esa ECOSPHERE

Asynchronous flowering patterns in saguaro cacti (*Carnegiea gigantea*)

Theresa Foley,[1] Don E. Swann,[2] Guadalupe Sotelo,[2] Nicholas Perkins,[2] and Daniel E. Winkler[3,†]

[1]*Sonora Environmental Research Institute, Inc. (SERI), P.O. Box 65782, Tucson, Arizona 85728 USA*
[2]*Saguaro National Park, 3693 South Old Spanish Trail, Tucson, Arizona 85748 USA*
[3]*U.S. Geological Survey, Southwest Biological Science Center, Tucson, Arizona 85719 USA*

Citation: Foley, T., D. E. Swann, G. Sotelo, N. Perkins, and D. E. Winkler. 2021. Asynchronous flowering patterns in saguaro cacti (*Carnegiea gigantea*). Ecosphere 12(12):e03873. 10.1002/ecs2.3873

Abstract. The saguaro cactus (*Carnegiea gigantea* [Engelm.] Britton & Rose) is a keystone species endemic to the Sonoran Desert of northern Mexico and the southwestern United States. The saguaro produces large white flowers near its stem apex (crown) during April–June, which bloom at night and close the following day. In 1924, Duncan Johnson reported that saguaro floral buds are likely to have an asymmetrical distribution in which buds occur in higher densities on the eastern half of a plant's crown. Using technology not available to Johnson, we tested his observations to determine whether flowers are asymmetrically distributed using repeat photography. We also tested whether there is a seasonal pattern of flowering that may explain Johnson's observations. We tracked intra-individual flowering phenology of 20 saguaros and measured 2372 flowers across two reproductive seasons in Saguaro National Park, Tucson, Arizona. Flowers first appeared on the east side of all saguaro crowns at the start of the reproductive season, and then spread radially in a counterclockwise direction as the season progressed. In contrast to previous reports, saguaro flowers were consistently more abundant on the northern part of the crown than in the eastern part. To our knowledge, this study is the first to document a seasonal, counterclockwise pattern of asynchronous flowering in saguaro or any angiosperm. We discuss potential drivers of this phenomenon as well as implications for saguaros responding to climate change.

Key words: *Carnegiea gigantea;* citizen science; columnar cactus; community science; desert plants; flower orientation; intra-individual flowering; phenology; phyllotaxis; reproductive strategy; saguaro; Sonoran Desert.

Received 24 May 2021; revised 26 July 2021; accepted 2 August 2021. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** dwinkler@usgs.gov

INTRODUCTION

Flowering phenology is perhaps the most common indirect measure of plant fitness and is often utilized to understand biotic interactions (Elzinga et al. 2007); phylogenetic dissimilarity (Kochmer and Handel 1986); plasticity and adaptive evolution (Anderson et al. 2012); and species and community responses to climate change (Mohan et al. 2019). Studies of phenological synchrony have been used to explain plant community dynamics (Augspurger 1983); the influence of microclimate variability on population success (Koenig et al. 2015); and the fitness consequences of warming as a driver of phenological mismatches between flowers and pollinating insects (Forrest and Thomson 2011, Kudo and Cooper 2019). Just as the timing of flowering is consequential to plant fitness, floral orientation and position can confer equally important fitness benefits by protecting pollen grains (Haverkamp et al. 2019), enhancing fertilization (Ushimaru et al. 2009), and facilitating ovule development (Wang et al. 2010, Figueroa-Castro and Valverde

2011). Flowers often orient toward the sun, presumably to take advantage of greater solar insolation and to provide optimal visual conditions for pollinators (Patiny 2011). Some species, most notably sunflowers, change their flower orientation to track the sun during the day (i.e., heliotropic flowers; Atamian et al. 2016). Alternatively, dioecious species may position flowers to enhance the presentation of female flowers over males (Hiraga and Sakai 2007). The fitness benefits of these patterns can include increased reproductive output via higher rates of pollination (Ushimaru et al. 2009, Lin and Forrest 2019) and temperature regulation to enable development of larger and more abundant seeds (Zhang et al. 2010). It is likely that flowering phenology and position both play a role in mediating individual plant fitness, but few studies have explored seasonal variation and intra-individual flowering patterns.

Many North American columnar cacti have flowers that primarily grow on the south-facing sides of their stems. Examples include the cardón (*Pachycereus pringlei*; Tinoco-Ojanguren and Molina-Freaner 2000) and the hairbrush cactus (*Pachycereus pecten-aboriginum*; Aguilar-Gastelum and Molina-Freaner 2015). Recent research suggests that this equatorial orientation may be related to the interception of photosynthetically active radiation, or PAR (Tinoco-Ojanguren and Molina-Freaner 2000, Warren et al. 2016*a*, 2017), which allows for a higher rate of carbon gain and therefore a higher production of flowers. South of the equator, columnar cacti have primarily north-facing flowers (Rundel 1974, Warren et al. 2016*b*). Although the majority of research on floral position in cacti has occurred in recent decades, work on the phyllotaxy, or arrangement of leaves, vascular tissues, and cephalia, is well-studied in the last half-century (Gibson 1973, 1978, Boke 1980, Cornejo and Simpson 1997, Altesor and Ezcurra 2003, Mauseth 2004, 2020). The relatively fixed arrangement of areoles in stem succulents may drive flowering strategies in columnar cacti species, although this has yet to be demonstrated. Testing this hypothesis may provide insight into the evolutionary ecology of adaptation in desert environments and other systems where high levels of light, radiation, and temperature play a critical role in determining ecosystem functioning (Noy-Meir 1973).

Perhaps the most iconic and well-studied columnar cactus is the saguaro (*Carnegiea gigantea* [Engelm.] Britton & Rose). Saguaros are unusual among columnar cacti in that nearly all flowers appear on the stem apex or crown, rather than along the sides of the stem. Floral buds arise from areoles located near the apex of the growing tip of the saguaro, which is “buried in a dense mass of white wool at the bottom of a cup-shaped depression two or three centimeters deep and from five to eight centimeters across” (Johnson 1924). Johnson noted that saguaro flowers are typically asymmetrically distributed, being more numerous on the eastern half and generally absent from the north side of the crown. He also observed that floral development is temporally advanced on the east or east-southeast side, with flowers opening on one side and progressing in two waves around the crown.

A century later, most sources on cactus bloom orientation cite Johnson’s (1924) observations and state that saguaro flowers occur primarily on the east or southeast side of the crown (Nobel 1978, Tinoco-Ojanguren and Molina-Freaner 2000, Anguilar-Gastelum and Molina-Freaner 2015). However, while collecting data during a multi-year study of saguaro flowering phenology in Saguaro National Park, we observed that flowering patterns are more complex than Johnson described. This paper revisits Johnson’s observations and tests them empirically for the first time by using technology that was not available 100 yr ago. Our goal was to determine how the location of flowers on the saguaro crown changes during the April–June reproductive season. In turn, we answer two questions: (1) Are flowers evenly distributed across individual saguaro crowns or are flowers asymmetrically distributed as Johnson (1924) observed; and (2) Do flowers appear in a particular order as the reproductive season progresses or is flowering phenology spatially random across the crown and temporally spread out during the reproductive season? We answered these questions with flowering data from 20 individual plants at Saguaro National Park, capturing 1766 photographs that enabled us to track 2372 saguaro flowers across two reproductive seasons. In doing so, our study documents novel flowering phenologies that have implications for understanding adaption in desert environments and the ability of the species to respond to changing climate.

