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Soil carbon release enhanced by increased tropical forest litterfall

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Tropical forests are a critical component of the global carbon cycle[1] and their response to environmental change will play a key role in determining future concentrations of atmospheric carbon dioxide (CO_2)[1,2]. Increasing primary productivity in tropical forests over recent decades has been attributed to CO_2 fertilization[3], and greater biomass in tropical forests could represent a substantial sink for carbon in the future[3,4]. However, the carbon sequestration capacity of tropical forest soils is uncertain and feedbacks between increased plant productivity and soil carbon dynamics remain unexplored[5,6]. Here, we show that experimentally increasing litterfall in a lowland tropical forest enhanced carbon release from the soil. Using a large-scale litter manipulation experiment combined with carbon isotope measurements, we found that the efflux of CO_2 derived from soil organic carbon was significantly increased by litter addition. Furthermore, this effect was sustained over several years. We predict that a future increase in litterfall of 30% with an increase in atmospheric CO_2 concentrations of 150 ppm could release about 0.6 t C ha^{-1} yr^{-1} from the soil, partially offsetting predicted net gains in carbon storage. Thus, it is essential that plant–soil feedbacks are taken into account in predictions of the carbon sequestration potential of tropical forests.

Tropical forests are fundamental in maintaining the balance of atmospheric CO_2 concentrations[2]. They contain about 30% of global soil carbon (C) stocks[7] but are characterized by rapid C turnover rates, which means that they are also the largest natural source of CO_2 (ref. 8). Rising atmospheric CO_2 levels have increased aboveground net primary productivity (NPP) in tropical forests, which is estimated to sequester 1.3×10^9 t C yr^{-1} (refs 3,4), but it is unclear whether this has increased or decreased C storage in the soil[6].

Plant–soil feedbacks play a decisive role in the potential of tropical forest soils to act as sources or sinks of atmospheric CO_2 (ref. 9). Typically, increases in forest NPP under increased CO_2 levels also increase litter production[10], leading to greater accumulation of organic matter on the forest floor[11]. If decomposition processes remain unchanged, this would involve a proportionate increase in soil CO_2 efflux but also of C stored in the soil, resulting in net C sequestration. However, increased inputs of fresh organic matter resulting from enhanced growth (for example, plant litter and root exudates) could result in 'priming effects'. Priming is the extra decomposition of soil organic matter that occurs when microbes are stimulated by the addition of easily decomposable organic matter[12,13], causing a disproportionate increase in soil CO_2 efflux. Such an effect would result in smaller net gains in soil C storage or even a net loss[6,14]. Recent work on temperate soil has shown that a greater proportion of soil organic carbon (SOC) could be susceptible to priming than previously thought, including C stored in deep soil horizons[15]. There is, therefore, considerable potential for changes in plant-litter inputs to have a significant impact on C dynamics in tropical forest soils with positive feedbacks to the atmospheric C pool.

So far, most studies of priming in response to increased litter inputs have been laboratory based, small-scale or short-term[16] and mainly limited to temperate ecosystems. In particular, the magnitude and sustainability of priming in tropical forests remains almost entirely unknown[5].

We used a unique long-term manipulative experiment altering litter inputs in a mature lowland semi-evergreen tropical forest in Panama, combined with a natural abundance isotope study, to quantify the effects of increased litter inputs on soil CO_2 efflux and the release of soil C to the atmosphere through priming. The experiment consisted of fifteen 45 m × 45 m plots where, starting in January 2003, the litter in five plots was removed monthly (L− plots), this litter was then added to five plots (L+ plots) and five plots were undisturbed controls (CT plots)[17]. We also established 2 m × 2 m subplots, where the forest litter was replaced with C_4 litter (*Saccharum spontaneum* L.) at the same rate as the CT and L+ treatments (CT_{C4} and $L+_{C4}$ subplots), to determine the contribution of litter to soil CO_2 efflux using the differences in isotopic signature ($\delta^{13}C$) between the soil and the C_4 litter[18].

