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Panama Rainforest Changes with Experimental Drought (PaRChED): Initial Effects of Partial Throughfall Exclusion on Soil Dynamics in Lowland Forests across Variation in Rainfall and Soil Fertility

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Panama Rainforest Changes with Experimental Drought (PaRChED)

Initial Effects of Partial Throughfall Exclusion on Soil Dynamics in Lowland Forests

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ABSTRACT. Changes in rainfall are predicted across tropical regions, with effects on nutrient, water, and carbon cycling. This chapter summarizes results from the first two years of a throughfall exclusion experiment in four lowland Panamanian forests that span a 1,000-mm change in rainfall and variation in soil fertility. Soil respiration (i.e., soil carbon dioxide [CO_2] flux) declined with throughfall exclusion, with a site*season interaction, and the radiocarbon age of respired carbon was older in exclusion versus control plots. The decline in soil CO_2 flux could be related to reduced fine root production and soil microbial biomass. Microbial community composition also changed with throughfall exclusion in infertile soils, and soil nutrients accumulated more in exclusion versus control plots during the dry season. The net effects on soil carbon storage will depend on the relative strengths of these effects over time. Continued research could improve predictions of tropical forest-climate feedbacks with changes in precipitation.

Keywords: drought; drying; rainforest; soil carbon storage; phosphorus; microbial community; root productivity; radiocarbon; nitrogen

INTRODUCTION

Tropical forests contain 25–40% of global terrestrial carbon stocks (Field et al., 1998; Jobbagy and Jackson, 2000). The tropics are projected to undergo large changes in precipitation with climate change, with large uncertainties and with both drying and increased rainfall severity and runoff predicted and observed for different regions (Arias et al., 2021). Understanding how changes in moisture will alter belowground soil carbon storage and related processes is crucial for predicting tropical forest-climate feedbacks.

This project focuses on assessing potential drying effects on tropical forest ecosystem processes. Climatic drying is predicted for many tropical forests (Feng et al., 2013; Duffy et al., 2015; Chadwick et al., 2016; Barkhordarian et al., 2019; Worden et al., 2021), and drying trends have already been documented in some tropical regions (Aleixo et al., 2019; Powers et al., 2020). Drying trends include longer and more intense dry seasons and chronic reductions in mean annual precipitation (MAP; Kharin et al., 2007; Joetzjer et al., 2013; Magrin et al., 2014; Boisier et al., 2015). Episodic drought can extend the dry season and has been associated with chronic reductions in rainfall through part or all of the wet season in Panama (e.g., El Niño events; Ropelewski and Halpert, 1987).

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Large throughfall exclusion experiments have indicated that drying is likely to alter nutrient and water cycling and carbon storage in seasonal forests in Brazil (Nepstad et al., 2002; Nepstad et al., 2007; da Costa et al., 2010). Because moisture regimes vary greatly across humid tropical forests, which can have natural dry seasons of zero to five months (FAO, 2012), and MAP from 2,000 to >8,000 mm/y (Holdridge et al., 1971), it is crucial to assess how drying scenarios will affect tropical forests across natural rainfall gradients.

We hypothesized that soil carbon dynamics and related ecosystem processes would be more resistant to drying in lower rainfall tropical sites with infertile soils, where plant and microbial communities are presumably better adapted to moisture stress. To assess this hypothesis, we used a partial throughfall exclusion experiment established in 2018 in four Panamanian forests that span natural variation in rainfall and soil fertility, excluding about 50% of throughfall from plots paired with controls. We measured soil carbon inputs, storage, and carbon loss, including measures of soil carbon stocks, litterfall and fine root productivity (carbon inputs to soil), soil respiration (carbon losses from soil), microbial community characteristics and activity, and soil nutrient availability. Here we describe the experimental design and preliminary results from the first two years of the experiment.

FIGURE 1. An example of one of the partial throughfall exclusion structures in the Panama Rainforest Changes with Experimental Drying (PaRChED), established in 2018 and diverting about 50% of throughfall away from 10 × 10 m plots (n = 4 structures at each of 4 sites; 32 plots total including controls).

