

RAPID ASSESSMENT OF SUSTAINABLE HARVESTING OF LEAVES FROM THE UNDERSTORY PALM, *CHAMAEDOREA RADICALIS*

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ABSTRACT—We explored a rapid-assessment protocol for *Chamaedorea radicalis*, an understory palm from which leaves are harvested for use in the cut-greens industry. We developed a multiple-regression model relating the finite rate of population growth to vegetative and reproductive variables from a 4-year demographic study across leaf-harvesting treatments in Reserva de la Biosfera El Cielo, Tamaulipas, Mexico. The resulting model, including total fecundity of adults and mean number of leaflets, was applied to 21 populations of *C. radicalis* using measurements collected from a single season. Predicted estimates of population-growth rate were 0.94–1.27, but 20 of the 21 populations had predictions bracketing the net-replacement rate = 1 for population growth. We then implemented a fixed-design, life-table-response experiment to explore whether measurements of annual transition probabilities provided a superior assessment; however, addition of transition probabilities only marginally increased predictive power of the model. Therefore, implementation of this protocol is limited by imprecision of estimates of population-growth rate.

RESUMEN—Hemos explorado un método de evaluación rápida para *Chamaedorea radicalis*, una palma del sotobosque en el que las hojas se cosechan para su uso en la industria de follaje verde. Hemos desarrollado un modelo de regresión múltiple que relaciona la tasa finita de crecimiento de las poblaciones a las variables vegetativas y reproductivas de un estudio demográfico de 4 años a través de tratamientos de cosecha de hojas en la Reserva de la Biosfera El Cielo, México. El modelo resultante, incluyendo la fecundidad total de adultos y el número medio de foliolos, se aplicó a 21 poblaciones de *C. radicalis* utilizando medidas tomadas en una sola temporada. Las estimaciones previstas de la tasa de crecimiento de las poblaciones varió desde 0.94 hasta 1.27, pero en 20 de las 21 poblaciones hubo intervalos de predicción incluyendo la tasa de sustitución neta = 1 de la tasa de crecimiento de las poblaciones. Por consiguiente implementamos un experimento de respuesta de tablas de vida de diseño-fijo para explorar si las medidas de las tasas anuales de transición proporcionan una evaluación superior; sin embargo, la adición de las tasas de transición sólo ligeramente aumentó la capacidad predictiva del modelo. Por lo tanto, la aplicación de este método es limitada por la imprecisión de las estimaciones de la tasa de crecimiento de las poblaciones.

In regions of high biodiversity and conservation value, local resources necessary for conservation often are limited. In an attempt to reconcile conservation of biological resources with their use in sustainable development initiatives, numerous integrated conservation and development projects have emerged (Kremen et al., 1994). These initiatives are based on the premise that if a sufficient economic value can be assigned to forestry resources, then the resulting financial incentive will serve to conserve resources and enable users to profit (Belcher et al., 2005). One such initiative is the sustainable use of non-timber forest products, defined as all biological products extracted from a forest, with the exception of timber (Belcher, 2003). The growing body of literature on non-timber forest products has emphasized their poten-

tial role in rural development through generation of significant economic returns and as a potentially viable alternative to more destructive uses of land (Nepstad and Schwartzman, 1992; Panayotou and Ashton, 1992; Plotkin and Famalore, 1992; Putz et al., 2001). About 4,000–6,000 species of non-timber forest products are used commercially (Iqbal, 1993; Secretariat of the Convention on Biological Diversity, 2001). In addition to worldwide use, sustainable management also is desirable because of reliance on these resources by rural-dwelling, impoverished people (Vedeld et al., 2004).

Successful implementation of programs to extract non-timber products from forests requires a thorough understanding of population ecology of the target species, and that implementation is situated firmly within

the appropriate socio-economic context. Absence of this critical information can result in threats to extractive programs and degradation of important resources (Vasquez and Gentry, 1989; Pandit and Thapa, 2003; Peres et al., 2003). While more research is needed on ecological impacts of harvesting on populations and communities of plants (Ticktin, 2004), addressing socio-economic pressures that might lead to over-exploitation of these resources is even more challenging (Arnold and Pérez, 2001; Wadt et al., 2008). Economic valuation of non-timber forest products is plagued with uncertainties (Peters et al., 1989; Godoy et al., 1993; Bennett, 2002), but, typically, local harvesters receive low prices for their products and are, thus, prone to engage in over-harvesting of resources (Browder, 1992). Ecological certification has been proposed as a mechanism that differentiates products based on method of production and increases the market price for non-timber forest products produced according to certain ecological and social standards (Kiker and Putz, 1997; Shanley et al., 2002). Such an initiative is being pursued for certification of leaves of palms of the genus *Chamaedorea* in Mexico and Central America (Committee for Environmental Cooperation of North America, <http://www.cec.org/Page.asp?PageID=122&ContentID=2128&SiteNodeID=358>).

Commercial trade in leaves of *Chamaedorea* is 14% of the floral cut-greens industry in the United States, as well as a considerable portion of material used for Palm Sunday in Christian congregations (Committee for Environmental Cooperation of North America, <http://www.cec.org/Page.asp?PageID=122&ContentID=2128&SiteNodeID=358>). One species, *C. radicalis*, is endemic to northeastern Mexico and harvesting its leaves is the principal source of income for many people in that region (Peterson, 2001). Local harvesters have expressed concern over reduced yield of leaves and declining abundance of *C. radicalis*, and have attributed this reduction to over-harvesting (Endress et al., 2004b). Implementation of a certification program could enhance sustainability of harvesting by providing a higher and more equitable price for leaves harvested in a sustainable manner. One of the first steps, however, in successful certification is establishment of ecological criteria to judge sustainability of harvesting. With goals of exploring utility of a rapid-assessment protocol to identify sustainable harvesting of leaves from *C. radicalis* and to facilitate the certification initiative, our objectives were to develop and assess validity of a set of ecological criteria for judging sustainability of harvesting leaves from *C. radicalis*, and to use this protocol to assess the current state of harvesting leaves from *C. radicalis* in Reserva de la Biosfera El Cielo.

