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STEM TILTING AND PSEUDOCEPHALIUM ORIENTATION IN *CEPHALOCEREUS COLUMN-TRAJANI* (CACTACEAE): A FUNCTIONAL INTERPRETATION

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Abstract. This paper analyzes the functional implications of stem tilting and pseudocephalium orientation in the giant columnar cactus *Cephalocereus column-trajani*. This species shows a consistent northern orientation of its pseudocephalium (a nonphotosynthetic hairy structure where flowers are produced) and stem tilting in the same direction. Analysis of pseudocephalium orientation was made on field data gathered from subpopulations of *C. column-trajani* from slopes with different exposures. Additionally, from morphometric characteristics measured in the field, a model cactus was constructed with the purpose of simulating radiation interception by different morphologies. Variations of this model cactus allowed the simulation of irradiance on erect and tilted cacti, as well as on plants with varying pseudocephalium orientation. Results of irradiance interception by different morphologies were related to actual data of growth rates, flowering period, and rainfall and temperature patterns on the study zone. Sampled individuals of *C. column-trajani* showed a significant north-northwest pseudocephalium orientation (angular mean = $339^\circ \pm 22^\circ$). Simulations showed that tilted cacti with pseudocephalia facing northwards increase yearly interception of direct solar radiation by the whole plant compared to erect cacti with or without a pseudocephalium (2 and 7% increase, respectively), and with tilted cacti with the pseudocephalium facing away from the north (9–10% increase). Additionally, the observed morphology decreases radiation interception during the hottest and driest period of the year. From our results, pseudocephalium orientation and stem tilting in *C. column-trajani* appear to be morphological adaptations that allow the fine-tuning of a columnar morphology to its thermal and radiation environment. However, the cost of tilting in this giant columnar cactus is that branching (which increases photosynthetic area and reproductive output) appears to be almost impossible without serious risk of stem breakage.

Key words: adaptation; functional morphology; growth rate; irradiance; photosynthetically active radiation (PAR); pseudocephalium; semiarid lands; thermal regulation; tilting; Zapotitlán, Mexico.

INTRODUCTION

Cephalocereus column-trajani (Karwinski ex Pfeiffer) Schumann is a giant, usually unbranched, columnar cactus, which forms dense populations on hills of the semiarid region of Puebla and Oaxaca in intertropical Mexico (Bravo-Hollis 1978). This spectacular plant (Fig. 1), known locally as cardón, reaches a height of 10–12 m and characterizes a vegetation unit named cardonal in the xerophytic scrub of the Valley of Zapotitlán (Zavala-Hurtado 1982).

An eye-catching feature of these populations is the marked stem tilting of the upper shoot of the cactus, which bends northwards with a similar orientation in almost all plants. In the concave side of the bent stem, and also facing approximately north, a pseudocephalium is found in all adult plants (Fig. 1; Greenwood 1964). The pseudocephalium is a cluster of densely

pubescent, flower-bearing areoles that are formed along the sides or at the top of a cactus stem, not including the shoot apex (Gibson and Nobel 1986). *C. column-trajani* individuals initiate the production of the pseudocephalium when they attain an average height of 3.35 m and become reproductive (Zavala-Hurtado and Díaz-Solís 1995). The developing flower buds are embedded, and hence protected, in the previously formed pseudocephalium hairs.

The surface of the pseudocephalium is not photosynthetic. On the one hand, the woolly cover impedes the arrival of light to the epidermis. On the other, the tissue surface under the hairy mat of the pseudocephalium is suberose and does not contain chloroplasts. Thus, this cactus species may lose a significant proportion (9–10%) of its potentially photosynthetic tissues with the development of the pseudocephalium. Because of their stem-succulent nature and their extremely low surface-volume relationship, giant columnar cacti maintain a large proportion of nonphotosyn-

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FIG. 1. Individual plant of *Cephalocereus columnna-trajani* in Zapotitlán, Mexico; the photograph was taken from the western side of the plant. The stem is tilted towards the north-northwest (as is the rest of the population visible in the background). The arrow shows the pseudocephalium.

thetic parenchyma, which lives at the expense of the relatively scarce chlorenchyma that is only found in the epidermis of the stem. Thus, on a whole-plant basis the compensation level for net photosynthesis is high (Nobel 1988), and the functionality of the stem epidermis as a light-capturing structure is extremely important. In this context, the evolution of a morphological trait such as the pseudocephalium, which has evolved at the cost of losing a significant amount of the photosynthetic epidermis, needs to be explored in terms of its functional morphology.

