

Female Fecundity Is Dependent on Substrate, Rather Than Male Abundance, in the Wind-Pollinated, Dioecious Understory Palm *Chamaedorea radicalis*

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ABSTRACT

We examined the impact of substrate, population density, and sexual composition on female reproductive success in harvested populations of the tropical understory palm *Chamaedorea radicalis*. Leaf harvest for the international floral greenery trade does not kill palms, but has been shown to reduce flowering frequency and has been projected to reduce population growth. Because *C. radicalis* is dioecious and wind-pollinated, a reduction in flowering density from leaf harvest or other anthropogenic factors may lower pollen movement between flowering conspecifics and lower fruit production. Such reduced fecundity in harvested populations can contribute to an Allee effect, where the per capita rate of population growth declines at low density. We tested for these effects by sampling *C. radicalis* along transects in ten populations, spanning a range of densities, during May (flowering peak) and August (fruiting peak) 2002. We applied path analysis using structural equation modeling (SEM) to test a set of hypothesized relationships between substrate, female size, several population parameters, and female fecundity. SEM models revealed that female fecundity was not dependent on any measure of population density or sexual composition, providing no evidence for an Allee effect. The strongest model ($R^2 = 92.9\%$) related *C. radicalis* reproductive output only to substrate, female size, flower number, and proportional fruit set. This model revealed that palms on rock outcrops were larger, produced more flowers, and had higher proportional fruit set than palms on the forest floor. This finding suggests that protection of females on outcrops should enhance population growth and viability.

Key words: Allee effect; Arecaceae; dioecy; fruit set; Mexico; path analysis; sex ratio.

POLLINATION SUCCESS IS OFTEN POSITIVELY CORRELATED with proximity to flowering conspecifics, and therefore individuals within low density or fragmented populations are susceptible to pollination limitation and reduced seed production. Such a decrease in per capita reproductive success with decreased population size or density is an example of the Allee effect (Allee *et al.* 1949, Stephens *et al.* 1999). The vulnerability of plant species to Allee effects depends on factors such as life history, breeding system, and phenology (Ghazoul 2005). For example, plants that are self-incompatible are more likely to suffer pollen limited seed set than self-compatible species, which have the potential to produce seeds in the absence of pollinators via self-pollination.

In this study, we examined the reproductive biology of the harvested palm *Chamaedorea radicalis*, which has several characteristics that predispose it to pollination limitation. Not only is *C. radicalis* dioecious, and therefore self-incompatible because each individual is either male or female, but this palm is wind-pollinated (Berry & Gorchov 2004). While wind pollination (anemophily) is common among temperate woody species, it is rarely found in tropical understory plants (Richards 1997), where low population densities and unfavorable environmental conditions (DiGiovanni & Kevan 1991) limit the movement of pollen between conspecifics. The influence of these constraints on wind pollination and their potential to cause Allee effects within tropical understory plants, however, is unclear, as most studies of these plants have focused on animal-pollinated systems (*e.g.*, House 1992, Cunningham 1995, Carlsson-Graner *et al.* 1998, Somanathan & Borges 2000, Wilcock & Neiland 2002, Ghazoul & Uma Shaanker 2004).

One of the best examples of the Allee effect in plants is *Banksia goodii*, where fruit set was correlated with declining population size because bird pollinators avoided the smallest and most isolated patches (Lamont *et al.* 1993). Several other studies of animal-pollinated plants have also reported low reproductive success at low population density due to density-dependent pollinator behavior (*e.g.*, Agren 1996, Kunin 1997, Ghazoul *et al.* 1998, Groom 1998, Somanathan *et al.* 2004). Although the Allee effect has not been reported among dioecious understory plants such as *C. radicalis*, studies of non-dioecious wind-pollinated species suggest that the efficiency of pollen transfer between conspecifics is affected by population density and the spatial distribution of pollen producers (Nilsson & Wästljung 1987, Smith *et al.* 1988, Allison 1990a, Knapp *et al.* 2001, Taylor *et al.* 2004), which in at least one case contributed to an Allee effect (Davis *et al.* 2004).

Understanding these relationships between population density and reproductive success is particularly important for land managers and conservationists who seek to maintain viable, productive populations of species that are of conservation or economic value (Ashman *et al.* 2004). Harvest practices that reduce population density can affect fecundity, lower population growth, and ultimately reduce density below some viability threshold, greatly increasing extinction risk (Dennis 1989, Groom 1998, Lande *et al.* 1998). Sustainable leaf harvest of *C. radicalis* is of particular concern within our study site, the El Cielo Biosphere Reserve (hereafter, El Cielo), where palm leaves are the only product that villagers are authorized to harvest and comprise the main source of income for most families (Peterson 2001). Although there is currently a concern of over-harvesting leaves, browsing by free-range livestock within El Cielo has a greater effect on *C. radicalis*, and has been projected by population models to cause population decline

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(Endress *et al.* 2004). However, these population models used for *C. radicalis*, as well as the published models for nearly all other dioecious plants (*e.g.*, Cipollini *et al.* 1994, Negrón-Ortiz *et al.* 1996, Bernal 1998), assume that female fecundity is independent of male density or sex ratio, which may not be true given the number of studies showing that the spatial distribution, sex ratio, and sexual identity of neighboring plants can influence female reproductive success (House 1992, Cunningham 1995, Carlsson-Graner *et al.* 1998, Somanathan & Borges 2000, Otero-Arnaiz & Oyama 2001, and others reviewed in Ghazoul 2005).

