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Effects of partial throughfall exclusion on the phenology of *Coussarea racemosa* (Rubiaceae) in an east-central Amazon rainforest

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Abstract Severe droughts may alter the reproductive phenology of tropical tree species, but our understanding of these effects has been hampered by confounded variation in drought, light and other factors during natural drought events. We used a large-scale experimental reduction of throughfall in an eastern-central Amazon forest to study the phenological response to drought of an abundant subcanopy tree, *Coussarea racemosa*. We hypothesized that drought would alter the production and the timing of reproduction, as well as the number of viable fruits. The study system comprised two 1-ha plots in the Tapajos National Forest, Para, Brazil: a dry plot where 50% of incoming precipitation (80% throughfall) was diverted from the soil during the six-month wet season beginning in January 2000, and a wet plot that received natural rainfall inputs. Fruit production of *C. racemosa* was quantified every 15 days using 100 litter traps ($0.5\ m^2$) in each plot. The production of new leaves and flowers was recorded monthly for *C. racemosa* individuals. Soil water, pre-dawn leaf water potential and solar radiation were measured to help interpret phenological patterns. Over the ~3.5-year period (April 2000 through December 2003), total fruit production remained similar between plots, declining by 12%. In 2003, production was four times higher in both plots than in previous years. In the dry plot, fruit fall shifted 40 and 60 days later into the dry season in 2002 and 2003, respectively. Total fruit fall dry mass production was variable across the study period. Foliage and flower production coincided with peak irradiance early in the dry season until delays in flowering appeared in the dry plot in 2002 and 2003. Plant water stress, through its influence on leaf developmental processes and, perhaps, inhibition of photosynthesis, appears to have altered both the timing of fruit fall and the quality and number of seeds produced.

Keywords Reproductive · Biology · Tropical · Forest · Drought

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Introduction

Droughts associated with Amazon deforestation (Silva Dias et al. 2002), biomass burning (Andreae et al. 2004), higher temperatures and evapotranspiration associated with global warming (Wang 2005), increasing El Niño Southern Oscillation (ENSO) frequency (Timmermann et al. 1999), and other oceanic temperature disruptions (Rohter 2005), are predicted to change forest productivity, carbon storage and vulnerability to fire over extensive areas of the Amazon

Table 1 Total incoming precipitation for each year of the drought treatment for the dry (panels off) and the wet (panels on) seasons

Year	Period of exclusion	Precipitation (mm)		
		Total incoming	Panels off	Panels on (throughfall excluded)
2000	02/01–08/07	2517	830	1687 (844)
2001	01/01–31/07	1882	171	1711 (856)
2002	01/01–31/07	1958	292	1665 (833)
2003	01/21–08/14	1690	394	1295 (648)
	Total	8047	1687	6358 (3179)

Approximately 50% of the incoming precipitation was excluded when the panels were on; these volumes are presented in parentheses

(Walther et al. 2002; Nepstad et al. 2002, 2004). Drying may also influence plant reproductive processes (Penuelas and Filella 2001; Ozanne et al. 2003), including the timing and amount of flower and fruit production, and thus affect future plant establishment (e.g., by changing the optimal timing of pollination, seed dispersal, seed germination and regeneration success; Walther et al. 2002). Such alterations in phenological patterns can also influence plant–animal interactions, as they may disrupt the timing of fruit and seed availability, seed dispersal patterns and seed predation (Curran and Leighton 2000; Curran and Webb 2000; Augspurger 1981, 1984).

Among the many factors controlling the phenology of tropical plants, subtle seasonal changes in day length that occur upon moving even short distances north or south of the equator have been proposed as the primary trigger of flowering in aseasonal tropical forests (Rivera and Borchert 2000; Rivera et al. 2002; Borchert et al. 2005). However, in areas that experience seasonal drought, plant water status is regarded as a more important mechanism influencing the variation in the timing of flower initiation (Borchert 1991; Borchert et al. 1994; William 1997). For example, mast fruiting of trees in SE Asia and supra-annual fruit production in the neotropics are associated with the droughts that occur during ENSO events (Curran et al. 1999; Wright et al. 1999), although it is unclear whether the proximal trigger for fruiting during ENSO is plant hydration following isolated rainfall events (Borchert et al. 2002), elevated radiation levels (Wright et al. 1999) or variations in temperature preceding ENSO (Ashton et al. 1988).

Prolonged drought, however, may have a negative effective on plant reproduction because of the substantial carbohydrate demands of both flowering and fruiting (Larcher 1995). Drought-induced reductions in leaf area and in quantum yield (Nepstad et al. 2002; Larcher 1995), or in stomatal conductance can inhibit photosynthesis, constraining the amount of carbohydrate available for investment in reproduction. The magnitude of the changes that severe droughts may impose on the reproductive phenology of diverse tropical forest tree species will depend upon their ability to cope with water stress through various adaptations, including: (1) stomatal regulation of water loss (Jones and Sutherland 1991), (2) internal adjustments in how carbohydrates are allocated (Chapin et al. 1990; Newell et al. 2002), (3) resistance to drought-induced cavitation (Cardiont, unpublished data), (4) drought avoidance through deep root systems (Nepstad et al. 1994), and (5) perhaps the ability to perform hydraulic redistribution of deep soil water (Oliveira et al. 2005).

