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SEASONAL DROUGHT AND LEAF FALL IN A TROPICAL FOREST[1]

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Abstract. Peak rates of leaf fall almost always occur during dry seasons in low-latitude, low-elevation tropical forests. The hypothesis that plant water stress is the proximal cue for leaf fall was tested by augmenting water supplies during the 4-mo dry season over two 2.25-ha plots of tropical moist forest on Barro Colorado Island (BCI), Panama. The manipulation maintained soil water potentials at or above field capacity throughout the dry season but did not affect atmospheric conditions in the canopy (i.e., relative humidity, temperature, windspeed, incident radiation). The manipulation ameliorated plant water status; for most species, dry-season leaf water potentials in the manipulated plots were similar to wet-season values and both were consistently greater than dry-season values in the control plots. The manipulation delayed leaf fall for 2 of 9 species of trees for which qualitative data are available and possibly for 2 of 20 species of trees and lianas for which quantitative data are available. The timing of leaf fall was indistinguishable in manipulated and control plots for the remaining 25 species. We conclude that plant water status is rarely the proximal cue for leaf fall on BCI. Atmospheric conditions may be important for some species, but there is no reason to presuppose that a majority of tropical plants are responsive to any single cue.

Key words: Barro Colorado Island; irrigation; leaf fall; leaf water potential; lianas; Panama; phenology; tropical forests; tropical seasons; tropical trees; water stress.

At higher latitudes, plant growth and reproduction are correlated with seasonal changes in temperature and photoperiod. In the tropics, temperature and photoperiod are relatively constant but similar correlations occur with seasonal changes in rainfall. For example, leaf fall peaks during dry seasons in low-latitude (<13°), low-elevation forests (<600 m) throughout the tropics (Central America: Frankie et al. 1974, Haines and Foster 1977; South America: Klinge and Rodriguez 1968, Cornforth 1970, Folster and de las Salas 1976, Franken et al. 1979, Cuevas and Medina 1986; Africa: Madge 1965, Hopkins 1966, John 1973, Swift et al. 1981, Songwe et al. 1988; Asia: Ogawa 1978, Rai and Proctor 1986, Schaik 1986), although there are exceptions (Cornforth 1970, Proctor et al. 1983). The ultimate cause for the association of leaf fall with tropical dry seasons may be the potential for damaging water stress that might otherwise occur when conditions are driest at the end of the dry season (e.g., Richards 1952, Longman and Jenik 1987). The proximal cue is less obvious, however, because leaf fall frequently peaks very early in the dry season, presumably before soil moisture content has fallen appreciably. Photoperiod, "night exposure," and subtle temperature changes have all been suggested as cues for leaf fall in the tropics (e.g., Richards 1952, Hopkins 1966, Longman and Jenik 1987).

Borchert (1980: 1073) proposed, however, that "Leaf abscission is the consequence of drought-induced tree water deficits and not, as expressed in many discussions of the adaptive value of deciduousness in tropical trees (e.g., Richards 1952), an anticipatory reaction to reduce further loss of water." Reich and Borchert (1984) proposed that water stress develops as the dry season progresses, and that water stress accelerates the senescence and shedding of leaves. Species with different capacities for water uptake and control of water loss might respond differently to the potential for dry-season water stress so that evergreen and deciduous species might co-occur, and individuals of a single species might respond differently if moisture availability or evaporative demand varied among microsites (Borchert 1980, Reich and Borchert 1984).

Under this hypothesis, water stress is the proximal cue for leaf fall. If the timing or severity of water stress is changed, the timing of leaf fall should change. In particular, if water stress is ameliorated or eliminated, leaf fall should be delayed. We have manipulated dry-season soil moisture content by adding water to two large plots of old forest on Barro Colorado Island (BCI), Panama. Numerous responses to the manipulation are under study. In this paper we report on leaf fall for 2 yr for 29 species of trees and lianas. The effect of the manipulation on plant water status is quantified directly with measurements of leaf water potentials.

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Study Site and Species

BCI (9°9′ N, 79°51′ W) supports tropical moist forest (Holdridge and Budowski 1956). Mean annual precipitation is 2600 mm (Windsor, *in press*). 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 88 mm (Leigh and Wright, *in press*). Mean maximum and minimum temperatures in the laboratory clearing are lowest in November (30.6°C) and October (22.8°), respectively, and climb steadily over the dry season to their highest values in April (32.3°) and May (23.6°), respectively (Windsor, *in press*). As the dry season progresses, gravimetric soil water content falls from ≈42% to ≈28% (Windsor, *in press*) and soil water potentials can fall to −2.0 MPa (Becker et al. 1988). A "veranillo" or little dry season occurs in August or September in most years (Rand and Rand 1982), but has little effect on soil water potentials (see Results: Moisture Availability, below). The community-wide rate of leaf fall peaks early in the dry season and remains high throughout the dry season (Haines and Foster 1977, Leigh and Smythe 1978). Many plants wilt by midday in the late dry season (S. J. Wright, *personal observation*), and 12% of the species of trees are deciduous some time during the dry season (Croat 1978). More detailed descriptions of BCI can be found in Croat (1978), Leigh et al. (1982) and Windsor (*in press*).

