



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

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20



21 **Abstract.** Across tropical ecosystems, global environmental change is causing drier climatic conditions and increases
22 in nutrient depositions. 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 whether nutrient availability affects the responses of three component NPP fluxes (stem growth,
25 fine roots production, and litterfall) to through-fall exclusion in 30-year-old unmanaged mixed plantations of six tree
26 species native to the tropical dry forest of Costa Rica. We used a factorial design with four treatments: control (CN),
27 fertilization (F), drought (D), and drought+fertilization (D+F). While we found that a 13-15% reduction in soil mois-
28 ture only led to modest effects in the studied ecosystem processes, NPP increased as a function of F and D+F. At the
29 same time, NPP increases with nutrient additions were larger in the plots without throughfall exclusion. The relative
30 contribution of each biomass flux to NPP varied depending on the treatment, with woody biomass being more im-
31 portant for F and root biomass for D+F and D. Moreover, seasonal canopy cover was maintained longer in the fertilized
32 plots. Belowground processes such as nodulation and microbial carbon use efficiency (CUE) also responded to exper-
33 imental treatments, with a decrease in nodulation for F plots and an increase in CUE for F and D plots. Species
34 functional type (i.e., N-fixation or deciduousness) and not the experimental manipulations were the main source of
35 variation in tree relative growth rates. Our results emphasize that nutrient availability moderately constrains ecosystem
36 processes in tropical dry forests, but this depends on water availability.

37



38 1 Introduction

39 Global environmental change is affecting primary productivity in tropical forest ecosystems. Among the main
40 factors behind this variation in productivity are the changes in the hydrologic regime due to an increase in rainfall
41 seasonality (Feng et al., 2013), increases in atmospheric water demand (McDowell et al., 2020), and regional decreases
42 in soil moisture (Seneviratne et al., 2010). In other words, the tropics are getting drier. Results from observational
43 studies in wet and tropical dry forests (TDFs) found that droughts may increase tree mortality rates (Powers et al.,
44 2020), reduce above-ground biomass productivity (Phillips et al., 2009; Castro et al., 2018), reduce the production of
45 seeds and flowers (O'Brien et al., 2018), and increase the abundance of high wood density and deciduous tree species
46 (Swenson et al., 2020; Aguirre-Gutiérrez et al., 2020; González-M et al., 2021). Collectively, this evidence suggests
47 that these ecosystems are changing in response to ongoing climatic variation. However, how tropical forests respond
48 to drought depends on other environmental factors, such as soil fertility, history of disturbance, and fire regime, among
49 others (Chazdon et al., 2005; Brando et al., 2014; Brodribb et al., 2020; Becknell et al., 2021; Wu et al., 2022). Ac-
50 counting for how these environmental variables modulate ecosystem responses to drought will enhance our under-
51 standing of the impacts of global environmental change on the carbon cycling (Bonan, 2008), particularly in tropical
52 forests, which play a disproportionate role in global carbon dynamics and provide ecosystem services to a quarter of
53 the world's population (Wright, 2005; Lewis, 2006).

54 One largely overlooked factor is the potential role of nutrient availability in mediating tropical forests' vul-
55 nerability to drought. Tropical forests exist in a highly heterogeneous mosaic of soil fertility, parent material, and
56 topography (Townsend et al., 2008; Augusto et al., 2017; Waring et al., 2021), properties that shape forest composition
57 (Condit et al., 2013; Werden et al., 2018a), and function (Clark and Clark, 2000). Nutrient-limited environments har-
58 bor a greater proportion of slow-growing, drought-tolerant species, whereas fast-growing drought-avoiding species
59 dominate nutrient-rich environments (González-M et al., 2021; Oliveira et al., 2021), which suggests that soils play
60 an important role in determining the heterogeneity of tropical forest ecosystem responses to drought. Moreover, an-
61 thropogenic activities can cause an increase in atmospheric nitrogen and phosphorus deposition across ecosystems
62 (Wang et al., 2017), and yet the consequences of these changes in combination with rainfall variation remain unknown
63 in tropical forests (Matson et al., 1999; Hietz et al., 2011). In summary, the empirical evidence needed to characterize
64 drought-nutrient interactions or the effects of soil characteristics on drought responses has yet to be documented but
65 is highlighted as a priority to parameterize vegetation dynamics models (Smith et al., 2014).

66 1.1 Nutrient and water availability affect primary productivity

67 In principle, high nutrient availability could alleviate drought stress as plants with higher leaf nitrogen
68 maximize water use efficiency at the cost of photosynthetic nitrogen use efficiency (Lambers et al., 2008). For
69 example, nutrient limitation negatively affects water use efficiency in crop species and tropical seedlings (Santiago,
70 2015). Soil fertility also affects the responses of forest productivity to rainfall variation, such that TDF stands
71 growing in more fertile soils tend to show higher increases in productivity with higher rainfall than stands in
72 nutrient-poor soils (Medvigy et al., 2019; Becknell et al., 2021).



73 Other processes besides primary productivity provide insight into ecosystem responses to global
74 environmental change. Leaves, and more precisely canopy cover, are the main center for carbon assimilation in
75 forest ecosystems. Recent evidence has shown that the patterns of leaf flushing and leaf shedding are changing at the
76 global scale as a consequence of climate change (Piao et al., 2019). While it is well documented that tropical leaf
77 phenological cycles depend on plant water status and the start of the rainy season (Frankie et al., 1974; Borchert,
78 1994), little is known about how soil fertility interacts with water availability to affect leaf production in TDFs. A
79 decrease in leaf canopy cover affects productivity by decreasing the photosynthetic area (Doughty and Goulden,
80 2008), while changes in the timing of leaf flushing/shedding may create a cascade of effects with unknown
81 consequences on other ecosystem processes, which will affect organisms that depend on these processes (Coley,
82 1998). Moreover, changes in the timing of leaf production could make plant species more susceptible to the presence
83 of herbivores in greater abundances (Janzen, 1981; Neves et al., 2014). Thus, quantifying the effects of rainfall
84 reductions on leaf production is key to disentangling the interactions between soil moisture and soil fertility, and to
85 understanding the coupling among primary productivity, canopy processes, and climate.

86 The extent to which the interactions between nutrient and water availability affect below-ground processes
87 is highly uncertain, particularly in TDFs (Phillips et al., 2016; Allen et al., 2017). Moreover, the increase of specific
88 nutrients, *i.e.*, via nitrogen deposition, might also cause an imbalance in stoichiometry or increase water demand
89 with unknown consequences for tropical forests as plants will adjust to compensate by increasing transpiration rates
90 or producing more root biomass (Lu et al., 2018; Waring et al., 2019). This evidence suggests that the effects of
91 drought on ecosystem productivity could vary depending on the edaphic conditions and atmospheric deposition of
92 nutrients. At the heart of this uncertainty is the degree to which soil microbial carbon use efficiency (CUE; the
93 proportion of total carbon consumed that is used to grow new biomass) either acclimates or shifts in response to
94 changes in water and nutrient availability. Theory suggests that microbes with high CUE produce more biomass that
95 upon death becomes protected from future microbial attack by adhering to mineral surfaces (Cotrufo et al., 2013).
96 Under drought, the CUE of the microbial community may decrease owing to the need to use carbon for survival
97 strategies rather than for growth (Schimel et al., 2007). When rainfall returns to these soils, this shift toward a low
98 CUE microbial community may drive significant soil carbon losses since available soil carbon will be metabolized
99 by a less efficient microbial community. However, there is the potential that reducing microbial nutrient limitation
100 may alleviate the impacts of drought on CUE due to microbes investing less energy in resource acquisition for
101 protective molecule production (Schimel et al., 2007). Given the potential for shifts in nutrient and precipitation
102 regimes to alter microbial CUE, identifying the extent to which these drivers alter CUE in TDFs is critical to
103 increasing our predictive understanding of soil carbon cycling in this important biome (Knorr et al., 2005; Chadwick
104 et al., 2016).

105 1.2 Experimental framework

106 Contrary to tropical rain forests, carbon cycling in TDFs is likely limited by both water and nutrient
107 availability (Lugo and Murphy, 1986; Castro et al., 2018; Medvigy et al., 2019; Becknell et al., 2021). This co-
108 limitation of resources highlights the importance of quantifying the individual and interactive roles of these two



109 factors in shaping ecosystem processes in this important and threatened biome (Hoekstra et al., 2005; Miles et al.,
110 2006). Large-scale manipulative experiments are needed to understand the interactions of drought and nutrient
111 limitation, although to date an experiment testing these two factors simultaneously has not been implemented in
112 tropical forests. While nutrient addition experiments have shown mixed (positive, weak and none) effects on tree
113 growth in tropical forests (Wright et al., 2018; Hou et al., 2020), results from throughfall exclusion experiments
114 suggest an initial decrease in woody productivity over the first two years and an increase in mortality after five years
115 (Meir et al., 2015). Most of these large-scale experiments have been conducted in wet tropical forests (mean annual
116 rainfall > 2000 mm) (Meir et al., 2015; Wright et al., 2018), even though TDFs seem to be equally vulnerable to
117 drought (Powers et al., 2020), and once accounted for up to 40% of tropical forest area (Murphy and Lugo, 1986).

118 To understand how both water and nutrient availability controls important primary productivity fluxes that
119 contribute to carbon cycling, we established a large-scale, fully factorial experiment in mixed-species plantations as
120 model TDF stands. We used rain-out shelters covering 50% of the forest floor area to reduce soil moisture and/or
121 fertilizer applications to increase soil nutrient availability to investigate four questions. First, how do tree species
122 differ in their growth responses to throughfall reduction and/or fertilization? Second, do experimental manipulations
123 affect phenological patterns of leaf production? Third, what is the role of nutrient availability and/or changes in soil
124 moisture in controlling root production, nodulation and soil microbial CUE? Fourth, to what extent does nutrient
125 addition affect the responses of primary productivity to experimental drought? We predicted that species-level
126 growth and ecosystem-scale primary productivity would be negatively affected by reduced throughfall, but that this
127 effect would be less in plots that were also fertilized.

