

1 **Drought and fire affect soil CO₂ efflux and use of non-structural carbon by roots**
2 **in forests of southern Amazonia**

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34 **Running Head:** Fire and Root Carbon Dynamics

35

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43

44 **Abstract**

45 Drought and fire events reduce the ability of tropical forests to cycle and store carbon due
46 to elevated tree mortality and reduced growth. However, the combined effects of drought
47 and fire on soil CO₂ efflux and subsurface carbon cycling remain poorly understood,
48 particularly in the Amazon. Here we evaluated how multiple burns and extreme drought
49 events affect soil CO₂ efflux and the use of non-structural carbon (NSC) in the roots of
50 forest species in southern Amazonia. We studied two different plots, one intact forest
51 (control) and another that was burned annually from 2004 until 2010 (burned). We
52 monitored: a) soil CO₂ efflux every three months between 2009 and 2012 (n = 25); b) the
53 amount of aboveground litterfall (n = 21); c) the production of fine roots (n = 16) every
54 three months for the same period; and d) estimated the age of NSC used in the production
55 of fine roots from radiocarbon (samples from 2009-2011; n = 15). Multiple fires in the
56 burn plot reduced soil CO₂ efflux by 18.7% compared to the control plot, and altered the
57 relationships between litter fluxes, soil temperature and soil CO₂ efflux. After the 2010
58 drought, soil CO₂ efflux in 2011 in the control plot was reduced by 17%. Relatively
59 freshly fixed C was used to produce new fine roots in 2009 (<2 years), but the age of C
60 used to grow new roots in 2010 and 2011 increased to 2-4 years old, especially in the
61 burned plot. Our results indicate that fire and drought events reduce soil CO₂ efflux and
62 vegetation productivity, and that the survival of some plants relies on the storage of NSC.

63

64 **Keywords:** Drought events, Burning, Perennial seasonal forest, Carbon allocation.

65

66 1. INTRODUCTION

67

68 Natural fires rarely occur in the Amazon (Hammond & ter Steege, 1998; Turcq et al.,
69 1998; Behling et al., 2001; Bush et al., 2004; Bush et al., 2007), but anthropogenic fires
70 can ignite large wildfires during episodic drought events (Nepstad et al., 1999; Moutinho
71 & Nepstad, 2001; Laurence & Vasconcelos, 2000). Under severe droughts, large areas of
72 Amazonian forests can dry out and drive increased fuel loads, resulting in increased forest
73 flammability. During the drought conditions in 1998, for example, an estimated one-third
74 of the Amazon region became flammable (Nepstad et al., 1999). The occurrence of
75 droughts in Amazonia may become more frequent in the future due to predicted climate
76 change (IPCC, 2007; Duffy et al., 2015). Fire thus is likely to become an even more
77 important component of the dynamics and trajectory of Amazonian forests in the future
78 (Brando et al., 2020).

79 Severe Amazon drought events impact the global carbon cycle. The extra area
80 burned in drought year fires drive increased CO₂ emissions (Alencar et al., 2006).
81 However, drought also can lead to net ecosystem C losses through increased tree mortality
82 and reduced C sinks from tree growth (Lewis et al. 2011). In 2005 and 2010, Lewis et al.
83 (2011) estimated these ‘committed’ fluxes as 1.6 PgC (0.8-2.6 95%CI) and 2.2 PgC (1.2
84 – 3.4, 95% CI), respectively. Previous studies have recorded similar effects of drought on
85 carbon stocks in Amazonian forests, for example, in 1992 and 1998 (Nepstad et al., 2004).

86 The transitional forests between Amazonia and the Cerrado are highly
87 vulnerable to compounding disturbances associated with fires and droughts. These
88 forests, located along the ‘Arc of Deforestation’ are highly fragmented (Marques et al.,
89 2020), and experience a prolonged dry season. They are among the fastest-warming
90 regions in the Amazon (Marengo et al., 2018), including an increase in seasonal drought

91 associated with a delay in the onset of the rainy season over the past ~40 years. They have
92 been an epicenter of fire activity in recent years, and some measurements of atmospheric
93 CO₂ suggest that these forests are becoming a net source of carbon to the atmosphere,
94 perhaps indicating a loss in resilience (Ivanauskas et al., 2004; Balch et al., 2008; Balch
95 et al., 2013). Severe droughts occurring with *El Niño* years in 2005, 2010 and 2016, make
96 them more vulnerable to fires that often start in cattle ranching and agricultural areas
97 (Brando et al., 2014; Alencar et al., 2004).

98 Studies of carbon impacts of forest fires and droughts in forests tend to focus on
99 changes in aboveground carbon that occur due to direct emissions from burning material
100 or committed emissions associated with tree mortality during and after drought events
101 (Lewis et al. 2011). Fewer studies have investigated belowground impacts, including the
102 legacy effects on above-and belowground productivity and the transfer of CO₂ from the
103 soil to the atmosphere (Brown & Lugo, 1982; Malhi, Aragon, Galbraith, et al., 2009;
104 Malhi, Aragon, Metcalfe, et al., 2009). Questions remain about whether drought
105 decreases or increases soil respiration in tropical forests (Lewis et al., 2011; Rocha et al.,
106 2013; Metcalfe et al., 2018). According to Vogt et al. (1996), a large portion of the carbon
107 stored in tropical forests is belowground, and root biomass accounts for half of the carbon
108 that is recycled annually by some forests. Although severe droughts and wildfires can
109 affect belowground processes (Rocha et al., 2013; Metcalfe et al., 2018), our
110 understanding of changes in root production, carbon allocation, and overall respiration
111 remains poorly quantified.

112 Fire has many effects on forest ecosystem dynamics. First, burning of surface
113 litter can reduce the input of organic matter into the soil, leading to reductions in not only
114 litter but also soil respiration (Nepstad et al., 1999b; Balch et al., 2008; Balch et al., 2013).
115 Second, fires kill trees and their roots, altering an important carbon input and source of

116 soil carbon efflux (Rocha et al., 2013; Doughty et al., 2015; Metcalf et al., 2018). Third,
117 fires alter species composition and competition for limiting resources, including light,
118 water, and nutrients, potentially increasing the growth of some species, and reducing
119 those of others, with unclear effects on soil carbon dynamics/soil respiration. Therefore,
120 the overall effect of forest fires on soil respiration and root production is complex
121 (Doughty et al., 2015) and requires further investigation.

122 Tropical trees in transitional forests have several adaptations to cope with dry
123 and hot conditions that allow the maintenance of high photosynthesis rates and carbon
124 storage during the long dry season. These include production of roots to access deeper
125 soil water, and in some species storage of nonstructural carbohydrate (NSC) reserves
126 (Hererra Ramírez et al. 2023). The role of NSC in seasonal and extreme drought is
127 complex and varies by plant organ and species (Ramierz et al. 2024). During periods of
128 C depletion caused by stomatal closure or leaf abscission associated with prolonged
129 drought, plants must utilize their reserves to maintain basic physiological processes
130 (Malhi et al., 2011; Doughty et al., 2015), such as respiration and growth. As carbon
131 limitation persists, plants will utilize older NSC reserves to maintain basic functions
132 (Richardson et al., 2015; Muhr et al., 2018; D'Andrea et al., 2019), including fueling new
133 root growth (Vargas et al., 2009). Thus, the age of the carbon used and respired by plants
134 can indicate the level of stress plants experience during droughts, as well as following
135 disturbances (Wurth et al., 2005; Sala et al., 2012).

