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# Chronic nitrogen addition causes a reduction in soil carbon dioxide efflux during the high stem-growth period in a tropical montane forest but no response from a tropical lowland forest in decadal scale

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## Abstract

Atmospheric nitrogen (N) deposition is rapidly increasing in tropical regions. We studied the response of soil carbon dioxide (CO<sub>2</sub>) efflux to long-term experimental N-addition (125 kg N ha<sup>-1</sup> yr<sup>-1</sup>) in mature lowland and montane forests in Panamá. In the lowland forest, on soils with high nutrient-supplying and buffering capacity, fine litterfall and stem-growth were neither N- nor phosphorus-limited. In the montane forest, on soils with low nutrient supplying capacity and an organic layer, fine litterfall and stem-growth were N-limited. Our objectives were to 1) explore the influence of soil temperature and moisture on the dynamics of soil CO<sub>2</sub> efflux and 2) determine the responses of soil CO<sub>2</sub> efflux from an N-rich and N-limited forest to elevated N input. Annual soil CO<sub>2</sub>-C efflux was larger from the lowland (15.20±1.25 Mg C ha<sup>-1</sup>) than the montane forest (9.36±0.29 Mg C ha<sup>-1</sup>). In the lowland forest, soil moisture explained the largest fraction of the variance in soil CO<sub>2</sub> efflux while soil temperature was the main explanatory variable in the montane forest. Soil CO<sub>2</sub> efflux in the lowland forest did not differ between the control and 9–11 yr N-addition plots, suggesting that chronic N input to nutrient-rich tropical lowland forests on well-buffered soils may not change their C balance in decadal scale. In the montane forest, first year N addition did not affect soil CO<sub>2</sub> efflux but annual CO<sub>2</sub> efflux was reduced by 14% and 8% in the 2- and 3 yr N-addition plots, respectively, compared to the control. This reduction was caused by a decrease in soil CO<sub>2</sub> efflux during the high stem-growth period of the year, suggesting a shift in carbon partitioning from below- to aboveground in the N-addition plots where stem diameter growth was promoted.

## 1 Introduction

Tropical forests contain more than 40% of the global carbon (C) stock in vegetation (IPCC, 2007), and they account for about one third of the global soil organic C storage down to a depth of one meter (Jobbágy and Jackson, 2000). Every year they cycle

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more than 10% of the atmospheric carbon dioxide (CO<sub>2</sub>), the most important anthropogenic greenhouse gas (IPCC, 2007), through photosynthesis, respiration and microbial decay (Malhi, 2005). A major term in this biosphere-atmosphere CO<sub>2</sub> exchange is soil respiration, the second largest flux in the global terrestrial C cycle. Despite its central role in the global C cycle soil respiration remains least understood among ecosystem C processes (Luo and Zhou, 2006).

Soil temperature and moisture are important abiotic factors regulating CO<sub>2</sub> production in tropical forest soils (Davidson et al., 2000; Schwendenmann et al., 2003). Generally, rates of enzymatic respiration processes increase with temperature. The common relationship with soil moisture is that CO<sub>2</sub> efflux is small under dry conditions which depress root and microbial activity, reaches a maximal rate at intermediate soil moisture, and decreases again when anaerobic conditions prevail. Another regulating factor for soil respiration is nutrient availability, which in the case of nitrogen (N) is drastically increasing in tropical regions due to enhanced agricultural use of N fertilizer, cultivation of N-fixing plants, combustion of fossil fuels and biomass burning (Galloway et al., 2003, 2008).

One way to evaluate potential future effects of N deposition on tropical forests is to create N-enriched conditions through N addition. Just three N-addition experiments have evaluated CO<sub>2</sub> efflux from tropical forest soils. Addition of 300 kg N ha<sup>-1</sup>yr<sup>-1</sup> to three submontane forests in Venezuela did not cause consistent trends in soil CO<sub>2</sub> efflux in the following year (Priess and Fölster, 2001). Soil CO<sub>2</sub> efflux was stimulated by three years of N addition (150 kg N ha<sup>-1</sup>yr<sup>-1</sup>) to a Costa Rican lowland forest on an Ultisol soil. This response was accompanied by an increase in the top-soil fine root biomass (Cleveland and Townsend, 2006). In contrast, two years of N addition at the same rate to a Chinese lowland forest on an Oxisol soil reduced soil CO<sub>2</sub> efflux during the warm and wet growing season, while no effect was observed at lower N-addition levels (50 and 100 kg N ha<sup>-1</sup>yr<sup>-1</sup>; Mo et al., 2008). These differing results elucidate that responses of soil CO<sub>2</sub> efflux to increasing N availability may depend on N loading levels and possibly soil characteristics.

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To address the question on how soil CO<sub>2</sub> efflux may respond to elevated N input the potential effects on root and microbial respiration need to be considered. Fine-root biomass and plant C allocation to mycorrhizal fungi typically decrease with rising N availability, which would reduce rhizosphere respiration, but conflictive fine-root production, turnover and maintenance respiration may increase (Nadelhoffer, 2000; Norby and Jackson, 2000; Treseder, 2004). N addition can indirectly enhance microbial respiration if plant primary production and hence substrate availability are boosted (Luo and Zhou, 2006). The effects of N addition on decomposition depend on its stage: decomposition rates of light soil C fractions/fresh litter are accelerated but decomposition rates of heavier soil C fractions/humified organic matter are suppressed (Neff et al., 2002). Finally, N enrichment may ultimately change soil chemical characteristics by increasing soil acidity, cation leaching (Lohse and Matson, 2005) and aluminum mobilization into the soil solution (Likens et al., 1996) which may decrease microbial biomass (DeForest et al., 2004) and root growth (Godbold et al., 1988), consequently reducing soil respiration.

