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# Rain forest nutrient cycling and productivity in response to large-scale litter manipulation

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*Abstract.* Litter-induced pulses of nutrient availability could play an important role in the productivity and nutrient cycling of forested ecosystems, especially tropical forests. Tropical forests experience such pulses as a result of wet–dry seasonality and during major climatic events, such as strong El Niños. We hypothesized that (1) an increase in the quantity and quality of litter inputs would stimulate leaf litter production, woody growth, and leaf litter nutrient cycling, and (2) the timing and magnitude of this response would be influenced by soil fertility and forest age. To test these hypotheses in a Costa Rican wet tropical forest, we established a large-scale litter manipulation experiment in two secondary forest sites and four old-growth forest sites of differing soil fertility. In replicated plots at each site, leaves and twigs (<2 cm diameter) were removed from a 400-$m^2$ area and added to an adjacent 100-$m^2$ area. This transfer was the equivalent of adding 5–25 kg/ha of organic P to the forest floor. We analyzed leaf litter mass, [N] and [P], and N and P inputs for addition, removal, and control plots over a two-year period. We also evaluated basal area increment of trees in removal and addition plots. There was no response of forest productivity or nutrient cycling to litter removal; however, litter addition significantly increased leaf litter production and N and P inputs 4–5 months following litter application. Litter production increased as much as 92%, and P and N inputs as much as 85% and 156%, respectively. In contrast, litter manipulation had no significant effect on woody growth. The increase in leaf litter production and N and P inputs were significantly positively related to the total P that was applied in litter form. Neither litter treatment nor forest type influenced the temporal pattern of any of the variables measured. Thus, environmental factors such as rainfall drive temporal variability in litter and nutrient inputs, while nutrient release from decomposing litter influences the magnitude. Seasonal or annual variation in leaf litter mass, such as occurs in strong El Niño events, could positively affect leaf litter nutrient cycling and forest productivity, indicating an ability of tropical trees to rapidly respond to increased nutrient availability.

*Key words: Costa Rica; decomposition; La Selva Biological Research Station; litter manipulation; litter production; nitrogen; phosphorus; rainfall; wet tropical forest; woody growth.*

## INTRODUCTION

In forested ecosystems, litterfall represents the main pathway of nutrient transfer from the aboveground vegetation to the soil (Vitousek 1982, Vitousek and Sanford 1986, Clark et al. 2001). That the majority of nutrients mineralized from these inputs are then recaptured and feed back positively to net primary productivity and nutrient cycling is an important paradigm of biogeochemical cycling in terrestrial ecosystems (Vitousek and Reiners 1975, Waring and Schlesinger 1985, Schlesinger 1998). The long lag between the timing of litter production and the subsequent release of those nutrients from the decomposed litter makes it difficult to quantify these linkages due to the difficulty in distinguishing effects of litterfall from those of other factors known to influence forest productivity, such as forest age, soil fertility, and seasonal changes in climate (Vitousek 1982, Nair 1989, Brown and Lugo 1990, Berg et al. 1993, Vitousek 1998, Wood et al. 2006). Because tropical forests have such high decomposition rates and tight coupling between the vegetation and the soil, they represent an ideal system for testing the link between litter production and leaf litter nutrient cycling (Aerts 1997, Aerts and Chapin 2000). We investigated the effect of litter quality and quantity on wood growth, leaf litter production, and nutrient cycling in a wet tropical forest in Costa Rica by experimentally manipulating forest floor litter in both young and old forest stands of contrasting soil fertility.

In tropical forests, the timing and magnitude of litter inputs is closely linked to seasonal variability in rainfall, with peak litterfall most often occurring toward the end

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of the dry season (Hopkins 1966, Klinge and Rodrigues 1968, Haines and Foster 1977, Kunkel-Westphal and Kunkel 1979, Cuevas and Medina 1986, Herbohn and Congdon 1993, Swamy and Proctor 1994, Wieder and Wright 1995, Newbery et al. 1997, Lawrence 2005). Although this trend is less evident in wet tropical forests, which experience more evenly distributed rainfall throughout the year, litter production does increase during short periods (2–4 weeks) of below average rainfall (D. Lawrence, *unpublished data*; D. A. Clark, *unpublished data*). Subsequent decomposition of this litter could result in pulsed availability of limiting nutrients (Lodge et al. 1994, McGrath et al. 2000). Potential responses to pulsed nutrient availability include increased aboveground net primary productivity (ANPP) in the form of increased wood growth (Tanner et al. 1990, 1992, Campo and Vazquez-Yanes 2004) and higher litter production (Vitousek 1998, Harrington et al. 2001), as well as an enhanced leaf litter [P] (Tanner et al. 1992, Wood et al. 2005), resulting in higher nutrient inputs to the soil within 12 to 18 months of nutrient application.

Forest age and soil fertility can also affect litter nutrient dynamics due to differences in the quality and quantity of litter inputs (Grubb 1977, Vitousek 1982, Hobbie 1992, Crews et al. 1995). Older secondary forests tend to have comparable or higher production and higher quality of leaf litter than old-growth forests (Ewel 1976, Brown and Lugo 1990, Read and Lawrence 2003, Lawrence 2005). Forests on lower fertility soils tend to produce similar quantities of litter as forests on high-fertility soils nearby, but of lower quality (Edwards 1982, Vitousek 1984, Vitousek and Sanford 1986, Crews et al. 1995, Aerts and Chapin 2000, McDonald and Healy 2000, Wood et al. 2006). Thus litter quality, but not necessarily quantity, is limited by local nutrient availability.

In addition to the influence of forest age and soil fertility on the litter itself, differences among these forest types can also affect decomposition rates, and hence the timing of nutrient availability (Ewel 1976, Vitousek 1982, Crews et al. 1995, Scowcroft et al. 2000, Xuluc-Tolosa et al. 2003, Vasconcelos and Laurance 2005). Because secondary forests tend to have higher litter nutrient concentrations, and in many instances higher soil nutrients than old-growth forests, forest floor turnover is likely to be more rapid (Ewel 1976, Brown and Lugo 1990, Wardle et al. 1997, Xuluc-Tolosa et al. 2003). Similarly, forests on more fertile soils also tend to have higher decomposition rates, and hence more rapid turnover of the forest floor than forests on less fertile soils (Swift et al. 1979, Brown and Lugo 1990, Hobbie 1992, Crews et al. 1995, Hattenschwiler et al. 2003, Xuluc-Tolosa et al. 2003). Differences in litter quality and in decomposition rates might lead to differences among forests in the timing and the magnitude of their response to litter inputs.

Conversely, nutrients contained in litterfall could also represent a loss of nutrients to the trees as a result of leaching, immobilization, and competition with other organisms (Chapin 1980, Aerts and Chapin 2000). Because tropical forests are most often limited by phosphorus (P), which has no substantial atmospheric component, the main source of the limiting nutrient is obtained from the longer-term process of weathering (Vitousek and Sanford 1986, Roy and Singh 1994, Crews et al. 1995, Herbert and Fownes 1995, Porder et al. 2006). Therefore, litter-derived P inputs likely provide an essential short-term supply of P to the vegetation (Walker and Syers 1976, Chapin 1980, Aerts and Chapin 2000).