128 2 Methods

129 Our experiment was conducted for four years (2016-2020) at Estación Experimental Forestal
130 Horizontes (hereafter Horizontes), in northwestern Costa Rica (10.711°N, 85.578°W) (Figure 1). Before Horizontes
131 was incorporated into Área de Conservación Guanacaste (ACG), the lands were used for grazing and crops (Werden
132 et al., 2018b). Since 1989, Horizontes has served as a large-scale ecological and forestry research laboratory, and the
133 ~7500 ha area encompasses a mosaic of TDF at different successional stages (0-80 years), 64 ha of timber
134 plantations trials of native TDF species (Gutiérrez-Leitón, 2018), restoration trials (Werden et al., 2020), a
135 Mesoamerican TDF arboretum (<http://www.arbnet.org/morton-register/arboretum-del-bosque-seco-tropical>), as well
136 as seed orchards of endangered precious wood species (M. Gutiérrez-Leitón *personal communication*). During the
137 study period total annual rainfall averaged ~1547 mm, with annual totals as follows: 1439 mm (2016), 2201 mm
138 (2017), 992 mm (2018), 919 mm (2019), and 2186 mm (2020), and median temperatures were 26.5 ± 1.6 °C during
139 the dry season and 25.6 ± 1.5 °C during the wet season (Fig. S1). Precipitation values were in range with the
140 historical average of ~1500 mm (Vargas G. et al., 2015). In Horizontes the start of the wet season is defined when
141 cumulative rainfall reaches 100 mm, which usually occurs in May and defines the beginning of the hydrological
142 year (*i.e.*, 12 months after cumulative rainfall reaches 100 mm) (Aragão et al., 2007; Waring et al., 2019). Therefore
143 our temporal scale is the hydrological year as in TDFs the start of the rainy season determines the beginning of leaf
144 production, seed germination, and other ecological processes (Murphy and Lugo, 1986).



145 2.1 Experimental design

146 We conducted our experiment in tree plantations that were established in 1991 (Gutiérrez-Leitón,
147 2018). The plantations consist of three 8-10 ha blocks that each contain one of three focal species combined with
148 one of four species from a pool of 11 species native to Northwestern Costa Rica (Fig. S2). The plantations have not
149 received any management (fertilization, liana cutting, thinning, etc.) for 25 years prior to our experiment, trees were
150 planted at a spacing of 3 x 3 m, and the understory now contains grasses, forbs, and a diverse community of 15
151 lianas and 50 trees/shrubs (Figure 1). We selected six species from the 11 that were planted (Table 1), which
152 represent functional types common to the TDF given the species ability to fix atmospheric nitrogen and their leaf
153 habit phenology (Xu et al., 2016; Powers and Tiffin, 2010). We took a tree-centered approach in locating the plots to
154 include at least six individuals of each focal species in the four treatments, with a minimum of 12 trees per plot. For
155 this reason, the plot area ranged from 120-360 m² and contained a two-species combination that we designated as
156 stand (Table S1). This experimental design was a compromise that allowed us to have at least four individuals of
157 each species within plots. Before selecting the plot locations, we did extensive surveys of tree diameters to ensure
158 that there were no systematic differences in tree diameters within species among treatments (Fig. S3). Soil samples
159 (0-10 cm depth) were collected in 2016 and 2021, by taking 7 to 10 cores (2.5 cm diameter) and compositing cores
160 by the plot. Particle size distribution was collected in 2016 (Table S2), extractable elements (Olson extractable Cu,
161 Zn, Mn, Fe, K, and P), and total C and N for samples collected in the fifth year (2021).

162 The experiment consisted of a fully factorial design with four experimental treatments: fertilization (F),
163 drought (D), drought+fertilization (D+F), and un-manipulated control (CN). We established four plot replicates, per
164 experimental treatment that each contained two of the six tree species, such that every species was represented in
165 one plot of each treatment. The D and D+F treatments consisted of a series of structures that covered 50% of the
166 surface area at each plot and were suspended at a 40° angle at distances from 0.4 to 2.5 meters above the ground
167 (Figure 1). The throughfall exclusion shelters were built with locally sourced materials including transparent
168 polycarbonate corrugated sheets, wood poles, and polyvinyl chloride pipes. To avoid lateral fine root growth outside
169 the throughfall exclusion structures, we dug a 50 cm deep trench around each exclusion plot that was covered with a
170 barrier of double folded 0.075 mm thick polyethylene film and then backfilled. Precipitation was routed off the
171 throughfall exclusion plots by a system of gutters and ground channels (Figure 1). For the F and D+F treatments, a
172 slow-release complete formula (macro- and micro-nutrients) nutrient fertilizer was broadcasted uniformly over the
173 entire plot area in two applications during the rainy season each year. From 2016 to 2018 we used Basacote® Plus
174 3M (Compo Expert GmbH), and then due to low market availability from 2018 through 2020 we used Osmocote®
175 Plus (The Scotts Company LLC) (Table S3). Nutrient addition rates were targeted to 150 kg N ha⁻¹ yr⁻¹ (Table S1),
176 similar to other large-scale tropical forest fertilization experiments (Wright et al., 2011; Alvarez-Clare et al., 2013;
177 Waring et al., 2019). Finally, because litterfall accumulated on the surfaces of the plastic panels, every two weeks
178 we used long brooms to sweep the litter off the panels and then place it under each panel.

179 2.2 Soil moisture



180 In each plot we quantified volumetric soil moisture at a 30 min frequency for the duration of the
181 experiment with an EM50 Digital data logger equipped with four 10-HS soil moisture probes (METER Group, Inc.
182 USA). Probes were distributed in two opposite pairs from the center of the plot, each pair consisting of a probe at 10
183 cm depth and another probe at 40 cm depth.

184 2.3. Aboveground processes

185 2.3.1. Tree growth

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

194 2.3.2. Canopy productivity

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

202 Leaf area index (LAI) was measured in seven points at each plot (four in each corner and three along the
203 center) every 10 to 30 days with an LAI-2200C Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, NE, USA).
204 The variation in sampling frequency was caused by logistical constraints that wet seasons occasionally imposed on
205 our ability to reach the plots. Because of the high abundance of species from the Fabaceae family in the plots, LAI
206 measurements were performed after sunrise (between 0900 to 1100 h) given the associated nastic movements in
207 leaves after dawn and before dusk (Minorsky, 2019). For that reason, we took each measurement using a 45° angle
208 cap towards the center of the plot and performed scattering correction before and after each measurement cycle
209 throughout the entire experiment (LI-COR Biosciences, Lincoln, NE, USA). LAI data were subsequently estimated
210 from the first four gap fractions using the software application FIV-2200 (LI-COR Biosciences, Lincoln, NE, USA).
211 In 2017 tropical storm Nate, which impacted 85% of the Costa Rican territory (Quesada-Román et al., 2020), caused
212 a significant LAI decrease during the month of November (Fig. S4). For that reason, we dropped the measurements



213 of November and December during 2017 from all the analyses involving LAI data. From the LAI data, we extracted
214 leaf area duration (LAD, $\text{m}^2 \text{m}^{-2} \text{d}^{-1}$), which describes the temporal dynamics and leaf persistence in the canopy of
215 broad-leaf plant communities (Ewert and Pleijel, 1999; Norby et al., 2003). LAD is defined as the area under the
216 non-linear curve of LAI as a function of the Julian day:

$$217 \quad LAD = \int_b^e LAI(t)$$

218 Where, b , describes the beginning of the growing season in Julian days; e , the end of the growing season in
219 Julian days; $LAI(t)$, the function of LAI temporal variation during the given growing season (Pokorný et al., 2008).
220 The growing season in this case is defined by leaf flushing and leaf fall (Norby et al., 2003). In our case, we
221 obtained the growing season parameters b and e from plot-specific and year-specific generalized additive models by
222 estimating the Julian days in which LAI starts to increase (positive slope change) from the minimum and when it
223 starts to decrease (negative slope change) after the maximum LAI (Methods S1). Then we fitted the LAI temporal
224 variation during the growing season and integrated it from b to e to obtain the area under the non-linear function
225 $LAI(t)$ (Fig. S5). In addition to LAD, for each plot, we calculated the maximum LAI value during the growing
226 season (LAI_{\max} , $\text{m}^2 \text{m}^{-2}$), minimum LAI during the dry season (LAI_{\min} , $\text{m}^2 \text{m}^{-2}$), leaf-less period (LLP, d), the
227 beginning of leaf flushing (GSB, d) and the seasonal LAI enlargement (LAE, %) which is the percentage change in
228 LAI from the dry season to the wet season (Pokorný et al., 2008).

229 2.4. Belowground processes

230 2.4.1 Fine-root and nodules production

231 We measured fine root productivity from July 2016 through December 2020 using the ingrowth core
232 method (Waring et al., 2016). To do this, we installed seven ingrowth cores in each plot to a depth of 15 cm. The 8
233 cm diameter cylindrical ingrowth bags were made from 2 mm nylon mesh. The cores were collected two months
234 after deployment and a subsequent new set of cores was installed after collection. While deploying the cores, we
235 filled them with sieved, root-free soil collected on-site. During the first year of the experiment, cores were sampled
236 in the dry season. However, the clay-rich soils harden greatly during the dry season, which increased the difficulty
237 of deploying new bags during these times. Therefore, for three years of experimental ingrowth bags were harvested
238 in June, August, and November. After collecting the cores, fine roots were separated from the soil by washing them
239 over a 2 mm sieve. We counted the number of nodules on each root sample if present. Finally, root samples were
240 dried for 72 hours at 60 °C and weighed to estimate total fine root productivity in $\text{kg m}^{-2} \text{yr}^{-1}$.