Species were included in the analyses of leaf fall for years for which litter traps collected at least 10 g of dried leaves from each of the four study plots (see Methods: Leaf Fall). Nine canopy trees, six subcanopy trees and five lianas met this criterion. Most are widely distributed in Central and northern South America, and all are common on BCI (Croat 1978). Adults of six of the canopy tree species are normally deciduous on BCI. *Anacardium excelsum* (2, 3, 2, 2), *Apeiba membranacea* (20, 9, 3, 6), and *Jacaranda copaia* (3, 9, 14, 7) are briefly deciduous early in the dry season (the numbers in parentheses are numbers of individuals >10 cm dbh on 1.4 ha of each plot). *Dipteryx panamensis* (4, 2, 2, 2) and *Trattannickia aspera* (8, 6, 8, 6) are briefly deciduous at the end of the dry season. *Quararibea asterolepis* (5, 5, 9, 6) exchanges leaves at the end of the dry season and again at the end of the wet season. *Guatteria dumetorum* (5, 3, 10, 5), *Licania platypus* (3, 2, 3, 2), and saplings of all nine canopy trees are evergreen. The six subcanopy trees, *Guarea guidonia* (10, 8, 19, 10), *Heisteria concinna* (6, 13, 11, 13), *Protium panamense* (13, 5, 11, 26), *Tetragastris panamensis* (31, 31, 28, 43), *Trichilia cipo* (22, 14, 14, 21), and *Virola sebifera* (20, 21, 10, 22), are all evergreen as are the five lianas, *Arrabidaea verrucosa, Doliocarpus olivaceus, Maripa panamensis, Prionostemma aspera,* and an unidentified Rhamnaceae. After first mention, species will be referred to by their generic names only. Nomenclature follows Croat (1978).

Methods

Two 2.25-ha plots were manipulated, and two similar plots served as controls. The forest on the plots is among the oldest on BCI (R. Foster, *personal communication*), and has escaped any substantial human disturbance for >500 years (Piperno, *in press*). The average distance between plots was >50 m. Water was added to the manipulated plots by 160 sprinklers placed at 15.3-m intervals in an hexagonal array. 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 manipulated plot received 135 Mg of water during 1.5 h of irrigation between 1100 and 1400 on each of 5 d. Mean soil water potentials were maintained at or slightly above field capacity (−0.04 MPa) throughout the dry seasons of 1986, 1987, and 1988. It was not necessary to irrigate between May and November. 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*). No point in the study plots was <75 m from the lake.

Moisture availability

Rainfall was monitored at the site. Relative humidity was measured at heights of 5, 15, and 25 m at the end of the dry season in March and April 1988. Psychrometers were raised into the canopy with ropes at three sites per treatment, and measurements were made for 1–3 d at each site. Wet and dry bulb temperatures were recorded with thermistors (LI-COR 1000-16), and air movement was maintained with battery-powered fans.

Three methods were used to monitor soil moisture content. Eight randomly located stations were established in the interior (>15 m from edge) of each plot in December 1985. Tensiometers (Soil Moisture Equipment Corporation, model 2725A) were installed at depths of 25 and 45 cm at each station in the manipulated plots. Soil psychrometers (Wescor, model PCT55) were installed at 25 cm at all 32 stations and at 50 cm at four randomly chosen stations in each plot following the methods of Becker et al. (1988). Access tubes for a hydroprobe (Campbell Nuclear Pacific, model 503) were installed at all 32 stations to allow measurements at depths of 25, 50, and 100 cm. All soil moisture measurements were recorded weekly. During the dry season, tensiometers were read thrice weekly, and the irrigation schedule was adjusted to maintain average tensiometer readings above −0.04 MPa. 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.