We created a large-scale litter manipulation experiment in secondary and old-growth forests of varying soil fertility in a wet tropical forest in Costa Rica. This experiment allowed us to determine the effects of sudden large inputs of organic matter on woody growth, leaf litter production, and litter nutrient cycling. By including both young and old as well as high- and low-fertility sites in this study, we were able to evaluate the full spectrum of litter quality and quantity (high inputs of high-quality litter, high inputs of low-quality litter, low inputs of high-quality litter, and low inputs of low-quality litter).

We hypothesized that: (1) An increase in the quantity and quality of litter inputs would have a positive effect on woody growth and leaf litter production, as well as leaf litter quality (N and P concentrations), by providing a pulse of limiting nutrients to the vegetation, while litter removal would have the opposite, negative effect. (2) The timing and magnitude of this response would be influenced by soil fertility and forest age, due to differences in litter quality, quantity, and decomposition rates. We predicted that secondary forests would exhibit the largest and earliest response to litter addition while old-growth forests located on low-fertility soils would display the smallest and most delayed response to addition. Alternatively, we might expect the low-fertility sites to demonstrate the largest response to litter addition due to greater nutrient limitation in these sites. We also hypothesized that the high-fertility sites would exhibit the smallest response to litter removal due to the potential for the soil nutrient pool to serve as a buffer against lower litter nutrient inputs.

## METHODS

### *Study site*

We conducted this research in both old-growth tropical wet forest and secondary forest regenerating from pasture at the La Selva Biological Research Station in Costa Rica (10°26′ N, 84°00′ W). La Selva receives on average 4300 mm of rainfall a year, with no month receiving <100 mm on average (Organization for Tropical Studies, *unpublished data* [*available online*]).[5] The drier period occurs between late January and late

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[5] ⟨http://www.ots.duke.edu/⟩

TABLE 1. Soil and litter characteristics of the six study sites at the La Selva Biological Research Station, Costa Rica.

| | Site name | | | | | |
|---|---|---|---|---|---|---|
| Site characteristics | A2 | A4 | L3 | L5 | Lindero Peje | Lindero Sur |
| Age | old growth | old growth | old growth | old growth | 23-yr | 15-yr |
| Soil type | Young Oxisol | Young Oxisol | Old Oxisol | Old Oxisol | Old Oxisol | Old Oxisol |
| Fertility | low | high | low | low | low | high |
| Annual litter input† ($Mg^{-1} \cdot ha^{-1} \cdot yr$) | 9.9 | 7.9 | 7.5 | 9.7 | 10.6 | 10.3 |
| Annual litter P input‡ ($kg^{-1} \cdot ha^{-1} \cdot yr$) | 6.4 | 6.4 | 5.2 | 6.6 | 6.4 | 7.5 |
| Total soil P§ (μg/g) | 836 | 1650 | 785 | 579 | 810 | 1300 |
| Bray-1 P¶ (μg/g) | 5.1 | 8.2 | 3.5 | 3.3 | 4.1 | 6.5 |
| Soil N§ (mg/g) | 5.5 | 4.6 | 4.8 | 5.2 | 4.5 | 3.9 |
| Soil N:P§ | 6.6 | 2.8 | 6.1 | 8.9 | 5.6 | 3.0 |

† Old-growth forest total fine litterfall (leaves, reproductive material, twigs <1 cm diameter) collected from nine pairs of 0.25-$m^2$ traps per plot (each standing basket trap paired with an equal-area quadrat demarcated on the ground) for one year prior to litter manipulation. The ground-level "traps" were used to collect litter items >50 cm long; all other fine litterfall was collected in the standing traps (D. A. Clark, *unpublished data*). Secondary 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 one year prior to litter manipulation (D. Lawrence, *unpublished data*).

‡ Annual litter P input was calculated as the annual litter input × mean leaf litter P concentration for the respective sites (T. E. Wood and D. Lawrence, *unpublished data*).

§ Old-growth soils were collected to 10 cm depth (Espeleta and Clark 2007); secondary soils were collected to 15 cm depth (D. Lawrence, *unpublished data*).

¶ Soils were collected to 5 cm depth. Analysis was conducted on air-dried, sieved (2 mm) soils.

May (Frankie et al. 1974, Sollins et al. 1994). The forest is evergreen, but a few emergent tree species are annually or sporadically deciduous (Frankie et al. 1974, Newstrom et al. 1994). A N-fixing legume, *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae/Mimosoideae), is the most dominant species, accounting for as much as 36% of the basal area (Lieberman et al. 1996).

### *Litter manipulation*

In June 2001 we manipulated litter at each of six locations (Table 1). Four old-growth sites which included two lower-fertility sites on older oxisols (L3, L5), one lower fertility site on younger oxisols (A2), and one higher fertility site on younger oxisols (A4) (Clark and Clark 2000, Espeleta and Clark 2007, Kleber et al. 2007). The two sites in secondary forest regenerated from pasture included low and high-fertility sites on older oxisols (Lindero Peje [LP; 15 yr] and Lindero Sur [LS; 23 yr], respectively) (Chazdon et al. 2005). The manipulation occurred outside of the normal dry-season peak in litter production to enable us to avoid the potentially confounding effects of the natural seasonal response and more conclusively determine the response to litter manipulation. Forest floor litter was removed from a >400-$m^2$ area. This litter was bagged, weighed, and then added to an adjacent area of 100 $m^2$ (see Plate 1). Woody material >2 cm in diameter was not removed and was left in the original plots. To quantify the treatment effect, we collected subsamples of forest floor litter from each of the removal plots. This litter was dried in an oven at 65°C and analyzed for percentage moisture and N and P concentration.

The manipulation resulted in a fourfold increase in existing forest floor mass and was the equivalent of adding 1–2 years of fresh litter and nutrient inputs to the system (Table 2). Adjacent to a control plot at each site (0.5-ha control in old-growth and 1.0 ha in secondary forest), we established two replicates each of removal and addition treatments at two sites located a minimum distance of 100 m apart. At each replicate site, we maintained a minimum distance of 10 m between removal, addition, and control plots. This distance represents the average canopy crown radius (D. A. Clark, *personal observation*). Replicates were limited to two in order to ensure that slope was the same in all treatments at a given forest site. The study sites span a wide range of soil fertility (579–1650 μg/g total P) and varied in the amount of forest floor mass (2.35–6.24 Mg/ha) and litter quality (0.5–1.1 mg/g P) (Table 2). Annual patterns in rainfall and temperature were similar during the two-year study period (Wood 2006).

### *Basal area increment*

We measured the diameter at breast height (dbh) of each of the trees $\geq$5 cm diameter in the addition and removal plots within two months of litter manipulation (August 2001). All stems were tagged and identified by species. The dbh was measured at 1.3 m unless irregularities such as buttresses or irregular boles were present, in which case dbh was measured above the irregularities. The measurement location for each tree was marked and the dbh of these trees was measured a second time one year later (August 2002).