136 In this study, we take advantage of a large-scale disturbance experiment in
137 southeastern Amazonia (Figure 1) to investigate the effects of drought stress and fire on
138 processes influencing soil CO₂ efflux and belowground carbon allocation in Cerrado-
139 Amazon transition forests. We evaluated soil temperature and moisture, soil and stem
140 respiration, fine root production, and the radiocarbon age of carbon used to grow new fine

141 roots in a large-scale disturbance experiment in southeastern Amazonia (Figure 1). The
142 experimental area consisted of three 50 ha experimental plots, one unburned [Control],
143 and two that were experimentally burned annually or triennially between 2004 and 2010
144 (Balch et al., 2008; Brando et al., 2012). The area was also affected by two drought events,
145 one in 2007 and another in 2010 (Brando et al., 2014). We were thus able to study the
146 effects of drought on belowground carbon cycling by comparing control plots in 2010
147 versus subsequent years, and fire effects (with and without drought) by comparing control
148 and fire plots. The effects of the combination of drought and fire on soil CO₂ efflux
149 processes and carbon allocation in the plants of the Cerrado-Amazon transition forests
150 can: 1) significantly reduce soil CO₂ efflux due to increased mortality and reduction of
151 the litter layer; 2) influence litter production by increasing seasonality, which may be
152 reinforced by a more intense drought period; 3) reduce the production of fine roots as a
153 result of fire and drought stress, reinforcing the importance of analyzing other variables
154 that explain interactions in the soil-plant-atmosphere system; and 4) allocate relatively
155 older non-structural carbon to build new structures, given that trees subjected to fire and
156 drought stress are expected to decrease photosynthesis.

157 Here, we aimed to evaluate the factors controlling soil carbon cycling in a
158 primary forest under natural and fire-affected conditions, as well as the effects of drought
159 and multiple burns capable of affecting processes such as soil CO₂ efflux and the use of
160 non-structural carbon (NSC) in root growth in southern Amazonia. We tested three
161 hypotheses: a) Drought alone will impact inputs by increasing aboveground litterfall in
162 the drought year, but reducing root productivity and new leaves that can fuel
163 decomposition in the subsequent year; b) Soil CO₂ efflux will be lower in the burned
164 forest than in the unburned forest area due to reductions in surface litter and fine root
165 production in areas that experienced high mortality from fire. This reduction in soil CO₂

166 efflux occurs despite increases in soil temperature, humidity, and overall necromass
167 production associated with tree mortality in the burned forest. b) Trees subjected to
168 combined drought and fire disturbance stresses allocate older nonstructural carbon
169 reserves to produce new roots.

170

171 2. METHODS

172 Soil CO₂ efflux combines several processes, including root respiration,
173 decomposition of surface litter, and decomposition of root litter and soil organic matter.
174 One of the goals of this study was to compare variations in the rates of CO₂ efflux with
175 the rates of inputs of fresh plant litter. Litter decomposition is typically rapid in tropical
176 forests given the high temperatures and moisture contents, as well as the need to recycle
177 nutrients (Montignini & Jordan, 2002). In this study, we measured seasonal and
178 interannual variations in fine root production and litterfall as inputs, as well as the overall
179 CO₂ efflux to study how fire and drought stresses influence these in a southeastern
180 Amazon forest.

181 2.1. Study site

182 The study area is located in Fazenda Tanguro (~85,000 ha), Mato Grosso state,
183 approximately 30 km north of the southern border of the Amazon Rainforest in Brazil
184 (130 04'35. 39 "S, 520 23'08. 85 W") (Figure 1). The area represents open ombrophilous
185 forests and is about 50 km from the Cerrado biome (IBGE, 1993). (IBGE, 1993). The
186 average annual precipitation is ~ 1770 mm (2005–2011), with a very intense dry season,
187 with monthly rainfall between May and August below 10 mm. The mean annual air
188 temperature is ~ 25°C, with an average daily and seasonal variation of 5°C above and
189 below the average. The soil type at the site is dystrophic Red-Yellow Latosol (Radam
190 Brasil, 1974; Brazilian soil classification), and soils are well-drained. Groundwater depth

191 is at ~15 m below the surface, and no soil layers prevented root penetration along the soil
192 profile. These soils of this region are among the least fertile in the Amazon (Table S1) and
193 are representative of much of the Eastern Amazon (Quesada et al., 2010; Quesada et al.,
194 2012). The study was conducted in a remnant fragment of transitional forest that was
195 maintained as a forest reserve protected by the owner, as mandated by Brazilian law. The
196 natural vegetation of the farm (44,000 ha) is classified as Perennial Seasonal Forest
197 (Ivanauskas et al., 2008). The average canopy height is ~20 meters, and the diversity of
198 plant species is relatively low when compared to the more humid forests typical of central
199 Amazonia (Balch et al., 2008), with only 97 species of trees and lianas per hectare larger
200 than 10 cm dbh [diameter at breast height 1.3 m above ground].

201

202

203 **2.2. Meteorological data**

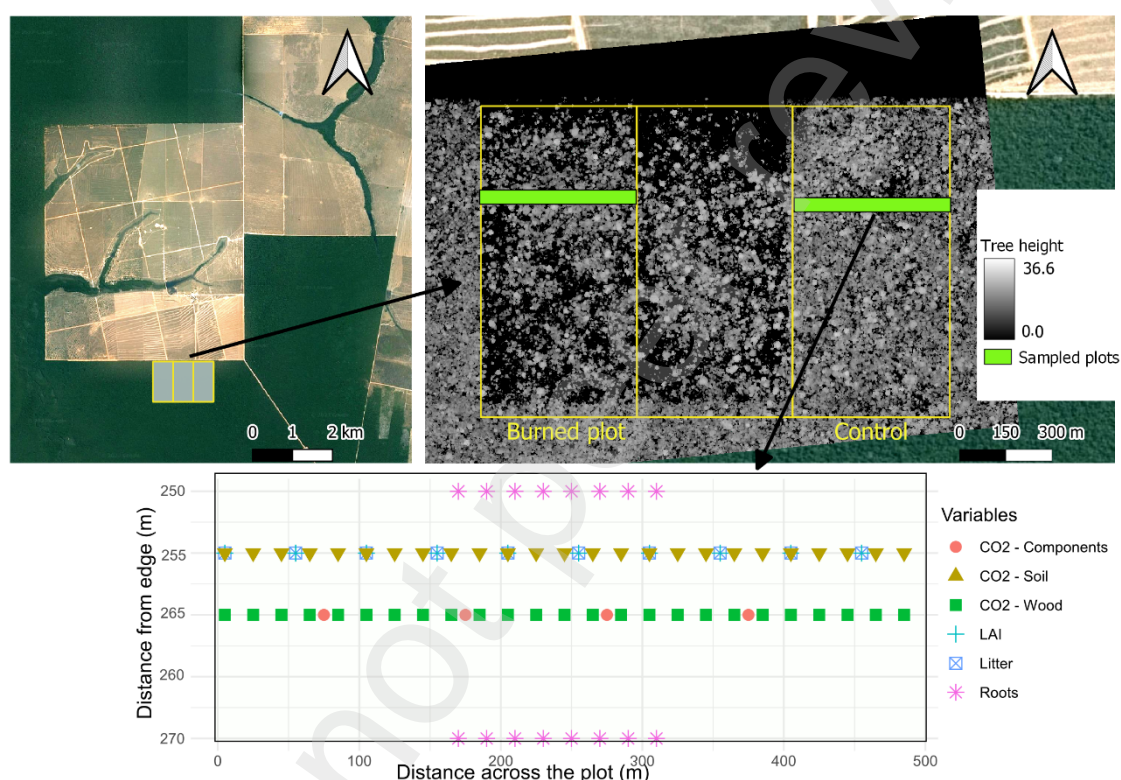
204 Solar radiation, air temperature, relative humidity, and rainfall time series data were
205 collected at an automatic weather station (AWS) located at 13.08 °S and 51.48 °W. The
206 original data were measured at an hourly time resolution from January 2009 to December
207 2012. We calculated maximum cumulative water deficit (MCWD), a well-established
208 drought index (Aragão et al., 2007), based on precipitation recorded at a weather station
209 located in an open area near the study plots.

