Based on the following set of assumptions: minimum surface resistance to water transport of 5 s cm⁻¹ and boundary layer resistance of 1.5 s cm⁻¹ (Kluge and Ting, 1970), night temperature of 15° (high estimate), night relative humidity ranging from 80% to 50%, and 10 hr of nightly

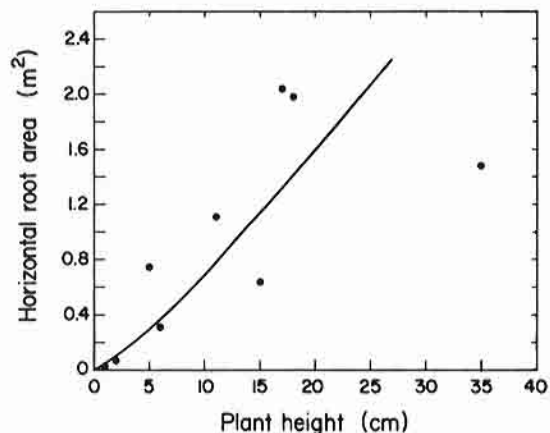


Fig. 4. Relationship between stem height and horizontal root area. Fitted curve is $Y = 0.0446 X^{1.19}$

Table 2. Density of individuals and ratio of horizontal root area to ground area in *Copiapoa*

Plot	Plant density (m ⁻²)	Root surface area
		Ground surface area
1	1.79	1.25
2	1.35	0.93
3	2.29	1.45
4	1.94	1.63

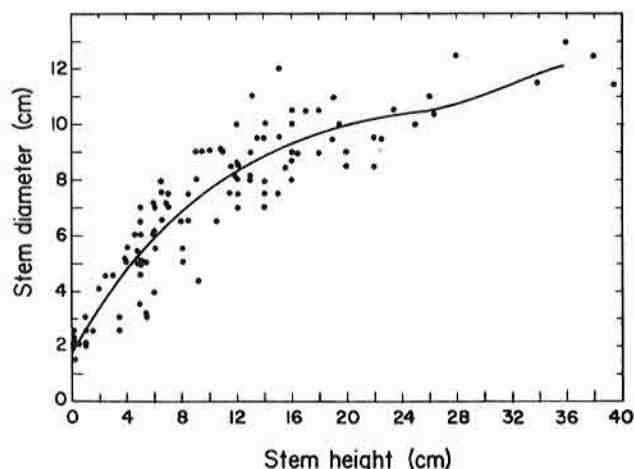


Fig. 5. Allometric relationship between stem height and stem diameter. Coefficients of the polynomial regression, from 0th order, are 1.78557, 0.850378, 0.0300861, 4.0073×10^{-4}

transpiration, maximum yearly water use in Plot 1 would be 2.4 to 6.0 l m⁻² yr⁻¹. Input from rainfall at 25 mm yr⁻¹ is 25 l m⁻² yr⁻¹.

Discussion and Conclusions

Our initial hypothesis was that competition among individuals for water was limiting the density of stands of *Copiapoa*, and that this competition would be demonstrable from plant-spacing pattern analysis. We used methods formulated to detect plant interaction effects on spacing even if the overall distribution of plant centers appeared random. All the results clearly indicated no putative competition effects on plant distribution.

That the ratio of horizontal root area to ground surface area exceeded 1.0 suggested that the plants could have saturated the available water uptake space. However, this assumes that the roots were uniformly distributed, and we do not know if this was the case. Also, the existing root mats were not densely branched (see Fig. 3).

The input of rainfall greatly exceeded the maximum potential water use within even the densest stands of cacti. However, since rainfall episodes are separated by rainless periods of up to six years' duration, water supply is clearly contingent on long-term storage in the plant stems. In Plot 1, the total stem volume of 1.04 l m⁻² is insufficient to store more than a small fraction of the water from a single storm. Available water from soil storage is unlikely, since the cacti are shallow rooted. Given this water storage limitation, a considerable degree of root overlap could be tolerated without any competition for moisture.

We estimated water use by assuming maximum nightly transpiration throughout the year. A cactus stem 22 cm tall that contained 80% water by volume could sustain these rates for 143 days, a 7 cm cactus for 90 days, and a 2 cm cactus for only 48 days, before the stored water was exhausted. From these figures, three points are clear: 1) Stomatal resistance must usually be much higher, and yearly water use much lower, than the estimated values. 2) Larger individuals can maintain transpiration, and thus photosynthesis, for longer periods than small ones. 3) Very small plants would have great difficulty maintaining a positive carbon balance during the rainless interludes.

We suggest that difficulty of establishment under conditions of very infrequent rainfall, rather than competition for water, limits population densities in *Copiapoa*. Plants smaller than 1.5 to 2 cm in diameter were never observed, despite careful examination of the plots and quadrats. It would appear that this is a critical size below which survival between rainstorms is highly unlikely.

There are only a few reported examples of regular spacing in desert perennial vegetation (Beals, 1968; Barbour, 1969; Woodell et al., 1969; Waisel, 1971; Fonteyn and Mahall, 1978; Moore and Bhadresa, 1978). Of these, three are based on *Larrea tri-*

dentata, and two on species of *Zygophyllum* in Israel. Most desert perennials form random or contagious distributions (e.g., Gulmon and Mooney, 1977). This prevailing pattern, in conjunction with our data, suggests that in the simple plant communities of the driest deserts, the primary selective force is not competition for available water, but survival during waterless periods.

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