

Defoliation and ENSO effects on vital rates of an understorey tropical rain forest palm

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Summary

1. Rain forest understorey plants suffer leaf area losses due to natural causes or when leaves are harvested as non-timber forest products. The negative effects of defoliation on plant fitness can be exacerbated during periods with strong water shortage and high temperatures, typical during ENSO (El Niño Southern Oscillation) years in Mexico and Central America. At present, the isolated and combined demographic effects of ENSO events and repeated defoliation on tropical rain forest plants are poorly understood.

2. We studied the consequences of repeated defoliation and an ENSO event on vital rates (mortality, growth, and reproduction) of the dioecious understorey palm *Chamaedorea elegans*. From March 1997 to March 2000 (including the 1998 ENSO year), we subjected 814 mature individuals to one of five defoliation treatments (0–100% of newly produced leaves were removed twice a year), recording mortality, growth (leaf production) and reproduction (inflorescence and seed production) every 6 months.

3. Increasing defoliation strongly reduced reproduction but had smaller effects on growth and mortality. Among non-defoliated palms, the probability of mortality increased with light availability, likely due to drought stress during the dry season, but this was not the case for the defoliated plants, probably because leaf area removal lowered transpiration and increased the root mass-to-leaf area ratio. During the ENSO year, growth and inflorescence production were stimulated, but survivorship and seed production diminished significantly, independent of defoliation level.

4. Synthesis. Variation in light availability and the occurrence of severe droughts can strongly affect demographic behaviour of understorey plants such as *C. elegans*, significantly influencing the effects of defoliation. Thus, strong episodic disturbance events (such as ENSO, insect outbreaks, strong storms, fires and landslides) should be taken into account to adequately understand the mechanisms that determine the population dynamics of forest plants and the potential for sustainable utilization of non-timber forest products.

Key-words: *Chamaedorea*, defoliation, ENSO, leaf harvesting, non-timber forest products, palm demography, tropical rain forest

Introduction

In tropical rain forests, understorey plants suffer leaf area losses due to herbivores (Coley & Barone 1996), falling canopy debris (e.g. Clark & Clark 1991), pathogens (e.g. García-Guzmán & Dirzo 2001) and, in some species, due to harvesting by humans as non-timber forest products (NTFP, Salafsky *et al.*

1993). Reductions in leaf area entail losses in terms of whole-plant carbon gain (Anten & Ackerly 2001), which can affect fitness components such as survival, growth and reproduction (Marquis 1984; Crawley 1989; Ehrlén 2003). However, plants can mitigate these losses through compensatory growth (Belsky 1986; Stowe *et al.* 2000). Knowledge of these adaptive responses has mostly emerged from studies carried out at the individual, functional level (e.g. McNaughton 1983; Oosterheld & McNaughton 1988; Anten *et al.* 2003). The demo-

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graphic consequences of leaf harvesting (e.g. Mendoza *et al.* 1987; Zuidema 2000; Endress *et al.* 2004a; b) or herbivory (e.g. Dirzo 1984; Ehrlén 2003) have been much less explored, especially under repeated defoliation (Endress *et al.* 2006) and climatic change scenarios.

The impact of defoliation events on vital rates of long-lived organisms such as tropical rain forest understorey palms depends on the intensity and frequency of leaf area loss (Trumble *et al.* 1993). The effects of single defoliation events on survival, growth and/or reproduction are generally small (e.g. Mendoza *et al.* 1987; Oyama & Mendoza 1990; Zuidema 2000), suggesting that understorey palms are reasonably tolerant to sporadic leaf harvesting. However, very little work (Chazdon 1991; Endress *et al.* 2004a,b) has been done on the long-term effects of repeated defoliation on vital rates (Ticktin 2004), even though defoliation is often recurrent and can be frequent (Anten & Ackerly 2001). Repeated defoliation can result in a depletion of carbohydrate reserves and thus in a reduced potential for compensatory growth (Kobe 1997). So while single defoliation events tend to have little effect on vital rates, repeated defoliation could significantly affect them, resulting in important impacts on plant demography (Endress *et al.* 2004a).

The effect of defoliation on vital rates depends on the environmental circumstances under which plants grow (Belsky 1986). Many palm species that are used for leaf harvesting reside in the understorey of old-growth tropical rain forest where plant survival, growth and/or reproduction are believed to be strongly dependent on light availability (Chazdon 1986; Martínez-Ramos *et al.* 1988). The negative impacts of defoliation may therefore decrease with increasing light availability. Indeed, in a greenhouse study, the palm *Chamaedorea elegans* exhibited stronger compensatory growth at 16% of daylight than at 5% (Anten *et al.* 2003). On the other hand, most understorey palms appear to be damaged by high or even moderately high-light intensities (Dransfield 1969; Chazdon 1986), and they have been reported to disappear from secondary forest or selectively logged forest (Dransfield 1969; Kiew 1972). To date, the interactive effects of light and defoliation on vital rates, under field conditions, has not been clearly investigated.

The consequences of defoliation on vital rates can be exacerbated under periods with water shortage and high temperatures (e.g. Howe 1990). Such severe drought events occur during ENSO (El Niño Southern Oscillation) years in many parts of the tropics with important effects for plant fitness (Aceituno 1988; Wright & Calderón 2006; Phillips *et al.* 2009). Stomatal closure induced by water shortages negatively affects a plant's carbon balance because of reduced photosynthesis and increased photorespiration (Lambers *et al.* 1998), which in turn may decrease survival and/or growth. On the other hand, high irradiance during ENSO years can enhance plant growth and reproduction, as shown in Barro Colorado Island (BCI), Panama (Wright *et al.* 1999). The combined consequences of repeated defoliation and ENSO events on vital rates of tropical rain forest plants have received little attention (Zuidema 2000). ENSO-related droughts are likely to become more frequent

and severe due to global climate warming (Meehl 1997; Timmerman *et al.* 1999). There is consequently an urgent need to assess the consequences of such climatic change on long-lived plant fitness and sustainable management of NTFPs.

This paper assesses the effects of repeated defoliation and ENSO events on vital rates (survival, growth and reproduction) of *C. elegans*, a long-lived understorey palm which is an important NTFP in Mesoamerica. By monitoring individual palms that were subjected to different experimental defoliation levels every 6 months for a 3-year period (including the 1997–98 ENSO event), we address the following questions: What are the cumulative effects of repeated defoliation on survival, growth and reproduction? To what extent do such effects depend on variation in light availability and soil depth, and on plant traits (leaf area and stem size)? What is the impact of temporary droughts such as those associated with ENSO?

The ENSO event examined in this study fell in the second year of our 3-year study. We recognize that this is an unreplicated event, from an experimental design perspective, and that the timing may uniquely interact with the cumulative defoliation events examined over the 3-year period. However, our ability to compare vital rates in the ENSO year with rates from the years before and after gives us increased confidence that the differences observed are in large measure due to the climate conditions. Experimental manipulation of climate, particularly the reduction in rainfall, would be essentially impossible in this system, so few alternatives exist to examine potential impacts of climatic variation on plant demography.

