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Experimental Warming and Drying Increase the Age of Soil Respired Carbon in Lowland Tropical Forests

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Abstract

Tropical forests account for over 50% of the global terrestrial carbon sink, but climate change threatens to alter the carbon balance of these ecosystems. We show that warming and drying of tropical forest soils may increase soil carbon vulnerability, by increasing the degradation of older carbon and decreasing decomposition of fresh inputs. *In situ* whole-profile heating by 4ºC and 50% throughfall exclusion both increased the average radiocarbon age of soil CO_2 efflux by ~2–3 years, but the mechanisms underlying this shift differed. Warming accelerated decomposition and loss of older carbon as soil CO_2 emissions reflecting increased decomposition and loss of older carbon. Drying suppressed microbial decomposition of fresh carbon inputs as soil CO_2 emissions decreased. These findings imply that both warming and drying, by accelerating the loss of older soil carbon and reducing the incorporation of fresh carbon, will exacerbate soil carbon losses in tropical forests under climate change.

MAIN

Introduction

Tropical forests exchange more CO_2 with the atmosphere than any other terrestrial biome[1], store nearly one-third of global soil carbon stocks[2], and have the highest soil CO_2 efflux of any ecosystem[3]. Climate projections suggest a future that will be both warmer and drier for much of the tropics[4] with increasing drought intensity and dry season length for the Neotropics[5, 6]. Despite the importance of tropical forests and their soils to the global carbon cycle and feedbacks to climate, uncertainty in predicting the response of tropical carbon cycling to future climate change remains high.

Soil CO_2 efflux is highly sensitive to temperature and moisture, which together have been shown to determine interannual patterns in emissions globally[7]. Even in tropical forests, where mean annual temperature is relatively high and temperature variability is relatively low, soil CO_2 efflux has been shown to increase with increasing temperature and peak at intermediate soil moisture content[8, 9]. Meta-analyses of warming experiments have reported average increases in soil CO_2 efflux with warming of 9%[10] to 12%[11]; and extrapolation of results from warming experiments suggest that climate warming will stimulate a net loss of global soil carbon to the atmosphere[12]. Importantly, none of the studies included in these analyses were conducted in the tropics. Field warming experiments in tropical forests have only recently been instigated and early results show large increases in soil CO_2 efflux with increased temperature[13] as have laboratory incubations of tropical soils[14, 15]. Soil moisture is also an important factor influencing soil microbial activity and respiration, and in the tropics the seasonal variation in moisture is often greater than that of temperature[8, 9, 16]. However, field drying experiments in tropical forests have reported mixed responses of soil CO_2 efflux to drying, including increases[17], decreases[18, 19] and no responses[20] across forests of differing rainfall and seasonality.

Moreover, previous work in tropical forests only considered total CO_2 efflux rates, which are important for determining the overall carbon balance of tropical forests[21], but are limited in their ability to uncover mechanisms behind observed change. Those mechanisms can be revealed by determination of ^{14}C values , which indicate the age of the carbon sources being metabolized and released as CO_2[22]. Given that temperature and moisture are the major climatic drivers of soil CO_2 efflux[7-9, 13, 16], and that in the tropics both significant warming and drying is predicted this century[23], there is a critical need for studies that assess the impact of warming and drying together on both the magnitude and source (i.e., age) of soil CO_2 efflux in tropical forests.

