Woodrat herbivory influences saguaro (Carnegiea gigantea) reproductive output

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1. Introduction

The saguaro (Carnegiea gigantea) is a keystone resource for Sonoran desert consumers of nectar, pollen, fruit, and cactus tissues. Saguaro tissue contains oxalic acid and is unavailable to most consumers. The white-throated woodrat (Neotoma albigula) is, however, able to consume foods with high oxalate content, and is strongly associated with desert succulents, primarily cacti of the genus Opuntia. N. albigula forages secondarily on saguaro tissues, reducing photosynthetic surface area and eliciting an energetically-demanding wound response that reduces energy stores available to fuel reproduction. We observed and quantified Neotoma herbivory on saguaros in a low desert environment. Evidence of Neotoma grazing was found on 44\% of all saguaros surveyed, and 13\% of all saguaros had >20\% of their surface area affected by Neotoma grazing. Neotoma herbivory on saguaros was predicted by the number of nearby succulents, presence of Neotoma middens, and saguaro age. When comparing similarly sized plants, saguaros with high levels (>20\% of surface) of herbivory produced fewer flowers and fruits than plants with no Neotoma herbivory. These findings suggest that periodic use of saguaros by N. albigula, such as during extended droughts with conditions unfavorable for Opuntia growth and establishment, may reduce long-term reproductive capacities in low-density saguaro populations.

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Although juvenile saguaros experience substantial mortality from rodent herbivory (Niering et al., 1963), adult cactus tissues are protected against herbivores by the plant’s epidermis, rows of spines, and high oxalic content of tissues. The white-throated woodrat (Neotoma albignula) overcomes these obstacles to herbivory, and survives without free-standing water through the intake of preformed water from succulent food sources (Schmidt-Nielsen, 1964). N. albignula is able to degrade oxalates through the action of its intestinal microbes, and can thereby tolerate secondary plant compounds that may be toxic to other herbivores (Shirley and Schmidt-Nielsen, 1967). Desert-dwelling Neotoma shows strong associations with Opuntia cacti, and may exhibit numerical responses to changes in Opuntia availability (Brown et al., 1972). Neotoma herbivory on saguaros represents use of a secondary food source when primary sources such as Opuntia are not readily available (Steenbergh and Lowe, 1977).

While conducting research near the northwestern extent of the Sonoran desert, we observed saguaros with extensive Neotoma herbivory. Where herbivory on saguaros occurs, a multi-layered, lignin-based callus tissue seals the wound and protects the plant’s internal tissues against evaporative water loss, insect attacks, and necrosis from bacterial infection (Steinkirch et al., 1967). The wounding response reduces the surface area of photosynthetic tissues and total interception of photosynthetically-active radiation (PAR), which limits CO2 uptake in cylindrical-stemmed cacti during much of the year (Nobel, 1977). Reduction in photosynthetically-active surface area from Neotoma herbivory thereby influences both short-term and long-term availability of energy resources for saguaro growth, maintenance, and reproductive output. Stem tissue damage by non-native herbivores has been documented in association with a >15% reduction in number of flowers and 8% fewer fruits in columnar cacti (Peco et al., 2011). In this study we evaluate the relationship between Neotoma herbivory and saguaro reproductive output, by: 1) quantifying the extent of herbivory on saguaros by Neotoma, and 2) testing whether herbivory on individual saguaros is associated with reduced flower and fruit production.

2. Materials and methods

2.1. Site description

We established monitoring points for saguaro reproductive output at ≥50 saguaros at each of 3 transects in southwestern Arizona. Transect locations were at the edge of La Posa Plain, La Paz County, beginning at 425 m elevation; near Kofa Mountain foothills, La Paz County, 475 m elevation; and near Table Top Mountain foothills, Pinal County, 500 m elevation. All transects occurred near the edge of the Lower Colorado River Valley subdivision of the Sonoran Desert, characterized by hot and arid conditions with low-density vegetation (Shreve, 1951) and saguaro populations with low demographic rates for both “births” (germination under moist and shaded conditions below nurse plants) and deaths (freeze-related mortality) (Drezner, 2006). Characteristic vegetation included low-density shrubs and trees including Larrea tridentata, Ambrosia dumosa, Encelia farinosa, and Parkinsonia microphylla, and cacti including C. gigantea, Opuntia bigelovii, and Opuntia acanthocarpa.