241 2.4.2 Microbial CUE and priming

242 To analyze microbial CUE, we collected ten soil samples (5 cm diameter, 15 cm depth) from each plot
243 during the wet season in August 2019 and homogenized into one soil sample per plot. The samples were expedited
244 back to the University of Minnesota where a laboratory microcosm experiment was performed. Microbial CUE was
245 assessed using the ^{13}C glucose tracing method (Frey et al., 2013), briefly >97% ^{13}C glucose (Cambridge Isotope



246 Laboratories) at a rate of 400 ug C g^{-1} soil was mixed with 25 g of each homogenized soil sample in 32 oz mason
247 jars (946.3 ml) with septa in the lids. Soil samples not rewet to maximum water-holding capacity (WHC) from D, F,
248 CN, and D+F plots were brought to 20% WHC with the addition of the glucose solution, with lab replications
249 yielding $n=4$. To examine the effects of rewetting, additional soil samples from each field treatment were rehydrated
250 with a glucose solution to maximum soil WHC ($n=4$). Additional control soils were incubated without the addition
251 of glucose and received the same amount of deionized water as non-rewet samples as a non-amended control,
252 bringing the total to 48 jar incubations. Soil microcosms were well mixed with water or substrate solution and
253 incubated for one week at room temperature. During this time the production of $^{13}\text{CO}_2$ and total CO_2 were assayed
254 every other day by taking gas samples from the microcosm headspace through the septa and inserting them into 12
255 ml Exetainer vials (Labco Limited). After gas samples were taken, jars were opened for ~ 20 minutes to allow for
256 gas exchange. After the experiment was complete, Exetainer vials were shipped to West Virginia University, where
257 each gas sample was measured using an LI-6400 (LI-COR Biosciences, Lincoln, NE, USA) and Picarro G2201-i
258 (Picarro Inc., Santa Clara, CA, USA). Glucose and soil organic matter-derived $\text{CO}_2 - \text{C}$ was calculated via mass
259 balance as described in Morrissey et al. (2017). Priming was then calculated as the difference in soil organic matter
260 $\text{CO}_2 - \text{C}$ between the microcosms that received substrate solution and those that received water. At the cessation of
261 the incubation, total microbial biomass was obtained by a chloroform fumigation method (Witt et al., 2000). Briefly,
262 8g of soil was suspended in 45 mL of 0.1 M K_2SO_4 with or without an additional 1ml of ethanol-free chloroform and
263 shaken for 4 hours (chloroform) or 2 hours (no chloroform) and filtered (90 mm GF/A filter paper). Extracts were
264 stored at -20°C until dissolved organic carbon was oxidized to CO_2 via persulfate digestion similar to Doyle et al.
265 (2004). Digestion efficiency was determined using a standard curve of yeast extract solution ranging from (0-200
266 mg C L^{-1}). The concentration and isotopic enrichment of the resulting CO_2 gas were measured on the Picarro. Total
267 and substrate-derived microbial biomass-C was calculated as the difference in C (mg) between chloroformed and
268 non-chloroformed soil extracts. Microbial CUE was calculated as substrate-derived biomass -C divided by the total
269 carbon consumed (substrate-derived $\text{CO}_2 - \text{C}$ and biomass -C) as described in Frey et al. (2013).

270 2.5. Ecosystem productivity

271 To quantify total net primary productivity (NPP) in $\text{kg m}^{-2} \text{ yr}^{-1}$, we summed total litterfall, wood, and
272 root production in each plot for a given year. To estimate wood production, we calculated stem aboveground
273 biomass (AGB) using allometric equations for tropical tree species (Chave et al., 2014). For the allometric
274 equations, we measured height of each stem using a Haglöf EC II-D electronic clinometer (Haglof Inc., Madison,
275 MS, USA) and obtained wood density data from a functional trait database for the TDF of Guanacaste (Powers and
276 Tiffin, 2010; Vargas G. et al., 2021). Mean wood density was substituted for species without wood density data.
277 Annual woody productivity then represented the sum of biomass increments from trees newly recruited into the 2.5
278 cm DBH size class plus biomass gain from increased diameters in planted and existing recruited trees. Additionally,
279 we calculated aboveground net primary productivity (ANPP) by summing only woody and litterfall productivity,
280 and the aboveground:belowground productivity ratios (AGB:BGB) by dividing ANPP by the root production in
281 each plot for each year.



282 2.6. Statistical analysis

283 To test whether the throughfall exclusion structures affected soil moisture, we performed a linear
284 mixed-model with the change in soil moisture for a given plot as the response variable, the presence of the
285 throughfall exclusion structure and the weekly timepoints from January 2017 to December 2020 were fixed effects,
286 and probe nested within plot nested within stand as a random intercept. We ran separate models for each depth (10
287 and 40 cm), and for the wet season and dry season due to the strong rainfall seasonality. To obtain the change in soil
288 moisture per plot, we divided the observation time into two periods, a pre-treatment (May 2016 to August 2016) that
289 consisted of wet season soil moisture data before the shelters were set up, and an experimental period (January 2017
290 to December 2020). We did not consider the period between August and December 2016 as the soil was saturated
291 when we established the rainout shelters. After removing outliers using the interquartile method, we calculated the
292 median pre-treatment soil moisture (SM_{PT} , $m^3 m^{-3}$) for each probe in each plot. We then calculated the treatment
293 effect as the percentage change between each soil moisture observation (SM_i , $m^3 m^{-3}$) and the SM_{PT} . This approach
294 was considered given the high spatial heterogeneity in soil properties among plots (Table S2), making it impossible
295 to compare values of volumetric water content. To investigate inter-annual variation in wet season soil moisture, we
296 fitted an additional linear mixed model to test whether soil moisture in plots without throughfall exclusion varied as
297 a function of year and depth, and probe nested within plot nested within stand as a random intercept. In both cases,
298 we calculated type III sum squares and the F-value for each model and performed Tukey's honest significant
299 difference test (Tukey's HSD) for multiple comparisons.

300 We tested the effects of the experimental treatments on aboveground and belowground processes by
301 fitting a series (one for each response variable) of a two-factorial linear mixed effects model. In these models
302 ecosystem processes were the response variables, the drought treatment was one factor, and the fertilizer treatment
303 the second factor, we included their interaction, and the experimental unit (*e.g.*, litterfall basket) nested within plot,
304 nested within stand as a random intercept. With this model, we were able to estimate the main effect of drought, the
305 main effect of fertilization, and the interaction between drought and fertilization. We then calculated type III sum
306 squares and the F-value for each model in an analysis of variance (ANOVA), with a Tukey's HSD for multiple
307 comparisons. To analyze the response of CUE from soils that were held at field soil moisture to soils that were
308 rewet, we calculated the natural log response ratio [*i.e.*, $\ln(RR)$], defined here as the mean of the rewet soils CUE
309 divided by the mean CUE of the field soil moisture soils. Values of $\ln(RR)$ 0 indicate a decline in CUE to rewetting.
310 All data management, and statistical analysis were done using R software for statistical computing version 3.6.3 (R
311 Core Team, 2021), and the packages *mev*g (Wood, 2004, 2011), *nlme* (Pinheiro et al., 2019), *car* (Fox and
312 Weisberg, 2019), and *tidyverse* (Wickham et al., 2019).

313 3 Results

314 3.1. Soil moisture and fertilization

315 At 40 cm depth, the change in soil moisture as a function of the pre-treatment period was larger in the
316 plots with a throughfall exclusion structure ($\sim -13\%$) than in the plots without it ($\sim -4\%$) (Figure 2). At 10 cm we



317 observed an average change of -15% in throughfall exclusion plots, but this was not significantly different when
318 compared to the non-droughted plots (-9.43%) (Figure 2). Weekly median soil moisture values in the throughfall
319 exclusion plots oscillated between 0.21-0.42 m³ m⁻³ at 10 cm depth and 0.25-0.44 m³ m⁻³ at 40 cm depth, compared
320 to 0.22-0.43 m³ m⁻³ at 10 cm depth and 0.25-0.45 m³ m⁻³ at 40 cm depth for plots without throughfall exclusion
321 (Figure 2). Wet season soil moisture followed the inter-annual rainfall variability in which the average volumetric
322 water content was around 0.39 m³ m⁻³ during 2016 and 2017, while it was around 0.32 m³ m⁻³ from 2018 to 2020
323 (Fig. S6). At the end of four years, extractable soil P increased by 2-3 fold in plots receiving fertilizer, and
324 extractable Fe also increased (Fig. S7); however, none of the other soil chemical variables we measured differed
325 among treatments.

326 3.2. Above-ground responses

327 3.2.1. Tree diameter relative growth rates (RGR_{dbh})

328 We found no evidence of changes in RGR_{dbh} as a function of drought (D) and fertilizer additions (F) for
329 either understory (D: $F\text{-}v = 0.03$, $d.f. = 1$, $p\text{-}v = 0.8601$; F: $F\text{-}v = 0.22$, $d.f. = 1$, $p\text{-}v = 0.6580$) or plantation trees (D:
330 $F\text{-}v = 2.35$, $d.f. = 1$, $p\text{-}v = 0.1489$; F: $F\text{-}v = 1.14$, $d.f. = 1$, $p\text{-}v = 0.3041$). We found moderate evidence of an
331 interaction between drought and fertilizer for both plantation ($F\text{-}v = 5.16$, $d.f. = 1$, $p\text{-}v = \mathbf{0.0499}$) and understory
332 trees ($F\text{-}v = 5.04$, $d.f. = 1$, $p\text{-}v = \mathbf{0.0659}$) (Figure 3). Moreover, nitrogen-fixing functional group explained the
333 differences in RGR_{dbh} for understory ($F\text{-}v = 21.11$, $d.f. = 1$, $p\text{-}v < \mathbf{0.0001}$) and plantation trees ($F\text{-}v = 4.18$, $d.f. = 1$,
334 $p\text{-}v = \mathbf{0.0512}$) (Figure 3) with non-N-fixers showing higher growth rates than N-fixers in both cases. On the other
335 hand, deciduous functional group showed weaker effects on RGR_{dbh} for plantation trees ($F\text{-}v = 3.95$, $d.f. = 1$, $p\text{-}v =$
336 $\mathbf{0.0639}$) (Table S4). In general, RGR_{dbh} varied idiosyncratically among plantation species in response to the
337 experimental treatments, and in many cases RGR_{dbh} in fertilized or drought+fertilizer plots was higher than in the
338 control or drought plots, but we did not find evidence of significant treatment effects (Fig. S8). We also found a
339 higher number of dead trees over the four years in plots with experimental manipulations and hence higher biomass
340 losses (Table S5). Mortality, recruitment, and survival for the trees and shrubs that were recruited in the plots did not
341 differ in response to the experimental treatments (Fig. S9).

