EFFECTS OF LEAF HARVEST ON *THRINAX RADIATA* PALM: IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

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CALVO-IRABIÉN LM, ZAPATA MT & IRIARTE-VIVAR S. 2009. **Effects of leaf harvest on** *Thrinax radiata* **palm: implications for management and conservation.** For centuries, Mayans have used *Thrinax radiata* leaves for roof thatching and broom manufacturing. To determine sustainable leaf harvest levels, an evaluation was done to study the effects of four harvest regimes on individual-level and leaf-level responses. Four leaf harvest (i.e. defoliation) intensities were simulated: control (0%); low (30%); intermediate (70%); and high (100%), following traditional practices. Readings were taken every six months over an 18-month period to record survival, trunk height, leaf production and new leaf nitrogen content. Low intensity harvest (30%) increased leaf size but had no effect on leaf production. On the contrary, six months after harvest, individuals in the 100% treatment produced more leaves than the control. However, this treatment negatively affected future growth, which was reflected in decreasing leaf number and size, 18 months post-harvest. New leaf nitrogen content was unaffected by harvest intensity, suggesting that the mechanism responsible for compensation of lost tissue in *T. radiata* is primarily mobilization of carbohydrate reserves, and not an increase in leaf nitrogen content. Thirty per cent defoliation of palm crown is suggested as a sustainable leaf harvest level to ensure no effect on leaf size and rapid recovery of initial leaf number.

Keywords: Defoliation, dry forest, non-timber forest product, Quintana Roo, sustainable harvest

CALVO-IRABIÉN LM, ZAPATA MT & IRIARTE-VIVAR S. 2009. **Kesan penuaian daun terhadap palma** *Thrinax radiata*: **implikasi kepada pengurusan dan pemuliharaan.** Orang Maya menggunakan daun *Thrinax radiata* untuk membuat atap berjerami dan penyapu selama berdekad-dekad. Bagi menentukan kadar penuaian daun yang mampan, penilaian dijalankan untuk mengkaji kesan empat kadar penuaian terhadap respons peringkat individu dan peringkat daun. Empat kadar penuaian daun (iaitu peranggasan) dijalankan: kawalan (0%), rendah (30%), pertengahan (70%) dan tinggi (100%) mengikut amalan tradisi. Nilai-nilai kemandirian, ketinggian batang, penghasilan daun dan kandungan nitrogen daun baru disukat setiap enam bulan selama 18 bulan. Penuaian berkadar rendah (30%) menambahkan saiz daun tetapi tidak mempengaruhi penghasilan daun. Sebaliknya, enam bulan selepas penuaian, individu yang mengalami 100% penuaian menghasilkan lebih daun daripada kawalan. Namun, penuaian 100% mempengaruhi pertumbuhan masa depan secara negatif, seperti yang ditunjukkan oleh bilangan daun yang berkurangan dan saiz daun yang lebih kecil, 18 bulan selepas penuaian. Kandungan nitrogen dalam daun baru tidak dipengaruhi oleh kadar penuaian. Ini menunjukkan mekanisme yang bertanggungjawab terhadap pampasan tisu yang hilang dalam *T. radiata* ialah pergerakan simpanan karbohidrat dan bukan penambahan kandungan nitrogen daun. Sebanyak 30% peranggasan silara palma dicadangkan sebagai kadar penuaian yang mampan bagi memastikan tiada kesan terhadap saiz daun dan bilangan daun kembali kepada asal dengan cepat.

INTRODUCTION

Palm leaves are one of the most important resources worldwide for rural people (Balick & Beck 1990) and are harvested for subsistence, cultural and commercial ends. This holds true for palms of the Yucatan Peninsula, where palms are of economic and ecological relevance (Orellana & Duran 1992, Sanchez-Sanchez & Islebe 2002).

Harvest and management of non-timber forest products (NTFP) have been proposed as an economic alternative that produces less impact on the structure and function of forest ecosystems than other productive activities (Nepstand & Schwartzman 1992). Although harvesting of NTFP may represent an economic alternative for household income and may

promote commitment among local people to forest conservation it may not always be ecologically sustainable.

The chit palm (*Thrinax radiata*, Arecaceae) was legally designated a threatened species in Mexico in 1994 (NOM-059-ECOL-2001). Nevertheless, illegal harvest and sale of this palm species is frequent. Chit palm populations are threatened primarily by habitat destruction from human activities (mainly tourism, agriculture and livestock raising), although direct use by local people, particularly harvesting whole individuals, and leaf harvest, are important threats (Olmsted & Alvarez-Buylla 1995, Calvo-Irabien & Ceballos-Gonzalez 2004). Under the current legislation, any commercial exploitation of this species requires a permit which includes clear statements of population status and effect of harvest.