In order to elucidate some of the possible impacts of severe droughts on the phenology of Amazonian trees, we excluded a portion of throughfall from an Amazon forest for four years in order to create severe soil moisture deficits. Specifically, we studied the vegetative and reproductive phenology of *Coussarea racemosa* (Rubiaceae), an abundant understory species, hypothesizing that the treatment would: (1) shift the temporal pattern of flowering and fruiting; (2) reduce total fruit production over the long term; and (3) reduce fruit quality (number of hollow fruits and of fruits with signs of predation) due to reduced energy for fruit filling and secondary metabolite production.

Methods

Climate and soils

This study was carried out in moist lowland tropical forest located in Brazil's Tapajós National Forest, in east-central Amazonia (2.897°S, 54.952°W). Measurements presented here were obtained between June 2000 and December 2003. Annual rainfall in the area ranges from 600 to 3,000 mm, with a mean of ~2,000 mm. The precipitation pattern is strongly seasonal, with an approximate six-month dry season extending from July to December. Soils at the study site are typical of the region, being deeply weathered Oxisol clays of the Haplustox group.

Treatment design

The throughfall exclusion experiment consists of two structurally and floristically similar 1-ha plots, 20 m distant from each other: a ‘‘dry plot’’ (treatment) and a ‘‘wet plot’’ (control). Approximately 50% of the incoming precipitation is diverted from the soil in the dry plot during the six-month wet season using a system of 5,660 plastic panels supported by wooden gutters located in the forest understory. The panels cover approximately 80% of the ground area in the dry plot. Both plots were isolated from the surrounding forest with a soil trench 1–3 m deep to prevent vegetation in the dry plot from accessing water from the surrounding area and to ensure a similar level of root system damage in the wet plot. Baseline measurements were collected in both plots over a one-year intercalibration period prior to treatment initiation, which began in late January 2000. For further description of the study site and experimental design, see Nepstad et al. (2002).

The study species

C. racemosa A. Rich (Rubiaceae) is an abundant subcanopy tree species in this forest, being represented by 143 and 223 individuals >2 cm dbh in the dry and wet plots, respectively. *C. racemosa* leaves are retained during the dry season, with an average longevity of 16 months (Brando and Xabregas, unpublished data). Flowers are arranged in terminal racemes with inferior ovaries. Fruits are drupes, presumably bird-dispersed, measuring an average 0.8 cm in length and 0.7 cm in diameter, containing a wrinkled, distinctive seed (Parrotta et al. 1995). *C. racemosa* is distributed in the Brazilian Amazon in the states of Acre, Bahia and Para, as well as in French Guyana, Guyana, Suriname and Ecuador (New York Botanical Garden 2006).

Phenological observations

Fruit production was measured using traps collected at two-week intervals. We used 100 (0.5 m^2; 0.8 × 0.62 m) traps made of nylon screen placed 1.5 and 1 m above the ground in the dry and wet plots, respectively, in 100 points in each of the plots according to a sampling grid with 6 × 17 m cells in the dry plot and 10 × 10 m cells in the wet plot. (The grid cell dimensions varied between plots in order to accommodate the drainage troughs constructed in the dry plot.) *C. racemosa* fruits were sorted manually, oven-dried (60 °C for 72 h), and weighed to the nearest 0.01 g. The present analysis concentrates on collections that were made over a 3.5-year period between April 2000 and December 2003. The mass and number of fruits produced were normalized between plots by dividing their dry mass by the basal area of study species individuals with dbh >9 cm (dry plot = 0.70 m^2 ha^{-1}; wet plot = 0.52 m^2 ha^{-1}) (see Results).

Visual assessments of the presence of new foliage and reproductive organs (buds, flowers, fruits) were conducted bimonthly between August 1999 and December 2002 for 21 (wet plot) and 22 (dry plot) *C. racemosa* individuals. These same parameters were recorded for all individuals (≥10 cm dbh) on a monthly basis between January and December 2003, when 46 and 44 individuals of the study species were observed in the dry and wet plots, respectively. At each census, the same observer noted the presence or absence of reproductive structures using binoculars, and examined many of the tree crowns from above using the site's six wooden towers and catwalks.

An intensive sample of the condition of *C. racemosa* fruits was made at the time of their peak production, in May and July 2003. A total of 100 fruits from litter traps in each plot collected on 23 (May) and 01 (July) were oven-dried and examined. For each fruit, we measured the lengths of the major and minor axes to the nearest 0.1 cm. The fruits were then opened and the presence of a seed, and whether there was evidence of predation, was noted.

