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TROPICAL FOREST LITTER DYNAMICS AND DRY SEASON IRRIGATION ON BARRO COLORADO ISLAND, PANAMA[1]

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Abstract. Moisture seasonality may control forest floor decomposition rates in tropical forests. We used a mass balance model and 5 yr (December 1986 through December 1990) of weekly litterfall and monthly forest floor mass measurements from control and dry season irrigated plots to test this hypothesis on Barro Colorado Island, Panama. Litterfall and forest floor mass were greater in the dry season than in the wet season. Irrigation affected neither the timing nor the quantity of litterfall. In contrast, dry season irrigation reduced forest floor mass throughout the year, not just during the dry season. Forest floor decomposition during the dry season was enhanced by irrigation. During the dry season, net decomposition (in grams per square metre per day) and exponential decay coefficients (per day) averaged 48 and 42% greater, respectively, in irrigated plots than in control plots. As a consequence, seasonal differences in decomposition rates were more pronounced in the control plots than in the irrigated plots. Net decomposition rates, for example, averaged 105 and 22% greater during the wet season than during the dry season on control and irrigated plots, respectively. Net decomposition was positively correlated with rainfall in the control plots, but not in the irrigated plots. These results support the hypothesis that moisture seasonality controls forest floor decomposition in tropical moist forests.

Key words: forest floor; irrigation; litter decomposition; litterfall; tropical moist forest.

INTRODUCTION

Leaf litter deposition and decomposition are critical pathways of organic matter and nutrient flux in tropical forest systems (cf. Golley et al. 1975, Swift et al. 1979, Sanchez et al. 1982, Anderson and Swift 1983, Golley 1983, Proctor 1983, 1984, Swift and Anderson 1989). In tropical forests with alternating dry and wet seasons, litter often exhibits a distinct seasonality. Although in some forests peak litterfall occurs during the wet season, more commonly maximum litterfall occurs during the dry season (cf. Wright and Cornejo 1990, Herbohn and Congdon 1993). In forests with pulsed dry season litterfall, an inhibition of litter decomposition, presumably because of moisture stress, results in a transient accumulation of litter on the forest floor during the dry season (Madge 1965, Golley et al. 1975, Swift and Anderson 1989). At the onset of the wet season, accelerated decomposition in the accumulated litter layer may result in an ephemeral enhancement of soil nutrient availability (cf. Swift et al. 1981, Swift and Anderson 1989, Lodge et al. 1994). Seasonal changes in litterfall and in forest floor litter mass have been well documented in tropical forests with marked wet and dry seasons (Haines and Foster 1977, Leigh and Smythe 1978, Martinez-Yrizou and Sarukhan 1990), but there is less evidence for an associated seasonality in litter decomposition rates (Swift et al. 1979, Anderson and Swift 1983, Swift and Anderson 1989). Therefore, over a 5-yr period, we collected litterfall and forest floor litter in a tropical moist forest on Barro Colorado Island (BCI), Panama. A mass balance approach was employed to test the hypothesis that litter decomposition on the forest floor exhibits seasonal variation, being substantially lower in the dry season than in the wet season. Furthermore, experimental dry season irrigation allowed us to test the hypothesis that litter decomposition rates are controlled by seasonality in moisture availability.

STUDY SITE

BCI (9°09′ N, 79°51′ W) receives ≈95% of its annual average of 2600 mm of rainfall during the 8-mo wet season, extending approximately from mid-April through mid-December (Fig. 1). During the remaining 4-mo dry season, monthly rainfall averages <60 mm (Windsor 1990). This precipitation regime supports lowland tropical moist forest vegetation (Holdridge and Budowski 1956) with both dry season deciduous and evergreen broadleaf species in the forest canopy. About 12% of the tree species shed their leaves at some time during the dry season (Croat 1978), and as a result litterfall deposition peaks early in the dry season and generally remains high throughout the dry season (Haines and Foster 1977, Leigh and Smythe 1978). Detailed descriptions of the geology, climate, and vegetation of BCI can be found in Woodring (1958),

