

Reproductive biology of the dioecious understory palm *Chamaedorea radicalis* in a Mexican cloud forest: pollination vector, flowering phenology and female fecundity

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Abstract: The reproductive biology of the dioecious understory palm *Chamaedorea radicalis* was investigated in order to identify the primary pollen vector and quantify the relationship between female fecundity and local neighbourhood sexual composition. The study was conducted in a montane mesophyll forest within the El Cielo Biosphere Reserve, Tamaulipas, Mexico. The species is considered vulnerable in Mexico and there are concerns about the sustainability of leaf harvest. We determined that wind is the primary pollen vector, based both on floral and pollen morphological characters, and on a pollinator enclosure experiment. Successful wind pollination of this understory palm was facilitated by the extended flowering period of males, which allows one male to be a source of pollen to receptive females for as long as a month. The number of flowers and fruits borne on a female were dependent on female size, however, no size parameter correlated well with fruit set. Fruit set was also not dependent on local sexual composition, male density or distance to the nearest male, suggesting that in this study area female reproductive success is not limited by the availability of pollen.

Key Words: Areaceae, *Chamaedorea radicalis*, dioecy, fruit set, Mexico, sex ratio, wind-pollination

INTRODUCTION

Reproductive success in dioecious systems is subject to many different ecological constraints. Although inbreeding is avoided, sexual reproduction requires a vector to transfer pollen between conspecifics. This dependence entails different risks associated with various pollination mechanisms: animal-pollinated species are bound by the ecological constraints of the foraging distance and the availability of pollinators (Somanathan & Borges 2000), while wind-pollinated systems are subject to factors such as impaction (on vegetation), precipitation and thermal processes (DiGiovanni & Kevan 1991). Each of these risks potentially affects female fecundity in dioecious populations.

At local scales, specific ecological factors such as spatial distribution, sex ratio and sexual identity of neighbours have been shown to influence female reproductive success. For example, the distance of the nearest flowering male negatively correlated with fruit set (fruits per flower) for the tropical dioecious species *Neolitsea dealbata*, *Litsea lefeana* and *Diospyros pentamera* (House 1992). The same

study also revealed a negative correlation between the amount of pollen trapped at females and the distance to local males (*Neolitsea* and *Diospyros*), and that for *Neolitsea* the amount of pollen trapped was positively related to fruit set. For the dioecious perennial herb *Silene dioica*, Carlsson-Graner *et al.* (1998) found that pollen availability limited seed production in populations with female-biased sex ratios. Anthropogenic influences may also compound these effects in disturbed plant communities. Somanathan & Borges (2000) documented a strong, negative correlation between the distance to the nearest male and both insect visitation and fruit set in three dioecious species (*Diospyros montana*, *D. sylvatica* and *Garcinia talbotii*) that are found in a fragmented, disturbed cloud-forest community in India, but no such effect on female reproductive success in a similar, undisturbed forest.

Most pollination research in the tropics has focused on entomophilous plant species, and indeed each of the above-reported local neighbourhood effects are mediated through pollinator behaviour. Little is known, however, about these effects for wind-pollinated tropical plants

(Bawa & Crisp 1980). A recent investigation of the wind-pollinated understory palm *Chamaedorea alternans* reported pollen limitation in some females, as indicated by a negative correlation between fruit production and distance to flowering males (Otero-Arnaiz & Oyama 2001); a result similar to those reported in some dioecious insect-pollinated plants.

From a management perspective, the ecological constraints associated with dioecy make it difficult to assess how reduction in male density or distribution would affect reproduction. *Chamaedorea radicalis* is one of several dioecious understory palms in the genus *Chamaedorea* considered vulnerable in Mexico or Central America due, at least in part, to harvest of leaves for sale as florist's greenery (Hodel 1992). Sustainability of the species as a non-timber forest product is of particular concern to villagers of El Cielo Biosphere Reserve for whom *C. radicalis* leaves are the only natural product that they are authorized to harvest. Jones & Gorchov (2000) found no significant correlation between palm density in forest stands and proximity to human settlement suggesting sustainable harvesting, however, they also observed that palm populations were more isolated near villages, possibly due to land uses such as grazing or agriculture. Endress *et al.* (in review) found that both leaf harvest and browsing by donkeys reduced survival rates, and using stage-structured transition (Lefkovich) matrices, projected browsing would reduce population growth rate in the long term. In nearly all published models for dioecious plants, a simplifying assumption is made that female fecundity is independent of male density or sex ratio (Bernal 1998, Cipollini *et al.* 1994, Negrón-Ortiz *et al.* 1996), but the dependence of female fecundity in systems studied by Carlsson-Graner *et al.* (1998), House (1992), Otero-Arnaiz & Oyama (2001), and Somanathan & Borges (2000) call this assumption into question. Relaxing the assumptions of the female dominant model necessitates development of a two-sex model (Caswell 2001, Meagher 1982) that parameterizes the effect of males on female fecundity.