342 3.2.2. Canopy productivity

343 The experimental manipulations showed no effects on fine litter production (drought: $F\text{-}v = 0.96$, $d.f. = 1$,
344 $p\text{-}v = 0.3473$; fertilizer: $F\text{-}v = 1.33$, $d.f. = 1$, $p\text{-}v = 0.2724$) and the production of leaves (drought: $F\text{-}v = 0.64$, $d.f. =$
345 1 , $p\text{-}v = 0.4404$; fertilizer: $F\text{-}v = 1.39$, $d.f. = 1$, $p\text{-}v = 0.2646$). Nevertheless, the control plots produced on average
346 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, 13% less
347 than 0.79 ± 0.24 kg m⁻² of the drought plots, and 8% lower than 0.75 ± 0.23 kg m⁻² in drought+fertilizer plots. We
348 also found a 40% decrease in the production of flowers, seeds, and fruits with nutrient additions ($F\text{-}v = 4.84$, $d.f. =$
349 1 , $p\text{-}v = \mathbf{0.0539}$) (Fig. S10), but no effects with the throughfall exclusion ($F\text{-}v = 1.54$, $d.f. = 1$, $p\text{-}v = 0.2449$). In all
350 the plots leaf area index (LAI) increased ~73% from the dry season (median LAI: 1.22) to the wet season (median



351 LAI: 5.10). All the metrics obtained from the LAI measurements showed some degree of change in response to the
352 fertilization treatment as these plots showed the highest maximum LAI (LAI_{max}), longest leaf area duration, shortest
353 leaf-less period, and on average leaf flushing started two weeks earlier than control plots (Fig. S11). However, these
354 changes were marginally significant only for LAI_{max} (F - $v = 3.36$, $d.f. = 1$, p - $v = 0.0928$).

355 3.3. Below-ground responses

356 3.3.1. Fine roots and nodule production

357 We found no evidence that differences in the production of fine roots were due to the throughfall
358 exclusions (F - $v = 0.25$, $d.f. = 1$, p - $v = 0.6227$) or nutrient additions (F - $v = 0.73$, $d.f. = 1$, p - $v = 0.4105$); despite that,
359 root productivity in the control plots ($0.112 \pm 0.06 \text{ kg m}^{-2}$) was ~15% less than in the drought plots with $0.133 \pm$
360 0.09 kg m^{-2} , ~27% less than in the fertilized plots with $0.154 \pm 0.09 \text{ kg m}^{-2}$, and ~24% less than in the
361 drought+fertilizer plots $0.149 \pm 0.12 \text{ kg m}^{-2}$. In general, we observed a decrease in the production of nodules in the
362 fertilization treatment ($\chi^2 = 4.95$, $d.f. = 1$, p - $v = 0.0262$), because only 1 nodule was observed in plots with nutrient
363 additions during the experimental manipulations. Interestingly, nodule production was the highest in plots with
364 drought and drought+fertilizer with 69 and 57 respectively, but we found little evidence this was different from 53
365 nodules counted in the control plots from 2016 to 2020 ($\chi^2 = 0.03$, $d.f. = 1$, p - $v = 0.8589$).

366 3.3.2. Microbial carbon use efficiency (CUE)

367 CUE was ~38% higher in soils from both the drought (F - $v = 4.31$, $d.f. = 1$, p - $v = 0.0621$) and fertilized
368 plots (F - $v = 4.10$, $d.f. = 1$, p - $v = 0.0678$) relative to control plots (Figure 4). When the soils were rewet in the lab,
369 the CUE exhibited a negative response as quantified by the $\ln(RR)$ for both the drought (F - $v = 5.66$, $d.f. = 1$, p - $v =$
370 0.0366) and fertilization treatments (F - $v = 0.73$, $d.f. = 1$, p - $v = 0.0809$) (Figure 4). There were interaction effects
371 between experimental treatments for both the CUE (F - $v = 5.33$, $d.f. = 1$, p - $v = 0.0462$) and $\ln(RR)$ (F - $v = 4.76$, $d.f.$
372 $= 1$, p - $v = 0.0597$), showing evidence of different responses to drought depending on nutrient availability and how
373 CUE was negatively affected by rewetting for drought plots (Figure 4). Soil priming was similarly influenced by
374 rewetting and across all treatments, the soils held at field soil moisture showed negative priming (Fig. S12).
375 Rewetting the soils in the lab led to greater soil C priming in the drought plots (F - $v = 5.33$, $d.f. = 1$, p - $v = 0.0497$),
376 but not in the fertilized plots (F - $v = 0.0191$, $d.f. = 1$, p - $v = 0.8932$) (Fig. S12).

377 3.4. Ecosystem productivity and biomass allocation

378 Ecosystem level fluxes were more responsive to nutrient additions than to the throughfall exclusion (Figure
379 5). Net primary productivity (NPP) increased with nutrient additions (F - $v = 7.86$, $d.f. = 1$, p - $v = 0.0178$), which led
380 to 17% and 19% higher NPP in fertilizer and drought+fertilizer plots respectively relative to the control plots
381 (Figure 5). Although we observed a 14% NPP increase in the drought plots (F - $v = 5.29$, $d.f. = 1$, p - $v = 0.0431$), we
382 found no evidence this was different from the control plots (Figure 5). Consistently, when considering only above-



383 ground net primary productivity (ANPP) we found that fertilizer increased the amount biomass produced (F - v =
384 5.81, $d.f.$ = 1, p - v = **0.0362**) which was 15% and 19% higher for fertilizer and drought+fertilizer plots respectively
385 relative to the control plots (Figure 5). Moreover, the drought treatment decreased ANPP (F - v = 4.58, $d.f.$ = 1, p - v =
386 **0.0575**). We found no evidence that the drought (F - v = 0.30, $d.f.$ = 1, p - v = 0.5960) or fertilizer plots (F - v = 0.35,
387 $d.f.$ = 1, p - v = 0.5645) allocated significantly more belowground biomass, despite the 13 and 15% reduction in the
388 aboveground to belowground ratio observed in the drought and fertilizer plots respectively relative to the control
389 plots (Figure 5). We did not observe interaction effects by the experimental treatments in either NPP (F - v = 1.13,
390 $d.f.$ = 1, p - v = 0.30), ANPP (F - v = 0.77, $d.f.$ = 1, p - v = 0.3991), or AGB:BGB (F - v = 0.34, $d.f.$ = 1, p - v = 0.5695),
391 although the response to nutrient additions in the plots without throughfall exclusions was three and four times
392 higher for NPP and ANPP respectively relative to plots in the drought treatment (Figure 5, panel b).

393 4 Discussion

394 Here we present the first attempt to experimentally test whether the responses of primary productivity and
395 microbial carbon use efficiency to drought are limited by nutrient availability in a tropical ecosystem (Beier et al.,
396 2012). Our experiment is also the only large-scale rainfall manipulation study in the tropical dry forest (TDF) biome
397 (Meir et al., 2015). We found that a 13-15% reduction in soil moisture only leads to modest effects in the studied
398 ecosystem processes. By contrast, extractable P increased in the fertilized plots severalfold (Fig. S7) causing an
399 increase in primary productivity (both NPP and ANPP) (Figure 5), a decrease in the nodule production, a decrease in
400 the production of seeds and flowers (Fig. S10), increases in LAI_{max} and LAD (Fig. S11), and an increase in CUE
401 when compared to the control plots (Figure 4). Variation in tree relative growth rates (RGR_{abh}) were mostly due to
402 functional types rather than the experimental treatments. However, there was a significant interaction in how
403 understory trees responded to both treatments leading to a reduction in the differences between N-fixing and non-N-
404 fixing trees (Figure 3). Collectively, these results suggest that reducing soil moisture by a modest amount is not
405 sufficient to drive large reorganizations in the ecosystem, and that soil nutrient availability has a mild control over
406 short-term changes in TDF productivity. Below, we further explore the implications of these results in the context of
407 how soil fertility could affect tropical ecosystem responses to global environmental change.

408 4.1. Nutrient and water limitations on ecosystem productivity

409 In a broad sense, we found that nutrient availability had a stronger control on forest productivity than a
410 ~15% reduction in soil moisture. While this result does not resonate with the expectation that water availability
411 imposes a greater limitation on productivity across environmental gradients than soil fertility (Harrington et al.,
412 1995; Santiago and Mulkey, 2005; Toledo et al., 2011; Sala et al., 2012; Poorter et al., 2016), it provokes the
413 question to what extent are tropical dry forests resilient to drought stress? Our data point to other aspects related to
414 drought intensity and not soil moisture alone that could be key factors in how water availability shapes TDF primary
415 productivity (Anderegg et al., 2013). Recent studies from northwestern Costa Rica have shown that abnormal
416 drought stress due to a strong ENSO event in 2015 caused biomass loss due to an increase in tree mortality, a



417 decrease in reproductive biomass production, and reductions in productivity (O'Brien et al., 2018; Castro et al.,
418 2018; Powers et al., 2020). The main characteristics of the 2015 ENSO were the elevated temperatures and a
419 substantial rainfall reduction for the region (Santoso et al., 2017), which can increase the severity of drought effects
420 in forest ecosystems due to increased atmospheric water demand (Brodrribb et al., 2020; McDowell et al., 2020).
421 Thus, while throughfall exclusion experiments manipulate soil moisture, it is possible that a combination of factors
422 such as the vapor pressure deficit, the rainfall patterns (intensity and seasonality), and their linkages to soil moisture,
423 is a more important aspect of drought stress for forested ecosystems.