Thrinax radiata trunks have been used in the construction of huts by the Mayans. Recently, trunks have been used to build lobster traps and tourism facilities (restaurants, huts, interior decorating, fences). Olmsted and Alvarez-Buylla (1995) studied the impact of stem harvest on population dynamics. Chit palm leaves have a wide variety of uses, including roof thatch, brooms, handcrafts and wrapping of food to be cooked in a hole in the ground. Its leaves also have several minor ritual, medicinal and ornamental uses (Calvo-Irabien & Ceballos-Gonzalez 2004). Although chit leaves have been used for centuries in the Yucatan Peninsula (Roys 1931), no ecological data have been generated to assess the impact and sustainability of its current harvesting regimes.

This kind of data is vital since many families depend on income from leaf harvest, while government institutions have the mission of preventing overexploitation of natural populations. Due to the rapid growth of tourism in Yucatan Península and the importance of chit leaves for roof thatching of tourism facilities, biological data will aid in precisely assessing leaf harvest impact, evaluating the potential for sustainable use or the risk of over-exploitation, and designing appropriate regulations for chit palm leaf harvest.

Partial defoliation of any plant entails a loss of photosynthetic tissue and can therefore negatively affect survival, growth and reproduction (Anten & Ackerly 2001, Anten *et al.* 2003). Long-term sustainability of chit palm leaf harvest depends on the ability of individual plants to survive defoliation and recover photosynthetic tissue after leaf removal. A plant's response largely depends on the severity of defoliation and its ability to mitigate the resulting damage through compensatory growth (Chazdon 1991, Anten *et al.* 2003, Rodriguez-Buritaca *et al.* 2005, Zuidema *et al.* 2007). Defoliation in the forest understorey aggravates the negative effect of light limitation by directly reducing plants' ability to capture light (Chazdon 1991, Anten *et al.* 2003). Several studies have emphasized the role played by carbohydrate reserves in compensation after defoliation of individual palms (Mendoza *et al.* 1987, Oyama & Mendoza 1990, Chazdon 1991). At the leaf level, a number of mechanisms have been proposed to explain compensation after defoliation: higher photosynthetic translocation rates in the remaining foliage; greater light availability due to diminished self-shading; changes in biochemical reaction rates associated with increased nitrogen availability; and changes in nitrogen partitioning within the leaf (Chazdon 1991, Anten & Ackerly 2001, Anten *et al.* 2003). A number of studies have reported a strong correlation between leaf nitrogen content and photosynthetic capacity of plants of a broad group of taxa (Field & Mooney 1986, Evans 1989, Reich *et al.* 1994) or between species across the same genus (Chazdon & Field 1987, Hogan 1988) because the photosynthetic machinery accounts for a large investment of nitrogen in a leaf (Field & Mooney 1986, Lambers *et al.* 1998).

Although responses to defoliation vary, the emerging general pattern in palm species is one of tolerance for even high levels of defoliation and an ability to recover effectively after treatment (Mendoza *et al.* 1987, Oyama & Mendoza 1990, Chazdon 1991, Zuidema & Werger 2000, Svenning & Macias 2002, Anten *et al.* 2003, Endress *et al.* 2004, Rodriguez-Buriticá *et al.* 2005, Endress *et al.* 2006, Valverde *et al.* 2006, Zuidema *et al.* 2007). Nevertheless, negative effects of defoliation, such as a decrease in leaf length (O'Brien & Kinnaird 1996, Ratsirarson *et al.* 1996, Endress *et al.* 2004), higher mortality rates in seedlings and juveniles (Mendoza *et al.* 1987) and especially reduced reproductive output (Ratsirarson *et al.* 1996, Anten *et al.* 2003, Endress *et al.* 2004, Valverde *et al.* 2006, Zuidema *et al.* 2007) have been reported for palm species.

The aim of the present study was to evaluate the ability of *T. radiata* to mitigate the negative

effects of defoliation, under different leaf harvest intensities. To do so, we used a manipulative experiment under natural conditions to simulate the current management practices of local users. Data on the leaf removal responses at the individual level (survival, leaf production) and at the leaf level (leaf size and nitrogen content) were used to determine sustainable leaf harvest levels.