We previously showed that fecundity in one population of *C. radicalis* was not dependent on sexual composition or male density at the local neighborhood scale (5–10 m radius; Berry & Gorchov 2004). However, the reduced palm densities found in other areas of El Cielo that are subject to more intensive palm harvest and livestock browse have greater average distances between males and females, creating a situation where the efficiency of pollen transfer among conspecifics may be reduced. To test this, we expanded from the neighborhood to the population scale, comparing many different populations that spanned a range of densities and sex ratios. Specifically, we addressed the following research questions: (1) Is female fecundity dependent on population sexual composition and proximity to males? and (2) Is female fecundity dependent on population density?

METHODS

STUDY SITE.—This study was conducted near the villages of San Jose (23°02' N, 99°14' W) and Alta Cimas (23°03' N, 99°12' W) within El Cielo, Tamaulipas, Mexico. El Cielo encompasses 144,530 hectares of the Sierra de Guatemala mountain range on the eastern slope of the Sierra Madre Oriental (Casas-González & Requena-Lara 2005). Although temperature and precipitation is variable within El Cielo and is dependent on elevation (range 200–2200 m; Casas-González & Requena-Lara 2005), nearby Rancho del Cielo averages 2500 mm/yr of precipitation and has an average temperature of 13.8°C (Davis *et al.* 1997). El Cielo contains a wide range of vegetation types (González-Medrano 2005), and this study was conducted primarily in montane mesophyll forests at elevations of 950–1500 m.

SPECIES DESCRIPTION.—*Chamaedorea radicalis* Mart. (Arecaceae) is a dioecious understory palm considered vulnerable in Mexico (FAO 1997), where mature leaves are harvested for sale to international cut-foilage markets. Adult plants have approximately 4–8 pinnately compound leaves and usually appear stemless, because their stem forms a “heel” that grows into the substrate (Hodel 1992). Unlike most tropical understory palms, *C. radicalis* is primarily wind-pollinated (Berry & Gorchov 2004). Although individual palms can be found flowering throughout the year, the population has an annual flowering pulse from March to June (Endress *et al.* 2004). Pistillate flowers on female *C. radicalis* have three ovules per flower, and therefore the potential to produce three seeds per fruit. However, only one seed develops after pollination and all fruits are one-seeded

drupes (Berry & Gorchov 2004); therefore, for this study the terms “fruit number” is synonymous with “seed number.”

DEMOGRAPHIC MEASURES.—For this study, a population was defined as a group of individuals that were spatially segregated from other individuals of *C. radicalis*. Ten populations were chosen according to spatial isolation, which within El Cielo is mostly due to topography, such as two populations on either side of a mountain ridge or a population in an isolated valley. Male and female adult palms in each population were sampled using the nearest individual transect method (Barbour *et al.* 1999) during early May 2002 (flowering peak). Sampled palms were marked and then re-censused in August 2002 (fruiting peak). Adults included both reproductive size classes defined by Endress *et al.* (2004): small adults (10–24 leaflets per leaf) and large adults (> 25 leaflets).

In each population, we established three 50 m transects, a minimum of 20 m apart, perpendicular to the contour of the slope from valley to ridge top. At five random points along each transect we recorded data for the nearest adult, nearest flowering adult, and for flowering adults only, the distance to the nearest flowering neighbor. The following information was collected for each flowering adult and its nearest flowering neighbor: distance (m) from sample point along transect, sex, leaflet number of the youngest fully-expanded leaf (YFL), number of leaves, sum of the length of inflorescence branches (cm) from first to last flower, and substrate (rock outcrop or forest floor). Leaflet number on YFL was recorded as the primary measure of palm size, because previous research confirmed it to be a stronger predictor of female flower number and fruit number than leaf length (cm) or leaf number (Berry & Gorchov 2004).