Materials and methods

STUDY SITE AND SPECIES

This study was conducted at the Chajul Biological Station, within the Montes Azules Biosphere Reserve in Chiapas, Mexico (16°06'N, 90°56'W). The station is located in lowland evergreen tropical forest with mean annual precipitation of about 3000 mm, a 4-month dry season from January through April with precipitation < 100 mm month⁻¹, and mean daily temperatures in the coldest (February) and warmest (May) months of 22 and 26.7 °C, respectively (Fig. 1a). During the 3 years of the study (March 1997 through February 2000) annual rainfall varied substantially (Fig. 1b). This variation was due to the impacts of the 1997–98 ENSO which caused a severe drought in south-eastern Mexico and northern Guatemala (Magaña *et al.* 2003). Using data of the Lacantún meteorological station (16°08' N, 90°54' W, 160 m.a.s.l.), < 10 km from our study site, we calculated a total precipitation of 41 mm during the dry season (January through May) of 1998, which was one order of magnitude lower than during normal (non-ENSO) years (Fig. 1c). During the dry season of 1998, mean maximum temperature and the number of days without rain were on average higher than during dry seasons of previous or subsequent years (Figs. 1b,d). Precipitation and the number of days without rain during the rainy season (June through October) of the ENSO year were also higher than in normal years (Figs. 1e,f).

The study was conducted with *C. elegans*, a dioecious, long-lived understorey palm of rain forests in southern Mexico, Belize and Guatemala (Hodel 1992). *Chamaedorea elegans* grows to maximum heights of < 1.5 m, is unbranched and produces

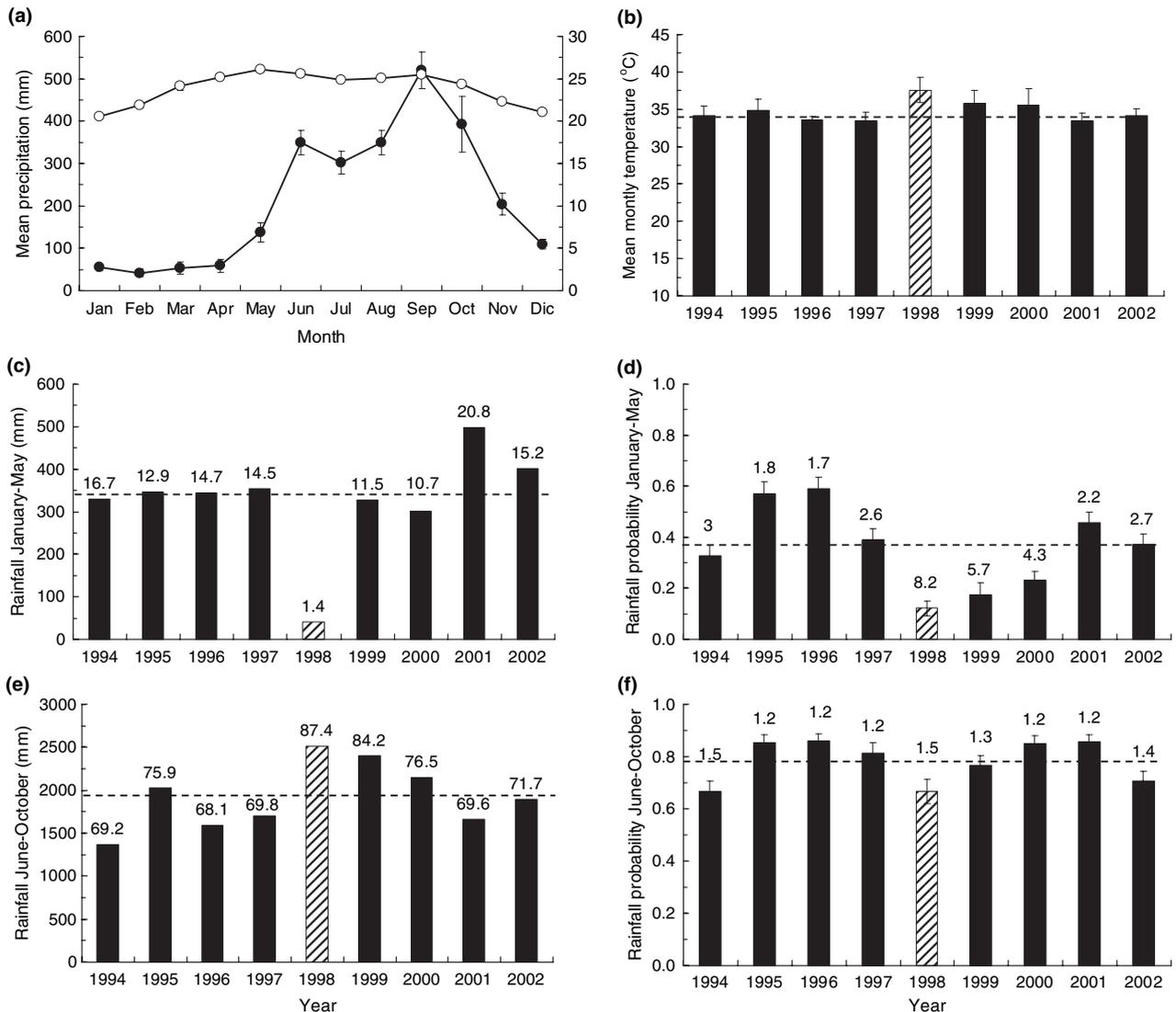


Fig. 1. Climatic regime at Chajul tropical rain forest, south-eastern Mexico (Lacantún meteorological station, CFE Mexico at < 10 km from our study site). (a) Average monthly precipitation (black dots) and median temperature (open dots) based on records of 9 years (1994–2004); (b) inter-annual variation in mean monthly maximum temperature during the dry season (January through May); (c) inter-annual variation in precipitation falling during the dry season; (d) inter-annual variation in the mean daily probability of rain (proportion of days with rain) during the dry season; (e) inter-annual variation in precipitation falling during the rainy season (June through October); (f) inter-annual variation in the mean daily probability of rain during the rainy season. In all cases vertical lines indicate one standard error. In (b) and (e), numbers above bars indicate percentage of rain (in respect to total precipitation of each year) falling during the dry or rainy season, respectively; in (d) and (f), numbers indicate the average number of days without rain (inverse the proportion of days with rain). Dashed bars indicate data for ENSO year (1998) and horizontal lines indicate average values across years (1994–2004).

leaves in a single cluster from the apical meristem. Inflorescences are produced mostly during winter and spring (from November to April), while fruit production occurs mostly in summer (July through October). The globular fruits (4–7 mm diameter) are single-seeded. In Chajul, this palm species is restricted to the karstic-range areas (300–700 m a.s.l.) where medium-sized forest (average canopy height about 18 m) develops on renzitic (pH ~ 7.0), shallow (< 20 cm depth), well-drained soil (Ibarra-Manríquez & Martínez-Ramos 2002). Leaves are harvested from natural populations for sale to the floral industry in North America and Europe (Hodel 1992). Leaf harvesters usually return to the same plant and remove 30–100% of the newly produced leaves (Reining *et al.* 1992).

