

1 **Throughfall exclusion and fertilization effects on tropical dry forest tree plan-**
2 **tations, a large-scale experiment**

3 German Vargas G.^{1,2,*}, Daniel Perez-Aviles³, Nannette Raczka⁴, Damaris Pereira-Arias³, Julián
4 Tijerín-Triviño⁵, L. David Pereira-Arias³, David Medvigy⁶, Bonnie G. Waring⁷, Ember Morrissey⁸,
5 Edward Brzostek⁴ and Jennifer S. Powers^{1,3}

6 ¹Department of Plant and Microbial Biology, University of Minnesota, St. Paul, MN USA 55108.

7 ²School of Biological Sciences, The University of Utah, Salt Lake City, UT 84112.

8 ³Department of Ecology, Evolution, & Behavior, University of Minnesota, St. Paul, MN USA 55108.

9 ⁴Department of Biology, West Virginia University, Morgantown, WV USA 26506.

10 ⁵Department. de Ciencias de la Vida, Grupo de Ecología Forestal y Restauración, Universidad de Alcalá, Madrid,
11 España 28801.

12 ⁶Department of Biological Sciences, University of Notre Dame, Notre Dame, IN USA 46556.

13 ⁷Grantham Institute on Climate Change and the Environment, Imperial College London, London UK, SW7 2AZ.

14 ⁸Division of Plant and Soil Sciences, West Virginia University, Morgantown, WV USA 26506.

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16 **Correspondence to:* German Vargas G. (gevargu@gmail.com)

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19 root productivity, soil microbial biomass.

20

21 **Abstract.** Across tropical ecosystems, global environmental change is causing drier climatic conditions and **increased**
22 **nutrient deposition.** Such changes represent large uncertainties due to unknown interactions between drought and
23 nutrient availability in controlling ecosystem net primary productivity (NPP). Using a large-scale manipulative exper-
24 iment, we studied **for four years** whether nutrient availability affects the **individual and integrated** responses of **above-**
25 **and below-ground ecosystem processes,** to through-fall exclusion in 30-year-old **mixed** plantations of **tropical dry**
26 **forest tree species in Guanacaste,** Costa Rica. We used a factorial design with four treatments: control (CN), fertiliza-
27 tion (F), drought (D), and drought+fertilization (D+F). While we found that a 13-15% reduction in soil moisture only
28 led to **weak** effects in the studied ecosystem processes, NPP increased as a function of F and D+F. The relative con-
29 tribution of each biomass flux to NPP varied depending on the treatment, with woody biomass being more important
30 for F and root biomass for D+F and D. Moreover, **the F treatment showed modest increases in maximum** canopy
31 cover, **Plant functional type (i.e., N-fixation or deciduousness) and not the experimental manipulations was the main**
32 **source of variation in tree growth.** Belowground processes also responded to experimental treatments, **as we found a**
33 decrease in nodulation for F plots and an increase in **microbial carbon use efficiency,** for F and D plots. Our results
34 emphasize that nutrient availability, **more so than modest reductions in soil moisture,** **limits** ecosystem processes in
35 tropical dry forests **and that soil fertility interactions with other aspects of drought intensity (e.g., vapor pressure def-**
36 **icit) are yet to be explored.**
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62 1 Introduction

63 Global environmental change is affecting primary productivity in tropical forest ecosystems. Among the main
64 factors behind this variation in productivity are the changes in the hydrologic regime due to an increase in rainfall
65 seasonality (Feng et al., 2013), increases in atmospheric water demand (McDowell et al., 2020), and regional decreases
66 in soil moisture (Seneviratne et al., 2010). In other words, the tropics are getting drier. Results from observational
67 studies found that droughts may increase **tropical** tree mortality rates (Powers et al., 2020; Chazdon et al., 2005),
68 reduce above-ground biomass productivity (Phillips et al., 2009; Castro et al., 2018), reduce the production of seeds
69 and flowers (O'Brien et al., 2018), and increase the abundance of high wood density and deciduous tree species
70 (Swenson et al., 2020; Aguirre-Gutiérrez et al., 2020). However, how tropical forests respond to drought depends on
71 other environmental factors, **such as soil fertility and the interaction with other disturbances** (Brando et al., 2014;
72 Brodrigg et al., 2020; Becknell et al., 2021). Accounting for how these environmental variables modulate ecosystem
73 responses to drought will enhance our understanding of the impacts of global environmental change in tropical forests,
74 which play a disproportionate role in global carbon dynamics and provide ecosystem services to a quarter of the
75 world's population (Wright, 2005; Lewis, 2006).

76 One largely overlooked factor is the potential role of nutrient availability in mediating tropical forests' vul-
77 nerability to drought. Tropical forests exist in a highly heterogeneous mosaic of soil fertility, parent material, and
78 topography (Townsend et al., 2008; Augusto et al., 2017; Waring et al., 2021), properties that shape forest composition
79 (Condit et al., 2013; Werden et al., 2018a), **and function** (Clark and Clark, 2000; Cunha et al., 2022). Nutrient-limited
80 environments harbor a greater proportion of slow-growing, drought-tolerant species, whereas fast-growing drought-
81 avoiding species dominate nutrient-rich environments (Oliveira et al., 2021), which suggests that soils play an im-
82 portant role in determining the heterogeneity of tropical forest responses to drought. Moreover, anthropogenic activi-
83 ties can cause an increase in atmospheric nitrogen and phosphorus deposition across ecosystems (Wang et al., 2017),
84 and yet the consequences of these changes in combination with rainfall variation remain unknown in tropical forests
85 (Matson et al., 1999; Hietz et al., 2011). In summary, the empirical evidence needed to characterize drought-nutrient
86 interactions **has yet to be documented but is highlighted as a priority to parameterize vegetation dynamics models**
87 (Smith et al., 2014).

88 1.1 Nutrient and water availability **modulate ecosystem processes**

89 **Soil fertility is an important factor modulating the responses of forest productivity to rainfall variation. For**
90 **instance, TDF stands growing in more fertile soils tend to show higher increases in productivity with higher rainfall**
91 **than stands in nutrient-poor soils** (Medvigy et al., 2019; Becknell et al., 2021). **High nutrient availability alleviates**
92 **drought stress because plants with higher leaf nitrogen maximize water use efficiency at the cost of photosynthetic**
93 **nitrogen use efficiency** (Lambers et al., 2008), **which will enhance photosynthetic capacity in favorable conditions.**
94 **At the same time, nutrient limitation negatively affects water use efficiency in crop species and tropical seedlings**
95 **with potential costs to productivity via reductions in carbon assimilation** (Santiago, 2015). **Other processes besides**
96 **primary productivity provide insight into ecosystem responses to global environmental change. Leaves, and more**

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119 precisely canopy cover, are the center for carbon assimilation in forest ecosystems. Recent evidence suggests that
120 the patterns of leaf flushing and leaf shedding are changing at a global scale because of climate change (Piao et al.,
121 2019). While it is well documented that tropical leaf phenological cycles depend on plant water status and the start
122 of the rainy season (Frankie et al., 1974; Borchert, 1994), phosphorus fertilization seems to reduce leaf life span in
123 Eastern Amazon forests (Cunha et al., 2022). A decrease in leaf canopy cover affects productivity by decreasing the
124 photosynthetic area (Doughty and Goulden, 2008), while changes in the timing of leaf flushing or shedding may
125 create a cascade of effects with unknown consequences, which will affect organisms that depend on these processes
126 (Coley, 1998). Thus, quantifying the combined effects of rainfall reductions and soil fertility on leaf production is
127 key to disentangling the interactions between primary productivity, canopy processes, nutrient availability, and
128 climate.

