



# 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*

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## Abstract

Rural people worldwide rely on non-timber forest products (NTFP) to generate income to meet livelihood needs. Ecological impacts of harvest are unknown in most cases, despite interest in NTFP for sustainable development and concerns over over-exploitation. Moreover, most studies are  $\leq 2$  years in duration, so may not capture long-term harvest impacts or reveal sustainable harvest levels, especially for long-lived species or when impacts are likely to be cumulative. We examined the effects of several leaf harvest regimes on the demography of the understory palm, *Chamaedorea radicalis*, whose leaves are harvested for use in the international cut-greens industry. From 1999 to 2005, we exposed 100 adult palms to each of five leaf harvest treatments ( $N = 500$ ): control (no harvest),  $1 \times$  (harvest once/year),  $2 \times$  (harvest twice/year),  $4 \times$  (harvest four times/year), and a modified  $4 \times$  treatment ( $4 \times m$ ) where only one leaf was removed per harvest and no palms were completely defoliated. Leaf production, leaf length, palm survival, and reproductive activity were monitored throughout the study. These data were incorporated with demographic data on seeds, seedlings, and juveniles to parameterize stage-based transition matrices for each year  $\times$  treatment combination to estimate  $\lambda$ , the finite rate of population growth. Leaf harvest increased mortality rates, and reduced palm growth and reproductive activity. Three of the harvest treatments reduced  $\lambda$  compared to the control treatment, and two of these ( $2 \times$ ,  $4 \times$ ) significantly below the replacement rate of 1.0. Only in the  $4 \times m$  treatment was  $\lambda$  not significantly different than the control. No differences in leaf yield were found among the harvest treatments; though yield generally averaged  $\leq 1$  leaf per palm per year, it did not decline over the 6 years. Incorporating the price of leaves with leaf yield indicated that income generated per hectare per year ranged from US\$ 7–31. Since the  $1 \times$  and  $4 \times m$  treatments had yields comparable to more intense harvest treatments with fewer ecological impacts, these treatments could serve as a foundation for the development of sustainable palm harvest and management plans. Harvesting only once per year is the most efficient strategy, as comparable yield is obtained in the fewest days of work. Conservation strategies, such as not harvesting from reproductively active plants, should enhance *C. radicalis* recruitment, with minimal impact on harvester income. Our findings indicate that sustainable *C. radicalis* harvest can be achieved with few modifications of current harvest practices. In general our conclusions are similar to those based on a two-year intensive study. It is not clear whether these findings apply to other harvested *Chamaedorea* species, since species differ in life history, habitats, and leaf selection criteria. © 2006 Elsevier B.V. All rights reserved.

**Keywords:** Arecaceae; Demography; Mexico; NTFP; Sustainable harvest; Xate; Population dynamics; El Cielo Biosphere Reserve

## 1. Introduction

Millions of people worldwide derive a considerable portion of their subsistence needs and income through the harvest of non-timber forest products (NTFP). There are over 4000 NTFP species used for commercial purposes (Iqbal, 1993), and

thousands more utilized for subsistence and cultural activities. In most cases, the ecological impact of harvest on the target species is unknown, despite the interest in NTFP for sustainable development and biodiversity conservation, as well as growing concerns over NTFP over-exploitation. This has led to vigorous debate on the value of NTFP harvest to conservation and the socio-economic well-being of rural and marginalized people (Panayotou and Ashton, 1992; Dove, 1993; Struhsaker, 1998; Arnold and Ruiz Pérez, 2001; Pattanayak and Sills, 2001; Marshall et al., 2003).

Ecological studies on NTFP are not easily generalized because reported impacts of harvest vary widely, with some

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species appearing quite tolerant to harvest (e.g. Zuidema and Boot, 2002; Ticktin et al., 2002), others showing dramatic negative impacts (e.g. Olmsted and Alvarez-Bullya, 1995; Zuidema, 2000; Soehartono and Newton, 2001), and still many other species exhibiting more subtle or conflicting responses (e.g. Svenning and Macía, 2002; Siebert, 2004). Because of the large number of NTFP species, the variety of plant parts collected, and considerable differences in harvest pattern and intensity, it has been difficult to synthesize findings from NTFP studies and develop a general understanding regarding the ecological impacts of harvest. An additional weakness of NTFP studies is their short time frame, with the majority lasting two or fewer years. A review of the NTFP literature (Ticktin, 2004) found that only 10% of NTFP studies monitored populations for more than 3 years, making it difficult to predict demographic effects of NTFP extraction.

In the past several years, there has been increased emphasis on manipulative experiments to determine the ecological effects of NTFP harvest (Ticktin et al., 2002; Endress et al., 2004a). Manipulative experiments are more robust than descriptive or observational approaches to determine harvest impacts on the target species, and can provide valuable information on the effects of harvest on plant vital rates, including growth, survival, and reproduction. While manipulative experiments have increased our understanding of species' tolerance to harvest and the effects of harvest on plant demography, most published manipulative experiments have been short-term in duration; only a handful have exceeded 2 years (but see Mendoza et al., 1987; Nakazono et al., 2004; Ticktin, 2005). The short-term nature of many experiments limits their ability to evaluate the effects of harvest on plant demography or determine sustainable harvest levels, especially for long-lived species or when harvest impacts are likely to be cumulative. To overcome this, modeling has been used extensively to explore long-term effects of harvest on NTFP demography and population dynamics (Svenning and Macía, 2002; Cropper and Anderson, 2002; Endress et al., 2004a; Rodríguez-Buritica et al., 2005). However, modeling alone is not sufficient to overcome a lack of empirical data, and modeling efforts can produce unrealistic or inaccurate results (Bierzychudek, 1999; Anderson and Putz, 2002). Moreover, demographic parameters needed for population modeling can be difficult to observe or estimate during short term studies, adding additional uncertainty into the models (Wood, 1994). Therefore, long-term empirical research is needed to inform our understanding of the ecological impacts of NTFP harvest.