STUDY SITES AND EXPERIMENTAL DESIGN

The Panama Rainforest Changes with Experimental Drying (PaRChED) manipulation was established in 2018 in four distinct forests in the lowlands of central Panama, including three sites within the Barro Colorado Nature Monument (BCNM) and one in the Bosque Protector San Lorenzo. The mean annual temperature at all sites is 26°C, and the mean monthly temperature varies by <1°C during the year (Windsor et al., 1990). Seasonality is driven by changes in rainfall, with a dry season from approximately late December through late April and a wet season the rest of the year.

The four forests span half of the larger rainfall gradient across the Isthmus of Panama and include the following: Gigante at 2,350 mm MAP on strongly weathered, infertile soil (GIG), two paired forests with 2,600 mm MAP on the Buena Vista Peninsula, one with strongly weathered infertile soil (P12), and one with less weathered fertile soil (P13), and San Lorenzo at 3,421 mm MAP on strongly weathered infertile soil. Site characteristics, including local meteorological data, root biomass, and soil properties, have been described previously, and these sites do not vary significantly in aboveground biomass (Cusack et al., 2018b). The sites have been shown to have seasonal trends in soil properties, including decreased soil moisture and decreased soil respiration during the dry season (Cusack et al., 2019).

In each of the four forests, we established four pairs of 10 m × 10 m plots in 2018. We constructed a 50% throughfall exclusion structure with aluminum support tubes and polyvinyl chloride PVC cross-tubes, with 50% of the surface area above the plots covered in transparent laminates (Fig. 1). The roof structures sloped down from the center of the plot and covered a ground area of 12 m × 12 m over each exclusion plot, with the structure extending 1 m beyond the plot edge. Plot edges were trenched to 50 cm, lined with heavy plastic, and backfilled. The other plot in each pair was left as a control. Plot pairings were based on a combination of spatial proximity and similarity of topography and tree cover. Plots were located on relatively flat ground, separated from each other by at least 10 m, and placed in locations where large trees (>30 cm diameter at breast height [dbh]) were absent to avoid having a plot dominated by one plant's root system. Roofing was cleaned every three weeks with a telescoping broom to return litterfall into plots.

Sampling within plots included (with sampling frequency in parentheses) the following: soil moisture and temperature probes at 5 cm and 20 cm depths (every 30 minutes); litterfall traps (tri-weekly); minirhizotron root observation tubes (tri-weekly); soil respiration surface flux collars (tri-weekly); soil respiration exclusion columns to separate root versus microbial respiration (tri-weekly); soil total carbon and nitrogen, extractable carbon, mineral nitrogen, resin-extractable phosphate, bulk density, pH, standing root stock, and arbuscular mycorrhizal fungi colonization of roots (quarterly); root ingrowth biomass (quarterly); stem diameter increment for all trees >5cm dbh (annually); radiocarbon content of soil respiration (bi-annually during year 2). Further details on construction, design, and sampling protocols are given in (Dietterich et al., 2022). We next summarize the initial results of this experiment from June 2018 to March 2020.

RESULTS AND DISCUSSION

Overview of Results

Over the first two years of throughfall exclusion, soil carbon dynamics varied with background rainfall and soil fertility, and key soil carbon processes responded to throughfall exclusion. Soil respiration initially declined in response to throughfall exclusion, with an interaction between site and season (Cusack et al., 2023); Fig. 2). Along with decreased respiration fluxes, the radiocarbon age of respired soil carbon was significantly older in throughfall exclusion versus control plots (McFarlane et al., in revision). The decline in soil respiration was associated with reductions in fine root (<2-mm diameter) production (Fig. 3), which mirror dry-season reductions in fine root production in surface soils (Fig. 4; (Cordeiro et al., in prep). Reduced soil respiration was also associated with reductions in microbial biomass, particularly during the wet season (Dietterich et al., 2022). Microbial community composition changed with throughfall exclusion in sites with infertile soils, where there was a convergence of microbial community composition toward a "drought microbiome" (Chacon et al., 2023). This convergence could be related to the accumulation of soil nutrients, particularly nitrogen, during the dry season (Fig. 5). The following sections provide details on each of these key results.