EXPERIMENTAL METHODS

We located natural populations of *C. elegans* about 4 km northwest of the Chajul station at about 300 m a.s.l., in a protected area without previous history of palm harvest activity. In March 1997, a study area of 1.12 ha was selected and divided into 23 subplots of approximately 500 m² (10 × 50 m). In total, 814 adult plants (≥ 0.10 m stem length) were mapped and tagged in all subplots. Plant height (measured vertically from the apex to the ground), stem length, number of leaves, reproductive status and the length of the most recent fully expanded leaf were measured in an initial census. Relative light intensity above each plant was measured three times (March 1997, October 1998 and February 2000) using a spherical concave densiometer (Model C,

Forest Densimeters, Bartlesville, OK, USA). The reliability of the densiometer measurements was tested by comparing them with readings of relative photon flux density obtained with quantum sensors (LI-190SA, Li-Cor, Lincoln, NE, USA; there was a good correspondence between the two methods, $r^2 = 0.952$; see Anten & Ackerly (2001). In March 2000, soil depth was measured at approximately 20 cm from the stem base of every palm in the experiment by measuring the length to which a metal pole (2 cm diameter, 1 m length) could penetrate the soil until touching solid rock.

Independent of subplots, all recorded plants were stratified by initial height and gender categories (male, female and non-reproductive) and then randomly assigned to one of five defoliation treatments: 0%, 33%, 50%, 66% and 100%. There were 190–196 replicates per treatment for the first four defoliation levels, but only 44 replicates at 100% defoliation because we expected these plants to die and wanted to maintain higher replication in the other treatments. Defoliation treatments were imposed at the initial census by removing the most recent fully expanded leaf and then removing every third (33%), every other (50%), two out of every three (66%) or all (100%) leaves. This protocol brackets the whole range of defoliation levels applied by leaf harvesters and allowed us to determine physiological traits as a function of leaf age after partial defoliation (Anten *et al.* 2003). This method of leaf removal likely has got reduced impact on plant growth compared with defoliation by harvesters, who tend to cut only young leaves.

Six subsequent censuses were conducted in October 1997, March and October 1998 and 1999, and February 2000. At each census, we recorded mortality and for surviving individuals the height, number of standing leaves, number of newly produced leaves, length of the most recent fully expanded leaf, gender and reproductive activity (inflorescence, infructescence and fruit production). After each census, defoliation treatments were maintained following the pattern of leaf removal initiated at the first census, i.e. one out of every three (33%), one out of every two (50%), two out of three (66%) or all (100%) newly produced leaves were removed. By the end of the experiment, 317 plants were recorded as male (M), 320 as female (F) and 177 as non-reproductive (N; no reproduction had been observed throughout the 3 years). For data analysis, a plant's reproductive status (M, F, N) was based on the cumulative observations, not on whether it was reproductive at a particular point in time.

Total leaf lamina area (=leaflets) was measured in 18 leaves of varying size selected from those removed for defoliation using a leaf area meter (LI3100). An allometric equation for leaf area (A , m²; $A = (2.12 \times 10^{-5}) \times L^{1.995}$, $r^2 = 0.986$) as a function of lamina length (L , cm) was obtained to estimate, non-destructively, leaf area of all individuals. Standing leaf area for a given census was calculated after leaf removal, to provide a measure of initial canopy size for the next growth period.

STATISTICAL ANALYSIS

In all statistical tests, we considered individuals as experimental replicates for each defoliation treatment. Individuals were assigned to treatments independent of their spatial position in the subplots in a complete randomized design. Using generalized linear models (analysis of deviance; Crawley 1993), we first assessed the effects of defoliation treatments, light availability, soil depth, plant size (leaf area and stem length) and gender on three vital rates (mortality, growth and reproduction), based on cumulative effects after 3 years. This was to determine the overall effects of defoliation, plant size and environmental conditions on vital rates. In this analysis, probability of mortality was quantified as the proportion of original individuals

that died during the 3 years after the first census date. In the case of growth and reproduction we excluded the 100% defoliation treatment as too few individuals in this treatment survived. Growth rates were quantified as the mean annual number of leaves produced per palm. Reproduction was analysed considering the frequency of reproduction (number of reproductive years per individual), the probability of flowering or fruiting (the proportion of mature individuals producing inflorescences or fruits [for females] per year and in 3 years) and reproductive effort (the mean annual number of inflorescences and fruits produced per reproductive plant). Because fruits are single-seeded, hereafter, fruit production will be treated as equivalent to seed production. A Poisson error and a log-link function were used for discrete, count variables (e.g. inflorescence and seed production), a binomial error and logistic-link function for binomial variables (e.g. mortality) and a normal error and identical-link function for continuous variables; for count and binomial variables, we rescaled models in cases of overdispersion (Crawley 1993).

We analysed the effects defoliation on the same vital rates on a year-by-year basis to determine the extent to which vital rates were affected by the ENSO year. We performed repeated-measures analyses of variance using the statistical package SYSTAT (ver. 11). All repeated subjects (individuals and the different mortality, leaf production and reproductive measurements along time) were fixed. Mortality was handled as a binary variable. Leaf production data were $\log(x + 1)$ -transformed prior to analysis to meet homoscedasticity and parametric criteria (Sokal & Rohlf 1998). Differences in mortality, growth and reproduction rates among defoliation treatments (DT), gender (G; male, female and non-reproductive individuals) and year (Y) were evaluated by $DT \times Y$, $G \times Y$ and $DT \times G \times Y$ interaction terms. Mauchly's criterion test for the compound symmetry of the variance-covariance matrix was obtained automatically, together with corrected significance levels in case of the rejection of the symmetry assumption (Greenhouse-Geisser and Huynh-Feldt corrections).

Results

POPULATION AND ENVIRONMENT CHARACTERIZATION

Out of the initial palm population, the female-to-male ratio (1.01) did not differ from 1:1. Males were significantly bigger than females and non-reproductive palms (mean stem length \pm SE = 44.1 \pm 1.3, 38.7 \pm 1.1, 37.4 \pm 1.7 cm, respectively; $F_{2,811} = 6.9$, $P < 0.001$). At the first census, males had significantly ($\chi^2 = 115.9$, d.f. = 2, $P < 0.001$) more leaves (6.5 \pm 0.1) than females (5.7 \pm 0.1), and females more than non-reproductive individuals (4.4 \pm 0.1). This resulted in males having a significantly ($F_{2,812} = 99.7$, $P < 0.0001$) greater total leaf area (0.135 \pm 0.003 cm²) than females (0.116 \pm 0.003), and females more than non-reproductive individuals (0.073 \pm 0.003).