Leaf harvest is one such extraction method where short-term studies may be inadequate to evaluate long-term impacts, as leaf harvest rarely results in the immediate death of the target plant, and effects are likely to be cumulative. Leaves from many plant species are used for a wide range of purposes, and palm leaves (Arecaceae) are one of the most important resources worldwide for rural people (Balick, 1988). Palms leaves are harvested for numerous subsistence, cultural and commercial purposes, including roof thatch, basketry, fiber, and ornamental uses. Leaf harvest from palms generally increases leaf production rates (Mendoza et al., 1987; Oyama and Mendoza,

1990; O'Brien and Kinnaid, 1996; Endress et al., 2004b; but see Anten et al., 2003), but often decreases leaf length (O'Brien and Kinnaid, 1996; Ratsirarson et al., 1996; Endress et al., 2004b). Defoliation has little to no effect on palm survival (Mendoza et al., 1987; Ratsirarson et al., 1996; Zuidema, 2000; Endress et al., 2004a), except for seedlings and juveniles where mortality rates can be high (Mendoza et al., 1987). Harvest does affect palm reproduction, and most studies have reported reduced inflorescence production, allocation of resources to reproductive structures, and/or the proportion of reproductive individuals (Ratsirarson et al., 1996; Flores and Ashton, 2000; Anten et al., 2003; Endress et al., 2004a). However, Mendoza et al. (1987) found that harvest could increase or decrease the probability of fruit production, depending on which leaves were removed. Reported effects of harvest on mortality and reproductive output may be underestimated however, since the majority of these studies measured demographic responses over just 2 years, and effects of harvest may be cumulative.

We investigated demographic effects associated with the harvest of *Chamaedorea* leaves in montane mixed mesophyll (tropical cloud) forest in northeastern Mexico over 6 years. Specifically, we examined the effects of several leaf harvest treatments on the demography of the understory palm, *Chamaedorea radicalis*. Previously, we reported the demographic and population level effects of different harvest levels over 2 years (Endress et al., 2004a,b). After 2 years, leaf harvest resulted in decreased leaf length, increased adult mortality, reduced flower and fruit production, but a modest increase in leaf production. Stage based transition matrix models (Caswell, 2001) incorporating these effects projected that the long-term effect of leaf harvest was to reduce population growth rate ( $\lambda$ ), but not to significantly lower than 1.0, indicating populations would not decrease in response to harvest.

We continued these leaf harvest treatments for an additional 4 years to assess the validity of these projections and detect cumulative effects. In this paper, we report the effect of harvest treatments on palm survival and reproduction, population growth rates, leaf production, leaf length, leaflet number, and yield over 6 years. We then discuss the implications of our results for *C. radicalis* populations and the sustainable management of *Chamaedorea* palms.

*Chamaedorea* palms occur in forest understories in Mexico, Central America, and northern South America. They are often a dominant component of the forest understory, and densities can reach >5000 palms/ha (Ataroff and Schwartzkopf, 1994; Jones and Gorchoy, 2000). At least seven species (*C. elegans*, *C. ernesti-augusti*, *C. oblongata*, *C. radicalis*, *C. seifrizii*, *C. tepijilote*, and *C. quetzalteca*) are harvested for use in the international cut-greens trade, and the vast majority of leaves harvested come from wild palms in the forests of Mexico and Guatemala (Current, 2002). Several of these species are listed as threatened or vulnerable (FAO, 1997). *Chamaedorea* leaves are an important part of the cut-greens industry (14% of US market), and are second in commercial value among NTFP in Mexico, with millions of leaves exported each year (Current, 2002). In 1999, over 2000 tons of *Chamaedorea* leaves were exported from Mexico, generating about \$20 million (Current,

2002). Evaluating the effects associated with wild *Chamaedorea* harvest is important because it is a widespread activity for many people, particularly those living within protected areas such as Biosphere Reserves. Harvest of *Chamaedorea* leaves for the cut-greens industry has occurred since the 1940s, and thousands of communities across Mexico and Guatemala participate in the collection of leaves (Current, 2002). *Chamaedorea* harvest has been reported in several protected areas including El Cielo (Jones and Gorchov, 2000), Maya (Reining et al., 1992), Monte Azules (Sánchez-Carillo and Valtierra-Pacheco, 2003), El Ocote (Current, 2002) La Sepultura (Current, 2002), and El Triunfo Biosphere Reserves (Current, 2002). Despite the ecological and socio-economic importance of *Chamaedorea* palms, little is known about long-term demographic effects of leaf removal or sustainable harvest rates.

## 2. Materials and methods

### 2.1. Species description

*C. radicalis* is a long-lived understory palm found in mountainous regions of Hidalgo, Nuevo León, Tamaulipas, and San Luis Potosí, Mexico, and is the most northerly of the 100 species of *Chamaedorea* (Hodel, 1992). At our study site in the El Cielo Biosphere Reserve, Tamaulipas, Mexico it is found from 200 m to above 1400 m, in a wide range of forest communities including semi-deciduous tropical, oak, mixed mesophyll (cloud forest) and pine-oak forests (Mora-Olivo et al., 1997; Jones and Gorchov, 2000). Palm density varies depending on plant community and topographic position, and ranges from 700–6000 palms/ha (Jones and Gorchov, 2000; Endress et al., 2004a).

*C. radicalis* is dioecious, and male and female plants are morphologically similar with the exception of their flowers. We recognized five life history stages for *C. radicalis*: seeds, seedlings (bifid leaves), juveniles (three to nine leaflets on youngest leaf and non-reproductive), small adults (10–24 leaflets), and large adults ( $\geq 25$  leaflets), following Endress et al. (2004a). Sex ratio is 1:1 (Endress et al., 2004a). Pollen is primarily dispersed by wind, and fruit set is not dependent on local or population sex composition, male density, or the distance to the nearest male (Berry and Gorchov, 2004, in press). Most individuals appear to have no stem because their stem forms a ‘heel’ that grows into the substrate, though some individuals develop an aboveground stem reaching 2–4 m in height (Gorchov and Endress, 2005). At our study site, marketable leaves are restricted to adult palms ( $\geq 10$  leaflets on youngest leaf), and only leaves  $\geq 40$  cm in length, with a deep green color, and minimal insect or fungal damage are harvested.

### 2.2. Study site

Research was conducted near the village of Alta Cima, which is located within the boundaries of the El Cielo Biosphere Reserve (hereafter El Cielo), Tamaulipas, Mexico. The region is characterized by karst limestone outcroppings and steep slopes

(Sánchez-Ramos et al., 2005). At nearby Rancho del Cielo (1100 m elevation), precipitation averages 2500 mm/year and temperatures average 13.8 °C (Puig and Bracho, 1987).

