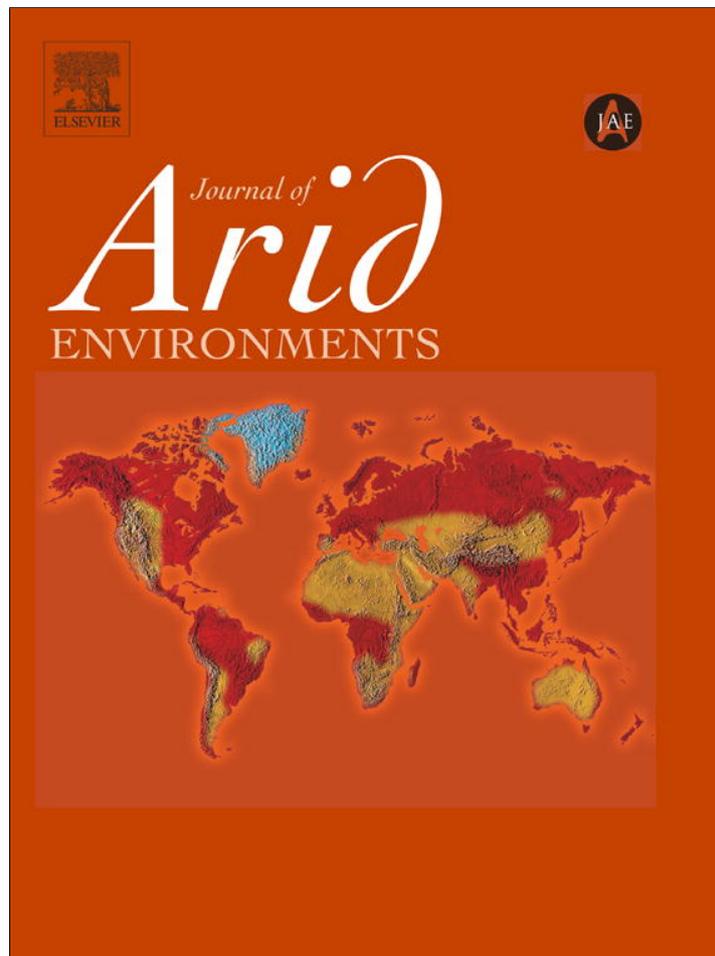


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Woodrat herbivory influences saguaro (*Carnegiea gigantea*) reproductive output

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ABSTRACT

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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1. Introduction

The saguaro (*Carnegiea gigantea*) is a massive, long-lived columnar cactus that serves as a keystone resource providing breeding substrate, thermal shelter, and nutrient-rich flowers and fruits to Sonoran desert fauna including volant and non-volant mammals, birds, and insect consumers of pollen, nectar, and stem tissues (Fleming and Valiente-Banuet, 2002). Reproductive output in saguaro represents a substantial investment of plant energy and resources. Individual saguaros may produce hundreds of fruits, each with ~2250 seeds (Steenbergh and Lowe, 1977), a mass of >25 g, and water content of ~80% (Wolf et al., 2002). Fully hydrated cactus stem tissue may have a water content of ≥90%, which in the absence of defenses against herbivory would become highly attractive and vulnerable to desert herbivores (Gibson and Nobel, 1986).

Saguaro populations are limited by recruitment (establishment and regeneration) within portions of the species range (Drezner,

2006). Latitudinal and elevational limits of saguaro distribution are largely determined by catastrophic freezes and subsequent necrosis of stem tissues, particularly near the northern extent of its range (Steenbergh and Lowe, 1976). In contrast to mortality-limited populations, saguaro abundance in the highly-arid northwestern Sonoran desert is related to the frequency of moist, warm-season conditions that promote germination (Turner, 1990). Once saguaros reach a reproductive maturity threshold (equivalent to 2.2 m in height), establishment of new seedlings is dependent upon the presence of monsoonal moisture conditions for germination (Steenbergh and Lowe, 1977), shading by nurse plants to prevent desiccation of seedlings (Turner et al., 1966), and survival from consumption and physical damage to seeds and seedlings (Niering et al., 1963).

Saguaro establishment occurs episodically at multi-decadal scales (Parker, 1993), with some cohorts being separated by 60 years or more (Drezner and Balling, 2002). Episodes of increased saguaro establishment often coincide with wetter periods, although this relationship becomes less consistent within the more freeze-limited (and less xeric) portions of the species' range (Pierson and Turner, 1998). Factors affecting saguaro recruitment therefore have a disproportionate effect on populations within the germination-limited portions of the species range, such as western Arizona (Drezner, 2008).