MATERIALS AND METHODS

Study site

The study was conducted at two forest sites located in the communally-held land of Kantunilkin and Solferino, which surround the Yumbalam Natural Protected Area (21° 13' to 21° 24' N; 87° 20' to 87° 26' W). Climate in the region is warm, subhumid with summer and winter rains. Annual average precipitation is 1100 mm, with a dry season from March till May. Annual mean temperature is 24.6 °C (Orellana *et al.* 1999). The environment is karstic, with soils being young, shallow and rocky. Vegetation is dry tropical forest (Holdridge 1967) with a mean height of 15 to 20 m. The most abundant tree and palm species include *Manilkara sapota, Simarouba glauca, Swartzia cubensis, Bursera simaruba, Sabal yapa* and *T. radiata* (La Torre-Cuadros & Islebe 2003).

The study area, in the northwest portion of the state of Quintana Roo, has been inhabited by humans for thousands of years, and is located within the ancient Mayan province known as Ecab. In 1527, the Spanish reported this area to be densely populated (Careaga 1979). Human communities are located in the Lázaro Cardenas district and the population is primarily rural. Local ethnic groups include Maya and Mestizo from Yucatan and Quintana Roo, as well as a small group of Totonac descendants originally from the state of Veracruz (La Torre-Cuadros & Islebe 2003). The main productive activities are agriculture and extraction of forest products, complemented by livestock, fishing and apiculture activities (La Torre-Cuadros & Islebe 2003).

Species description

Thrinax radiata is found in the Bahamas, Cuba, Jamaica, Haiti, Florida and the Yucatan Peninsula; it is the only species of this genus in Mexico

(Quero 1992). Chit palm is a single-trunk palm that reaches sub-canopy to canopy heights in the semi-evergreen forest and coastal dunes of the states of Quintana Roo and Yucatan (Olmsted & Alvarez-Buylla 1995, Sanchez-Sanchez & Islebe 2002). Leaves are fan-shaped, number from 5 to 25 and can measure up to 1.8 m in diameter (mean: 70 cm). The ramified inflorescence is 50 to 60 cm long, and can bear up to 11 000 small (ca. 5 mm), bisexual flowers. Plants reach reproductive maturity when approximately 3 m tall, and yearly produce between 300 and 3000 white-coloured fruits per individual (Olmsted & Alvarez-Buylla 1995). Each fruit contains one seed, and these seeds are plain, shiny, brown in colour and measure 7 mm in diameter (Quero 1992). This species grows slowly and growth rate depends mainly on light conditions; a 15 m tall palm is approximately 70 to 100 years old (Olmsted & Alvarez-Buylla 1995).

Several characteristics of the chit palm leaf blade, such as its size, form and resistance to rapid decay, have led this species to its wide-spread use as roof thatch and for broom manufacture in the Yucatan Peninsula (Orellana & Duran 1992, Olmsted & Alvarez-Buylla 1995, Arellano *et al.* 2003). An average of 12 leaves is harvested to make a broom, whereas thatching requires large numbers of leaves: 2000 to 3000 leaves for a typical traditional Mayan-style house; 5000 to 8000 leaves for tourist structures such as huts or restaurants. Dried chit palm thatch can last as long as 15 years (Calvo-Irabien & Ceballos-Gonzalez 2004, Zapata 2004).

Twenty men, with experience in chit leaf harvesting, from Kantunilkin and Solferino, were interviewed. A semi-structured interview was implemented to describe leaf harvesting practices. Leaves are harvested year round from juvenile palms between 0.5 and 2.5 m trunk height. Only leaves with fully expanded leaf blades are cut and those between 50 and 70 cm in diameter are typically preferred. Large, undamaged leaf blades are the most valuable (Zapata 2004). Sixty per cent of interviewed harvesters left uncut half of the leaves on an individual, while the other 40% of interviewed harvesters, left only three leaves in the palm crown, which represents an 80% defoliation of the palm crown, based on an average leaf number of 14.6 per individual (Zapata 2004). Under the current market leaf demand, repeated harvest of the same palm individual within a year

is rarely performed (Zapata 2004); only 20% of the interviewed harvesters mentioned to have repeated leaf harvest on the same individual within six months, most harvesters performed a repeated harvest at least one year later. Chit leaves and brooms are sold mainly in local stores or through personal arrangements with buyers in nearby tourist areas such as Isla Holbox or Cancun (Zapata 2004).

