

Effects of seasonality, litter removal and dry-season irrigation on litterfall quantity and quality in eastern Amazonian forest regrowth, Brazil

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Abstract: Litterfall quantity and quality may respond to alterations in resource availability expected with ongoing land-use and climate changes. Here, we quantify the effects of altered resource availability on non-woody litterfall quantity and quality (nitrogen and phosphorus concentrations) in eastern Amazonian forest regrowth (Brazil) through two multi-year experimental manipulations: (1) daily irrigation (5 mm d⁻¹) during the dry season; and (2) fortnightly litter removal. Consistent with other tropical forest data litterfall exhibited seasonal patterns, increasing with the onset of the dry season and declining with the onset of the rainy season. Irrigation did not affect litterfall mass and had little impact on nitrogen (N) or phosphorus (P) concentrations and return, except for decreasing litter P concentration at the end of two irrigation periods. Litter removal did not alter litterfall mass or P concentration, but progressively reduced litterfall N during the course of the experiment. Overall, these results suggest significant resistance to altered resource availability within the bounds of our experimental treatments; our findings may help to constrain carbon and nutrient cycling predictions for tropical forests in response to land-use and climate changes.

Key Words: dry-season irrigation, litter removal, nitrogen, non-woody litterfall, phosphorus, resource manipulation, secondary forest

INTRODUCTION

Litterfall represents the major process of nutrient transfer from above-ground vegetation to soils (Vitousek & Sanford 1986), and fine litterfall comprises a significant fraction of above-ground net primary productivity in forests (Clark *et al.* 2001a). Litter nitrogen and phosphorus cycling are of particular importance since these nutrients usually are the most limiting for tropical forest productivity (Vitousek 1984). Low phosphorus availability is likely a common constraint for tropical forest regrowth. Nitrogen limitation appears significant for forests re-establishing after several episodes of slash-and-burn, which lead to substantial losses of nitrogen

through volatilization (Davidson *et al.* 2004, Gehring *et al.* 1999).

Litterfall rates, dynamics and quality have been shown to be associated with soil moisture and nutrient availability. In seasonal tropical forests, litterfall usually peaks during the dry season (Wieder & Wright 1995), but a direct effect of soil moisture availability on litterfall quantity and timing has not been demonstrated (Cavelier *et al.* 1999, Wieder & Wright 1995). However leaf litterfall quantity may be negatively related to rainfall in drier seasonal forests (Whigham *et al.* 1990). Litterfall quality may also vary according to rainfall seasonality, but litterfall nutrient concentrations were not affected during a 5-y irrigation experiment in Panama (Yavitt *et al.* 2004). Litterfall quantity has been shown to be limited by nutrient availability (Vitousek 1984), with fertilization resulting in higher litterfall rates in a dry tropical forest in Mexico (Campo & Vázquez-Yanes 2004) and wet tropical

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Table 1. Characteristics of rainfall distribution and intensity during the experimental period at the site. Dry months are defined by rainfall less than 100 mm. Dry-season rainfall includes precipitation from August to December. NA stands for not available.

	Year						
	1999	2000	2001	2002	2003	2004	2005
Annual rainfall (mm)	2577	2399	3179	2301	2895	3038	2793
Minimum monthly rainfall (mm)	NA	66	34	56	42	8	13
Maximum monthly rainfall (mm)	NA	291	489	385	499	611	476
Number of dry season months	NA	3	5	4	2	3	3
Total dry season rainfall (mm)	NA	694	304	400	647	445	615
Total irrigation (mm)	NA	NA	665	790	680	630	685

forest sites in Hawaii (Harrington *et al.* 2001) and Puerto Rico (Li *et al.* 2006).

Quantification of soil moisture and nutrient effects on litterfall quantity and quality could facilitate projections of carbon and nutrient dynamics under altered conditions of resource availability. In this context, long-term (> 1–2 y) observational and resource-manipulation studies on litterfall quantity and quality are important for understanding the effects of interannual variability in carbon and nutrient dynamics, and developing reliable estimates of fine litterfall (Clark *et al.* 2001b). Experimental manipulations of moisture availability include water addition or exclusion, whereas nutrient manipulation involves fertilizer addition or litter removal (Eviner *et al.* 2000, Hanson 2000). Long-term data on litterfall quantity and quality, as well as data on the effect of resource (water and nutrient) manipulations on litterfall, are scarce for Amazonian tropical forest regrowth, which represents a significant and dynamic component of forest landscapes in this region (Fearnside 1996, Zarin *et al.* 2001).

The primary objective of this study was to investigate the effects of moisture and nutrient availability on non-woody litterfall within the context of two manipulative experiments consisting of dry-season irrigation and litter removal. The initial response of non-woody litterfall quantity to these manipulative experiments encompassing the pre-treatment (22 mo) and treatment (18 mo) periods were reported in Vasconcelos *et al.* (2004). Here we present long-term data on litterfall quantity for the treatment period, including 35 additional months of resource manipulation, as well as pre-treatment and treatment data on litterfall quality. We hypothesized that (1) dry-season irrigation would increase non-woody litterfall quantity and quality, and (2) litter removal would reduce non-woody litterfall quantity and quality.

STUDY SITE

This study was conducted at a field station belonging to Universidade Federal Rural da Amazônia (UFRA),

near the city of Castanhal (1°19'S, 47° 57'W) in the state of Pará, Brazil. Since July 2001, daily rainfall was measured 500 m from the experimental area using a standard rain gauge. Prior to July 2001, rainfall data reported here are from the meteorological station at Castanhal (1°17'53" S, 47°56'56"W) located ~3 km from our site, but no longer in operation. From 70–90% of annual rainfall occurs between January and July, resulting in a dry period from August to December. Annual rainfall during the experimental period (Table 1) was consistent with the values recorded from 1990–1999 (mean \pm SE = 2461 \pm 271 mm) at the Castanhal meteorological station. The number of dry months (rainfall < 100 mm mo⁻¹) during the experimental period varied from 2 to 5 per year (Table 1).