System water balance and PAR

Soil water was quantified using time domain reflectometry (TDR, Topp et al. 1980). Volumetric soil water content (WVC) was measured each month using a series of paired probes situated beside (0–30 cm deep; vertical orientation) and within (50–1,100 cm deep; horizontal orientation) five deep soil shafts in both plots (Nepstad et al. 2002). The VWC measurements were used to derive estimates of plant available water (PAW) by assuming that the global minimum value for VWC observed at each depth interval in the dry plot corresponded to the permanent wilting point. The average maximum values for PAW in the wet plot, excluding extreme values immediately following a rain, were used to estimate field capacity. PAW for the 11-m-deep profile was determined by summing the difference (field capacity–wilting point) for each depth interval. Oliveira et al. (2005) found that the diameter of *C. racemosa* tap roots was markedly reduced at 1 m depth, suggesting that this species is not very deep-rooted. We report PAW as a percentage of the maximum value (% PAW max) up to a 200 cm depth.

Pre-dawn leaf water potential (LWPpre) of *C. racemosa* was determined at biweekly–monthly intervals using a pressure chamber (SoilMoisture 3,005–1,422; Scholander et al. 1965) beginning in January 2000. For each date, samples consisted of four leaves collected from each of three mature individuals (≥10 cm dbh) in each plot. Leaves were clipped before sunrise, placed in plastic bags and stored on ice until measurements could be made (Nepstad et al. 2002).

Photosynthetically active radiation (PAR) was measured using a quantum sensor (Type QS2, Delta-T Devices Ltd, Cambridge, UK) located on top of a 33-m tall tower that extended above the main canopy in the dry plot.

Dendrometer bands were used to quantify the increments of stems ≥10 cm dbh on a monthly basis between 1999 and 2003 in both plots. These estimates were available for 34 individuals (dry plot) and 35 individuals (wet plot). The frequency and sensitivity of these measurements allowed us to identify seasonal patterns of stem expansion and shrinkage associated with water storage (Reich and Borchert 1982).

Statistical analyses

Temporal patterns of fruiting were assessed using circular statistics (Zar 1999). Fruiting events, assessed twice-monthly, were treated as a binomial response variable and given a value of 1 or 0 depending on whether fruits were present or absent in each litter trap, respectively. The mean number of fruiting events (a) and the vector length (r) were calculated by transforming the date of the event into an angle between 0 and 360°, where 0° corresponds to 1 January, as follows:

$$\begin{aligned} a &= \arctan(Y/X) \quad \text{if } X>0 \text{ or} \\ a &= 180+\arctan(Y/X) \quad \text{if } X<0 \end{aligned} \tag{1}$$

and,

$$r=\sqrt{X^2+Y^2} \tag{2}$$

where $X=(\sum f_i \cos a_i)/n$, $Y=(\sum f_i \sin a_i)/n$, $n=\sum f_i$, where f_i represents the number of events (number of traps with fruits present), and a_i is the midpoint of the measurement interval (i) expressed as an angle. The length of the vector provides a measure of concentration. To test the uniformity of fruiting throughout each year, we applied the Rayleigh test (Zar 1999): January corresponded to 0–30°, February to 31–60°, March to 61–90°, and so on.

We used a Mann–Whitney test to test for differences in fruit production as dry mass between plots during each year of the study. This approach was taken because the normality assumptions of parametric analyses could not be met. Degrees of freedom for this analysis were provided by the biweekly observations made in each plot. One-tailed tests were used in accordance with our stated hypothesis that drought would cause a reduction in fruit production. A 2×2 contingency table analysis was used to assess differences between plots in terms of fruit condition (number of hollow fruits and fruits with signs of predation) for the intensive samples in May and July 2003. Degrees of freedom for this analysis were provided by the number of litter traps containing at least two *C. racemosa* fruits. To assess similarity of cycles of soil recharge between dry and wet plots, we carried out a cross-correlation analysis for the years 2000, 2001, 2002 and 2003, according to Venables and Ripley (2002).

Results

Structures of *Coussarea racemosa* population

C. racemosa was the third most important species according to the importance value index (4%) in the two experimental hectares, and the most important species in the Tapajos National Forest (IVI = 30.2%,) followed by *Erisma uniciatum* (IVI = 15.5%) (Vieira 2003). The reproductive population of *C. racemosa* was

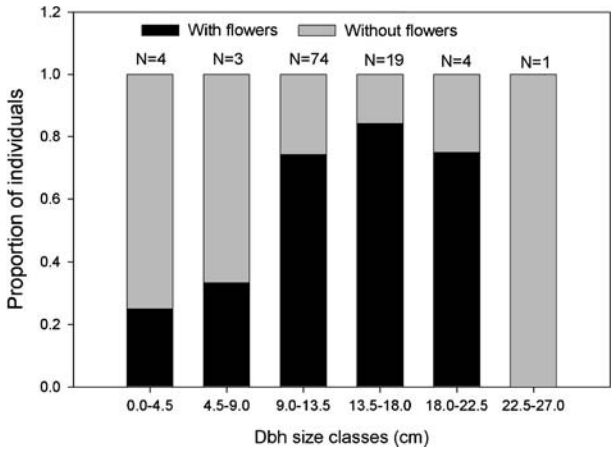

Fig. 1 The percentage of reproductive and nonreproductive individuals of *C. racemosa*, according to five different dbh (diameter breast height, 1.3 m) size classes. *N* represents the number of individuals used in each size class; both dry and wet plots were combined

