

Variation in leaf litter nutrients of a Costa Rican rain forest is related to precipitation

TANA E. WOOD^{1,*}, DEBORAH LAWRENCE¹ and DEBORAH A. CLARK²

¹*Department of Environmental Sciences, University of Virginia, PO Box 400123, Charlottesville, Virginia 22904-4123, USA;* ²*Department of Biology, University of Missouri, St. Louis, 8001 Natural Bridge Road, St. Louis, MO 63121;* **Author for correspondence (e-mail: tana@virginia.edu; phone: 434-242-0881; fax: 434-982-2137)*

Received 11 September 2003; accepted in revised form 8 June 2004

Key words: El Niño/Southern Oscillation, Litter, Nutrients, Seasonality, Tropical rain forest

Abstract. By assessing current leaf litter nutrient dynamics, we may be able to predict responses of nutrient cycling in tropical ecosystems to future environmental change. The goal of this study was to assess whether nutrient cycling is related to seasonal variation in rainfall in a wet tropical forest. We examined leaf litter of an old-growth tropical rain forest in N.E. Costa Rica over a 4-year period to explore seasonal and inter-annual changes in leaf litter nutrient concentrations, and to evaluate potential short- and long-term drivers of variation in litter nutrient concentration, particularly that of phosphorus (P) and nitrogen (N). We also examined the temporal dynamics of calcium, potassium, and magnesium in the leaf litter. Leaf litter [P] and %N changed significantly with time, both seasonally and inter-annually. Seasonal changes in leaf litter [P] were strongly positively correlated with rainfall from the previous 2 weeks; cations, however, were inversely related to this measure of current rainfall, while %N was not related to rainfall. We propose that the positive relationship between current rainfall and leaf litter [P] is due to a response by the vegetation to an increase in nutrient availability and uptake. In contrast, given the negative relationship between current rainfall and cation concentrations, leaching from live leaf tissue is a more likely driver of short-term changes in cations. Should global climate change include altered rainfall patterns in this biome, one class of ecosystem-level responses could be significant changes in P and cation cycling.

Introduction

Traditionally, tropical rain forests were frequently viewed as static communities that function under optimal climatic conditions (ample moisture, consistently warm temperatures). More recently, however, the dynamism and temporal variability of processes in these forests have been recognized (cf., Tian et al. 1998; Clark et al. 2003). The goal of our research was to (1) evaluate seasonal and inter-annual patterns of leaf litter nutrient cycling in a wet tropical forest, (2) determine whether variation of leaf litter nutrient concentrations is related to climatic and environmental variables, and (3) generate hypotheses concerning the possible mechanisms driving this variation.

Most litterfall studies in tropical forests have demonstrated a strong seasonality of leaf litterfall, with the peak at the end of the dry (/drier) season

(Hopkins 1966; Klinge and Rodrigues 1968; Haines and Foster 1977; Kunkel-Westphal and Kunkel 1979; Herbohn and Congdon 1993; Swamy and Proctor 1994; Wieder and Wright 1995; Lawrence and Foster 2002). Following such a seasonal peak in litterfall, there can be a pulse of increased soil nutrient availability at the beginning of the rainy season (Lodge et al. 1994; Campo et al. 1998; McGrath et al. 2000). This pulse can lead to high nutrient concentrations in live leaf tissue, often coinciding with the peak-growing season (Cuevas and Medina 1986; Palma et al. 2000; Son et al. 2000; Salifu and Timmer 2001). Despite evidence indicating the influence of seasonality on patterns of nutrient cycling, the seasonality of leaf litter nutrient concentrations has not been well characterized for tropical rain forests (Cuevas and Medina 1986; Scott et al. 1993). This gap in knowledge limits our understanding of overall nutrient cycling in such forests due to the possibility that the soil nutrient supply is not constant (Lodge et al. 1994; Campo et al. 2001). Given the low apparent intra-year variability in mean temperature and solar radiation in tropical wet forests, seasonal changes in leaf litter nutrient concentrations could serve as a constraint on net primary productivity. Because N and P are the nutrients most likely to limit primary productivity in tropical forests (Vitousek 1984), we used the N:P ratio to evaluate seasonal changes in N and P limitation. Prior research has shown that foliar N:P > 16 are P limited systems, while foliar N:P of 14–16 are co-limited by N and P (Koerselman and Meuleman 1996; Aerts and Chapin 2000). Although these limits were developed for wetland vegetation, more recent work suggests that the critical values are relevant for forests as well (Tessier and Raynal 2003; Richardson et al. 2004; Knecht and Goransson 2004).

Tropical forests can also experience significant inter-annual climatic variability. Clark et al. (2003) suggest that Costa Rican tropical rain forest tree species are highly sensitive to climate, resulting in significant variation in canopy tree growth from year to year. Other studies have shown that tropical dry and wet forest trees show increased tree mortality during exceptionally hot and/or dry years (Murphy and Lugo 1986; Condit et al. 2000; Clark 2004). Phenological patterns of tropical species are also influenced by climatic variability, with major reproductive events occurring irregularly or supra-annually in some tropical regions (Stocker et al. 1995; Curran et al. 1999; Wright et al. 1999; Wich and Van Schaik 2000). Although ample evidence indicates the importance of inter-annual climatic variability in tropical ecosystems, studies of leaf litter nutrient cycling in tropical rain forests extending beyond a single year are rare (see Herbohn and Congdon 1998 (moist); Cuevas and Medina 1986 (wet); Newbery et al. 1997 (wet)). The lack of long-term litterfall nutrient measurements spanning the strong inter-annual climatic variability seen by tropical rain forests limits our understanding of these systems (Murphy and Lugo 1986; Martinez-Yrizar and Sarukhan 1990).

Neither the timing of phenological events in tropical forests nor the seasonality of leaf litter nutrient concentrations have been attributed to a single environmental factor (Murphy and Lugo 1986; Herbohn and Congdon 1998).

A variety of mechanisms have been proposed to explain short-term (0–4 weeks) variation in leaf litter nutrient concentrations. One potential mechanism includes the impact of rainfall on nutrient availability and plant uptake (Escudero et al. 1992; Salisbury and Ross 1992; McGrath et al. 2000). Soil moisture affects nutrient diffusion through the soil to roots. With higher rainfall, effective soil nutrient availability could increase, leading to high live tissue concentrations. Root growth and uptake are limited by soil moisture, so if nutrient-rich surface soils dry out during the dry season (Cuevas 1995; Holbrook et al. 1995), leaf nutrient concentrations could also decline. Thus, during periods of high rainfall, leaf litter nutrient concentration could be higher than in drier periods.

A relationship between high precipitation and high leaf litter nutrient concentrations could also be the consequence of an increase in green leaf (live) litterfall (Cuevas and Lugo 1998). Often, strong precipitation events bring high winds. High winds could mechanically remove nutrient-rich green leaf tissue. A positive relationship between precipitation and leaf litter nutrient concentration would then result; however, this relationship would be independent of potential changes in soil nutrient availability (Lodge et al. 1991; Veneklaas 1991; Cuevas and Lugo 1998). Another mechanism through which precipitation could influence leaf litter nutrient concentrations is through the leaching of nutrients from live tissue (Epstein 1972; Marschner 1995; Killingbeck 1996; Aerts and Chapin 2000; Chuyong et al. 2000). Most tropical tree species have evolved leaf structures (e.g. smooth surface) to counteract this loss (Dean and Smith 1978). However, leaching might still be an important influence on seasonal patterns of leaf litter nutrients. In contrast with the high soil moisture-high soil nutrient availability-high litter nutrients hypothesis, leaching from live leaves would result in lower nutrient concentrations in leaf litter during high rainfall periods. In addition to increasing the nutrient loss from live tissue, high rainfall could also lead to increased rates of soluble nutrient loss from the soil as well as a decrease in decomposition rates and mineralization due to lower oxygen concentrations (Aerts and Chapin 2000; Schuur and Matson 2001). Lower soil nutrient availability during periods of heavy rain could lead to decreased nutrient concentrations in foliar tissue. Thus, as with leaching from live foliage, leaching from the soil would lead to lower leaf litter nutrient concentrations.