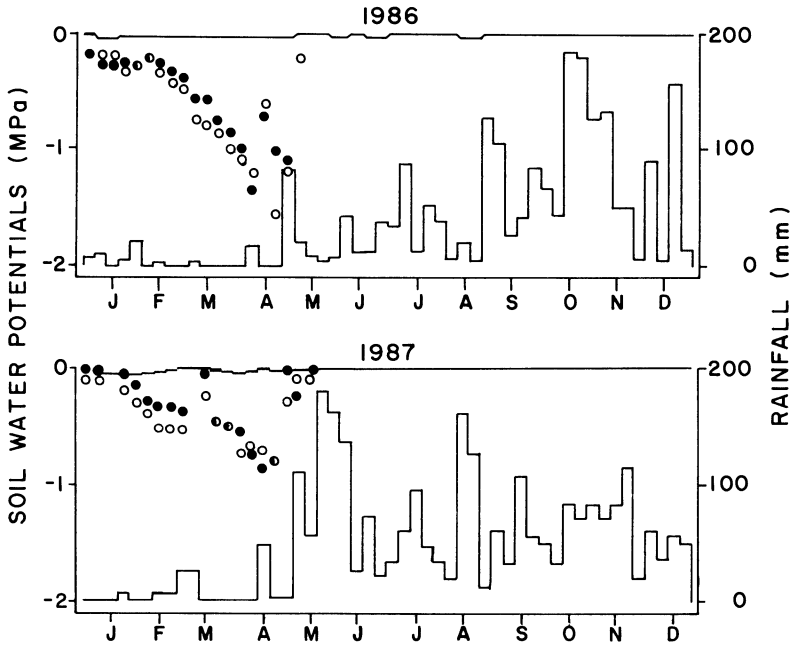

FIG. 1. Weekly rainfall and soil water potentials. The histogram represents rainfall. Open and closed circles represent dry-season soil water potentials for the two control plots. The solid line at the top of each graph represents soil water potentials in the manipulated treatment. All soil water potentials were measured at 25 cm depths. The week that includes the first Monday in each month is marked along the abscissa.

Leaf water potentials

Midday leaf water potentials were measured for 10 species of trees and treelets. Measurements were made with a portable pressure chamber (PMS Instrument Company) between 1100 and 1400 for two individuals of each species in each plot. Leaves were shot down from as close to the top of each tree as possible and were immediately sealed in airtight bags. Measurements were made within 20 min of collection. Averages for two leaves are reported for most individuals. Dry- and wet-season measurements were taken in 1987 between 27 March and 24 April and 27 November and 2 December, respectively. Dry-season measurements were interrupted by a substantial rain on 5 April (Fig. 1) and were resumed on 23 April. Mean gravimetric soil water contents in the control plots were 27.1, 32.2 and 28.2% on 25 March, 8 April, and 22 April, respectively.

Leaf water potentials determined just before dawn reflect the ability of a plant to recover water lost during the day, and may better indicate the water status of the plant. Predawn leaf water potentials could not be determined for large trees and lianas because leaves could not be collected from the canopy in the predawn darkness. Predawn leaf water potentials were determined for the common understory shrub *Hybanthus prunifolius*. Measurements were made between 0430 and 0630 for two leaves of 20 widely scattered individuals in each plot in mid-March 1988 and for another 12 individuals on 7 October 1988. Leaves were excised with clippers, and determinations were made within 2 min.

ANOVA was used to analyze dry-season leaf water potentials with plots as a random factor nested within treatments. If the plot effect did not explain variation in leaf water potentials ($P > .25$), it was omitted and a second ANOVA was performed with plots disregarded (Winer 1971: 378). Small sample size precluded a two-way nested ANOVA with season and treatment as main effects. Seasonal differences are therefore evaluated by inspection.

Leaf fall

Randomly located litter traps were emptied weekly. Ten traps were installed on each plot on 18 November 1985, and an additional five traps were installed on each plot on 3 March 1986. No trap was <15 m from the edge of a plot or <2 m from an adult *Oenocarpus panamanus*. The fronds of this palm redirect falling litter, often creating a bare zone in the immediate vicinity. Traps were constructed of plastic screening (1.2-mm mesh), had a surface area of 0.25 m^2, and were mounted 40 cm above the ground. Trap contents were dried to a constant mass at 60°. Leaves were identified to species and weighed to the nearest 0.1 g.

Leaf fall was analyzed for species for which >10 g of dried leaves were collected in each plot in a single year. The two study years actually included 52 weekly censuses beginning on 17 December 1985 and 16 De-

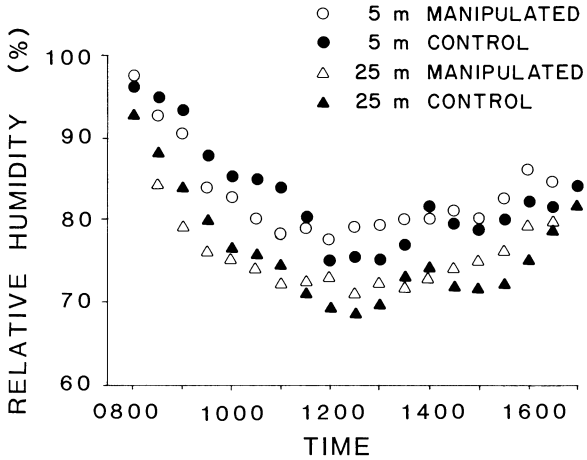

FIG. 2. Diurnal course of relative humidity late in the dry season. Open and closed symbols represent averages for manipulated and control treatments, respectively. Circles and triangles represent heights of 5 and 25 m above the forest floor, respectively.

cember 1986 and are referred to as 1986 and 1987, respectively. Analyses were performed separately for 1986 and 1987. Analyses for 1986 are based on the first 40 traps. The addition of traps part way through a year could introduce spurious seasonal effects. Analyses for 1987 are based on all 60 traps.

The timing of leaf fall was investigated separately for each species using time-series analysis and repeated-measures ANOVA. Leaf dry mass was summed over all traps in each treatment for each week to create a time series for each treatment. Cross correlations were calculated for these series. Cross correlations consist of Pearson product-moment correlation coefficients that are calculated for two series lagged one against the other. In this instance, leaf masses from the control treatment for week t were correlated with leaf masses from the manipulated treatment for week $t + x$, where x is the lag. Positive lags would indicate that leaf fall occurred later in the manipulated treatment.

