# NON-TIMBER FOREST PRODUCT EXTRACTION: EFFECTS OF HARVEST AND BROWSING ON AN UNDERSTORY PALM

BRYAN A. ENDRESS,<sup>1,3</sup> DAVID L. GORCHOV,<sup>1</sup> AND ROBERT B. NOBLE<sup>2</sup>

<sup>1</sup>Department of Botany, Miami University, Oxford, Ohio 45056 USA <sup>2</sup>Department of Mathematics and Statistics, Miami University, Oxford, Ohio 45056 USA

*Abstract.* Despite the advocacy for non-timber forest product (NTFP) extraction as a form of sustainable development, the population ecology of many NTFPs remains unstudied, making it difficult to assess the ecological impacts of extraction. We investigated the demography and population dynamics of the harvested, understory palm, *Chamaedorea radicalis* in the El Cielo Biosphere Reserve, Mexico. Our objectives were: (1) to describe patterns of *C. radicalis* abundance and population size structure, (2) to document *C. radicalis* demography, (3) to test experimentally how this demography was affected by different leaf harvest regimes and livestock browse intensities, and (4) to project their effects on transient and long-term population dynamics.

Data on palm abundance and population size structure were collected from belt-transects along hillsides. We also exposed 100 adult palms to each of five leaf harvest treatments (N = 500): control, harvest once per year, harvest twice per year, harvest four times per year, and a modified four times per year harvest where only one leaf was removed each harvest. Browse experiments were conducted to assess the effect of burro browse on demography. Experiments were monitored over two years, and results were incorporated with other demographic data to parameterize stage-based (Lefkovitch) matrices for each year  $\times$ treatment combination.

Topographic position influenced both population size structure and density, with a gradient from valleys (727 palms/ha) to upper slopes (5513 palms/ha). Palm demography was characterized by low mortality, low reproductive activity, and high seed germination rates. Leaf harvest increased adult mortality and reduced fecundity, and it was projected to reduce  $\lambda$  (finite rate of increase). However,  $\lambda$  for harvested populations did not differ significantly from 1. Browsing increased mortality of seedlings, juveniles, and small adults, resulting in populations projected to decline ( $\lambda < 1$ ).

These findings indicate that browsing by free-range livestock impacts *C. radicalis* populations more than leaf harvest and could explain the low density and skewed size structure in valleys. The modest impact of leaf harvest treatments is due in part to the reduction in the availability of marketable leaves. Detection of such feedbacks exemplifies how the incorporation of human management practices enhances the insights that experiments bring to studies of the population ecology of NTFPs.

Key words: Chamaedorea radicalis; El Cielo; Lefkovitch matrix; livestock browse; Mexico; nontimber forest products; palm; plant demography; population dynamics; sustainable harvest.

#### INTRODUCTION

Over the past decade, the extraction of non-timber forest products (NTFPs) has been promoted as part of a balanced approach to the conservation of tropical forests (Panayotou and Ashton 1992, Plotkin and Famolare 1992). NTFP harvest is thought to have fewer negative impacts on forest communities and ecosystem processes than other land use activities, while providing communities with a source of income to meet livelihood needs. Despite the interest and advocacy for NTFP extraction, the population ecology of most

Manuscript received 6 November 2002; revised 20 October 2003; accepted 28 October 2003; final version received 4 December 2003. Corresponding Editor: A. Townsend.

<sup>3</sup> Present address: Department of Forest Science, Oregon State University, 1401 Gekeler Lane, La Grande, Oregon 97850 USA. E-mail: bryan.endress@oregonstate.edu NTFPs remains unstudied, making it difficult not only to assess the conservation status of NTFP species, but also the sustainability of extraction (Boot and Gullison 1995, Ticktin and Johns 2002).

Leaves of palms (Arecacaceae) are important for millions of people worldwide and are used for weaving, thatching, basketry, broom construction, and ornamental uses. Because leaf removal rarely results in the immediate death of individual palms, leaf harvest has been considered a sustainable use of tropical forests (Reining et al. 1992, Salafsky et al. 1993, Zuidema 2000). Despite the cultural and economic importance of palm leaves and their potential for sustainable extraction, little is known about the effects of leaf harvest on palm demography or population dynamics. This has limited the ability of ecologists and resource managers to assess the ecological impacts of leaf harvest or provide technical assistance concerning palm resource management.

Several studies have sought to determine the effect of leaf harvest on palm populations by experimentally testing the effects of defoliation on vital rates (growth, survival, and fecundity) of individual palms and extrapolating population level effects from their results. Results from these studies indicate that leaf harvest did not affect palm survival (Ratsirarson et al. 1996, Zuidema 2000; N. P. R. Anten, M. Martinez-Ramos, and D. D. Ackerly, unpublished manuscript) and had little impact on leaf production (O'Brien and Kinnaird 1996, Ratsirarson et al. 1996), though there are exceptions (Zuidema 2000). In some cases, defoliation actually increased leaf production rates over the short term (O'Brien and Kinnaird 1996, Anten and Ackerly 2001), though subsequent leaves were often smaller (Joyal 1996, O'Brien and Kinnaird 1996, Ratsirarson et al. 1996). Leaf harvest may also decrease inflorescence or seed production (Ratsirarson et al. 1996, Flores and Ashton 2000).

While these studies provide valuable information regarding the response of individual palms to defoliation, extrapolating population level impacts from these experiments is difficult, because other relevant factors must also be considered, including (1) the demography of all life history stages of the target species, (2) the pattern of leaf harvest, and (3) harvest frequency.

Assessing the impact of leaf removal on population dynamics is difficult because of problems in quantifying its effects on lifetime growth, survival, and reproduction. One powerful way to explore harvest impacts is to integrate field harvest experiments that simulate actual harvest practices with population matrix models. Population matrix models utilize data on growth, survival, and fecundity to gain insight on the importance of different life history stages to demographic structure and the direction and rate of population change. These models are useful in exploring the consequences of NTFP extraction on palm populations (Pinard and Putz 1992) and have been used to examine the effects of stem (Pinard 1993, Olmsted and Alvarez-Bullya 1995), palm heart (Zuidema 2000), seed (Ratsirarson et al. 1996, Bernal 1998), and leaf harvest (Joyal 1996, Zuidema 2000).

Results from Joyal (1996) and Zuidema (2000) suggest that palm populations are resilient to leaf harvest. Zuidema (2000) studied a one-time defoliation of the clonal palm, *Geonoma deversa*, and found no effect on survival, but reduced individual leaf production, stem growth, vegetative production, and fecundity. However, this had little impact on population structure or finite rate of increase ( $\lambda$ ). Periodic harvests at a frequency greater than the recovery time of individual palms ( $\geq$ 4 yr) were projected to be sustainable. Joyal (1996) constructed a matrix model to examine the growth rate of a harvested population of *Sabal uresana* in Mexico, and found  $\lambda > 1$ , suggesting leaf harvest

was not seriously threatening the population. Few other studies have used population matrix models to explore the effects of leaf harvest on palm resource management or population dynamics (but see Svenning and Macía 2002). Additional studies are needed to better understand population level responses of palms to defoliation, and the importance of harvest pattern and intensity on population dynamics.

Throughout northeastern Mexico, leaves from wild populations of the understory palm Chamaedorea radicalis Mart. are harvested for use by the cut foliage industry in the United States and Europe. Chamaedorea radicalis is listed as vulnerable by FAO (1997). The harvest of C. radicalis leaves is critically important for communities living within the El Cielo Biosphere Reserve, Tamaulipas, Mexico. Since the creation of the reserve in 1985, these leaves have been the only forest resource residents are allowed to harvest for commercial purposes (Trejo 1992). As a result, C. radicalis has become the principal source of income for many communities in El Cielo, resulting in intense leaf harvesting within the reserve. Local palm collectors (palmilleros) are concerned that overharvesting has reduced palm abundance and is currently threatening their primary source of income (Peterson 2001). In addition to leaf harvest, another factor which may threaten C. radicalis is browsing by free-range livestock (Jones and Gorchov 2000).

Despite the importance of C. radicalis for many people throughout northeastern Mexico, and the concerns of overharvesting, little is known about the population ecology of C. radicalis or the effects of leaf harvest on palm population dynamics. Therefore, in collaboration with two communities in El Cielo, we conducted a study to explore the demography of C. radicalis and the effects of harvest and livestock browse on population dynamics. Specifically our objectives were (1) to describe patterns of C. radicalis abundance and population size structure in relation to topography and substrate type, (2) to document C. radicalis demography, (3) to experimentally test how this demography is affected by different leaf harvest regimes and livestock browse intensities, and (4) to project the effect of harvest and browse on transient and long-term population dynamics.

