Two cholla species exhibit adaptive plasticity in their solar radiation avoidance strategies

Josiah Berkov-Kemp[1], Tyler Hannum[2], and Cassidy Ricks[3]

[1]University of California, Los Angeles; [2]University of California, Santa Cruz, [2]University of California, San Diego

Intense solar radiation in desert ecosystems drives adaptation in cacti. Several Mojave Desert members of the cactus genus *Cylindropuntia* may exhibit morphological adaptations to reduce the impact of solar irradiation, such as light-blocking spines and the ability to point their new growth parallel to the sun's rays. To detect adaptive morphologies in three *Cylindropuntia* species, we measured the orientation, spine density, and pigmentation of the new growth on the southwest and northeast sides of the plant. Additionally, we took morphometric measurements such as segment size to better understand how cacti allocate their resources and growth to cope with the sun. We found that two species of *Cylindropuntia* (*C. echinocarpa* and *C. acanthocarpa*) cacti do grow in line with the sun's rays. We found no relationship between spine coverage and side of plant across all three species. For *C. ramosissima*, which bore the least number of spines on each of its segments, the results of damaging UV rays were frequently apparent in the form of stem-flattening somatic meristem mutations, despite their apparent investment in other pigment-based forms of defense. Two *Cylindropuntia* species display adaptive orientation but likely do not use spine density to avoid solar radiation. These results suggest that segment orientation is a more plastic trait than spine coverage in *Cylindropuntia*.

Keywords: Cylindropuntia, solar radiation, adaptive plasticity, spine density, somatic mutation

INTRODUCTION

Desert ecosystems are some of harshest environments on earth and contain many of the most resilient organisms alive. Extreme temperature fluctuations, periods of intense drought, and constant solar radiation are just a few of the selective pressures that drive adaptation in desert plants (Owens 2020). A set of desert specialists is the group of cacti known commonly as chollas. Chollas are members of the genus *Cylindropuntia*, and are characterized by cylindrical stems separated into spine-covered segments that branch radially outward and upward from a central base. Chollas are foundation species in the Mojave Desert, providing shade, protection, and nutrition for desert flora and fauna (Owens 2020). Chollas are well-adapted to the desert environment, as evidenced by their abundance throughout the American southwest. Investigating the evolutionary strategies that allow chollas to thrive in such harsh environments is crucial for understanding not only the life history of these desert foundation species but also the ecosystems they support.

One of the primary selective factors in the desert is sunlight (solar radiation). Desert plants need the energy transferred through solar radiation to photosynthesize, but excess radiation can accelerate transpiration (water loss) and increase somatic mutation rates. Recent research indicates that solar radiation can also cause damage to cactus photosynthetic organs (De la Rosa-Manzano et al. 2016). All three of these stressors can decrease fitness and increase mortality in cholla exposed to high levels of solar radiation like those present in the Mojave Desert. Many desert plant species exhibit phototropic (sun-tracking) adaptations to avoid damage by excess sunlight, keeping their leaves parallel to the sun's rays and thus reducing direct impact (Ehleringer and Forseth 1980). This phenomenon is an example of adaptive plasticity, which in this case refers to the tendency for a plant to change its morphology in response to environmental pressures (Miller 2016).

In 1987, Geller and Nobel described the tendency of chollas to orient and grow their segments directly toward the greatest incidence of solar radiation. They explained this as an adaptation to maximize photosynthetic capacity by pointing the smallest surface area of each segment toward the sun, thereby limiting self-shading and allowing more sunlight to filter into the photosynthetic canopy of the cholla. This explanation assumes that access to solar radiation is a limiting factor for cholla growth, which seems unlikely because cholla live in deserts where they are constantly exposed to direct sunlight. We posit that this orientation towards solar incidence may instead limit concentrated solar radiation on a few segments by distributing the sunlight over a larger area of the cholla plant, diluting the harmful effects of the excess sunlight. Pointing segments toward the sun also forces solar radiation to travel orthogonally through all the rows of spines on a given segment before it hits the interior segments behind it. These spines may disperse the sunlight as it passes through them, providing added solar protection to cholla segments oriented toward the sun.