129 The extent to which nutrient and water availability interactions affect below-ground processes is highly
130 uncertain, particularly in TDFs (Phillips et al., 2016; Allen et al., 2017). The increase of specific nutrients (i.e., via
131 nitrogen deposition) might cause an imbalance in stoichiometry or increase water demand, which plants will adjust
132 by increasing transpiration rates or producing more root biomass (Lu et al., 2018; Waring et al., 2019; Cunha et al.,
133 2022). It is also highly uncertain how these changes may affect the microbial processes that determine carbon
134 cycling. For instance, whether soil microbial carbon use efficiency (CUE; the proportion of total carbon consumed
135 that is used to grow new biomass) can acclimate in response to changes in water and nutrient availability is not
136 known. Current knowledge suggests that microbes with high CUE produce more biomass that upon death becomes
137 protected from future microbial attack by adhering to mineral surfaces (Cotrufo et al., 2013). Under drought, the
138 CUE of the microbial community may decrease owing to the need to use carbon for survival strategies rather than
139 for growth (Schimel et al., 2007). However, it is possible that reducing microbial nutrient limitation may alleviate
140 the impacts of drought on CUE due to microbes investing less energy in resource acquisition (Schimel et al., 2007).
141 Other aspects of soil microbial processes may be affected by drought or modulated by soil nutrient availability
142 (Ahmed et al., 2018). Soil priming refers to the decomposition of older recalcitrant organic matter following the soil
143 microbial community's stimulation by adding labile organic matter (Liu et al., 2020). If drought alters patterns of
144 fine root growth and rhizodeposition (Preece and Peñuelas, 2016), this may lead to altered priming with altered
145 consequences of soil organic carbon storage. Identifying the extent to which shifts in nutrient and precipitation
146 regimes alter soil carbon cycling in TDFs is critical to increasing our understanding of climate change consequences
147 in this important biome (Knorr et al., 2005; Chadwick et al., 2016).

148 1.2 Experimental framework

149 Carbon cycling in TDFs is likely limited by both water and nutrient availability (Lugo and Murphy, 1986;
150 Castro et al., 2018; Medvigy et al., 2019; Becknell et al., 2021). This co-limitation of resources highlights the
151 importance of quantifying the individual and interactive roles of these two factors in shaping ecosystem processes in
152 this important and threatened biome (Hoekstra et al., 2005; Miles et al., 2006). Large-scale manipulative
153 experiments are needed to understand the interactions between drought and nutrient limitation, although to date an
154 experiment testing these two factors simultaneously has not been implemented in tropical forests. While nutrient

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194 addition experiments have shown mixed (~~strong~~, weak and none) effects on tree growth in tropical forests (Wright et
195 al., 2018; Hou et al., 2020; Cunha et al., 2022), results from throughfall exclusion experiments suggest an initial
196 decrease in woody productivity over the first two years and an increase in mortality after five years (Meir et al.,
197 2015). Most of these large-scale experiments have been conducted in wet tropical forests (mean annual rainfall >
198 2000 mm) (Meir et al., 2015; Wright et al., 2018), ~~despite TDF's documented vulnerability to drought~~ (Powers et al.,
199 2020).

200 To ~~investigate whether nutrient availability modulates changes in ecosystem processes in response to~~
201 ~~reduced rainfall manipulations we established a large-scale, fully factorial experiment in mixed-species plantations~~
202 ~~as model TDF stands~~. We used rain-out shelters covering 50% of the forest floor area to reduce soil moisture and/or
203 fertilizer applications to increase soil nutrient availability (Fig. 1). ~~We focused data collection on above- and below-~~
204 ~~ground ecosystem processes that contribute to carbon cycling. For over a 4-yr period, we performed measurements~~
205 ~~on tree diameter growth, canopy cover, and litterfall production as aboveground processes, and measurements of on~~
206 ~~fine roots production, nodulation, microbial CUE, and soil priming as belowground processes. We then integrated~~
207 ~~ecosystem-level responses to the experimental manipulations by quantifying net primary productivity, aboveground~~
208 ~~primary productivity, and the carbon allocation between above and belowground biomass~~.

209 2 Methods

210 Our experiment was conducted for four years (2016-2020) at Estación Experimental Forestal
211 Horizontes (hereafter Horizontes), in northwestern Costa Rica (10.711°N, 85.578°W) (Fig. 1). Before Horizontes
212 was incorporated into Área de Conservación Guanacaste (ACG), the lands were used for grazing and crops (Werden
213 et al., 2018b). Since 1989, Horizontes has served as a large-scale ecological and forestry research laboratory, and the
214 ~7500 ha area encompasses a mosaic of TDF at different successional stages (0-80 years), 64 ha of timber
215 plantations trials of native TDF species (Gutiérrez-Leitón, 2018), restoration trials (Werden et al., 2020), ~~and a~~
216 ~~Mesoamerican TDF arboretum (<http://www.arbnet.org/morton-register/arboretum-del-bosque-seco-tropical>)~~. During
217 the study period, total annual rainfall averaged ~1547 mm, ~~and median temperatures were 26.5 ± 1.6 °C during the~~
218 ~~dry season and 25.6 ± 1.5 °C during the wet season~~ (Fig. S1). Precipitation values were in range with the historical
219 average of ~1500 mm (Vargas G. et al., 2015). In Horizontes the start of the wet season is defined when cumulative
220 rainfall reaches 100 mm, which usually occurs in May and defines the beginning of the hydrological year (*i.e.*, 12
221 months after cumulative rainfall reaches 100 mm) (Aragão et al., 2007; Waring et al., 2019). Therefore our temporal
222 scale is the hydrological year as in TDFs the start of the rainy season determines the beginning of leaf production,
223 seed germination, and other ecological processes (Murphy and Lugo, 1986).

224 2.1 Experimental design

225 We conducted our experiment in tree plantations that were established in 1991 (Gutiérrez-Leitón,
226 2018). The plantations consist of three 8-10 ha blocks that each ~~contains~~ one of three focal species combined with
227 one of four species from a pool of 11 species native to Northwestern Costa Rica (Fig. S2). The plantations have not

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Deleted: four questions. First, to what extent does nutrient addition affect the responses of primary productivity to experimental drought? Second, do experimental manipulations affect phenological patterns of leaf production? Third, what is the role of nutrient availability and/or changes in soil moisture in controlling soil microbial CUE? Fourth, how do tree species differ in their growth responses to throughfall reduction and/or fertilization? We predicted that species-level growth and ecosystem-scale primary productivity would be negatively affected by reduced throughfall, but that this effect would be less in plots that were also fertilized.

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260 received any management for 25 years prior to our experiment, trees were planted at a spacing of 3 x 3 m, and the
261 understory now contains a diverse community of 15 lianas and 50 trees/shrubs (Fig. 1). We selected six species that
262 represent functional types common to the TDF based on species' ability to fix atmospheric nitrogen and leaf habit
263 phenology (Table 1) (Xu et al., 2016; Powers and Tiffin, 2010). We took a tree-centered approach in locating the
264 plots to include at least six individuals of each focal species in the four treatments, with a minimum of 12 trees per
265 plot. For this reason, the plot area ranged from 120-360 m² and contained a two-species combination that we
266 designated as a stand (Table S1). This experimental design was a compromise that allowed us to have at least four
267 individuals of each species within plots per treatment. Before selecting the plot locations, we did extensive surveys
268 of tree diameters to ensure that there were no systematic differences in tree diameters within species among
269 treatments (Fig. S3). Soil samples (0-10 cm depth) were collected in 2016 and 2021, by taking 7 to 10 cores (2.5 cm
270 diameter, one on each corner and three to six in the center line of the plot) and compositing cores by the plot.
271 Particle size distribution was collected in 2016 (Fig. S4), extractable elements (Olson extractable Cu, Zn, Mn, Fe, K,
272 and P), and total C and N for samples collected in the fifth year (2021) (Table S2).