### **METHODS**

# Study area

The study was conducted in the montane mesophyll forests of the El Cielo Biosphere Reserve, Tamaulipas, Mexico in the communities of Alta Cima  $(23^{\circ}08' \text{ N}, 99^{\circ}09' \text{ W};$  elevation 950 m) and San José  $(23^{\circ}03' \text{ N}, 99^{\circ}12' \text{ W};$  elevation 1300 m). El Cielo straddles the Sierra Madre Oriental with elevations ranging from 200 to 2200 m. The region is characterized by rugged karst topography, with ~98% of the reserve having slopes >20% (Davis et al. 1997). Precipitation at the nearby

Life history stage	No. leaflets on youngest fully expanded leaf	Reproductive?	Marketable leaves?
Seed (S)	NA	NA	NA
Seedling (Ss)	2	no	no
Juvenile (J)	3–9	no	no
Small adult (A1)	10-24	yes, rarely	yes
Large adult (A2)	≥25	yes	yes

 

 TABLE 1. Life history stages of Chamaedorea radicalis based on leaf morphology and reproductive activity from tagged palms in Cañón del Diablo, Alta Cima (El Cielo Biosphere Reserve, Tamaulipas, Mexico).

Note: Abbreviations (in parentheses) are used throughout the tables and figures.

Rancho del Cielo averages 2500 mm/yr, with a mean temperature of 13.8°C (Davis et al. 1997). San José has  $\sim$ 75 residents, and Alta Cima  $\sim$ 250 residents. Both communities are heavily dependent on the collection of *C. radicalis* leaves for their livelihood (Peterson 2001). The collection of *C. radicalis* leaves occurs year-round, and palmilleros are able to collect hundreds of leaves per day (Endress et al. 2004). Suitable leaves for harvest are pinnately compound leaves from adult palms that are  $\geq$ 40 cm in length with minimal insect or fungal damage. Collectors harvest all marketable leaves on individuals, occasionally defoliating palms completely. Leaves are sold for approximately US\$0.01–0.02 each (B. A. Endress, *personal observation*, 2001).

### Study species

*Chamaedorea radicalis* is a long-lived, dioecious, understory palm found in northeastern Mexico (Hodel 1992). The distribution of *C. radicalis* within El Cielo ranges from 200 m elevation in seasonal tropical forests to pine–oak forests above 1400 m (Mora-Olivo et al. 1997). The palm is slender, erect, and usually lacks an aboveground stem, though some individuals have a well-developed stem reaching 3–4 m in height. Seedlings have bifid leaves, while adult palms generally have 4–8 pinnately compound leaves (Hodel 1992).

We recognized five life history stages of *C. radicalis*: seeds, seedlings, juveniles, small adults, and large adults (Table 1). Stages were classified based on leaf morphology and reproductive activity of marked palms in El Cielo between 1999 and 2001, which showed that: (1) palms with >10 leaflets on the youngest leaf are not reproductively active, and (2) large adults are more than twice as likely to flower or produce fruit than small adults (Endress 2002).

Male and female palms are morphologically similar, with the exception of their flowers (Hodel 1992). The palm is wind pollinated (Berry and Gorchov, 2004); seed dispersers are unknown.

### Palm abundance and stage structure

Previous studies indicate that the abundance and stage structure of populations of other understory palm

species are influenced by topographic variation and/or microhabitat heterogeneity (Clark et al. 1995, Svenning 2001a, b). If such variation is present in populations of C. radicalis, it may confound or mask the effects of leaf harvest or livestock browse. Therefore, during July–August 2000, we sampled palm populations using belt transects along five hillsides within Cañón del Diablo, Alta Cima (1000-1200 m elevation) to better understand patterns of abundance and population stage structure in relation to substrate type and topographic position. At each hillside, three transects were randomly located and placed perpendicular to the slope's aspect. Transects ran from the midpoint of the valley to the midpoint of the ridge and ranged in length from 74 to 144 m. Transects were 2 m wide for a total area sampled of 2915 m<sup>2</sup>.

Transects were partitioned into both topographic position and substrate type categories. Five topographic positions were recognized: valleys (the area between the midpoint of the valley to the bottom of the slope), three slope categories of equal length (lower, mid-, and upper slope), and ridges (top of hillside's slope to the midpoint of the ridge). Along transects, three categories of substrate type were also recognized: soil (areas with  $\geq$ 50% soil cover), rock (areas with >50% rock cover), and rock outcrop (large rocks that emerged >1 m from the surrounding substrate). All palms encountered were counted, classified into a life history stage, and palm density and the proportion of palms in each life history stage were calculated.

A mixed-model generalized linear model on the ranked data was used to test for the effect of topographic position and substrate type on palm density. Ranks were used because densities were not normally distributed, and transformations were unsuccessful in normalizing the data. Topographic position was considered a fixed effect, substrate type a random effect, and hillsides were used as replicates (N = 5). Thus, data from the three transects on each hillside were first pooled, and then densities were calculated for each combination of topographic position and substrate type for each hillside.

To examine differences in stage structure in relation to topographic position, we combined data from the transects to determine the overall, or pooled stage structure. We then compared the pooled structure with the population structure of C. radicalis in each of the topographic position categories using log-likelihood goodness-of-fit tests ( $G^2$ ). Valley and lower slope categories were combined due to low sample sizes, and contingency tests used a Bonferonni adjusted  $\alpha$  value ( $\alpha = 0.05/4 = 0.0125$ ) to identify significant differences. Keyfitz's index of dissimilarity,  $\Delta$ , was also calculated to explore differences between the pooled stage structure and C. radicalis structure along the topographic gradient.  $\Delta$  is the sum of the positive differences between the two populations in the proportion of individuals in each class, and provides insight on the overall differences between population structures (Caswell 2001). Similar analyses were done to test for differences between the pooled stage structure and the stage structures on soil, rock, and rock outcrop substrates ( $\alpha = 0.05/3 = 0.0166$ ).

## Leaf harvest experiment

In January 1999, we established 10 plots within Cañón del Diablo to conduct our leaf harvest experiment. Plots were located on mid- and upper hillsides (elevation ranged from 1039 to 1120 m) and ranged in size from 53 to 290 m<sup>2</sup>. Dominant canopy species within the plots included Cercis canadensis, Chione mexicana, Clethra pringlei, Quercus germana, and Wimmeria concolor (Endress 2002). Each plot contained 50 adult palms with leaves of marketable size (n =500). Palms in the plots were exposed to leaf harvest prior to January 1999 and many had evidence of past harvest (cut rachises). However, no differences were found in the mean number of cut rachises per palm among treatments (Endress et al. 2004). The plots were then divided into five subplots of 10 palms each, with one subplot randomly assigned to each of five harvest treatments (split-plot design; n = 100 palms/treatment). The treatments were: (1) control, no leaf removal; (2)  $1\times$ , all marketable leaves removed once per year (in August); (3), 2×, all marketable leaves removed twice per year (in August and February); (4),  $4\times$ , all marketable leaves removed four times per year (in February, May, August, and November), and (5),  $4 \times$  modified, same as treatment 4 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.

Treatments were designed to test a range of harvest regimes and were developed in collaboration with palmilleros in Alta Cima. The  $4 \times$  treatment approximated the current harvest regime in El Cielo, as palmilleros indicated they visit the same location at least four times per year to collect leaves (Endress et al. 2004). The  $4 \times$  modified (hereafter " $4 \times$ m") treatment simulates current harvest practices in terms of the frequency of visits, but avoids complete defoliation. Treatments were initiated in May 1999, and leaves harvested in accordance with local harvest practices; harvested leaves were  $\geq$ 40 cm in length and free of fungal and insect damage.

The treatments were based on the frequency of visits and local harvest selection criteria, not on the number or proportion of leaves removed per palm, and are thus different from other leaf harvest studies (e.g., O'Brien and Kinnaird 1996, Ratsirarson et al. 1996; N. P. R. Anten, M. Martinez-Ramos, and D. D. Ackerly, *unpublished manuscript*). In our study the number of leaves removed per palm depended on the number of marketable leaves present, as occurs during actual harvest.

All palms were permanently tagged, and the following data recorded for each individual: number of leaves, number of leaflets on each leaf, leaf length, and, if present, the phenological stage and sex of inflorescences and fruit number. The youngest leaf on each plant was marked to measure leaf production. Palms were recensused monthly through August 2001.

The demography of smaller palms (seedlings and juveniles) was measured in nested plots within five of the permanent plots ( $3 - \times 3$ -m subplots). Palms in these subplots were tagged and censused every three months (in February, May, August, and November). New recruits within the subplots were also tagged and measured.

Seed germination experiments were conducted for both years of the study (1999–2000 and 2000–2001). Two 0.25-m<sup>2</sup> seed plots, one positioned on a slope and the other on level ground, were established adjacent to each of the 10 harvest plots. Seeds were collected in late August of each year from palms outside of the plots, and 20 were sown into each seed plot (N = 400). Emerging seedlings were counted monthly through August 2001.