424 We observed the strongest experimental signal in the fertilization treatment (F and D + F) regardless of the
425 throughfall reductions. Such responses agree with known evidence of nutrient limitation on productivity in various
426 tropical forests (Alvarez-Clare et al., 2013; Wright et al., 2018; Waring et al., 2019), which has also been observed
427 in ecosystem models for the TDF (Medvigy et al., 2019). Interestingly the contribution of each biomass flux to NPP
428 depended on the combined effects of drought and fertilization, with root productivity contributing more to droughted
429 plots and woody productivity to fertilized plots (Fig. S13). Such changes in root and woody biomass production are
430 comparable to responses in secondary wet tropical forests to nutrient additions (Wright et al., 2018). In a nearby
431 secondary TDF Waring et al. (2019) found no significant effect of nitrogen and/or phosphorus additions on
432 productivity, however, in contrast to that study, our experiment included the additions of both macro and micro-
433 nutrients (Table S2). Moreover, the increase in productivity as a function of fertilization depended on the presence
434 of throughfall structures with non-drought showing the greatest increase (Figure 5, panel b). This confirms the
435 colimitation of water availability and soil fertility on TDF productivity, where forests in fertile soils are more
436 responsive to increases in rainfall than forests in infertile soils (Becknell et al., 2021). At the same time, our results
437 are comparable to other throughfall exclusion experiments in which fine litter production was not affected by the
438 drought treatment in a consistent manner (Nepstad et al., 2002; Brando et al., 2006; Schwendenmann et al., 2010),
439 with a lot of its variation possibly linked to climatic variability (Brando et al., 2008).

440 **4.2 Canopy dynamics and tree growth**

441 Canopy dynamics did not show strong variation in response to the experimental treatments The timing of
442 leaf flushing, period of no leaves, leaf area duration, and maximum canopy cover showed some mild responses to
443 the fertilization treatment, indicating that added nutrients may allow plants to retain canopy cover for longer periods
444 (Fig. S11). It is possible that the timing of leaf phenology may also depend on intra- and interspecific responses to
445 environmental factors that shape soil water availability including temperature, atmospheric water demand, and soil
446 water retention. For example, the tree species *Coussarea racemosa* A. Rich modified its vegetative and reproductive
447 phenology in response to a rainfall manipulation in the eastern Amazon (Brando et al., 2006), while at the forest
448 level changes were observed in LAI_{max} but not the timing of leaf production (Brando et al., 2008). In a throughfall
449 exclusion experiment combined with fertilization in loblolly pine (*Pinus taeda* L.) plantation there were no changes
450 in the LAI_{max} in response to rainfall reduction but an increase in the LAI_{max} in the fertilized plots (Samuelson et al.,
451 2014), which is qualitatively consistent with our data.



452 No species showed significant changes in RGR_{dbh} , but the understory trees showed a reduction in the
453 differences between N-fixing and non-N-fixing trees. For F and D this was due to a reduction in growth rates by
454 non-N-fixing trees, while for D+F due to an increase in the growth rates by N-fixing trees (Figure 4). One possible
455 reason for these patterns could be increased resource availability due to decreased competition. The D+F plots in
456 which these three species were present experiences the highest biomass losses due to mortality during the four years
457 of experimental manipulation (Table S5; Fig. S11). Even though it is hard to determine the cause of death, an initial
458 spike in tree mortality has been observed in a long-term throughfall exclusion experiment in the Amazon (Costa et
459 al., 2010), which also caused an increase in growth rates of remaining trees (Rowland et al., 2015). Interestingly,
460 Meir et al. (2018) found that tree growth and mortality in the same experiment reached an equilibrium in the long-
461 term (> 10 years), reporting similar values to trees in a 1 ha plot without rainfall manipulation. The lack of
462 responsiveness in the F and D plots, in addition to the biomass losses in some of the D+F plots (Table S5), supports
463 the idea that the availability of resources could be the cause of higher RGR_{dbh} in the D+F compared to the other
464 treatments (Fig. S14). The lowest RGR_{dbh} were found in plots with the D treatment, with the strongest experimental
465 effect on *D. retusa*, *E. cyclocarpum*, and *S. glauca* (Fig. S8). These results are very similar to what has been found
466 in other tropical throughfall exclusion experiments (Meir et al., 2015), in which there is an overall negative effect in
467 tree diameter growth by a decrease in soil moisture.

468 4.3 Belowground responses

469 The fertilized plots showed no nodule production. This observed trend suggests that nutrient addition
470 alleviates limitations for legumes (Toro et al. 2022), and confirms the facultative nature of nodulation (Barron et al.,
471 2011). On the other hand, nodule production was the highest for both drought treatments (D and D+F). In part, a
472 decrease in soil moisture slows down the rate of nitrogen mineralization and limits plant nutrient uptake (Borken and
473 Matzner, 2009; He and Dijkstra, 2014). Comparable to our results, the legume species *Robinia pseudoacacia* L. also
474 increased nodulation in a drought experiment (Wurzburger and Miniat, 2014). Moreover, trees tend to rely more on
475 deeper water sources with less access to nutrients (Querejeta et al., 2021), which might also enhance nodulation in
476 legumes. Collectively, our data and these studies suggest that the effects of soil moisture reduction go beyond
477 ecosystem water/carbon balance and could cause a domino effect that might alter forest biogeochemistry.

478 Our soil incubation results suggest that global change has the potential to alter microbial CUE and the
479 susceptibility of soil carbon to pulse rainfall events in tropical dry forests. After three years of treatment, soil
480 microbes in the D and F soils had significant increases in CUE (Figure 4). Increases in CUE are commonly
481 attributed to shifts in the microbial community (Domeignoz-Horta et al., 2020) or a reduction in carbon investment
482 by microbes in enzymes to fuel the nutrient acquisition (Manzoni et al., 2012). In this experiment, however, the
483 increases in CUE in the D and F soils but not the D + F soils hinder our ability to narrow down which of these
484 mechanisms may be driving our results. Quantifying the shifts in microbial community composition, as well as the
485 identity of microbes that are active decomposers, may shed light on the mechanistic underpinning of the CUE
486 response observed here. Importantly, these differences in CUE across treatments also appeared to impact the
487 response of the soils to large, simulated rainfall events. Regardless of treatment, rewetting the soils to water holding



488 capacity led to a large reduction in CUE (Figure 4). While not statistically significant, there was a clear trend of
489 greater CUE declines in the treatment soils, particularly the D soils. This trend suggests that when large rainfall
490 events occur in disturbed soils; these decreases in microbial CUE could potentially lead to a stronger Birch Effect
491 and enhance the soil C loss (Schimel, 2018). In support, we found that rewetting the soils also led to the glucose
492 addition driving greater priming of soil carbon losses, a result that was particularly pronounced for the D soils (Fig.
493 S12). By contrast, the glucose addition in soils that were held at field soil moisture conditions led to the net
494 mineralization of soil C by the microbial community. Collectively, our soil incubation results highlight a critical
495 need for more research on the potential for global change to lead to shifts in microbial community composition and
496 traits in TDFs.

497 **5 Conclusions**

498 Our results highlight that forest productivity responses to is sensitive to soil fertility and that this modulates
499 how TDFs tree species respond to reductions in soil moisture. However, despite adding both macro- and micro-
500 nutrients, our results confirm that the short-term responses of tropical trees to fertilization treatments are modest at
501 best. At the same time, the nodulation data indicate that there might be a tight coupling between nutrient availability
502 and water availability in this system. Studying the role of soil moisture on plant nutrient acquisition dynamics
503 remains a largely unexplored venue in TDF ecology. Moreover, little is known of how these belowground processes
504 interact with microbial community dynamics, such as CUE, also affected by nutrient additions or reductions in soil
505 moisture. Beyond these processes, disentangling the causes and consequences of colimitation by water and nutrients
506 in productivity could help to elucidate how future climatic conditions will affect carbon cycling in the TDF.

507 **6 Data availability**

508 The data reported in this publication and associated R code for statistical analysis can be found in the
509 following DRYAD repository: Vargas G., German et al. (2022), Throughfall exclusion and fertilization effects on
510 tropical dry forest tree plantations, a large-scale experiment, Dryad, Dataset,
511 <https://doi.org/10.5061/dryad.5x69p8d6r>

512 **7 Author contribution**

513 GVG, BGW, DM, DPA and JSP designed the experiments. GVG, DPA, LDPA, DPAR, JTT and NR
514 performed field measurements. NR and EM performed CUE laboratory measurements. GVG processed the field
515 data. GVG and NR performed statistical analyses with input from EB and JSP. GVG wrote the initial draft with
516 input from JSP. All authors contributed with edits and feedback in subsequent versions.

517 **8 Competing interests**



518 David Medvigy is a member of the editorial board of Biogeosciences. The remaining authors have no
519 conflicts of interest to declare.

