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REGULAR ARTICLE

No short-term change in soil properties following four-fold litter addition in a Costa Rican rain forest

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Abstract We experimentally manipulated forest floor litter to investigate the influence of litter quality and quantity on soil properties over the short-term (weeks to months) in a wet tropical forest in NE Costa Rica. The study included old growth forest on high fertility soils, old growth forest on low fertility soils, and secondary forest on intermediate fertility soils. Forest floor litter was removed from a 16 m^2 area and added to an adjacent 4 m^2 area in March 2003, resulting in a one to four-fold increase in the annual litter input to the forest floor. We created three addition, three removal and three control plots per forest type. We measured treatment effects on variation in soil moisture, temperature, pH, and Bray-1 P (plant available) over a 5-month period that captured the dry-wet season transition. Litter manipulation had no effect on any of the soil properties measured during the 5-month study period. Significant variability through time and a similar temporal pattern across the three forest stands suggest that climatic variability is driving short-term patterns in these soil properties rather than seasonal inputs of litter. In general, soils were warmer, drier and more basic with higher available P during dry season months. Even in wet tropical forests, small variability in climate can play an important role in soil dynamics over periods of weeks to months. Although litter manipulation did not influence soil properties over the 5-month study period, a longer lag may exist between the timing of litter inputs and the influence of that litter on soil properties, especially plant available P.

Keywords Bray-1 P · La Selva · Litter manipulation · pH · Phosphorus · Seasonality · Soil moisture · Temperature

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Introduction

Litter quality and quantity are hypothesized to exert a strong control on short-term variability in the physical and chemical characteristics of soil in many ecosystems, including tropical forests (Jenny 1941; Wedin and Tilman 1990; Berendse 1994; Lodge et al. 1994; Reich et al. 2005; Sayer 2005). The difficulty in testing this theory with observational studies, however, is in distinguishing litter effects from those driven by seasonal variation in climate (Aerts 1997; Binkley and Giardina 1998; Powers and Schlesinger 2002; Wood et al. 2006). We manipulated litter inputs in a

wet tropical forest to separate effects of variability in litter quality and quantity from short-term effects of climate on soils.

Climatic variability in the tropics occurs in the form of drying and rewetting cycles, even in wet tropical forests characterized by only 3 to 4 months per year of rainfall <200 mm/month (Walsh and Newbery 1999). These cycles can affect soil processes via the influence of precipitation on soil moisture, litter production, decomposition rates, microbial activity and soil nutrients (Lodge et al. 1994; McGrath et al. 2000; Cleveland et al. 2004). During dry season months, litter accumulates on the forest floor as the amount of litterfall increases, decomposition rates slow, and immobilization is high (Singh et al. 1989; Lodge et al. 1994; Cleveland et al. 2006). With the onset of the wet season, decomposition rates and turnover of microbial biomass increases, leading to a pulse of nutrients to the soil (Ladd et al. 1977; Singh et al. 1989; Lodge et al. 1994; McGrath et al. 2000; Campo et al. 2001). Therefore, the amount of available nutrients in the soil is likely to be highest just after the onset of the wet season when nutrients from accumulated litter are mineralized.

In addition to pulsed nutrient release from decomposing litter, seasonal fluctuations in the thickness of the litter layer may also impact soil processes by influencing the exchange of water and energy between the soil and atmosphere (Putuhena and Cordery 1996; Ogée and Brunet 2002). Thicker litter layers tend to support higher soil moisture and temperature, serving as a buffer against small variations in climatic conditions (Putuhena and Cordery 1996 [pine and eucalyptus forest, Australia]; Ogée and Brunet 2002 [pine forest, France]). Moreover, thick layers of decomposing organic matter may lead to local acidification of the soil in the short-term due to the production of organic acids (Killham 1994; Sayer 2005). Therefore, soil pH is likely to be highest in the dry season when the forest floor is at its thickest and decrease as the wet season progresses. In addition, sites with thick forest floors will likely demonstrate less seasonal variation in soil moisture and temperature than sites with thin forest floors.

