Individual and demographic responses of the palm *Brahea aculeata* to browsing and leaf harvesting in a tropical dry forest of Northwestern Mexico (#107875)

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Individual and demographic responses of the palm *Brahea aculeata* to browsing and leaf harvesting in a tropical dry forest of Northwestern Mexico

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Background. The leaves of many palm species represent important non-timber forest products (NTFPs), which may be intensively harvested by local people in many tropical areas. Additionally, in some regions livestock graze in natural forests, and they may browse on palm leaves, especially during the dry season. Thus, harvesting and browsing can result in the loss of leaf area of individual palms, which may alter functional traits of individuals and change demographic patterns of populations. Currently, there are few studies that analyze the effects of multiple disturbances on these traits. The goals of this study were to evaluate the effects of browsing and leaf harvesting as well as the interaction between these two factors on individual traits and demographic patterns of the *Brahea aculeata* palm in northwestern Mexico.

Methods. A browsing and leaf harvesting experiment was conducted on natural populations of the species. Individuals were subjected to different harvesting intensities and the presence or absence of cattle. Annual censuses were conducted from 2011 to 2014, and individual traits and demographic patterns were monitored.

Results. In general, at the individual level, most of the analyzed attributes showed an increase especially during the first two years of monitoring. Thus, palms experiencing any leaf harvesting and browsing had 1.5 to 6.0 times higher values than control palms in leaf production, especially juveniles and small adults. At the demographic level, the effects of browsing and leaf harvest were low or null, as survival was not affected by them. Browsing positively affected the growth of *B. aculeata* individuals in the first 2 of the 3 years analyzed, while leaf harvesting had a negative effect for the 3 years. We also found a positive relationship between probability of reproduction and leaf harvest; however, in contrast, 2.0 to 3.0 times fewer fruits were produced with the increase of leaf harvesting. Thus, after 3 years of simulated management, *B. aculeata* changed the resource allocation patterns, and many of the analyzed attributes decreased. Based on our results, *B. aculeata* can be considered a species that tolerates high levels of defoliation for 2 years. This study contributes basic ecological information useful for the conservation and management of *B. aculeata*, but overall it also highlights that different anthropogenic activities may act as drivers affecting the functional response and demography of NTFP species and they should be considered for the long-term integral management of these species.

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Abstract

Background. The leaves of many palm species represent important non-timber forest products (NTFPs), which may be intensively harvested by local people in many tropical areas. Additionally, in some regions livestock graze in natural forests, and they may browse on palm leaves, especially during the dry season. Thus, harvesting and browsing can result in the loss of leaf area of individual palms, which may alter functional traits of individuals and change demographic patterns of populations. Currently, there are few studies that analyze the effects of multiple disturbances on these traits. The goals of this study were to evaluate the effects of browsing and leaf harvesting as well as the interaction between these two factors on individual traits and demographic patterns of the *Brahea aculeata* palm in northwestern Mexico.

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Introduction

The harvest of non-timber forest products (NTFPs) represents an important source of income and contributes to the welfare of many rural communities across the globe (*Krishnakumar, Fox & Anitha, 2012; Shackleton et al., 2024*). With appropriate management practices, the harvest of NTFPs may also contribute to the conservation of natural resources and biodiversity (*Gaoue et al., 2016; Rodrigues de Melo et al., 2023*). Intensive use and overexploitation of NTFPs, however, may negatively affect individuals and populations (*Endress, Gorchov & Berry, 2006; Duarte & Montúfar, 2012; Lopez-Toledo et al., 2012*).

Different structures such as stems, bark, fruits and leaves are removed from plants and used as NTFPs, which may cause changes in individuals and population dynamics. The study of the responses of functional individual traits to stress factors, such as leaf area loss (caused by leaf harvesting or browsing), can provide insight regarding the anatomical and physiological responses of plants and how this relates to changes at the population level (*Briske & Richards, 1995; Poorter, 1999; Violle et al., 2007*). Vital rates (reproduction, growth and survival) are also important for exploring the response to disturbances such as management practices and for identifying the sustainable use of NTFP (*Zuidema et al., 2007; Martínez-Ballesté & Martorell, 2015; Ohse et al., 2023*). Thus, studying the effects of different harvest and management practices on both individual and demographic traits of harvested populations may help to identify optimal management strategies (*Anten, Martinez-Ramos & Ackerly, 2003; Hernández-Barrios et al., 2012; Gaoue et al., 2016; Ticktin et al., 2023*).

Leaves are important organs for essential processes, such as capturing light energy, carbohydrate production and water conservation (*Wright et al., 2004*). Thus, the loss of leaf area can affect plants' essential functions, such as growth, reproduction and/or individuals' survival.

Plants usually undergo multiple leaf area loss events caused by reoccurring biotic and physical damage (herbivory, fallen branches; *Martínez-Ramos & Álvarez-Buylla, 1995; Cepeda-Cornejo & Dirzo, 2010*). For plants used as NTFPs, leaf harvesting may represent a large increase in the amount and frequency of leaf area loss. This reduction may alter the allocation of resources to different plant functions, such as reproduction, growth and maintenance. Plants may compensate for the reduction in leaf material by shifting resources from reproduction to leaf production and/or mobilizing stored reserves to produce new leaves (*McNaughton, 1983; Belsky et al., 1993; Cunningham, 1997; Anten, Martinez-Ramos & Ackerly, 2003; Lopez-Toledo et al., 2012; Sun, Shafiti & Rundel, 2022*). In scenarios with higher frequency and/or higher intensities of leaf area loss, which can occur during the harvest of some NTFPs, plants' capacity to compensate can be reduced, however, as stored reserves are depleted, potentially resulting in growth reduction and increased mortality (*Anten, Martinez-Ramos & Ackerly, 2003; Endress, Gorchov & Noble, 2004; Farrington et al., 2008; Martínez-Ramos, Anten & Ackerly, 2009; Lopez-Toledo et al., 2012; Ward, Jones, & Barsky, 2022*).

Many palm species are culturally and/or economically important NTFPs. The leaves of several palm species are used for many products, including roof thatch and handicrafts, and represent an important source of income for local economies especially in rural areas (*Joyal, 1996; Svenning & Macia, 2002; Pulido & Caballero, 2006; Coronel & Pulido, 2010; Briseño-Tellez & Pulido-Silva, 2023; Briseño Tellez et al., 2023; Sander, Pulido-Silva & da Silva, 2023*). Multiple studies have been conducted on palms used as NTFPs to analyze the effects of leaf harvesting on leaf production and the vital rates of individuals (*Endress, Gorchov & Berry, 2006; Hernández-Barrios et al., 2012; Lopez-Toledo et al., 2012; Martínez-Ramos, Anten & Ackerly, 2009; Mandle & Ticktin, 2012; Martínez-Ballesté & Martorell, 2015*). Some studies reported no effect of harvesting on individual palm's vital rates (growth, reproduction and survival) when the harvest is restricted to a few defoliation events, even with complete defoliation. In some cases, defoliated plants even show elevated levels of growth and reproduction because of overcompensation (*Anten, Martinez-Ramos & Ackerly, 2003; Martínez-Ramos, Anten & Ackerly, 2009; Gaoue et al., 2016*). Other studies, however, indicated that repeated defoliation over multiple years negatively affects leaf production and vital rates, and these negative effects intensify with increased harvest intensity or frequency (*Martínez-Ramos, Anten & Ackerly, 2009; Hernández-Barrios et al., 2012; Lopez-Toledo et al., 2012*).

On the other hand, in many tropical regions, cattle ranching is a common land use in forests, grasslands and other natural areas (*Herrera, 1995; Meghan, Graydon & Cushman, 2013*), and livestock may also browse or/graze on species that are also NTFPs. It has also been shown that cattle may modify soil compaction and other physical and chemical properties (*Fleischner 1994*), and, in the long term, these effects may become evident in the structure (*Stern et al., 2002*) and in the architecture of the stems and vegetation (*Breceda et al., 2005*). Moreover, browsing may have even stronger effects on plant vital rates than defoliation for NTFP harvesting since NFTP harvesting is generally restricted to a particular leaf or individual plant characteristics (e.g., leaf size and shape) and, therefore, more selective than browsing by livestock that usually consume all available leaves.

Several studies have evaluated the effect of leaf harvesting on individual plant responses, especially in palms (*Svenning & Macia, 2002; Arango, Duque & Muñoz, 2010; Hernández-Barrios et al., 2012; Martínez-Ballesté & Martorell, 2015*). Few studies, however, have analyzed the interactive effects of two factors or more on the individual and demographic patterns of plants (*Berry et al., 2008; Mandle & Ticktin, 2012; Mandle, Ticktin & Zuidema, 2015; Sinasson*

& Shackleton, 2023). These studies demonstrated interactions among two or more drivers regarding vital rates of individuals and population dynamics. *Berry et al. (2008)* found significant interactions among substrate site, topographic position, human management and herbivory regarding the population dynamics of *Chamaedorea radicalis* in Mexico. Their results showed that herbivory reduced survival and fecundity on the forest floor, which in the absence of seed migration resulted in a projected decline of forest floor palms (sinks). With seed dispersal, however, the palms persisted, and the total population growth for both substrates was projected to be positive, indicating that seed dispersal from non-browsed palms on rock outcrops (sources) was sufficient to sustain *C. radicalis* on the forest floor. Similarly, *Mandle, Ticktin & Zuidema (2015)* found that the population dynamics of *Phoenix loureiroi* palms in India are driven by interactive effects among fire, grazing, leaf harvest and abiotic conditions.