Adult palms were removed from analyses if: (1) they died prior to August 1999 (the first sampling date for construction of the matrix models; N = 20), (2) they regressed to the juvenile stage prior to August 1999 (N = 16), or (3) they were browsed by cattle (N = 21). In addition, 18 smaller palms (juveniles and seedlings) died prior to August 1999 and 12 were browsed, and thus also excluded from analyses.

# Livestock browse experiment

To evaluate the effect of livestock browse on palm demography, we exposed a palm population to two intensities of burro browse. Burros were chosen because they are one of the most numerous domestic animals in Alta Cima and San José (Peterson 2001) and can browse on slopes inaccessible to cattle and horses.

A 600-m<sup>2</sup> study area near San José was established in a location with minimal, if any, browsing in the past. This site was similar to our study plots in Cañón del Diablo in terms of elevation (1050 m), *C. radicalis* density, and species composition of the forest overstory (Endress 2002). All *C. radicalis* individuals within the site were tagged and measured in January 1999 for the variables specified in the leaf removal experiment. The site was fenced to prevent accidental leaf harvest or livestock browsing, and then separated into six  $10 \times 10$ -m plots containing ~75 palms each. The following three treatments were randomly assigned to two plots each: (1) no browse (control); (2) 1× browse, one-time browse in February 2000; (3) 2× browse, two-time browse conducted in August 1999 and February 2000.

For each browsing event, the burro was placed just inside of the plot entrance, and was allowed to browse within the plot as long as it wanted. The gate was left open to allow the burro to exit the site at any time. Burros, on average, spent 10 min browsing. Before and after each browsing episode, we censused each palm for the leaf and inflorescence variables specified in the leaf harvest experiment, as well as recorded any browsing damage.

# Effects on mortality and reproduction

Differences in mortality between each leaf harvest treatment and the control were analyzed by two-tailed Fisher's exact tests, because low mortality rates prevented the analysis of one contingency table. Adult palms in the control treatments for both the harvest and browse experiments were pooled for these analyses, as these sites were similar in C. radicalis density, elevation, and tree composition. Separate  $2 \times 2$  contingency tables were constructed for each year of the study (1999-2000, 2000-2001), consisting of the number of adults that survived and died that year. Small and large adults were pooled together for these analyses because mortality rates were very low. A Bonferroni adjusted P value was used to account for the multiple comparisons ( $\alpha = 0.05/4 = 0.0125$ ). Similarly, Fisher's exact tests were used to analyze the effect of each browse treatment vs. the pooled control on mortality of each stage (seedling through large adult) for the year browse occurred (1999-2000), and the year following browse (2000–2001), with Bonferroni adjusted  $\alpha = 0.05/2 =$ 0.025.

Differences among control, harvest, and browse treatments in the proportions of small and large adults flowering were determined by log-likelihood goodness-of-fit tests ( $7 \times 2$  contingency table). For palms that did flower in each year, differences in the mean number of inflorescences produced per palm were analyzed by Kruskal-Wallis tests for small and large adults. This was done since data violated assumptions required for parametric analyses.

Differences in the proportion of palms producing fruit were analyzed by constructing six,  $2 \times 2$  contingency tables comparing the pooled control to each of the harvest and browse treatments (Bonferonni adjusted  $\alpha = 0.05/6 = 0.0083$ ) using Fisher's exact tests. Because few palms produced fruit, small and large adults were again pooled for analyses.



FIG. 1. Life cycle graph for *Chamaedorea radicalis*. Abbreviations: S, seed; Ss, seedling; J, juvenile; A1, small adult; A2, large adult. Arrows indicate transitions among life history stages.

### Matrix model parameterization and analysis

Demographic data collected from the leaf removal and browse experiments were used to construct population matrix models. Stage-structured (Lefkovitch) models were used in this study because demographic parameters of understory palms correlate better with an individual's size or stage rather than age (Pinard and Putz 1992).

Although C. radicalis is a dioecious species, a onesex model was used to assess population dynamics. One-sex models assume (1) no difference between males and females in growth and survival rates and (2) female fecundity is independent of sex ratio and male density. Population dynamics of dioecious species are often modeled using one-sex models when male and female growth and survival are similar, or when there are insufficient data on differences between male and female demography (Bernal 1998, Caswell 2001). Our populations met the first assumption since we found no differences in growth or survival between males and females (Endress 2002). In addition Berry and Gorchov (2004) found fruit production in female C. radicalis individuals was not dependent on neighborhood or population male density or sex ratio, indicating female fecundity is independent of male abundance.

A life cycle graph (Fig. 1) illustrates the transitions among the five life history stages. Population matrix models followed the following form:  $\mathbf{n}(\mathbf{t} + \mathbf{1}) = \mathbf{A} \times \mathbf{n}(\mathbf{t})$ , where  $\mathbf{n}(\mathbf{t})$  represents the stage structure ( $\mathbf{n}$ ) of the population at time  $\mathbf{t}$ ,  $\mathbf{n}(\mathbf{t} + \mathbf{1})$  is the stage structure at the next time interval (the next year), and  $\mathbf{A}$  is a matrix containing the transition probabilities and fecundity estimates of each life history stage.

To construct each population matrix, three parameters were estimated for each stage: (1) the probability an individual will survive and remain within that stage class during one year, (2) the probability that an individual will survive and grow into another stage during one year, and (3) reproductive output or fecundity. Fecundity was estimated by calculating the mean number of fruit produced per palm per stage (small or large adults). *Chamaedorea radicalis* was modeled as birthpulse population with a postbreeding census since reproduction follows seasonal patterns (Endress 2002).

	Propo	rtion of po life histo	pulation i ry stage				
Position and substrate	Seedling	Juvenile	Small adult	Large adult	N	Р	Δ
Topographic position							
Valley/lower slope	0.35	0.08	0.29	0.28	107	0.015	30
Midslope	0.30	0.14	0.42	0.14	283	0.444	8
Upper slope	0.29	0.16	0.37	0.18	406	0.628	3
Ridge	0.31	0.11	0.38	0.20	126	0.822	6
Pooled	0.30	0.14	0.38	0.18	922		
Substrate type							
Soil	0.32	0.13	0.41	0.14	68	0.730	10
Rock	0.34	0.14	0.39	0.13	593	0.012	10
Rock outcrop	0.21	0.13	0.35	0.31	261	< 0.0001	32
Pooled	0.30	0.14	0.38	0.18	922		

TABLE 2. Population structure of C. radicalis across topographic positions and substrate types.

*Note:* P values are from  $G^2$  tests.  $\Delta$  is Keyfitz's index of dissimilarity.

We used August as a census date to calculate annual transition rates because C. *radicalis* seed maturation peaks that month (Endress 2002).

Seeds of C. radicalis have been shown to lose viability rapidly, suggesting that they do not remain viable in the soil after one year (Rojas Agil et al. 2000). While most seedlings emerged 7-11 months after planting, 2.5% of seeds emerged in the second year (2001). We therefore had to estimate the seed-to-seed transition rate. This was done by dividing 2.5% by the germination rate of nondormant seeds (37%; 0.025/0.37 =0.067). Thus, we estimated that 6.7% of seeds remained in the seed bank, of which 37% germinated the following year. Because the study ended in August 2001, we did not have an estimate for the percentage of seeds remaining dormant for the second cohort of seeds (planted in August 2000). In this case, we assumed the same germination rate for dormant seeds (2.5%) and divided this by the germination rate of nondormant seeds for that year (28.3%) resulting in a seed-to-seed transition of 0.088.

Transition matrices were constructed for each year of the study (1999–2000 and 2000–2001) for each of the leaf removal and browse treatments. The control transition matrix was constructed by combining palms from the control treatments in both the browse and leaf harvest experiments. Because leaf harvest is restricted to adult palms, the transition probabilities for seeds, seedlings, and juveniles were identical for each of the leaf harvest treatments. We have no reason to believe harvest affects the demography of these stages, as collectors avoid trampling seedlings while collecting (Jones and Gorchov 2000).

Transition matrices for the leaf harvest and browse treatments were analyzed to explore both short-term (transient) and long-term (asymptotic) population dynamics. Eigenanalysis was performed to estimate  $\lambda$ , the finite rate of increase, and stable stage distributions. We use  $\lambda$  to describe the rate at which a population changes each year once it reaches its stable stage distribution; it describes the long-term dynamics of the population. If  $\lambda > 1$ , then the population is projected to increase over time. The population is stable when  $\lambda = 1$ , while if  $\lambda < 1$ , the population is projected to decline. The stable stage distribution is the structure of the population (percentage of individuals in each stage class) when the population is growing at  $\lambda$ . All analyses were done in SAS using PROC IML (SAS Institute 2000).

Confidence intervals (95%) for  $\lambda$ s were constructed by bootstrap analysis, and data was resampled in the same manner as it was collected (McPeek and Kalisz 1993). The procedure involved generating 2000 resampled matrices for each year × treatment combination, and solving for  $\lambda$  for each matrix. We then estimated 95% confidence intervals using the bootstrap percentile interval method (Caswell 2001). Significant differences between  $\lambda$ s of the treatments were determined by nonoverlapping confidence intervals.