A comprehensive approach to evaluating sustainability is establishment of long-term demographic research assessing ecological impacts of harvesting on the population (Peters, 1996). Under this assessment protocol, the classical determinant of sustainability is the finite rate of

population growth derived from matrix models, with a finite rate of population growth >1 considered sustainable (Hall and Bawa, 1993). Existence of long-term demographic studies, such as those for *C. radicalis* (Endress et al., 2004a, 2004b, 2006), may permit formulation of rapid-assessment-of-sustainable-harvest protocols that can be used to accurately assess sustainability of harvesting within a short timeframe (M. Martínez-Ramos, in litt.). First, we explored development of a rapid-assessment-of-sustainable-harvest protocol by establishing a direct predictive relationship between finite rate of population growth and important ecological correlates of harvesting, using data from the long-term demographic study. This model was used to assess current state of harvesting leaves within populations we sampled in Reserva de la Biosfera El Cielo. Second, we explored whether estimates of annual transition probabilities improved assessments of sustainability. To accomplish this, we used a life-table-response experiment, a retrospective analysis that decomposes differences in finite rate of population growth into individual contributions from demographic parameters (Horvitz et al., 1997; Caswell, 2001). Results of the life-table-response experiment were used to identify which annual transition probabilities constituted the largest contribution to differences in finite rate of population growth across treatments. We then assessed utility of these probabilities in predicting finite rate of population growth in conjunction with the rapid-assessment-of-sustainable-harvest model.

MATERIALS AND METHODS—Our study was conducted in Reserva de la Biosfera El Cielo, Tamaulipas, Mexico, a 144,530-ha site that straddles the Sierra de Guatemala Mountains (22°55'–23°30'N, 99°02'–99°30'W). Reserva de la Biosfera El Cielo has rugged karst topography, with ca. 98% of the region having slopes $>20\%$ (Artigas and Rodríguez, 2005). Populations of *C. radicalis* were sampled near four communities: Gómez-Farías (200 m elevation), Alta Cima (950 m), San José (1,300 m), and La Gloria (1,600 m). Average annual rainfall and temperatures in the region ranged from 1,800 mm and 22.8°C in Gómez-Farías to 2,500 mm and 13.8°C at Rancho del Cielo (1,100 m; Davis et al., 1997).

Chamaedorea radicalis is a long-lived, dioecious understory palm, endemic to northeastern Mexico (Hodel, 1992). Within Reserva de la Biosfera El Cielo, *C. radicalis* occurs in a diversity of habitats and elevations, ranging from semi-deciduous tropical forest at ca. 200 m elevation to pine-oak forest at $>1,400$ m elevation (Mora-Olivo et al., 1997). The life cycle has been divided into five stages: seeds, seedlings (bifid leaves), juveniles (3–9 leaflets on the youngest, fully expanded leaf; non-reproductive), small adults (10–24 leaflets on the youngest, fully expanded leaf; rarely produces reproductive structures), and large adults (≥ 25 leaflets on the youngest, fully expanded leaf; reproductive; Endress et al., 2004a). Marketable leaves are only on adult palms and must be without insect or fungal damage and >40 cm in length (Endress et al., 2004b). *Chamaedorea radicalis* responds to frequent harvesting in a number of ways, including stunted development of leaves and reduced fruit-set (Endress et al., 2004a). Additionally, demo-

graphic projections predict continued harvesting will shift the stable-stage distribution toward more adults and fewer seedlings (Endress et al., 2004a).

We identified and sampled spatially distinct populations in forests surrounding each of four communities during May–July 2006 ($n = 21$; Gómez-Farías, $n = 4$; Alta Cima, $n = 8$; San José, $n = 5$; La Gloria $n = 4$). Through conversations with local harvesters, an attempt was made to sample along a gradient of intensity of harvesting and to locate unharvested populations. The history of extraction of leaves in Reserva de la Biosfera El Cielo and relative proximity to communities suggests that unharvested populations likely experienced harvesting in the past; however, there was no indication of recent harvesting. In total, three unharvested populations were located and intensity of harvesting was quantified independently at each site.

Each population was sampled using five 2 by 50-m, parallel belt transects spaced according to relative area of the population and topography (5–25 m apart). A target of 100 individuals/population was set and additional transects were established as needed. Due to topographical constraints, total area sampled for each population was 430–798 m². For each palm, we recorded number and length of all leaves, number of leaflets on each leaf, presence of male-female inflorescences, number of fruits, and number of cut leaves. Fruits were counted and categorized based on size and color: 1, immature (small and green); 2, mature and unripe (green and same size or slightly smaller than category 3); 3, mature and ripe (greenish-yellow to red). Fecundity was calculated as mean number of mature fruits for adult palms. Number of cut leaves was used as a measure of intensity of harvesting. A pilot study on longevity of cut leaves revealed that they remain on individuals for ≤ 1.5 years, and therefore, are informative with regard to recent harvesting activity. These measurements of individuals were used to calculate values for comparisons of populations. Mean values and proportions were calculated relative to total number of adult palms (small plus large adults) in each population.

Demographic methods for the 4-year study, including construction of matrix models and eigenanalysis, were described by Endress et al. (2006). In brief, plots were established in Alta Cima, in January 1999, and individual adult palms were marked and subjected to one of the following experimental treatments: control with no leaves removed; all marketable leaves removed once per year; all marketable leaves removed twice per year; all marketable leaves removed 4 times/year; and a modified 4 times/year treatment, where a maximum of 1 leaf/palm was removed each harvest and a minimum of two leaves were necessary for a leaf to be harvested (to prevent complete defoliation). Each palm was measured prior to initiation of treatments in May 1999 and at quarterly censuses. Germination of seeds and demography of seedlings and juveniles were assessed in nested subplots. Treatments and demographic censuses continued through May 2005, resulting in 4 years of demographic data across all treatments.