We calculated the net increase in basal area (square meters per hectare) for all removal and addition plots. New stems $\geq$5 cm diameter and trees that died during the study period were excluded from this analysis. Trees were considered to be dead when they were completely dry with no new leaves or green shoots visible. Because data on stems 5–9.9 cm dbh were unavailable for the old-growth control plots, we calculated basal area increment for the old-growth treatment and control plots using stems $\geq$10 cm dbh. For these study sites, stems 5–9.9 cm dbh account for 7.6% of the total basal

TABLE 2. Parameters of the forest floor litter manipulation.

| Site name (plot no.) | Forest floor mass† (Mg/ha) | Forest floor litter P† (mg/g) | Forest floor turnover‡ (month) | Litter added§ (Mg/ha) | C added¶ (Mg/ha) | N added¶ (kg/ha) | P added¶ (kg/ha) |
|---|---|---|---|---|---|---|---|
| Old growth, Young Oxisol | | | | | | | |
| A2 (1) | 4.7 | 0.66 | 5.8 | 19.0 | 8.2 | 325 | 12.5 |
| A2 (2) | 4.8 | 0.58 | 5.9 | 19.3 | 7.6 | 249 | 11.2 |
| A4 (1) | 3.1 | 1.18 | 4.7 | 12.3 | 4.6 | 179 | 14.5 |
| A4 (2) | 5.8 | 1.06 | 8.9 | 23.3 | 9.1 | 331 | 24.7 |
| Old growth, Old Oxisol | | | | | | | |
| L3 (1) | 4.8 | 0.42 | 7.7 | 19.2 | 8.5 | 333 | 8.1 |
| L3 (2) | 4.5 | 0.55 | 7.3 | 18.2 | 7.8 | 229 | 10.0 |
| L5 (1) | 3.3 | 0.55 | 4.1 | 13.2 | 5.5 | 235 | 7.3 |
| L5 (2) | 4.6 | 0.58 | 5.6 | 18.3 | 7.1 | 245 | 10.5 |
| Secondary forest, Old Oxisol | | | | | | | |
| Lindero Peje (1) | 5.4 | 0.72 | 6.1 | 21.5 | 10.2 | 384 | 15.5 |
| Lindero Peje (2) | 6.2 | 0.75 | 7.1 | 25.0 | 8.5 | 352 | 18.6 |
| Lindero Sur (1) | 2.3 | 0.52 | 2.7 | 9.4 | 4.5 | 165 | 4.9 |
| Lindero Sur (2) | 2.6 | 0.55 | 3.1 | 10.6 | 5.0 | 177 | 5.8 |

† Forest floor litter was collected from a 400-$m^2$ area in June 2001. Wood larger than 2 cm diameter was excluded.

‡ Forest floor turnover time = (forest floor mass/annual litter input) × 12 months.

§ Total forest floor litter collected from a 400-$m^2$ area and added to a neighboring 100-$m^2$ area.

¶ Total forest floor litter added to the 100-$m^2$ area × the nutrient concentration (%) of that litter.

area of stems $\geq$5 cm dbh (D. A. Clark, *unpublished data*). In secondary forest sites these smaller stems accounted for 8.3% (R. L. Chazdon, *unpublished data*). The most common dominant species of control, addition, and removal plots were *Pentaclethra macroloba* and *Goethalsia meiantha* (Table 3; Appendix A).

### *Litter collection*

Two 0.64-$m^2$ litterfall traps were placed within each removal and addition treatment plot. For the control plots, leaf litter was collected as part of ongoing research (old-growth, nine 0.25-$m^2$ standing basket traps per 0.5-ha plot [D. A. Clark]; secondary, four 0.64-$m^2$ traps in a 1.0-ha area [D. Lawrence]). All fine litter was collected biweekly for 28 months and dried in an oven at 65°C. Old-growth litter was dried to constant mass. Secondary forest and treatment plots were dried for a full week and then weighed. Litter was then separated into three fractions (fruit/flower, small twigs, and leaves) and weighed. Leaves were ground to pass through a 1-mm mesh screen. We analyzed a subset of monthly samples (August–December) from both the year of forest floor manipulation and the following year. We chose this subset of samples based on the estimated forest floor turnover time for this forest.

### *Expected timing of litter effects*

To determine the time frame for potential feedbacks of litter inputs, we analyzed decomposition rates in two ways. First, we calculated the forest floor turnover time (litter pool/litter input) for each of the study sites. We divided the forest floor mass (as measured at the time of our manipulation (total dry mass removed/400 $m^2$ area; Table 2) by the total annual litter input from the prior year for the respective control plots (D. A. Clark and D. Lawrence, *unpublished data*; Table 1). To estimate relative rates of decomposition as well as the rate at which nutrients are lost from decomposing litter at the different sites, we conducted a decomposition study in the control plots. For each of the six study sites, litter (leaves, reproductive material, and stems <2 cm diameter) was collected in mesh sheets tied up above the ground and later air-dried. Each decomposition bag was filled with 10 g of litter (bags 10 × 15 cm; 1-mm plastic mesh screen; 1 cm wide holes were sewed at the top in order to allow larger invertebrates to enter). Litterbags containing local litter were set out at their respective sites within one month of litter manipulation (July 2001) and collected on four subsequent dates (after 2, 6, 10, and 14 weeks). On each of the collection dates, two bags were collected at each site. Decomposition bags were dried in an oven at 65°C. The litter was then weighed and ground to pass through 1-mm mesh screen.

### *Nutrient and statistical analyses*

All leaf litterfall, soil, and litter decomposition samples were digested using a modified Kjeldahl digestion on a Tecator 2000 Digestion System (Perstorp Analytical, Silver Spring, Maryland, USA). Bray-1 P extractions were performed on 2 g of sieved, air-dried soil collected from each of the study sites. The soil was mixed with 20 mL of 1.0 mol/L $NH_4F$ and 0.5 mol/L HCl and shaken for 5 min (Bray and Kurtz 1945). This mixture was then filtered for 10 min through Schleicher and Schuell 597 filter paper (110 mm). Both the digestate and Bray extracts were analyzed for P colorimetrically using an Alpkem Flow Solution IV Auto Analyzer (OI Analytical, College Station, Texas, USA). Carbon (C) and N concentrations were determined by combustion using a Carlo Erba (Model NA 2500; Carlo Erba, Milan, Italy).

TABLE 3. Vegetation characteristics of the treatment plots.

| Site name (plot no.) | Basal area (m$^2$/ha)† | | | Dominant species (% basal area)† | | |
|---|---|---|---|---|---|---|
| | Control | Addition | Removal | Control | Addition | Removal |
| Old growth, Young Oxisol | | | | | | |
| A2 (1) | 21 | 20 | 39 | *Pentaclethra macroloba* (29) | *Ocotea hartshorniana* (69) | *Pentaclethra macroloba* (63) |
| A2 (2) | | 41 | 24 | | *Pentaclethra macroloba* (92) | *Pentaclethra macroloba* (37) |
| A4 (1) | 27 | 19 | 44 | *Pentaclethra macroloba* (45) | *Lacmellea panamensis* (28) | *Ilex skutchii* (53) |
| A4 (2) | | 36 | 13 | | *Sacoglottis trichogyna* (76) | *Goethalsia meiantha* (44) |
| Old growth, Old Oxisol | | | | | | |
| L3 (1) | 24 | 13 | 30 | *Pentaclethra macroloba* (31) | *Macrolobium costaricense* (28) | *Pentaclethra macroloba* (61) |
| L3 (2) | | 9 | 32 | | *Iriartea deltoidea* (51) | *Carapa guianensis* (33) |
| L5 (1) | 23 | 21 | 23 | *Pentaclethra macroloba* (33) | *Minquartia guianensis* (47) | *Pentaclethra macroloba* (63) |
| L5 (2) | | 42 | 27 | | *Ampelocera macrocarpa* (72) | *Pentaclethra macroloba* (46) |
| Secondary forest, Old Oxisol | | | | | | |
| Lindero Peje (1) | 28 | 22 | 24 | *Goethalsia meiantha* (19) | *Pentaclethra macroloba* (49) | *Pentaclethra macroloba* (26) |
| Lindero Peje (2) | | 43 | 3 | | *Inga leiocalycina* (53) | *Pentaclethra macroloba* (36) |
| Lindero Sur (1) | 22 | 54 | 22 | *Goethalsia meiantha* (28) | *Goethalsia meiantha* (69) | *Goethalsia meiantha* (61) |
| Lindero Sur (2) | | 10 | 17 | | *Goethalsia meiantha* (36) | *Goethalsia meiantha* (40) |

