Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere

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Terrestrial biosphere–atmosphere carbon dioxide (CO_2) exchange is dominated by tropical forests, where photosynthetic carbon (C) uptake is thought to be phosphorus (P)-limited. In P-poor tropical forests, P may also limit organic matter decomposition and soil C losses. We conducted a field-fertilization experiment to show that P fertilization stimulates soil respiration in a lowland tropical rain forest in Costa Rica. In the early wet season, when soluble organic matter inputs to soil are high, P fertilization drove large increases in soil respiration. Although the P-stimulated increase in soil respiration was largely confined to the dry-to-wet season transition, the seasonal increase was sufficient to drive an 18% annual increase in CO_2 efflux from the P-fertilized plots. Nitrogen (N) fertilization caused similar responses, and the net increases in soil respiration in response to the additions of N and P approached annual soil C fluxes in mid-latitude forests. Human activities are altering natural patterns of tropical soil N and P availability by land conversion and enhanced atmospheric deposition. Although our data suggest that the mechanisms driving the observed respiratory responses to increased N and P may be different, the large CO_2 losses stimulated by N and P fertilization suggest that knowledge of such patterns and their effects on soil CO_2 efflux is critical for understanding the role of tropical forests in a rapidly changing global C cycle.

carbon cycle | nutrient availability | soil respiration | nitrogen | phosphorus

Tropical forests contain up to 40% of global terrestrial biomass carbon (C), and they account for at least one-third of annual biosphere–atmosphere carbon dioxide (CO_2) exchange and global soil organic C storage (1–3). Because of their dominant role in the terrestrial C cycle, even small changes in tropical CO_2 fluxes can modify the global C budget, climate, and atmospheric composition (2, 4). The biogeochemical importance of tropical rain forests has been clearly established, but the role of nutrients in regulating C cycling in this vast biome is poorly understood. Many studies have shown that nitrogen (N) availability directly controls terrestrial C uptake and losses in mid- and high-latitude ecosystems (5, 6), but the nature and extent of nutrient limitation on C storage in low-latitude tropical ecosystems are still poorly understood. However, such data are essential prerequisites to effective predictions of how the C cycle in tropical forests may respond to global environmental change.

Direct tests of nutrient limitation in tropical rain forests are rare, but those that do exist suggest that nutrient regulation of net primary production (NPP) may be fundamentally different from that in temperate systems. Many lowland tropical forests grow on highly weathered soils that are relatively N-rich (7) but that are depleted in "rock-derived" essential elements, especially phosphorus (P) (8, 9). As a result, many lowland tropical rain forests are characterized by low soil P availability (9, 10) and high foliar and litter N:P ratios (11, 12), and they respond to P fertilization by increases in the production and P content of litterfall (13). These observations, among others, have led to the widespread belief that P availability limits NPP in lowland tropical forests on highly weathered soils.

Low P availability may limit tropical NPP, but understanding the effects of nutrient availability on ecosystem C storage requires insight into how it regulates the balance between both NPP (C uptake) and organic matter decomposition (C loss). Data demonstrating how soil P availability controls decomposition in tropical forests are similarly rare; they have been limited primarily to simple analyses of nutrient effects on leaf litter-mass loss, and they show inconsistent responses to the addition of nutrients. For example, in a highly weathered Hawaiian soil, where P availability limits NPP, the addition of P increased the rates of litter-mass loss (14); but in P-poor sites in the Brazilian Amazon (15) and southwestern Costa Rica (ref. 16 and described here), the addition of P had no effect. Such inconsistencies suggest complex interactions between soil nutrient availability and organic matter decomposition in tropical rain forests, and they highlight our incomplete understanding of the response of the tropical C cycle to future changes in nutrient availability.