In this study, we determined how warming and drying impact the amount and age of carbon released as soil CO_2 efflux in lowland tropical forest. We measured the $\Delta^{14}C$ and $\delta^{13}C$ of soil respired CO_2 in lowland tropical forests in Panama (Table S1 and Fig. S1) that are subject to either *in situ* experimental soil warming (4 °C above ambient temperature to 1.2 m depth[13] or *in situ* experimental drying (50% throughfall exclusion)[24]. Our study sites are seasonally moist, semi-deciduous forests within the Barro Colorado Nature Monument (the warming experiment site and one drying site), which enabled us to directly compare how warming and drying both affect the soil CO_2 efflux for this type of forest, and on the northern side of the isthmus where mean annual precipitation is greater (a second drying site). Given the seasonality of these forests, we performed measurements at stages of the seasonal cycle for which we expected the largest variation in CO_2 efflux based on previous studies[13, 16, 25] – the wet season and dry season or dry-to-wet season transition (see methods). We hypothesized that warming and drying both increase the relative contribution of older soil carbon to CO_2 efflux relative to reference control plots, but via two different mechanisms. Specifically, warming stimulates the decomposition of older soil carbon by increasing the activity of microbes, via priming effects and/or a switch in resource use following the depletion of fresh organic matter[26]. In contrast, drying reduces microbial activity and limits the mobility, incorporation, and decomposition of recent inputs of plant organic matter ('fresh carbon') in soils. This restricts microbial access to fresh carbon in soils, reducing its contribution to net CO_2 efflux. Thus, under both experimental treatments of warming and drying we hypothesized an increase in the age of the dominant carbon source contributing to CO_2 efflux.

Effects of experimental warming on the average age of respired CO_2

We investigated the effects of soil warming at the Soil Warming Experiment in Lowland Tropical Rainforest (SWELTR)[13]. Soil warming increased the ^{14}C value of respired CO_2 during the wet season, indicating greater efflux of modern 'bomb" carbon under warmed and wet conditions (Figure 1a). Specifically, $\Delta^{14}C$ of respired CO_2 was 12 ± 5 ‰ higher in warmed plots than control plots in the wet season ($p = 0.02$). In the warmed plots, $\Delta^{14}C$ of respired CO_2 was 11 ± 5 ‰ higher in the wet season than in the dry season ($p = 0.03$).

The observed increase in the $\Delta^{14}C$ of respired CO_2, indicates that carbon fixed nearer to the bomb spike (circa 1963; see Figure S4 for reference), or decadal-aged carbon, contributed more to soil CO_2 flux under warmer and wetter conditions (with warming in the wet season) compared to cooler and drier conditions. Neither $\Delta^{14}C$ nor $\delta^{13}C$ (Figure S3) values differed between total and root-free CO_2 flux (using root exclusion columns). Considering roots typically respire CO_2 with $\Delta^{14}C$ values close to current atmosphere (see Methods)[22], this suggests this shift was attributable to microbial (not live root) CO_2 flux. These results suggest increased decomposition and loss of decadal-aged soil carbon under warmer and wetter conditions, while recently fixed carbon was the dominant source of carbon respired under drier and cooler conditions.

