

Orientation and its Consequences for *Copiapoa* (Cactaceae) in the Atacama Desert

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Summary. Three species of the barrel cactus *Copiapoa* (*C. cinerea*, *C. columna-alba*, *C. haseltoniana*) were investigated in their native habitats along the cool, arid coastal regions of the Atacama Desert in northern Chile. All species orient towards the north with a high degree of precision. Two consequences of adaptive value result from this northerly orientation. First, tissue temperatures of the meristematic and floral regions on the tip of the cactus receive high solar radiation loads which result in high temperatures (30°–40° C) relative to air temperatures (15°–20°) during winter and spring months when adequate soil moisture for growth is available. Second, absorption of solar radiation by the sides of the cactus is minimized, which reduces both the potential detrimental effects of light and heat load on the cactus and probably balances daily quanta absorbed for photosynthesis with nighttime CO₂ uptake rates during drought stress periods.

Introduction

The Atacama Desert of northern Chile is perhaps the driest desert in the world. Along the coastal plains and canyons which drain into the Pacific Ocean, the vegetation of this arid zone is dominated by succulents (Rundel 1976; Rundel and Mahu 1976; Rundel et al. 1979). Members of the genus *Copiapoa* (Cactaceae) are the principal succulents in this area. In certain parts of the Atacama Desert, species of *Copiapoa* form essentially monospecific stands (See Gulmon et al. 1980, for a stand photograph) and attain densities of 2 plants per square meter (Gulmon et al. 1979). *Copiapoa* are frequently found along the coast both below and above but not within the fog zone.

From casual observations, species of *Copiapoa* are intriguing because these barrel cacti appear to be orientated in a non-random fashion, generally facing north to the equator. Mooney et al. (1977) have made initial observations of this orientation and of cactus surface temperatures for *C. haseltoniana*. They reported that the range of cactus body orientations were within 30° of due north. A similar phenomenon occurs in plants found in the Sonoran Desert in North America. Here species of the barrel cactus *Fero-cactus* generally face south to the equator, although quantitative data are not available (Humphrey, 1936).

The purposes of this study were to first quantify the orientation

of species of *Copiapoa* in the Atacama Desert, second to measure the consequences of such an orientation, and third to determine the possible adaptive values of this phenomenon.

Methods and Materials

Species of *Copiapoa* were studied in their native habitat along the coast in northern Chile. Populations of *Copiapoa cinerea* Britton and Rose were sampled 10 km northeast of Paposo (longitude 70° 30' W, latitude 25° 5' S) and at Tal Tal (longitude 70° 34' W, latitude 25° 25' S), *C. columna-alba* Ritter (= *C. cinerea* v. *columna-alba* (Ritter) Backebg.) at Pan de Azucar (longitude 70° 37' W, latitude 25° 25' S), and *C. haseltoniana* Backebg. at Paposo. Measurements of azimuth and angle of the cactus body, length, and width were collected on 50 to 100 randomly chosen cacti at each site. Additionally, the absorptances to photosynthetically active radiation (400–700 nm) by different parts of the cactus body were measured using an Ulbricht integrating sphere (Ehleringer and Björkman 1978).

Detailed measurements of microclimate and cactus surface temperatures were measured on *C. columna-alba* at Pan de Azucar during September, 1978. Diurnal measurements of cactus surface temperatures were made by inserting 24 gauge copper-constantan thermocouples just below the epidermal surface. Thermocouples were placed under the surface in the four compass directions as well as on the base of the hairs on the top of the cactus. Solar radiation components were measured with a net radiometer, quantum sensor, and solar radiometer. Humidity was measured using an aspirated wet bulb psychrometer and wind speed with a cup anemometer.

Simulations of solar radiation absorption by *Copiapoa* were based on equations describing the path of solar radiation through the day and throughout the year from List (1968) and Gates (1963). Calculations of the solar quantum flux absorbed by the cactus assumed the cactus to be an octahedral cylinder with a top perpendicular to the sides of the cactus.