Our study reports the impact of longterm N addition (125 kg N ha<sup>-1</sup> yr<sup>-1</sup>) on soil CO<sub>2</sub> efflux from two species-rich, old-growth tropical forests in Panama with contrasting N status: lowland forest on deeply-weathered Cambisol and Nitisol soils and montane forest on less-developed Andosol soils. In the lowland forest annual fine litterfall, leaf litter decomposition rates (Kaspari et al., 2008), stem diameter growth and fine-root biomass at 0–0.2 m depth were not affected by chronic N addition (Wright, S. J., unpublished results). Soil pH and base saturation were decreased after 8 years of N addition (0–0.5 m depth; Koehler et al., 2009). In the montane forest, annual fine litterfall increased during the first 2 years of N addition (Adamek et al., 2009) while 1.5 years of N-addition did not influence fine-root biomass, production or turnover in the organic layer and 0–0.2 m mineral soil (Adamek, 2009). Based on these site characteristics we hypothesized that:

1) due to the increased soil acidity and resulting nutrient imbalances soil CO<sub>2</sub> efflux in the lowland forest will be smaller from the 9–11 yr N-addition than the control plots;

2) due to the increase in aboveground substrate supply for microbial decomposition soil CO<sub>2</sub> efflux in the montane forest will be larger from the 1–3 yr N-addition than the control plots.

This is the first study to evaluate 1) soil CO<sub>2</sub> effluxes in response to long-term N-addition (i.e. 3 yr) to an N-limited tropical montane forest and 2) soil CO<sub>2</sub> effluxes after decadal N addition to an N-rich tropical lowland forest.

## 2 Materials and methods

### 2.1 Study area

The lowland study site (between 25–61 m elevation) consists of an old-growth (>300 years) semi-deciduous tropical forest (Leigh et al., 1996) and is located on Gigante Peninsula (9°06' N, 79°50' W) which is part of the Barro Colorado Nature Monument, Republic of Panama. On nearby Barro Colorado Island, annual rainfall (1995–2007) averages 2650±146 mm with a dry season from January to mid-May during which 297±40 mm of rainfall is recorded. Ambient N deposition from rainfall was 9 kg N ha<sup>-1</sup> yr<sup>-1</sup>, measured bi-weekly from 2006 to 2007 at the shore of Gigante Peninsula near the study site. Annual air temperature averages 27.4±0.1°C. The soil is derived from a dense basalt flow, has a heavy clay texture, and is classified as Endogleyic Cambisol in the lower and Acric Nitisol in the upper part of the landscape, respectively (FAO classification; alternatively Dystrudepts in USDA classification). The soil aluminum (Al) saturation (0–0.05 m depth) was increased after 8 years of N addition (3.1±2.9 and 26.6±9.1% Al on cation exchange capacity in the control and N-addition plots, respectively).

The montane study site (between 1200–1300 m elevation) consists of an old-growth lower montane rainforest (Grubb, 1977) and is located in the Fortuna Forest Reserve in the Cordillera Central (8°45' N, 82°15' W), Chiriquí province, Republic of Panama. Mean annual rainfall is 5532±322 mm (1997–2007), and rainfall distribution exhibits a

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weak seasonality (11 yr average of 244–288 mm month<sup>-1</sup> from February to April and 403–683 mm month<sup>-1</sup> from March to January). Ambient N deposition from rainfall was 5 kg N ha<sup>-1</sup> yr<sup>-1</sup>, measured bi-weekly from 2006 to 2007 at a forest clearing near the study site. The average monthly air temperature is 19°C from December to March and 21°C for all other months (annual mean 20.1±0.1°C; 1999–2007). Monthly stem diameter increments are largest between July and December and clearly smaller in the rest of the year (Adamek et al., 2009). The soil is derived from volcanic ash deposits, has a sandy loam texture, a substantial organic layer (median thickness of 8 cm) and is classified as Aluandic Andosols (FAO) or Hapludands (USDA). Before treatment, this soil had lower pH and base saturation and larger exchangeable aluminum content than the control and 8 yr N-addition lowland forest soil. 3 yr N addition did neither affect top soil pH (4.33±0.10 and 4.38±0.13 at 0–0.05 m depth in the control and N-addition plots, respectively) nor pH down to a depth of 0.4 m (4.76±0.14 and 4.72±0.16 in the control and N-addition plots, respectively). The increase in chronic mineral soil extractable NO<sub>3</sub><sup>-</sup> concentrations, which was statistically undistinguishable from the control during the first 2 years of N addition, was significant concerning the 3 yr N-addition period ( $P=0.0152$ ). Detailed soil characteristics, forest structure, and temporal patterns of soil mineral N concentrations in both sites can be found in Koehler et al. (2009).

## 2.2 Experimental design

In the lowland, our study was conducted in the only ongoing chronic nutrient addition experiment in old-growth forest. The experiment includes N-addition and control plots laid out in four replicates across a 26.6 ha area in a stratified random design. N addition started in June 1998. In the montane forest, the experiment was set up in a paired-plots random design with four replicates. N addition started in February 2006. At both sites, each plot is 40×40 m in size and plots are separated by at least 40 m distance. The N-addition plots received 125 kg urea-N ha<sup>-1</sup> yr<sup>-1</sup> split in four equal applications. In the lowland forest, N was applied during wet season with six to eight weeks between

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applications. In the montane forest, the N applications were spread during the year with at least seven weeks time-lag. For further details please see Koehler et al. (2009).