Elasticity analyses were conducted to explore the relative contribution of each transition element in the matrix to  $\lambda$ , and the stable stage distribution was determined for each treatment  $\times$  year combination. Differences in the stable stage distributions of the control, harvest, and browse treatments were analyzed using Kefitz's index of dissimilarity,  $\Delta$ . The observed population structure used in this analysis came from the 922 palms sampled along the belt transects within Cañón del Diablo.

In cases where the observed population structure differs greatly from the stable stage distribution, the population will not grow at  $\lambda$ . Instead, the population growth rate from one year to the next will be influenced by the current population structure in addition to the transition rates in the population matrix. Thus, transient analyses may provide a more accurate assessment of short-term population dynamics than long-term analyses. Transient analysis involves matrix multiplication and follows the same formula as above:  $\mathbf{n}(\mathbf{t} + \mathbf{1}) = \mathbf{A} \times \mathbf{n}(\mathbf{t})$ . For each leaf harvest treatment, we multiplied the 2000–2001 transition matrix **A**, by the population structure  $\mathbf{n}(\mathbf{t})$ , to determine the population size and structure for the following year,  $\mathbf{n}(\mathbf{t} + \mathbf{1})$  (2001–2002). The column vector  $\mathbf{n}(\mathbf{t} + \mathbf{1})$  is then multiplied by **A** to determine the population size and structure for the following year,  $\mathbf{n}(\mathbf{t} + \mathbf{2})$  (2002–2003). This procedure was repeated to simulate 25 years of population change for each of the harvest treatments. The 2001–2002 matrices were used in this analysis because these transitions should more closely reflect the demography of palms subjected continuously to leaf harvest than the transitions in 1999–2000. For transient dynamics of browsed populations, the 1999–2000 matrices were used because no browsing occurred during 2000–2001.

### RESULTS

## Palm abundance and stage structure

Results showed a significant effect of topographic position on *C. radicalis* density (df = 4,2; F = 10.835; P < 0.0001). Mean palm densities per hectare (±1 sE) were lowest in valleys (727 ± 232) and lower slopes (1273 ± 191), and highest on mid-slope (3967 ± 423), upper slope (5513 ± 416), and ridge sites (5053 ± 508). Substrate type had no significant effect on palm density (P = 0.197).

Of the 922 individual palms recorded along the transects, 56% were adults (18% large adults, 38% small adults), 14% were juveniles, and 30% were seedlings. The stage structure in valley/lower slope sites differed significantly from the pooled stage structure, resulting in  $\Delta = 30$  (Table 2). These valley/lower slope areas contained a greater proportion of large adults, while small adults and juveniles were underrepresented. No differences were found in the stage structures of midslope, upper slope, or ridge sites and the pooled structure.

The stage structure of populations on rock outcrops also differed significantly from the pooled stage structure, as large adults were overrepresented (31%) while seedlings were underrepresented (21%), resulting in a  $\Delta = 32$  (Table 2). Soil and rock substrates  $\Delta$  values were much lower, though a marginally significant difference was found between the stage structure on rocks and the pooled population.

## Seed germination

Of the 400 seeds planted in 1999, 39.5% germinated. Of these, 97.5% emerged 7–11 months after planting (March–July 2000), and 10 seeds remained dormant through 2000 and germinated the following May (2001). Germination rates were lower for the 2000– 2001 cohort, as 28.3% of seeds germinated, though this does not include any dormant seeds. Germination rates did not differ between level and sloped areas in 1999– 2000 ( $\chi^2 = 0.844$ , P = 0.358) or 2000–2001 ( $\chi^2 =$ 0.112, P = 0.738).



FIG. 2. Adult mortality in each leaf harvest treatment for 1999–2000 ( $G^2 = 12.27$ , df = 4, P = 0.0154) and 2000–2001 ( $G^2 = 7.99$ , df = 4, P = 0.0918). The figure shows data for small and large adults, pooled. There was no leaf removal or browsing in control plots (0×); all marketable leaves were removed once, twice, or four times per year in treatments 1×, 2×, and 4×, respectively. For modified treatment 4×m, at most one leaf was removed at each of four harvests per year, but only if the palm had at least two leaves.

#### Effects of harvest and browse on survival

Leaf harvest increased mortality of adult *C. radicalis* individuals. During 1999–2000, mortality rates differed significantly among treatments, with the control treatment having the lowest mortality and the 4× treatment the highest (P = 0.0154; Fig. 2). In the second year of the study (2000–2001) the control treatment again had the lowest mortality, with the highest mortality in the 1× and 4×m treatments; however, the treatments did not differ significantly (P = 0.0919).

Burro browse increased mortality of all size classes of *C. radicalis*. Of the 152 palms in the  $1\times$  browse treatment, 60.5% were browsed, including 50% of seedlings, 56% of juveniles, 71% of small adults, and 67% of large adults. Many palms browsed were either killed immediately (uprooted) or died by August 2000. Browsed seedlings were most likely to die (47.5%), followed by large adults (20%), juveniles (12.5%), and small adults (7.2%). The 2× browse treatment had a



FIG. 3. Mortality in control,  $1 \times$  browse, and  $2 \times$  browse treatments for each life history stage. Significant differences, at P < 0.05, between the control and browse treatments are shown by different letters. Values above bars indicate sample sizes (*n*). There was no leaf removal or browsing in control plots; in the browse treatments, burros were allowed to browse once (February 2000,  $1 \times br$ ) or twice (August 1999 and February 2000,  $2 \times br$ ).

similar proportion of palms browsed (63.2%), though the mortality rates for browsed palms were higher, with seedlings having 50% mortality, followed by small adults (36%), juveniles (35%), and large adults (29%).

Mortality due to browsing, in addition to mortality of some unbrowsed palms, resulted in significant differences in mortality among browse and control treatments (Fig. 3). In 1999–2000, seedling mortality was over four times higher in browse treatments than in the control treatment. For both juveniles and small adults, mortality was much greater in the 2× browse treatment than in the control, but differences between the 1× browse and control were not significant. Mortality of large adults ranged from 0% (control) to 13.3% (2× browse) though differences were only marginally significant with the Bonferonni-adjusted  $\alpha$  (1× browse vs. control, P = 0.046; 2× browse vs. control, P = 0.072).

In the year following browsing (2000–2001), mortality rates were again higher than the control, though significantly only for seedlings in the 2× browse treatment (P = 0.0057; Fig. 3). In addition, a large proportion of juveniles and small adults that were browsed but not killed in 1999–2000 regressed to smaller life history stages in 2000–2001. Over five times as many juveniles regressed in the 1× browse (37.5% regressed; P = 0.0130) and 2× browse treatments (38.5% regressed; P = 0.0171) than in the control treatment (6.5%). Small adults in the browse treatments showed the same trend, with the 1× browse (11.4% regressed; P = 0.005) and 2× browse (52.8% regressed; P < 0.0001) treatments differing significantly from the control (1.1%). No differences were found in the proportion of large adults regressing to smaller size classes among the control (11.7% regressed) and browse treatments (1× browse: 9.7%, 2× browse: 10%).

## Effects of harvest and browse on reproduction

Between January 1999 and August 2001, 148 different palms flowered (23.3% of adult palms). Of these 68 (46%) were male and 80 (54%) were female; this did not significantly differ from a 1:1 sex ratio ( $G^2 = 0.9484$ , df = 1, P = 0.33). No differences were found between the proportion of males or females flowering in either year; in 1999–2000, 52.2% of known males and 60.5% of known females flowered ( $G^2 = 1.05$ , P = 0.305), while in 2000–2001, 63.8% of males and 67.8% of females flowered ( $G^2 = 1.17$ , P = 0.280). During 1999–2000, 10.4% of small adults flowered, compared to 24.8% of large adults, while in 2000–2001, 9.8% of small adults, and 32.9% of large adults flowered.

In 1999–2000, more large adults flowered in the control treatment than in the harvest or browse treatments, but this trend was not significant ( $G^2 = 10.84$ , df = 6, P = 0.093; Fig. 4). The proportion of large adults that produced flowers in 2000–2001 was also significantly



FIG. 4. Percentage of *C. radicalis* adults (small and large) that flowered in 1999–2000 and 2000–2001. See Figs. 2 and 3 legends for treatment descriptions.

	No. fruiting palms		Percen adults p fr	tage of roducing uit	Mean no fruitin	. fruit per g palm	Р		
Treatment <sup>†</sup>	1999-2000	2000-2001	1999-2000	2000-2001	1999-2000	2000-2001	1999-2000	2000-2001	
$0 \times (\text{control})$	14	13	8.8	8.3	26.5	16.5			
1×	1	2	1.1	2.4	35.0	17.5	0.009	0.059	
$2 \times$	3	1	3.3	1.2	10.7	19.0	0.072	0.020	
$4 \times m$	1	3	1.2	3.5	3.0	54.7	0.012	0.119	
$4 \times$	6	1	6.5	1.4	10.5	11.0	0.347	0.030	
$1 \times$ browse	1	1	1.0	0.9	8.0	8.0	0.011	0.007	
$2 \times$ browse	5	4	6.2	6.5	19.8	27.3	0.336	0.444	

TABLE 3. Fruit production in control, harvest, and browse plots for 1999–2000 and 2000–2001.