Results

Measurements on randomly selected individuals of *C. columna-alba* revealed a strong tendency for the body of the cactus to face north (Fig. 1). Out of a sample of 100 individuals, the orienta-

Table 1. Morphological characteristics of species of *Copiapoa*. The cactus body angle is the angle of the main axis of the body from the horizontal, the wax length is the length of the body from the tip covered with waxes, and the hair width is the width of the top surface diameter covered by wooly hairs. N is the sample size. Values are means and standard deviation

	Cactus angle (°)	Length (cm)	Wax length (cm)	Width (cm)	Hair width (cm)	N
<i>C. cinerea</i> -Paposo	44.6 ± 6.3	38.3 ± 14.5	6.3 ± 3.9	14.2 ± 2.4	6.4 ± 1.7	50
<i>C. cinerea</i> -Tal Tal	65.6 ± 8.6	30.6 ± 8.8	14.5 ± 4.7	12.9 ± 1.8	3.0 ± 1.0	50
<i>C. columna-alba</i>	51.9 ± 8.6	23.6 ± 9.0	5.0 ± 2.2	10.0 ± 1.4	3.6 ± 1.2	100
<i>C. haseltoniana</i>	42.1 ± 8.8	37.6 ± 9.3	10.9 ± 3.1	14.9 ± 2.3	6.2 ± 1.4	50

Table 2. Absorptances to solar radiation in the 400–700 nm waveband by various parts of the cactus surface for different species of *Copiapoa*. Measurements were made in the field on fresh tissues and are means of 5 samples. Units of solar absorptance are percent

	Absorptance (400–700 nm)		
	hairs	wax surface	glabrous surface
<i>C. cinerea</i> -Paposo	76.3	75.3	83.8
<i>C. cinerea</i> -Tal Tal	78.7	67.0	76.2
<i>C. columna-alba</i>	72.6	60.5	84.4
<i>C. haseltoniana</i>	69.7	65.5	80.3

tion of 93% of these individuals was within 20° of north. No individuals deviated more than 40° from north. A similar pattern was observed for the two populations of *C. cinerea* and for *C. haseltoniana*, although these data are not presented.

There are differences between the three species with respect to gross morphological characteristics (Table 1). Cactus body angles from species growing at elevations below the fog zone averaged 42.1° for *C. haseltoniana* and 51.9° for *C. columna-alba*. Above the fog zone the population of *C. cinerea* from Paposo had a mean body angle of 44.6°, while the population from Tal Tal had a value of 65.6°.

The species of *Copiapoa* range in length from a mean of 23.6 cm (*C. columna-alba*) to 38.3 cm (*C. cinerea*) (Table 1). A portion of the upper part of the cactus body is covered with a reflective waxy surface. The extent of this wax layer varies widely between populations. At Paposo, this wax layer covers only 16% of *C. cinerea*, whereas at Tal Tal this layer extends over 47% of the cactus surface. In *C. columna-alba* and *C. haseltoniana*, the waxy layer covers 21% and 29% of the surface, respectively.

The upper portion or top of the cactus is covered by the same waxy layer that appears on the cactus sides, except for the central meristematic region which is covered with hairs. This meristematic hair layer covers 23 to 45% of the body width depending on the species.

Measurements of absorptance to solar radiation between 400–700 nm were made on the various surfaces for each species. The waxy layer was consistently the most reflective (lowest absorptance) surface of the cactus in all species (Table 2). The glabrous sides of the cacti had the highest absorptance (76%–84%), while the hairs were of intermediate value between the glabrous and waxy surfaces.