Soil CO_2 efflux (R_{SOIL}), soil temperature and soil water content were measured monthly over the mineral soil in all plots, C_4 subplots and in additional root-free (trenched) subplots[19] from May 2007 to June 2008 (ref. 19). The contribution of SOC-derived CO_2 (R_{SOC}) to total annual soil CO_2 efflux (R_{YEAR}) was calculated from differences among treatments. We used trace-gas isotope ratio mass spectrometry to determine the $\delta^{13}C$ of litter-derived and belowground CO_2 efflux (that is, from soil and roots) from gas samples taken in July 2009. The IsoError model[20] was used to partition C_4 litter- and SOC-derived CO_2 in the samples using isotopic signatures (Supplementary Information).

R_{SOIL} was significantly higher in the L+ treatments when compared with the controls (L+ treatment, $P = 0.019$; $L+_{C4}$ treatment, $P < 0.001$), but there was no effect of litter removal. The seasonal pattern of R_{SOIL} (Fig. 1) was reflected in significant effects of sampling date and temperature (CT and L+, $P = 0.019$ and

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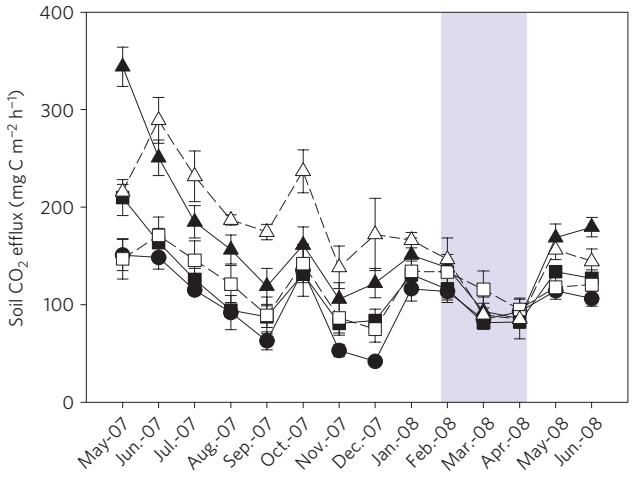

Figure 1 | Comparison of measured soil CO_2 efflux in litter-manipulation treatments in lowland tropical forest in Panama, Central America. Squares represent controls, triangles represent litter addition and circles represent litter-removal treatments; filled symbols with solid lines denote main treatments and open symbols with dashed lines denote treatments with C_4 litter; purple shading indicates the dry season; error bars show ± s.e.m. for $n = 5$ plots.

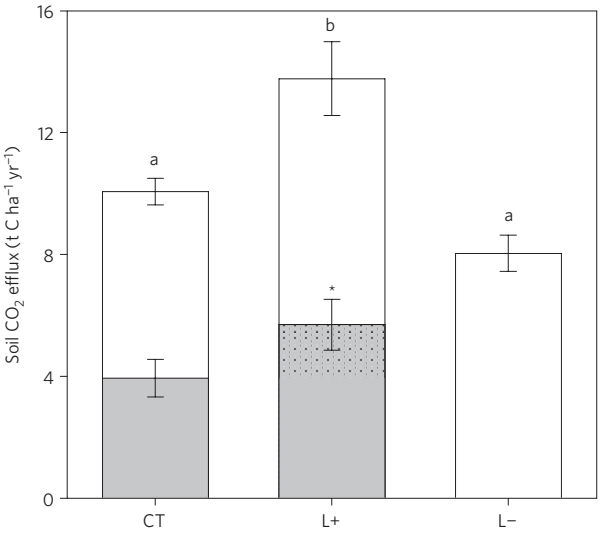

Figure 2 | Effects of litter quantity on soil respiration in litter-manipulation treatments in lowland tropical forest in Panama. White bars show annual total soil CO_2 efflux in the main litter-manipulation treatments and grey bars show the contribution of SOC-derived soil CO_2 to annual total soil CO_2 efflux in the litter addition and control treatments; CT is control, L+ is litter addition and L− is litter removal; the dotted portion of SOC-derived soil CO_2 is the estimated release of soil carbon as CO_2 through priming effects in the L+ treatment; different letters above bars denote significant differences at $P < 0.05$ for total soil CO_2 efflux and the asterisk denotes a significant difference from the controls at $P < 0.05$ for SOC-derived CO_2; error bars show ± s.e.m. for $n = 4$ plots (SOC-derived CO_2) and $n = 5$ plots (annual total CO_2 efflux).