### 2.3 Soil CO<sub>2</sub> efflux, temperature and moisture measurements

From January 2006 to January 2009 we measured soil CO<sub>2</sub> efflux, soil temperature and soil moisture every six weeks on all plots and more intensively on the N-addition plots (two to five times within a six week period following N addition). In each plot, four permanent chamber bases were inserted ~0.02 m into the soil in a stratified random design along two perpendicular 20 m long transects that cross the plot's central point. Therefore, all chambers were surrounded (buffered) by at least 10 m of forest receiving the same treatment. Soil CO<sub>2</sub> efflux was measured during the day using vented static chambers (area 0.04 m<sup>2</sup>, height 0.25 m). A study on nearby Barro Colorado Island had indicated that day and night soil CO<sub>2</sub> efflux was statistically undistinguishable (Kursar, 1989). Four gas samples (100 mL each) were removed at 2, 12, 22 and 32 min after chamber closure and stored in pre-evacuated glass containers with a teflon stopcock. Gas samples were analyzed using a gas chromatograph (Shimadzu GC-14B, Germany) equipped with an electron capture detector (Lofffield et al., 1997) which was calibrated with three to four standard gases (360, 706, 1505 and 5012 ppm CO<sub>2</sub>, Deuste Steiningger GmbH, Mühlhausen, Germany). Gas fluxes were calculated from the concentration increase in the chamber versus time, and were adjusted for air temperature and atmospheric pressure measured at the time of sampling. To account for the decreasing diffusion gradient over time caused by the chamber feedback we fitted both a linear and a quadratic regression model if CO<sub>2</sub> concentrations increased asymptotically (Wagner et al., 1997). We chose the statistically more adequate model based on the Akaike Information Criterion. The quadratic model was used in ~30% of the gas flux calculations. If the concentration increase leveled out but the quadratic model was statistically inferior we excluded the respective last data points and calculated the flux based on a linear model. This data screening and calculation procedures provide that we minimized underestimations which may occur if a linear model was

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uncritical applied to static chamber flux data (e.g. Livingston et al., 2006). Two pre-treatment measurements in the montane forest indicated that initial soil CO<sub>2</sub>-efflux did not differ between control and N-addition plots before manipulation. We do not have pre-treatment measurements of soil CO<sub>2</sub> efflux from the 9–10 yr N-addition plots of the lowland forest. The annual gaseous C losses were approximated by applying the trapezoid rule on time intervals between measured flux rates, assuming constant flux rates per day.

Parallel to gas sampling, soil temperature was measured at 0.05 m depth near each of the four chamber bases per plot. For soil moisture, four samples of 0–0.05 m mineral soil (and additionally from the organic layer at the montane site) were collected within the inner 10×10 m of each plot and pooled. A subsample was oven-dried at 105°C for 24 h. Soil moisture is expressed as percentage of water-filled pore space, assuming a particle density of 2.65 g cm<sup>-3</sup> for mineral soil (Linn and Doran, 1984) and of 1.4 g cm<sup>-3</sup> for organic layer (Breuer et al., 2002).

## 2.4 Statistical analyses

If data sets were rightly skewed a square-root or logarithmic transformation was applied before analysis. If data sets were left-skewed a quadratic or cubic transformation was applied before analysis. Regression analyses (on treatment means) were conducted to investigate the influence of soil moisture and temperature on soil CO<sub>2</sub> efflux. For the lowland forest, the data of the control and N-addition plots were pooled to increase the robustness of parameter estimates. This was justified by their comparable soil CO<sub>2</sub> efflux, temperature and moisture (see Sect. 2). In multiple regression or if including squared terms the explanatory variables  $x$  were mean-centered and normalized before analysis [ $x^*=(x-\text{mean}(x))/\text{standard error}(x)$ ]. Multiple regression analyses were conducted by first fitting the maximal model (containing all linear, squared and interaction terms) and progressing to the minimal adequate model through a series of single-term deletions based on F-tests (Crawley, 2002). Variance inflation factors as multicollinearity measure were <2 in all models. Model significance was assessed by

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regression analysis of variance. Linear mixed effects models (on plot means) were used to test for the “fixed effect” of treatment (N addition), site (lowland vs. montane forest) or season on the time-series of the response variables (i.e. the repeated measurements of soil CO<sub>2</sub> efflux, soil temperature and water-filled pore space). The spatial replication nested in time was included as “random” effect. The models were specified as explained in Koehler et al. (2009) and the significance of the fixed effect was evaluated using analysis of variance (Crawley, 2002). For soil characteristics, treatment effects and/or differences between sites were assessed using independent *t*-tests. In all analyses concerning CO<sub>2</sub> efflux, only the chronic fluxes measured at least 6 weeks after an N-application were considered (see Sect. 2). Effects were considered significant if *P* value ≤0.05. Mean values in the text are given with ±1 standard error, regression parameter estimates are given with the 95% confidence level. Analyses were conducted using R 2.9.0 (R Development Core Team, 2009).

### 3 Results

#### 3.1 Water-filled pore space and temperature in the control forest soils

Water-filled pore space (WFPS) showed a seasonal pattern in the lowland forest where it varied by 34% between dry and wet seasons (Fig. 1a). In the montane forest, WFPS was larger in the mineral soil than in the organic layer. WFPS varied less throughout the year than in the lowland (16% and 21% in organic layer and mineral soil, respectively; Fig. 1b). In contrast, soil temperature at 0.05 m depth varied seasonally by only 1.7°C (annual mean of 25.5°C) in the lowland (Fig. 1c) but by 3.8°C (annual mean of 18.1°C) in the montane forest (Fig. 1d). An unusually low-rainfall period in the montane forest (February to April 2007 with ~40% less rain than the 11 yr average) caused a reduction in the WFPS in both mineral soil and organic layer. With the onset of higher rainfall the WFPS re-increased in the mineral soil while it remained smaller in the organic layer until the end of the study (Fig. 1b). WFPS and soil temperature did not differ between

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control and N-addition plots at either site.