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529 **10 References**

- 530 Aguirre-Gutiérrez, J., Malhi, Y., Lewis, S. L., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T. R.,
531 Gvozdevaite, A., Hubau, W., Moore, S., Peprah, T., Ziemnińska, K., Phillips, O. L., and Oliveras, I.: Long-term
532 droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity,
533 *Nature Communications*, 11, <https://doi.org/10.1038/s41467-020-16973-4>, 2020.
- 534 Allen, K., Dupuy, J. M., Gei, M. G., Hulshof, C., Medvigy, D., Pizano, C., Salgado-Negret, B., Smith, C. M.,
535 Trierweiler, A., Bloem, S. J. V., Waring, B. G., Xu, X., and Powers, J. S.: Will seasonally dry tropical forests be
536 sensitive or resistant to future changes in rainfall regimes?, *Environ. Res. Lett.*, 12, 023001,
537 <https://doi.org/10.1088/1748-9326/aa5968>, 2017.
- 538 Alvarez-Clare, S., Mack, M. C., and Brooks, M.: A direct test of nitrogen and phosphorus limitation to net primary
539 productivity in a lowland tropical wet forest, *Ecology*, 94, 1540–1551, <https://doi.org/10.1890/12-2128.1>, 2013.
- 540 Anderegg, L. D. L., Anderegg, W. R. L., and Berry, J. A.: Not all droughts are created equal: translating
541 meteorological drought into woody plant mortality, *Tree Physiol*, 33, 672–683,
542 <https://doi.org/10.1093/treephys/tpt044>, 2013.
- 543 Aragão, L. E. O. C., Malhi, Y., Roman-Cuesta, R. M., Saatchi, S., Anderson, L. O., and Shimabukuro, Y. E.: Spatial
544 patterns and fire response of recent Amazonian droughts, *Geophysical Research Letters*, 34,
545 <https://doi.org/10.1029/2006GL028946>, 2007.
- 546 Augusto, L., Achat, D. L., Jonard, M., Vidal, D., and Ringeval, B.: Soil parent material—A major driver of plant
547 nutrient limitations in terrestrial ecosystems, *Global Change Biology*, 23, 3808–3824,
548 <https://doi.org/10.1111/gcb.13691>, 2017.
- 549 Barron, A. R., Purves, D. W., and Hedin, L. O.: Facultative nitrogen fixation by canopy legumes in a lowland
550 tropical forest, *Oecologia*, 165, 511–520, <https://doi.org/10.1007/s00442-010-1838-3>, 2011.



- 551 Becknell, J. M., Vargas G., G., Pérez-Aviles, D., Medvigy, D., and Powers, J. S.: Above-ground net primary
552 productivity in regenerating seasonally dry tropical forest: Contributions of rainfall, forest age and soil, *Journal of*
553 *Ecology*, 109, 3903–3915, <https://doi.org/10.1111/1365-2745.13767>, 2021.
- 554 Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Körner, C., Boeck, H. de, Christensen, J.
555 H., Leuzinger, S., Janssens, I. A., and Hansen, K.: Precipitation manipulation experiments – challenges and
556 recommendations for the future, *Ecology Letters*, 15, 899–911, <https://doi.org/10.1111/j.1461-0248.2012.01793.x>,
557 2012.
- 558 Bonan, G. B.: Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests, *Science*, 320,
559 1444–1449, <https://doi.org/10.1126/science.1155121>, 2008.
- 560 Borchert, R.: Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees,
561 *Ecology*, 75, 1437–1449, <https://doi.org/10.2307/1937467>, 1994.
- 562 Borken, W. and Matzner, E.: Reappraisal of drying and wetting effects on C and N mineralization and fluxes in
563 soils, *Global Change Biology*, 15, 808–824, <https://doi.org/10.1111/j.1365-2486.2008.01681.x>, 2009.
- 564 Brando, P. M., Ray, D., Nepstad, D., Cardinot, G., Curran, L. M., and Oliveira, R.: Effects of partial throughfall
565 exclusion on the phenology of *Coussarea racemosa* (Rubiaceae) in an east-central Amazon rainforest, *Oecologia*,
566 150, 181–189, <https://doi.org/10.1007/s00442-006-0507-z>, 2006.
- 567 Brando, P. M., Nepstad, D. C., Davidson, E. A., Trumbore, S. E., Ray, D., and Camargo, P.: Drought effects on
568 litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction
569 experiment, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 1839–1848,
570 <https://doi.org/10.1098/rstb.2007.0031>, 2008.
- 571 Brando, P. M., Balch, J. K., Nepstad, D. C., Morton, D. C., Putz, F. E., Coe, M. T., Silvério, D., Macedo, M. N.,
572 Davidson, E. A., Nóbrega, C. C., Alencar, A., and Soares-Filho, B. S.: Abrupt increases in Amazonian tree mortality
573 due to drought–fire interactions, *PNAS*, 111, 6347–6352, <https://doi.org/10.1073/pnas.1305499111>, 2014.
- 574 Brodribb, T. J., Powers, J., Cochard, H., and Choat, B.: Hanging by a thread? Forests and drought, *Science*, 368,
575 261–266, <https://doi.org/10.1126/science.aat7631>, 2020.
- 576 Castro, S. M., Sanchez-Azofeifa, G. A., and Sato, H.: Effect of drought on productivity in a Costa Rican tropical dry
577 forest, *Environ. Res. Lett.*, 13, 045001, <https://doi.org/10.1088/1748-9326/aaacbc>, 2018.
- 578 Chadwick, R., Good, P., Martin, G., and Rowell, D. P.: Large rainfall changes consistently projected over
579 substantial areas of tropical land, *Nature Climate Change*, 6, <https://doi.org/10.1038/nclimate2805>, 2016.
- 580 Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T.,
581 Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W. A., Muller-Landau, H. C.,
582 Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan,
583 C. M., Saldarriaga, J. G., and Vieilledent, G.: Improved allometric models to estimate the aboveground biomass of
584 tropical trees, *Global Change Biology*, 20, 3177–3190, <https://doi.org/10.1111/gcb.12629>, 2014.
- 585 Chazdon, R. L., Redondo Brenes, A., and Vilchez Alvarado, B.: Effects of Climate and Stand Age on Annual Tree
586 Dynamics in Tropical Second-Growth Rain Forests, *Ecology*, 86, 1808–1815, <https://doi.org/10.1890/04-0572>,
587 2005.



- 588 Clark, D. B. and Clark, D. A.: Landscape-scale variation in forest structure and biomass in a tropical rain forest,
589 *Forest Ecology and Management*, 137, 185–198, [https://doi.org/10.1016/S0378-1127\(99\)00327-8](https://doi.org/10.1016/S0378-1127(99)00327-8), 2000.
- 590 Coley, P. D.: Possible Effects of Climate Change on Plant/Herbivore Interactions in Moist Tropical Forests,
591 *Climatic Change*, 39, 455–472, <https://doi.org/10.1023/A:1005307620024>, 1998.
- 592 Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R., and Turner, B. L.: Species distributions in response to
593 individual soil nutrients and seasonal drought across a community of tropical trees, *PNAS*, 110, 5064–5068,
594 <https://doi.org/10.1073/pnas.1218042110>, 2013.
- 595 Costa, A. C. L. da, Galbraith, D., Almeida, S., Portela, B. T. T., Costa, M. da, Junior, J. de A. S., Braga, A. P.,
596 Gonçalves, P. H. L. de, Oliveira, A. A. de, Fisher, R., Phillips, O. L., Metcalfe, D. B., Levy, P., and Meir, P.: Effect
597 of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest,
598 *New Phytologist*, 187, 579–591, <https://doi.org/10.1111/j.1469-8137.2010.03309.x>, 2010.
- 599 Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., and Paul, E.: The Microbial Efficiency-Matrix
600 Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do
601 labile plant inputs form stable soil organic matter?, *Global Change Biology*, 19, 988–995,
602 <https://doi.org/10.1111/gcb.12113>, 2013.
- 603 Domeignoz-Horta, L. A., Pold, G., Liu, X.-J. A., Frey, S. D., Melillo, J. M., and DeAngelis, K. M.: Microbial
604 diversity drives carbon use efficiency in a model soil, *Nat Commun*, 11, 3684, <https://doi.org/10.1038/s41467-020-17502-z>, 2020.
- 606 Doughty, C. E. and Goulden, M. L.: Seasonal patterns of tropical forest leaf area index and CO₂ exchange, *Journal*
607 *of Geophysical Research: Biogeosciences*, 113, <https://doi.org/10.1029/2007JG000590>, 2008.
- 608 Ewert, F. and Pleijel, H.: Phenological development, leaf emergence, tillering and leaf area index, and duration of
609 spring wheat across Europe in response to CO₂ and ozone, *European Journal of Agronomy*, 10, 171–184,
610 [https://doi.org/10.1016/S1161-0301\(99\)00008-8](https://doi.org/10.1016/S1161-0301(99)00008-8), 1999.
- 611 Feng, X., Porporato, A., and Rodriguez-Iturbe, I.: Changes in rainfall seasonality in the tropics, *Nature Clim*
612 *Change*, 3, 811–815, <https://doi.org/10.1038/nclimate1907>, 2013.
- 613 Fox, J. and Weisberg, S.: *An {R} Companion to Applied Regression*, Third., Sage, Thousand Oaks, CA, 2019.
- 614 Frankie, G. W., Baker, H. G., and Opler, P. A.: Comparative Phenological Studies of Trees in Tropical Wet and Dry
615 Forests in the Lowlands of Costa Rica, *Journal of Ecology*, 62, 881–919, <https://doi.org/10.2307/2258961>, 1974.
- 616 Frey, S. D., Lee, J., Melillo, J. M., and Six, J.: The temperature response of soil microbial efficiency and its
617 feedback to climate, *Nature Clim Change*, 3, 395–398, <https://doi.org/10.1038/nclimate1796>, 2013.
- 618 González-M, R., Posada, J. M., Carmona, C. P., Garzón, F., Salinas, V., Idárraga-Piedrahita, Á., Pizano, C., Avella,
619 A., López-Camacho, R., Norden, N., Nieto, J., Medina, S. P., Rodríguez-M, G. M., Franke-Ante, R., Torres, A. M.,
620 Jurado, R., Cuadros, H., Castaño-Naranjo, A., García, H., and Salgado-Negret, B.: Diverging functional strategies
621 but high sensitivity to an extreme drought in tropical dry forests, *Ecology Letters*, 24, 451–463,
622 <https://doi.org/10.1111/ele.13659>, 2021.
- 623 Gutiérrez-Leitón, M.: Opciones para reforestación comercial con especies nativas en zonas secas de Costa Rica,
624 *Ambientico*, 267, 28–31, 2018.