Materials and Methods

Study site and species

This study was conducted in the western Tucson Mountain District of Saguaro National Park (Fig. 1; 32.25, −111.20), approximately 20 km northwest and at a similar elevation (approximately 800 m asl) as Johnson's study site on Tumamoc Hill (Johnson 1924). The Tucson Mountain District is comprised of about 24,000 acres of low Sonoran Desert ecosystem, 90% of which is composed of thorn scrub and saguaro habitat (McAulifee 1996). Our study site (Fig. 1) is located on the east slope of a monticule at 792 m asl, approximately 367 m northeast of the Red Hills Visitor Center.

The iconic saguaro cacti (*Carnegiea gigantea*) is a large columnar cactus endemic to the Sonoran Desert of the southwestern United States and Sonora, Mexico. It is a keystone species in the Sonoran Desert, providing resources to more than 100 species, including many insects, birds, and the lesser long-nosed bat (*Leptonycteris curasoae yerbabuenae*; Drezner 2014). The saguaro reaches reproductive age at approximately 35–65 yr of age and may live for 150+ years (Steenbergh and Lowe 1983). The saguaro is of great cultural importance to members of the Tohono O'odham Nation, who utilize the fruit as a food source (Brum 1973) and the rib wood as building material (Pater and Siquieros 2000). Other visually dominant plants of the Sonoran Desert

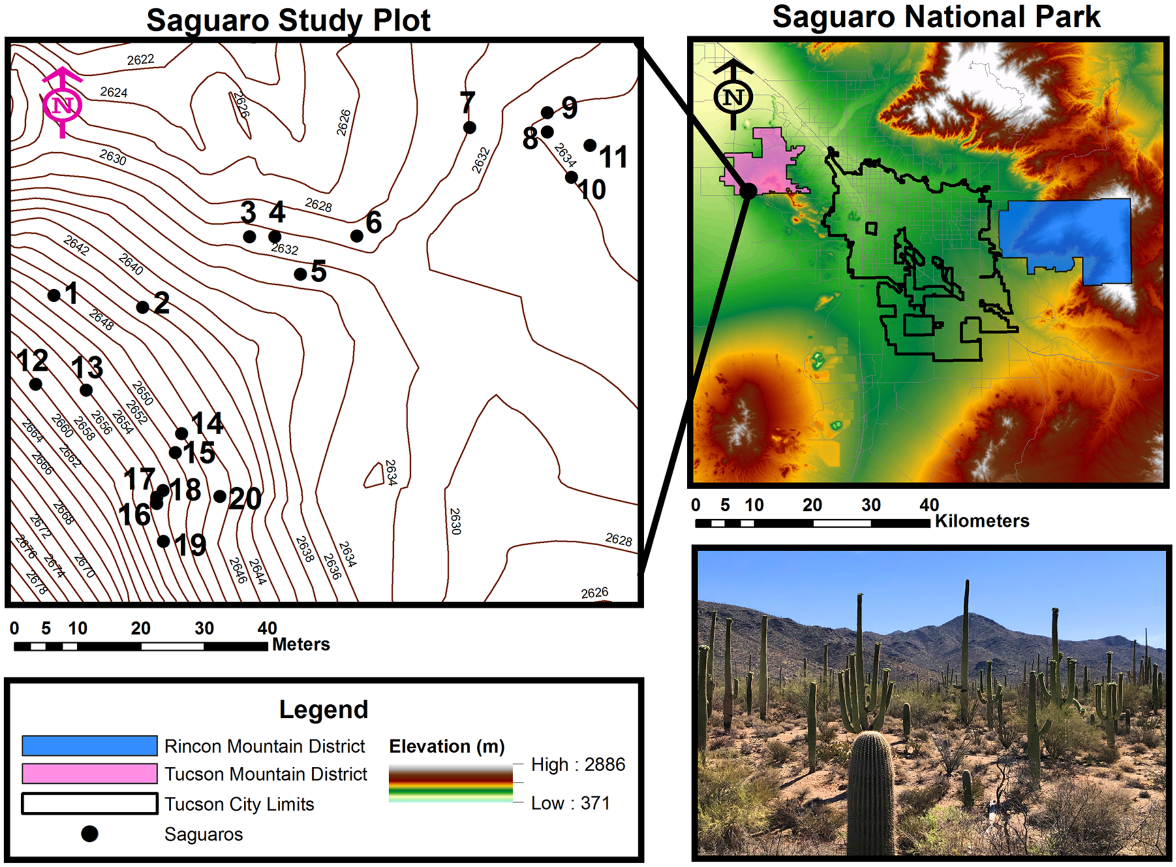

Fig. 1. Topographic distribution of the 20 individual saguaros in the present study. Saguaro National Park has two districts, with the City of Tucson (black outline) located between them. The Tucson Mountain District (pink polygon) is located to the west of the Tucson city limits, and the Rincon Mountain District (blue polygon) is located to the east of the city. Also pictured is the population of saguaros tracked in the present study. Photograph by Theresa Foley.

include leguminous trees such as foothill palo verde (*Parkinsonia microphyllum*), blue palo verde (*P. floridum),* and velvet mesquite (*Prosopis velutina*), which shelter and protect young saguaros from environmental extremes (Turner 1963).

Precipitation in the Sonoran Desert has a bimodal distribution. The first rainy season occurs during the winter and early spring, when westerly frontal systems bring rain to the desert. The North American Monsoon (and to a lesser degree, dissipating tropical cyclones from the eastern Pacific Ocean) is responsible for a second rainy season from approximately the beginning of July to early autumn (Weiss et al. 2009). The saguaro typically begins producing floral buds during the last two weeks of April in the northern portion of its range (Steenbergh and Lowe 1977), triggered by winter rains as well as warmer temperatures and increasing day length (Bowers 1996, Renzi et al. 2019), with flowers typically appear during May and June. Each flower is open for approximately 24 h, initially opening around nightfall (Steenbergh and Lowe 1977). The saguaro fruit, which ripens in late June to mid-July, is an important source of food and moisture during the hot season between the winter and monsoonal rains (Drezner 2014). Germination of seeds occurs with the arrival of the summer rains. Renzi et al. (2019) found that warmer temperatures were correlated with an earlier onset of saguaro blooming and a higher number of flowers, while increased precipitation appeared to delay blooms and reduce the number of flowers.

Field protocol

We recorded the height, number of branches (arms), and GPS coordinates of 20 saguaros from the study plot. All saguaros were >2 m tall (the approximate height of first reproduction; Steenbergh and Lowe 1983) and less than 8 meters tall (the length of our photographic pole). To photograph individual saguaro crowns, we attached a digital camera (Nikon Coolpix S3700, Minato City, Tokyo, Japan) to a 0.6 m PVC pipe mounted 0.5 m from the top of an extendable flagpole. The camera connected to a Lenovo Yoga (LenovoPad YT3-850F, Quarry Bay, Hong Kong) via the tablet's Wireless Mobile Utility application, so that the tablet holder had a live view of what the camera lens was capturing (Fig. 2).