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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 albigula*) 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. albigula* 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 (Steelink 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 reproductively 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. albigula* (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. albigula* 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, $\leq 20\%$ 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

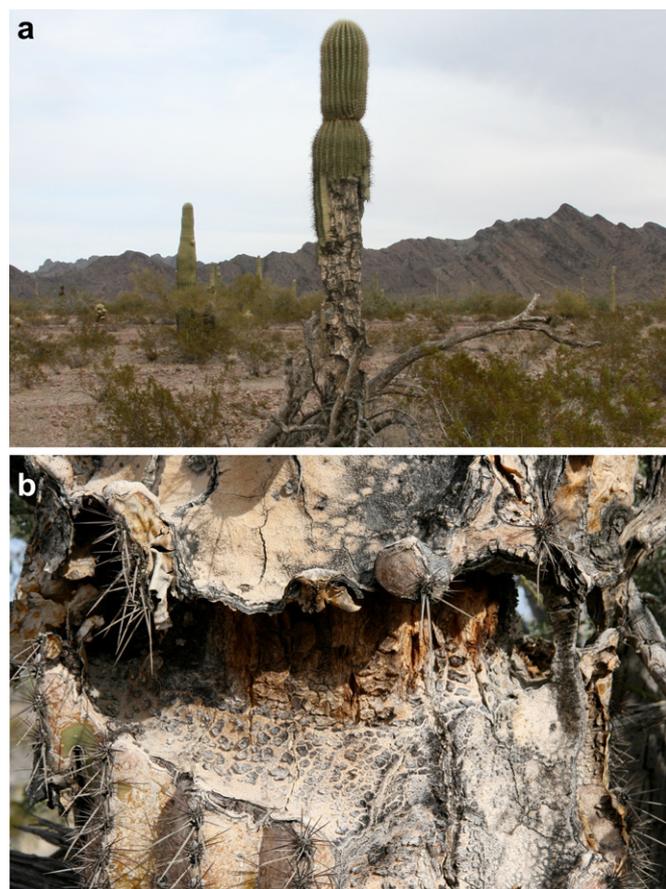


Fig. 1. (a) Extensive damage to saguaro from *Neotoma* grazing on succulent stem tissues. *Neotoma albigula* herbivory reduces the photosynthetic surface area of the plant and generates a wound response that is necessary to protect grazed saguaro tissues from desiccation, freezing, and infection of exposed tissue. (b) Damage from *N. albigula* herbivory is characterized by staircase-like patterns around the stem where feces from the grazing rodents may be found.

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 $\sim 15 (\pm 3)$ 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 ($\alpha = 0.05$) 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, $\alpha = 0.05$), 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 ($0.38 \leq P \leq 0.91$). 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

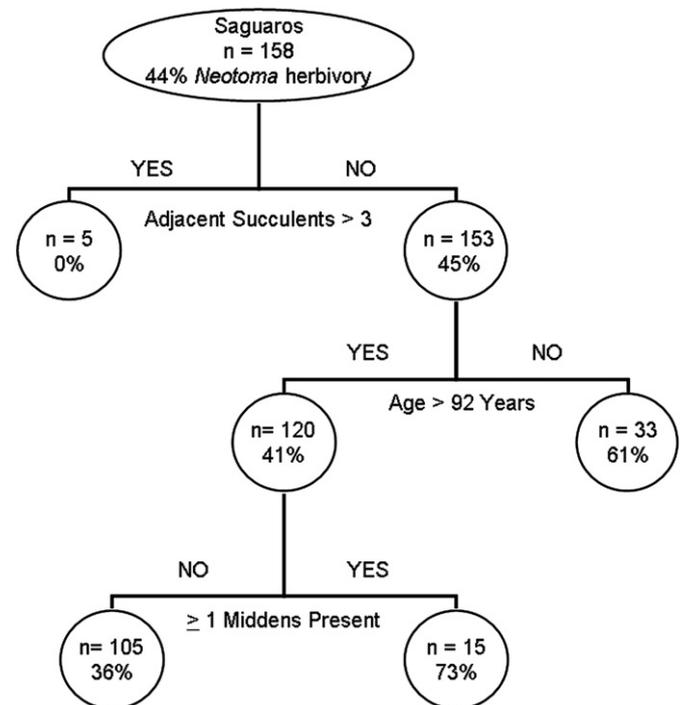


Fig. 2. Classification tree showing predictive factors for the presence/absence of observed *Neotoma* grazing on saguaros. The branch-defining condition is labeled at each split in the tree, and the number of plants and percentage with *Neotoma* herbivory are given at each node. Conditions associated with a higher frequency of herbivory are listed on the right side of each split.