### 3.2 Soil CO<sub>2</sub> efflux of the control forests

Soil CO<sub>2</sub> effluxes were larger from the lowland (189.60±7.95 mg C m<sup>-2</sup> h<sup>-1</sup>) than the montane forest (107.29±4.68 mg C m<sup>-2</sup> h<sup>-1</sup>,  $P=0.004$ , Table 1). In the lowland, they ranged between 83.45±17.69 and 283.99±36.08 mg C m<sup>-2</sup> h<sup>-1</sup>, displaying a distinct seasonal pattern with lower effluxes during dry season (136.96±16.82 mg C m<sup>-2</sup> h<sup>-1</sup>) than during wet season (205.20±6.60 mg C m<sup>-2</sup> h<sup>-1</sup>,  $P<0.001$ , Fig. 2). 26.75±2.06% of the annual CO<sub>2</sub> efflux occurred during the ~130 days of dry season. WFPS explained a larger fraction of the variance in soil CO<sub>2</sub> efflux than soil temperature. Soil CO<sub>2</sub> effluxes were maximal at an intermediate WFPS and decreased below and above this value (Fig. 4a). A regression between soil CO<sub>2</sub> efflux and temperature illustrates that temperature was only a relevant explanatory variable if CO<sub>2</sub> production was not limited by low soil moisture (Fig. 5a). Based on a regression tree moisture limitation of soil CO<sub>2</sub> production took place below a WFPS of ~38%. Accordingly, the minimal adequate multiple regression model contains not only WFPS (and its quadratic term) and soil temperature but also the interaction-term of both factors (parameter estimates ±95% CI):

$$\text{CO}_2 = 189.07 (\pm 12.18) + 3.24 (\pm 1.51) T^* + 2.09 (\pm 1.18) \text{WFPS}^* - 0.22 (\pm 0.14) \text{WFPS}^{*2} - 0.28 (\pm 0.21) \text{WFPS}^* T^* \quad (1)$$

where CO<sub>2</sub> is mean soil CO<sub>2</sub> efflux (mg C m<sup>-2</sup> h<sup>-1</sup>),  $T$  is soil temperature at 0.05 m depth (°C), WFPS is water-filled pore space (%) and \* indicates that the variable was mean-centered and normalized before analysis ( $n=47$ ,  $R^2=0.650$ ,  $P<0.001$ ).

Soil CO<sub>2</sub> effluxes from the montane forest varied less than in the lowland, between 51.27±3.22 and 165.01±6.26 mg C m<sup>-2</sup> h<sup>-1</sup>. In 2007 and 2008 they were larger during the high stem-growth period than during the other months ( $P=0.001$ , Fig. 3). No relationship was detected between soil CO<sub>2</sub> efflux and WFPS (in either organic layer or

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mineral soil, Fig. 4b), while soil CO<sub>2</sub> efflux increased with increasing soil temperature (Fig. 5b).

### 3.3 Effects of elevated N input on the chronic soil CO<sub>2</sub> efflux

Often, during the time when soil extractable N concentrations were artificially elevated within a month following an N application (Koehler et al., 2009), transitory peaks occurred in soil CO<sub>2</sub> efflux (Figs. 2a and 3a). Because we are interested in evaluating the ultimate long-term effects of an N-enriched soil N-cycle on soil CO<sub>2</sub> efflux we excluded these transitory effects from the subsequent analyses and only considered the “chronic” fluxes measured at least 6 weeks after an N-application, which are reported in the following. In the lowland forest, soil CO<sub>2</sub> efflux did not differ between the control and 9–11 yr N-addition plots (176.59±8.64 mg C m<sup>-2</sup> h<sup>-1</sup>, Fig. 2b). In the montane forest, soil CO<sub>2</sub> efflux did not differ between the control and N-addition plots during the first year of N addition (112.14±11.53 mg C m<sup>-2</sup> h<sup>-1</sup>). In the second year of N addition, soil CO<sub>2</sub> efflux was smaller from the N-addition than the control plots during the high stem-growth period (i.e. July to December, *P*=0.0247). These diminished CO<sub>2</sub> effluxes resulted in 14% reduction of the mean annual soil CO<sub>2</sub> efflux relative to the control (Fig. 6a, Table 1). A reduction of soil CO<sub>2</sub> efflux from the N-addition plots was observable during the high stem-growth period in the third year as well, but these fluxes were statistically undistinguishable from the controls (*P*=0.1625; Figs. 3b, 6b, Table 1).

## 4 Discussion

### 4.1 Soil moisture and temperature regulation on soil CO<sub>2</sub> efflux from the control forests

The importance of soil moisture and temperature in regulating soil CO<sub>2</sub> efflux, through their influence on CO<sub>2</sub> production by microbial and root respiration, differed between

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the lowland and montane forests. We did not calculate apparent  $Q_{10}$  values of soil  $CO_2$  efflux because in the field the influence of plant phenology and soil temperature variation at an arbitrarily chosen depth can not be separated (Davidson et al., 2006). The influence of plant phenology on soil respiration is mainly due to different timing of litterfall, root growth, and root turnover (Curiel Yuste et al., 2004). In the lowland forest, the seasonality in rainfall and thus in soil moisture strongly influences plant phenology as well as decomposition. Leaf fall peaks during dry season when decomposition is limited by low soil moisture (Cornejo et al., 1994), while nutrient mineralization rates (except for potassium) are much greater during wet than during dry season (Yavitt et al., 2004). Fine root productivity is also restricted by low water supply and hardened soil during dry season. Fine roots grow rapidly during the first half of wet season and much less during the remainder of the year, and maximum fine root biomass occurs in the transition between dry and wet season (Cavelier et al., 1999; Yavitt and Wright, 2001). The soil  $CO_2$  efflux reflected these patterns in decomposition and plant phenology. The effluxes were largest in the first half of wet season and decreased thereafter, reaching their minimum at the end of dry season (Fig. 2b). The regression analyses confirmed the strong influence of soil moisture on soil  $CO_2$  efflux (Fig. 4a). The interaction term between soil moisture and temperature in the multiple regression model (Eq. 1) reflects that soil  $CO_2$  efflux only increased with temperature if  $CO_2$  production was not limited by low soil moisture content (Fig. 5a). The annual soil  $CO_2$  efflux is comparable to values reported from other old-growth tropical lowland forests (Raich and Schlesinger, 1992).