Short-term variation in leaf litter nutrients could also be influenced by source–sink interactions. As new plant tissue is produced, greater translocation of mobile nutrients from old tissue (source) to new (sink) occurs (Nambiar and Fife 1991; Newbery et al. 1997). Therefore, if senescing leaves are a good source of mobile nutrients, lower leaf litter nutrient concentrations could occur when fruit production is high, when trees are flushing new leaves, or at times of peak production of either wood or roots.

In addition to short-term variation in leaf litter nutrient concentrations, we also expected to see significant inter-annual variation. Our study period (October 1997–April 2001) included the latter portion of the 1997–1998 El

Niño event. In N.E. Costa Rica, El Niño years intensify the seasonality of precipitation (a wetter wet season followed by a drier dry season) (Waylen et al. 1996). In this region, a particularly strong ENSO could result in significant moisture stress during the drier season months. For example, the longest recorded period with total precipitation not exceeding 5 mm at La Selva Biological Station, Costa Rica was in March and April of the 1983 ENSO year (30 days; Sanford et al. 1994). This short-term drought resulted in a 40% reduction in total soil moisture content in the upper 70 cm of soil (Luvall 1984; Parker 1985; in Sanford et al. 1994)). In March–April 2000 there was another such block of 30 consecutive days with ≤ 5 mm rain (Figure 1). Because tropical wet forests infrequently experience any significant soil drying, water stress could lead to premature senescence of leaves (Wright and Cornejo 1990; del Arco et al. 1991; Wieder and Wright 1995; Sizer et al. 2000). Premature senescence may result in incomplete nutrient resorption and thus higher nutrient concentrations in leaf litterfall when precipitation values are low. This effect should be enhanced in lower-fertility sites where the plants may be more susceptible to water stress due to a lower ability to maintain osmotic pressure in the leaves (Cuevas and Medina 1986; Murphy and Lugo 1986).

For secondary forests in our study area, leaf litterfall was negatively correlated with the amount of precipitation during the 2-week collection period (D. Lawrence unpublished data). This short-term link between precipitation and leaf litter production, if paralleled in the old-growth forest that is the subject of this study, could play an important role in the longer-term seasonality of leaf litter nutrient concentrations through the subsequent release of nutrients during decomposition. Hence, increases in leaf litterfall in response to periods of low rainfall could have a positive influence on subsequent leaf litter nutrient concentrations, and the time lag would depend on the rate at which litter nutrients become incorporated into the soil and available to the plants. The turnover time of the forest floor for this area is 19–24 weeks (Gessel et al. 1980; T.E. Wood and D. Lawrence unpublished data). Thus, we expected that the lag time for the influence of precipitation-linked changes in leaf litter

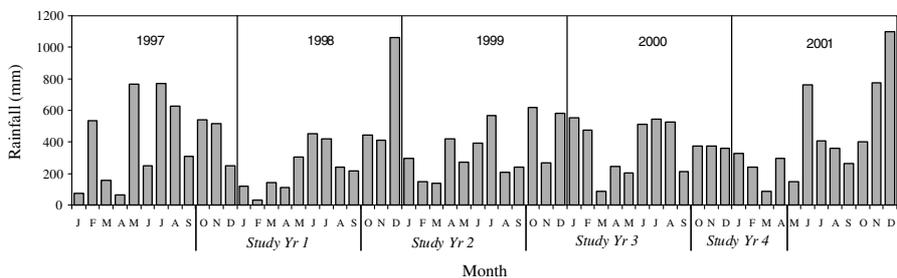


Figure 1. Monthly rainfall (mm) over the 4-year sample period (October 1997–April 2001). 1997–1998 was a strong El Niño year for the region. Dry season months are February–April (OTS unpublished meteorological records).

production would be no greater than 20 weeks. In addition, because nutrients tend to be immobilized during the initial stages of decomposition (Ewel 1976), we set a lower bound of 12 weeks for the influence of prior precipitation and leaf litterfall on leaf litter nutrient concentrations.

To summarize, we explored short-term variability in leaf litter nutrients that might be due to positive effects of rainfall on soil nutrient availability, plant uptake and live leaf losses, negative effects of rainfall on leaching and nutrient mineralization, or rainfall-neutral effects of source–sink interactions. We also explored the hypothesis that long-term variability is influenced by positive feedbacks from decomposition following heavy litterfall. The patterns we find will mark a first step towards assessing possible drivers of leaf litter nutrient variation.

Methods

Study region

The study occurred in old growth, tropical lowland forest at La Selva Biological Research Station in Costa Rica (10°26'N, 84°00'W; Organization for Tropical Studies [OTS]). Mean annual rainfall is 4200 mm, with no month averaging less than 150 mm. The monthly mean temperature for our study period (1997/1998–2000/2001) was 26 °C, with a mean difference of approximately 9 °C between maximum and minimum daily temperatures (OTS unpublished meteorological records). The study region is Tropical Wet Forest under the Holdridge Life Zone System (Holdridge 1947). The landscape is of volcanic origin, and the topography varies from flat, alluvial terraces to moderate hills (Sollins et al. 1994). The drier season lasts from late January through April, with a less pronounced and short-term decrease in rainfall also occurring during September or October ('veranillo') (OTS unpublished meteorological records).

The forest is evergreen, but a few of the emergent tree species are annually or sporadically deciduous. The most common tree species, *Pentaclethra macroloba*, accounts for 34% of the basal area and 13% of stems (Lieberman et al. 1996; Clark and Clark 2000). Tree species differ in the timing and synchronicity of leaf flushing and leaf fall. Forest-level peak litterfall occurs during the latter part of the drier season (Frankie et al. 1974; D.A. Clark unpublished data).

Leaf litter collection and nutrient analysis

Eighteen 0.50-ha plots were established by the CARBONO Project at La Selva (cf. Clark and Clark 2000) in the three major old-growth edaphic conditions (inceptisol terrace, ultisol plateau, ultisol on steep slope; Figure 2). The La Selva GIS was used to site the plots in an unbiased, replicated design to sample

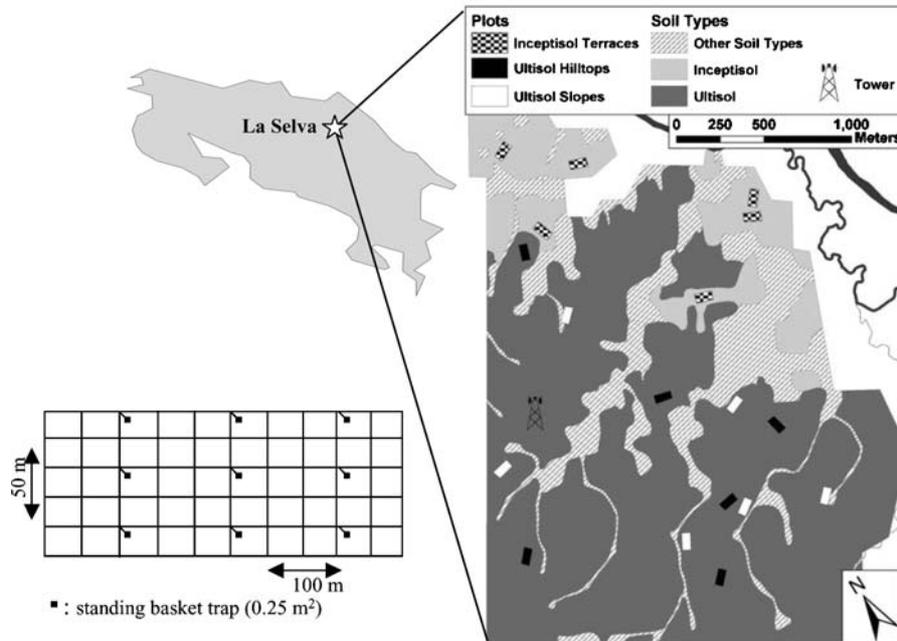


Figure 2. Map of study region and plots at La Selva Biological Station, Costa Rica. The 18 0.50 ha plots were stratified across the three main soil types: inceptisol terraces, ultisol hilltops and ultisol slopes (Clark and Clark 2000; map prepared by A. Trabucco).

the three edaphic types. Within each plot, leaf litterfall was collected from nine 0.25 m² litterfall traps every 2 weeks beginning in September 1997 (Figure 2). Samples were bulked by plot, then sorted by litter material (leaves, reproductive material, wood < 1 cm in diameter), and dried at 65 °C to constant mass. The leaf material is then run through a Wiley Mill to pass through a 1 mm mesh screen.