273 The experiment consisted of a fully factorial design with four experimental treatments: fertilization (F),
274 drought (D), drought+fertilization (D+F), and un-manipulated control (CN). We established four plot replicates, per
275 experimental treatment that each contained two of the six tree species, such that every species was represented in
276 one plot of each treatment. The D and D+F treatments consisted of a series of structures that covered 50% of the
277 surface area at each plot and were suspended at a 40° angle at distances from 0.4 to 2.5 meters above the ground
278 (Fig. 1). The throughfall exclusion shelters were built with transparent polycarbonate corrugated sheets, wood poles,
279 and polyvinyl chloride pipes. To avoid lateral fine root growth outside the throughfall exclusion structures, we dug a
280 50 cm deep trench around each exclusion plot that was covered with a barrier of double-folded 0.075 mm thick
281 polyethylene film and then backfilled. Precipitation was routed off the throughfall exclusion plots by a system of
282 gutters and ground channels (Fig. 1). For the F and D+F treatments, a slow-release complete formula (macro- and
283 micro-nutrients) nutrient fertilizer was broadcasted uniformly over the entire plot area in two applications during the
284 rainy season each year. From 2016 to 2018 we used Basacote® Plus 3M (Compo Expert GmbH), and then due to low
285 market availability from 2018 through 2020, we used Osmocote® Plus (The Scotts Company LLC) (Table S3).
286 Nutrient addition rates were targeted to 150 kg N ha⁻¹ yr⁻¹ (Table S1), similar to other large-scale tropical forest
287 fertilization experiments (Wright et al., 2011; Alvarez-Clare et al., 2013; Waring et al., 2019). We placed fertilized
288 plots more than 50 m away from other plots or down the slope from control and drought plots whenever we could
289 not find enough trees 50 m away. These measures were considering the possibility of nutrient leaching from one plot
290 to another one. Finally, because litterfall accumulated on the surfaces of the plastic panels, every two weeks we used
291 long brooms to sweep the litter off the panels and then place it under each panel.

292 2.2 Soil moisture

293 We quantified volumetric soil moisture at a 30 min frequency for the duration of the experiment with
294 an EM50 Digital data logger equipped with four 10-HS soil moisture probes (METER Group, Inc. USA). Probes

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306 were distributed in two opposite pairs from the center of each plot, each pair consisting of a probe at 10 cm depth
307 and another probe at 40 cm depth in the soil.

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308 2.3. Aboveground processes

309 2.3.1. Tree growth

310 From 2016 to 2020, we measured the diameter at breast height (DBH) for all stems greater than 2.5 cm
311 DBH annually at the end of the growing season. These measurements included the plantation trees and every stem
312 that recruited into the 2.5 DBH size class before and during the experiment. All trees and shrubs were identified to
313 species level and classified into nitrogen fixation and leaf habit (evergreen or deciduous) functional types. For stems
314 between 2.5 cm and 10 cm DBH, diameter was measured with a diameter tape at a marked point 130 cm above the
315 ground. In the case of stems > 10 cm DBH, we measured DBH increments using band dendrometers set at 130 cm.
316 For each stem we calculated relative growth (RGR) as $RGR_{i-f} = \log(DBH_f/DBH_i)/((DC_f-DC_i)/365)$, where DC
317 represents the day of the century, i and f final DBH and DC values for a given stem (Wright et al., 2011).

318 2.3.2. Canopy productivity

319 We measured canopy productivity using two complementary methods: litterfall traps and leaf area index.
320 To measure litterfall production, we deployed three 0.25 m² traps ~ 0.4 m above the ground in a transect along the
321 center of each plot. In plots with throughfall exclusion structures, traps were in the spaces between the
322 polycarbonate sheets. Litter was collected monthly from each trap, dried for 72 hours at 60 °C, and sorted into
323 leaves, small branches, flowers, fruits, and frass, and then weighed separately. We then calculated the annual
324 litterfall productivity in kg m⁻² yr⁻¹ for total litterfall (leaves, small branches, flowers, and fruits), only leaves, and
325 reproductive litterfall (flowers and fruits).

326 Leaf area index (LAI) was measured in seven points at each plot (four in each corner and three along the
327 center) every 10 to 30 days with an LAI-2200C Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, NE, USA).
328 The variation in sampling frequency was caused by logistical constraints that wet seasons occasionally imposed on
329 our ability to reach the plots. Because of the high abundance of species from the Fabaceae family in the plots, LAI
330 measurements were performed after sunrise (between 0900 to 1100 h) given the associated nastic movements in
331 leaves after dawn and before dusk (Minorsky, 2019). For that reason, we took each measurement using a 45° angle
332 cap towards the center of the plot and performed scattering correction before and after each measurement cycle
333 throughout the entire experiment. LAI data were subsequently estimated from the first four gap fractions using the
334 software application FIV-2200 (LI-COR Biosciences, Lincoln, NE, USA). In 2017 tropical storm Nate, which
335 impacted 85% of the Costa Rican territory (Quesada-Román et al., 2020), caused a significant LAI decrease during
336 the month of November (Fig. S5). For that reason, we dropped the measurements of November and December 2017
337 from all the analyses involving LAI data. From the LAI data, we extracted leaf area duration (LAD, m² m⁻² d⁻¹),
338 which describes the temporal dynamics and leaf persistence in the canopy of broad-leaf plant communities (Ewert

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343 and Pleijel, 1999; Norby et al., 2003). LAD is defined as the area under the non-linear curve of LAI as a function of
344 the Julian day:

$$345 \quad LAD = \int_b^e LAI(t)$$

346 Where, b , describes the beginning of the growing season in Julian days; e , the end of the growing season in
347 Julian days; $LAI(t)$, the function of LAI temporal variation during the given growing season (Pokorný et al., 2008).

348 The growing season in this case is defined by leaf flushing and leaf fall (Norby et al., 2003). We obtained the
349 growing season parameters b and e from plot-specific and year-specific generalized additive models by estimating
350 the Julian days in which LAI starts to increase (positive slope change) from the minimum and when it starts to
351 decrease (negative slope change) after the maximum LAI (Methods S1). Then we fitted the LAI temporal variation
352 during the growing season and integrated it from b to e to obtain the area under the non-linear function $LAI(t)$ (Fig.
353 S6). In addition to LAD, for each plot, we calculated the maximum LAI value during the growing season (LAI_{max} ,
354 $m^2 m^{-2}$), minimum LAI during the dry season (LAI_{min} , $m^2 m^{-2}$), leaf-less period (LLP, d), the beginning of leaf
355 flushing (GSB, d) and the seasonal LAI enlargement (LAE, %) which is the percentage change in LAI from the dry
356 season to the wet season (Pokorný et al., 2008).

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357 2.4. Belowground processes

358 2.4.1 Fine-root and nodules production

359 We measured fine root productivity from July 2016 through December 2020 using the ingrowth core
360 method (Waring et al., 2016). To do this, we installed seven ingrowth cores in each plot to a depth of 15 cm. The 8
361 cm diameter cylindrical ingrowth bags were made from 2 mm nylon mesh. The cores were collected two months
362 after deployment and a subsequent new set of cores was installed right after collection. While deploying the cores,
363 we filled them with sieved, root-free soil collected on-site. During the first year of the experiment, cores were
364 sampled in the dry season. However, the clay-rich soils harden greatly during the dry season, which increased the
365 difficulty of deploying new bags during these times. For the following three years, ingrowth bags were harvested in
366 June, August, and November, with the modification that the bags harvested in June were deployed in November. We
367 acknowledge that roots may have grown, died, or decomposed during the dry season (Kummerow et al., 1990).
368 However, this effect will lead to minimal bias in annual productivity totals, as dry season root growth and
369 decomposition are expected to be negligible in the TDF (Kavanagh and Kellman, 1992). After collecting the cores,
370 fine roots were separated from the soil by washing them over a 2 mm sieve. We counted the number of nodules on
371 each root sample if present. Finally, root samples were dried for 72 hours at 60 °C and weighed to estimate total fine
372 root productivity in $kg m^{-2} yr^{-1}$.