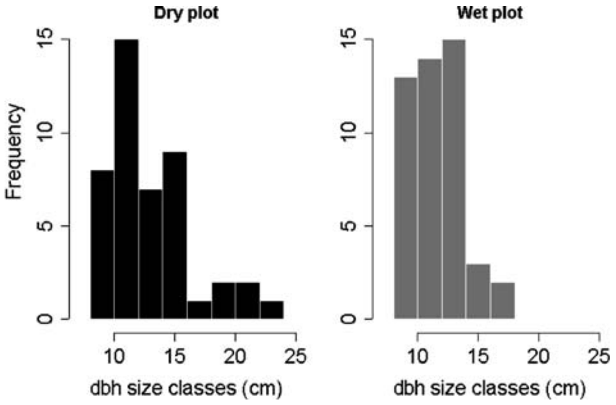

Fig. 2 Diameter distributions of the reproductive populations of *C. racemosa* (individuals >9 cm in dbh) for the dry and wet plots

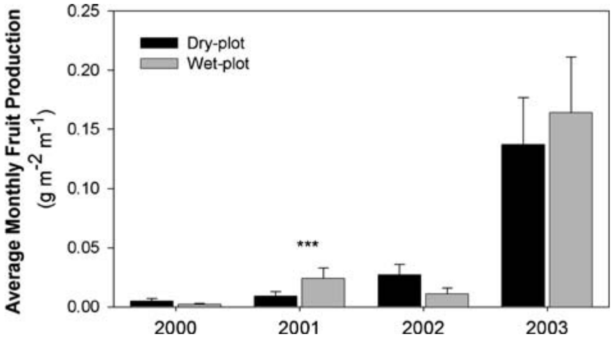

Fig. 3 Monthly fruit production (dry mass (g) per m^2) of *C. racemosa* in the dry and wet plots in each year of the experiment. *Error bars* indicate ±1 SE **P* <0.1; ***P* <0.05; ****P* <0.01

established on the basis of an observed relationship between dbh and percentage reproductively active individuals, when ~80% of individuals flowered (Fig. 1). This reproductive population with dbh >9 cm consisted of 49 and 45 individuals in the dry and wet plots, respectively. The diameter distributions were similar in both plots, ranging from 9.0 to 23.9 cm dbh (mean = 12.9±1.06) in the dry plot and from 9.0 to 17.6 cm dbh (mean = 11.9±0.7) in the wet plot (Fig. 2).

Mortality rates for this species remained similar in both plots throughout the 3.5-year study period, 1.9 (binomial confidence interval: upper = 3.78; lower = 0.89) and 1.0 (binomial confidence interval: upper = 2.28; lower = 0.39) % year^{-1} for the dry and wet plots, respectively (Tohver et al., unpublished data).

Quantitative phenology

C. racemosa reproduced every year during the study period, with large pulses of fruiting occurring on a supra-annual basis (Fig. 3). In 2003, mean fruit production in both plots was over eightfold greater than in 2001 and 2002 (only nine months of records were available in 2000). The duration of fruit fall was broad in both plots during all years of the study, ranging from as brief as five months in the wet plot in 2002 to as long as 11 months in the dry plot in 2003 (Table 2).

Annual fruit production was variable between plots over time. For example, in 2001 and 2003, production was 64% (*P*=0.006, Mann–Whitney *U*) and 17% (*P*=0.417) higher in the wet plot than the dry plot, respectively (Fig. 3). By contrast, production was ~2.5 times higher in the dry plot than the wet plot in both 2000 (*P*=0.070, Mann–Whitney *U*) and 2002 (*P*=0.040). Overall, the drought treatment does not appear to have had a dramatic impact on overall fruit production between plots; yet monthly averages determined over the entire study period were approximately 12% lower in the dry plot (0.044 g m^{-2} 30 d^{-1}) than in the wet plot (0.050 g m^{-2} 30 d^{-1}). This slight cumulative difference over the study was due to higher production in the wet plot than the dry plot in 2003, when fruit production was four times higher than all of the previous years combined.

