Drought and fire affect soil CO_2 efflux and use of non-structural carbon by roots in forests of southern Amazonia

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ABSTRACT

Drought and fire events reduce the ability of tropical forests to cycle and store carbon. However, the combined effects of drought and fire on soil CO_2 efflux and subsurface carbon cycling remain poorly understood, particularly in the Amazon. Here we evaluated how multiple burns and extreme drought events affect soil CO_2 efflux and the use of non-structural carbon (NSC) in the roots of forest species in southern Amazonia. We studied one intact forest (control) and another burned annually from 2004 until 2010 (burned). We monitored: a) soil CO_2 efflux every three months between 2009 and 2012 (n = 25); b) the litterfall (n = 21); c) the fine roots production (n = 16); and d) estimated the age of NSC used in the production of fine roots from radiocarbon (samples from 2009 to 2011; n = 15). Multiple fires in the burn plot reduced soil CO_2 efflux by 18.7 % compared to the control plot, and altered the relationships between litter production, soil temperature and soil CO_2 efflux. After the 2010 drought, soil CO_2 efflux in 2011 in the control plot was reduced by 17 %. Relatively freshly fixed C was used to produce new fine roots in 2009 (<2 years), but the age of C used to grow new roots in 2010 and 2011 increased to 2–4 years old, especially in the burned plot. Our results suggest that fire and drought events reduce soil CO_2 efflux and root growth, with post-disturbance root growth likely relying on stored non-structural carbohydrates (NSC).

1. Introduction

Natural fires rarely occur in the Amazon (Bush et al., 2007; Feldpausch et al., 2022), but anthropogenic fires can ignite large wildfires during episodic drought events (Brando et al., 2019; Nepstad et al., 1999; Zong et al., 2024). Under severe droughts, large areas of

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Amazonian forests can dry out and drive increased fuel loads, resulting in increased forest flammability. During the drought conditions in 1998, for example, an estimated one-third of the Amazon region became flammable (Nepstad et al., 1999). The occurrence of droughts in Amazonia may become more frequent in the future due to predicted climate change (Duffy et al., 2015; IPCC, 2023). Fire thus is likely to become an even more important component of the dynamics and trajectory of Amazonian forests in the future (Brando et al., 2020).

Severe Amazon drought events impact the global carbon cycle. The extra area burned in drought year fires drive increased CO_2 emissions (Brando et al., 2019; da Silva Junior et al., 2022). However, drought also can lead to net ecosystem C losses through increased tree mortality and reduced C sinks from tree growth (Doughty et al., 2015; Kannenberg et al., 2022; Lewis et al., 2011). In 2005 and 2010, (Lewis et al., 2011) estimated these 'committed' fluxes as 1.6 PgC (0.8–2.6 95 %CI) and 2.2 PgC (1.2–3.4, 95 % CI), respectively. These findings highlight the critical role of Amazonian droughts and fires in accelerating carbon losses and weakening the forest's ability to function as a long-term carbon sink.

The transitional forests between Amazonia and the Cerrado are highly vulnerable to compounding disturbances associated with fires and droughts. These forests, located along the 'Arc of Deforestation' are highly fragmented (Marques et al., 2020), and experience a prolonged dry season. They are among the fastest-warming regions in the Amazon (Marengo et al., 2024), including an increase in seasonal drought associated with a delay in the onset of the rainy season over the past ~40 years. They have been an epicenter of fire activity in recent years, and some measurements of atmospheric CO_2 suggest that these forests are becoming a net source of carbon to the atmosphere, perhaps indicating a loss in resilience (Balch et al., 2008; Gatti et al., 2021). Severe droughts occurring with *El Niño* years in 2005, 2010 and 2016, make them more vulnerable to fires that often start in cattle ranching and agricultural areas (Barlow et al., 2020; Brando et al., 2014).

Studies of carbon impacts of forest fires and droughts in forests tend to focus on changes in aboveground carbon that occur due to direct emissions from burning material or committed emissions associated with tree mortality during and after drought events (Brando et al., 2019; Lewis et al., 2011). Fewer studies have investigated belowground impacts, including the legacy effects on above- and belowground productivity and the transfer of CO_2 from the soil to the atmosphere (Balesdent et al., 2018; Malhi et al., 2009). Questions remain about whether drought decreases or increases soil respiration in tropical forests (Metcalfe et al., 2018; Rocha et al., 2014). According to Vogt et al. (1995) and Tsegay and Meng (2021), a large portion of the carbon stored in tropical forests is belowground, and root biomass accounts for half of the carbon that is recycled annually by some forests. Although severe droughts and wildfires can affect belowground processes (Brando et al., 2019; Metcalfe et al., 2018; Rocha et al., 2014), our understanding of changes in root production, carbon allocation, and overall respiration remains poorly quantified.

Fire has many effects on forest ecosystem dynamics. First, burning surface litter can reduce the input of organic matter into the soil, leading to reductions in not only litter but also soil respiration (Balch et al., 2008; Pellegrini et al., 2022). Second, fires kill trees and their roots, altering an important carbon input and source of soil carbon efflux (Doughty et al., 2015; Pellegrini et al., 2022; Rocha et al., 2014). Third, fires alter species composition and competition for limiting resources, including light, water, and nutrients, potentially increasing the growth of some species, and reducing those of others, with unclear effects on soil carbon dynamics/soil respiration. Therefore, the overall effect of forest fires on soil respiration and root production is complex (Doughty et al., 2015; Pellegrini et al., 2022) and requires further investigation.