The soils are classified as Dystrophic Yellow Latosol Stony Phase I (Tenório *et al.* 1999) in the Brazilian Classification, corresponding to Sombrustox in U. S. Soil Taxonomy. Soil granulometric composition in the first 20 cm is 20% clay, 74% sand and 6% silt. Concretions represent 16% of the soil volume in the upper 10 cm of soil. In the surface soil (0–10 cm), pH is 5.0, organic carbon (C) is 2.2%, organic C stock is 2.9 kg m⁻², total nitrogen (N) is 0.15%, C:N is 14.4, and Mehlich-1 extractable phosphorus is 1.58 mg kg⁻¹ (Rangel-Vasconcelos 2002). This level of extractable soil phosphorus (P) suggests low availability at our study site compared with other soil types and land uses in Amazonia (McGrath *et al.* 2001).

Forest regrowth, annual crops, and active and degraded pastures characterize the landscape surrounding the field station. The stand under study was last abandoned in 1987 following multiple cycles of shifting cultivation, beginning in the 1940 s when the old-growth forest was cleared. Each cycle of 1–2 y included cultivation of *Zea mays* L., *Manihot esculenta* Crantz, and *Vigna unguiculata* (L.) Walp, followed by fallow. Typical shifting-cultivation cycles lasted 7–10 y (G. Silva e Souza & O. L. Oliveira pers. comm.). Trees are mostly evergreen, with a few species (e. g. *Annona paludosa* Aubl. and *Rollinia exsucca* (DC. ex Dunal) A. DC.) showing deciduousness during the dry season. The four most abundant overstorey species are *Lacistema pubescens* Mart., *Myrcia sylvatica* (G. Mey.) DC., *Vismia guianensis* (Aubl.) Choisy and *Cupania*

scrobiculata Rich., representing 71% of all stems in the stand. In November 1999, mean stem density for trees with diameter at breast height (dbh) greater than 1 cm at 1.3 m height was 213 individuals per 100 m², basal area was 13 m² ha⁻¹, average tree height was 4.9 m for the stand (Coelho *et al.* 2004), and above-ground biomass was 51.2 Mg ha⁻¹ (unpubl. data).

Experimental design

Treatment plots were established in August 1999, when the forest regrowth was 12 y old. Each treatment plot was 20 × 20 m with a centrally nested 10 × 10-m measurement subplot. There were four replicate plots for the irrigation treatment, four plots for the litter removal treatment, and four control plots. Adjacent plots were spaced 10 m from each other.

Irrigation was applied at a rate of 5 mm d⁻¹, for about 30 min, during the dry seasons of 2001 to 2005 in the late afternoon. We used rainfall and soil water potential to define approximate boundaries for the dry and wet seasons as described in Vasconcelos *et al.* (2004). The amount of daily irrigation applied corresponds to regional estimates of daily evapotranspiration for regrowth and old-growth-forest sites in Amazonia (Jipp *et al.* 1998, Lean *et al.* 1996, Shuttleworth *et al.* 1984, Sommer *et al.* 2002). Irrigation was distributed through tapes with microholes every 15 cm. In 2001, irrigation tapes were spaced 4 m from each other. In the subsequent irrigation periods we reduced the distance between tapes to 2 m to facilitate more even distribution of water. The total amount of irrigation applied ranged from 630 to 790 mm per dry season, representing an increase of 100–200% of water input during the dry season, and an increase of 21–34% in annual rainfall.

In the litter-removal plots, leaf and branch fall were removed from the forest (20 × 20-m plots) with plastic rakes every 2 wk, beginning in August 2001 with the removal of the pre-treatment litter layer (5380 ± 350 kg ha⁻¹, n = 8); carbon and nitrogen stocks of the pre-treatment litter layer were 2230 ± 146 and 73 ± 5 kg ha⁻¹, respectively (n = 8). Pre-treatment mass and nutrient stocks were estimated on two sets of data collected in previous dry (n = 4) and wet (n = 4) seasons. Total new non-woody litterfall removed during the treatment period (from August 2001 to December 2005) was 35.7 ± 1.4 Mg ha⁻¹ (n = 12). Carbon and nitrogen concentrations of pre-treatment litterfall were 47.9% ± 0.2% and 1.2% ± 0.02%, respectively, corresponding to a C:N ratio of 40 ± 0.7 (n = 12). Phosphorus concentration of pre-treatment litterfall was 0.28 ± 0.01 mg g⁻¹ (n = 12). Pre-treatment surface soil (0–10 cm) and litter N and P stocks, as well as the amount of N and P removed by raking, are shown in Table 2.

Table 2. Nutrient stocks and experimental nutrient removal in a tropical forest regrowth stand in eastern Amazonia, Brazil. All values are total nutrient concentrations except for soil phosphorus which is Mehlich-1 extractable phosphorus. NA stands for not available.

Nutrient	Pre-treatment nutrient stocks (kg ha ⁻¹)		Litterfall nutrient removed during treatment period (kg ha ⁻¹)
	Soil (0–10 cm)	Litter Layer	
Nitrogen	2010	73	305
Phosphorus	2.1	NA	9.9

Soil water potential measured with tensiometers (10 cm depth) was significantly higher (less negative) in irrigated than in control plots during the dry season (Vasconcelos *et al.* 2004). This difference in soil water status between control and irrigated plots was reflected in dry-season differences in soil carbon dioxide efflux (Vasconcelos *et al.* 2004) and in pre-dawn leaf water potential for an understory species (*Miconia ciliata*); in November 2001 pre-dawn leaf water potential for control plants was about -1.2 MPa while irrigated plants were about 1 MPa less negative (Fortini *et al.* 2003).