On average, canopy openness (% CO) above palms was 4.6 \pm 0.1% (range: 0.5–36%) and varied positively with stem length ($F_{1,812} = 3.80$, $P = 0.05$), but especially with the height (H) at which leaves were displayed above ground ($F_{1,812} = 7.16$, $P = 0.0076$; % CO = 4.08 \pm 0.013 \times H). Average soil depth for the whole population was 21.0 \pm 0.5 cm (SE) and it did not differ for palms of different gender or size ($P > 0.10$).

MORTALITY

Control population

From the 196 palms in the non-defoliation treatment recorded in March 1997, 16% died after 3 years with a mean annual mortality rate of 0.055 ± 0.002 (ind ind⁻¹ year⁻¹). Mean annual mortality rate of non-reproductive individuals was higher (0.141 ± 0.016) than that of the reproductive ones (0.04 ± 0.004 ; $\chi^2 = 9.85$, d.f. = 2, $P = 0.007$). Females and males did not differ in mortality rate. Based on observed patterns of damage on dead plants we estimated that vertebrate (20.7%, caused by moles) and insect (3.4%, damage to apical meristem by caterpillars) predation accounted for about a quarter of total mortality in 3 years, falling canopy debris (tree and branch falls) for 7.0%, and 69% was due to undetermined causes.

Mean annual mortality rate decreased with leaf area and increased with light availability and soil depth. All these effects were independent from each other and together explained about 15% of the observed deviance in mortality (Table 1a). In this analysis that corrects for differences in plant size, there was no significant gender effect, suggesting that the lower mortality rate of reproductive plants can be explained by their greater leaf area. According to the adjusted model, the probability of mortality sharply increases for individuals with small leaf areas and for those found in forest spots with moderate to high-light levels (10–30% canopy openness; Fig. 2a), such as tree fall gaps. Mortality of plants with greater leaf areas increased more gradually with increasing light intensity.

Defoliation effects

Across all treatments, the defoliation effect on cumulative mortality over 3 years was significant and independent of palm

gender (Table 1b). The 66% and to a greater extent the 100% defoliation treatments differed significantly from the other ones (Table 2). In the 0–66% defoliation treatments, the non-reproductive individuals exhibited significantly higher mortality than the reproductive ones in every defoliation level (Table 1b; Table 2). In all these analyses, there was no significant effect of either light intensity or soil depth on mortality, but mortality decreased with leaf area and increased with stem length (Table 1b). The effect of leaf area did depend on gender (i.e. mortality declined faster with leaf area in non-reproductive than in reproductive palms, data not shown), although such interactions and the effects of leaf area and stem length were minor, and combined they explained < 3% of total variation in mortality (Table 1b).

ENSO effects

Mortality rates differed between years and these differences did not depend on the level of defoliation, but varied with gender (Table 3). Overall, mortality rates in the ENSO year (1998) were two to five times higher (mean \pm SE = 0.154 ± 0.013 ind ind⁻¹ year⁻¹), than in 1997 (0.029 ± 0.006), and 1999 (0.069 ± 0.010). This result was consistent for all defoliation treatments except the 100% treatment, where mortality increased progressively from the 1997 to 1999 (Fig. 3a).

GROWTH

Control population

A linear regression model showed that leaf production increased both with the amount of standing leaf area and with light availability (% canopy openness, % CO), but that the former explained four-fold more variation than the latter (Fig. 2b; Table 1a). Gender also affected leaf production with

Table 1. Results from the Analysis of Deviance used to assess the effects of gender, palm size (stem length), total leaf area (Leaf Area), depth soil (Soil) and light intensity (% canopy openness, Light) on mortality rate (ind ind⁻¹ 3-year⁻¹), growth (mean annual leaf production) and four measures of reproduction (reproduction frequency in years, and inflorescence and seed production per year) of *Chamaedorea elegans* palms

	Mortality	Growth	Frequency of reproduction	Inflorescences per palm	Inflorescences per reproductive palm	Seeds per palm
(a) Natural population						
Leaf area	0.001 (0.061)	< 0.001 (0.220)	< 0.001 (0.206)	< 0.001 (0.271)	< 0.001 (0.209)	< 0.001 (0.270)
Light	0.002 (0.059)	0.001 (0.050)	–	–	–	–
Soil	0.030 (0.027)	–	–	–	–	–
Gender	–	0.032 (0.030)	–	–	–	–
(b) With defoliated palms						
Treatment	< 0.001 (0.131)	–	< 0.001 (0.150)	< 0.001 (0.140)	–	–
Leaf area	< 0.001 (0.011)	< 0.001 (0.060)	0.001 (0.040)	< 0.001 (0.090)	< 0.001 (0.200)	< 0.001 (0.070)
Light	–	< 0.001 (0.080)	0.005 (0.020)	0.006 (0.040)	0.013 (0.050)	0.013 (0.020)
Gender	< 0.001 (0.045)	< 0.001 (0.050)	0.014 (0.010)	0.040 (0.010)	–	–
Stem length	< 0.001 (0.014)	< 0.001 (0.020)	–	0.010 (0.020)	–	–
Gender \times leaf area	0.025 (0.001)	–	–	–	–	–

(a) Natural population (i.e. control, non-defoliated palms) and (b) including defoliation treatments (Treatment). The numbers in the table represent significant P -values (< 0.05) with R^2 for each factor in parentheses ($P(R^2)$). Error type used in these analyses was logistic for mortality, normal for growth and log for reproduction (see text).

