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SEASONAL DROUGHT AND THE PHENOLOGY OF UNDERSTORY SHRUBS IN A TROPICAL MOIST FOREST¹

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Abstract. The vegetative and reproductive growth of tropical forest plants often occurs in short bursts separated by longer quiescent periods. Seasonal changes in moisture availability may be a cause and, if so, may cue growth in a proximate sense or limit growth in an ultimate sense. Two 2.25-ha plots of mature forest were irrigated for three consecutive dry seasons on Barro Colorado Island, Panama, to discriminate among the various possibilities. The responses of three *Piper* species and four *Psychotria* species are reported.

Irrigation disrupted the timing of leaf flush for all seven species. Irrigation increased annual leaf production for just one species, however, and had no effect on annual inflorescence production for the *Psychotria* nor on stem radial growth. These responses are consistent with the hypothesis that water stress constrains the timing of growth while only rarely limiting total annual growth. However, leaf turgor potentials observed among control plants may not have been sufficiently low to constrain leaf and inflorescence production, and other effects of irrigation cannot be discounted. Possible phenological cues that were affected by irrigation include soil moisture content, air temperature, relative humidity, and the timing of nutrient inputs from decaying litter. There was no evidence that a “water stress requirement” must be met during the dry season before wet season budbreak. The gradual decay in synchrony for leaf production for all four *Psychotria* species suggests that endogenous rhythms contribute to growth periodicities in this genus.

Key words: Barro Colorado Island; dry season; forest; irrigation; Panama; *Piper*; plant phenology; *Psychotria*; tropical forest; water stress.

INTRODUCTION

The vegetative and reproductive growth of tropical forest plants is frequently limited to a short period each year even though physical conditions are favorable at other times (e.g., Richards 1952, Njoku 1963, Hopkins 1970). A number of factors may select for periodic growth by tropical plants. Examples include selection to produce fruit at times that are optimal for dispersal (Janzen 1967) or germination (Garwood 1983), selection to produce leaves synchronously to satiate herbivores (Aide 1988, 1989), and selection to produce flowers and fruit synchronously to attract pollinators or satiate seed predators (Augspurger 1980, 1981). Whatever the ultimate selective factor, some proximate mechanism must initiate and synchronize plant growth. Possibilities include endogenous plant rhythms and responses to changes in the physical environment.

A number of physical factors have been identified that may cue periodic growth by tropical plants. Both photoperiod and temperature can be important (e.g., Njoku 1958, 1964, Longman 1969, 1978, Wycherley 1973, Ashton et al. 1988). Their general utility has been questioned, however, because their seasonal variation is small in the tropics (Borchert 1980, 1983, Reich and Borchert 1984). Photoperiod is invariant at the equa-

tor, and diurnal changes in temperature are most often greater than seasonal changes. Rainfall and moisture availability are much more seasonal in many tropical forests, and may influence growth periodicities in several ways. Water stress may limit growth during the dry season (e.g., Reich and Borchert 1984). Even when water stress is not directly limiting, changes in moisture availability may act as proximate cues for growth (e.g., Alvim and Alvim 1978). Finally, changes in moisture availability may affect other physical factors, such as nitrogen mineralization (e.g., Birch 1964), which in turn affect plant growth.

The evidence that relates moisture availability to the growth of tropical plants comes from manipulations in plantations and growing houses (e.g., Alvim 1960, Murray 1965, Sale 1970) and from correlations between climatic variables and the timing of growth of forest plants (e.g., Frankie et al. 1974, Opler et al. 1976, 1980, Alvim and Alvim 1978, Reich and Borchert 1984). Extrapolation from plantation and growing-house experiments to forest conditions and inferences of causation from field correlations have generally been made circumspectly for two reasons (e.g., Njoku 1963, Longman 1978). First, the different environmental conditions found in plantations, growing houses, and forests may affect responses to changes in moisture availability. Second, climatic variables covary in the field in ways that make it difficult to establish causality. The two experimental manipulations of moisture

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availability in a tropical forest established that wetting after drought can cue anthesis in a gregariously flowering shrub (Augsburger 1980, 1981) and a gregariously flowering tree (Reich and Borchert 1982). For several other tropical species that flower gregariously after heavy rains, it has been shown that the cue is a temperature drop associated with the rain and not an increase in moisture availability (reviewed by Wycherley [1973]).

To investigate the relation between seasonal changes in moisture availability and plant growth in a tropical moist forest, two large plots of mature forest were irrigated for three consecutive dry seasons on Barro Colorado Island (BCI), Panama. The water content of the soil on the irrigated plots was kept near field capacity year-round. Two control plots experienced normal conditions during the 4-mo dry season. A variety of responses were studied. This paper considers leaf and inflorescence production for seven species of understory shrubs from the genera *Piper* and *Psychotria*. The following questions are addressed: Does dry season moisture stress limit annual leaf and inflorescence production? Do seasonal changes in moisture availability affect the timing and synchrony of production? If timing is disrupted, does the response suggest that endogenous rhythms maintain the periodicity of growth?

STUDY SITE AND SPECIES

BCI (9°9' N, 79°51' W) supports tropical moist forest (Holdridge Life Zone system, Holdridge and Budowski 1956). Mean annual precipitation is 2600 mm (Windsor 1990). A dry season begins in December (or rarely in November or January) and ends in April or May. Median rainfall for the first 13 wk of the calendar year is just 84 mm (Windsor 1990). As the dry season progresses, gravimetric soil water content falls from $\approx 42\%$ to $\approx 28\%$ (Windsor 1990), and soil water potentials can fall to -2.0 MPa (Becker et al. 1988). Mean monthly maximum temperatures at 1 m in the forest understory are lowest in November (27.6°C) and climb steadily over the dry season to their highest value in April (30.0°C). Mean monthly minimum temperatures at 1 m in the forest understory vary by just 1°C among months, the extremes being 22.4°C in January and 23.4°C in June (Windsor 1990). More detailed descriptions of BCI can be found in Croat (1978), Leigh et al. (1982), and Windsor (1990). The forest at the study site is among the oldest on BCI (R. Foster, *personal communication*) and has escaped any substantial human disturbance for > 500 yr (Piperno 1990).

Shrubs of the genera *Piper* and *Psychotria* are conspicuous components of many tropical forests. More than 1000 species of *Piper* and 1,650 species of *Psychotria* have been described (Burger 1972, Hamilton 1989a). Twenty-one species of *Piper* and 20 species of *Psychotria* can be found on BCI (Croat 1978). The seven study species germinate, grow, and reproduce in the shaded understory on BCI (N. Garwood, *personal*

communication; this study). Habitat and geographic distributions according to Croat (1978) and Hamilton (1989a, b) follow: *Piper aequale* Vahl, *Psychotria horizontalis* Sw., *Psychotria limonensis* Krause, and *Psychotria marginata* Sw. range from Mexico into South America; *Psychotria furcata* DC. ranges from Costa Rica into South America; and *Piper cordulatum* C. DC. and *Piper perlasense* Yunck. are only known from Panama. *Piper perlasense* is limited to tropical moist forest. The other six species can also be found in premontane wet forest and/or tropical wet forest, and *Psychotria horizontalis* also inhabits tropical dry forests. The species were chosen to include a variety of seasonal patterns of leaf flush and inflorescence production within each genus.

METHODS

Two 2.25-ha plots were irrigated, and two 2.25-ha plots served as controls. Sprinklers were placed at 15.3-m intervals in a hexagonal array, and water was sprayed 15.3 m so that each point (except at plot borders) would have received water from three or more sources were it not for interception by the vegetation. Sprinklers were mounted 1.8 m above the ground, and water reached heights of ≈ 4 m. During a typical week in the dry season, each irrigated plot received 675 Mg of water. This is equivalent to 30 mm of water spread uniformly over each plot. Water was drawn from Gatun Lake, where nutrient concentrations are lower than in rain water collected on BCI (Gonzalez et al. 1975, R. Stallard, *personal communication*). The study plots were > 75 m from the lake.