Data were collected by Saguaro National Park staff, interns, and volunteer community scientists, who photographed the crown of the main stem and the saguaro arms, typically 6 d/week from ca. 6:00–8:00 local time. When we started observations on 18 April 2017, 14 of the 20 study saguaros already had floral buds. To capture saguaro flowering as well as bud formation, in 2018 we began our surveys on 4 April when only one saguaro had buds. For simplicity, we report only flowering data but discuss floral buds when appropriate. We confined our analysis to the crown of the main saguaro stems because branches sometimes twist in response to environmental factors (Steenbergh and Lowe 1976).

Photographic analyses

To orient each saguaro crown, we laid a line on the ground that ran due magnetic north approximately 2 m from the base of the saguaro. We photographed each saguaro crown with the reference line; oriented photographs toward true north; and overlaid a transparent, digital compass over each photograph. The angle of declination is +9° 35′ east in Tucson. We divided the compass into 12 ordinal directions that each span 30° (Fig. 2). Appendix S1: Table S1 lists the degree ranges, names, and abbreviations of each ordinal direction. For example, the North direction encompasses 345–15°.

We counted the number of open flowers in each ordinal direction for every photograph and recorded the presence and absence of floral buds. We did not count individual buds because they varied greatly in size and were oftentimes, too numerous to count accurately. Given that buds and flowers can be up to 12 cm in length and will sometimes bend, we assigned individual buds and flowers to the ordinal direction where each floral base was located. On occasional days when photographs were of poor quality or not available, we used photographs from the days prior and after to count the flowers and determine the presence or absence of buds. One-day-old flowers appear slightly open, often with some of the white petals still visible, and two-day-old flowers have a textured-yellow top (Renzi et al. 2019).

Statistical analyses

We found that rose diagrams best illustrated the seasonal pattern of saguaro flower

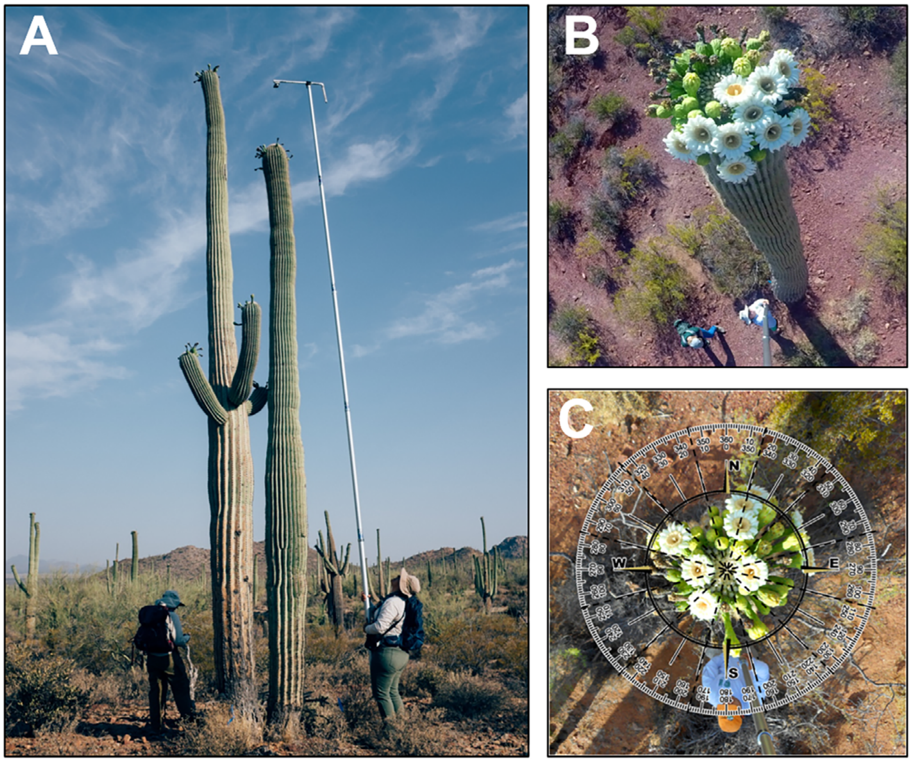

Fig. 2. Photographing the top of a saguaro using an extendable flagpole with a camera mounted on top and connected wirelessly to a tablet (A and B). Photograph of saguaro crown with compass superimposed, used to determine the ordinal direction of buds and flowers (C). Photographs by the National Park Service.

distributions over the saguaro crown, while box, and whisker plots best illustrated inter-individual variability for the beginning and end of the flowering period for each direction. We visualized the total number of flowers surveyed each year and calculated the mean angle of flowers across all individuals using the procedures of Zar (1976). We also visualized the total number of flowers and calculated the mean angle for each individual saguaro (see Appendix S1). To determine whether the spatial distribution of flowers is not uniform, we performed a circular chi-square goodness-of-fit test on the total number of flowers produced each year as well as on the individual saguaros (Watson 1987). Because the circular chi-squared analysis requires a minimum of 30 data points, we did not calculate the mean angle for saguaros having fewer than 30 flowers.

We also created rose diagrams to visualize the change in flower production over the entire reproductive season. To minimize the number of figures required without diminishing the visual representation of the seasonal progression, we collapsed data into four-day intervals. Last, we combined this with box and whisker plots to illustrate inter-individual variability in the first and last flower produced each year for each ordinal direction. Statistical analyses were carried out in R 4.0.4 (R Core Team, 2021) and Microsoft Office. Data are publicly accessible in the National Park Service's Data Store (IRMA: Integrated Resource Management Applications Portal; https://irma.nps.gov/DataStore; dataset 2287617).

RESULTS

We tracked a total of 972 flowers across 20 individual saguaros in 2017, and 1,400 flowers in 2018. Overall, flowers were most abundant in the NNW direction in 2017 (mean angle = 332°) and were not uniformly distributed (χ^2 = 130.96,

$P < 0.001$; Table 1; Fig. 3). The distribution of flowers varied slightly in 2018 and were more abundant in the North direction (mean angle = 345°) but, similar to the previous year, were not uniformly distributed (χ^2 = 80.10, $P < 0.001$; Table 1; Fig. 3). Saguaros produced fewer flowers in 2017 compared to 2018, and total counts varied by direction. For example, saguaros produced 33 flowers in the SSE direction in 2017 (Appendix S1: Table S2) but 89 flowers in the same direction in 2018 (Appendix S1: Table S3). Flower production doubled in the ENE direction in 2018 (total flowers = 124) compared to 2017 (total flowers = 62). Overall, saguaros produced more flowers in each direction in 2018, although the magnitude of change varied between years (Fig. 3).

The 2017 and 2018 total flowers produced by each saguaro show a spatial pattern of fewer flowers in the southerly directions of the crown (Appendix S1: Tables S2, S3; Appendix S1: Figs. S1, S2). The 2017 mean angle of flowers produced by each individual varied from 77–358° but was generally in the WNW to North directions (Appendix S1: Table S4). The 2018 mean angle of flowers produced by each individual varied from 6–355° but was generally in the North to NNE directions (Appendix S1: Table S5). Though not directly tested, there does not appear to be a relationship between total flowers produced and the height or number of branches of each individual. The average height of the 20 saguaros included in this study was 5.49 m (range = 2.04–7.9 m) and fewer than half of the individuals tracked had one or more branches (Appendix S1: Tables S4, S5).