† Old-growth control data are from 0.5-ha plots and include stems $\geq$10 cm dbh (D. B. Clark and D. A. Clark, *unpublished data*). Secondary forest control data are from 1.0-ha plots and include stems $\geq$5 cm dbh (R. L. Chazdon, *unpublished data*). Addition, 100-m$^2$ area; removal, 400-m$^2$ area. Both estimates include stems $\geq$5 cm dbh.

We analyzed leaf litter mass, leaf litter N and P concentrations, and leaf litter N and P inputs (litter mass/interval × associated nutrient concentration) for a response to litter treatment both the year of manipulation and the year following manipulation using PROC Mixed analysis in SAS (SAS Institute 2002). We blocked the data by soil fertility (high, A4, LS; low, A2, L3, L5, LP) and age (old growth, A2, A4, L3, L5; secondary, LS, LP). When the homogeneity of variance assumption was not met, we log-transformed the data, which successfully corrected this problem in all instances. In addition, if the blocked effects of age and fertility were not significant in the model, they were included as random effects in the PROC Mixed analysis. We performed a two-way analysis of variance (ANOVA) to determine whether woody growth varied among treatments and forest types. When significant, a post hoc test (Tukey-Kramer) was performed to determine where significant differences occurred.

To determine which factors might be driving the response of production or inputs to litter manipulation, we regressed the basal area increment, and cumulative leaf litter production and N and P inputs for both the addition and removal sites against the factors most likely to drive variation in the magnitude of the response. We considered the following factors: quantity of litter added/removed, quality of litter added/removed ([N] and [P]), quantity of nutrients in the added litter/removed, and soil nutrients (total N and P, Bray-1 P). In addition, we evaluated whether the stoichiometry (C:N, C:P, N:P) of the added/removed litter or the soil affected the magnitude of the response. We defined the cumulative effect as the total production (or inputs) summed over the study period of interest (e.g., total litter or inputs summed from August–December 2001). Finally, we determined whether site effects, such as forest floor turnover time, basal area, and stem density, explained variability among sites in their response to litter manipulation. All regressions were performed in SigmaPlot (SPSS 2001).

## RESULTS

### *Effect of litter manipulation on woody growth and litter production*

Leaf litter production was significantly higher in the addition plots than in both the control and removal plots for the period two to six months following litter addition (mean 22% increase, as high as 92%; August–December 2001; PROC Mixed, treatment effect, $F = 3.41$, df = 2, 135, $P = 0.0359$, Tukey-Kramer; Fig. 1). This positive effect was greatest in October and November (Fig. 1). Leaf litter production changed significantly with time (PROC Mixed, time effect, $F = 7.07$, df = 4, 135, $P = 0.0002$). However, leaf litter production from August to December did not vary significantly with age or fertility,

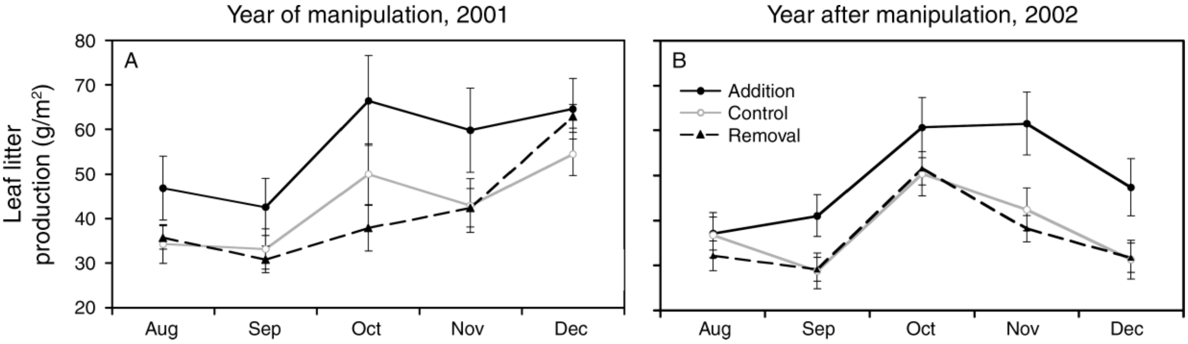

FIG. 1. Leaf litter production (mean ± SE) by treatment (A) in the year of litter manipulation and (B) in the year following manipulation. Data are pooled across all sites as no significant effect of fertility or age class was found.

nor did these forest types differ in the timing of their response to litter manipulation (PROC Mixed, forest type effect, n.s. [not significant]; forest type × time × treatment effect, n.s.). The effect of litter manipulation on leaf litter production persisted into the second study year, with leaf litter production significantly higher than removal and control plots from August to December 2002 (PROC Mixed, treatment effect, $F = 3.54$, df = 4, 171, $P = 0.0311$, Tukey-Kramer; Fig. 1). Similar to the first study year, leaf litter production did not differ by fertility or forest age (PROC Mixed, fertility and age effects, n.s.). The mean basal area increment (woody growth) did not differ significantly among treatments. Contrary to expectations, litter removal did not significantly affect basal area increment or litter production.

### *Effect of litter manipulation on litter N and P concentrations*

Leaf litter [N] and [P] did not differ significantly among treatments, either in the months following or in the year after litter manipulation (Figs. 2 and 3). Leaf litter [P] changed significantly with time and was significantly higher in the high-fertility sites (0.88 vs. 0.82 mg/g for low-fertility sites) (PROC Mixed, time effect, $F = 5.08$, df = 4, 129, $P = 0.0008$; fertility effect, $F = 12.14$, df = 1, 31, $P = 0.0015$, Tukey-Duncan). Leaf litter [N] did not change significantly with time (PROC