Demographic data from the 4 years were used to parameterize stage-structured, population-projection matrices as described by Caswell (2001). Matrix elements indicate the stage-specific probabilities of transition and fecundity. The first row of the matrix indicated stage-specific fecundity, or mean number of fruits produced per palm, while other elements of the matrix consist of the probability of surviving and remaining in a given stage, probability of survival and growth from one stage to a

larger stage, and probability of survival and regressing to a smaller stage. Transition matrices were constructed for each of the five treatments for the 4 years of demographic data ($n = 20$). Because harvesting was limited to adult stages of life history, matrix elements for seeds and smaller palms were equal across treatments as reported by Endress et al. (2004a). To evaluate population-level impacts of harvesting, eigenanalysis was employed to determine finite rate of population growth for each year and harvest-treatment combination.

For the first model of rapid assessment of sustainable harvesting, we computed all possible multiple-regression models to relate the finite rate of population growth to vegetative and reproductive variables from the 4-year study (4 years times five treatments resulted in $n = 20$). The response variable for the model was the estimate of finite rate of population growth from eigenanalysis of the transition matrix for each year and harvest-treatment combination. Predictor variables included mean number of leaflets on the youngest, fully expanded leaf, proportion of adults that were reproductive, and fecundity. These variables were selected because they showed sufficient overlap in their ranges between the sampled populations and long-term dataset, thus, minimizing extrapolation in output of the model (i.e., estimation of a new value outside the range of data employed for derivation of the model). We employed Akaike's Information Criteria (AIC) and the information-theoretic approach to assess multiple-regression models as described by Burnham and Anderson (2002) and selected the most-parsimonious predictive model of finite rate of population growth. To account for small samples, we used corrected AIC-values (AIC_c).

The resulting multiple-regression model was used to generate an estimate of finite rate of population growth for each population sampled in 2006. For each of the 21 populations, we entered the value for each predictor variable into the final regression model to generate an estimate of the finite rate of population growth. Given the uncertainty of estimates derived from regression models (Zar, 1999), we generated a 95% prediction interval for each estimate of finite rate of population growth as described by Gotelli and Ellison (2004). Prediction intervals are similar to confidence intervals, but bracket uncertainty around an estimate based on existing data (in this instance, the 4-year study) and the new data (in this instance, the sampled populations). Additionally, we related predicted estimates of finite rate of population growth to three direct measures of intensity of harvesting: proportion of palms with cut leaves, mean number of cut leaves on adult palms, and a ratio of cut:intact leaves on adult palms. Regression analysis was conducted using R version 2.11 (R Development Core Team, Vienna, Austria).

We used a fixed-design, life-table-response experiment, as described by Caswell (2001), to assess relative contributions of individual matrix elements across treatments and years to differences in finite rate of population growth in the 4-year study. Life-table-response-experiment analysis has been used for similar purposes in determining the influence of management regime on dynamics of populations of non-timber forest products (Martínez-Ballesté et al., 2005) and in an alternative approach to evaluating sustainability of harvesting (Zuidema et al., 2007). Using a factorial design described by Caswell (2001), we modeled finite rate of population growth as a linear function of the yearly transition interval, treatment, and an interaction

term to determine main effects, as well as individual contributions from parameters in the transition matrix. Because harvesting is limited to adults and because transitions between seedlings and juveniles were modeled as equivalent across treatments, we report only results of the life-table-response experiment associated with adults. Additionally, the primary objective of the life-table-response experiment was to assess the impact of year and treatment on differences in finite rate of population growth, so we report only effects of the main treatment (interactions are reported in Ash, 2007). Sensitivity analysis was conducted using MATLAB 7.1 (The MathWorks, Inc., Natick, Massachusetts).

We assessed whether prediction of finite rate of population growth by rapid assessment of sustainable harvesting would be improved by incorporating demographic rates; specifically, the annual transition probabilities that had the largest contribution to finite rate of population growth based on the life-table-response experiment. Transition probabilities with large contributions were included in the final rapid-assessment-of-sustainable-harvest regression model to determine if predictive power of the model was improved by these additional variables.

RESULTS—Populations displayed a wide range of means across all variables (Table 1). Of critical importance, the three unharvested populations exhibited evidence of minimal recent harvesting as determined by the low number of cut leaves. Total fecundity of adults was either zero or negligible among most populations with the pronounced exception of unharvested population 21 (4.0 fruits/adult). Flowering was more common than fruiting at the time of sampling, with nearly all populations containing flowering palms and unharvested populations containing the highest proportions. Mean number of leaflets on the youngest, fully expanded leaf was highest in two of the unharvested populations (4 and 21). Populations in Gómez-Farías exhibited higher than average values for most individual and population-level variables, including mean number of leaflets and length of leaves. These populations, however, also had the highest proportion of harvested palms (with the exception of the unharvested population), lowest densities, and lowest proportion of seedlings.

Multiple-regression analysis and selection of the AIC_c model revealed that the most-parsimonious model in explaining variation in finite rate of population growth was a univariate model of total fecundity of adults. However, given the number of zero values for this variable in sampled populations, we selected a bivariate model that included total fecundity of adults and mean number of leaflets on the youngest, fully expanded leaf (finite rate of population growth = $1.06 + 0.08 \times \text{total adult fecundity} - 0.003 \times \text{mean number of leaflets}$, $F_{2,17} = 17.10$, $P < 0.001$, $R^2 = 0.67$, $\Delta\text{AIC}_c = 2.95$). Each predictor variable exhibited a positive relationship with finite rate of population growth (Fig. 1).