*Note:* P values are reported for Fisher's exact tests, testing differences in the percentage of palms fruiting between the control and experimental treatments (critical P = 0.0083).

<sup>†</sup> There was no leaf removal or browsing in control plots; all marketable leaves were removed once, twice, or four times per year in treatments  $1\times$ ,  $2\times$ , and  $4\times$ , respectively. For modified treatment  $4\times m$ , at most one leaf was removed at each of four harvests per year, but only if the palm had at least two leaves. In the browse treatments, burros were allowed to browse once (February 2000) or twice (August 1999 and February 2000).

affected by treatments ( $G^2 = 22.48$ , df = 6, P = 0.001; Fig. 4). The control treatment had the highest proportion of flowering large adults, while the 4× treatment had the lowest proportion. The same trend appeared for small adults, but differences were not significant in either 1999–2000 ( $G^2 = 5.50$ , df = 6, P = 0.482) or 2000–2001 ( $G^2 = 10.42$ , df = 6, P = 0.101).

For palms that did flower, no differences were found in the number of inflorescences produced between treatments for small or large adults in either year. For small adults, the mean number of inflorescences produced per flowering palm in 1999–2000 ranged from 1.00 (1× browse) to 1.20 (4×; N = 50, df = 6,  $\chi^2 =$ 8.705, P = 0.191); inflorescence production in large adults ranged from 1.00 (2× harvest) to 2.25 (4×m; N = 55, df = 6,  $\chi^2 = 9.916$ , P = 0.128). For 2000– 2001, inflorescence production in small adults ranged from 1.00 (1× browse) to 2.00 (2× browse; N = 39, df = 6,  $\chi^2 = 4.591$ , P = 0.597), and for large adults, 1.00 (2× harvest) to 1.91 (4×m harvest; N = 82, df = 6,  $\chi^2 = 10.732$ , P = 0.097).

In 1999–2000, 39% of known females produced fruit (range: 1–71 fruits per palm), while in 2000–2001, 32% produced fruit (range: 1–88 fruits per palm). In total, 44 palms produced 1171 mature fruit between August 1999 and August 2001. Over half (55.2%) of these fruit were borne by 10 individuals.

Fruit production varied among treatments (Table 3). The control treatment contained the largest proportion of fruit-bearing palms in both years. The only treatment where the proportion of fruiting palms was significantly different than the control was the  $1 \times$  browse treatment in 2000–2001.

# Population dynamics

Transition matrices summarizing the demography of *C. radicalis* are reported in Table 4. Differences in the demography of palms in the leaf harvest and browse treatments resulted in significantly lower finite rates of increase ( $\lambda$ ) for these populations as compared to the

control treatment (Table 5). The only exception was the 4×m treatment in 2000–2001, which did not differ significantly from the control treatment. For most of the treatments,  $\lambda$  changed little from 1999–2000 to 2000–2001, except the 4×m and 1× browse treatments, which increased considerably. Although the population growth rates of leaf harvest treatments were significantly lower than the control, they did not differ significantly from 1. The finite rate of increase of 1× browse treatment on the other hand was significantly <1 for the year of the browse event.

The stable stage distributions derived from the matrices indicated that leaf harvest and burro browse resulted in drastically different stable stage distributions (Table 6). The 1999–2000 matrices for the control,  $4\times$ harvest, and  $2 \times$  browse treatments generated stable stage distributions similar to the observed stage structure. The  $4 \times m$  harvest and the  $1 \times$  browse showed the opposite pattern, with few seeds and seedlings, and a large proportion of small and large adults. For the 2000-2001 matrices, the stable stage distribution of the control treatment differed considerably from all other treatments, except for the  $4 \times m$  treatment. With that exception, as the frequency of leaf harvest visits per year increased (from 1 to 4 per yr), differences in the stable stage distribution increased, from populations dominated by seeds, seedlings, and juveniles to ones dominated by large adults. These differences largely reflect the differences in fecundity among treatments.

The elasticity matrices for each treatment  $\times$  year combination revealed that  $\lambda$  was most sensitive to proportional changes in stasis (individuals that survived but did not grow or regress), and in particular, the stasis of large and small adults (Fig. 5, Table 7). Elasticity of matrix elements corresponding to regression and fecundity were quite low compared to growth and survival.

Although the current population structure of *C. radicalis* differed greatly from the stable stage distribu-

$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			1999–2000				2000-2001					
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Treatment	Stage	S	Ss	J	A1	A2	S	Ss	J	A1	A2
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$\overline{0 \times (\text{control})}$	S	0.068	0	0	0.664	5.660	0.088	0	0	0.134	3.350
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	. ,	Ss	0.370	0.691	0.036	0	0	0.283	0.642	0.065	0	0
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		J	0	0.235	0.393	0.047	0	0	0.224	0.226	0.010	0.017
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		A1	0	0	0.500	0.720	0.226	0	0.030	0.710	0.495	0.100
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		A2	0	0	0	0.178	0.774	0	0	0	0.494	0.833
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$1 \times$	S	0.068	0	0	0.356	0.333	0.088	0	0	0	0.543
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		Ss	0.370	0.691	0.036	0.017	0	0.283	0.642	0.065	0.021	0
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		J	0	0.235	0.393	0.051	0	0	0.224	0.226	0.063	0
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		A1	0	0	0.500	0.712	0.181	0	0.030	0.710	0.458	0.029
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		A2	0	0	0	0.186	0.727	0	0	0	0.354	0.943
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$2 \times$	S	0.068	0	0	0	1.129	0.088	0	0	0.614	0
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		Ss	0.370	0.691	0.036	0.016	0	0.283	0.642	0.065	0	0
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		J	0	0.235	0.393	0.048	0	0	0.224	0.226	0	0
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		A1	0	0	0.500	0.774	0.290	0	0.030	0.710	0.544	0.120
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		A2	0	0	0	0.065	0.677	0	0	0	0.439	0.800
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$4 \times m$	S	0.068	0	0	0.063	0	0.088	0	0	1.810	2.316
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		Ss	0.370	0.691	0.036	0	0	0.283	0.642	0.065	0.024	0
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		J	0	0.235	0.393	0	0	0	0.224	0.226	0.024	0
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		A1	0	0	0.500	0.750	0.158	0	0.030	0.710	0.714	0.026
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		A2	0	0	0	0.229	0.711	0	0	0	0.238	0.895
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$4 \times$	S	0.068	0	0	0.230	1.531	0.088	0	0	0.256	0
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		Ss	0.370	0.691	0.036	0.033	0	0.283	0.642	0.065	0	0
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		J	0	0.235	0.393	0.033	0	0	0.224	0.226	0.023	0
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		A1	0	0	0.500	0.574	0.250	0	0.030	0.710	0.419	0.097
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		A2	0	0	0	0.148	0.689	0	0	0	0.488	0.903
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$1 \times$ browse	S	0.068	0.289	0	0.110	0	0.088	0	0	0	0.250
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		Ss	0.370	0.289	0	0	0	0.283	0.500	0.375	0.056	0
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		J	0	0.105	0.188	0.012	0	0.000	0.147	0.063	0.056	0.031
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		A1	0	0	0.688	0.614	0.200	0	0	0.563	0.611	0.063
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		A2	0	0	0	0.265	0.667	0	0 .	0	0.250	0.875
Ss         0.370         0.519         0         0.049         0         0.283         0.742         0.357         0.350         0           J         0         0.111         0.235         0.082         0.100         0         0.097         0.143         0.125         0           A1         0         0.074         0.412         0.459         0.150         0         0         0.071         0.325         0.091           A2         0         0         0.142         0.459         0.150         0         0         0.071         0.100         0.811	$2 \times$ browse	S	0.068	0	0	0.082	4.700	0.088	0	0	0.500	3.870
J         0         0.111         0.235         0.082         0.100         0         0.097         0.143         0.125         0           A1         0         0.074         0.412         0.459         0.150         0         0         0.357         0.325         0.09           A2         0         0         0         0.148         0.650         0         0         0.071         0.100         0.81		Ss	0.370	0.519	0	0.049	0	0.283	0.742	0.357	0.350	0
A1 0 0.074 0.412 0.459 0.150 0 0 0.357 0.325 0.09 A2 0 0 0 0.148 0.650 0 0 0.071 0.100 0.81		J	0	0.111	0.235	0.082	0.100	0	0.097	0.143	0.125	0
		A1	0	0.074	0.412	0.459	0.150	0	0	0.357	0.325	0.091
A2 0 0 0 0.148 0.050 0 0 0.071 0.100 0.81		A2	0	0	0	0.148	0.650	0	0	0.071	0.100	0.818

TABLE 4. Stage transition matrices for C. radicalis in each treatment in 1999–2000 and 2000–2001.