El Cielo is a United Nations designated protected area where the goals are to reduce biodiversity loss, improve livelihoods, and enhance social, economic and cultural conditions for environmental sustainability. Several small communities are found within the reserve. Logging or other types of forest conversion are prohibited, but *C. radicalis* harvest is permitted. As a result, *C. radicalis* harvest is the principal livelihood activity for over 90% of families in Alta Cima and the nearby village of San José (Peterson, 2001). Leaves have been harvested in the region for over 40 years. Since the creation of El Cielo in 1987, *C. radicalis* has become the primary livelihood activity for people living within the reserve, and palm populations have been subject to intense, continual harvest. Current harvest intensity in the area is near its maximum, with nearly every marketable leaf harvested by collectors (Endress et al., 2004b). Intense leaf harvest, coupled with herbivory by free-range livestock, has led to dwindling palm resources and concerns over *C. radicalis* populations in El Cielo (Endress et al., 2004a).

Leaves are harvested throughout the year and Alta Cima (population of around 200) collects around 1.68 million leaves per year (Endress et al., 2004b). Alta Cima (1152 ha) is an *ejido* entirely within El Cielo. An *ejido* is a legally recognized form of collective land-tenure where members (*ejidatarios*) have usufruct rights to natural resources. In Alta Cima, individual *ejidatarios* have the right to harvest palm leaves anywhere on *ejido* land (except in other *ejidatario*'s home gardens, fields and agroforestry areas). Collectors from surrounding communities are prohibited from harvesting in Alta Cima. Other *ejidos* in and near El Cielo manage palm resources in the same manner (Peterson, 2001). More detailed descriptions the importance of *C. radicalis* to local communities and local palm management strategies can be found in Peterson (2001) and Endress et al. (2004b).

### 2.3. Experimental design

The experiment was conducted using 10 plots in Cañón del Diablo near Alta Cima. Plots were located on hillsides (elevation 1039–1120 m) where dominant canopy species included *Cercis canadensis*, *Chione mexicana*, *Clethra pringlei*, *Quercus germana*, and *Wimmeria concolor* (Endress, 2002). Each plot contained 50 adult palms ( $n = 500$ ). Plots were divided into five subplots of 10 palms each, and subplots randomly assigned to one of five harvest treatments ( $n = 100$  palms/treatment). The treatments were: control: no leaf removal; 1x: all marketable leaves removed once per year (August); 2x: all marketable leaves removed twice per year (August and February); 4x: all marketable leaves removed four times per year (February, May, August, and November), and 4xm: same as 4x, but at most one leaf per palm was removed each harvest, and for a leaf to be harvested, the palm had to have at least two leaves (this prevented complete defoliation). Treatments were designed to test a range of harvest regimes and



were developed in collaboration with local palm harvesters. The 4× treatment approximated the current harvest regime in El Cielo (Endress et al., 2004b). The 4×m treatment was designed to eliminate major defoliation events, as interviews with palm harvesters suggested that complete defoliation of individuals may increase mortality and result in shorter leaves (Peterson, 2001).

In January 1999, all palms were permanently tagged, and the following data recorded: number of leaves, number of leaflets on each leaf, leaf length, and inflorescence or fruit production. Newly emerging leaves were marked to monitor leaf production. Palms were surveyed monthly through August 2001, and every 3 months thereafter through May 2005. At each census we recorded survival, number of new leaves, leaf length and the number of leaflets, and any inflorescence or fruit production. Reproductive activity was only recorded for 5 years (May 1999–May 2004). Palms that died or regressed to the juvenile stage before August 1999 or were browsed by livestock ( $n = 37$ ) were excluded from all analyses, which resulted in the following sample sizes for each treatment: control,  $n = 81$ ; 1×,  $n = 96$ ; 2×,  $n = 96$ ; 4×m,  $n = 94$ ; and 4×,  $n = 96$ .

The harvest treatments were initiated in May 1999 and continued through May 2005. Eduardo Padrón Serrano, a local palm harvester and collaborator on the project, conducted the harvest treatments in accordance with local harvest practices. Since the treatments were based on the frequency of visits and local selection criteria, the number of leaves removed per palm within the same treatment varied, depending on the number of marketable leaves present, as occurs during actual harvest.

#### 2.4. Effects on survival

In order to determine whether adult palm survival differed among treatments, cumulative mortality data were analyzed using the LIFETEST procedure in SAS (SAS Institute, 2000). Differences among treatments were analyzed using the log-rank  $\chi^2$ -test statistic. We then used the covariance matrix from the log-rank  $\chi^2$ -statistic to calculate Z-statistics for each pairwise comparison of the treatments (Fox, 2001) using a Bonferonni adjusted  $\alpha$  value to identify significant differences ( $\alpha = 0.05/10 = 0.005$ ).

#### 2.5. Effects on reproduction

Evaluating the effects of leaf harvest on *C. radicalis* reproductive activity was difficult, because only a small proportion of palms in the experiment reproduced during the study. Differences among treatments in the proportion of palms flowering at least once during the experiment were determined by a log-likelihood contingency test ( $5 \times 2$  table). For palms that did flower and survived over the course of the experiment, differences in the median number of inflorescences produced per palm were analyzed by a Kruskal–Wallis test (data violated the assumptions required for parametric analyses). Differences among treatments in the proportion of palms producing fruit and the mean number of fruit produced per fruiting palm were determined in the same manner.

#### 2.6. Effects on population growth rate

To integrate all demographic effects of each harvest treatment and assess their effect on population growth, we parameterized a stage transition matrix (Caswell, 2001) for each treatment for each of the 4 years for which we had complete data (1999–2000 through 2003–2004). Matrix models included the five life history stages of *C. radicalis*: seeds, seedlings, juveniles, small adults, and large adults (Endress et al., 2004a). We used a birth-pulse, post-breeding census model, with August as the census date. We used a one-sex, female-dominant model (Caswell, 2001) for this dioecious population, since it met the assumptions of no apparent sexual dimorphism in vital demographic rates (Endress, 2002) and no dependence of female fecundity on male density, nearest male distance, or sex ratio (Berry and Gorchov, 2004; Berry and Gorchov, in press). As there is no sex-ratio bias in the population (Endress, 2002; Berry and Gorchov, in press), we assumed half the seeds and half the adults in each stage were female, and calculated fecundity for each adult stage as: (1/2 total number of fruits)/(1/2 total number of individuals).