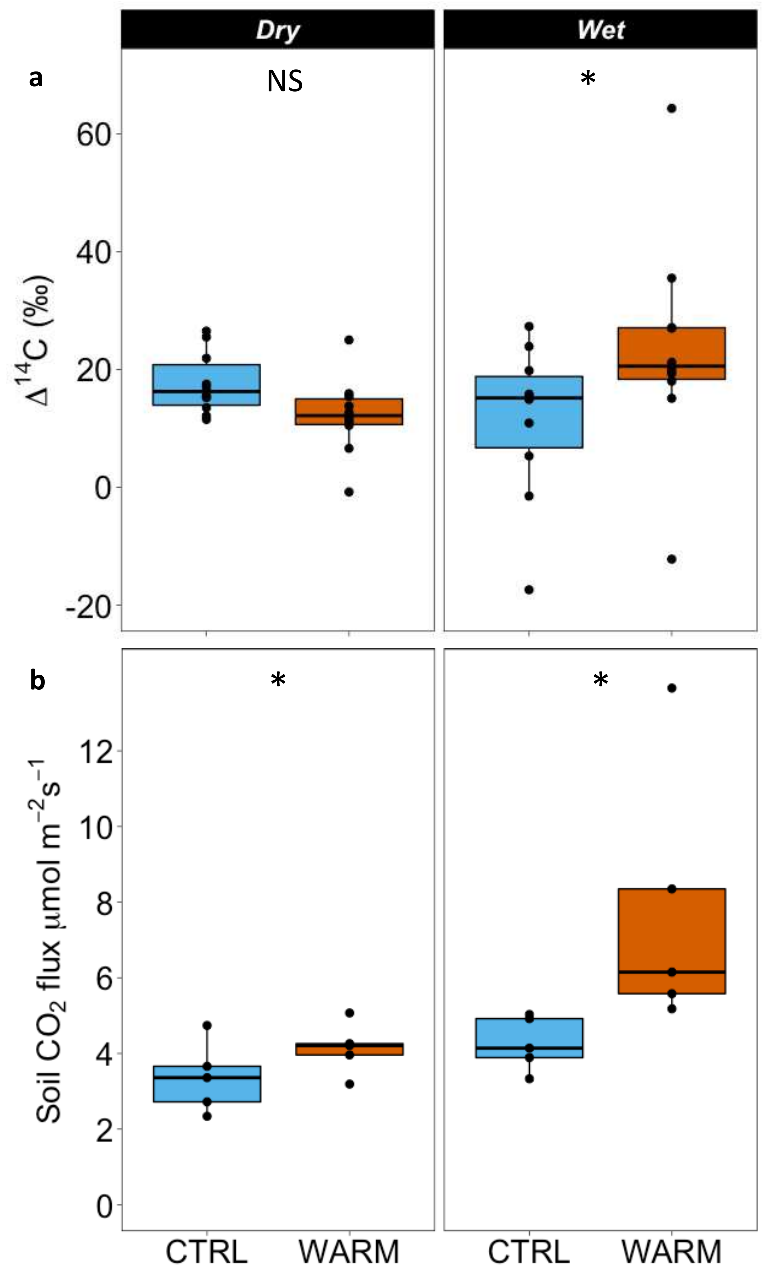

Fig. 1: Soil warming effects on total soil respired CO_2 flux and ^{14}C values during the dry and wet season in 2019. a, ^{14}C of respired CO_2 from single time-point measurements for n=2 per plot (total n = 10). **b,** Monthly average total soil respired CO_2 flux for March and October 2019 (n = 5 paired plots). The figures show plots warmed by +4°C (WARM) and controls (CTRL). Lines indicate medians, ends of boxes show the upper (Q3) and lower (Q1) quartiles, whiskers indicate minimum and maximum ranges (calculated from quartiles), solid points are individual observations. Asterisks indicate statistically significant differences between control and warmed plots where $p \leq 0.05$ whereas NS indicates non-significant differences ($p > 0.05$).

During the time periods of our study, total soil CO_2 flux rates were also higher in warmed and wet conditions (Fig. 1b). We found that total soil CO_2 flux increased from the dry season (March) to the wet season (October) by 60% ($p = 0.03$) and that experimental warming increased total soil CO_2 flux from 3.8 ± 0.4 μmol CO_2 m^{-2} s^{-1} in control plots to 6.0 ± 1.4 μmol CO_2 m^{-2} s^{-1} in warmed plots ($p = 0.03$). The partitioning of total soil CO_2 flux for the sampling periods in this study into heterotrophic (soil-derived) and autotrophic (root-derived) CO_2 flux from root exclusion and ingrowth cores, showed that 74 ± 7 % of total soil CO_2 flux was heterotrophic (Fig. S2). These results are consistent with a published 2-year time series of soil CO_2 flux from this experiment[13], which showed a 55% increase in soil CO_2 flux with warming that was attributed primarily to soil microbial (rather than live root) CO_2 flux.

Our results unequivocally show that warming caused an increase in the emission of older carbon (with a higher $\Delta^{14}C$ value) from soil organic matter into the atmosphere, which can be explained by different mechanisms that are not mutually exclusive. First, warming-stimulated soil CO_2 efflux during the 18-24 months preceding our measurements[13] may have depleted the pool of fresh soil organic carbon (i.e., with a $\Delta^{14}C$ value closer to 0%) leading to a switch in microbial substrate use to older pools of carbon[27]. Second, warming may have increased the degradation of older carbon pools via priming, whereby the rapid metabolism of plant-carbon inputs provided the necessary energy for microbes to synthesize enzymes to access to more longer-lived carbon pools[26] – a process that may be exacerbated in forests like our study sites where microbial growth is N and/or P limited[28]. In support of this mechanism, during the wet season in warmed soil we observed increased soil CO_2 efflux (Figure 1)[13], increased activity of soil extracellular enzymes[13], and increased variability in $\Delta^{14}C$ of respired CO_2 reflecting increased connectivity of soil organisms with a wider variety of carbon sources available for microbial metabolism.