Soil Carbon Losses: Respiration

Soil respiration is typically the dominant pathway for carbon loss from terrestrial ecosystems, and soil respiration from tropical forests is one of the largest natural sources of annual CO_2 flux to the atmosphere (Raich and Schlesinger, 1992). In PaRChED, soil respiration over the first two years of the experiment declined in response to throughfall exclusion, with an interaction between site and season (Fig. 2; Cusack et al., 2023). This result mirrored the background pattern of decreased soil respiration during the natural dry season across a broader set of 15 Panamanian forests, where the magnitude of the wet-season soil respiration increase was positively correlated with the difference between mean monthly rainfall in the wet and dry seasons as well as with site-scale available phosphorus and base cations (Cusack et al., 2019). Although all four PaRChED forests had significant reductions in soil respiration with throughfall exclusion for at least part of the year, the seasonal distribution and the extent of this decline varied among sites (Fig. 2). The strongest and most consistent declines occurred at our wettest San Lorenzo site.

We measured the radiocarbon signature of soil respiration in the field in the early (May) and late wet season (December) of the first full year (2019) of the experiment. The radiocarbon age of respired soil carbon was two to three years older in throughfall exclusion versus control plots, as indicated by more enriched $\Delta^{14}C$‰ (McFarlane et al., in revision). We partitioned soil respiration between roots and heterotrophs using root exclusion soil columns. It appears that the decline in soil respiration and the increased radiocarbon age of respired carbon were related to changes in the radiocarbon content of microbial respiration, not to root respiration. The radiocarbon signature measured in the throughfall exclusion plots indicates a shift toward older carbon. One explanation for this change could be reduced delivery of fresh carbon to soil microbes with throughfall exclusion through the slowed decomposition of leaf litter, reduced carbon inputs from roots, and reduced hydrological transport of fresh dissolved organic carbon from the forest floor into mineral soils.

Soil Carbon Inputs: Root Dynamics, Stem Increment, and Litterfall

Throughfall exclusion suppressed fine root production across sites for 0- to 10-cm depths in surface root ingrowth cores (Fig. 3) but not in minirhizotron image analyses to 1-m depth (Fig. 4). There was no significant throughfall exclusion treatment effect on tree stem increment, litterfall biomass, root biomass, or root production during the initial two years of the experiment. Also, there were clear seasonal and depth patterns in root production, as indicated in the repeated sampling of minirhizotron images to 1.2 m. Specifically, root production tended to increase with the onset of the rainy season in surface soils (0- to 30-cm depth) at the drier sites and during the dry season in surface soils and the deepest soils (60- to 100-cm depth) at our wettest site (San Lorenzo, 60- to 90-cm depth; Fig. 4).

Soil Carbon Stocks

PaRChED has not yet assessed changes in soil carbon stocks with throughfall exclusion. Other work has shown that soil carbon in the BCNM exhibits seasonal patterns, such that soil carbon increases during the wet season and declines during the dry season, particularly in mineral-associated soil fractions (Turner et al., 2015; Cusack et al., 2018a). On BCI, an irrigation experiment eliminated a similar seasonal pattern in soil carbon (Yavitt and Wright, 2002). The seasonal pattern was attributed to dry-season desorption of organic matter from clay surfaces in these sites, but the pattern was not observed across a broader set of 14 lowland forests in Panama (Dietterich et al., 2021), although there was a general accumulation of the free debris soil carbon fraction (i.e., low-density particulate organic matter) during the dry season across sites. These shifts in soil carbon stocks and fractions with seasonal drying, and with irrigation, provide clues to how soil carbon stocks might be changing with throughfall exclusion in PaRChED. Going forward, we hypothesize that chronic drying will negatively affect soil carbon stock sizes in clay-rich soils where mineral-associations dominate carbon storage. Drying in these soils appears to promote desorption of soil carbon and subsequent decomposition. Future work will test these hypotheses by looking at seasonal and experimental effects on total soil carbon and soil carbon fractions in these sites.