$P < 0.001$, respectively; CT_{C4} and $L+_{C4}$, $P < 0.001$ and $P < 0.001$, respectively), but there were no significant interactions between treatment and temperature, or treatment and sampling date in any of the models (Supplementary Table S1). Thus, the treatment effects were a direct result of differences in litter inputs. R_{YEAR} was 13.8 ± 1.2 t C ha^{-1} yr^{-1} in the L+ plots, 10.0 ± 0.5 t C ha^{-1} yr^{-1} in the controls and 8.4 ± 0.6 t C ha^{-1} yr^{-1} in the L− plots (main treatment effect, $P = 0.002$, $F_{2,14} = 11.44$). R_{YEAR} in the L+ plots was significantly greater than in the controls (Dunnett's $P = 0.01$) whereas the L− plots and controls did not differ (Fig. 2).

The CT_{C4} and $L+_{C4}$ treatments were highly representative of the CT and L+ treatments (Supplementary Fig. S1), with no significant differences between treatments with C_4 litter and treatments with forest litter for any of the variables measured. Although the estimates of R_{SOC} derived from the isotope study were strongly correlated with those obtained from the main treatments ($n = 8$, $r = 0.85$, $P < 0.01$; Supplementary Fig. S2) they were slightly higher because the isotope study was carried out during the rainy season, when soil respiration is typically high (Supplementary Information).

On the basis of treatment differences (discounting the 35% and 21% root respiration measured in the CT and L+ treatments, respectively), the contribution of R_{LITTER} to R_{YEAR} was 26% in the CT plots and 38% in the L+ plots. The contribution of R_{SOC} to R_{YEAR} was 39% in the control plots and 41% in the L+ plots.

The estimates of total annual SOC-derived CO_2 were significantly higher in the L+ treatments (5.7 ± 0.8 t C ha^{-1} yr^{-1}) when compared with the controls (3.9 t C ha^{-1} yr^{-1}; $t_{n=4} = 3.26$, $P = 0.023$; Fig. 2). We therefore estimate the release of soil C as CO_2 by priming in the litter-addition treatment as 1.8 ± 0.5 t C ha^{-1} yr^{-1}. Importantly, we measured no difference in microbial biomass C between the CT and L+ treatments (E.J.S., E.V.T. and J.S. Powers, unpublished data). Consequently, we are confident that the greater proportion of SOC-derived CO_2 in the L+ plots was a result of priming and not enhanced heterotrophic respiration due to greater microbial biomass[21].

Our study shows that priming of soil organic matter is likely to become a significant source of CO_2 as NPP increases in tropical forests under increased atmospheric CO_2 (refs 3,4). On the basis of an estimate using a simple linear relationship between the intensity of priming effects and the quantity of fresh organic matter inputs, our results indicate that priming could release about 0.6 t C ha^{-1} yr^{-1} from tropical forest soils under an increase of about 30% in litterfall at CO_2 concentrations of 150 ppm above ambient[10]. However, data from a laboratory study indicate that CO_2 efflux resulting from priming effects approaches an asymptote at relatively low amounts of added litter[22] and accordingly, doubling litter inputs would cause a smaller relative release of soil C than a 30% increase in litterfall (Supplementary Information). If the same applies to tropical forest soils, our estimate could be considered conservative (Supplementary Fig. S3).

The long-term impacts of priming effects on tropical forest soil C storage are hard to predict at present because of the paucity of data for tropical soils. Importantly, a large proportion of the C inputs associated with increased NPP has short turnover times[11], whereas the C released from the soil by priming effects is relatively stable[13,14]. Consequently, more stable soil C would be replaced with C that is more susceptible to microbial decomposition. This acceleration of soil C turnover could reduce the stability of SOC over the long term despite there being no immediate net decrease in overall soil C stocks.