In the montane forest, only soil temperature explained a significant fraction of the variance in soil  $CO_2$  efflux. This site receives almost double annual rainfall than the lowland forest and has lower air and soil temperatures. The fine litterfall exhibits a seasonal pattern with larger amounts falling in the windier period between ~November and February. In spite of the availability of fresh substrate for microbial decomposition, soil  $CO_2$  effluxes were smaller during this colder period of the year (Figs. 1d, 3b). This suggests that the increase of soil  $CO_2$  efflux in May was prompted by the simultaneously

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rising soil temperature, and that CO<sub>2</sub> production was hampered by low temperatures during ~February to April. The annual soil CO<sub>2</sub> efflux is comparable to values reported from other old-growth tropical montane forests (Raich, 1998; Priess and Fölster, 2001). In the lowland forest, where soil temperature varies little throughout the year, seasonal changes in soil CO<sub>2</sub> efflux were mainly triggered by differences in soil moisture while the opposite was the case in the montane forest.

## 4.2 Effects of N addition on soil CO<sub>2</sub> efflux from the lowland forest

Soil CO<sub>2</sub> efflux did not differ between the control and N-addition plots in the lowland forest (Fig. 2b, Table 1) and, in combination with results from studies on fine roots, litterfall and decomposition, this suggests that both root and microbial respiration were resilient to the observed N-induced changes in soil chemical characteristics. Our measured bulk soil CO<sub>2</sub> efflux does not allow us to distinguish between the CO<sub>2</sub> sources. It is possible that an increase in CO<sub>2</sub> production from one source was offset by a decrease from the other source. However, our assumption that neither root nor microbial respiration were strongly influenced by chronic N addition is in line with previous findings: 1) fine root biomass in 0–0.2 m depth had not changed by 3- and 11 yr N addition (Wright, S. J., unpublished results) and 2) neither annual leaf litterfall nor leaf litter mass loss rates were influenced by 6 yr N addition (Kaspari et al., 2008).

Our result that elevated N input did not affect soil CO<sub>2</sub> efflux contrasts the findings from an N-addition study in an N-rich Costa Rican lowland forest on an Ultisol soil. In that study, laboratory experiments with root-free soil showed that microbial respiration was not altered by N addition (Cleveland et al., 2006; Cleveland and Townsend, 2006). In the field, however, soil CO<sub>2</sub> efflux was boosted by 3 yr addition of 150 kg N ha<sup>-1</sup> yr<sup>-1</sup>. This rise was partly attributed to a parallel increase in the top-soil fine root biomass. A possible explanation for the contrasting results in our study and theirs is that root responses on a smaller scale of nutrient manipulation (5×5 m treatment plots in Costa Rica) may differ from – and might not reflect – responses to fertilization across entire root systems occupying larger soil volumes (40×40 m treatment plots in this study;

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Raich et al., 1994; Ostertag, 2001; Cleveland and Townsend, 2006).

The fact that soil CO<sub>2</sub> efflux did not change under chronic N addition despite alterations in soil chemical traits (i.e. decrease in pH and base saturation, increase in Al saturation) may be explained by the initial soil characteristics of our site. Our soils have a higher pH, effective cation exchange capacity and base saturation than Ferral-sols/Oxisols (Koehler et al., 2009), and a very low Al saturation. The supply of available phosphorus (P) is possibly sufficient, i.e. litterfall and stem diameter growth did not respond to P-addition (Wright, S. J., unpublished results). Data on dissolved ions indicate that active weathering occurs in both the control and chronic N-addition plots (Corre, M. D., unpublished results). After 8 years of N addition, the top soil pH (4.5±0.1) was still in the upper part of the range wherein acidity is neutralized by Al solubilization from silicates and hydrous oxides (pH 3–5, Van Breemen et al., 1983). Therefore, despite the observed increase in Al saturation, the Al concentrations may not have reached a level where toxicity effects on roots and microbial biomass are expressed. After a decade of N addition, the good nutrient-supplying and buffering capacity in our soils still mitigates acidity- or Al-induced reductions of soil respiration.

With N addition ongoing we expect that our studied forest will eventually exhibit a decline in soil CO<sub>2</sub> efflux, as reported from N-enriched temperate forests (Bowden et al., 2004) and an N-saturated tropical lowland forest on an Oxisol soil in China. The Chinese site has been receiving high atmospheric deposition of >30 kg N ha<sup>-1</sup> yr<sup>-1</sup> for several decades. Aboveground primary production (fine litterfall and stem growth) was not affected by N addition (Mo et al., 2008; Mo, J., personal communication). Already the control top soil pH (3.76±0.01) is in the lower part of the Al-buffer range and hence a progressing N-induced acidification may increasingly manifest Al-toxicity on roots and microbial biomass. The observed decrease in soil CO<sub>2</sub> efflux within 2 yr experimental addition of 150 kg N ha<sup>-1</sup> yr<sup>-1</sup> was indeed accompanied by a decline in microbial biomass, fine root biomass (both in the top soil) and litter decomposition rates (Mo et al., 2006, 2008). Our finding that soil CO<sub>2</sub> efflux did not change with chronic N addition to an old-growth tropical lowland forest differs from both previous studies but

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this is explicable by scale-related differences in root responses to N addition on the one hand and site-specific soil characteristics as well as exposure time and N loading level on the other hand.

### 4.3 Effects of N addition on soil CO<sub>2</sub> efflux from the montane forest

5 Soil CO<sub>2</sub> efflux did not differ between the control and 1 yr N-addition plots but was diminished during the high stem-growth period in the second and third year of N addition (statistically distinguishable only in the second year, Fig. 3). This decrease in soil CO<sub>2</sub> efflux can neither be supported by soil acidification and pH-related changes in soil chemistry nor by changes in decomposition. First, 3 yr N addition did not alter  
10 the pH from the organic layer down to 0.4 m depth. Secondly, a reduction in microbial respiration rates would be expected if substrate quantity and/or decomposition rates decreased with N addition. Instead, the total fine litterfall was 0.97 t C ha<sup>-1</sup> larger during the first two years of N addition compared to the control (Adamek et al., 2009; the reported biomass increase was converted using a C content of 48%). This increase in  
15 the aboveground substrate input for decomposition was opposed by a reduction in soil CO<sub>2</sub> efflux of 1.00±0.29 t C ha<sup>-1</sup> yr<sup>-1</sup> with 2–3 yr N addition (Table 1). The magnitude and direction of these changes imply that- even if decomposition rates may have declined with N addition- a decrease in microbial respiration alone could not fully account for the observed reduction in soil CO<sub>2</sub> efflux.