For each female measured, flower number was counted as the sum of flower buds, open flowers, and flower scars on all inflorescence branches. Because of copious male flower production (*ca* 1000 flowers per individual) it was not practical to directly count flowers for each individual, and therefore, male flower number (*M*) was estimated from inflorescence length (*I*, in cm) with the equation: $M = -98.7 + 18.3 * I$. This equation from Berry & Gorchov (2004) is based on a significant regression of total male flowers on an inflorescence versus inflorescence branch length from first to last flower ($R^2 = 66.0\%$, $P < 0.0005$). For females only, we also recorded fruit number and distance to the nearest flowering male. For non-flowering adults, only size data was available, as it is impossible to sex palms without reproductive structures. For each population the density of adult palms and of flowering palms was estimated with the equation: density = $1/2$ (average distance from transect in m)² (Barbour *et al.* 1999). For flowering palms, the density of each sex was calculated as the percentage for each sex multiplied by the total flowering palm density of both males and females. Population sexual composition was quantified as population sex ratio (males:females) and flower sex ratio (staminate:pistillate). However, both parameters were operational values, as only flowering individuals were sexed. Two measures of fecundity were scored for each female: total fruit number (based on direct counts of mature fruit) and proportional fruit set (number of fruits divided by number of flowers).

PATH ANALYSIS.—Path analysis using structural equation modeling (SEM; Hatcher 1994, McCune & Grace 2002) was used to test if the data support a set of hypothesized relationships between substrate, palm size, several population parameters, and female fecundity (Fig. 1). SEM is particularly useful for complex data sets, because unlike more common analyses such as multiple regression, SEM allows for a statistical evaluation of multivariate hypotheses that contain multiple causal pathways and multiple dependent variables (McCune & Grace 2002). These hypotheses can be concisely presented in a path diagram (Fig. 1), where arrows indicate the causal relationships among the different variables. The postulated causal relationships among variables in each of our models were based primarily on information from previous field studies of *C. radicalis* (Jones & Gorchov 2000, Berry & Gorchov 2004, Endress *et al.* 2004).

The basic path diagram (Model 1, Fig. 1) proposed that female reproductive success is influenced by size, which is affected by substrate. Within El Cielo, rock outcrops (rocks protruding ≥ 1 m) have a higher density of large adult *C. radicalis* than forest floor substrates of rock or soil (Endress *et al.* 2004). Because size, which is measured by the number of leaflets on the youngest fully expanded leaf (YFL), is a significant predictor of flower number and fruit number in *C. radicalis* (Berry & Gorchov 2004), we expect these larger palms on rock outcrops to have more available resources, allowing a higher proportion of flowers to produce fruit (*i.e.*, higher proportional fruit set).

Alternative Models 2–4 included the same basic path diagram from Model 1, but incorporated additional pathways in order to test

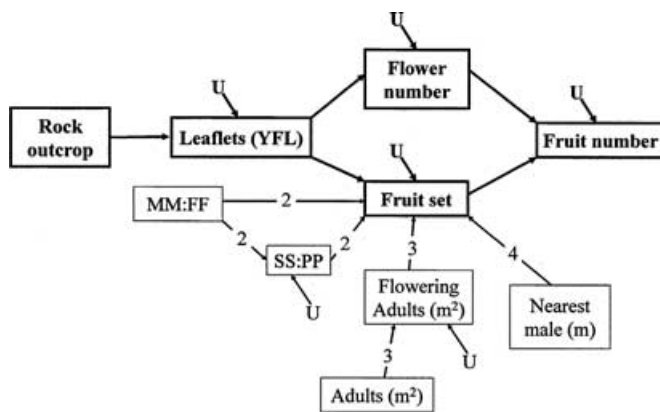


FIGURE 1. Path diagram of hypothesized determinants of reproductive success in female *C. radicalis*. Arrows indicate postulated causal relationships among variables and the letter U represents the total effect of unexplained factors on a given variable. The basic Model 1 includes only those paths without numbers and that are in bold. Numbers and non-bold text indicate paths that were added to the basic model to construct alternate models 2–4 (Table 3). For example, Model 4 is identical to Model 1 except for the addition of a path from nearest male distance to proportional fruit set. YFL = youngest fully expanded leaf; MM:FF = ratio of males to females in the population; SS:PP = ratio of staminate to pistillate flowers in the population.

the effect of different population parameters on female fruit number (Fig. 1). Specifically, Model 2 incorporated the impact of population sex ratio (MM:FF) and flower sex ratio (SS:PP), Model 3 incorporated palm density, and Model 4 incorporated nearest male distance (Fig. 1). Although models 3 and 4 appear to be addressing the same question, namely that palm abundance influences proportional fruit set, they approach the question based on different assumptions. As discussed by Allison (1990a), expressing plant abundance as plant density (Model 3) is appropriate for wind-pollinated plants because it emphasizes that the origin of pollen reaching a plant is diffuse rather than from a single point, especially in a tropical forest understory where wind direction is generally inconsistent. Alternately, the specific use of distance between flowering individuals as a measure of plant abundance (Model 4) takes into consideration the leptokurtic dispersal pattern of wind-borne pollen, which suggests that pollination is most influenced by the proximity of the nearest flowering neighbor, or nearest male in the case of dioecious species (Allison 1990b). Evaluation of both models enables us to infer whether plant density (Model 3) or plant spacing (Model 4) is more important to pollination in *C. radicalis*.