Experimental design

At each forest site (Kantunilkin and Solferino), one permanent plot (2000 m^2) was established. In these two plots, three leaf harvest intensities were implemented: low, 30% of fully expanded leaves on an individual removed; medium, 70%; and high, 100%; and a control treatment (0% defoliation). For palms that did not have exactly 10 leaves, the 30 and 70% treatments were performed by rounding to the next highest integer if the first decimal figure of the number of leaves to be harvested was higher than 0.5 (e.g. 2.7 = 3 harvested leaves), and to the next lowest integer if the value was equal or lower than 0.5 (e.g. 2.1 = 2 harvested leaves). Fifteen individuals were randomly assigned to each of the four treatments. A total of 60 palm individuals were studied in each permanent plot. ANOVA tests showed no significant differences in initial mean trunk height ($F_{(7, 112)}$ = 1.41 p = 0.208) or initial leaf number ($F_{(7, 112)}$ = 1.130 p = 0.350) for palm individuals in the four different leaf harvest intensity treatments. Initial trunk height averaged 1.4 m (S.E. = 0.48, range 50 to 250 cm) and, average initial leaf number was 11.4 (SE = 0.23, range = 6 to 17 leaves). Experimental palm individuals had not been previously harvested. In order to have control over the defoliation treatments, permanent plots were selected in areas rarely visited by harvesters.

Leaf harvest followed local harvest technique for chit palm, as described in the interviews (see species description section; Zapata 2004). Whole leaves were cut with a machete at the base of the petiole. The newly emerged, unfolded leaf was not harvested as part of any defoliation treatment. The number of leaves removed per individual in the same treatment varied depending on the initial number of leaves present. Defoliations were performed once, in November 2002. According to interviewees, the

experimental individuals had not been harvested in the previous year.

The youngest, unopened leaf was marked on the petiole to aid in recording new leaf production. Leaves were considered as new leaves when the foliar blade was fully expanded. Leaf production was used to assess palm growth because trunk increases in height with new leaf production (Olmsted & Alvarez-Buylla 1995). Data were obtained at three, six-month intervals following defoliation (i.e. at 6, 12 and 18 months). Survival, trunk height, new leaf production (number of new leaves) and radius of each leaf (from hastula to end of foliar lamina) were recorded for all experimental individuals. Leaf area was indirectly estimated based on 35 randomly sampled leaves. A scaled digital image was taken of each foliar lamina. Digital images were edited and transformed to black and white format (Scion image software) and Idrisi software (Eastman 1999) was used to calculate image area for each sampled leaf. Based on the radius and leaf area data for the 35 leaves, the following regression equation was developed: log leaf area = -0.8894 + 0.824*radius (adjusted R = 0.78, $F_{(1, 33)}$ = 39.37 p < 0.001), and used to estimate total leaf area of each experimental individual in the field.

Effects on individual growth

The effect of leaf harvest intensity at the individual level was tested using repeated-measures ANOVA (Von Ende 1993) for two response variables: number of new leaves and leaf size. The Site and Defoliation factors were considered as the main effects and Time was the repeated measure factor. Three time periods were analysed for each Site/Defoliation combination. Site, Defoliation and Time were treated as fixed effects, and therefore a completely fixed effects model was used (Wiener *et al.* 1991). *A posteriori* Tukey tests (Sokal & Rohlf 1995) were done for each time period (6, 12 and 18 months after harvest) to compare the effects of leaf harvest intensity. Data were pooled across sites for this multiple comparison analysis.

Effects on leaf nitrogen content

Quantitative assessment of the effects of leaf harvest intensity on leaf photosynthetic capacity was done by measuring relative nitrogen content

in new leaves. A subsample of six individuals (replicates) from each harvest treatment was selected for this purpose. Four leaf sections were removed from new, fully expanded, leaves. Leaf discs were removed from the leaf apex using a 1 inch diameter cork borer. In cases where four leaves could not be found on an individual, samples were taken from the available new leaves. Plant materials were transported on ice to the laboratory. Biomass (dry weight) of leaf discs was measured on an analytic top-loading balance. All plant materials were ovendried for 48 hours at 60 °C to constant weight. Plant samples were analysed for total nitrogen content, after acid digestion, by the micro-Kjeldahl method (Labconco Corporation 1998). Nitrogen content was measured at 6 and 12 months post-harvest and relative leaf nitrogen content was calculated on a dry weight basis. Changes in new leaf N content were analysed using the same experimental design as described above. Based on the available data, however, the repeated-measures ANOVA was only done for two time periods (6 and 12 months). All statistical analyses were done with the SYSTAT v.12 program (Systat 2002). When needed, data were transformed to improve for normality and variance homogeneity.