The inconsistent responses of decomposition to the addition of nutrients in tropical rain forests may be partly explained by soluble organic matter dynamics in decomposing litter. Mass loss during decomposition consists of two distinct processes: direct mineralization of organic matter to CO_2 in the litter layer, and leaching and transport of soluble organic material from the litter layer to the soil (17). If mass loss is dominated by direct microbial C mineralization in the litter layer itself, then the potential for strong nutrient constraints on litter decomposition clearly exists. However, if leaching (a physical process) is the dominant mass-loss vector, then decomposition may be decoupled from nutrient availability, and it may be more a product of litter solubility and rainfall (18, 19). In tropical rain forests, frequent, heavy rainfall interacts with large amounts of potentially soluble litter C, favoring relatively high litter-mass rate loss by leaching. The frequent transport of soluble organic C from the litter layer into the soil can be an important control over soil CO_2 efflux to the atmosphere and a significant component of overall C balance (20–22).

Because litter decomposition in tropical rain forests may be dominated by leaching, accurate assessments of the C balance of tropical forests should also account for potential nutrient constraints on the mineralization of soluble organic C transported to the soil. Microbial decomposition of soluble, labile organic matter accounts for the majority of heterotrophically respired soil CO_2 (23), and previous data showed that in P-poor tropical soils, soil P availability can strongly limit the rates and magnitude of soluble organic matter that is respired (16, 24). In a soil-incubation experiment, Cleveland *et al.* (16) showed that CO_2 flux in soils receiving C + P was significantly higher than rates observed after adding C alone. In the same experiment, however,

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Abbreviations: ha, hectare; NPP, net primary production.

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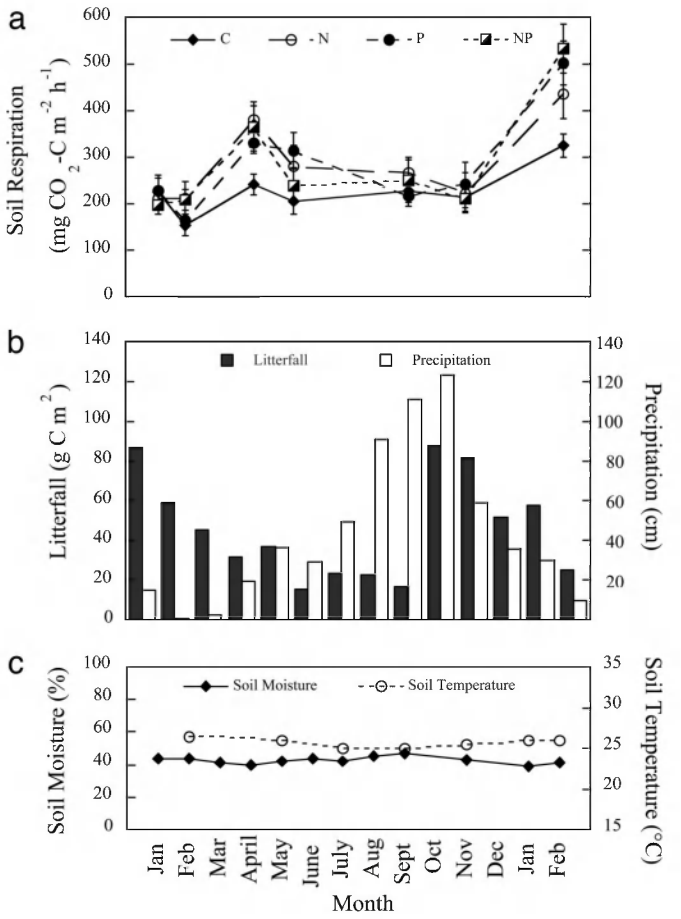

Fig. 1. Seasonal dynamics of soil CO_2 efflux, litterfall, precipitation, and soil temperature and moisture. (*a*) Soil respiration (CO_2 efflux) from January 2004 through February 2005 in control (filled diamonds), +N (open circles), +P (filled circles), and +NP (black and white squares) plots. Each point represents a mean of 10 measurements; error bars are ± 1 SE. (*b*) Monthly litterfall (filled bars) and precipitation (open bars). (*c*) Soil moisture (filled diamonds) and soil temperature (open circles) associated with the respiration data shown in *a*.