2.2. Saguaro survey protocols

We established transects 100 m in width, with length determined by quota sampling. Observers walked transects in a randomly-selected direction until 50 saguaros had been identified, and then walked slowly in the opposite direction while thoroughly searching for any additional saguaros that were not located during the first pass along the transect. At each saguaro we recorded plant height (using a graduated telescoping pole), plant diameter at a height of 1 m, number of arms (≥30 cm or with reproductive structures), number of reproductive stems (arms plus the main stem if at a productively mature height), and the number of other cacti and Neotoma middens present within 10 m, a distance equal to 17–87% of the reported movement radius of N. albignula (Brown and Zeng, 1989; Chew and Chew, 1970). We calculated saguaro ages from site specific age—height and growth—precipitation regression equations developed by Drezner (2003).

We assessed N. albignula herbivory through a visual classification system to quantify the percentage of damaged plant surface tissues (Turner and Funicelli, 2000), and a training set of 108 saguaros near the study area that were photographed from multiple directions. Neotoma herbivory exhibited characteristic grazing patterns, including circular staircases chewed into the outer stem tissue, long troughs or tunnels of surface tissue excavation, and/or presence of Neotoma feces within these excavated pathways (Fig. 1). In contrast, tissue damage from lagomorph herbivory was confined to the basal portion of the stem, generally affected a greater width of stem tissue, and in some cases was accompanied by lagomorph feces near the base of the stem. We categorized surface impacts of herbivory (including contiguous areas of tissue necrosis or epidermal collapse) for each saguaro as no Neotoma herbivory, ≤20% of the surface affected, or >20% of the surface damaged by herbivory.

We conducted visual counts of reproductive structures (flowers and fruits, in any stage of development) present on transect
saguaros during peak flowering and fruiting periods (mid-May and mid- to late-June, respectively) in 2008. Two observers using 10× binoculars counted flowers and fruits by standing on opposite sides approximately 10 m away from the plant. Observers counted reproductive structures on each side of the stem, and communicated with each other to ensure against skipped or duplicate counts of reproductive structures. In 2009, we counted flower and fruit production on paired, mature saguaros (empirically determined to be ≥2.5 m tall) with no Neotoma herbivory and with >20% herbivory. Saguaro pairings matched plants on the same transect that had distinct (0 vs. >20%) levels of Neotoma herbivory, and were similar in height, age, and number of arms. When mature saguaros with 0 or >20% herbivory could not be paired with other saguaros on the transect, we extended transect surveys to complete saguaro pairings and recorded information on new saguaros until ~15 (±3) pairs were surveyed on each transect.

2.3. Statistical analyses

We constructed classification and regression trees (Breiman et al., 1984; Salford Systems, 2006) to analyze relationships between the presence/absence of Neotoma herbivory and environmental variables (middens and succulents present, saguaro age, transect), and for analysis of 2008 saguaro reproductive output and plant attributes (height, diameter, arms, surface herbivory, and transect). We determined variable splits with the Gini impurity criterion for classification trees and sum of squares for regression trees, and identified optimal trees from repeated cross-validations to find the smallest trees whose model errors fell within 1 SE of the minimum error (De’ath and Fabricus, 2000). Variable importance scores reflected changes in misclassification associated with each variable, expressed on a scale of 0–100 (Breiman et al., 1984). We calculated the year of establishment by subtracting saguaro age from the year of observation, and evaluated temporal uniformity of saguaro establishment using Kolmogorov–Smirnov tests. We used Wilcoxon paired tests to determine whether 2009 flower and fruit production in saguaros with no Neotoma herbivory was significantly increased (α = 0.05) relative to saguaros with >20% surface herbivory, and to test for differences between reproductive output of individual plants between 2008 and 2009. Paired t-tests (two-tailed, α = 0.05), evaluated differences in all other attributes of paired saguaros (height; number of reproductive stems, \( \sqrt{x + 0.5} \) transformation; diameter; age) (R Development Core Team, 2011).

3. Results

3.1. Saguaro attributes

We surveyed 158 saguaros on 3 transects in 2008. Saguaro densities on transects ranged from 3.0 to 8.3 plants/ha. Observed saguaros varied in height from 0.3 to 10.0 m. The shortest saguaros observed with flowers and fruits were 3.3 and 2.5 m tall, respectively, which corresponded to a minimum reproductive age of 83 years. The distribution of saguaro establishment was not uniform across years (\( D = 3.2, P < 0.001 \)).

Herbivory occurred on 57% of all saguaros observed, and evidence of Neotoma herbivory was present on 44% of all saguaros. Neotoma herbivory affected 0 to >70% of surface area of individual plants. Thirteen percent of observed saguaros exhibited the highest category of surface herbivory impacts (>20%). The presence or absence of Neotoma herbivory on a saguaro was successfully predicted in 65% of all cases, using the number of other cacti present, saguaro age, and the number of Neotoma middens present as predictive variables (Fig. 2). The predictive model had high specificity (81% of saguaros without herbivory correctly assigned) but relatively low sensitivity (45% correct assignment for plants with Neotoma herbivory). No saguaros containing >3 cacti present within 10 m exhibited any evidence of herbivory.