In this paper, we advance the hypothesis that pseudocephalium orientation and stem tilting in *Cephalocereus columnna-trajani* actually have functional advantages in terms of radiation interception compared with unbranched erect cacti with no pseudocephalium and tilted cacti with pseudocephalium orientations different from the observed one. Additionally, we hypothesized that the northwestern orientation of the pseudocephalium and stem tilting protect the flowers from direct solar radiation. This hypothesis is explored by means of: (a) a statistical description of the orientation of the pseudocephalium in *Cephalocereus col-*

umna-trajani in plain terrain, and in north, south, east, and west slopes; (b) simulations of irradiance received by a model cactus with the pseudocephalium at different azimuths, and with and without tilting of the trunk, and (c) analysis of radiation interception curves in terms of their relationship with growth rate, flowering, and rainfall and temperature curves.

METHODS

Study site

Field data were gathered from a *cardonal* in a hill at the semiarid valley of Zapotitlán ($18^{\circ}20' N$, $97^{\circ}28' W$, 1550 m elevation), a local basin of the Tehuacán Valley in the Pueblan-Oaxacan Region in the Mexican State of Puebla (Vite et al. 1992). Climate in this zone is semiarid with summer rains. Annual mean temperature is $18^{\circ}\text{--}22^{\circ}\text{C}$ and precipitation is $\sim 400 \text{ mm/yr}$. The soils are shallow, stony, and halomorphic (Byers 1967). Semiarid conditions are imposed by the rain shadow of the Sierra Madre Oriental, which intercepts humid winds from the Gulf of Mexico. The vegetation has been classified as a xerophytic scrub (matorral xerófilo; Rzedowski 1978).

Orientation of the pseudocephalia in the field

Five samples of 50 individuals of *C. columnna-trajani* each were drawn from five different conditions: eastern, western, northern, and southern slopes and an unobstructed plain. The azimuth of the pseudocephalium for each individual was measured using a Brunton compass corrected for true north. Angular mean and circular deviation of pseudocephalium azimuth for each sample were calculated using circular statistics (Zar 1974).

Modeling plant morphology

The irradiance received by a *Cephalocereus columnna-trajani* individual was estimated from that computed for a three-dimensional figure made up of 209 intercepting planes, or facets, each with specific dimensions, azimuth, tilting angle, and suppressed photosynthetic area due to the pseudocephalium. The data for the construction of the geometric model cactus were gathered from ten randomly selected adult individuals with a mean height of 5.63 m (minimum = 4.91 m; maximum = 6.82 m; SD = 0.63 m) growing in an unobstructed plain. We measured cactus heights to the nearest centimeter using a 10-m extendible pole gauge. Shoot diameter was measured to the nearest millimeter using a caliper. Measurements were taken every meter starting from the cactus base. Additionally, we recorded pseudocephalium length and width every 0.5 m using a measuring tape. Tilting angle of the cactus shoot was measured for each of three 2 m high segments from a vertical reference on printed photographs taken from a sample of 35 randomly selected adult individuals growing in the same plain, with a mean height of

6.74 m (minimum = 5.80 m; maximum = 7.80 m; SD = 0.52 m; we used a larger sample for this measurement in order to obtain accurate regression estimations of tilting). With these data, a geometric model cactus was constructed as described in the Appendix.

The simulations were run for six theoretical morphologies: (a) erect plants without a pseudocephalium (tilting angle = 0° and number of facets covered by the pseudocephalium = 0 for all segments); (b) erect plants with north-northwestern pseudocephalia (tilting angle = 0° for all segments); (c) tilted plants with north-northwestern pseudocephalia; (d) tilted, east-oriented pseudocephalia (azimuth of facets rotated 111°); (e) tilted, west-oriented pseudocephalia (azimuth of facets rotated -69°); and (f) tilted, south-oriented pseudocephalia (azimuth of facets rotated -159°). Model cacti with no pseudocephalium have a photosynthetic surface of 5.70 m². In model cacti with a pseudocephalium the photosynthetic surface becomes reduced in 9.4% (although the total surface area is the same).

Simulation analyses

A computer program simulating direct solar radiation (Ezcurra et al. 1991) was supplied with data describing the azimuth, inclination, and area of the 209 intercepting planes, plus the latitude and the date to be simulated. Using standard astronomical equations (Meeus 1988), the program calculates the apparent position of the sun from sunrise to sunset at 10-min intervals and estimates the interception efficiency of each individual plane at each time.

Based on the fact that the pathway of the solar beam through the atmosphere becomes shorter as the sun approaches the zenith, the proportion of direct solar radiation that is damped by the air mass was calculated as a function of the angular elevation of the sun above the celestial horizon (Ross 1981). The estimations were done following Gates' (1980) method, which calculates direct solar radiation (in watts per square meter) intercepted by a given body with a known surface at a given hour of the day under a given air transmittance (which ranges between 0.5 and 0.8 in most desert areas). The simulations were run for three different dates: the equinox, the summer solstice, and the winter solstice, using an air transmittance value of 0.7 for each date. An extension of this program integrates the daily direct solar radiation (in joules per square meter per day), allowing the estimation for a whole year. Resulting figures of irradiance were multiplied by the photosynthetic area of the model cactus in order to estimate total irradiance received by the photosynthetic surface of the simulated plant.