MATERIALS AND METHODS

Litterfall

From October 1999 to December 2005, litterfall was collected weekly in each of three 1 × 1-m screen litter traps in the 10 × 10-m measurement subplots. The weekly frequency of litterfall collection was chosen to minimize mass and nutrient losses due to leaching of trapped litter (Luizao 1989). The plant material collected in each trap was air-dried in the laboratory to remove excess moisture before storage. At 4-wk intervals, material from the same collector was mixed and then separated into woody and non-woody fractions. Leaves and their petioles, foliar rachises, and reproductive parts were included in non-woody litterfall. Our non-woody fraction corresponds to the fine litter (or small litter) defined in several studies (Smith *et al.* 1998), except for the non-inclusion of woody material. In fine litter, small-diameter woody material – usually < 1–2 cm diameter (Clark *et al.* 2001b, Proctor 1983) – is included assuming that this woody fraction has turnover times comparable to other components of non-woody material (mostly foliar and reproductive material) and may represent material produced from current year's growth. Thus, our estimate of non-woody material may represent a slight underestimation of fine litter.

We weighed woody and non-woody litterfall after drying at 60–70 °C until constant weight. Litterfall data for April 2003 were lost due to a malfunction of the oven that resulted in burning of litterfall samples; for this period,

we used for each trap a value of litterfall estimated from the mean relative contribution of April to annual litterfall per trap ($6.3 \pm 0.2\%$ for all traps). Estimated data for April 2003 were used to analyse annual litterfall response to treatments, but not for monthly litterfall.

Composite samples of non-woody litterfall were ground with a coffee grinder (Krups, US) and stored in 60-ml scintillation vials for subsequent analysis of N and P. Nitrogen and phosphorus concentrations were determined in the Laboratory of Plant Ecophysiology and Propagation at Embrapa Amazônia Oriental (Brazil) in samples collected from January 2000 to December 2004. The Kjeldahl digestion was used to determine total N (Anderson & Ingram 1996). Phosphorus concentrations were determined colorimetrically after digestion of 0.1-g sample in sulphuric acid and peroxide (Murphy & Riley 1962). Following the criteria in Boone *et al.* (1999), all the samples were analysed in duplicate for P, while 10% of the samples were randomly selected for duplicate analyses for N. Mean coefficient of variation in duplicate analyses was 2.1% for N ($n = 542$) and 4.1% for P ($n = 2096$). Per cent error in the analysis of standard reference material (peach leaves, NIST SRM 1547) was $-14 \pm 1.6\%$ for N ($n = 22$) and $2.0 \pm 1.0\%$ ($n = 24$) for P.

To calculate N and P fluxes in non-woody litterfall (nutrient return), nutrient concentrations were multiplied by mass for each trap per month.

Litter stock

At the end of the 2004 wet season (25 August) and dry season (29 December), we collected samples ($n = 4$) of forest-floor litter from randomly chosen areas (25×50 cm) in each of the control and irrigated plots and processed as for litterfall. Non-woody litter stock was calculated by dividing the amount of dry material per collection area (g m^{-2}).

Statistical analysis

We used SAS version 9.00 for all statistical analyses. We analysed the effects of treatment, date, and treatment-by-date interaction on the variables non-woody litterfall mass, N and P concentration and return, and litter stock with PROC MIXED using a repeated-measures analysis with compound symmetric and autoregressive covariance structures for monthly and annual data, respectively. The compound symmetric structure assumes constant variance at all dates and equal correlations between all pairs of measures on the same experimental unit, i.e. litterfall trap for the litterfall variables and plot for litter stock, while in the autoregressive structure yearly measurements are

related to each other at an exponentially decreasing rate. Because we considered the irrigation and litter removal manipulations as two independent experiments, we ran separate tests that compared each treatment with the control. Within this analysis, significant treatment effects would have indicated temporally consistent differences between treatment and control measurements both pre- and post-treatment and across seasons, significant date effects were generally indicative of seasonal trends that affected both treatment and control measurements, and treatment-by-date effects indicated a significant difference between treatment and control measurements that occurred after the treatment was initiated. Thus, the treatment-by-date effect represents the best test of treatment effect when there were no pre-existing differences among plots prior to the treatment. We used a priori CONTRAST statements to explicitly test whether the measured variables differed between seasons and between treatments within each season (wet and dry).

When necessary, we performed logarithmic and square-root transformations to meet the model assumptions of normality, based on the criteria of $P > 0.05$ in the Kolmogorov–Smirnov test, and equal variances, based on the absence of a pattern of heteroscedasticity in plots of residual versus predicted values. Multiple comparisons of means were performed with Tukey–Kramer adjustments. All results are reported as significant when $P < 0.05$.

RESULTS

Irrigation experiment

Monthly non-woody litterfall mass was significantly higher in the dry season than in the wet season (777 ± 12 and $605 \pm 9 \text{ kg ha}^{-1} \text{ mo}^{-1}$, respectively; $P < 0.0001$) (Table 3, Figure 1a-b). For annual non-woody litterfall mass, there was a significant treatment \times date interaction (Table 3, Figure 2a), and values tended to be higher (about 20%) in irrigated plots than in control plots (8990 ± 550 and $7420 \pm 630 \text{ kg ha}^{-1} \text{ y}^{-1}$, respectively) in 2003. Annual litterfall of control and irrigation plots was poorly correlated with water input through rainfall and irrigation ($r = 0.479$, $P = 0.115$, $n = 12$, Pearson correlation).

Monthly non-woody litterfall N concentration was significantly different by date only (Table 3, Figure 1c). The effect of date was not due to seasonal differences in litterfall N concentration (dry = $1.24\% \pm 0.01\%$ vs. wet = $1.27\% \pm 0.01\%$ N, $P = 0.98$).