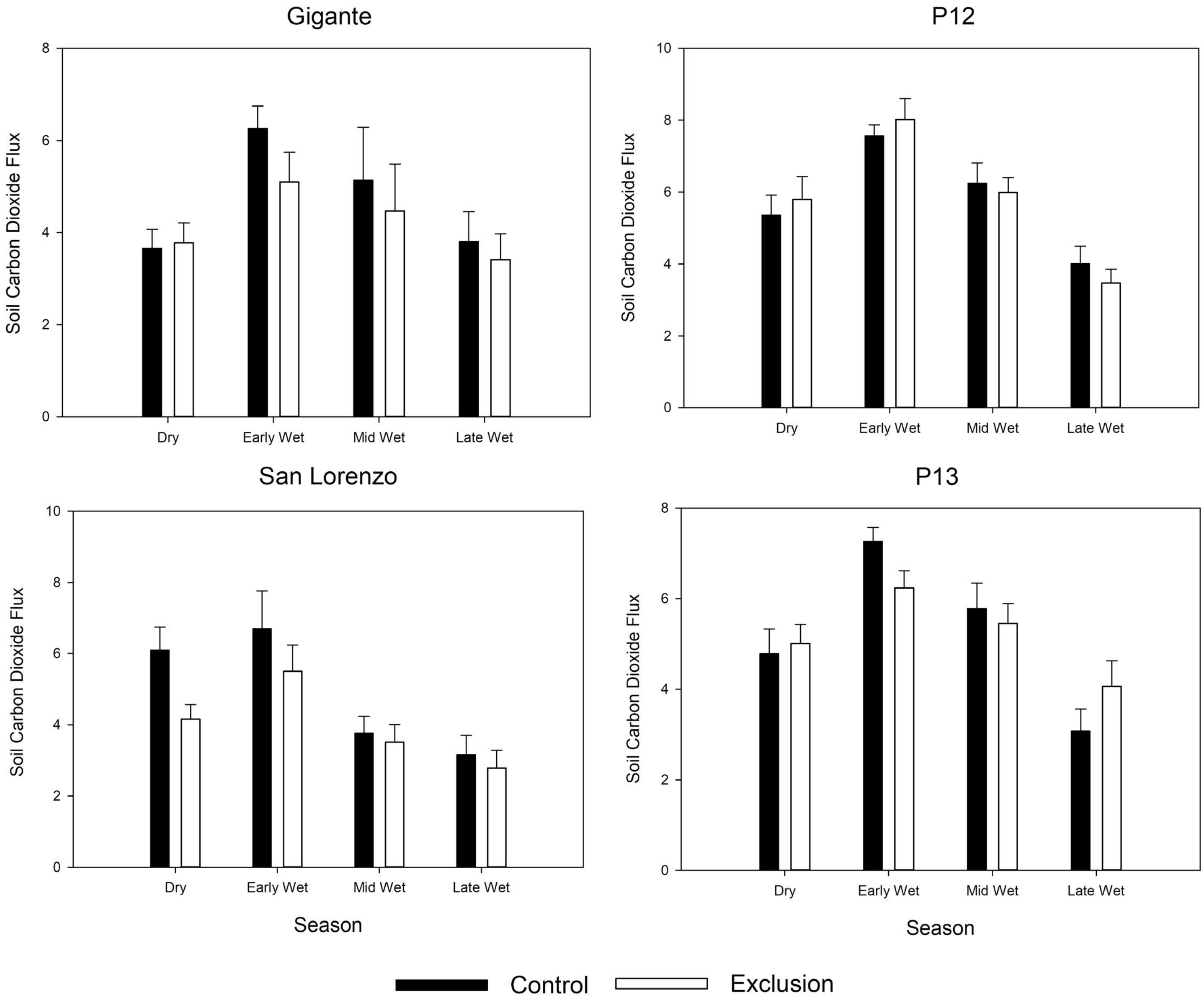

FIGURE 2. Soil carbon dioxide fluxes (µmol m^{-2} s^{-1}; i.e., soil respiration) across seasons and treatments for control and throughfall exclusion plots for the four Panama Rainforest Changes with Experimental Drying (PaRChED) forest sites. Data are averaged over two post-treatment years (2018–2020), separating the wet season into early, mid. and late. Bars present means ±1 SE (n = 4 plots per site). The sites are (i) Gigante (2,350 mm MAP, infertile soils), (ii) P12 (2,600 mm MAP, infertile soils), (iii) San Lorenzo (3,421 mm MAP, infertile soils), and (iv) P13 (2,600 mm MAP, fertile site). Overall, there were significant effects of site, season, and treatment, with interactions. All sites had a peak in soil respiration during the early wet season followed by declines later in the wet season. The mid-rainfall sites (P12 and P13) had the highest overall soil carbon dioxide fluxes, and every site had suppressed soil carbon dioxide fluxes in throughfall exclusion plots versus control plots for some portion of the year.