As in most giant columnar cacti, the stem of *C. columnna-trajani* is ribbed, and its total stem surface is ~5% larger than in the facet projection we used for our simulations. The simulated radiation interception per unit photosynthetic surface may be referred either to the "true" (i.e., ribbed) surface, or to the unribbed

geometric projection of the stem. For simplicity, we referred our results to the unribbed projection. If the results are referred to ribbed plants, then the intercepted radiation per unit area is proportionally less, but the relative differences between morphologies do not change.

The simulation data were supplemented with climatic information and with data on growth and flower production. Mean temperature and rainfall data (1990–1991) were provided by the climatological station of Zapotitlán Salinas (Servicio Meteorológico Nacional, Mexico). Average number of flowers per individual per month for 75 individuals of *C. columnna-trajani* in 1990–1991 were drawn from our own unpublished data. Finally, mean monthly growth rates for the same two years were estimated from data of Zavala-Hurtado and Díaz-Solís (1995).

RESULTS

Orientation of the pseudocephalia in the field

The five populations showed a significant mean direction ($P < 0.001$) according to a Raleigh test (Zar 1974). The mean azimuth and circular standard deviation of the pseudocephalium in plants from the unobstructed plain were $339^\circ \pm 21.8^\circ$. This orientation (hereafter called north-northwestern) was considered as the typical natural orientation, and hence, the one to be evaluated in terms of efficiency in light interception.

Two-sample tests using the method of Watson and Williams (1956, cited in Zar 1974) revealed that there were nonsignificant differences ($P > 0.1$) in pseudocephalium orientation between cacti from the northern and southern slopes and the unobstructed plain. Cacti from the eastern slope showed significantly different ($P < 0.001$) pseudocephalium azimuth from cacti of all the other four sites. The same occurred with cacti from the western slope, which showed significantly different ($P < 0.001$) pseudocephalium azimuth from cacti of all the other sites, excepting the northern slope (Fig. 2).

Simulation analyses

In our model, an erect cactus with no pseudocephalium intercepts 11652 MJ/yr of direct solar radiation (Table 1). The presence of a pseudocephalium in erect plants reduced light interception in values ranging from 11.6% when the structure faced east, to 3.1% in northern orientations. An erect cactus bearing a pseudocephalium with north-northwestern azimuth would reduce its light interception by 5.1%, compared with an erect cactus with no pseudocephalium.

Bending of the shoot in plants with a pseudocephalium dramatically increased light interception (Table 1). A tilted cactus with a north-facing pseudocephalium intercepts more (4.0%) light than an erect one without a pseudocephalium. In tilted cacti, minimum light interception would occur for a plant with a pseu-

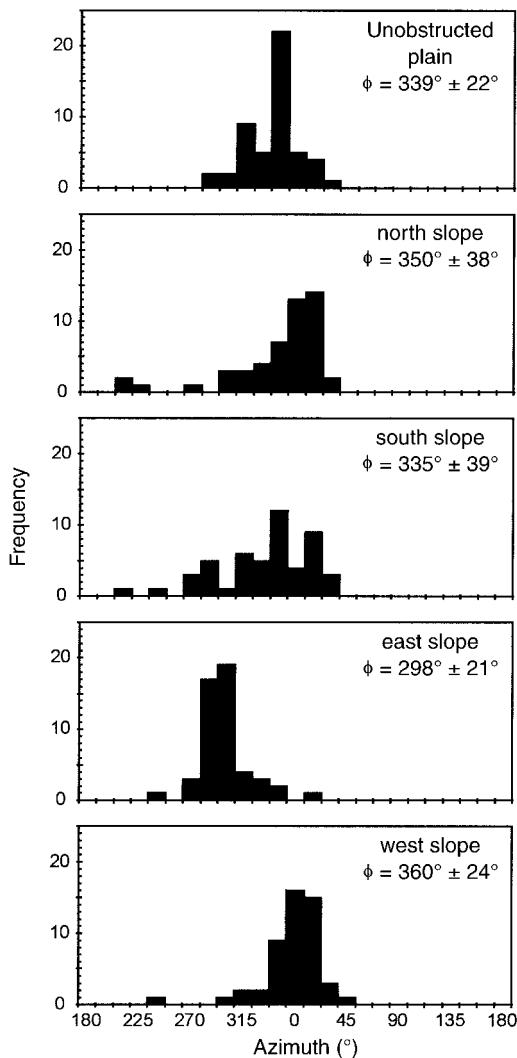


FIG. 2. Frequency distributions of pseudocephalium azimuth of 50 individuals of *Cephalocereus column-trajani* from different slope aspects in the valley of Zapotitlán, Mexico. Angular means (ϕ) and circular standard deviations of pseudocephalium azimuth are shown for each slope.

docephalium facing south. The average observed cactus morphology (tilted, with a north-northwestern pseudocephalium) intercepts 1.7% more light than that received by an erect individual with no pseudocephalium.