- 625 Harrington, R. A., Fownes, J. H., Meinzer, F. C., and Scowcroft, P. G.: Forest growth along a rainfall gradient in
626 Hawaii: Acacia koa stand structure, productivity, foliar nutrients, and water- and nutrient-use efficiencies,
627 *Oecologia*, 102, 277–284, <https://doi.org/10.1007/BF00329794>, 1995.
- 628 He, M. and Dijkstra, F. A.: Drought effect on plant nitrogen and phosphorus: a meta-analysis, *New Phytologist*, 204,
629 924–931, <https://doi.org/10.1111/nph.12952>, 2014.
- 630 Hietz, P., Turner, B. L., Wanek, W., Richter, A., Nock, C. A., and Wright, S. J.: Long-Term Change in the Nitrogen
631 Cycle of Tropical Forests, *Science*, 334, 664–666, <https://doi.org/10.1126/science.1211979>, 2011.
- 632 Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., and Roberts, C.: Confronting a biome crisis: global disparities of
633 habitat loss and protection, *Ecology Letters*, 8, 23–29, <https://doi.org/10.1111/j.1461-0248.2004.00686.x>, 2005.
- 634 Hou, E., Luo, Y., Kuang, Y., Chen, C., Lu, X., Jiang, L., Luo, X., and Wen, D.: Global meta-analysis shows
635 pervasive phosphorus limitation of aboveground plant production in natural terrestrial ecosystems, *Nat Commun*,
636 11, 637, <https://doi.org/10.1038/s41467-020-14492-w>, 2020.
- 637 Janzen, D. H.: Patterns of Herbivory in a Tropical Deciduous Forest, *Biotropica*, 13, 271–282,
638 <https://doi.org/10.2307/2387805>, 1981.
- 639 Knorr, W., Prentice, I. C., House, J. I., and Holland, E. A.: Long-term sensitivity of soil carbon turnover to warming,
640 *Nature*, 433, 298–301, <https://doi.org/10.1038/nature03226>, 2005.
- 641 Lambers, H., Chapin, F. S., and Pons, T. L.: Photosynthesis, in: *Plant Physiological Ecology*, edited by: Lambers,
642 H., Chapin, F. S., and Pons, T. L., Springer, New York, NY, 11–99, https://doi.org/10.1007/978-0-387-78341-3_2,
643 2008.
- 644 Lewis, S. L.: Tropical forests and the changing earth system, *Philosophical Transactions of the Royal Society B:*
645 *Biological Sciences*, 361, 195–210, <https://doi.org/10.1098/rstb.2005.1711>, 2006.
- 646 Lu, X., Vitousek, P. M., Mao, Q., Gilliam, F. S., Luo, Y., Zhou, G., Zou, X., Bai, E., Scanlon, T. M., Hou, E., and
647 Mo, J.: Plant acclimation to long-term high nitrogen deposition in an N-rich tropical forest, *PNAS*, 115, 5187–5192,
648 <https://doi.org/10.1073/pnas.1720777115>, 2018.
- 649 Lugo, A. E. and Murphy, P. G.: Nutrient dynamics of a Puerto Rican subtropical dry forest, *J. Trop. Ecol.*, 2, 55–72,
650 <https://doi.org/10.1017/S0266467400000602>, 1986.
- 651 Manzoni, S., Taylor, P., Richter, A., Porporato, A., and Ågren, G. I.: Environmental and stoichiometric controls on
652 microbial carbon-use efficiency in soils, *New Phytologist*, 196, 79–91, [https://doi.org/10.1111/j.1469-
653 8137.2012.04225.x](https://doi.org/10.1111/j.1469-), 2012.
- 654 Matson, P. A., McDowell, W. H., Townsend, A. R., and Vitousek, P. M.: The globalization of N deposition:
655 ecosystem consequences in tropical environments, *Biogeochemistry*, 46, 67–83,
656 <https://doi.org/10.1007/BF01007574>, 1999.
- 657 McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clark, J. S.,
658 Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein,
659 J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., Turner, M. G., Uriarte, M., Walker, A. P., and Xu, C.:
660 Pervasive shifts in forest dynamics in a changing world, *Science*, 368, eaaz9463,
661 <https://doi.org/10.1126/science.aaz9463>, 2020.



- 662 Medvigy, D., Wang, G., Zhu, Q., Riley, W. J., Trierweiler, A. M., Waring, B. G., Xu, X., and Powers, J. S.:
663 Observed variation in soil properties can drive large variation in modelled forest functioning and composition during
664 tropical forest secondary succession, *New Phytologist*, 223, 1820–1833, <https://doi.org/10.1111/nph.15848>, 2019.
- 665 Meir, P., Wood, T. E., Galbraith, D. R., Brando, P. M., Da Costa, A. C. L., Rowland, L., and Ferreira, L. V.:
666 Threshold Responses to Soil Moisture Deficit by Trees and Soil in Tropical Rain Forests: Insights from Field
667 Experiments, *BioScience*, 65, 882–892, <https://doi.org/10.1093/biosci/biv107>, 2015.
- 668 Meir, P., Mencuccini, M., Binks, O., da Costa, A. L., Ferreira, L., and Rowland, L.: Short-term effects of drought on
669 tropical forest do not fully predict impacts of repeated or long-term drought: gas exchange versus growth,
670 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, 20170311,
671 <https://doi.org/10.1098/rstb.2017.0311>, 2018.
- 672 Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., Kapos, V., and Gordon, J. E.: A global
673 overview of the conservation status of tropical dry forests, *Journal of Biogeography*, 33, 491–505,
674 <https://doi.org/10.1111/j.1365-2699.2005.01424.x>, 2006.
- 675 Minorsky, P. V.: The functions of foliar nyctinasty: a review and hypothesis, *Biological Reviews*, 94, 216–229,
676 <https://doi.org/10.1111/brv.12444>, 2019.
- 677 Morrissey, E. M., Mau, R. L., Schwartz, E., McHugh, T. A., Dijkstra, P., Koch, B. J., Marks, J. C., and Hungate, B.
678 A.: Bacterial carbon use plasticity, phylogenetic diversity and the priming of soil organic matter., *The ISME journal*,
679 11, 1890–1899, <http://dx.doi.org/10.1038/ismej.2017.43>, 2017.
- 680 Murphy, P. G. and Lugo, A. E.: Ecology of tropical dry forest, *Annu. Rev. Ecol. Syst.*, 17, 67–88,
681 <https://doi.org/10.1146/annurev.es.17.110186.000435>, 1986.
- 682 Nepstad, D. C., Moutinho, P., Dias-Filho, M. B., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna,
683 N., Chambers, J., Ray, D., Guerreiros, J. B., Lefebvre, P., Sternberg, L., Moreira, M., Barros, L., Ishida, F. Y.,
684 Tohler, I., Belk, E., Kalif, K., and Schwalbe, K.: The effects of partial throughfall exclusion on canopy processes,
685 aboveground production, and biogeochemistry of an Amazon forest, *Journal of Geophysical Research:*
686 *Atmospheres*, 107, LBA 53-1-LBA 53-18, <https://doi.org/10.1029/2001JD000360>, 2002.
- 687 Neves, F. S., Silva, J. O., Espírito-Santo, M. M., and Fernandes, G. W.: Insect Herbivores and Leaf Damage along
688 Successional and Vertical Gradients in a Tropical Dry Forest, *Biotropica*, 46, 14–24,
689 <https://doi.org/10.1111/btp.12068>, 2014.
- 690 Norby, R. J., Sholtis, J. D., Gunderson, C. A., and Jawdy, S. S.: Leaf dynamics of a deciduous forest canopy: no
691 response to elevated CO₂, *Oecologia*, 136, 574–584, <https://doi.org/10.1007/s00442-003-1296-2>, 2003.
- 692 O'Brien, M. J., Pérez-Aviles, D., and Powers, J. S.: Resilience of seed production to a severe El Niño-induced
693 drought across functional groups and dispersal types, *Global Change Biology*, 24, 5270–5280,
694 <https://doi.org/10.1111/gcb.14416>, 2018.
- 695 Oliveira, R. S., Eller, C. B., Barros, F. de V., Hirota, M., Brum, M., and Bittencourt, P.: Linking plant hydraulics
696 and the fast–slow continuum to understand resilience to drought in tropical ecosystems, *New Phytologist*, 230, 904–
697 923, <https://doi.org/10.1111/nph.17266>, 2021.