Tropical trees in transitional forests have several adaptations to cope with dry and hot conditions that allow the maintenance of high photosynthesis rates and carbon storage during the long dry season. These include production of roots to access deeper soil water, and in some species storage of nonstructural carbohydrate (NSC) reserves

(Herrera-Ramírez et al., 2023). The role of NSC in seasonal and extreme drought is complex and varies by plant organ and species (Ramirez et al., 2024). During periods of C depletion caused by stomatal closure or leaf abscission associated with prolonged drought, plants must utilize their reserves to maintain basic physiological processes (Doughty et al., 2015; Malhi et al., 2011), such as respiration and growth. As carbon limitation persists, plants will utilize older NSC reserves to maintain basic functions (D'Andrea et al., 2019; Muhr et al., 2018; Richardson et al., 2015), including fueling new root growth (Vargas et al., 2009). Thus, the age of the carbon used and respired by plants can indicate the level of stress plants experience during droughts, as well as following disturbances (Sala et al., 2012; Würth et al., 2005).

The effects of the combination of drought and fire on soil CO_2 efflux processes and carbon allocation in the plants of the Cerrado-Amazon transition forests can: 1) significantly reduce soil CO_2 efflux due to increased mortality and reduction of the litter layer; 2) influence litter production by increasing seasonality, which may be reinforced by a more intense drought period; 3) reduce the production of fine roots as a result of fire and drought stress, reinforcing the importance of analyzing other variables that explain interactions in the soil-plant-atmosphere system; and 4) allocate relatively older non-structural carbon to build new structures, given that trees subjected to fire and drought stress are expected to decrease photosynthesis.

In this study, we take advantage of a large-scale disturbance experiment in southeastern Amazonia (Fig. 1) to investigate the effects of drought stress and fire on processes influencing soil CO_2 efflux and belowground carbon allocation in Cerrado-Amazon transition forests. We aimed to evaluate the factors controlling soil carbon cycling in a primary forest under natural and fire-affected conditions, as well as the effects of drought capable of affecting processes such as soil CO_2 efflux and the use of non-structural carbon (NSC) in root growth in southern Amazonia. We tested three hypotheses: a) Drought alone will impact inputs by increasing aboveground litterfall in the drought year, but reducing root productivity and new leaves that can fuel decomposition in the subsequent year; b) Soil CO_2 efflux will be lower in the burned forest than in the unburned forest area due to reductions in surface litter and fine root production in areas that experienced high mortality from fire. This reduction in soil CO_2 efflux occurs despite increases in soil temperature, humidity, and overall necromass production associated with tree mortality in the burned forest. c) Trees subjected to combined drought and fire disturbance stresses allocate older nonstructural carbon reserves to produce new roots.

2. Methods

2.1. Study site

The study area is located in Fazenda Tanguro (~85,000 ha), Mato Grosso state, approximately 30 km north of the southern border of the Amazon Rainforest in Brazil (13°.04'35.39" S, 52°.23'08.85" W) (Fig. 1). The natural vegetation of the farm (44,000 ha) is classified as Perennial Seasonal Forest (Ivanauskas et al., 2008). The average canopy height is ~20 m, and the diversity of plant species is relatively low when compared to the more humid forests typical of central Amazonia (Balch et al., 2008), with only 97 species of trees and lianas per hectare larger than 10 cm dbh [diameter at breast height 1.3 m above ground].

The data was collected in two experimental plots with area of 50 ha each (Fig. 1), one unburned [Control], and one that were experimentally burned annually between 2004 and 2010 (Fig. 1; (Balch et al., 2008; Brando et al., 2012)). The average annual precipitation is ~ 1770 mm (2005–2011), with a well-marked dry (May-September) and wet (October-April) season. The prescribed fires occurred at the end of the dry season, usually towards the end of August or early September. The mean annual air temperature is ~ 25°C, with a seasonal variation of 5°C. The area studied was affected by two drought events, one in 2007 and another in 2010 (Fig. 2; (Brando et al., 2014)).
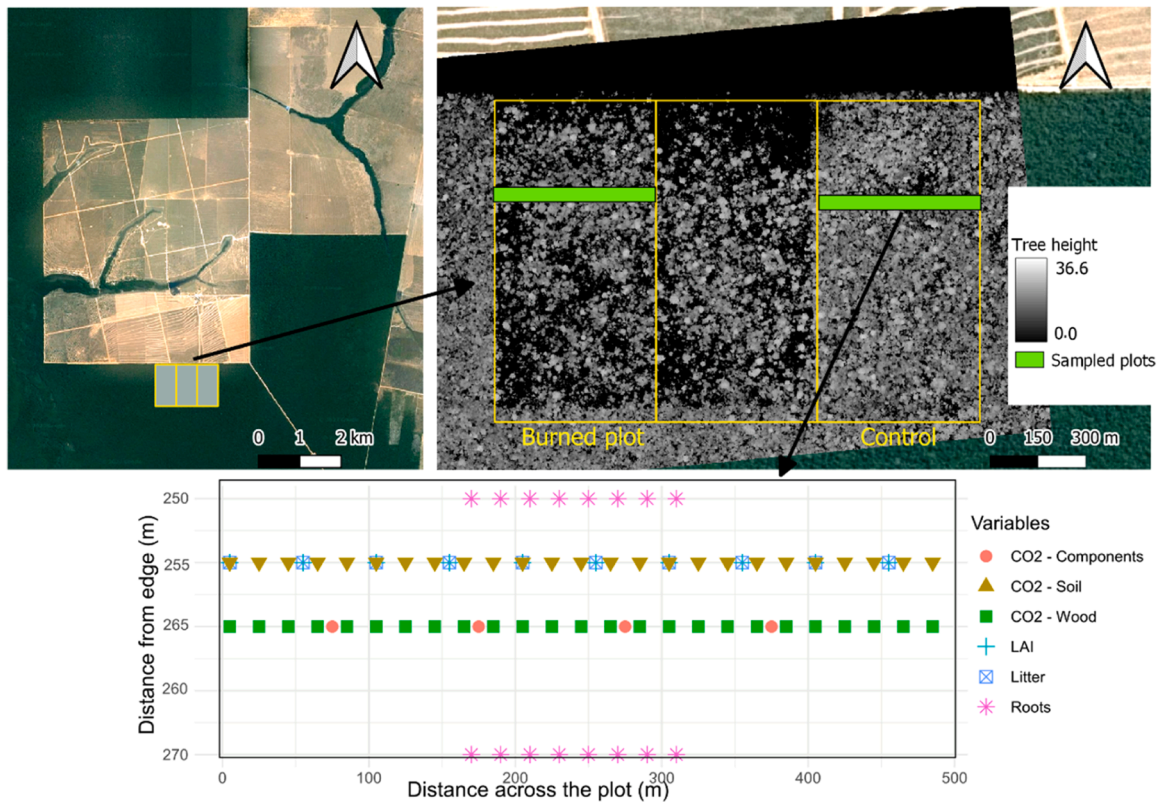
Fig 1. Location of the study area on Tanguro Farm (left on the image). Colors indicate vegetation type and land use (forest=green; crop=gray/beige). On the right is the control plot (no fire), on the left is the burned plot (burned every year). The light green stripes indicate transect F, where all collection points was allocated according to the graph below.