Looking at the yearly pattern of light interception (Fig. 3a), it can be seen that the average observed cactus morphology shows the highest light interception during fall and winter when relatively low temperatures prevail in the region (Fig. 3b). This estimated radiation-interception pattern contrasts with the theoretical patterns of erect cacti without a pseudocephalium, and especially of south-tilted cacti, which would maximize light interception during the relatively hot summer months. Additionally, the less efficient east- and west-tilted cacti would show lower interception values throughout the year. It also can be seen that tilting

TABLE 1. Total annual direct solar radiation intercepted by 11 simulated plants differing in location of pseudocephalium and tilting (see Appendix for details of model cacti). Percentages are relative to an erect cactus with no pseudocephalium.

Type of simulated pseudocephalium	Erect		Tilted	
	Radiation intercepted (MJ/d)	%	Radiation intercepted (MJ/d)	%
None	11 652	100		
North-northwest facing	11 062	94.9	11 853	101.7
North facing	11 285	96.9	12 113	104.0
East facing	10 303	88.4	10 825	92.9
South facing	10 324	88.6	10 615	91.1
West facing	10 303	88.4	10 825	92.9

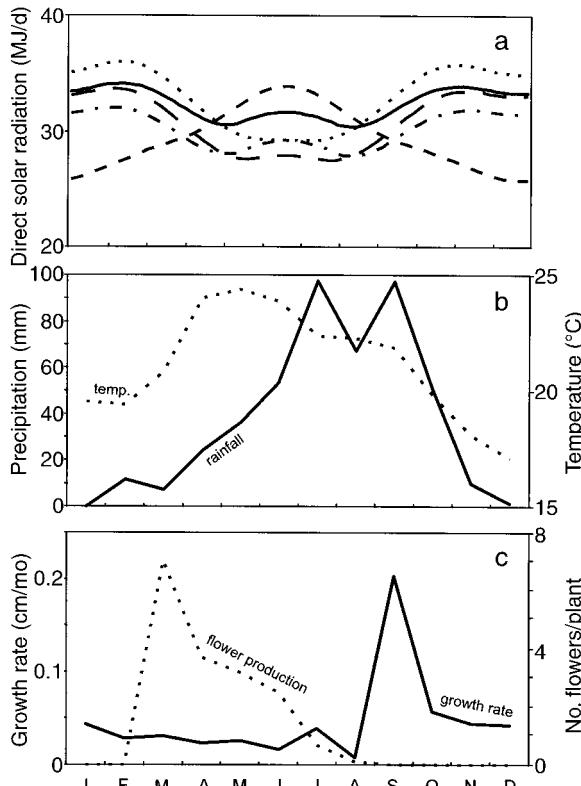


FIG. 3. (a) Simulated intercepted solar radiation by five different model cacti (continuous line, erect cactus with no pseudocephalium; long-dashed line, erect cactus with pseudocephalium facing north-northwest; dotted line, tilted cactus with pseudocephalium facing north-northwest; dash-dot line, tilted cactus with pseudocephalium facing east or west; and dashed line, tilted cactus with pseudocephalium facing S). (b) Average rainfall (solid line) and mean monthly temperature (dotted line) from the Zapotitlán Salinas climatological station during 1990–1991. (c) Mean growth rate (solid line) and mean number of flowers produced per individual (dotted line) from a population of 75 *Cephalocereus column-trajani* individuals during 1990–1991.

improves light interception from September to March in cacti with north-northwestern azimuths in relation to the interception pattern of cacti showing the same orientation of the pseudocephalium but no shoot bending.

Maximization of light interception during fall in the average cactus morphology (Fig. 3a) coincides with the peak in growth rate of *Cephalocereus column-trajani* (Fig. 3c) and with the September rainfall period in the study site (Fig. 3b) for the analyzed years. Flower blooming presents a peak in March (Fig. 3c), during a period of high incident radiation (Fig. 3a) and relatively low temperatures, before the onset of the rainy season (Fig. 3b).

The simulations of the daily patterns of light interception are presented only for the three most efficient morphologies: (a) erect plants with no pseudocephalium; (b) erect plants with a north-northwestern pseudocephalium; and (c) north-northwestern tilted plants with a pseudocephalium (Fig. 4). Simulations were performed for the equinox (Fig. 4a), the summer solstice (Fig. 4b), and the winter solstice (Fig. 4c).