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373 2.4.2 Microbial CUE and priming

374 To analyze microbial CUE, we collected ten soil samples (5 cm diameter, 15 cm depth) from each plot
375 during the wet season in August 2019 and homogenized them into one soil sample per plot. The samples were

380 expedited back to the University of Minnesota where a laboratory microcosm experiment was performed. Microbial
381 CUE was assessed using the ^{13}C glucose tracing method (Frey et al., 2013), briefly >97% ^{13}C glucose (Cambridge
382 Isotope Laboratories) at a rate of $400 \mu\text{g C g}^{-1}$ soil was mixed with 25 g of each homogenized soil sample in 32 oz
383 mason jars (946.3 ml) with septa in the lids. Soil samples ~~that did~~ not rewet to maximum water-holding capacity
384 (WHC) from D, F, CN, and D+F plots were brought to 20% WHC with the addition of the glucose solution, with lab
385 replications yielding $n=4$. To examine the effects of rewetting, additional soil samples from each field treatment
386 were rehydrated with a glucose solution to maximum soil WHC ($n=4$). Additional control soils were incubated
387 without the addition of glucose and received the same amount of deionized water as non-rewet samples as a non-
388 amended control, bringing the total to 48 jar incubations. Soil microcosms were well mixed with water or substrate
389 solution and incubated for one week at room temperature. During this time the production of $^{13}\text{CO}_2$ and total CO_2
390 were assayed every other day by taking gas samples from the microcosm headspace through the septa and inserting
391 them into 12 ml Exetainer vials (Labco Limited). After gas samples were taken, jars were opened for ~ 20 minutes
392 to allow for gas exchange. After the experiment was complete, Exetainer vials were shipped to West Virginia
393 University, where each gas sample was measured using an LI-6400 (LI-COR Biosciences, Lincoln, NE, USA) and
394 Picarro G2201-i (Picarro Inc., Santa Clara, CA, USA). Glucose and soil organic matter-derived $\text{CO}_2 - \text{C}$
395 was calculated via mass balance as described in Morrissey et al. (2017). Priming was then calculated as the difference in
396 soil organic matter $\text{CO}_2 - \text{C}$ between the microcosms that received substrate solution and those that received water.
397 At the cessation of the incubation, total microbial biomass was obtained by a chloroform fumigation method (Witt et
398 al., 2000). Briefly, 8g of soil was suspended in 45 mL of 0.1 M K_2SO_4 with or without an additional 1ml of ethanol-
399 free chloroform and shaken for 4 hours (chloroform) or 2 hours (no chloroform) and filtered (90 mm GF/A filter
400 paper). Extracts were stored at -20°C until dissolved organic carbon was oxidized to CO_2 via a persulfate digestion
401 (Doyle et al., 2004). Digestion efficiency was determined using a standard curve of yeast extract solution ranging
402 from (0-200 mg C L^{-1}). The concentration and isotopic enrichment of the resulting CO_2 gas were measured on the
403 Picarro. Total and substrate-derived microbial biomass-C was calculated as the difference in C (mg) between
404 chloroformed and non-chloroformed soil extracts. Microbial CUE was calculated as substrate-derived biomass -C
405 divided by the total carbon consumed (substrate-derived $\text{CO}_2 - \text{C}$ and biomass -C) (Frey et al., 2013).

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406 2.5. Ecosystem productivity

407 To quantify total net primary productivity (NPP) in $\text{kg m}^{-2} \text{yr}^{-1}$, we summed total litterfall, wood, and
408 root production in each plot for a given year. To estimate wood production, we calculated stem aboveground
409 biomass (AGB) using allometric equations for tropical tree species (Chave et al., 2014). For the allometric
410 equations, we measured the height of each stem using a Hagl f EC II-D electronic clinometer (Haglof Inc.,
411 Madison, MS, USA) and obtained wood density data from a functional trait database for the TDF of Guanacaste
412 (Powers and Tiffin, 2010). Mean wood density was substituted for species without wood density data. Annual
413 woody productivity then represented the sum of biomass increments from trees newly recruited into the 2.5 cm DBH
414 size class plus biomass gain from increased diameters in planted and existing recruited trees. Additionally, we
415 calculated aboveground net primary productivity (ANPP) by summing only woody and litterfall productivity, and

419 the aboveground:belowground productivity ratios (AGB:BGB) by dividing ANPP by the root production in each
420 plot for each year.

421 2.6. Statistical analysis

422 To test whether the throughfall exclusion structures affected soil moisture, we performed a linear
423 ~~mixed model~~ with the change in soil moisture for a given plot as the response variable, the presence of the
424 throughfall exclusion structure and the weekly time points from January 2017 to December 2020 were fixed effects,
425 and probe nested within plot nested within stand as a random intercept. ~~This approach allowed us to test the effect~~
426 ~~on soil moisture after the onset of the throughfall exclusion structures~~ (Reid et al., 2015), ~~while also accounting for~~
427 ~~the intra-annual variation in soil moisture typical of the TDF~~ (Schwartz et al., 2022). We ran separate models for
428 each depth (10 and 40 cm), and for the wet season and dry season due to the strong rainfall seasonality. To obtain
429 the change in soil moisture per plot, we divided the observation time into two periods, a pre-treatment (May 2016 to
430 ~~late August~~ 2016) that consisted of wet season soil moisture data before the shelters were set up, and an
431 experimental period (January 2017 to December 2020). We ~~excluded from this analysis the data collected between~~
432 ~~September~~ and December 2016 as we ~~finished establishing the rainout shelters three months into the rainy season.~~
433 After removing outliers using the interquartile method, we calculated the median pre-treatment soil moisture (SM_{PT} ,
434 $m^3 m^{-3}$) for each probe in each plot. We then calculated the treatment effect as the percentage change between each
435 soil moisture observation (SM_i , $m^3 m^{-3}$) and the SM_{PT} . To investigate inter-annual variation in wet season soil
436 moisture, we fitted ~~additional linear mixed models~~ to test whether soil moisture in plots without throughfall
437 exclusion varied as a function of year and depth, and ~~the~~ probe nested within ~~the~~ plot nested within ~~stands~~ as a
438 random intercept. In both cases, we calculated type III sum squares and the F value for each model and performed
439 Tukey's honest significant difference test (Tukey's HSD) for multiple comparisons.

440 We tested the effects of the experimental treatments on aboveground and belowground ~~ecosystem~~
441 processes by fitting a series (one for each response variable) of a two-factorial linear mixed effects model.
442 ~~Ecosystem~~ processes were the response variables, the drought treatment was one factor, and the fertilizer treatment
443 ~~was~~ the second factor, we included their interaction, and the experimental unit (e.g., litterfall basket) nested within
444 ~~the plot~~, nested within ~~stands~~ as a random intercept. With this model, we were able to estimate the main effect of
445 drought, the main effect of fertilization, and the interaction between drought and fertilization, ~~while also accounting~~
446 ~~for the effects of the plantation stand and the plot~~. We then calculated type III sum squares and the F value for each
447 model in an analysis of variance (ANOVA), with a Tukey's HSD for multiple comparisons. To analyze the response
448 of CUE from soils that were held at field soil moisture to soils that were rewet, we calculated the natural log
449 response ratio [*i.e.*, $\ln(RR)$], defined here as the mean of the rewet soils CUE divided by the mean CUE of the field
450 soil moisture soils. Values of $\ln(RR)$ ~~below~~ 0 indicate a decline in CUE to rewetting. All data management, and
451 statistical analysis were done using R software for statistical computing version 3.6.3 (R Core Team, 2021), and the
452 packages mcvg (Wood, 2004, 2011), nlme (Pinheiro et al., 2019), car (Fox and Weisberg, 2019), and tidyverse
453 (Wickham et al., 2019).