210

211 **2.3. Soil CO₂ efflux, Temperature, and Humidity**

212 Total soil CO₂ efflux for each month was measured at 25 points (Figure 1) along
213 transects spanning the length of each plot, at a distance of 250 m from the edge. CO₂
214 efflux was measured by circulating air between headspace within a flow-through chamber
215 with an infrared gas analyzer or IRGA (EGM-4 IRGA and SRC-1, PP Systems, Hitchin,

216 UK). The chamber top was fit onto plastic (PVC) tubes that were permanently fixed in
 217 the soil so that each location was measured repeatedly. The tubes were 12 cm in diameter
 218 and 10 cm long, with a small portion inserted at a depth of 2 cm into the soil. At the time
 219 of each flux measurement, soil surface temperature (depth of 10 centimeters) was
 220 measured with a thermometer (T260 probe, Testo Ltd., Hampshire, UK), and moisture
 221 was measured using a *Hydrosense* probe (Campbell Scientific Ltd., Loughborough, UK).



222

223 **Figure 1.** Location of the study area on Tanguro Farm (left on the image). Colors indicate
 224 vegetation type and land use (forest = green; crop = gray/beige). On the right is the control
 225 plot (no fire), on the left is the burned plot (burned every year), and in the center is the
 226 plot burned every third year (not studied here). The light green stripes indicate transect F,
 227 where all collection points in plots A and C are located.

228

229 **2.4. Collection of surfaces litterfall**

230 For litter collection, we installed 25 trays (60 cm long \times 40 cm wide) at a height
231 1 m from the ground. Trays were installed every 20 m along the transect within each plot
232 (Figure 1), and collected every two weeks. The collected litter was divided into leaf and
233 non-leaf materials, stored in labeled paper bags, oven-dried at 65°C for 48h, and then
234 weighed.

235 **2.5. Root collections**

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

251 **2.6. Analysis of ^{14}C age of carbon used to grow new roots**

252 We used the method of tracking 'bomb' radiocarbon to estimate the age of
253 carbon used to grow new roots. This method relies on the fact that, following a sudden
254 increase caused by atmospheric nuclear weapons testing in 1964, the radiocarbon content

255 of atmospheric CO₂ has declined with time as this excess was taken up by biota and the
256 oceans and been diluted by ¹⁴C-free CO₂ emitted from fossil fuel burning. Photosynthesis
257 in any of the past 40 years will fix CO₂ with the ¹⁴C signature equal to that year's
258 atmospheric ¹⁴CO₂. C that is stored for several years in plants will reflect that it was fixed
259 in the past by having a higher ¹⁴C content – that reflects how many years elapsed since
260 its C was originally fixed from the atmosphere. For more details see Trumbore (2009);
261 Muhr et al. (2014), Hilman et al. (2021).

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

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

280 We estimated the mean age of carbon in fine root structural tissues by comparing
281 the measured $\Delta^{14}\text{C}$ with the $\Delta^{14}\text{C-CO}_2$ in the atmosphere as reported for the southern
282 Hemisphere Zones 1 and 2 (Hua et al. 2022), or the time elapsed since the C used to
283 produce root tissues was fixed from the atmosphere. This mean age represents the time
284 elapsed since the atmosphere last had the $\Delta^{14}\text{C}$ value measured in the sample (Hilman et
285 al. 2021). Samples of annual plants sampled over several years at the Tanguro ranch
286 correspond to the southern hemisphere curve of Hua et al. (2022) and indicate there are
287 no local factors influencing the atmospheric $\Delta^{14}\text{C-CO}_2$ at this site.

288 **2.7. Statistical Analysis**

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

295

296 **3. RESULTS**

297

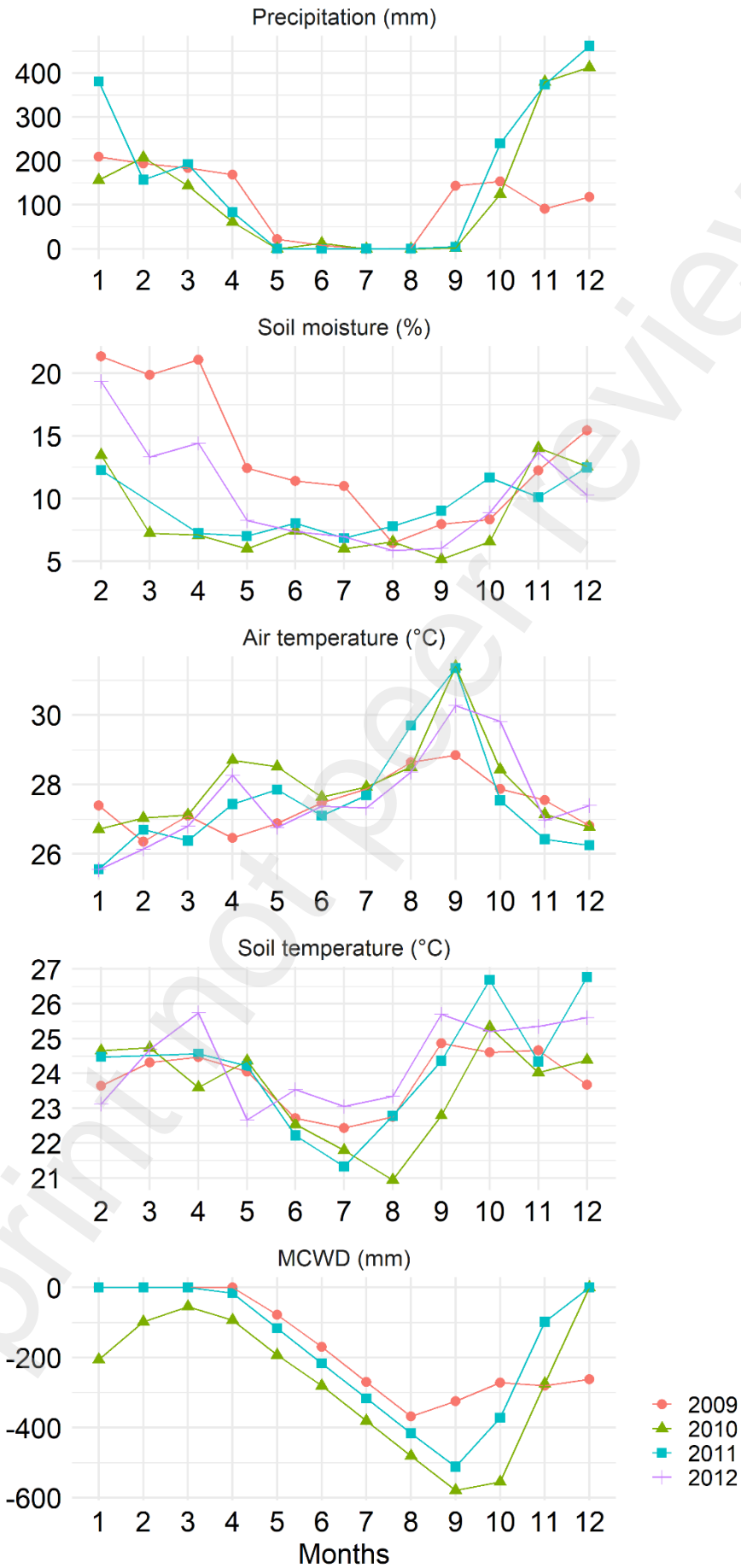
298 **3.1. Differences between treatments**