To determine %N and [P] of the leaf litter, we performed a modified Kjeldahl digestion on a Tecator 2000 Digestion System (Perstorp Analytical; Sweden). This method uses 30% hydrogen peroxide and concentrated sulfuric acid at 360 °C to hydrolyze organic N and P to an inorganic form. Digested samples were kept refrigerated until further analysis. The matrix was analyzed colorimetrically on an Alpkem Flow Solution IV Auto analyzer (OI Analytical; College Station, Texas, USA) in accordance with the US EPA method for total P and total Kjeldahl N determination.

Leaf litter calcium (Ca), magnesium (Mg), and potassium (K) were analyzed at the Cornell Nutrient Analysis Laboratory (CNAL) using an HNO₃/H₂O₂ block digestion at 150 °C. The samples were then re-dissolved in 50 ml of 10% nitric acid for analysis using Spectro CIROS CCDE Inductively Coupled Argon Emission Plasma Spectrometry (ICP).

Seasonal and inter-annual variability

We analyzed seasonal changes in leaf [P], %N and N:P. Month-to-month variation was analyzed by repeated measures analysis of variance (RANOVA) on one leaf litter sample every 4 weeks collected from three inceptisol and three ultisol plots over the 2-year period October 1997–September 1999 (fine resolution; 48 dates; 288 samples). The degree of P versus N limitation was determined using the N:P ratio (Koerselman and Meuleman 1996; Aerts and Chapin 2000; Knecht and Goransson 2004).

Inter-annual variability in leaf litter [P], %N, [Ca], [K], and [Mg] were evaluated using a longer, 4-year data set. Samples from the peak, minimum and midseason litterfall periods spanning October 1997 through April 2001 were used. For P and N, data include samples from all 18 CARBONO plots (coarse resolution; 11 dates; 198 samples); for cations, data from 12 plots were used (4 ultisol slopes, 4 ultisol plateaus, 4 inceptisols; 11 dates; 132 samples). Changes in leaf litter nutrient concentrations over the 4-year period were determined using a two-way ANOVA by year and by soil type. We followed up with a two-factor ANOVA within each soil type (by plot and by year) to determine when inter-annual differences occurred when the Tukey–Duncan *post hoc* test was not significant. All ANOVAs were performed using SAS System for Windows V8 (1999–2001; SAS Institute Inc.).

Regressions with leaf litter nutrient concentration: short-term

Using univariate regression, we related local precipitation and wind data to leaf litter [P], %N, [K], [Ca], and [Mg]. Time lags of 0 and 2 weeks were used to examine whether precipitation directly influenced leaf litter nutrients, with precipitation summed over the 2-week collection period or over the 2 weeks immediately prior to the collection period. Hourly and maximum wind speeds averaged over the entire 2-week collection period were also related to leaf litter nutrient concentrations.

Regressions with leaf litter nutrient concentration: long-term

To determine the relationship between long-term precipitation patterns and litter [P] and %N caused by precipitation-linked changes in litter production, time lag regressions were performed between litter nutrients and precipitation 12, 14, 16, 18 and 20 weeks prior. Due to the number of comparisons, an α value of 0.0125 was used for all of the long-term precipitation analyses with multiple comparisons (Bonferonni Correction: $[0.05/n-1]$). All regressions were conducted using SigmaPlot (2001; SPSS Inc.).

To determine the direct source–sink relationship between litter production and litter [P] and %N, time-lag regressions were performed using contempo-

aneous leaf litter production data for all 18 CARBONO plots (2 week collection period; D.A. Clark unpublished data). Leaf litter production was averaged across soil type in order to minimize factors that might lead to variation in time lags such as differences in decomposition rates and the timing of soil nutrient availability.

We used fruit/flower litter production data to test the source–sink interaction hypothesis. Fruits and flowers collected in the litter traps (indicative of previous fruit and flower production) were used for these analyses because data on actual fruit and flower production were unavailable. We compared leaf litter nutrient levels with the mass of fruit/flower litter at the same time, and 6, 8, 10, and 12 weeks into the future. Positive lags were used because we assumed that the nutrient demands of fruit and flower production were provided by translocation of nutrients from litter falling during formation and maturation.

To examine the hypothesis that high leaf litter production feeds back positively on future leaf litter nutrient concentrations, we compared leaf litter [P] with litter mass from 12, 14, 16, 18 and 20 weeks prior. Leaf litter production was averaged for each site for each of the 2-week collection periods compared. Values were averaged by soil type in order to minimize factors that might lead to variation in time lags such as differences in decomposition rates and the timing of soil nutrient availability.

Results

Seasonal patterns and inter-annual variability

Leaf litter [P] changed significantly with time over the 2-year monthly sample period (RANOVA, time effect, $p = 0.047$, $F = 1.60$, $df = 27$). In both years, leaf litter [P] reached a maximum during the rainy season 3–5 mo following peak litterfall (June–August/weeks 40–48; peak litterfall = March–April/weeks 24–28; Figure 3a). The maximum [P] for inceptisols was 1.42 mg/g and the maximum for ultisol plateaus was 0.96 mg/g. There was no discernable seasonal pattern for the occurrence of leaf litter P minima (Figure 3a).

Leaf litter %N also changed significantly with time over the 2-year monthly sample period (RANOVA, time effect, $p < 0.0001$, $F = 4.07$, $df = 23$). A distinctive peak in %N occurred during the ENSO year (1997–1998) for both inceptisols (2.8%; March/week 24) and ultisols (3.9%; February/week 20). The lowest %N values occurred in the subsequent study year (inceptisols: 1.6%, November/week 8 [year2]; ultisols: 1.4%, July/week 44 [year2]; Figure 3b). Whereas %N in the ultisols decreased during the wet season months of both years (July/week 44 for both years), the inceptisols showed a wet season decline in the ENSO year only (July/week 40; Figure 3b). The N:P ratio followed a very similar pattern to that of %N (Figure 3c). The ratio changed significantly with time (RANOVA; time effect, $p < 0.0001$, $F = 4.62$, $df = 23$) and the maxima and minima of N:P occurred on the same dates as those for %N. An