Landscape scale variability in soil fertility could lead to differences in the timing and magnitude of seasonal variation in soil characteristics due to differences in microclimate, litter quality, litter production (Ewel 1976; Swift et al. 1979; Read and Lawrence 2003; Lawrence 2005; Wood et al. 2006) and decomposition rates (Ewel 1976; Swift et al. 1979; Xuluc-Tolosa et al. 2003; Torn et al. 2005) among the different forest types. High fertility soils tend to have higher nutrient concentrations in the litter and faster decomposition rates of both litter and soil organic matter than lower fertility sites (Van den Driessche 1974; Swift et al. 1979; Vitousek 1982; Hobbie 1992; Zech et al. 1997; Torn et al. 2005). Therefore, forests on higher fertility soils are likely to have an earlier and larger influx of pulsed nutrients than forests on lower fertility soils.

In addition to differences in soil nutrient availability, forest age can also play an important role in soil properties. Secondary forests can differ from old growth forests in microclimate, litter production, litter quality, and soil nutrient status. In general, the microclimate of secondary forests tends to have higher air temperatures and evaporative drying rates and lower relative humidity (Arunachalam and Arunachalam 1999; Didham and Lawton 1999; Martius et al. 2004b; Vasconcelos and Laurance 2005). Secondary forests also have high litter production accompanied by high nutrient concentrations relative to their old growth counterparts (Brown and Lugo 1990; Read and Lawrence 2003; Lawrence 2005; however, see Martius et al. 2004a). Additionally, secondary forest soils may have higher soil pH and cation exchange capacity than older forests (McGrath et al. 2001). Therefore, secondary forest regenerated from pasture is likely to have higher soil temperature and soil pH accompanied by lower soil moisture than old growth forest. In addition, the high litter nutrient inputs combined with the dry, warm microclimate found in secondary forests could lead to lower dry season nutrient availability when litter accumulation is high and decomposition rates are low, followed by a larger pulse of available soil nutrients with the onset of the wet season when decomposition rates increase.

In this study, we evaluated the influence of both the quality and quantity of forest floor litter on soil temperature, moisture, pH, and Bray-1 phosphorus (P) from the dry to wet season transition in a wet tropical forest in Costa Rica. We manipulated forest floor litter in three forest types (secondary-intermediate P, old growth-low P, old growth-high P), which enabled us to evaluate a wide range of litter quality and quantity. We hypothesized that: (1) available soil P, moisture and acidity would increase and soil

temperature would decrease as the wet season progressed due to increased decomposition of forest floor litter with the onset of the wet season, (2) soil temperature and moisture would increase with the quantity of litter inputs due to the impact of forest floor litter on the exchange of water and energy between the soil and the atmosphere, while soil pH would decrease due to greater organic acid production, (3) additions of high P litter (e.g. high quality) would have a positive effect on available soil P, and the positive effect would occur earlier in sites with high P litter than sites with low P litter due to associated differences in decomposition rates, (4) the secondary-intermediate P site would have higher soil temperatures and pH accompanied by lower soil moisture than old growth forest due to the warm, dry microclimate of secondary forest sites. We also hypothesized that the secondary forest site would demonstrate the largest increase in available soil P with the onset of the wet season due to the greater quantity and quality of litter produced relative to old growth forest.

Materials and methods

Study sites

This research was conducted at La Selva Biological Station in northeast Costa Rica (10°26′ N, 84°00′ W). La Selva is classified as a tropical wet forest, receiving on average 4300 mm of rainfall per year (OTS *unpublished data*). The driest period lasts from January to April, with an average of 100–200 mm of rainfall per month (Chazdon et al. 2005). The soils are highly weathered with a low base-exchange capacity, and are classified as oxisols according to US Taxonomy (Kleber et al. 2007).