The weather at Pan de Azucar during the measurement periods was typical of spring conditions. Mornings were frequently cloudy and overcast, with the cloud cover burning off by mid-day, before reforming in the late afternoon. Air temperatures fluctuated from a high of 18–20° C to an overnight low of 11–13° C. Relative

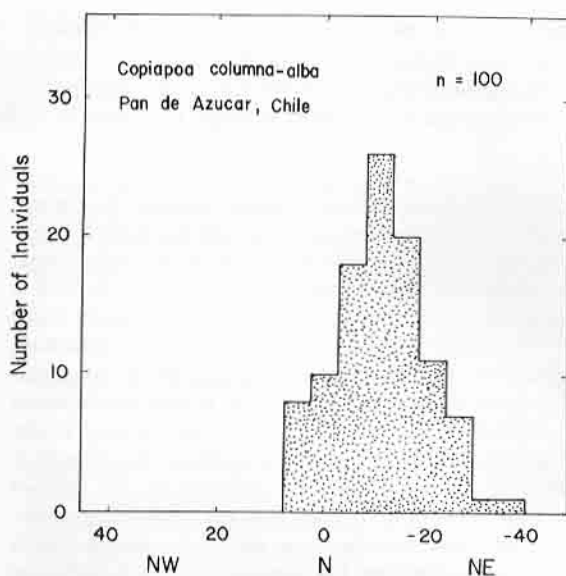


Fig. 1. Azimuth (direction) frequency histogram for orientation of *Copiapoa columna-alba* at Pan de Azucar, Chile

humidities typically varied between 80% and 95%. Diurnal measurements of air and cactus surface temperatures are presented for *C. columna-alba* at Pan de Azucar (Fig. 2). Air temperatures in this cool, coastal habitat ranged from 13.0°–19.9° C during the daylight hours. The temperatures of the meristematic hair region on the top of the cactus are by far the warmest temperatures of any part of the cactus. During most of the daylight hours, temperatures in this region were between 30°–40° C, some 15°–20° C above the air temperature. The sides of the cactus warm up above air temperatures also, but not nearly to the same extent as the meristematic region. The east facing side of the cactus peaks at 27.2° C in the morning, while the west facing side of the cactus peaks at 31.0° C in the afternoon. The south facing side of the cactus, like the top, peaks at midday.

Calculation of the solar quantum flux (400–700 nm) absorbed by different sides of the cactus were made using standard equations for the path and attenuation of sunlight during the course of a day (List 1968; Gates 1963) and the mean solar diffuse component measured on September 12, 1978. These calculations revealed a pattern of solar quanta absorption similar to the measured daily fluctuations in surface temperature for various sides of the cactus body (Fig. 3). The magnitudes of solar quantum flux on the sides of the cactus are also quite similar to observed deviations in cactus surface temperature from air temperature, and so it is likely that solar radiation is the principal component causing cactus temperatures to exceed air temperature.

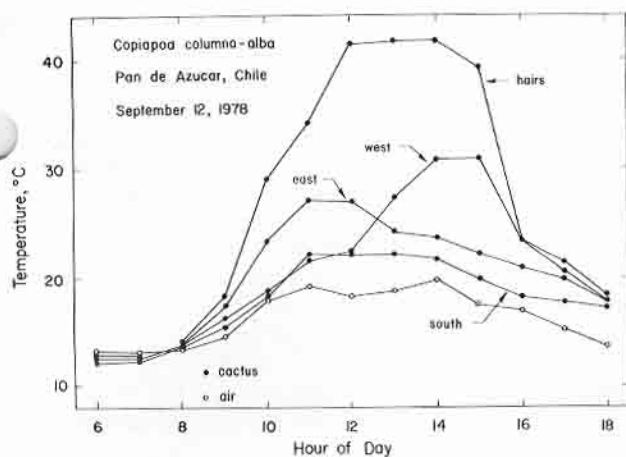


Fig. 2. Daily course of air temperature and surface temperatures on different parts of the cactus body of *Copiapoa columna-alba* at Pan de Azucar, Chile on September 12, 1978