Matrices for the first 2 years were published in Endress et al. (2004a) and those for the last 2 years followed the same methods. For the last 2 years, transition probabilities for seeds, seedlings, and juveniles were obtained from seedling establishment experiments and censuses of seedlings and juveniles in the same area as the harvest experiments (Berry et al., in preparation). Because no leaves are harvested from these three life history stages, their transition probabilities for any given year were used in matrices for all five treatments. Transitions for small and large adults (including fecundity, regression, stasis, and growth) were distinct for each harvest treatment, and were based on the marked individuals. For each transition matrix, we obtained  $\lambda$ , the finite rate of increase, by Eigenanalysis using Matlab 7.1 To assess the ‘average’ demography in each harvest treatment, we calculated the geometric mean of the four  $\lambda$ s for the 4 years. The confidence interval of each geometric mean  $\lambda$  was calculated following Bland and Altman (1996): first calculating the mean ( $x$ ) and standard error (S.E.) of the logarithms of the four  $\lambda$ s, then calculating  $(x - 1.96\text{S.E.})$  and  $(x + 1.96\text{S.E.})$ , and finally the anti-logs of these two sums.

Since fruit production is dominated by a few individuals, and leaf harvest reduced fruit production after 2 years (Endress et al., 2004a), protecting reproductively active individuals to increase *C. radicalis* recruitment rates may offset some of the negative demographic consequences of leaf harvest. To explore the potential population-level implications of protecting reproductive palms, we estimated population growth of harvested populations by modifying each year’s 4×m transition matrix to include the fecundity values of the control treatment, determining  $\lambda$  by eigenanalysis, then calculating the geometric mean of the  $\lambda$ s for the 4 years.

#### 2.7. Effects on leaf production and growth

Annual leaf production for each palm was determined for 6 years (from June 1999–May 2000 to June 2004–May 2005)

and included all leaves initiated during each year. Palms that died prior to, or during, a given year were not included in the analysis for that year. Treatment effects on annual leaf production were analyzed with generalized linear models constructed for each year of the study (GLM procedure in SAS). These were mixed models with both random (plot) and fixed (treatment) effects. Cumulative leaf production throughout the entire study was also analyzed with a generalized linear model restricted to palms that survived the 6-year study period. The treatment  $\times$  plot mean square error was used as the error term for the  $F$ -tests for treatment effects (Potvan, 2001).

We also used mixed-generalized linear models as described above to evaluate the effect of the harvest treatments on mean length of the youngest fully expanded leaf. For this analysis, the length of the youngest fully expanded leaf for each palm was determined for seven time periods: May 1999 (pre-treatment), May 2000, May 2001, May 2002, May 2003, May 2004, and May 2005; again excluding palms that died prior to, or during, the year under analysis.

The number of leaflets on the youngest fully expanded leaf is a measure of an individual's life history stage; this number increases with age, except following major stress such as browsing (Endress et al., 2004a), and is positively correlated with reproductive activity (Endress et al., 2004a; Berry and Gorchoy, 2004). To determine if leaf harvest affected the leaflet number on the youngest leaf, we tested for mean differences in leaflet number prior to treatment initiation (May 1999) and again in May 2005 using a mixed generalized linear model. Only palms that survived throughout the study were included in the May 2005 analysis. We also used a mixed-generalized linear model to test for mean differences in the change in leaflet number from the beginning of the study to the end (number in May 1999 – number in May 2005).

## 2.8. Effects on leaf yield

To evaluate the effects of the harvest treatments on leaf yield, we calculated the cumulative number of leaves actually harvested from each palm between May 1999 and May 2005, and tested for mean differences in leaf yield among the harvest treatments using a generalized linear model with both random (plot) and fixed (treatment) effects. Plants that died during the experiment were not included in this analysis. We also examined the data for differences in the proportion of productive palms (palms producing at least 1 marketable leaf) for each year of the study using a series log-likelihood contingency tests ( $5 \times 2$  contingency tables), one for each year of the study.

We also examined differences in leaf yield incorporating palm mortality into the analysis. This allowed for an analysis at the population-level and provides insight into the potential yield and income generation over time of populations exposed to different harvest scenarios. To do this, we included all palms in the analysis, and once a palm died, its yield was recorded as 0, and the data set was then analyzed as described above.

We then integrated yield data with the density of adult palms in the area (1171 per ha, Endress et al., 2004a) to estimate the income generated by the harvest treatments on a per-hectare basis. We did this analysis for each year of the study as well as for the cumulative yield over 6 years. To estimate the mean number of leaves harvested per hectare per treatment, we multiplied the mean number of leaves harvested by the current stock of palms producing marketable leaves (1171), and then multiplied this by the current leaf price (US \$0.02 per leaf).

## 3. Results

### 3.1. Effects on survival

A significant difference in adult palm survivorship curves was found over the study ( $\chi^2 = 12.34$ , d.f. = 4,  $P = 0.015$ ;

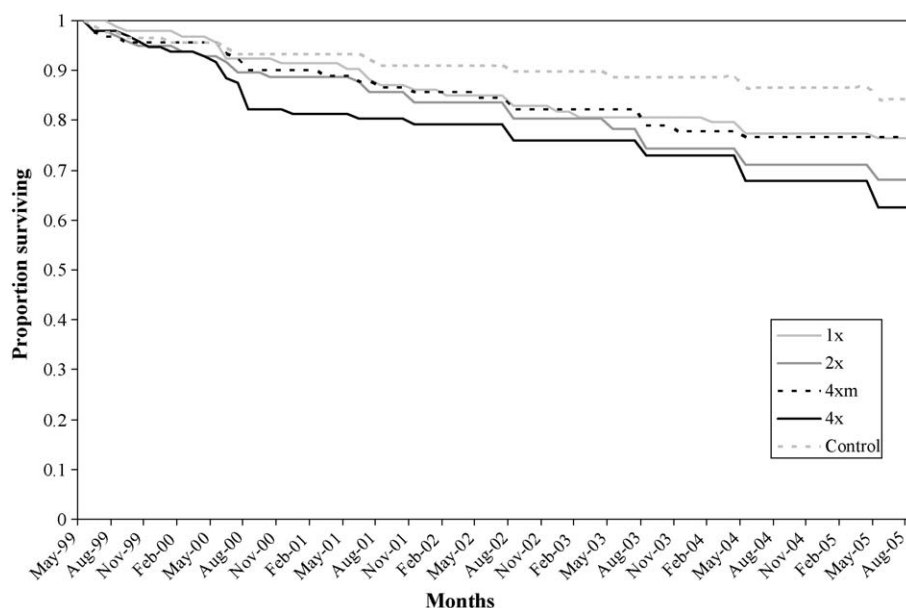


Fig. 1. Survivorship curves for adult *Chamaedorea radicalis* individuals exposed to five different leaf harvest treatments over 6 years (May 1999–May 2005).