This study examined the reproductive biology of *Chamaedorea radicalis* (Arecaceae), specifically addressing the following questions: Are insects or wind the primary pollen vector for *C. radicalis*? Is reproductive success of female *C. radicalis* dependent on local neighbourhood spatial distribution and sexual composition?

STUDY SITE AND SPECIES

Study site

This study was conducted near the village of San José (23°08'N, 99°09'W) within the El Cielo Biosphere Reserve, Tamaulipas, Mexico. El Cielo straddles the

Sierra Madre Oriental with elevations of 200–2200 m (Perrine & Gorchov 1994). The study sites are located in a montane mesophyll forest community at elevations of approximately 1400–1600 m (Puig & Bracho 1987). Although temperature and precipitation within the Reserve are dependent on elevation, nearby Rancho del Cielo averages 2500 mm y⁻¹ of precipitation and has an average temperature of 13.8 °C (Davis *et al.* 1997). El Cielo contains a wide range of vegetation types (Davis *et al.* 1997, Perrine & Gorchov 1994), including the northernmost extension of tropical cloud forest in North America (Rzedowski 1978).

Species description

Chamaedorea radicalis Mart. is one of approximately 100 *Chamaedorea* species, all of which are dioecious understory palms. *Chamaedorea radicalis* is considered the most cold-tolerant and northerly *Chamaedorea* (Hodel 1992), and in El Cielo is found at elevations above 1400 m (Mora-Olivo *et al.* 1997). Adult plants have approximately 4–8 pinnately compound leaves, while seedlings have bifid leaves (Hodel 1992). Most adult individuals appear stemless, because their stem typically forms a 'heel' that grows into the substrate. Individuals that develop with an erect, above-ground stem, however, can reach 2–4 m in height (Gorchov & Endress, in press).

The inflorescences on females of *C. radicalis* are unbranched or branched with 2–10 rachillae. Male inflorescences are branched with as many as 20 rachillae (Hodel 1992). Although individual palms can be found flowering at almost any given time throughout the year, the population has an annual flowering pulse from March to June (Endress *et al.*, in review).

No pollination vector has been suggested for *C. radicalis* and different modes of pollen dispersal are found within the genus. Previously described insect-pollinated *Chamaedorea* species include *C. costaricana* (Henderson 1986), *C. ernesti-augustii* (Hodel 1992) and *C. wendlandiana* (Croat 1978). Wind-pollination was reported for *C. alternans* (Otero-Arnaiz & Oyama 2001), and *C. exorrhiza* (Bawa *et al.* 1985). For *C. pinnatifrons* wind is the primary vector, but pollen release is dependent on insects disturbing the anther (Listabarth 1992); a pollination syndrome referred to as insect-induced wind pollination.

METHODS

Reproductive biology

The reproductive biology of *C. radicalis* was examined via a pollinator exclusion experiment and observations

of reproductive characteristics, including flowering phenology, morphology of floral parts, morphology of external pollen features and identification of insect visitors. Some insect visitors were also collected for identification at El Instituto de Ecología, UAT in Tamaulipas, Mexico and El Instituto de Ecología A.C., Xalapa, Veracruz, Mexico.