The main effects for the repeated-measures ANOVA were treatment and census interval, with repeated measures on census interval. A significant interaction between treatment and census interval would indicate that the timing of leaf fall differed between treatments. A significant census-interval main effect would indicate that leaf fall was not uniform throughout the year. The treatment main effect is of limited interest because there are no a priori predictions, and an overall treatment effect could be introduced by chance differences between treatments in species abundances and in the proximity of individuals to litter traps. Census intervals were created whenever leaf fall fell to zero by grouping data into 26 two-week, 17 three-week, 13 four-week, or 10 five-week intervals. The shortest interval which maintained nonzero variances was used for each species. Analyses were performed on logarithms of the sum of leaf dry masses for all traps in each plot. Degrees of freedom were adjusted to correct for possible violations of the compound symmetry assumption of repeated-measures ANOVA (Huynh and Feldt 1976).

RESULTS

Moisture availability

Total rainfall for 1986 and 1987 was 2069 and 2593 mm, respectively. In the control treatment, soil water potentials declined steadily during the dry season except for brief increases after heavy rains (Fig. 1). In the manipulated treatment, average soil water potentials were always above −0.04 MPa (Fig. 1). In the wet season, soil water potentials were most often 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 (data not shown) paralleled those at 25 cm, but were less responsive to dry-season rains. About 90% of all roots are found in the upper 40 cm of soil on BCI (Odum 1970, S. J. Wright and A. P. Smith, *personal observation*).

The manipulation did not affect relative humidity 5, 15, and 25 m above the forest floor (Fig. 2, data from 15 m not shown). This result may be due partly to mixing of the air column by the dry-season trade winds and partly to the apparent absence of a treatment effect on stomatal behavior in the canopy (see Discussion, and Sternberg et al. 1989). The manipulation does change relative humidity at 1.3 m (S. J. Wright, *unpublished manuscript*), but this height is well below the leaves of adults of all study species except *Hybanthus*. The manipulation also had no effect on temperature, windspeed, and incident radiation in the canopy (data not shown).

Leaf water potentials

In the dry season, there was a significant treatment effect on midday leaf water potentials for *Dipteryx, Hirtella triandra, Prioria copaifera* and *Quararibea* (Table 1). The manipulation moderated leaf water potentials for all four species (Fig. 3). Furthermore, at least three of the four dry-season measurements from the control treatment were more negative than all four dry-season measurements from the manipulated treatment for *Alseis blackiana, Beilschmiedia pendula, Faramea occidentalis,* and *Trichilia* (Fig. 3). This result suggests that the treatment moderated leaf water potentials for these species also. The absence of a statistically significant effect is not surprising given the low power of the analyses (one and two degrees of freedom) for these species (Table 1). Leaf water potentials were nearly constant under all conditions for *Jacaranda,* and were highly variable under all conditions for *Virola* (Fig. 3).

Inspection of Fig. 3 suggests seasonal differences in

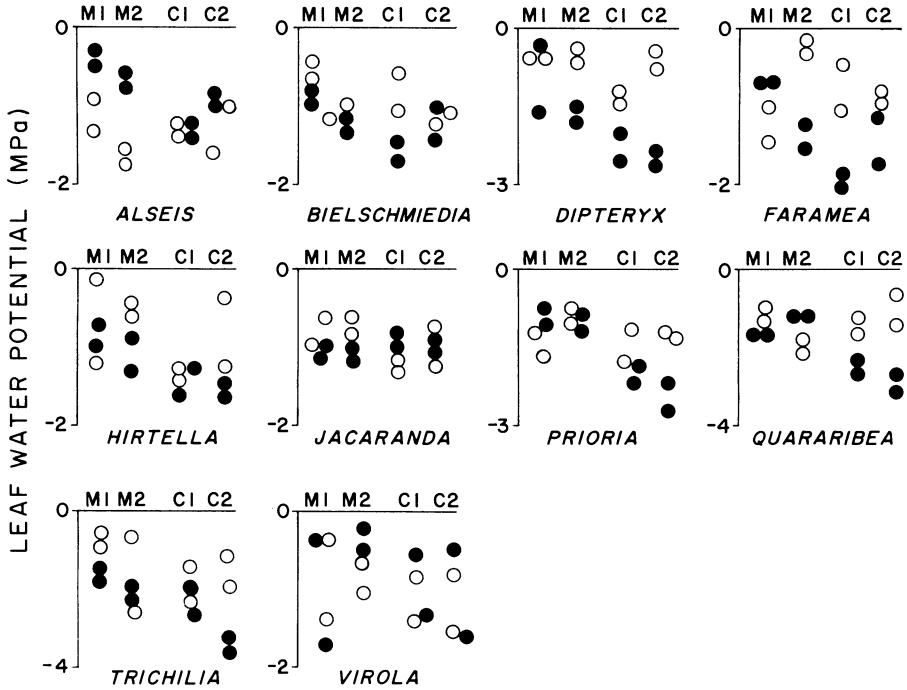

FIG. 3. Midday leaf water potentials for trees and treelets in the wet (○) and dry (●) seasons. Plots are separated along the abscissa. M1 and M2 refer to manipulated plots and C1 and C2 to control plots. Each symbol represents a plant. The scale on the ordinate varies among species.