RESULTS

Individual-level response to leaf harvest intensity

No individual mortality was registered during the study period. The number of new leaves produced over time was significantly different between harvest treatments (Time × Defoliation; Table 1 and Figure 1). The interaction, Time × Defoliation × Site was not significant, indicating that the effect of the defoliation treatments was equal between sites (Table 1). *A posteriori* Tukey tests showed that for the 30 and 70% treatments, defoliation did not have a negative impact. Defoliated individuals produced similar number of new leaves than undisturbed palms (Figure 1). In the high intensity treatment (100%), six months post-harvest defoliated individuals produced significantly more leaves than the control (Figure 1). Nevertheless, 18 months post-harvest, individual palms under the 100% defoliation treatment produced significantly fewer leaves than the control and 30% treatments (Figure 1). F and p values for the *a posteriori*

Tukey tests were F$_{(3, 116)}$ = 3.44; p = 0.019, F$_{(3, 116)}$ = 2.18; p = 0.097 and F$_{(3, 116)}$ = 3.16; p = 0.027; for 6, 12 and 18 months respectively.

Leaf size was significantly affected by harvest intensity and varied over time (Time × Defoliation; Table 2; Figure 2). The effect of defoliation on leaf size was equal between study sites, as shown by the non-significant interaction Time × Defoliation × Site (Table 2 and Figure 2). Tukey tests indicated that 6 and 12 months after harvest, defoliation had a positive effect on leaf size. Individuals in the 30% treatment produced larger leaves than those in the control (Figure 2). In contrast, the effect of leaf removal in the high intensity defoliation treatment had a negative impact on leaf size. Twelve and 18 months post-harvest, individuals in the 100% treatment produced smaller leaves compared with individuals under the 30 and 70% treatments, but leaf size was equal to undefoliated individuals (Figure 2). F and p values for the *a posteriori* Tukey tests were F$_{(3, 116)}$ = 2.93; p = 0.04, F$_{(3, 116)}$ = 8.39; p < 0.0001 and F$_{(3, 116)}$ = 4.70; p = 0.004 for 6, 12 and 18 months respectively.

Leaf-level response to leaf harvest intensity

At both sites, leaf nitrogen content was unaffected by leaf harvest intensity (Figure 3), as indicated by the Time × Defoliation interaction and the Time × Defoliation × Site interaction in the repeated-measures ANOVA (Table 3). Regardless of harvesting intensity, leaf nitrogen content in new leaves was higher 6 months post-harvest (18.8 $\pm$ 0.28) than 12 months post-harvest (15.6 $\pm$ 0.21; Figure 3).

DISCUSSION

During the 18-month study period, no individual mortality was observed, not even when 100% of the fully opened leaves were harvested. In general, this result is consistent with other studies on neotropical palm species (Mendoza *et al.* 1987, Oyama & Mendoza 1990, Chazdon 1991, Martinez-Balleste 2006, Zuidema *et al.* 2007). The limited period of our study did not allow us to conclude about the long-term effect of harvest intensity, or repeated defoliation events on mortality rates of *T. radiata*. Zuidema *et al.* (2007), who studied defoliation response of 10 understorey palm species, found that survival was either not affected or hardly affected by

Table 1   Repeated measures ANOVA for effects of leaf harvest intensity on new leaf production 6, 12 and 18 months after harvest. Probabilities were corrected for sphericity using the Greenhouse-Geisser correction (G-G).