Another important morphological mechanism that chollas may use to combat harmful solar radiation is their spine density. De la Rosa-Manzano et al. 2016 proposed that spines are used to limit photosynthetic damage to cactus tissue by shading cactus stems. Cacti of the *Opuntia* genus (proximate to *Cylindropuntia*) have also been observed to increase spine development when exposed to direct sunlight (Leding 1934). Another study on *Opuntia* showed that some species of these cacti also use UV blocking pigmentation within their segments to shield themselves from harmful solar radiation (Cockell et al. 2004).

In order to examine solar radiation avoidance techniques in *Cylindropuntia*, we conducted an observational study on three species of cholla: silver cholla (*C. echinocarpa*), buckhorn cholla (*C. acanthocarpa*), and pencil cholla (*C. ramosissima*). We measured various attributes of spine morphology, segment orientation, and pigmentation in these species to answer three questions related to three potential radiation avoidance techniques:

Segment Orientation: Do segments orient towards the angle of maximum sunlight incidence (sun azimuth angle)?

Spine Density: Are there more spines on segments on the southwest side of plants (where average solar irradiation is highest)?

Pigmentation: Is pigmentation used as a replacement for high spine count in pencil cholla?

Through these inquiries we sought to determine the extent to which *C. echinocarpa, C. acanthocarpa,* and *C. ramosissima* use segment orientation and spine morphology to protect their segments from damaging solar radiation.

METHODS

Research was carried out in the flat lands immediately surrounding the Sweeney Granite Mountains Desert Research Center, at the base of the Granite Mountains (elevation ~1220 m) in the southern Mojave Desert of San Bernardino County, CA between February 24 and 28, 2021. Predominant species on the landscape include buckhorn cholla (*Cylindropuntia acanthocarpa*), pencil cholla (*C. ramosissima*), silver cholla (*C. echinocarpa*), Mojave yucca (*Yucca shindigera*), creosote bush (*Larrea tridentata*), as well as numerous low-growing woody perennials and ephemeral desert annuals. As is typical of deserts, the region's average annual precipitation is extremely low, with most rainfall occurring in late fall through winter (Hereford et al. 2005). This region is positioned in a rain-shadow, causing a general lack of cloud cover and directly exposing its resident organisms to the sun's rays.

In order to test the effects of sun angle on cholla growth, we randomly selected four segments on the northeast and southwest sides of each cholla. We chose these directions due to our position in the northern hemisphere, as most direct incoming solar radiation comes from the south and west and much less from the north and east. We used a compass to measure the segments' directional bearing. We then removed the segment and measured circumference using a piece of string wrapped around the widest point. Due to *C. ramosissima*'s thinner and less-variable segment width, circumference for that species was estimated by measuring the stem diameter at its widest point and multiplying this value by π. Segment length was measured by holding the segment to a meter stick and quantifying the length of green photosynthetic segment tissue. To understand the differences in spine abundance on various parts of the plant, we assessed the number of spines per areole by counting the number of spines protruding from four areoles on each cut segment and averaging them. Lastly, we counted the total number of areoles on a given segment, marking counted areoles with a Sharpie to avoid double counting. To test our hypothesis that spine count might be used as a replacement for pigmentation in *C. ramosissima*, we visually estimated the percentage pigmentation cover on each cut segment from that species in addition to counting the total number of spines.

Surface area was calculated by treating cholla segments as cylinders with one circular face (Fig. 1) using the formula *Surface Area = CL+(C2)2* where *C* is segment circumference and *L* segment length.

Azimuth angle of incoming solar radiation was found using Casio's online solar elevation angle calculator with the latitude and longitude coordinates 34°48'31.9"N, 115°37'42.1" and time of day set as 12 noon when incoming radiation would be at its greatest.