Table 1. Total observed flowers each year (*n*), the mean angle and associated direction, and χ^2 testing whether 2017 and 2018 flower distributions were not uniform.

Year	*n*	Mean angle	Direction	χ^2	*P*
2017	972	332	NNW	130.96	<0.001
2018	1400	345	N	80.10	<0.001

Flower production data collapsed into four-day intervals showed a strong seasonal trend each year, with flowers appearing first in the east, then in north and west before finishing production in the south (Figs. 4 and 5). Although saguaros were producing flowers in new directions as the season progressed, production continued in other directions as well and peaked in mid to late May in both 2017 and 2018. The spatial and temporal progression of flowering is most evident in the timing of the first and last flowers produced in each direction (Fig. 6).

The start and end of the flowering season varied between years and individuals (Appendix S1: Tables S4, S5). Saguaros started flowering earlier in 2017 (20 April; DOY = 110)

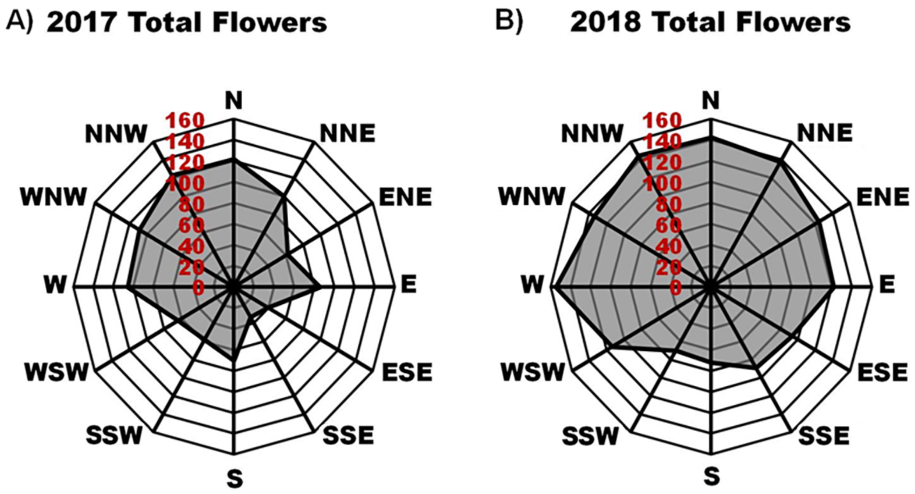

Fig. 3. Rose diagrams illustrating the total number of flowers produced in each ordinal direction across the 20 study saguaros. Flower counts are presented for (A) 2017 and (B) 2018.

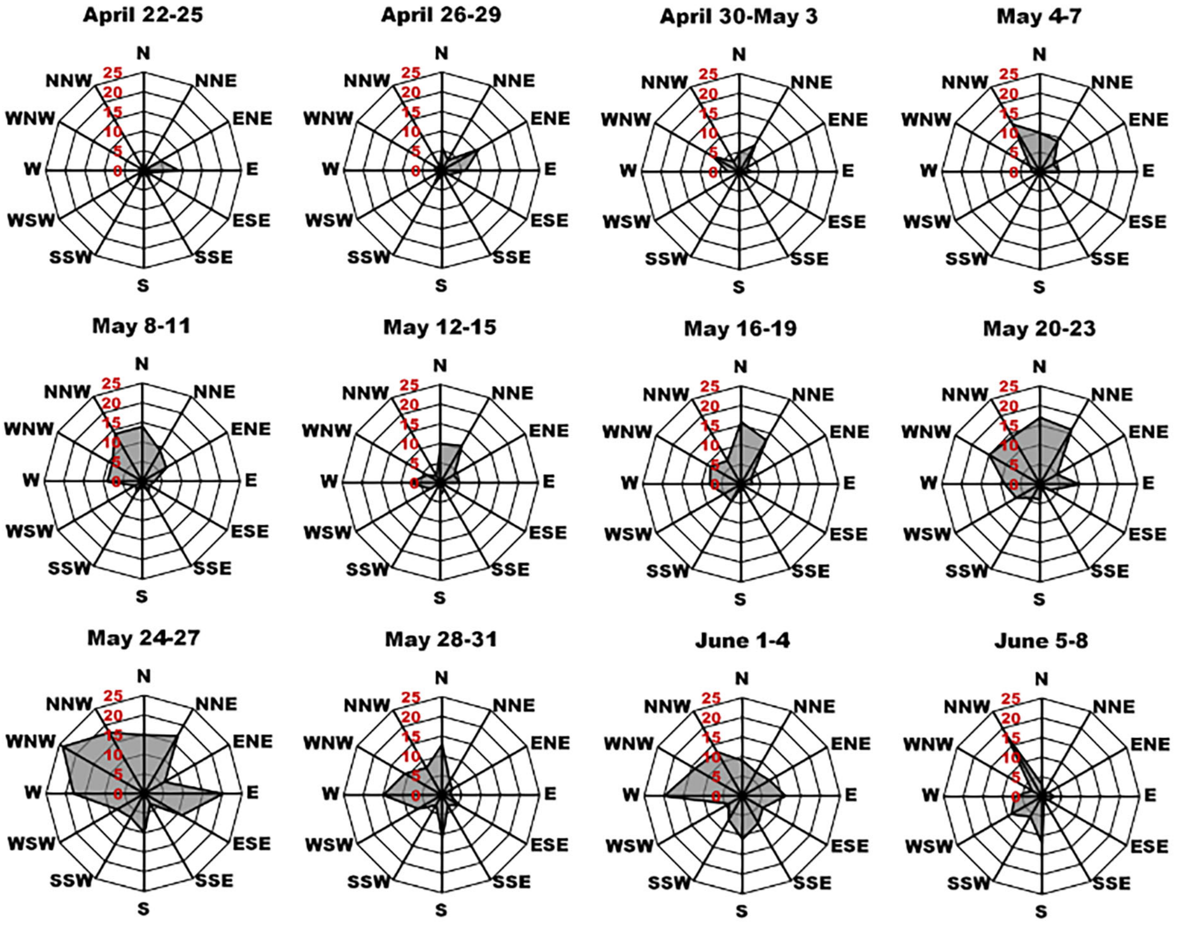

Fig. 4. Rose diagrams of the total number of flowers produced in 2017 in each ordinal direction across the 20 study saguaros. Data are separated into 4-d periods to illustrate the seasonal progression of flowering, moving left to right across each row. Shaded portions of each diagram represent the total number of flowers open during each 4-d period.

compared to 2018 (28 April; DOY = 118), and they stopped flowering later in 2017 (27 June; DOY = 178) compared to 2018 (20 June; DOY = 171). The day of first flower across all directions on the saguaro crown ranged from 110–146 in 2017 and 118–164 in 2018. The last day of flower ranged from 131–178 in 2017 and 127–171 in 2018. The duration of flowering ranged from 7–45 d in 2017 (excluding one individual that did not flower) and 2–32 d in 2018. Overall, 2017 was a longer, more variable flowering season among individuals across the different directions measured (i.e., higher variation between days of first and last flowers). 2018 was shorter and less variable, despite saguaros producing 30% more flowers than they did in 2017.

