



8-27-2014

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Taly Dawn Drezner
York University, Canada, drezner@yorku.ca

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Recommended Citation

Drezner, Taly Dawn (2014) "Regional branching relationships in *Carnegiea gigantea*, a keystone cactus," *Western North American Naturalist*. Vol. 74 : No. 2 , Article 2.

Available at: <https://scholarsarchive.byu.edu/wnan/vol74/iss2/2>

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REGIONAL BRANCHING RELATIONSHIPS IN *CARNEGIEA GIGANTEA*, A KEYSTONE CACTUS

Taly Dawn Drezner¹

ABSTRACT.—The large columnar cactus *Carnegiea gigantea* branches to increase reproductive output. The branches of this keystone species also provide shelter to a large portion of the Sonoran Desert's fauna. In this study, branch length was used to reconstruct branch establishment at 2 populations to determine branching patterns over time and the relationship across populations. Branches showed high establishment but relatively low survival. Either more branches establish than eventually survive or growth is slow when branches are smaller, thereby biasing the distribution of lengths due to the differences in growth rate. Also, the distribution of branch lengths (i.e., branch generation over time) reflects a cohort pattern, indicating that there are favorable and poor years for branch production. Further, a significant relationship in peaks and troughs is detected between the 2 very different populations, suggesting a regional influence over branching that extends beyond a population or local area.

RESUMEN.—El gran cactus columnar *Carnegiea gigantea* se ramifica para aumentar su potencial reproductivo. Las ramas y los frutos adicionales de esta especie clave también proveen refugio a una gran porción de la fauna del Desierto de Sonora. En este estudio, la longitud de la rama se usó para reconstruir el establecimiento de la rama en dos poblaciones para determinar los patrones de ramificación a lo largo del tiempo y la relación entre distintas poblaciones. Las ramas mostraron un alto establecimiento, pero una supervivencia relativamente baja. Se establecieron más ramas de las que al final sobrevivieron, el crecimiento fue más lento cuando las ramas eran más pequeñas, separando de este modo la distribución de longitudes debidas a diferencias en la tasa de crecimiento. También, la distribución de la longitud de las ramas (es decir, generación de ramas a lo largo del tiempo) refleja un patrón de cohorte, indicando que hay años pobres y otros favorables para la producción de ramas. Además, se detectó una relación significativa en los picos y los puntos mínimos entre dos poblaciones muy diferentes, sugiriendo una influencia regional en la ramificación que se extiende más allá de una población o de un área local.

Carnegiea gigantea (Engelm.) Britton & Rose (Cactaceae, saguaro) establishes in cohorts that are often separated by decades with little to no regeneration (e.g., Turner 1990). Favorable periods include adequate to ample precipitation, lack of freezes, and mild temperatures (Brum 1973, Steenbergh and Lowe 1976, 1983, Pierson and Turner 1998), and cohort establishment has been linked to conditions associated with El Niño (Drezner and Balling 2002) and periods of active volcanism worldwide (Drezner and Balling 2008). Survivorship is far below 0.01% from seed to one year of age (Steenbergh and Lowe 1977), and mortality then quickly diminishes in the first few years, until old-age mortality begins (Steenbergh and Lowe 1983).

Flowers and fruits are produced on new growth on branches and on the stem apex (Johnson 1924, Steenbergh and Lowe 1977). Individuals produce branches to increase seed production. The first branch essentially doubles

the reproductive output of the plant; the second branch triples reproductive output, and so forth (Steenbergh and Lowe 1983). Individuals located in regions that receive more winter rainfall take advantage of the extra water to produce branches (Drezner 2003a), whereas branches are added sparingly in drier areas to conserve water (Yeaton et al. 1980, Geller and Nobel 1986).