For monthly non-woody litterfall P concentration and N:P ratio, there was a significant treatment \times date interaction (Table 3, Figure 1d-e). Litterfall P concentration was significantly higher in control plots than in irrigated plots for some months during early to mid-dry

Table 3. F statistics and associated significance levels for the effects of treatments (irrigation and litter removal), sampling date, and their interaction on non-woody litterfall mass and nutrients in a tropical forest regrowth stand in eastern Amazonia, Brazil. The level of significance is indicated (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, ns: not significant).

Non-woody litterfall	Irrigation experiment			Litter-removal experiment		
	Treatment	Date	Treatment \times Date	Treatment	Date	Treatment \times Date
Monthly mass	0.28 ^{ns}	25.3 ^{***}	1.14 ^{ns}	0.08 ^{ns}	15.5 ^{***}	0.82 ^{ns}
Monthly N concentration	0.07 ^{ns}	17.0 ^{***}	0.65 ^{ns}	3.77 ^{ns}	17.6 ^{***}	1.54 [*]
Monthly P concentration	0.64 ^{ns}	35.3 ^{***}	1.85 ^{***}	1.54 ^{ns}	31.9 ^{***}	0.74 ^{ns}
NP ratio	0.11 ^{ns}	31.6 ^{***}	1.47 [*]	0.04 ^{ns}	29.8 ^{***}	0.70 ^{ns}
Annual mass	0.46 ^{ns}	1.87 ^{ns}	3.28 [*]	0.09 ^{ns}	3.49 [*]	0.62 ^{ns}
Annual N concentration	0.07 ^{ns}	264 ^{***}	1.02 ^{ns}	4.31 ^{ns}	158 ^{***}	3.72 [*]
Annual N return	0.20 ^{ns}	17.1 ^{***}	1.86 ^{ns}	0.21 ^{ns}	17.5 ^{***}	1.18 ^{ns}
Annual P concentration	0.70 ^{ns}	130 ^{***}	1.80 ^{ns}	1.58 ^{ns}	77.8 ^{***}	0.52 ^{ns}
Annual P return	0.24 ^{ns}	45.2 ^{***}	2.93 [*]	0.08 ^{ns}	15.9 ^{***}	0.85 ^{ns}

season (November 2001 and September 2002) and late-dry to early wet seasons (January and February in 2002 and 2003) (Figure 1d). Also during these months, irrigated plots showed significantly higher N:P ratio values (Figure 1e). Litterfall P concentration was slightly but significantly lower in the dry season than in the wet season ($0.38 \pm <0.01$ and $0.40 \pm <0.01$ mg P g⁻¹, respectively; $P < 0.0001$).

Annual N (Figure 2c) and P concentrations (Figure 2g), as well as annual return of N (Figure 2e) were significantly different by date only (Table 3). The significant treatment \times date interaction on annual return of P is not consistently tied to a treatment effect (Table 3, Figure 2i), although irrigation plots tended to have higher P return than control plots in 2003.

The stock of non-woody litter was significantly higher towards the end of the dry season (December 2004) than at the end of the wet season (August 2004) (6800 ± 540 and 4350 ± 360 kg ha⁻¹, $n = 8$, respectively; $P < 0.001$). There were no significant treatment effects ($P = 0.203$) or treatment \times date interaction ($P = 0.271$).

Litter-removal experiment

Monthly non-woody litterfall mass was significantly different by date only (Table 3, Figure 3a–b), with significantly higher values in the dry season than in the wet season (746 ± 11 and 604 ± 9 kg ha⁻¹ mo⁻¹, respectively; $P < 0.0001$). Annual non-woody litterfall mass was significantly different by date only (Table 3, Figure 2b).

For non-woody litterfall N concentration, there was a significant treatment \times date interaction (Table 3, Figure 3c), with treatment data showing significantly different means only after treatment began. During the treatment period, mean litterfall N concentration was about 12% higher for control plots than for litter-removal plots ($1.26\% \pm 0.01\%$ and $1.13\% \pm 0.01\%$ N, respectively; $P = 0.01$).

Non-woody litterfall P concentration was significantly different by date only (Table 3, Figure 3d). Phosphorus concentration during the wet season was slightly but significantly higher than during the dry season ($0.40 \pm <0.01$ and $0.36 \pm <0.01$ mg P g⁻¹, respectively; $P < 0.0001$).

The nitrogen:phosphorus ratio was higher in the dry season than in the wet season (36 ± 0.5 vs. 33 ± 0.4 , respectively; $P < 0.0001$) (Table 3, Figure 3e), although the difference was slight.

For annual N concentration, there was a significant treatment \times date interaction (Table 3), with significantly higher values in control than in litter-removal plots from 2002 to 2004 (Figure 2d). The difference in annual N concentration between control and litter-removal plots increased from $\sim 11\%$ in 2002 to $\sim 16\%$ in 2004, which correspond to $\sim 5\%$ (2002) and $\sim 11\%$ (2004) after accounting for pre-treatment differences.

Annual P concentration was significantly different by date only (Table 3, Figure 2h). Annual return of N and P were significantly affected by date (Table 3); N return in 2001 was significantly higher than in the other years (Figure 2f), while higher return rates in 2003 and 2004 than in the other years were observed for P (Figure 2j).