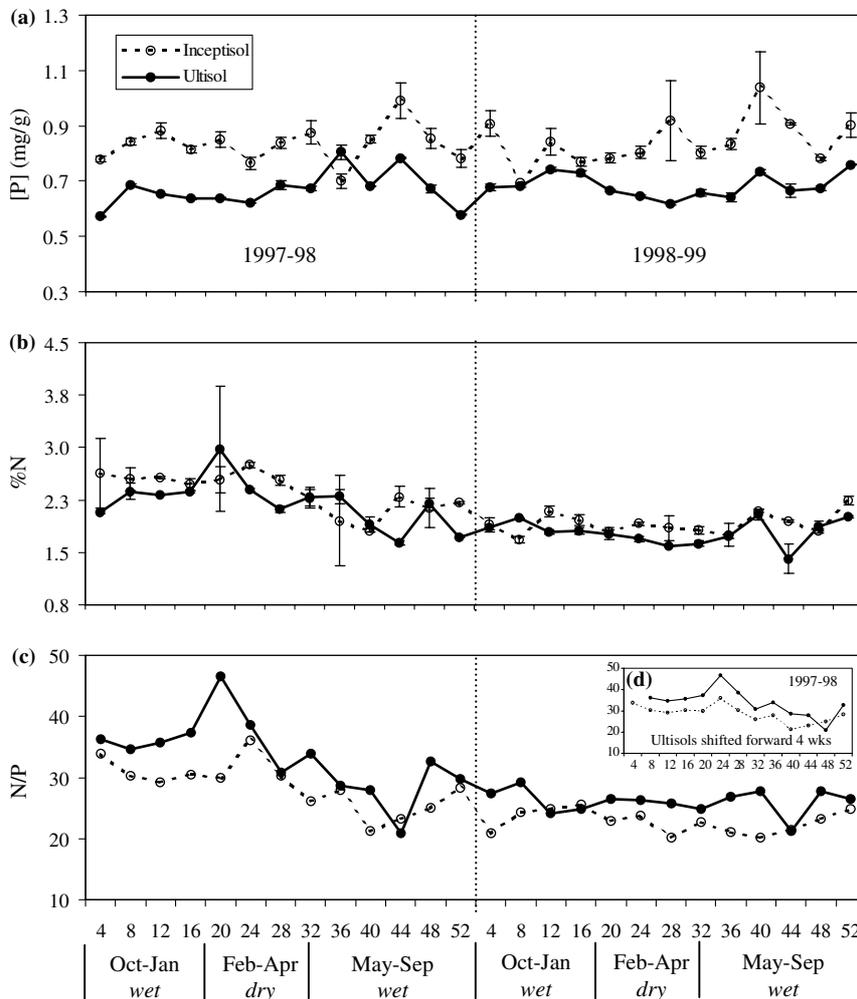


Figure 3. Seasonal trends of (a) Leaf litter [P], (b) %N, (c) N:P over a 2-year period by soil type and (d) seasonal N:P for the ENSO year with ultisol values shifted 4 weeks forward. Means \pm 1S.E. for three inceptisol plots and three ultisol plots for each 4 week sample. All six plots varied significantly with time.

asynchrony in the N:P ratio occurred between the inceptisols and ultisols in the ENSO year. While the pattern of change is similar between the two soil types, the ultisols responded 4 weeks earlier than the inceptisols (Figure 3c, d).

The 4-year coarse-resolution data (18 sites; 3 dates/year \times 4 years) revealed significant differences in leaf litter [P] among years (Table 1; two-way ANOVA, time effect $p=0.0373$; $F=2.879$, $df=3$) and among the three edaphic conditions. Leaf litter [P] for ultisols declined in 1999–2000 and then recovered in 2000–2001 (Table 1; Tukey–Duncan). Although the decrease in 1999–2000 was

not significant for inceptisols, the trend was the same. Leaf litter %N decreased over the first three study years and leveled out in the third and fourth study years. Across all soil types, leaf-litter [K] and [Mg] significantly increased in year three (Table 1; two-way ANOVA; time effect $p=0.001$, $F=5.733$, $df=3$ (K), $p=0.0278$, $F=3.144$, $df=3$ (Mg)). Both [K] and [Mg] were no different in the fourth sample year from their values prior to the increase (Table 1). Calcium concentrations did not differ between years (Table 1; two-way ANOVA, $p=0.563$; $F=0.685$, $df=3$).

Regressions of leaf litter nutrient concentration

Over the 4-year time frame, leaf litter [P] and current precipitation were positively related in all three edaphic types (Figure 4a–c; $R^2=0.67$, $n=11$, $p=0.0038$ (inceptisol); $R^2=0.773$, $n=11$, $p=0.0008$ (ultisol plateau); $R^2=0.51$, $n=11$, $p=0.0135$ (ultisol slope)). For both the inceptisol and ultisol plateau, a single outlier was removed from the regression (Figure 4b, c; open circles). Outliers were determined using the DFITTS statistic. (Sigma Plot 2001). Both outliers occurred in October of the 1997–1998 El Niño year. This period was unusually wet for the ‘veranillo’ season. Approximately 370–580 mm more rain fell from August–October 1997 than in the subsequent three study years; hence this date

Table 1. Mean annual leaf litter nutrient concentrations by soil type for the 4 study years (3 dates/year \times 6 sites/soil type)

	1997–1998	1998–1999	1999–2000	2000–2001
N (%)	a	b	c	c
inceptisol	2.34 \pm 0.06	1.94 \pm 0.05	1.63 \pm 0.06	1.48 \pm 0.03
ultisol plateau	2.05 \pm 0.07	1.72 \pm 0.07	1.35 \pm 0.04	1.41 \pm 0.09
ultisol slope	2.01 \pm 0.16	1.77 \pm 0.03	1.36 \pm 0.03	1.54 \pm 0.09
P (mg g ⁻¹)	ab	a	b	ab
inceptisol	0.82 \pm 0.03	0.89 \pm 0.03	0.84 \pm 0.04	0.81 \pm 0.03
ultisol plateau	0.63 \pm 0.02	0.67 \pm 0.03	0.60 \pm 0.03	0.66 \pm 0.02
ultisol slope	0.70 \pm 0.02	0.70 \pm 0.02	0.64 \pm 0.02	0.70 \pm 0.03
K (mg g ⁻¹)	a	a	b	ab
inceptisol	2.82 \pm 0.24	3.31 \pm 0.28	3.84 \pm 0.68	3.33 \pm 0.42
ultisol plateau	1.67 \pm 0.03	1.77 \pm 0.11	2.52 \pm 0.43	2.28 \pm 0.37
ultisol slope	2.16 \pm 0.18	2.16 \pm 0.03	2.80 \pm 0.32	1.85 \pm 0.36
Mg (mg g ⁻¹)	a	a	b	ab
inceptisol	1.98 \pm 0.14	2.05 \pm 0.04	2.13 \pm 0.15	1.95 \pm 0.06
ultisol plateau	2.16 \pm 0.02	2.04 \pm 0.06	2.58 \pm 0.22	2.26 \pm 0.02
ultisol slope	1.97 \pm 0.20	1.91 \pm 0.09	2.07 \pm 0.18	1.92 \pm 0.06
Ca (mg g ⁻¹)	a	a	a	a
inceptisol	8.00 \pm 0.68	8.2 \pm 0.29	8.02 \pm 0.63	7.48 \pm 0.013
ultisol plateau	8.06 \pm 0.22	7.64 \pm 0.36	8.79 \pm 0.47	8.69 \pm 0.22
ultisol slope	7.51 \pm 0.34	6.58 \pm 0.55	7.11 \pm 0.17	7.02 \pm 0.03

Different letters indicate significant differences among years.

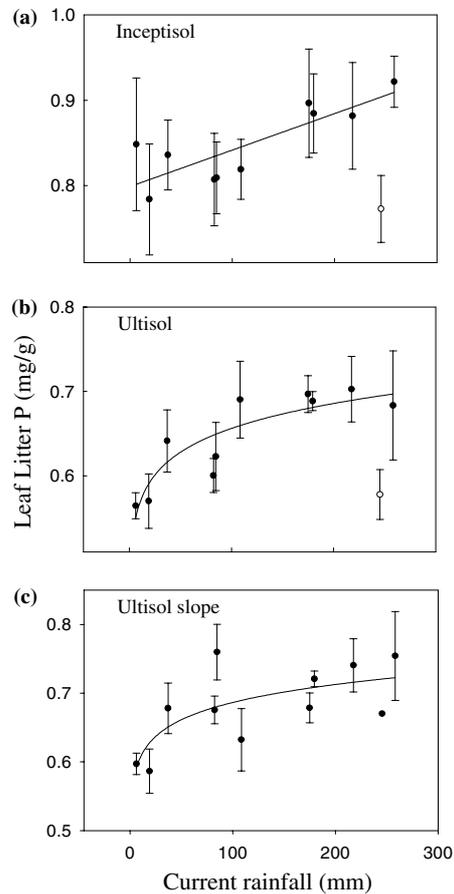


Figure 4. The effect of current rainfall on mean leaf litter [P] (a) inceptisol ($R^2=0.67$, $p=0.0038$, $n=11$), (b) ultisol plateau ($R^2=0.77$, $p=0.0008$, $n=11$), (c) ultisol slope ($R^2=0.51$, $p=0.0135$, $n=11$). Current precipitation defined as the rain falling during the 2-week litter collection period. The open circles in figures (b) and (c) are outliers (DFITTS statistic, SigmaPlot). Both outliers occurred in October 1997 (El Niño year), which received more rainfall than is usual for this period.

was anomalous in the amount of precipitation it received (Figure 1). Neither mean wind speed nor maximum wind speed were significantly related to leaf litter [P]. There was no significant relationship between current rainfall and %N.

