THE SOUTHWESTERN NATURALIST 45(4):421–430 DECEMBER 2000

PATTERNS OF ABUNDANCE AND HUMAN USE OF THE VULNERABLE UNDERSTORY PALM, *CHAMAEDOREA RADICALIS* (ARECACEAE), IN A MONTANE CLOUD FOREST, TAMAULIPAS, MEXICO

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ABSTRACT—The pinnate leaves of a vulnerable understory palm species, *Chamaedorea radicalis,* are gathered from wild populations within the El Cielo Biosphere Reserve, Tamaulipas, Mexico, by local people for sale to international cut foliage markets. Conservation implications of leaf harvesting within natural populations requires collection of ecological information on abundance of palms in different habitats and environmental factors that determine palm abundance. Densities of *C. radicalis* and associated environmental parameters were sampled in 28 stands of montane cloud forest to determine the relationship of *C. radicalis* abundance to tree community composition and environmental factors. Ordination of associated tree species importance values was performed using detrended correspondence analysis (DCA) and palm density was regressed against environmental factors using simple and multiple regression analyses. Palm density averaged 4,411 individuals/ha with a maximum 14,000 individuals/ha. Density of *C. radicalis* was greater in stands with high percentage of rock substrate, low tree basal area, and stands dominated by *Quercus germana* and *Harpalyce arborescens.* Densities of *C. radicalis* and the percentage of palms showing evidence of harvesting were unrelated to the time traveled away from the nearest settlement, suggesting that long term harvesting of the leaves may not have had a discernible effect on population densities. However, these results must be viewed within the context of larger landscape patterns of land-use within the reserve.

RESUMEN—Las hojas pinnadas de *Chamaedorea radicalis,* una especie de palma del sotobosque considerada vulnerable son colectadas de las poblaciones silvestres por los lugareños de la Reserva de la Biosfera El Cielo, Tamaulipas, México, para su venta al mercado internacional de hojas. Implicaciones conservacionistas sobre las cosechas en poblaciones naturales requiere recopilar informaciones ecológicas sobre la abundancia de palmas en diferentes habitats y sobre los factores ambientales que determina su abundancia. Densidad de *C. radicalis* y los parámetros ambientales en 28 áreas de muestreo en el bosque mesófilo de montaña fueron medidos para determinar la relación entre la abundancia de *C. radicalis* con la composición florística y los factores ambientales. Se calculó la ordenación de los valores de importancia de las especies de árboles asociados usando análisis de correspondencia (DCA) y se hicieron regresiones simples y múltiples de la densidad de la palma contra factores ambientales. La densidad promedia de la palma fue 4,411 plantas/ha, con un máximo de 14,000 plantas/ha. La densidad de *C. radicalis* fue más alta en las áreas de muestreo con mayor porcentaje de substrato rocosa, menor área basal de árboles, y areas dominadas por *Quercus germana* y *Harpalyce arborescens.* Ni las densidades ni los porcentajes de *C. radicalis* con evidencia de cosecha mostraron relaciones con el tiempo de viaje al poblado más cercano, lo que sugiere que la cosecha de hojas a largo plazo posiblemente no tenga un efecto notable en las densidades poblacionales. Sin embargo, estos resultados deben ser vistos desde un contexto paisajístico más amplio sobre uso de tierra dentro de la reserva.

Management strategies promoting the conservation of tropical ecosystems through extraction of non-timber forest products have received much opinion and advocacy (Peters et al., 1989; Plotkin and Famolare, 1992; Panayotou and Ashton, 1992; Nations, 1992; Nepstad and Schwartzman, 1992) but relatively little analysis (Godoy et al., 1993; Hall and Bawa, 1993). In recent years, population modeling has been applied to assess the sustainability of harvesting of non-timber forest products from wild plant populations (Peters, 1990, 1991; Pinard and Putz, 1992; Olmsted and Alvarez-Buylla, 1995; Ratsirarson et al., 1996). Extraction of non-timber forest products has been proposed as one method of sustainable land use for rural inhabitants of developing nations (Panayotou and Ashton, 1992; Nepstad and Scwartzman, 1992). Collection of non-timber forest products has fewer negative impacts on forest communities and ecosystem processes than other land uses such as logging (Gorchov, 1993; Boot and Gullison, 1995). Therefore, collection of non-timber forest products may offer a way for local communities to meet their livelihood needs while preserving biodiversity and maintaining ecosystem function.