Although the three types of cacti showed similar trends in their daily patterns of direct solar radiation interception, some relevant differences must be highlighted: (a) erect cacti with no pseudocephalium showed a symmetric pattern around noon; (b) cacti bearing a north-northwestern pseudocephalium (both erect and tilted) intercepted more radiation before noon in the summer solstice and in the equinox, compared to the radiation intercepted after midday; (c) tilted cacti with pseudocephalium showed the highest direct solar radiation interception of all morphologies during the equinox (33.7 MJ/d) and the winter solstice (34.1 MJ/d), and present an intermediate value during the summer solstice (29.5 MJ/d); (d) erect cacti with a pseudocephalium showed the lowest radiation interception of all morphologies in the three simulations (31.1 MJ/d on the equinox, 28.1 MJ/d on the summer solstice, and 32.2 MJ/d in the winter solstice); (e) erect cacti with no pseudocephalium showed intermediate values of radiation interception in the equinox and winter solstice (32.5 and 32.3 MJ/d, respectively), and the maximum value of all morphologies during the summer solstice (31.8 MJ/d).

DISCUSSION

Orientation in the flowering structures of columnar cacti is well known. For example, in *Carnegiea gigantea* it has long been reported that flowers are primarily produced on the east-southeast side of the top of the plant (MacDougall and Spaulding 1910, cited in Nobel 1981; Johnson 1924), i.e., exactly on the opposite side from that for *C. column-trajani*. For this northern species (*C. gigantea*), flower development seems to be enhanced by high surface temperatures achieved on the southern side of stem. Conversely, *Trichocereus chilensis* and *T. litoralis*, two species of co-

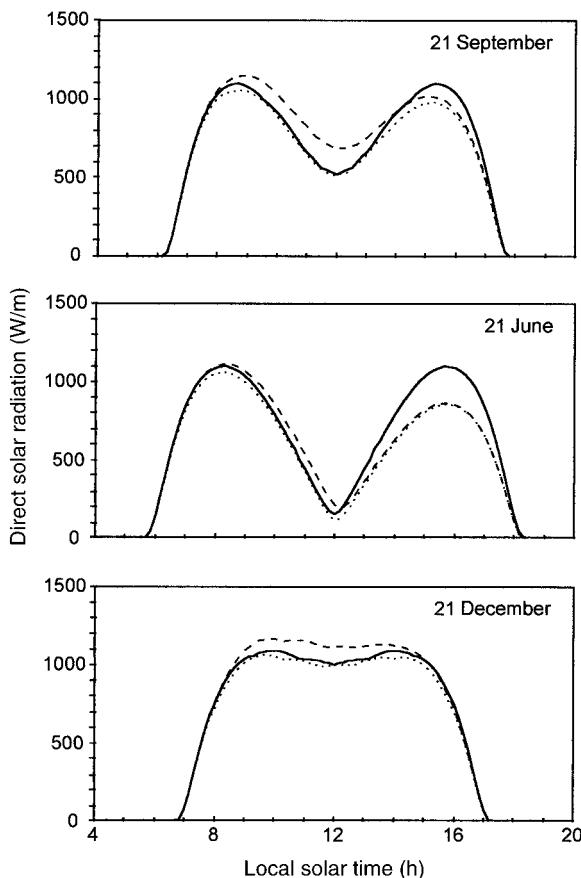


FIG. 4. Simulated daily interception of direct solar radiation (W/m^2) for cactus models of different morphology (—, erect cactus with no pseudocephalium; ·····, erect cactus with pseudocephalium facing north-northwest; and - - -, tilted cactus with north-northwest-facing pseudocephalium). Graphs show intercepted radiation during (a) autumn equinox (the same simulation curve is obtained for 21 March, the spring equinox); (b) summer solstice; and (c) winter solstice.

lumnar cacti from the southern hemisphere, produce flowers mainly in the warmer, northern side of the stem (Rundel 1974).

Stem tilting, however, has only been studied in barrel cacti, a life form with relatively short stems. Nobel (1988) argued that giant columnar cacti do not tilt because gravity would exert a considerable bending moment on their massive stems, causing their breakage. Indeed, from the many giant columnar species in the Tehuacán Valley, *C. column-trajani* is the only one that exhibits stem tilting, and is also one of the only two species that do not usually branch. Additionally, stem breakage is a very frequent cause of physical injury on these plants (Zavala-Hurtado and Díaz-Solís 1995). Some barrel cactus species (e.g., *Ferocactus* spp. in North America and *Copiapoa* spp. in South America) expose their apical region (in which flowers are produced) to the south and north, respectively (i.e., toward the equator) by means of a stem tilting. The

northern azimuth and tilting in three species of *Copiapoa* were explained by Ehleringer et al. (1980) as a mean of increasing apical temperatures by enhancing meristematic activity during the winter and spring months. The equatorwards tilting of barrel cacti does not improve PAR interception and CO₂ uptake for the whole plant. On the contrary, the bending of the longitudinal stem axis towards the sun's trajectories in fact leads to less PAR annually incident on the stem (Nobel 1988). The functional advantages of tilting, hence, are possibly more related to temperature control than to a maximization of intercepted PAR.