The experimental fires were conducted between 2004 and 2010 during the peak dry season (July–September). The treatment plot was burned annually for three consecutive years and three additional times over the six-year period, with no prescribed fires in 2008. The initial fires (2004–2006) were of low intensity, but drought events in 2007 and 2010 increased fuel loads and dryness, leading to abrupt rises in fireline intensity. Before the first burn, the control plot had 11 % higher aboveground biomass (AGB) than the treatment plot, though canopy greenness, vegetation height, and tree density were comparable across treatments (Figure S1; (Balch et al., 2008)). Surprisingly, initial tree mortality following the first burn was low (Balch et al., 2008), despite the known sensitivity of Amazonian trees to fire (Barlow and Peres, 2008; Brando et al., 2012). However, in subsequent years, severe droughts in 2007 and 2010 exacerbated fire impacts, causing sharp increases in fire-induced tree mortality rates and significant reductions in forest biomass (Brando et al., 2014). Over the course of the experiment, the cumulative effects of recurrent prescribed fires substantially altered forest structure and biomass. Fire severity was higher in plots burned every three years, as longer intervals allowed for greater fuel accumulation, increased fuel production, and higher understory air dryness. Consequently, post-fire mortality of large trees was higher in the three-year fire treatment, where our sampling was conducted for this study. The soil type at the site is dystrophic Red-Yellow Latosol (RADAM and BRASIL, 1974); Brazilian soil classification), and soils are well-drained. Groundwater depth is at ~15 m below the surface, and no soil layers prevented root penetration along the soil profile. These soils of this region are among the least fertile in the Amazon (Table S1) and are representative of much of the Eastern Amazon (Quesada et al., 2012, 2010).

2.2. Meteorological data

Solar radiation, air temperature, relative humidity, and rainfall time series data were collected at an automatic weather station (AWS) located at 13.08 °S and 51.48 °W, one kilometer away from the experimental forest studied. The original data were measured at an hourly time resolution from January 2009 to December 2012. We calculated maximum cumulative water deficit (MCWD), a well-established drought index (Aragão et al., 2007), based on precipitation recorded at a weather station located in an open area near the study plots.

2.3. Soil CO_2 efflux, temperature, and humidity

Total soil CO_2 efflux for each month was measured at 25 points (Fig. 1) along transects spanning the length of each plot, at a distance of 250 m from the edge. CO_2 efflux was measured by circulating air between headspace within a flow-through chamber with an infrared gas analyzer or IRGA (EGM-4 IRGA and SRC-1, PP *Systems,* Hitchin, UK). The chamber top was fit onto plastic (PVC) tubes that were permanently fixed in the soil so that each location was measured repeatedly. The tubes were 12 cm in diameter and 10 cm long, with a small portion inserted at a depth of 2 cm into the soil. At the time of each flux measurement, soil surface temperature (depth of 10 centimeters) was measured with a thermometer (T260 probe, Testo Ltd., Hampshire, UK), and moisture was measured using a *Hydrosense* probe (Campbell Scientific Ltd., Loughborough, UK).