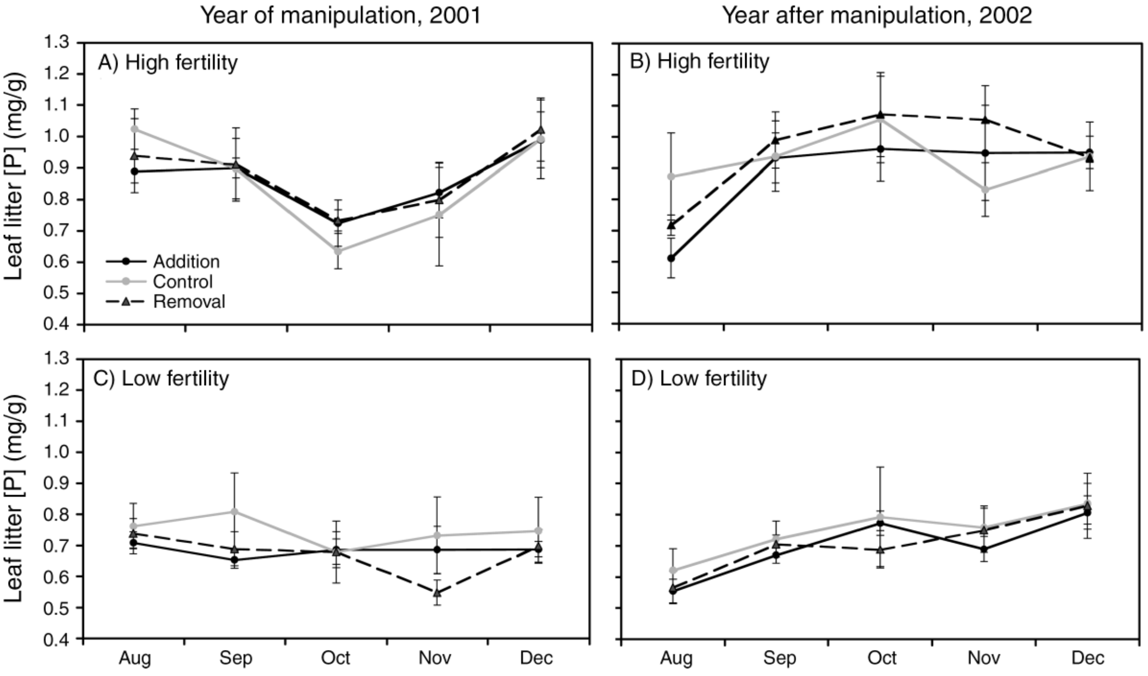

FIG. 2. Leaf litter P concentration (mean ± SE) for (A, B) high-fertility and (C, D) low-fertility sites by treatment in both the year of litter manipulation and the year following litter manipulation. Soil fertility significantly influenced the magnitude of leaf litter [P]. High-fertility sites include A4 and LS; low-fertility sites include A2, L3, L5, and LP (A = Young Oxisol, L = Old Oxisol, LS = Lindero Sur, LP = Lindero Peje). See Table 1 for a description of sites.

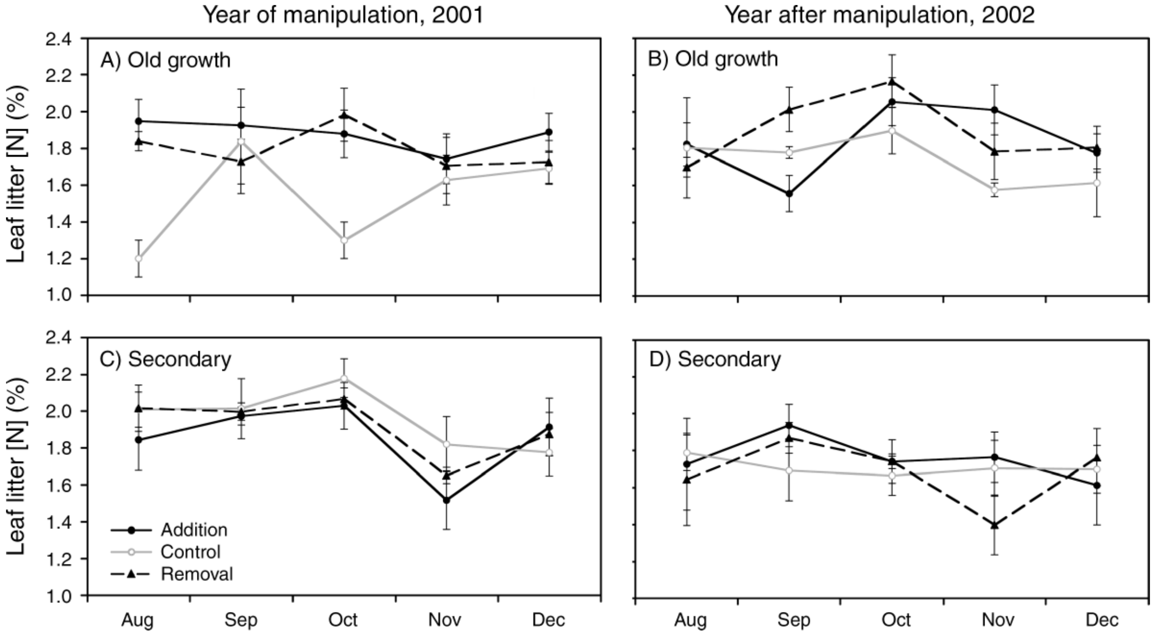

FIG. 3. Leaf litter N concentration (mean ± SE) for (A, B) old-growth and (C, D) secondary-forest sites by treatment in both the year of litter manipulation and the year following litter manipulation. Age class significantly influenced the magnitude of leaf litter [N]. Old-growth sites include A4, A2, L3, L5; secondary-forest sites include LS and LP.

Mixed, time effect, n.s.) and was significantly higher in the secondary forests than in the old-growth forest plots (1.93% vs. 1.76%) (PROC Mixed, age effect, $F = 4.41$, df $= 1, 31$, $P = 0.0034$, Tukey-Duncan). These results held for both study years (PROC Mixed, time effect, n.s.; age effect, $F = 4.75$, df $= 1, 31$, $P = 0.0307$). Soil fertility did not affect leaf litter [N] in either of the two study years.

### *Effect of litter manipulation on litter N and P inputs*

From two to six months following litter addition (August–December 2001), monthly litter P inputs were

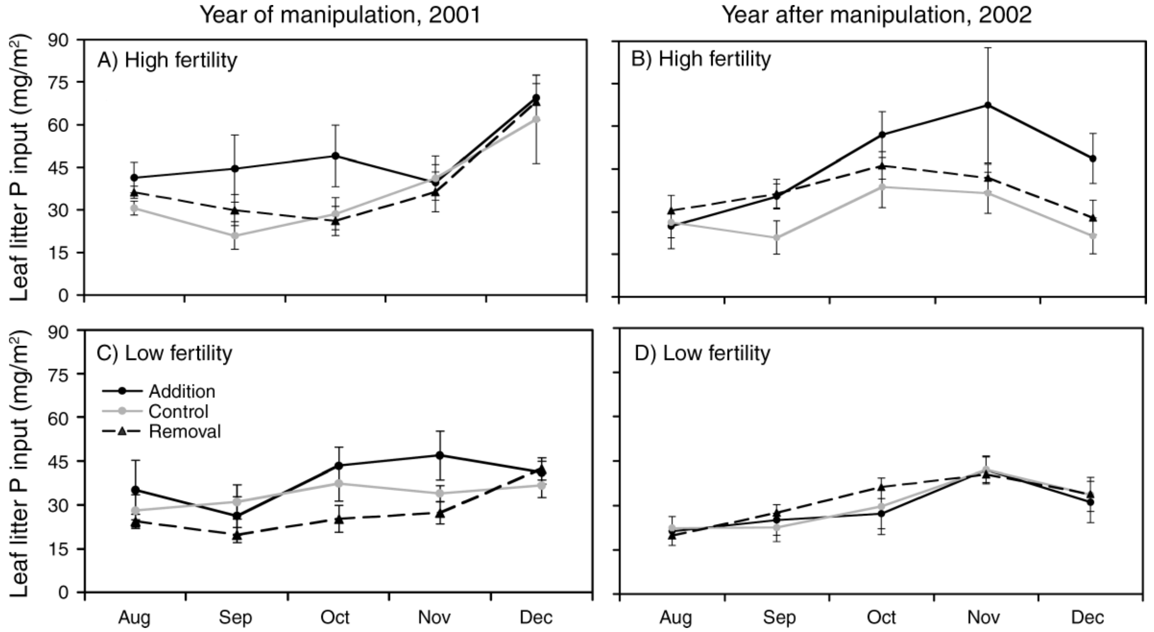

FIG. 4. Leaf litter P inputs (mean ± SE) for (A, B) high-fertility and (C, D) low-fertility sites by treatment in both the year of litter manipulation and the year following litter manipulation. Soil fertility significantly influenced the magnitude of leaf litter P inputs. High-fertility sites include A4 and LS; low-fertility sites include A2, L3, L5, and LP.