Soil Microbial Biomass and Community Composition

Tropical forest soils commonly have a positive relationship between soil moisture and soil microbial biomass, as observed in a seasonal forest in Belize (Eaton, 2001) and a drying experiment in a wet forest in Costa Rica (Waring and Hawkes, 2015). In the PaRChED experiment, we found similar results. There was significantly less microbial biomass in throughfall exclusion versus

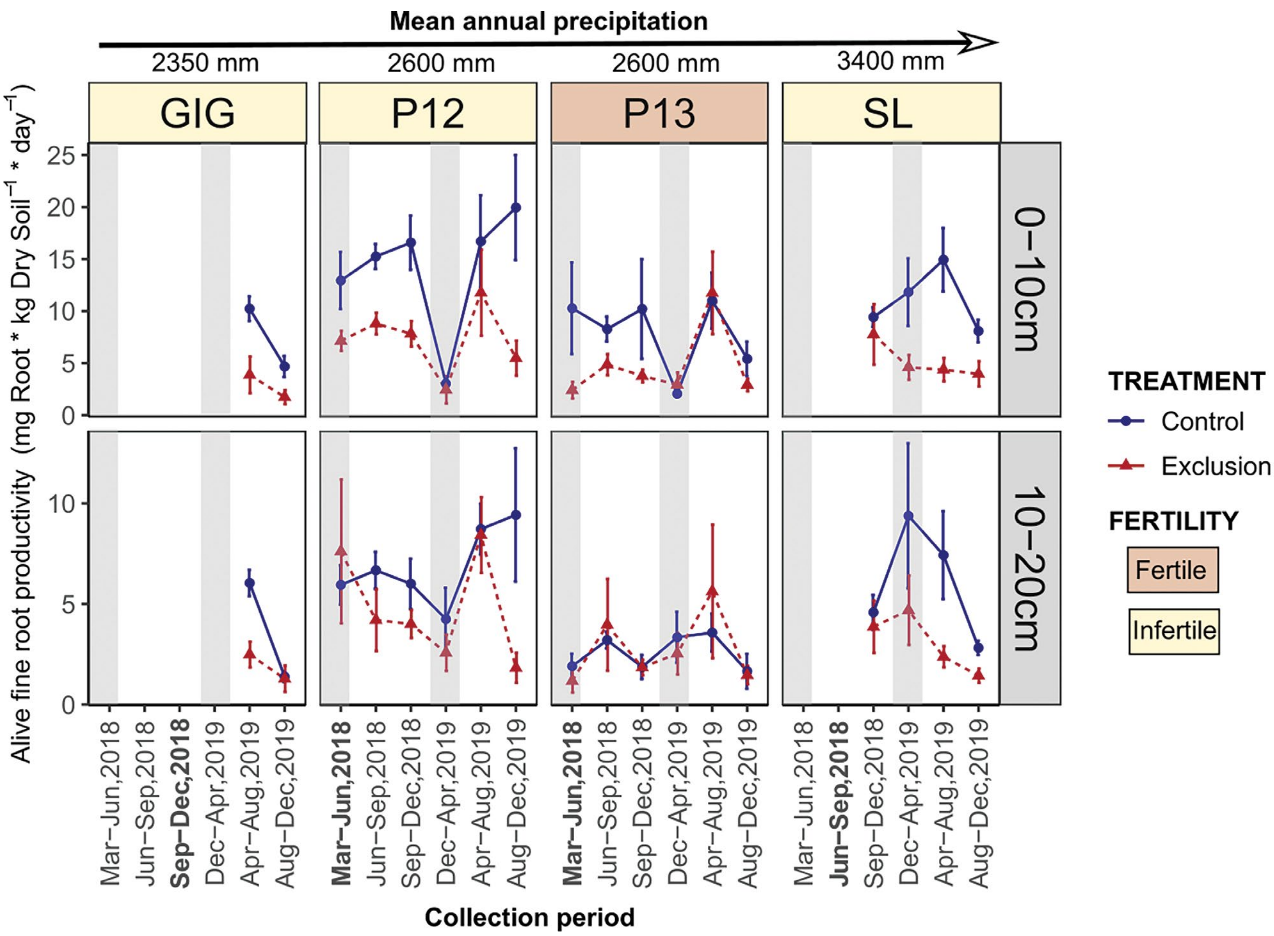

FIGURE 3. Root production from root ingrowth cores for two soil depths for the four Panama Rainforest Changes with Experimental Drying (PaRChED) forests during the first two years of the experiment. Throughfall exclusion significantly suppressed surface root growth, and site, time, depth, and site*time were also significant predictors of root production. Means (±1 SE, n = 4 plots) are shown. Shaded areas represent the dry season. The dry seasons are Mar–Jun 2018 and Dec–Apr 2019. Bold dates on the horizontal axis indicate the dates throughfall exclusion was initiated at each site.

control plots, including decreased fungal biomass (Chacon et al., 2023), which mirrored background trends of decreased microbial biomass during the dry season in these sites (Dietterich et al., 2022).

We also observed a change in microbial community composition with throughfall exclusion in the sites with infertile soils (Gigante, P12, and San Lorenzo) (January 2020), as indicated by amplicon sequencing. After 18 months of rainfall redirection, the shift in the infertile sites resulted in a convergence of microbial community composition in exclusion plots toward a common "drought microbiome" (Chacon et al., 2023). These results suggest that the sensitivity of tropical soil microbial communities to drying depends in part on soil fertility. Similar to these results, a throughfall exclusion experiment in an aseasonal Puerto Rican forest also resulted in large shifts in community composition (Bouskill et al., 2013) and function (Bouskill et al., 2016). The functional impact of the observed shifts in microbial biomass and community composition deserves further investigation in the Panama sites, particularly in relation to decreased soil respiration and possible effects on soil carbon storage.

Soil Chemistry

Throughfall exclusion promoted the accumulation of soil nutrients during the dry season, particularly for extractable dissolved nitrogen and mineral nitrogen (Dietterich et al., 2022), notably nitrate (Fig. 5). This pattern of nutrient accumulation was an accentuation of the background pattern of nutrient accumulation during the dry season, as seen in control plots for these sites (Fig. 5). A literature review of seasonally dry tropical forests