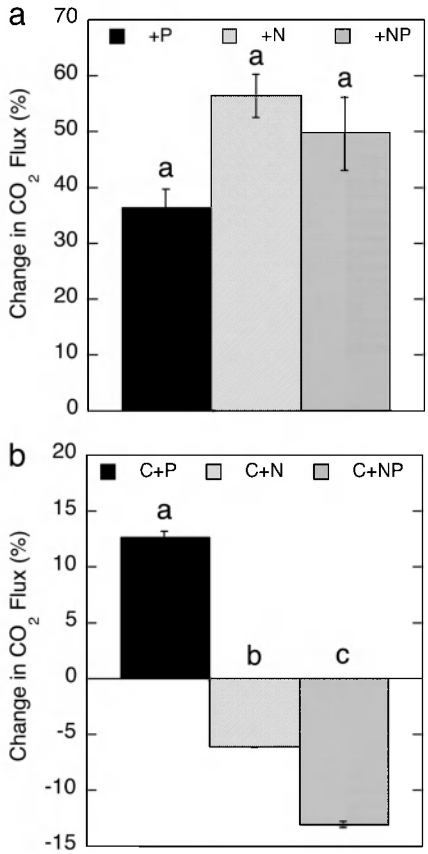

Fig. 2. Relative effects of nutrient fertilization on soil CO_2 fluxes in field and laboratory experiments. (*a*) Relative effects of the addition of nutrient on soil respiration in field experiments. Responses represent the change in soil CO_2 fluxes in fertilized plots relative to fluxes measured in control plots at the time of annual peak soil respiration in April 2004. Respiration rates in all treatments were significantly higher than rates measured in control plots ($\alpha = 0.05$). Error bars represent ± 1 SE, and significant differences among treatments are denoted by different lowercase letters ($\alpha = 0.05$). (*b*) Relative effects of the addition of nutrients on soil respiration in soil incubation experiments (for complete details, see ref. 16). Responses represent the change in total CO_2 respired after the addition of C to fertilized plot soil samples relative to fluxes measured after the addition of C to control plot soil samples. Error bars represent ± 1 SE. Significant differences among all treatments are denoted by lowercase letters ($\alpha = 0.05$). Respiration rate in C + N samples was not significantly different from rates in samples receiving C alone.

the addition of N had neutral to negative effects on heterotrophic soil respiration rates, suggesting that when labile C is plentiful, P availability exerts primary control over microbial respiration of that labile C.

Our laboratory assays (16, 24) provided compelling evidence for the P limitation of soil respiration in tropical rain forests. The goal of the current research was to determine how increases in nutrient availability could affect *in situ* rates of soil respiration and how such changes might, in turn, alter tropical rain forest C balance. To address these questions, we used a matrix of fertilization plots (N × P in a full factorial design) to investigate how nutrient availability regulates soil CO_2 losses in a lowland Costa Rican tropical rain forest site with highly weathered, P-poor soils (25). Based on data obtained in the previously conducted laboratory assays (16, 24), we hypothesized that P fertilization would increase soil C losses to the atmosphere but that the addition of N would not significantly affect soil CO_2 fluxes.

Results and Discussion

As expected, after 3 yr of fertilization, the additions of P stimulated *in situ* soil respiration in the fertilization plots (Fig. 1*a*). In April, when soil respiration reached a seasonal maximum (Fig. 1*a*), CO_2 fluxes were 37% higher in +P plots than in control plots (Fig. 1*a*; $P < 0.05$). The most dramatic nutrient-stimulated increases in soil respiration occurred during this dry-to-wet season transition, but the seasonal, P-stimulated increase in soil respiration was still sufficient to drive an ≈18% increase in total annual CO_2 flux in the +P plots relative to the controls; over the course of 2004, CO_2 efflux from control plots was 1,880 g of $C{\cdot}m^{-2}{\cdot}yr^{-1}$, whereas +P plots respired 2,227 g of $C{\cdot}m^{-2}{\cdot}yr^{-1}$. These results corroborate those obtained in the laboratory assays (16); in both cases, P fertilization significantly enhanced soil respiration rates (Fig. 2). Together, these data provide strong evidence that P availability strongly limits soil respiration in this ecosystem and that P input to the soil may stimulate significant CO_2 losses to the atmosphere.