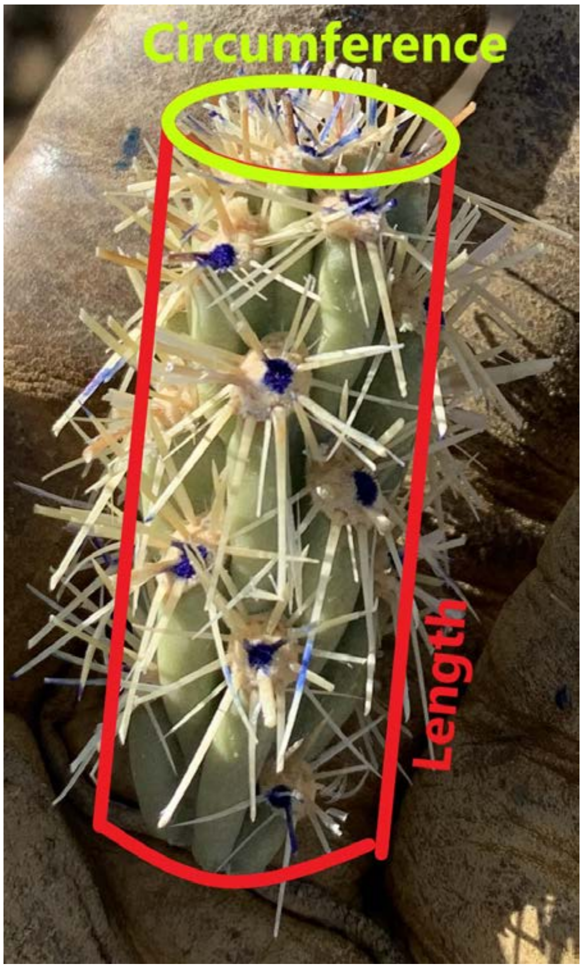

Figure 1. Buckhorn cholla segment illustrating representation as one-faced cylinder with circumference and length. We treated individual segments as cylinders with a single face, using the circumference at their widest point and overall length to create values for surface area. Length measurements were taken from the segment's point of attachment to the rest of the plant to the extent of their green, fleshy, photosynthetic shoot.

Statistical analyses were performed using JMP pro 15 statistical software (developed by SAS Institute, latest release October 2019) and RStudio (version 1.4.1103, latest release January 2021). To understand the relationship between sun azimuth angle and segment direction, we performed t-tests using the side of the plant (NE or SW) as an independent variable and segment direction (compass bearing, in degrees) as a dependent variable for each of our three species. An average azimuth angle of 206.1° was calculated from the 53 data points provided by Casio's solar elevation angle calculator and compared with the means of each group in order to determine whether segments grow towards the sun's azimuth and thus reduce their exposure to its damaging radiation. Additionally, in order to discern whether the cholla species were displaying adaptive plasticity on their sunny southwest sides, we performed a Bartlett test of heteroskedasticity comparing the variation in segment direction between the southwest and northeast sides of each cactus species. We used a t-test with individual cholla as a random effect to determine if there was a difference in spine density between the southwest and northeast sides of the chollas. To determine the effect of spines on pigmentation in *C. ramosissima* we performed a linear regression using individual cholla as a random effect.

RESULTS

Segment Orientation: The southwest-facing segments of all three cacti demonstrated a tendency to grow in line with the sun's azimuth angle of 206°, with southwest side *C. acanthocarpa* segments averaging 222° in orientation, southwest *C. echinocarpa* 234°, and southwest *C. ramosissima* 204° (Fig. 2). The Bartlett test for heteroskedasticity revealed that two of the three cactus species exhibited less orientation variability on their southwest sides than their northeast sides (*C. acanthocarpa*: K-squared = 12.9, p <0.001; *C. echinocarpa*: K-squared = 7.56, p<0.01). *C. ramosissima* showed no variance between the orientation of segments on the northeast and southwest side (K-squared = 0.644, p = 0.422).