2.4. Collection of surface litterfall

For litter collection, we installed 25 trays (60 cm long × 40 cm wide) at a height 1 m from the ground. Trays were installed every 20 m along the transect within each plot (Fig. 1), and collected every two weeks.
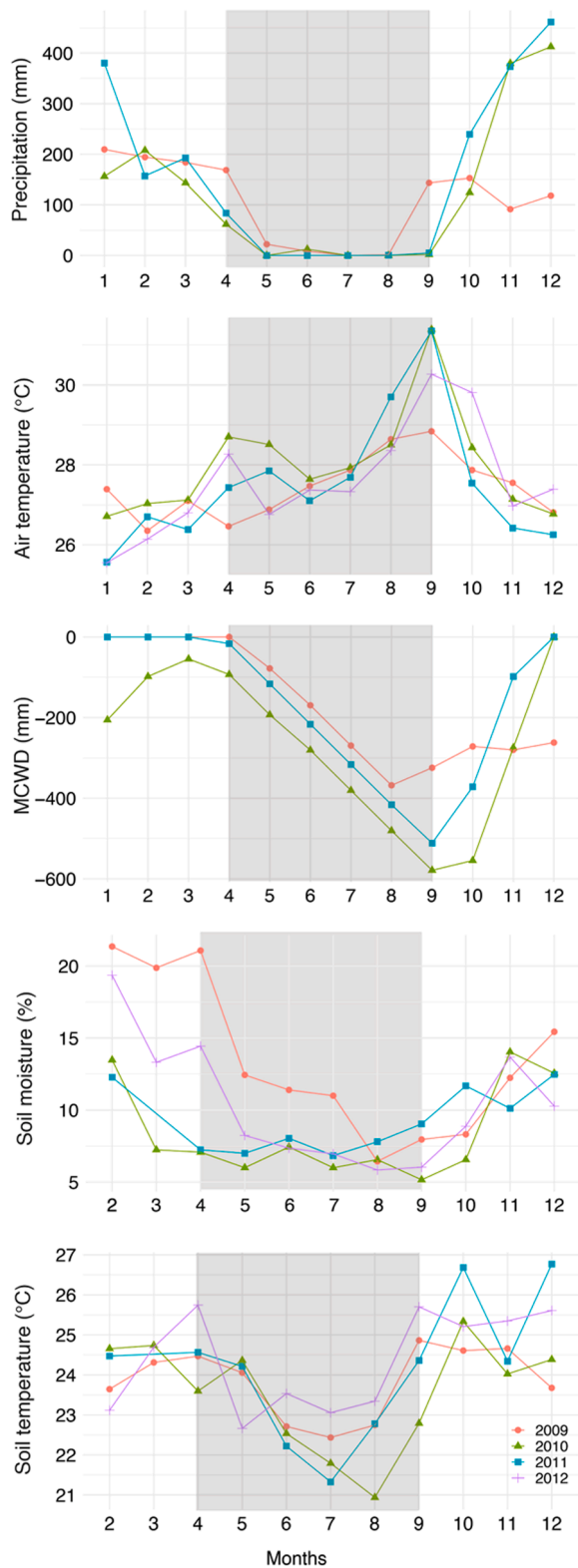
Fig 2. Seasonal climate data averages for monthly precipitation (2009–2011), soil moisture (2009–2012), air temperature, soil temperature (depth of 10 centimeters), and climatological maximum soil water deficit of the MCWD between 2009 and 2011 from top to bottom on the graph. All variables were recorded at a weather station located in an open area near the study plots, except for soil moisture, which was recorded using sensors installed in each plot. The gray area represents the dry season.

The collected litter was divided into leaf and non-leaf materials, stored in labeled paper bags, oven-dried at 65°C for 48 h, and then weighed.

2.5. Root collections

To estimate fine root production, 16 root ingrowth collars were installed in each plot (control and burned). Ingrowth collars had dimensions of 40 cm in length and 20 cm in diameter. They were filled with root-free soil and equipped with screens to allow the entrance of fine roots. Ingrowth cores were installed (using the methodology of Vogt et al. (1998) every 20 m in each plot (Fig. 1). Collections began in February 2009 and ended in October 2011. Every three months, the cores were removed, and the roots that had grown in through the screens were manually removed from the soil in each core according to the root extraction methodology of Metcalfe et al. (2007). Roots were picked for a period of 40 minutes, while a relationship between the time of picking and the cumulative mass of root extraction over time a range of time intervals was used to predict overall root mass (Metcalfe et al., 2007). The root-free soil from each core was returned to and the core reinstalled in the plot. Thus, the same soil was used repeatedly over the 2-year period. The roots collected from each ingrowth core were washed thoroughly, oven dried at 65°C for 48 h until a constant mass was reached, and then weighed. After weighing, the collected root samples were stored in sealed paper bags.

2.6. Analysis of ^{14}C age of carbon used to grow new roots

We used the method of tracking 'bomb' radiocarbon to estimate the age of carbon used to grow new roots. This method relies on the fact that, following a sudden increase caused by atmospheric nuclear weapons testing in 1964, the radiocarbon content of atmospheric CO_2 has declined with time as this excess was taken up by biota and the oceans and been diluted by ^{14}C-free CO_2 emitted from fossil fuel burning. Photosynthesis in any of the past 40 years will fix CO_2 with the ^{14}C signature equal to that years' atmospheric $^{14}CO_2$. C that is stored for several years in plants will reflect that it was fixed in the past by having a higher ^{14}C content–that reflects how many years elapsed since its C was originally fixed from the atmosphere. For more details see Gaudinski et al. (2001), Hilman et al. (2021).

In this study, roots picked from the ingrowth cores were known to have grown within the previous 3 months. In total, 15 individual root samples were selected per plot (control and burned): 10 from cores sampling root growth during the rainy and/or post-fire periods for each year (2009 and 2010) and five from cores sampling roots grown during the dry season for each year (2009–2011). Sample selection was uneven due to the costs of ^{14}C analyses and was focused on times with higher root production.

These samples were analyzed in the ^{14}C laboratory at the Max Planck Institute for Biogeochemistry in Germany. First, they were extracted with an acid-base-acid washes to remove soluble components such that the main C analyzed represented structural C. Then the dried extracted samples were ground, combusted, converted to graphite and subsequently analyzed using Accelerator Mass Spectrometry (Steinhof et al., 2017). Results are reported as Δ ^{14}C, the difference (in parts per thousand [‰]) between measured (in 2012) root samples and a preindustrial wood standard. Using this notation, $Δ^{14}C$ of 0 ‰ means that the $^{14}C/^{12}C$ of the standard is equal to that of the preindustrial sample. Positive values of $Δ^{14}C$ indicate that the C in the sample was fixed from the atmosphere since the 1960s, while negative values of ^{14}C indicate that sufficient time (e.g., hundreds to thousands of years) has elapsed since C fixation for radioactive decay of ^{14}C.