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474 **3 Results**

475 **3.1. Soil moisture and fertilization**

476 At 40 cm depth, we found evidence ($p < 0.05$) of a ~ 13% reduction in soil moisture as a function of
477 the pretreatment period in the plots with a throughfall exclusion structure, contrary to a weak ~ 4% reduction in soil
478 moisture in the plots without throughfall exclusion (Fig. 2). At 10 cm we observed an average change of -15% in
479 throughfall exclusion plots, but this was not significantly different when compared to the non-droughted plots (-
480 9.43%) (Fig. 2). In both plots with throughfall exclusion and plots without exclusion there was strong evidence ($p <$
481 0.001), across all depths and in both seasons, that soil moisture increased or decreased following seasonal rainfall
482 patterns. Weekly median soil moisture values in the throughfall exclusion plots oscillated between 0.21-0.42 $m^3 m^{-3}$
483 at 10 cm depth and 0.25-0.44 $m^3 m^{-3}$ at 40 cm depth, compared to 0.22-0.43 $m^3 m^{-3}$ at 10 cm depth and 0.25-0.45 m^3
484 m^{-3} at 40 cm depth for plots without throughfall exclusion (Fig. 2). Wet season soil moisture followed the inter-
485 annual rainfall variability in which the average volumetric water content was around 0.39 $m^3 m^{-3}$ during 2016 and
486 2017, while it was around 0.32 $m^3 m^{-3}$ from 2018 to 2020 (Fig. S7). At the end of four years, extractable soil P
487 increased by 2-3 fold in plots receiving fertilizer, and extractable Fe also increased (Fig. S8); however, none of the
488 other soil chemical variables we measured differed among treatments.

489 **3.2. Above-ground responses**

490 **3.2.1. Tree diameter relative growth rates (RGR_{dbh})**

491 We found no evidence of changes in RGR_{dbh} as a function of drought (D) and fertilizer additions (F) for
492 either understory (D: $F_v = 0.03$, $df = 1$, $p_v = 0.8601$; F: $F_v = 0.22$, $df = 1$, $p_v = 0.6580$) or plantation trees (D: $F_v =$
493 2.35 , $df = 1$, $p_v = 0.1489$; F: $F_v = 1.14$, $df = 1$, $p_v = 0.3041$). We found moderate evidence of an interaction between
494 drought and fertilizer for plantation trees ($F_v = 5.16$, $df = 1$, $p_v = 0.0499$) but not for understory trees ($F_v = 5.04$, $df =$
495 1 , $p_v = 0.0659$) (Fig. 3), whereas the effects of fertilization caused an increase in RGR for trees in drought plots
496 and a decrease for trees in non-drought plots (Fig. S9). The nitrogen-fixing plant functional type (PFT) explained the
497 differences in RGR_{dbh} for understory ($F_v = 21.11$, $df = 1$, $p_v < 0.0001$) and plantation trees ($F_v = 4.18$, $df = 1$, $p_v =$
498 0.0512) (Fig. 3) with non-N-fixers showing higher growth rates than N-fixers in both cases. On the other hand, the
499 deciduous PFT showed weaker effects on RGR_{dbh} for plantation trees ($F_v = 3.95$, $df = 1$, $p_v = 0.0639$) (Table S4).
500 RGR_{dbh} varied idiosyncratically among plantation species in response to the experimental treatments, but we did not
501 find evidence of significant treatment effects (Fig. S10). We also found a higher number of dead trees over the four
502 years in plots with experimental manipulations and hence higher biomass losses (Table S5). Mortality, recruitment,
503 and survival for the trees and shrubs that were recruited in the plots did not differ in response to the experimental
504 treatments (Fig. S11).

505 **3.2.2. Canopy productivity**

506 The experimental manipulations showed no effects on fine litter production (drought: $F_v = 0.96$, $df = 1$, $p_v =$
507 0.3473 ; fertilizer: $F_v = 1.33$, $df = 1$, $p_v = 0.2724$) and the production of leaves (drought: $F_v = 0.64$, $df = 1$, $p_v =$

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552 0.4404; fertilizer: $F_v = 1.39, df = 1, p_v = 0.2646$). Nevertheless, the control plots produced on average 0.69 ± 0.14 kg
553 m^{-2} of fine litter, which was 12 % lower than in the fertilized plots with 0.78 ± 0.14 $kg\ m^{-2}\ yr^{-1}$, 13% less than $0.79 \pm$
554 0.24 $kg\ m^{-2}\ yr^{-1}$ of the drought plots, and 8% lower than 0.75 ± 0.23 $kg\ m^{-2}\ yr^{-1}$ in drought+fertilizer plots. We also
555 found a 40% decrease in the production of flowers, seeds, and fruits with nutrient additions ($F_v = 4.84, df = 1, p_v =$
556 **0.0539**) (Fig. S12), but no effects with the throughfall exclusion ($F_v = 1.54, df = 1, p_v = 0.2449$). In all the plots leaf
557 area index (LAI) increased ~73% from the dry season (median LAI: 1.22) to the wet season (median LAI: 5.10).
558 None of the metrics obtained from the LAI measurements changed in response to the experimental manipulations
559 (Fig. S13), the only exception being maximum LAI (LAI_{max}) which we found to be marginally higher for fertilized
560 plots ($F = 3.36, df = 1, p = 0.0928$).

561 3.3. Below-ground responses

562 3.3.1. Fine roots and nodule production

563 We found no evidence that differences in the production of fine roots were due to the throughfall
564 exclusions ($F_v = 0.25, df = 1, p_v = 0.6227$) or nutrient additions ($F_v = 0.73, df = 1, p_v = 0.4105$); despite that, root
565 productivity in the control plots (0.112 ± 0.06 $kg\ m^{-2}\ yr^{-1}$) was ~15% less than in the drought plots with 0.133 ± 0.09
566 $kg\ m^{-2}\ yr^{-1}$ ~27% less than in the fertilized plots with 0.154 ± 0.09 $kg\ m^{-2}\ yr^{-1}$ and ~24% less than in the
567 drought+fertilizer plots 0.149 ± 0.12 $kg\ m^{-2}\ yr^{-1}$. In general, we observed a decrease in the production of nodules in
568 the fertilization treatment ($\chi^2 = 4.95, df = 1, p_v = 0.0262$), because only 1 nodule was observed in plots with nutrient
569 additions during the experimental manipulations. Interestingly, nodule production was similar for drought,
570 drought+fertilizer, and control plots with 69, 57, and 53 respectively ($\chi^2 = 0.03, df = 1, p_v = 0.8589$).