20 On the other hand, a decrease in root respiration can be supported by the fact that the decline in soil CO<sub>2</sub> efflux occurred during the periods when N addition stimulated tree growth. The growth rates of stems in the 0.3–0.5 m diameter at breast height class were promoted during the high-growth phase of the second (Adamek et al., 2009) and third year N addition (Pame-Baldos, 2009). The fact that the decline in soil CO<sub>2</sub> efflux  
25 occurred during the same time suggests a shift in C partitioning from below- to above-ground. Even though 1.5 yr N addition did not affect fine root biomass, production or turnover in the organic layer and 0–0.2 m mineral soil (Adamek, 2009) a reduced belowground C flux during high stem-growth periods could result in smaller specific root

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respiration rates, and hence a decline in rhizosphere respiration. Moreover, mycorrhizal C allocation – which has not been investigated in our site- might decrease in response to N addition (Treseder, 2004). A similar response as in our studied Panamanian forest has been found in a nutrient-limited tropical Eucalyptus plantation where fertilization (with N, P, potassium and micronutrients) increased wood productivity as well as total litterfall but decreased C allocation to fine roots and reduced soil CO<sub>2</sub> efflux by 18% (Giardina et al., 2004). Also, a recent analysis of annual C budgets for 63 forest ecosystems from temperate, boreal and tropical regions strongly supported the assumption that enhanced nutrient availability generally increases C partitioning to aboveground net primary production while it decreases partitioning to the total belowground C flux (Litton et al., 2007). A possible decline in microbial respiration would not suffice to explain our observed decrease in soil CO<sub>2</sub> efflux while the temporal synchrony with an enhanced stem-growth suggests that a diminution of rhizosphere respiration contributed a major fraction to the reduction in soil respiration.

## 5 Consequences of chronic N deposition on carbon cycling in tropical forests

Biological demand for N (i.e. presence or absence of N limitation on vegetation growth) was an important qualitative predictor of the response of soil CO<sub>2</sub> efflux to elevated soil N availability. For tropical lowland forests on soils with high nutrient-supplying and buffering capacity, where primary productivity is not N-limited, we do not expect that chronic N addition will affect their C balance in the short term or decadal scale. In the long term, soil CO<sub>2</sub> efflux (and forest productivity) may eventually decline as N enrichment is accompanied by a progressing soil acidification and changing soil chemical traits. However, our results suggest that this condition may take several years to develop. The onset of a decrease in soil CO<sub>2</sub> efflux should be strongly determined by the N loading and initial soil characteristics (e.g. pH, cation exchange capacity and base saturation). On the other hand, N addition might cause a reduction in soil CO<sub>2</sub> efflux from tropical montane forests which have N-limited primary productivity. Once N limi-

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tation is alleviated a relatively quick shift in C partitioning from below- to aboveground may occur during periods of high stem growth. In the longer term, such shift would cause imprints on the magnitude of soil C storage.

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**Table 1.** Annual soil CO<sub>2</sub> efflux (Mg C ha<sup>-1</sup>, mean ±SE, n=4) for control and N-addition plots. Only the chronic CO<sub>2</sub> effluxes measured at least 6 weeks after an N addition have been used for this calculation.

Site	Treatment	2006	2007	2008
Montane	Control	9.93±0.62	9.17±0.55	8.99±0.55
	1–3 yr N addition	(11.03±0.51*)	7.88±0.35	8.28±0.22
Lowland	Control	17.12±1.59	15.63±0.91	12.84±1.29
	9–11 yr N addition	16.30±0.92	15.45±0.87	13.08±0.89

\*The two pre-treatment measurements from January and February 2006 were not included in this calculation. Note that this annual value is biased towards an overestimation because the high chronic CO<sub>2</sub> efflux measured in May 2006 is not representative for the integration time it represents.

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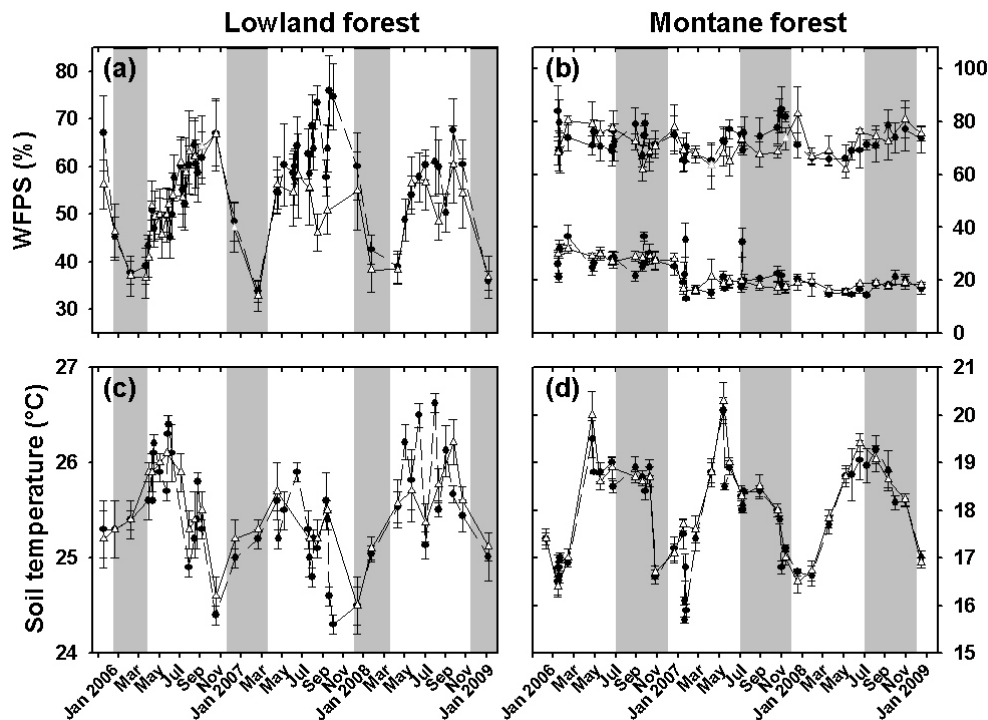
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**Fig. 1.** Mean ( $\pm$ SE,  $n=4$ ) water-filled pore space (WFPS) and soil temperature at 0.05 m depth in the control ( $\Delta$ ) and N-addition ( $\bullet$ ) lowland (a) and (c) and montane (b) and (d) forest. For WFPS in the montane forest, the upper and lower values are for the 0–0.05 m mineral soil and organic layer, respectively. Grey shading marks the dry seasons in the lowland forest, and the high stem-growth periods in the montane forest.