299 Soil moisture (<20 cm depth) had large seasonal variation but minor differences
300 between control and burned plots (Figure 2, Table 1). The highest soil moisture was
301 observed in the second half of the rainy season (February–March) and the lowest soil
302 moisture was observed at the end of the dry season (September) in both plots. The
303 minimum soil moisture occurred at the end of the dry period of 2010 in both plots (5.16%
304 (v/v) and 5.32% in the control and burned plots, respectively). In contrast, the highest soil

305 moisture content occurred in the burned (22.48%) and control (21.36%) plots during the
306 2012 and 2009 rainy periods. Water deficits expressed as monthly maximum cumulative
307 water deficit (MCWD) increased over the dry season months (Figure 2). Greatest MCWD
308 values occur in 2010, the drought year.

309 Mean soil temperature (depth of 10 centimeters) varied according to seasonality
310 and plot (Figure 2). Highest soil temperatures occurred in the dry season (September-
311 December) in the fire-disturbed plots, and lowest temperatures between May and July
312 (Figure 2, Table 1). There was considerable interannual variation in soil temperature
313 (Figure 2, Table 1). For example, in 2009, the highest soil temperatures were observed in
314 March (25.6°C) and September (24.8°C). However, in 2010, the highest temperatures
315 were recorded in December (27.4°C) and October (25.3°C). The highest temperatures in
316 2011 were recorded in the dry season in August and December (27.9°C and 26.7°C). In
317 2012, the highest temperatures recorded were (28.3°C) in September and (25.7°C) in
318 April (Figures 2 and 3, Table 1).

319



321

322 **Figure 2.** Seasonal climate data averages for monthly precipitation (2009–2011), soil
323 moisture (2009–2012), air temperature, soil temperature (depth of 10 centimeters), and
324 climatological maximum soil water deficit of the MCWD between 2009 and 2011 from
325 top to bottom on the graph. All variables were recorded at a weather station located in an
326 open area near the study plots, except for soil moisture, which was recorded using sensors
327 installed in each plot.

328

329 **3.2. Soil CO₂ efflux**

330 Soil CO₂ efflux varied among treatments, seasons, and years (2009–2012)
331 (Figure 3, Table 1). Across all years of observation, average soil CO₂ efflux was 18.7%
332 lower in the burned plot than in the control plot. Despite this difference, both treatments
333 had similar seasonal patterns, with lower soil CO₂ efflux rates during the dry season and
334 higher rates during the wet season (Figure 3). On average, soil CO₂ efflux was ~15%
335 higher in both plots during the rainy season than in the dry season.

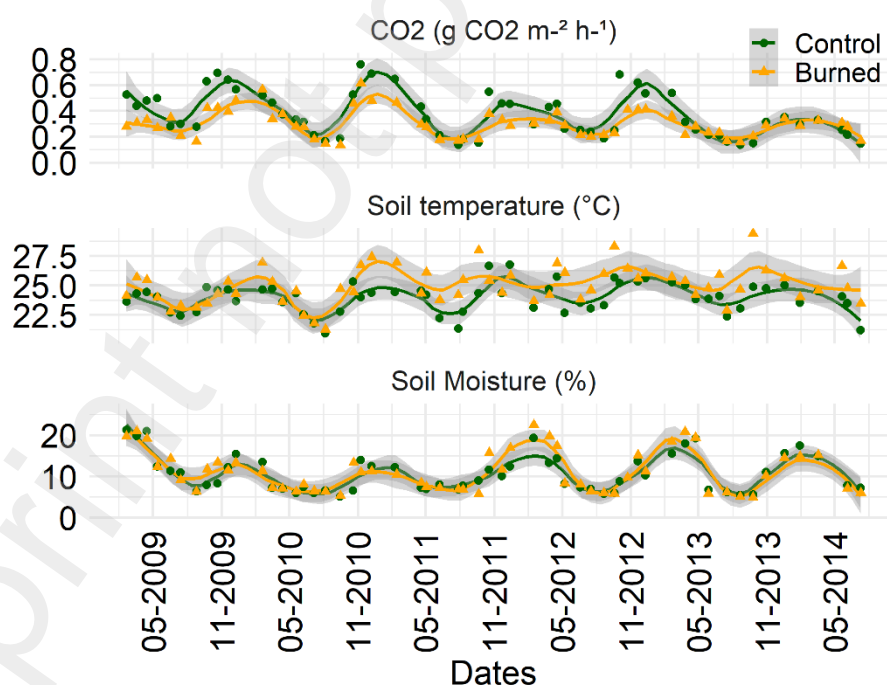
336 In addition to the variability in soil CO₂ efflux between the two plots and
337 seasons, we observed high interannual variability in CO₂ efflux (Table 1). In particular,
338 the driest sampling years (2010 and 2011) had lower CO₂ efflux rates in both plots. For
339 example, in 2011, CO₂ efflux (0.13 $\mu\text{mol CO}_2 \text{ m}^2 \text{ s}^{-1}$) was the lowest recorded, while in
340 2010, the lowest recorded was (0.16 $\mu\text{mol CO}_2 \text{ m}^2 \text{ s}^{-1}$). In 2012, the lowest soil CO₂ efflux
341 rate (0.18 $\mu\text{mol CO}_2 \text{ m}^2 \text{ s}^{-1}$) was recorded during the dry season in August of that year
342 (Figure 3, Table 1).

343

344 **Table 1.** Variation in soil CO₂ fluxes ($\mu\text{mol CO}_2 \text{ m}^2 \text{ s}^{-1}$) from the soil, with minimum,
 345 mean, and maximum values for each year in the control and burned plots during the
 346 sampling period.