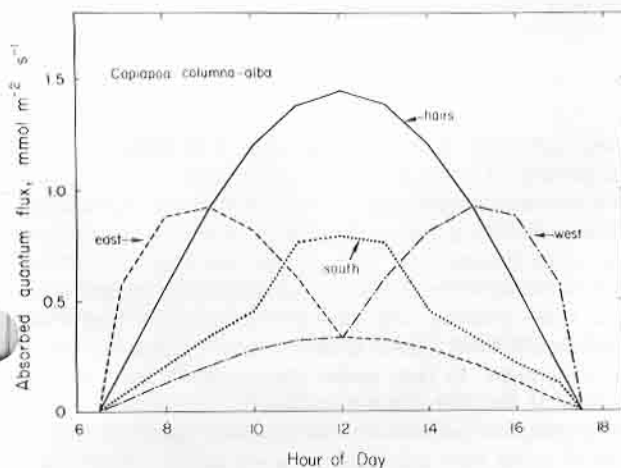


Fig. 3. Calculated solar irradiances on different parts of the cactus body of *Copiapoa columna-alba* at Pan de Azucar, Chile for September. Calculations assume an average diffuse radiation component of 40%, which is similar to the value measured for September 12, 1978 (see Fig. 2)

Discussion

The coastal parts of the Atacama Desert are cool and extremely arid. Species of the cactus genus *Copiapoa* are found in the driest portions of this desert where plants can still survive. Rainfall in these regions averages less than 25 mm annually and 2–10 year droughts are not uncommon. Gulmon et al. (1979) have studied the distributions, spacing and sizes of *C. columna-alba* at Pan de Azucar, Chile, where these plants form monospecific stands. They found a random distribution of plants, suggesting competition was not responsible for structuring the community, and they also found a lack of small sized *C. columna-alba*. It was their conclusion that the inability to survive extended periods of drought was the principal reason that small individuals were not found. If this is the case, we should expect the structure, morphology, and physiology of the larger cactus to possess characteristics that enhance the plant's ability to survive long periods of drought.

Physiologically, species of *Copiapoa* possess the CAM photo-

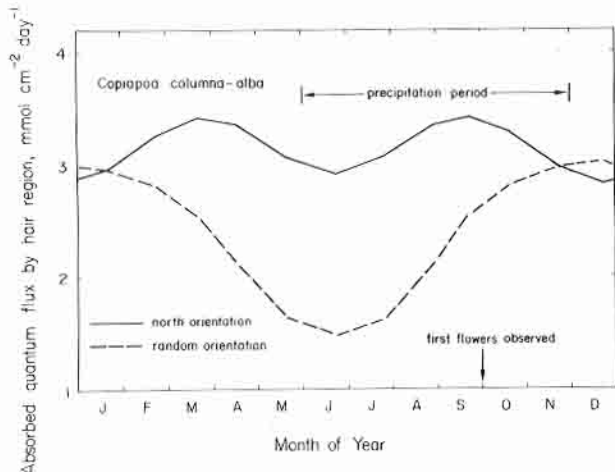


Fig. 4. Calculated daily absorbed quantum flux (400–700 nm) by the meristematic hair region at the tip of *Copiapoa columna-alba* throughout the year for cacti that face north and for those with a hypothetical random orientation. Both sets of calculations assume a cactus body angle of 51.9°

synthetic pathway (Mooney et al. 1975). This enables the plants to open their stomates and take up CO_2 at night when relative humidities are highest and vapor pressure deficits are lowest. It is likely that during extended periods of drought or even late in the summer drought season these plants may be in an "idling mode", not even opening their stomates at night but instead refixing internally generated CO_2 . Such a phenomenon has been observed in other cactus including the barrel cactus, *Ferocactus acanthodes* (Nobel 1977).

The three species of *Copiapoa* observed in this study and presumably most other *Copiapoa* species orient in a northerly direction. It is our hypothesis that this orientation has several predictable consequences to the cactus which may be of adaptive benefit. First, we suggest that by facing north in a cool temperature habitat, *Copiapoa* maximize interception of heat (solar radiation) in the meristematic and reproductive regions, thereby significantly raising tissue temperatures (to the $30^\circ\text{--}40^\circ\text{C}$ range). Second, we suggest that by facing north, *Copiapoa* minimize the interception of light and heat (solar radiation) by the sides of cactus. Our evidence which follows utilizes *C. columna-alba* as being representative of the general phenomenon.