Branches begin forming on plants of different ages and different heights across their range (Drezner 2013). Steenbergh and Lowe (1983) suggest branching is controlled by apical dominance. A study in Organ Pipe Cactus National Monument (OPCNM) suggested that branching may start at a minimum plant diameter (Yeaton et al. 1980). Winter rain increases branching (Drezner 2003a), but the trigger for branching is not well understood; Bowers (1996) found that winter rain is the initial trigger of flowering. Branches establish disproportionately to the south of the plant (Drezner 2003b),

¹Department of Geography, N430 Ross, York University, 4700 Keele Street, Toronto, Ontario M3J 1P3, Canada. E-mail: drezner@yorku.ca

and branch positioning maximizes photosynthetic surface area (Geller and Nobel 1986). The additional photosynthetic surface area available on any given branch, as well as the additional water storage, do not always fully offset the cost of producing more branches and reproductive structures (Geller and Nobel 1986). When individuals are in close proximity, conspecific competition for water reduces branching (McAuliffe and Janzen 1986) because *Carnegiea* have shallow surface roots (McAuliffe 1984). In the more arid west, the reduced branching is coupled with lower susceptibility to freezing mortality in the characteristically lower elevations there (Drezner 2006a). Very little research has been done on branching patterns of columnar cacti (Cody 1984) or on branch growth rates (e.g., Steenbergh and Lowe 1983).

This study aims to evaluate population-wide branch demographics to determine whether branches establish periodically or consistently through time. I tested whether branching occurs in cohorts, similar to the establishment of the plant itself, rather than evenly over time. Thereafter, I examined the data for regional similarities in branch cohorts.

METHODS

Study Site

The Sonoran Desert is characterized by 2 seasons of rainfall. In winter, extratropical cyclones sweep through the region and bring widespread rainfall (Sheppard et al. 2002), whereas in summer, the monsoon drives localized thunderstorm development (Carleton 1986, 1987).

The Tucson Mountain District of Saguaro National Park (SNP-W; Fig. 1) is home to dense stands of *Carnegiea gigantea*, estimated at ≥ 4 plants $\cdot 100 \text{ m}^{-2}$, and generally high vegetation cover (perhaps 75%; Drezner 2006a) that results from the relatively high rainfall enjoyed at this locale, both in winter and summer. January precipitation averages 24.6 mm at the nearby Tucson 17 NW (#028795) meteorological station, and July precipitation averages 51.3 mm (mean annual precipitation 326.1 mm). SNP-W is within the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951, Turner and Brown 1994) at an elevation of about 750 m (at SNP-W), with mean maximum temperatures of 38.3 °C in July (at Tucson 17 NW).

The Kofa site is located at the boundary of the Kofa National Wildlife Refuge (Fig. 1), in the arid western part of the species' range. Rainfall in both seasons is much lower at Kofa NWR than at SNP-W, averaging 13.0 mm in January and 12.2 mm in July (mean annual precipitation 127.8 mm) at the nearby Quartzsite (#026865) meteorological station. Rainfall ultimately limits the species not far to the west (Turner et al. 1995). Average maximum temperatures in July are 42.3 °C (Quartzsite) at this Lower Colorado River Valley subdivision site (Shreve 1951, Turner and Brown 1994), which is found at about 400 m elevation. As a result, vegetation cover is lower (7%) than at SNP-W, and *Carnegiea* densities have been estimated at 0.2 plants $\cdot 100 \text{ m}^{-2}$ (Drezner 2006a).

Field and Statistical Methods

At SNP-W, data collection commenced near the visitor center. At Kofa (33°32' N, 114°10' W), sampling began at the boundary of the Kofa National Wildlife Refuge where it intersects with a dirt road. A back and forth sweeping motion was used across the site to sample individuals. Only branched plants were sampled, and unhealthy individuals were excluded. Large washes were also excluded because they concentrate surface water availability locally and may thus bias results. A total of 209 branches were sampled at the 2 sites. For each branched individual, branch length was determined using a telescoping leveling rod that measured to the nearest centimeter.