Phenological data were collected daily for flowering females ($n=11$ inflorescence branches on 8 plants) and flowering males ($n=10$ branches on 4 plants) throughout the entire field season (May–June 2001). For both sexes the following qualitative information was collected for each inflorescence branch: date first flower opened, if flowering sequence was acropetal or basipetal, date of last blooming flower, and inflorescence branch length at beginning and end of anthesis. For individual flowers the following was recorded: date perianth first opened, date anther first dispersed pollen (males) or stigma first became receptive (females), and date flower first appeared past anthesis. For females the date that first immature fruits appear was also recorded. The criterion for fruit development was when the ovary, which is normally ≤ 4 mm (Hodel 1992), and typically in this population ~ 2 mm (*pers. obs.*), swelled to ≥ 4 mm in diameter while becoming oblong in appearance. The oblong appearance is a reliable indicator of successful pollination, because in pollinated *C. radicalis* flowers, only one of three ovules develop into a seed, making immature fruits appear swollen on one side (*pers. obs.*).

Inflorescence, flower and pollen morphology were examined and described for comparison to wind and insect pollination syndromes. Initial observations were made in the field with a $14\times$ hand lens. Some flowers were stored in small vials with FAA preservative and later examined under a scanning electron microscope (SEM). Pollen was collected on male flowers in small glassine envelopes for later examination in the laboratory using micro-acetolysis similar to the technique of Genise *et al.* (1990). This method uses a mixture of anhydrous acetic acid and sulphuric acid, which is heated to prepare pollen for examination under a light microscope. We also examined flowers from both sexes and pollen under SEM.

Male and female flowers were checked for the presence of nectar using Diastix[®] reagent strips that are commonly used to detect sugar in urine. This particular test tape indicates the presence of glucose in concentrations as low as 2% (2 g dL^{-1}). One reagent strip per flower was dipped in the droplet that formed on female flowers and one was pressed against each male flower, since no liquid was observed.

Insect exclusion similar to Sacchi & Price (1988) was used to test the effect of insects and wind on pollination. To determine potential of fruit set in the absence of pollinators, one treatment involved bagging female inflorescence branches with a fine nylon mesh

(pore size $\sim 1500\ \mu\text{m}$) that excluded visitors, but still permitted wind-dispersed pollen. Although pollen was confirmed to pass through the mesh by visual inspection of wind-blown pollen, it is likely the mesh had some effect on wind velocity, potentially restricting pollen movement. A second treatment used pollen bags for crop plants (pore size $\sim 500\ \mu\text{m}$) to exclude both pollinators and wind-dispersed pollen from female inflorescences. The final treatment was unmanipulated female inflorescences exposed to both wind and insect pollination modes (open pollination). Fifteen females were randomly assigned to each of the three treatments. Plants observed to have suffered insect damage, however, were removed from the analysis, which meant sample sizes for some treatments were less than 15. Fruit-set data (Fruit set = number of mature fruit/number of flowers) from this experiment were analysed with a one-way ANOVA to test for differences among the treatment-level means. Tukey's pairwise comparisons were employed to compensate for unequal sample sizes with a family error rate of 0.05 and an individual error rate of 0.0196.

Factors influencing female fecundity

The influence of local neighbourhood composition and spatial distribution on female fecundity was examined through an analysis of total fruit and fruit set for 33 focal females. Although fruit number may seem the most direct parameter for quantifying reproductive success, calculating fruit set as a ratio of flowers to fruit is more common (House 1992, Rathcke 2000, Somanathan & Borges 2000), as it controls for initial flower number, facilitating comparisons among different-sized females. Flower number for each male and female was estimated from the sum of inflorescence branch lengths using separate regressions (male, female) of total number of flowers on an inflorescence vs. the inflorescence length from first to last flower. This relationship was quantified by manually counting flower number and measuring inflorescence length for individuals of both sexes.

For this study the local neighbourhood size was established at two different thresholds of 10 m and 5 m radial distance from the focal female. These threshold distances are plausible for this species based on field observations of density and distribution of flowering palms. *Chamaedorea radicalis* is often found in small groups of several individuals patchily distributed throughout the forest understorey with few palms between the patches (*pers. obs.*). Results from the smaller radius indicate the influence of only the most immediate flowering conspecifics, while the larger radius encompasses most palms within a given patch. To test for differences among patches in fruit number or fruit set, we used patch as a random factor in a one-way ANOVA. For multiple

Table 1. Flowering duration and flower production for females and males of *Chamaedorea radicalis* at El Cielo Biosphere Reserve, Mexico. Means \pm 1 SE and results of two-sample t-tests are presented for each parameter.