Note: Stages are as defined in Table 1; treatments are as defined in Table 3.

tions projected for most treatments, the transient dynamics followed by each treatment was still similar to that projected by  $\lambda$  (Fig. 6a). Changes in the number of adults in *C. radicalis* populations exposed to harvest and browse is of particular interest to palmilleros, since only adults produce harvestable leaves. Simulations based on transition matrices project that browsing (both  $1 \times$  and  $2 \times$  treatments) would have the most drastic impact on the number of adults over the next 25 years (Fig. 6b). The  $2 \times$  browse treatment had the largest

TABLE 5. Finite rate of increase ( $\lambda$ ) for each harvest and browse treatment for 1999–2000 and 2000–2001, and their 95% confidence limits.

	19	99–2000	2000-2001			
Treatment	λ	CI (95%)	λ	CI (95%)		
$\overline{0 \times (\text{control})}$	1.18	1.10, 1.25	1.18	1.11, 1.25		
1×	1.02	0.93, 1.08	1.03	0.94, 1.09		
$2 \times$	0.97	0.88, 1.05	0.98	0.90, 1.05		
4×m	0.94	0.87, 1.00	1.16	0.95, 1.26		
4×	0.99	0.89, 1.07	1.00	0.98, 1.02		
$1 \times$ browse	0.89	0.79, 0.98	0.96	0.90, 1.01		
$2 \times$ browse	0.95	0.80, 1.07	0.96	0.84, 1.09		

decline, a 60.5% reduction number of adults in the first five years.

# DISCUSSION

# Demography

Chamaedorea radicalis demography was characterized by both low mortality and low reproductive activity. Mortality averaged  $\sim 9\%$  per year in the control plots for seedlings and decreased for later life history stages; over the two years of this study, no large adults in the control treatment died. Low mortality rates for large or reproductive individuals are typical for longlived understory/subcanopy palms (Piñero et al. 1984, Oyama and Mendoza 1990, Pinard 1993, Olmsted and Alvarez-Bullya 1995, Zuidema 2000). Additionally, only a fraction of adults flowered, and fewer produced fruit. The majority of fruit production was restricted to a few individuals (10 individuals produced  $\sim$ 55% of fruit). A similar pattern was reported for Chamaedorea alternans (Otero-Arnaiz and Oyama 2001). The demography of these rare individuals that produce a large proportion of the population's seeds requires further examination. While elasticity analyses indicated that  $\lambda$ 

browse treatments.

					meannent							
Year and stage	Observed distribution	0× (control) (%)	1× (%)	2× (%)	2× (%) 4×m (%)		1× browse (%)	2× browse (%)				
1999-2000												
Seed Seedling Juvenile Small adult Large adult A	29.0 21.3 9.9 26.9 12.8	39.4 30.6 10.0 13.9 6.1 39.5	17.7 22.9 11.0 29.4 19.0 22.6	12.4 20.5 12.1 45.2 9.9 40.6	3.2 5.2 2.2 44.3 45.1 99.4	22.7 31.4 13.4 22.0 10.5 27.1	5.5 3.4 2.1 41.0 48.1 98.7	37.6 33.9 7.8 13.8 6.8 42.4				
2000-2001												
Seed Seedling Juvenile Small adult Large adult A	29.0 21.3 9.9 26.9 12.8	45.6 24.4 6.1 9.4 14.5 42.8	23.7 18.7 6.0 10.4 41.2 56.8	14.0 12.4 3.7 20.4 49.5 73.4	44.6 25.5 6.4 12.4 11.0 39.6	4.1 3.6 1.5 14.7 76.1 126.6	14.0 14.8 5.2 17.0 49.0 72.4	29.3 53.1 6.9 4.6 6.1 64.1				

*Note:* The observed population structure comes from data collected along belt transects (N = 922).  $\Delta$  is Keyfitz's index of dissimilarity.

was relatively insensitive to changes in fecundity, a large change in fruit production by this subset of large adults would likely have a pronounced effect of population dynamics.

*Euterpe precatoria* (Zuidema 2000) to  $\lambda = 1.258$  for Euterpe edulis (Silva Matos et al. 1999), and suggests the study years were benign for this species.

# Effects of browsing

Despite the low proportion of palms producing fruit, the control treatment was projected to increase  $\sim 18\%$ per year. This estimate is on the high end of population growth rates reported for palms, for which estimates of undisturbed populations range from  $\lambda = 0.979$  for



FIG. 5. Elasticities summed across stage classes showing the relative importance of stasis, growth, regression, and fecundity to  $\lambda$ , in the harvest and browse treatments, based on 2000–2001 matrices. See Figs. 2 and 3 legends for treatment descriptions.

Results from our browse experiment showed that burro browse significantly reduced the population growth rate of C. radicalis, even after a single browse episode. The low growth rates of browsed populations were the result of high mortality rates of seedlings, juveniles, and small adults. Additionally, some palms regressed to smaller size classes in response to browsing.

The effect of browsing on fruit production is less clear. Browsing reduced fruit production in the  $1 \times$ browse, while the  $2 \times$  browse treatment had one of the largest fecundity estimates in the study. Fruit production in the  $2 \times$  browse treatment may have been unusually high because the plots contained five large females that were responsible for 100% of seed production; these individuals were located on rock outcrops and thus inaccessible to the burro. This suggests that topographic factors have the potential to greatly influence the severity of browse events on C. radicalis populations. Populations found in rugged areas, such as those found on mid- and upper slopes of mountains, may be completely inaccessible to livestock, while populations in valleys and lower slopes may be browsed frequently. In areas easily accessible to livestock, palms located on rock outcrops escape browsing. Thus, the impact of browsing across the landscape may range from local extirpation to no impact at all, depending on topography.

These results support the hypothesis that livestock browsing is the cause of reduced palm abundances and unique population structures of C. radicalis on lower

		1999–2000					2000-2001				
Treatment	Stage	S	Ss	J	A1	A2	S	Ss	J	A1	A2
$\overline{0 \times (\text{control})}$	S	0.005	0	0	0.018	0.066	0.007	0	0	0.002	0.081
	Ss	0.084	0.121	0.002	0	0	0.083	0.102	0.003	0	0
	J	0	0.086	0.047	0.008	0	0	0.073	0.018	0.001	0.003
	A1	0	0	0.091	0.183	0.025	0	0.013	0.075	0.081	0.025
	A2	0	0	0	0.091	0.174	0	0	0	0.110	0.322
$1 \times$	S	0.004	0	0	0.033	0.020	0.004	0	0	0	0.044
	Ss	0.053	0.128	0.003	0.004	0	0.044	0.078	0.003	0.001	0
	J	0	0.060	0.048	0.017	0	0	0.042	0.014	0.007	0
	A1	0	0	0.074	0.280	0.046	0	0.006	0.046	0.051	0.013
	A2	0	0	0	0.066	0.166	0	0	0	0.056	0.593
$2 \times$	S	0.003	0	0	0	0.037	0.004	0	0	0.044	0
	Ss	0.037	0.114	0.004	0.006	0	0.044	0.088	0.003	0	0
	J	0	0.046	0.046	0.021	0	0	0.041	0.012	0	0
	A1	0	0	0.064	0.370	0.030	0	0.005	0.038	0.163	0.087
	A2	0	0	0	0.067	0.155	0	0	0	0.087	0.385
$4 \times m$	S	0.001	0	0	0.014	0	0.008	0	0	0.047	0.053
4×m	Ss	0.014	0.043	0.001	0	0	0.099	0.129	0.003	0.002	0
	J	0	0.015	0.011	0	0	0	0.090	0.023	0.005	0
	A1	0	0	0.014	0.422	0.090	0	0.015	0.091	0.178	0.006
	A2	0	0	0	0.090	0.285	0	0	0	0.059	0.194
$4 \times$	S	0.005	0	0	0.016	0.052	0.001	0	0	0.008	0
	Ss	0.068	0.175	0.004	0.006	0	0.008	0.016	0.001	0	0
	J	0	0.078	0.055	0.008	0	0	0.008	0.003	0.003	0
	A1	0	0	0.081	0.153	0.032	0	0.001	0.011	0.063	0.076
	A2	0	0	0	0.083	0.185	0	0	0	0.076	0.724
$1 \times$ browse	S	0.001	0	0	0.016	0	0.001	0	0	0	0.011
	Ss	0.016	0.008	0	0	0	0.011	0.021	0.006	0.003	0
	J	0	0.012	0.005	0.006	0	0	0.020	0.003	0.009	0.014
	A1	0	0.004	0.018	0.316	0.121	0	0	0.036	0.129	0.038
	A2	0	0	0	0.121	0.356	0	0	0	0.063	0.635
$2 \times$ browse	S	0.007	0	0	0.003	0.085	0.006	0	0	0.005	0.052
	Ss	0.088	0.111	0	0.004	0	0.057	0.271	0.017	0.011	0
	J	0	0.043	0.021	0.013	0.008	0	0.085	0.016	0.010	0
	A1	0	0.050	0.064	0.125	0.020	0	0	0.046	0.028	0.010
	A2	0	0	0	0.113	0.246	0	0	0.032	0.030	0.325

TABLE 7. Elasticity matrices for all treatments in 1999-2000 and 2000-2001.