Other experiments that warmed the soil profile (by 4.5 °C) have reported increases in annual soil CO_2 flux of approximately 35 % in temperate forest[29] and 14% in boreal peat forest[30], considerably less than the 55% increase in soil CO_2 flux with whole-profile warming reported for our site[13]. Few warming experiments have published $\Delta^{14}C$ values of respired CO_2. No change in the $\Delta^{14}C$ values of respired CO_2 was reported by warming experiments in two temperate forests where emissions were sustained by decadal-aged C[29, 31]. However, more similar to our observations, a 31% increase in summer soil CO_2 flux coincided with increased $\Delta^{14}C$ of respired CO_2 with warming in a boreal forest[32], indicating a greater contribution of decadal-aged carbon to the total flux. Experimental warming also increased the age of CO_2 in porewater profiles in a boreal bog[33] and in soil pore spaces in tundra[34]. These results suggest a variable, but potentially widespread, shift toward increased mobilization and loss of older soil carbon with climate warming.

Experimental drying effects on the average age of respired CO_2

We investigated the effects of soil drying at two sites that are part of the Panama Rainforest Changes with Experimental Drying (PARCHED) study[24]. We selected the P12 site for its similarity to the warming experiment as the two sites have equivalent MAP and similar soils, while the San Lorenzo (SL) experimental drying site receives about 800 mm more annual rainfall than the other two sites. We found that experimental drying led to an increase in the $\Delta^{14}C$ of respired CO_2 of 8 ± 3 ‰ averaged across sites and sampling periods ($p = 0.03$, Fig. 2b). Soil CO_2 $\Delta^{14}C$ values decreased from the wet-to-dry season transition in May to the late wet season in

November/December by 6 ± 3 ‰ averaged across sites and treatment ($p < 0.01$), possibly reflecting increased utilization of newer carbon as litter from the previous dry season was decomposed during the wet season. The $\Delta^{14}C$ of respired CO_2 did not differ between the drier (P12) and wetter (SL) site (Fig. 3) and did not differ between total and root-free soil CO_2 flux (Fig. S7).