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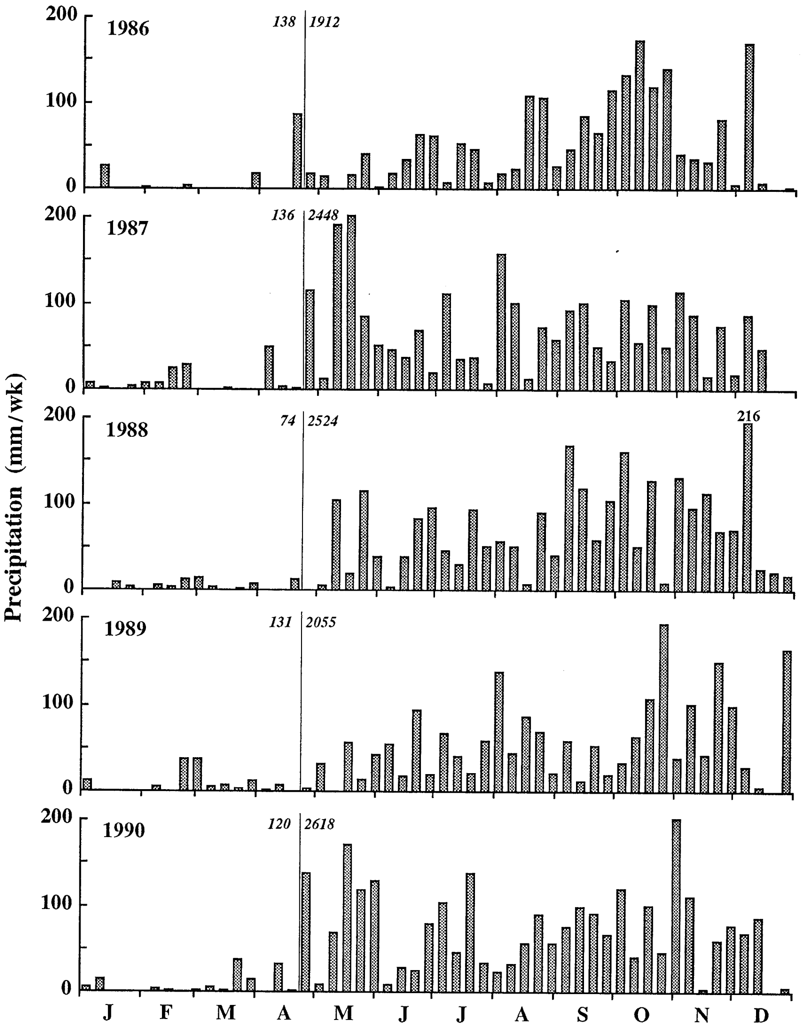

FIG. 1. Total weekly rainfall on BCI over the 5-yr duration of the study. The vertical line in each panel denotes the separation between the dry season and the wet season. Italicized values on either side of the vertical line are total dry season and wet season rainfall (millimetres).

Knight (1975), Croat (1978), Leigh et al. (1982), and Windsor (1990).

Forest irrigation

The main study site was located on Poacher's Peninsula, the southernmost extension of BCI. The soils are Alfisols and the forest in this area has been relatively undisturbed by human activity for >500 yr (Piperno 1990). Four 2.25-ha plots were established, two to serve as controls and two to be manipulated by dry season irrigation. Irrigation was accomplished using 160 sprinklers, elevated 1.8 m above the ground, and placed 15.3 m apart in an hexagonal array. The irrigation schedule was continuously adjusted to maintain soil water potential near −0.03 MPa (cf. Wright 1991). During a typical dry season week, irrigation water was applied for 3 h/d on each of five successive days, so that each plot typically received ≈675 Mg of water per week (equivalent of 30 mm/wk of rainfall). Irrigation water was taken from Gatun Lake, in which nutrient concentrations are typically lower than in rainwater collected on BCI (Gonzalez et al. 1975).

METHODS

Litterfall and forest floor litter collection

Litterfall and forest floor mass were collected over a 5-yr period from December 1986 through December 1990. Litterfall was collected weekly in 40 screened traps (10 traps in each plot), each with a surface area of 0.25 m^2, elevated above the forest floor surface (see Wright and Cornejo 1990). Forest floor litter was collected monthly within 2 m of each litterfall trap from a randomly located 29.5 × 29.5 cm area which was marked and excluded from future forest floor collections. Pieces of litterfall or forest floor litter with a diameter ≥2 cm were excluded from all collections. The boundary between the organic forest floor layer and the underlying mineral soil was consistently distinct. Collected litterfall or forest floor litter samples were returned to the laboratory, oven-dried at 60°C, and weighed. In addition, for all forest floor litter samples collected between July 1986 and August 1988, 0.5 g subsamples were combusted at 800°C in a muffle furnace; organic matter was calculated as loss on ignition.

Quantification of litter decomposition

In using a mass balance approach to estimate decomposition rates, it was assumed that: (1) litterfall began to decompose as soon as it landed in one of the raised screen traps, (2) litterfall in the traps decomposed at the same rate as litterfall on the ground, (3) the rate of litterfall deposition was equal for each of the 7 d of the interval between litterfall collection dates, and (4) litter decomposition follows a simple exponential decay function.