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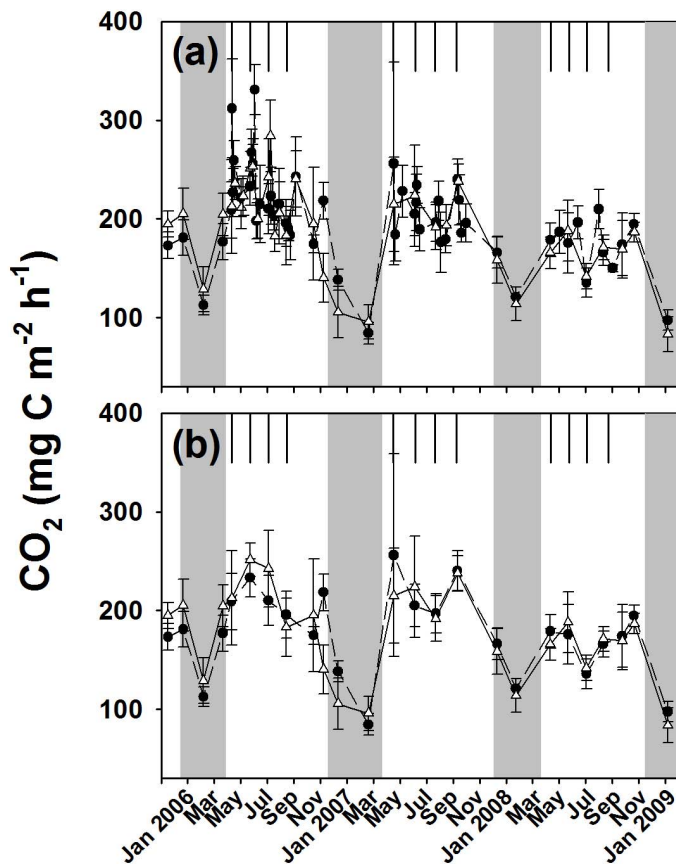
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**Fig. 2.** Mean ( $\pm$ SE,  $n=4$ ) soil  $\text{CO}_2$  efflux from the control ( $\Delta$ ) and N-addition ( $\bullet$ ) lowland forest with **(a)** including the transitory fertilization effects and **(b)** showing only the chronic fluxes at least 6 weeks after an N addition. Black vertical lines indicate dates of N addition. Grey shadings mark the dry seasons.

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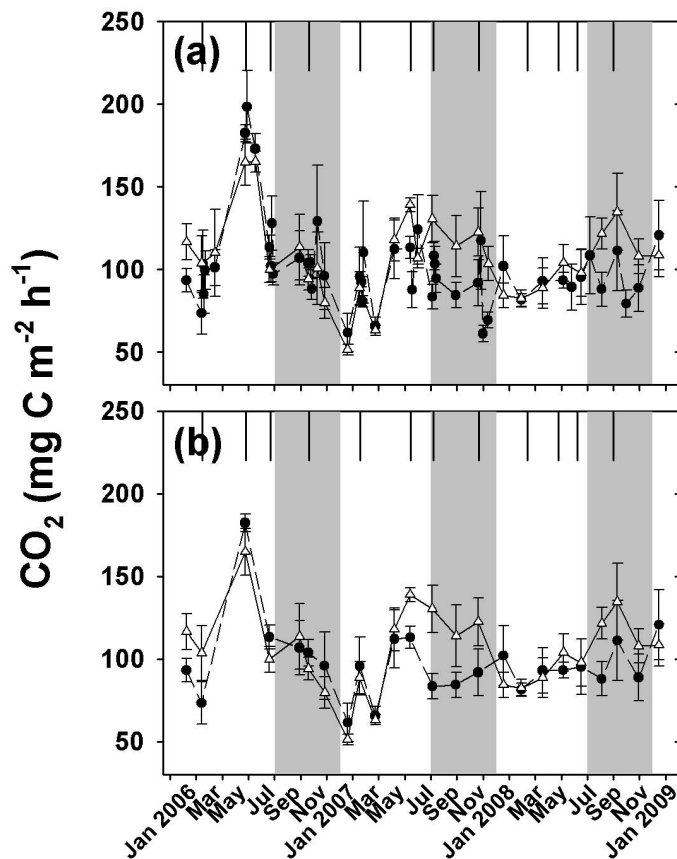
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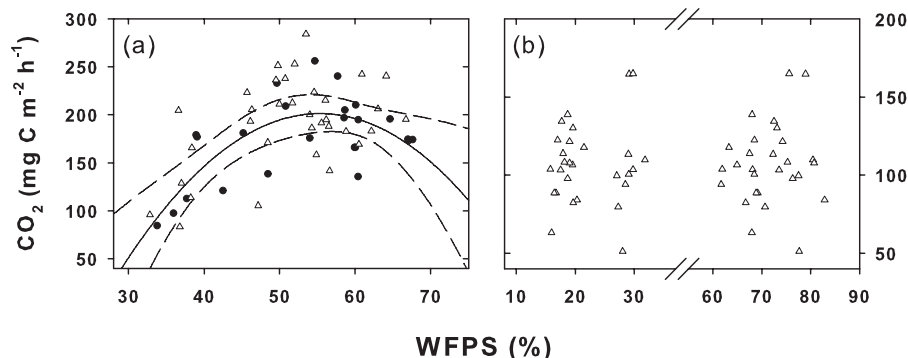


**Fig. 3.** Mean ( $\pm$ SE,  $n=4$ ) soil CO<sub>2</sub> efflux from the control ( $\Delta$ ) and N-addition ( $\bullet$ ) montane forest with **(a)** including the transitory fertilization effects and **(b)** showing only the chronic fluxes at least 6 weeks after an N addition. Black vertical lines indicate dates of N addition. Grey shadings mark the high stem-growth periods.