DISCUSSION

Our study was inspired by natural history observations of the iconic saguaro cactus that remained untested for nearly 100 yr (Johnson 1924). Major technological advances since then and the commitment of volunteer community scientists enabled us to revisit and expand upon some of the observations in Johnson (1924). In doing so, we identified novel flowering phenology patterns that, prior to this study, had never been measured in saguaros or any other angiosperm that we are aware of. Using measurements of 2372 flowers from 20 individual plants across two reproductive seasons at Saguaro National Park, we show that flowers are asymmetrically

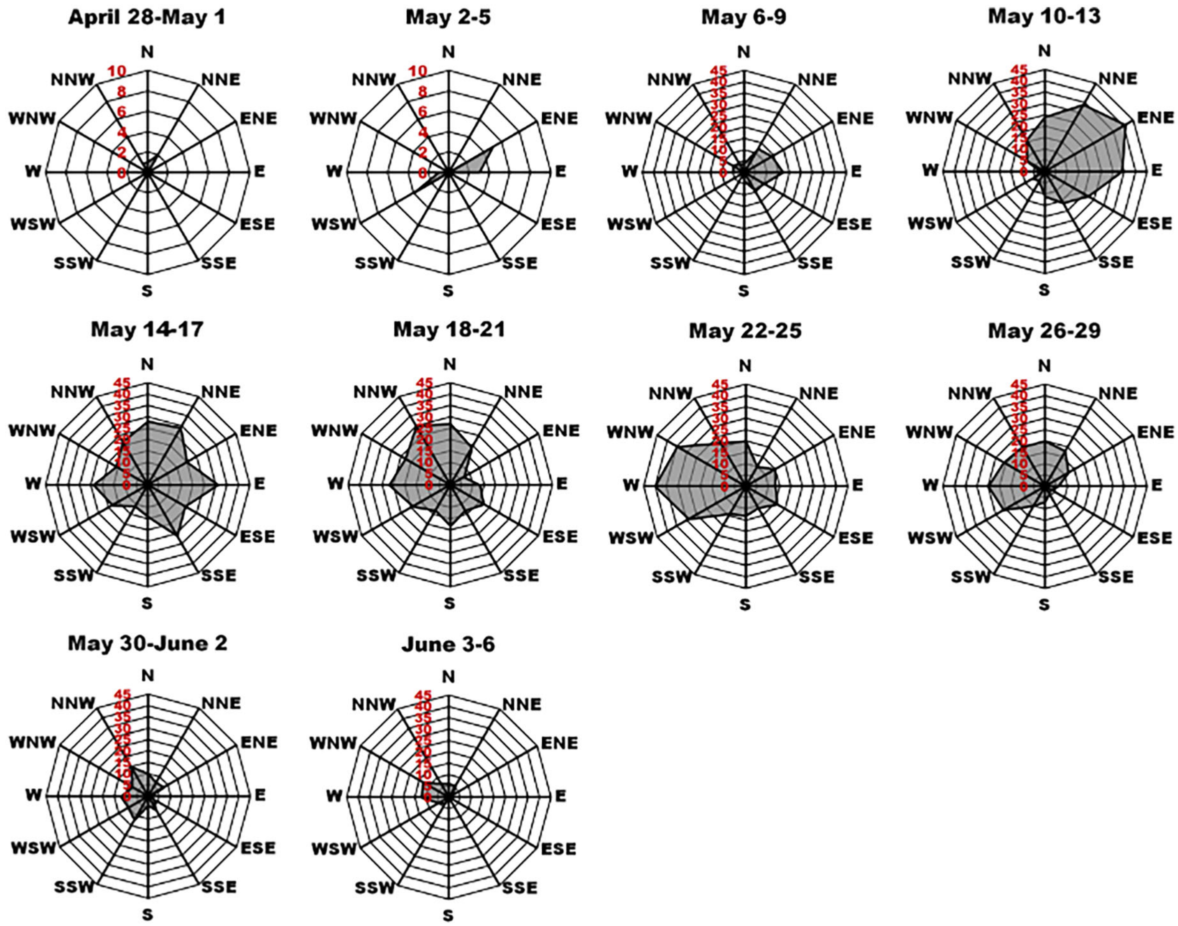

Fig. 5. Rose diagrams of the total number of flowers produced in 2018 in each ordinal direction across the 20 study saguaros. Data are separated into 4-d periods to illustrate the seasonal progression of flowering, moving left to right across each row. Note the smaller scale for the first two periods displayed, which was done so to make the relatively few flower observations visible. Shaded portions of each diagram represent the total number of flowers open during each 4-d period.

distributed across individual plant crowns, and the distribution appears to vary across years.

More importantly, our results demonstrate that flower production occurs in a predictable pattern across individual saguaros. That is, flowering is spatially asynchronous within individuals, with flowers blooming in a counterclockwise pattern starting on the portion of the crown facing east. In addition, flowering is mostly temporally synched in each direction across individual plants. Our results also confirm Johnson's (1924) observation that flowers develop first on the eastern side of the crown, but contradict his statement that most or all of the buds on the north side of the stem will not mature. In our study, flowers in northern areas of the crown not only reached maturity but were also more abundant over the course of the entire season than flowers with eastern and southern aspects. Together, these insights provide a better understanding of the flowering phenology of a keystone species that supports at least 100 additional species across the Sonoran Desert (Drezner 2014) and also suggest a multitude of avenues for future research to examine how saguaros and related species are responding and will continue to respond to changing climate.

This paper results from a long-term, community science, saguaro phenology study initiated