571 3.3.2. Microbial carbon use efficiency (CUE)

572 CUE was ~38% higher in soils from both the drought ($F_v = 4.31, df = 1, p_v = 0.0621$) and fertilized plots (F_v
573 $= 4.10, df = 1, p_v = 0.0678$) relative to control plots (Fig. 4). When the soils were rewet in the lab, the CUE
574 exhibited a negative response as quantified by the $\ln(RR)$ for both the drought ($F_v = 5.66, df = 1, p_v = 0.0366$) and
575 fertilization treatments ($F_v = 0.73, df = 1, p_v = 0.0809$) (Fig. 4). There were interaction effects between experimental
576 treatments for both the CUE ($F_v = 5.33, df = 1, p_v = 0.0462$) and $\ln(RR)$ ($F_v = 4.76, df = 1, p_v = 0.0597$), showing
577 evidence of different responses to drought depending on nutrient availability and how CUE was negatively affected
578 by rewetting for drought plots (Fig. 4). Soil priming was similarly influenced by rewetting and across all treatments,
579 the soils held at field soil moisture showed negative priming (Fig. S14). Rewetting the soils in the lab led to greater
580 soil C priming in the drought plots ($F_v = 5.33, df = 1, p_v = 0.0497$), but not in the fertilized plots ($F_v = 0.0191, df =$
581 $1, p_v = 0.8932$) (Fig. S14).

582 3.4. Ecosystem productivity and biomass allocation

Deleted: -v... = 1.39, df = 1, p-v... = 0.2646). Nevertheless, the control plots produced on average 0.69 ± 0.14 kg m^{-2} of fine litter, which was 12 % lower than in the fertilized plots with 0.78 ± 0.14 kg $m^{-2}\ yr^{-1}$ kg m^{-2} ... [2]

Deleted: kg m^{-2} ... f the drought plots, and 8% lower than 0.75 ± 0.23 kg $m^{-2}\ yr^{-1}$ kg m^{-2} ... in drought+fertilizer plots. We also found a 40% decrease in the production of flowers, seeds, and fruits with nutrient additions ($F_v = 4.84, df = 1, p_v = 0.0539$) (Fig. S10...12), but no effects with the throughfall exclusion ($F_v = 1.54, df = 1, p_v = 0.2449$). In all the plots leaf area index (LAI) increased ~73% from the dry season (median LAI: 1.22) to the wet season (median LAI: 5.10). None of All... the metrics obtained from the LAI measurements changed in response to the experimental manipulations (Fig. S13), the only exception being showed some degree of change in response to the fertilization treatment as these plots showed the highest... maximum LAI (LAI_{max}) which we found to be marginally higher for fertilized plots ($F = 3.36, df = 1, p = 0.0928$), longest leaf area duration, shortest leaf-less period, and on average leaf flushing started two weeks earlier than control plots (Fig. S11)... However, these changes were marginally significant only for LAI_{max} ($F_v = 3.36, df = 1, p_v = 0.0928$). ... [3]

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Deleted: -v... = 0.25, df = 1, p-v... = 0.6227) or nutrient additions ($F_v = 0.73, df = 1, p_v = 0.4105$); despite that, root productivity in the control plots (0.112 ± 0.06 kg $m^{-2}\ yr^{-1}$ kg m^{-2} ... was ~15% less than in the drought plots with 0.133 ± 0.09 kg $m^{-2}\ yr^{-1}$ kg m^{-2} ... ~27% less than in the fertilized plots with 0.154 ± 0.09 kg $m^{-2}\ yr^{-1}$ kg m^{-2} ... and ~24% less than in the drought+fertilizer plots 0.149 ± 0.12 kg $m^{-2}\ yr^{-1}$ kg m^{-2} ... In general, we observed a decrease in the production of nodules in the fertilization treatment ($\chi^2 = 4.95, df = 1, p_v = 0.0262$), because only 1 nodule was observed in plots with nutrient additions during the experimental manipulations. Interestingly, nodule production was the highest ... similar in plots with... or drought, t and drought+fertilizer... fertilizer, and control plots with 69, and 57, and 53 respectively,... but we found little evidence this was different from 53 nodules counted in the control plots from 2016 to 2020 ... $\chi^2 = 0.03, df = 1, p_v$... [4]

Deleted: -v... = 4.31, df = 1, p-v... = 0.0621) and fertilized plots ($F_v = 4.10, df = 1, p_v = 0.0678$) relative to control plots (Fig. 4). When the soils were rewet in the lab, the CUE exhibited a negative response as quantified by the $\ln(RR)$ for both the drought ($F_v = 5.66, df = 1, p_v = 0.0366$) and fertilization treatments ($F_v = 0.73, df = 1, p_v = 0.0809$) (Fig. 4). There were interaction effects between experimental treatments for both the CUE ($F_v = 5.33, df = 1, p_v = 0.0462$) and $\ln(RR)$ ($F_v = 4.76, df = 1, p_v = 0.0597$), showing evidence of different responses to drought depending on nutrient availability and how CUE was negatively affected by rewetting for drought plots (Fig. 4). Soil priming was similarly influenced by rewetting and across all treatments, the soils held at field soil moisture showed negative priming (Fig. S14)... Rewetting the soils in the lab led to greater soil C priming in the drought plots ($F_v = 5.33, df = 1, p_v = 0.0497$), but not in the fertilized plots ($F_v = 0.0191, df = 1, p_v = 0.8932$) (Fig. S12) ... [5]

697 Ecosystem level fluxes ~~were~~ more responsive to fertilization than to the throughfall exclusion (Fig. 5). Net
 698 primary productivity (NPP) increased with nutrient additions ($F_v = 7.86, df. = 1, p_v = 0.0178$), which led to 17% and
 699 19% higher NPP in fertilizer and drought+fertilizer plots respectively relative to the control plots (Fig. 5). Although
 700 we observed a 14% NPP increase in the drought plots ($F_v = 5.29, df. = 1, p_v = 0.0431$), we found no evidence this
 701 was different from the control plots ~~after looking at the multiple comparisons~~ (Fig. 5). Consistently, when
 702 considering only above-ground net primary productivity (ANPP) we found that fertilizer increased the amount
 703 biomass produced ($F_v = 5.81, df. = 1, p_v = 0.0362$) which was 15% and 19% higher for fertilizer and
 704 drought+fertilizer plots respectively relative to the control plots (Fig. 5). Moreover, the drought treatment decreased
 705 ANPP ($F_v = 4.58, df. = 1, p_v = 0.0575$). We found no evidence that the drought ($F_v = 0.30, df. = 1, p_v = 0.5960$) or
 706 fertilizer plots ($F_v = 0.35, df. = 1, p_v = 0.5645$) allocated more belowground biomass (Fig. 5). We did not observe
 707 interaction effects by the experimental treatments in either NPP ($F_v = 1.13, df. = 1, p_v = 0.30$), ANPP ($F_v = 0.77, df.$
 708 $= 1, p_v = 0.3991$), or AGB:BGB ($F_v = 0.34, df. = 1, p_v = 0.5695$), although the response to nutrient additions in the
 709 plots without throughfall exclusions was slightly higher for NPP and ANPP relative to plots in the drought treatment
 710 (Fig. 5, panel b).

711 4 Discussion

712 Here we present the first attempt to experimentally test whether ~~integrated ecosystem responses to rainfall~~
 713 ~~manipulations~~ are limited by nutrient availability in the tropical dry forest (TDF) biome (Beier et al., 2012; Meir et
 714 al., 2015). We found that a 13-15% reduction in soil moisture only leads to modest effects in the studied ecosystem
 715 processes. By contrast, extractable P increased in the fertilized plots severalfold (Fig. S8) causing an increase in
 716 primary productivity (both NPP and ANPP) (Fig. 5), a decrease in the nodule production, a decrease in the
 717 production of seeds and flowers (Fig. S12), increases in LAI_{max} (Fig. S13), and an increase in CUE when compared
 718 to the control plots (Fig. 4). Variation in tree relative growth rates (RGR_{dbh}) were mostly due to plant functional
 719 types rather than the experimental treatments. However, there was a significant interaction in how understory trees
 720 responded to both treatments leading to a reduction in the differences between N-fixing and non-N-fixing trees (Fig.
 721 3). Collectively, these results suggest that reducing soil moisture by a modest amount is not sufficient to drive large
 722 reorganizations in ecosystem processes, and that soil nutrient availability mildly modulate short-term changes in
 723 productivity. Below, we further explore the implications of these results in the context of how soil fertility could
 724 affect tropical ecosystem responses to global environmental change.