Rare precipitation events come during the winter and spring months of June through November. Growth and flowering, if they are to occur during a particular year, occur at this time. Since air temperatures are cool at this time of the year ($10^\circ\text{--}15^\circ\text{C}$), increases in meristematic and flower tissue temperatures would enable these processes to proceed at a faster rate. Using computer simulations, we calculated the solar radiation (as 400–700 nm quantum flux, which is a constant 50% of the total solar radiation load) that would be absorbed by the tops of *C. columna-alba* oriented due north versus those oriented in a random fashion (Fig. 4). A random orientation is actually the average of north, east, west, and south facing cacti. From these calculations, it is clear that during the spring months when usable moisture is most likely to be available the tops of north facing cacti absorb more heat than randomly facing cacti. In fact, absorption by the tops of north facing cacti can be almost twice as great as that of randomly oriented plants in the winter months and can be 40% higher in the spring months.

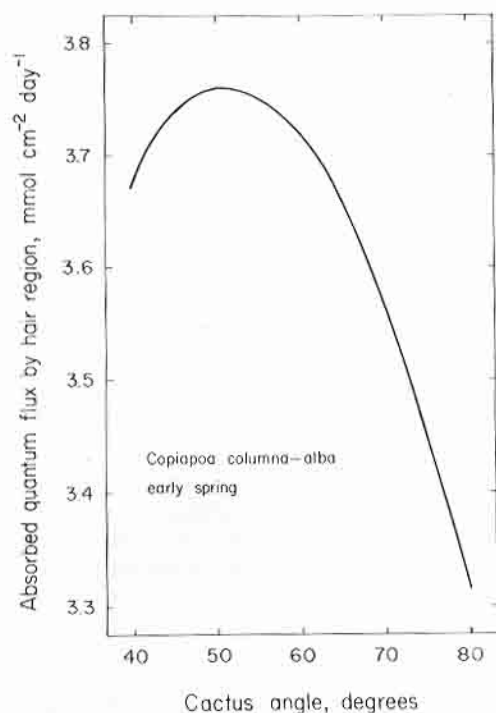


Fig. 5. Calculated daily absorbed quantum flux (400–700 nm) by the tip hair region of *Copiapoa columna-alba* during the early spring when apical and floral development is occurring as a function of the cactus body angle. Angle is measured from the horizontal

Flowering was first observed in the cactus on about October 1. This date is very close to the predicted date of maximum solar radiation absorption by the tops of northerly oriented cacti and some 3 months before the predicted maximum solar radiation absorption by randomly oriented plants. *Trichocereus*, a vertically oriented columnar cactus, which also occurs in the Atacama Desert of Chile shows a similar phenomenon. In *Trichocereus*, flowering occurs on only the north side of the top of the cactus (Rundel 1974).

If a northerly orientation is being used to maximize heat absorption by the meristematic and flowering regions of the cactus, we would expect that the cactus body angle would also have a strong influence on the degree of heat absorption. For northerly oriented *C. columna-alba*, we calculated the effect of changes in cactus body angle on the absorbed quantum flux by the top portion of the cactus during the early spring (Fig. 5). As expected, the cactus body angle strongly affects the absorbed quantum flux. The cactus body angle for maximum heat or quantum absorption is 50°, with a precipitous decline in quantum absorption below 40° and above 60°. From Table 1, the measured cactus body angle of 51.9° for *C. columna-alba* is very close to the predicted optimum value. Cactus body angles of the other *Copiapoa* species fall within the general range of 40°–60°, and thus it seems unlikely that the variations in body angle between populations are of much significance.