So far, the long-term sustainability of priming effects under repeated inputs of fresh organic matter remains unknown[16]. In our study, priming effects continued for at least six years after the initiation of the experiment[5], despite organic C concentrations of only about 5% in the surface soil at our study site[23]. Our estimates of CO_2 released through priming represent about 13% of total belowground respiration in the litter-addition treatment. Surprisingly, this is similar to estimates from litter-addition studies in temperate forests (11.5–21%; ref. 26), where SOC content is much higher. This may be because accelerated turnover of SOC through priming is more likely to occur in soils with low nutrient availability[24,25], which is often characteristic of tropical forest soils[26].

Alternatively, it may indicate that a larger proportion of SOC is susceptible to priming than previously assumed[14,15]. The stocks of SOC in the top 0.5 m of the soil in the study area are estimated as about 90 t ha^{-1} (ref. 23), but so far it has not been possible to estimate which proportion of this could be susceptible to priming.

Global change phenomena other than increasing atmospheric CO_2 (for example, changes in rainfall patterns) can also affect NPP (ref. 27) and potentially cause priming effects. At our study site, we measured no significant differences in soil respiration among treatments during the dry season (Fig. 1), indicating that no priming occurred when litter decomposition and heterotrophic respiration were inhibited by dry conditions. Droughts could therefore reduce C release from the soil by restricting microbial decomposition. However, as trees respond to drought stress by shedding leaves, the resulting large pulses of litter inputs could ultimately enhance priming effects as soon as conditions favourable for decomposition returned[1,5].

It is clear that increased C uptake through enhanced growth in tropical forests, predicted under climate change, could be offset by accelerated turnover of SOC. Our estimate of priming under a 150 ppm increase in atmospheric CO_2 concentrations (0.6 t C ha^{-1} yr^{-1}) is larger than the estimated climate-induced increase in forest biomass in Amazonia over recent decades (0.45 t ha^{-1} yr^{-1}; 1975–2005; refs 4,27). The magnitude of priming effects may even be greater than we report because, as well as increased litterfall, root biomass and root exudates are expected to increase under increased CO_2 concentrations, which would further exacerbate soil C release due to priming[14,16]. Although our measurements were made in a lowland tropical forest, similar priming effects have been observed in a wide range of forest soils[21,24], which casts doubts on present estimates of the C sequestration capacity of forest ecosystems. A better understanding of tropical forest carbon dynamics, in particular of plant–soil feedbacks, is clearly needed to explain present trends. This will improve predictive models of global carbon stocks and allow greater preparedness for the consequences of climate change.

Methods

Experimental design. The study was conducted within a large-scale litter-manipulation experiment in mature lowland semi-evergreen tropical forest in Panama. Briefly, the experiment consists of fifteen 45 m × 45 m plots where, starting in January 2003, the litter in five plots was raked up once a month (L− plots), the removed litter was added to five plots (L+ plots) and five plots were undisturbed controls (CT plots); see ref. 17 for a detailed description.

We determined the contribution of litter to belowground respiration using differences in isotopic signatures ($\delta^{13}C$) of the litter and soil[18] by replacing the forest litter in one 2 m × 2 m subplot in each CT and L+ plot with *Saccharum spontaneum* (L.) leaves, an invasive C_4 plant (henceforth C_4 litter; Supplementary Information). The litter standing crop in each subplot was replaced with an equivalent mass of air-dried C_4 litter in October 2005 and a wire-mesh tent over each subplot excluded forest litterfall. From October 2005 to October 2006 and May 2007 to May 2009, C_4 litter was added every month in amounts equivalent to the monthly mean litterfall mass in the CT plots and double the mean litterfall in the L+ plots (henceforth CT_{C4} and $L+_{C4}$ subplots).

Measurements. Four measurement collars were installed in each main treatment plot in 2005 (refs 5,19). One collar was installed in the centre of each CT_{C4} and $L+_{C4}$ subplot and in root-free (trenched) subplots, described in ref. 19. Soil CO_2 efflux from the mineral soil (R_{SOIL}), soil temperature and soil water content were measured in all plots and subplots as described in ref. 19 once a month from May 2007 to June 2008.