Soil CO ₂ efflux rates ($\mu\text{mol CO}_2 \text{ m}^2 \text{ s}^{-1}$)						
	Control			Burned		
	Minimum	Average	Maximum	Minimum	Average	Maximum
2009	0.27	0.48	0.69	0.16	0.32	0.47
2010	0.16	0.41	0.76	0.13	0.34	0.61
2011	0.13	0.35	0.65	0.17	0.27	0.46
2012	0.18	0.38	0.68	0.20	0.30	0.41

347



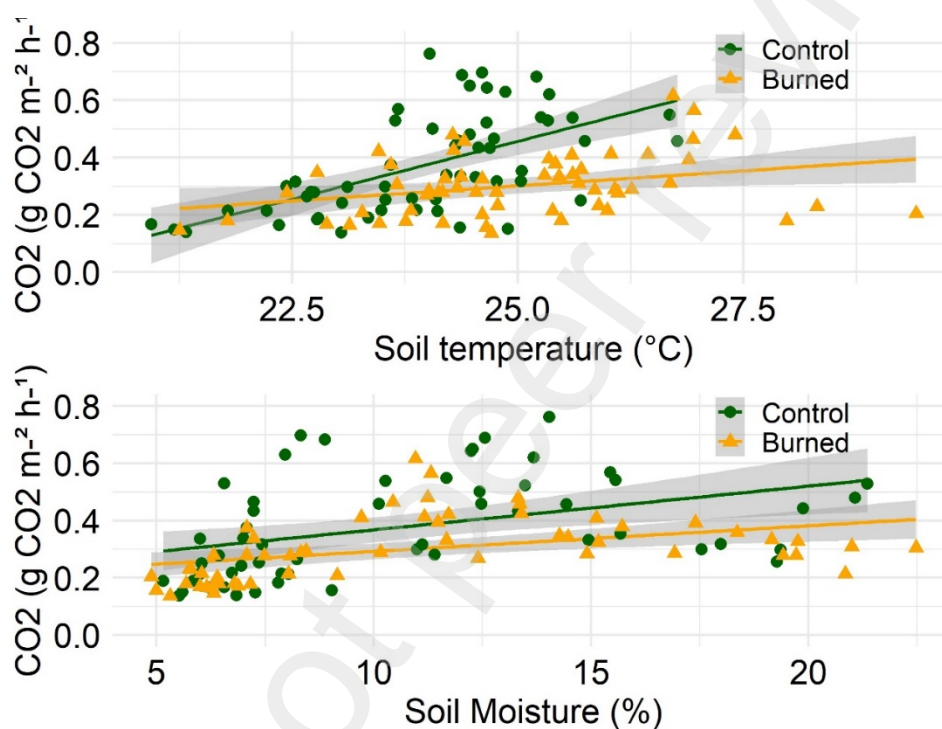
348

349 **Figure 3.** Mean \pm standard error of the seasonal variation in the control and burned plots
 350 of soil carbon dioxide, temperature, and soil moisture measured at the time of collection
 351 between 2009 and 2012 from top to bottom.

352

353 Soil CO₂ efflux was strongly influenced by soil moisture ($P < 0.001$, $R^2 = 0.26$;
 354 Figure 4) and temperature ($P < 0.001$, $R^2 = 0.32$). The relationship between CO₂ fluxes
 355 and temperature was stronger for control than burned plots (Figure 4a), while both
 356 treatments responded similarly to soil moisture variation (Figure 4b).

357



358

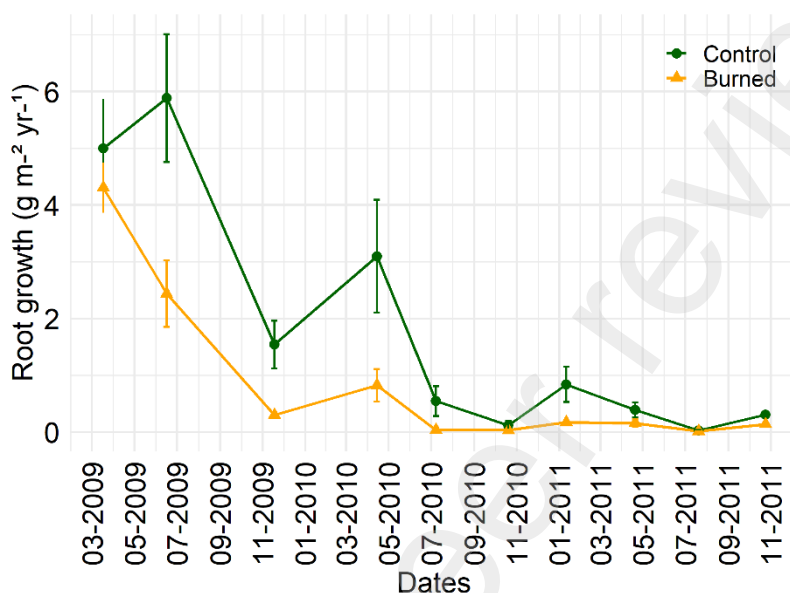
359 **Figure 4.** Relationships between soil CO₂ efflux and temperature (a), and moisture (b) in
 360 both treatment plots.

361

362 3.3. Fine Root Production

363 The mass of new root biomass in ingrowth cores showed a strong reduction over
 364 time but was higher in the control compared to burned plots (Figure 5). For example, in
 365 2009, the control plot had much higher average fine root production compared to the
 366 burned plot (4.14 g m⁻² year⁻¹ versus 2.34 g m⁻² year⁻¹). In 2010, root production declined
 367 in both plots, but the average root production in the control plot was still much higher

368 (1.25 g m⁻² year⁻¹) than in the burned plot (0.29 g m⁻² year⁻¹). Both plots strongly
 369 decreased in average root production over time, and the decline was more pronounced in
 370 the burned plots. For example, in the first year of the study, root production was 2.34 g
 371 m⁻² year⁻¹, but in the last year, it was 0.10 g m⁻² year⁻¹ (Figure 5).