When the resulting bivariate model was applied to data from the sampled populations, the predicted estimates of finite rate of population growth were 0.94–1.27 (Fig. 2);

however, 20 of the 21 populations had prediction intervals bracketing the net rate of replacement = 1. For the other population (unharvested population 21), the full prediction interval was >1 for finite rate of population growth, suggesting a population with positive long-term growth. The other two unharvested populations had estimates of finite rate of population growth <1, but prediction intervals that bracketed 1. The predicted estimates of finite rate of population growth showed a negative trend with each of the three measures of intensity of harvesting; however, these regressions were not significant and explained only a minimal amount of variation in finite rate of population growth (Fig. 3).

The life-table-response experiment revealed that differences in finite rate of population growth across years (Fig. 4) and treatments (Fig. 5) in the 4-year study primarily were attributed to differences in two demographic rates; annual growth from small to large adult and fecundity of large adults. Matrix elements corresponding to probability of surviving and remaining in a given stage and probability of survival and regressing to a smaller stage contributed only minimally to differences in finite rate of population growth for main effects of year and treatment. These matrix elements also exhibited more variability, with both positive and negative influences on finite rate of population growth.

Fecundity of large adults consistently made the largest contribution to differences in finite rate of population growth across years and treatments, while fecundity of small adults contributed minimally to differences in finite rate of population growth (Figs. 4 and 5). Contributions of fecundity always were negative, indicating that treatments and years had a negative effect on finite rate of population growth relative to the control.

The matrix element corresponding to growth from small to large adult also consistently had a substantial negative contribution to differences in finite rate of population growth, with the exception of the 2000–2001 census (Fig. 5). However, only in one treatment (4 times/year with a maximum of 1 leaf/palm removed each harvest) did relative contribution from the growth transition exceed the contribution of fecundity of large adults. The main effect of year often exceeded that of treatment, but treatment nonetheless constituted a substantial negative contribution. Because these two elements (annual transition probability of growth and fecundity of large adults) had the largest contributions to finite rate of population growth across the five treatments and 4 years, we explored whether their inclusion would improve the rapid-assessment-of-sustainable-harvest model. Because total fecundity of adults was already a variable in the model, the matrix element for fecundity of large adults would have been redundant and, therefore, was not added to the model. The univariate relationship between the annual transition probability of growth and finite rate of population growth was significant ($F_{1,18} = 4.79$, $P = 0.042$, $R^2 = 0.21$); however,

TABLE 1—Parameters measured for 21 populations of the understory palm *Chamaedorea radicalis* in Reserva de la Biosfera El Cielo, Tamaulipas, Mexico, summer 2006. Asterisks (*) indicate unharvested populations.

Site	Plot	Elevation (m)	Density (individuals/ha)	Average number of leaves	Average length of youngest, fully expanded leaf (cm)	Average number of leaflets on youngest, fully expanded leaf	Proportion of seedlings
Gómez-Farías	1	539	2,019	2.2	65.2	32.4	0.1
	2	349	1,533	2.5	56.8	29.0	0.1
	3	409	2,269	2.2	51.0	26.0	0.0
	4*	367	1,661	3.6	65.6	33.5	<0.1
Alta Cima	5	909	8,918	2.4	49.9	25.5	0.2
	6	1,120	4,339	2.3	51.4	25.4	0.2
	7	944	4,979	2.0	47.7	26.5	0.4
	8	947	3,596	2.5	57.0	29.4	0.5
	9	1,086	4,260	2.5	53.1	25.0	0.2
	10	1,069	3,280	2.2	53.6	27.9	0.4
	11	1,215	5,200	2.7	60.2	27.4	0.4
San José	12	939	4,718	2.4	52.6	24.4	0.4
	13	1,046	7,080	2.3	57.4	28.0	0.2
	14	1,287	5,587	2.1	50.7	26.9	0.2
	15	1,222	12,860	2.2	52.8	27.2	0.2
La Gloria	16*	1,374	4,660	2.8	60.7	25.5	0.1
	17	1,362	2,311	2.3	68.1	28.4	0.1
	18	1,178	6,880	2.3	54.2	27.4	0.3
	19	1,677	5,000	2.0	54.6	28.0	0.2
	20	1,291	9,020	2.2	59.3	26.5	0.2
	21*	1,002	6,340	2.9	77.4	35.4	0.3

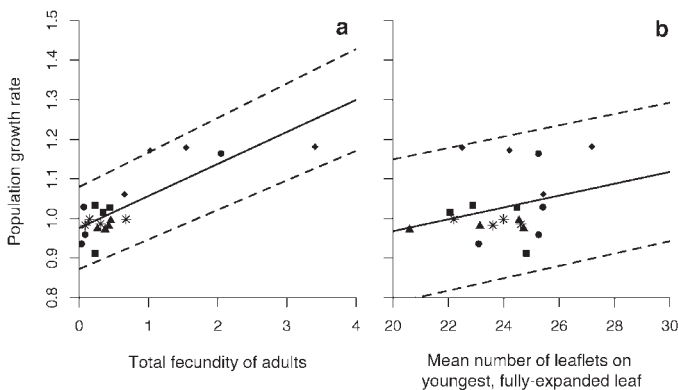


FIG. 1—Univariate regressions of finite rate of population growth on each selected predictor variable from the rapid-assessment-of-sustainable-harvesting model for 21 populations of the understory palm *Chamaedorea radicalis* in Reserva de la Biosfera El Cielo, Tamaulipas, Mexico. Each point represents the finite rate of population growth and a) total fecundity of adults ($F_{1,18} = 35.63$, $P < 0.001$, $R^2 = 0.66$) or b) mean number of leaflets on the youngest, fully expanded leaf ($F_{1,18} = 1.47$, $P = 0.240$, $R^2 = 0.08$) for each year and harvest-treatment combination ($n = 20$): ♦, control with no leaf removed; ■, all marketable leaves removed once per year; ▲, all marketable leaves removed twice per year; ●, 4 times/year with a maximum of 1 leaf/palm removed each harvest (unless only one leaf was present); and *, all marketable leaves removed four times/year. Dashed lines represent the 95% prediction intervals.