Spine Density: Spine density did not vary from the northeast side of the plant to the southwest side for any of the three species. (*C. ramosissima:* N = 104, F = 0.0235, p = 0.879; *C. echinocarpa*: N = 89, F = 0.328, p = 0.568; *C. acanthocarpa:* N = 104, F = 0.135, p = 0.714).

Pigmentation: Pigmentation cover on the segments of *C. ramosissima* was not affected by total spine number (N=104, F = 1.45, p = 0.231).

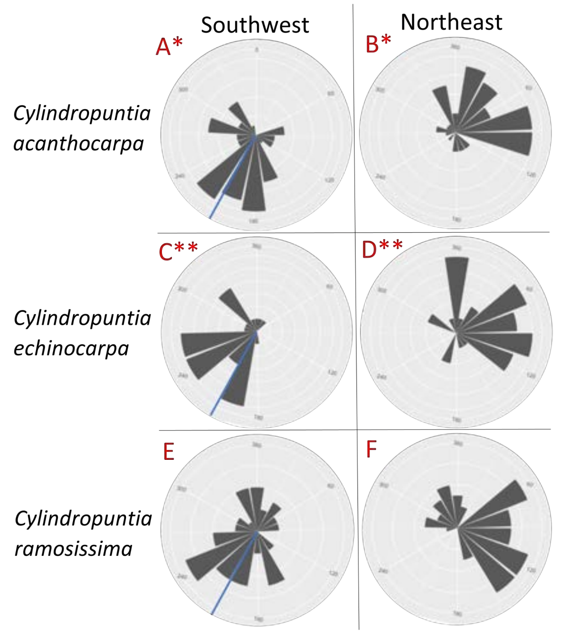

Figure 2. Orientation of segments on southwest sides of two cholla species demonstrate adaptive plasticity to grow with sun's azimuth angle. Circular histograms comparing orientation of observed segments on southwest and northeast sides of three cholla species. Direction of black bar indicates segment compass direction, and size of bar represents number of segments observed in that orientation. Segments on the southwest sides of buckhorn and silver cholla (A and C, respectively) demonstrate significantly lower variation in observed orientation than segments of the same species on the northwest side (B and D) based on the results of a Bartlett's test of heteroskedasticity (*C. acanthocarpa*: K-squared = 12.9, p < 0.001; *C. echinocarpa*: K-squared = 7.56, p < 0.01). This indicates a degree of adaptive plasticity allowing these species to match the sun's noon azimuth angle (when its radiation is most intense; 206°, indicated by blue line) and thereby reduce their exposure to its damaging direct rays. Significant pairings marked with asterisks.

DISCUSSION

C. echinocarpa, and *C. acanthocarpa* displayed segment orientation adaptive plasticity. Segments on the southwest side of the plate were oriented in a specific direction, towards the southwest, while segments on the northeast side were oriented randomly. On the southwest side of *C. echinocarpa*, and *C. acanthocarpa*, segments are directly exposed to UV radiation, and were found to orient themselves close to the 206° average azimuth. This orientation of the segments likely limits the amount of surface area that is exposed to sun rays, which in turn limits the amount of UV damage and water lost to transpiration. The relationship found between segment orientation and sun location concurs with the results of a study conducted by Zavala Hurtado et al. (1998) that the stem tilting of *Cephalocereus columna-trajani* minimizes the amount of sun exposure during the hottest seasons of the year. Our results imply that the position of the segment is an adaptive response to the sun's placement.

There was no difference in spine density between the southwest and the northeast side of the chollas. This suggests that spine density is a static morphological trait that is not affected by environmental factors such as sunlight. This is a surprising finding because it contrasts with studies that have documented similar species of cacti altering their spine production in response to sunlight (Leding 1934). Our results also contradict a 2016 study by De la Rosa-Manzano et al. which postulated that cactus spines are used primarily for sun shading.