Brahea aculeata (Brandegee) H.E.Moore is an endemic palm of northwestern Mexico. The leaves are harvested for roof thatching and the production of handicrafts (baskets, etc.). Cattle also graze on the leaves of *B. aculeata* (*Joyal, 1996; Lopez-Toledo, Horn & Endress, 2011*). It is likely that defoliation, whether from harvesters or livestock, alone or combined, may affect the individual and demographic responses. This paper aims to understand the effects of grazing and leaf harvesting, as well as the ~~and the~~ interaction of these two factors on the individual traits and demographic patterns of *B. aculeata*. We expected that (i) individuals of *Brahea aculeata* would tolerate browsing and low to moderate leaf harvest; however, if the leaf area had been permanently lost over three years, especially at high intensity, individual traits may ~~have shown~~ important negative outcomes. In terms of demographic impact, we expected that (ii) harvest and livestock browsing would negatively affect survival, growth and reproduction and (iii) that the magnitude of these negative effects would increase over time.

Furthermore, ~~and that~~ after three years, the cumulative leaf area loss would have stronger effects both on individual and demographic traits.

Materials & Methods

Study site

The study was conducted within the Área de Protección de Flora y Fauna Sierra de Alamos-Río Cuchujaqui (APFFSA-RC), a 92,890-ha federal protected area in the northern Mexican state of Sonora (27 ° 12'30 " - 26 ° 53'09 " N and 109 ° 03'00 "-108 ° 29'32" W). Within the APFFSA-RC, elevations range from 300 to 1600 m and promote a vegetation gradient ranging from tropical deciduous to pine-oak forest (*Haro, 2009*). Precipitation is highly variable with a mean of 650 mm, ranging from 190 and 1120 mm/year (*Lopez-Toledo, Horn & Endress, 2011*). During this research, precipitation ranged from 360 (2011) to 472 (2014) mm, which is lower than the annual average recorded. In the region, the dry season is very pronounced and lasts up to 8 months (November to June). The mean annual temperature is 21.5 °C and ranges from 10 °C and 41°C as minimum and maximum temperatures (*Haro, 2009; Lopez-Toledo, Horn & Endress, 2011*).

Study species

Brahea aculeata (Brandegee) H. E. Moore (*Erythea aculeata* Brandegee) is a solitary-stemmed palm with hermaphrodite reproduction that reaches ~10 m in height (*Quero, 2000*). The species flowers between March and May, and fruits ripen during May and November. Moreover, individuals usually become reproductive after 1.0 m of height. Our study species is endemic to northwestern Mexico (in the states of Sonora, Sinaloa, Chihuahua and Durango). It is patchily distributed and can be found from sunny mountains slopes to shadier areas along arroyos and canyon bottoms in tropical dry forest and lower oak and pine-oak woodlands (*Lopez-Toledo et al., 2011*). It has a wide altitudinal distribution ranging from 320-1500 m. *B. aculeata* appears on the IUCN Red List as "vulnerable," as well as "endangered" in the Mexican Red List because of habitat loss and intensive management (*Quero, 1998; Felger, Johnson & Wilson, 2001; SEMARNAT, 2002*).

Management of *Brahea aculeata*

Within the APFFSA-RC, *B. aculeata* is a very important species in terms of structure of the vegetation and as an NTFP (*Joyal, 1996*). Commercial leaf harvesting in the region has been performed for at least 50 years, with local residents developing traditional strategies for leaf harvest and palm management (*Joyal, 1996; Lopez-Toledo, Horn & Endress, 2011*). Within the APFFSA-RC, there are two leaf harvesting schemes: i) that conducted by native people from inside the reserve, hereafter defined as "low harvest" and that ii) conducted by nonnative people from larger cities or from coastal towns who use the leaves for thatching roofs of beach resorts, hereafter named "high harvest." The former usually involves harvesting only mature leaves, and always only the two youngest leaves and spear leaves are left. In contrast, the latter involves a more aggressive harvesting scheme, cutting all available leaves and spears. Depending on demand for the product, some areas may be harvested every 6 months or every year. Furthermore, within the reserve cattle ranching is very common, with the cattle placed in different plots of land of 30-50 ha within a farm and rotated every 2-3 months (*Quiséhuatl-Medina et al., 2020*). During the dry season when many of the deciduous trees have dropped their leaves, *B. aculeata* leaves may be consumed by cattle, which may damage palm individuals

<250 cm high (*Lopez-Toledo, Horn & Endress, 2011*). Leaf harvesting is applied to juveniles and adult plants because they produce good-sized leaves for both harvesting schemes, while cattle activity may affect all life stages through grazing, trampling and soil compaction (*Quiséhuatl-Medina et al., 2020*). Leaf harvesting occurs in January, which coincides with the best climate and results in the highest leaf quality for weaving and thatching.

Sampling design

To evaluate the effect of cattle grazing and leaf harvesting on *Brahea aculeata,* we established six permanent plots of 75 x 25 m (0.1875 ha) in 2011. Two treatments were randomly assigned to these plots: 1) grazing and 2) non-grazing. For the former treatment, unrestricted livestock grazing was allowed, while the latter plots were fenced to prevent cattle access. Trying to simulate the local management, the cattle were allowed for about 3 months (April to June) each year within the plot.

Each plot was then divided into three subplots of 25 x 25 m (625 m^2) where three regional harvest schemes were randomly assigned and applied annually in January each year: 1) no harvest, 2) low harvest and 3) high harvest. We applied these harvesting schemes for each palm ≥ 10 cm in height and quantified the number of total leaves and harvested leaves. Harvesting treatments resulted in a gradient from 0 to 100% of harvested leaves in both grazing treatments. We obtained the necessary permits from Dirección General de Vida Silvestre-Secretaria de Medio Ambiente y Recursos Naturales to collect leaves (DGVS / 01991/10 and DGVS / 00837/14).

Annual censuses were conducted from January 2011 to January 2014. At each census, for each palm we marked the second youngest leaf, which represented a fully developed leaf; thus, we were able to measure new leaf production each year. We measured eight traits for each palm: i) length of stem, ii) leaf production, iii) lamina length (of the marked leaf and hereafter defined as "leaf length"), iv) petiole length (of the marked leaf), v) percentage of leaves harvested, vi) survival (alive or dead), vii) stem length (measured from the base of the stem to the base of the new leaf) and viii) number of fruits (except for 2011 to 2012). We classified individuals into one of three size classes: a) *Juveniles*, individuals of 10.1-100 cm and base diameter > 5 cm; b) *Adults I,* which comprised individuals of 100.1-250 cm) and d) *Adults II*, individuals >250 cm. Overall, we marked and monitored a total of 1,194 individuals during the three-year period of the study with 197-228 individuals per plot. This included the following number of individuals per treatment: 120-125 juveniles, 45-63 Adults I and 32-40 Adults II.

Data analysis

We included seven different response variables including three at individual and four at demographic level, respectively. The individual traits analyzed were related to leaf area and included leaf production (LP), leaf length (LL) and petiole length (PL). The demographic rates analyzed included mortality (M), stem growth (SG), probability of reproduction (PR) and fruit production (FP). To assess the responses of browsing and leaf harvesting on *Brahea aculeata* at the individual and demographic level, we developed mixed models considering the following explanatory variables: Time ('T' with three levels: 2012, 2013 and 2014), Grazing (included as a categorical variable 'Gr' with the levels Grazing and Non-Grazing), Harvest ('H' expressed as a proportion of harvested leaves/total leaves varying from 0 to 100% harvest). We also included the interaction term Harvest:Time to consider the cumulative effects of harvesting through time, which we expected would become stronger through the monitoring. For all analyses, these were used as fixed factors. To reflect the nested design of the experiment, the “plot/subplot” of the browsing/harvesting treatments and the repeated measurements of individuals through time, we used mixed models, which can include these terms as random effects (*Pinheiro & Bates, 2000; Bates et al., 2015*). All the analyses were conducted using the linear mixed-effects model (LMM) for continuous response variables (e.g., leaf length, petiole length and stem growth) and the generalized linear mixed model (GLMM) for variables that were counts (e.g., leaf production and fruit production) and binomials (e.g., probability of reproduction). We did not conduct analysis for mortality, given the very low number of dead individuals (9 in total) during the monitoring period. For LMM analyses, when required, response variables were log(x) or log (x + 1) transformed to meet normality criteria (*Crawley, 2012*). For GLMM analyses, we used Poisson error for counts and binomial error for binomial variables. The model presented for each response variable represents the full model including all terms mentioned above. The trend line presented in the results was plotted based on the coefficients of these models; see Supplementary Information section (SI). All analyses were completed using the *lme4* package 1.1-21version (*Bates et al., 2015*) in the R program version 3.5.2 (The R Foundation for Statistical Computing, 2018). To test significance of factors, we used the *lmerTest* package version 3.1-0 for LMM (*Kuznetsova, Brockhoff & Bojesen-Christensen, 2016*) and the parametric bootstrap method available in the *pbkrtest* package ver. 0.4-7 for GLMMs (*Halekoh & Højsgaard, 2014*).

Results

Individual traits

In general, we found that the effects of leaf harvesting were stronger than browsing (χ^2 = 45.3, p<0.001). Thus, for the three individual traits analyzed, the leaf harvest had significant effects.

The palms' performance, however, was similar between browsing treatments (Fig 1). Furthermore, the null effects of browsing were similar for the three size classes analyzed (Tables 1-3). Leaf production ranged from 0 to 35 leaves/yr and differed among size categories (Fig. 1). Overall, the lowest leaf production rate was registered for juveniles (mean ± SE: 5.3 ± 0.05 leaves/yr), while the highest was for adults II (mean ± SE: 12.8 ± 0.3 leaves/yr) (Fig. 1). For the three size classes, we found that palms showed a positive response to harvesting, that is, the leaf production rate significantly increased with the increase of proportion of harvesting (Fig 1; Table 1). Although this relationship was positive for the three years, the slope had a variation with higher values in the second year, while for the third year the slope declined (Fig. 1ab; Table S1).