addition of the transition probability of growth to the rapid-assessment-of-sustainable-harvest model only minimally improved explanatory ability (finite rate of population growth = $1.07 + 0.08 \times \text{total adult fecundity} - 0.004 \times \text{mean}$

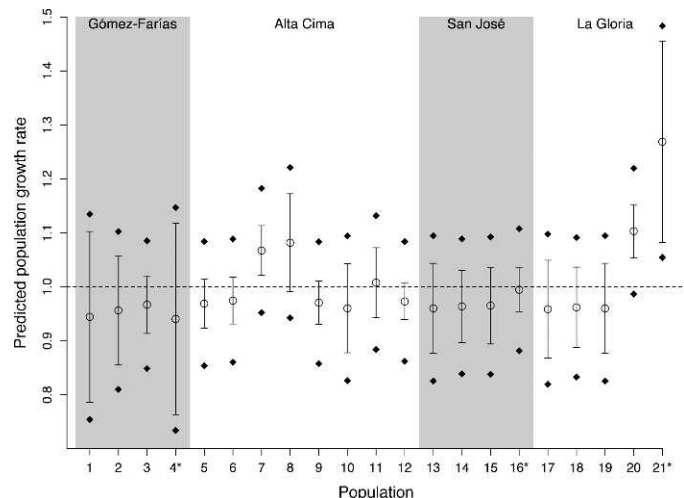


FIG. 2—Predicted estimates of finite rate of population growth for 21 populations of the understory palm *Chamaedorea radicalis* in Reserva de la Biosfera El Cielo, Tamaulipas, Mexico, using the rapid-assessment-of-sustainable-harvest regression model. Populations are grouped by community and unharvested populations are denoted by asterisks (*). Error bars indicate 95% confidence intervals and 95% prediction intervals are denoted by ♦.

TABLE 1—Extended.

Proportion of juveniles	Proportion of small adults	Proportion of large adults	Proportion flowering	Proportion fruiting	Total adult fecundity	Average number of cut leaves	Proportion harvested
<0.1	0.2	0.7	0.1	<0.1	0.0	1.8	0.7
<0.1	0.2	0.6	<0.1	0.0	0.0	2.1	0.8
<0.1	0.4	0.5	<0.1	0.0	0.0	1.9	0.9
<0.1	0.2	0.8	0.4	<0.1	0.0	<0.1	<0.1
<0.1	0.3	0.4	<0.1	<0.1	0.0	1.0	0.5
<0.1	0.4	0.4	<0.1	<0.1	<0.1	1.0	0.6
<0.1	0.2	0.3	<0.1	<0.1	1.2	1.2	0.5
<0.1	0.1	0.3	<0.1	<0.1	1.5	0.8	0.4
<0.1	0.4	0.3	0.1	<0.1	0.0	0.7	0.4
<0.1	0.2	0.4	<0.1	0.0	0.0	1.3	0.6
<0.1	0.3	0.3	<0.1	<0.1	0.6	0.7	0.4
<0.1	0.3	0.3	<0.1	<0.1	0.0	0.6	0.3
<0.1	0.3	0.4	<0.1	0.0	0.0	1.0	0.6
<0.1	0.3	0.4	<0.1	0.0	0.0	0.5	0.3
<0.1	0.3	0.4	<0.1	<0.1	<0.1	0.8	0.5
<0.1	0.4	0.4	0.1	<0.1	0.3	<0.1	<0.1
<0.1	0.3	0.6	0.2	<0.1	0.0	0.3	0.2
0.1	0.2	0.4	<0.1	<0.1	0.0	0.5	0.4
<0.1	0.2	0.5	0.1	<0.1	0.0	0.9	0.6
<0.1	0.3	0.4	<0.1	<0.1	1.7	0.6	0.4
<0.1	0.1	0.5	0.2	<0.1	4.0	<0.1	<0.1

number of leaflets, + 0.07*annual growth, $F_{3,16} = 11.28$, $P < 0.001$, $R^2 = 0.68$). Considering all possible multiple-regression models with the three predictor variables (total fecundity of adults, annual transition probability of growth, and mean number of leaflets), a modified rapid-assessment-of-sustainable-harvest model with total fecundity of adults and annual-transition probability of growth was

equivalent to the original model ($\Delta AIC_c = 2.60$ versus 2.95).

DISCUSSION—The rapid-assessment-of-sustainable-harvest model was parameterized with the ultimate goal of identifying sustainable harvesting by using finite rate of population growth as a measure of population vigor.