In the mountains of the El Cielo Biosphere Reserve in northeastern Tamaulipas, the mature pinnate leaves of the understory palm, *Chamaedorea radicalis,* are harvested by rural people (palmilleros) from wild populations of palms in primary and mature secondary forests. Large quantities of *Chamaedorea* leaves are exported from Mexico each year for use as ornamental green foliage in large cut-flower arrangements. *Chamaedorea radicalis* leaves are the only authorized natural products extracted from the Biosphere Reserve and represent a significant source of external income for rural people (Trejo-Hernandez, 1992).

Mexico is the world's leading producer of cut foliage from *Chamaedorea* (Reining and Heinzman, 1992). Several species of *Chamaedorea,* including *C. radicalis,* have been overexploited in their native habitats along the eastern coast of Mexico (Marshall, 1989; González-Pacheco, in Oyama, 1992; Hodel, 1992). *Chamaedorea radicalis* is considered a vulnerable species in Mexico (Hodel, 1992) and may become endangered if habitat destruction and overexploitation continue. Efforts to reduce the impact of harvesting on populations of *Chamaedorea* by restricting trade in the leaves (CITES, 1989) have been stalled, in part because of insufficient knowledge of the abundance of the species and the effect of leaf harvesting on wild populations (Marshall, 1989).

Potentially, *Chamaedorea* leaves are commercially viable and sustainable non-timber forest products. Because the apical meristem is undamaged by leaf removal, a palmillero can return to the same plant over several years to harvest additional leaves. However, information on the effect of long term leaf harvesting on *Chamaedorea* growth, survival, and reproduction remains unclear. For *Chamaedorea tepejilote,* leaf production was increased by partial and complete defoliation, and reproduction was increased by partial defoliation during a two-year study period (Oyama and Mendoza, 1990). Studies of palms of other genera suggest that leaf removal often increases leaf production initially (Oyama and Mendoza, 1990; Chazdon, 1991; O'Brien and Kinnaird, 1996; Ratsirarson et al. 1996), though defoliation eventually may lead to increased palm mortality (Mendoza et al., 1987; O'Brien and Kinnaird, 1996). Leaf removal also may decrease seed production (Mendoza et al., 1987; Oyama and Mendoza, 1990; Ratsirarson et al., 1996) or result in a reduction in leaf length at maturity (O'Brien and Kinnaird, 1996; Ratsirarson et al., 1996).

The major stimulus for our research was reports from local palmilleros that palm abundances were lower in areas near human settlements and people were walking increasingly farther into the forests each year to collect leaves of the palm. Furthermore, efforts are currently underway to establish plantations of *C. radicalis* in El Cielo Biosphere Reserve in areas where the palm has presumably been depleted because of overharvesting (Jiménez et al., 1996). This suggests that heavy harvesting of the palm near human settlements may lead to lower palm abundances (Reining et al., 1992). However, before we can assess how leaf removal affects abundance of *C. radicalis,* we need to understand how its abundance varies with environmental factors, because large levels of variability can mask observed effects of overexploitation on wild species (Ludwig et al., 1993; Osenberg et al., 1994). Knowledge of environmental and human factors that are associated with *C. radicalis* distribution and abundance within its range should provide the information necessary to evaluate its conservation status, judge the sustainability of harvesting, and suggest ways in which the resource can be managed. We addressed three questions in this study. Which tree communities and soil substrates are associated with variation in densities of *C. radicalis*? Is abundance of *C. radicalis* positively correlated with time traveled away from human settlements? Are palm densities lower in areas that are experiencing greater harvesting pressure?