Across all soil types, [K] and [Mg] strongly declined with increased rainfall during the 2-week collection period (Figure 5a–f). This relationship was most pronounced for K, which decreased very rapidly to a minimum when precipitation exceeded 50 mm (Figure 5a–c). Calcium concentrations declined with increased precipitation in the ultisol plots (Figure 5h).

Due to the negative relationship between leaf litter production and precipitation (D. Lawrence unpublished data) and the hypothesized link between

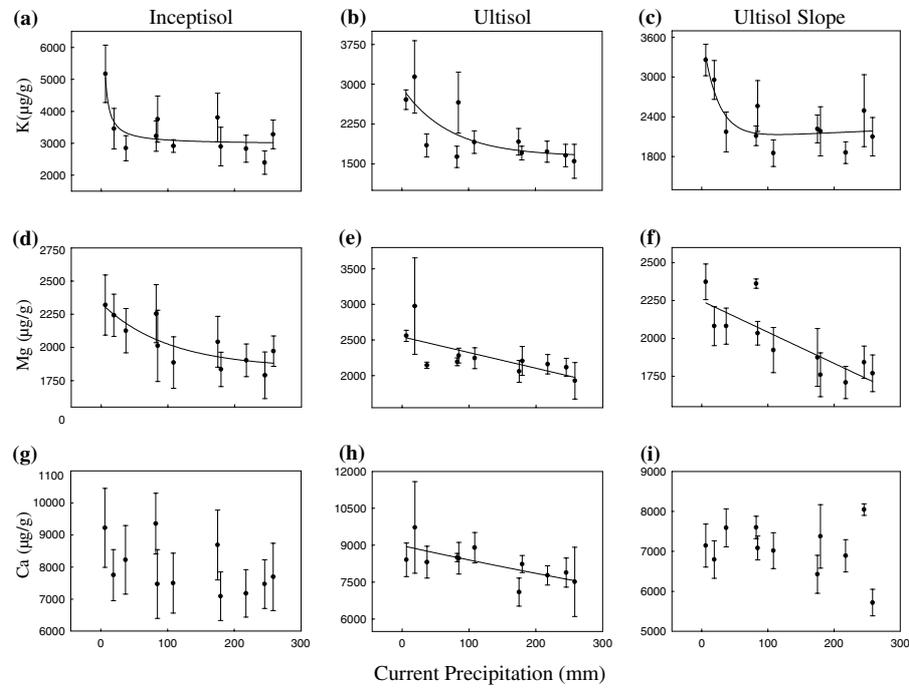


Figure 5. The effect of current precipitation on leaf litter [K] ((a) inceptisol ($R^2=0.67$, $p=0.0119$, $n=11$), (b) ultisol plateau ($R^2=0.59$, $p=0.0296$, $n=11$), (c) ultisol slope ($R^2=0.72$, $p=0.0239$, $n=11$)), [Mg] ((d) inceptisol ($R^2=0.70$, $p=0.008$, $n=11$), (e) ultisol plateau ($R^2=0.50$, $p=0.0148$, $n=11$), (f) ultisol slope ($R^2=0.67$, $p=0.002$, $n=11$)), and [Ca] ((g) inceptisol (n.s., $n=11$), (h) ultisol plateau ($R^2=0.50$, $p=0.0145$, $n=11$), (i) ultisol slope (n.s., $n=11$)).

decomposing litter, soil nutrient availability, and subsequent litter nutrient concentrations, we expected [P] and %N to be negatively related to precipitation with a long time lag. As expected, mean leaf litter [P] across soil types declined significantly with precipitation from 16 weeks previous in the ultisols and ultisol slopes, and from 18 weeks previous in the inceptisols (Figure 6a–c). In contrast, %N was not related to precipitation at any of the time lags tested.

Leaf litter [P] and leaf litter production 12 weeks prior showed a positive trend for ultisol soil types (Figure 7b, c); in ultisol plateaus, the relationship was significant. Leaf litter [P] and leaf litter production 16 weeks prior also showed a positive relationship in inceptisols (Figure 7a). Leaf litter production from 10 to 12 weeks prior was significantly positively related to %N for all soil types (Figure 7d–f; inceptisols: 10 weeks, $R^2=0.46$, $p=0.031$, $n=10$; ultisols: 12 weeks, $R^2=0.81$, $p=0.001$, $n=10$; ultisol slopes: 10 weeks, $R^2=0.46$, $p=0.032$, $n=10$).

Fruit/flower litterfall was not significantly related to leaf litter [P] at any of the time lags tested. However, %N was positively related to fruit/flower litter mass 8 weeks later in ultisol slope sites ($R^2=0.66$, $p=0.002$, $n=11$).

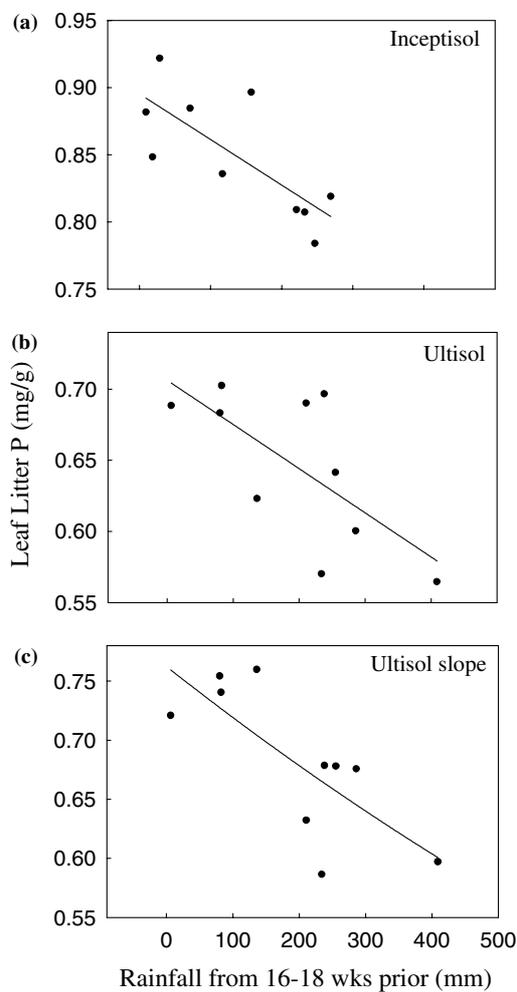


Figure 6. The effect of prior rainfall on leaf litter [P] by soil type (average of 6 sites for a given date). (a) inceptisols ($R^2=0.58$, $p=0.0108$, $n=10$), (b) ultisol plateaus ($R^2=0.47$, $p=0.0287$, $n=10$), (c) ultisol slopes ($R^2=0.57$, $p=0.0115$, $n=10$).

