

**CORRELATION BUT NO CAUSATION BETWEEN LEAF
NITROGEN AND MAXIMUM ASSIMILATION: THE ROLE OF
DROUGHT AND REPRODUCTION IN GAS EXCHANGE IN
AN UNDERSTORY TROPICAL PLANT
MICONIA CILIATA (MELASTOMATACEAE)¹**

DÉBORA V. ARAGÃO,² LUCAS B. FORTINI,³ STEPHEN S. MULKEY,⁴
DANIEL J. ZARIN,^{3,5} MARISTELA M. ARAUJO,² AND
CLÁUDIO J. R. DE CARVALHO⁶

²Universidade Federal Rural da Amazônia, Departamento de Ciências Florestais, Av. Presidente Tancredo Neves, nº2501—Bairro Terra Firme—Caixa Postal 917. CEP 66077-530—Belém—Pará—Brazil; ³School of Forest Resources and Conservation, Institute of Food and Agricultural Sciences, University of Florida, P.O. Box 11070, Gainesville, Florida 32611-0760 USA; ⁴Department of Botany, College of Liberal Arts and Sciences, University of Florida, P.O. Box 118526, Gainesville, Florida 34002-8526 USA; and ⁵Laboratório de Ecofisiologia e Propagação de Plantas, Empresa Brasileira de Pesquisa Agropecuária—Amazônia Oriental, Trav. Dr. Enés Pinheiro S/N—Bairro Marco—Caixa Postal 48. CEP 66092-100—Belém—Pará—Brazil

Alternative hypotheses were tested to explain a previously reported anomaly in the response of leaf photosynthetic capacity at light saturation (A_{\max}) in *Miconia ciliata* to dry-season irrigation. The anomaly is characterized by an abrupt increase in leaf A_{\max} for nonirrigated plants at the onset of the rainy season to values that significantly exceeded corresponding measurements for plants that were irrigated during the previous dry season. Hypothesis 1 posits that a pulse in leaf nitrogen increases CO_2 assimilation in nonirrigated plants at the onset of the wet season and is dampened for irrigated plants; this hypothesis was rejected because, although a wet-season nitrogen pulse did occur, it was identical for both irrigated and nonirrigated plants and was preceded by the increase in assimilation by nonirrigated plants. Hypothesis 2 posits that a reproduction-related, compensatory photosynthetic response occurs in nonirrigated plants following the onset of the wet season and is dampened in irrigated plants; consistent with hypothesis 2, high maximum assimilation rates for control plants in the wet season were significantly correlated with fruiting and flowering, whereas irrigation caused flowering and fruiting in the dry season, spreading *M. ciliata* reproductive activity in irrigated plants across the entire year.

Key words: Amazon; compensatory photosynthesis; drought seasonality; nitrogen content; reproductive phenology; secondary forest.

Seasonal and interannual differences in frequency, duration, and intensity of rain events in tropical forests have important ecological consequences for tropical plants (Engelbrecht et al., 2002). Drastic drought events can cause changes in plant mortality as well as in population structure and dynamics (Wright and Cornejo, 1990; Borchert, 1992; Mulkey et al., 1996; Wright, 1996; Tezara et al., 1998; Priori and Eamus, 1999; Tobin et al., 1999; Engelbrecht et al., 2002; Nepstad et al., 2002). When water deficiency is sufficient to hinder carbon assimilation, drought also limits the productivity of tropical plants (Mulkey et al., 1996) and hinders their phenological development (Borchert, 1996; Borchert et al., 2002; Schongart et al., 2002).

Mineral nutrition is also responsive to drought and is a primary determinant of growth and morphogenesis. In general, high amounts of nitrogen are associated with high rates of

maximum photosynthesis across contrasting taxa, due to the high organic nitrogen requirement of photosynthetic enzymes (Field and Mooney, 1986; Evans and Seeman, 1989; Osaki and Shinano, 2001). Nitrogen content variation may be associated with rapid changes in soil and litter moisture that cause the decomposition of organic material and stimulate microorganisms in the litter (Lodge et al., 1994). In Amazonian forests, re-wetting of seasonally dry soil results in a pulse of nitrogen mobilization (Luizão et al., 1992).