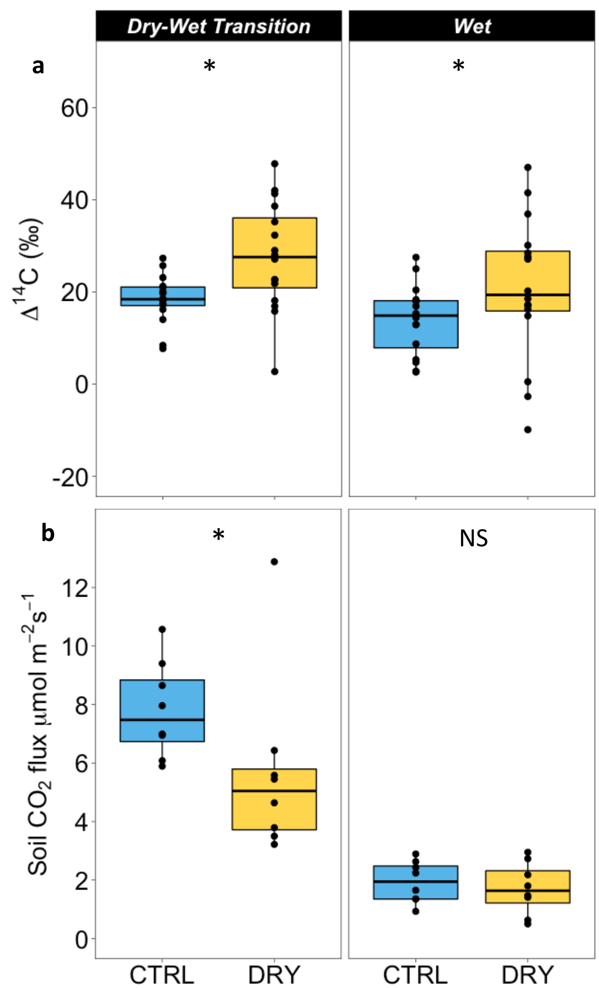

Fig. 2: Soil drying effects on total soil respired CO_2 flux and ^{14}C values during the dry-to-wet transition and wet season in 2019 from single-time point measurements at PARCHED. a, ^{14}C of respired CO_2 for both P12 and SL for n=2 per plot (total n = 16). **b,** Single time-point total soil respired CO_2 efflux for both P12 and SL (n = 8 paired plots). The figures show plots with 50% of throughfall excluded (DRY) and controls (CTRL). Lines indicate medians, ends of boxes show the upper (Q3) and lower (Q1) quartiles, whiskers indicate minimum and maximum ranges (calculated from quartiles), solid points are individual observations. Asterisks indicate statistically significant differences between control and throughfall exclusion plots where $p \leq 0.05$ whereas NS indicates non-significant differences ($p > 0.05$).