The amount of irrigation was continually adjusted to maintain mean soil water potentials at or slightly above field capacity (-0.04 MPa). Soil water potentials were monitored with tensiometers (model 2725A; Soil Moisture Equipment Corporation, Pasadena, California, USA) installed at depths of 25 and 45 cm at eight randomly located stations in the interior (> 15 m from edge) of each irrigated plot. Tensiometers were read three times each week during the dry season and once each week during the wet season. During the dry season each plot was irrigated for 1.5–2 h between 1000 and 1400 on 5 to 7 d/wk. It was not necessary to irrigate between May and November, nor for 1–3 d after heavy dry-season rains.

Moisture availability

Soil moisture was monitored in two ways in addition to tensiometers. Eight randomly located stations were also established in the interior (> 15 m from edge) of each control plot. Soil psychrometers (model PCT55; Wescor, Logan, Utah, USA) were installed at 25-cm depth at all 32 stations and at 50-cm depth at four randomly chosen stations in each plot. Access tubes for a hydroprobe (model 503; Campbell Nuclear Pacific, Oxnard, California, USA) were installed at all 32 stations to allow measurements at depths of 25, 50,

and 100 cm. Psychrometer and hydroprobe measurements were recorded weekly. All but two of the psychrometers had failed by 5 June 1986. Regressions between hydroprobe counts and soil water potentials for 1986 were used to convert hydroprobe counts to soil water potentials for 1987 and 1988.

The soil moisture measurements complement one another. Soil psychrometers are not accurate for soil water potentials > -0.2 MPa, and tensiometers fail at soil water potentials ≤ -0.1 MPa. For this reason, tensiometers were not installed in the control plots, and the only reliable wet-season measurements of soil water potential are from tensiometers in the irrigated plots. The water retention characteristics of the soils did not differ between treatments (R. Radulovich and S. J. Wright, *unpublished data*), and there is no reason to suspect treatment differences in soil water potentials during the wet season.

Rainfall was monitored with a gauge mounted on a stump in Gatun Lake immediately adjacent to the site. Relative humidity and air temperature were measured weekly 1 m above the ground with a sling psychrometer at the 32 stations described above.

Leaf water relations

The effect of irrigation on plant water status was evaluated directly through late dry-season measurements of pre-dawn leaf water potentials and turgor loss points in 1986 and mid-day measurements of leaf water potentials in 1987 and 1988. *Piper perlasense* was excluded from these destructive measurements because all known individuals were part of the phenology census. All measurements were made with a portable pressure chamber (PMS Instrument Company, Corvallis, Oregon, USA). Pre-dawn leaf water potentials were determined between 0400 and 0530 on 25 and 28 March 1986. Mid-day leaf water potentials were determined between 1100 and 1300 for the four *Psychotria* species and for *Piper cordulatum* in April 1987 and for *Psychotria limonensis* and *Psychotria marginata* in April 1988. Measurements for the other species were disrupted by rain in 1988. Leaf water potentials were determined for two leaves from three to seven individuals for each species and treatment. Excised leaves were immediately sealed in airtight plastic bags, and water potentials were determined within 10 min of excision. Turgor loss points were estimated from pressure-volume analyses (Tyree and Jarvis 1982) for one leaf from each of six individuals for each species in March 1986. Excised leaves were allowed to rehydrate overnight in the absence of light before pressure-volume analyses were undertaken.

Phenology censuses

Censuses were conducted at 2-wk intervals beginning in March 1985. The censuses initially included ≥ 5 reproductively mature individuals of each species in each plot except for *Psychotria limonensis* for which

just one individual could be located in one plot and *Piper perlasense* for which 6, 4, 4, and 3 individuals were located in the four plots. Individuals that died or lost $\geq 25\%$ of their branches were replaced. Replacement individuals were judged to have been reproductively mature in 1985 on the basis of size. Individuals are only included in an analysis if they were present on the census for the entire year of analysis. All individuals were initially in the shaded understory. A few individuals survived in small gaps created by treefalls or limbfalls. The stem diameter of each census plant was measured 20 cm above the ground in March 1986 and July 1988 using dial calipers.

Each newly macroscopic leaf and inflorescence was marked with a date-specific tag during each census. Bud initiation was not monitored. Dates of anthesis were equivocal for the *Psychotria* because single inflorescences often had buds and flowers for a month or more. Analyses of *Psychotria* reproduction were therefore based on the dates that inflorescences were first marked. Analyses of *Piper* reproduction were not attempted because inflorescences are dormant for variable amounts of time, flowers are microscopic, and dates could not be determined accurately.

The proportion of annual production that occurred in each census will be used to describe the phenological data. For individual i , let $f_i(x)$ represent the proportion of annual production that occurred in census x . Then the mean proportion of annual production for census x is

$$\bar{f}(x) = \sum_i f_i(x)/N, \quad (1)$$

where the sum is over the N individuals in the population. The mean census of production for the population is

$$\mu = \sum_x x \bar{f}(x),$$

where the sum is over the number of biweekly censuses each year.

The population variance of census of production (PV) and its between- (BIV) and within- (WIV) individual components will be used to describe the synchrony of production. Let μ_i represent the mean census of production for individual i , and let $f(\mu_i)$ represent the observed probability distribution of the μ_i . Then

$$PV = \sum_x x^2 \bar{f}(x) - \mu^2, \quad (2a)$$

$$WIV = \sum_i \left[\sum_x x^2 f_i(x) - \mu_i^2 \right] / N, \quad (2b)$$

$$BIV = \sum_i \mu_i^2 f(\mu_i) - \mu^2, \quad (2c)$$

and $PV = BIV + WIV$ (Roughgarden 1974). In words, WIV is the average of the individual variances, and

BIV is the variance of the individual means. WIV will be small when individuals limit production to short periods. BIV will be small when different individuals limit production to the same period. If irrigation reduces population synchrony, PV will increase. If irrigation reduces synchrony among individuals, BIV will also increase.

Analyses

Analysis of covariance was used to test the null hypothesis that irrigation did not affect the growth of the basal area of the stem. The dependent variable was basal area in July 1988, and the covariate was basal area in March 1986. The main effects were treatment and species. Plots were nested within treatments. This analysis (and the following analyses of leaf and inflorescence production) could not be performed for *Psychotria limonensis* due to lack of replication in one plot.

Repeated-measures analyses of covariance were used to test the null hypotheses that irrigation did not change total annual production and that irrigation did not change the timing of production. The main effects for these analyses were treatment and census interval. Repeated measures occurred on census interval. The covariate was the basal area of each plant. Plots were nested within treatments. As an aid to interpretation, a significant between-subject effect of treatment would indicate that total annual production differed between treatments. A significant within-subject effect treatment would indicate that the timing of production differed between treatments. A significant within-subject effect of census interval would indicate that production was not uniform over census intervals. The analyses were performed on logarithms of numbers of leaves or inflorescences produced in each census interval. It was necessary to perform separate analyses for 1986, 1987, and 1988 because many individuals died and were replaced during the study. Because three analyses were performed for each species, significance levels were adjusted by dividing by three, following the conservative Bonferroni procedure (Sokal and Rohlf 1981: 779–782). When the nested plot effect was not significant at $P < .25$, its mean square error was pooled with the overall experimental mean square error (Sokal and Rohlf 1981:285). Basal area varied little among individuals for some analyses. When basal area was not a significant covariate (at $P < .25$), a new analysis was performed which omitted basal area. Repeated-measures analyses assume compound symmetry of the variance-covariance matrix. Multivariate analyses do not make this problematical assumption and were used to validate significance levels from the repeated-measures analyses (Milliken and Johnson 1984).

Censuses were grouped into intervals to maintain nonzero variances; zero variance would otherwise occur whenever production fell to zero for all individuals of a species. Inflorescence production was highly synchronous for the three *Psychotria* species for which

analyses could be performed, and intervals were short. The first and final intervals included variable numbers of censuses in order to include the earliest and latest inflorescences. Otherwise, intervals included two consecutive censuses for *Psychotria marginata* and single censuses for *Psychotria furcata* and *Psychotria horizontalis*.