372

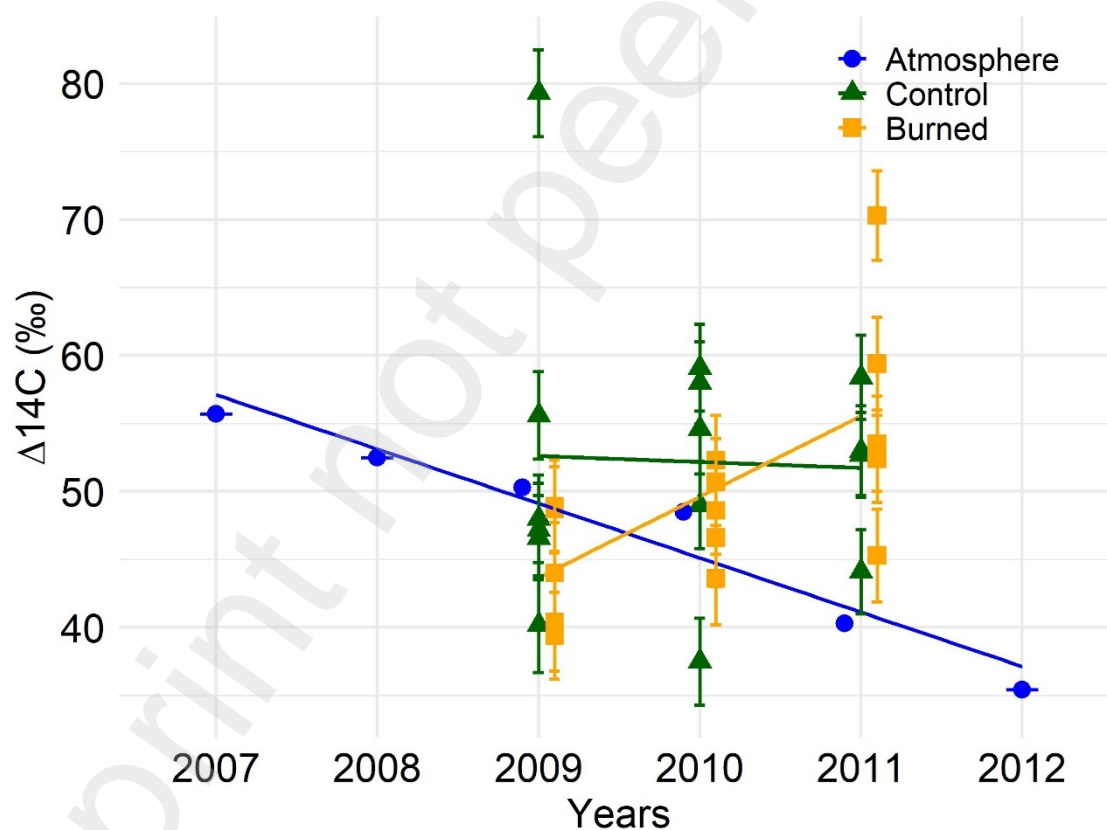
373 **Figure 5.** Means plus standard error of root growth in ingrowth cores up to 30 cm depth
 374 in the burned plot (yellow) and control plot (green) throughout the collection period.

375

376 3.4. Age of fine root carbon

377 Radiocarbon contents of fine (<2mm) roots picked from the ingrowth cores
 378 between 2009 and 2011 showed considerable variation. During the same period,
 379 atmospheric $\Delta^{14}\text{C}$ was declining at a rate averaging ~ 4.2 ‰ per year (based on Hua et
 380 al. 2022), in agreement with annual plant measurements. In 2009, most ingrown root
 381 samples from both control and burned plots (80%) had $\Delta^{14}\text{C}$ values close to those
 382 measured in annual plants and atmospheric CO_2 samples collected during the same year
 383 ($\Delta^{14}\text{C}$ of 50.9‰ versus 50.3‰ of the atmosphere $\Delta^{14}\text{C}$), indicating that the carbon
 384 allocated to root construction was fixed from the atmosphere in the same year. Notably,

385 one of the individual roots sampled from the control plot in 2009 had a high $\Delta^{14}\text{C}$ value
 386 (79.3‰, equivalent to 5-year-old carbon used to grow the new root [Figure 6]). In 2011,
 387 differences between $\Delta^{14}\text{C}$ of individual root samples and the $\Delta^{14}\text{C}$ of the atmospheric CO_2
 388 were larger. For example, the $\Delta^{14}\text{C}$ of the control plot samples averaged 52.1‰, that of
 389 the burned plot averaged 56.2‰, and the $\Delta^{14}\text{C}$ of the atmosphere that year averaged
 390 40.3‰. Especially in the burn plot, new roots in 2011 were grown from carbon fixed from
 391 the atmosphere on average ~ 4 -years previously, with the estimated time since fixation
 392 tending to increase from 2009-2011. As the source of this older C must be stored reserves
 393 in the living root system, the increase in the age of C used for growing roots in the burn
 394 plot could indicate greater reliance on storage reserves.



395

396 **Figure 6.** Differences in the carbon allocation period $\Delta^{14}\text{C}$ (‰) for the root analyses of
 397 the burned and control plots (2009–2011). The control plot is green, burned is yellow,
 398 while blue points represent annual plants collected in each year as a measure of growing

399 season atmospheric $\Delta^{14}\text{CO}_2$. Vertical error bars indicate analytical error for each sample
 400 ($\pm 2\text{-}4\%$).

401

402 3.5. Litter production

403 Litter production between 2009 and 2012 was higher in the control than the
 404 burned plots (Table 4). In both plots, with highest litterfall occurred during the dry season
 405 (May - September) and lowest fluxes during the wet season (October - April) (Table 4).
 406 For example, in the control plot, the highest average monthly production (12 Mg biomass
 407 $\text{ha}^{-1} \text{ year}^{-1}$) occurred during the dry period of 2009. The lowest average (2.58 Mg biomass
 408 $\text{ha}^{-1} \text{ year}^{-1}$) was recorded during the 2012 rainy season. However, in the burned plot, the
 409 highest monthly average litter production occurred during the dry period of 2009 (11.52
 410 Mg biomass $\text{ha}^{-1} \text{ year}^{-1}$). The lowest average (1.61 Mg biomass $\text{ha}^{-1} \text{ year}^{-1}$) was recorded
 411 in March 2012 (Table 4), which was the rainy season.

412

413 **Table 4.** Leaf litter production (Mg biomass $\text{ha}^{-1} \text{ month}^{-1}$) with minimum, mean, and
 414 maximum values during the study years between the control and burned plots.

Litter production (Mg biomass $\text{ha}^{-1} \text{ m}^{-1}$)						
	Control			Burned		
	Minimum	Average	Maximum	Minimum	Average	Maximum
2009	3.22	6.16	12	2.36	5.51	11.50
2010	2.64	6.22	10	2.47	5.39	9.50
2011	2.63	5.07	9.3	1.73	4.67	8.03
2012	2.58	6.12	11.45	1.61	4.00	6.89