We estimated the mean age of carbon in fine root structural tissues by comparing the measured Δ ^{14}C with the Δ ^{14}C-CO_2 in the atmosphere as reported for the southern Hemisphere Zones 1 and 2 (Hua et al., 2022), or the time elapsed since the C used to produce root tissues was fixed from the atmosphere. This mean age represents the time elapsed since

the atmosphere last had the $\Delta^{14}C$ value measured in the sample (Hilman et al., 2021). Samples of annual plants sampled over several years at the Tanguro ranch correspond to the southern hemisphere curve of Hua et al. (2022) and indicate there are no local factors influencing the atmospheric $\Delta^{14}C\text{-}CO_2$ at this site.

2.7. Statistical analysis

The possible differences in soil CO_2 efflux between the plots studied (control and burned) and between the seasons (dry and rainy) were verified using analysis of variance (ANOVA) with two factors, followed by Tukey's test. A simple regression analysis was used to verify the relationship between soil CO_2 efflux, soil humidity, and temperature. Throughout the text, the means are presented as the standard error ($\pm$ SE). All statistical analyses were performed using R software (R Core Team, 2024).

3. RESULTS

3.1. Differences between treatments

Soil moisture (<20 cm depth) had large seasonal variation but minor differences between control and burned plots (Fig. 2). The highest soil moisture was observed in the second half of the rainy season (February–March) and the lowest soil moisture was observed at the end of the dry season (September) in both plots. The minimum soil moisture occurred at the end of the dry period of 2010 in both plots (5.16 % (v/v) and 5.32 % in the control and burned plots, respectively). In contrast, the highest soil moisture content occurred in the burned (22.48 %) and control (21.36 %) plots during the 2012 and 2009 rainy periods. Water deficits expressed as monthly maximum cumulative water deficit (MCWD) increased over the dry season months (Fig. 2). The greatest MCWD values occurred in 2010, the drought year.

Mean soil temperature (depth of 10 centimeters) varied according to season and plot (Fig. 2). Highest soil temperatures occurred in the dry season (September-December) in the fire-disturbed plots, and lowest temperatures between May and July (Fig. 2). There was considerable interannual variation in soil temperature (Fig. 2). For example, in 2009, the highest soil temperatures were observed in March (25.6°C) and September (24.8°C). However, in 2010, the highest temperatures were recorded in December (27.4°C) and October (25.3°C). The highest temperatures in 2011 were recorded in the dry season in August and December (27.9°C and 26.7°C). In 2012, the highest temperatures recorded were (28.3°C) in September and (25.7°C) in April (Figs. 2 and 3).

3.2. Soil CO_2 efflux

Soil CO_2 efflux varied among treatments, seasons, and years (2009–2012) (Fig. 3, Table 1 and S2). Across all years of observation, average soil CO_2 efflux was 18.7 % lower in the burned plot than in the control plot. Despite this difference, both treatments had similar seasonal patterns, with lower soil CO_2 efflux rates during the dry season and higher rates during the wet season (Fig. 3). On average, soil CO_2 efflux was ~15 % higher in both plots during the rainy season than in the dry season.

In addition to the variability in soil CO_2 efflux between the two plots and seasons, we observed high interannual variability in CO_2 efflux (Table 1 and S2). In particular, the driest sampling years (2010 and 2011) had lower CO_2 efflux rates in both plots. For example, in 2011, CO_2 efflux (0.13 μmol CO_2 m^{-2} s^{-1}) was the lowest recorded, while in 2010, the lowest recorded was (0.16 μmol CO_2 m^{-2} s^{-1}). In 2012, the lowest soil CO_2 efflux rate (0.18 μmol CO_2 m^{-2} s^{-1}) was recorded during the dry season in August of that year (Fig. 3, Table 1 and S2).

Soil CO_2 efflux was strongly influenced by soil moisture (P < 0.001, R^2=0.26; Fig. 4) and temperature (P < 0.001, R^2=0.32). The
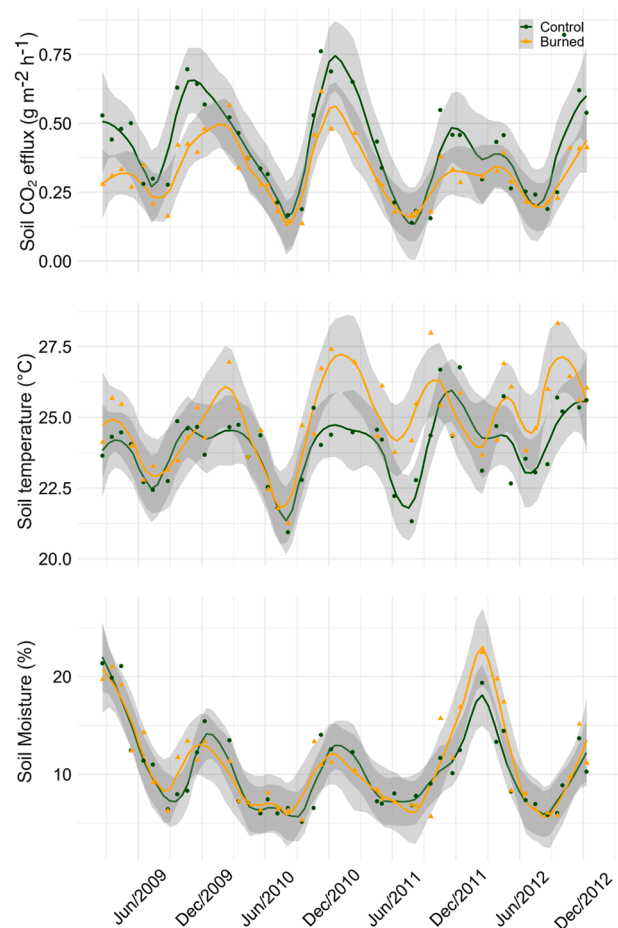