Recent research on a common second-growth understory species, *Miconia ciliata* (Rich.) DC, found leaf water status and gas exchange strongly affected by changes in water availability caused by dry-season irrigation and occasional rain events (Fortini et al., 2003). Individuals in nonirrigated plots responded to the first wet-season rains with an abrupt recovery of gas exchange, exhibiting maximum assimilation values well above those of individuals located in irrigated plots during the same period. This phenomenon could be attributed to a wet-season nutrient pulse (e.g., Lodge et al., 1994) or to compensatory photosynthesis by control plants in response to an increase in carbon sink strength caused by concentrated flowering and fruiting in the rainy season, as suggested by Fortini et al. (2003). The objective of the present study was to test these alternative hypotheses for the abrupt wet-season increase in leaf photosynthetic capacity at light saturation (A_{\max}) for control plants relative to values for irrigated plants. Hypothesis 1 posits that a pulse in leaf nitrogen is related to the increase

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⁵ Author for reprint requests (e-mail: zarin@ufl.edu).

of CO₂ assimilation of control plants at the onset of the wet season and is dampened for irrigated plants, for which the drought constraint on N mobilization and uptake has been reduced throughout the dry season. Hypothesis 2 posits that a reproduction-related compensatory photosynthetic response occurs in control plants following the onset of the wet season and is dampened in irrigated plants that spread their reproduction over a longer time.

MATERIALS AND METHODS

Site description—The study was carried out at the UFRA field station (Universidade Federal Rural da Amazônia, 1°17'46" S and 45°55'28" W) near the city of Castanhal, in the Bragantina Region of Pará, Brazil. The Bragantina Region is distinguished from other Amazon regions by the predominance of secondary vegetation, resulting from constant human occupation since the rubber boom at the beginning of the 20th century (Ludovino, 2001). Previously covered by humid tropical forest, the study area was first cleared in 1939. Corn and manioc were the main crops of the slash-and-burn agriculture in the area. After six to eight cycles of slash and burn, the area was abandoned and allowed to regrow for the past 15 yr. Mean annual temperature is 26°C, average relative humidity is 80%, and mean annual precipitation is 2500 mm. A dry season extends from July to December with at least 1 mo with total rainfall less than 60 mm (Diniz, 1986). Daily precipitation was measured at the site from February 2001 to September 2003. The predominant soil type is dystrophic yellow latosol, stony phase I, in the Brazilian classification (Tenório et al., 1999), corresponding to Sombriustox in U.S. soil taxonomy. Soils are well-drained and shallow to laterite. Predominant botanical families are Lacistemataceae, Clusiaceae, and Myrtaceae.

Study species—*Miconia ciliata* (Rich.) DC, Melastomataceae family, is a woody, shallow-rooted understory shrub with most individuals below 2 m tall (Fortini et al., 2003). *Miconia ciliata* is a common roadside plant and is often present in the understory during early secondary succession; it is the third most common understory species at the study site (Coelho et al., 2004).

Experimental design—The study was conducted in eight 20 × 20 m treatment plots separated by 10-m buffer strips. Four plots were randomly selected to receive dry-season irrigation; the other four served as untreated controls. Nested 10 × 10 m measurement plots were located in the center of each 20 × 20 m plot. Irrigation provided the equivalent of 5 mm daily precipitation during rainless dry-season days through an irrigation tape system, corresponding to regional estimates of daily evapotranspiration (Shuttleworth et al., 1984; Lean et al., 1996; Jipp et al., 1998). Plots were irrigated from July to December during the 2001 and 2002 dry seasons. Data reported here were collected from May 2002 to October 2003.

Gas exchange—Gas exchange was measured monthly in three plants per plot on one healthy and fully developed leaf per individual between 0900 and 1500 hours with a portable photosynthesis system (LI-6400, Licor, Lincoln, Nebraska, USA) at ambient H₂O and CO₂ concentrations with flow rate of 400 μmol/s. Temperature in the measurement chamber was kept below 32°C. Measured variables include photosynthetic capacity at light saturation (A_{max}), stomatal conductance (g_s), and intercellular CO₂ concentration (C_i). The A_{max}/g_s ratio was evaluated as a parameter of intrinsic water use efficiency. Photosynthetic capacity at light saturation was reached by initially exposing leaves to 10 μmol · m⁻² · s⁻¹ photosynthetic photon flux density (PPFD) until complete stabilization of CO₂ assimilation. After stabilization, the leaf was exposed to 800 μmol · m⁻² · s⁻¹, until it reached a steady state of assimilation (see Fortini et al., 2003). Data logged at 5-s intervals during the stabilization of assimilation were plotted graphically and a representative value of A_{max} was chosen. Values of stomatal conductance and internal carbon concentration associated with the representative A_{max} value were automatically selected.