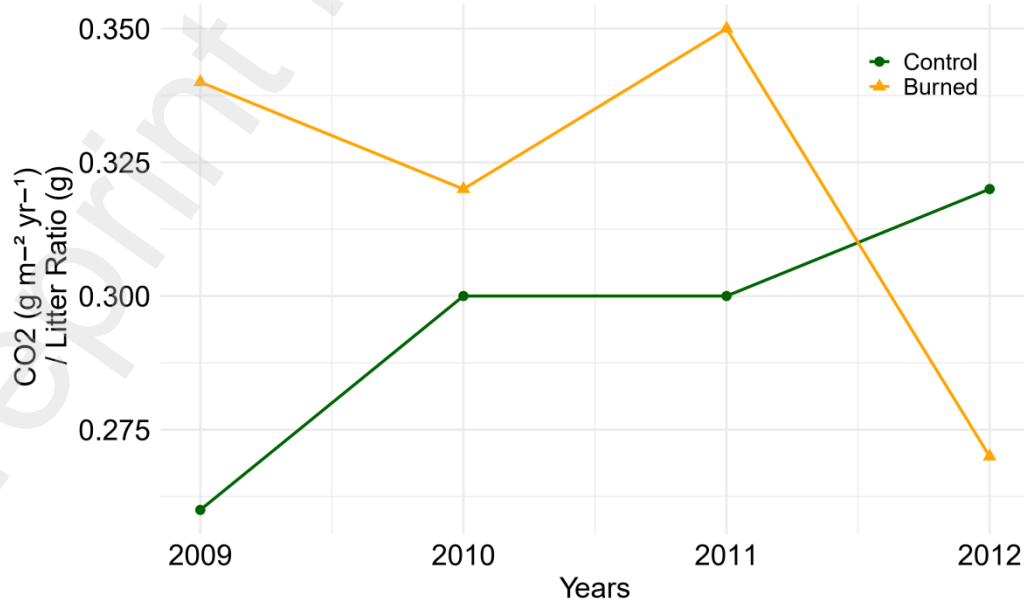
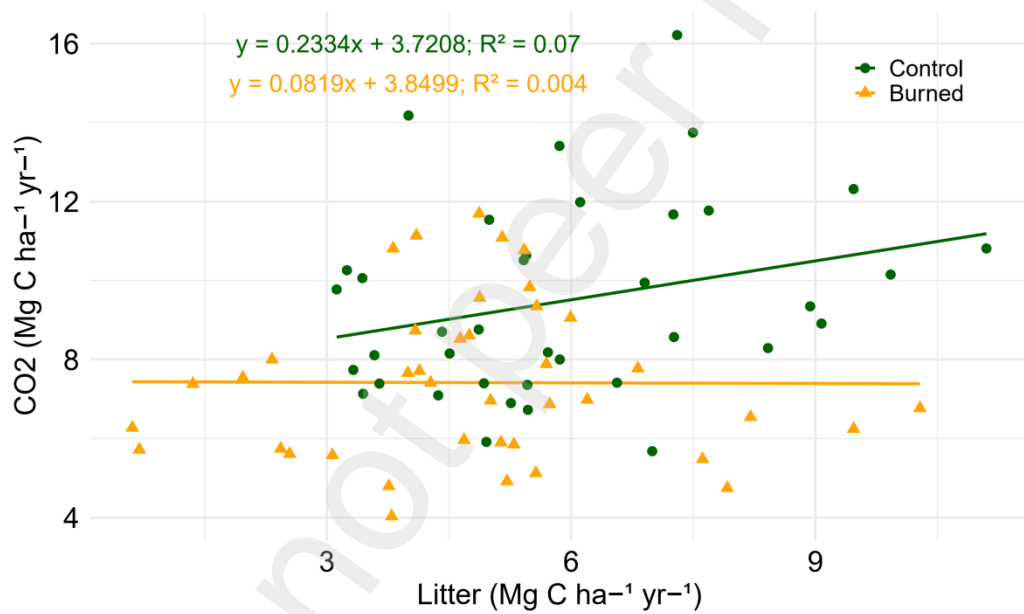
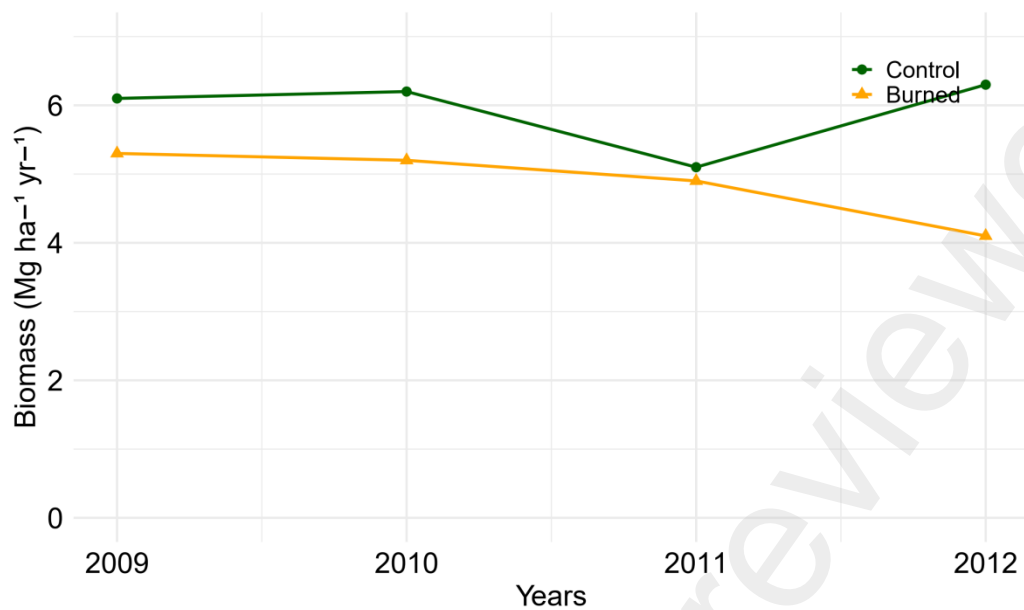
415

416 We observed large interannual variability in litter production, with lower values
417 in the years following the 2010 drought event. For example, during the years 2009, 2010
418 and 2011, the control plot litter production was 6.16 (2009), 6.22 (2010) and 5.07 (2011)
419 Mg biomass ha⁻¹ year⁻¹, and burned plot litter production declined from 5.51 (2009) to
420 5.39 (2010) and 4.67 (2011) Mg biomass ha⁻¹ year⁻¹. In 2012, production increased again
421 in the control plot (6.12 Mg biomass ha⁻¹ year⁻¹), but continued to decrease in the burned
422 plot (4.00 Mg biomass ha⁻¹ year⁻¹) (Table 4, Figure 7).

423

424 **3.6. Relationship between litter and soil CO₂ efflux**

425 The relationship between soil CO₂ efflux and litter production was weak (Figure
426 7), although litter decomposition annually accounted for roughly a third of the CO₂
427 effluxes measured in the soils of both plots (Figure 10). For example, the ratio of soil CO₂
428 efflux to litter production between the plots was 0.29 in the control plot and 0.32 in the
429 burned plot (Figure 7).



431 **Figure 7.** From top to bottom in the graph, annual averages of litter production in Mg
432 biomass ha⁻¹ year⁻¹; relationship between soil CO₂ efflux and litter production;
433 relationship between soil CO₂ efflux; annual relationship between soil CO₂ efflux (Mg
434 CO₂ m² s⁻¹) and litter production (Mg biomass ha⁻¹ year⁻¹) between burned and control
435 plots (2009–2012).

436

437 **4. DISCUSSION**

438 This study examined the effects of fire and drought on soil moisture, root
439 productivity, and soil CO₂ efflux in an Amazonian transitional forest, as well as the age
440 of carbon utilized to grow new roots. Analyzing a control forest plot that suffered from
441 severe drought, in contrast to a forest that was frequently subjected to fires, helped us
442 understand the effect of combined fire and drought disturbance, demonstrating that
443 repeated fires and drought reduced litter and fine root production, altered the allocation
444 of carbon to root growth and significantly reduced soil CO₂ efflux. Declines in soil CO₂
445 efflux are mainly related to increased tree mortality from compounding of fire and
446 drought stresses (Brando et al. 2014), leading to diminished inputs of fast-decomposing
447 fine litter in the burned plots. Although litter inputs were lower, surface litter production
448 made up a greater proportion of soil CO₂ efflux in the burn plots in most years. Soil
449 temperatures were higher in burn plots although no large effect on soil moisture was
450 observed. However, CO₂ efflux in the burned plots was less sensitive to soil temperature
451 than in control plots.