The behavior of *C. columnatajani* contrasts with previous reports on this problem in various aspects. First, *C. columnatajani* is the only giant columnar species known to show a conspicuous stem tilting. Second, the species tilts away from the equator, and not towards it. Third, the flowers, which are embedded in the pseudocephalium, are also oriented away from the equator, in contrast with other columnar species that produce their flowers on the warmer side of the columnar stem facing the equator. And fourth, this cactus species is endemic to the intertropical zone, while all the previous reports of nonrandom orientation in columnar or barrel cacti are for subtropical plants growing either north of the Tropic of Cancer or south of the Tropic of Capricorn.

The importance of photosynthetically active radiation (PAR) as a limiting factor for cacti has been previously documented (Nobel 1980, 1981, 1982, Geller and Nobel 1986, 1987). PAR limitation occurs because of the opacity, rigidity, and vertical orientation of the photosynthetic surfaces of most cacti and of other CAM plants such as cactoid Euphorbiaceae. The capture of light in these desert succulents implies necessarily the risk of overheating their photosynthetic tissues. Many perennial desert plants, including succulent and non-succulent evergreen species, present their chlorenchyma vertically oriented (e.g., Woodhouse et al. 1980, Nobel 1982, 1986, Cano-Santana et al. 1992, Ezcurra et al. 1991, 1992, Valverde et al. 1993). As a general rule, a vertically oriented structure will intercept more light in the morning and afternoon, and less light at midday, when the sun is near the zenith. Thus, the vertical orientation helps to solve the compromise between capturing light and avoiding overheating during the warmer hours of the day. In the Tehuacán Valley, opuntioid, barrel, and columnar cacti establish under the shade of nurse plants, and their seedlings do not survive a dry season if they are exposed to direct solar radiation (Valiente-Banuet et al. 1991, Valiente-Banuet and Ezcurra 1991). Adult plants manage to survive direct exposure to the sun because of their vertical orientation. Felled individuals of *C. columnatajani*, exposed horizontally to direct solar radiation, attain midday temperatures in their chlorenchyma above 55°C, while the normal erect plants are only slightly above air temperature, and around 35°C (J. A. Zavala-Hur-

tado, unpublished data). In *Opuntia pilifera* the horizontal exposure of the usually vertical cladodes increases their midday temperature from 35°C to 47°C (Cano-Santana et al. 1992). Most cacti will show an abrupt increase in chlorophyll fluorescence (an indicator of decreasing electron flow in Photosystem I during photosynthesis) between 50° and 56°C. Furthermore, the electron transport involved in Photosystem II starts to decrease in cacti when the photosynthetic tissues reach temperatures between 40° and 50°C (Nobel 1988). Thus, even if the plant survives high midday temperatures, its photosynthetic system may lose much of its functional capacity if the chlorenchyma reaches temperatures above 45–50°C. The columnar life form allows cacti to avoid the potentially harmful effects of high temperatures by maximizing PAR interception in the early morning and late afternoon. The strategy, however, has a cost, as PAR interception becomes suboptimal. For example, while horizontal cladodes of *Opuntia pilifera* in Zapotitlán intercept in one day as much as 41 mol photons/m² of cladode area, vertical cladodes facing east and west will intercept 23 mol photons/m², and vertical cladodes facing north and south will intercept only 5 mol photons/m² (Cano-Santana et al. 1992). In the case of *C. columnatajani*, an approximate conversion of our model's predictions from direct solar radiation into PAR indicates that the plants in the field intercept ~12 mol photons·m⁻²·d⁻¹. Although this value is well above the compensation level reported for cacti, which is ~3 mol photons·m⁻²·d⁻¹, it is also below the daily PAR level that results in maximum net uptake of CO₂, which is ~30 mol photons·m⁻²·d⁻¹ (Nobel 1988), and it is also well below the maximum measured PAR interception for a plane surface in the region (41 mol photons·m⁻²·d⁻¹).

In this framework, tilting appears to be a morphological adaptation that allows the fine-tuning of a columnar morphology to its thermal and radiation environment. By tilting north-northwestwards with an angle that is greater than the northern declination of the sun during the summer solstice, the plant achieves a series of changes in its radiation-interception pattern. It intercepts less radiation at midday and during the afternoon than a vertical columnar plant during the hotter months of the year (Figs. 4 and 5). This is especially important as it is frequently the case that summer rains may arrive as late as July. The tilted stem intercepts more light than an erect structure during the September equinox, the time of the year when the summer rains have commenced and the soils are moister, and also when the plant shows greatest growth (Fig. 3). By tilting the stem, the nonphotosynthetic pseudocephalium can develop without significantly losing PAR interception. In fact, tilting actually improves global PAR interception by ~2%, and it particularly improves PAR interception during favorable seasons and during the most favorable hours of the day. The spiny pseudocephalium, in turn, protects the flowers from potential