No relationship was found between the spine density on a segment and the percent of pigmentation coverage on *C. ramosissima*. This pigmentation is likely an adaptation to protect the segment from UV radiation (Cockell et al. 2004), but no pattern in the presence of the pigmentation was found . *C. ramosissima* also did not display segment orientation plasticity, or spine density plasticity. Overall, *C. ramosissima* had fewer solar protection adaptations than *C. echinocarpa* and *C. acanthocarpa*. This lack of protection may account for the presence of mutations in *C. ramosissima* segments, as excessive UV radiation can cause mutation in plants (Evans et al. 2001). Out of the 50 *C. ramosissima* plants surveyed in the area studied, 5 were found with mutations, while no *C. echinocarpa* or *C. acanthocarpa* surveyed had mutations.

The three species of *Cylindropuntia* examined in this study displayed segment orientation plasticity that likely helps them prosper in the harsh environment of the Mojave Desert. The morphological adaptations used by the three cholla species help us understand organisms' adaptations to this harsh and unique ecosystem. Future studies can build off of the results of our study by researching the role of spine sheaths in the photosynthetic processes of *Cylindropuntia*. All spines on *Cylindropuntia* cacti are covered with reflective paper-like sheaths. The origin and purpose of these sheaths is unclear, but they may diffuse or filter out harmful radiation before it reaches the vulnerable tissue of the segments. A future study could investigate these properties by experimentally removing sheaths from some cholla segments and measuring variation in water retention and fitness across the plant. Another possible study could further investigate the somatic mutations we observed in pencil cholla. Levels of solar radiation could be experimentally varied between different segments of plants. Segments could also be separated by spine coverage, pigmentation, and orientation. Frequency of mutation could be used as a response variable for all these treatments.

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REFERENCES

Cockell, C. S., J. Berry, A. Southern, A. Herrera, and C. Yackulic. 2004. Protection from UV radiation in the economic crop, *Opuntia* SPP. *Economic Botany* **58:**S88–S100.

De la Rosa-Manzano, E., J. Flores, and P. Delgado-Sanchez. 2016. Effects of spine-shading on aspects of photosynthesis for three cactus species. *Botanical Sciences* **94:**301–310.

Drezner, T. D. 2020. The importance of microenvironment: *Opuntia* plant growth, form and the response to sunlight. *Journal of Arid Environments* **178:**104144.

Ehleringer, J., & Forseth, I. (1980). Solar tracking by plants. *Science* **210(4474):**1094–1098. doi:10.1126/science.210.4474.1094

Evans, Lance S., J. H. Sullivan, and M. Lim. 2001. Initial effects of UV-B radiation on stem surfaces of *Stenocereus thurberi* (organ pipe cacti). *Environmental and Experimental Botany* **46:**181–187.

Geller, G. N. and P. S. Nobel. 1987. Comparative cactus architecture and PAR interception. *American Journal of Botany* **74:**998–1005.

Hereford, R., R. H. Webb, and C. I. Longpre. Precipitation history of the Mojave Desert region, 1893–2001. Fact Sheet 117-03. U.S. Department of the Interior, U.S. Geological Survey, Flagstaff, Arizona, USA.

Huang, F., and W. Guo. 2013. Structural and mechanical properties of the spines from *Echinocactus grusonii* cactus. *Journal of Materials Science*. **48:**5420–5428.

Leding, A. R. 1934. A new spine character in cactus: *Echinocereus* from Texas shows "woolly" character in juvenile stage. *Journal of Heredity* **25:**327–328.

Miller, T. J. 2016. The causes and consequences of phenotypic plasticity in *Clarkia concinna* (Onagraceae). https://escholarship.org/uc/item/4p42x8cd

Owen, M. B. 2020. Variety is the spice of desert bird life: foundation plant species provide habitat heterogeneity for bird communities in the Mojave Desert. York University. http://hdl.handle.net/10315/37927.

Zaval-Hurtado, J. A., F. Vite, and E. Ezcurra. 1998. Stem tilting and pseudocephalium orientation in *Cephalocereus columna-trajani* (Cactacae): A Functional Interpretation. *Ecology* **79:**340–348.