In March 2003, during peak litterfall, we manipulated forest floor litter in high fertility old growth forest (high P), low fertility old growth forest (low P), and secondary forest regenerated from pasture on intermediate fertility soil (intermediate P; Table 1). We define high fertility as having high soil/litter P because P is the main limiting nutrient for the study area (Wood et al. 2005). *Pentaclethra macroloba* is

Table 1 Site characteristics of the three study sites

Site characteristics	Site name		
	A4	L5	Lindero Peje
Fertility (soil P level)	High	Low	Intermediate
Age	Old growth	Old growth	23-years
Annual litter input (Mg ha^{-1} year^{-1})[a, b]	8.9	8.7	11.6
Annual litter P input (kg ha^{-1} year^{-1})[c]	8.5	5.3	9.3
Leaf litter [P] (mg g^{-1})[d]	0.96	0.61	0.80
Total soil P (μg g^{-1})[e, f]	1650	579	810
Bray-1 P (μg g^{-1})[g]	11.93	6.03	5.41
Soil N (mg g^{-1})[e, f]	4.56	5.16	4.5
Soil N:P[e, f]	2.76	8.91	5.56
Soil C (mg g^{-1})[e, f]	51.16	61.93	52.13

[a] Old growth forest total fine litterfall (leaves, reproductive material, twigs <1 cm diameter) was collected from nine pairs of 0.25 m^2 traps in a 0.5 ha area (each standing basked trap paired with an equal-area quadrat demarcated on the ground) for 1 year prior to litter manipulation. The ground-level "traps" were used to collect litter items >50 cm long; all other fine litter was collected in the standing traps (DA Clark *unpublished data*)

[b] Secondary (23-year) total fine litterfall (leaves, reproductive material, twigs <1.8 cm diameter) was collected from 20 0.64 m^2 traps in a 1.0 ha area for 1 year prior to litter manipulation (D Lawrence *submitted*)

[c] Annual Litter P Input was calculated as the Annual litter input × Mean leaf litter P concentration for the respective sites (Wood et al. 2008)

[d] Mean leaf litter [P] (Wood et al. 2008)

[e] Old growth soils were collected to 10 cm depth (Espeleta and Clark 2007)

[f] Secondary (23-year) soils were collected to 15 cm depth (D Lawrence *unpublished data*)

[g] Soils collected to 5 cm depth (*this study*)

the dominant species in the old growth forest sites, while *Goethalsia meiantha* is the dominant species in the secondary forest site (D.A. Clark *unpublished data*, R.L Chazdon *unpublished data*). The annual litter input was highest in the secondary forest (11.6 Mg ha^{-1} $year^{-1}$), followed by the high and low P old growth stands (8.9 and 8.7 Mg ha^{-1} $year^{-1}$, respectively; D.A. Clark and D. Lawrence *unpublished data*). Mean forest floor turnover time (stock divided by flux) was fastest in the high P old growth site, followed by the secondary and low P old growth sites (2.9, 3.7, and 9.0 months, respectively; Table 2).

Within each forest type, we established three replicates for each of three treatments: addition, removal, and control. Leaves and twigs <2 cm in diameter were removed from a 16 m^2 area (removal), weighed and then added to a neighboring 4 m^2 area (addition). We moved 350–377 g m^{-2} (3.5–3.8 Mg ha^{-1}) in the secondary forest plots, 570–791 g m^{-2} (5.7–7.9 Mg ha^{-1}) in the low fertility old growth site, and 185–256 g m^{-2} (1.9–2.6 Mg ha^{-1}) in the high fertility old growth site (dry weight; Table 2). This resulted in a four-fold increase in forest floor mass, an 85–367% increase in annual litter inputs to the forest floor, and a one to three-fold increase in annual organic P inputs (Tables 1 and 2). For the controls, we established three 5 m linear transects. Within a forest type, all treatments were established at least 10 m apart to minimize treatment interactions.

Within each treatment (addition, removal, control) we collected initial soil samples (5 cm deep) and measured soil temperature (at 5 cm) immediately prior to litter manipulation. Subsequently these data were collected 1, 3, 8, 15, and 20 weeks after manipulation. Based on mean forest floor turnover time (Table 2) and a decomposition study conducted in this forest, we assumed that much of the mass and P would be lost by 20 weeks (50% P loss after 4 months; Wood et al. 2008). This time frame (March–August) also allowed us to fully capture the dry to wet season transition (Fig. 1). During this time, mean monthly ambient temperature declined from 25.8°C to 25.4°C, maximum declined from 32.6°C to 31.0°C and minimum increased from 21.1°C to 22.8°C. Monthly rainfall increased from 44 to 560 mm over the same time period (Fig. 1). The coefficient of variation (CV) over the 5-month period was much lower for monthly mean temperature than for monthly rainfall (4–7% vs. 53% CV).