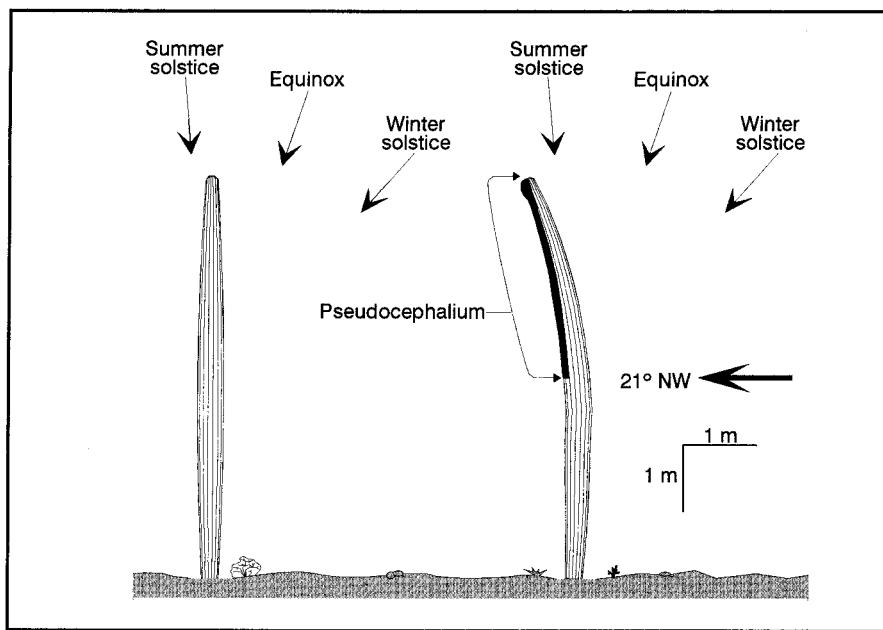


FIG. 5. Angle of incidence of direct solar radiation at midday for an erect unbranched columnar cactus compared with an average *C. columnatajani*, for the summer and winter solstices, and for the equinox. NW = northwest.

nectar robbers, and also keeps the night-blooming flowers shaded during the day. Finally, the simulation shows that by shifting the pseudocephalium north-northwest instead of directly north, the plant increases light interception during the cooler hours of the morning (when the apparent position of the sun is in the east), and decreases interception in the afternoon (when the sun is in the west).

Thus, tilting has a direct bearing on the plant's reproductive system, and ultimately on its fecundity, as a mechanism that allows the protection of the flowers (that bloom in the dry season) from excessive evaporative demand and from potential predators. Additionally, tilting does not hinder PAR interception, which is fundamental for successful plant growth. In short, our simulations suggest that tilting may have a positive effect on plant reproduction (an important component of fitness) without compromising plant growth (a second fundamental component of fitness). The obvious cost of tilting in a giant columnar cactus such as our study species is that branching becomes almost impossible without serious risk of stem breakage. Thus, *C. columnatajani* faces a trade-off compared with other columnar species in the region, such as *Neobuxbaumia tetetzo*: while tilting may increase its capacity to intercept PAR and at the same time to passively regulate stem temperature, the species cannot benefit from the increased PAR interception and CO₂ uptake (Geller and Nobel 1986, 1987), as well as the increased reproductive potential (Yeaton et al. 1980) that derive from stem branching.

This interpretation of the results of our model can be tested with field data on the orientation of the pseu-

docephalia. In open plain habitats, the azimuth of the pseudocephalium is north-northwest (angular mean = 339°), but in plants growing on steep slopes, which obstruct part of the incoming radiation, the angular location of the pseudocephalium is shifted towards the slope, i.e., both tilting and the development of the pseudocephalium shift in the direction where the plant receives less direct solar radiation and less PAR.

It is interesting to note that the geographic range of this species is extremely restricted in terms of latitude. *C. columnatajani* is only found in the Tehuacán Valley between Zapotilán and Zinacatepec, ranging from 97°13' to 97°30' W, and from 18°18' to 18°21' N (Bravo-Hollis 1978). That is, the species traverses the Tehuacán Valley occupying some 40 km from east to west, but less than 10 km from north to south. The development of a tilting stem may be adaptive in this narrow area, but could be nonadaptive at other latitudes, as the success of the tilting strategy is strongly dependent on the apparent position of the sun during the growing season, and hence on the latitude of the site. The extreme degree of architectural specialization of this species may be at the same time the cause of its local success and also of its geographic rareness.