Daily litterfall was not calculated by dividing the mass of the collected litterfall by 7, because this approach fails to take into consideration that litterfall within the trap undergoes decomposition (cf. Kirita and Hozumi 1969). Thus, daily litterfall was estimated as

$$\mathrm{LFD} = \frac{\mathrm{LFW}}{\sum_{i=1}^{7} e^{-ki}}, \tag{1}$$

where LFW is the weekly litterfall rate in grams per square metre per week (dry mass of the litter collected in the litterfall traps each week), LFD is the daily litterfall rate in grams per square metre per day (assuming that equal amounts of litterfall were deposited on each day of the week), k is the exponential decay constant (d^{-1}), and i indexes the seven days of a week.

Decomposition rates (k values) were estimated by assuming that the mass of litter on the forest floor (FFLM) at month x is equal to the mass of litter on the forest floor at month $x - 1$ adjusted for 28 d of decomposition at a rate of k, plus each day's litterfall inputs during the month (Eq. 1) adjusted for the number of days within the month for which that litterfall decomposed at a rate of k, or

$$\mathrm{FFLM}_{\mathrm{month}\,x} = \mathrm{FFLM}_{\mathrm{month}\,x-1} \times e^{-28k} + \sum_{w=1}^{4} \sum_{i=1}^{7} \mathrm{LFD}_w \times e^{-k\{29-[7\times(w-1)+i]\}}, \tag{2}$$

where w indexes the 4 wk of each month and LFD_w denotes the daily litterfall for each of the 4 wk of the month. This equation was fit to the weekly litterfall and monthly forest floor littermass data using nonlinear least squares regression (PROC NLIN; SAS 1989) with the stipulation that estimated k values could not be <0.

Net decomposition during a 28-d interval (NETDEC; grams per square metre per day) was estimated as the forest floor mass at the beginning of the 28-d sampling interval plus litterfall inputs during the interval minus the forest floor littermass at the end of the 28-d interval:

$$\mathrm{NETDEC} = \left(\mathrm{FFLM}_{\mathrm{month}\,x} + \sum_{j=1}^{28} \mathrm{LFD}_j - \mathrm{FFLM}_{\mathrm{month}\,x+1}\right) \Big/ 28, \tag{3}$$

where j indexes the 28 d of the interval. Net decomposition was estimated using k values calculated separately for each plot and litterfall and forest floor mass values for each of the 40 sampling locations.

Statistical analysis

Weekly litterfall, monthly forest floor littermass, and daily net decomposition data were analyzed using repeated measures analysis of variance. A repeated measures design is appropriate because litterfall and forest floor littermass were collected from the same 40 locations (10 in each plot) throughout the duration of the study. The analyses were performed with between-subjects effects of irrigation (control vs. irrigated plots) and plot nested within the irrigation effect (two control and two irrigated plots), within-subjects effects of year and season (dry season vs. wet season), and all possible interactions. The significance of each term in the analysis was evaluated using the multivariate Wilks' lambda test (cf. PROC GLM; SAS 1989). To facilitate statistical analysis, we somewhat artificially set the respective durations of the dry season and wet season to be the same in each of the five years of the study. This delimitation is consistent with the experimental design in that the dry season closely corresponded to the period of experimental irrigation.

RESULTS

Litterfall

Total litterfall averaged 1239 $\mathrm{g\cdot m^{-2}\cdot yr^{-1}}$ (Table 1; Fig. 2). Litterfall was greater in the dry season than in the wet season, but the magnitude of the difference between wet season and dry season litterfall was not consistent across all years (significant year by season interaction in the ANOVA; Table 2). Weekly litterfall rates ranged from 1.4 to 1.8 times greater during the dry season than during the wet season. Dry season irrigation did not affect litterfall (non-significant irrigation effect and season by irrigation interaction; Table 2).

Forest floor litter

Forest floor littermass was consistently lower in the irrigated plots than in the control plots (Table 1, Fig. 3; significant irrigation effect, but no significant interactions with irrigation in Table 2). Superimposed on the irrigation effect, forest floor littermass consistently was greater during the dry season than during the wet season, but the magnitude of the season effect was not consistent across all years (Fig. 3; significant year by

TABLE 1. Tropical forest litterfall and forest floor littermass during the dry season and the wet season in the control and irrigated plots for each of the five years of the study.

Year	Treatment	Total annual litterfall ($g \cdot m^{-2} \cdot yr^{-1}$)	Mean litterfall ± 1 SE ($g \cdot m^{-2} \cdot wk^{-1}$)		Mean forest floor mass ± 1 SE (g/m^2)	
			Dry season	Wet season	Dry season	Wet season
1986	Control	1420	33.7 ± 1.4	24.2 ± 1.2	914 ± 48	892 ± 45
	Irrigated	1380	33.2 ± 1.4	23.3 ± 1.0	840 ± 44	723 ± 29
1987	Control	1411	35.9 ± 1.4	22.9 ± 1.0	1005 ± 55	729 ± 23
	Irrigated	1315	32.9 ± 1.1	21.6 ± 0.6	743 ± 31	581 ± 19
1988	Control	1210	32.3 ± 1.7	18.9 ± 0.9	877 ± 28	608 ± 21
	Irrigated	1227	34.2 ± 1.2	18.4 ± 0.6	686 ± 28	431 ± 13
1989	Control	1172	33.7 ± 1.6	17.1 ± 1.1	870 ± 44	710 ± 24
	Irrigated	1229	33.1 ± 1.3	19.0 ± 1.1	663 ± 39	562 ± 19
1990	Control	1016	26.1 ± 1.2	16.4 ± 0.7	676 ± 28	592 ± 25
	Irrigated	1010	26.7 ± 1.2	15.9 ± 0.6	480 ± 21	480 ± 29