The length of each of the branches was listed, and a frequency distribution was created for each site. A weighted mean of 9 was calculated for each locale for smoothing. For example, the weighted mean for 10-cm branches is $[\text{freq } 6\text{cm} + 2(\text{freq } 7\text{cm}) + 3(\text{freq } 8\text{cm}) + 4(\text{freq } 9\text{cm}) + 5(\text{freq } 10\text{cm}) + 4(\text{freq } 11\text{cm}) + 3(\text{freq } 12\text{cm}) + 2(\text{freq } 13\text{cm}) + \text{freq } 14\text{cm}]/25$. Growth rates of whole plants at SNP-W are nearly twice those of whole plants at Kofa (Drezner 2005). Branch growth rates are unknown (though branching and reproductive effort is related to growth rate [Steenbergh and Lowe 1983]) making graphical comparisons and correlation difficult. Drezner (2003c) developed a method to estimate apical plant growth. Drezner's (2003c) model involves a general growth curve and a multiplicative site-specific factor that adjusts for differences in main stem growth rates under different



Fig. 1. Range of *Carnegiea* in the northern Sonoran Desert. Range adapted from Turner et al. (1995). The Kofa and SNP-W field sites are marked.

environmental and climatic conditions (Drezner 2003c). This factor is an index value that can be used to compare growth rates in different populations. Although the relationship between branch growth rate and primary stem growth under varying environmental conditions is also unknown, relative growth rates of branches surely reflect differences in the environment. I assume that if a plant grows twice as fast at site A than at site B (for example), then branch growth will similarly be twice as fast at any given length. For example, at any given height, a plant with a factor of 0.70 will grow twice as fast as plant with a factor of 0.35. It is important to highlight that this ratio has been previously established for these 2 sites (Drezner and Balling 2002, Drezner 2003c) and has simply been applied here. These values were

not established in this study nor manipulated to fit the current study. Thus, I applied Drezner (2003c) to the branch lengths specifically for the *relative* growth rate (the multiplicative factor), but not for the actual age calculation of the branch. Because *Carnegiea* growth varies over the plant's lifetime and the age-height relationship is nonlinear for the main stem, applying the model to branch growth for age is questionable because we do not know the variation in branch growth from year to year or at different lengths. Some data suggest that the very slow growth observed in the main stem is not paralleled in branch growth, such as third year branches already being reproductive at 15 cm in length (Steenbergh and Lowe 1977). Previous research (Drezner 2005) found that the growth rate index value at Kofa