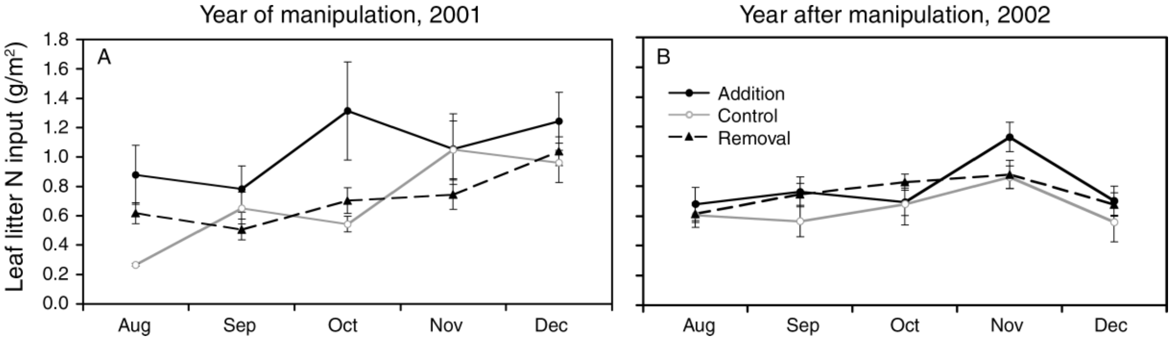

FIG. 5. Leaf litter N inputs (mean ± SE) by treatment (A) in the year of litter manipulation and (B) in the year following manipulation. Data are pooled across all sites as no significant effect of fertility or age class was found.

significantly higher in the addition plots than in both control and removal plots (mean 31% increase, as high as 85%, Fig. 4; PROC Mixed, treatment effect, $F = 3.59$, df = 2, 156, $P = 0.030$). As with litter production, the increase in P inputs in the addition plots was highest in October and November. However, unlike leaf litter production, leaf litter P inputs did not differ among treatments in the subsequent study year (Fig. 4). Leaf litter P inputs changed significantly with time in both study years (PROC Mixed time effect, $F = 15.22$, df = 4, 156, $P < 0.0001$). Leaf litter P inputs were significantly greater (by 26%) in the high-fertility sites; however, there was no significant effect of fertility on the timing of the response to litter manipulation (PROC Mixed fertility effect, $F = 4.83$, df = 1, 156, $P = 0.0295$; time × fertility × treatment, n.s.). There was no significant effect of litter removal on monthly litter P inputs.

As with leaf litter P inputs, leaf litter N inputs were also significantly higher in the addition than in the control and removal plots the year of litter manipulation (mean 46% increase, as high as 156%; PROC Mixed, $F = 4.72$, df = 2, 165, $P = 0.0102$, Tukey-Kramer; Fig. 5). Leaf litter N inputs changed significantly with time both the year of addition and the subsequent study year (PROC Mixed, time effect, $F = 10.03$, df = 4, 165, $P < 0.0001$). The magnitude of monthly N inputs did not differ with age or fertility, nor did the timing of the response to litter manipulation (PROC Mixed, age and fertility effects, n.s.; time × age/fertility × treatment effect, n.s.). There was no effect of litter removal on leaf litter N inputs.

### *Drivers of variability in the cumulative litter manipulation effect*

As much as 41–62% of the variation in the cumulative leaf litter, litter N, and litter P inputs of the addition plots was explained by the total P in added litter (Fig. 6; litter production, $R^2 = 0.48$, $P = 0.012$; P input, $R^2 = 0.62$, $P = 0.005$; N input, $R^2 = 0.41$, $P = 0.026$). Litter C:P was also significantly related to cumulative leaf litter mass, litter N, and litter P inputs (35–55% of the variance explained; data not shown). The P concentration of added litter was significantly related to the cumulative leaf litter ($R^2 = 0.37$, $P = 0.035$) and P input ($R^2 = 0.51$, $P = 0.009$) but not to N inputs. As expected, litter [P], litter C:P, and total P added in litter covaried, but total P added best explained the response to litter addition.

The high-fertility secondary forest site, LS, had a relatively low response to forest floor addition. This was likely due to low forest floor P stocks and hence a lower P litter treatment relative to other high-fertility sites. The low forest floor P stocks at this site may be due to the high forest floor turnover time and hence a rapid loss of nutrients and mass from litter (Table 2). The low-fertility sites, L3 and L5, also had low forest floor P stocks and a net negative response to litter addition (L3, 180 vs. 218 mg/m$^2$; L5, 264 vs. 288 mg/m$^2$ [total leaf litter 2–6 months following manipulation in addition vs. control plots]). Cumulative N and P inputs for all sites responded positively to litter addition, regardless of age and soil fertility.

None of the soil properties evaluated (total soil N, P, Bray-1 P, C:N, and C:P), or site characteristics (stem density, basal area, turnover time) were related to the litter manipulation effect for the addition sites. However, both Bray-1 P and total soil P were positively correlated with forest floor [P] ($r^2 = 0.50$, $P = 0.01$; data not shown). Furthermore, sites with higher forest floor [P] also tended to have larger P inputs in the manipulation.

We also evaluated the relationship between the cumulative litter removal effect and the forest floor mass, quality, and nutrients that were removed. The C:P and [P] of the removed forest floor litter explained 39–42% of the variability in the cumulative leaf litter input in the removal sites, respectively (Fig. 7; C:P, $R^2 = 0.39$, $P = 0.02$; [P], $R^2 = 0.42$, $P = 0.02$). Neither the total forest floor mass nor the quality of the litter removed influenced the cumulative leaf litter N and P inputs of the removal sites.