For each model described above, total fruit number was the final dependent variable and was used as the primary measure of reproductive output for *C. radicalis*. Fruit number is a comprehensive measure of individual reproductive success because it incorporates both flower number and proportional fruit set (fruits/flower), which is a measure of pollination success. Because proportional fruit set is calculated as a *ratio* of fruits to flowers, it controls for flower number, facilitating comparisons of pollination success between females of different size and flower production. Therefore, we constructed our models so that the paths of population parameters that tested for pollen limitation led to fruit number via proportional fruit set (Fig. 1). Other studies of plant reproductive success have also incorporated both fruit set and fruit number as fecundity parameters in SEM (*e.g.*, Mitchell 1994, Torres *et al.* 2002). However, unlike these studies of animal-pollinated plants, we did not include a path between flower number and proportional fruit set. Because *C. radicalis* is wind-pollinated and is not dependent on floral display to attract pollinators, we did not expect that individuals with more flowers would have greater pollination success and a higher proportional fruit set.

STATISTICAL ANALYSES.—All SEM analyses were performed using the CALIS procedure in SAS 8.02 (SAS Institute 1999), which allows simultaneous significance testing for individual path coefficients and uses the maximum likelihood method to estimate standardized path coefficients. All analyses were performed on the variance-covariance matrix. SEM provides a test of the null hypothesis that the theoretical model fits the data, expressed as a goodness-of-fit χ^2 . If the model is a good fit, then the χ^2 value will be small and the *P* value large (*e.g.*, > 0.05). However, this test can be influenced by factors such as departures from multivariate normality, sample size, and model complexity, and should therefore be interpreted with caution (Hatcher 1994). For this study we supplement the χ^2 test with the following additional fit indices: Goodness of Fit Index (GFI; Tanaka & Huba 1985), Bentler's (1989) Comparative Fit

Index (CFI), and Bentler and Bonnett's (1980) Normed Fit Index (NFI). Each of these indices ranges from 0–1, with values over 0.9 indicating a good fit (Hatcher 1994). Alternate models were compared with the basic model 1 using a χ^2 difference test, which tests whether each alternate model was significantly different ($P < 0.05$) than the basic model in its overall fit with the data.

To prepare the data for SEM, bivariate regression was used to identify the best linear transformations for indicator variables (Grace *et al.* 2000). The following parameters were transformed: flower number (natural log), fruit number (square root), proportional fruit set (arcsine square root), flowering adult density (inverse), adult palm density (inverse), nearest male (square root). Proportional fruit set was not measured directly, but was calculated from flower number and fruit number. Consequently, proportional fruit set and fruit number are not independent, and therefore allowing the path coefficient between these two variables to be freely estimated would artificially improve the model's overall fit (Loehlin 1987). To address this problem while still retaining this path in the model, we followed Albert *et al.* (2001) and Torres *et al.* (2002) in fixing the effect of proportional fruit set on fruit number to its standardized partial regression coefficient from the equation: Fruit number = $-5.08 + 1.41 * \text{Flower number} + 6.14 * \text{Proportional fruit set}$ ($R^2 = 93.1\%$, $F = 781.3$, $df = 117$, $P < 0.001$). Fixing this value prevented the SEM from estimating a coefficient for this path, and therefore the effect of proportional fruit set on fruit number was not included in the calculations of goodness-of-fit statistics for any of the models. However, fixing this path coefficient does not mean that the data for proportional fruit set are fixed (*i.e.*, there is still variation, and therefore error, when estimating proportional fruit set), and because of the variation in this data it was still possible for SEM to calculate other important statistics for proportional fruit set, such as R^2 , t values, total variance, and unexplained variance (U). Except for this strong correlation between proportional fruit set and fruit number, all variables were free of multicollinearity.

Sample size for all SEM models was the total number of individual adult females from the ten populations ($N = 118$). Pooling the data is appropriate for these analyses because preliminary results showed that population did not correlate with any of the variables included in our models. For each population parameter (adult density, flowering adult density, sex ratio [MM:FF], flower sex ratio [SS:PP]), a value was calculated for each population ($N = 10$; Table 1), and then assigned to each female within that population. For all other parameters, values were measured directly from each individual female ($N = 118$; Table 2).

RESULTS

POPULATION DENSITY AND SEXUAL COMPOSITION.—Across the ten populations, an average of 20.7 percent (SD = 9.1%, $N = 10$) of sampled adults produced inflorescences during the 2002 flowering season. As most palms did not flower, estimated flowering adult palm density was much lower than the overall adult palm density (Table 1). Mean flowering palm density varied con-

TABLE 1. Population density and operational sex ratio parameters from populations of *Chamaedorea radicalis* within El Cielo, Tamaulipas, Mexico. Reported for each parameter are population values calculated from 15 random points sampled along three transects. Also reported for each parameter is an overall mean and standard deviation ($N = 10$ populations).