Parameter	Females		Males		t	P
	n	Mean \pm SE	n	Mean \pm SE		
Inflorescence flowering duration (d)	11	10.6 \pm 0.5	10	31.0 \pm 1.2	-15.8	< 0.005
Individual flower duration (d)	21	6.0 \pm 0.7	14	2.6 \pm 0.5	4.0	< 0.005
Flower number per inflorescence branch	90	46.8 \pm 2.0	17	207.8 \pm 6.7	-23.1	< 0.005
Flower number per inflorescence*	31	63.9 \pm 6.4	30	1086.0 \pm 126.0	-8.1	< 0.005

* Estimated values for male inflorescences based on the sum of inflorescence branch lengths (cm), using the regression equation: flower number = $-98.7 + 18.3 \times$ infl. length ($R^2 = 66.0\%$, $P < 0.0005$).

comparisons we employed Tukey's pairwise comparisons (family error rate = 0.05).

The following quantitative information was collected for each focal female: flower number (using estimator as calculated above), number of immature fruits, fruit set, number of leaves, length of youngest fully expanded leaf, number of leaflets on youngest leaf and height of above-ground stem. For the local neighbourhood around each focal female we recorded the sex of all individuals that had flowering periods overlapping the focal female (to calculate the operational sex ratio MM:FF), distance of nearest flowering male, number of male flowers (estimated from inflorescence lengths) and number of female flowers. From this information we also calculated for both radial thresholds the flower sex ratio (MM:FF), and the density of flowering palms.

We used linear regression to determine which independent variable best predicted each measure of female fecundity (fruit set, fruit number) at each neighbourhood size (radius). To meet the model's assumption of normally distributed data, the predictor variable inflorescence length was square-root-transformed, and the response variables flower number and fruit number were \log_{10} -transformed. We also used stepwise regression (Alpha 0.15 to add or remove), including local composition parameters and the strongest single predictor from the focal female parameters, to construct a multiple regression model using Number Cruncher Statistical Software (Hintze 2001).

RESULTS

Flowering phenology

Males and females within the study population flowered synchronously during most of the field season (May–June 2001). All females and nearly all males were past anthesis by 8 June 2001. Each palm produced only one inflorescence over the duration of this study. Individual inflorescence branches of both sexes showed a basipetal flowering sequence, however, while male inflorescences always flowered basipetally, female stalks showed this

characteristic in only 9 of 11 branches. The two sexes also exhibited differences in flowering phenology and flower production (Table 1). Staminate flowers averaged fewer days at anthesis than pistillate flowers, but due to the much greater flower production on male inflorescences, total mean flowering progression (first flower at anthesis to last flower past anthesis) averaged three times longer on male than female inflorescences. Additionally, male inflorescences averaged almost five branches each, while most females had an unbranched inflorescence (79% unbranched, $n = 33$).

Floral and pollen morphology

Staminate flowers (Figure 1a) of *C. radicalis* are small (2–3 mm diameter), green and inconspicuous with no noticeable scent or nectar. The perianth is composed of three sepals and three petals, which are free, distinct and light green in colour. The top edge of the calyx turns a dark shade of brown as the flower opens. There are six free and distinct stamens with anthers borne on long, thin filaments that are exerted beyond the rim of the perianth during anthesis. The anthers produce abundant, dry pollen (Figure 1d) that is dispersed in very small clouds of several cm in diameter when blown off by wind. This pollen is small, ~ 20 – $25 \mu\text{m}$ in diameter (Erdtman 1945), with a smooth, unornamented exine. Carpels are absent in staminate flowers, however, there is a prominent pistillode (Figure 1a and 1c).

