FACTORS AFFECTING THE NUMBER OF ARMS ON A SAGUARO (*CARNEGIEA GIGANTEA*)

RICHARD L. HUTTO

Division of Biological Sciences, University of Montana, Missoula, MT 59812
Correspondent: hutto@mso.umt.edu

ABSTRACT—The average number of arms on a saguaro (*Carnegiea gigantea*) increases with saguaro height, but there is considerable variation among saguaros for any given height. This variation has been largely attributed to variation in water availability among individual plants. To test this hypothesis, I recorded the height and number of arms of a sample of 425 saguaros within Organ Pipe Cactus National Monument along with values of three variables that should affect arm production through their effect on water availability: (1) the number of neighboring saguaros under the same nurse tree canopy, (2) the presence of a wash within 5 m, and (3) the presence and identity of any living or dead plant associate. Deviation from the number of arms expected for a given saguaro height was negatively related to the number of saguaro neighbors and positively related to the presence of a nearby wash. Saguaros growing with live associates also had fewer arms than those growing alone, and saguaros growing with dead associates had more arms than those growing alone. Each of these results is consistent with the idea that arm production is affected by water availability.

RESUMEN—El número promedio de brazos en un saguaro (*Carnegiea gigantea*) aumenta con su altura, a pesar de que existe variación considerable para cualquier altura. Esta variación se ha atribuido mayormente a la variación en la disponibilidad de agua entre individuos de saguaro. Para probar esta hipótesis, registré la altura y el número de brazos de una muestra de 425 saguaros dentro del Organ Pipe Cactus National Monument, además de valores de tres variables que pudieran afectar la producción de brazos por su efecto en la disponibilidad de agua: (1) el número de saguaros vecinos bajo el mismo dosel del árbol nodriza, (2) la presencia de un arroyo dentro de 5 m, y (3) la presencia e identidad de cualquier planta asociada viva o muerta. La desviación del número de brazos esperados para una dada altura estuvo relacionada negativamente con el número de saguaros vecinos y relacionada positivamente con la presencia de un arroyo cercana. Los saguaros creciendo en asociación con plantas vivas también tuvieron menos brazos que los que crecieron solos, y los saguaros creciendo con plantas asociadas muertas tuvieron más brazos que los que crecían sin ellas. Cada uno de estos resultados es consistente con la idea de que la producción de brazos se ve afectada por la disponibilidad de agua.

A conspicuous feature of many saguaros (*Carnegiea gigantea*) is the presence of arms, which serve to increase the number of fruits and seeds produced by the plant (Steenbergh and Lowe, 1977), ultimately increasing its reproductive potential (Yeaton et al., 1980; Steenbergh and Lowe, 1983). Still, why some saguaros display more than a dozen arms while other cacti never produce a single one is not entirely clear. It takes time to accrue arms, and the earliest age at which a saguaro might branch is around 60 years, or after it has reached about 4 m in height (Steenbergh and Lowe, 1977, 1983). Additional arms take time to develop, so we would expect saguaro height, which increases with age, to be correlated with the number of arms a saguaro has accrued. Indeed, a relationship between saguaro height and number of arms has been documented by McAuliffe and Janzen (1986), who provided a height–arm regression equation for a series of about 100 saguaros, and by Drezner (2003*a*), who provided another height–arm regression based on 238 saguaros. In both studies, saguaro height accounted for only about 10% of the variation in number of arms, so other factors must affect arm production as well.

In addition to age, water availability was suggested decades ago (e.g., Yeaton et al., 1980) to be the key to understanding variation in saguaro morphology, but it was not until the work of McAuliffe and Janzen (1986) that the effect of water availability on the number of saguaro arms was investigated more directly. McAuliffe and Janzen (1986) showed not only that the presence of saguaro neighbors produced a measurable effect on water uptake during rainfall events, but that the number and closeness of saguaro neighbors was, in turn, negatively related to the number of arms at a given saguaro height. Taken together with information from correlative studies of water availability and branching patterns (Yeaton et al., 1980; Steenbergh and Lowe, 1983; Drezner, 2003*a*), water