3.2. Reproductive output and herbivory

Mean counts of mature saguaro reproductive outputs were 33.1 flowers (range 0–165) and 23.2 fruits (range 0–111) per plant in 2008. Mature saguaros failed to produce flowers and fruits in 27.1% and 24.1%, respectively, of observed cases. Each classification or regression tree for presence/absence or total output of flower and fruit production identified plant height and the number of reproductive stems present as the variables with the highest importance scores (Fig. 3). Importance values for the Neotoma herbivory variable were relatively low, but non-zero (5.8–10.4), in the optimal trees for classifying or quantifying reproductive output. None of the optimal regression trees for quantifying or classifying presence of saguaro reproductive output included transect as a predictive variable.

We identified 46 pairs of structurally similar saguaros with distinct categories of herbivory (no Neotoma herbivory vs. >20% of surface affected) in 2009. Numbers of flowers and fruits on mature saguaros with no observed Neotoma herbivory increased significantly compared to paired saguaros with >20% herbivory (Table 1). No comparisons of other paired saguaro variables approached significance (0.38 < P < 0.91). For individual plants surveyed in both 2008 and 2009, no significant differences in flower (\( W = 178, P = 0.424 \)) or fruit (\( W = 182, P = 0.078 \)) production occurred between years.

4. Discussion

Deserts are water-limited systems that produce significant challenges for the plants and animals inhabiting those
Characteristics of paired saguaros with no woodrat herbivory and with high (>20%) levels of surface tissue damage.

<table>
<thead>
<tr>
<th>Saguaro attributes</th>
<th>Mean plant values</th>
<th>Signif.</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>No Neotoma herbivory (h_0)</td>
<td>&gt;20% surface herbivory (h_20)</td>
</tr>
<tr>
<td>N</td>
<td>46</td>
<td>46</td>
</tr>
<tr>
<td>Flowers</td>
<td>38.1</td>
<td>26.3</td>
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<tr>
<td>(n observed)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruits (n observed)</td>
<td>43.7</td>
<td>25.2</td>
</tr>
<tr>
<td>Height (m)</td>
<td>5.4</td>
<td>5.4</td>
</tr>
<tr>
<td>Diameter (cm)</td>
<td>39.0</td>
<td>38.9</td>
</tr>
<tr>
<td>Reproductive Stems^b (n)</td>
<td>2.0</td>
<td>2.2</td>
</tr>
<tr>
<td>Age (years)</td>
<td>129.1</td>
<td>129.3</td>
</tr>
</tbody>
</table>

^a P-values for tests comparing variables between paired plants: \( P(h_0 \leq h_{20}) \), Wilcoxon pairs test, for counts of flowers and fruits; \( P(x_{n} - x_{o}) \), paired t-test, for height, diameter, arms, and age of paired saguaros.

^b Untransformed values. Transformed values (\( \sqrt{x + 0.5} \)) were used to meet assumptions of the paired t-tests for differences in attributes between saguaro pairs.

Environments (Noy-Meir, 1973). Extended drought conditions in the Sonoran desert lead to the loss of plants that normally comprise the primary food sources for *N. albigena*, including *Opuntia* spp. and other small cacti (McAuliffe and Hamerlynck, 2010). Shifting of *N. albigena* grazing pressure to saguaro stems results in short-term consequences that are compounded through the life of the saguaro, as reduced surface for PAR interception limits the plant’s ability to generate long-term energy stores. We found that *Neotoma* herbivory had significant effects on flower and fruit production of saguaros; counts of flowers and fruits were 31% and 42% lower on heavily-grazed vs. ungrazed plants, respectively. Saguaro seeds germinate only under environmental conditions that occur intermittently in space and in time: under nurse trees or shrubs, and often at multi-decadal scales (Parker, 1993; Pierson and Turner, 1998; Shreve, 1910). Saguaro establishment requires a sufficient seed supply to reach suitable or “safe” sites, and the presence of favorable ambient conditions for seed survival and germination (Andersen, 1989). Because saguaro seeds and seedlings are both subject to high mortality rates from herbivores and abiotic factors (Niering et al., 1963; Steenbergh and Lowe, 1977), decreases in seed output may translate to reduced magnitude of episodic recruitment pulses that are vital to the growth and maintenance of cactus populations. In the following discussion we consider implications to regional saguaro population demographics from the effects of *Neotoma* grazing on reproductive output, and project how increasing regional air temperatures and reductions in seasonal precipitation will affect the persistence of saguaros in the Sonoran desert.