In the dry plot, the timing of peak fruit fall shifted later into the dry season as the drought treatment progressed. Early on, in 2001, the peak of fruit fall occured during the latter half of the wet season (early May) in both plots (Rayleigh Test, dry-plot, *P*=0.312; wet plot, *P*=0.058) (Table 2). However, in 2002, a

Table 2 Results from a circular statistical analysis carried out to determine the time of peak fruiting for *C. racemosa*

Years	Months and mean vector (*a*, degrees)		*r* (concentration)		Chi-squared test
	Dry plot	Wet plot	Dry plot	Wet plot	
2001	May (128)	May (129)	0.414	0.324	0.90
2002	August (138)	April (99)	0.477	0.702	<< 0.01
2003	July (201)	May (149)	0.515	0.489	<< 0.01

Presented are the month and associated mean vector (*a*), and the length of the mean vector (*r)* for reproduction events in both plots from July 2000 to December 2003. Chi-squared probabilities associated with significance tests comparing the dry and wet plots are provided by treatment year

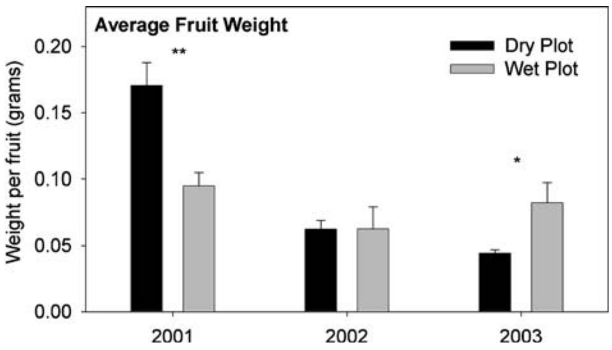

Fig. 4 Average fruit dry mass for fruits of *C. racemosa* in the dry and wet plots in each year of the experiment; number of traps with fruits. *Error bars* indicate ±1 SE. N=4 and 12 for 2001; 14 and 8 for 2002; 19 and 16 for 2003 in the dry and wet plots, respectively, *P <0.1; **P <0.05; ***P <0.01

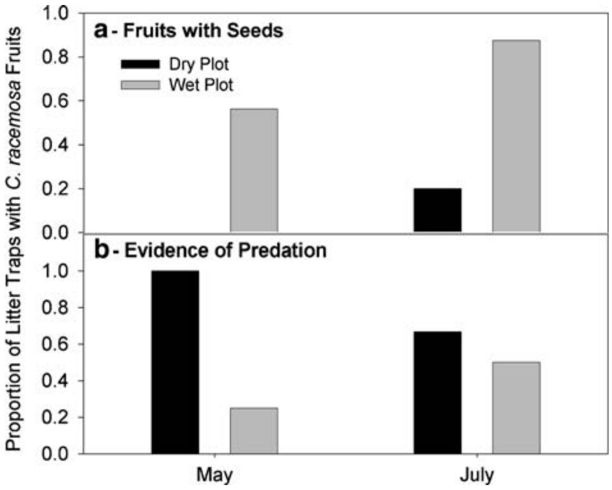

Fig. 5a–b Proportion of traps with fruits of *C. racemosa* in May and July 2003, representing the peak of fruit fall: **a** represents the proportion of traps in which fruits contained seeds and **b** the proportion of traps containing fruits that showed evidence of predation

significant shift in the timing of this peak was observed in the dry plot, occuring ~40 days later (Table 2). An even larger shift was observed in 2003, the year of maximum production, when peak fruit fall occurred almost two months later in the dry than in the wet plots (Table 2).

The drought treatment appears to have provoked changes in fruit morphology over time. For example, the mass of an average *C. racemosa* fruit produced in 2001 was 1.8 times higher in the dry plot than the wet plot, yet these values were nearly equal in 2002, and eventually became ~50% higher in the wet plot by 2003 (Fig. 4). These observations suggest a trend towards lighter fruits being produced in response to the persistent drought treatment (Fig. 4). However, changes in fruit weight were not accompanied by alterations in fruit size (data not shown).

Large differences were also observed in fruits that contained seeds and the number of fruits showing evidence of predation between dry and wet plots for the samples collected in May and July of 2003 (Fig. 5). For example, only 14% (3 out of 22) of the litter traps with fruits in the dry plot contained seeds compared to 75% (30 out of 40 traps) in the wet plot (P<0.000, Yates corrected chi-square test). Moreover, a significantly higher percentage of fruits showed evidence of predation in the dry plot, where 17 out of 22 traps (77%) with fruits showed signs of damage, compared to 16 out of 40 traps (40%) in the wet plot (P=0.011). Less than 1% of the fruits we examined in the dry plot (1 out of 103) both contained seeds and lacked evidence of predation. The corresponding value was ~20-fold higher in the wet plot, where 19 out of 102 fruits contained seeds that were in good condition.

Environmental correlates for leaf and flowering phenology

C. racemosa initiated both leaf and flower production early in the dry season (Fig. 6a,b,f,g). In each year of the study, inflorescenses were initially observed in August or September (Fig. 6b), coincident with the formation of new leaves (Fig. 6a). The proportion of the sampled population with flowers was highest in 2002, when 60% of the reproductively mature individuals were flowering in both plots (Fig. 6b). In this year, in the dry plot we observed two waves of leaf flushing and flowering after a mid-dry season rainfall event (Fig. 6g), the second wave coinciding with partial stem hydration of *C.racemosa* individuals (Fig. 6e).