Soil sampling and analysis

Soil samples for each plot were a composite of five soil cores. Temperature measurements were taken next to the soil cores with a soil thermometer (five measures per plot). To measure soil moisture, 5 g of field-wet soil were dried in an oven at 100°C for 24 h. Gravimetric soil moisture (field moist mass minus

Table 2 Forest floor litter treatment

Site name (plot #)	Forest floor litter added (Mg ha^{-1})	Forest floor litter [P] (mg g^{-1})	Total forest floor P added (kg ha^{-1})	Bray-1 P Pool (kg ha^{-1} to 5 cm)	[a]Litter added relative to annual litter input (%)	[b]Total P added relative to Bray-1 P pool (%)	[c]Forest floor turnover time (months)
Old growth-high P							
A4 (1)	7.6	0.82	6.2	2.8	85	220	2.5
A4 (2)	10.3	0.65	6.7	6.2	116	108	3.4
A4 (3)	8.4	0.75	6.3	4.3	94	148	2.8
Old growth-low P							
L5 (1)	24.1	0.54	13.1	2.3	277	581	8.2
L5 (2)	23.0	0.70	16.1	3.2	264	500	7.9
L5 (3)	31.9	0.61	19.4	3.0	367	657	10.9
Secondary-intermediate P							
Lindero Peje (1)	15.2	0.54	8.1	2.3	131	355	3.9
Lindero Peje (2)	14.1	0.70	9.9	2.2	122	444	3.6
Lindero Peje (3)	14.0	0.65	9.1	1.3	121	693	3.6

[a] Forest floor litter added divided by the total annual litter input for each site × 100%

[b] Forest floor P added divided by the total Bray-1 P pool (5 cm depth) for each site × 100%

[c] Pool of forest floor litter divided by the total annual litter input for each site

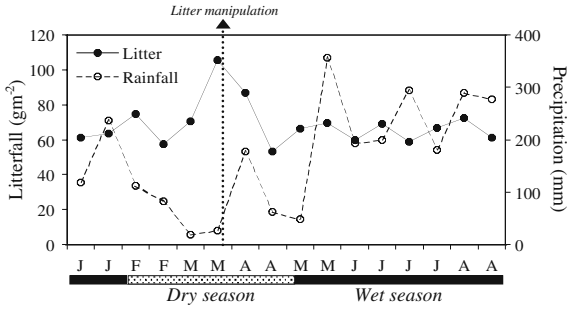

Fig. 1 Bi-weekly variation in rainfall and litter inputs during the study period (*rainfall*: OTS *unpublished meteorological records*; *Litterfall*: D. Lawrence *unpublished data*). The *arrow* indicates when litter manipulation occurred (March 2003)

oven dried mass divided by oven dried mass) was measured on initial soil samples as well as soils collected 1, 3, and 8 weeks after litter manipulation. The remaining soil was air dried and sieved to pass through a 2 mm sieve. Soil pH was determined on air-dried soils using a 1:5 soil–water ratio. This soil–water mixture was shaken for 10 min and allowed to settle for 20 min. Measurements were then taken with an Orion pH meter (model 720A). The Bray-1 extract removes acid-soluble Al- and Fe-phosphates through the formation of fluoride complexes with Al and Fe (Stevenson 1986), and is widely used as an indicator of plant-available P. Bray-1 P extractions were performed on 2 g of sieved, air-dry soil. The soil was mixed with 20 mL of 1.0 M NH_4F and 0.5 M HCl and shaken for 5 min (Bray and Kurtz 1945). This mixture was then filtered for 10 min through Schleicher & Schuell 597 filter paper (110 mm) and analyzed colorimetrically on an Alpkem Flow Solution IV using the standard EPA method for total P.

Statistical analysis

Data were analyzed using Proc Mixed analysis in Statistical Analysis System (SAS) to determine if soil properties differed among litter treatments and forest stands, and if they changed significantly with time (SAS System for Windows V8.0, 2002, SAS Institute). Proc Mixed uses a restricted maximum likelihood approach for the estimation of model parameters (as opposed to the least squares approach of general linear model procedure (Proc GLM)), and is more suited for the repeated measures experimental design than Proc GLM. When significant differences were found, we used a post-hoc test (Tukey–Duncan) to determine where these differences occurred. If the difference among treatments was significant for the initial sample collection within a site, the data were "normalized" by subtracting the initial value of each individual plot from all subsequent values so that all sites started with an initial value of zero. Normalizing the data enabled us to determine whether treatment effects were in response to litter manipulation rather than a consequence of natural variability within and among sites.