The northern orientation of the flowers in *C. columnatajani* and the tilting away from the equator, in contrast with the equatorwards tilting and flower production in other cacti, deserve some attention. The difference between our study species and other reported cactus species with stem directionality lies in the fact that *C. columnatajani* grows in a frost-free intertropical zone, where a vertically oriented columnar plant receives light on both its southern and northern face at

different times of the year (Peters 1993). By tilting slightly to the north, this species intercepts less radiation during the hotter months of the year. Tilting thus allows the passive regulation by the plant of its thermal and radiation environment. Extratropical cacti, on the other hand, are often limited both by low temperatures in winter and high temperatures in summer. The apparent position of the sun for these plants is always towards the equinox. Tilting towards the equator may help to regulate radiation interception during the hot summers, while still allowing the interception of significant amounts of radiation during the cold months of the year. The interaction between the yearly radiation pattern, the radiation interception by tilted stems, and the growth season, remains to be studied in more detail for these plants.

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APPENDIX

Characteristics of the model cactus and their variations, used in this study for estimating the irradiance received by an actual or hypothetical *Cephalocereus column-trajani* individual with similar characteristics.

Total heights and stem diameters were used for obtaining the overall shape of a cactus by means of the following regression equation:

$$D(H) = [0.03844 + 0.09673H/T - 0.1080(H/T)^2]T \quad (\text{A.1})$$

where $D(H)$ = stem diameter (in centimeters) at any height (H) of the stem (in centimeters) and T = total height of an individual (in centimeters). This equation was obtained by polynomial regression on field data from 10 plants growing in open plain areas ($R^2 = 0.75$; $F_{2,59} = 86.5$; $P < 0.00001$).

With the tilting angles measured for the plant segments, a data set was constructed for statistical analyses. As tilting of the upper part of the plant may bend the lower part of the stem in the opposite direction, negative signs were assigned to the angles of sectors that were bent away from the azimuth of the pseudocephalium. The tilting angles for the midpoint of these three categories were fitted to an arbitrary exponential function ($r = 0.72$ on a semilog scale; $n = 105$; $P < 0.05$), which allowed us to interpolate the mean angle of deviation from the basal point for any height of the stem. The function obtained was

$$\beta = [3.8798 \times \exp(1.2777 H)] - 7.0 \quad (\text{A.2})$$

where β is the angle of deviation and H is the height of a standardized plant 6 m high. This function allowed us in turn to model the tilting angle of any specific stem segment.

For a plant with a total height of 600 cm, Eq. A.1 was used in the computation of diameters at every 50 cm from 0 to 550 m high, and at 595 cm high. With these data, each of the 12 stem stretches was approximated as a truncated pyramid composed by 16 equal trapezoidal sides, or facets. The calculated diameters at each height were ascribed to the maximum width of the bottom and the top of the truncated pyramids. Finally, the plant apex was simulated by a 5 cm high truncated pyramid with 16 lateral sides and a 8.45 cm wide flat top. Eq. A.2 was used to calculate the expected tilting angle of the stem axis for each of the 12 segments. Standard trigonometric equations were used for assigning an azimuth and a vertical angle to each truncated pyramid with respect to the main axis of the stem. Spherical trigonometry was used to calculate the azimuth and the inclination of each facet with respect to the local horizontal coordinates, knowing their azimuth and inclination with respect to the main axis of the stem and the inclination and azimuth of each stem sector.

Thus, the basic characteristics of the model plant (which are similar to the mean characteristics of actual plants in the field) were as shown in Table A1.

TABLE A1. Morphometric characteristics of a model cactus used in the simulations analysis. Figures are based on average measurements on 35 individuals of *Cephalocereus column-trajani* in the field.

No. of segment	Height class (cm)	Stem diameter (cm)	Tilting angle (°)	Number of facets	Facet area (cm ²)	Segment area (cm ²)	Pseudocephalium	
							No. of facets	% covered
1	0–50	23.06	-2.68	16	246.60	3945.60	0	0.00
2	150–100	27.45	-1.71	16	284.94	4559.00	0	0.00
3	100–150	30.94	-0.58	16	314.49	5031.87	0	0.00
4	150–200	33.52	0.74	16	335.28	5364.43	0	0.00
5	200–250	35.21	2.28	16	347.30	5556.84	0	0.00
6	250–300	36.00	4.05	16	350.58	5609.20	0.40	2.48
7	300–350	35.88	6.11	16	345.10	5521.52	0.99	6.22
8	350–400	34.87	8.47	16	330.86	5293.77	1.59	9.96
9	400–450	32.96	11.17	16	307.86	4925.84	2.19	13.71
10	450–500	30.14	14.23	16	276.10	4417.55	2.79	17.45
11	500–550	26.43	17.68	16	235.54	3768.67	3.39	21.19
12	550–595	21.82	21.33	16	170.14	2722.24	3.99	24.93
13	595–600	16.89	21.53	16	16.04	256.64	4.59	28.68
14	(crown)	8.45		1	56.81	56.81	0	0.00