452 The reduction in soil CO₂ efflux in the annually burned area is a partially
453 unexpected result. Fire events increase tree mortality (Balch et al., 2008; Brando et al.,
454 2012; Silverio et al., 2019) and the amount of dead wood decomposition, which would
455 contribute to soil CO₂ efflux (Rocha et al., 2013; Metcalf et al., 2018). However, the

456 opposite was observed: a reduction in CO₂ efflux from the soil in the burned plot
457 compared with the control. Three processes are likely to have influenced this reduction:
458 1) Root productivity was lower in burned plots than in control plots (Figure 5). Owing to
459 the high tree mortality after the passage of the 2007 experimental fires (Brando et al.,
460 2014), the number of living remnant trees growing in the annually burned plot was
461 drastically reduced - thus, both root productivity and root respiration declined. 2) Leaf
462 litter production also declined, coinciding with a reduction in leaf area index in the burned
463 plots compared to control plots during this period (Brando et al. 2019). 3) While indeed
464 more dead wood may be present, this was not necessarily well sampled by our soil CO₂
465 efflux chambers; further higher air temperatures in burn plots could be associated with
466 overall drier wood and reductions in decomposition rate.

467

468 **4.1. Fire and drought induce changes in the soil components of transitional forests**

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

475 Considering the period of observations in this study, 2010 stood out with lower
476 productivity in both the control and burned plots compared to the other years studied.
477 Fine root production was reduced in the burned plot, probably because of the reduced
478 number of trees growing in the burned plot compared with the control plot (Balch et al.,
479 2008; Balch et al., 2011; Brando et al., 2012; Balch et al., 2013; Rocha et al., 2013;
480 Metcalf et al., 2018). However, a gradual reduction in root production was also observed

481 in control plots over time. This pattern of reduction in root production in both plots was
482 unexpected because there were no major changes in the dynamics and structure of the
483 control plot, nor were surface litter fluxes declining. Although the ingrowth core is a well-
484 established method to quantify fine root growth, several studies suggest that the
485 disturbance associated with core installation, as well as alterations in soil characteristics
486 when the root-free soil is repeatedly placed back into the cores after new roots are
487 removed is a limitation (Hendricks et al., 2006). Particularly given the very nutrient-poor
488 soils at Tanguro, the lack of new nutrients from root turnover could lead to fewer new
489 roots exploring the ingrowth core and explain the reductions in root production observed
490 in both control and burned plots over time in our study.

491

492 **4.2. Changes in soil CO₂ efflux processes**

493 In the present study, fire, in conjunction with drought episodes, caused a
494 decrease in soil CO₂ efflux rates as well as a reduction in the seasonal variation of CO₂
495 efflux (Figure 3). The extrapolated annual CO₂ efflux ($7.24 \pm 1.9 \text{ MgC ha}^{-1} \text{ year}^{-1}$) for the
496 control site are higher than other published estimates for the Amazon region (Doff Sotta
497 et al., 2004) ($6.45 \pm 1.2 \text{ MgC ha}^{-1} \text{ year}^{-1}$), and southern Amazonia ($6.6 \pm 2.0 \text{ MgC ha}^{-1}$
498 year^{-1}) (Metcalf et al., 2018), with 95% confidence interval. In a forest with more
499 pronounced dry season in Acre, Brazil, Salimon et al. (2004) found similarly higher
500 annual soil C efflux in a study carried out in a secondary forest, a primary forest, and a
501 pasture area, with the highest CO₂ efflux observed in the forest during the rainy season.
502 These results suggest that forests with a more pronounced dry season tend to have higher
503 CO₂ flux compared to more continuously wet systems.

504 The relationships between temperature, moisture and soil CO₂ efflux differed for
505 burned and control forests. In general, in the control forest, higher soil temperatures meant

506 higher soil CO₂ efflux (Figure 4). In contrast, the correlation between soil CO₂ efflux and
507 temperature in the burned plot was not strong, despite experiencing overall higher soil
508 temperatures (Figure 4). Similarly, soil CO₂ efflux increased with litterfall in the control
509 forests, but the relationship was not so marked in the burn plots, despite a larger
510 percentage of the overall flux coming from litter (Figure 7).

511

512 **4. 3. Fire and drought alter belowground C allocation**

513 In this study, we found that fire and drought, in addition to causing a decrease in
514 soil CO₂ efflux rates, likely caused an increase in the age of the carbon allocated to grow
515 new roots (Figure 7), with mostly fresh photosynthetic products used to grow new roots
516 in 2009, but with 2–4-year-old C reserves used in 2010 and 2011, particularly in burned
517 plots. Our results are in accord with other studies (e.g., Vargas et al. 2015, Richardson et
518 al. 2014), and indicate that trees under fire and drought stress rely more on older stored
519 nonstructural carbon to grow new roots. This can indicate overall greater vulnerability of
520 the remnant trees in the burned plots, compared to the control plots that have greater
521 allocation of fresh photosynthetic products belowground. Together, our results suggest
522 that fire and drought significantly reduce carbon cycling and create stressful conditions
523 that can affect mortality in remaining trees not already killed by fire. With ongoing
524 climate change, extreme drought and increased forest flammability can lead to
525 degradation of forests and reduced carbon stocks through higher mortality, accompanied
526 by reduction in CO₂ efflux in the immediate years after disturbance.

527

528

529 **5. CONCLUSION**

530 Consecutive fire and extreme drought events in the seasonal forests of southern
531 Amazonia significantly reduced both above- and below-ground litter production and soil
532 CO₂ efflux. Reductions in litter production were associated with higher tree mortality due
533 to fire, while reductions in soil humidity during drought periods also reduced biological
534 activity.

535 Using root ingrowth cores, we saw a pronounced reduction in the production of
536 fine roots in the burned plot, as well as a more gradual reduction in root production in the
537 control plot. Given that these were not accompanied by similar declines either in
538 aboveground litterfall or soil CO₂ efflux, we conclude that it is important to use other
539 measures of productivity in addition to ingrowth cores, or to replace the soil used in the
540 cores with each deployment in multi-year studies.

541 Trees subjected to fire and drought stress allocated relatively older nonstructural
542 carbon to build new structures. Photosynthetic production is by fire and drought through
543 reduced leaf area and increased stomatal closure, and reduced availability of fresh
544 assimilation products can force trees to increase the use of reserves previously allocated
545 to storage in the burned and control plots for growth of new fine roots.

546

547

548

549 **AUTHOR CONTRIBUTIONS**

550 PMB and ST who conceived the project; WRS did the data collection and adjustments;
551 DVS, LMS and WRS did the formal analysis and visualization of the data collected with
552 the guidance of PMB; DVS and LMS helped with the visualization and validation of the
553 data; LGM, PMB, ST helped with the visualization and validation of the data; WRS and
554 PMB wrote the draft with revisions and edits by all the authors.

555

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569

570

571 DATA AVAILABILITY STATEMENT

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

574

575 DECLARATION OF COMPETING INTEREST

576

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

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