Fig. 1). The control treatment had the highest survival rate (84%), followed by the 4×m (76%), 1× (76%), 2× (68%) and 4× (63%) treatments. Pairwise comparisons indicated that survivorship in the control treatment was significantly higher than in the 2× ( $Z = 2.33$ ,  $P = 0.0099$ ) and 4× treatments ( $Z = 3.23$ ,  $P = 0.00006$ ), but not significantly different than in the other harvest treatments.

### 3.2. Effects on reproduction

The proportion of palms that flowered at least once differed among treatments ( $G^2 = 10.71$ , d.f. = 4,  $P = 0.0301$ ); it was greatest in the control (56%), followed by the 4×m (50%), 1× (45%), 2× (43%), and 4× treatments (31%). For palms that did flower, no difference was found in the median number of inflorescences produced between June 1999 and May 2004 ( $\chi^2 = 4.686$ , d.f. = 4,  $P = 0.3210$ ) with values ranging from  $1.68 \pm 0.14$  S.E. inflorescences/palm (2×) to  $2.44 \pm 0.26$  S.E. inflorescences/palm (control).

Because inflorescence production was rare, only 60 palms (13%) were identified as female, and of these, 47 (78%) produced fruit (Table 1). Since we previously reported a 1:1 sex ratio for our marked palms (Endress et al., 2004a), this indicates that just over 20% of females produced fruit over 5 years. Fruit production was dominated by just a few individuals, with 10 individuals responsible for just over 61% of fruit produced. Not only did few palms fruit, but seed set varied considerably, ranging from 1 to 156 fruits/female over the study period.

A significant difference was found in the proportion of palms fruiting among treatments ( $G^2 = 12.482$ , d.f. = 4,  $P = 0.0141$ ), with a considerably greater proportion of palms in the control treatment fruiting. Values ranged from 9% (4×m treatment) to 38% of females (control). However, there was no significant difference in the mean number of fruit produced per fruiting palm ( $\chi^2 = 3.919$ , d.f. = 4,  $P = 0.4172$ ; Table 1). These patterns resulted in considerable differences in the total number of fruit produced over the study period among treatments, with the control treatment producing 3.1–5.7 times as many fruit as each harvest treatment (Fig. 2).

### 3.3. Effects on population growth rate

For each harvest treatment, for each year with complete data (1999–2000 to 2003–2004), a stage transition matrix (see online Supplementary Documents for matrices) was parameterized incorporating the above effects on survival and

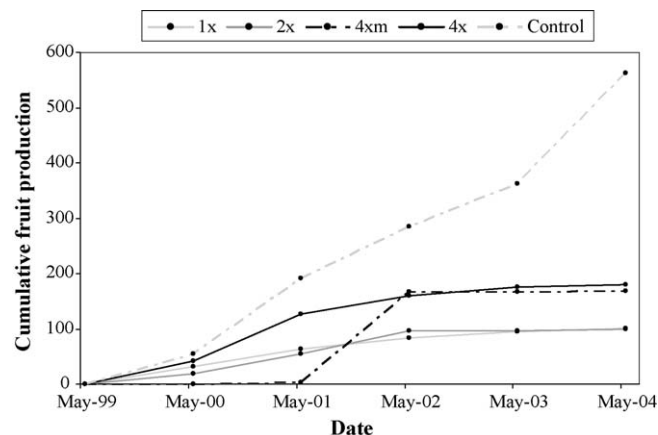


Fig. 2. Cumulative fruit production for *C. radicalis* among leaf harvest treatments from June 1999 to February 2004.

reproduction, as well as changes in stage (regression, growth) of adults and demography of seeds, seedlings, and juveniles. For the control treatment,  $\lambda$ , the finite rate of increase, was above 1.0 each year, with a geometric mean of 1.15 (Table 2), indicating population growth. For the 2× and 4× harvest treatments, all  $\lambda$ s were below 1.0 and the geometric mean  $\lambda$  significantly below 1.0 (Table 2). In contrast, for the 1× and 4×m treatments  $\lambda$  was below 1.0 some years and above 1.0 other years, with the geometric mean not significantly different than 1.0 (Table 2). Our model of a population in which reproductively active plants were protected (i.e. not harvested; 4×m treatment with control fecundity values) had a geometric mean  $\lambda$  of 1.11, significantly higher than 1.0 and comparable to that of the control (Table 2; See online Supplementary Documents for matrices).

### 3.4. Effects on leaf production and growth

Leaf harvest had little effect on annual leaf production rates with mean rates ranging from 1.7 (control, year 4) to 2.2 (2×, year 2). As we reported in earlier (Endress et al., 2004b) productions rates differed significantly in the second year of the study, with the 2× harvest treatment producing significantly more leaves than the control treatment. In subsequent years, no differences in leaf production were found among treatments. Additionally, no differences were found among treatments in the mean number of leaves produced per palm throughout the entire study; d.f. = 4,36,  $F = 1.076$ ,  $P = 0.3827$ , with production ranging from 10.2 leaves/palm (control) to 10.8 leaves/palm (1×).

Table 1

Fruit production summary statistics for *Chamaedorea radicalis* under five leaf harvest treatments over 60 months (May 1999–May 2004)

Treatment	No. known females	No. fruiting palms	Percentage of females producing fruit (%)	Mean no. fruit per fruiting palm $\pm$ S.D.
Control	18	17	94	33.1 $\pm$ 36.3
1×	10	9	90	11.2 $\pm$ 8.4
2×	12	6	50	16.5 $\pm$ 11.9
4×m	9	4	44	42.3 $\pm$ 35.9
4×	11	11	100	16.4 $\pm$ 16.5

Known females are individuals that produced  $\geq 1$  female inflorescence during the study.