Leaf length also differed among palm size categories, and juveniles had the smallest leaves (mean ± SE: 48.3 ± 0.2 cm), while adults I and adults II had 1.5-1.2 times larger leaves, respectively (Fig. 2; Table S1). We detected effects of browsing only for Adults I but not for juveniles (Table 2). Harvesting and the H:T interaction were found to be significant for the three categories and for juveniles the first year. Based on the coefficients of the model, harvesting produced positive effects (slope = 5.7 cm/prop of harvesting): larger leaves at higher harvesting. For the second year, leaf size decreased with harvesting, and, for the third year, this relationship became negative (slope=0.5 cm/prop of harvesting, Table S2). For Adults I and Adult II, harvesting did not produce changes during the first and second year, but for the third the relationship become negative (Fig, 2; Table 2 and S2).

Petiole length was a very sensitive trait, and generally the palms exposed to high harvesting intensities showed a positive effect during the two first years, with an increase of up to 55% in length. For the third year, though, the petiole decreased (Table 3; Fig. 3). By contrast, we did not find any effect from browsing on petiole size (Table 3).

Demographic rates

Similarly, to the individual traits, we did not find a significant effect from browsing on any of the demographic rates of *Brahea aculeata*. Specifically, for the case of mortality, browsing and harvesting did not show any effect. We could not test their effect given the low number of individuals' death (9 individuals corresponding to 7 juveniles and 2 Adults I). For stem growth, we found a large range of variation with 0 and 25 cm yr^{-1} as the minimum and maximum, mainly because of palm size with the Adults I and Adults II, which showed the higher and lowest growth (Fig 4). For the case of browsing, the statistical model did not detect differences among plants in the browsing and non-browsing plots and it indicated higher growth for the third year but negative for the second year. The effects of harvesting were negative during the three years (Table 4; Fig. 4a, b).

Palms that had leaf area loss showed apparently contrasting effects on attributes related to reproduction. In general, the probability of reproduction increased with leaf area loss, while the number of fruits produced decreased with harvesting intensity. The positive effect of harvesting on the probability of reproduction was especially evident in Adults I, which also showed an increase along time with a higher probability of reproduction. Thus, harvesting intensities > 20% increased this probability, and, after 40% harvest, the probability reached its maximum (Fig. 5a, Table 5). Moreover, the statistical model indicated that the probability of reproduction varied positively with the size of individuals, and larger individuals had higher reproduction probabilities. This also changed, however, among years, and the model indicated that cumulative effects of harvests resulting in smaller sized palms reproducing. Thus, in the final period, smaller palms increased the probability of reproduction (Table 5; Fig. 5b). Fruit production varied largely among individuals from 2 to 657 fruit/individual, and a noteworthy variation among years was also recorded (Fig. 5c) This variation was partly explained by the harvesting proportion, time and stem length, but browsing had no effect (Table 5). The statistical model indicated a negative effect of harvesting, and, for the most part, large intensities of harvesting reduced the fruit production about 50% of (Fig. 5 c). Although we found a high variation in fruit production, palm size had a positive relationship, with large palms producing more fruits (Fig. 5d).

Discussion

Overall, we found that *Brahea aculeata* is resilient to browsing and leaf-harvesting, as these two factors alone had only minor or no effects on most of the analyzed traits.

Individual traits

To our knowledge, few studies have tested the effects of different drivers and their interactions on non-timber forest products (NTFP) (e.g., *Endress, Gorchov & Noble, 2004; Mandle & Ticktin, 2012; Mandle, Sinasson & Shackleton, 2023*), yet these experimental designs are necessary to simulate real management practices where NTFPs are exposed to other disturbance factors in addition to harvest. Our study contributes to this goal by documenting the effect of multiple drivers on both individuals and populations. During the first two years, we found that loss of leaf area had limited effects on *Brahea aculeata,* and individuals were able to recover from defoliation. After 3 years of defoliation, however, individuals subjected to both high browsing and high harvesting rates were the more negatively affected. This is consistent with research on *Phoenix loureiroi*, the mountain date palm, where grazing and harvest reduced growth (*Mandle & Ticktin, 2012*).

The management practices simulated on *Brahea aculeata* only negatively affected one of the four individual traits analyzed (petiole length). Although petiole size is not relevant for the management of the species, it is an architectural attribute important for structural support (*Niinemets et al., 2004*). The changes we found may help to understand the low or null effect on leaf size and maybe indicate possible trade-offs among functions such as light acquisition and support structures (*Niinemets et al., 2004*). Leaf size and leaf production generally responded positively, and we did not find any effect on the total number of leaves per plant. Although leaf production and leaf size showed a reduction in the three size-categories, this was not lower than the first-year values. Therefore, this species may be considered resilient: capable of recovering from damage caused by defoliation even at high leaf area loss intensities (*Walker, Kinzig & Langridge, 1999; Lopez-Toledo et al., 2012*), at least in the short term. This coincides with findings for other palms species subject to low defoliation intensity treatments and few events of harvesting (*Anten, Martinez-Ramos & Ackerly, 2003; Martínez-Ballesté, Martorell & Caballero, 2008; Hernández-Barrios et al., 2012; Mandle, Ticktin & Zuidema, 2015; Pulido & Coronel-Ortega, 2016*). *Mandle, Ticktin and Zuidema (2015,)* studying *Phoenix loureiroi* in India, reported that this species is resilient to low (~15 %) harvest rates with an annual harvest scheme.

In the case of *Brahea aculeata*, the increase in leaf production and leaf size is likely due to an increased allocation of resources to these attributes. This response can be considered an overcompensatory response (*Bazzaz, Ackerly & Reekie, 2000; Anten & Ackerly, 2001; Anten, Martinez-Ramos & Ackerly, 2003*), which has been explained as follows: i) a result of the mobilization of resources from other plant structures, such as stems or roots that store nonstructural carbohydrates and nutrients; ii) a reallocation at the expense of some functions such as reproduction or iii) a response caused by an adjustment in the photosynthesis rate in the remaining leaves (*McPherson & Williams, 1998; Bazzaz, Ackerly & Reekie, 2000; Boege, 2005; Endress, Gorchov & Berry, 2006; Lopez-Toledo et al., 2012; Martínez-Ballesté & Martorell, 2015*). For example, defoliated *Chamaedorea elegans* palms allocated more resources to lamina growth at the expense of the other plant structures, especially those related to reproduction (*Anten, Martinez-Ramos & Ackerly, 2003*). Studies of other palm species under more intensive management schemes (semiannual harvest and high harvesting intensities) have also found a higher leaf production rate (*Martínez-Ballesté, Martorell & Caballero, 2008; Coronel & Pulido, 2010*). In a study of two species of *Sabal* (*S. yapa* and *S. mexicana*) from the Mexican Yucatan Peninsula, *Martínez-Ballesté* and *Martorell (2015)* also concluded that adults individuals could compensate for leaf production even at higher harvest intensities (twice each year) for 2 years. As part of the experiment, however, 1 to 3 young leaves per palm were left, which allowed them to recover. In our case, intensive management included the harvest of all leaves and spears, and, even under this scenario, we did not find negative effects on *Brahea aculeata* for the first two years, which highlights the resilience of this species.

Except in a few cases, most of the defoliation studies have been short-term (*Endress, Gorchov & Noble, 2004; Martínez-Ballesté, Martorell & Caballero, 2008; Duarte & Montúfar, 2012; Pulido & Coronel-Ortega, 2015*). To evaluate the effect of leaf area loss, especially in the context of the sustainability of non-timber forest products, it is important to conduct long-term studies, as short-term studies may miss interannual variability and may not detect the cumulative effects of leaf area loss. In the case of *Brahea aculeata,* simulating real management practices over 3 years showed an increase in all the variables analyzed, with the highest levels in the second year and a drop in the third year, especially for juveniles. This decline may indicate the cumulative effects of three years of browsing and harvesting. In other palm species, multiple defoliation events and intensive harvesting lead to a depletion of reserves (*Martínez-Ramos, Anten & Ackerly, 2009*). For example, a defoliation experiment on *Chamaedorea elegans* performed every 6 months for 3 years led to a large reduction in leaf traits and an even larger reduction in reproductive attributes, such as inflorescences, flowers and fruits, especially at high harvesting intensities (*Lopez-Toledo et al., 2012*).

For *Brahea aculeata*, after the three-year experiment, the effect of harvest and browsing on leaf attributes was greater on intermediate sizes than on smaller and larger individuals. This was due to the interactive effects of browsing and harvesting. The intermediate-sized palms (10-250 cm height) can be easily harvested, and the leaves are more accessible to livestock. In contrast, smaller and larger individuals (seedlings and adults II) were only subjected to either browsing or harvesting but not both. The low effect on adults II is remarkable, given that adults need to allocate resources for reproductive structures. Regardless, they did not show any negative effect, which also indicates the high resilience of these size classes. In large adults, the stored resources are, in general, more abundant, which explains the lower effect we found (*Anten, Martinez-Ramos & Ackerly, 2003; Boege, 2005*). Several studies, however, have found that plants have thresholds at which they can tolerate some degree of disturbance, but once this is exceeded, however, accumulated reserves are reduced or depleted, and individuals are no longer able to compensate for the damage (*Anten & Ackerly, 2001; Staffan & Mendez, 2005*). It is likely that in the case of *Brahea aculeata* we did not reach this threshold, and it may have been reached by the increasing of frequency of harvesting. This question will remain open, however.