For analyses of leaf production, the entire year was divided into intervals that included equal numbers of censuses. Each dry season was divided into two intervals, and the following wet season was divided into three (1987 and 1988) or four (1986) intervals of equal length. The same intervals were used for all species. The transitions between seasons were identified using soil moisture content in the control plots. The annual dry season was defined to include censuses during which soil moisture content declined continuously, with interruptions of not more than one week following a rain. The wet season was defined to include censuses during which soil moisture content increased or fluctuated without trend. Using the above definitions of dry and wet seasons, the timing of the transitions between seasons was identical for gravimetric soil water content from the upper 10 cm of soil (S. J. Wright, unpublished data) and for hydroprobe counts from 25-cm depth. These depths are appropriate because the roots of shrubs are concentrated in the upper 20 cm of soil on BCI (Odum 1970, Rundel and Becker 1987). The average percentage of root surface area in the upper 20 cm of soil for three large individuals of *Piper cordulatum* and *Psychotria horizontalis* was 79% and 96%, respectively (Becker and Castillo 1990).

RESULTS

Moisture availability

Total rainfall for 1986, 1987, and 1988 was 2069, 2593, and 2602 mm, respectively. In the control plots, soil water potentials declined steadily during the dry season except for brief increases after heavy rains (Fig. 1). In the irrigated plots, average soil water potentials at 25 cm were always above -0.04 MPa (Fig. 1). In the wet season, soil water potentials were normally close to zero, but fell to -0.02 to -0.04 MPa during three relatively dry periods in 1986 (Fig. 1). Soil water potentials at 50 cm and hydroprobe counts at 100 cm (data not shown) paralleled those at 25 cm but were less responsive to dry season rains.

Irrigation also reduced seasonal differences in temperature and relative humidity. Mid-day temperatures averaged 1–2°C lower and relative humidity averaged 6–12% higher in the irrigated plots than in the control plots throughout most of the three dry seasons (Fig. 2).

Leaf water relations

Irrigation increased leaf water potentials for all species (Tables 1 and 2). In March 1986, mean pre-dawn leaf water potentials in the control plots were indistin-

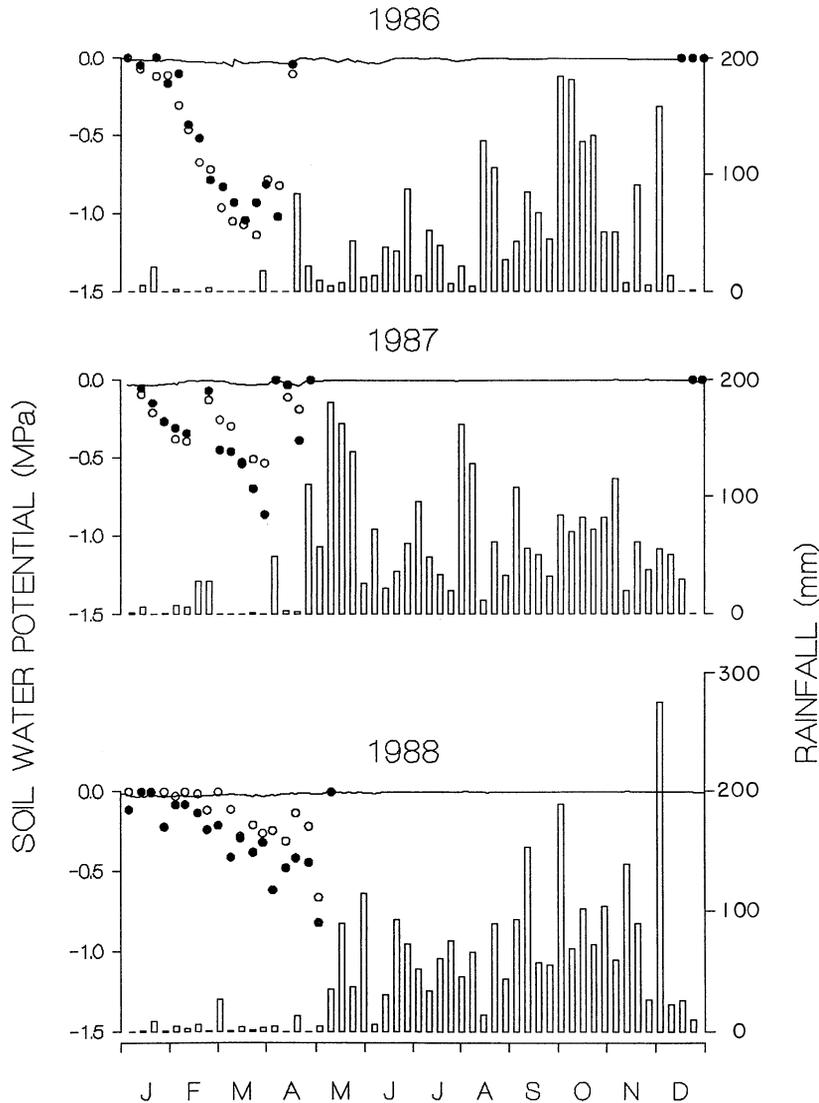


FIG. 1. Weekly rainfall and soil water potentials on Barro Colorado Island, Panama. The histogram represents rainfall. Open and closed circles represent mean dry-season soil water potentials in the two control plots. The solid line at the top of each plot represents mean soil water potentials in the irrigated plots. All soil water potentials were measured at 25-cm depth (see *Methods: Moisture availability*). The open and closed circles are depicted for each week that met the criterion used to define the dry season (see *Methods: Analyses*) and for the first week of the wet season. The data for 1986 and 1987 were previously published in Wright and Cornejo (1990b).

guishable from turgor loss points for all four *Psychotria* species (Table 1), and many individuals were clearly wilted at 0500 (S. J. Wright, *personal observation*). At the same time, mean pre-dawn leaf water potentials in control plots were 0.4 MPa and 0.6 MPa greater than turgor loss points for *Piper aequale* and *Piper cordulatum* (Table 1). The *Piper* species were better buffered against water stress than were the *Psychotria* species.

Mid-day leaf water potentials also showed a clear treatment effect (Table 2). In 1987, mid-day leaf water potentials were close to the turgor loss points estimated in 1986 (Table 1) for *Piper cordulatum*, *Psychotria horizontalis*, and *Psychotria marginata* and well below the

turgor loss point for *Psychotria furcata*. Mid-day wilting was observed for *Psychotria furcata*, *Psychotria horizontalis*, and *Psychotria marginata* in control plots in 1987 and 1988, but pre-dawn wilting did not occur (S. J. Wright, *personal observation*).

Basal area

Irrigation did not affect basal area growth for *Piper aequale*, *Piper cordulatum*, *Piper perlasense*, *Psychotria horizontalis*, and *Psychotria marginata* (Table 3). *Psychotria furcata* could not be included in the analysis because too few individuals survived between stem diameter measurements. The nested plot effect was not

TABLE 1. Pre-dawn leaf water potentials and turgor loss points for 26 and 28 March 1986, on Barro Colorado Island, Panama. Entries are means \pm 1 SE for three to seven individuals.

Species	Pre-dawn leaf water potential (MPa)		Turgor loss point (MPa)
	Control	Irrigated	
<i>Piper aequale</i>	-0.62 \pm 0.17	-0.07 \pm 0.02	-1.06 \pm 0.06
<i>P. cordulatum</i>	-0.45 \pm 0.03	-0.06 \pm 0.02	-1.06 \pm 0.03
<i>Psychotria furcata</i>	-1.65 \pm 0.33	-0.22 \pm 0.02	-1.61 \pm 0.15
<i>P. horizontalis</i>	-1.53 \pm 0.33	-0.15 \pm 0.02	-1.54 \pm 0.05
<i>P. limonensis</i>	-1.35 \pm 0.18	-0.13 \pm 0.02	-1.30 \pm 0.08
<i>P. marginata</i>	-1.60 \pm 0.18	-0.22 \pm 0.02	-1.67 \pm 0.03

significant (at $P < .25$), and its mean square error was pooled with the overall experimental mean square error (Sokal and Rohlf 1981:285). Preliminary analyses (not shown) verified the homogeneity of slopes assumption of analysis of covariance for the treatment main effect and the treatment \times species interaction. Slopes were heterogeneous for the species main effect (Table 3).