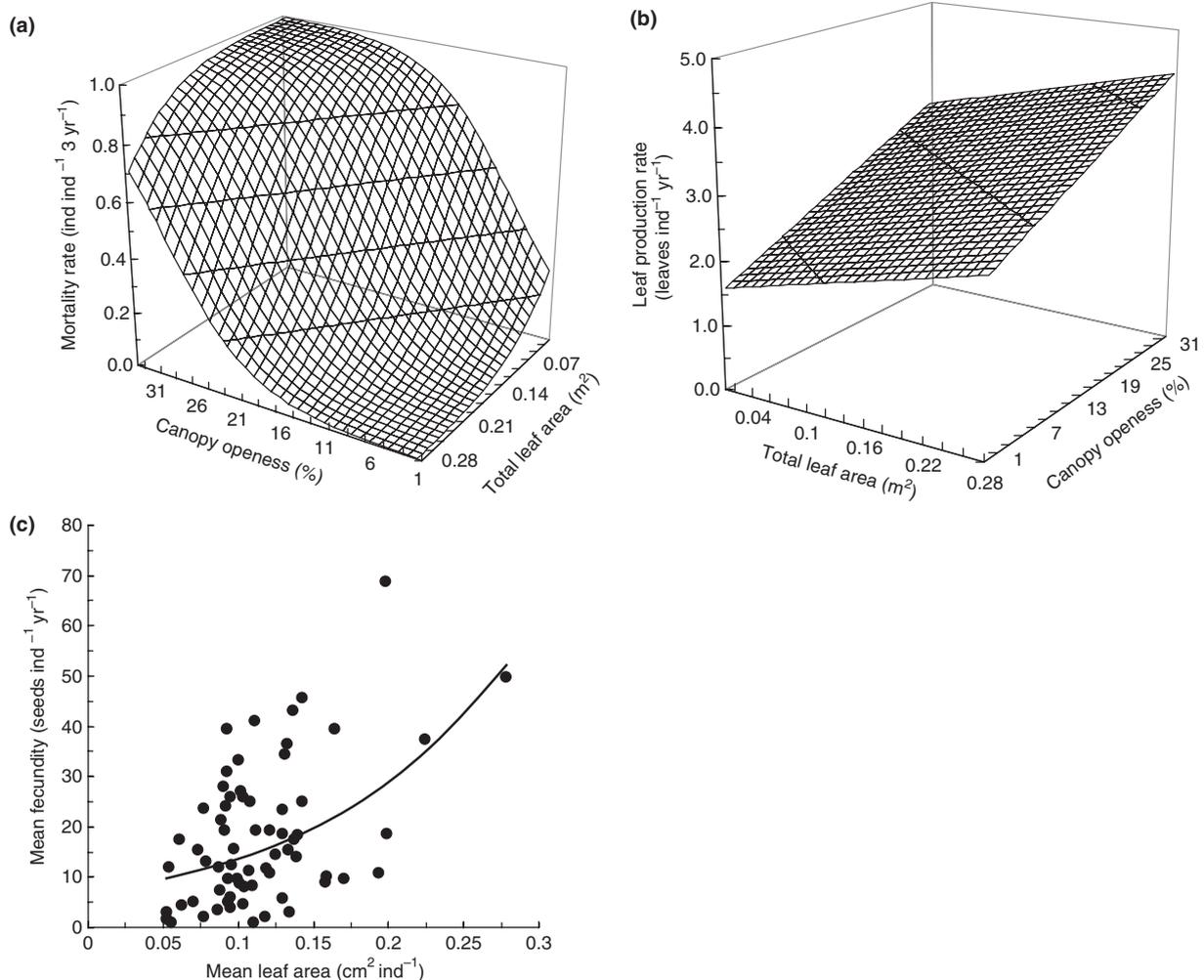


Fig. 2. Mortality, growth and reproduction responses to environmental factors in a natural population (non-defoliated palms) of *Chamaedorea elegans* at Chajul, south-eastern Mexico. (a) Predicted mortality rate (q_x) for palms found in sites with average soil depth (SD = 21.1 cm) as a function of light (% canopy openness, % CO) and plant leaf area [LA; logistic regression model: $q_x = \exp(-1.78 - 18.8 \times \text{LA} + 0.22 \times \% \text{CO} + 0.04 \times \text{SD}) / (1 + \exp(-1.78 - 18.8 \times \text{LA} + 0.22 \times \% \text{CO} + 0.04 \times \text{SD}))$]. (b) Predicted annual leaf production rates (LPR) for female palms as a function of leaf area and light (linear regression model: $\text{LPR} = 1.48 + 3.93 \times \text{LA} + 0.053 \times \% \text{CO}$; intercept for males = 1.55 and for non-reproductive palms = 1.4). (c) Mean fecundity (mean annual seed production rate, SP) as a function of leaf area of individual palms [log-regression model: $\text{SP} = 7.6 \times (\exp(-0.09 + 7.3 \times \text{LA}))$], where 7.6 is the scale factor used in the analysis of deviance to correct overdispersion].

non-reproductive palms producing fewer leaves than females and males, which did not differ significantly from each other (see 0% defoliation in Table 2).

Defoliation effects

Defoliation treatments did affect mean annual leaf production rate (LPR) ($F_{3,617} = 4.0$, $P = 0.008$). Leaf production decreased with defoliation level but only the 66% treatment was significantly different from 0% (Table 2). This effect disappeared when gender, plant size (leaf area and stem length) and light intensity were included in the analysis (Table 1b). On average, as in the natural population, males had significantly higher leaf production than females and both were higher than non-reproductive palms at all defoliation levels (Table 2). Mean annual LPR increased with leaf area (LA), light intensity (% CO) and stem length (SL) (Table 1b; adjusted model:

$\text{LPR} = G + 2.93 \times (\text{LA}) + 0.06(\% \text{CO}) + 0.003(\text{SL})$; values of G, females = 2.13, males = 2.32, non-reproductive individuals = 1.96).

ENSO effects

On average, excluding palms with 100% defoliation, LPRs increased 26–30% in the ENSO year, compared with the other 2 years, independent of gender and defoliation treatment (Table 3, Fig. 3b). In all years, leaf production was 19–37% higher in males than in females and non-reproductive plants (data not shown). In the third year (1999), females had the lowest LPRs compared with the other genders, particularly in the 66% defoliation treatment (females: 1.37 ± 0.12 ; males: 2.16 ± 0.10 ; non-reproductive palms: 1.59 ± 0.10 ; see significant year \times gender \times defoliation treatment interaction, Table 3).

Table 2. Effect of defoliation treatments on mean \pm SE (calculated for the three studied years) mortality (ind ind⁻¹ 3-year⁻¹), leaf production (lf ind⁻¹ year⁻¹), frequency (years) and probability of reproduction (ind ind⁻¹ year⁻¹), inflorescence production (infl ind⁻¹ year⁻¹), and fecundity (seeds ind⁻¹ year⁻¹) for palms of different gender (NR = non-reproductive) and combining all palms

Gender	Treatment (%)	Mortality	Leaf production	Frequency of reproduction	Probability of reproduction	Inflorescence production	Fecundity
Female	0	0.12 (0.04)	2.17 (0.06)	2.2 (0.8)	0.99 (0.01)	1.3 (0.1)	12.4 (1.7)
	33	0.12 (0.04)	2.19 (0.05)	2.0 (0.1)	0.92 (0.03)	1.0 (0.1)	10.0 (1.8)
	50	0.18 (0.05)	2.10 (0.06)	1.6 (0.1)	0.75 (0.05)	0.8 (0.1)	8.4 (1.6)
	66	0.18 (0.05)	2.05 (0.05)	1.1 (0.1)	0.59 (0.06)	0.5 (0.1)	7.3 (1.3)
	100	0.91 (0.09)	1.34 (–)	–	–	–	–
Male	0	0.12 (0.04)	2.41 (0.06)	2.3 (0.1)	0.97 (0.02)	1.4 (0.1)	
	33	0.16 (0.04)	2.31 (0.06)	2.3 (0.1)	1.00 (0.00)	1.3 (0.1)	
	50	0.12 (0.05)	2.33 (0.05)	1.7 (0.1)	0.85 (0.04)	1.0 (0.1)	
	66	0.15 (0.05)	2.26 (0.06)	1.3 (0.1)	0.74 (0.06)	0.8 (0.1)	
	100	0.94 (0.06)	2.38 (–)	–	–	–	
NR	0	0.37 (0.09)	1.93 (0.08)				
	33	0.41 (0.08)	1.75 (0.06)				
	50	0.34 (0.07)	1.82 (0.06)				
	66	0.41 (0.07)	1.79 (0.06)				
	100	1.00 (0.0)	–				
All palms	0	0.16 (0.03) ^a	2.25 (2.04) ^b	2.3 (0.1) ^c	0.98 (0.01) ^c	1.37 (.06) ^b	
	33	0.19 (0.03) ^a	2.17 (0.03) ^b	2.0 (0.1) ^c	0.96 (0.02) ^c	1.17 (0.06) ^b	
	50	0.19 (0.03) ^a	2.15 (0.03) ^{ab}	1.5 (0.1) ^b	0.81 (0.04) ^b	0.90 (0.06) ^b	
	66	0.24 (0.03) ^b	2.05 (0.03) ^a	1.1 (0.1) ^a	0.66 (0.04) ^a	0.61 (0.06) ^a	
	100	0.95 (0.03) ^c	–	–	–	–	