Demographic patterns

Other palms such as *Phoenix loureiroi,* which is an NTFP from Indian tropical dry forests, has been found to be resilient to low levels of leaf area loss resulting from the combination of multiple interacting factors (fire, harvesting and grazing). Nevertheless, chronic and higher levels of these multiple factors have severe negative consequences for populations (*Mandle & Ticktin, 2012*). *Martínez-Ballesté* and *Martorell (2015),* studying the *Sabal yapa* palm from tropical dry forest ecosystems, also found that the species is resilient to harvest. In this case, *S. yapa* was resilient to any leaf harvesting regime and could maintain positive demographic rates. For *Brahea aculeata*, we concluded that this species is also resilient but only under a management that includes 2 years of harvesting with annual cycles at even high levels of harvesting. If this management continues for a third year, however, the resource allocation patterns changed considerably, and some demographic patterns reduced drastically. There are other species such as *Chamaedorea*, which had been reported to be more susceptible to leaf harvesting. Although these species grow in different ecosystems (understory palms from humid tropical forests) than *B. aculeata*, the allocation resources and effects of harvesting may be used to compare our results. For some *Chamaedorea* species, several authors have found that high harvesting intensities (> 66%) strongly affected demographic rates and population dynamics, even after few events (*Martínez-Ramos, Anten & Ackerly, 2009; Hernández-Barrios et al., 2012; Lopez-Toledo et al., 2012*). The difference may be due in part to environmental conditions and the frequency of defoliation. In these studies, *Chamaedorea* harvesting was performed biannually, whereas in our present study, harvesting was conducted only once a year (to simulate one of the most frequent practices). Furthermore, browsing was conducted during a short season of the year (May to July). Therefore, during the first two years of monitoring, it is likely that the time (one entire year) between events of defoliation may be sufficient for *B. aculeata* to recover from the leaf area lost. In addition, there may be a differential response comparing an understory palm such as *Chamaedorea* to a canopy species such as *Brahea*.

In previous studies, the first defoliation event can cause an increase in the probability of reproduction, flowers or fruits (*Martínez-Ramos, Anten & Ackerly, 2009*). The cumulative effects of multiple defoliation events, however, led to declines in reproductive output (*Endress, Gorchov & Noble, 2004; Zuidema, de Kroon & Werger, 2007; Martínez-Ramos, Anten & Ackerly, 2009; Hernández-Barrios et al., 2012*). This reduction has been explained based on the amount of carbohydrates and the carbon gain by photosynthesis, which decreased through defoliation (*Klinkhamer et al., 1992; Boege, 2005*). Although leaf harvesting for *Brahea aculeata* increased the probability of reproduction, fruit production was 2 to 3 times lower as compared with control palms. Thus, it is likely that the frequency and intensity of defoliation applied to *Brahea aculeata* was sufficient to reach that threshold, indicating that the stored resources for reproduction become reduced. For further studies, it will be interesting to explore whether more frequent harvests or chronic harvesting over the long term affect the reproductive success or the fate of descendants. In the Alamos area, the species has been chronically and intensively harvested for at least 50 years. Therefore, it is likely that the reproductive variables may have been affected given the low recruitment of seedlings observed in the field studies. This is an unanswered question, however, and further studies related to reproductive success and germination are necessary.

Brahea aculeata is a long-lived species, and, therefore, low mortality is expected for adults. We found high survival rates and no impact on survival by browsing or harvesting. For other species, effects on mortality have been found, but this may be due to the greater frequency and intensity of harvesting or differences in the natural history of the species (*Endress, Gorchov & Berry, 2006; Martínez-Ramos, Anten & Ackerly, 2009; Hernández-Barrios et al., 2012; Mandle & Ticktin, 2012*).

Finally, the positive effect of browsing on growth may be an indirect effect of livestock activity. The cover of herbaceous plants was extremely high in the non-browsing plots, while in the browsing plots the livestock either trampled or ate the vegetation. This may eliminate the competition for resources, such as light, water or nutrients and make them available for palms (*Herrera, 1995; Heckel et al., 2010*).

Implications for management

Palms are ecologically and economically important in many tropical regions, and especially the leaves are intensively used for different purposes, including thatching roofs and handicrafts, which generate important income for local people (*Joyal, 1996; Anten, Martinez-Ramos & Ackerly, 2003; Endress, Gorchov & Noble, 2004; Arango, Duque & Muñoz, 2010; Coronel & Pulido, 2010; Duarte & Montúfar, 2012*). Our results indicate that *Brahea aculeata* under a two-year management that includes cycles of annual harvesting at moderate and even high leaf harvesting intensity may be considered sustainable, and, therefore, any intent of management for 3 or more years should be completely avoided.

Our results have important implications for the management of the species, as to date *B. aculeata* is a red listed species under Mexican and international norms, and no permissions are legally allowed. Within our study area, however, at some properties the management may be even more intensive with semiannual harvest (*Lopez-Toledo, Horn & Endress, 2011*). Many area residents depend on the leaf harvest of this species, and, therefore, we believe our results may contribute basic ecological information for the sustainable management of the species. These results may be implemented and contribute to an economically important activity. Note that characteristics such as leaf production rate and leaf length have direct implications for the use of many palms. Many handicrafts and roofs made of palm require only longer leaves (*Pulido & Caballero, 2006; Pulido & Coronel-Ortega, 2015*). Therefore, in this specific case, harvesting and browsing can be considered as positive – at least in the short term - leading to an increase in the length of leaves.

Nevertheless, it is still necessary to explore the effect of resting time and a more intensive management, which is applied in some areas (such as semiannual harvesting), and to evaluate the effects on the demography and population dynamics of the species. These questions, however, will also remain open for further studies (*Hernández-Barrios et al., 2012; Lopez-Toledo et al., 2012*).

Conclusions

Based on our experiment in field condition in northwestern Mexico, we state that *Brahea aculeata* demonstrated considerable resilience to simultaneous defoliation and browsing events; however, it was able to compensate for these effects only during the initial two years. Defoliation had a more pronounced impact than browsing and on some of the analyzed variables. Studies that simultaneously evaluate the combined effects of multiple factors on the performance of non-timber forest products (NTFPs) are essential for addressing management scenarios that reflect the realities faced by various species in the field. Despite being protected under the Mexican Red List (NOM-059-SEMARNAT-2010), this endemic and threatened species is still harvested and managed by various groups who rely on it for their livelihoods. Understanding the effects of harvesting, browsing and other potential factors affecting performance of these palms will be crucial for informing effective management and future conservation efforts.

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References

1. Anten NPR, Ackerly DD. 2001. A new method of growth analysis for plants that experience periodic losses of leaf mass. *Functional Ecology* 15:804-811.
2. Anten NPR, Martinez-Ramos M, Ackerly DD. 2003. Defoliation and growth in an understory palm: quantifying the contributions of compensatory responses. *Ecology* 84:2905–2918.
3. Arango DA, Duque AJ, Muñoz E. 2010. Dinámica poblacional de la palma *Euterpe oleracea* (Arecaceae) en bosques inundables del Chocó, Pacífico colombiano. *Revista de Biología Tropical* 58:465-481.

4. Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48.
5. Bazzaz FA, Ackerly DD, Reekie EG. 2000. Reproductive allocation in plants. In: Fenner M, ed. *Seeds: The ecology of regeneration in plant communities*. CAB International, 1-29.
6. Belsky A, Carson W, Jensen C, Fox G. 1993. Overcompensation by plants– herbivore optimization or red herring. *Evolutionary Ecology* 7:109–121.
7. Berry EJ, Gorchov DL, Endress BA, Stevens MHH. 2008. Source-sink dynamics within a plant population: the impact of substrate and herbivory on palm demography. *Population Ecology* 50:63-77.
8. Boege K. 2005. Influence of plant ontogeny on compensation to leaf damage. *American Journal of Botany* 92:1632–1640.
9. Breceda A, Ortiz V, Scrosati R. 2005. Mauto (*Lysiloma divaricatum*, Fabaceae) allometry as an indicator of cattle grazing pressure in a tropical dry forest in Northwestern Mexico. *Rangeland Ecology & Management* 58:85-88.
10. Briseño-Tellez JM, Pulido-Silva MT. 2023. Uso de la palma dulce (*Brahea dulcis*) en Actopan y Pachuca para el Día de la Candelaria. *Herreriana* 5:41-47.
11. Briseño-Tellez JM, Pulido Silva MT, Bautista K, García Mera A, Larios-Lozano O, López Gutiérrez BN, López López YA, Mendoza Cruz Y, Monzalvo R, Ortega-Meza D, Sánchez Trejo EC, Zepeda-Hernández ZK. 2023. Palm Sunday in central Mexico: among sellers, palms and syncretism. *Journal of Ethnobiology and Ethnomedicine* 19:22.
12. Briske DD, Richards JH. 1995. Plant responses to defoliation: a physiological, morphological and demographic evaluation. *Wildland plants: physiological ecology and developmental morphology* 635-710.
13. Cepeda-Cornejo V, Dirzo R. 2010. Sex-related differences in reproductive allocation, growth, defense and herbivory in three dioecious neotropical palms. *PloS one* 5:e9824.
14. Coronel MO, Pulido MT. 2010. Uso artesanal, fenología y cosecha optima de la palma *Brahea dulcis* (Kunth) Mart. en el estado de Hidalgo, México. In: Moreno Fuentes A, Pulido Silva MT, Mariaca Méndez R, Valadez Azúa R, Mejía Correa P, Gutiérrez Santillán TV, Eds. *Sistemas Biocognitivos tradicionales: paradigmas en la conservación biológica y el fortalecimiento cultural*. Primera edición. México, 24-29.