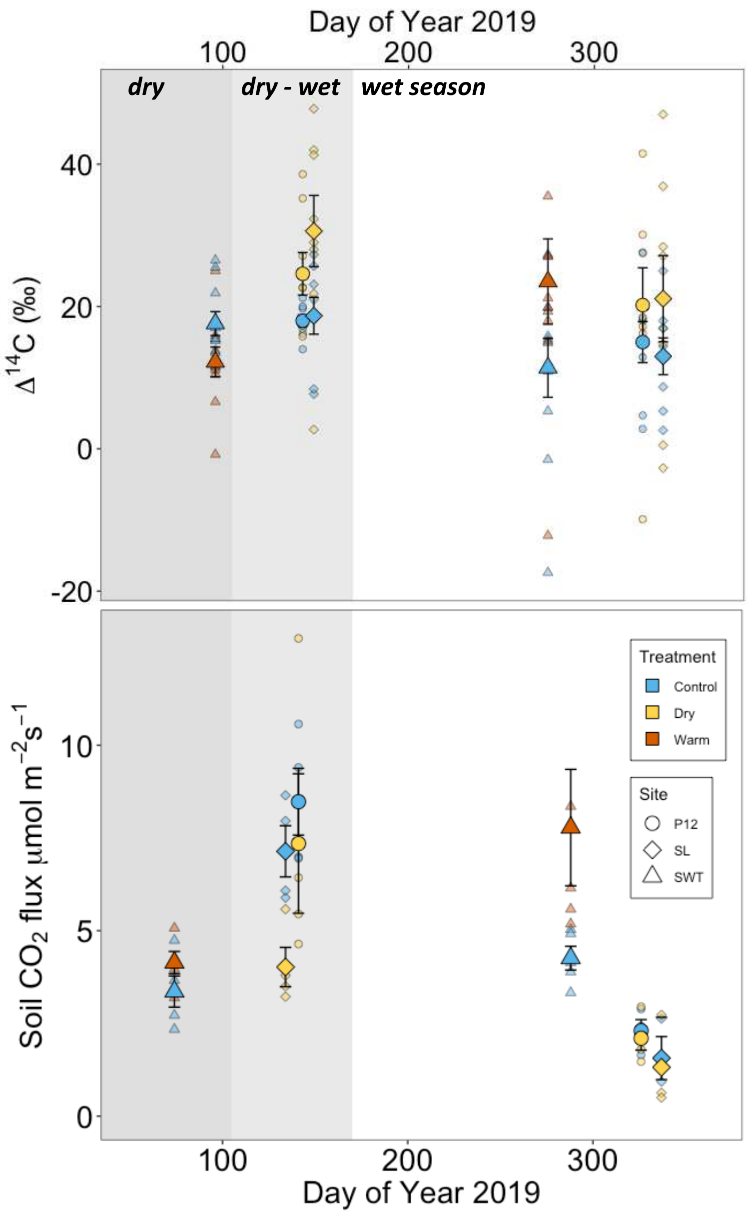

Fig. 3: Total soil respired CO_2 flux and ^{14}C values over 2019 at SWELTR, P12, and San Lorenzo. a, Total soil respired CO_2 flux rates are monthly averages for SWELTR and single time-point measurements at P12 and San Lorenzo **b,** Single time-point ^{14}C of respired CO_2.The figures show means as large symbols with standard errors and individual measurements as small symbols. Dark gray shading denotes the dry season, light gray shading denotes the dry-to-wet seasonal transition period, and no shading denotes the wet season.

During our study period, experimental drying led to decreased total soil CO_2 efflux, from 7.8 ± 0.5 μmol CO_2 m^{-2} s^{-1} (control plots) to 5.7 ± 1.0 μmol CO_2 m^{-2} s^{-1} (throughfall exclusion plots), during the dry-to-wet season transition (p <0.01, Fig. 2a). Partitioning of soil CO_2 efflux into heterotrophic (soil-derived) and autotrophic (root derived) components suggested that this response was driven by a reduction in heterotrophic CO_2 flux rates ($p < 0.01$), since root CO_2 flux was unaffected by treatment (Fig. S5). Overall, total, root, and heterotrophic soil CO_2 flux rates were higher during the dry-to-wet season transition compared to the wet season ($p < 0.01$), consistent with seasonal trends based on time-series reported for these and other sites in the region[25].

Drought decreases soil respiration as moisture limits both microbial activity and the transport of organic matter[35] as demonstrated following throughfall exclusion in other tropical forests[18, 36, 37]. Our finding that the $\Delta^{14}C$ of respired CO_2 increased under partial throughfall exclusion (Fig. 2) is consistent with this idea, indicating a reduced contribution of fresh plant-carbon inputs to soil respiration. However, our finding has further, potentially major, implications: it suggests that the turnover of older decadal-aged carbon was less affected by drying than the turnover of recent plant carbon inputs. We suggest that this reflects a greater contribution to surface CO_2 efflux of soil organic matter from deeper in the soil profile, where soil moisture is higher[36], soil carbon is older, and microbial activity is less affected by changes in the surface soil moisture, litter inputs, and litter decomposition rates. At the same time, decomposition of fresh litter and transport of new carbon may slow under drying treatments, reducing the accessibility of young soil organic matter to soil microbes, and necessitating a shift toward slightly older, but accessible, C sources. Indeed, throughfall exclusion decreased litter decomposition rates in a forest in Costa Rica[38] and increased accumulation of forest floor material in temperate forests[39, 40]. Furthermore, a suppression of respiration at all four PARCHED sites with throughfall exclusion has been attributed to a reduction in vertical flushing and nutrient delivery to soils[25]. Together, these mechanisms explain our observation of higher $\Delta^{14}C$ of respired CO_2 in the dry-to-wet seasonal transition than in the late wet season when soil moisture is higher.

Surprisingly, the increase in $\Delta^{14}C$ of respired CO_2 in drying plots relative to control plots observed in the dry-to-wet season transition persisted into the wet season as respiration rates decreased and wetter conditions should have resulted in a greater connectivity among soil organisms and fresh carbon inputs even in throughfall exclusion plots. Our observed pattern could reflect a decrease in surface fine root production or turnover in the drying plots, which would reduce inputs of fresh root-derived carbon to soils even though root respiration flux did not change with treatment. Preliminary data from the drying sites suggests that indeed drying suppresses surface root growth, which may be moving to deeper soils (<60 cm) to access water (Cordeiro et al, unpublished). Such a shift of root activity to deeper depths to access available water was observed in Amazonian rainforest[19, 41], and is a general pattern across tropical forests during dry seasons and droughts[42].