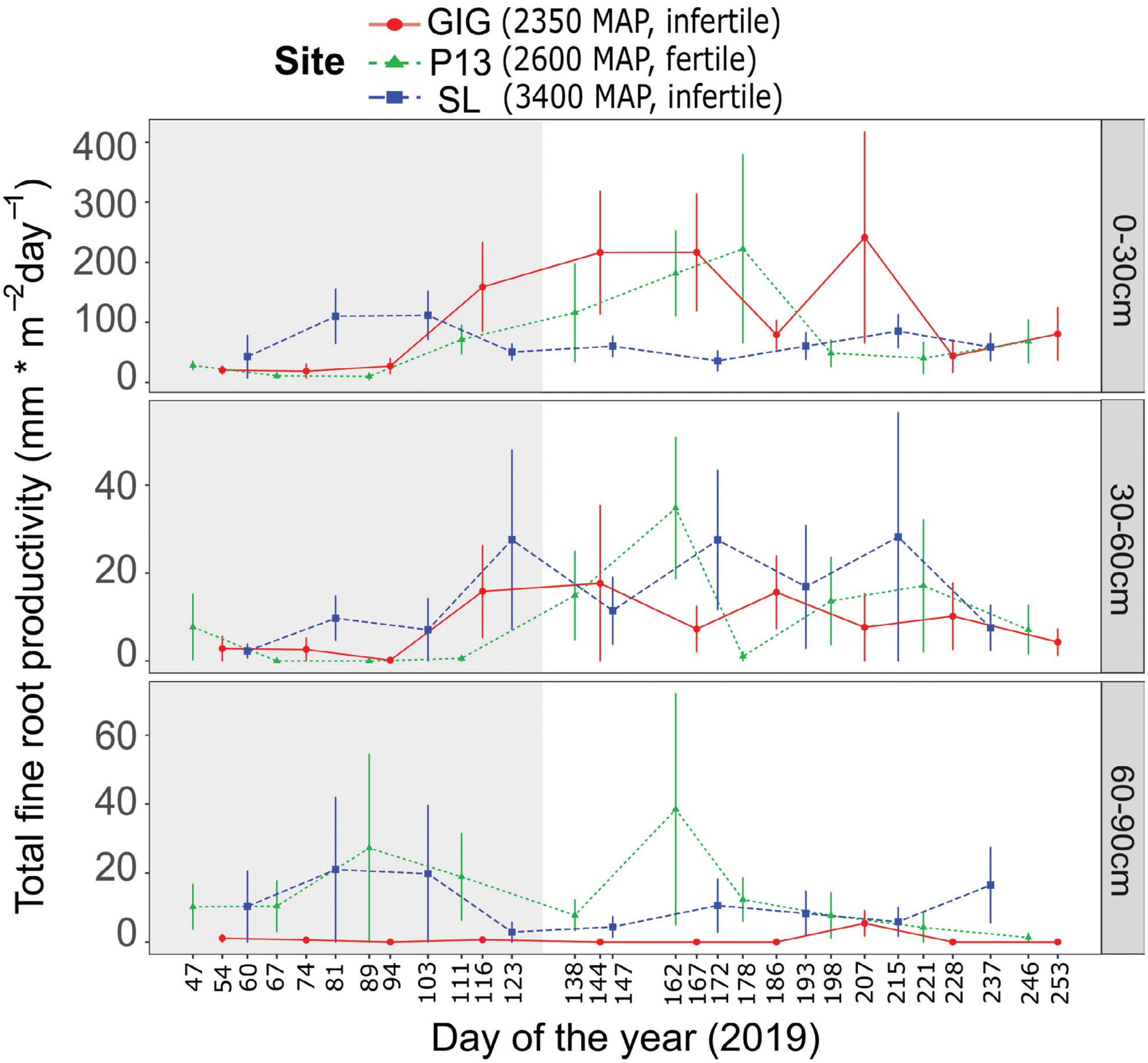

FIGURE 4. Root production from minirhizotron images for three depth increments for three of the Panama Rainforest Changes with Experimental Drying (PaRChED) forests during the first year of the experiment. The dry season is shaded and extended from December 20 (Day 354) to May 10 (Day 130). Mean (±1 SE, n = 8 plots) values combine exclusion and control plots because there was no treatment effect during this period.

also found accumulation of nitrogen and phosphorus during dry seasons (Allen et al., 2017). A study across different Neotropical forests with varying MAP also found greater soil nitrogen availability in drier sites as indicated by soil ^{15}N values (Posada and Schuur, 2011). Reinforcing our finding, an irrigation experiment on BCI found that watering through the dry season diminished the retention of nitrate in soils (Yavitt et al., 1993; Yavitt and Wright, 1996). Together with our data, these results suggest that the accumulation of nutrients in surface soils, and particularly of nitrate, is directly linked to moisture. In our study, throughfall exclusion could promote nitrate accumulation as a result of the declines in microbial biomass and root production that we observed, if nitrifying bacteria decreased and/or root uptake of nitrate declined with throughfall exclusion.