TABLE 1. Analyses of variance for dry-season leaf water potentials. Analyses were performed on mean leaf water potentials for manipulated and control individuals.

Species	Source	SS	df	MS	F
Alseis blackiana	Treatment	70.51	1	70.51	4.63
	Plot	30.39	2	15.20	19.6**
	Error	3.09	4	0.77	
Beilschmiedia pendula	Treatment	32.00	1	32.00	1.86
	Plot	34.31	2	17.16	6.2
	Error	11.06	4	2.77	
Dipteryx panamensis†	Treatment	287.4	1	287.04	12.3*
	Error	140.28	6	23.38	
Faramea occidentalis	Treatment	92.82	1	92.82	2.2
	Plot	84.20	2	42.10	6.7
	Error	25.16	4	6.29	
Hirtella triandra†	Treatment	60.23	1	60.23	14.6**
	Error	24.77	6	4.13	
Jacaranda copaia†	Treatment	0.63	1	0.63	1.5
	Error	2.61	6	0.44	
Prioria copaifera†	Treatment	351.13	1	351.13	32.7**
	Error	64.47	6	10.75	
Quararibea asterolepis	Treatment	380.47	1	380.47	20.45*
	Plot	37.20	2	18.60	9.7*
	Error	7.66	4	1.92	
Trichilia tuberculata	Treatment	225.79	1	225.79	2.90
	Plot	155.66	2	77.83	17.2*
	Error	18.06	4	4.52	
Virola sebifera†	Treatment	17.26	1	17.26	0.6
	Error	258.4	6	43.1	

* $P < .05$, ** $P < .01$.
† The nested plot effect was not significant ($P > .25$), and a second ANOVA that disregarded plots is reported.

midday leaf water potentials when dry-season measurements from the control treatment are compared to wet-season measurements. At least three of the four dry-season measurements from the control treatment were more negative than all eight wet-season measurements for *Beilschmiedia, Dipteryx, Faramea, Hirtella, Prioria, Quararibea,* and *Trichilia* (Fig. 3).

Inspection of Fig. 3 also suggests that the manipulation ameliorated these seasonal differences for most species. Dry-season leaf water potentials from the manipulated plots were similar to wet-season measurements for 8 of the 10 species. This was unexpected. Possible seasonal changes in tissue osmotic concentrations, stomatal behavior, and leaf orientation may have combined with augmented soil moisture content to offset the high evaporative demand created by reduced humidity and increased windspeed, air temperature, and incident radiation characteristic of the late dry season. For *Alseis,* dry-season measurements from the manipulated plots were actually greater than wet-season measurements (Fig. 3). Dry season measurements for *Alseis* were made shortly after leaf exchange, and the relatively large values may reflect changes in the ability to retain water, which occur with leaf age (Reich and Borchert 1988). For *Dipteryx,* dry-season leaf water potentials from the manipulated plots were generally more negative than wet-season measurements (Fig. 3).

Predawn leaf water potentials (mean ± 2 SE) for *Hybanthus* were 0.17 ± 0.03 MPa in October; in March they were 0.24 ± 0.03 and 0.25 ± 0.03 MPa in the manipulated plots, and 0.87 ± 0.13 and 0.73 ± 0.09 MPa in the control plots, respectively. The manipulation created conditions in the understory that allowed nearly complete rehydration overnight. Petioles are short in *Hybanthus* (<2 mm), and stem had to be included in all samples to use the pressure chamber. This stem tissue may explain why leaf water potentials closer to zero were not obtained.

Leaf fall

Leaf fall was analyzed for 13 and 19 species for 1986 and 1987, respectively, including 12 species that were analyzed in both years. Cross correlations were not significant (at three standard errors of the correlation coefficient) for any lag for *Heisteria, Maripa* in 1986, *Pouteria,* and *Virola.* For the remaining analyses, the lag associated with the largest correlation coefficient was equitably distributed around zero, being negative, zero, or positive for 9, 7, and 10 analyses, respectively (Fig. 4). The only analyses for which the lag associated with the largest correlation coefficient was positive and >3 wk were *Doliocarpus* for 1987, *Prionostemma* for 1986, and *Dipteryx* for the one year that it qualified for analysis. *Prionostemma* also showed a strong positive lag of 3 wk for 1987, while *Doliocarpus* showed a negative lag of 1 wk for 1986 (Fig. 4).

The treatment × census interval interaction was significant for just 3 of the 32 repeated-measures ANOVAs (Table 2). The cross-correlation analysis indicated that leaf fall occurred >3 wk late in the manipulated treatment for the same three analyses, namely for *Doliocarpus* for 1987, *Prionostemma* for 1986, and *Dipteryx* (Fig. 4). The Huynh-Feldt adjustment to degrees of freedom did not affect the significance of the interaction for any of the analyses (Table 2).