15. Crawley MJ. 2012. *The R Book*. 2nd Edition. Wiley United Kingdom.
16. Cunningham SA. 1997. The effect of light environment, leaf area, and stored carbohydrates on inflorescence production by a rain forest understory palm. *Oecologia* 111:36–44.
17. Duarte N, Montúfar R. 2012. Effect of leaf harvest on wax palm (*Ceroxylun echinulatum* Galeano) growth, and implications for sustainable management in Ecuador. *Tropical Conservation Science* 5:340-351.
18. Endress BA, Gorchev DL, Noble RB. 2004. Non-timber forest product extraction: effects of harvest and browsing on an understory palm. *Ecological Applications* 14:1139-1153.
19. Endress BA, Gorchov DL, Berry EJ. 2006. Sustainability of a non-timber forest product: Effects of alternative leaf harvest practices over 6 years on yield and demography of the palm *Chamaedorea radicalis*. *Forest Ecology and Management* 234:181-191.
20. Farrington SJ, Muzika RM, Drees D, Knight TM. 2008. Interactive effects of harvest and deer herbivory on the population dynamics of American Ginseng. *Conservation Biology* 23:719-728.
21. Felger R, Johnson MB, Wilson MF. 2001. *The trees of Sonora, Mexico*. USA Arizona: Oxford University Press,
22. Fleischner TL. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8:629-644.
23. Gaoue OG, Jiang J, Ding W, Agusto FB, Lenhart S. 2016. Optimal harvesting strategies for timber and non-timber forest products in tropical ecosystems. *Theoretical Ecology* 9:287-297.
24. Halekoh U, Højsgaard S. 2014. A kenward-roger approximation and parametric bootstrap methods for tests in linear mixed models–the R package pbkrtest. *Journal of Statistical Software*, *59*, 1-32.
25. Haro JM. 2009. Sierra Mayo-Yaqui, Sonora y Chihuahua. In Ceballos G, Martínez L, García A, Espinoza E, Bezaury J, Dirzo R, Eds. *Diversidad, amenazas y áreas prioritarias para la conservación de las Selvas Secas del Pacífico de México*. Primera edición. Fondo De Cultura Económica, CONABIO, WWF-MÉXICO, CONANP, UNAM, ECOCIENCIA S.C., 41-61.

26. Heckel CD, Bourg NA, McShea WJ, Kalisz S. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology* 91:319-326.
27. Hernández-Barrios JC, Anten NPR, Ackerly DD, Martínez-Ramos M. 2012. Defoliation and gender effects on fitness components in three congeneric and sympatric understorey palms. *Journal of Ecology* 100:1544-1556.
28. Herrera J. 1995. Acorn predation and seedling production in a lowdensity population of cork oak (*Quercus suber* L.). *Forest Ecology and Management* 76:197-201.
29. Joyal E. 1996. The use of Sabaluresana (Arecaceae) and other palms in Sonora, Mexico. *Economic Botany* 50:429-445.
30. Klinkhamer PGL, Meelis E, de Jong TJ, Weiner J. 1992. On the analysis of size-dependent reproductive output in plants. *Functional Ecology* 6:308–316.
31. Krishnakumar J, Fox J, Anitha V. 2012. Non-timber forest products livelihoods and conservation. *Economic & Political Weekly* 52:132-139.
32. Kuznetsova A, Brockhoff PB, Bojesen-Christensen RH. 2016. Package ‘ImerTest’: Tests in Linear Mixed Effects Models. Version 2.0-33.
33. Lopez-Toledo L, Anten NPR, Endress BA, Ackerly DD, Martínez-Ramos M. 2012. Resilience to chronic defoliation in a dioecious understory tropical rain forest palm. *Ecology* 100:1245-1256.
34. Lopez-Toledo L, Horn C, Endress BA. 2011. Distribution and population patterns of the threatened palm *Brahea aculeata* in a tropical dry forest in Sonora, Mexico. *Forest Ecology and Management* 261:1901-1910.
35. Mandle L, Ticktin T, Zuidema PA. 2015. Resilience of palm populations to disturbance is determined by interactive effects of fire, herbivory and harvest. *Journal of Ecology* 103:1032–1043.
36. Mandle L, Ticktin T. 2012. Interactions among fire, grazing, harvest and abiotic conditions shape palm demographic responses to disturbance. *Journal of Ecology* 100:997-1008.
37. Martínez-Ballesté A, Martorell C, Caballero J. 2008. The effect of Maya traditional harvesting on the leaf production, and demographic parameters of Sabal palm in the Yucatán Peninsula, Mexico. *Forest Ecology and Management* 256:1320-1324.

38. Martínez-Ballesté A, Martorell C. 2015. Effects of harvest on the sustainability and leaf productivity of populations of two palm species in Maya homegardens. *PloS One* 0:1-17.
39. Martínez-Ramos M, Álvarez-Buylla E. 1995. Ecología de poblaciones de plantas en una selva húmeda de México. *Boletín de la Sociedad Botánica de México* 56:121-153.
40. Martínez-Ramos M, Anten NPR, Ackerly DD. 2009. Defoliation and ENSO effects on vital rates of an understorey tropical rain forest palm. *Journal of Ecology* 97:1050–1061.
41. McNaughton SJ. 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40:329-336.
42. McPherson K, Williams K. 1998. The role of carbohydrate reserves in growth, resilience and persistence of cabbage palm seedlings (*Sabal palmetto*). *Oecologia* 117:460–468.
43. Meghan JS, Graydon DJ, Cushman JH. 2013. Community-level consequences of cattle grazing for an invaded grassland: variable responses of native and exotic vegetation. *Journal of Vegetation Science* 24:332–343.
44. Niinemets Ü, Al Afas N, Cescatti A, Pellis A, Ceulemans R. 2004. Petiole length and biomass investment in support modify light interception efficiency in dense poplar plantations. *Tree physiology* 24:141-154.
45. Ohse B, Compagnoni A, Farrior CE, McMahon SM, Salguero-Gómez R, Rüger N, Knight TM. 2023. Demographic synthesis for global tree species conservation. *Trends in Ecology & Evolution* 38:579-590.
46. Pinheiro JC, Bates DM. 2000. *Mixed-effects models in S and S-Plus*. New York, Springer-Verlag.
47. Poorter L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional ecology* 13:396-410.
48. Pulido MT, Caballero J. 2006. The impact of shifting agriculture on the availability of non-timber forest products: the example of *Sabal yapa* in the Maya lowlands of Mexico. *Forest Ecology and Management* 222:399-409.
49. Pulido MT, Coronel-Ortega M. 2015. Ethnoecology of the palm *Brahea dulcis* (Kunth) Mart. in central Mexico. *Journal of ethnobiology and ethnomedicine* 11:1-17.
50. Quero HJ. 1998. *Brahea aculeata*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 27 March 2015.

51. Quero HJ. 2000. El complejo *Brahea-Erythea* (Palmae: Coryphoideae). Informe final Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (CONABIO). Mexico City. Mexico.
52. Quisehuatl-Medina A, Averett JP, Endress BA, Lopez-Toledo L. 2020. Removal of cattle accelerates tropical dry forest succession in Northwestern Mexico. *Biotropica* 52:457-469.
53. Rodrigues de Mello NG, Gulinck H, Van den Broeck P, Parra C. 2023. A qualitative analysis of Non-Timber Forest Products activities as a strategy to promote sustainable land use in the Brazilian Cerrado. *Land Use Policy* 132:106797.
54. Sander NL, Pulido-Silva MT, da Silva CJ. 2023. Usos de las palmas en Latinoamérica. *CRV, Porto Alegre, Brazil*.
55. SEMARNAT. 2002. Norma Oficial Mexicana NOM-059-SEMARNAT-2010, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo.
56. Shackleton CM, Garekae H, Sardeshpande M, Sanni GS, Twine WC. 2024. Non-timber forest products as poverty traps: Fact or fiction? *Forest Policy and Economics*, 158:103114.
57. Sinasson S GK, Shackleton CM. 2023. The concurrent impacts of drought and leaf harvesting on two traditional African vegetable non-timber forest product species. *Plos one* 18:e0283900.
58. Staffan PK, Méndez M. 2005. The resource economy of plant reproduction. In: E Reekie, FA Bazzaz, eds. *Reproductive allocation in plants.* Oxford, UK. 1 Elsevier academic.
59. Sun JW, Sharifi MR, Rundel PW. 2022. Plasticity in Compensatory Growth to Artificial Defoliation and light availability in four neotropical understory and forest edge herb species. *Biology* 11:1532.
60. Stern M, Quesada M, Stoner K.E. 2002. Changes in composition and structure of a tropical dry forest following intermittent cattle grazing. Revista de Biología Tropical 50:1021-1034.
61. Svenning JC, Macia MJ. 2002. Harvesting of *Geonoma macrostachys* Mart. Leaves for thatch: an exploration of sustainability. *Forest Ecology and Management* 167:251-262.

62. Ticktin T, Charitonidou M, Douglas J, Halley JM, Hernández-Apolinar M, Liu H, Mondragón D, Pérez-García EA, Tremblay RL, Phelps J. 2023. Wild orchids: A framework for identifying and improving sustainable harvest. *Biological Conservation* 277:109816.
63. Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* 116:882-892.
64. Walker B, Kinzig A, Langridge J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2:95-113.
65. Ward JS, Jones CC, Barsky JP. 2022. Multiyear defoliations in southern New England increases oak mortality. *Canadian Journal of Forest Research* 52:269-279.
66. Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821-827.
67. Zuidema PA, de Kroon H, Werger MJA. 2007. Testing sustainability by prospective and retrospective demographic analyses: evaluation for palm leaf harvest. *Ecological Applications* 17:118–128.

Figure 1

Leaf production of Brahea aculeata individuals subjected to different intensities of browsing and harvesting of leaves in the tropical dry forest of Alamos, Sonora.