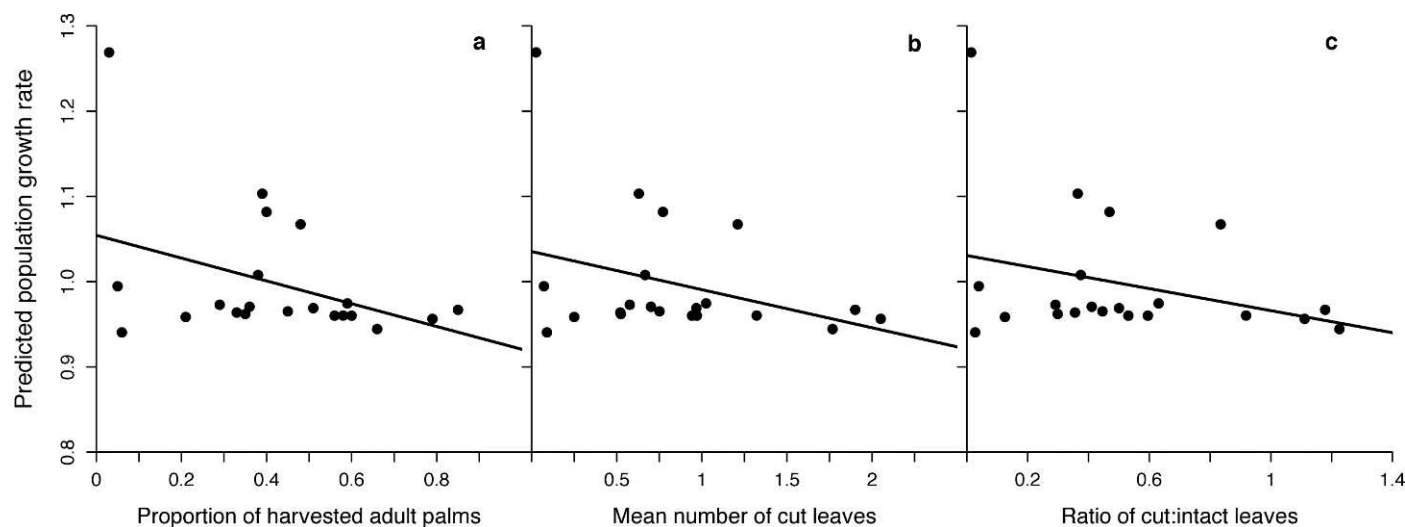


FIG. 3—Regression models between predicted finite rate of population growth from the rapid-assessment-of-sustainable-harvest model and different measures of intensity of harvesting among 21 populations of the understory palm *Chamaedorea radicalis* in Reserva de la Biosfera El Cielo, Tamaulipas, Mexico, 2006: a) proportion of harvested palms ($F_{1,19} = 3.40$, $P = 0.080$, $R^2 = 0.15$); b) mean number of cut leaves ($F_{1,19} = 2.34$, $P = 0.140$, $R^2 = 0.11$); and c) ratio of cut:intact leaves ($F_{1,19} = 1.97$, $P = 0.180$, $R^2 = 0.09$).

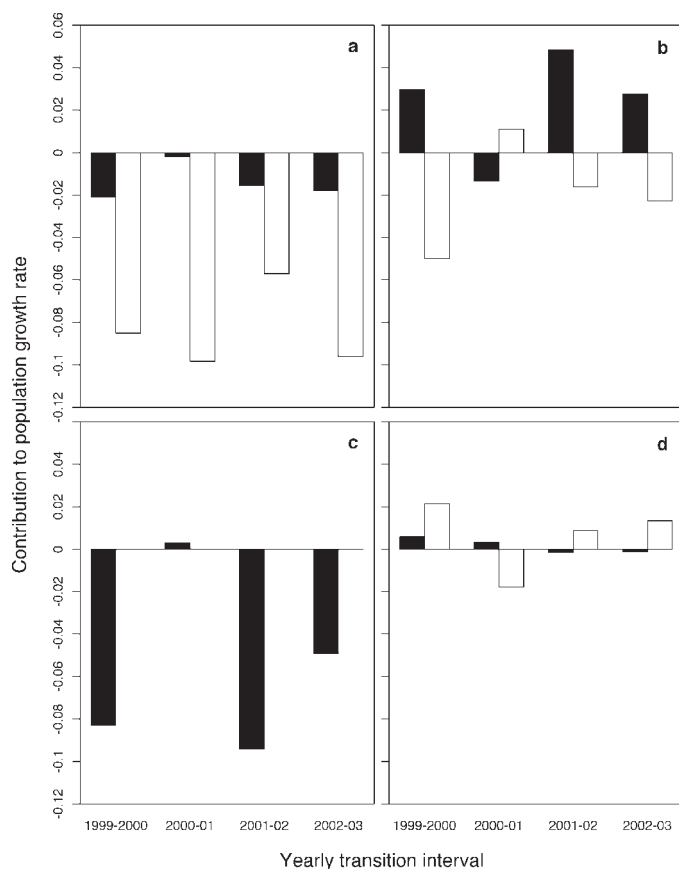


FIG. 4—Results of the life-table-response experiment for the main effect of year on differences in finite rate of population growth for 21 populations of the understory palm *Chamaedorea radicalis* in Reserva de la Biosfera El Cielo, Tamaulipas, Mexico. The main effect of year is determined relative to the control matrix; i.e., finite rate of population growth^(y) minus finite rate of population growth^(c), where finite rate of population growth^(y) is derived for each year. Results for small (■) and large (□) adults are grouped by category of transition probability: a) mean number of fruits produced per palm (fecundity); b) probability of surviving and remaining in a given stage; c) probability of survival and growth from one stage to a larger stage; and d) probability of survival and regressing to a smaller stage.

Sustainable harvesting was identified definitively in only one of the 21 populations using the conservative criterion of finite rate of population growth plus or minus interval of prediction >1.0 . Conversely, no population was projected to have a finite rate of population growth with a prediction interval completely <1.0 ; therefore, none can be considered definitively as experiencing unsustainable levels of leaf harvesting. Overall utility of the rapid-assessment-of-sustainable-harvest model was thus limited by imprecision of estimates of finite rate of population growth. A complete assessment of utility of the model, however, also requires an examination of its validity and applicability.