Given the relatively minor influence of the addition of N on soil CO_2 fluxes in the laboratory assays (ref. 16 and Fig. 2*b*), we hypothesized that N input would not significantly affect soil respiration in the field-fertilization experiment. Contrary to our expectations, the addition of N strongly stimulated soil CO_2 losses in the fertilization plots; soil respiration rates in both the +N and +NP plots were similar to those observed when we added P alone (Fig. 1*a*). Again, at the time of maximum seasonal

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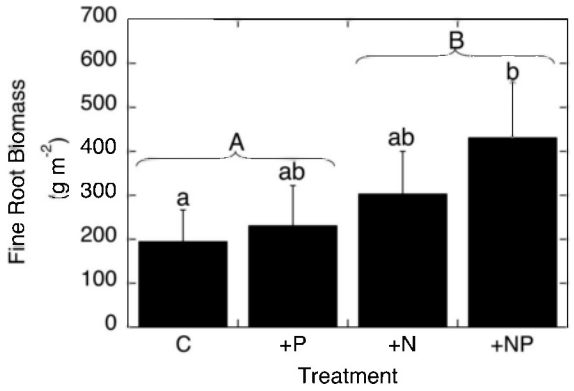

Fig. 3. Total fine-root biomass (0–10 cm) in experimental plots collected in February 2005. Error bars are ± 1 SD. Significant differences ($\alpha = 0.05$) among all treatments are denoted by lowercase letters, and significance differences between N-treated and non-N-treated soil are denoted by uppercase letters.

soil respiration in April 2004, CO_2 fluxes were 56% higher in +N plots ($P < 0.01$) and 49% higher in +NP plots ($P < 0.05$) than in control plots (Fig. 2*a*). On an annual basis, soil respiration rates in the N-fertilized plots were also much higher than rates in the control plots; CO_2 fluxes were 2,310 g of $C{\cdot}m^{-2}{\cdot}yr^{-1}$ and 2,139 g of $C{\cdot}m^{-2}{\cdot}yr^{-1}$ in the +N and +NP plots, respectively, versus 1,880 g of $C{\cdot}m^{-2}{\cdot}yr^{-1}$ in the controls.

The results of our field-fertilization experiment, combined with the results of the laboratory assays (16), provide a powerful means of assessing the specific effects of nutrient availability on soil respiration, and together, they provide compelling evidence that mechanisms driving the observed CO_2 responses to N may be different from those driving responses to P. Soil CO_2 fluxes represent both the activity of soil heterotrophs (dominated by microorganisms) and live-root respiration (26). After plot fertilization, higher CO_2 fluxes could arise from more rapid decomposition by the microbial community, greater root respiration, or both. In the field experiment, our data suggest that the observed P-stimulated increase in soil respiration was a heterotrophic response. Measurements of fine-root biomass from all plots revealed no difference between control and +P treatments ($P = 0.87$), indicating that the observed increase in soil respiration in response to the addition of P was not driven by increases in fine-root biomass (Fig. 3). Similarly, CO_2 fluxes in the laboratory assays (which removed all roots and all possible effects of root activity) also increased significantly after P fertilization (Fig. 2*b*), suggesting that increased P availability can drive higher soil CO_2 fluxes by more rapid microbial (heterotrophic) respiration.