DISCUSSION

Seasonal patterns

Non-woody litterfall rates and seasonality measured in this study are consistent with other reports for tropical forests (Dantas & Phillipson 1989, Scott *et al.* 1992, Smith *et al.* 1998, Wieder & Wright 1995). The magnitude of interannual variability over 6 y varied from 9% for irrigated plots to 16% for litter-removal plots, lower than that reported for a Panamanian old-growth forest (38%) (Wieder & Wright 1995). Annual litterfall was not related to annual rainfall, suggesting that litterfall production is not controlled by rainfall intensity for

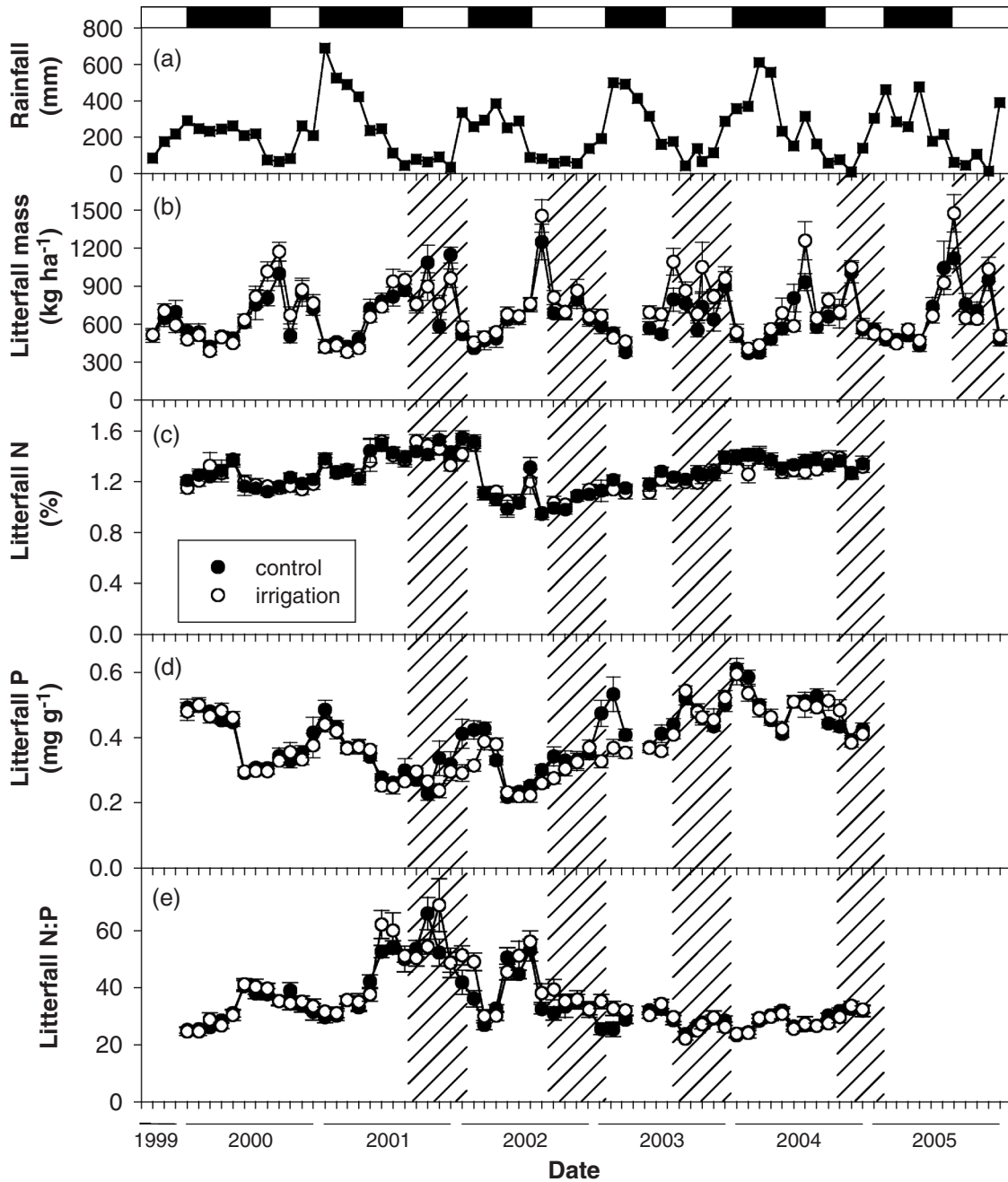


Figure 1. Effects of manipulation of moisture availability on monthly non-woody litterfall mass and nutrient dynamics in an eastern Amazonian forest-regrowth stand, Brazil. Monthly rainfall (a) and non-woody litterfall mass (b), nitrogen concentration (c), phosphorus concentration (d), and nitrogen:phosphorus ratio (e) for control and irrigation plots. In (b) to (e), each symbol represents the mean \pm SE, $n = 12$. Hatched area indicates the irrigation periods. White and black horizontal bars mark the dry and wet seasons, respectively.

this forest regrowth stand. However, Lawrence (2005) found a positive relationship between annual litterfall and annual rainfall for tropical seasonal forests at a global scale. Interannual variability in litterfall nutrient concentration was higher for P (49%) than for N (21%) in control plots, suggesting that N is cycled more tightly than P.

There were no detectable effects of rainfall seasonality on litterfall N concentration, although Yavitt *et al.* (2004) reported higher N concentration in leaf fall during the wet season for a Panamanian old-growth forest, and Wood *et al.* (2005) reported a wet-season decline in leaf litterfall N concentration for a Costa Rican old-growth forest.