Phenology censuses

For the year prior to irrigation (1985) the timing of production was similar between the treatments-to-be for all species except possibly *Psychotria limonensis* (Figs. 3, 4, and 5). The slight differences for *Psychotria*

limonensis are probably an artifact of the low number of leaves and inflorescences produced (Table 4) and of the relatively low level of synchrony of production (Figs. 4 and 5).

Piper

Control plants of *Piper aequale* and *Piper perlasense* produced large numbers of leaves at the beginning of the wet season while control plants of *Piper cordulatum* produced leaves throughout the wet season and into the early dry season (Fig. 3). Irrigated plants of all three species produced leaves in the dry season, and the early wet-season peak for *Piper aequale* and *Piper perlasense* occurred earlier and was less pronounced (Fig. 3). Irrigation significantly changed the timing of leaf production for *Piper aequale* in 1986 and 1988, for *Piper cordulatum* in 1987, and for *Piper perlasense* in 1988 (Table 5). Irrigation did not affect total annual leaf production for *Piper aequale* nor for *Piper perlasense* (Table 5). Irrigation significantly increased total annual leaf production for *Piper cordulatum* in 1988 (Table 5).

The variance of the individual means (between-individual variance, BIV) was consistently small relative to the population variance of the census of production (PV) for all three *Piper* species, and there were no treatment differences nor trends through time in PV and BIV (Fig. 6).

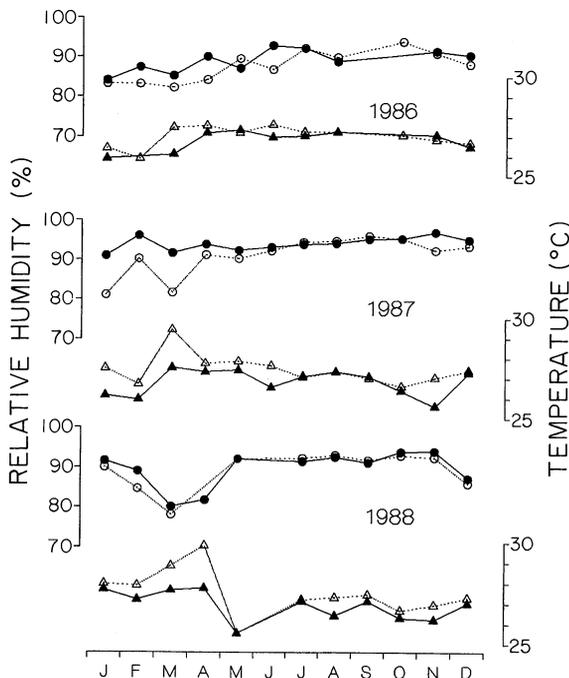


FIG. 2. Mid-day temperatures and relative humidities 1 m above the ground in the shaded forest understory on Barro Colorado Island, Panama. Open and closed symbols represent mean values for control and irrigated plots, respectively. Circles and the left ordinate represent relative humidities. Triangles and the right ordinate represent temperatures. Standard errors were smaller than the symbols.

TABLE 2. Mid-day leaf water potentials for April 1987 and April 1988 on Barro Colorado Island, Panama. Entries are means \pm 1 SE for three to seven individuals.

Species	Mid-day leaf water potential (MPa)	
	Control	Irrigated
1987		
<i>Piper cordulatum</i>	-1.11 \pm 0.07	-0.57 \pm 0.10
<i>Psychotria furcata</i>	-2.27 \pm 0.26	-1.07 \pm 0.09
<i>P. horizontalis</i>	-1.57 \pm 0.19	-0.71 \pm 0.09
<i>P. limonensis</i>	-1.09 \pm 0.15	-0.52 \pm 0.07
<i>P. marginata</i>	-1.58 \pm 0.07	-0.63 \pm 0.07
1988		
<i>Psychotria limonensis</i>	-1.09 \pm 0.15	-0.46 \pm 0.07
<i>P. marginata</i>	-1.40 \pm 0.04	-0.67 \pm 0.11

TABLE 3. Analysis of covariance for changes in stem basal area in *Piper* and *Psychotria* species on Barro Colorado Island, Panama. The dependent variable is basal area in July 1988, and the covariate is basal area in March 1986.

Source of variation	Sum of squares	df	Mean square	F
Basal area (mm ²)	184 352	1	184 352	76.53***
Treatment	212	1	212	0.09
Species	27 764	4	6 941	2.88*
Treatment × species	17 347	4	4 337	1.80
Basal area × species	59 459	4	14 865	6.17***
Error	122 860	51	2 409	

* $P < .05$; *** $P < .001$.

Psychotria leaf production

Control plants of all four species produced large numbers of leaves in the first three censuses of the wet season, although the intensity of this peak varied among species (Fig. 4). Synchrony was greatest for control plants of *Psychotria furcata*. Leaf production was bimodal for control plants of *Psychotria horizontalis* and *Psychotria marginata*, with secondary peaks in the late wet season. Synchrony was least for control plants of *Psychotria limonensis*, which produced leaves year-round.

The timing of leaf production changed gradually among irrigated plants for all four *Psychotria* species (Fig. 4). PV increased from 1986 to 1987 and again from 1987 to 1988 for irrigated individuals of all four species, and BIV increased by equal amounts for *Psychotria furcata* (Fig. 7). Irrigation significantly changed the timing of leaf production for *Psychotria furcata* and *Psychotria horizontalis* in 1987 and 1988 and for *Psychotria marginata* in 1988 (Table 6). Irrigation did not affect total annual leaf production for *Psychotria furcata* nor for *Psychotria marginata* (Table 3). There was a significant effect on total annual leaf production for *Psychotria horizontalis* in 1986 and 1988 (Table 3). The distribution of basal areas among treatments suggests that this last result was an artifact, however. The four individuals of *Psychotria horizontalis* with the smallest basal areas were in control plots (mean = 101

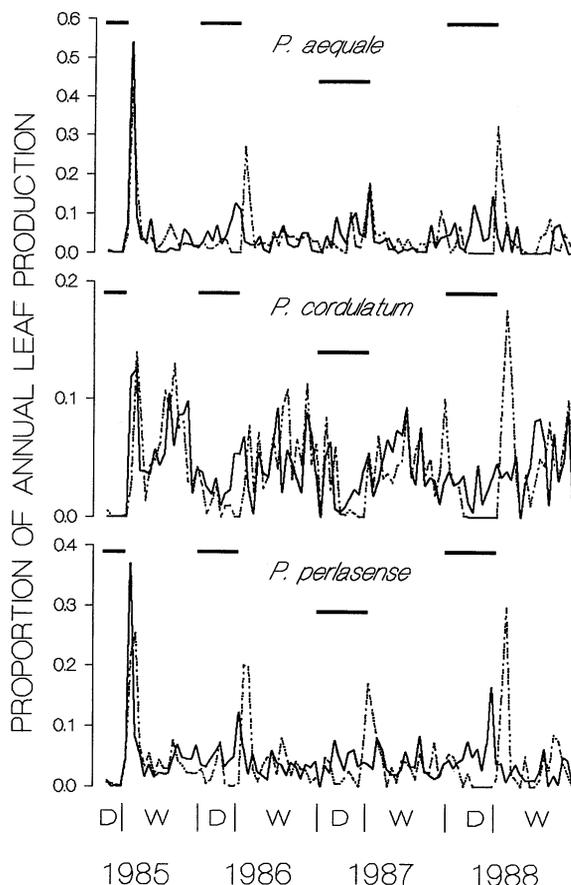


FIG. 3. The timing of leaf production for three species of *Piper* on Barro Colorado Island, Panama. The solid and broken lines represent irrigated and control plants, respectively. Ninety-nine censuses taken each 2 wk are arranged chronologically along the abscissa. The ordinate represents the mean proportion of annual production that occurred during each biweekly census interval (see Eq. 1). The scale on the ordinate differs among species. The vertical lines along the abscissa and the heavy horizontal lines at the top of each plot demarcate dry (D) and wet (W) seasons. Proportions are based on years, which run from the beginning of each dry season through the end of the following wet season, except for 1985 when censuses began on 4 March. Note that the broken line is sometimes hidden by the solid line.