Leaf production of *Brahea aculeata* individuals subjected to different intensities of browsing and harvesting of leaves in the tropical dry forest of Alamos, Sonora: a) Juveniles, b) Adult I and c) Adult II. In the charts the different surfaces/trend lines represent the values predicted by the model for each year of sampling. Note the differences in the Y-axis scale.

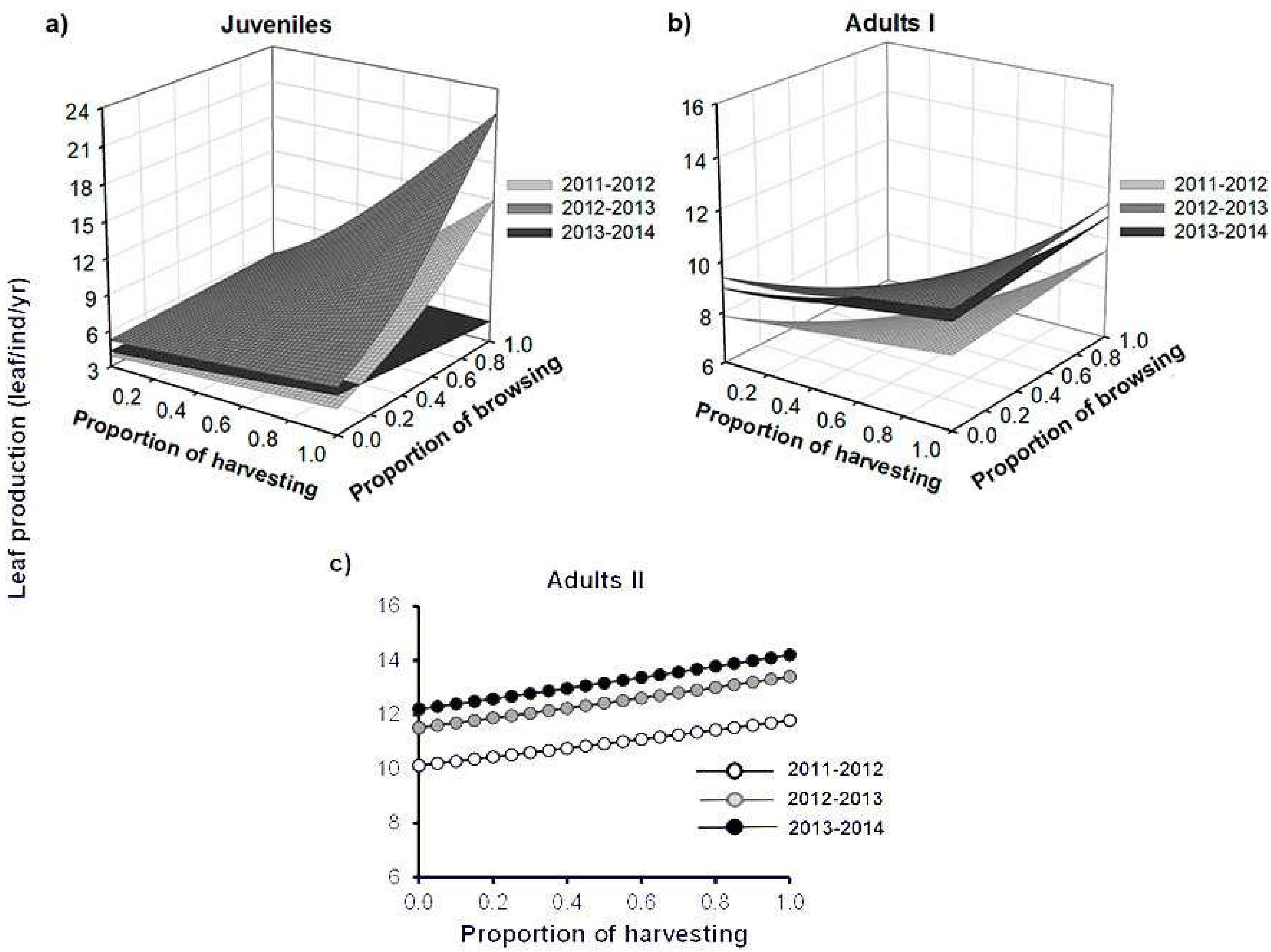

Figure 2

Leaf length of *Brahea aculeata* individuals subjected to different intensities of browsing and harvesting of leaves in the tropical dry forest of Alamos, Sonora

Leaf length of *Brahea aculeata* individuals subjected to different intensities of browsing and harvesting of leaves in the tropical dry forest of Alamos, Sonora: a) Juveniles, b) Adult I and c) Adult II. In the charts b) and c) the different surfaces represent the values predicted by the model for each year of sampling. In d) the letters represent significant differences for years of sampling. Note the differences in the Y-axis scale.

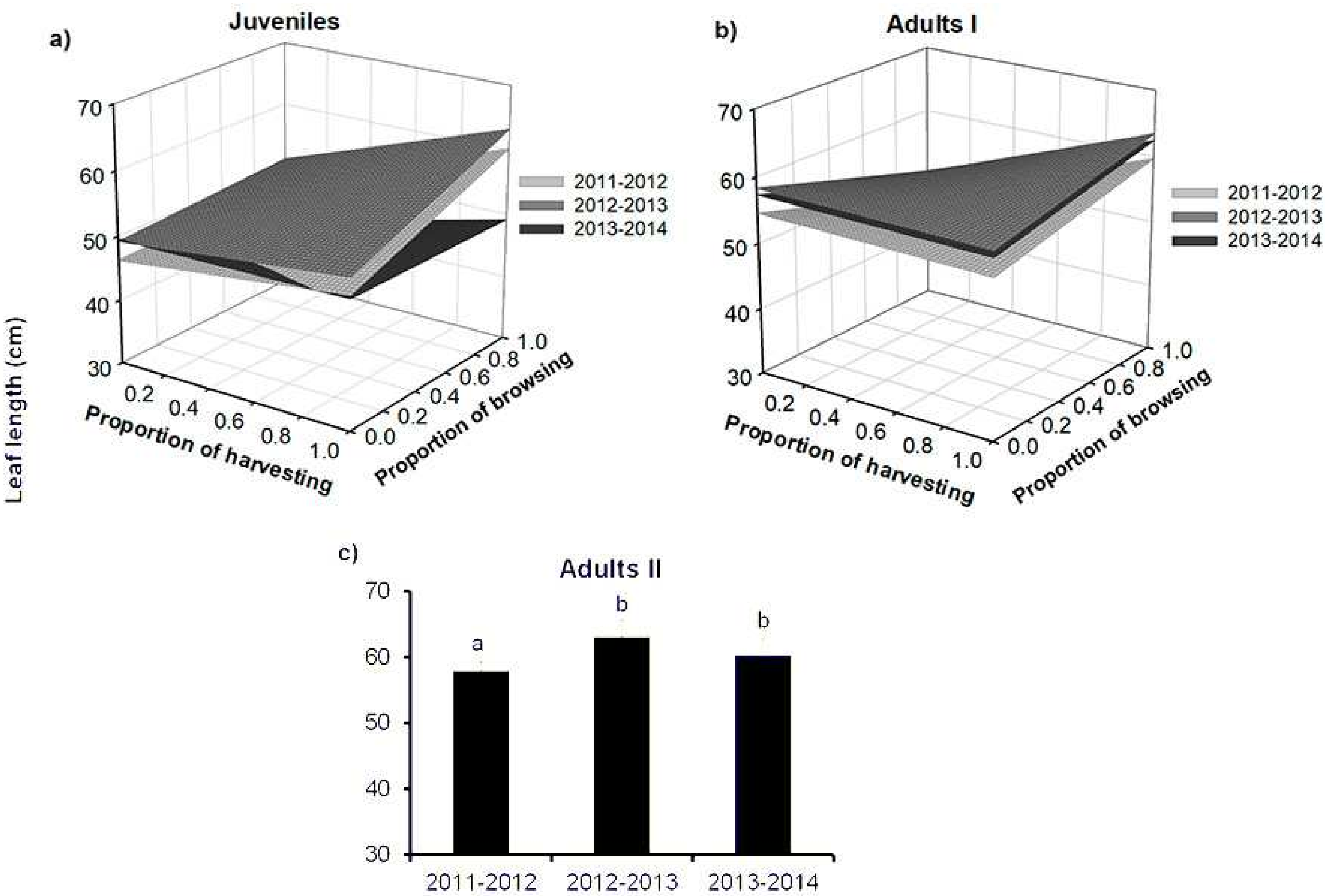

Figure 3

Petiole length of *Brahea aculeata* individuals subjected to different intensities of browsing and harvesting of leaves in the tropical dry forest of Alamos, Sonora

Petiole length of *Brahea aculeata* individuals subjected to different intensities of browsing and harvesting of leaves in the tropical dry forest of Alamos, Sonora: a) Seedlings, b) Juveniles, c) Adult I and d) Adult II. In graph a) the letters represent significant differences for years of sampling; while in b), c) and d) the different surfaces/trend lines represent the values predicted by the model for each year of sampling. Note the differences in the Y-axis scale.