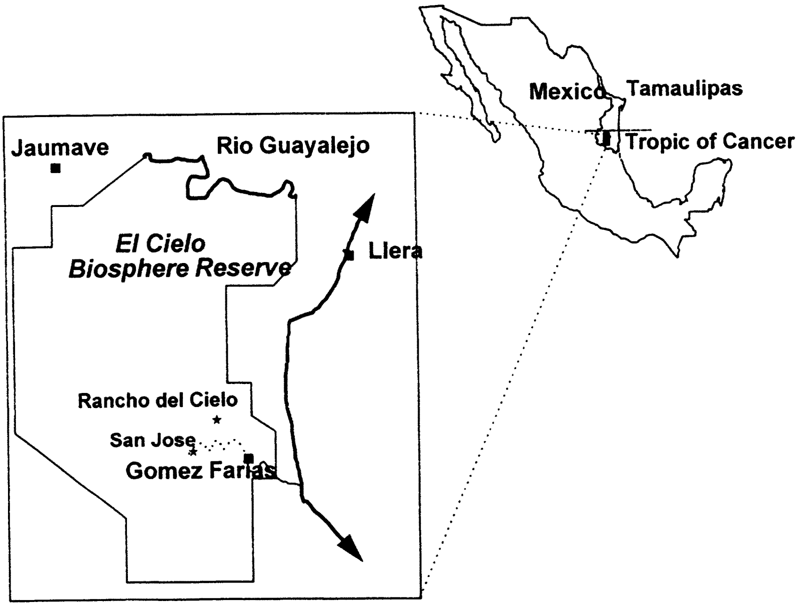


FIG. 1—The El Cielo Biosphere Reserve, Tamaulipas, Mexico, showing the community of San José, the area where this study was conducted.

MATERIALS AND METHODS—*Study Area*—This study was conducted in the cloud forests of the El Cielo Biosphere Reserve (between 22°55′ to 23°30′N and 99°02′ to 99°30′W), near the El Canindo Field Station (elevation 1,410 m), ejido San José. El Cielo is situated in the Sierra de Guatemala, in the front ranges of the Sierra Madre Oriental, in the northeastern Mexican state of Tamaulipas (Fig. 1). The Sierra is composed mostly of karstic limestone outcroppings (Puig, 1993) of Cretaceous origin (Heim, 1953). Annual precipitation in the Reserve depends on elevation and averages 1,800 mm in the village of Gómez Farías (elevation 200 m) and 2,500 mm at Rancho del Cielo (1,100 m—Davis et al., 1997); average annual temperature for these localities is 22.8 and 13.8°C, respectively (Davis et al., 1997).

The El Cielo Biosphere Reserve encompasses a wide diversity of vegetation types including tropical dry forest, tropical semi-deciduous forest, montane mesophyll (cloud) forests, pure and mixed oak forests, oak-pine forests, and chaparral (Perrine and Gorchov, 1994; Davis et al., 1997). The reserve contains the northern-most extension of tropical cloud forest in North America (Rzedowski, 1978) and was established as a biosphere reserve to protect this diverse forest type. The cloud forests of El Cielo Biosphere Reserve are limited to the mid-elevations of the Sierra from 800 to 1,500 m, encompass more than 100 km^2, and are similar floristically to those found in Teocelo, Veracruz (Vázquez-García, 1993). Several floristic inventories have been conducted in the area (Sharp et al., 1950; Hernández et al., 1951; Martin, 1958; Puig et al., 1983; Puig and Bracho, 1987; Puig, 1993), and an annotated bibliography of the botanical literature of El Cielo Biosphere Reserve and environs (Perrine and Gorchov, 1994) has been completed.