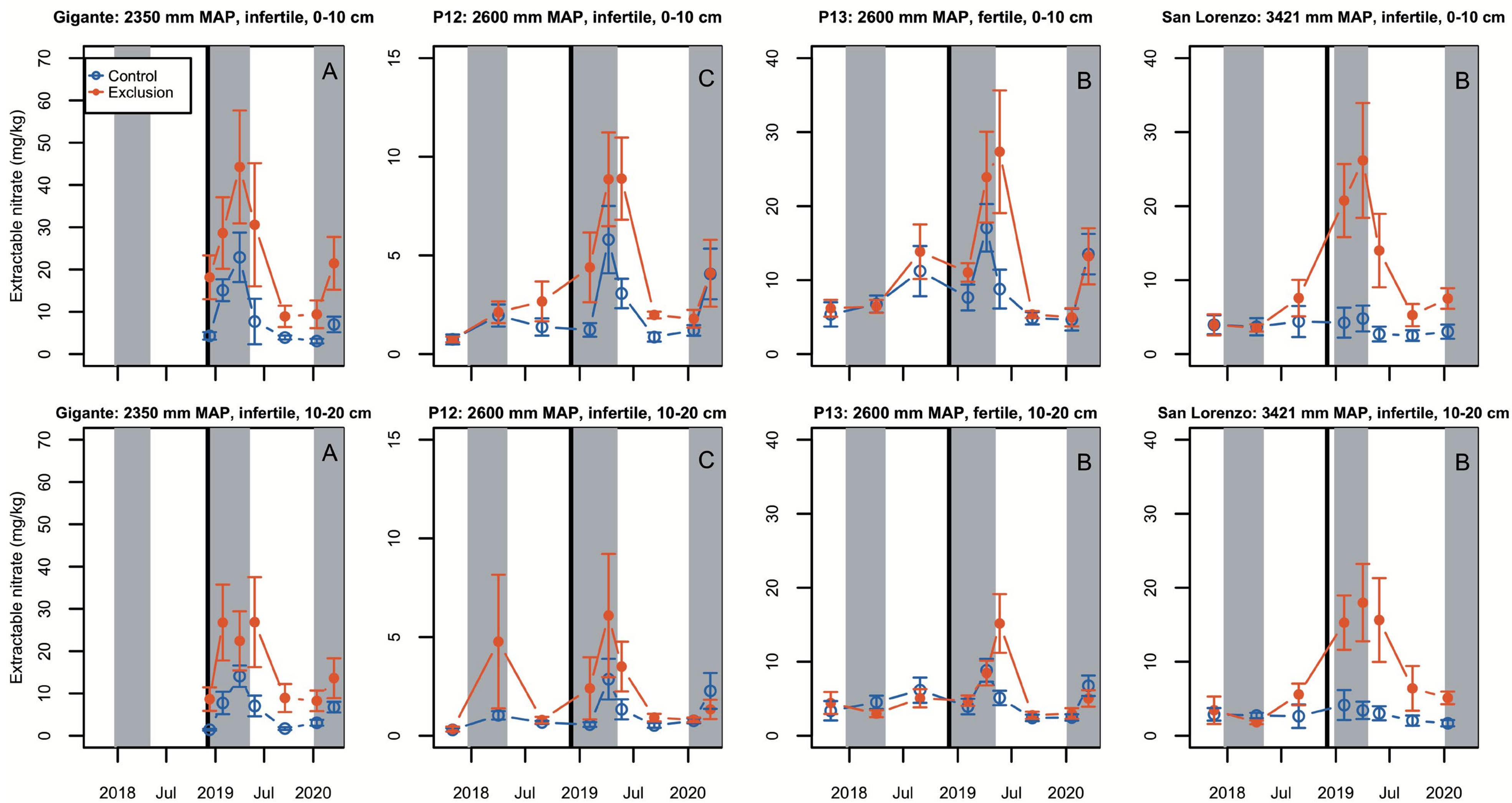

FIGURE 5. Extractable nitrate (NO_3^-) levels by throughfall exclusion treatment, site, time, and depth. Sites are arranged in order of increasing mean annual precipitation (MAP; Gigante < [P12, P13] < San Lorenzo), with 0–10 cm depth on top and 10–20 cm depth for each site underneath. Data shown are averages (±1 SE, $n = 4$). White background indicates wet seasons, gray background indicates dry seasons, and vertical black lines indicate the dates throughfall exclusion structures were completed. Overall, time, season, treatment, and their interactions were significant, with larger NO_3^- accumulation in throughfall exclusion plots versus control plots during the dry season. Note that the vertical axis scale differs among sites.

Understanding mechanistic links among these changes in ecosystem processes and properties will be the focus of future work in PaRChED.

CONCLUSION

Our results suggest that drying in seasonal tropical forests is likely to alter soil carbon storage, although the net balance between reduced soil respiration, reduced root production, and changes in microbial processes remains to be seen in the PaRChED experiment. Continued research at these sites will contribute to the development and parameterization of ecosystem models coupled to Earth system models to improve predictions of future carbon storage and land-climate feedbacks in tropical forests.

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