TABLE 4. Numbers of leaves and inflorescences produced each year on Barro Colorado Island, Panama. Entries are means ± 1 SE.

Species	1986	1987	1988
Leaves			
<i>Piper aequale</i>	73 ± 29.2	64 ± 21.8	87 ± 25.8
<i>P. cordulatum</i>	31 ± 4.7	29 ± 4.8	25 ± 4.6
<i>P. perlasense</i>	55 ± 6.8	63 ± 6.9	56 ± 7.6
<i>Psychotria furcata</i>	102 ± 18.6	67 ± 10.6	50 ± 6.0
<i>P. horizontalis</i>	69 ± 6.7	74 ± 8.7	72 ± 8.2
<i>P. limonensis</i>	14 ± 3.0	14 ± 3.2	16 ± 3.6
<i>P. marginata</i>	43 ± 5.8	55 ± 6.3	53 ± 6.9
Inflorescences			
<i>Psychotria furcata</i>	61 ± 13.8	43 ± 11.8	26 ± 7.2
<i>P. horizontalis</i>	8.5 ± 3.0	8.0 ± 2.4	5.5 ± 1.9
<i>P. limonensis</i>	3.4 ± 0.9	3.9 ± 1.0	5.0 ± 1.7
<i>P. marginata</i>	7.9 ± 1.4	14 ± 3.1	13 ± 2.5

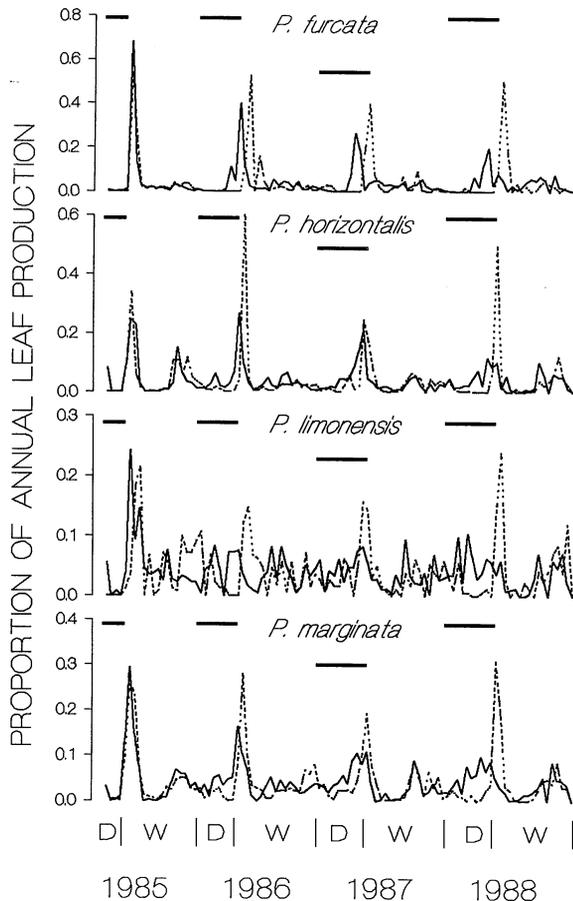


FIG. 4. The timing of leaf production for four species of *Psychotria* on Barro Colorado Island, Panama. Data display is explained in the caption to Fig. 3. Note that the scale on the ordinate differs among species and that the solid line sometimes hides the broken line.

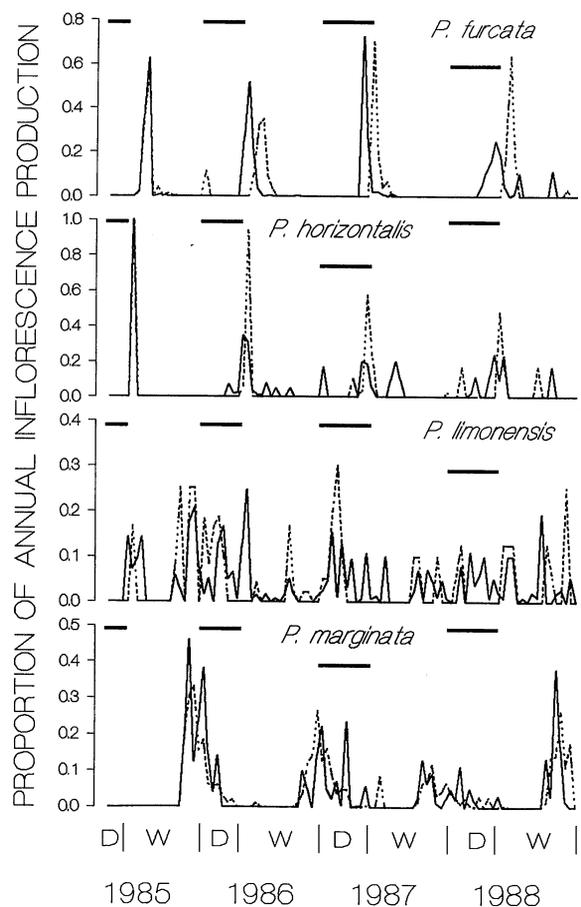


FIG. 5. The timing of inflorescence production for four species of *Psychotria* on Barro Colorado Island, Panama. Data display is explained in the caption to Fig. 3. Note that the scale on the ordinate differs among species and that the solid line sometimes hides the broken line.

mm²), and the five largest (mean = 537 mm²) were in irrigated plots. There was a strong trend for larger individuals to have greater leaf production, although basal area was not a significant covariate because a few mid-sized individuals had the largest annual leaf production (data not shown).

Psychotria inflorescence production

There were a variety of patterns of inflorescence production among control plants (Fig. 5). *Psychotria furcata* and *Psychotria horizontalis* produced inflorescences in synchronous peaks early in the wet season. *Psychotria limonensis* produced inflorescences in every month of the year. *Psychotria marginata* produced inflorescences in a broad peak which began late in the wet season and continued into the early dry season (analyses were for years that began on 1 June).

Irrigation significantly changed the timing of inflorescence production for *Psychotria furcata* in 1987 and 1988 and for *Psychotria horizontalis* in 1986 (Table 7).

Irrigation did not affect total annual inflorescence production (Table 7).

PV and BIV both increased by two orders of magnitude for *Psychotria furcata* in 1988 (Fig. 8). PV and BIV did not show consistent differences among years for inflorescence production for the other three *Psychotria* species (Fig. 8). PV and BIV were unusually large for *Psychotria limonensis* (Fig. 8).

DISCUSSION

Two mechanisms have been proposed which relate water stress to the growth of tropical forest plants. Alvim (1960) proposed a mechanism by which water stress might serve as a proximate cue for tropical plant growth. Alvim posited a critical "water stress requirement" that must be satisfied before increases in moisture availability break bud dormancy. This water stress requirement was likened to the cold stress requirement observed in many plants at higher latitudes. The existence of a critical water-stress requirement has been demonstrated for anthesis in coffee (Alvim 1960, Ma-

TABLE 5. Analyses of covariance for *Piper* leaf production on Barro Colorado Island, Panama. Analyses were performed on logarithms of numbers of leaves produced by each plant. Repeated measures occur on census intervals (see *Methods: Analyses*). The covariate is basal area. If the nested plot effect was not significant (at $P < .25$), it was pooled with the error mean square. If the between-subject effect of basal area was not significant ($P > .25$), a new analysis was performed that omitted basal area. Sums of squares, degrees of freedom, and F statistics are for the univariate repeated-measures model. For within-subject effects, significance levels are only reported if the univariate and multivariate models were in agreement. The within-subject effect of basal area is not reported.