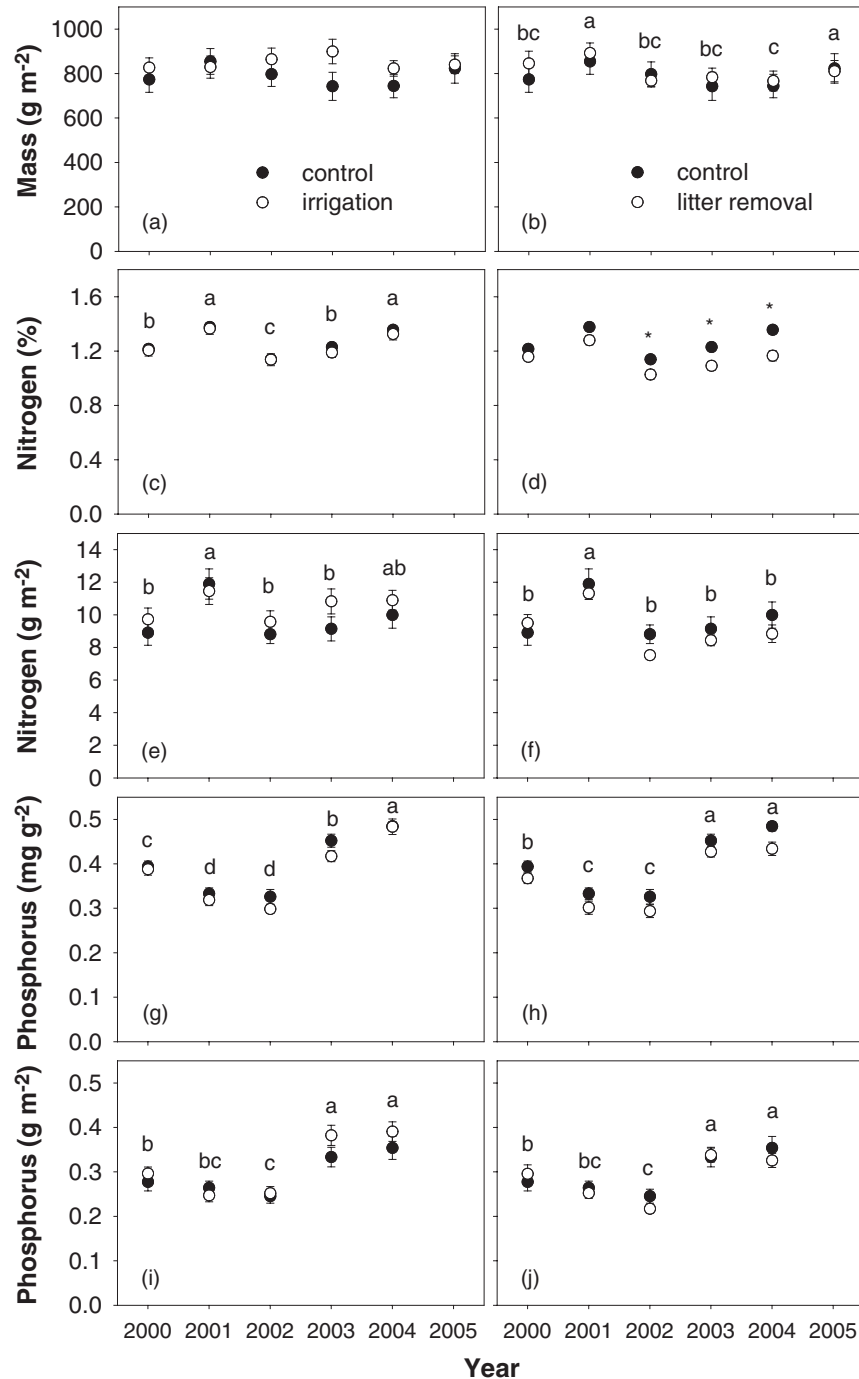


Figure 2. Effects of manipulation of moisture and nutrient availability on annual non-woody litterfall mass and nutrient dynamics in an eastern Amazonian forest-regrowth stand, Brazil. Annual non-woody litterfall mass (a, b), nitrogen concentration (c, d), nitrogen return (e, f), phosphorus concentration (g, h), and phosphorus return (i, j) in response to dry-season irrigation and litter removal. Each symbol represents the mean \pm SE, $n = 12$. Different letters indicate that treatment means differ significantly among years and asterisks indicate that treatments differ significantly within years at $P < 0.05$ (Tukey's test).

Non-woody litterfall P concentration was lower during the dry season than in the wet season in the present study, with some lower values of litterfall P associated with peaks in litterfall, and some higher values of P occurring during lower litterfall rates in the wet season. These results for

litterfall P are consistent with data reported for dry tropical secondary forest in Mexico (Read & Lawrence 2003) and an old-growth forest in Costa Rica (Wood *et al.* 2005).

Most annual litterfall P peaks occurred during the first 1–2 mo of the wet season, when rapid decomposition