Carpellate flower buds are indistinguishable from staminate flower buds, as the perianth of both is similar and neither flower produces a noticeable scent. Unlike staminate flowers, however, carpellate flowers produce a large drop of nectar (glucose content $> 2\%$) from a gland (Figure 1e) in the septum tissue of the ovary. When open, carpellate flowers are recognizable by the absence of stamens and the presence of a large ovary composed of three fused carpels, which extend beyond the rim of the perianth of mature flowers (Figure 1b). The stigma is large (~ 0.5 mm in diameter), three-lobed and sits directly

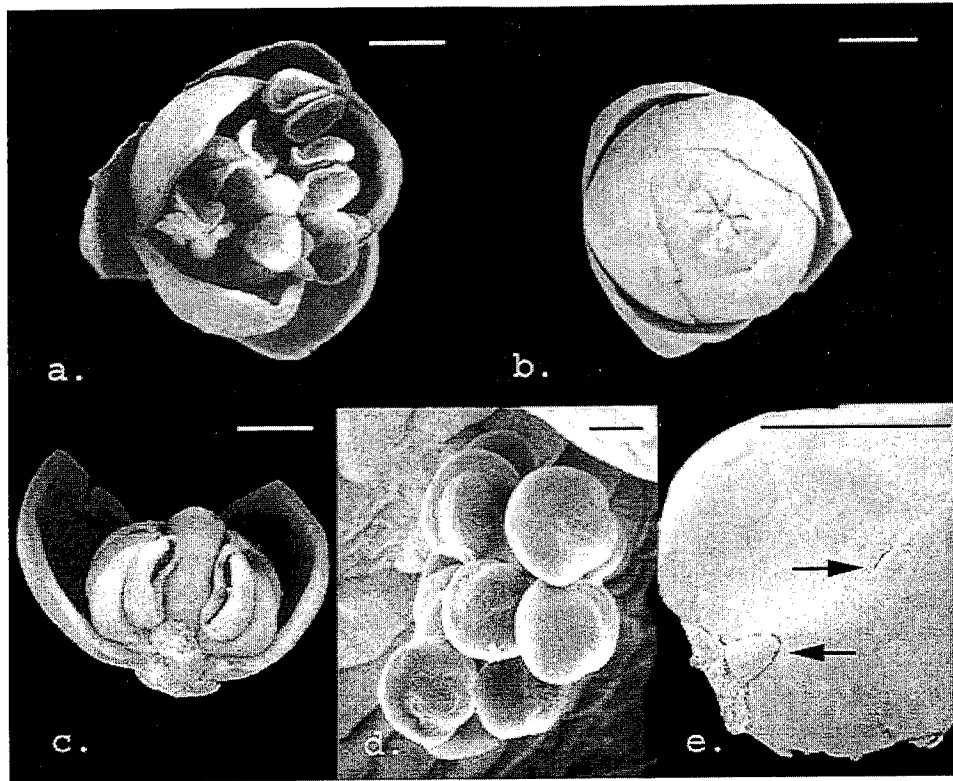


Figure 1. Scanning electron micrographs of *Chamaedorea radicalis* reproductive organs. (a) Staminate flower. (b) Carpellate flower. (c) Cross-section of staminate flower, showing partially developed pistillode. (d) Pollen grains on anther epidermal tissue. (e) Female ovary showing nectar gland (top arrow) and staminode (bottom). Scale bars for all micrographs except (d) = 1000 μ m in length; scale bar in (d) = 10 μ m in length.

on the ovary on a very reduced style. During anthesis the stigma lobes are moist and covered with many white papillae.

Pollinator exclusion experiment and insect visitors

Fruit set was significantly lower in the insect/wind enclosure than in the other two treatments (Figure 2). Fruit set in the insect-only enclosure, however, was not significantly different from the control, indicating that pollination occurs in the absence of insects.

Visitors to flowers of both sexes were primarily from the Drosophilidae and the Clorotidae, but ants (Formicidae) and spiders (Opilioniidae) were also observed visiting females during anthesis. Insects from the following families visited immature fruits on female plants only after anthesis, and are therefore not possible pollinators, but may be seed or fruit predators: Blatidae, Tettigonidae (brown cricket), Cleridae, Derbidae (green cricket) and Forficulidae (earwigs). Although not quantified in this study, some insect(s) caused substantial damage to immature fruits on several different individuals.