Study Species—*Chamaedorea radicalis* Mart. is a slender, erect palm that can appear stemless at a young age, but can reach a full height of 3 to 4 m. *Chamaedorea radicalis* is found on limestone outcroppings in oak forests throughout the eastern states of Hidalgo, Nuevo Leon, San Luis Potosi, and Tamaulipas (Hodel, 1992). Within El Cielo Biosphere Reserve, *C. radicalis* is found in a number of forest communities ranging from seasonal tropical forest (ca. 200 m) to the pine-oak forest found above 1,400 m elevation (Mora-Olivo et al., 1997). *Chamaedorea radicalis* has been listed as a threatened species in Mexico by Oyama (1992) and is of indeterminate status in Tamaulipas (Malda Barrera, 1990).

Stand Selection—Twenty-eight forest stands were sampled from June through August 1993 in the mountains surrounding San José. Stands were selected so as to sample the range of *C. radicalis* densities within the different forest tree communities at multiple distances away from San José. Because of the long time period of extraction (>40 years, M. Camacho and B. A. Endress, pers. comm.) and the thoroughness of local palmilleros, sampling of unharvested populations was not possible. We avoided sampling in forest stands where livestock grazing of the understory, tree fall gaps, and severe topographic obstacles (e.g., cliffs, rock outcrops, and sinkholes) were apparent.

We established five 25-m transects 10 m apart and perpendicular to the contour of the slope of the stand. At each of five random points along each transect, we recorded the distance, diameter at breast height (dbh), and species of the nearest individual tree >3 cm diameter, the number of individuals of *C. radicalis* within a 2-m radius, whether the substrate was rock or leaf litter, and the cardinal direction of the aspect of the slope. The spacing of points and transects was sufficient to avoid resampling of individual trees. We established a 10 by 10 m (100 m^2) plot in each stand and counted the number of individuals, including seedlings, of *C. radicalis*. For each individual, we recorded the presence of severed petioles, a clear indication of previous harvest activity.

Analysis of Community Composition—Relative density and basal area for each tree species were calculated from absolute values for each tree species in each stand, and these two relative values were averaged to create an importance percentage for each species in each stand. We developed a dominance-type classification (Whittaker, 1978) based on the species with the highest importance percentage in each stand.

We performed detrended correspondence analysis (DCA), an indirect gradient analysis method, on the importance percentages for each of the tree species in the 28 stands using CANOCO (Ter Braak, 1988). Environmental variables for each stand and stand scores from the first four axes of the DCA were used as independent variables in stepwise multiple regression and simple linear regressions to examine the distribution of palms along environmental gradients and among different communities. We used simple linear regressions to examine the contribution of environmental factors in explaining variation in the DCA stand scores and biological variables.

Analysis of Factors Influencing C. radicalis *Density*—The density of *C. radicalis* per ha was estimated from the average of the 25, 2-m radius (12.6 m^2) plots sampled in each stand. We transformed each of the slope aspects, A (where $A = \Sigma A'/25$, $A' = cos(135 - A_i) + 1$, the A_is are the aspects of the 25 individual points). This transformation is based on Beers et al. (1966) and yields highest scores for southeastern aspects and lowest values for northwestern aspects, reflecting the patterns found for *C. radicalis* density (Jones, 1994). Percent palms harvested per stand was estimated by percent palms in the 100-m^2 plot with severed petioles.

We employed forward stepwise linear regression (Neter et al., 1996) to regress density of *C. radicalis* against environmental and biological variables. Stepwise multiple regression is a combination of forward and backward regression that enters, retains, and removes parameters based on the alpha value for each parameter. The selection level entry and stay values in the multiple regression model were $P < 0.20$ and $P < 0.10$, respectively. Environmental factors entered in the regression model included elevation (m), percent rock in stand (defined as the percentage of the 25 points falling on rock substrate), and the average of transformed aspects. Biological variables entered in the analysis were axes 1 through 4 of the DCA, species richness in the stand, total tree basal area, and total tree density. Log transformation of *C. radicalis* density provided a better fit and therefore was used in all analyses (Sokal and Rohlf, 1995). We used simple linear regression models to estimate the contribution of individual factors in explaining variation in the abundance of *C. radicalis*.