Results

Soil moisture

Gravimetric soil moisture in the top 5 cm did not differ significantly among the three litter treatments. The level of soil moisture was, however, significantly influenced by forest age. The secondary forest site had a quarter to a third lower soil moisture than both old growth forest sites (Fig. 2; Proc Mixed, type effect: df=2, n=18, F=6.79, P=0.0064, Tukey–Kramer). Soil moisture changed significantly with time (Proc Mixed, time effect: df=3, n=108, F=11.67, P<0.0001), varying across all treatments from 17% to 87% (absolute difference of 70%) throughout the course of the study. Soil moisture was highest at the end of the wet season month of May (70–100%; Fig. 2). The temporal variability in soil moisture was not influenced by treatment or forest type.

Soil temperature

Litter manipulation had no effect on soil temperature at 5 cm depth. However, the old growth-high P forest had significantly higher temperatures (22.3°C) than both secondary and old growth-low P forest (21.3 and 21.5, respectively; Proc Mixed, site effect, df=2, n=27, F=202.47, P<0.0001). Soil temperature decreased significantly from April to August (2–7% lower in August; Proc Mixed, time effect: df=4, n=135, F=35.91, P<0.0001). These patterns were not influenced by forest type or litter treatment (Fig. 3).

Soil pH

As with soil temperature, litter manipulation had no effect on the pH of the top 5 cm of soil (Fig. 4). The old growth-high P forest had significantly lower pH

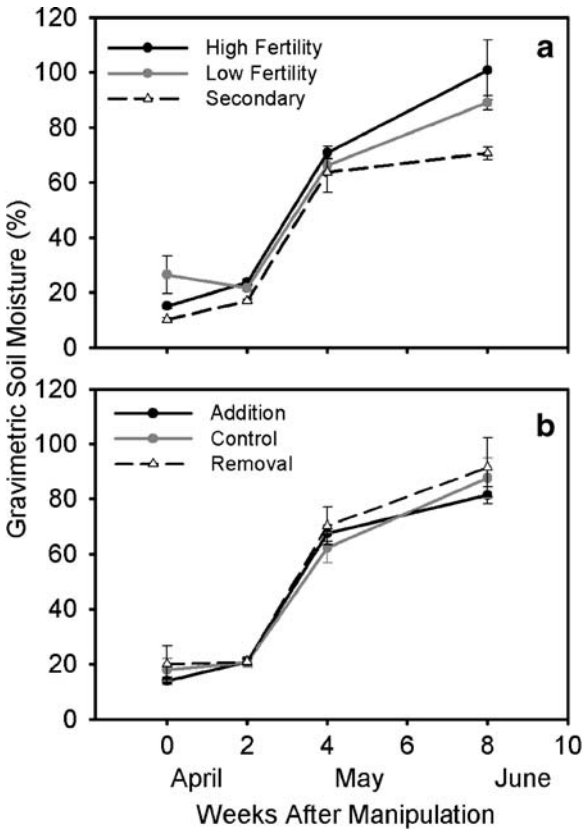

Fig. 2 Gravimetric soil moisture (%) for **a** the three forest types and **b** the three litter treatments. Mean ± 1 S.E. are presented as there was no significant treatment effect

(mean of 3.77) than soils in both secondary and old growth forest on low P soils (means of 3.97 and 3.84, respectively; Proc Mixed, site effect: df=2, n=27, F=6.47, P=0.0037). Soil pH changed significantly with time, decreasing by 6–12% as the wet season progressed from April to August (Proc Mixed, time effect: df=4, n=135, F=15.61, P<0.0001).