For the all palm cases, those treatments not sharing same superscript letter differed significantly at $P < 0.05$. SE values indicated in parentheses.

Table 3. Results from the repeated-measures ANOVA used to assess the effects of defoliation treatment (DT; 100% treatment excluded), gender (G) and year (Y) on annual mortality rate (ind ind⁻¹ year⁻¹), growth rate (annual number of leaves produced per palm) and five measures of fecundity (annual rates)

Trait	Effects			
	Y	Y \times DT	Y \times G	Y \times DT \times G
Mortality	< 0.0001	< 0.0001	0.356	0.436
Growth	< 0.0001	0.066	0.169	0.044
Inflorescences per individual	< 0.0001	0.069	0.485	0.054
Inflorescences per reproductive individual	< 0.0001	0.501	0.149	0.223
Probability of flowering	< 0.0001	0.157	0.149	0.022
Seed production per female	< 0.0001	0.001	–	–
Seed production per reproductive female	< 0.0001	0.001	–	–
Probability of fruiting	< 0.0001	0.001	–	–

Values indicate significance levels; in the last three reproductive traits, only females were considered and therefore no gender effect was tested (–).

REPRODUCTION

Control population

During the 3-year study, male and female palms had on average about the same frequency of reproductive years (FR, 2.1 ± 0.01), and probability of reproduction (Table 2). FR increased with LA), but it was not affected either by other factors [adjusted model: $FR = \text{Exp}(-0.095 + 5.90 \times LA)$; Table 1a]. Similar results were obtained for the mean annual number of inflorescences produced per year per individual (including reproductive and non-reproductive palms; IP, adjusted model: $IP = \text{Exp}(-0.83 + 7.7 \times LA)$] or for inflo-

rescence production per reproductive palm [IPR, adjusted model: $IPR = \text{Exp}(-0.39 + 5.1 \times LA)$; Table 1a). Also, fecundity (mean number of seeds produced per female per year) increased with leaf area, and was independent of other factors. An adjusted log regression model indicated that a five-fold increase in leaf area produced a similar increase in fecundity (Fig. 2c).

Defoliation effects

Defoliation treatment had a strong negative effect on both the frequency of reproduction and the mean annual number of inflorescences produced per palm, independently of gender

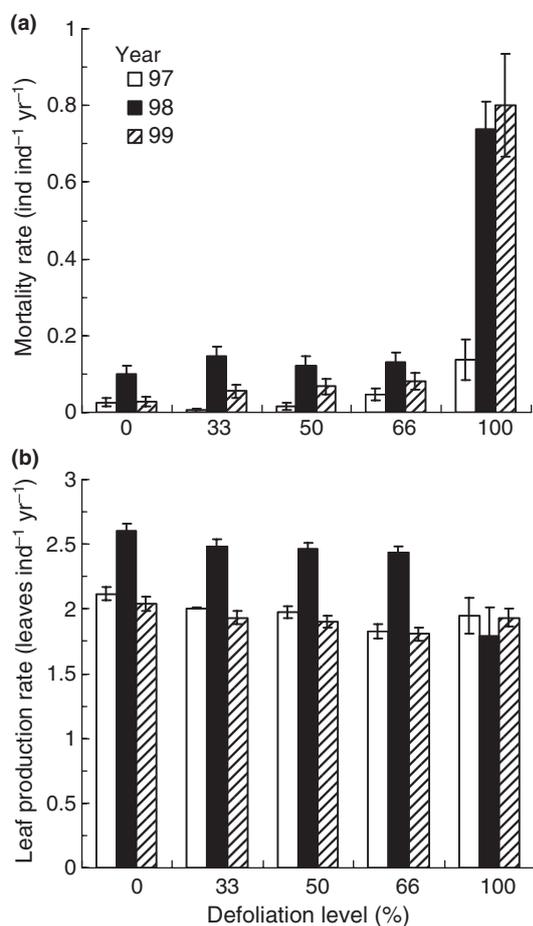


Fig. 3. Year and defoliation effects on vital rates of *Chamaedorea elegans* palms at Chajul, south-eastern Mexico. (a) mortality rates, (b) leaf production rates, (c) fecundity (annual production of seeds per individual). In all cases, bars indicate mean values and vertical lines indicate one standard error.

(Table 1b). For example, by the third year, the 66% defoliation treatment had resulted in a more than 50% reduction in both variables (Fig. 4). Across all defoliation treatments females had fewer reproductive years and produced fewer inflorescences than males (Tables 1b and 2). Overall, leaf area and light intensity (as well as stem length in the case of inflorescence production) had significant and positive effects on both reproductive variables. These effects, however, explained less variation in reproduction than defoliation treatment (Table 1b).

Defoliation effect on inflorescence production rate was mostly due to its effect on the probability of flowering rather than on reproductive effort (Table 1b; Fig. 4). Flowering probability was significantly higher in males than in females at every defoliation level (Table 2), and increased with leaf area, light intensity and stem length (Table 1b). Inflorescence production in reproductive palms (IPR) increased with light intensity but mostly with leaf area (Table 1b; adjusted model: $IPR = \exp(-53 + 0.04 \times \% CO + 5.24 \times LA)$).

Fecundity significantly increased with leaf area and light intensity, while stem length and soil depth had no effect (Table 1b). Leaf area had a two-fold larger effect than light

intensity. When the effect of leaf area was accounted for, defoliation treatment had no significant effect (Table 1b).

ENSO effects

The production of inflorescences per palm was significantly greater during the ENSO year than during the other 2 years (Table 3; Fig. 4). Among the control palms, this difference was about 60%. The year effect was independent of defoliation treatment. The probability of reproduction and the production of inflorescences per reproductive individual varied in a similar way among years (Table 3; Fig. 4b,e), although a significant year \times treatment \times gender effect was found on the probability of reproduction. Thus, the increase in reproductive effort in the ENSO year could be attributed both to an increase in the probability of flowering and to an increase in the number of inflorescences per reproducing individual.