Percent palms with severed petioles (evidence of past harvest) in each stand was regressed on the variables by use of logistic regression. These included environmental variables, percent rock, time traveled from San José, and elevation, as well as biological variables, total tree basal area, total tree density, and log-transformed *C. radicalis* density.

RESULTS—*Tree Community Composition*—The dominance type analysis revealed that forests surrounding San José are composed of communities dominated by an unidentified oak, hereafter *Quercus* sp. 3, *Quercus germana, Liquidambar styraciflua, Meliosma alba, Acacia angustissima, Harpalyce arborescens, Nectandra sanguinea, Wimmeria concolor, Zanthoxylum cf. caribaeum, Diosporos riojae,* and several unidentified taxa. *Quercus* sp. 3 is the most common dominant tree species in the forest communities surrounding San José.

Eigenvalues of the first four ordination axes were 0.51, 0.34, 0.20, and 0.13, respectively. Eigenvalues in this ordination analysis are considered to represent the proportion of the variation in the species/stand matrix accounted for by each axis. Stands dominated by *Q. germana, Quercus* sp. 3, *L. styraciflua,* and *H. arborescens* cluster in different areas when plotted on the first and second axes stand scores (Fig. 2). Stands dominated by other species are not easily identified as clusters. Regressions of the DCA axes 1 and 2 against the environmental variables did not reveal significant relationships ($P > 0.05$).

Density of Chamaedorea radicalis—*Chamaedorea radicalis* density ranged from 0 to 14,000 individuals/ha and averaged 4,411 individuals/ha ($SE = 631.2$) for the 28 stands sampled. Stepwise multiple regression indicated that the total tree basal area ($P < 0.01$), DCA axis 1 (P