Table 2

Finite rates of increase ( $\lambda$ ) for stage transition matrices parameterized for each leaf harvest treatment during each 1-year period for which complete data are available, and the geometric mean  $\lambda$  for each treatment

Year	Control	1×	2×	4×m	4×	4×m protected
1999–2000	1.179	1.016	0.972	0.936	0.998	1.180
2000–2001	1.172	1.033	0.981	1.164	0.998	1.143
2001–2002	1.061	0.912	0.995	1.029	0.986	1.000
2002–2003	1.181	1.028	0.974	0.959	0.983	1.130
Geometric mean $\lambda$	1.147	0.996	0.980	1.018	0.991	1.111
Confidence interval of geometric mean $\lambda$	1.090–1.207	0.940–1.055	0.970–0.991	0.925–1.121	0.984–0.999	1.035–1.193

The 4×m ‘protected’ treatment simulates a population exposed to the 4×m treatment in which reproductive individuals are not harvested by using fecundity estimates from the control treatment. The 24 stage transition matrices are reported in [Supplementary Documents](#). Lambdas ( $\lambda$ ) for the control, 1×, 2×, 4×m, and 4× treatments from 1999 to 2000 and 2000 to 2001 are from [Endress et al. \(2004a\)](#).

Leaf harvest led to a significant reduction in leaf length for all time periods after treatment initiation ([Table 3](#), [Fig. 3](#)), and pairwise contrasts revealed that all harvest treatments differed significantly from the control treatment (all  $P$  values  $\leq 0.0001$ ). In May 1999, prior to treatment initiation, the leaf length for all palms averaged 49 cm, with no differences among treatments. By May 2006, leaf length in the control treatment increased by more than 14 cm to 63 cm, while leaf length in each harvest treatment was not different than its pretreatment value ([Fig. 3](#)).

Table 3

Analysis of variance (ANOVA) tables of length of youngest fully expanded leaf of *C. radicalis* adults in May of each year under different leaf harvest treatments

Year	Source	d.f.	MS	F	P > F
1999	Treatment	4	152.62	0.99	0.4271
	Plot	9	878.19	6.64	<0.0001
	Treatment × plot	36	154.65	1.17	0.2372
	Error	414	132.35		
2000	Treatment	4	1311.94	7.04	0.0003
	Plot	9	1610.76	13.27	<0.0001
	Treatment × plot	36	186.48	1.54	0.0281
	Error	373	121.36		
2001	Treatment	4	1494.30	6.31	0.0006
	Plot	9	910.04	7.35	<0.0001
	Treatment × plot	36	236.68	1.91	0.0018
	Error	345	123.76		
2002	Treatment	4	1544.43	6.69	0.0004
	Plot	9	1010.19	8.69	<0.0001
	Treatment × plot	36	230.86	1.99	0.0010
	Error	328	116.22		
2003	Treatment	4	1539.47	5.72	0.0011
	Plot	9	1383.06	9.82	<0.0001
	Treatment × plot	36	269.02	1.91	0.0019
	Error	320	140.82		
2004	Treatment	4	2853.46	11.56	<0.0001
	Plot	9	1054.69	8.03	<0.0001
	Treatment × plot	36	246.89	1.88	0.0025
	Error	303	131.37		
2005	Treatment	4	3470.429	21.3	<0.0001
	Plot	9	840.493	5.1	0.0002
	Treatment × plot	36	386.412	2.4	0.0036
	Error	291	163.08		

The 1999 analysis occurred prior to treatment initiation.

Prior to treatment initiation, there were no differences among treatments in the mean number of leaflets on the youngest fully expanded leaf (mean = 22.4 leaflets). In May 2005, a significant difference in the mean number of leaflets among treatments was found (d.f. = 4,36,  $F = 4.52$ ,  $P = 0.0046$ ) with the control treatment averaging the highest number of leaflets ( $32.9 \pm 1.12$ S.E.), and the 4× treatment the lowest ( $26.8 \pm 0.91$ S.E.). Palms in the control treatment had a average increase of 11.8 leaflets over the study period ([Fig. 4](#)), which was significantly greater ( $P < 0.0001$ ) than each of harvest treatments, which averaged  $2.1 \pm 1.2$ S.E. (4×),  $5.0 \pm 1.1$ S.E. (4×m),  $5.8 \pm 1.0$  (1×), and  $6.1 \pm 1.1$  (2×).

### 3.5. Effects on leaf yield

When palms that died were not included in the analysis, considerable differences in the mean number of leaves harvested per palm were found among the harvest treatments (d.f. = 3,27,  $F = 9.95$ ,  $P < 0.0001$ ). The 4× treatment averaged the highest yield ( $7.2 \pm 0.6$ S.E. leaves per palm) followed by the 4×m ( $5.8 \pm 0.6$ S.E.), 2× ( $5.7 \pm 0.5$ S.E.) and 1× ( $4.6 \pm 0.5$ S.E.) treatments. However, incorporating mortality into the analysis resulted in no significant differences among treatments (d.f. = 3,27,  $F = 2.4$ ,  $P < 0.09$ ; [Fig. 5](#)), with cumulative yield values ranging from 4 to 6 leaves per palm

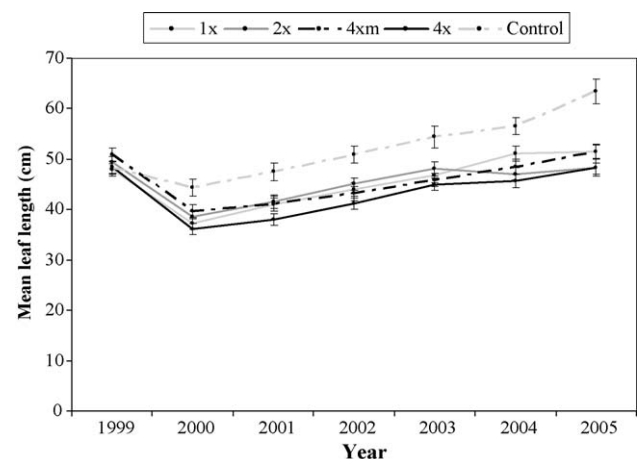


Fig. 3. Effects of different leaf harvest treatments on mean leaf length (+S.E.) of *C. radicalis*.