Soil phosphorus

Litter manipulation had no effect on Bray-1 P in the top 5 cm. However, the high P site had significantly higher Bray-1 P than both lower P sites (11.9 μg/g old growth-high P forest; 6.0 μg/g old growth-low P forest; 5.4 μg/g secondary-intermediate P forest; Proc Mixed, site effect: df=2, n=27, F=56.07, P<0.0001). Bray-1 P varied significantly with time (Proc Mixed, time effect: df=4, n=135, F=8.81, P<0.0001). In both intermediate and low P sites, Bray-1 P increased by 37% to 44%, respectively, 1 month after peak litterfall (March) and declined as the rainy season progressed (Fig. 5). In the high P site, Bray-1 P also increased 1 month after peak litterfall by 54%. However, in contrast to the low P sites, the high P site experienced a second large spike in Bray-1 P in mid-July, 3 months after litter manipulation and 4 months after peak litterfall (Fig. 5). Despite this apparent difference, neither forest site or litter treatment influenced the temporal variation in Bray-1 P.

Discussion

Litter manipulation did not significantly influence any of the soil properties measured (soil moisture, temperature, pH, and Bray-1 P) during the 5 months following treatment. These soil characteristics significantly vary among the three forest stands. In all sites, the soil was drier, hotter, and more basic during the dry season with higher plant available P than in the

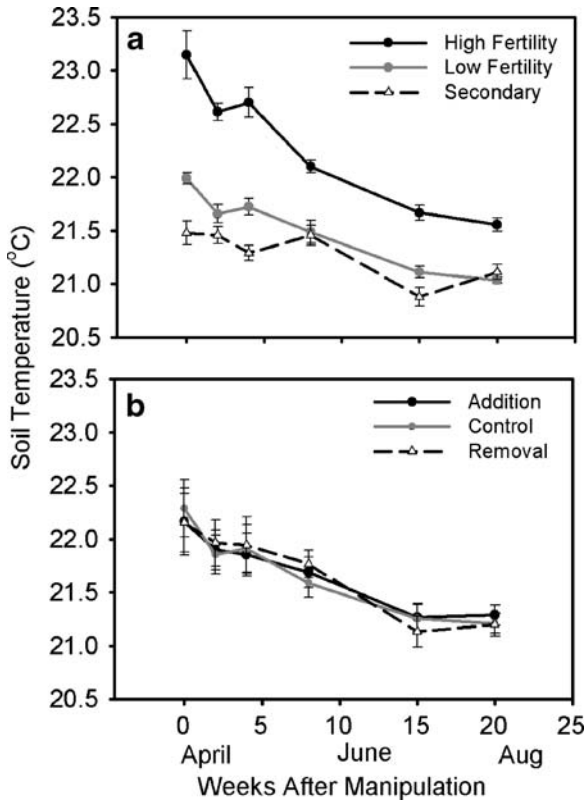

Fig. 3 Soil temperature taken at 5 cm depth across **a** forest types and **b** the three litter treatments. Mean ± 1 S.E. are presented as there was no significant treatment effect

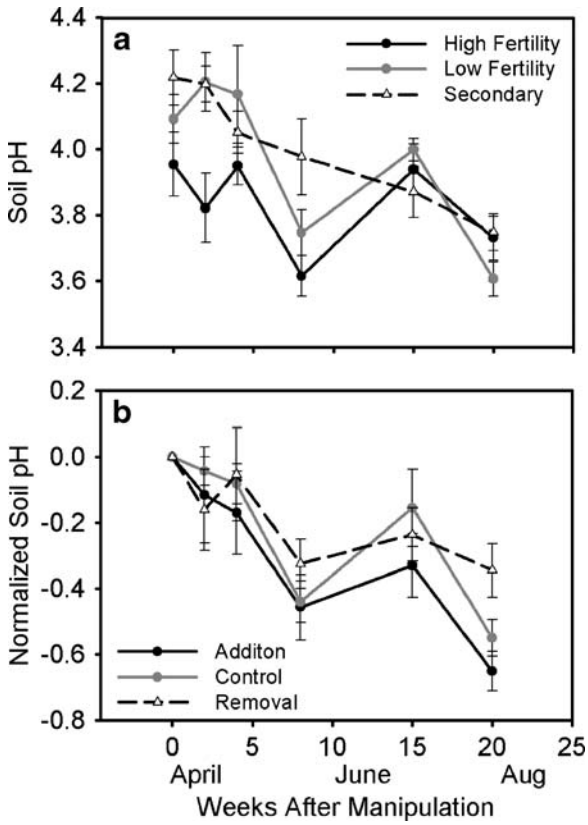

Fig. 4 Soil pH (in water) across the three forest types (**a**) and among the three litter treatments (**b**). The initial soil pH values differed significantly among the three treatments. Therefore, pH values were "normalized" by subtracting the initial value from all measures. Subsequently, the three treatments did not differ significantly. Mean ± 1 S.E. are presented as there was no significant treatment effect