The census-interval main effect was significant in 17 of the 32 repeated-measures ANOVAs (Table 2). In each case leaf fall was concentrated in the dry season. For *Licania* in 1987 and for *Arrabidaea, Jacaranda,* and *Tetragastris,* the Huynh-Feldt adjustment to degrees of freedom negated the significance of the census-interval main effect. Leaf fall appeared to be concentrated in the dry season for each of these species, but violations of the assumptions of repeated-measures ANOVA reduced the power of the analysis and the effect was not statistically significant. Species for which the null hypothesis of aseasonal leaf fall could not be rejected include *Guatteria, Heisteria, Maripa, Pouteria, Protium,* and *Virola.* Visual inspection confirms that leaf fall is approximately aseasonal for all of these species except *Pouteria.* For *Pouteria,* leaf fall was concentrated at different times of year in each plot.

Discussion

The manipulation maintained soil water potentials at field capacity throughout the dry season (Fig. 1) and moderated dry-season leaf water potentials for most species (Table 1, Fig. 3), yet had no effect on the timing of leaf fall for most species (Table 2, Fig. 4). Direct observation of leaf fall from deciduous trees confirms this last result. In addition to the deciduous species mentioned above, individuals of *Apeiba tibourbou, Spondias mombin, S. radlkoferi, Tabebuia guayacan, T. rosea, Pseudobombax septenatum, Sapium caudatum, Zuelania guidonia,* and *Pterocarpus rohrii* were present on the manipulated plots. The manipulation delayed leaf fall into the wet season for *Dipteryx* and *T. guayacan* in 1986, 1987, and 1988, but had no effect on the timing of leaf fall for the 13 remaining deciduous species (Table 2, S. J. Wright, *personal observation*).

Borchert (1980, 1983) and Reich and Borchert (1982, 1984) developed the hypothesis that plant water status is the proximal cue for leaf fall and bud break in tropical trees. Our results support their hypothesis for leaf fall for *Dipteryx* and *T. guayacan* and possibly for the lianas *Doliocarpus* and *Prionostemma.* However, maintaining soil water potentials at field capacity throughout the dry season had no effect on the timing of leaf fall for 25 additional species. At least two possibilities may reconcile the hypotheses of Reich and Borchert with these results. First, Reich and Borchert (1984: 71) hypothesized that "the effects of water stress on the time of leaf fall . . . are moderate" for evergreen species. "Moderate" effects might not be detectable for the 13 evergreen species treated here. Second, the hypotheses of Reich and Borchert were developed from pheno-