### *Forest floor turnover time and decomposition rates*

The youngest, high-fertility site (LS) had the shortest forest floor turnover time (3 months; Table 2), while the older, secondary forest site (LP) had a turnover time

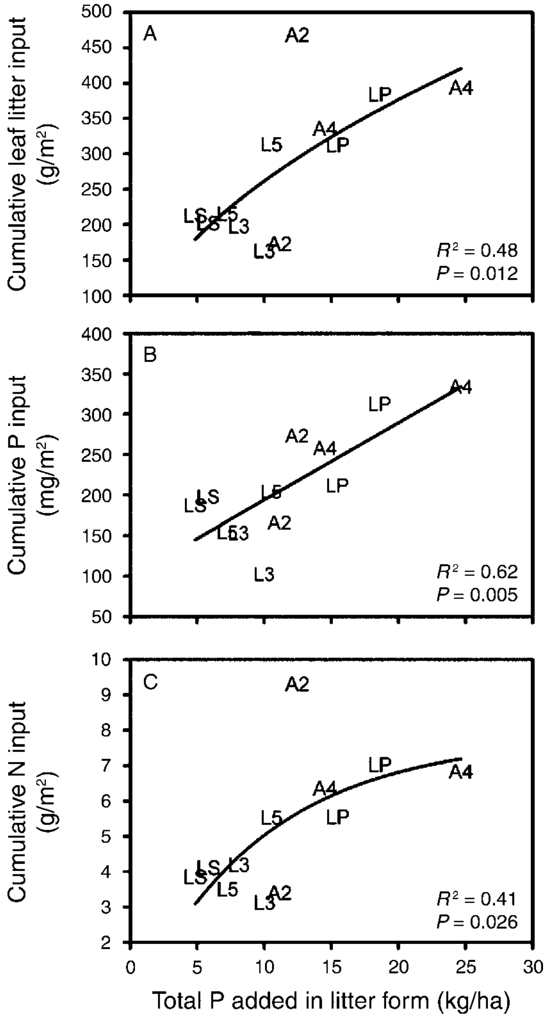

FIG. 6. Relationships between the total P added in litter form and the cumulative (A) leaf litter input, (B) leaf litter P inputs, and (C) leaf litter N inputs in the litter addition plots. The cumulative input is defined as the sum of total leaf or nutrient inputs from August to December in the year of litter manipulation.

similar to that of old-growth sites with similar soil fertility (6–7 months; Table 2). Contrary to expectations, one of the low-fertility sites (L5) had a relatively rapid forest floor turnover time (5 months; Table 2), and one plot at the highest fertility old-growth forest (A4) had the slowest forest floor turnover time (9 months; Table 2). Decomposition rates, as measured by litterbags, did not differ significantly with age or with fertility, although rates were slightly faster in the higher fertility sites. After four months of decomposition in our study, the litter had lost on average 42% of its original mass (range, 19–67%) and 50% of its initial P (range, 16–67%; data not shown). The decomposition rates estimated with decomposition bags were slower than those estimated by the forest floor turnover calculation.

## DISCUSSION

### *Forest productivity*

Over all forest types, increasing forest floor litter mass led to an average 22% increase in leaf litter production 2–6 months following litter application. This increase in litter production, ~2 Mg/ha/yr, is the equivalent of 19–27% of average annual production (Fig. 1). The increase in leaf litter productivity coincided with the time when 50% of P had been lost from decomposing litter. The rapid response of the vegetation to litter addition is reflective of the high forest floor turnover rate (3–9 months; Table 2) and a tight link between leaf litter nutrient cycling and forest productivity.

Given that the typical leaf life span of tropical trees ranges from 1 to 5 years (mean of two years; e.g., Reich et al. 1991), it is improbable that a complete cycle of new leaf production and senescence occurred within the time frame of this study. Rather, the increase in leaf litter production is most likely the result of trees shedding old leaves in favor of creating new leaves during periods of high soil nutrient availability. Similarly, evidence of a decoupling of leaf production and leaf life span has been found in other fertilization studies. For example, Harrington et al. (2001) found that in addition to

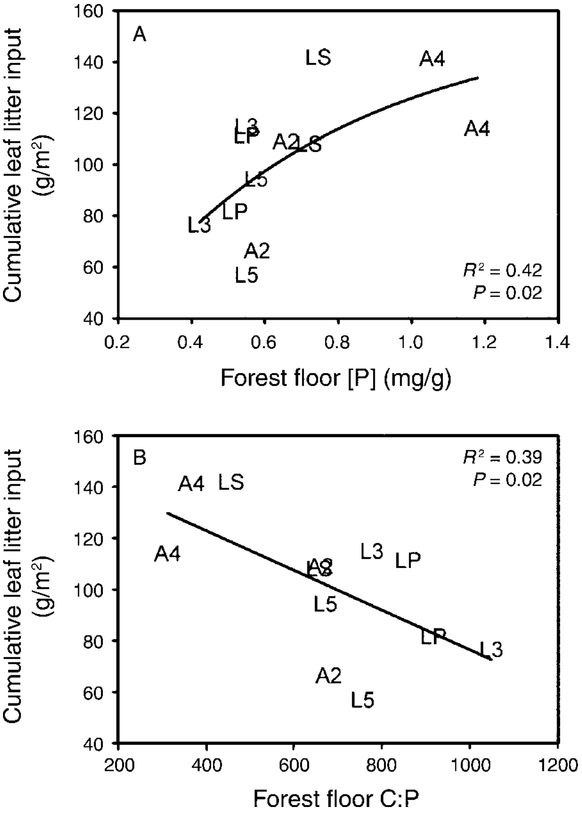

FIG. 7. Relationships between the cumulative leaf litter input in the removal plots vs. the (A) forest floor [P] and (B) forest floor C:P. The cumulative leaf litter input is defined as the sum of the total leaf litter produced from August to December the year of litter manipulation.

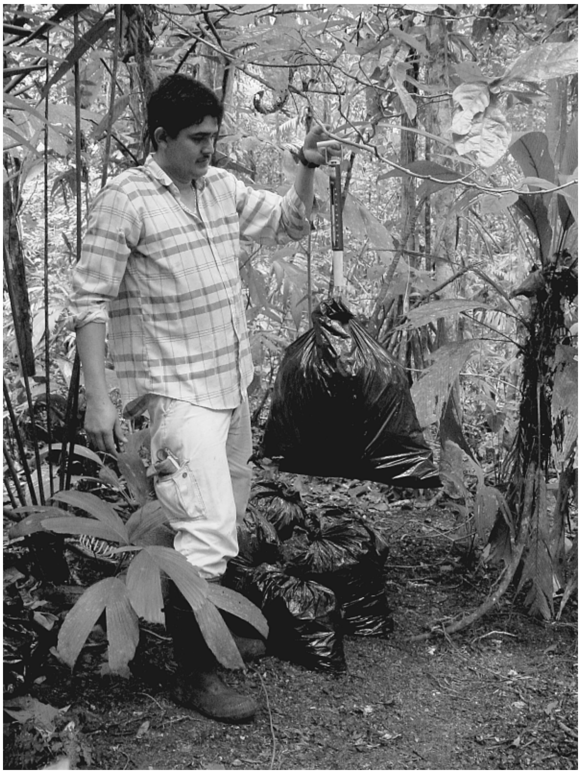

PLATE 1. Juan Romero weighs bagged forest floor litter before it is transferred to the neighboring addition plot. Photo credit: T. E. Wood.

increased litter production, the leaf area index (LAI) also increased in response to fertilization. The increase in litter production we report, in response to forest floor litter manipulation rather than the addition of nutrients in their mineral form, suggests highly efficient cycling of leaf litter nutrients.

The fourfold increase in forest floor litter could have also influenced litter production and nutrient inputs via its influence on soil properties such as soil moisture, pH, and temperature (Facelli and Pickett 1991, Ostertag et al. 2003, Sayer 2005). Lower soil moisture, high acidity, and temperatures as a result of a thick litter layer could cause trees to drop leaves prematurely as a result of the accompanying environmental stress. However, a similar experiment conducted at three of the six study sites found no effect of litter manipulation on soil pH, soil moisture, or temperature (Wood and Lawrence 2008). Therefore, the effect of forest floor litter manipulation on new litter production is likely due to microbially mediated nutrient release from the added litter rather than a change in physical or chemical soil characteristics.