Discussion

Seasonal variation in N, P and N:P

Based on the average 2-year N:P ratio, this system is limited by P (Koerselman and Meuleman 1996; Knecht and Goransson 2004). The N:P values for this region are average for a tropical rain forest (26–29 versus 28 (mean); T.E. Wood unpublished data). The N:P ratio changed significantly with time over

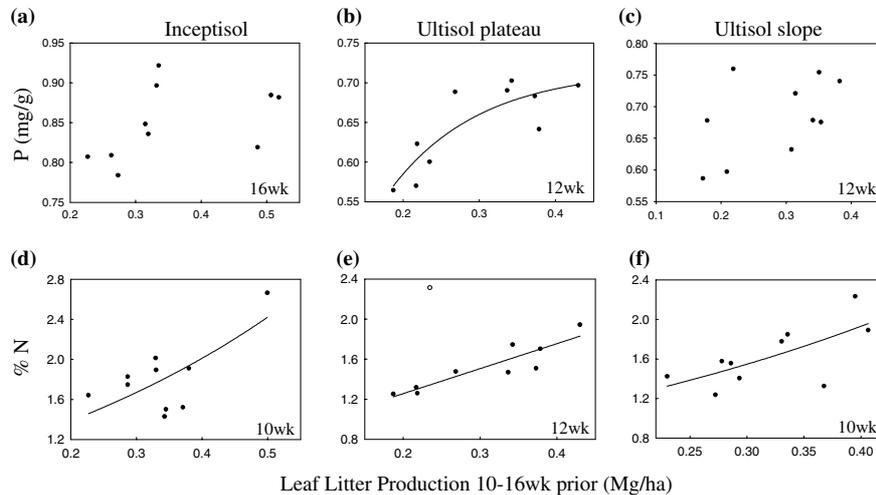


Figure 7. The effect of prior leaf litter production on leaf litter [P] ((a) inceptisols ($R^2=0.337$, $p=0.079$, $n=10$), (b) ultisol plateaus ($R^2=0.74$, $p=0.0015$, $n=10$), (c) ultisol slopes ($R^2=0.27$, $p=0.0996$, $n=10$)) and %N ((d) inceptisols ($R^2=0.46$, $p=0.031$, $n=10$), (e) ultisol plateaus ($R^2=0.81$, $p=0.001$, $n=10$), (f) ultisol slopes ($R^2=0.46$, $p=0.032$, $n=10$)).

the 2-year study period. This variation was driven mainly by changes in N (CV = 14–18% (N) versus 8–9% (P)).

In both the first and second study years, the wet season months (June–August/weeks 36–52) were characterized by lower N:P ratios as a result of lower leaf litter %N and higher leaf litter [P] (Figure 3c). These results are contrary to those of Chuyong et al. (2000, wet forest) and Read and Lawrence (2003, dry forests) where leaf litter %N decreased during the dry season months. The lower N:P ratio during the wet season months could be due to a shift in the relative amounts of N and P availability in the soil and/or a change in the vegetative demand for these nutrients (source–sink interactions) (Nambiar and Fife 1991; Newbery et al. 1997).

The N:P ratios peaked during the dry season months of the ENSO year (February–April/weeks 20–32; 47 ultisols, 36 inceptisols; Figure 3c). The occurrence of high N:P ratios during the extended ENSO dry season suggests a shift towards greater P demand relative to N during this period. In addition to high N:P ratios, there was a striking asynchrony in N:P values between ultisols and inceptisols during the ENSO year, such that ultisols responded 4 weeks earlier than inceptisols. Hence, the positive shift in N:P ratio occurred one month earlier in the less fertile ultisols (Figure 3c, d). In contrast, the second study year did not exhibit the same inceptisol-ultisol N:P asynchrony. Differences in N:P between soil types was minimal and N:P ratios were on average lower. The discrepancy in N:P patterns between the two

years suggests that this system responds to environmental variation on a supra-annual basis and may reflect a response to ENSO related climatic variability.

Inter-annual variation

With the exception of Ca, all of the leaf litter nutrient concentrations varied across years (Table 1). Significant variation occurred among the first three study years, with no change for any of the nutrients between years 3 and 4 (Table 1). This pattern of inter-annual variation suggests that leaf litter nutrient cycling responded to an environmental forcing present during the first two study years and not in the subsequent 2 years. The ENSO of 1997–1998 is the most likely cause.

Overall, leaf litter %N showed the greatest inter-annual variation. The greater inter-annual variation of N compared with the other nutrients indicates that N is not cycled as tightly as P and the cations (Vitousek 1984).

Regressions with leaf litter nutrient concentration

Leaf litter [P] increased with the amount of precipitation during the collection period. Hence, while leaching may have a small negative effect on leaf litter [P], the net positive relationship suggests that leaching is not the major driver of variation. Possible explanations include (1) live tissue concentrations change in response to soil nutrient availability while nutrient resorption remains constant (Cuevas and Medina 1986; Vitousek and Sanford 1986; Aerts and Chapin 2000; McGrath et al. 2000; Cleveland et al. 2004; however, see Newbery et al. 1997) (2) a decrease in P demand by the vegetation in response to a wet season phenological event (i.e. source–sink interactions) (Nambiar and Fife 1991; Newbery et al. 1997) (3) reduced nutrient resorption in response to increased effective soil nutrient availability associated with wet season months (Boerner 1985; Cuevas and Medina 1986; del Arco et al. 1991; Escudero et al. 1992; McGrath et al. 2000; Cleveland et al. 2004; however, see Chapin and Moilanen 1991; Aerts 1996; Aerts and Chapin 2000). Given that we observed no relationship between leaf litter [P] and wind velocity, the temporal pattern of leaf litter [P] was probably not due to an increase in nutrient-rich green leaf tissue in the litter traps.

In contrast to the positive relationship between current precipitation and [P], the negative relationship between [K] and [Mg] and precipitation is most likely the result of leaching from live leaf tissue. This is especially true of K, which is highly soluble and not bound to any known organic compounds (Epstein 1972; Veneklaas 1991; Schlesinger 1997). The lack of a significant trend in Ca for two of the three edaphic types may be because Ca is

incorporated into leaf structures, reducing the concentration of mobile Ca in leaf tissue.

Alternatively, a negative relationship between cation concentrations and rainfall could be due to leaching/decomposition in the litter traps; however, if this were occurring during the 2 week collection period, we would expect N and P, which are also susceptible to leaching, to decline as well. A litter decomposition study conducted in Guatemala showed that Mg and P are lost from litter at similar rates during the first 2 weeks (Ewel 1976). The positive relationship between P, but not Mg, and rainfall leads us to conclude that cation leaching is most likely occurring in the canopy rather than in the litter traps.

This study suggests that long-term patterns of precipitation (16–18 weeks) influence leaf litter nutrient cycling. As with short-term variability in precipitation, changing soil nutrient availability should be further investigated as the proximate mechanism for changing litter chemistry. Whereas the immediate effects of precipitation should occur due to the mediating influence of soil moisture, the long-term effects may occur due to the negative impact of precipitation on the amount of leaf litter that falls. In support of this developing hypothesis, we found a negative relationship between rainfall and leaf litter [P] on a long time lag (16–18 weeks). We also found a weak positive relationship between litterfall mass and [P] on a shorter-time lag (12–16 weeks) that accommodates a negative link between precipitation and litterfall in mature forests. The timing of these lags coincides with documented rates of nutrient cycling through the litter–soil system (Figure 8). In the Guatemalan decomposition study, approximately 80% of P was lost from leaf litter within the first 10 weeks of decomposition (Ewel 1976). In our study, we found a positive relationship between leaf litterfall 12–16 weeks prior and current leaf litter [P]. In addition, maximum leaf litter [P] occurred in the wet season just 12–16 weeks after peak leaf litter production, within the same time frame as the demonstrated lag between leaf litter production and leaf litter [P]. Hence, it is likely that leaf litter production does feed back positively on subsequent leaf litter nutrient concentrations (Figure 8).

The 10–12 week time lag between leaf litter production and %N also supports a positive feedback from litter production (Figure 8). That the relationships were significantly earlier than those for leaf litter [P] may reflect less immobilization of N than of P. This result is consistent with the P limitation suggested above. Leaf litter %N was significantly positively related to a proxy for current fruit/flower development (+ 8 week lag). One explanation may be that more N leads to greater photosynthesis (Reich et al. 1997) and thus more carbohydrates for fruit production.

To better understand feedbacks among precipitation, litter production and litter chemistry, further research should focus on forest floor and belowground processes that control nutrient availability such as decomposition and immobilization, as well as controls on nutrient resorption from leaf tissue (e.g. Figure 8).