Higher soil CO_2 fluxes in the +P plots also correlated with differences in the soil concentration of soluble organic C between the +P and control plots, providing direct evidence that P fertilization stimulated higher rates of heterotrophic respiration. In April 2004, soil respiration in the +P plots was 37% higher than the rate in control plots (Fig. 2*a*), and at the same time, water-extractable (soluble) organic C was significantly lower in the P-fertilized plots (35.8 ± 3.1 μg of C per g of soil) than in control plots (43.3 ± 2.1 μg of C per g of soil). The lower concentration of water-extractable (soluble) C in the P-fertilized plots at the time of maximum soil respiration is consistent with their high soil respiration rates at that time, and it indicates that a relatively higher proportion of soluble soil C had been respired in the P-fertilized plots than in the controls. Thus, several lines of evidence unambiguously demonstrate that increases in P availability in tropical rain forests (27, 28) could drive higher CO_2 losses by P-stimulated increases in soil heterotrophic respiration.

The inconsistent effects of N fertilization on soil CO_2 fluxes in the laboratory assays and the field-fertilization experiment are noteworthy, and they may represent opposite responses of plants and the microbial community to the addition of N (Fig. 2). Even in sites where N availability clearly limits NPP, laboratory and field additions of N frequently elicit neutral or negative effects on microbial respiration (29, 30), just as we observed in our laboratory experiment (16; Fig. 2*b*). However, N fertilization stimulated soil respiration in our field experiment (Figs. 1 and 2*a*). How can the decreases in soil respiration in the laboratory experiment after the addition of N be resolved with the field data showing N stimulation of soil CO_2 fluxes? Our data suggest that higher soil respiration in the plots receiving N could be a product of fine-root responses to N fertilization; plots receiving N (alone or with P) had significantly higher fine-root biomass than those that did not receive N ($P < 0.05$; Fig. 3). Higher fine-root biomass in the N-fertilized plots does not necessarily explain their high rates of soil respiration, but it does provide a plausible explanation for both the unexpected increase in soil respiration in the N-fertilized plots and the inconsistent effects of N on soil CO_2 fluxes in the laboratory and field experiments. Root proliferation in response to high N availability in the fertilization plots, combined with previous data showing that N does not stimulate microbial respiration in laboratory incubations, suggests that the increase in soil respiration in the N-fertilized plots may have been driven, at least in part, by changes in fine-root dynamics (31, 32).

The effects of nutrient availability on *in situ* soil respiration showed strong seasonal variation (Fig. 1*a*). Soil respiration in control plots was at an annual low of 151 mg of $C{\cdot}m^{-2}{\cdot}h^{-1}$ during the relatively dry month of February 2004, but after the onset of heavy daily rains, it increased 40% to an annual high of 242 mg of $C{\cdot}m^{-2}{\cdot}h^{-1}$ in April. However, the effects on CO_2 fluxes of adding nutrients were more than or equal to those of seasonal changes in rainfall. In February 2004, there were no significant differences in soil respiration among all plots. By April, respiration rates had increased by 40% in the control plots, whereas rates increased by 80% in the +N plots, by 83% in the +NP plots, and by 100% in the +P plots. The seasonal variation in soil respiration would seem to highlight the well established importance of climate as a control of soil respiration; but surprisingly, there were no strong relationships between soil respiration and surface (0–10 cm) soil temperature and moisture because both remained remarkably constant throughout the year (Fig. 1*c*).

Instead, our field data suggest that the seasonal patterns in soil respiration are driven by interactions between leaf litterfall (a large, labile C source) and precipitation, which provides a vehicle for the movement of decomposable C from the litter to the soil. As at most tropical rain forests, annual C inputs at this site are dominated by a large, dry-season litterfall pulse (Fig. 1*b*). During the transition to the wet season, rainfall can leach substantial amounts of water-soluble C to the soil as dissolved organic matter (16, 33). We observed large increases in soil respiration in both early 2004 and 2005 (Fig. 1*a*), shortly after several relatively dry months in which >50% of the annual litter fell (Fig. 1*b*). In both 2004 and 2005, the highest rates of soil respiration occurred during periods of significant daily rainfall that were preceded by profound inputs of leaf litter, and in each case, the magnitude of the CO_2 pulse was proportional to the overall litterfall C pulse received in the preceding 3 mo (Fig. 1).