While the [P] and C:P of added litter were also significantly related to the cumulative litter effect, these factors explained less of the variability in leaf litter production than total P added. Increased leaf litter production in response to addition of total P added is consistent with results from other fertilization studies (Tanner et al. 1990, 1992, Vitousek and Howarth 1991, Crews et al. 1995, Herbert and Fownes 1995, Aerts and Chapin 2000, Harrington et al. 2001). Contrary to expectations, neither soil fertility nor forest age influenced the magnitude of the leaf litter response to forest floor litter addition. Rather, the total P added in litter form drove the observed variability in leaf litter production (Fig. 6). This finding supports our hypothesis that tropical rain forest vegetation is sensitive to inputs of limiting nutrients from litter on short timescales.

Although soil fertility did not directly influence leaf litter production, both total and available P (Bray-1) were positively correlated with forest floor [P], and sites with high forest floor [P] tended to also have higher total P inputs. Therefore, there is an indirect effect of soil fertility on leaf litter production via its influence on litter quality. Soil fertility may also influence the response to increased litter inputs by acting as a buffer against nutrient immobilization. For example, the low-fertility sites, L3 and L5, demonstrated a net negative response to litter addition. The combination of large inputs of low-quality litter and low soil P might have led to net immobilization, such that the microbes acted as a sink for added nutrients rather than a source (Chapin 1980, Lodge et al. 1994, Cleveland et al. 2006). In contrast, the secondary forest site, LS, had high soil fertility and low forest floor P inputs (Table 2). The response of leaf litter production to litter addition at LS was not negative; however, it was low compared to sites with higher forest floor P stocks (Fig. 1). In this case, high soil quality mitigated the negative effect of low total P inputs.

Contrary to expectations, litter removal had no significant effect on forest productivity or nutrient cycling. Although forest floor litter was removed from a relatively large area when compared with the addition treatment (400 $m^2$ vs. 100 $m^2$), the treatment itself was much smaller (onefold removal vs. fourfold addition). More intense litter removal over a longer time period is likely needed before an effect of litter removal on forest productivity and nutrient cycling is observable (Sayer 2005). The cumulative leaf litter inputs in the removal plots were, however, significantly related to the concentration of P in the forest floor litter (Fig. 7). That the quality of the forest floor litter, rather than the available and/or total nutrient pools in the soil explained such a large degree of the variation in the cumulative leaf litter inputs in these sites further highlights the importance of litter as a source of limiting nutrients in this system.

In addition to our expectation that litter addition would positively influence leaf litter production, we also hypothesized that litter augmentation would have a positive effect on woody growth. However, over one year, woody growth did not differ between removal and addition treatments. Hence over the short term, trees initially put nutrients derived from high litter inputs into new leaf production rather than wood growth. Further research is needed to determine how wood growth responds to litter inputs over a longer time frame.

### *Litter nutrient cycling*

Tropical trees have been shown to increase both foliar and senesced leaf nutrient concentrations in response to more intense fertilization with inorganic nutrients over 12 months to 11 years (Tanner et al. 1990, 1992, Vitousek 1998, Mirmanto et al. 1999, Harrington et al. 2001). In this study, litter manipulation had no effect on leaf litter [N] and [P] over 20 months, or the timing of changes in N and P concentrations. Instead, leaf litter [P] was significantly higher in the high-fertility sites, while leaf litter [N] was significantly higher in the secondary forest sites. Hence, the observed temporal variation in leaf litter nutrient concentrations is not a response to short-term pulses in nutrient availability. The processes that might alter leaf litter nutrients, such as resorption, are apparently not responding to nutrients from decomposing litter. Higher leaf litter nutrient concentrations in response to litter addition may not be observed until leaves created under higher nutrient availability are later senesced (i.e., 1–5 years later). Further research is needed to test this hypothesis.

Both leaf litter N and P inputs increased significantly in response to litter addition (mean 46%, 31%, respectively, over the course of three to four months; Figs. 4 and 5). Given that leaf litter nutrient concentrations did not differ among the litter treatments, the increase in N and P inputs occurred mainly in response to changes in leaf litter production. The effect of litter addition on both N and P inputs was short-lived (Figs. 4 and 5; no effect the year following litter manipulation). This rapid return of litter N and P inputs to "normal" conditions indicates a very tight cycling of N and P, and would suggest a high adaptability of this forest to climatic variability. In contrast, elevated leaf litter inputs persisted into the subsequent study year (Fig. 1), indicating a continued positive feedback of increased litter production on future leaf litter productivity.

Although mean leaf litter [N] and [P] as well as P inputs varied significantly among forest types (Figs. 2–4), forest type did not influence the timing or the magnitude of the response to litter addition. As with litter production, the total P in added litter, rather than soil classification, better predicted the response (Fig. 6). Across sites, the maximal effect of litter addition occurred in October–November of the year of addition, regardless of litter quality. The similar timing of this response, indicates that microbes are responding to climate first, and to litter quality second. This hypothesis is further supported by the similar decomposition rates among the six study sites. Although surprising, our decomposition results are consistent with the findings of Cleveland et al. 2006, who conducted a large decomposition experiment in similar forest in Costa Rica. It is possible that there is a longer lag in the response of sites with low litter [P] to litter addition (i.e., switch from net immobilization to net mineralization) that was not captured during the time frame of this study.

## CONCLUSIONS

Sudden large inputs of litterfall in response to major climatic events are not uncommon for tropical forests. Although not important for this forest, hurricanes and major storm events, common to many tropical forests, can lead to massive defoliation of trees and create up to a twofold increase in forest floor mass (Lodge et al. 1991, Ostertag et al. 2003). The high nutrient content and thus high decomposition rate of green leaves vs. senesced leaves could lead to a larger and more rapid response of these forests to elevated litter inputs (Lodge et al. 1991, Fonte and Schowalter 2004). In addition, during especially dry years, such as those that occur during ENSO events, litter production can increase as much as 20% (D. A. Clark, *unpublished data*). For this forest, experimentally increasing litter inputs to the forest floor resulted in a net positive feedback on leaf litter production and nutrient inputs to the soil. Tropical wet forests appear efficient at recapturing nutrients lost in prior litterfall. Efficient nutrient recapture may confer adaptability of tropical trees in the face of short-term climatic change (ENSO) or longer-term shifts in climate regime in both secondary and old-growth forests. Variability in the response of vegetation to litter addition was driven by variability in the total amount of the most limiting nutrient (P) in added litter rather than total organic matter inputs to the soil or soil fertility, and these nutrients were put toward new leaf production rather than wood growth. These results suggest that in the short term, trees initially put nutrients obtained from decomposing litter into leaf production rather than wood. Should predictions of more frequent ENSO events and more intense wet–dry seasonality in tropical forests hold true (Hulme and Viner 1998), we may expect a shift in the timing of phenological events (i.e., leaf flushing) to coincide with seasonal pulses of nutrient availability.

## ACKNOWLEDGMENTS

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## APPENDIX

Top 10 tree species for each of the treatment plots (*Ecological Archives* E090-007-A1).