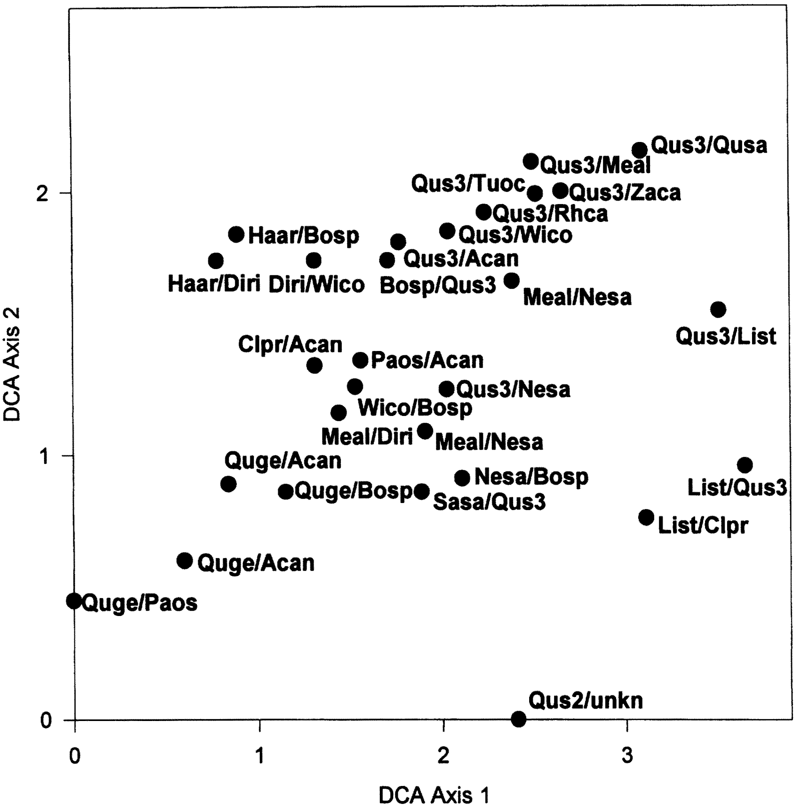
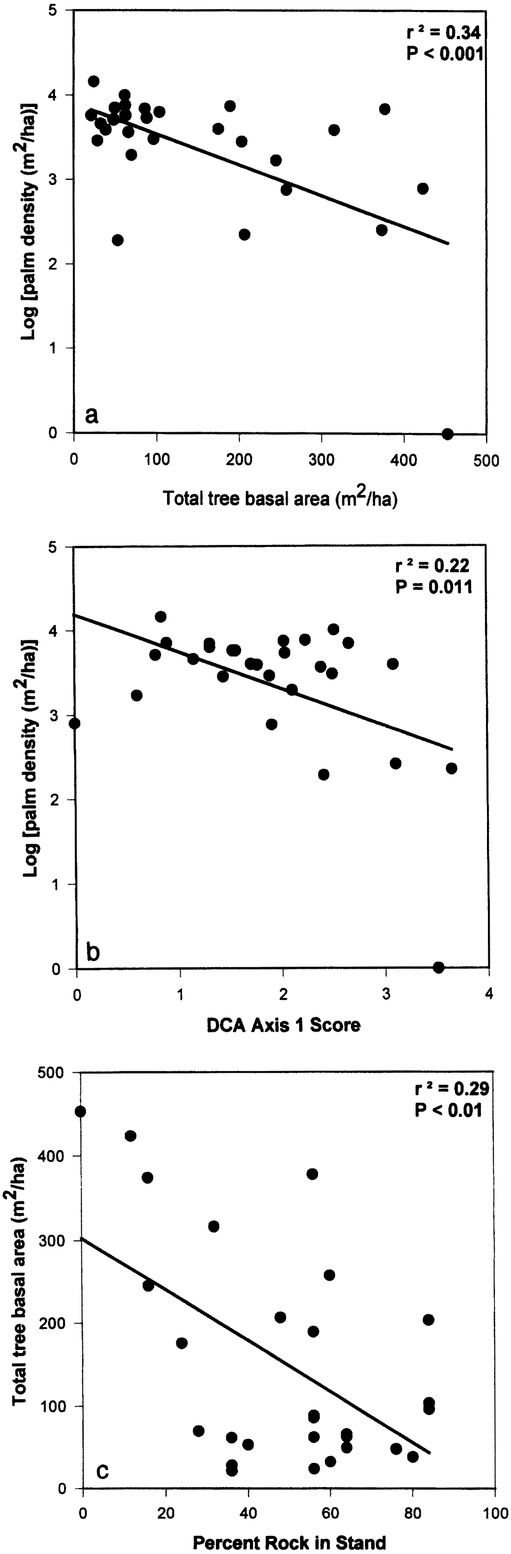


FIG. 2—The ordination diagram for detrended correspondence analysis (DCA) axis 1 and axis 2 stand scores labeled by their dominance type classification from 28 forest stands near San José, El Cielo Biosphere Reserve, Tamaulipas, México. Species abbreviations are Acan = *Acacia angustissima*; Bosp = "Borrego" species; Clpr = *Clethra pringleii*; Diri = *Diosporos riojae*; Haar = *Harpalyce arborescens*; List = *Liquidambar styraciflua*; Meal = *Meliosma alba*; Nesa = *Nectrandra sanguinea*; Paos = "Palo de oso"; Quge = *Quercus germana*; Qus2 = *Quercus* species 2; Qus3 = *Quercus* species 3; Raca = *Rhamnus caroliniana*; Sasa = *Sapindus saponaria*; Tuoc = *Turpina occidentalis*, unkn = unknown species; Wico = *Wimmeria concolor*; Zaca = *Zanthoxylum* cf. *caribaeum*.