Leaf water potential—We selected three *M. ciliata* individuals per plot for leaf water potential. We did not do these measurements on the individuals

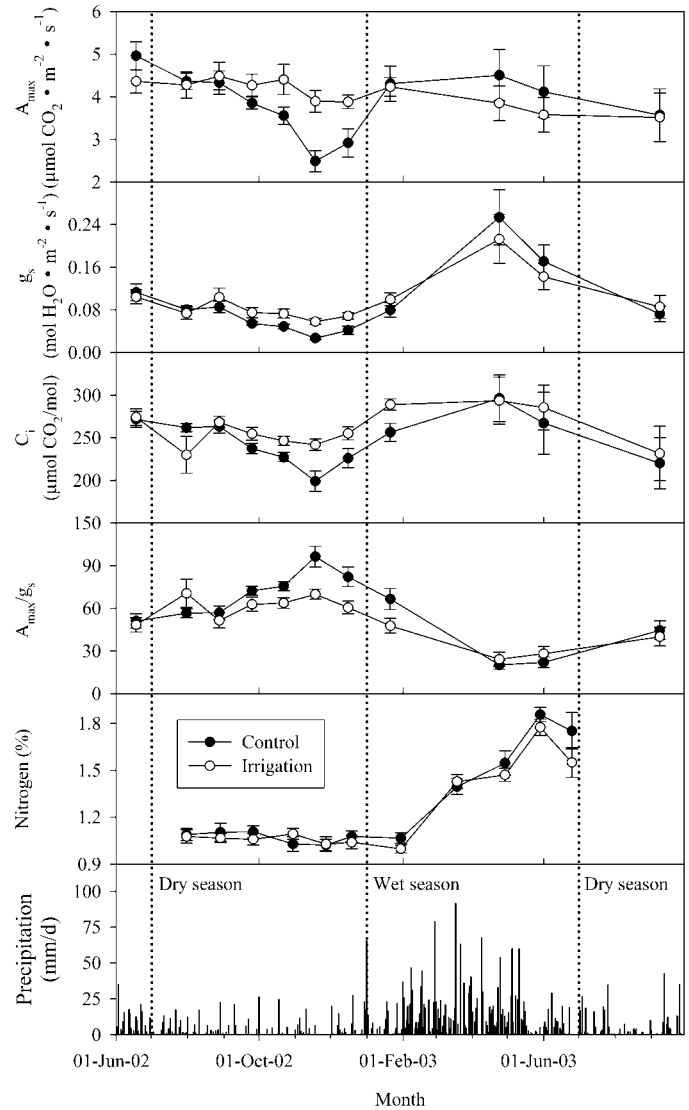


Fig. 1. *Miconia ciliata* leaf gas exchange, leaf nitrogen concentration, and daily precipitation from June 2002 to September 2003 (±1 SE). A_{max}, photosynthetic capacity at light saturation; g_s, stomatal conductance; C_i, internal CO₂ concentration.

used for leaf gas exchange because individuals were small and leaves were removed monthly for sampling. Two sets of measurements were made on a monthly basis using a PMS pressure bomb (Corvalis, Oregon, USA), one set in the mid afternoon (1400–1500 hours) and one set at pre-dawn (0300–0400 hours). One leaf per individual per measurement was used since leaf-to-leaf variation for same individuals was low.

Phenological observations—Flowering and fruiting phenology were recorded for the same individuals used for gas exchange measurements. Observations were made monthly from January 2002 to June 2003 during the period of leaf gas exchange measurements.