This shift in the timing of leaf flushing and flowering may have disrupted the synchrony between flowering and peak PAR observed in 2000 and 2001 in the dry plot and in all years in the wet plot. In 2003, when a mid-dry season rain event was associated with rapid stem rehydration, peaks of flowering were observed in August (wet plot, 40% of reproductive individuals) and November (dry plot, 48%). Flowering had almost ceased by December in both plots (wet plot, 0% of reproductive individuals; dry plot, 7% of reproductive individuals). The tight temporal synchrony between flower and leaf production was observed in all years. This synchrony was maintained even when differences in reproductive and vegetative phenological patterns between parcels existed.

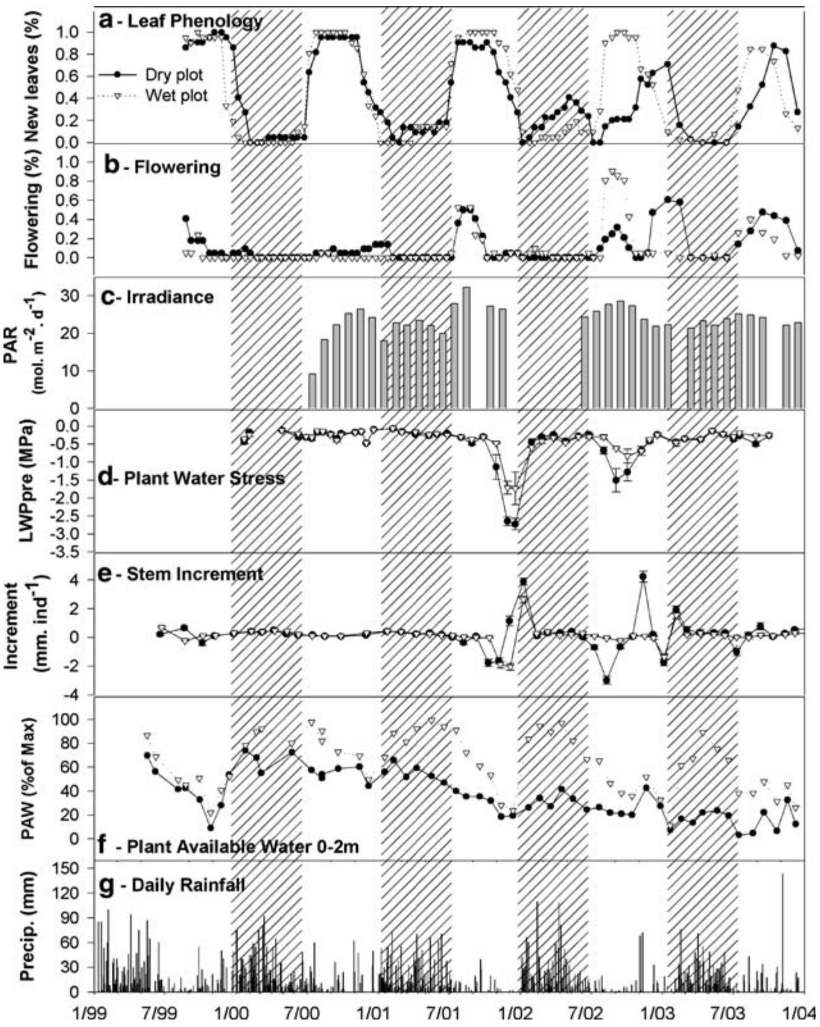

Fig. 6a–g Temporal trends in ecological parameters of *C. racemosa*, and environmental factors in treatment and control plots during the throughfall exclusion experiment, Tapajós National Forest. **a** Proportion of individuals with new leaves and **b** proportion of individuals flowering (n=21 and n=20 in the wet and dry plots, respectively, in 2002, and n=46 and n=49 in 2003). **c** Photosynthetic active radiation (PAR) in mol m^{-2} day^{-1}. **d** Pre-dawn leaf water potential of three individuals per plot and n=4 leaves per individual; means ± SE. **e** Stem radial growth increment of trees; means ± SE, n=34 and n=35 in the control and treatment plots, respectively. **f** Plant-available water, % of maximum, from 0 to 200 cm depth. **g** Daily rainfall measured in a forest clearing 500 m from the study plots. The *shaded areas* represent the throughfall exclusion period

Discussion

The altered phenology of *Cousarea racemosa* documented in this study in response to partial throughfall exclusion supports the hypothesis that increasing frequency and severity of drought, as has been predicted for the Amazon Basin, may have profound implications for the reproductive biology of this tree species (Penuelas and Filella 2001; Ozanne et al. 2003; Nepstad et al. 2002). While *C. racemosa* does not appear to have suffered increased mortality, and exhibits some resistance to drought-induced cavitation of water conducting xylem (Cardinot et al., unpublished data), reproductive behavior responded strongly to the four-year drought treatment, as evidenced by progressive delays in the formation of new leaves, production of flowers and maturation of fruits. In addition to the temporal shifts provoked by the drought, lighter fruits were produced, the fruits that were formed were more likely to be hollow, and those fruits that did contain seeds were more likely to have been destroyed by seed predators.