< 0.05), DCA axis 2 scores ($P < 0.01$), and richness ($P < 0.01$) accounted for 71% (Table 1) of the variation in *C. radicalis* density ($Y = 2.056 - 0.002*(\text{tree basal area}) + 0.133*(\text{richness}) - 0.471*(\text{DCA 1}) + 0.642*(\text{DCA 2})$. Simple regressions revealed that *C. radicalis* density is negatively correlated with total tree basal area (Fig. 3a) and DCA axis 1 (Fig. 3b). Simple regression analysis further revealed that total tree basal area was negatively related to per-

TABLE 1—A summary of the stepwise linear regression procedure for log-transformed *Chamaedorea radicalis* density regressed against the environmental and biological variables. $C(p)$ is Mallow's coefficient, a measure of the total squared error of the model. Total model $R^2 = 0.71$.

Variable entered	Partial R^2	Model R^2	$C(p)$	F	P
Total tree basal area	0.35	0.35	27.96	13.78	0.001
DCA axis 1 stand score	0.10	0.45	22.04	4.49	0.044
DCA axis 2 stand scores	0.14	0.59	12.69	8.32	0.008
Richness	0.12	0.71	5.41	9.11	0.006



cent rock (Fig. 3c) and that *C. radicalis* density was positively related to percent rock ($y = 2.04 + 0.0194x$, $R^2 = 0.30$, $P < 0.01$).

Chamaedorea radicalis density showed no relationship to time traveled in minutes from San José ($P > 0.05$) or to percent palms harvested in each stand ($P > 0.05$). Percent palms showing evidence of harvesting averaged 18.9% per stand ($SE = 2.95$), and ranged from a maximum 49.3% and minimum of 0% per stand. Percentage of *C. radicalis* with evidence of past leaf harvest was greater in areas with greater *C. radicalis* density (Logit $P = -10.208 + 3.429x$, 2 Log(L) $= 17.827$, $P < 0.05$) and with greater percentage of rock (Logit $P = -1.722 + 0.0665x$, 2 Log(L) $= 23.042$, $P < 0.05$).

DISCUSSION—The negative relationship between *C. radicalis* density and tree basal area may be due to variation in rockiness of the substrate. Stands with higher percent rock had both lower tree basal area and higher *C. radicalis* density. Percent rock did not enter into the stepwise regression procedure because of its colinearity with total tree basal area. Rock substrate apparently limits the growth of large trees, so these areas would have low canopy cover, hence greater light available to the understory, and a higher average temperature of the forest floor (Sukachev and Dylis, 1964), both of which may benefit *C. radicalis*. Palmilleros indicated that there are a greater amount of palms in chaparrito, areas of small trees and a rocky substrate, than in the forest, an observation consistent with our results.

The positive relationship between rock and *C. radicalis* density may alternatively have a direct, edaphic explanation. Other studies have shown that soil moisture and drainage are important in determining densities of the palms

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FIG. 3—Regressions of log-transformed *C. radicalis* density against: a) total tree basal area, and b) DCA axis 1 score, and of c) total tree basal area against percent rock, for 28 forest stands near the community of San Jose, El Cielo Biosphere Reserve. Regression equations are: a) $y = 3.90 - 0.00363x$, $R^2 = 0.34$, $P < 0.001$; b) $y = 4.19 - 0.440x$, R^2 0.22, $P < 0.01$; and c) $y = 302.4 - 3.08x$, $R^2 = 0.29$, $p < 0.01$.

Lepidocaryum temanii (Kahn and Mejia, 1987) and *Chamaedorea bartlingiana* (Ataroff and Schwarzkopf, 1992). These species have higher densities (2,300 and 10,000 individuals/ha, respectively) in well-drained sites with low soil humidity. Also, exposed and broken limestone within a forest stand may increase the available microsites for *C. radicalis* establishment.

Another possible cause for the greater *C. radicalis* density in elevated rocky stands is the lower accessibility of these stands to free-ranging livestock (F. A. Jones, pers. obser.). Although not quantified in this study, grazing also may account for the observed low density and absence of this palm near trails and roads, and should be considered as a limiting factor in future studies of these populations.