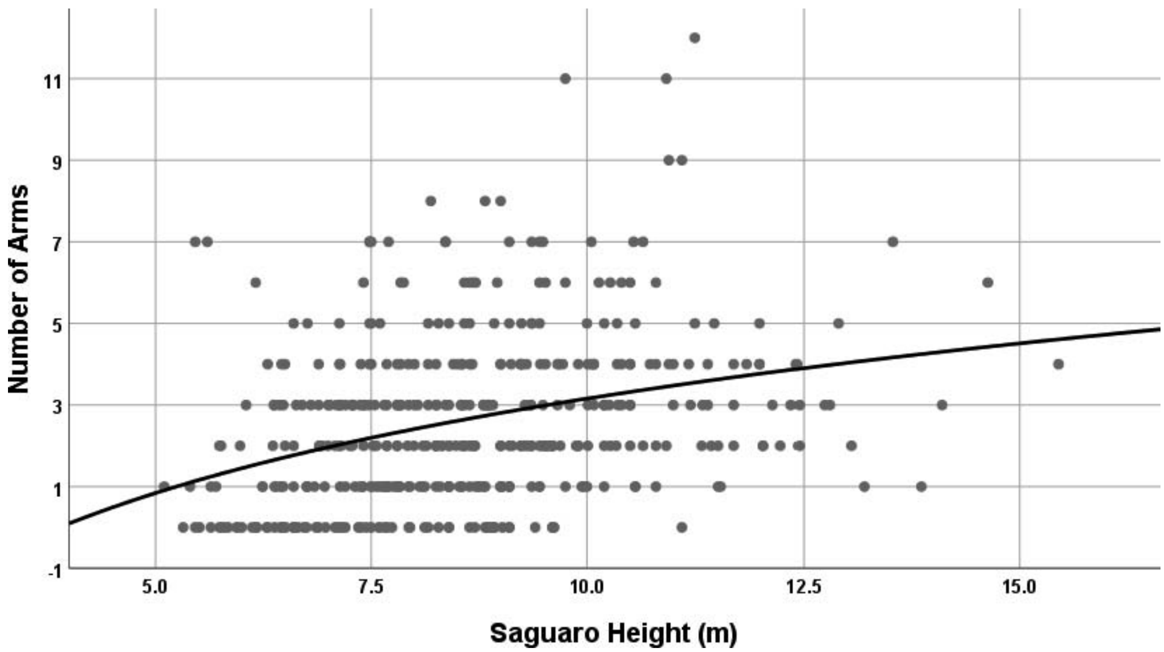

FIG. 1—Relationship between the number of saguaro arms present and saguaro height. The line represents the best least-squares fit of $y = 3.34 \times \log(x) - 4.53$.

availability appears to be a key driver behind arm production.

I sought to further explore the role of water by using a saguaro-centered study where the following potential influences on water availability were recorded for a series of subject saguaros: (1) the number of nearby saguaros if the subject saguaro was growing beneath the canopy of a nurse tree, (2) the presence of a wash nearby, and (3) the presence and identity of any plant associate. I predicted that if water availability is a significant driver behind the number of arms a saguaro has, the number of saguaro arms would be significantly correlated with values of each of these factors after controlling for saguaro height.

METHODS—*Field Methods*—Between 18 and 26 March 2000, I walked several 1-km-long straight-line transects in random directions in each of four locations within Organ Pipe Cactus National Monument: west of the campground area (31°56′35.52″N, 112°49′3.72″W), on the flats south of the campground area (31°55′33.5994″N, 112°48′45.36″W), on the basalt flats northeast of the campground (31°58′12.7194″N, 112°47′52.0794″W), and around the visitor center (31°57′22.6794″N, 112°48′5.7594″W). For every saguaro >4 m in height that fell within 5 m of a transect line, I recorded the height, number of arms, identity of any plant associate (defined as a plant whose canopy touched the saguaro), number of other saguaros associated with the same nurse plant, and the presence or absence of the edge of a wash (defined as any distinct gulley that would funnel water during a rain event) within 5 m of the subject saguaro.