Important demographic indicators of harvesting intensity were identified in the 4-year study and projected

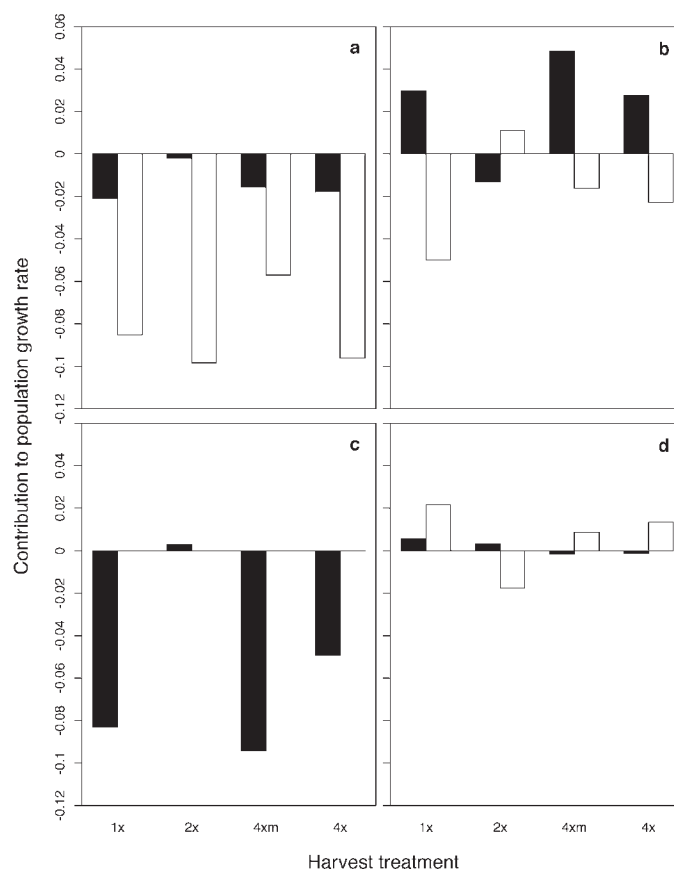


FIG. 5—Results of the life-table-response experiment for the main effect of harvesting treatment on differences in finite rate of population growth for 21 populations of the understory palm *Chamaedorea radicalis* in Reserva de la Biosfera El Cielo, Tamaulipas, Mexico. Results for small (■) and large (□) adults are grouped by category of transition probability: a) mean number of fruits produced per palm (fecundity); b) probability of surviving and remaining in a given stage; c), probability of survival and growth from one stage to a larger stage; and d) probability of survival and regressing to a smaller stage. Harvesting treatments are: 1x, all marketable leaves removed once per year; 2x, all marketable leaves removed twice per year; 4xm, 4 times/year with a maximum of 1 leaf/palm removed each harvest (unless only one leaf was present); and 4x, all marketable leaves removed 4 times/year.

finite rate of population growth varied across the gradient of harvesting intensity as noted by Endress et al. (2006). Therefore, development of the rapid-assessment-of-sustainable-harvest model is really an extension of this direct correlation between demographic indicators, intensity of harvesting, and projected finite rate of population growth. Nonetheless, determination of long-term dynamics from short-term measures poses a significant ecological challenge and requires biologically realistic models. There is a sound biological basis for inclusion of fecundity as a predictor of finite rate of population growth in the rapid-assessment-of-sustainable-harvest model, as the dynamics of a population are tied intimately to its reproductive output. Dependence of finite rate of

population growth on number of leaflets on the youngest, fully expanded leaf is less intuitive. However, a clear correlation was established via the 4-year study by Endress et al. (2006); harvested palms exhibited a developmental response, producing leaves with fewer leaflets, while populations exhibited a demographic response evidenced by lower finite rate of population growth.

With only a single season of data for the 21 populations, there is no way to validate the model through independent derivation of finite rate of population growth, either from observed changes in size of populations or parameterization of transition matrices as was done in the 4-year study by Endress et al. (2006). There is some evidence that suggests the rapid-assessment-of-sustainable-harvest model produced valid and meaningful estimates of finite rate of population growth. The relationship between each measure of harvesting intensity and estimates of finite rate of population growth, while not significant, was negative as expected from the results obtained from the short-term and long-term experiments of leaf harvesting reported by Endress et al. (2004a, 2006).

In contrast, the model also provided results that were contrary to local perceptions and measurements of intensity of harvesting. Two of the three unharvested populations had predicted estimates of finite rate of population growth <1 , suggesting that their demography was indicative of a population in decline. While this seems counterintuitive to measurements in the field that indicated these populations were not harvested, it is possible that the historical legacy of harvesting was still being reflected in current population dynamics. These populations likely have experienced harvesting in the past, so it may not have been detected as the elapsed time exceeded longevity of remnants of cut leaves. Additionally, the relatively low density of palms in these populations may make them unattractive for harvesting, as harvesters target high-density populations (Table 1). Another possible influence on population growth is the effect of browsing by livestock. Browsing substantially impacts dynamics of populations of *C. radicalis* by influencing survival and fecundity of browsed individuals (Endress et al., 2004a; Berry et al., 2008). The community of Alta Cima had instituted mandatory fencing of pastures to prevent livestock from damaging *C. radicalis* and other forestry resources. Alleviation of the impact of browsing can be observed in two populations we sampled (7 and 8), which were recovering from intense browsing and exhibited two of the highest predicted finite rate of population growth from the rapid-assessment-of-sustainable-harvest model (Fig. 2). In contrast, the community of San José had free-ranging livestock and, while there was no indication of active browsing in the four populations we sampled, these populations had low predicted estimates of finite rate of population growth, albeit not substantially different from other populations. It may be

that periodic exposure to browsing (i.e., not detectable at time of sampling) is substantial enough to influence dynamics of populations.