725 4.1. Nutrient and water limitations on ecosystem productivity

726 In a broad sense, we found that nutrient availability had a stronger control on forest productivity than a
 727 ~15% reduction in soil moisture. While this result does not resonate with the expectation that water availability
 728 imposes a greater limitation on productivity across environmental gradients than soil fertility (Harrington et al.,
 729 1995; Santiago and Mulkey, 2005; Toledo et al., 2011; Sala et al., 2012; Poorter et al., 2016), it provokes the
 730 question to what extent are tropical dry forests resilient to drought stress? Our data point to other aspects related to

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771 drought intensity and not soil moisture alone that could be key factors in how water availability shapes TDF primary
772 productivity (Anderegg et al., 2013). Recent studies from northwestern Costa Rica have shown that abnormal
773 drought stress due to a strong ENSO event in 2015 caused biomass loss due to an increase in tree mortality, a
774 decrease in reproductive biomass production, and reductions in productivity (O'Brien et al., 2018; Castro et al.,
775 2018; Powers et al., 2020). The main characteristics of the 2015 ENSO were the elevated temperatures and a
776 substantial rainfall reduction for the region (Santoso et al., 2017), which can increase the severity of drought effects
777 in forest ecosystems due to increased atmospheric water demand (Brodrribb et al., 2020; McDowell et al., 2020).
778 Thus, while throughfall exclusion experiments manipulate soil moisture, it is possible that a combination of factors
779 such as the vapor pressure deficit, the rainfall patterns (intensity and seasonality), and their linkages to soil moisture,

780 is a more important aspect of drought stress for forested ecosystems than soil moisture alone.
781 We observed the strongest experimental signal in the fertilization treatment (F and D + F) regardless of the
782 throughfall reductions. Such responses agree with known evidence of nutrient limitation on productivity in tropical
783 forests (Alvarez-Clare et al., 2013; Wright et al., 2018; Waring et al., 2019; Cunha et al., 2022), which has also been
784 observed in ecosystem models for the TDF (Medvigy et al., 2019). Interestingly the contribution of each biomass
785 flux to NPP depended on the combined effects of drought and fertilization, with root productivity contributing more
786 in droughted plots and woody productivity in fertilized plots (Fig. S15). Increases in root and woody productivity in
787 response to nutrient additions have been observed in secondary wet tropical forests (Wright et al., 2018) and Eastern
788 Amazon forests (Cunha et al., 2022). In a nearby secondary TDF Waring et al. (2019) found no significant effect of
789 nitrogen and/or phosphorus additions on productivity, however, in contrast to that study, our experiment included
790 the additions of both macro and micro-nutrients (Table S2). Moreover, the increase in productivity as a function of
791 fertilization showed a bigger, yet not significant, increase without the presence of throughfall structures (Fig. 5,
792 panel b). This trend resembles observed patterns in nearby stands of TDF, where forests in fertile soils are more
793 responsive to increases in rainfall than forests in infertile soils (Becknell et al., 2021). At the same time, our results
794 are comparable to other throughfall exclusion experiments in which fine litter production was not affected by the
795 drought treatment in a consistent manner (Nepstad et al., 2002; Brando et al., 2006; Schwendenmann et al., 2010),
796 with a lot of its variation possibly linked to inter-annual climatic variability (Brando et al., 2008).

797 4.1.1 Canopy dynamics and tree growth

798 While maximum canopy cover (LAI_{max}) showed a mild increase in the fertilization treatment, the temporal
799 dynamics of leaf phenology, showed no changes (Fig. S13). It is possible that the timing of leaf phenology may also
800 depend on intra- and interspecific responses to environmental factors that shape soil water availability including
801 temperature, atmospheric water demand, and soil water retention. For example, the tree species *Coussarea racemosa*
802 A. Rich modified its vegetative and reproductive phenology in response to a rainfall manipulation in the eastern
803 Amazon (Brando et al., 2006), while at the forest level changes were observed in LAI_{max} but not the timing of leaf
804 production (Brando et al., 2008). However, the opposite was observed in a fertilization experiment in the same
805 region where nutrient additions reduced leaf life span and had no effects on LAI_{max} (Cunha et al., 2022). In a
806 throughfall exclusion experiment combined with fertilization in loblolly pine (*Pinus taeda* L.) plantations, there

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831 were no changes in the LAI_{max} in response to rainfall reduction but an increase in the LAI_{max} in the fertilized plots
832 (Samuelson et al., 2014), which is qualitatively consistent with our data. This body of knowledge suggests that the
833 effects of experimental manipulations on canopy cover might be context-dependent.

834 No species showed significant changes in RGR_{dbh}, but the understory trees showed a reduction in the
835 differences between N-fixing and non-N-fixing trees. For F and D this was due to a reduction in growth rates by
836 non-N-fixing trees, while for D+F due to an increase in the growth rates by N-fixing trees (Fig. 4). One possible
837 reason for these patterns could be increased resource availability due to decreased competition. The D+F plots in
838 which these three species were present experienced the highest biomass losses due to mortality during the four years
839 of experimental manipulation (Table S5; Fig. S1L). Even though it is hard to determine the cause of death, an initial
840 spike in tree mortality has been observed in a long-term throughfall exclusion experiment in the Amazon (Costa et
841 al., 2010), which also caused an increase in growth rates of remaining trees (Rowland et al., 2015). Interestingly,
842 Meir et al. (2018) found that tree growth and mortality in the same experiment reached an equilibrium in the long-
843 term (> 10 years), reporting similar values to trees in a 1 ha plot without rainfall manipulation. The lack of
844 responsiveness in the F and D plots, in addition to the biomass losses in some of the D+F plots (Table S5), supports
845 the idea that the availability of resources such as light could be the cause of higher RGR_{dbh} in the D+F compared to
846 the other treatments (Fig. S1G). The lowest RGR_{dbh} were found in plots with the D treatment, with the strongest
847 experimental effect on *D. retusa*, *E. cyclocarpum*, and *S. glauca* (Fig. S1Q). These results are very similar to what
848 has been found in other tropical throughfall exclusion experiments (Meir et al., 2015), in which there is an overall
849 negative effect on tree diameter growth by a decrease in soil moisture.

850 4.1.2 Belowground responses

851 The fertilized plots showed no nodule production. This observed trend suggests that fertilizer addition
852 alleviates nutrient limitations for legumes (Toro et al. 2022), and confirms the facultative nature of nodulation
853 (Barron et al., 2011). While not statistically significant, nodule production was the highest for both drought
854 treatments (D and D+F). In part, a decrease in soil moisture slows down the rate of nitrogen mineralization and
855 limits plant nutrient uptake (Borken and Matzner, 2009; He and Dijkstra, 2014). Comparable to our results, the
856 legume species *Robinia pseudoacacia* L. also increased nodulation in a drought experiment (Wurzburger and
857 Miniati, 2014). Moreover, trees tend to rely more on deeper water sources with less access to nutrients (Querejeta et
858 al., 2021). This allocation of root biomass might also enhance nodulation in legumes as there might be changes in
859 the vertical profile of nutrients in the soil, particularly in arid environments where plants can have deep roots
860 (Tumber-Dávila et al., 2022). However, the lack of data on root production beyond the top 15 cm in our experiment
861 makes it hard to confirm this is the case.