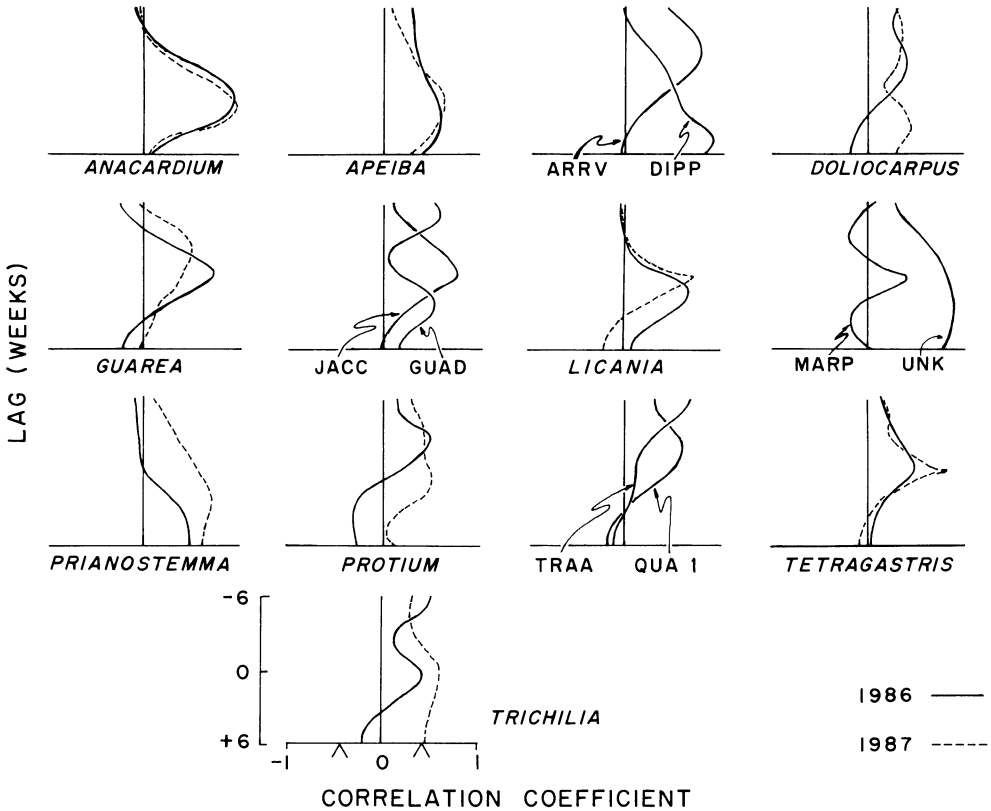

FIG. 4. Correlograms for leaf fall. Pearson product-moment correlation coefficients are plotted on the abscissa, and lags are plotted on the ordinate. Positive lags indicate that leaf fall occurred later in the manipulated treatment than in the control. Arrows (.) along the abscissa of the lower left panel represent plus and minus three standard errors of the correlation coefficient for lags of ±6 wk. For species analyzed in both years, the solid and dashed lines represent 1986 and 1987, respectively. Codes for species analyzed in only one year follow: ARRV, *Arrabidaea*; DIPP, *Dipteryx*; GUAD, *Guatteria*; JACC, *Jacaranda*; MARP, *Maripa*; TRAA, *Trattinnickia*; QUA1, *Quararibea*; and UNK, unknown Rhamnaceae.

logical data that came primarily from tropical dry forest on the Pacific coast of Costa Rica (Daubenmire 1972, Borchert 1980, Reich and Borchert 1982, 1984). BCI is in a different biome (Holdridge and Budowski 1956), and it is possible that the more severe dry seasons typical of tropical dry forests do in fact control leaf fall.

A final possibility is that, even in tropical dry forest, plant water stress is only rarely the proximal cue for leaf fall. The hypotheses of Reich and Borchert were developed from correlations between leaf fall and plant water status as inferred from changes in trunk diameter, and from correlations between phenologies and inferred moisture availability at different sites. These correlations may not be causal. Reich and Borchert (1984) present phenologies for two species of trees from "irrigated forest" at La Pacifica, Costa Rica. For *Cochlospermum vitifolium*, the timing of leaf fall was unaffected. For *Enterolobium cyclocarpum* the first date of leaf fall was unaffected, but the duration of leaf fall was protracted. Leaf fall in *C. vitifolium* and *Genipa americana* also was unaffected by dry-season irrigation in the extremely seasonal environment of the Venezuelan llanos (V. Kapos, *personal communication*).

Three observations from our experiment suggest that many leaves fall before substantial water stress occurs. First, there is a strong peak in leaf fall summed over all species in the first month of the dry season (Wright and Cornejo, *in press*). Second, soil water potentials are still high at this time (Fig. 1). Third, given adequate soil moisture, the water absorption and retention capacities of most species are adequate to maintain leaf water potentials even under the atmospheric conditions present at the driest time of year, at the end of the dry season (Fig. 3). Thus, it is unlikely that water stress is widespread during the peak of leaf fall at the beginning of the dry season.

We will now consider what might cue leaf fall for the many species that do not respond to soil moisture availability. Environmental factors not affected by irrigation include photoperiod, windspeed, incident radiation, and, in the canopy, relative humidity (Fig. 2) and temperature. Properties of the plant not affected include leaf age and possible endogenous rhythms

TABLE 2. Repeated-measures analyses of variance for leaf fall. Analyses were performed on logarithms of the dry mass of leaves per manipulated and control plot through time during each year.

	Anacardium				*Apeiba*				*Arrabidaea*	
	1986§		1987‖		1986‖		1987†		1987†	
Source of variation	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Treatment	0.17	0.01	0.59	6.19	2.69	0.13	2.16	0.32	17.1	3.01
Error	55.6		0.10		20.2		6.78		5.60	
Census interval¶	5.68	5.90**	3.42	8.93**	4.69	5.83**	3.73	3.21**	1.27	2.15
Treatment × interval	0.81	0.84	0.27	0.70	0.80	0.99	0.45	0.39	0.39	0.66
Error	0.96		0.38		0.80		1.16		0.59	

	Dipteryx		*Doliocarpus*				*Guarea*			
	1987‖		1986‖		1987§		1986†		1987‡	
Source of variation	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Treatment	18.6	4.83	1.20	0.29	1.91	0.75	34.1	52.2*	15.4	59.5*
Error	3.85		4.21		2.56		0.65		0.26	
Census interval	8.39	24.5**	2.06	4.23*	1.16	5.07**	1.73	2.74**	1.44	3.80**
Treatment × interval	1.03	3.02*	0.99	2.04	0.69	3.02**	0.39	0.61	0.49	1.31
Error	0.34		0.49		0.23		0.63		0.38	

	Guatteria		*Heisteria*		*Jacaranda*		*Licania*			
	1987‡		1987‡		1986§		1986‖		1987§	
Source of variation	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Treatment	0.88	0.05	1.99	0.16	2.71	0.32	18.1	5.50	15.1	2.04
Error	16.7		12.2		8.50		3.29		7.40	
Census interval	0.29	1.03	1.69	1.68	0.82	2.88	6.09	6.47**	3.24	2.41
Treatment × interval	0.30	1.05	0.68	0.68	0.11	0.38	1.67	1.78	0.91	0.68
Error	0.28		1.00		0.29		0.94		1.34	