Fig 3. Mean $\pm$ standard error of the seasonal variation in the control and burned plots of soil carbon dioxide efflux, temperature, and soil moisture measured at the time of collection between 2009 and 2012.

relationship between CO_2 fluxes and temperature was stronger for control than burned plot (Fig. 4a), while both treatments responded similarly to soil moisture variation (Fig. 4b).

3.3. Fine root production

The mass of new root biomass in ingrowth cores showed a strong reduction over time but was higher in the control compared to burned plots (Fig. 5). For example, in 2009, the control plot had much higher average fine root production compared to the burned plot (4.14 g m^{-2} year^{-1} versus 2.34 g m^{-2} year^{-1}). In 2010, root production declined in both plots, but the average root production in the control plot was still much higher (1.25 g m^{-2} year^{-1}) than in the burned plot (0.29 g m^{-2} year^{-1}). Both plots strongly decreased in average root production over time, and the decline was more pronounced in the burned plot. For example, in the first year of the study, root production was 2.34 g m^{-2} year^{-1}, but in the last year, it was 0.10 g m^{-2} year^{-1} (Fig. 5).

3.4. Age of fine root carbon

Radiocarbon contents of fine (<2 mm) roots picked from the ingrowth cores between 2009 and 2011 showed considerable variation. During the same period, atmospheric $\Delta^{14}CO_2$ was declining at a rate averaging ~4.2 ‰ per year (based on Hua et al. (2022)), in agreement with annual plant measurements. In 2009, most ingrown root samples from both control and burned plots (80 %) had $\Delta^{14}C$ values close to those measured in annual plants and atmospheric CO_2 samples collected

Table 1

Comparison of average annual and seasonal soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) and leaf litter production (Mg biomass ha^{-1} month^{-1}) in the control and burned treatments.

	Control			Burned		
	Yearly average	Dry season	Wet season	Yearly average	Dry season	Wet season
Soil CO_2 efflux	0.37 ± 0.02	0.25 ± 0.0.02	0.49 ± 0.02	0.30 ± 0.01	0.23 ± 0.01	0.37 ± 0.02
Litter production	5.76 ± 0.16	7.18 ± 0.25	4.74 ± 0.20	4.97 ± 0.16	7.01 ± 0.27	3.48 ± 0.16

Fig 4. Linear relationships between soil CO_2 efflux and temperature (a), and moisture (b) in both treatment plots.
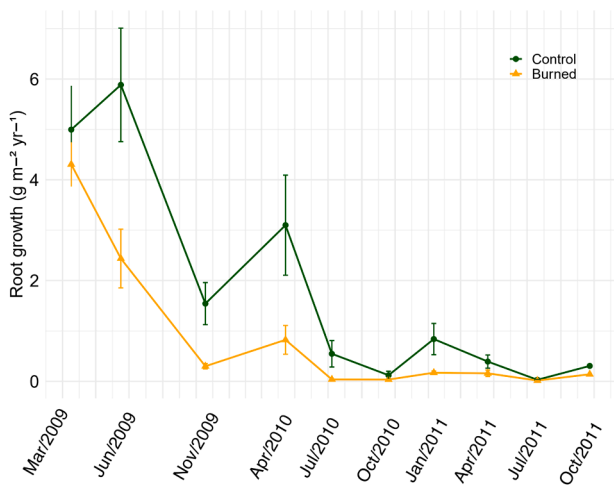

Fig 5. Means plus standard error of root growth in ingrowth cores up to 30 cm depth in the burned plot (yellow) and control plot (green) throughout the collection period.

Fig 6. Differences in the carbon allocation period Δ^{14}C (‰) for the root analyses of the burned and control plots (2009–2011). The control plot is green, burned is yellow, while blue points represent annual plants collected in each year as a measure of growing season atmospheric $\Delta^{14}CO_2$. Vertical error bars indicate analytical error for each sample ($\pm$ 2–4 ‰).

As the source of this older C must be stored reserves in the living root system, the increase in the age of C used for growing roots in the burn plot could indicate greater reliance on storage reserves.

3.5. Litter production

Litter production between 2009 and 2012 was higher in control than the burned plots (Table 1 and S2). In both plots, the highest litterfall occurred during the dry season (May - September) and lowest fluxes during the wet season (October - April) (Table 1 and S2). For example, in the control plot, the highest average monthly production (12 Mg biomass ha^{-1} year^{-1}) occurred during the dry period of 2009. The lowest average (2.58 Mg biomass ha^{-1} year^{-1}) was recorded during the 2012 rainy season. However, in the burned plot, the highest monthly average litter production occurred during the dry period of 2009 (11.52 Mg biomass ha^{-1} year^{-1}). The lowest average (1.61 Mg biomass ha^{-1} year^{-1}) was recorded in March 2012 (Table 1 and S2), which was the rainy season.