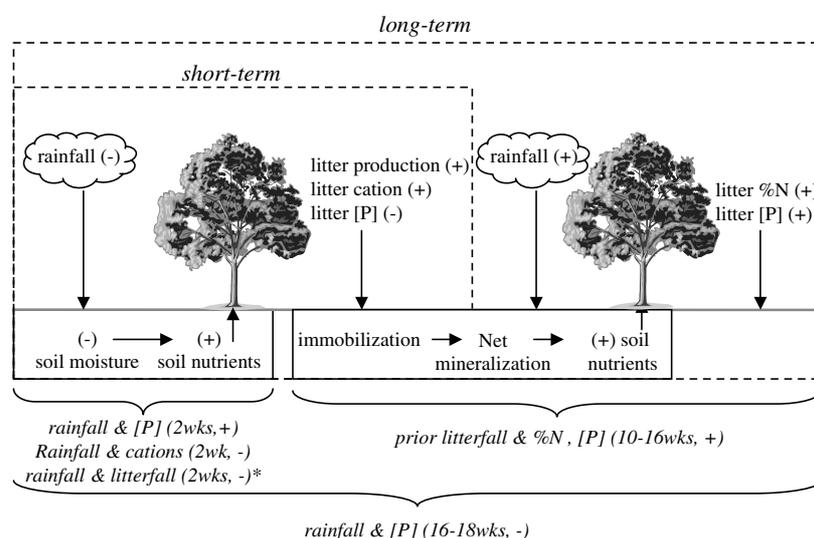


Figure 8. Time scale of short- and long-term relationships among leaf litter nutrient concentrations, precipitation, and leaf litter production demonstrated in this study. Short-term changes in leaf litter [P] and cations are likely driven by rainfall, via the influence of rain on soil moisture, nutrient uptake and leaching. Long-term variation in leaf litter [P] and %N appears to be partially influenced by pulses of nutrient availability provided by the decomposition of litter. *D. Lawrence, unpub. data.

Conclusion

The N:P ratios changed over the 2-year study period with lower ratios consistently in the wet season months. We propose that this seasonal variation is due to changes in the relative availability of these nutrients in the soil and/or a shift in nutrient demand by the vegetation. In the ENSO year, P appeared to be more limiting than in the subsequent year, and this P limitation was more pronounced in the less fertile ultisols than in the inceptisols. The pattern of N:P variation also differed between edaphic types such that the ultisols responded 4 weeks earlier than inceptisols. These results indicate that during periods of high P demand relative to N, differences in leaf litter nutrient cycling between ultisols and inceptisols are exacerbated.

Overall, precipitation appears to be a major driver of short-term variation in leaf litter P and cation concentrations. This was especially true when precipitation levels were below 150 mm. An increase in soil nutrient availability associated with higher soil moisture is proposed as an explanatory mechanism for further study. Dynamics in the major cations K and Mg (but not Ca) suggest that leaching from leaf tissue in the canopy is an important source of variation in these nutrients.

Longer-term variation in [P] and %N is consistent with pulses of nutrient availability provided by the decomposition of leaf litter (Figure 8). Inter-an-

nual variation of leaf litter nutrients indicates that single-year studies could potentially miss important responses of nutrient cycling to climatic variability. Although controversial, one of the projected consequences of global climate change is an expectation of more intense and frequent ENSO events. The associated intensification of seasonality in precipitation could lead to intensified pulses of nutrient availability through changes in leaf litter production, quality, and decomposition rates. Ultimately, changes in the rate of nutrient supply could have longer-term effects on net primary productivity, carbon storage, and species composition.

Acknowledgements

Research in the CARBONO plots was based upon work supported by the National Science Foundation under Grant DEB-9629245 and the Department of Energy Grant DE-FG02-96ER62289. Funding was also provided by a grant from the Andrew W. Mellon Foundation.

References

- Aerts R. 1996. Nutrient resorption from senescing leaves of perennials: Are there general patterns? *J. Ecol.* 34(4): 597–608.
- Aerts R. and Chapin F.S. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30: 1–67.
- Boerner R.E.J. 1985. Foliar nutrient dynamics, growth, and nutrient use efficiency of *Hamamelis virginiana* in three forest microsites. *Can. J. Bot.* 63: 1476–1481.
- Campo J., Jaramillo V.J. and Maass J.M. 1998. Pulses of soil phosphorus availability in a Mexican tropical dry forest: effects of seasonality and level of wetting. *Oecologia* 115: 167–172.
- Campo J., Maass J.M., Jaramillo V.J., Martinez-Yrizar A. and Sarukhan J. 2001. Phosphorus cycling in a Mexican tropical dry forest ecosystem. *Biogeochemistry* 53: 161–179.
- Chapin F.S. and Moilanen L. 1991. Nutritional controls over nitrogen and phosphorus resorption from Alaskan Birch leaves. *Ecology* 72(2): 709–715.
- Chuyong G.B., Newbery D.M. and Songwe N.C. 2000. Litter nutrients and retranslocation in a central African rain forest dominated by ectomycorrhizal trees. *New Phytol.* 148: 493–510.
- Clark D.A. 2004. Sources or sinks?: the responses of tropical forests to current and future climate and atmospheric composition *Philos. Trans. R. Soc. Lond. Ser. B* 359: 477–491.
- Clark D.B. and Clark D.A. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecol. Manage.* 137: 185–198.
- Clark D.A., Piper S.C., Keeling C.D. and Clark D.B. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proc. Natl. Acad. Sci. USA* 100(10): 5852–5857.
- Cleveland C.C., Townsend A.R., Constance B.C., Ley R.E. and Schmidt S.K. 2004. Soil microbial dynamics in costa rica: seasonal and biogeochemical constraints. *Biotropica* 36(2): 184–195.
- Condit R., Ashton P.S., Baker P., Bunyavejchewin S., Gunatilleke S., Gunatilleke N., Hubbell S.P., Foster R.B., Itoh A., LaFrankie J.V., Lee H.S., Losos E., Manokaran N., Sukumar R. and Yamakura T. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414–1418.
- Cuevas E. 1995. Biology of the belowground system of tropical dry forests. In: Mooney H. A., Bullock S.H. and Medina E. (eds), *Seasonally Dry Tropical Forests*. Cambridge University Press, Cambridge, pp. 362–383.