Note: Stages are as defined in Table 1; treatments are as defined in Table 3.

slopes and valleys. Of the large adults encountered in valley/lower slopes along our belt transects, 90% were in areas we considered inaccessible to livestock, either because they were found on rock outcrops or were surrounded by rugged topography that prohibited livestock access. These protected palms may then act as seed sources in valley/lower slope areas, resulting in seedling recruitment. This situation would likely result in a population with large proportions of seedlings and large adults, and such overrepresentation of these size classes was found in the stable stage distributions of browsed C. radicalis populations. Alternatively, low densities in lower slopes and valleys may be the result of reduced palm establishment or survival due to unfavorable environmental conditions such as low light levels or large accumulations of leaf litter that bury seedlings (e.g., Molofsky and Augspurger 1992, Svenning 2001*a*, *b*).

The impact of livestock browsing on *C. radicalis* demography highlights the importance of examining factors beyond human extraction when assessing the population dynamics of non-timber forest products (NTFP). While ecologists recognize that many biological, environmental, and historical variables influence

a species distribution, abundance, and population dynamics, most NTFP-related studies focus only on the impact of human extraction, without exploring alternative factors that may explain observed trends in NTFP distribution or population dynamics, such as livestock browsing. By examining additional factors when studying NTFPs, ecologists may gain a better understanding of the relative contribution of these factors in influencing patterns of abundance and their population dynamics.

# Effects of leaf harvest

Leaf harvest significantly reduced  $\lambda s$  for both years of the study with one exception (4×m treatment in 2000–2001). Increased mortality appears to be the primary factor that contributed to reduced population growth rates. Although the differences in mortality were sometimes modest, elasticity analyses indicated that survival and stasis of small and large adults have a relatively large effect on  $\lambda$ . In addition, harvested populations had reduced fecundity. As in other palm defoliation studies, leaf harvest reduced inflorescence production and/or the number of females producing fruit (Ratsirarson et al. 1996, Flores and Ashton 2000).



FIG. 6. (a) Projected transient dynamics of *C. radicalis* populations (excluding the seed stage) under different harvest and browse regimes, based on 2000–2001 matrices. The initial population structure estimate (N = 922) came from belt transects (Table 3); (b) Projected changes in the number of adults (small and large) between control, harvest, and browse treatments based on the 2000–2001 transition matrices and population structure from belt transects (N = 516 adults). See Figs. 2 and 3 legends for treatment descriptions.

However, in 2000–2001, the  $4 \times m$  treatment had similar fecundity estimates as the control and similar population growth rates, suggesting that avoidance of complete defoliation minimizes detrimental impacts on flowering females.

Despite the wide range of harvest frequencies used in the experiment, few differences were seen in their effects on palm demography and population dynamics. This was due to the fact the annual per capita leaf production rates were quite low (1.71-2.18 leaves/year) and thus multiple visits to a site to harvest leaves only resulted in modest increases in leaf yield (Endress et al. 2004). Therefore the actual number of leaves removed per palm was quite similar among the 1×, 2×, and 4×m treatments, ranging from 1.06 to 1.25 leaves/year in 1999–2000 (Endress et al. 2004). The 4× treatment averaged considerably more leaves harvested per palm that year (1.59) and, as a result, had twice the mortality rate of the other harvest treatments.

We expected that in the second year of the study, mortality rates in the harvest treatments would increase, as palms were subjected to harvest over a longer period of time. This did not occur, and in fact, mortality rates decreased in 2000–2001 in the 2× and 4× treatments. This appears to be a result of a reduction in the number of leaves harvested in 2000-2001 because C. radicalis responded to harvest by producing leaves <40 cm in length, which are not marketable, and were therefore not harvested. During 1999-2000, leaf harvest rates ranged from 1.06 to 1.59 leaves/palm while the following year rates were much lower, ranging from 0.55 leaves/palm ( $1 \times$  treatment) to 0.71 leaves/palm  $(4 \times m \text{ treatment}; \text{ Endress et al. 2004})$ . This response to leaf harvest may be critical to the maintenance of harvested C. radicalis populations, as intensely harvested palms are removed from the harvest pool (by not producing marketable leaves), and thus are allowed a respite from harvesting. However, the economic implication of this response is troubling to palmilleros as leaf harvest quickly reduced the number of marketable leaves produced per year, resulting in decreased yields (Endress et al. 2004).

Despite lower population growth rates in harvested populations,  $\lambda s$  did not significantly differ from 1, the standard threshold many researchers have used to determine ecological sustainability of non-timber forest product extraction (Peters 1990, Pinard and Putz 1992, Bernal 1998, Zuidema 2000, Svenning and Macía 2002). However, all of the 95% confidence intervals for our estimates of  $\lambda$  ranged from below to above 1, suggesting that leaf harvest may result in declining C. radicalis populations. Our results should be treated with caution as our models were based on only two years of demographic data, and species can exhibit considerable spatiotemporal variation in their demography in response to a variety of biological and environmental factors (Horvitz and Schemske 1995, Caswell 2001). It is possible that the two years of our study were benign for C. radicalis. In addition, the models developed in this study were deterministic, and did not incorporate density dependence or environmental stochasticity. Additional years of data would provide a better understanding of the effects of leaf harvest on population dynamics, and this study highlights to need for longer term studies on the effects of NTFP extraction on population dynamics.

Our approach of simulating actual harvest practices rather than using traditional experimental defoliation treatments highlighted the dynamics between the intensity of harvest and the future production of marketable leaves, a critical factor influencing the effect of harvest on *C. radicalis* population dynamics. This feedback between palms and harvesters resulted in temporal differences in harvesting intensity, with some years many leaves being harvested, while in others very few. In most other defoliation studies, this interaction has not been recognized, because the experimental defoliations were based on the proportion of leaves removed per palm and were constant through time (Ratsirarson et al. 1996, O'Brien and Kinnaird 1996; N. P. R. Anten, M. Martinez-Ramos, and D. D. Ackerly, unpublished manuscript). While this approach is useful for documenting an individual's response to a particular level of harvesting, extrapolating population level effects of harvest from these studies may be inappropriate, because the treatments selected in the studies may be different from the decisions harvesters make when selecting leaves, i.e., harvest varies in both space and time depending on the availability of desirable leaves. Leaf harvesters are likely selective when collecting leaves, particularly when they are to be used for weaving, basketry, thatch, or commercial use, and the interaction between harvest and the production of useful leaves can have a profound impact on short and longterm population dynamics of NTFPs. Despite the importance of integrating local harvest strategies with ecological experiments to understand the impact of NTFP extraction on population dynamics, only a handful of studies have taken this approach (Joyal 1996, Velásquez Runk 1998, Svenning and Macía 2002, Ticktin et al. 2002).

Our approach to evaluating the effects of different harvest frequencies differs from that of Zuidema (2000). Zuidema (2000) modeled defoliation of an understory palm every 4, 8, or 16 years by multiplying by the appropriate sequence of matrices parameterized from defoliation, recovery, and undisturbed years. That approach is appropriate for supra-annual harvests, but not for harvests that are more frequent than the recovery time of individual palms.

Results from defoliation studies, including this one, suggest that leaf harvest generally has a greater impact on NTFP populations than seed or fruit harvest, but less of an impact than extraction that kills individuals, such has stem or palm-heart extraction (Peters 1991, Olmstead and Alvarez Bullya 1995, Bernal 1998, Zuidema 2000, Soehartono and Newton 2001, Ticktin 2004). Moreover, within a given species, the tolerance to harvest is mediated by human management practices in space and time. Incorporating human management practices into experimental studies of NTFP extraction will provide better insights on the effects of harvest on population dynamics and result in a greater applicability of research studies in addressing conservation or resource management issues.

### ACKNOWLEDGMENTS

This research was funded by the Department of Botany, Miami University and the Garden Club of Ohio. A. Townsend, T. Crist, E. Jurado, A. Greenberg, M. Vincent, A. Huerta, and two anonymous reviewers provided helpful comments on earlier versions of this manuscript. We thank Alta Cima and San José for their generous help and hospitality. We thank Eduardo Padrón Serrano, the Gonzáles family, and La Fe for their field assistance and logistical support. We also thank SEDUE of Tamaulipas and the Instituto de Ecología y Alimentos, Tamaulipas, especially L. Trejo-Hernández and C. González-Romo.