Population	Adult density (m ²)	Flowering density (m ²)	Male density (m ²)	Female density (m ²)	Sex ratio	Floral sex ratio
1	0.113	0.033	0.017	0.016	1.08	12.6
2	0.727	0.109	0.066	0.044	1.78	21.4
3	0.377	0.030	0.015	0.014	1.36	11.8
4	0.595	0.040	0.022	0.018	1.59	22.5
5	0.215	0.026	0.018	0.008	3.00	51.7
6	0.789	0.047	0.025	0.022	1.33	11.1
7	0.601	0.053	0.021	0.032	0.75	4.0
8	0.109	0.030	0.016	0.014	1.44	20.9
9	0.814	0.032	0.020	0.011	2.22	15.1
10	0.200	0.038	0.022	0.016	1.90	14.5
Mean	0.454	0.044	0.024	0.019	1.65	18.6
SD	0.283	0.024	0.015	0.011	0.63	12.9

siderably among the populations, but within several populations, flowering male density and flowering female density were similar (Table 1). The operational sex ratio (MM:FF) of most populations appeared male-biased, with only one population having fewer males than females, and the overall mean sex ratio of 1.65 males to females was statistically greater than an even ratio of 1.0

TABLE 2. Female size and fecundity parameters for *Chamaedorea radicalis*. Reported for each parameter are population means calculated from N females sampled within each population. Also reported is the overall mean, standard deviation, and the coefficient of variation (CV) for each parameter based on pooled data for all females ($N = 118$). YFL = youngest fully expanded leaf.

Population	N	Leaf number	Leaflet number (YFL)	Inflorescence length (cm)	Flower number	Proportional fruit set	Fruit number
1	10	2.7	31.3	23.8	46.2	0.12	9.6
2	12	2.7	33.5	16.7	40.8	0.27	13.6
3	12	2.2	29.4	16.2	56.1	0.13	9.1
4	13	2.4	26.7	15.2	50.6	0.16	8.7
5	9	2.4	28.8	16.6	53.7	0.18	9.6
6	14	1.9	31.4	19.9	62.1	0.23	13.9
7	18	2.1	29.9	17.6	60.8	0.25	18.6
8	11	2.6	33.0	15.5	52.6	0.33	21.1
9	10	1.7	29.4	18.0	64.5	0.12	7.5
10	9	2.4	29.5	15.9	51.6	0.25	16.2
Mean		2.3	30.3	17.5	53.9	0.20	12.8
SD		0.3	2.0	2.6	7.3	0.07	4.6
CV (%)		13.6	6.6	14.9	13.5	35.00	35.9

($P = 0.003$). Operational floral sex ratio showed similar variation among the populations (Table 1), but males produced considerably more flowers per individual than females, and therefore, all populations produced more staminate than pistillate flowers.

FEMALE SIZE AND FECUNDITY.—Mean female size, as measured by leaf number and leaflet number, varied among the different populations (Table 2). Likewise, mean female inflorescence length and flower number, which measure reproductive effort, varied across the ten populations. However, the parameters that varied most among populations were proportional fruit set (which measures pollination success) and fruit number (which measures reproductive output). An analysis of the same size and reproductive data partitioned by substrate type revealed that palms on rock outcrops were significantly larger (more leaflets on YFL), developed longer inflorescences with more flowers, and produced on average nearly twice as many fruits as those on the forest floor (Fig. 2). In contrast, results from two-sample t -tests showed that mean proportional fruit set and leaf number were not significantly different ($P > 0.05$) between the substrates.

PATH ANALYSIS.—Estimation of the basic model 1 (Figs. 1 and 3) revealed a non-significant χ^2 -value, implying a good fit with the data. More specifically, a non-significant test statistic from this analysis indicated that the covariance structure specified in the model should be accepted given the covariance structure of the data. All other goodness-of-fit indices (GFI, CFI, NFI) were near 1.0, providing additional evidence that this model was consistent with the data (Table 3). This model explained a large proportion of the variation in fruit number ($R^2 = 92.9\%$) and smaller but still significant proportions of variation in the other dependent variables: proportional fruit set ($R^2 = 13.9\%$), flower number ($R^2 = 22.1\%$), and leaflet number ($R^2 = 15.3\%$). R^2 -values in these analyses represent the percent variance in these variables explained by their direct antecedents in the model (Hatcher 1994). All the path coefficients in this model were of meaningful magnitude and were statistically

significant ($P < 0.05$), and results of diagnostic tests did not reveal any paths that might be added or deleted to improve the model.

Model 2 was identical to the basic Model 1 with the addition of the paths from population sex ratio and flower sex ratio to female proportional fruit set (Fig. 1). When compared, the two models were not statistically different ($P > 0.05$), and consequently the goodness-of-fit indices for Model 2 were very similar to Model 1 (Table 3). The additional paths in this model had little or no effect on the R^2 values for most of the dependent variables, although population sex ratio was a very good predictor of flower sex ratio ($R^2 = 60.0\%$). The paths from sex ratio and flower sex ratio to proportional fruit set were the only ones in the model that did not have statistically significant t values ($P < 0.05$), indicating that neither of these parameters explained a significant amount of the variation in proportional fruit set.