Source of variation	1986			1987			1988		
	ss	df	F	ss	df	F	ss	df	F
<i>Piper aequale</i>									
Between subjects									
Treatment	0.3	1	0.2	5.7	1	7.8	3.4	1	0.8
Plot	3.0	2	1.6	1.5	2	1.6	8.6	2	7.5*
Basal area	15.8	1	16.4**	4.3	1	9.3*	1.9	1	3.2
Error	11.5	12		5.5	12		5.5	9	
Within subjects									
Interval	3.4	5	1.5	6.8	4	3.6*	6.4	4	4.4**
Treatment	12.9	5	5.5**	10.9	4	1.8	25.0	4	9.0*
Plot				11.9	8	3.2*	5.6	8	1.9
Error	32.7	70		22.7	48		13.1	36	
<i>Piper cordulatum</i>									
Between subjects									
Treatment	1.2	1	1.2	0.6	1	0.3	6.2	1	23.1**
Plot				3.5	2	2.7			
Basal area	23.1	1	23.0**	15.4	1	24.4**	8.4	1	31.5**
Error	21.1	21		10.7	17		4.8	18	
Within subjects									
Interval	5.0	5	2.0	6.2	4	3.7*	2.9	4	1.3
Treatment	4.5	5	1.8	6.7	4	4.1**	6.9	4	1.7
Plot							8.0	8	1.8
Error	53.1	105		31.1	76		35.4	64	
<i>Piper perlasense</i>									
Between subjects									
Treatment	0.5	1	0.3	0.2	1	0.2	1.2	1	0.8
Basal area				3.2	1	2.7	13.4	1	8.9*
Error	28.0	15		16.9	14		21.0	14	
Within subjects									
Interval	13.1	5	5.2**	1.4	4	0.8	2.4	4	1.3
Treatment	4.9	5	0.9	3.1	4	1.6	21.5	4	10.9**
Plot	10.5	10	2.1						
Error	32.9	65		25.9	56		27.6	56	

* $P < .05$, ** $P < .01$.

galhaes and Angelocci 1976) and for leaf flush in cacao (Alvim and Alvim 1978). For both species, continuous irrigation delayed budbreak and reduced total budbreak. In this study, irrigation prevented plants from experiencing water stress (Tables 1 and 2). The response to irrigation was nearly the opposite of that observed in coffee and cacao, however. When timing was affected it was advanced rather than delayed (Figs. 3, 4, and 5), and total annual production never declined. These responses are not consistent with a critical water stress requirement for budbreak, and a water stress requirement can be discounted for both genera.

Reich and Borcher (1984) proposed that water stress is the ultimate factor limiting plant function during the dry season in tropical forests. They proposed a continuum of responses to dry-season conditions depending upon plant xeromorphy and dry-season soil moisture

content. For mesomorphic plants in tropical dry forests, they proposed that leaf fall and deciduousness should occur in response to developing water stress early in the dry season, and that subsequent bud break should only occur after a substantial rain. For relatively xeromorphic plants in tropical wet forests, they proposed that water stress should enhance leaf senescence and leaf fall and inhibit budbreak. The tropical moist forests of BCI are intermediate between tropical dry and wet forests. Most plants on BCI are evergreen. In fact, no shrubs and just two herbaceous species, two liana species, and 10% of the tree species are deciduous (Croat 1978). Still, during the 4-mo dry season potential evapotranspiration can exceed precipitation by > 500 mm (Dietrich et al. 1982). Indications of severe plant water stress have been observed on BCI during the 5–6 mo dry seasons that sometimes occur in central

TABLE 6. Analyses of covariance for *Psychotria* leaf production on Barro Colorado Island, Panama. See caption to Table 5 and *Methods: Analyses* for details of the analysis.

Source of variation	1986			1987			1988		
	ss	df	F	ss	df	F	ss	df	F
<i>Psychotria furcata</i>									
Between subjects									
Treatment	0.7	1	0.2	2.2	1	1.1	0.4	1	0.3
Plot							3.1	2	1.9
Error	18.6	10		26.5	14		10.6	13	
Within subjects									
Interval	96.7	5	19.2**	36.6	4	12.5**	49.7	4	14.4**
Treatment	6.1	5	0.6	12.7	4	4.5**	44.9	4	8.8*
Plot	21.7	10	2.1				10.2	8	1.5
Error	50.3	50		39.6	56		45.0	52	
<i>Psychotria horizontalis</i>									
Between subjects									
Treatment	13.7	1	13.3**	1.0	1	0.6	13.4	1	12.0**
Error	16.5	16		30.9	19		20.0	18	
Within subjects									
Interval	57.4	5	16.1**	38.0	4	12.5**	21.4	4	9.0**
Treatment	11.9	5	3.5	9.6	4	3.4*	44.3	4	6.6*
Plot							13.4	8	2.8*
Error	53.8	80		53.3	76		38.0	64	
<i>Psychotria marginata</i>									
Between subjects									
Treatment	0.2	1	0.3	0.2	1	0.1	2.1	1	1.1
Plot							3.7	2	1.9
Basal area	15.3	1	17.3**	8.0	1	5.4	7.7	1	4.1
Error	14.2	16		25.2	17		18.1	16	
Within subjects									
Interval	2.9	5	0.8	3.8	4	2.0	0.9	4	0.4
Treatment	13.7	5	3.7	4.3	4	2.3	36.7	4	10.0**
Plot							7.4	8	1.6
Error	59.5	80		31.5	68		38.0	64	

* $P < .05$, ** $P < .01$.

Panama during El Niño southern oscillations (Fetcher 1979, Robichaux et al. 1984). However, water stress may not limit plant function during more representative dry seasons on BCI (Rundel and Becker 1987).

Responses to irrigation indicate that water stress only rarely limits the growth of *Piper* and *Psychotria* species. Irrigation had no effect on stem basal area growth after 2.33 yr (Table 3) and/or no effect on annual leaf and inflorescence production after 3 yr (Tables 5, 6, and 7) for six species of *Piper* and *Psychotria*. The only significant growth response was an increase in leaf production in the third year of irrigation for *Piper cordulatum* (Table 5). An apparent increase in leaf production for *Psychotria horizontalis* was discounted due to a nonrandom treatment distribution of plant sizes (see *Results: Psychotria leaf production*).

Other evidence suggests that water stress only rarely limits carbon gain by the *Psychotria*. Irrigation had no effect on total non-structural carbohydrate reserves in leaf and stem tissue for *Psychotria furcata*, *Psychotria limonensis*, and *Psychotria marginata* (D. Tissue and S. J. Wright, unpublished data). Irrigation also had limited effects on photosynthetic rates. Photosynthetic rates

were measured in the field during the late dry season for irrigated and control plants for *Psychotria limonensis* in four years, *Psychotria marginata* in three years, and *Psychotria furcata* in two years. Irrigation had a significant effect on photosynthetic rates for just two of these nine species-year combinations (Mulkey et al. 1991, S. S. Mulkey, S. J. Wright, and A. P. Smith, unpublished data).

Water stress could well affect the timing of growth without reducing total annual growth. Cell growth is the plant process that is most susceptible to water stress (Hsiao et al. 1976). Leaf and inflorescence production involve cell growth, and their timing might be affected by levels of water stress that do not affect photosynthesis and total annual growth. Irrigation caused significant changes in the timing of leaf and inflorescence production in 12 of 26 analyses (Tables 5, 6, and 7). The widespread effects of irrigation on timing are consistent with the limiting water-stress hypotheses of Reich and Borchert (1984). Irrigation may have had other effects on the timing of plant growth, however, and more direct evidence for the limiting water-stress hypothesis is needed. The hypothesis can be evaluated

TABLE 7. Analyses of covariance for *Psychotria* inflorescence production on Barro Colorado Island, Panama. See caption to Table 5 and *Methods: Analyses* for details of the analysis.