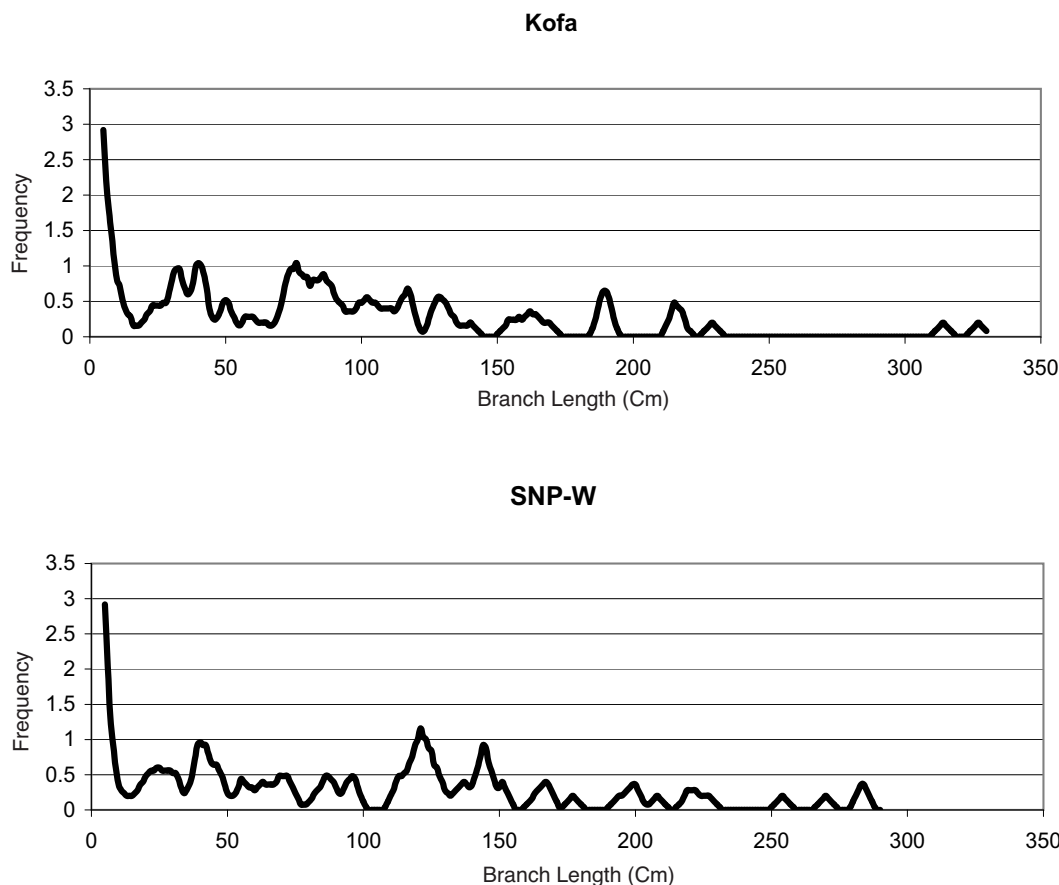


Fig. 2. Distribution of branch lengths at Kofa and Saguaro National Park, West (SNP-W), smoothed using a weighted mean. The horizontal axis represents branch lengths (cm). The vertical axis represents the frequency (smoothed) of branches at each given length. These data also represent establishment frequencies (coupled with the survivorship of those branches).

is 0.411, whereas at SNP-W it is 0.743. The branch lengths at Kofa were multiplied and adjusted to match the growth rate at SNP-W. Each branch length (in cm) in the weighted frequency distribution for Kofa was multiplied by 0.411/0.743.

The frequency distribution for SNP-W, along with the adjusted frequency distribution for Kofa (to match SNP-W), were analyzed. A Pearson product-moment correlation was run to find the relationship between the frequencies at the 2 sites. To reduce bias from the high frequencies for the shortest lengths, I ran 2 correlations: a broad analysis from 20 to 290 cm and a second analysis that focused on the concentration of data, spanning the lengths from 10 to 120 cm. These lengths were selected based on a visual inspection of the frequency distribution (Fig. 2).

RESULTS

Sampled branch lengths varied from 1 to 327 cm ($n = 106$) at Kofa, and 1 to 284 cm ($n = 103$) at SNP-W. The most distinct feature of the branch frequency histogram (by height) is the large number of very small branches at both sites, followed by the relative flattening of the frequency curve (Fig. 2). For example, at Kofa, there are 23 branches that are 1–5 cm in length and only 5 that are 6–10 cm. Similarly, at SNP-W, there are 25 branches that are 1–5 cm and only 3 that are 6–10 cm.

The results of the Pearson correlations for the frequencies of branches at different lengths at the 2 sites were significant for both the 20–290 cm range ($n = 271$, $r = 0.430$, $P = 1.3 \times 10^{-13}$) and the 10–120 cm range ($n = 111$,

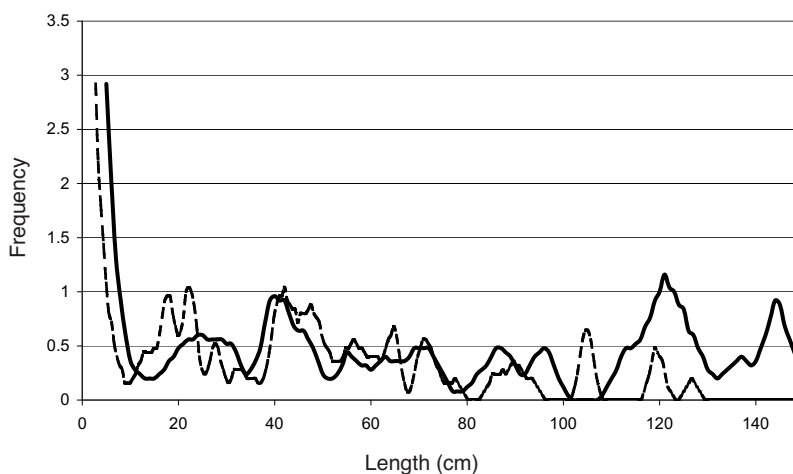


Fig. 3. Kofa (dashed line) and SNP-W (solid line) branching adjusted for growth rate. The horizontal axis represents branch lengths (cm) at SNP-W. The vertical axis represents the frequency (smoothed) of branches at each given length. The data for Kofa are adjusted for different growth rates at the 2 sites, making horizontal axis units irrelevant for the Kofa site. That is, plants at Kofa grow at about 55% the rate of those at SNP-W. Thus, branch lengths were multiplied to adjust them to the SNP-W frequency curve.