Model 3, which added paths for palm density to the basic model (Fig. 1), had a significant χ^2 goodness-of-fit, suggesting a very poor fit with the data, and it was a significantly poorer fit than Model 1 (Table 3). As with Model 2, the additional paths in this model had little impact on the R^2 -values of most dependent variables, although adult palm density explained a reasonable proportion of the variance in flowering palm density ($R^2 = 28.0\%$). However, the path from flowering palm density to proportional fruit set was not statistically significant and the coefficient for this path was not meaningful in magnitude (< 0.005), suggesting that flowering palm density is not a good predictor of proportional fruit set.

Model 4 added a path to the basic Model 1 from nearest male distance to female proportional fruit set (Fig. 1). This model was not statistically different from Model 1, and there was very little difference among the goodness-of-fit test statistics of the two models (Table 3). The only path that was not statistically significant was from nearest male distance to proportional fruit set. This result suggests that while the overall model was acceptable, female proportional fruit set was not dependent on the distance to the nearest flowering male and that path did not contribute to the overall explanatory power of the model.

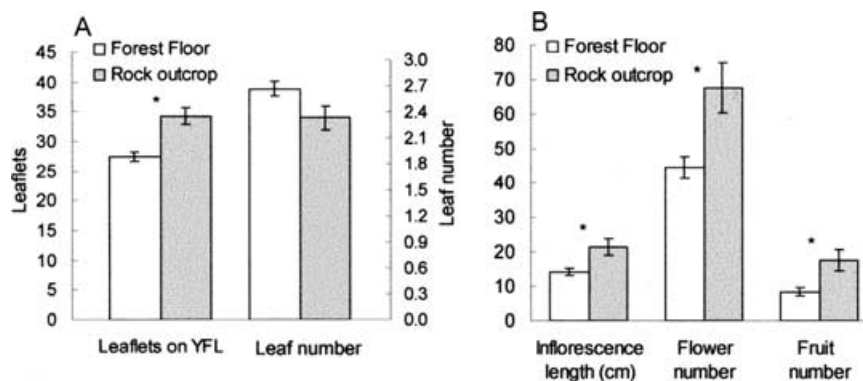


FIGURE 2. Mean size (A) and fecundity (B) variables for flowering female *Chamaedorea radicalis* sampled in May and August 2002 on two substrate types. Forest floor includes both rock and soil substrate types. Mean ($\pm$ SE) values were calculated from data pooled from ten populations ($N = 70$ females on forest floor and 48 on rock outcrops). Significant differences ($P \leq 0.05$) according to a two-sample t -test are indicated by an asterisk (*). YFL = youngest fully expanded leaf.

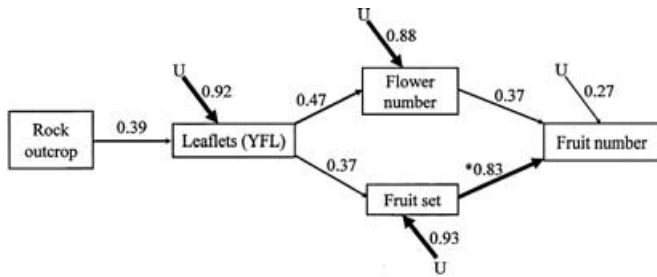


FIGURE 3. Path diagram of Model 1 showing the effects of substrate and size on female fruit number in populations of the palm *Chamaedorea radicalis*. The thickness of each arrow corresponds with the size of each standardized path coefficient, which is labeled above each arrow. For this model all paths were significant ($\alpha = 0.05$) and positive. *Fixed to its partial regression coefficient (see Methods).

For each model, unexplained variables (U) accounted for a substantial portion of the variance in the dependent variables. Therefore, to statistically test the explanatory power of the models, we compared each model against a hypothetical null model where there existed no paths or correlations among any of the variables. In addition to testing the usefulness of our models, the null model also provided a baseline of χ^2 values to compare against the other models (Hatcher 1994). For each of the models proposed in this study there was a large and statistically significant ($P < 0.05$) reduction in χ^2 compared to the null model (Table 3), providing strong support for each model. The most dramatic improvement in χ^2 was for Model 1, which was also the most parsimonious model, as it accounted for as much of the variance in the data as the other models with fewer paths.