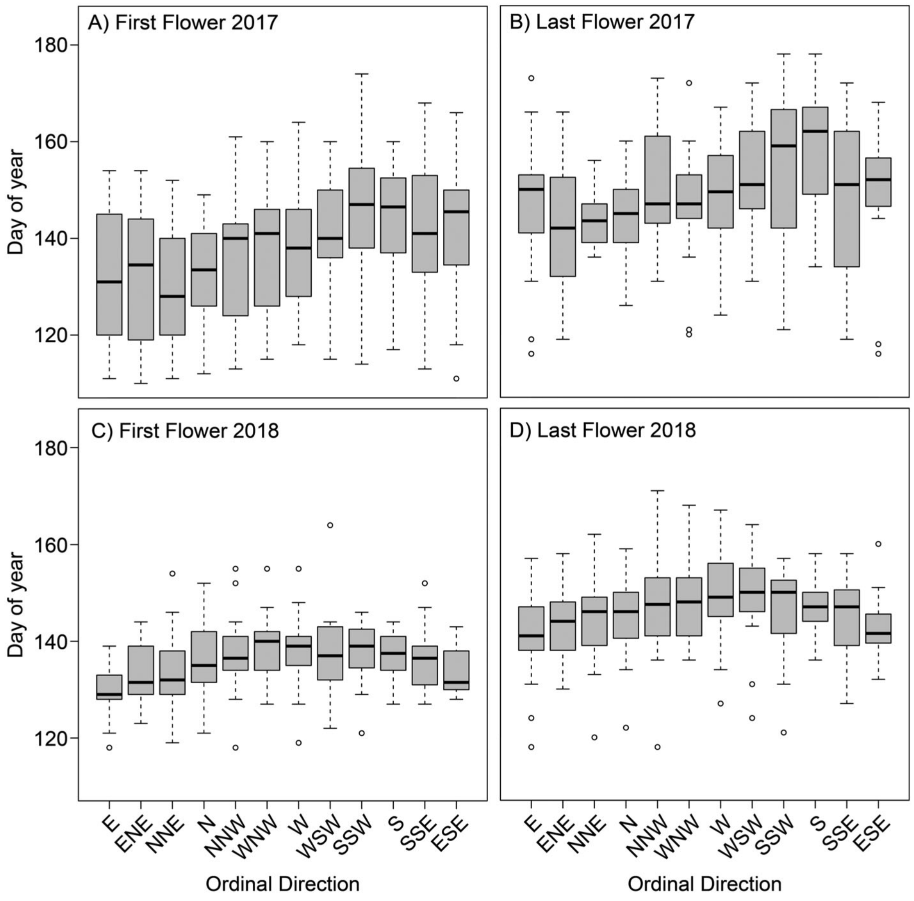

Fig. 6. Box and whisker plots representing inter-individual (*n*#x2009;= =#x2009;= 20) variability in saguaro flowering phenology. Day of year of the first flower (A) and last flower (B) produced in each ordinal direction in 2017; and first flower (C) and last flower (D) produced in each ordinal direction in 2018. The bottom and top of each box denote the 1st and 3rd quartile, the thick black link indicates the median value, and the whiskers are 1.5× the interquartile range. Individual points are any values outside the whiskers range.

by the National Park Service, which is researching how warmer temperatures and drier conditions will affect saguaro flowering. When Johnson made his saguaro observations a century ago in 1915, the Sonoran Desert was cooler. In Saguaro National Park, the average temperature has increased 1.2 ± 0.2°C/century from 1950 to 2010, as compared to the nationwide average of 0.3 ± 0.2°C/century from 1895 to 2010 (Gonzalez et al. 2018). Renzi et al. (2019) found that warmer temperatures were correlated with earlier saguaro blooming and higher flower yields, while increased precipitation was correlated with the delayed onset of flowering and decreased flower yields. Steenberg and Lowe (1977) observed that, in Tucson, saguaro bud development usually begins during the last 15 d of April. In 2017, we began our observations within this time window on 18 April and most saguaros already had buds. To capture the beginning of saguaro budding, we began our 2018 observations on 4 April. While most of the 2018 budding occurred within the last two weeks of April, even on 4 April we observed some buds. The earlier observation of buds could be attributed to photography, which enabled us to see tiny buds up to 8 m off the ground not visible to the human eye. Another explanation is that warmer temperatures could be causing saguaros to bloom earlier. Future research planned at this site should provide additional understanding regarding saguaro phenological controls and cues.

We cannot be certain why our results differ from Johnson's frequently cited conclusion that saguaro flowers generally occur in the eastern half of the crown, although we acknowledge future work with additional years of data should aim to disentangle this. Nonetheless, our study site in Saguaro National Park is at a similar elevation, only 20 km from Johnson's site at the Desert Research Laboratory. The most plausible explanation is the length of the two studies: Johnson visited the Tucson area from the east coast, conducted his research at the beginning of the blooming season during April and May of 1915, and appears to have left Tucson sometime in May. We carried out our observations from April to June and observed that flowering peaked during the last two weeks of May and the first week of June. Renzi et al. (2019) found that higher temperatures are correlated with earlier blooming and a larger number of flowers in saguaros. Under the cooler temperatures of a century ago, it is possible that flowering may have peaked even later in the season and that Johnson's conclusions were based on limited seasonal data.

More difficult to explain is why saguaro flowers do not tend to have an equatorial orientation. In most columnar cacti, flowers appear on the side of the stem with an equatorial direction that maximizes exposure to sunlight. In the Northern Hemisphere, they tend to produce flowers on the south side of the stem (Tinoco-Ojanguren and Molina-Freaner 2000, Aguilar-Gastelum and Molina-Freaner 2015), while cacti in the Southern Hemisphere have flowers facing predominantly north (Warren et al. 2016*b*, 2017). Warren et al. (2017) make the case that location of flowers in the Atacama Desert cactus Eulychnia saintpieana (*Eulychnia breviflora*) is more energetically favorable, because it reduces the energy needed to translocate photosynthetic products to the non-photosynthetic reproductive tissue. There may also be some selection pressure from pollinators that prefer warmer flowers (Patiny 2011) or may even serve as a defense mechanism against potential pests (Navas et al. 1991). This is likely evidenced by the fact that saguaros produce flowers on areoles near the apex of their stems and lower occurring areoles solely produce spines for defense. Additionally, in the Northern Hemisphere cardón espinoso (*Pachycereus weberi*) flowers facing southward produced more ovules and seeds that were heavier (Figueroa-Castro and Valverde 2011). Although we did not measure reproductive output in terms of fruit or seed production, a saguaro 4.5 meters tall is capable of producing 100 fruits a year even before it grows arms. With an estimated 2,250 seeds per fruit, this equates to upwards of 225,000 seeds capable of being produced per individual per season (Steenbergh and Lowe 1977). Given that flower production varied widely between individuals and years, future work may examine the potential impacts of floral location on reproductive output in saguaros.

We speculate that non-equatorial flower orientation in the saguaro may be due to physiological constraints related to having apex flowers while growing in a region where freezing temperatures are possible as late as March. Saguaro meristem growth produces phyllotactic ribs (orthostichies) that give rise to the saguaro's characteristic morphology and this in turn yields areoles that are uniformly arranged on the surfaces of the stem (Mauseth 2021). Saguaro flowers are thus constrained by the fixed location of areoles near the apex of the plant (Barthlott and Hunt 1993) and the corresponding microclimate conditions at the surface location of each areole. The saguaro is the most northern columnar cacti species and has evolved to be relatively cold tolerant (Lowe and Steenbergh 1981, Steenbergh and Lowe 1983), since freezing temperatures are a part of the annual climate cycle in the northern Sonoran Desert (Steenbergh and Lowe 1976, Weiss and Overpeck 2005). Adaptations to cold temperatures may place constraints on how much heat reproductive organs can tolerate during the warm, dry Sonoran Desert fore-summer.

Our novel observations that flower locations change seasonally in saguaros, appearing initially in the east, then counterclockwise in other ordinal directions of the crown may also be related to saguaro physiological constraints. We are not aware of previous studies that looked at progressive changes in location of saguaro flowers over a season, although Johnson (1924) anecdotally observed that "...flowers open in a quite definite succession..." Producing flowers near the stem apex, and altering placement during the course of the season, could allow saguaros to take advantage of warmer temperatures and greater insolation during the cooler early spring while minimizing the more deleterious heat effects later in the season. A reasonable hypothesis is that as temperature and/or PAR vary seasonally, different parts of the crown produce flowers in response to these changes. Previous work has shown that temperature thresholds are required to produce flowers in other cacti species (Rowher and Heins 2007, Chu and Chang 2020, Drezner 2021). This is likely true in saguaros as well, though it has yet to be explicitly tested. Thermal regulation as a driver of floral development and subsequent position may also help the saguaro to reduce moisture loss, especially during the hot and dry weather plants experience in late May and early June. Yeaton et al. (1980) found that saguaros on moisture limited slopes have significantly narrower inter-rib distances, deeper inter-rib depths, and longer spines on the southern side of their stems as compared to the northern side. There were no such north–south differences with saguaros on the flats with relatively higher available soil moisture, suggesting that these differences were moisture conserving adaptations. Steenberg and Lowe (1983) state that the role of saguaro spines in thermoregulation needs further study. The role of saguaro bud and flower position on the crown for moisture conservation and thermoregulation has not yet been studied in the peer-reviewed literature.