Statistical Methods—To establish the quantitative relationship between observed number of arms on a saguaro and saguaro height, I fit a simple logarithmic regression. I then conducted a multiple regression with ln(height), number of saguaro neighbors, and presence of wash nearby as variables to examine whether each contributes significantly to variation in number of arms. For each value associated with the three independent variables of interest, I calculated the mean deviation from the regression-predicted number of arms and conducted an analysis of variance to determine whether the deviations differed significantly across values.

RESULTS—Because branching is a developmental process, there will necessarily be a relationship between age (as reflected in saguaro height) and the number of arms a saguaro has acquired. As others (McAuliffe and Janzen, 1986; Drezner, 2003*a*) have found in their studies, I found a significant ($F_{1,473} = 47.4$, $P < 0.001$) relationship between saguaro height and number of arms in a sample of 425 saguaros (Fig. 1). In my sample, saguaro height accounted for 10% ($R^2 = 0.10$) of the variation in arm number. By including three variables in a multiple regression, I also found that height, number of saguaro neighbors, and presence of a wash within 5 m each contribute significantly ($F_{3,381} = 22.1$, $P < 0.001$) to predicting the number of saguaro arms; together they account for about 15% ($R^2 = 0.148$) of the variation in arm number. The partial correlation between number of arms and number of saguaro neighbors was −0.15 ($P =$ 0.003), and between number of arms and the presence of a wash nearby was 0.21 ($P < 0.001$).

Using the expected number of arms derived from the arm–height relationship, I found a significant ($F_{4,393} =$ 3.2, $P = 0.014$) negative relationship between the number of saguaros growing under the same nurse tree canopy and the mean deviation from the expected number of arms for a given saguaro height. Moreover, the negative effect is incremental across the number of saguaro

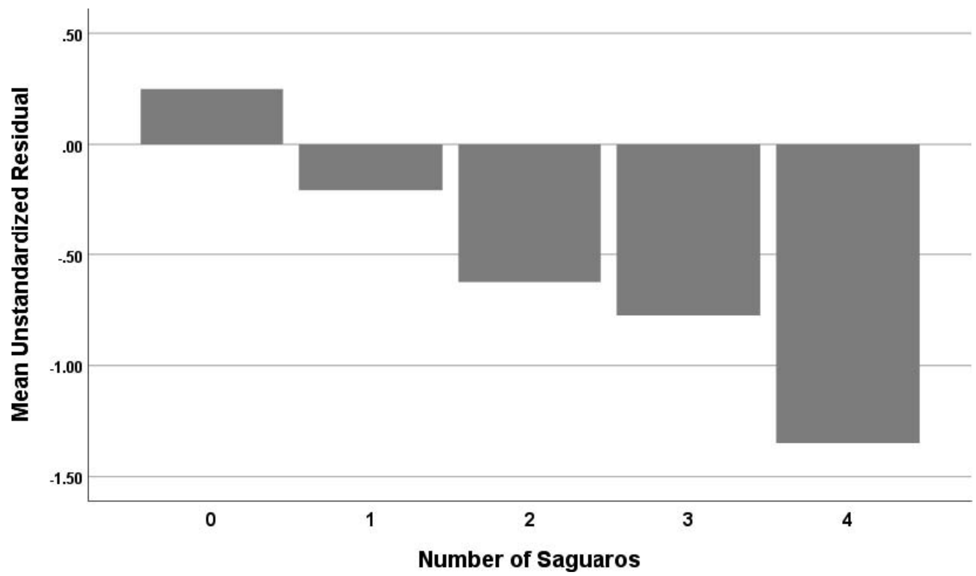

FIG. 2—Mean residual from the expected number of arms for a given saguaro height is plotted against the number of saguaros growing with the subject saguaro under the same nurse plant.

neighbors, revealing an ever-decreasing mean deviation with numbers of saguaro neighbors (Fig. 2).

Because I recorded only the presence or absence of a wash within 5 m and did not measure absolute distance from a subject saguaro to the nearest wash, it was not possible to examine evidence for incremental change in mean residual value with distance to wash. Nonetheless, deviation from the expected number of arms for a given saguaro height was significantly ($F_{1,383} = 20.4$, $P < 0.001$) positively related to whether or not a saguaro was growing near a wash, with saguaros growing near a wash having more than the expected numbers of arms (mean deviation = 0.85 arms) and saguaros growing farther than 5 m from a wash having fewer than the expected numbers of arms (mean deviation = −0.20 arms).