	Maripa				*Pouteria*			
	1986‡		1987‡		1986‡		1987‖	
Source of variation	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Treatment	14.5	13.4	5.74	1.02	2.75	0.18	10.3	3.45
Error	1.09		5.61		15.6		2.98	
Census interval	0.84	1.64	0.55	1.03	0.74	0.69	1.46	2.00
Treatment × interval	0.81	1.59	0.56	1.05	1.20	1.13	0.83	1.14
Error	0.51		0.55		1.07		0.73	

	Prionostemma				*Protium*				*Quararibea*	
	1986‡		1987†		1986‖		1987‡		1987†	
Source of variation	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Treatment	0.74	0.03	0.80	0.03	0.29	0.03	0.51	0.08	17.3	0.96
Error	21.8		28.6		8.47		6.74		18.1	
Census interval	1.45	2.04*	1.66	2.49**	2.09	1.66	1.76	1.61	3.58	5.51**
Treatment × interval	1.42	2.00*	0.85	1.27	1.02	0.81	1.89	1.73	0.79	1.21
Error	0.71		0.67		1.26		1.10		0.65	

	Tetragastris				*Trattinnickia*		*Trichilia*			
	1986†		1987†		1987‡		1986†		1987‡	
Source of variation	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Treatment	71.5	8.26	51.1	50.7	4.84	0.26	31.2	6.80	37.9	15.5
Error	8.66		1.01		18.9		4.59		2.45	
Census interval	1.13	2.28	1.19	3.34	4.10	2.06*	1.28	2.50*	1.54	3.71**
Treatment × interval	0.55	1.11	0.44	1.23	1.22	0.61	0.38	0.75	0.31	0.74
Error	0.49		0.36		2.00		0.51		0.42	

TABLE 2. Continued.

	Virola				Unknown	
	1986†		1987‡		1987§	
Source of variation	MS	*F*	MS	*F*	MS	*F*
Treatment	14.3	3.43	2.28	0.07	1.50	0.50
Error	4.17		32.1		2.99	
Census interval	1.61	1.07	2.07	1.90	4.04	8.80**
Treatment × interval	1.19	0.79	0.83	0.77	0.55	1.21
Error	1.50		1.09		0.46	

* $P < .05$; ** $P < .01$.

†, ‡, §, ‖ Degrees of freedom for interval main effect and for treatment × interval interaction are 25, 50; 16, 32; 12, 24; and 9, 18, respectively, before the Huynh-Feldt adjustment.

¶ Period of the year.

(Borchert 1978). Between 1971 and 1979 the timing of the community-wide peak of leaf fall on BCI closely matched year-to-year variation in the timing of the onset of the dry season (D. Windsor and S. J. Wright, *personal observation*). This implicates physical factors that change with the onset of the dry season, and suggests that photoperiod and leaf age, which are unaffected by variation in the onset of the dry season, are relatively unimportant.

The high evaporative demand created by dry-season atmospheric conditions is a possible proximal cue for leaf fall. Humidity declines and windspeed and incident radiation increase sharply at the beginning of the dry season on BCI (Becker 1987, Windsor, *in press*). This will increase the vapor pressure deficit between the atmosphere and the leaf mesophyll. Increasing vapor pressure deficits lead to stomatal closure (Schulze 1986), and this effect may be particularly strong in tropical plants (e.g., Whitehead et al. 1981, Mooney et al. 1983). Carbon isotope ratios of leaves that had only experienced dry-season conditions differed between control and manipulated plots for understory saplings but not for canopy trees of the same species (Sternberg et al. 1989). This result suggests that the manipulation affected stomatal behavior in the understory where humidity is also affected but not in the canopy where humidity is unaffected. If stomates closed in response to increasing vapor pressure deficits and remained closed regardless of soil moisture availability and tissue water potentials, then leaf damage and abscission might follow. Possible causes of leaf damage after stomatal closure include photoinhibition and increases in leaf temperature as a result of decreases in transpiration, evaporative cooling, and leaf internal carbon dioxide concentrations. For evergreens, older leaves with diminished capacities to prevent water loss (Reich and Borchert 1988) may be abscised as a consequence of increasing vapor pressure deficits while younger leaves are retained, leading to an improvement in overall water status (Addicott 1982). Valerie Kapos (*personal communication*) has independently arrived at the hypothesis that atmospheric conditions cue leaf fall for trees in the Venezuelan llanos.

Finally there is no reason to presuppose that any single environmental factor controls the timing of leaf fall for large numbers of tropical plants. Tropical floras include a multitude of species that inhabit a wide range of microenvironments and present a diversity of responses to variation in the physical environment (Robichaux et al. 1986, Rundel and Becker 1987, Reich and Borchert 1988). Moreover, leaf fall is the final step in a complex process, and environmental factors may influence this process in many different ways (Hopkins 1966, Addicott 1982). We have shown that soil moisture availability and realized plant water status affect leaf fall for a very few species in one tropical forest. Further experimentation will be necessary to elucidate the effects of moisture stress in other tropical forests and to test the hypothesis that vapor pressure deficits cue leaf fall.

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