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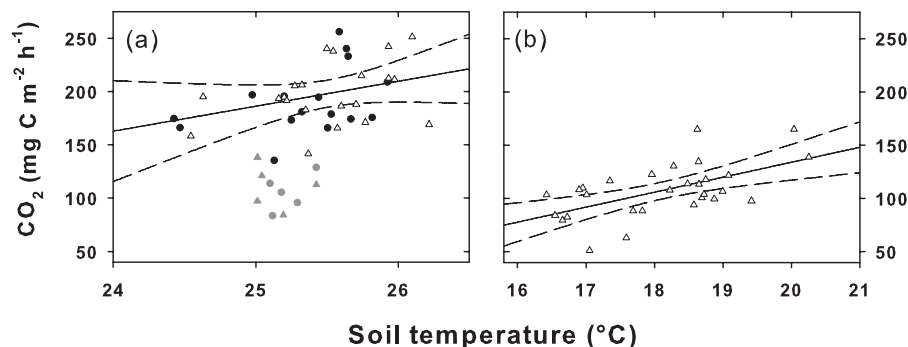
**Fig. 4.** Regression analyses (parameter estimates  $\pm 95\%$  CI) between mean water-filled pore space (WFPS) and  $\text{CO}_2$  efflux of the control ( $\Delta$ ) and N-addition ( $\bullet$ ) plots ( $n=4$  for each treatment) for the (a) lowland [ $y=204.45(\pm 13.06) + 1.78(\pm 1.32)x^* - 0.35(\pm 0.16)x^{*2}$ ,  $R^2=0.417$ ,  $n=60$ ,  $P<0.001$ , \* denotes that the variable  $x$  was mean-centered and normalized before analysis] and (b) montane forest (no significant relationship). For the lowland forest, the analysis was conducted on the pooled data of the control and N-addition plots (see Sect. 2.4). For the montane forest, data points to the left and right of the x-axis break are for the organic layer and mineral soil, respectively. For both sites, only the chronic fluxes measured at least 6 weeks after an N addition were included in this calculation.

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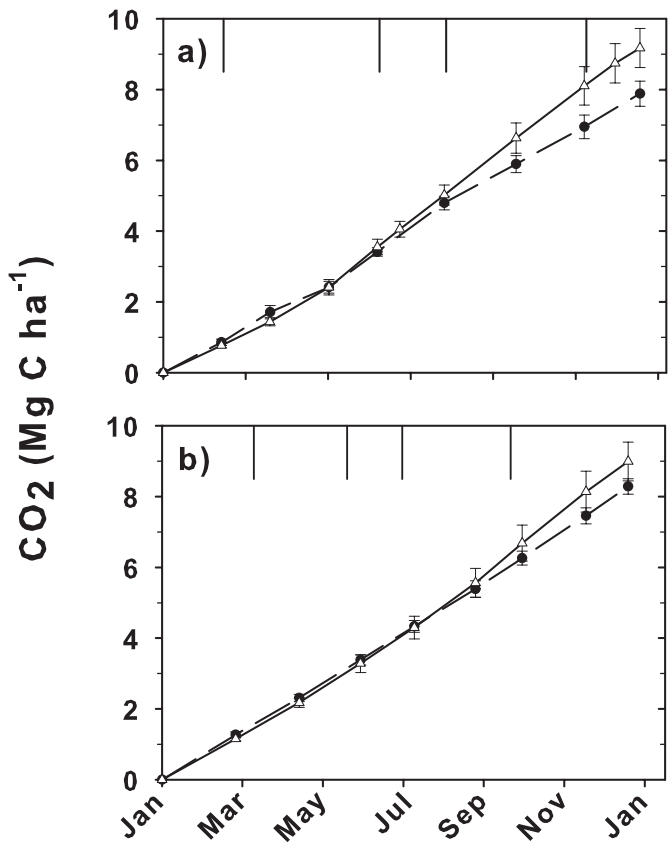
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**Fig. 5.** Linear regressions (parameter estimates  $\pm 95\%$  CI) between mean soil temperature (0.05 m depth) and  $\text{CO}_2$  efflux of the control ( $\Delta$ ) and N-addition ( $\bullet$ ) plots ( $n=4$  for each treatment) for the **(a)** lowland [ $y = -484.45 (\pm 551.25) + 26.71 (\pm 21.67) x$ ,  $R^2 = 0.152$ ,  $n = 51$ ,  $P = 0.017$ ] and **(b)** montane forests [ $y = -147.04 (\pm 141.11) + 14.05 (\pm 7.78) x$ ,  $R^2 = 0.337$ ,  $n = 28$ ,  $P < 0.001$ ]. For the lowland forest, the analysis was conducted on the pooled data of the control and N-addition plots (see Sect. 2.4) and excluded ten data points (grey) of which soil  $\text{CO}_2$  production was limited by low soil moisture content. For both sites, only the chronic fluxes measured at least 6 weeks after an N addition were included in this calculation.

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**Fig. 6.** Mean ( $\pm$ SE,  $n=4$ ) cumulative soil CO<sub>2</sub> efflux from the control ( $\Delta$ ) and N-addition ( $\bullet$ ) montane forest in (a) 2007 (2yr N addition) and (b) 2008 (3yr N addition). Only the chronic fluxes measured at least 6 weeks after an N addition were included in this calculation. Black vertical lines indicate dates of N addition.

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