season interaction in Table 2). Mean dry season forest floor littermass, averaged across control and irrigated plots, was 1.5 times greater than mean wet season forest floor littermass in 1988, but only 1.1 times greater than mean wet season forest floor littermass in 1986 and 1990.

Litter decomposition

The exponential decay model produced estimates of k that ranged from 0 to 0.0347 d^{-1} (0 to 12.7 yr^{-1}) and averaged (over all 5 yr and over control and irrigated plots) 0.0089 d^{-1} (3.2 yr^{-1}; Fig. 4). Expressed on an annual basis and averaged over the 5 yr, mean dry season k values were 2.40 and 3.41 yr^{-1} for the control and irrigated plots, respectively, and mean wet season k values were 2.96 and 3.68 yr^{-1} for the control and irrigated plots, respectively (Table 3). Based on these overall averages, k values in irrigated plots were 1.42 times those of control plots during the dry season, but only 1.24 times those of control plots during the wet season. Moreover, k values in the wet season were 1.23 times greater than those in the dry season for control plots, but only 1.07 times greater than those for the dry season in irrigated plots.

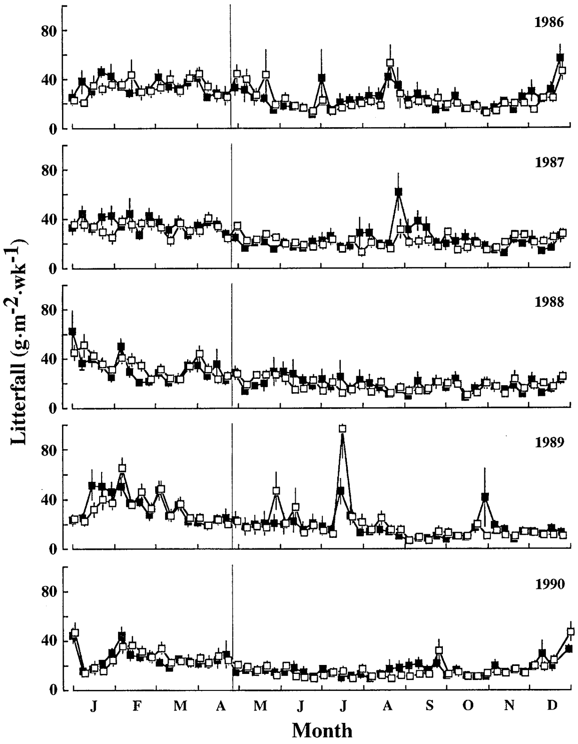

FIG. 2. Litterfall (means ± 1 SE; n = 20) for the control (-■-) and irrigated (-□-) plots. The vertical line in each panel denotes the beginning of the wet season, which extends through the last collection in December of each year. The peak in litterfall recorded in July 1989 was associated with an unusually severe windstorm.

"Litter turnover coefficients," k_L, defined as the total annual litterfall divided by the mean forest floor littermass, ranged from 1.53 to 2.41 yr^{-1} (Table 3), corresponding to mean residence times ($1/k_L$) ranging from 151 to 239 d. Averaged over the 5-yr period, annual k_L values were 27% greater for the irrigated plots than for the control plots. The net effect of dry season irrigation was to reduce the mean residence time of leaf litter on the forest floor from 222 d in control to 174 in irrigated plots (averaged across all 5 yr).

Regarding net decomposition (grams per square metre per day; Fig. 5), the most interesting statistical result is the nearly significant season by irrigation effect (P = 0.0514, Table 2). Averaged across all years (which is reasonable given the nonsignificant year by season by irrigation effect), mean dry season net decomposition values were 1.85 and 2.73 $g \cdot m^{-2} \cdot d^{-1}$ for the control and irrigated plots, respectively, and mean wet season net decomposition values were 3.80 and 3.35 $g \cdot m^{-2} \cdot d^{-1}$ for the control and irrigated plots, respectively (Table 3). Based on these overall averages, net decomposition values in irrigated plots were 1.48 times those of control plots during the dry season, but only 0.88 times those of control plots during the wet season. Moreover, net decomposition values in the wet season were 2.05 times greater than those in the dry season for control plots, but only 1.23 times greater than those for the dry season in irrigated plots.