An alternative hypothesis for our observed patterns of flower production is that as areas of the crown become filled with buds, and then flowers and fruit, new buds must then form in unoccupied areas. Areas that have optimal conditions in terms of PAR interception and temperature are occupied by buds first, then successive areas are occupied, with the least optimal areas occupied last. Although not explicitly tested, we did observe anecdotally that individual saguaros that produced buds later in the season when temperatures were much higher also tended to produce buds first in the east and north, and later in the west and south. Flower location could also change in relation to seasonal changes in pollinator species, although there is little evidence to support this in saguaros. Columnar cacti in the Sonoran Desert reduce inter-species competition for pollinators by the timing of flower opening (Fleming 2000). Cardón (*Pachycereus pringlei*), organ pipe (*Stenocereus thurberi*), and senita (*Lophocereus schottii*) cacti open their flowers right at sunset and usually close before noon the next day. Saguaro flowers open one and a half to two hours after sunset and do not close until the late afternoon of the next day, enabling saguaros to have both daytime and nighttime pollinators. The lesser long-nosed bat (*Leptonycteris curasoae yerbabuenae*), white-winged dove (*Zenaida asi atica*), native bees, and honeybees are all effective saguaro pollinators (Fleming 2000).

Results from our study suggest that the location of reproductive structures in saguaros may be more complex than originally suggested by Johnson (1924). Because digital photography and other new technology now makes collecting highly detailed, long-term data on flowering ecology much simpler than in the past, we anticipate new developments in our understanding of reproductive patterns in saguaro cacti that could provide insights into flowering and environmental conditions in other cacti and succulents. Moreover, with changes in climate there may be some potential in using patterns in bud and flower locations as a more precise monitoring tool, and the saguaro may be used as ecological indicator of change. The dearth of studies on seasonal, intra-individual flowering patterns in plants, including in cacti, suggests that more work is needed to explore flowering ecology at finer levels and relate this to biotic and abiotic selection pressures that can be used to explain differences between taxa. The evolutionary histories of columnar cacti are only recently being deciphered and diversification among related taxa has at times been explained by strong selection from environmental conditions during periods of hyperaridity (Merklinger et al. 2021). Studying the production of flowers around the saguaro crown will improve our understanding of flowering ecology in general, particularly in cacti that also exhibit flowering on cylindrical perennial stems.

ACKNOWLEDGMENTS

This study was supported by the Friends of Saguaro National Park, Western National Parks Association, and Latin Heritage Internship Program. Contributions from DEW were supported by the Ecosystems and Land Resources Mission Areas of the U.S. Geological Survey and National Park Service. We thank the staff of Saguaro National Park for support, and numerous community science volunteers and park interns who ventured out daily into the summer heat to photograph saguaros, especially Blu Au, Melisa Bohlman, Emma Fajardo, and Martha Tullis. We thank Perry Grissom, Rob Massatti, Kenneth Chapin, and the anonymous reviewers for helpful comments on the manuscript. This study would not be possible without the inspiration and guidance of saguaro *aficionado* William Peachey. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Aguilar-Gastelum, I., and F. Molina-Freaner. 2015. Orientación de las flores de dos poblaciones norteñas de Pachycereus pecten-aboriginum (Cactaceae). Botanical Sciences 93:241–247.

Altesor, A., and E. Ezcurra. 2003. Functional morphology and evolution of stem succulence in cacti. Journal of Arid Environments 53:557–567.

Anderson, J. T., R. I. Colautti, D. W. Inouye, A. M. McKinney, and T. Mitchell-Olds. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proceedings of the Royal Society B: Biological Sciences 279:3843–3852.

Atamian, H., B. K. Blackman, E. A. Brown, N. M. Creux, A. G. Garner, and S. L. Harmer. 2016. Circadian regulation of sunflower heliotropism, floral orientation, and pollinator visits. Science 353:587–590.

Augspurger, C. K. 1983. Phenology, flowering synchrony, and fruit set of six neotropical shrubs. Biotropica 15:257–267.

Barthlott, W., and D. R. Hunt. 1993. Cactaceae Flowering plants· Dicotyledons. Pages 161–197. Springer, Berlin, Heidelberg.

Boke, N. H. 1980. Developmental morphology and anatomy in Cactaceae. BioScience 30:605–610.

Bowers, J. E. 1996. Environmental determinants of flowering date in the columnar cactus Carnegiea gigantea in the northern Sonoran Desert. Madroño 43:69–84.

Brum, G. D. 1973. Ecology of the saguaro (Carnegiea gigantea): phenology and establishment in marginal populations. Madroño 22:195–204.

Chu, Y.-C., and J.-C. Chang. 2020. Regulation of floral bud development and emergence by ambient temperature under a long-day photoperiod in white-fleshed pitaya (*Hylocereus undatus*). Scientia Horticulturae 271:109479.

Cornejo, D. O., and B. B. Simpson. 1997. Analysis of form and function in North American columnar cacti (tribe Pachycereeae). American Journal of Botany 84:1482–1501.

Drezner, T. D. 2014. The keystone saguaro (Carnegiea gigantea, Cactaceae): a review of its ecology, associations, reproduction, limits, and demographics. Plant Ecology 215:581–595.

Drezner, T. D. 2021. Areole spacing and numbers on Opuntia littoralis cladodes are not associated with environmental conditions. Southwestern Naturalist 64:235–239.

Elzinga, J. A., A. Atlan, G. Bernasconi, A. Biere, L. Gigord, A. E. Weis, and G. Bernasconi. 2007. Time after time: flowering phenology and biotic interactions. Trends in Ecology and Evolution 22:432–439.

Figueroa-Castro, D., and P. Valverde. 2011. Flower orientation in Pachycereus weberi (Cactaceae): effects on ovule production, seed production and seed weight. Journal of Arid Environments 75:1214–1217.

Fleming, T. H. 2000. Pollination of cacti in the Sonoran Desert. American Scientist 88:432–439.

Forrest, J. R., and J. D. Thomson. 2011. An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. Ecological Monographs 81:469–491.

Gibson, A. C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). Biotropica :29–65.

Gibson, A. C. 1978. Architectural designs of wood skeletons in cacti. Cactus and Succulent Journal of Great Britain 40:73–80.

Gonzalez, P., M. Notaro, D. J. Vimont, F. Wang, and J. W. Williams. 2018. Disproportionate magnitude of climate change in United States national parks. Environmental Research Letters 13:104001.

Haverkamp, A., I. T. Baldwin, B. S. Hansson, M. Knaden, X. Li, and F. Yon. 2019. Flower movement balances pollinator needs and pollen protection. Ecology 100:e02553.

Hiraga, T., and S. Sakai. 2007. The effects of inflorescence size and flower position on biomass and temporal sex allocation in *Lobelia sessiliflora*. Plant Ecology 188:205–214.