We observed large interannual variability in litter production, with lower values in the years following the 2010 drought event. For example, during the years 2009, 2010 and 2011, the control plot litter production was 6.16 (2009), 6.22 (2010) and 5.07 (2011) Mg biomass ha^{-1} year^{-1}, and burned plot litter production declined from 5.51 (2009) to 5.39 (2010) and 4.67 (2011) Mg biomass ha^{-1} year^{-1}. In 2012, production increased again in the control plot (6.12 Mg biomass ha^{-1} year^{-1}), but continued to decrease in the burned plot (4.00 Mg biomass ha^{-1} year^{-1}) (Table 1 and S2, Fig. 7).

3.6. Relationship between litter and soil CO_2 efflux

The relationship between soil CO_2 efflux and litter production was weak (Fig. 7), although litter decomposition annually accounted for roughly a third of the CO_2 effluxes measured in the soils of both plots

during the same year (Δ^{14}C of 50.9 ‰ versus 50.3 ‰ of the atmosphere $\Delta^{14}CO_2$), indicating that the carbon allocated to root construction was fixed from the atmosphere in the same year. Notably, one of the individual roots sampled from the control plot in 2009 had a high Δ^{14}C value (79.3 ‰, equivalent to 5-year-old carbon used to grow the new root [Fig. 6]). In 2011, differences between Δ^{14}C of individual root samples and the Δ^{14}C of the atmospheric CO_2 were larger. For example, the Δ^{14}C of the control plot samples averaged 52.1 ‰, that of the burned plot averaged 56.2 ‰, and the Δ^{14}C of the atmosphere that year averaged 40.3 ‰. Especially in the burn plot, new roots in 2011 were grown from carbon fixed from the atmosphere on average ~ 4-years previously, with the estimated time since fixation tending to increase from 2009 to 2011.
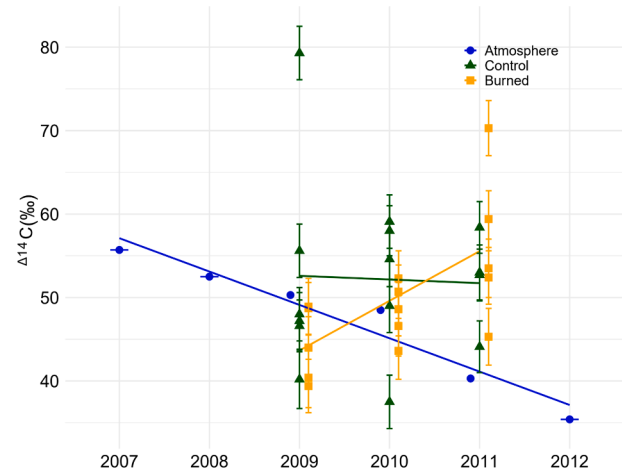
Fig 7. From top to bottom in the graph, annual averages of litter production in Mg biomass ha^{-1} $year^{-1}$; relationship between soil CO_2 efflux and litter production; annual relationship between soil CO_2 efflux (g m^{-2} yr^{-1}) and litter production (g ha^{-1} $year^{-1}$) between burned and control plots (2009–2012).

(Fig. 7). For example, the ratio of soil CO_2 efflux to litter production between the plots was 0.29 in the control plot and 0.32 in the burned plot (Fig. 7).

4. Discussion

This study examined the effects of fire and drought on soil moisture, root productivity, and soil CO_2 efflux in an Amazonian transitional forest, as well as the age of carbon utilized to grow new roots. Analyzing a control forest plot that suffered from severe drought, in contrast to a forest that was frequently subjected to fires, helped us understand the effect of combined fire and drought disturbance, demonstrating that repeated fires and drought reduced litter and fine root production, altered the allocation of carbon to root growth and significantly reduced soil CO_2 efflux. Declines in soil CO_2 efflux are mainly related to increased tree mortality from compounding of fire and drought stresses (Brando et al., 2014), leading to diminished inputs of fast-decomposing fine litter in the burned plots. Although litter inputs were lower, surface litter production made up a greater proportion of soil CO_2 efflux in the burn plots in most years. Soil temperatures were higher in burn plots although no large effect on soil moisture was observed. However, CO_2

efflux in the burned plots was less sensitive to soil temperature than in control plots.

The reduction in soil CO_2 efflux in the annually burned area is a partially unexpected result. Fire events increase tree mortality (Balch et al., 2008; Brando et al., 2012; Silvério et al., 2019) and the amount of dead wood decomposition, which would contribute to soil CO_2 efflux (Metcalfe et al., 2018; Rocha et al., 2014). However, the opposite was observed: a reduction in CO_2 efflux from the soil in the burned plot compared with the control. Three processes are likely to have influenced this reduction: 1) Root productivity was lower in burned than in control plot (Fig. 5). Owing to the high tree mortality after the passage of the 2007 experimental fires (Brando et al., 2014), the number of living remnant trees growing in the annually burned plot was drastically reduced - thus, both root productivity and root respiration declined. 2) Leaf litter production also declined, coinciding with a reduction in leaf area index in the burned plots compared to control plots during this period (Brando et al., 2019). 3) While indeed more dead wood may be present, this was not necessarily well sampled by our soil CO_2 efflux chambers; further higher air temperatures in burn plots could be associated with overall drier wood and reductions in decomposition rate.

4.1. Fire and drought induce changes in the soil components of transitional forests

Seasonality had a strong influence on the production of litter, with the largest contributions of material between May and September (Fig. 7), influenced by falling branches and leaves during the period of low rainfall in the region. Results from other areas of semi-deciduous tropical forests have identified increases in litter during the drier period of the year (Boinski and Fowler, 1989; Dantas and Phillipson, 1989; Scott et al., 1992; Songwe, Fasehun, et al., 1988).