Leaf nitrogen content and leaf specific mass—From July 2002 to September 2003, six leaf samples were collected monthly for analysis of leaf N in three individuals per plot. Three leaf disks were collected for calculation of leaf specific mass from three plants per plot. Because *M. ciliata* is a small plant and we needed to conserve material for repeated measures of photosynthesis, we could not destructively sample the plants used for gas exchange measurements. Therefore, leaf material for determinations of nitrogen content

TABLE 1. Statistical results for leaf gas exchange (treatment \times time interaction term) in *Miconia ciliata*.

Variables ^a	Wilk's lambda			Univariate G-G ^b		
	df	F	P	df	F	P
A_{\max}	10, 7	2.78	0.09	5.73, 91.66	1.93	0.09
g_s	10, 7	2.41	0.13	2.75, 43.93	0.50	0.67
C_i	10, 7	1.30	0.37	4.3, 68.8	3.51	0.01
A_{\max}/g_s	10, 7	2.24	0.15	5.44, 87.05	2.89	0.02

^a A_{\max} photosynthetic capacity at light saturation; g_s stomatal conductance; C_i internal CO_2 concentration.

^b G-G, Geisser and Greenhouse adjustment.

and leaf specific mass was collected from plants that were growing close to those used for gas exchange measurements. Leaves were dried at 64°C until constant mass. Nitrogen was analyzed by micro-Kjeldahl digestion and colorimetric determination using the method described by Kandeler and Gerber (1988) with NIST reference standard 1547. Leaf specific mass was computed as the ratio between the leaf area of each disc and its dry mass, then averaged for the three discs. We collected the discs during representative dry- and wet-season months (October 2002 and April 2003, respectively). These values of leaf specific mass were used to estimate mass-based assimilation in plants used for photosynthesis.

Statistical analysis—Statistical analyses of the data were performed with JMP software, version 3.2.6 (SAS Institute, Cary, North Carolina, USA). A repeated measures MANOVA model with treatment as the only effect was used to evaluate time and treatment effects on A_{\max} and leaf nutrient data. Each monthly measurement was considered as a dependent variable and time was used as the effect between dependent variables. We used the Wilk's lambda statistic to evaluate the MANOVA results. The Geisser and Greenhouse (G-G) adjustment allowed us to perform a univariate repeated measures ANOVA parallel to the multivariate testing (SAS Institute, 1998). In both ANOVA and MANOVA models the effect of treatment on photosynthetic capacity was tested as the irrigation \times month interaction. We also used ANOVA to test the effect of the interaction between reproductive event and months on photosynthetic capacity for irrigated and control plots separately. All results are reported as significant when $P < 0.05$. We report marginal significance when $0.05 \leq P < 0.10$.

RESULTS

Seasonal and interannual leaf gas exchange—Throughout the dry season, irrigated plants maintained higher A_{\max} , g_s , C_i , and lower A_{\max}/g_s values, than did control plants (Fig. 1). Control plants exhibited a trend of slow decline in A_{\max} , g_s , and C_i from the end of the rainy season to the end of the dry season. Control A_{\max} values were lowest in the driest months (October, November, and December) with related significant treatment effects within-subjects (October, $F = 5.5$; $P_{1,16} < 0.03$; November, $F = 34.6$; $P_{1,16} < 0.002$; December, $F = 7.8$; $P_{1,16} < 0.01$). We found marginally significant treatment effects for A_{\max} in the multivariate model for leaf gas exchange variables. In the univariate model, C_i and A_{\max}/g_s showed significant treatment effects, and A_{\max} showed marginally significant treatment effects (Table 1). Similar to the results of Fortini et al. (2003), gas exchange and stomata conductance in control plants were higher than in irrigated plants at the onset of the wet season (Fig. 1).