Saguaro densities on our transects ranged from 13 to 36% of mean regional densities documented across the drier, northwestern portion of saguaro range, and were only 2–5% of mean densities where saguaros grow in conditions near their environmental optimum (Drezner, 2006). Saguaro densities were comparable to those reported by Brum (1973) at a low-density site where reproductive output was considered insufficient to prevent population declines. Low saguaro densities and delayed onset of reproduction are consistent with populations where infrequent monsoon rains limit saguaro recruitment (Brum, 1973; Drezner, 2008). The observed non-uniformity of saguaro ages at our study sites further suggests that recruitment is linked to intermittent periods when conditions are favorable for saguaro establishment.

Assessing the impacts of *N. albigena* herbivory or other factors on reproductive output of saguaros must be viewed in the context of the established relationship between plant size and reproductive output (Parker, 1989; Pecol et al., 2011; Schmidt and Buchmann, 1986). Increased plant height is indicative of saguaro age...
exceeding the maturity threshold, a developmental stage where branching may occur to provide additional reproductive surfaces, increased photosynthetic surface for PAR interception, and increased energy stores. Once saguaros reach a height indicating maturity, they are generally successful in translating energy stores to reproductive output, even during adverse environmental conditions such as drought (Steenbergh and Lowe, 1977; Thackery and Leding, 1929). Our results similarly identified plant height as the strongest predictor of reproductive output among all saguaros surveyed, while comparisons of paired, morphologically-similar plants allowed us to isolate the negative effects to saguaro reproductive output associated with the permanent loss of photosynthetic surface area from Neotoma herbivory.

Observed saguaro reproductive output was substantially lower than previously reported (Niering et al., 1963; Schmidt and Buchmann, 1986; Steenbergh and Lowe, 1977; Thackery and Leding, 1929). These differences may be largely methodological, as we did not obtain complete counts of reproductive output throughout the season, but instead quantified reproductive structures present at single visits during peak flowering and fruiting periods. Although direct comparisons of reproductive output among studies are precluded, our study sites exhibited a frequency of mature-sized plants lacking reproductive structures and a delayed timing to maturity that was characteristic of saguaros in marginal habitats undergoing an apparent population decline (Brum, 1973). The observed reduction in reproductive output from saguaros with high (>20%) levels of herbivory translates to an estimated loss of 0.48 kg of fruit (containing 0.36 kg of water) and 41,625 seeds produced per plant annually.

Neotoma herbivory on saguaros was observed regularly at our study sites, and was associated with presence of nearby Neotoma middens (active or currently unoccupied), lower numbers of other succulents that may serve as primary food and water sources for N. albigula, and saguaro age. Neotoma is precluded from subsisting entirely on non-succulent desert vegetation due to species’ water requirements and the need to avoid potential toxic effects from ingested plant compounds (Karasov, 1989). Loss of Opuntia from the home range of a Neotoma requires the animal to abandon its home range, or find more drought-resistant sources of succulent food to replace Opuntia in its diet. The massive saguaro is one of the few plant species that can survive and provide a moisture-rich food source under conditions where Opuntia may not be able to persist. Saguaro may experience establishment peaks and/or population increases over extended periods (>100 years) when other desert plant species exhibit climate-related population declines (Turner, 1990). Saguaro are the plants most likely to be affected by diet switching and N. albigula herbivory during periodic extended droughts, and may experience reversed or disrupted mutualistic interactions with grazers that normally serve as seed dispersers (McCluney et al., 2012). The magnitude of these cascading drought-related impacts from native herbivore diet-switching exceeds observed depressions in reproductive output associated with columnar cacti stem tissue damage from multiple introduced herbivores (Peco et al., 2011).

Climate modeling for the southwestern United States projects increases in mean annual temperatures of ≥3°C by the end of the century, along with decreases in mean annual precipitation (IPCC, 2007). Climate projections for the southwestern United States include disproportionate seasonal decreases in precipitation and moisture conditions during winter (Christensen et al., 2004). Extended drought periods, particularly during winter, hinder the establishment of new Opuntia plants (Bowers, 2005). The most severe impacts of climate change on Sonoran desert Opuntia are expected where Opuntia and other cacti currently exist at low densities or under sub-optimal conditions. If future climate conditions are insufficient for Opuntia establishment rates to replace mortality of adult plants, our results predict increased frequency of Neotoma grazing on cactus tissues, which is associated with substantial reductions in reproductive output. Diminished saguaro reproductive output reduces the availability of energy and moisture from flowers and fruits that are important resources for Sonoran desert fauna, and has potential demographic implications for saguaro populations.

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