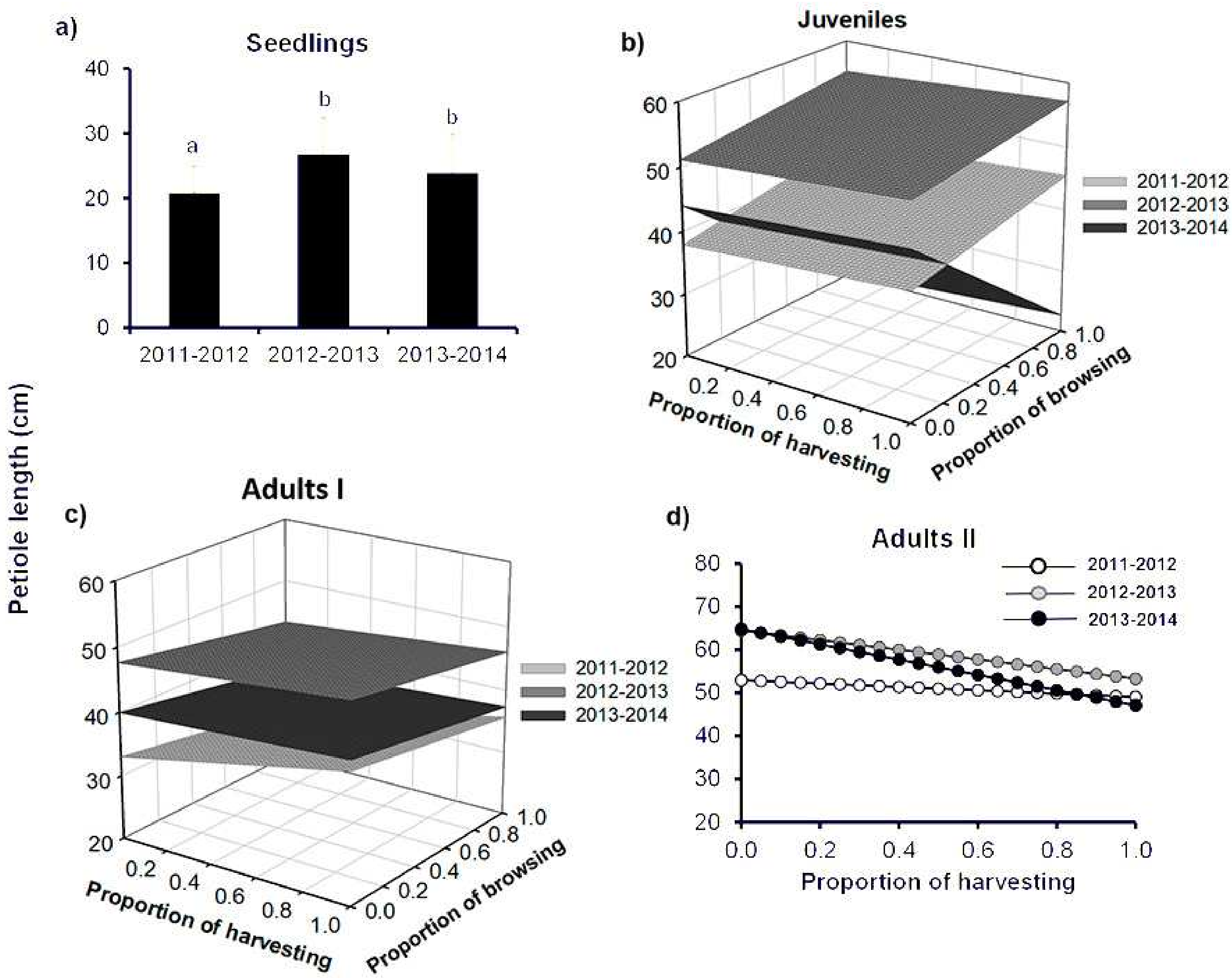
Petiole length (cm)
a)
Seedlings
40
30
20
10
0
a
b
b
2011-2012
2012-2013
2013-2014
b)
Juveniles
60
50
40
30
20
0.2
0.4
0.6
0.8
1.0
Proportion of harvesting
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of browsing
2011-2012
2012-2013
2013-2014
c)
Adults I
60
50
40
30
20
0.2
0.4
0.6
0.8
1.0
Proportion of harvesting
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of browsing
2011-2012
2012-2013
2013-2014
d)
Adults II
80
70
60
50
40
30
20
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of harvesting
2011-2012
2012-2013
2013-2014

Figure 4

Stem growth for *Brahea aculeata* individuals subjected to different intensities of browsing and harvesting of leaves in the tropical dry forest of Alamos, Sonora

Stem growth for *Brahea aculeata* individuals subjected to different intensities of browsing and harvesting of leaves in the tropical dry forest of Alamos, Sonora: a) stem growth and b) stem growth. In both charts the circles represent the observed values and the different colors represent the sampling years. The trend lines represent the values predicted by the model for each year of sampling. Note the logarithmic scale of the vertical axis in the plot.

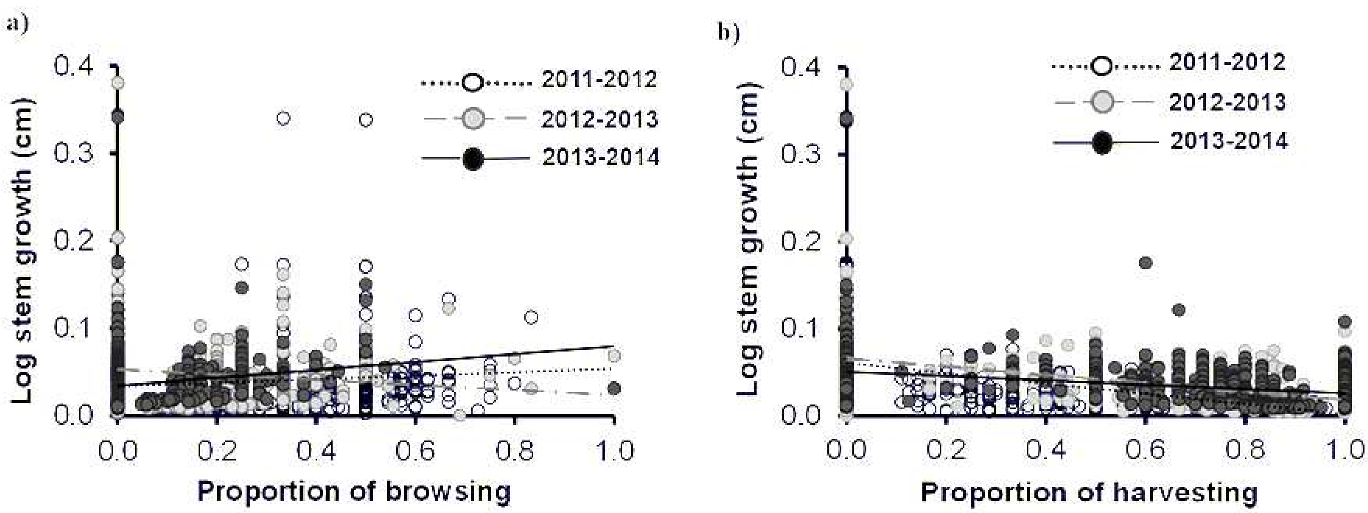

Figure 5

Reproductive attributes for *Brahea aculeata* under different harvesting intensities in the tropical dry forest of Alamos, Sonora

Reproductive attributes for *Brahea aculeata* under different harvesting intensities in the tropical dry forest of Alamos, Sonora. a) Reproduction probability as a function of harvesting, b) reproduction probability as a function of size and c) fruit production as a function of harvesting, d) fruit production as a function of size. In all the graphs the circles represent the observed values, the lines represent the values predicted by model and, the different colors in circles and lines represent the sampling years, in both charts lines represent the values predicted by the model.

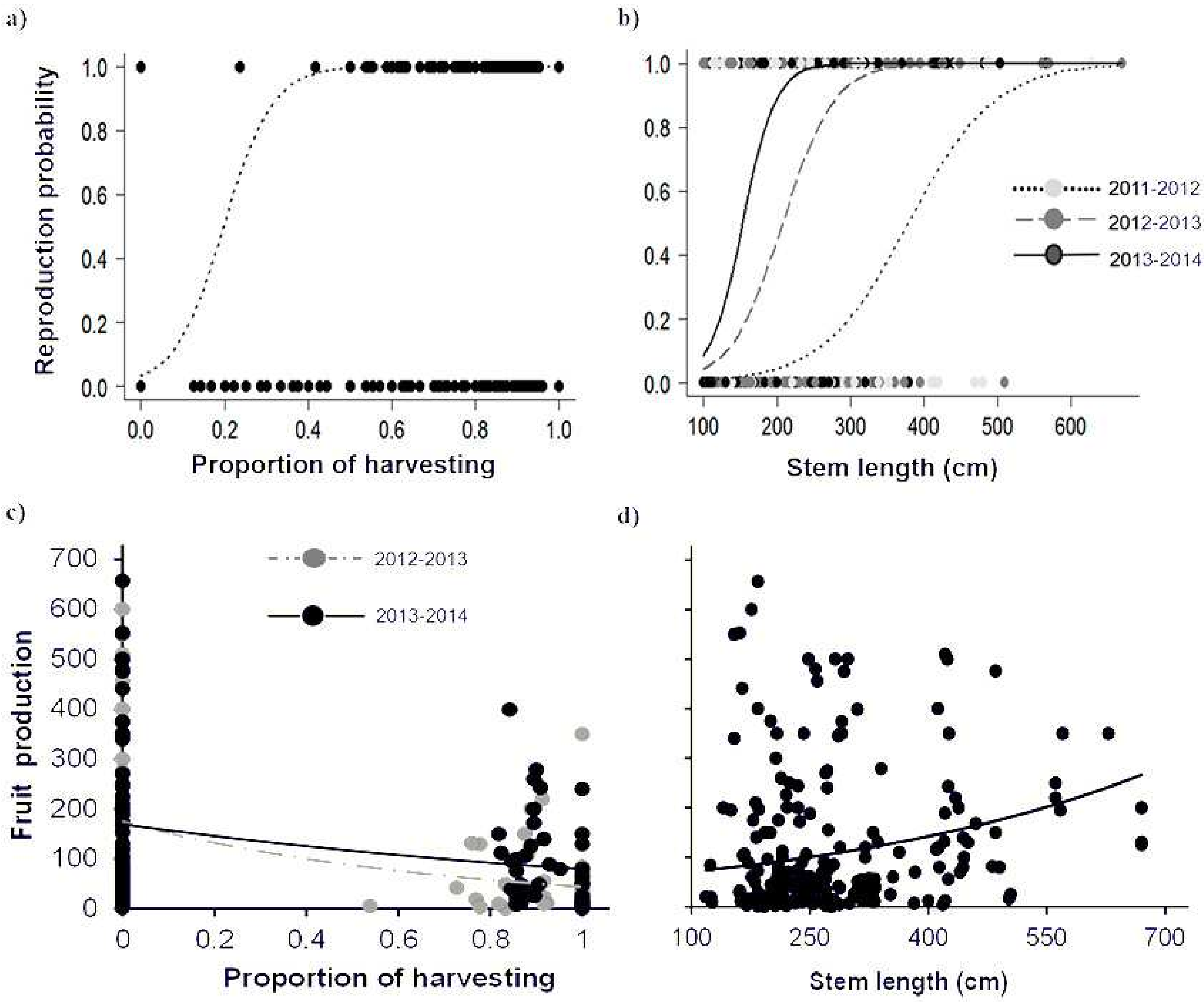
a)
Reproduction probability
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of harvesting
b)
1.0
0.8
0.6
0.4
0.2
0.0
2011-2012
2012-2013
2013-2014
100
200
300
400
500
600
Stem length (cm)
c)
Fruit production
700
600
500
400
300
200
100
0
2012-2013
2013-2014
0
0.2
0.4
0.6
0.8
1
Proportion of harvesting
d)
100
250
400
550
700
Stem length (cm)