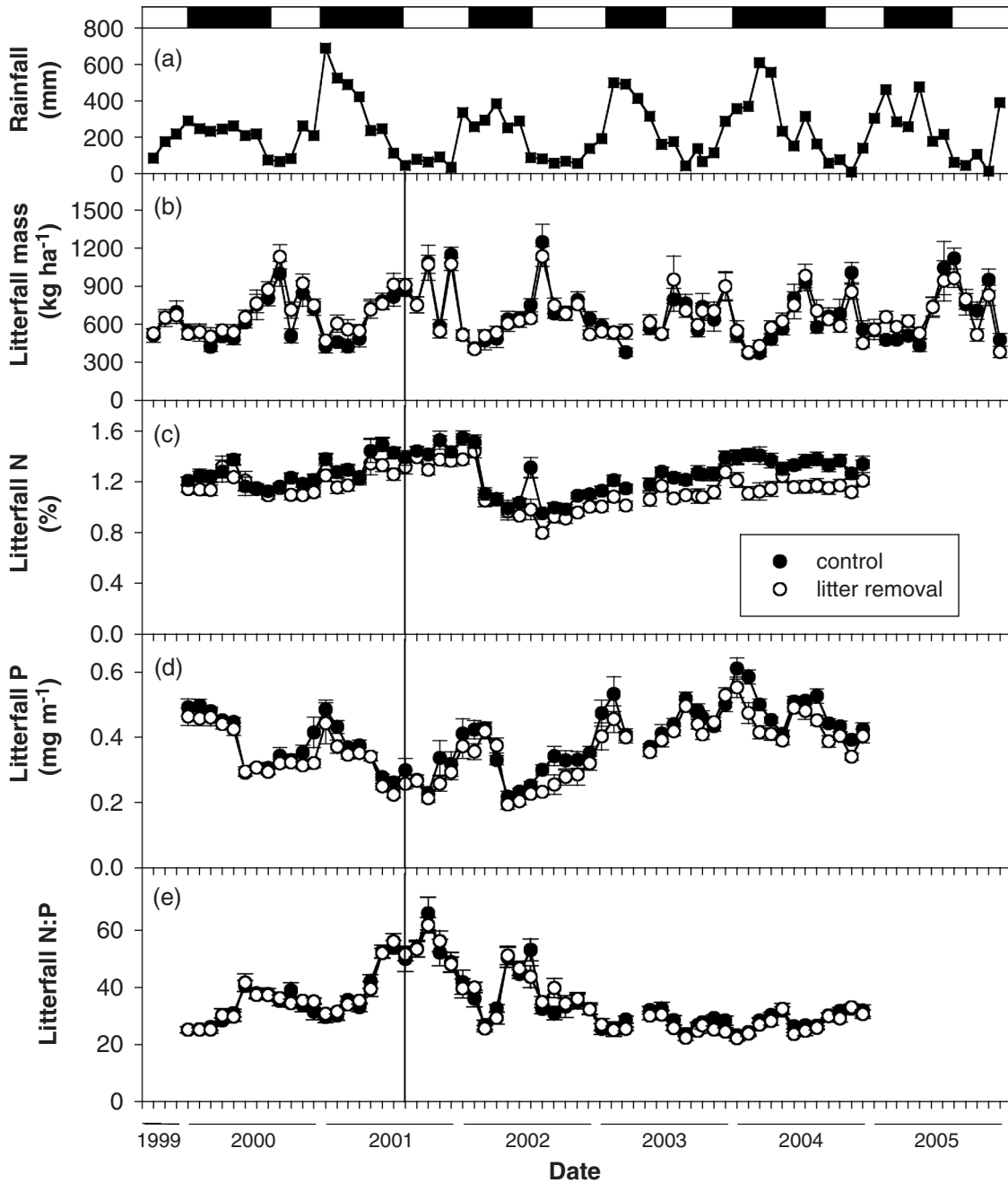


Figure 3. Effects of manipulation of nutrient availability on monthly non-woody litterfall mass and nutrient dynamics in an eastern Amazonian forest-regrowth stand, Brazil. Monthly rainfall (a) and non-woody litterfall mass (b), nitrogen concentration (c), phosphorus concentration (d), and nitrogen:phosphorus ratio (e) for control and litter removal plots. In (b) to (e), each symbol represents the mean \pm SE, $n = 12$. The vertical line indicates the beginning of the litter removal treatment. White and black horizontal bars mark the dry and wet seasons, respectively.

of litter accumulated during the dry season could have supplied a pulse of nutrients to plants with the onset of rainfall (Lodge *et al.* 1994, Wood *et al.* 2005). Lower litterfall P concentration in irrigated plots during dry-wet season transitions (2001–2002 and 2002–2003), associated with the strongest dry-season irrigation periods, are consistent with the pulse hypothesis, i.e.

irrigation could have prevented litter accumulation and, therefore, diminished the nutrient mineralization pulse with the onset of rainfall. Alternatively the seasonal and treatment effects on litterfall P may be caused by differences in P resorption between treatments and/or differences in the contribution of P-rich, reproductive litterfall (flowers and fruits) during dry-wet transitions.

Reproductive litterfall has been shown to have higher P concentration than leaf litterfall for tropical forests (Scott *et al.* 1992, Zagt 1997), and to peak (number of seeds m^{-2}) during dry-wet season transitions for our experimental site, although no irrigation effects have been observed in two consecutive evaluation years (Dias 2006).

Litter stock measured in this study is within the range reported for tropical forests (Luizão *et al.* 2004, Scott *et al.* 1992, Smith *et al.* 1998). Increased litter stock in the dry season is consistent with higher litterfall and lower decomposition rates during this period at the study site (Vasconcelos *et al.* 2007), as also reported for an old-growth forest in Panama (Wieder & Wright 1995).

Limited impact of dry-season irrigation

The lack of dry-season irrigation effects on non-woody litterfall rates previously reported for the initial 18 mo of treatment (Vasconcelos *et al.* 2004) persisted during two subsequent irrigation periods. These results are consistent with those found for a dry-season irrigation experiment in a semi-deciduous lowland forest in Panama (Cavelier *et al.* 1999, Wieder & Wright 1995), which added approximately 30 mm water wk^{-1} , and further confirm that soil moisture availability may not alter litterfall amounts in tropical forests, even when dry-season precipitation inputs are doubled or tripled. However since both irrigation studies were carried out at sites with mean annual rainfall > 2500 mm, i.e. the higher end of seasonal forests, the observed response of litterfall to irrigation may not be readily extrapolated to drier tropical forest sites.

Dry-season irrigation did not alter N and had only small effects on P concentrations in non-woody litterfall, consistent with the results from a water manipulation study in a Panamanian old-growth forest (Yavitt *et al.* 2004). The limited impacts of dry-season irrigation in this study contrasts with the potential for increased N and P availability in irrigated plots due to higher litter decomposition in irrigated plots (Vasconcelos *et al.* 2007). Thus, these results suggest that low litter quality – indicated by the high C:N and lignin:N ratios of leaf litter (Vasconcelos *et al.* 2007) and non-woody litterfall – may be a stronger control over N and P availability than soil water status at this site, favouring microbial immobilization of nutrients (Aerts 1997). Furthermore, consistent with results from an irrigation study in Panama (Yavitt & Wright 1996), dry-season irrigation had no influence on soil net nitrification rates at our site (Vasconcelos *et al.* 2004).