Interestingly, the mean annual seed production per individual (considering reproductive and non-reproductive palms) and the annual probability of fruiting decreased significantly in the ENSO year (Table 3). For both variables, there was a significant interaction between defoliation treatment and year (Table 3). Non-defoliated palms, and to a lesser degree those of the 33% defoliation level, had their greatest seed production after the ENSO year (1999) while palms subjected to 50% defoliation and, mainly, those suffering 66% defoliated had their lowest performance in that year (Fig. 4c,d). When the analysis was conducted only considering fruiting individuals, the effect of year and that of the interaction between year and defoliation treatment were not significant (Table 3). Seed production per reproductive palm was similar in all years, except in the 66% defoliation treatment where reproductive output declined with time (Fig. 4f).

Discussion

Our results show that sustained defoliation, interacting with variation in light availability (due to forest canopy dynamics), severe drought (such as those occurring in ENSO years) and soil properties, strongly influences the demography of a shade-tolerant palm. The opportunistic nature of our study regarding the ENSO analysis limits the generality of the results. However, our study clearly documents the strong impact that such a disturbance event can have on population dynamics of tropical rain forest understorey plants.

EFFECTS OF DEFOLIATION

Defoliation had a strong negative effect on reproduction, which is contrary to most other studies, which found very small or no negative effects after single defoliation events (e.g. Mendoza *et al.* 1987; Oyama & Mendoza 1990). The only other study that we know that applied repeated defoliation found results similar to ours (Endress *et al.* 2004a,b, 2006). Thus, applying repeated defoliation treatments is crucial to adequately analysing the demographic conse-

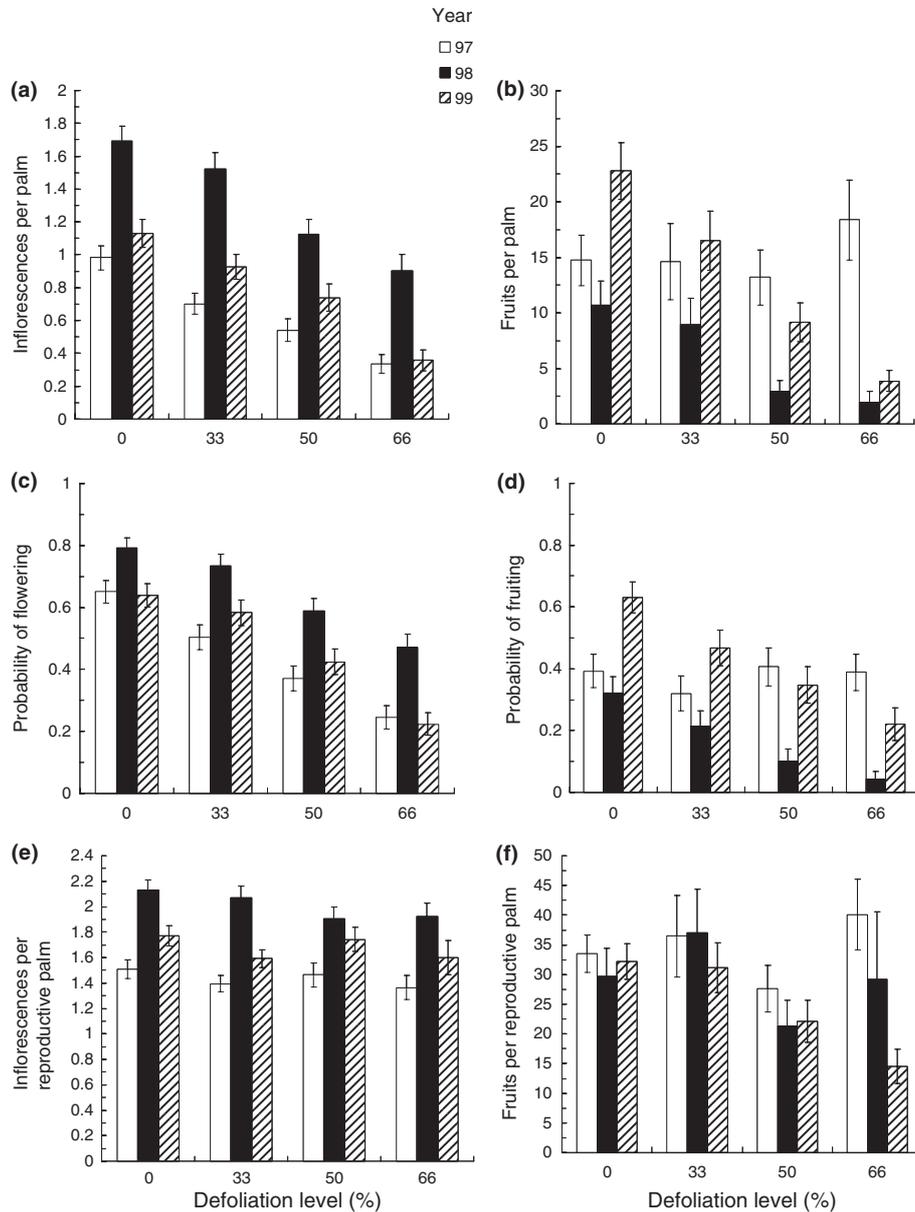


Fig. 4. Year and defoliation effects on reproductive components of *Chamaedorea elegans* palms at Chajul, south-eastern Mexico. (a) Mean annual number of inflorescences produced per female individual, (b) mean annual number of seeds (fruits) produced per individual, (c) mean annual probability of flowering, (d) mean annual probability of seed production, (e) mean number of inflorescences produced per flowering plant and (f) mean number of seeds produced per fruiting palm. Vertical lines indicate one standard error. Note that the results presented in panels (a) and (b) are the product of those presented in (c) and (e), and (d) and (f), respectively.

quences of leaf harvesting and herbivory, which can endure for several years.

The negative effect of defoliation was mainly through its effect on the probability of reproduction (flowering and fruiting); the number of inflorescences and seeds produced per reproductive plant was much less affected, as was also documented for *Chamaedorea radicalis* (Endress *et al.* 2006). These results concur with the observation that in tropical understory palms the probability of reproduction is a more plastic trait than reproductive output (Piñero & Sarukhán 1982). Flowering can be triggered after plants reach a threshold level of carbohydrates (Klinkhamer *et al.* 1992). It is likely that the ability of palms to reach such a threshold is lowered as leaf

area, and therefore carbon gain, is reduced by increased levels of defoliation.

Demographically a defoliation-induced reduction in the probability of reproduction may have important consequences. As defoliation levels increase, reproduction tends to be concentrated among fewer individuals. In our study, the percentage of females reproducing every year declined from 33% in the control treatment to 5% in the 66% defoliation treatment. Thus, populations subjected to herbivory or leaf harvesting are potentially at greatest risk because the few reproductive plants may die either by deterministic factors (e.g. diseases), stochastic effects (e.g. physical damage) or as result of defoliation, leaving the population without regenera-

tive potential. Also, studies conducted on tropical long-lived palms indicate that large reproductive population sizes are needed to reduce the risk of negative genetic effects (Eguiarte *et al.* 1992, 1993).