We suggest that the dry-to-wet season increases in soil respiration (and the corresponding large responses to the additions of P) were stimulated by inputs of leached organic C to the soil during that time. Maximum annual litter-mass loss rates (i.e., >40% in 60 days) (16) during this transition coincide with the highest rates of soil respiration, suggesting that the large pulses of soluble organic C leached from the litter to the soil during the dry-to-wet season transition may have had a natural priming

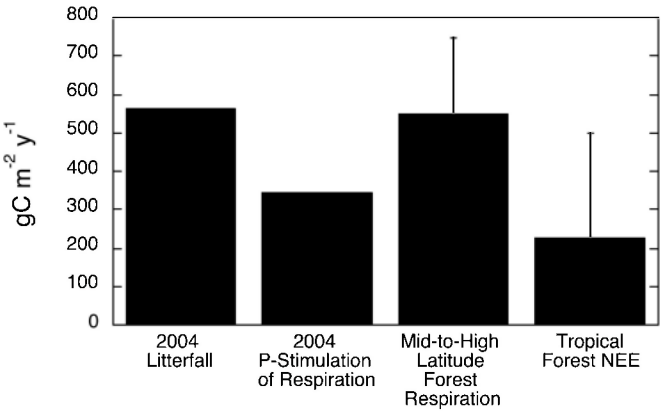

Fig. 4. Annual litterfall and net annual P-stimulated increase in soil respiration from the Costa Rican sites compared with a mean of soil respiration values from mid- and high-latitude forest biomes and with a mean of net ecosystem exchange (NEE) values from several tropical forest sites. The mid-latitude forest soil respiration value is the mean of values from deciduous temperate forests, coniferous temperate forests, and boreal forests (44). The NEE value is derived from seven recent estimates based on eddy-covariance flux tower measurements, including sites in Costa Rica (45) and the Brazilian Amazon (36, 46). "Mean NEE" represents a net uptake of C, but for comparative purposes, it is depicted here as a positive value.

effect on the microbial community, with P fertilization enhancing the respiratory response to high labile C availability. Several lines of evidence support this hypothesis, including: (*i*) leaf litter in these forests has a large soluble fraction that can be easily leached by rainfall (16); (*ii*) experimental additions of litter-derived soluble organic C to the soil cause rapid, significant increases in soil respiration; (*iii*) the size of those increases is a function of P availability; and (*iv*) P fertilization caused substantially larger CO_2 fluxes (Figs. 1 and 2). However, the data also indicate that soil respiration patterns are not entirely a function of the litter–climate interactions because a significant litter pulse combined with high rainfall in late 2004 did not cause an immediate soil respiration pulse in any of the experimental plots.

Some of the potential mechanisms behind our results remain unclear, but the implications are not; our data clearly show the potential for changes in nutrient availability to affect CO_2 emissions from tropical rain forest soils. Despite the fact that *in situ* soil respiration responses to the addition of P were most pronounced in the early wet season (Fig. 1*a*), those episodic, nutrient-stimulated CO_2 losses were large enough to stimulate an annual increase in CO_2 efflux from the P-fertilized plots that approached annual soil respiration rates measured in higher-latitude forest biomes (Fig. 4). It is still unclear whether P limitation of soil respiration is widespread in the lowland tropics or whether chronic increases in atmospheric N and P deposition in tropical latitudes (27, 34) will cause increases in soil CO_2 efflux. However, the soil at our site is relatively P-rich compared with many other tropical soils (25), suggesting that subtle changes in P inputs to these even more P-poor tropical forests could stimulate soil CO_2 losses like those we observed. Such changes are already occurring in tropical ecosystems, where natural soil fertility is being influenced by land-use perturbations that alter soil-nutrient dynamics and availability both directly (25) and indirectly [by changes in atmospheric deposition of both N and P (27, 34)].