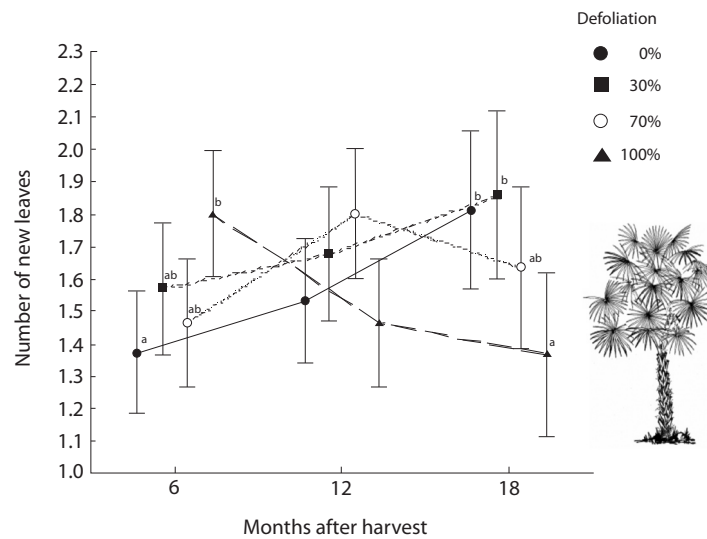| Source of variation	df	MS	F	p	G-G
Site	1	6.14	2075.39	0.0000	
Defoliation	3	0.97	14.16	0.0003	
Site × Defoliation	3	0.50	2.25	0.0869	
Error	112	0.43	1.08	0.3692	
Time	2	0.69	2.14	0.1198	0.1200
Time × Site	2	0.55	1.73	0.1803	0.1803
Time × Defoliation	6	1.25	3.89	0.0010	0.0010
Time × Defoliation × Site	6	0.50	1.55	0.1622	0.1620
Error	224	0.32			

Figure 1   Effects of leaf harvest intensity on new leaf production of *Thrinax radiata*. Data are means $\pm$ 95% confidence interval. Means with the same letter are not significantly different within each time period in a post hoc Tukey test ($p \leq 0.05$).

Table 2   Repeated measures ANOVA for effects of leaf harvest intensity on leaf size (m^2) 6, 12 and 18 months post-harvest. Probabilities were corrected for sphericity using the Greenhouse-Geisser correction (G-G).

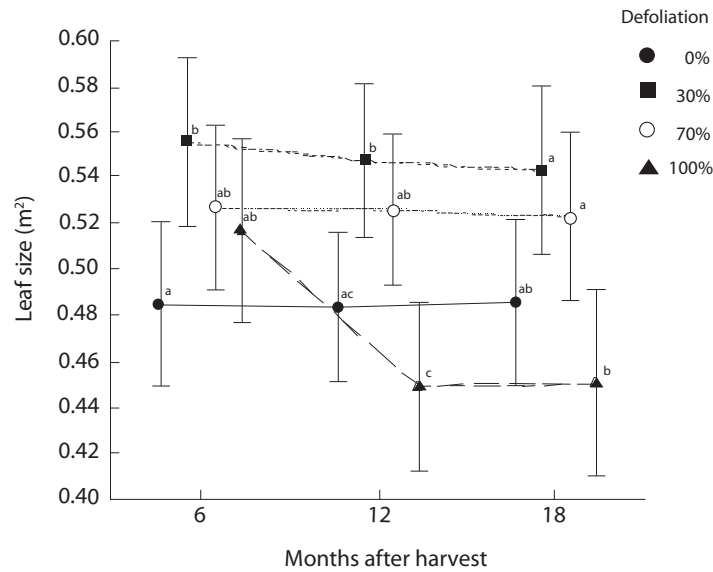| Source of variation	df	MS	F	p	G-G
Site	1	0.038	1.54	0.2169	
Defoliation	3	0.103	4.20	0.0076	
Site × Defoliation	3	0.010	0.39	0.7593	
Error	105	0.025			
Time	2	0.015	9.39	0.0001	0.0001
Time × Site	2	0.003	1.69	0.1861	0.1901
Time × Defoliation	6	0.008	5.31	0.00004	0.00004
Time × Defoliation × Site	6	0.002	1.19	0.3086	0.3110
Error	210	0.002			

Figure 2   Effects of leaf harvest intensity on leaf size (m²) of *Thrinax radiata*. Data are means ± 95% confidence interval. Means with the same letter are not significantly different within each time period in a post hoc Tukey test (p ≤ 0.05).

Table 3   Repeated measures ANOVA for the effect of leaf harvest intensity on leaf nitrogen content (mg g⁻¹), 6, 12 and 18 months after harvest