We hypothesized that irrigation would result in increased above-ground productivity and, consequently, higher annual non-woody litterfall rates. However, after 5 y of dry-season irrigation, no consistent effect of irrigation on litterfall was detected. Litterfall rates tended

to be higher (21%) for the irrigated plots in 2003, but that was in the year with the weakest dry season over the whole experimental period, when we would have expected the least effect of dry-season irrigation on forest processes. Recent results from a temperate deciduous forest suggest that there may be a lag effect of drought on litterfall (Newman *et al.* 2006). Such an effect may be implicated in the increased annual litterfall recorded in our irrigated plots in 2003, due to the extended drought in the preceding dry season (Table 1). However, statistical analyses of correlations between annual litterfall and previous year rainfall revealed no significant effect during the study period, suggesting that either the lag effect is absent, or that the range and/or quantity of our data are insufficient to adequately test for it.

Litter removal reduces litterfall N concentration

Nitrogen and phosphorus concentrations and inputs in litterfall are comparable to values reported for forests of the Brazilian Amazon and elsewhere in the tropics (Cuevas & Medina 1986, Luizao 1989, Markewitz *et al.* 2004, Mirmanto *et al.* 1999, Scott *et al.* 1992). Increased differences in N concentrations between control and litter-removal plots are consistent with the recognized role of nutrient cycling in litter as a significant source of N for tropical forest plants (Markewitz *et al.* 2004, Vitousek & Sanford 1986).

Mean litterfall P concentration for the control plots in this forest regrowth stand (0.04%) coincides with the threshold value proposed by Vitousek (1984) to distinguish between high and low P levels for tropical forests. For most months from 2000 to 2003, litterfall P concentrations were below this threshold, which may reflect the low availability of soil phosphorus, as suggested by the low soil extractable P reported for the site (Rangel-Vasconcelos 2002).

Our litter manipulation treatment removed about four to five times initial P stocks in above-ground fine litter and soil (0–10 cm). Despite this apparent dramatic effect of litter removal, litterfall P concentration did not differ from control plots, which may be explained by sufficient supply of P from soil sources. While weathering processes are not likely a substantial source of P in highly weathered tropical soils deprived of primary P-containing minerals (Sanchez 1976), mineralization of P from soil organic matter may represent a significant source of P for plants, even after 40 mo of fortnightly litter removal. Recent studies have determined substantial amounts of (potentially) labile organic-P fractions (NaOH- and NaHCO_3 -extractable) for Amazonian forest regrowth sites in Brazil (Frizano *et al.* 2003, Markewitz *et al.* 2004), and a simulation study concluded that N and P stored in (deeply buried) soil organic matter can sustain C accumulation

rates under conditions of limited input of such nutrients in tropical forest regrowth (Herbert *et al.* 2003). In addition, some secondary-forest trees colonizing sites with low soil P availability probably present mechanisms to improve P acquisition such as mycorrhizal associations and high phosphatase exudation rates (Marschner 1995). Uhl (1987) hypothesized that high incidence of mycorrhizal infection and efficient uptake and nutrient use may be necessary for establishment of successional trees under the limiting nutrient conditions typical of abandoned lands after slash-and-burn in the tropics. Similarly, Gehring *et al.* (1999) suggested that the growth of two early successional tree species in an Amazonian forest site was not limited by soil P availability because of efficient mycorrhizal associations.

Since litter is one of the main sources of most nutrients in tropical forests (Markewitz *et al.* 2004, Vitousek & Sanford 1986), we expected that chronic litter removal would have resulted in nutrient deficiency, and consequently reduced litterfall quantities. But, thus far, this study indicates that the quantity of non-woody litterfall was insensitive to the reduction in nutrient availability (indicated by reduced litter N concentration) imposed by the litter manipulation treatment, consistent with the results obtained by Sayer (2005) for a 2-y litter-removal study in Panama. It is possible that extending the litter removal period will further reduce nutrient concentrations in litter, leading to a critical point where productivity will be significantly constrained. Nutrient manipulation effects on ecosystem processes are usually not immediate, and litter-removal studies may have slower effects on litterfall responses than fertilization studies (Campo & Vázquez-Yanes 2004, Mirmanto *et al.* 1999).

Nitrogen:phosphorus ratio

Monthly non-woody litterfall N:P mass ratio for control plots averaged 35 (range: 23–66) over the experimental period, which is similar to the ratio (37) calculated for a 19-y-old forest regrowth in eastern Amazonia (Markewitz *et al.* 2004), and also consistent with the range for tropical forests (Cuevas & Medina 1986, Luizao 1989, Mirmanto *et al.* 1999, Scott *et al.* 1992, Wood *et al.* 2005). Our N:P values further suggest that the studied forest regrowth stand is limited by P, according to the threshold established (N:P > 16) to characterize P-limited systems (Aerts & Chapin 2000, Koerselman & Meuleman 1996).

Soil moisture availability may change with altered rainfall patterns associated with climate and land-use changes in Amazonia (Lean *et al.* 1996, Trenberth & Hoar 1997), possibly leading to replacement of tropical forest by savanna in eastern Amazonia, especially with associated increases in the incidence of wildfire (IPCC 2007). Altered

nutrient input and storage are expected with land-use changes and fire events, reducing forest regrowth rates (Zarin *et al.* 2005). Forest biogeochemical models that attempt to simulate carbon and nutrient cycling responses to climate and land-use changes should take into account the results of experimental resource manipulations on litterfall.

We conclude that non-woody litterfall quantity and quality are not sensitive to increased moisture availability during the dry season and reduced nutrient availability imposed on this forest regrowth stand, except for a progressive reduction in litterfall N during long-term litter removal. Below-ground mechanisms to improve water and nutrient acquisition may confer resistance to this alteration in resource availability, and merit further study. Additional years of manipulation may allow us to test if this forest regrowth stand will maintain unaltered rates of non-woody litter production under likely lower nutrient availability associated with continued litter removal. Likewise, lengthening the manipulation period increases our chance of capturing consecutive, dry years, which would be a more adequate scenario to test irrigation effects on forests under relatively high annual rainfall.

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