Johnson, D. S. 1924. The influence of insolation on the distribution and on the developmental sequence of the flowers of the giant cactus of Arizona. Ecology 5:70–82.

Kochmer, J. P., and S. N. Handel. 1986. Constraints and competition in the evolution of flowering phenology. Ecological Monographs 56:303–325.

Koenig, W. D., J. M. Knops, W. J. Carmen, and I. S. Pearse. 2015. What drives masting? The phenological synchrony hypothesis. Ecology 96:184–192.

Kudo, G., and E. J. Cooper. 2019. When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. Proceedings of the Royal Society B: Biological Sciences 286:20190573.

Lin, S.-Y., and J. R. Forrest. 2019. The function of floral orientation in bluebells: interactions with pollinators and rain in two species of Mertensia (Boraginaceae). Journal of Plant Ecology 12:113–123.

Lowe, C. H., and W. F. Steenbergh. 1981. On the Cenozoic ecology and evolution of the sahuaro (Carnegiea gigantea). Desert Plants 3:83–86.

Mauseth, J. D. 2004. Giant shoot apical meristems in cacti have ordinary leaf primordia but altered phyllotaxy and shoot diameter. Annals of Botany 94:145–153.

Mauseth, J. D. 2020. Shoot Apical Meristem Stability and Non-Fibonacci Phyllotaxy in Ribbed Cacti. International Journal of Plant Sciences 181:518–528.

Mauseth, J. D. 2021. Shoot apical meristem growth in saguaro (Carnegiea gigantea, Cactaceae) is episodic and radially asymmetrical rather than uniform. International Journal of Plant Sciences 182:161–173.

McAuliffe, J. R. 1996. Saguaro cactus dynamics. University of Arizona Press, Tucson, Arizona, USA.

Merklinger, F. F., M. Arakaki, T. Böhnert, F. Luebert, D. Quandt, and M. Weigend. 2021. Quaternary diversification of a columnar cactus in the driest place on earth. American Journal of Botany 108:184–199.

Mohan, J. E., J. T. Anderson, K. Benavides, P. T. Frankson, R. Hannifin, L. M. Kueppers, and D. E. Winkler. 2019. Plant reproductive fitness and phenology responses to climate warming: results from native populations, communities, and ecosystems Ecosystem Consequences of Soil Warming. Pages 61–102. Elsevier, Cambridge, MA.

Navas, S. V., R. Beshear, J. Funderburk, T. Mack, and S. Olson. 1991. Seasonal patterns of *Frankliniella* spp. (Thysanoptera: Thripidae) in tomato flowers. Journal of Economic Entomology 84:1818–1822.

Nobel, P. S. 1978. Surface temperatures of cacti-influences of environmental and morphological factors. Ecology 59:986–995.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Pater, M. J., and B. Siquieros. 2000. Saguaro cactus: cultural significance and propagation techniques in the Sonoran Desert. Native Plants Journal 1:90–94.

Patiny, S. 2011. Evolution of plant-pollinator relationships. Volume 81. Cambridge University Press, Cambridge, UK.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Austria, Vienna.

Renzi, J. J., K. L. Gerst, and W. D. Peachey. 2019. A decade of flowering phenology of the keystone saguaro cactus (*Carnegiea gigantea*). American Journal of Botany 106:199–210.

Rohwer, C. L., and R. D. Heins. 2007. Daily light integral, prevernalization photoperiod, and vernalization temperature and duration control flowering of easter cactus. HortScience 42:1596–1604.

Rundel, P. 1974. Trichocereus in the Mediterranean zone of central Chile. Cactus and Succulent Journal 46:79–81.

Steenbergh, W. F., and C. H. Lowe. 1976. Ecology of the saguaro: I. The role of freezing weather in a warm-desert plant population. *Research in the Parks: Transactions of the National Park Centennial symposium, National Park Service Symposium Series No. 1*, 49–92.

Steenbergh, W. F., and C. H. Lowe. 1977. Ecology of the saguaro, II: reproduction, germination, establishment, growth, and survival of the young plant. *Research in the Parks: Transactions of the National Park Centennial symposium, National Park Service Symposium Series No. 1*, 228 pages.

Steenbergh, W. F., and C. H. Lowe. 1983. Ecology of the saguaro, III: growth and demography. *Research in the Parks: Transactions of the National Park Centennial symposium, National Park Service Symposium Series No. 1*, 242 pages.

Tinoco-Ojanguren, C., and F. Molina-Freaner. 2000. Flower orientation in Pachycereus pringlei. Canadian Journal of Botany 78:1489–1494.

Turner, R. M. 1963. Growth in 4 species of Sonoran Desert trees. Ecology 44:760–765.

Ushimaru, A., I. Dohzono, F. Hyodo, and Y. Takami. 2009. Flower orientation enhances pollen transfer in bilaterally symmetrical flowers. Oecologia 160:667–674.

Wang, Y., Y. W. Duan, L. H. Meng, and Y. P. Yang. 2010. Change in floral orientation in Anisodus luridus (Solanaceae) protects pollen grains and facilitates development of fertilized ovules. American Journal of Botany 97:1618–1624.

Warren, S. D., L. E. Aguilera, and L. S. Baggett. 2016*a*. Directional orientation of reproductive tissue of *Eulychnia breviflora* (Cactaceae) in the hyperarid Atacama Desert. Revista Chilena De Historia Natural 89:10.

Warren, S. D., L. S. Baggett, and H. Warren. 2016*b*. Directional floral orientation in Joshua trees (Yucca brevifolia). Western North American Naturalist 76:374–378.

Warren, S. D., L. E. Aguilera, L. S. Baggett, and M. Zuñiga. 2017. Floral orientation in Eulychnia acida, an arborescent cactus of the Atacama Desert, and implications for cacti globally. Ecosphere 8:e01937.

Watson, R. E. 1987. Two educational comparisons of linear and circular statistics. Dissertations 2501. Loyola University, Chicago, IL.

Weiss, J. L., C. L. Castro, and J. T. Overpeck. 2009. Distinguishing pronounced droughts in the Southwestern United States: seasonality and effects of warmer temperatures. Journal of Climate 22:5918–5932.

Weiss, J. L., and J. T. Overpeck. 2005. Is the Sonoran Desert losing its cool? Global Change Biology 11:2065–2077.

Yeaton, R. I., R. Karban, and H. B. Wagner. 1980. Morphological growth patterns of saguaro (*Carnegiea gigantea*: Cactaceae) on flats and slopes in Organ Pipe Cactus National Monument, Arizona. Southwestern Naturalist 25:339–349.

Zar, J. H. 1976. Two-sample and multisample testing of circular data. Behavior Research Methods and Instrumentation 8:329–330.

Zhang, S., H.-L. Ai, D.-Z. Li, H. Wang, and W.-B. Yu. 2010. Flower heliotropism of Anemone rivularis (Ranunculaceae) in the Himalayas: effects on floral temperature and reproductive fitness. Plant Ecology 209:301–312.

DATA AVAILABILITY STATEMENT

Data are available from the National Park Service's Data Store IRMA (Integrated Resource Management Applications): https://irma.nps.gov/DataStore/Reference/Profile/2287617

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3873/full