Factors influencing female fecundity

For focal females in the study population (n = 33), average fruit set was 43% with a mean fruit number of 32, however, both measures showed considerable variation

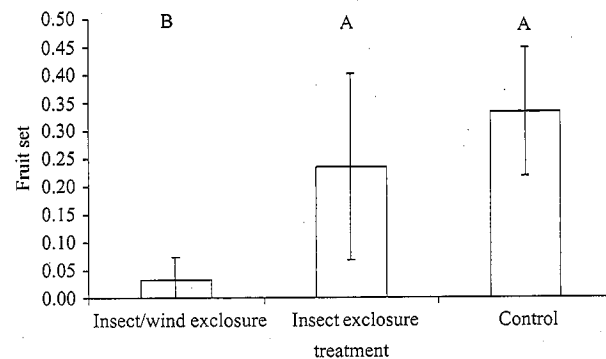


Figure 2. Mean fruit set of female *Chamaedorea radicalis* in three enclosure treatments (ANOVA, $F = 24.00$, $df = 30$, $P < 0.005$), including standard deviations around the means. Different letters represent significant differences indicated by Tukey's pairwise comparisons (family error rate of 0.05).

Table 2. Summary of single predictor regressions of female *Chamaedorea radicalis* size variables on three measures of fecundity (n = 33 females). Statistically significant results ($P \leq 0.05$) are in bold. YFL = Youngest fully expanded leaf.

Predictor	Flower number		Fruit number ^b		Fruit set	
	R ²	P	R ²	P	R ²	P
Inflorescence length (cm) ^a	91.2%	< 0.005	81.3%	< 0.005	13.5%	0.035
Length of YFL (cm)	30.6%	0.001	24.3%	0.005	6.3%	0.159
Leaflet number of YFL	27.2%	0.002	20.1%	0.011	8.1%	0.109
Leaf number	3.5%	0.299	4.9%	0.232	1.1%	0.556
Above-ground stem height (cm)	0.1%	0.884	1.8%	0.471	1.7%	0.473

Analyses based on data transformed by: square root^a and \log_{10} ^b.

(fruit set range: 0–86.3%, fruit number range: 0–224 fruits). Of the five size parameters measured on these females, the best predictor of flower number and fruit number was inflorescence length (Table 2). Fruit set was mostly independent of female size, having only a weak association with inflorescence length (Table 2). For each of the response variables, stepwise linear regression of these size parameters resulted in a model with only a single predictor, inflorescence length.

Both fruit number and fruit set of focal females were independent of patch in this population (ANOVA fruit number $F = 1.41$, $P = 0.244$, $df = 32$; fruit set $F = 0.98$, $P = 0.477$, $df = 32$). Results of both fruit number and fruit set on the local neighbourhood parameters revealed that no single predictor variable explained a significant amount of variation in either measure of female fecundity or at either neighbourhood scale (5-m or 10-m radius). Stepwise linear regression of each response variable at each neighbourhood scale on the strongest size parameter, inflorescence length, and all of the local neighbourhood parameters yielded one-parameter models including only inflorescence length.

DISCUSSION

Pollen vector and floral biology

The correlation of several floral and pollen morphological characters with the wind-pollination syndrome, and the results of our enclosure experiment, indicate that wind is the primary pollen vector of *Chamaedorea radicalis*. The floral morphology of *C. radicalis* correlates with the wind-pollination syndrome as both staminate and pistillate flowers are small and inconspicuous, and lack any noticeable scent to attract pollinators. Specific floral characteristics that promote pollination by wind include (1) fertile reproductive organs of both sexes exerted beyond the rim of the perianth, (2) numerous smooth, dry pollen grains released from staminate flowers,

and (3) large, moist stigmas in carpellate flowers. The strongest evidence for anemophily is that the enclosures showed no statistical difference in fruit set between females in the control group (exposed to all pollination vectors) and those exposed only to wind-borne pollen. These results also revealed a low level of fruit set (~4%) in the treatment designed to exclude pollen, suggesting some agamosperous fruit production in this population. However, agamospermy has not been previously documented within *Chamaedorea* and another plausible explanation is that the pollen exclusion bags allowed some pollen to pass through. This conclusion is perhaps more likely, as individual *C. radicalis* pollen grains were found to be smaller than the pore size of the pollen bags.