TABLE 2. Results of repeated measures analyses of variance conducted separately on the weekly litterfall, monthly forest floor mass, and net daily decomposition data. All statistical tests were conducted using the multivariate Wilks' lambda test. Test results (the df column gives the numerator and denominator degrees of freedom), are given for each of the between-subjects and within-subjects tests.

		Litterfall			Forest floor mass			Net decomposition		
	df	Test statistic	*F*	*P*	Test statistic	*F*	*P*	Test statistic	*F*	*P*
Between-subjects effects										
Irrigation	1, 36	0.9996	0.0132	0.9090	0.7827	9.9970	0.0032	0.9997	0.0124	0.9119
Plot(irrigation)	2, 36	1.0000	0.0001	0.9999	0.9870	0.2363	0.7908	0.9515	0.9183	0.4083
Within-subjects effects										
Year	4, 33	0.4392	10.5353	0.0001	0.2764	21.6006	0.0001	0.5045	8.1040	0.0001
Year × irrigation	4, 33	0.9411	0.5163	0.7242	0.9195	0.7227	0.5827	0.9758	0.2043	0.9342
Year × plot(irrigation)	8, 66	0.9068	0.4137	0.9088	0.7465	1.3106	0.2538	0.8925	0.4826	0.8643
Season	1, 36	0.2828	91.3194	0.0001	0.6282	21.3091	0.0001	0.7009	15.3600	0.0004
Season × irrigation	1, 36	1.0000	0.0012	0.9725	0.9991	0.0310	0.8612	0.8986	4.0601	0.0514
Season × plot(irrigation)	2, 36	0.9705	0.5467	0.5836	0.8524	3.1167	0.0564	0.9817	0.3346	0.7178
Year × season	4, 33	0.6785	3.9096	0.0105	0.2570	23.8460	0.0001	0.5254	7.4512	0.0002
Year × season × irrigation	4, 33	0.8822	1.1012	0.3724	0.9645	0.3037	0.8734	0.8271	1.7245	0.1681
Year × season × plot(irrigation)	8, 66	0.7027	1.5920	0.1442	0.6835	1.7293	0.1080	0.7361	1.3661	0.2278

DISCUSSION

Litterfall, forest floor mass, and estimates of decomposition

Total annual litterfall values (Table 1) are similar to those previously reported for forests in Panama (Golley et al. 1975, Leigh 1975, Haines and Foster 1977, Leigh and Smythe 1978) and are near the upper end of the ranges previously reported for semideciduous tropical forests in seasonally wet climates (Proctor 1984, Heaney and Proctor 1989, Scott et al. 1992, Sampaio et al. 1993). Furthermore, the magnitude of interannual variability in litterfall (38% greater in 1986 than in 1990) is similar to that reported for other tropical forests (e.g., Blasco and Tassey 1975, Leigh and Smythe 1978, Lim 1978, Jordan and Murphy 1982, Martinez-Yrizou and Sarukhan 1990, Herbohn and Congdon 1993). Experimental irrigation did not affect the timing or quantity of litterfall. Similarly, timing of litterfall was unaffected by irrigation for 25 of 29 individual tree and liana species studied during the first 2 yr of the irrigation study (Wright and Cornejo 1990). Dry-season irrigation did improve the leaf water status of many tree and liana species (Wright and Cornejo 1990), but similar quantities of litterfall in control and irrigated plots suggest that this improved water status was not manifested as increased leaf production. Forest floor littermass values (Table 1) are within the ranges previously reported for semideciduous tropical forests in seasonally wet climates (cf. Anderson and Swift 1983, Proctor et al. 1983, Heaney and Proctor 1989, Lugo et al. 1990, Scott et al. 1992).

Our overall average k value is equivalent to 3.2 yr^{-1} (cf. Table 3). For tropical forests, k values for leaf litter decomposition are typically >1.0 yr^{-1} (Olson 1963, Anderson and Swift 1983). Using Brown and Lugo's (1982) data for tropical moist and wet forests, Sampaio et al. (1993) estimated k values ranging from 0.62 to 3.3 yr^{-1}. Our overall average litter turnover coefficient, k_L, of 1.87 yr^{-1} is within the range of values previously reported for other tropical moist forests (see Anderson