Dry season rainfall was 21% higher in 2002 than in 2001. This interannual variation in rainfall within dry seasons is correlated with significant interannual differences in gas exchange of control plants between this study and that of Fortini et al. (2003) (Wilk's test, $F = 7.36$, $P_{3,16} < 0.003$. Univariate test,

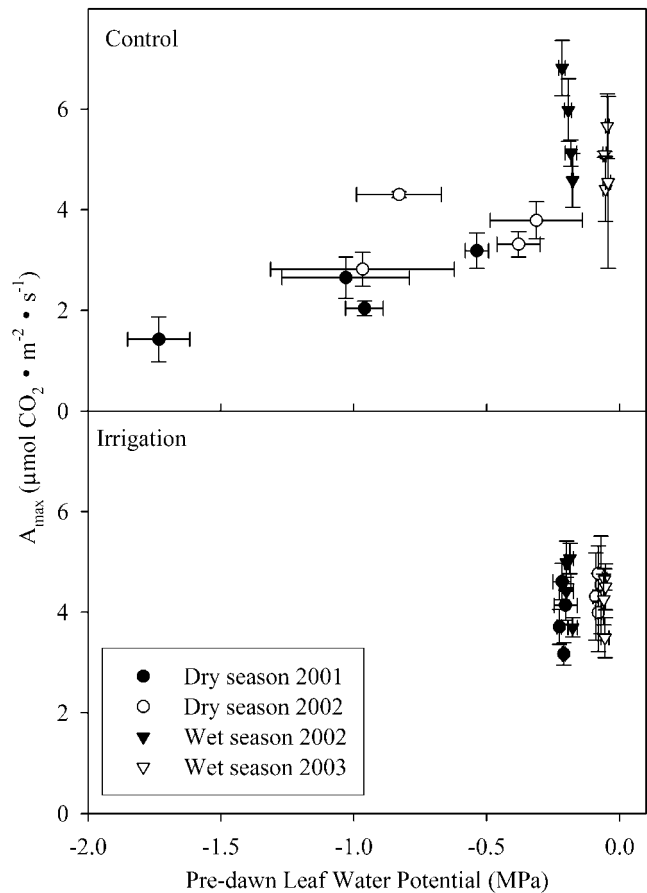


Fig. 2. Plot-level correlation between photosynthetic capacity at light saturation (A_{\max}) and leaf water potential in *Miconia ciliata* for representative dry- and wet-season months. Squared Pearson product-moment: for control data, $R^2 = 0.82$, $P < 0.01$; for irrigation data, $R^2 = 0.10$, $P = 0.88$. Each point represents the average of all plants in each plot and error bars represent standard errors. Dry season 2001 and wet season 2002 data from Fortini et al. (2003).

$F = 7.40$, $P_{2,1,37.9} > 0.99$). Despite the milder 2002 dry season, a positive correlation between control leaf water potential and leaf gas exchange was still observed while no such correlation was found for irrigated plots (Fig. 2).

Leaf nitrogen periodicity and A_{\max} —A peak in nitrogen concentration for both treatments occurred following the onset of the wet season (Fig. 1), and a positive correlation between leaf nitrogen content and A_{\max} was apparent for control plots but not for irrigated plots (Fig. 3). However, the timing of the increase in N content (30 January through 29 March 2003) lagged behind the increase in A_{\max} (16 December 2002 through 21 January 2003). No treatment differences were detected for leaf nitrogen content during the experimental period (Wilk's test, $F = 2.54$, $P_{10,3} > 0.24$; univariate test, $F = 1.97$, $P_{3,19,38.33} > 0.13$).

Periodicity of phenology and A_{\max} —Flowering and fruiting events of *M. ciliata* were sensitive to climatic conditions (Fig. 4). In control plots, the number of individuals in flower was concentrated in the wet season, peaking from March to May. Control plants had high numbers of flowers and fruits in the early wet season (Table 2). The peaks in flowering and fruiting