DISCUSSION

POPULATION DENSITY, SEXUAL COMPOSITION, AND FRUIT SET.—Although there was considerable variation in both adult density and flowering density among the different populations, we found no evidence that flowering females in low-density populations suffered from reduced fecundity, and therefore no evidence for an Allee effect in these populations. Indeed, Model 3, which incorporated the paths for population density and flowering density, was the only model to fail the χ^2 goodness-of-fit test (Table 3). And while the models that included paths to proportional fruit set from population sex ratio (Model 2) and distance to the nearest flowering male (Model 4) passed the overall goodness-of-fit tests, these models were acceptable despite the addition of these parameters, not because they added anything to the explanatory power of the overall model. These models had lower goodness-of-fit scores than Model 1, which did not include any population parameters, indicating that the additional paths decreased the accuracy of the model. Therefore, these findings suggest that at current population levels, differences in reproductive output are not driven by population density or male distribution. This lack of dependence of female fecundity on male density is

TABLE 3. Goodness-of-fit indices for the basic path analysis Model 1 and alternate models (Fig. 1) describing reproductive output in female *Chamaedorea radicalis*. Reported are χ^2 difference comparisons between model 1 and each of the alternate models 2–4, as well as the null model, which represents a hypothetical path diagram where no paths exist among the variables. A significant χ^2 difference test ($P < 0.05$) indicates that the two path models being compared have statistically different χ^2 goodness-of-fit values; the model with the lower χ^2 is the better fit to the data.

Model	Goodness-of-fit						Comparison		
	GFI	CFI	NFI	χ^2	df	P	χ^2	df	P
Model 1	0.98	1.00	0.98	5.9	6	0.43	—	—	—
Model 4 ^a	0.98	1.00	0.98	6.8	9	0.66	0.9	3	NS
Model 2 ^b	0.96	0.99	0.97	17.8	13	0.17	11.9	7	NS
Model 3 ^c	0.94	0.97	0.94	24.7	14	0.04	18.8	8	< 0.025
Null Model	—	—	—	385.6	10	< 0.005	379.7	4	< 0.005

Notes: $N = 118$. GFI = Goodness of Fit Index, CFI = Bentler's Comparative Fit Index, NFI = Bentler-Bonnett Normed Fit Index. For each of these indices values range from 0–1, with values over 0.9 indicating a good fit.

^aIdentical to Model 1, except path from nearest male distance was added.

^bIdentical to Model 1, except paths from population sex ratio (MM:FF) and flower sex ratio (SS:PP) were added.

^cIdentical to Model 1, except paths from adult palm density and flowering palm density were added.

typically assumed but rarely tested in population models of dioecious plants (e.g., Cipollini & Whigham 1994, Negrón-Ortiz *et al.* 1996, Bernal 1998), and enables birth to be modeled as a female-dominant process based solely on the demography of females.

However, we would caution that these findings do not imply that female fecundity could never be limited by male distribution or abundance. Leaf harvest and livestock management practices that negatively impact growth, survival, or flowering and fruiting frequencies may drive down flowering palm densities in the future to a point where reproduction is pollen limited. For example, the impacts of herbivory from free-range livestock are projected to reduce *C. radicalis* populations in forest areas exposed to livestock (Endress *et al.* 2004), and there is evidence from other wind-pollinated plants that long-term animal browsing can reduce plant density and pollen production to a level where seed production is limited (Allison 1990b). While the negative effects of leaf harvest and livestock browsing on *C. radicalis* flowering frequency have been well documented (Endress *et al.* 2004), the impacts on operational sex ratios have not been elucidated. Although we found no evidence that *C. radicalis* proportional fruit set was affected by current levels of variation in sex ratio and flower sex ratio, local sex ratio was shown to affect fruit initiation in another understory palm, *Calyptranthes ghiesbreghtiana* (Cunningham 1995).

PALM SIZE AND FECUNDITY.—In the absence of pollen limitation, natural differences in available resources, such as light, water, or nutrients, are often the cause of variation in plant fecundity. Since there

is assumed to be a trade-off between investments in stored reserves, vegetative growth, and reproduction (Chapin *et al.* 1990), females with more available resources are better able to increase fecundity by either producing more flowers or increasing proportional fruit set (*i.e.*, aborting fewer flowers). Although it varies among species, several studies have shown increased flower production in response to an increase in some limiting resource, such as light (Chazdon & Fetcher 1984, Niesenbaum 1992, Niesenbaum 1993, Cunningham 1997a, Svenning 2002) or water (Delph 1986, Herrera 1991). However, because most studies do not measure natural resource availability, plant size parameters are often substituted as a surrogate measure of plant resources, a substitution that has been justified by several studies showing that plant size is a good predictor of resource availability (Solbrig 1981, Cunningham 1997a, Sugiyama & Bazzaz 1998, Svenning 2002). Plant size has been shown to impact both flower production and flowering frequency (Aker 1982, Snow & Whigham 1989, Cipollini & Stiles 1991, Herrera 1991), and for palms in particular, fecundity correlates with size parameters such as height (Oyama 1990, Scariot *et al.* 1995, Barot & Gignoux 1999) and leaf number (Barot & Gignoux 1999).