$r = 0.414$, $P = 6.2 \times 10^{-6}$). The relationship in branch establishment at the 2 sites can be seen graphically as well (Fig. 3).

DISCUSSION

I observed that the distribution of branch lengths (i.e., branch generation over time) reflects a cohort pattern. There are peaks and troughs in the establishment of branches over time. This pattern suggests that branch production is triggered by temporally varying climatic conditions. The peaks and troughs overlap at the 2 study sites, particularly for shorter branches. Branches established during many of the same periods at both sites, and there are common “good years.” Despite differences in precipitation receipt, presence of vegetation, and growth rate (Drezner 2006b), the correlation between the 2 sites is statistically significant. This relationship suggests that a regional (or larger area-scale) influence (likely rainfall) triggers branching. *Carnegiea* establishes in cohorts due to climatic requirements for establishment and short-term survival (Turner 1990, Pierson and Turner 1998), including notable temporary weather fluctuations such as El Niño (Drezner and Balling 2002) and changes associated with global volcanic eruptions (Drezner and Balling 2008). Large winter rain events and high rainfall totals

trigger flowering (Bowers 1996), number of branches (Drezner 2003a), and branching at lower heights on the plant (Drezner 2013). Thus, winter rainfall is likely important for triggering branching in any given year, thus promoting branch cohorts in good years (though branch development does not necessarily occur exclusively during favorable years).

The significant correspondence between these 2 sites after adjustment of stem growth supports the idea that branch growth rates reflect overall growth rate at that site and lends support to the possibility that the growth factor of branches may be similar (or proportional) to that of the main stem.

There also appears to be a mortality curve for branches that is somewhat similar to that of the plant itself. Of the $<0.1\%$ of seeds that germinate, $<0.5\%$ survive their first year of life, and mortality then declines (Steenbergh and Lowe 1977, 1983). The pattern for branches, although less extreme, similarly shows high establishment but relatively low “survival” of the branches generated. Either more branches establish than eventually survive in the first few years or, like the plant itself, growth is slow when branches are smaller, and thus short branches are overrepresented. Steenbergh and Lowe (1977) note that 3-year-old branches may reach 8–16 cm in length and may already be producing fruits; although data are geographically

(and thus environmentally) limited, this suggests that slow growth rate alone cannot explain this pattern and that some attrition of branches occurs. If branches are indeed lost in higher numbers shortly after development, the cause is unknown. It may be weather related (e.g., wet winter triggers branch development, and those branches are subsequently lost) or even related to faunal consumption or interference, but these ideas are entirely speculative.

The peaks and troughs in each curve suggest that branching is not regular in any population, but rather, just as good and bad years define the natural cohort structure of *Carnegiea* populations, so do certain favorable years for branch establishment. Because there is no method to estimate branch age, these high and low periods cannot be matched to real dates and thus also cannot be matched to climate or other temporal data to ascertain the precise driving variables, though precipitation (including winter precipitation) would be expected to be important based on past research (Bowers 1996, Drezner 2003a). The significant relationship in peaks and troughs between these 2 very dissimilar sites further suggests that the underlying variables that determine the good and bad years or periods for branch production are likely regional in scale (at least), though some local effects would be expected in any situation. Further, the data suggest that the branches may be a microcosm of the plant, as branches exhibit a cohort structure like the population, and may well be characterized as having a mortality curve, as the plants themselves do.

ACKNOWLEDGMENTS

I thank Kevin Gelfand for field assistance.

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Received 17 May 2013
Accepted 28 February 2014