In July 2009, CO_2 efflux from the mineral soil was sampled in four CT_{C4} and four $L+_{C4}$ subplots. Samples were also taken in two L− plots to determine the combined $\delta^{13}CO_2$ from soil and roots (Supplementary Information). Samples (20 ml) were taken using a gas-tight syringe and injected into 15-ml evacuated vials. One sample was taken at ambient [CO_2] and five subsequent samples were taken in steps of 150 ppm, resulting in six samples per collar with [CO_2] of 400–1200 ppm. The [CO_2] in the headspace rose linearly in all cases, indicating that gas diffusion was not inhibited and sampling over this range would not affect the isotope ratio of the respired CO_2 (ref. 18). The $\delta^{13}C$ of the samples was determined by trace-gas isotope ratio mass spectrometry. The samples were injected into a trace-gas preconcentrator coupled to an Isoprime isotope ratio mass spectrometer using a gas-tight syringe. Water was eliminated with a perchlorate chemical trap and the CO_2 was cryogenically preconcentrated before gas chromatography column separation and trace-gas isotope ratio mass spectrometry analysis.

Calculations. Total annual soil CO_2 efflux (R_{YEAR}) was estimated by interpolation (Supplementary Information). The contribution of litter-derived CO_2 (R_{LITTER}) to R_{YEAR} was calculated using two approaches. First, R_{LITTER} in the CT plots was calculated as the difference in R_{YEAR} between the *i*th CT and L− plots:

$$R_{LITTERi} = R_{YEAR-CTi} - R_{YEAR-L-i}$$

R_{LITTER} in the corresponding L+ plots was double the control values.

The second approach partitioned the sources of CO_2 by isotopic signature using the IsoError model[20], which includes propagated errors by considering the variability in $\delta^{13}C$ of the source materials and the CO_2 mixture (Supplementary Information). As sources we used the $\delta^{13}C$ values of the C_4 litter (−11.84‰) and of R_{SOIL} from the L− plots (−22.55‰; mineral soil with roots but without litter; Supplementary Information). The $\delta^{13}C$ of the CO_2 mixture in the gas samples was determined by linear regression from Keeling plots[28].

Root-rhizosphere-derived CO_2 (R_{ROOTS}) for the *i*th plot in treatment *j* (CT or L+) was calculated from root-free (trenched) subplots[19]:

$$R_{ROOTSij} = R_{YEARij} - R_{ROOTFREEij}$$

SOC-derived CO_2 in the *i*th CT and L+ plot was then calculated as:

$$R_{SOCij} = R_{YEARij} - R_{LITTERij} - R_{ROOTSij}$$

Finally, CO_2 efflux as a result of priming in the *i*th L+ plot was:

$$C_{PRIMEi} = R_{SOC-L+i} - R_{SOC-CTi}$$

Statistics. We used one-way analysis of variance (ANOVA) to investigate treatment effects on R_{YEAR}, *t*-tests to investigate differences in R_{SOC} between CT and L+ plots and repeated-measures ANOVA to investigate differences in soil water content and soil temperature among treatments and between main treatment plots and C_4 subplots.

We used linear mixed-effects models (lme command in R.2.12; ref. 29) to model the effects of treatment, soil temperature and sampling date on R_{SOIL} for main treatments and C_4 subplots separately. Treatment, date and soil temperature were used as fixed effects and experimental plots as the random effect (Supplementary Table S1). Models were fitted using maximum likelihood and selected by stepwise backward selection based on the Akaike information criterion[30]. We excluded soil water content from the models because it covaried with temperature and did not differ significantly among treatments; the strong seasonality of soil water content was taken into account by including sampling date.

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Author contributions

E.J.S. and E.V.J.T. conceived the experiment. E.J.S. designed and carried out the experiment. T.R.M. and E.J.S. analysed the data. H.K.G. carried out the isotope analyses. E.J.S. and M.S.H. wrote the paper. All authors commented on the analysis and presentation of the data.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at http://www.nature.com/reprints. Correspondence and requests for materials should be addressed to E.J.S.