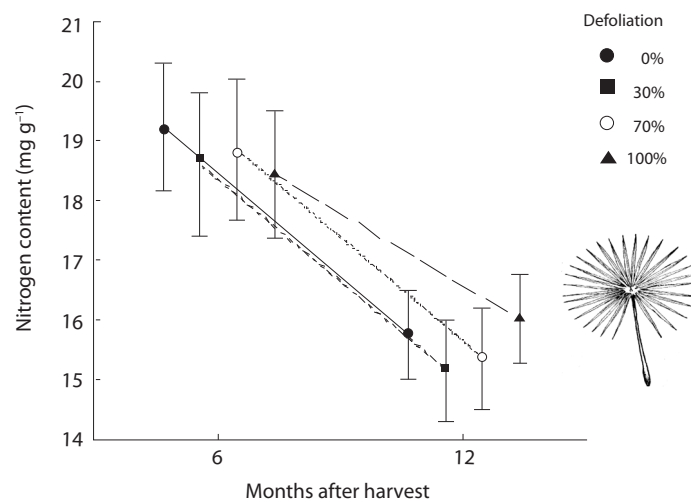| Source of variation	Df	MS	F	p
Site	1	6.95	2.85	0.1001
Defoliation	3	1.39	0.57	0.6387
Site × Defoliation	3	6.75	2.77	0.0557
Error	36	2.44		
Time	1	218.84	85.69	0.0000
Time × Site	1	8.93	3.50	0.0696
Time × Defoliation	3	1.57	0.62	0.6088
Time × Defoliation × Site	3	2.39	0.94	0.4332
Error	36	2.55		

Figure 3   Effects of leaf harvest intensity on leaf nitrogen content of new leaves of *Thrinax radiata*. Data are means ± 95% confidence interval.

defoliation regardless of study period, intensity or frequency of the experiment. Defoliation did not affect new leaf production in the low (30%) and medium (70%) harvest intensity treatments (Figure 1). Numerous defoliation studies for palm species have shown similar results (Mendoza *et al.* 1987, Oyama & Mendoza 1990, Chazdon 1991, Ratsirarson *et al.* 1996, Endress *et al.* 2006, Martinez-Balleste 2006, Valverde *et al.* 2006). In contrast, as a consequence of high intensity harvest (100%), individual palms produced higher number of new leaves compared with undisturbed palms. This is in accordance with the results of Oyama and Mendoza (1990) and Ratsirarson *et al.* (1996).

This finding suggests that *T. radiata* individuals have a short-term response to recover from total loss of fully opened leaves. Nevertheless, this allocation implies a cost for future growth as shown by the significant decline in the number of new leaves produced 18 months after harvest. This associated cost was also observed in new leaf size, since highly defoliated individuals (100%) produced smaller leaves than those under low and medium harvest intensity treatments (Figure 2). The precise physiological mechanisms responsible for this finding are unclear. Similar results have been reported for *Chamaedorea radicalis* (Endress *et al.* 2004, 2006) and *Livistona rotundifolia* (O'Brien & Kinnaird 1996). They suggested that early unfolding of leaves in heavily harvested palms lead to smaller leaf size.

Several studies evaluating defoliation responses at the individual level have emphasized the critical role of carbohydrate reserves, stored in trunk tissue or rootstocks, in maintaining vegetative and reproductive activities following defoliation (Mendoza *et al.* 1987, Oyama & Mendoza 1990, Chazdon 1991, Endress *et al.* 2004, 2006). In contrast, few studies have assessed palm response to defoliation at the leaf level (Anten & Ackerly 2001, Anten *et al.* 2003). As a result of these studies, an alternative explanation suggested that compensatory leaf production of defoliated palm individuals results from increased carbon assimilation rates in the remaining leaves, due to higher photosynthetic rates.

Our findings suggest that the studied palm individuals, in the 100% defoliation treatment, used stored carbohydrate reserves to compensate for the higher loss of photosynthetic tissue. In this treatment individuals were left only with the youngest unopened leaf. The fact that nitrogen content, an indirect indicator of photosynthetic capacity in the field (Field & Mooney 1986, Hogan 1988), was not affected by harvest intensity, suggests that the mechanism responsible for compensation of lost tissue is primarily mobilization of carbohydrate reserves and not an increase in photosynthesis. The limited period of our study and the fact that we did not directly measure leaf photosynthetic capacity did not allow us to make a definite conclusion.