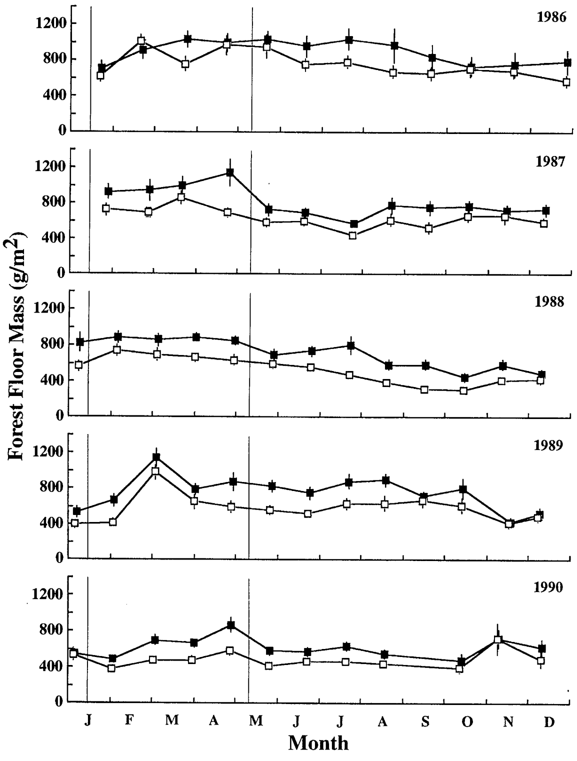

FIG. 3. Forest floor littermass (means ± 1 SE; n = 20) for the control (-■-) and irrigated (-□-) plots. The vertical lines in each panel denote the beginning of the dry season (January) and the beginning of the wet season (May) for each of the five years.

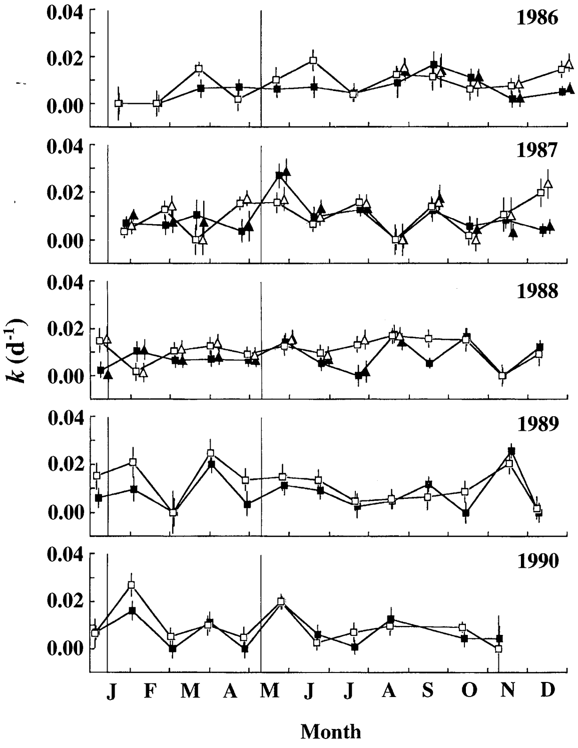

FIG. 4. Exponential decay k values (estimates ± asymptotic standard errors; n = 20) for the control (-■-) and irrigated (-□-) plots. The vertical lines in each panel denote the beginning of the dry season (January) and the beginning of the wet season (May) for each of the five years. From August 1986 through August 1988, exponential decay k values (estimates ± asymptotic standard errors; n = 20) calculated using forest floor organic matter masses (based on ash-corrected dry mass values) and litterfall organic matter masses (assuming that litterfall was 95% organic matter) are shown for the control (-▲-) and irrigated (-△-) plots.

and Swift 1983, Heaney and Proctor 1989, Swift and Anderson 1989, Scott et al. 1992).

Using the mass balance approach, we estimated litter decomposition rates on a monthly basis in control and dry season irrigated plots over a 5-yr period. Consistency of our results with those obtained using more traditional methodologies supports the validity of the mass balance approach for quantitatively evaluating temporal dynamics in litter decomposition in tropical forests.

Forest floor litter dynamics on BCI

The patterns obtained for k values, litter turnover coefficients, and net decomposition values lead to the same conclusion: the overall effect of dry season irrigation was to enhance the rate of litter decomposition during the dry season, thereby diminishing the normal (control plot) seasonal differences in decomposition rate and leading to a more rapid annual turnover of forest floor litter in irrigated plots than in control plots. It should be noted that forest floor littermass was lower in the irrigated plots than in the control plots throughout each year, not just during the dry seasons.

Both our study and a concurrent litterbag study of leaf decomposition conducted during the 1987 dry season (Cornejo et al. 1994) concluded that irrigation enhances decomposition during the dry season. Even in the absence of irrigation, however, considerable dry season decomposition occurred. In control plots, 16–30% of the total annual decomposition took place during the dry seasons of 1987–1990. During the mild El Niño year of 1986, the dry season in central Panama was especially severe (cf. Fig. 1) and dry season decomposition was minimal in both control and irrigated plots (cf. Table 3).