Source of variation	1986			1987			1988		
	ss	df	F	ss	df	F	ss	df	F
<i>Psychotria furcata</i>									
Between subjects									
Treatment	0.0	1	0.0	0.9	1	1.4	0.6	1	0.5
Plot							2.4	2	5.0
Basal area	5.3	1	14.9**	6.5	1	9.5*	0.3	1	1.3
Error	3.2	9		6.9	10		2.4	10	
Within subjects									
Interval	18.6	5	3.2*	2.5	4	1.1	6.9	5	1.8
Treatment	40.6	5	2.4	31.8	4	13.3**	31.9	5	5.0*
Plot	34.0	10	2.9*				12.9	10	1.7
Error	40.9	35		23.8	40		38.4	50	
<i>Psychotria horizontalis</i>									
Between subjects									
Treatment	0.1	1	0.1	1.3	1	1.3	0.0	1	0.0
Plot	3.0	2	1.7	2.0	2	1.8	1.0	2	1.8
Error	6.1	7		3.9	7		2.2	8	
Within subjects									
Interval	9.6	4		6.1	4	3.6*	1.4	5	0.7
Treatment	11.5	4	10.6**	3.1	4	1.8	2.4	5	1.2
Plot	4.1	8	5.6*						
Error	6.4	28	2.3	15.1	36		20.1	50	
<i>Psychotria marginata</i>									
Between subjects									
Treatment	0.0	1	0.0	0.3	1	0.3			
Plot	7.5	2	7.3						
Error	5.6	11		14.2	14				
Within subjects									
Interval	2.9	5	1.3	6.1	5	3.1*			
Treatment	5.8	5	1.3	2.0	5	0.5			
Plot	8.9	10	1.9	8.1	10	2.0			
Error	25.1	55		24.0	60				

* $P < .05$, ** $P < .01$.

directly by determining whether levels of water stress observed among control plants in the dry season were sufficient to constrain leaf and inflorescence production.

Turgor potential is known to affect many plant physiological processes (Hsiao et al. 1976) and will be used to evaluate levels of plant water stress. Leaf turgor potentials were determined toward the end of the 1986 and 1989 dry seasons. Analyses of leaf and inflorescence production were not attempted for 1989 because extensive treefalls damaged or changed the light environments of many of the plants on the phenology census. Median rainfall between 1 January and 31 March is 84 mm on BCI (Windsor 1990). In 1986 and 1989, rainfall in this period was 60% and 132%, respectively, of the long-term median. In March 1986, pre-dawn leaf turgor potentials of control plants of the four *Psychotria* species were indistinguishable from zero (Table 1). In March 1989, pre-dawn leaf turgor potentials of control plants varied between 0.5 MPa for *Psychotria limonensis* and 1.0 MPa for *Psychotria furcata*

and *Psychotria marginata*, and leaf turgor potentials were >0.2 MPa throughout the day for all four *Psychotria* species (S. J. Wright, J. L. Machado, S. S. Mulkey, and A. P. Smith, *unpublished manuscript*). Turgor potentials were only determined for the *Piper* species in March 1986, when pre-dawn values were 0.4 MPa and 0.6 MPa for *Piper aequale* and *Piper cordulatum*, respectively (Table 1). The *Piper* species were better buffered against water stress than were the *Psychotria* species in 1986. Rundel and Becker (1987) also observed that *Piper cordulatum* was relatively well buffered against dry season water stress.

The observed turgor potentials suggest that water stress is sufficient to limit metabolism for some species in some years. However, other species on BCI have been observed to produce leaves and/or flowers at turgor potentials lower than the minimum values observed for the *Piper* species in 1986 and for the *Psychotria* species in 1989. As an example, irrigated individuals of the canopy tree *Quararibea asterolepis* Pitt. produced leaves in April 1989, when their leaf

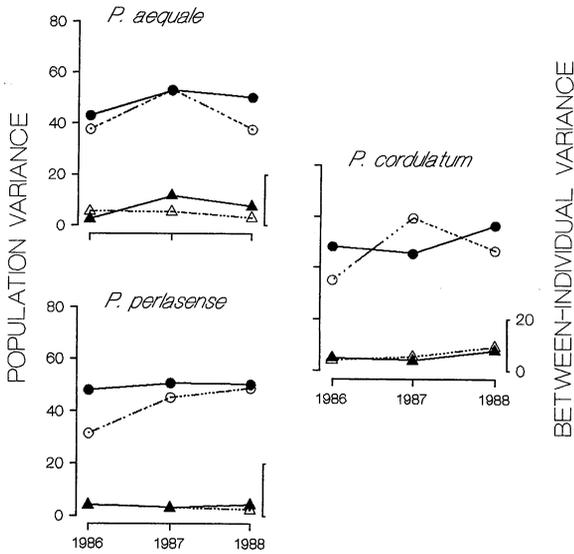


FIG. 6. The synchrony of leaf production for three species of *Piper* on Barro Colorado Island, Panama. Circles and the left ordinate represent the population variance of census of production (PV, from Eq. 2a). Triangles and the right ordinate represent the between-individual component of the population variance (BIV, from Eq. 2c). Solid and open symbols represent irrigated and control plants, respectively.

turgor potentials averaged <0.1 MPa throughout the afternoon (S. J. Wright, R. Cordero, L. Schultz, and M. Garcia, unpublished manuscript). This suggests that the mild levels of water stress observed for the *Piper* species and in some years for the *Psychotria* species may not be sufficient to explain the near absence of leaf and inflorescence production in the dry season.

Other physical factors that differ between the seasons on BCI and that might affect plant phenology include photoperiod, cloud cover, incident radiation, wind-speed, relative humidity, and forest understory temperature (Windsor 1990). Irrigation had no effect on photoperiod, cloud cover, windspeed, and incident radiation at the forest canopy, and these factors can be discounted as causes of plant responses.

At least five other possibilities cannot be discounted so easily. Short-term decreases in temperature of as little as 2°C initiate flowering in some tropical forest plants (e.g., Wycherley 1973, Ashton et al. 1988). Irrigation reduced forest understory temperatures (Fig. 2), and this might mask small temperature changes associated with storms. Alternatively, the $1\text{--}3^{\circ}\text{C}$ decrease in understory temperatures associated with irrigation may have been sufficient to affect leaf or inflorescence production. A second possibility is suggested by the sensitivity of plants to the red : far-red ratio of light (Sweeney 1987). The spectral distribution of light in the forest understory could vary independently of incident radiation at the forest canopy if overstory leaf fall changed. In fact, irrigation did not affect overstory

leaf fall (Wright and Cornejo 1990 a, b) nor understory light levels (S. J. Wright, unpublished data). Since the amount of light and its spectral distribution are highly correlated in the forest understory on BCI (Lee 1987), it seems unlikely that the spectral distribution of light differed between treatments. A third possibility is that changes in soil moisture content act as a proximate cue for plant growth, instead of limiting plant growth through water stress.

A fourth possibility is suggested by the observation that phosphorus is limiting in many tropical forests (Vitousek 1984). Soil phosphate concentrations average $2\ \mu\text{g}/(\text{g dry soil})$ and may limit plant growth at the study site (J. B. Yavitt, K. Wieder, and S. J. Wright, unpublished manuscript). Irrigation changed the timing of litter decomposition and nutrient release (K. Wieder and S. J. Wright, unpublished data). In particular, inputs of inorganic, plant-available phosphorus showed a sharp peak early in the wet season in control plots but not in irrigated plots (J. B. Yavitt and S. J. Wright, unpublished data). The possibility that seasonal flushes of phosphate from decaying litter synchronize plant activity cannot be discounted.