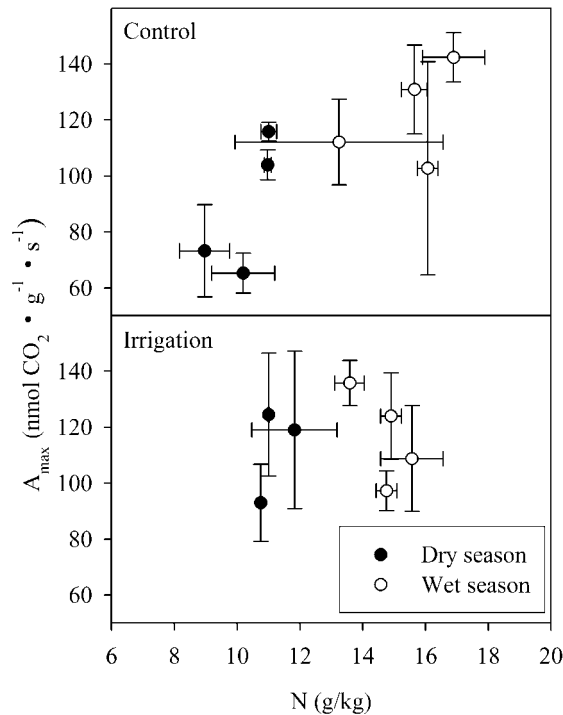


Fig. 3. Plot-level correlation between estimated mass-based A_{max} and leaf nitrogen content in *Miconia ciliata* for representative dry- and wet-season months. Squared Pearson product-moment: for control data, $R^2 = 0.60$, $P < 0.03$; for irrigation data, $R^2 = 0.002$, $P = 0.92$. Each point represents the average of all plants in each plot and error bars represent standard errors. Y-axis standard error bars reflect A_{max} variance and do not include propagation of variances in leaf specific mass.

of *M. ciliata* following the onset of the wet season are associated with high photosynthetic rates for the control plants (chi-square, $p < 0.005$). In contrast with reproductive phenology of control plants, the number of irrigated plants in flower was relatively constant through the experimental period.

DISCUSSION

Miconia ciliata's pattern of decreasing photosynthetic potential with increasing drought stress agrees with results from previous studies with this plant (Fortini et al., 2003) and with other understory tropical forest species (Mulkey and Wright, 1996; Brodribb et al., 2002; Nepstad et al., 2002). The irrigation treatment maintained relatively constant A_{max} for *M. ciliata* individuals throughout the measurement period. For control plants, the magnitude of A_{max} response to drought is regulated by duration and amount of rainfall, determined by intra- and interannual precipitation patterns. Rainfall has a critical role in CO_2 assimilation and stomatal conductance for this species because its low dry-season water status is evidently related to soil water availability (Tezara et al., 1998). *Miconia ciliata*'s superficial root system may contribute to its fast recovery of water status during occasional rain events during the dry season. Because rain does not initially penetrate quickly into the soil and water is retained near or at surface by litter and humus, plants with superficial root systems have an advantage in water status recovery (Cao and Booth, 2001). Because of the higher frequency of rainy days during the 2002

TABLE 2. Average number of months during which individual plants of *Miconia ciliata* were flowering or fruiting (SE). Wet season data from January to July 2002 (Fortini et al., 2003); dry season data from August to December 2002.

Treatment	Flowering		Fruiting	
	Wet season	Dry season	Wet season	Dry season
Control	2.9 (0.8)	0.3 (0.2)	2.8 (0.7)	0.0
Irrigation	1.0 (0.5)	1.2 (0.4)	1.3 (0.6)	0.9 (0.3)

dry season, relatively low drought stress was evidenced in control plants compared to data collected from the previous dry season (Fortini et al., 2003).

Despite the positive correlation between averaged photosynthesis and averaged leaf nitrogen content for control plants (Fig. 3), the abrupt increase of A_{max} for these plants occurred from the onset of the wet season while the leaf nitrogen pulse occurred much later in the wet season (Fig. 1). Hence, the observed nitrogen pulse correlates with A_{max} across the entire wet season, but cannot have caused the observed increase at the beginning of the wet season. The increase in leaf nitrogen content and stomatal conductance jointly occurred after abrupt increases in A_{max} during the wet season, suggesting that stomatal function and changes in N cycling occur concurrently, following changes in water and plant-available N.

The increase in leaf nitrogen content is also related positively with the observed production of new leaves in both control and irrigated plants at the end of the wet season (Borchert et al., 2002). We observed that leaves were exchanged more frequently during the wet season, a process that could result in a crown of younger leaves with higher leaf nitrogen content. This phenomenon may mean that increased nitrogen availability causes increases in whole plant assimilation but that remains to be tested. We found no support for the hypothesis that a pulse in leaf nitrogen is related to the increase of leaf A_{max} for control plants at the onset of the wet season.