#### LITERATURE CITED

- Anten, N. P. R., and D. D. Ackerly. 2001. Canopy-level photosynthetic compensation after defoliation in a tropical understory palm. Functional Ecology 15:252–262.
- Bernal, R. 1998. Demography of the vegetable ivory palm *Phytelephas seemannii* in Columbia, and the impact of seed harvesting. Journal of Applied Ecology **35**:64–74.
- Berry, E. J., and D. L. Gorchov. 2004. Reproductive biology of the dioecious understory palm, *Chamaedorea radicalis* (Arecaceae) in a Mexican cloud forest: pollination vector, flowering phenology, and female fecundity. Journal of Tropical Ecology 20:1–8.
- Boot, R. G. A., and R. E. Gullison. 1995. Approaches to developing sustainable extraction systems for tropical forest products. Ecological Applications **5**:896–903.
- Caswell, H. 2001. Population matrix models. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Clark, D. A., D. B. Clark, R. M. Sandoval, and M. V. C. Castro. 1995. Edaphic and human effects on landscapescale distribution of tropical rain forest palms. Ecology 76: 2581–2594.
- Davis, S. D., V. H. Heywood, O. Herra-MacBryde, J. Villa-Lobos, and A. C. Hamilton. 1997. Centers of plant diversity: a guide and strategy for their conservation. Volume 3. The Americas. World Wildlife Fund and IUCN (World Conservation Union), Cambridge, UK.
- Endress, B. A. 2002. Population dynamics, conservation, and management of the palm, *Chamaedorea radicalis* Mart. in the El Cielo Biosphere Reserve, Tamaulipas, Mexico. Dissertation. Miami University, Oxford, Ohio, USA.
- Endress, B. A., D. L. Gorchov, M. B. Peterson, and E. P. Serrano. 2004. Harvest of the palm *Chamaedorea radicalis*, its effects on leaf production, and implications for sustainable management. Conservation Biology **18**:1–9.
- FAO (Food and Agriculture Organization of the United Nations). 1997. Non-wood forest products. 10: tropical palms. Food and Agriculture Organization of the United Nations, Bangkok, Thailand.
- Flores, C. F., and P. M. S. Ashton. 2000. Harvesting impact and economic value of *Geonoma deversa*, Arecaceae, an understory palm used for roof thatching in the Peruvian Amazon. Economic Botany 54:267–277.
- Hodel, D. R. 1992. *Chamaedorea* palms. International Palm Society, Lawrence, Kansas, USA.
- Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs 65:155–192.
- Jones, F. A., and D. L. Gorchov. 2000. Patterns of abundance and human use of the vulnerable understory palm, *Chamaedorea radicalis* (Arecaceae), in a montane cloud forest, Tamaulipas, Mexico. Southwestern Naturalist 45:421–430.
- Joyal, E. 1996. The palm has its time: an ethnoecology of *Sabal uresana* in Sonora, Mexico. Economic Botany **50**: 446–462.
- McPeek, M. A., and S. Kalisz. 1993. Population sampling and bootstrapping in complex designs: demographic analysis. Pages 232–252 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- Molofsky, J., and C. K. Augspurger. 1992. The effect of leaf litter on early seed establishment in a tropical forest. Ecology **73**:68–77.
- Mora-Olivo, A., J. L. Mora Lopez, J. P. Jiménez Pérez, and J. S. Silva. 1997. Vegetación y flora asociada a la palmilla (*Chamaedorea radicalis*) en la Reserva de la Biosfera "El Cielo." Biotam 8:1–10.
- O'Brien, T. G., and M. F. Kinnaird. 1996. Effect of harvest on leaf development of the Asian palm *Livistona rotundifolia*. Conservation Biology **10**:53–58.

1152

- Olmsted, I., and E. R. Alvarez-Bullya. 1995. Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. Ecological Applications **5**: 484–500.
- Otero-Arnaiz, A., and K. Oyama. 2001. Reproductive phenology, seed-set and pollination in *Chamaedorea alternans*, an understory dioecious palm in the rain forest in Mexico. Journal of Tropical Ecology **17**:745–754.
- Oyama, K., and A. Mendoza. 1990. Effects of defoliation on growth, reproduction, and survival of a Neotropical dioecious palm, *Chamaedorea tepejilote*. Biotropica 22:86–93.
- Panayotou, T., and P. S. Ashton. 1992. Not by timber alone: economics and ecology for sustaining tropical forests. Island Press, Washington, D.C., USA.
- Peters, C. M. 1990. Population ecology and management of forest fruit trees in Peruvian Amazon. Pages 86–98 in A. Anderson, editor. Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest. Columbia University Press, New York, New York, USA.
- Peters, C. M. 1991. Plant demography and management of tropical forest resources: a case study of *Brosimum alicastrum* in Mexico. Pages 265–272 *in* A. Gomez-Pompa, T. C. Whitmore, and M. Hadley, editors. Rainforest regeneration and management. UNESCO (United National Educational Scientific and Cultural Organization), Paris, France.
- Peterson, M. B. 2001. Resource use and livelihood strategies of two communities in the El Cielo Biosphere Reserve, Tamaulipas, Mexico. Thesis. Miami University, Oxford, Ohio, USA.
- Pinard, M. 1993. Impacts of stem harvesting on populations of *Iriartea deltoidea* (Palmae) in an extractive reserve in Acre, Brazil. Biotropica **25**:2–14.
- Pinard, M. A., and F. E. Putz. 1992. Population matrix models and palm resource management. Bulletin de Institut Francais Etudes Andines 21:637–649.
- Piñero, D., M. Martinez-Ramos, and J. Sarukhán. 1984. A population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. Journal of Ecology **72**:977–991.
- Plotkin, M., and L. Famolare, editors. 1992. Sustainable harvest and marketing of rain forest products. Island Press, Washington, D.C., USA.
- Ratsirarson, J., J. A. Silander, and A. F. Richard. 1996. Conservation and management of a threatened Madagascar palm species, *Neodypsis decaryi*, Jumelle. Conservation Biology 10:40-52.
- Reining, C. C. S., R. M. Heinzman, M. C. Madrid, S. López, and A. Solórzano. 1992. Non-timber forest products of the

Maya Biosphere Reserve, Peten, Guatemala. Conservation International, Washington, D.C., USA.

- Rojas Agil, M., E. Jurado, G. Sánchez-Ramos, L. Trejo-Hernández, and F. L. Ríos. 2000. Rapid viability loss in seeds of palmilla (*Chamaedorea radicalis* Mart.) from El Cielo Biosphere Reserve. Southwestern Naturalist 45:373–375.
- Salafsky, N., B. L. Dugelby, and J. W. Terborgh. 1993. Can extractive reserves save the rain forest? An ecological and socioeconomic comparison of nontimber forest product extraction systems in Péten, Guatemala, and West Kalimantan, Indonesia. Conservation Biology 7:39–52.
- SAS Institute. 2000. SAS. Version 8.1. SAS, Cary, North Carolina, USA.
- Silva Matos, D. M., R. P. Freckleton, and A. R. Watkinson. 1999. The role of density dependence in the population dynamics of a tropical palm. Ecology 80:2635–2650.
- Soehartono, T., and A. C. Newton. 2001. Conservation and sustainable use of tropical trees in the genus Aquilaria II. The impact of gaharu harvesting in Indonesia. Biological Conservation 97:29-41.
- Svenning, J. C. 2001a. Environmental heterogeneity, recruitment limitation and the mesoscale distribution of palms in a tropical montane rain forest (Maquipucuna, Ecuador). Journal of Tropical Ecology 17:97–113.
- Svenning, J. C. 2001b. On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). Botanical Review 67:1–53.
- Svenning, J. C., and M. J. Macía. 2002. Harvesting Geonoma macrostachys Mart. leaves for thatch: an exploration of sustainability. Forest Ecology and Management 167:251– 262.
- Ticktin, T. 2004. The ecological consequences of NTFP harvest: a review. Journal of Applied Ecology **41**:11–21.
- Ticktin, T., and T. Johns. 2002. Chinateco management of *Aechmea magdalenae*: implications for the use of TEK and TRM in management plans. Economic Botany **56**:177–191.
- Ticktin, T., P. Nantel, F. Ramirez, and T. Johns. 2002. Effects of variation on harvest limits for nontimber forest species in Mexico. Conservation Biology **16**:691–705.
- Trejo, H. L. 1992. La palmilla (*Chamaedorea* spp.) un recurso forestal no maderable en la Reserva de la Biosphera "El Cielo". La Revista de la Universidad Autonoma de Tamaulipas 21:53–55.
- Velásquez Runk, J. 1998. Productivity and sustainability of a vegetable ivory palm (*Phytelephas aequatoralis*, Arecacaeae) under three management regimes in northwestern Ecuador. Economic Botany **52**:168–182.
- Zuidema, P. A. 2000. Demography of exploited tree species in the Bolivian Amazon. PROMAB (Programa Manejo de Bosques de la Amazonía Boliviana), Beni, Bolivia.