The effects of increasing N inputs on tropical soil CO_2 fluxes are more difficult to predict from our results. Higher respiration and fine-root biomass in the N-fertilized plots, combined with a lack of evidence for N stimulation of microbial respiration in the laboratory assays (Fig. 2), suggest that the N-stimulated increases in soil respiration in the field could have been the result of changing root dynamics in the small (5 × 5 m), relatively N-rich plots (31, 32). However, natural N inputs, which are likely to occur at the landscape scale, may elicit root responses that are much different from those we observed. For example, large-scale increases in tropical soil N availability may drive decreases in fine-root biomass allocation and overall declines in root (and hence soil) respiration (35). Nonetheless, the profound increase in soil respiration we observed in response to N fertilization suggests the importance of further work resolving how large-scale, chronic N inputs may alter fine-root dynamics, soil respiration, and the overall C balance in tropical rain forests.

The potential influence of N and P availability on the tropical C balance remains largely ignored. To date, most analyses have focused on the direct role of climate and disturbance on tropical C fluxes (36, 37), without significant attention to how nutrient availability may interact with each of those drivers. For example, Saleska *et al.* (36) indicated that sizable wet-season CO_2 losses from a central Amazon forest were caused by the decomposition of C inputs from a past disturbance. Our results suggest that the respiration of such disturbance-driven pulses of organic matter may be further regulated by variations in soil fertility. If so, future increases in soil nutrient (particularly P) availability may drive substantial soil C losses from the majority of tropical forests growing on P-poor soils. However, predicting the true nature and extent of such nutrient controls will require better knowledge of spatial and temporal changes in soil N and P availability and a better mechanistic understanding of their effects on soil C turnover in a range of tropical rain forest sites.

Materials and Methods

Site Description. The study site is a diverse, primary, lowland tropical rain forest in southwest Costa Rica, located on the north end of the Osa Peninsula in the Golfo Dulce Forest Reserve (8°43′ N, 83°37′ W). Annual rainfall averages >5,000 mm·yr^{-1}, and like most tropical rain forests, precipitation is seasonally variable (38); peak rainfall occurs between June and October, and it decreases during a pronounced dry season between December and April (Fig. 1*b*). Over an 8-yr period (1980–1987), December–May rainfall averaged <250 mm·mo^{-1} at the Sirena Biological Station, 25 km southwest of our sites (39). In contrast, over the same period, May–November rainfall averaged >500 mm·mo^{-1}, and every month between May and November received >250 mm of rainfall (39). Leaf senescence and litterfall reach a maximum during the dry season (Fig. 1*b*).

The entire Osa Peninsula was formed in three large seafloor volcanic events that occurred between 75 and 40 × 10^6 yr ago, but some parts of the region were below sea level in more recent geologic eras (40). These phenomena created a wide range in parent material and soil, and forests in the region thus occur on three general soil types: (*i*) old, highly weathered Ultisols on steeply dissected terrain that rarely exceeds a few hundred meters elevation; (*ii*) much younger (2–4 × 10^6 yr old) Ultisols on roughly similar upland terrain; and (*iii*) the highly fertile Mollisols found on the alluvial plains. Our experiment was conducted on a P-poor Ultisol soil that developed on a steeply dissected landscape in the Osa basaltic complex (41).

Soil Fertilization Plots. To assess the effects of soil nutrient availability on soil C fluxes in a P-poor, lowland tropical rain forest, we established a soil N and P fertilization experiment. Starting in 2001, we fertilized 5- × 5-m plots with N and P in a full factorial design (10 replicates per treatment). Plots were randomly selected to receive treatments, and they were fertilized twice per year [in January (dry season) and June (wet season)] by hand-broadcasting N [150 kg of N·hectare (ha)$^{-1}$·yr^{-1} as NH_4NO_3; +N], P (150 kg of P·ha^{-1}·yr^{-1} as KH_2PO_4; +P), or N and P in combination (150 kg of N and P·ha^{-1}·yr^{-1}; +NP); 10 control plots at each site were not fertilized. Fertilized plots

received N, P, or N + P at a high rate and at a 1:1 weight ratio to account for the for high P-sorption capacity of the Ultisol soil (42) and to remove all possible nutrient constraints by N and P (14). All plots received 2 full yr of fertilizer before soil respiration measurements began.