The negative relationship of *C. radicalis* to DCA axis 1 reflects that stands dominated by *L. styraciflua* and *Quercus* sp. 3 had lower densities than those stands dominated by *Q. germana* and *H. arborescens*. That *L. styraciflua* is particularly abundant in the second growth forests after logging or agriculture (Sosa and Puig, 1987) suggests that previous anthropogenic disturbance may limit establishment or survival of *C. radicalis* in these stands.

The absence of relationships between DCA axes and environmental variables suggests that more complete studies are necessary to determine the environmental gradients that account for the distribution of these tree communities. Tree communities that clustered in the DCA diagram were dominated by species of holoarctic origin, such as *L. styraciflua* and the *Quercus* sp. which are the dominant trees of the cloud forest canopy stratum in El Cielo Biosphere Reserve (Puig et al., 1987) and have the highest basal areas of trees in these forests (Puig et al., 1983). The stands that were not easily identified as clusters are dominated by species of tropical origin, such as *M. alba, A. angustissima, W. concolor, Sapindus saponaria, N. sanguinaria,* and *H. arborescens*. These tree species have a shrubby habit, lower basal area, and are characteristic species of the lower strata of the forest (Puig et al., 1983).

Although percent palms with evidence of harvesting was best predicted by percent rock in the stand, both of these variables were correlated with *C. radicalis* density. Therefore, we suggest that the most relevant biological factor involved in determining percent palms harvested in a stand is density of the palms. Salafsky et al. (1993) also report that density-dependent collection of *Chamaedorea* palm leaves has been observed in the Petén.

We cannot infer the effect of harvesting on *C. radicalis* populations because the data presented here represent status of these populations at a single point in time and we do not know the past history of harvesting in the different stands. Densities of *C. radicalis* were not lower near human settlement as expected and as has been found for *Chamaedorea oblongata* and *Chamaedorea elegans* in the Petén (Reining et al., 1992), and palm density was greater, not lower, in areas with a high percentage of plants harvested.

That we found no correlation between population density and distance from human settlements contrasts with claims of local collectors. This pattern might suggest that the palms are being harvested sustainably in the San José region. Alternatively, populations near settlements may be so fragmented that they are unattractive for harvesting. Although populations of high density do exist near human settlements, they appear more isolated, due to other land uses and a greater impact of grazing by free-range livestock. This fragmentation results in a low palm density at the large scale. Because collectors take leaves from numerous populations in a day, on a spatial scale many times greater than our study plots, these near-settlement areas may not produce sufficient leaves to warrant frequent collection. Our findings may not be representative of areas where palm harvesting is more intense, e.g., near the settlements of Alta Cimas and Gómez Farías, where elevations are lower and the forest is more tropical. Therefore we caution the application of our results to the management of wild and planted *C. radicalis* populations in these areas. Future studies that examine the interaction between palm density, leaf production, leaf harvest intensity and frequency, free-range livestock, environmental factors, and landscape heterogeneity would contribute greatly to our understanding of the effects of harvesting on palm populations. Towards this end, we are collaborating in a multi-year study to determine the effect of leaf harvesting and grazing on *C. radicalis* leaf production, demography, and population growth to assess the sustainability of harvest regimes within the El Cielo Biosphere Reserve.

This study was funded by grants to FAJ from the Ohio Academic Challenge Fund and the W. S. Turell Herbarium Fund. We thank L. Trejo, A. Mora, and C. Gutierrez of the Instituto de Ecología y Alimentos, Universidad Autónoma de Tamaulipas for their assistance in the field and plant identification. J. Vankat, W. H. Eshbaugh, and three anonymous reviewers provided helpful comments that greatly improved the work. M. Ortega created the map. Additionally, we would like to thank C. Gonzalez, S. Medellín, and D. Kaufman for their insight and assistance throughout the work. Finally, this work would not have been possible without the cooperation, assistance, and kindness of the people of San José. This work is for them.

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Submitted 9 March 1999. Accepted 29 November 1999. Associate Editor was David B. Wester.