Our results showed that even under a single defoliation event, the high intensity leaf harvest treatment had negative effect on size and number of new leaves, suggesting that complete removal of opened leaves is not a sustainable harvest practice on the long run, particularly under a scenario of repeated defoliation. Empirical knowledge of chit harvesters coincides with this finding since none of the 20 interviewed harvesters mentioned complete removal of the palm crown as a local harvest practice. Palm individuals under the 30% defoliation treatment showed larger leaves than undisturbed individuals 6 and 12 months after harvest. To our knowledge, no other study of palm defoliation has shown a short-term increase in leaf size as a result of defoliation. This short-term compensation response to leaf harvest showed no associated cost on future growth. Eighteen months after defoliation, experimental individuals under the 30% treatment had new leaf size equal to undisturbed individuals. This finding, together with the fact that individuals under this treatment produced equal number of new leaves (and total leaf area; data not shown) than undisturbed individuals, suggests that defoliation of 30% of the palm crown is a sustainable harvesting regime. Spatial heterogeneity had minor effect on the response of chit palm individuals to different harvest intensities. Site effect was not statistically significant, suggesting that our findings could be used in similar sites of the Yucatan Peninsula where *T. radiata* leaves are harvested.

Significant seasonal and year to year variation has been reported for leaf production in *T. radiata* (Olmsted & Alvarez-Buylla 1995). This could be the explanation for the increase in leaf production over time in non-defoliated palms (Figure 1).

Numerous studies have emphasized the negative impact of leaf harvest on palm

reproductive output (Anten *et al.* 1993, Ratsirarson *et al.* 1996, Endress *et al.* 2004, Valverde *et al.* 2006, Zuidema *et al.* 2007). Although the effects of harvesting on reproduction were not assessed in this study, life history characteristics of *T. radiata* suggest that leaf harvesting may have minimum impact on reproductive outcome. Unlike most experimental defoliation studies in palms, which analyse understorey species (Mendoza *et al.* 1987, Oyama & Mendoza 1990, Chazdon 1991, Zuidema 2000, Svenning & Macias 2002, Anten *et al.* 2003, Endress *et al.* 2004, Rodriguez-Buriticá *et al.* 2005, Endress *et al.* 2006, Valverde *et al.* 2006), *T. radiata* reaches the forest canopy. Calvo-Irabien & Ceballos-Gonzalez (2004) found that approximately 1% of the reproductive individuals were 3 m height, and as reported in the interviews, chit palm leaf harvesters occasionally use individuals up to 3 m height. Therefore, leaf harvesters rarely, if ever, use leaves from reproductive chit palms. This together with the fact that no mortality was recorded as a result of defoliation, suggests that the demographic impact of leaf harvest in this palm species may not be signficant. Nevertheless, we suspect that intense and continued harvesting would reduce the growth rates of harvested palms. This retards the transition from juvenile stages to reproductive palms, which may have consequences on population viability.

Management guidelines

Our results appear consistent with the 20 to 30% leaf harvest recommendations for other neotropical palm species (Obrien & Kinnaird 1996, McKean 2003). *Thrinax radiata* individuals under the 30% defoliation treatment averaged 1.5, 1.7 and 1.8 new leaves after 6, 12 and 18 months of harvesting respectively. This gives a total of five new leaves in 1.5 years. Based on these results, a sustainable harvest would be five leaves per individual palm each 1.5 years. Managing chit palm harvest at 30% of total leaf crown and harvesting individuals between 0.7 and 2.5 m trunk height would yield an estimated leaf production of 657 harvestable leaves/ ha every 1.5 years. This estimate considers the average density found in the two studied forests (150 ± 7.1 individuals per hectare), as well as an average leaf number of 14.6 ± 0.5 per individual (Zapata 2004). This quota of 30% harvest of

palm crown will not lead to reduced leaf size and allows individuals to quickly (2–3 years) regain initial leaf number. This practice is therefore not highly restrictive and is consistent with traditional harvesting practices.

Maintaining this defoliation level makes chit palm leaf harvesting sustainable under the present market leaf demand conditions. An increase in leaf demand and therefore leaf harvest frequency would require longer term studies to assess the effects of repeated defoliation.

Under the current scenario, ecological data show potential sustainability for chit palm leaf harvest. However, sale of chit leaves can be difficult because the permit procedure is complex and many harvesters cannot successfully apply without technical support from the Secretariat of the Environment (SEMARNAT). Currently, the main obstacles to sustainable chit palm management and leaf sale are not related to resource management or abundance but to the incipient stage of harvester organizations aimed at establishing prices, signing contracts and attaining certification, as well as control of illegal leaf harvest. Harvesters consider *T. radiata* a locally abundant resource, making enforcement of harvest restrictions rather difficult. The present results provide support for sustainable use of this resource within traditional harvest levels by minimizing the risk of over-exploitation. If sustainable leaf harvest is to be attained, local communities must actively participate in managing the resource (Ticktin 2004). This will be much more feasible if their traditional practices are considered and harvest limits are established within current ranges.

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