The dry period (non-rainy season) in the Atacama Desert extends from December through May. This is also the period during which fog and/or overcast skies are least likely to be present (Espinosa 1967), so that the drought period is characterized by high solar radiation loads in addition to lack of water. From

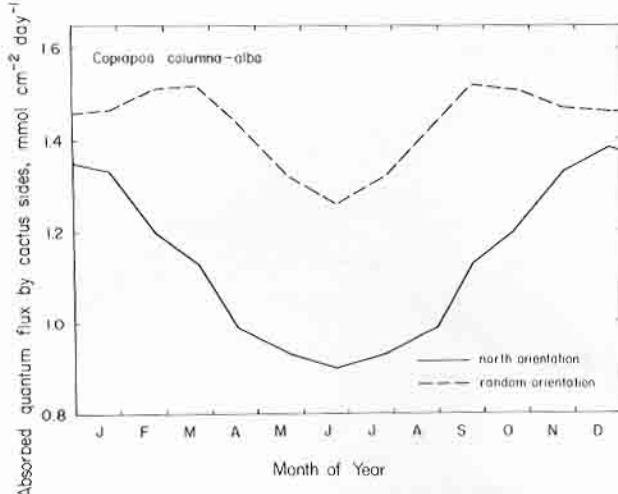


Fig. 6. Calculated daily absorbed quantum flux (400–700 nm) by the sides (surface of cactus without the tip hair region) of *Copiapoa columna-alba* throughout the year for cacti facing north and for cacti with a hypothetical random distribution. Both sets of calculations assume a cactus body angle of 51.9°

previous studies on other species of cacti, it is known that the daily nighttime CO₂ uptake (daily carbon gain) is proportional to the daily quantum absorption (Nobel 1977) and also that the daily nighttime CO₂ uptake is inversely proportional to the level of water stress (Szarek et al. 1973; Szarek and Ting 1975; Nobel 1977). From these observations, we suggest that under conditions of water stress resulting from extended periods of drought that *Copiapoa* require fewer quanta to reduce the CO₂ captured during the previous night. In fact, excess absorption of light may be detrimental to the photosynthetic process.

Using computer simulations, the absorbed quantum flux by the sides of cactus were calculated for north facing and randomly facing *C. columna-alba* (Fig. 6). At all times of the year a northerly orientation results in a much lower absorbed quantum flux by the cactus sides. This is particularly true during the late summer and fall drought periods when northerly oriented cacti sides may be absorbing only 70–80% of what randomly oriented cactus sides absorb. By reducing the quantum absorption during drought periods, northerly oriented cacti conceivably not only maintain a quantum absorption more in balance with the "potential" night CO₂ uptake, but also reduce the heat load and potential detrimental effects of excess light on the sides of the cactus. The reflective wax layer on the sides and top of the cactus accentuates this effect.

If we assume that *C. columna-alba* from Pan de Azucar are cylindrical, then the mean surface area of the top is 79 cm² and of the sides is 741 cm², more than nine times larger in area than the top. Yet from Figs. 4 and 6, it appears that the top of the cactus is absorbing more than two and a half times as much quanta as the sides. What this implies is that the relative heat load of the entire plant (ratio of total heat absorbed to plant volume) is reduced dramatically as plants increase in size. Small plants, even though they orient in a northerly direction and are covered with a reflective waxy material, are subject to the highest heat loads by virtue of the top/side surface area ratio. It is possible that these higher heat loads on small cacti will result in a high mortality rate than larger cacti under normal conditions. Relative-

ly higher heat loads on smaller individuals and the observation that the time between rain storms is long compared to the water storage capacity of the plant stems, especially in smaller individuals (Gulmon et al. 1980) are likely explanations of why Gulmon et al. (1980) found so few small individuals of *C. columna-alba* in their study plots.

In the much wetter Sonoran Desert of North America, several species of the barrel cactus, *Ferocactus*, orient towards the south in a manner analogous to the northerly orientation of *Copiapoa* (Humphrey 1936). Microclimatology and cactus surface temperatures have been measured on *F. acanthodes* (Mozingo and Comanor 1975; Lewis and Nobel 1977), where they find a temperature pattern similar to what we have described for *C. columna-alba*. It is possible that a pattern similar to *Copiapoa* may be occurring in *Ferocactus*, but as of yet no evidence is available.

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