- Cuevas E. and Lugo A.E. 1998. Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. *Forest Ecol. Manage.* 112: 263–279.
- Cuevas E. and Medina E. 1986. Nutrient dynamics within amazonian forest ecosystems. I. Nutrient flux in fine litter fall and efficiency of nutrient utilization. *Oecologia* 68: 466–472.
- Curran L.M., Caniago I., Paoli G.D., Astianti D., Kusneti M., Leighton M., Nirarita C.E. and Haeruman H. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286: 2184–2188.
- Dean J.M. and Smith A.P. 1978. Behavioral and morphological adaptations of a tropical plant to high rainfall. *Biotropica* 10: 152–154.
- del Arco J.M., Escudero A. and Garrido V.M. 1991. Effects of site characteristics on nitrogen retranslocation from senescing leaves. *Ecology* 72(2): 701–708.
- Epstein E. 1972. *Mineral Nutrition of Plants: Principles and Perspectives*. John Wiley & Sons, Inc., New York.
- Escudero A., del Arco J.M., Sanz I.C. and Ayala J. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia* 90: 80–87.
- Ewel J.J. 1976. Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *J. Ecol.* 64: 293–307.
- Frankie G.W., Baker H.G. and Opler P.A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881–919.
- Gessel S.P., Cole D.W., Johnson D. and Turner J. 1980. The nutrient cycles of two Costarican forests. *Prog. Ecol.* 3: 23–44.
- Haines B. and Foster R.B. 1977. Energy flow through litter in a Panamanian forest. *J. Ecol.* 65: 147–155.
- Herbohn J.L. and Congdon R.A. 1993. Ecosystem dynamics at disturbed and undisturbed sites in north Queensland wet tropical rain forest. II. Litterfall. *J. Trop. Ecol.* 9: 365–380.
- Herbohn J.L. and Congdon R.A. 1998. Ecosystem dynamics at disturbed and undisturbed sites in North Queensland wet tropical rain forest. III. Nutrient returns to the forest floor through litterfall. *J. Trop. Ecol.* 14: 217–229.
- Holbrook N.M., Whitbeck J.L. and Mooney H.A. 1995. Drought responses of neotropical dry forest trees. In: Mooney H.A., Bullock S.H. and Medina E. (eds), *Seasonally Dry Tropical Forests*. Cambridge University Press, Cambridge, pp. 243–276.
- Holdridge L.R. 1947. Determination of world plant formations from simple climatic data. *Science* 105(2727): 367–368.
- Hopkins B. 1966. Vegetation of the Olokemeji Forest Reserve, Nigeria. *J. Ecol.* 54: 687–703.
- Klinge H. and Rodrigues W.A. 1968. Litter production in an area of Amazonian Terra Firme forest. Part I. Litterfall, organic carbon and total nitrogen contents of litter. *Amazoniana* 1: 287–302.
- Knecht M.R. and Goransson A. 2004. Terrestrial plants require nutrients in similar proportions. *Tree Phys.* 24(4): 447–460.
- Koerselman W. and Meuleman A.F.M. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J. App. Ecol.* 33(6): 1441–1450.
- Killingbeck K.T. 1996. Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology* 77(6): 1716–1727.
- Kunkel-Westphal I. and Kunkel P. 1979. Litter fall in a Guatemalan primary forest, with details of leaf-shedding by some common tree species. *J. Ecol.* 67: 665–686.
- Lawrence D. and Foster D. 2002. Changes in forest biomass, litter dynamics and soils following shifting cultivation in southern Mexico: an overview. *Interciencia* 27(8): 400–408.
- Lieberman D., Lieberman M., Peralta R. and Hartshorn G.S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecol.* 84: 137–152.
- Lodge D.J., McDowell W.H. and McSwiney C.P. 1994. The importance of nutrient pulses in tropical forests. *TREE* 9(10): 384–387.

- Lodge D.J., Scatena F.N., Asbury C.N. and Sanchez M.J. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. *Biotropica* 23(4): 336–342.
- Marschner H. 1995. *Mineral Nutrition of Higher Plants*, 2nd ed. Academic Press, San Diego.
- Martinez-Yrizar A. and Sarukhan J. 1990. Litterfall patterns in a tropical deciduous forest in Mexico over a five-year period. *J. Trop. Ecol.* 6(4): 433–444.
- McGrath D.A., Comerford N.B. and Duryea M.L. 2000. Litter dynamics and monthly fluctuations in soil phosphorus availability in an Amazonian agroforest. *Forest Ecol. Manage.* 131(13): 167–181.
- Murphy P.G. and Lugo A.E. 1986. Ecology of tropical dry forest. *Ann. Rev. Ecol. Syst.* 17: 67–88.
- Nambiar E.K.S. and Fife D.N. 1991. Nutrient retranslocation in temperate conifers. *Tree Physiol.* 65: 185–207.
- Newbery D.M., Alexander I.J. and Rother J.A. 1997. Phosphorus dynamics in a lowland African rain forest: The influence of ectomycorrhizal trees. *Ecol. Monogr.* 67(3): 367–409.
- Palma R.M., Defrieri R.L., Tortarolo M.F., Raue J. and Gallardo J.F. 2000. Seasonal changes of bioelements in the litter and their potential return to green leaves in four species of the Argentine Subtropical Forest. *Ann. Bot.* 85: 181–186.
- Read L. and Lawrence D. 2003. Litter nutrient dynamics during succession in dry tropical forests of the Yucatan: regional and seasonal effects. *Ecosystems* 6(8): 747–761.
- Reich P.B., Walters M.B. and Ellsworth D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. USA* 94: 13730–13734.
- Salifu K.F. and Timmer V.R. 2001. Nutrient retranslocation response of *Picea mariana* seedlings to nitrogen supply. *Soil Sci. Soc. Am. J.* 65(3): 905–913.
- Richardson S.J., Peltzer D.A., Allen R.B., McGlone M.S. and Parfitt R.L. 2004. Rapid development of phosphorus limitation in temperate forest along the Franz Josef soil chronosequence. *Oecologia* 139: 267–276.
- Salisbury F.B. and Ross C.W. 1992. *Plant Physiology*. Wadsworth Publishing Company, Belmont.
- Sanford R.L., Paaby P., Luvall J.C. and Phillips E. 1994. Climate, geomorphology, and aquatic systems. In: McDade L.A., Bawa K.S., Hespeneheide H.A. and Hartshorn G.S. (eds), *La Selva: Ecology and Natural History of a Neotropical Rainforest*. University of Chicago Press, Chicago, pp. 34–53.
- Schlesinger W.H. 1997. *Biogeochemistry: An Analysis of Global Change*. Academic Press, San Diego.
- Schuur E.A.G. and Matson P.A. 2001. Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia* 128(3): 431–442.
- Scott D.A., Proctor J. and Thompson J. 1993. *Ecological Studies on a Lowland Evergreen Rain Forest on Maraca Island, Roraima, Brazil. II. Litter and Nutrient Cycling*. *J. Ecol.* 80(4): 705–717.
- Sizer N.C., Tanner E.V.J. and Kossman Ferraz I.D. 2000. Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia. *J. Trop. Ecol.* 16: 853–863.
- Sollins P., Sancho F.M., Mata R.C. and Sanford R.L. 1994. Soils and soil process research. In: McDade L.A., Bawa K.S., Hespeneheide H.A. and Hartshorn G.S. (eds), *La Selva: Ecology and Natural History of a Neotropical Rainforest*. University of Chicago Press, Chicago, pp. 34–53.
- Son Y., Lee I.K. and Syu R. 2000. Nitrogen and phosphorus dynamics in foliage and twig of pitch pine and Japanese larch plantations in relation to fertilization. *J. Plant Nutr.* 23(5): 697–710.
- Stocker G.C., Thompson W.A., Irvine W.A., Fitzsimon J.D. and Thomas P.R. 1995. Annual patterns of litterfall in a lowland and tableland rainforest in tropical Australia. *Biotropica* 27(4): 412–420.
- Swamy H.R. and Proctor J. 1994. Litterfall and Nutrient Cycling in Four Rainforests in the Sringeri Area of the Indian Western Ghats. *Global Ecol. Biogeogr.* 4(5): 155–165.
- Tessier J.T. and Raynal D.J. 2003. Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. *J. App. Ecol.* 40: 523–534.

- Tian H., Melillo J.M., Kicklighter D.W., McGuire A.D., Helfrich J.V.K.I., Moore B. III and Vorosmarty C.J. 1998. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* 396: 664–667.
- Vitousek P.M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285–298.
- Vitousek P.M. and Sanford R.L. 1986. Nutrient cycling in moist tropical forest. *Ann. Rev. Ecol. Syst.* 17: 137–167.
- Veneklaas E.J. 1991. Litterfall and nutrient fluxes in two montane tropical rainforests, Columbia. *J. Trop. Ecol.* 7(3): 319–336.
- Waylen P.R., Quesada M.E. and Caviedes C.N. 1996. Temporal and spatial variability of annual precipitation in Costa Rica and the Southern Oscillation. *Int. J. Climatol.* 16(2): 173–193.
- Wich S.A. and Van Schaik C.P. 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *J. Trop. Ecol.* 16: 563–577.
- Wieder R.K. and Wright S.J. 1995. Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. *Ecology* 76(6): 1971–1979.
- Wright S.J. and Cornejo F.H. 1990. Seasonal drought and leaf fall in a tropical forest. *Ecology* 71(3): 1165–1175.
- Wright S.J., Carrasco C., Calderon O. and Paton S. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80: 1632–1647.