For *C. radicalis*, much of the variation in female reproductive output was explained by the greater flower production and pollination success (proportional fruit set) of larger individuals (Fig. 3), which is generally consistent with our earlier neighborhood-scale study that reported significant effects of female size on both flower number and fruit number (Berry & Gorchov 2004). However, by using path analysis with SEM in this study, we were able to go beyond basic correlations of palm size and fecundity, and test for specific causal relationships; an approach that has been successfully applied to study reproduction in other plants (*e.g.*, Murren & Ellison 1996, Albert *et al.* 2001). For example, the present study across several populations revealed a significant relationship between palm size and proportional fruit set that we did not detect at the neighborhood scale (Berry & Gorchov 2004).

Females on outcrops had higher reproductive output than those on the forest floor. While path analysis indicates that this difference is primarily due to the larger size of females on outcrops, an alternative explanation is that females on rock outcrops receive greater quantities of unimpeded pollen by being raised above the surrounding vegetation. This explanation is not supported in our system because females on rock outcrops did not have significantly higher proportional fruit set (pollination success) than females on the forest floor. Rather, our findings indicate that there is sufficient pollen transfer to *C. radicalis* females on both substrates, and therefore the lower proportional fruit set found in smaller females is likely due to fruit abortion caused by resource limitation.

OTHER FACTORS INFLUENCING FRUIT NUMBER.—Although not examined in this study, a plant's current level of reproduction could be influenced by the energetic costs associated with previous reproductive events (Snow & Whigham 1989). Furthermore, there is evidence that for sexually dimorphic plants, such as *C. radicalis*, the cost of reproduction is greater for females than males (Cipollini & Whigham 1994, Nicotra 1999). This greater cost of reproduction for females is one likely explanation for the slight overall male bias

we observed in operational sex ratios. Being freed of the cost of fruit production, males in these populations likely flower with greater frequency than females of similar size, which has the consequence of reducing the likelihood of pollen limitation. However, to fully assess the impact of resources on reproduction, it would be necessary to also incorporate data from mature individuals that are not flowering in the current year.

An alternative explanation to pollen or resource limitation is that some of the observed variation in female fruit production was due to pathogens or flower and fruit predators. If seed predation is high enough, it can overwhelm the effects of pollen limitation on seed production that might otherwise be present (Cunningham 1997b). Several types of insects visit *C. radicalis* flowers and fruits, and some insects cause significant damage to immature fruits (Berry & Gorchov 2004). However, in this study there was no obvious or widespread damage from insect pests on *C. radicalis* fruits, suggesting that predation did not play a large role in the variation of fruit production among females.

THE ROLE OF SUBSTRATE ON SIZE AND FECUNDITY.—Our finding that females on rock outcrops were larger and had a greater fruit number suggests that growth and/or survival of these palms differs from those on other substrates. This could explain differences in palm abundance and population structure between rock outcrops, rock, and soil substrates previously reported for El Cielo (Jones & Gorchov 2000, Endress *et al.* 2004). The distribution and abundance of other Neotropical palms have also been shown to correlate with topographic–edaphic variables (Clark *et al.* 1995, Svenning 2001). One likely explanation for the observed size and fecundity differences of palms on rock outcrops in El Cielo is the inaccessibility of these individuals to livestock, such as cattle, mules, and burros that range freely in the forests. Browsing from livestock appears to account for more herbivory on *C. radicalis* than native herbivores, and has been shown to adversely affect population growth (Endress *et al.* 2004). The greater fecundity of females on inaccessible rock outcrops suggests that this may play a crucial role in population persistence. Not only are rock outcrops more productive microsites for *C. radicalis*, seed dispersal from rock outcrops has been projected to sustain the rest of the population, where the population growth rate is otherwise below the replacement rate of 1 (E. Berry, unpublished data). Thus, population dynamics can be modeled as a variant of the source-sink model (*sensu* Pulliam 1988) based on the demographic variation between rock outcrops (putative sources) and the forest floor (putative sinks).

IMPLICATIONS FOR CONSERVATION.—For species such as *C. radicalis* that are of conservation or economic value, it is important to understand how patterns of human disturbance not only influence plant reproduction, but how these impacts ultimately affect population viability. While not all variation in seed production at the plant level translates into an effect on population growth, it has been postulated that species whose population dynamics are most sensitive to changes in seed production are those with life-history characteristics such as no clonal growth, few reproductive episodes, and lack of a significant seed bank (Ashman *et al.* 2004). These life-history traits are found in *C. radicalis* and are common among

other species of palms, many of which are harvested from tropical forests as important non-timber forest products (Uhl & Dransfield 1987, Balick & Beck 1990). There are 21 commercial species in the genus *Chamaedorea* alone, and due to a large demand from international floral and horticulture markets, several of these species have been overexploited in their native habitats and are currently threatened (CEC 2002). The influence of harvest on patterns of reproduction has been studied in few species, and further investigation into the causes and consequences of reduced fecundity in these populations is required to help ensure the long-term viability of these economically important species.

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