Utility of the rapid-assessment-of-sustainable-harvest approach is impeded by lack of precision in estimates of finite rate of population growth. A remedy to the problem of imprecise estimation of a parameter is to increase sample size used for generation of the model. However, in this instance, each sample used to generate the model involved considerable data, including repeated surveys of marked palms. The long-term study of *C. radicalis* conducted by Endress et al. (2006) was one of the few studies of non-timber forest products that employed a wide gradient of harvesting regimes based on actual strategies of harvesters. The realistic nature of experimental treatments permitted a more sound comparison between the long-term study and the populations we sampled within Reserva de la Biosfera El Cielo. However, reliance of the rapid-assessment-of-sustainable-harvest model on this substantial demographic dataset limits options for improving precision of the model. Stage structure was not recorded in the long-term 4-year study and consequently did not allow the inclusion of these variables in development of the rapid-assessment-of-sustainable-harvest model. Measures of stage or size structure in parameterization datasets should improve rapid-assessment-of-sustainable-harvest models, as populations with a disproportionate representation of smaller size classes theoretically are expected to be increasing or at least experiencing net replacement. Use of data on size structure to make inferences about population growth has a long-standing legacy within forest ecology (Lorimer, 1980; Ogden, 1985; Read et al., 1995; Condit et al., 1998). Feeley et al. (2007) detected significant relationships between direction of population growth and the coefficient of skewness, a measure of the relative proportion of small to larger stems in a population (Bendel et al., 1989). Similarly, Peres et al. (2003) discovered that two measures of size structure were significantly related to the legacy of harvesting seeds from the Brazil nut (*Bertholletia excelsa*), although they did not predict population dynamics. For palms such as *C. radicalis*, parameters for size structure, such as proportion of seedlings, may be significant predictors of long-term growth of populations.

Another problem with the rapid-assessment-of-sustainable-harvest approach is inclusion of reproductive measures for species with seasonal reproduction, such as *C. radicalis*. This problem can be reduced by limiting sampling to periods of reproduction or measuring more persistent structures, for instance, the longer-lived female inflorescences of *C. radicalis*.

Imprecision of estimates of finite rate of population growth from the rapid-assessment-of-sustainable-harvest model argues that a better method is needed to infer dynamics of harvested populations and to assess whether a harvesting practice is sustainable. For this reason, we

explored whether inclusion of annual transition probabilities would improve the prediction of finite rate of population growth. The life-table-response experiment revealed a substantial influence of fecundity of large adults and the annual transition probability of growth from small to large adults on differences in finite rate of population growth across harvesting treatments in the 4-year study by Endress et al. (2006). We did not have estimates for annual transitions for the sampled populations, but addition of the annual transition probability of growth did little to improve the explanatory ability of the rapid-assessment-of-sustainable-harvest model. A protocol for assessment based on measuring annual rates of transition would require a substantially larger investment in marking individual palms and returning for a yearly census, so it does not appear to provide a cost-effective alternative.

While transition probabilities, or demographic rates in general, appear not to be an efficient addition to rapid assessment of sustainable harvesting, they might be an appropriate focus for a framework of sustainability that does not involve estimation of finite rate of population growth (Zuidema et al., 2007; Schmidt et al., 2011). In this framework, important demographic rates as determined by elasticity analysis would be monitored as direct measures of sustainability of harvesting. This is similar to the approach suggested by Zuidema et al. (2007), where harvesting is considered sustainable if those vital rates that exhibit high elasticity contribute minimally to differences in finite rate of population growth across treatments, as determined by life-table-response-experiment analysis. While this novel approach to evaluating sustainability may address concerns associated with estimation of finite rate of population growth (Zuidema and Franco, 2001), it does not resolve the need for rapid assessments of sustainability of non-timber forest products. Our suggestion is that harvested populations are assessed periodically for values of important demographic rates identified by elasticity analysis; an initial certification of sustainability could then be re-evaluated based on these rates. For *C. radicalis*, fecundity of adults is an important demographic rate for harvested populations and could be a useful parameter in a monitoring framework of sustainable harvesting. To account for year-to-year variation and environmental drivers of production of seeds (i.e., drought), measures of stage structure also could be monitored. Proportion of seedlings or juveniles is likely a more stable indicator of recruitment and health of a population.

Models based on experimental periodic harvesting of leaves of *C. radicalis* have projected that harvesting can be sustainable (Endress et al., 2004a, 2004b, 2006), but the current status of harvested wild populations in Reserva de la Biosfera El Cielo is necessary to inform ongoing efforts for certification. While our study does not conclusively provide a rapid-assessment framework, it does identify

limitations of predicting sustainability of harvesting from short-term measurements. The expansive breadth of the long-term dataset for *C. radicalis* was not sufficient to overcome limitations of this type of prediction and develop a satisfactory rapid-assessment-of-sustainable-harvest model. Nonetheless, these limitations do not negate the need for accredited certifiers to have a reliable method to quickly and accurately determine the state of extraction for non-timber forest products. If certification of non-timber forest products is to be a significant enhancer of their sustainable use, the issue of how best to evaluate and determine the sustainability of extraction needs to be resolved. For *C. radicalis*, this may be best achieved through adherence to best-management practices. Recent initiatives have assessed current demand in the United States for ecologically certified leaves of palms through a series of pilot studies for Palm Sunday (Committee for Environmental Cooperation of North America, <http://www.cec.org/Page.asp?PageID=122&ContentID=2128&SiteNodeID=358>). For a recent initiative exclusively considering the sale of leaves of *C. radicalis* from Reserva de la Biosfera El Cielo, a harvester had to adhere to the following guidelines to receive the enhanced price: 1, no felling of stemmed palms to obtain leaves; 2, no harvesting from palms bearing fruits; 3, no complete defoliation of harvested palms. These best-management practices are not arbitrary, but akin to the rapid-assessment-of-sustainable-harvest model in the sense that they are informed by years of collection of demographic data and experimental work on *C. radicalis*. Initiatives such as this are crucial for management of ecological and economic sustainability of non-timber forest products.

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