Table 1 (on next page)

Five tables are included in a .docx file

Legends of five tables are included in a .docx file

Individual and demographic responses of the palm *Brahea aculeata* to browsing and leaf harvesting in a tropical dry forest of Northwestern Mexico

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TABLES

Table 1. Result of Generalized Linear Mixed-Effects Models (GLMMs) used to assess the cumulative effects of browsing and harvesting of leaves on leaf production of *Brahea aculeata* in the tropical dry forest of Alamos, Sonora. The terms tested in the models were the time (T), browsing proportion (Br), harvesting proportion (H) and the interactions among these terms (Br:H). The statistics are provided *F* and χ2, degrees of freedom in brackets (*gl*) and *P* valor with based in maximum likelihood ratio test; *ns* indicates that there was no significant effect; (–) indicates that the factor was not significant and therefore it was removed from the model (See Figure 1).

	Leaf production							
	Seedlings		***Juveniles***		***Adults I***		***Adults II***	
Factors	$F/LRT\chi^2_{(gl)}$	P	$F/LRT\chi^2_{(gl)}$	P	$F/LRT\chi^2_{(gl)}$	P	$F/LRT\chi^2_{(gl)}$	P
Time (T)	-	-	$41.8_{(2,1987)}$	<0.001	$40.5_{(2)}$	<0.001	$19.9_{(2)}$	<0.001
Browsing (Br)	-	-	$6.9_{(1,1987)}$	0.008	$12.5_{(1)}$	<0.001		
Harvesting (H)	NA	NA	$97.5_{(1,1987)}$	<0.001	$5.4_{(1)}$	0.01	$4.5_{(1)}$	0.03
T:Br	-	-	$0.7_{(2,1985)}$	*ns*	-	-		
T:H			$3.8_{(2,1987)}$	0.02	-	-	-	-
Br:H			$6.8_{(1,1987)}$	0.008	$3.9_{(1)}$	0.04		
T:Br:H			$5.4_{(2,1985)}$	0.004	-	-		

Table 2. Result of Linear Mixed-Effects Models (LMM) used to assess the cumulative effects of browsing and harvesting of leaves on leaf length of *Brahea aculeata* in the tropical dry forest of Alamos, Sonora. The terms tested in the models were the time (T), browsing proportion (Br), harvesting proportion (H) and the interactions among these terms (Br:H). The statistics are provided *F* and χ2, degrees of freedom in brackets (*gl*) and *P* valor with based in maximum likelihood ratio test; *ns* indicates that there was no significant effect; (–) indicates that such factor was not significant and therefore it was removed from the model (See Figure 2).

Leaf length								
	Seedlings		***Juveniles***		***Adults I***		***Adults II***	
Factors	$F/LRT\chi^2_{(gl)}$	P	$F/LRT\chi^2_{(gl)}$	P	$F/LRT\chi^2_{(gl)}$	P	$F/LRT\chi^2_{(gl)}$	P
Time (T)	-	-	$28.1_{(2,1982)}$	<0.001	$68.9_{(2)}$	<0.001	$22.8_{(2)}$	<0.001
Browsing (Br)	-	-	$1.2_{(1,1982)}$	ns	$11.2_{(1)}$	<0.001		
Harvesting (H)			$21.3_{(1,1982)}$	<0.001	$0.7_{(1)}$	ns	-	-
T:Br	-	-	$3.5_{(2,1982)}$	<0.02	-	-		
T:H			$17.8_{(2,1982)}$	<0.001	-	-	-	-
R:H			$6.3_{(1,1982)}$	0.01	$6.3_{(1)}$	0.01		
T:Br:H			-	-	-	-		

Table 3. Result of Linear Mixed-Effects Models (LMM) used to assess the cumulative effects of browsing and harvesting of leaves on petiole length of *Brahea aculeata* in the tropical dry forest of Alamos, Sonora. The terms tested in the models were the time (T), browsing proportion (Br), harvesting proportion (H) and the interactions among these terms (Br:H). The statistics are provided *F* and χ2, degrees of freedom in brackets (*gl*) and *P* valor with based in maximum likelihood ratio test; *ns* indicates that there was no significant effect; (–) indicates that such factor was not significant and therefore it was removed from the model (See Figure 3).

	Petiole length							
	Seedlings		***Juveniles***		***Adults I***		***Adults II***	
Factors	$F/LRT\chi^2_{(gl)}$	*P*	$F/LRT\chi^2_{(gl)}$	*P*	$F/LRT\chi^2_{(gl)}$	*P*	$F/LRT\chi^2_{(gl)}$	*P*
Time (T)	$15.2_{(2)}$	<0.001	$139.5_{(2,1988)}$	<0.001	$175.09_{(2,891)}$	<0.001	$9.04_{(2,283)}$	<0.001
Browsing (Br)	-	-	$0.7_{(1,1988)}$	ns	$6.2_{(1,891)}$	0.01		
Harvesting (H)			$5.1_{(1,1988)}$	0.02	$2.3_{(1,891)}$	ns	$13.6_{(1,283)}$	<0.001
T:Br	-	-	$9.6_{(2,1988)}$	<0.001	-	-		
T:H			-	-	$4.5_{(2,891)}$	0.01	$6.7_{(2,283)}$	0.001
R:H			-	-	-	-		
T:Br:H			-	-	-	-		

Table 4. Result of Linear Model Using Generalized Least Squares (GLS) used to assess the cumulative effects of browsing and harvesting of leaves on stem growth *Brahea aculeata* in the tropical dry forest of Alamos, Sonora. The terms tested in the models were time (T), browsing proportion (Br), harvesting proportion (H), stem length (SL) and the interactions among these factors. The statistics are provided (χ2, degrees of freedom in brackets and *P* value based in maximum likelihood ratio test; ns indicates no significant effect of the term and – indicates that such factor was not significant and therefore it was removed from the model. Three and four way interactions (SL:T:Br, SL:T:H, SL:Br:H, T:Br:H, SL:T:Br:H) were not significant and were removed from the model and therefore they are not included in the table (See Figure 4).

Stem growth		
Factors	χ^2	*P*
Stem length (SL)	$253.5_{(1)}$	<0.001
Time (T)	$23.5_{(2)}$	<0.001
Browsing (Br)	$8.9_{(1)}$	<0.01
Harvesting (H)	$1.1_{(1)}$	ns
SL:T	$7.27_{(2)}$	0.02
SL:Br	-	-
SL:H	-	-
T:Br	$7.08_{(2)}$	0.02
T:H	$7.08_{(2)}$	0.02
Br:H	-	-

Table 5. Result of Generalized Linear Mixed-Effects Models (GLMMs) or Generalized Linear Mixed Models using AD Model Builder (glmmADMB) used to assess the cumulative effects of browsing and harvesting of leaves on reproductive attributes *Brahea aculeata* in the tropical dry forest of Alamos, Sonora. The terms tested in the models were time (T), browsing proportion (Br), harvesting proportion (H), stem length (SL) and the interactions among these factors. We used *glmer* for the reproduction probability and *glmmadmb* for the fruit number. The statistics are provided (χ2, degrees of freedom in brackets and P value based in maximum likelihood ratio test; ns indicates no significant effect of the term and – indicates that such factor was not significant and therefore it was removed from the model). Three and four way interactions (SL:T:Br, SL:T:H, SL:Br:H, T:Br:H, SL:T:Br:H) were not significant and were removed from the model and therefore they are not included in the table (See Figure 5).

	Reproductive attributes			
	Probability of reproduction		**Fruit production**	
Factors	χ^2	*P*	χ^2	*P*
Stem length (SL)	$20.8_{(1)}$	<0.001	$17.68_{(1)}$	<0.001
Time (T)	$1.01_{(2)}$	ns	$6.9_{(2)}$	0.03
Browsing (Br)	-	-	-	-
Harvesting (H)	$8.59_{(1)}$	0.003	$10.18_{(2)}$	0.006
SL:T	$26.06_{(2)}$	<0.001	-	-
SL:Br	-	-	-	-
SL:H	-	-	-	-
T:Br	-	-	-	-
T:H	-	-	$3.9_{(1)}$	0.04
Br:H	-	-	-	-