The observed seasonal pattern in soil CO_2 efflux likely reflects a combination of favorable conditions for microbial activity during seasonal rewetting: litter accumulated over the dry season provides ample substrate[16, 43], dissolved organic carbon (DOC) production and transport facilitate microbial access to substrate[44], and rewetting of soil following drought strongly stimulates microbial activity[19, 45]; while the effect of throughfall exclusion in decreasing soil moisture attenuates during the wet season. In these seasonally moist forests, litter and free organic debris builds up over the dry season and it is likely that this buildup of fresh organic matter fuels the sharp increase in respiration rates that we report during the dry-to-wet season transition period at P12 and SL[16, 25]. Indeed, studies in nearby forests including the warming site[13, 46] and elsewhere in the tropics[19, 41] show a similar increase in soil respiration rates during this dry-to-wet transition period, driven by seasonal patterns of moisture availability, microbial biomass[24], and leaf-litterfall input[43].

Discussion: Potential combined effects of warming and drying

Climate change is expected to alter rates of soil carbon cycling in tropical forests through warming[47] and altered rainfall regimes[48]. Unfortunately, no experiments have manipulated warming and drying together, although climate warming and drying are expected to occur together throughout much of the tropics and currently occur together during cycles of the El Niño-Southern Oscillation. Our results, based on individual responses to *in situ* experimental soil warming and soil drying, demonstrate that warming and drying change, not only the emission of CO_2 from soils, but also the age of the carbon being emitted. Specifically, we found that warming increased the utilization of older soil carbon (while increasing total CO_2 efflux) and drying reduced the utilization of new carbon inputs (while decreasing total CO_2 efflux). Thus, warming and drying together may result in the loss of older soil carbon.

The consequences of our findings will have wider implications when the impact of warming and drying on aboveground processes are considered alongside belowground effects. Both warming and drying have been shown to have detrimental effects on tropical forest productivity, based on *in situ* drying[48] and warming[49] experiments as well as field studies[50] that show limited evidence for acclimation of photosynthetic activity. In the context of our results, warming and drying together may decrease inputs of fresh carbon to soils as well as degradation rates of detritus, with negative effects on plant growth as nutrients remain immobilized in undecayed litter. Meanwhile increased CO_2 release from warmed subsoil carbon will continue, decreasing soil carbon storage, until drying extends to deeper soil horizons.

Importantly, our reported increases in ^{14}C with experimental warming and drying reflect changes in the average age of carbon being respired (the equivalent of 2–3 years in the mean age of respired carbon, see Fig. S4) but do not provide insight into the distribution of carbon ages contributing to these averages. Our ongoing work using $\Delta^{14}C$ to study soil carbon storage and cycling in these and other sites along the Panama Canal-zone rainfall gradient shows that soils in these forests store large amounts of young soil carbon (Finstad et al., unpublished). Thus, we conclude that our observed shifts in the age of respired carbon are striking, especially considering that these results were observed following relatively short-term (1 to 3 years) experimental treatments.

5. Conclusions

In summary, we demonstrate how warming and drying affect the rate and age of soil carbon emission to the atmosphere in tropical forests, by determining the $\Delta^{14}C$ of soil CO_2 efflux following experimental soil warming (whole-profile heating by 4ºC) and soil drying (50% throughfall exclusion). Experimental warming increased soil CO_2 efflux and, during the wet season, increased the age of respired soil carbon by roughly 2–3 years. In contrast, experimental drying decreased heterotrophic respiration rates and increased the age of respired soil carbon by about two years. Together, these results indicate an increase in the vulnerability of soil carbon and a relative shift in microbial carbon use towards older sources: warming by depleting the pool of rapidly cycling carbon and stimulating the decomposition of old carbon; drying by reducing the accessibility and subsequent decomposition of new carbon inputs. These findings imply a destabilization of old soil carbon under warming and a suppression of new carbon turnover under drying, which will have major implications for the tropical forest biogeochemical cycles under climate change. Our findings of differential responses of soil respiration rates and carbon sources to experimental warming and drying point to a need to study the effects of modified soil moisture and temperature together to improve our understanding of these interacting controls on soil respiration and carbon cycling and better represent these controls in soil carbon and land surface models.

Acknowledgments, Samples, and Data

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