862 Our soil incubation results suggest that global environmental change has the potential to alter microbial
863 CUE and the susceptibility of soil carbon to pulse rainfall events in tropical dry forests. After three years of
864 treatment, soil microbes in the D and F soils had significant increases in CUE (Fig. 4). Increases in CUE are
865 commonly attributed to shifts in the microbial community (Domeignoz-Horta et al., 2020), changes in the
866 availability of soil C (Morris et al., 2022), or a reduction in carbon investment by microbes in enzymes to fuel the

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Deleted: Collectively, our data and these studies suggest that the effects of soil moisture reduction go beyond ecosystem water/carbon balance and could cause a domino effect that might alter forest biogeochemistry.

880 nutrient acquisition (Manzoni et al., 2012). In this experiment, however, the increases in CUE in the D and F soils
881 but not the D + F soils hinder our ability to narrow down which of these mechanisms may be driving our results.
882 Quantifying the shifts in microbial community composition, as well as the identity of microbes that are active
883 decomposers, may shed light on the mechanistic underpinning of the CUE response observed here. Importantly,
884 these differences in CUE across treatments also appeared to impact the response of the soils to large, simulated
885 rainfall events. Regardless of treatment, rewetting the soils to water holding capacity led to a large reduction in CUE
886 (Fig. 4). While not statistically significant, there was a clear trend of greater CUE declines in the treatment soils,
887 particularly the D soils. This trend suggests that when large rainfall events occur in disturbed soils, a decrease in
888 microbial CUE could potentially lead to a stronger Birch Effect and enhance the soil C loss (Schimel, 2018). In
889 support, we found that rewetting the soils also led to the glucose addition driving greater priming of soil carbon
890 losses, a result that was particularly pronounced for the D soils (Fig. S14). By contrast, the glucose addition in soils
891 that were held at field soil moisture conditions led to the net mineralization of soil C by the microbial community.
892 Collectively, our soil incubation results highlight a critical need for more research on the potential for global change
893 to lead to shifts in microbial community composition and traits in TDFs.

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894 4.2 Conclusions

895 Our results highlight that forest productivity is sensitive to soil fertility and that this might interact with
896 changes in soil moisture. However, despite adding both macro- and micro-nutrients, our results confirm that the
897 short-term responses of tropical dry forest trees to fertilization treatments are modest at best, contrary to the
898 observed strong responses in nutrient-depleted eastern Amazon forests (Cunha et al., 2022). At the same time, the
899 nodulation data indicate that there might be a tight coupling between nutrient availability and water availability in
900 this system. Studying the role of soil moisture on plant nutrient acquisition dynamics remains a largely unexplored
901 venue in TDF ecology. Considering the observed patterns, a total throughfall exclusion will be necessary to cause
902 soil moisture to decrease by greater than 15 % and manipulations of the atmospheric water demand (e.g., vapor
903 pressure deficit) could help to improve our understanding of drought in tropical forests. Moreover, little is known of
904 how these belowground processes interact with microbial community dynamics, such as CUE, also affected by
905 nutrient additions or reductions in soil moisture. Beyond these processes, disentangling the causes and consequences
906 of colimitation by water and nutrients in productivity could help to elucidate how future climatic conditions will
907 affect carbon cycling in the TDF.

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1251 **TABLES AND FIGURE CAPTIONS**

1252 **Table 1.** Focal tree species present in the experimental manipulations and their functional and hydraulic traits
 1253 measured in other studies (Data from Powers and Tiffin, 2010; Powers et al, 2020). Here we present species leaf
 1254 habit (LH), nitrogen fixation (NF), specific leaf area (SLA, cm² g⁻¹), wood density (WD, g cm⁻³), water potential at
 1255 turgor loss point (Ψ_{TLP} , Mpa), and the water potential at 50 % accumulation of embolisms (Ψ_{P50} , Mpa).

Family	Species	LH	NF	SLA	WD	Ψ_{TLP}	Ψ_{P50}
Bignonaceae	<i>Handroanthus impeteginosus</i> (Mart. ex DC.) Mattos	DC	N	97.85	0.71	-1.95	-3.15
Fabaceae	<i>Dalbergia retusa</i> Hemsl.	DC	Y	67.70	0.80	-1.99	-4.71
Fabaceae	<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	DC	Y	145.51	0.38	-1.75	-2.73
Fabaceae	<i>Hymenaea courbaril</i> L.	SD	N	69.45	0.84	-1.91	-4.2
Meliaceae	<i>Swietenia macrophylla</i> King.	DC	N	68.86	0.67	-1.65	-2.92
Simaroubaceae	<i>Simarouba glauca</i> DC.	EV	N	54.89	0.41	-1.98	-2.81

1256

1257 **Fig. 1. a)** Geographical location and layout of a throughfall exclusion by fertilization experiment in Northwestern
1258 Costa Rica. **b)** Picture of a throughfall exclusion structure in a 30-year-old *Swietenia macrophylla* King. and
1259 *Hymenaea courbaril* L. plantation.

1260
1261 **Fig. 2.** Volumetric soil moisture records at two depths for plots with a throughfall exclusion structure and plots
1262 without it. **a)** Temporal variability at a weekly resolution median volumetric soil moisture with its associated 75 and
1263 25 percentiles, where the dashed vertical line represents the date when the structures were established. **b)** Histogram
1264 distribution of the percent difference between soil moisture during the experiment (SM_{Exp}) and the soil moisture
1265 preceding the experimental treatments (SM_{Pre}) for each depth during the dry season and the wet season, where the
1266 vertical lines represent the median $SM_{Exp} - SM_{Pre}$ percent value for plots with a throughfall exclusion structure
1267 (dashed) and plots without it (continuous). Reported results from a linear mixed effect model comparing weekly
1268 $SM_{Exp} - SM_{Pre}$ percent values for each depth during the dry and wet seasons.

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1270 **Fig. 3.** Diameter relative growth rate responses (RGR) of plantation (panel a) and understory (panel b) trees to
1271 fertilization (F), drought (D), and drought plus fertilization (D + F) over a period of four years (2016-2020). Bar
1272 plots showing the mean RGR with the associated standard error (error bars) were obtained from a total of 194
1273 plantation trees and 462 understory trees in 16 experimental plots. Lowercase letters stand for multiple comparisons
1274 among experimental treatments from a Post-Hoc Tukey's honest significance difference test.

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1276 **Fig. 4.** Microbial carbon use efficiency (CUE) and the log-response ratio between lab rewet and non-rewet samples
1277 $\ln(RR)$ in control, fertilization (F), drought (D), and drought plus fertilization (D + F) during the wet season of 2019.
1278 Panel a) shows bar plots with the mean response with the associated standard error ($n=4$) and panel b) shows
1279 interaction plots among experimental treatments. No significant differences were present after performing a Post-
1280 Hoc Tukey's honest significance difference test, despite the evidence of a moderate effect of F and D in both CUE
1281 and $\ln(RR)$.

1282
1283 **Fig. 5.** Responses of ecosystem net primary productivity (NPP), aboveground net primary productivity (ANPP), and
1284 aboveground to belowground ratios to fertilization (F), drought (D), and drought plus fertilization (D + F) over a
1285 period of four years (2016-2020). Panel a) shows median values for each experimental manipulation with their
1286 associated standard error ($n=4$) with significance values after performing a Post-Hoc Tukey's honest significance
1287 difference test where $p < 0.05$ (*) and $p < 0.1$. Panel b) shows the interactions between F and D treatments where for
1288 NPP and ANPP there was a greater response of non-drought plots to fertilization.

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