To examine the effect of plant associates on saguaro arm production, I considered only those saguaros growing in the absence of other saguaros nearby, which reduced the number of sampled saguaros from 425 to 274. Although the presence and identity of a plant associate did not contribute significantly ($F_{8,265} = 0.82$, $P = 0.58$) to explaining the number of arms a saguaro had, the pattern of deviations from the regression associated with each associate category (Fig. 3) still suggested a biologically meaningful relationship between associates and water availability. Specifically, the effect of growing in association with a living plant relative to growing alone was consistently negative (Fig. 3), and the larger (nurse) plants (*Olneya*, *Prosopis*, *Cercidium*) seemed to exert a greater negative effect than smaller associates did. It was also noteworthy that when a nurse plant was dead, the growing conditions appeared to exert a positive effect on the number of arms a saguaro had relative to the number it would have had if growing alone.

DISCUSSION—A strong relationship between saguaro age and height has been well established (Steenbergh and Lowe, 1977, 1983; Pierson and Turner, 1998; Drezner, 2003*b*), as has the relationship between saguaro height and onset of reproduction (Steenbergh and Lowe, 1977; Drezner, 2008). McAuliffe and Janzen (1986) were the first to record a relationship between saguaro height and number of arms (the tips of which support flowers). They argued that if water availability influences arm production, then intraspecific crowding (or anything else that affects water availability) should also affect arm production. By measuring water uptake after seasonal rains, McAuliffe and Janzen (1986) showed that competition with other nearby saguaros reduced water uptake and, indeed, influenced the number of saguaro arms. I, therefore, expected to find that, for a given saguaro height, the number of arms a saguaro had ought to be affected by whether they were growing in the presence of other saguaros, growing near a wash or not, or growing in close association with other plants.

Two of the variables I measured (number of saguaro neighbors and presence or absence of a wash within 5 m) were significantly related to the number of arms a saguaro has at a given height, and one variable (presence and identity of any associate) exerted an influence that, although not statistically significant, also revealed a likely influence of water availability on arm production. Indeed, others (Steenbergh and Lowe, 1983; McAuliffe and Janzen, 1986; Drezner, 2003*a*) have argued that water availability (especially winter water availability; Drezner, 2003*a*), has an important influence on the production of saguaro arms. Because washes funnel water during rain events, any saguaro growing near a wash ought to receive the benefit of increased moisture availability relative to a saguaro growing farther from a wash. Therefore, it is not