wet (Figs. 2, 3, 4 and 5). These observed trends in soil moisture, soil temperature and soil pH support our original hypotheses. However, the decline in Bray-1 P after the initial wet season spike was unexpected. The overall higher dry season Bray-1 P may reflect low rates of P diffusion through the soil matrix to roots during the dry season, followed by high leaching of P during wet season months (Vitousek 1982; Attiwill and Adams 1993; Cleveland et al. 2006). Alternatively, this trend could be explained by lower dry season plant demand followed by maximal plant uptake as the wet season progresses and nutrient demand increases (Ladd et al. 1977; Stark and Jordan 1978; McGrath et al. 2001).

In addition to the observed seasonal variation in soil characteristics, these characteristics also differed significantly among the three forest types. Soil moisture was as much as a third lower in the younger forest than in the two old growth forests. The lower soil moisture is indicative of the low relative humidity and high evaporative rate found in tropical secondary forests (Arunachalam and Arunachalam 1999; Didham and Lawton 1999; Martius et al. 2004b; Vasconcelos and Laurance 2005). In addition to lower soil moisture, the secondary forest also had higher soil pH than the two old growth forests. High pH in the secondary forest relative to the old growth sites supports previous findings that combustion of forest biomass upon conversion to agricultural land adds base cations to the soil and hence increases soil pH (McGrath et al. 2001).

As expected, the old growth-high P site had higher plant available P than the sites located on less P-rich soils, regardless of forest age (Fig. 5). Therefore, higher total soil P results in greater plant available P. The old growth-high P site also had significantly higher soil temperatures than the two lower P sites.

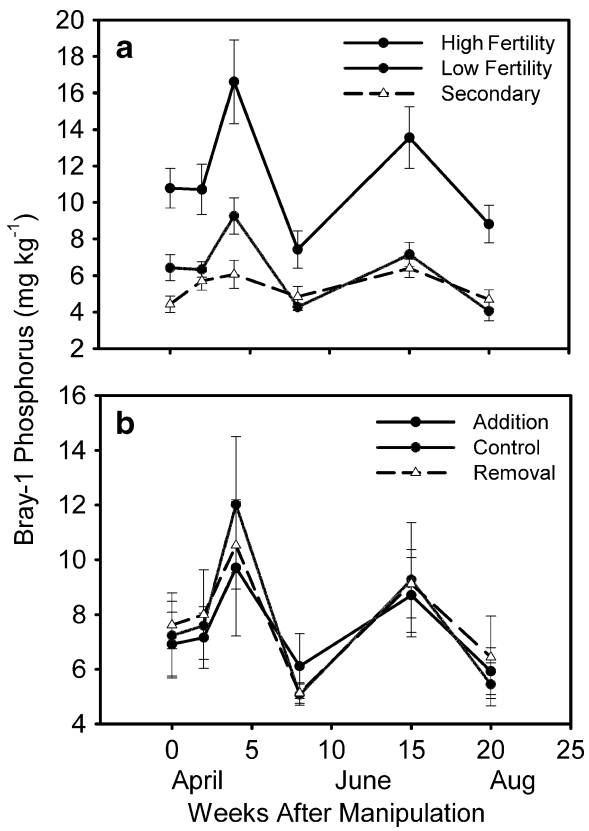

Fig. 5 Bray-1 P across the three forest types (**a**) and among the three litter treatments (**b**). Mean ± 1 S.E. are presented as there was no significant treatment effect

This finding is contrary to our expectation that the secondary forest site would have the highest soil temperatures. One explanation might be that the old growth high-P site had a thinner forest floor layer relative to the secondary and old growth-low P sites (Table 2). A thinner forest floor could result in more direct solar radiation due to the reduced litter-layer buffer, and hence greater soil warming (Sayer 2005). Alternatively, the consistently high soil temperature found in the old growth-high P site could be the consequence of a slightly later sample time relative to the other two forest sites (approximately 1 h; Doff Sotta et al. 2004).