Laboratory Soil Incubations. Cleveland *et al.* (16) conducted an incubation experiment to determine the effect of nutrient availability on heterotrophic soil respiration. One hundred grams of mixed litter collected from the soil surface during the dry season was air-dried and leached in 1 liter of deionized water for 24 h at 22°C. After extraction, the leachate was filtered to 0.45 μm, and its C content was measured by using a TOC 5050A total organic C analyzer (Shimadzu). Ten 15-g (dry weight) fresh soil samples collected from control, +N, +P, and +NP plots were sieved to remove roots, placed in 900-ml glass jars, and preincubated for 24 h. After the initial incubation, samples were amended with 5 ml (i.e., an amount to bring soil to 50% of water-holding capacity) of one of two solutions: dissolved organic C (422 μg of C per g of soil) or 5 ml of water (as control). After the addition of treatments, incubation vessels were capped with lids equipped with rubber septa for gas sampling and sampled for CO_2 at 3, 6, 9, 12, 15, 24, 32, and 48 h by using gas-tight syringes; sample CO_2 concentrations were determined by using a GC-14 gas chromatograph equipped with a thermal-conductivity detector (Shimadzu).

***In Situ* Soil Respiration Analyses.** Soil respiration was measured during 2004 and early 2005 by using a vented, closed, soil-chamber system (LI-6400, Li-Cor, Lincoln, NE). Before each analysis, 80-cm^2 polyvinylchloride collars were inserted 10 cm into the soil at random positions within each of the 40 experimental plots, and chambers were allowed to equilibrate for at least 48 h before soil CO_2 flux measurements began. For each measurement, the Li-Cor soil respiration chamber was placed on the collar, and the CO_2 flux was calculated from linear regression of increasing CO_2 concentrations over the 3–5 min after chamber equilibration. All measurements occurred during daytime hours, and simultaneous surface soil temperature and soil moisture content (gravimetric) were determined in each plot. For each of the four treatments, average CO_2 efflux rates were calculated from the 10 chamber measurements obtained during a single sampling event. Daily mean soil CO_2 efflux rates for each treatment were obtained by linear interpolation between sampling events and then summed to estimate annual soil CO_2 efflux and nutrient-stimulated increases in soil respiration.

Litterfall. Litterfall was collected in 12 0.25-m^2 litter traps placed haphazardly throughout the fertilization plot matrix. Organic material was collected every 1–2 weeks, dried, separated into litter categories (e.g., leaves, twigs, seeds, etc.), and weighed. The data shown in Fig. 1*b* represent the total mass of all litter categories.

Fine-Root Biomass. Soil fine-root mass was measured in February 2005 by harvesting roots within each experimental plot. Cores (5 cm × 10 cm) were collected by using a hand corer, and roots were separated by washing and sieving to 2 mm, dried at 60°C for 48 h, and weighed to determine total fine-root biomass (43).

Soluble Soil Organic C. Soluble soil organic C was determined on fresh surface (0–10 cm) soil samples collected from all plots immediately after soil respiration measurements. After collection, soil samples were sealed in plastic bags, placed on ice, and returned to the laboratory at the University of Colorado. Soil samples were coarsely sieved to remove rocks, roots, and debris. One-gram samples were extracted in 10 ml of deionized water, shaken at 300 rpm for 2 h, and filtered by using prerinsed Whatman no.1 filter paper. Organic C in extracted sample leachates was determined by using a TOC 5050A total organic C analyzer.

Statistical Analyses. Before analysis, all data were tested for homoscedasticity (the Levene test for equality of variances), normality, and skewedness (SPSS, Chicago). When data were heterogeneous, they were log (ln) transformed before analysis. Spatial (i.e., between-treatment) and temporal differences in soil respiration rates and root biomass were determined with one-way ANOVA. Relationships among soil respiration, soil temperature, and soil moisture were examined with linear regression. Significant effects were determined at $P < 0.05$.

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