An interesting exception to the wind-pollination syndrome is the presence of nectar in carpellate flowers; this nectar was harvested by flying insects that were also infrequent visitors to male plants during anthesis and are, therefore, potential pollinators. While the enclosures experiment confirmed wind as the primary pollen vector, mean fruit set in the control (insects and wind) was approximately 10% higher than in the insect enclosure (wind only). Although this difference was not statistically significant, the higher mean fruit set in the control could be attributed to some pollen transfer by insect visitors. Indeed, it is not uncommon for apparent wind-pollinated species to receive appreciable quantities of insect-dispersed pollen (Richards 1997). While in most palms wind is thought to play a secondary role to insects (Anderson *et al.* 1988, Henderson 1986, Scariot & Lleras 1991), in the genus *Chamaedorea* there are multiple examples of primarily wind-pollinated species that have documented insect visitors (Listabarth 1992, Otero-Arnaiz & Oyama 2001, Oyama 1990). Another explanation for the presence of nectar in this wind-pollinated species is that anemophily in *C. radicalis* is a derived syndrome, and the nectar glands have been retained from an insect-pollinated ancestor. Our results also confirm complete dioecy in the population; although both sexes have vestigial reproductive organs, carpellate

flowers lack stamens to produce pollen and the pistillode in staminate flower was never observed to produce fruit.

Our finding that *C. radicalis* is wind-pollinated helps identify specific ecological constraints on pollen transfer, which may ultimately affect female reproductive success. Unlike most tropical palms that are entomophilous and affected by biotic factors (e.g. pollinator behaviour and abundance), we expect pollination of *C. radicalis* to be primarily influenced by abiotic factors, such as wind (speed and direction), turbulence and precipitation (DiGiovanni & Kevan 1991). Partly due to such environmental constraints, the wind-pollination syndrome is rare in tropical forest understoreys (Richards 1997). While the habitat for *C. radicalis* is indeed tropical, montane mesophyll forest (Puig & Bracho 1987), many days throughout the flowering season are dry with substantial air movement in the understorey (*pers. obs.*). This airflow is presumably sufficient to move the palm's small, dry-powdery pollen between conspecifics. Successful pollination is also facilitated by the extended flowering period of males; sequential anthesis on male inflorescence branches allows one male to be a source of pollen to receptive females for as long as 1 mo.

Factors influencing female fecundity

Fruit set in females did not correlate with palm size and had only a weak association with inflorescence length, a measure of reproductive effort. As with fruit set, fruit number was most strongly associated with inflorescence length, however, it also correlated with female size variables (length and leaflet number in youngest fully expanded leaf). These results are consistent with other palm studies that reported significant relationships between female fecundity and size variables, such as palm height (Barot & Gignoux 1999, Oyama 1990, Scariot & Lleras 1995) and leaf number (Barot & Gignoux 1999). To fully assess the relationship of female fecundity to size, however, it would be necessary to incorporate in analyses those females not flowering in the current year. Furthermore, our study does not address the costs associated with current reproduction, which can affect future growth and reproductive success. Other studies of dioecious plants reported delayed costs of reproduction in females, both in terms of subsequent growth and future reproduction (Cipollini & Whigham 1994, Fox & Stevens 1991, Nicotra 1999). These studies also found that for sexually dimorphic plants, like *C. radicalis*, these costs tend to be greater in females than males (Cipollini & Whigham 1994, Nicotra 1999).

For *C. radicalis*, the correlation between fruit production and simple female size characteristics can be valuable in the management of natural populations in El Cielo,

where leaves are intensively harvested by villagers called palmilleros. For example, since leaf harvest has been shown to reduce the proportion of large adults that flower (Endress *et al.*, in review), restricting leaf harvest of known females would enhance seed production. Of course, we expect there is some threshold male density below which fruit set would be reduced. Indeed, this has been reported in the palm *C. alternans*, where fruit set was shown to be dependent on the proximity of flowering males, leading to pollen limitation in some females (Otero-Arnaiz & Oyama 2001). However, at current densities, female fecundity of *C. radicalis* was not dependent upon the proximity or distribution of males within a 5-m or 10-m radius, as no local neighbourhood parameter or combination of parameters explained a significant amount of the variation in fruit number or fruit set. Both measures of fecundity were quite variable among females; this could be due to pathogens or flower and seed predation by insect visitors. Our findings that female fecundity was independent of male density or sex ratio indicate that for this population birth can be modelled as a female-dominant process, and population models of this species can be based solely on the demography of females.

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