In the absence of irrigation, *M. ciliata* produces flowers and fruits during the wet season. Studies in tropical dry forests reveal that phenological development is strongly affected by seasonal drought (Schongart et al., 2002). Because physiological processes are linked to many plant functions that simultaneously determine reproductive events and CO_2 assimilation (Ackerly et al., 2000), high demand for assimilates may have a positive effect on assimilation (Watson and Casper, 1984; Reekie and Bazzaz, 1987; Tonsor and Goodnight, 1997). Our data are consistent with the hypothesis that the wet-season increase of control plant A_{max} relative to irrigated plant values was caused by a reproduction-related, compensatory photosynthetic response that occurs in control plants during the wet season.

Conclusions—This study confirmed the role of moisture availability as the primary constraint on A_{max} for *M. ciliata* at this site, as reported by Fortini et al. (2003) and replicated the measurement of increased A_{max} for wet-season control plants relative to the A_{max} for irrigated plants. We have additionally demonstrated that dry-season irrigation accelerates flowering and fruiting, spreading the peaks of reproductive phenology of the *M. ciliata* across the entire year. In the absence of irrigation, higher photosynthesis is associated with reproductive plants during the wet season, providing support for the hy-

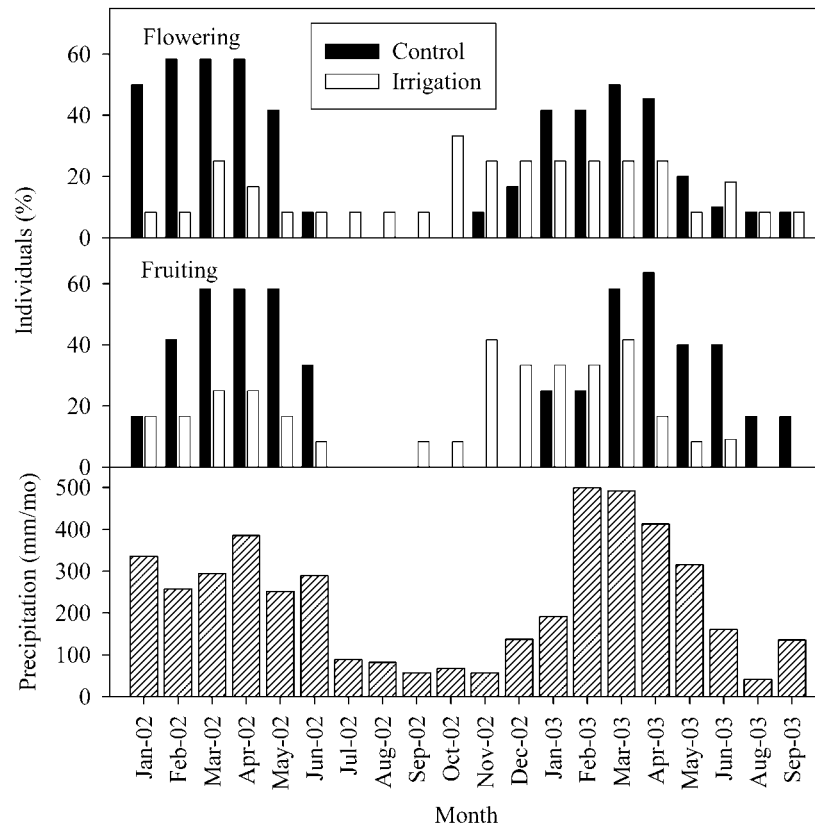


Fig. 4. Temporal distribution of fruiting and flowering for *Miconia ciliata*.

pothesis that reproductive phenology, triggered by the sustained increase in soil moisture associated with the onset of the rainy season, elicits a compensatory photosynthetic response from control plants. Thus, water availability and reproductive phenology triggered by increased water availability are the primary factors that explain variance in gas exchange for this species. The magnitude of gas exchange is responsive to interannual variations in the intensity and frequency of precipitation, and flower and fruit production depend on changes in water availability. Changes in reproductive phenology could be among the first responses of fast regional climate changes and could have serious consequences for plants and animals that depend on the periodic availability of plant resources (Corlett and LaFrankie, 1998). Despite the increase of leaf nitrogen during the wet season, the hypothesis of a nutrient pulse-induced increase in A_{\max} was not supported by our study. Because the increase in N content was preceded by the increase in A_{\max} , a nitrogen pulse cannot be the cause of the observed increase in assimilation.

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