In contrast to reproduction, growth and survival were only slightly affected by repeated defoliation, as found in other studies (e.g. Endress *et al.* 2004b, 2006). In long-lived plant species with slow growth and reproduction, but high survival rates, population growth rate tends to be most sensitive to changes in adult survival and much less responsive to changes in fecundity or growth (Batista *et al.* 1998; de Kroon *et al.* 2000; Franco & Silvertown 2002; Silvertown *et al.* 1996; Zuidema *et al.* 2007). Among the control *C. elegans* palms we observed that survival rates were positively correlated with total leaf area and that the effect of this trait was greater than that of any other factor. Thus, safeguarding leaf production in favour of reproductive output in response to damage would be beneficial for this species as it helps maintain adult survival. Overall these responses may enable understory palms to maintain populations near equilibrium stages even under relatively severe and repeated defoliation, suggesting that leaf harvesting can be biologically sustainable (Endress *et al.* 2004b, 2006). However, as we will discuss below, this conclusion does not consider the effects of extreme events, nor does it consider the points noted above, that reproduction tends to become concentrated among fewer individuals or that seedling recruitment potential may be negatively affected by defoliation.

LIGHT AND SOIL DEPTH EFFECTS AND INTERACTIONS WITH DEFOLIATION

Among control plants, both reproduction and growth increased mostly with standing leaf area. Total leaf area determines the amount of light captured by a plant and, therefore, its photosynthetic capacity. *Chamaedorea elegans* exhibits little self-shading within its crown and a greater leaf area is associated with a proportional increase in carbon gain (Anten & Ackerly 2001). Interestingly, however, light availability had a much smaller effect on most demographic rates than leaf area, and no significant effect on flower and seed production. This result might be associated with the low light saturated rates of leaf photosynthesis (A_{\max}) and low plasticity in this trait documented for *C. elegans* (Anten & Ackerly 2001). A low A_{\max} implies that shade-tolerant plants cannot efficiently utilize high-light conditions for photosynthesis (Givnish 1988; Chazdon 1992).

Contrary to growth and reproduction, mortality increased with light availability. In understory shade-tolerant plants, high-light conditions can damage the photosynthetic system and/or increase water transpiration losses (Lambers *et al.* 1998). Some individuals were growing in gaps with 20–30% canopy openness, where high respiratory rates, caloric loads and/or photoinhibition can be expected. Field observations noted bleaching of leaf laminas of *C. elegans* palms in tree fall gaps, suggesting that mortality effects of light were partly due to photoinhibition. Regarding water stress, understory plants

are especially susceptible to drought due to their shallow rooting systems (Wright 1992) and low capacity for hydraulic plasticity (Valladares *et al.* 2005). Our palm population was growing on very shallow soil (<20 cm for most plants), and plant death tended to occur during or shortly after the dry season.

Interestingly in defoliated plants, unlike in control plants, mortality was not positively related with light availability. Two factors may have produced this result. First, defoliation seemed to increase mortality at low light. This result was to be expected as the capability of compensatory growth in response to defoliation declines under shaded conditions (Anten *et al.* 2003; Wise & Abrahamson 2007). Second, defoliation implies the direct removal of transpiring tissue, but does not immediately affect root mass. Anten *et al.* (2003) showed that defoliated *C. elegans* palms have a greater root-to-leaf-area ratio, which probably increased the water supply to the remaining leaves, as has been demonstrated in herbaceous plants (e.g. Coughenour *et al.* 1990; Van Staalduinen & Anten 2005; Wise & Abrahamson 2007). Thus, it could be that in our study leaf removal relieved some of the water stress to which plants were subjected and that this might have contributed to their survival. More generally, our defoliation results illustrate that light availability and leaf damage may interactively affect demographic behaviour of rain forest understory plants.

ENSO EFFECTS

In our study, the increase in mortality and decrease in fecundity during the El Niño year occurred during the dry season while increases in leaf production and flowering occurred during the subsequent rainy season. As described above, we recorded a very strong reduction in rainfall between January and May 1998, but rainfall subsequently resumed to above normal (cf. Fig. 1c,e). The ENSO effect therefore aggravated drought during the dry season and thus increased mortality. Extreme ENSO events have led to increased mortality and reduced growth among several tropical trees (e.g. Condit *et al.* 1995; Gilbert *et al.* 2001; Delissio & Primack 2003; Wright 2005; Phillips *et al.* 2009). Also, such drought stress could have limited the development and maturation of fruits in palms that produced their inflorescences during the previous flowering season (November 1997 through April 1998). To what extent this drought period affected pollination is unknown.

We noted that the canopy was considerably more open and that there was a much thicker layer of dead leaves on the forest floor during the March census in the ENSO year, although we did not measure radiation at that time. Also, during the wet season (June through October) of the ENSO year, there were fewer rainy days than normal (cf. Fig. 1f). Considering that rainy days are usually more overcast than rain-free days, this suggests that more light was available in the understory during the growing (wet) season. Therefore, once rainfalls resumed the growth and flowering of surviving plants might have been significantly stimulated by a temporary increase in

light availability. In BCI, Panama, it has been observed that flowering activity among understorey tree species notoriously increases during El Niño years, which has been explained by the prevalence of high solar radiation and less cloudiness during those years (Wright & Calderón 2006).

On balance, however, the ENSO effects on the population dynamics in our study were most likely negative. As noted above, population growth rates of long-lived species such as *C. elegans* tend to be much more sensitive to changes in survival than to changes in any other demographic rate. A doubling of the mortality rate therefore probably had a much greater effect than a 40–60% increase in flowering. This indicates that severe drought events, such as occur during El Niño, may play an important role in determining the long-term population dynamics of *C. elegans*.

The strong increase in mortality during the ENSO event was apparent across all defoliation treatments. This may have important consequences for determining sustainability of leaf harvesting. As noted above, one study (Endress *et al.* 2004b, 2006) estimated that populations of the understorey palm *Chamaedorea radicalis* can remain near equilibrium under repeated defoliation, suggesting that leaf harvesting can be sustainable as long as recruitment is ensured (Endress *et al.* 2006). This study, however, did not mention any evidence of drought effects on palm defoliation effects. It has been pointed out that conclusions regarding sustainability of leaf harvesting should thus be taken with care as environmental conditions can vary considerably from one year to the next (e.g. Horvitz & Schemske 1995; Caswell 2001).

Conclusion

In this study, we show that occurrence of severe droughts can strongly aggravate the negative effects of herbivory and leaf harvesting, and that these effects should be quantified when assessing the ecological effects of herbivores and sustainability of leaf harvesting. This is especially urgent since ENSO-related droughts are expected to become more frequent and severe under the present global climatic change scenario (e.g. Meehl 1997; Timmerman *et al.* 1999). More generally, our results illustrate how research conducted during 'normal' years may overlook the impact of severe events and may therefore fail to identify critical mechanisms that control population dynamics of forest plants.

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