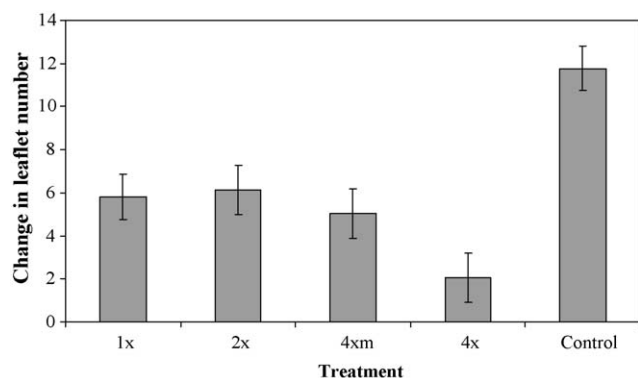


Fig. 4. Mean change in leaflet number ( $\pm 1$ S.E.) between May 1999 and May 2005 in the different leaf harvest treatments.

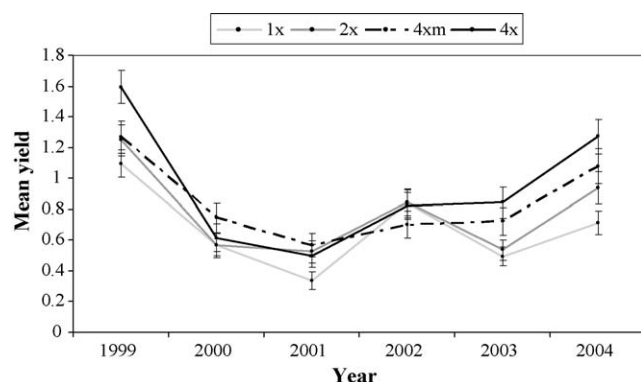


Fig. 5. Mean annual leaf yield (number harvested) per palm ( $\pm 1$ S.E.) for *C. radicalis* under different leaf harvest treatments.

over 6 years. On an annual basis, yield varied through time, and ranged from 0.4 to 1.3 leaves/year. The proportion of productive palms (palms producing at least one marketable leaf) varied among years (range 29–82%), but no treatment differences were found within any year. In year 1, 76% of palms (in all harvest treatments pooled) had at least one marketable leaf; in subsequent years productivity was lower with 44%, 38%, 54%, 49%, and 62% in years 2–6, respectively.

Incorporating the price of leaves with leaf yield indicated that income generated per hectare ranged from US \$7.37 (1 $\times$  treatment during 2001–2002) to \$31.34 (4 $\times$  treatment in year 1999–2000). Revenue followed leaf yield patterns (Fig. 5), and cumulative income generated per hectare over the 6 years was estimated in US\$ as: \$80 (1 $\times$ ), \$93 (2 $\times$ ), \$98 (4 $\times$ m), and \$112 (4 $\times$ ).

## 4. Discussion

### 4.1. Effects on demographic rates and leaf yield

Continual leaf harvest resulted in significant effects on the demographic rates of *C. radicalis*. Adult survival was reduced by two of the leaf harvest treatments, 2 $\times$  and 4 $\times$ , whereas reproduction and growth (in terms of leaf size) were reduced in all four treatments. New leaf production was not affected. These findings suggest that individuals respond to leaf loss by

allocating resources to replacing lost leaf tissue, at the expense of improvements in plant status that are associated with production of inflorescences and larger leaves. This pattern is similar to that reported for *C. elegans*, where experimental defoliation reduced all growth parameters, but increased the allocation to leaves relative to allocation in reproductive structures (Anten et al., 2003).

While harvest increased leaf production versus control in the second year (Endress et al., 2004b), this increase was not maintained in subsequent years. This short-term enhancement of leaf production was similar to, but smaller, than, those reported in studies of defoliation in other palms (Mendoza et al., 1987; Oyama and Mendoza, 1990; O'Brien and Kinnaird, 1996). Short-term increases in leaf production are likely limited to healthy, previously un-harvested palms with sufficient stored reserves to immediately compensate for defoliation. In our case, palms had been subject to harvest for many years prior to the experiment, with only a 6 month respite, so they likely only had modest reserves. Short-term increases in leaf production rates are thus unlikely to be maintained over time in any palm, and should not be used to estimate long-term leaf yield and income for commercial leaf harvest. Our findings also differed from Anten et al. (2003) who measured leaf production rates 1 year after *C. elegans* was exposed to experimental defoliation; they reported a small decrease in leaf production in response to leaf removal.

The drop in leaf yield and the proportion of productive palms after the first year suggests that palms initially had a high stocking of harvestable leaves, due to the absence of harvest during the 6 months before the initiation of the treatments, and were subsequently able to maintain a steady but lower production of marketable leaves while subject to harvest. The reduction in leaf size in the second year was presumably due to precocious leaf expansion in response to defoliation (Endress et al., 2004b), but in subsequent years leaf size gradually increased, suggesting the internal status of harvested palms gradually recovered. The decline in leaf length in response to harvest mediates harvest intensity in *C. radicalis*, as leaves <40 in length are not harvested. Harvested palms also had fewer leaflets on the youngest fully expanded leaf than un-harvested palms, indicating that harvest slows *C. radicalis* development. However, individuals in the harvest treatments that survived over the 6 years still gained, not lost leaflets. Decreases in leaflet number are a sign of plant stress for *C. radicalis* (Endress et al., 2004a), and reproductive activity is positively correlated with leaflet number. Therefore, while harvest slowed the development of *C. radicalis*, many palms continued to progress to larger size classes.

### 4.2. Effects on population growth and implications for palm management

Incorporation of all demographic effects of harvest via matrix models revealed that the 1 $\times$ , 2 $\times$ , and 4 $\times$  harvest treatments all reduced the population growth rate below that of the control treatment, and in the case of the 2 $\times$  and 4 $\times$  treatments, below the replacement rate of  $\lambda = 1.0$ . In contrast,



the population growth rate in the 4×m treatment was quite variable, with a geometric mean  $\lambda$  slightly above 1.0 and not different than the control. Thus, two of the harvest treatments (1× and 4×m) appear to be sustainable, both in terms of maintaining population size ( $\lambda \geq 1$ ) and non-declining leaf yield. Our finding that the harvest treatment with the highest geometric mean  $\lambda$  was the 4×m treatment, suggests that taking at most one leaf per visit, and never defoliating a palm, minimizes stress and its demographic consequences. Among the four harvest treatments, this treatment also had the highest 6-year survival rate, proportion flowering at least once, and number of fruits per fruiting palm.