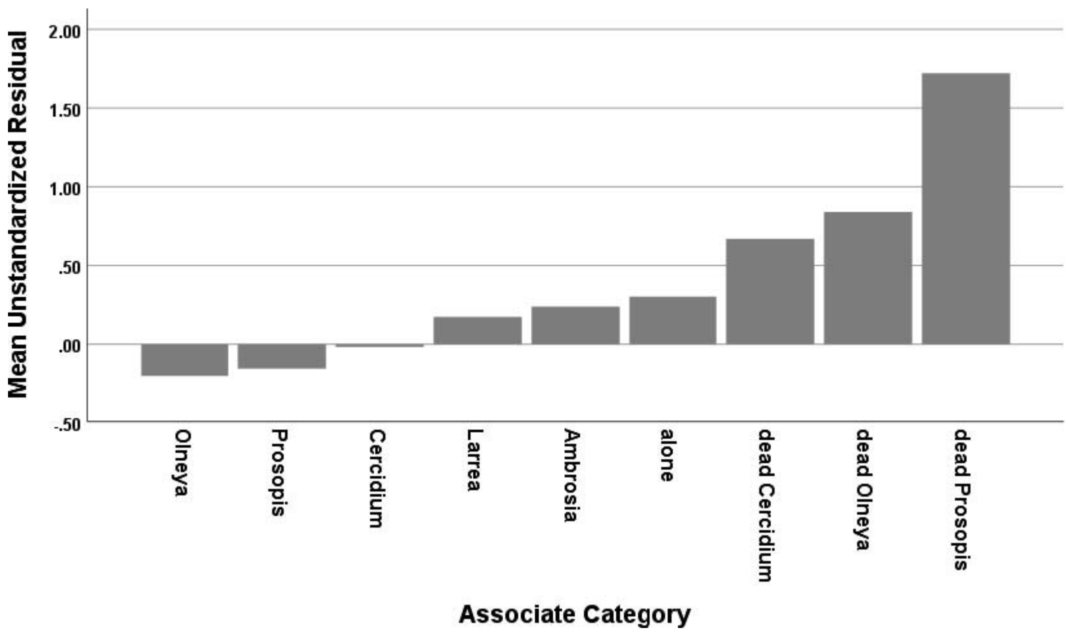

FIG. 3—Mean residual from the expected number of arms for a given saguaro height is plotted against whether the subject saguaro was growing alone or with any of eight categories of associate plant. Associate categories are named after the genus of the associate.

surprising that the presence of a nearby wash was significantly positively related to arm production. Similarly, the negative effects of growing close to another individual of the same species is abundantly clear here; with every additional saguaro growing beneath the same nurse tree, a given saguaro has an incremental decrease in the number of arms it produces (Fig. 2). This is undoubtedly related to direct competition for water, as others (Steenbergh and Lowe, 1983; McAuliffe and Janzen, 1986; Drezner, 2003*a*) have suggested.

Early subjective impressions (e.g., Shreve, 1931; Niering et al., 1963) and a subsequent quantitative analysis of saguaro distribution relative to available space (Hutto et al., 1986) reveal that saguaros grow more often beneath the canopies of large shrubs than expected on the basis of chance alone. Larger plants probably influence seed distribution patterns through several possible means: (1) they serve as preferred perch sites for bird species that consume saguaro seeds and then deposit seeds beneath their perch sites (Hutto et al., 1986), (2) they can influence seed distribution patterns by somehow reducing levels of seed predation beneath their canopy (Steenbergh and Lowe, 1969), or (3) they serve as places where seeds accumulate in blowing winds. Large desert shrubs and trees can also serve to improve germination success and survivorship of young saguaros either through protection from predation (Steenbergh and Lowe, 1969) or protection from harsh abiotic conditions (Turner et al., 1966; Steenbergh and Lowe, 1969, 1977; Drezner and Garrity, 2003; Drezner, 2007). Because of these potential benefits that saguaros receive by growing under the canopy of large shrubs and trees, the large plant associates of saguaros are now known as "nurse trees" in both the scientific and popular literature.

However, the commensal relationship between saguaros and their nurse trees appears to change through time. In the present study, I found that all living plant associates of established saguaros (especially the larger associates) exert a measurable negative effect on saguaro arm production, and that the negative effect appears to turn to a positive effect once again after the associate dies. Indeed, in a variety of ecological systems, the balance of facilitation and competition may vary with the life stages of the interacting species such that positive effects that exist when beneficiaries are young and small turn to competitive effects when the associates are older and larger (Callaway and Walker, 1997). As evidence, Callaway and Walker (1997:1960) note that often ". . . seedlings of beneficiary species are found spatially associated with nurse plants, whereas adults are not, which suggests that the balance of competition and facilitation shifts among the various life stages of the beneficiary and the benefactor."

Across the life of a saguaro–nurse association, the nurse tree creates conditions that facilitate saguaro establishment, but then competition for water shifts the overall effect from the positive side toward the negative side before it shifts back again to the positive side after the saguaro associate dies. The earliest positive interactions can be extended, at least for a while, before competitive effects overwhelm the nurse (Montesinos-Navarro et al., 2019) until, eventually, the nurse plant in the presence of a saguaro dies earlier than if the saguaro associate were not present (McAuliffe, 1984). Thus, trees that "nurse" saguaros early on in a saguaro's life may become competitive later on, before again becoming facilitators (as evidenced by the positive deviation in number of arms for a given height when a nurse tree is dead). A final twist to this story is that, frequently, nurse trees also facilitate the establishment of multiple saguaros beneath their canopies, which means that any benefactor stands a good chance of undergoing competition for water with other saguaros throughout its life. So, the benefits and costs of growing beneath a nurse tree appear to shift not only with time, but with circumstance as well.

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