Considering the period of observations in this study, 2010 stood out with lower productivity in both the control and burned plots compared to the other years studied. Fine root production was reduced in the burned plot, probably because of the reduced number of trees growing in the burned plot compared with the control plot (Balch et al., 2013, 2011, 2008; Brando et al., 2012; Metcalfe et al., 2018; Rocha et al., 2014). However, a gradual reduction in root production was also observed in control plots over time. This pattern of reduction in root production in both plots was unexpected because there were no major changes in the dynamics and structure of the control plot, nor were surface litter fluxes declining.

Although the ingrowth core method is widely used to quantify fine root growth, it has limitations due to the disturbance associated with core installation and repeated soil manipulation. Several studies suggest that these disturbances, combined with alterations in soil structure and nutrient availability when root-free soil is continuously reused, may constrain root regrowth over time (Hendricks et al., 2006). In our study, the sharp reduction in root production observed in later sampling periods is likely a result of both these methodological constraints and the inherently nutrient-poor soils at Tanguro, which may have further limited root regeneration. The repeated removal of newly formed roots may have progressively depleted the soil's capacity to sustain additional root growth, particularly in the burned plots, where fire-induced changes in nutrient cycling could exacerbate this effect. To mitigate this limitation in future studies, we recommend installing a fraction of ingrowth cores in undisturbed soil during each sampling period. This approach would allow for a more representative measurement of root production while minimizing soil depletion effects over time.

4.2. Changes in soil CO_2 efflux processes

In the present study, fire, in conjunction with drought episodes, caused a decrease in soil CO_2 efflux rates as well as a reduction in the seasonal variation of CO_2 efflux (Fig. 3). The extrapolated annual CO_2 efflux (7.24 ± 1.9 MgC ha^{-1} $year^{-1}$) for the control site are higher than

other published estimates for the Amazon region (Sotta et al., 2004) (6.45 ± 1.2 MgC ha^{-1} year^{-1}), and southern Amazonia (6.6 ± 2.0 MgC ha^{-1} year^{-1}) (Metcalfe et al., 2018), with 95 % confidence interval. In a forest with more pronounced dry season in Acre, Brazil, Salimon et al. (Salimon et al., 2004) found similarly higher annual soil C efflux in a study carried out in a secondary forest, a primary forest, and a pasture area, with the highest CO_2 efflux observed in the forest during the rainy season. These results suggest that forests with a more pronounced dry season tend to have higher CO_2 flux compared to more continuously wet systems.

The relationships between temperature, moisture and soil CO_2 efflux differed for burned and control forests. In general, in the control forest, higher soil temperatures meant higher soil CO_2 efflux (Fig. 4). In contrast, the correlation between soil CO_2 efflux and temperature in the burned plot was not strong, despite experiencing overall higher soil temperatures (Fig. 4). Similarly, soil CO_2 efflux increased with litterfall in the control forests, but the relationship was not so marked in the burn plots, despite a larger percentage of the overall flux coming from litter (Fig. 7).

4.3. Fire and drought alter belowground C allocation

In this study, we found that fire and drought, in addition to causing a decrease in soil CO_2 efflux rates, likely caused an increase in the age of the carbon allocated to grow new roots (Fig. 7), with mostly fresh photosynthetic products used to grow new roots in 2009, but with 2–4-year-old C reserves used in 2010 and 2011, particularly in burned plots. Our results are in accord with other studies (e.g., (Brunner et al., 2015; Maguire and Kobe, 2015)), and indicate that trees under fire and drought stress rely more on older stored nonstructural carbon to grow new roots. This can indicate overall greater vulnerability of the remnant trees in the burned plot, compared to the control plot that have greater allocation of fresh photosynthetic products belowground. Together, our results suggest that fire and drought significantly reduce carbon cycling and create stressful conditions that can affect mortality in remaining trees not already killed by fire. With ongoing climate change, extreme drought and increased forest flammability can lead to degradation of forests and reduced carbon stocks through higher mortality, accompanied by reduction in CO_2 efflux in the immediate years after disturbance.

5. Conclusion

Our findings indicate that recurrent fire and extreme drought events in the seasonal forests of southern Amazonia significantly alter carbon cycling dynamics, reducing both aboveground and belowground carbon inputs and limiting soil CO_2 efflux. The reduction in litter production was closely linked to increased tree mortality in burned areas, whereas decreased soil moisture during drought events suppressed biological activity, further restricting CO_2 release from the soil.

The decline in fine root production, particularly in the burned plot, suggests long-term disruption of belowground carbon allocation. The shift toward the use of older non-structural carbon (NSC) for root growth indicates that trees in burned areas rely on stored carbon reserves, evidence of reduced capacity for photosynthesis, and carbon assimilation. This physiological response suggests that trees in burned areas sustain metabolic stress, which may compromise their long-term survival and the capacity of these forests to recover carbon stocks.

The increasing frequency of extreme droughts and rising flammability of Amazonian forests associated with ongoing climate change are likely to exacerbate the carbon cycle disruptions observed in this study. Reductions in soil CO_2 efflux and root production suggest that fire and drought not only reduce the short-term capacity of forests to sequester carbon but also hinder their long-term resilience. These findings highlight the urgent need for fire prevention and climate adaptation strategies to avoid a reduction in Amazonian forest resilience.

CRediT authorship contribution statement

Wanderley Rocha: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Divino Vicente Silvério:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maracahipes-Santos Leonardo:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis. **Trumbore Susan:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Malhi Yadvinder:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Martorano Lucieta Guerreiro:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Conceptualization. **Brando Paulo Monteiro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that might appear to influence the work reported in this document.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122584.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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