While these findings suggest that some of the leaf harvest treatments are ecologically sustainable, our estimates for population growth, which are most sensitive to demographic variation in large adults (Endress et al., 2004a) remain near the replacement rate of  $\lambda = 1.0$  only because adult palm mortality is very low in the harvest treatments. Such low mortality may ensure population stability, but without recruitment, it is not possible to increase population growth above  $\lambda = 1.0$ , no matter how long adults live. Indeed, our harvest model that incorporated fecundity values from protected palms projected rates of population growth for most years that were substantially higher than 1.0. Therefore, in addition to taking no more than one leaf per visit, and never defoliating a palm, another sound conservation management strategy is to enhance *C. radicalis* recruitment by protecting reproductively active individuals. Reproductive individuals could be protected in several ways. One option would be to prohibit leaf harvesting from females that produce the majority of fruit. Since these plants represent only about 2% of adult plants (Endress, unpublished data), the impact on harvester income is negligible. This would require identifying and marking these females and community agreements to not harvest from such plants. An alternative approach would be to not harvest leaves from reproductively active individuals (presence of inflorescence or infructescence). Again, since only a small proportion of adults are reproductively active at any time, impacts on income would likely be small. This second approach may be more easily discernible for harvesters, because inflorescences and infructescences are readily identified, and this approach does not require extensive marking of individuals across large, often remote areas.

All of these treatments were less productive than assumed by local harvesters, as they averaged only about one leaf per palm per year. Given the similarities among treatments in leaf yield, the 1× treatment is the most efficient – it yields as many leaves as the other treatments with less expenditure of time and risk of injury. Palms in this treatment generally had higher demographic rates than those in the 2× and 4× treatments. A once per year harvest protocol would be quite different from current practices, where areas are visited by the same and different harvesters multiple times per year, but could be adopted by communities. For example, an ejido might delineate 12 harvest areas, with one open for harvesting each month, and systematically rotate harvest areas.

#### 4.3. Long-term versus short-term studies

Several of the qualitative conclusions reached after 2 years of study (Endress et al., 2004a,b) were not changed after 3 additional years of study (2 years in the case of reproduction). The findings of this manuscript that harvest reduced growth (as measured by leaf length) and reproduction were evident in the 2-year study, as was the increase in mortality, although mortality rates were not statistically significant after 2 years. While Endress et al. (2004a) projected all harvest treatments to have  $\lambda$ s not significantly different than 1.0, but significantly lower than an unharvested population (Endress et al., 2004a), this longer term study found that three of the harvest treatments reduced  $\lambda$  compared to the control treatment, and two of these (2×, 4×) significantly below the replacement rate of 1.0. Moreover, only in the 4×m treatment was  $\lambda$  not significantly different than the control. Thus, the additional 4 years of data allowed us to detect treatment differences that were not evident after just 2 years.

The fact that several conclusions reached after 2 years were qualitatively similar to our conclusions in this paper does not mean that short-term studies are sufficient in all cases to determine long-term harvest impacts. In the case of *C. radicalis*, the similarities observed between the 2- and 6-year leaf harvest data were most likely only because our experiment utilized populations that have been exposed to intense leaf harvest for several decades. Thus, individual palms had little if any stored reserves to compensate for leaf loss. The consistent patterns observed throughout the study suggest that additional years of similar harvest patterns are unlikely to reveal radically different responses; therefore these likely represent the cumulative long-term demographic effects of leaf harvest for this species. Experiments conducted using previously harvested NTFP populations are rare (Ticktin, 2004), but our findings suggest that this approach can be advantageous for understanding cumulative, long-term demographic effects more quickly than when using previously unharvested populations. Moreover, short-term experimental studies on previously unharvested populations may have the greatest risk of failing to identify ecological impacts of NTFP harvest.

#### 4.4. Resiliency and ecological sustainability

While *C. radicalis* appears quite resilient to some harvest practices, a comprehensive assessment of ecological sustainability would need to consider the effects of harvest on ecological relationships, patterns, and processes. For example, the reductions in *C. radicalis* fruit production documented here might affect local bird or rodent populations. Because of the difficulties in assessing absolute ecological sustainability, it is perhaps more useful to compare different land use activities and their relative impacts on ecological systems (Ticktin et al., 2003). From this perspective, *C. radicalis* harvest clearly has fewer impacts than other land use activities such as logging, ranching, or intensive agriculture, and is certainly a more preferable land use activity than many others, particularly in protected areas.

Several factors contribute to the resiliency of harvested *C. radicalis* populations. First, the species is widely distributed throughout a range of forest types, and is often highly abundant (Mora-Olivo et al., 1997; Jones and Gorchov, 2000; Endress et al., 2004a). Additionally, although harvesting is intense, collection is restricted to adult plants, which account for approximately 40% of the overall population, leaving 60% of individuals un-harvested (Endress et al., 2004a). The species also responds to harvest by producing shorter leaves, some of which are too small to be marketable, and thus are not harvested. This response provides a respite from harvesting for these individuals, which allowed them to recover from past harvest before being harvested again. Because of this response, and because other leaves produced are not marketable due to their coloration or the presence of insect or fungal damage, only 40–50% of adult plants produced marketable leaves in any given year. Therefore, only about 20% of individuals within the entire *C. radicalis* population are subject to harvest in a given year. These factors may explain the persistence of *C. radicalis* populations that have been exposed to intense harvest for decades.

#### 4.5. Conservation and management of other *Chamaedorea* spp.

It remains unclear if other species of *Chamaedorea* respond to harvest in similar ways as *C. radicalis*. Despite the importance of *Chamaedorea* to rural people in Mexico and Guatemala, and its importance to the cut-greens industry, little is known about how other species respond to harvest. Palm species in general, including other *Chamaedorea* species, respond to harvest similarly (see Introduction and citations within), and the other *Chamaedorea* species used in the floriculture industry have similarities (Hodel, 1992). However, differences exist among the species in their morphology, habitats, and life history, making comparisons without empirical data between the species difficult. Moreover, land tenure, local palm management strategies, micro-economics, and leaf selection criteria (the cut-greens industry has a range of leaf sizes) vary considerably across Mexico and Guatemala, further compounding the difficulties developing appropriate generalizations. Future work on *Chamaedorea* and other NTFP should focus on examining and integrating biological, social, and economic data across regions to provide better insight on the sustainability of NTFP harvest.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2006.07.020.

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