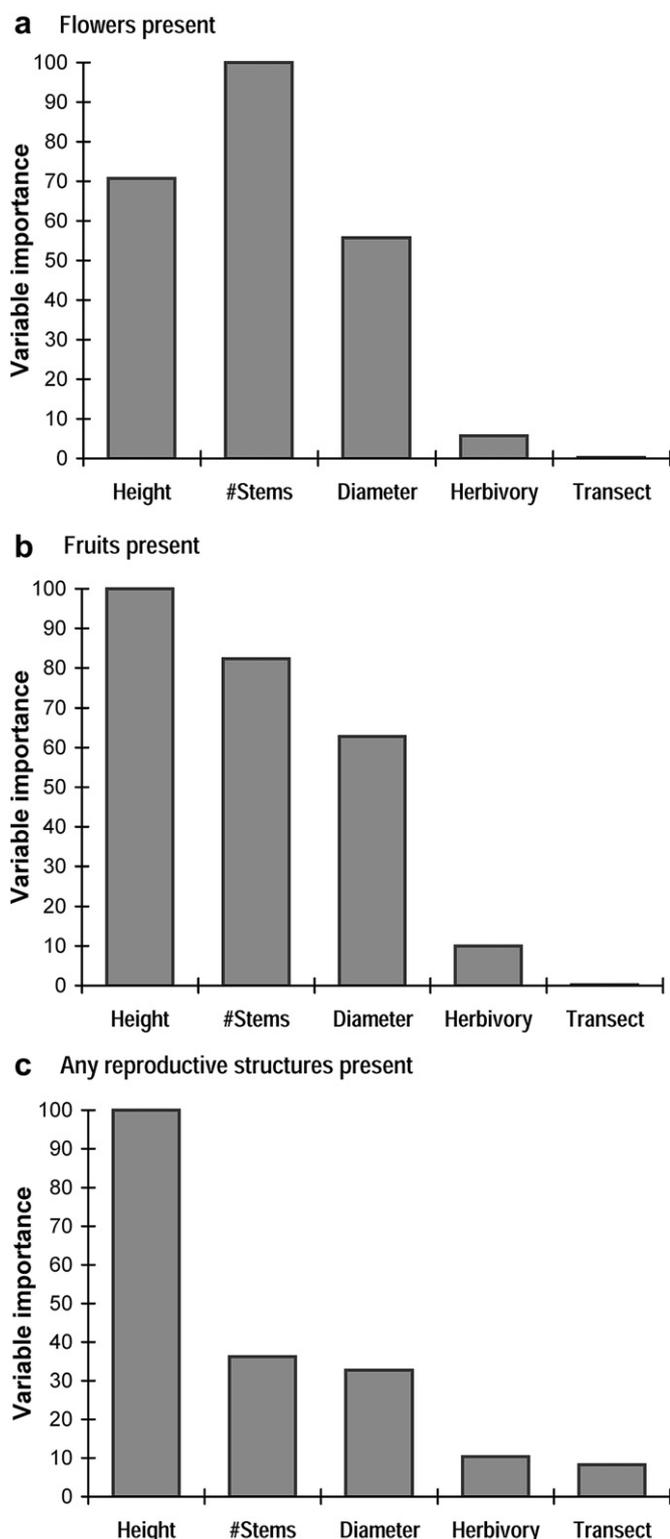


Fig. 3. Relative importance values for variables used to predict presence/absence of saguaro (a) flowers, (b) fruits, and (c) any reproductive structures (flowers or fruits). Variables included: total height of the plant (*Height*), the number of arms plus stems above the maturity threshold (*#Stems*), plant diameter at 1 m above ground (*Diameter*), the extent of surface impacts of herbivory, by category (*Herbivory*), and the transect number for each plant (*Transect*).

Table 1

Characteristics of paired saguaros with no woodrat herbivory and with high (>20%) levels of surface tissue damage.

Saguaro attributes	Mean plant values			Signif. ^a
	No <i>Neotoma</i> herbivory (h_0)	>20% surface herbivory ($h_{>20}$)	Difference ($\bar{x}_{h_0} - \bar{x}_{h_{>20}}$)	
<i>N</i>	46	46		
Flowers (<i>n</i> observed)	38.1	26.3	11.7	0.026
Fruits (<i>n</i> observed)	43.7	25.2	18.5	0.008
Height (m)	5.4	5.4	0.02	0.91
Diameter (cm)	39.0	38.9	0.1	0.88
Reproductive Stems ^b (<i>n</i>)	2.0	2.2	-0.2	0.38
Age (years)	129.1	129.3	-0.2	0.91

^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; $P(\bar{x}_{h_0} = \bar{x}_{h_{>20}})$, 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. albigula*, including *Opuntia* spp. and other small cacti (McAuliffe and Hamerlynck, 2010). Shifting of *N. albigula* 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, north-western 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 monsoonal 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. albigula* 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; Peco 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. Saguaros 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). Saguaros 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 saguaro 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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