Nagy and Macauley (1982) concluded that substantial leaf litter decomposition may occur at relative humidities and moisture contents within the litter layer as low as 32 and 5%, respectively. It does occasionally rain during the dry season (Fig. 1), but these sporadic, low-intensity rain events apparently do not affect decomposition. For the control plots neither the k values nor the net decomposition values were correlated with 28-d rainfall totals recorded during the dry season (Table 4). Nonetheless, for the control plots, significant correlations between k values and rainfall, calculated

TABLE 3. Mean k values and daily net decomposition for the dry and wet seasons in the control and irrigated plots, and k_L values for each of the five years of the study.

		Mean k (d^{-1})			Mean daily net decomposition ± 1 SE (g·m^{-2}·d^{-1})	
Year	Treatment	Dry season	Wet season	k_L (yr^{-1})	Dry season	Wet season
1986	Control	0.00334	0.00751	1.58	0.14 ± 1.55	4.36 ± 1.38
	Irrigated	0.00409	0.01039	1.81	−0.56 ± 1.81	5.00 ± 1.14
1987	Control	0.00679	0.00904	1.73	2.37 ± 2.15	4.48 ± 1.06
	Irrigated	0.00776	0.01093	2.08	3.07 ± 1.54	3.86 ± 0.94
1988	Control	0.00762	0.00851	1.76	3.99 ± 1.38	4.05 ± 0.72
	Irrigated	0.00844	0.01192	2.41	4.16 ± 1.18	3.86 ± 0.58
1989	Control	0.00832	0.00804	1.53	1.84 ± 2.04	3.32 ± 0.92
	Irrigated	0.01476	0.00912	2.07	3.28 ± 1.98	3.05 ± 0.79
1990	Control	0.00685	0.00791	1.63	0.93 ± 1.17	2.79 ± 0.96
	Irrigated	0.01166	0.00806	2.10	3.70 ± 1.02	1.00 ± 1.12

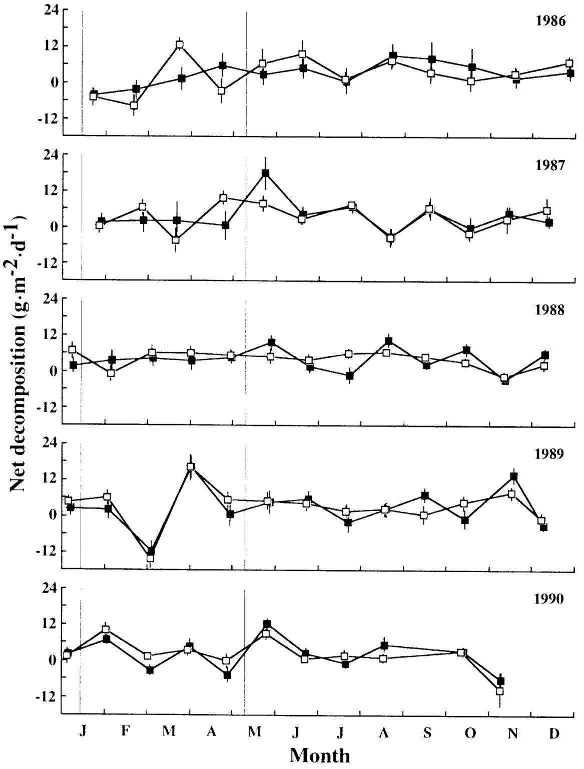

FIG. 5. Net decomposition values (means ± standard errors; n = 20) for the control (-■-) and irrigated (-□-) plots; negative values indicate that the measured increase in forest floor mass during a sampling interval exceeded the measured input of litter via litterfall. The vertical lines in each panel denote the beginning of the dry season (January) and the beginning of the wet season (May) for each of the five years.

TABLE 4. Pearson product moment correlations between 28-d rainfall totals and estimated k values or mean net decomposition values for control and irrigated plots. Correlations were calculated separately regardless of season (n = 55), for the dry season alone (n = 20) and for the wet season alone (n = 35).

	Season		
	Both	Dry	Wet
k value (d^{-1})			
Control plots			
r*	0.2596	−0.2728	0.3248
P	0.0217	0.1223	0.0191
Irrigated plots			
r*	−0.0013	−0.2074	−0.0463
P	0.4959	0.1902	0.3869
Mean net decomposition (g·m^{-2}·d^{-1})			
Control plots			
r*	0.2430	−0.2585	0.2362
P	0.0296	0.1356	0.0685
Irrigated plots			
r*	−0.0450	−0.2249	−0.1618
P	0.3653	0.1702	0.1561

* Correlation coefficients (r) are given along with P values for a one-sided test of the hypothesis that higher rainfall should be associated with higher measures of decomposition. For the irrigated plots, correlations also were calculated with 30 mm/wk added to the measured rainfall during the dry season, accounting for the added irrigation water. This correction did not affect the correlation coefficients calculated separately for the dry or wet seasons, and had only a minimal effect on the correlations calculated regardless of season, changing the P values by <0.03 and therefore not affecting the interpretations.

either regardless of season or for the wet season alone, and significant correlations between net decomposition and rainfall regardless of season, suggest that seasonality in rainfall drives seasonality in decomposition. In contrast, for the irrigated plots, none of the correlations between decomposition and rainfall were significant (Table 4). Thus, the effect of dry season irrigation was to remove the normal seasonal dependence of decomposition on rainfall.