In contrast to the significant seasonal and spatial variation in soil properties, none of the measured soil characteristics responded to litter manipulation. This lack of response is surprising given the magnitude of the litter treatment. We added the equivalent of one to four times the annual litter input (approximately 7.6–31.9 Mg ha^{-1}; Table 2). The P contained in this litter accounted for one to seven times the Bray-1 P soil pool (Table 2). In addition, the experiment was established during peak dry season; hence, the effect of litter addition should have been maximized due to the thicker forest floor found during this time of year. However, despite large additions of litter and P, there was no effect on soil temperature, moisture, pH or available soil P after 5 months. In fact, as previously discussed, Bray-1 P tended to decline with the progression of the wet season, contradicting our hypothesis that plant available P would be amplified in the litter addition sites as P from the decomposing litter is mineralized (Lodge et al. 1994). This trend (initial increase followed by depletion) combined with the lack of response to elevated litter inputs would indicate that nutrient mineralization of accumulated dry season litter is not the main driver of short-term variation in soil P. Rather, the seasonal spike in Bray-1 P observed after the onset of the wet season could reflect P release from lysed microbial cells (Lodge et al. 1994; Singh et al. 1989). During dry season months, microorganisms accumulate intracellular solutes, which then cause them to lyse upon re-wetting (Lodge et al. 1994). Alternatively, the lack of response to litter manipulation in the soil could be an indication of plants taking up P maximally as it is mineralized from decomposing litter via root growth directly into the litter layer (Stark and Jordan 1978; Attiwill and Adams 1993; McGrath et al. 2000; Sayer et al. 2006). A large-scale litter manipulation conducted in these same sites resulted in leaf litter production increasing significantly 2 to 4 months later (Wood et al. 2008). The increase in leaf litter production in response to litter addition supports the hypothesis that nutrients mineralized from decomposing litter are taken up immediately by the vegetation, rather than being transferred to the soil. It would also explain the similar Bray-1 P concentrations in the soil regardless of forest floor treatment. Alternatively, the temporal data are consistent with microbes taking P out of the soil to process newly fallen litter (Vitousek 1982; Singh et al. 1989). If a period of immobilization occurs, the lag between the timing of litter inputs and subsequent enhancement of soil P availability may be greater than the 5-month duration of this study.

Conclusions

In general, soils were drier, warmer and more basic during the dry season months. Contrary to expectations, Bray-1 P initially increased with the onset of the wet season, but steadily decreased as the wet season progressed. The high dry season Bray-1 P may be due to low rates of P diffusion through the soil matrix to roots combined with lower plant demand during this period (McGrath et al. 2001). This trend could also be explained by release of microbial-bound P as a result of the lysing of microbial cell walls with the onset of the wet season (Lodge et al. 1994).

Soil characteristics differed significantly among the three forest types. As expected, the old growth high-P forest had higher plant available-P than the two lower P sites. In addition, soil pH was higher and soil moisture was lower in the secondary forest versus the two old growth forests. However, contrary to our expectations, soil temperature was highest in the old growth high-P site. This difference could be due to differences in the thickness of the litter layer, or an artifact of a slightly later sampling time at this site. Despite differences in the magnitude of the measured variables among the three forest types, their temporal patterns were the same, regardless of age or fertility. This similarity in temporal patterns across sites would indicate that climate is a more important driver of short-term variation in soil characteristics than the quality and quantity of litter inputs.

Finally, despite significantly increasing both the litter and nutrient inputs to the soil, none of the soil characteristics measured responded to litter manipulation after 5 months of decomposition. This result could indicate maximal plant uptake of nutrients from decomposing litter via root growth directly into the litter layer (Stark and Jordan 1978; Sayer et al. 2006). It is also possible that the period of immobilization is longer than what was captured in this study. Future research should expand on these findings by incorporating more frequent sampling over a longer time period, increasing the number of replicate forest types, and manipulating litter at different times throughout the year.

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