Timing of leaf flushing, flowering and fruiting

Given that environmental cues such as temperature and subtle changes in day length (Wright 1996) were not altered by the treatment, the delays in the timing of flowering and leaf flushing indicate that this species is dependent on water availability for flowering and new leaf production. Borchert et al. (2004) asserted that these two processes, especially in trees with terminal inflorescence such as *C.racemosa*, require cell expansion, and thus positive tree water status may trigger phenological events. Augspurger (1981) found similar responses when using sprinklers to induce *Hybanthus prunifolius* individuals to flower prior to the normal triggering rainfall events in Panama.

The delay in flowering led to a corresponding delay in fruit fall in the dry plot relative to the wet plot

(Table 2). As a result, the majority of seeds arrived on the forest floor early in the dry season in the dry-plot, as opposed to the wet plot, where fruit fall was concentrated in the wet season. Many tropical species appear to time fruit fall to precede the optimal time for germination, which, in most cases, coincides with the wet season (Frankie et al. 1974; Garwood 1983). Hence, the shift in fruitfall may negatively impact on the long-term viability of *C. racemosa* by diminishing the likelihood of seed germination and subsequent seedling establishment.

Fruit production and seed quality

Fruit production in both plots (dry mass) was about fourfold greater in 2003 compared to the other years of this study. This pattern of high fruit production was observed not only for *C. racemosa*, but for all species combined in both plots (D. Nepstad, unpublished data). Several authors argue that higher levels of PAR during dry years increase fruit production due to high photosynthetic yields. For instance, Graham et al. (2003) provoked an increase in fruit production for two Panamanian tree species by artificially increasing PAR. However, drought-induced restrictions on photosynthesis (Nepstad et al. 2002) may have limited the reproductive success of *C. racemosa* by two mechanisms: by reducing the number of seeds per fruit and by lowering fruit resistance to seed predators through defense mechanisms such as second secondary metabolites and physical barriers (Janzen 1969; Chapin et al. 1990). In addition to potential changes in fruit morphology driven by the drought treatment, two ecological effects may have contributed to the increased number of fruits with signs of predation in the dry plot. First, the shift in timing of fruit fall, occurring later in the dry season, may alter the interaction between the population of *C. racemosa* and its seed predators (Curran and Leighton 2000; Curran and Webb 2000; Augspurger 1981, 1984). Second, the 18.5% decrease in leaf area index in the dry plot relative to the wet plot that occurred from 2000 to 2003 (Nepstad et al., unpublished data) may have made it easier for seed predators to find the fruits of *C. racemosa*.

Conclusion

While the drought treatment was linked to a decline in the average mass per fruit of *C. racemosa*, the most provocative responses were those related to the delay in flowering and fruiting, and the diminished number of mature fruits containing seeds. The delay in flowering/fruiting was best explained by the dependence of inflorescence production and new leaf production on plant water status, which was significantly affected by the drought treatment. It appears that plant water stress altered reproductive phenology by delaying the onset of leaf production further into the dry season, and it may also have diminished reproductive success by increasing the failure of seed set and enhancing seed predation. In addition, lower levels of photosynthetic yields for *C. racemosa* in the dry plot (Nepstad et al. 2002) may have contributed to the reduced reproductive success of this species in 2003.

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References

Andreae MO, Rosenfeld D, Artaxo P, Costa AA, Frank GP, Longo KM, Silva-Dias MAF (2004) Smoking rain clouds over the Amazon. Science 303:1337–1342

Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Nat 132:44–66

Augspurger CK (1981) Reproductive synchrony of a tropical shrub: experimental studies on effects on pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). Ecology 62:775–788

Augspurger CK (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705–1712

Borchert R (1991) Growth periodicity and dormancy. In: Raghvendra AS (ed) Physiology of trees. Wiley, New York, pp 221–245

Borchert R (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75:1437–1449

Borchert R, Rivera G, Hagnauer W (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. Biotropica 34:27–39

Borchert R, Meyer SA, Felger RS, Porter-Bolland L (2004) Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. Glob Ecol Biogeogr 13:409–425

Borchert R, Renner SS, Calle Z, Navarrete D, Tye A, Gautier L, Spichiger R, von Hildebrand P (2005) Photoperiodic induction of synchronous flowering near the equator. Nature 433:627–629

Chapin FS III, Schulze E-D, Mooney HA (1990) The ecology and economics of storage in plants. Annu Rev Ecol Syst 21:423–447

Curran LM, Leighton M (2000) Vertebrate responses to spatio-temporal variation in seed production by mast-fruiting Bornean Dipterocarpaceae. Ecol Monogr 70:101–128

Curran LM, Webb CO (2000) Spatio-temporal scale of seed predation in mast-fruiting Dipterocarpaceae: experimental studies of regional seed availability. Ecol Monogr 70:129–148

Curran LM, Caniago I, Paoli GD, Astiani D, Kusneti M, Leighton M, Nirarita C, Haeruman H (1999) Impact of El Niño and logging on canopy tree recruitment in Borneo. Science 286:2184–2188

Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J Ecol 62:881–919

Garwood NC (1983) Seed germination in a seasonal tropical forest in Panama a conmunity study. Ecol Monogr 53:159–181

Graham EA, Mulkey SS, Wright SJ, Kitajima K, Phillips NG (2003) Cloud cover limits productivity in a tropical rain forest tree during La Nina. Proc Nat Acad Sci 100:572–576

Janzen DH (1969) Seed-eaters vs. seed size, number, toxicity, and dispersal. Evolution 23:1–27

Jones HG, Sutherland RA (1991) Stomatal control of xylem embolism. Plant Cell Environ 14:607–612

Larcher W (1995) Physiological plant ecology. 3rd edn. Springer, Berlin Heidelberg New York

Nepstad DC, Carvalho CJR, Davidson EA, Jipp P, Lefebvre PA, Negreiros GH, Silva ED, Stone TA, Trumbore SE, Vieira S (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372:666–669

Nepstad DC, Moutinho PRS, Dias-Filho MB, Davidson EA,Cardinot G, Markewitz D, Figueiredo R, Viana N, Lefebvre PA, Ray DG, Chambers JQ, Barros L, Ishida FY, Belk E, Schwalbe K (2002) The effects of rainfall exclusion on canopy processes and biogeochemistry of an Amazon forest. J Geophys Res 107:1–18

Nepstad DC, Lefebvre P, Da Silva UL, Tomasella J, Schlesinger P, Solorzano L, Moutinho P, Ray D, Benito JG (2004) Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. Glob Change Biol 10:704–717

New York Botanical Garden (2006) New York Botanical Garden virtual herbarium: online specimen search. New York Botanical Garden, Bronx, NY (see http://sciweb.nybg.org/Science2/vii2.asp, last accessed 19th July 2006)

Newell EA, Mulkey SS, Wright SH (2002) Seasonal patterns of carbohydrate storage in four neotropical tree species. Oecologia 133:333–342

Oliveira RS, Dawson TE, Burgess SSO, Nepstad D (2005) Hydraulic redistribution in three Amazonian trees. Oecologia 145:354–363

Ozanne CMP, Anhuf D, Boulter SL, Keller M, Kitching RL, Körner C, Meinzer FC, Mitchell AW, Nakashizuka T, Silva Dias PL, Stork NE, Wright SJ, Yoshimura M (2003) Biodiversity meets the atmosphere: a global view of forest canopies. Science 301:183

Parrotta JA, Francis JK, Almeida RR (eds)(1995) Trees of Tapajos: A photographic field guide. General Technical Report IITF-1, United States Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Rio Pedras, Puerto Rico

Penuelas J, Filella I (2001) Responses to a warming world. Science 294:793–795

Reich P, Borchert R (1982) Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). Ecology 63:294–299

Rivera G, Borchert R (2000) Induction of flowering in tropical trees by a 30-min reduction in photoperiod: evidence from field observations and herbarium specimens. Tree Physiol 21:201–212

Rivera G, Elliott S, Caldas LS, Nicolossi G, Coradin VTR, Borchert R (2002) Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. Trees 16:445–456

Rohter L (2005) A record Amazon drought, and fear of wider ills. New York Times, 11 Dec 2005

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. Science 148:339–46

Silva-Dias MS, Rutledge S, Kablat P, Dias PS, Nobre CA, Fish G, Dolman A, Zipser E, Garstang M, Manzi AO, Fuentes JD, Rocha HR, Marengo JÁ, Fattori AP, Sá LDA, Alvalá RCS, Andreae MO, Artaxo P, Gielow R, Gatti L (2002) Cloud and rain processes in a biosphere atmosphere interaction context in the Amazon Region. J Geophys Res 107(D20):8072–8092

Topp GC, Davis JL, Annan AP (1980) Electromagnetic determination of soil water content: measurements in coaxial transmission lines, vol. 16. Water Resources Research, Washington, pp 574–582

Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398:694–696

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, Berlin Heidelberg New York

Vieira S (2003) Mudanças Globais e Taxa de Crescimento de Espécies Arbóreas da Amazônia. Doctoral Thesis. University of São Paulo, São Paulo, Brazil

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee T JC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Wang GL (2005) Agricultural drought in a future climate: results from 15 global climate models participating in the IPCC 4th Assessment. Climate Dyn 25:739–753

Williams RJ, Myers BA, Muller WJ, Duff A, Eamus D (1997) Leaf phenology of woody species in a North Australian tropical savanna. Ecology 78:2542–2558

Wright SJ (1996) Phenological responses to seasonality in tropical forest plants. In: Mulkey SD, Chazdon RL, Smith AP (eds) Tropical forest ecophysiology. Chapman & Hall, New York, pp 440–460

Wright SJ, Carrasco C, Calderón O, Paton S (1999) The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest. Ecology 80:1632–1647

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice-Hall, Upper Saddle River, NJ, p 931