A fifth possibility is that atmospheric vapor pressure deficits affect plant phenologies (Wright 1905, Wright and Cornejo 1990b). The irrigation experiment provides two lines of evidence consistent with this possibility. The first comes from a comparison among forest strata. Irrigation increased atmospheric humidity in the understory (Fig. 2) and changed the phenologies of most shrubs (this study) and understory saplings (S. J. Wright, unpublished data). Irrigation did not affect relative humidity in the forest canopy and had no effect on the phenology of flowering and leaf

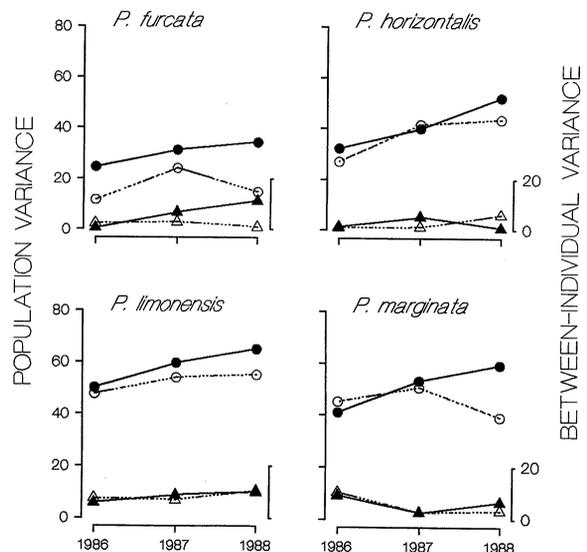


FIG. 7. The synchrony of leaf production for four species of *Psychotria* on Barro Colorado Island, Panama. Data display is explained in the caption to Fig. 6.

fall for most species of canopy trees and lianas (Wright and Cornejo 1990a, b).

The second line of evidence that suggests that atmospheric drought affects plant phenologies comes from a comparison of the phenologies of the *Piper* and *Psychotria* species for different years. Substantial rains occurred in February and April of 1987, and relative humidities averaged 90% in the control plots in both months (Figs. 1 and 2). By way of contrast, relative humidities never averaged >85% in the control plots during February, March, and April of 1986 and 1988 (Fig. 2). For control plants of most of the *Piper* and *Psychotria* species, leaf and inflorescence production occurred earlier and less synchronously in 1987 than in 1986 and 1988 (Figs. 3, 4, and 5). In addition, the population variance of date of leaf production (Figs. 6 and 7) was greater for irrigated plants than for control plants for 13 of 14 comparisons for 1986 and 1988 ($P = .0009$, binomial test) but only for 4 of 7 comparisons for 1987 ($P = .5$, binomial test).

An effect of atmospheric conditions on plant phenology could reconcile the observation that many canopy trees fail to flower after unusually rainy dry seasons on BCI (Foster 1982) with the observation that understory irrigation does not affect flowering in many of the same species (Wright and Cornejo 1990a, b). For example, 409 mm, or 487%, of median rainfall fell between 1 January and 31 March 1970, and many canopy trees failed to flower during the following wet season (Foster 1982). Irrigation added about 450 mm of water between 1 January and 31 March, yet the same species of canopy trees flowered normally (Wright and Cornejo 1990a, b). Natural rainfall will affect atmospheric conditions in the canopy that were not affected by understory irrigation.

Atmospheric conditions may have an advantage over soil conditions as a potential phenological cue. Edaphic properties can vary tremendously with microsite. Individual plants separated by a few metres might be rooted in soil derived from different parent materials with different water-retention properties. Over only slightly larger distances individuals rooted in stream beds and on ridge tops might experience dramatic differences in soil moisture availability. Changes in atmospheric conditions occur more uniformly over larger areas and may more effectively synchronize the growth of forest plants. Wright and Cornejo (1990b) suggest a mechanism by which atmospheric conditions might affect plant phenology.

To summarize, the responses of the *Piper* and *Psychotria* species to irrigation are consistent with the hypothesis that dry season water stress affects the timing of leaf and inflorescence production (Borchert 1980, 1983, Reich and Borchert 1982, 1984). However, the levels of water stress observed for the *Piper* species and in some years for the *Psychotria* species may not be sufficiently severe to affect leaf and inflorescence production. In addition, other possible cues for plant phe-

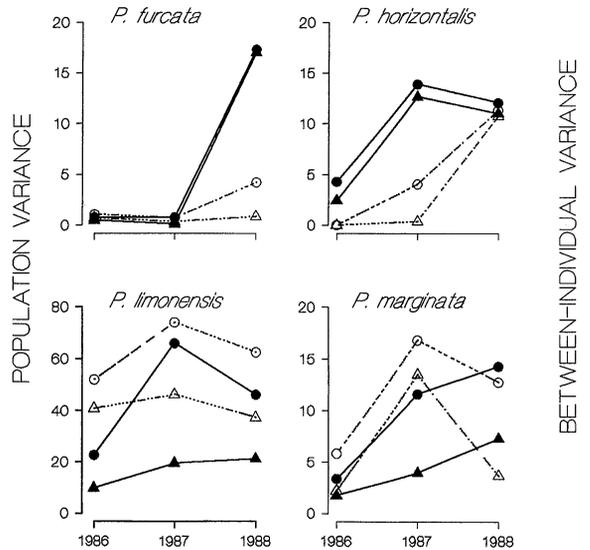


FIG. 8. The synchrony of inflorescence production for four species of *Psychotria* on Barro Colorado Island, Panama. Data display is explained in the caption to Fig. 6. Note that the scale on the ordinate differs for *P. limonensis*.

nology cannot be discounted. Possible cues that were affected by irrigation in addition to soil water content include understory humidity and temperature and the timing of nutrient and particularly phosphate release from decomposing litter.

Endogenous rhythms

If budbreak is affected by endogenous rhythms and by an exogenous cue that is disrupted by irrigation, then timing should change gradually as irrigation continues and as the last exogenous cue that entrained individuals becomes more remote in time. The gradual responses of the *Psychotria* suggest that endogenous rhythms affect budbreak. Synchrony, as represented by the population variance of census of leaf production (PV), increased from year to year for irrigated plants of the four *Psychotria* species but not for control plants (Fig. 7) nor for irrigated plants of the three *Piper* species (Fig. 6). The timing of production also changed gradually for the *Psychotria* species. This effect is clearest for leaf and inflorescence production by *Psychotria furcata* (Figs. 4 and 5) and for leaf production by *Psychotria horizontalis* and *Psychotria marginata* (Fig. 4). In each instance the early wet-season peak diminished in importance for irrigated plants (decreasing synchrony), and the residual peak occurred earlier each year (changes in timing). By 1988, peak production occurred in the late dry season for these irrigated plants (Figs. 4 and 5).

The loss of population synchrony for the *Psychotria* could be caused by loss of synchrony among individuals (an increase in BIV) or by loss of synchrony within individuals (an increase in WIV). Changes in the pop-

ulation variance of the census of production (PV) were paralleled by changes of equal magnitude in BIV for *Psychotria furcata* (Figs. 7 and 8), and the loss of population synchrony was caused by loss of synchrony among individuals. There were no systematic changes in BIV for the other three *Psychotria* species (Figs. 7 and 8).

Annual rhythms may be maintained by root-to-shoot asynchronies (Borchert 1978), by photoperiodic cues, or by true circannian rhythms (Sweeney 1987). Photoperiodic cues, which were not affected by irrigation, cannot explain gradual responses to irrigation. Root-to-shoot asynchronies are unlikely to explain the sudden decline in synchrony observed for inflorescence production by *Psychotria furcata* in the third year of the experiment, especially after synchrony was unaffected for the first two years (Fig. 8). True circannian rhythms have never been demonstrated for whole plants, and field experiments cannot satisfy the criteria set forth by Sweeney (1987:127–128) to establish true circannian rhythms. Nevertheless, the data for the *Psychotria* and especially for *Psychotria furcata* are suggestive, and these plants might be a suitable place to begin the necessary laboratory studies.

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