We note that the nature and magnitude of wet season vs. dry season differences in litterfall, forest floor littermass, k values, and net decomposition values were considerably different from year to year (significant year by season interaction in all three ANOVAs in Table 2). Statistical analyses allowed interpretations that substantiated our hypotheses of seasonality of litter decomposition and the influence of moisture availability, but had this study been limited to only a single year, the interpretations might well have been different.

We feel compelled to comment that in our study plots the accumulation of leaf litter on the forest floor during the dry season appears much more dramatic by visual perception in the field than by inspection of the data obtained in this study. During the dry season, the forest floor is completely covered with what appears to be several layers of dry, relatively undecomposed leaf litter. In contrast, at the end of the wet season the litter layer is discontinuous. Patches of exposed mineral soil are common, and the leaf litter that is found is wet and appears to be fairly highly decomposed. This difference between perception and the actual forest floor mass data may be attributable to several factors. First, compaction of wet leaves as the wet season progresses may create a visual impression of mass loss that exceeds the true mass loss via decomposition. Second, leaf litter on the forest floor during the wet season may be denser than leaf litter on the forest floor during the dry season. Species with high specific leaf area (in square centimetres per gram) decompose more rapidly that those with a low specific leaf area (Cornejo et al. 1994). Seasonal changes in the overall mean specific leaf area of forest floor litter could contribute to a disparity between visually perceived changes in the quantity of litter on the forest floor and actual mass changes. Third, high water availability during the wet season or in irrigated plots during the dry season not only could stimulate microbially mediated organic matter mineralization, but also could result in contamination of the leaf litter with mineral soil particles splashed onto the leaf surfaces by the physical impaction of raindrops on soil. From July 1986 through August 1988, organic matter

TABLE 5. Results of repeated measures analysis of variance conducted on percent organic matter of the collected forest floor material. All statistical tests were conducted using the multivariate Wilks' lambda test. Because percent organic matter was determined only for forest floor samples collected between July 1986 and August 1988, we did not include the within-subjects effect of year in this analysis.

	df	Test statistic	*F*	*P*
Between-subjects effects				
Irrigation	1, 36	0.9991	0.0313	0.8607
Plot(irrigation)	2, 36	0.9277	1.4038	0.2588
Within-subjects effects				
Season	1, 36	0.4205	49.6094	0.0001
Season × irrigation	1, 36	0.8711	5.3265	0.0269
Season × plot(irrigation)	2, 36	0.8550	3.0529	0.0596

concentration of the forest floor litter revealed a significant season by irrigation interaction (Table 5), with organic matter concentrations averaging 84 and 80% in the dry and wet seasons, respectively, in the control plots and averaging 83 and 81%, respectively, in the irrigated plots. Thus, seasonal variation in ash concentrations may have contributed to the disparity between visually perceived vs. measured changes in the quantity of litter on the forest floor. Nonetheless, the temporal patterns for k values estimated using organic matter mass rather than dry mass data were very similar to the temporal patterns for k estimated from dry mass data (Fig. 4). Therefore, we conclude that our interpretations throughout this paper are not substantially confounded by using dry mass data, rather than organic matter mass data.

The application of a mass-balance approach with spatially and temporally intensive measurement of litterfall and forest floor littermass, coupled with experimental dry season irrigation over a 5-yr period, support the hypothesis that in the tropical moist forests of BCI, seasonality in moisture availability drives seasonality in litter decomposition on the forest floor. The notion that forest floor litter dynamics and soil nutrient availability may be linked in tropical forest ecosystems (e.g., Swift et al. 1981, Swift and Anderson 1989, Lodge et al. 1994), although conceptually compelling, is not strongly supported by available data. In the litterbag study conducted by Cornejo et al. (1994) during the 1987 dry season, irrigation resulted in an enhanced release of potassium from leaf litter of all species, but the effects of irrigation on the release of other nutrients were inconsistent among species. Within the litter layer, nutrient dynamics and organic matter dynamics appear to be decoupled, so the seasonal patterns and the effect of dry-season irrigation on decomposition documented here provide no direct insights into seasonal patterns of nutrient flux through the forest floor litter layer. However, the mass balance approach could be extended by determining nutrient concentrations in litterfall and the forest floor litter to estimate net mineralization/immobilization of nutrients within the litter layer. Such an analysis may be fruitful in unraveling linkages between litter dynamics and soil nutrient availability.

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