- 698 Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G., Malhi, Y.,
699 Monteagudo, A., Peacock, J., Quesada, C. A., Heijden, G. van der, Almeida, S., Amaral, I., Arroyo, L., Aymard, G.,
700 Baker, T. R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., Oliveira, Á. C. A. de, Cardozo, N. D., Czimczik,
701 C. I., Feldpausch, T. R., Freitas, M. A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C.,
702 Morel, A., Neill, D. A., Nepstad, D., Patiño, S., Peñuela, M. C., Prieto, A., Ramírez, F., Schwarz, M., Silva, J.,
703 Silveira, M., Thomas, A. S., Steege, H. ter, Stropp, J., Vásquez, R., Zelazowski, P., Dávila, E. A., Andelman, S.,
704 Andrade, A., Chao, K.-J., Erwin, T., Fiore, A. D., C. E. H., Keeling, H., Killeen, T. J., Laurance, W. F., Cruz, A. P.,
705 Pitman, N. C. A., Vargas, P. N., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J., and Torres-
706 Lezama, A.: Drought Sensitivity of the Amazon Rainforest, *Science*, 323, 1344–1347,
707 <https://doi.org/10.1126/science.1164033>, 2009.
- 708 Phillips, R. P., Ibáñez, I., D’Orangeville, L., Hanson, P. J., Ryan, M. G., and McDowell, N. G.: A belowground
709 perspective on the drought sensitivity of forests: Towards improved understanding and simulation, *Forest Ecology*
710 *and Management*, 380, 309–320, <https://doi.org/10.1016/j.foreco.2016.08.043>, 2016.
- 711 Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., and Zhu, X.: Plant phenology
712 and global climate change: Current progresses and challenges, *Global Change Biology*, 25, 1922–1940,
713 <https://doi.org/10.1111/gcb.14619>, 2019.
- 714 Pinheiro, J., Bates, D., DebRoy, S., Starkar, S., and R Core Team: *nlme: Linear and Nonlinear Mixed Effects*
715 *Models*, 2019.
- 716 Pokorný, R., Tomášková, I., and Havránková, K.: Temporal variation and efficiency of leaf area index in young
717 mountain Norway spruce stand, *Eur J Forest Res*, 127, 359–367, <https://doi.org/10.1007/s10342-008-0212-z>, 2008.
- 718 Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., Boukili, V.,
719 Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Craven, D., de Almeida-Cortez, J. S., Cabral, G. A. L., de
720 Jong, B. H. J., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., Espírito-Santo, M. M.,
721 Fandino, M. C., César, R. G., Hall, J. S., Hernandez-Stefanoni, J. L., Jakovac, C. C., Junqueira, A. B., Kennard, D.,
722 Letcher, S. G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J. A.,
723 Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y. R. F., Ochoa-Gaona, S., de Oliveira, A. A., Orihuela-
724 Belmonte, E., Peña-Claros, M., Pérez-García, E. A., Piotta, D., Powers, J. S., Rodríguez-Velázquez, J., Romero-
725 Pérez, I. E., Ruíz, J., Saldarriaga, J. G., Sanchez-Azofeifa, A., Schwartz, N. B., Steininger, M. K., Swenson, N. G.,
726 Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M. D. M., Vester, H. F. M., Vicentini, A.,
727 Vieira, I. C. G., Bentos, T. V., Williamson, G. B., and Rozendaal, D. M. A.: Biomass resilience of Neotropical
728 secondary forests, *Nature*, 530, 211–214, <https://doi.org/10.1038/nature16512>, 2016.
- 729 Powers, J. S. and Tiffin, P.: Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit
730 versus taxonomic approaches, *Functional Ecology*, 24, 927–936, <https://doi.org/10.1111/j.1365-2435.2010.01701.x>,
731 2010.
- 732 Powers, J. S., Vargas G., G., Brodribb, T. J., Schwartz, N. B., Pérez-Aviles, D., Smith-Martin, C. M., Becknell, J.
733 M., Aureli, F., Blanco, R., Calderón-Morales, E., Calvo-Alvarado, J. C., Calvo-Obando, A. J., Chavarría, M. M.,
734 Carvajal-Vanegas, D., Jiménez-Rodríguez, C. D., Chacon, E. M., Schaffner, C. M., Werden, L. K., Xu, X., and



- 735 Medvigy, D.: A catastrophic tropical drought kills hydraulically vulnerable tree species, *Global Change Biology*, 26,
736 3122–3133, <https://doi.org/10.1111/gcb.15037>, 2020.
- 737 Querejeta, J. I., Ren, W., and Prieto, I.: Vertical decoupling of soil nutrients and water under climate warming
738 reduces plant cumulative nutrient uptake, water-use efficiency and productivity, *New Phytologist*, 230, 1378–1393,
739 <https://doi.org/10.1111/nph.17258>, 2021.
- 740 Quesada-Román, A., Ballesteros-Cánovas, J. A., Granados-Bolaños, S., Birkel, C., and Stoffel, M.:
741 Dendrogeomorphic reconstruction of floods in a dynamic tropical river, *Geomorphology*, 359, 107133,
742 <https://doi.org/10.1016/j.geomorph.2020.107133>, 2020.
- 743 R Core Team: R: A language and environment for statistical computing, 2021.
- 744 Reich, P. B. and Borchert, R.: Water Stress and Tree Phenology in a Tropical Dry Forest in the Lowlands of Costa
745 Rica, *Journal of Ecology*, 72, 61–74, <https://doi.org/10.2307/2260006>, 1984.
- 746 Rowland, L., da Costa, A. C. L., Galbraith, D. R., Oliveira, R. S., Binks, O. J., Oliveira, A. a. R., Pullen, A. M.,
747 Doughty, C. E., Metcalfe, D. B., Vasconcelos, S. S., Ferreira, L. V., Malhi, Y., Grace, J., Mencuccini, M., and Meir,
748 P.: Death from drought in tropical forests is triggered by hydraulics not carbon starvation, *Nature*, 528, 119–122,
749 <https://doi.org/10.1038/nature15539>, 2015.
- 750 Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbágy, E., and Peters, D.: Legacies of precipitation fluctuations on
751 primary production: theory and data synthesis, *Philosophical Transactions of the Royal Society B: Biological*
752 *Sciences*, 367, 3135–3144, <https://doi.org/10.1098/rstb.2011.0347>, 2012.
- 753 Samuelson, L. J., Pell, C. J., Stokes, T. A., Bartkowiak, S. M., Akers, M. K., Kane, M., Markewitz, D., McGuire, M.
754 A., and Teskey, R. O.: Two-year throughfall and fertilization effects on leaf physiology and growth of loblolly pine
755 in the Georgia Piedmont, *Forest Ecology and Management*, 330, 29–37,
756 <https://doi.org/10.1016/j.foreco.2014.06.030>, 2014.
- 757 Santiago, L. S.: Nutrient limitation of eco-physiological processes in tropical trees, *Trees*, 29, 1291–1300,
758 <https://doi.org/10.1007/s00468-015-1260-x>, 2015.
- 759 Santiago, L. S. and Mulkey, S. S.: Leaf productivity along a precipitation gradient in lowland Panama: patterns from
760 leaf to ecosystem, *Trees*, 19, 349–356, <https://doi.org/10.1007/s00468-004-0389-9>, 2005.
- 761 Santoso, A., Mcphaden, M. J., and Cai, W.: The Defining Characteristics of ENSO Extremes and the Strong
762 2015/2016 El Niño, *Reviews of Geophysics*, 55, 1079–1129, <https://doi.org/10.1002/2017RG000560>, 2017.
- 763 Schimel, J., Balsler, T. C., and Wallenstein, M.: Microbial Stress-Response Physiology and Its Implications for
764 Ecosystem Function, *Ecology*, 88, 1386–1394, <https://doi.org/10.1890/06-0219>, 2007.
- 765 Schimel, J. P.: Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes, *Annu. Rev.*
766 *Ecol. Evol. Syst.*, 49, 409–432, <https://doi.org/10.1146/annurev-ecolsys-110617-062614>, 2018.
- 767 Schwendenmann, L., Veldkamp, E., Moser, G., Hölscher, D., Köhler, M., Clough, Y., Anas, I., Djajakirana, G.,
768 Erasmí, S., Hertel, D., Leitner, D., Leuschner, C., Michalzik, B., Propastin, P., Tjoa, A., Tschardtke, T., and
769 Straaten, O. V.: Effects of an experimental drought on the functioning of a cacao agroforestry system, Sulawesi,
770 Indonesia, *Global Change Biology*, 16, 1515–1530, <https://doi.org/10.1111/j.1365-2486.2009.02034.x>, 2010.



- 771 Seneviratne, S. I., Corti, T., Davin, E. L., Hirschi, M., Jaeger, E. B., Lehner, I., Orlowsky, B., and Teuling, A. J.:
772 Investigating soil moisture–climate interactions in a changing climate: A review, *Earth-Science Reviews*, 99, 125–
773 161, <https://doi.org/10.1016/j.earscirev.2010.02.004>, 2010.
- 774 Smith, N. G., Rodgers, V. L., Brzostek, E. R., Kulmatiski, A., Avolio, M. L., Hoover, D. L., Koerner, S. E., Grant,
775 K., Jentsch, A., Fatichi, S., and Niyogi, D.: Toward a better integration of biological data from precipitation
776 manipulation experiments into Earth system models, *Reviews of Geophysics*, 52, 412–434,
777 <https://doi.org/10.1002/2014RG000458>, 2014.
- 778 Swenson, N. G., Hulshof, C. M., Katabuchi, M., and Enquist, B. J.: Long-term shifts in the functional composition
779 and diversity of a tropical dry forest: a 30-yr study, *Ecological Monographs*, 90, e01408,
780 <https://doi.org/10.1002/ecm.1408>, 2020.
- 781 Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leñaño, C., Licona, J. C., Llanque, O., Vroomans,
782 V., Zuidema, P., and Bongers, F.: Climate is a stronger driver of tree and forest growth rates than soil and
783 disturbance, *Journal of Ecology*, 99, 254–264, <https://doi.org/10.1111/j.1365-2745.2010.01741.x>, 2011.
- 784 Townsend, A. R., Asner, G. P., and Cleveland, C. C.: The biogeochemical heterogeneity of tropical forests, *Trends*
785 *in Ecology & Evolution*, 23, 424–431, <https://doi.org/10.1016/j.tree.2008.04.009>, 2008.
- 786 Vargas G., G., Werden, L. K., and Powers, J. S.: Explaining Legume Success in Tropical Dry Forests Based on Seed
787 Germination Niches: A New Hypothesis, *Biotropica*, 47, 277–280, <https://doi.org/10.1111/btp.12210>, 2015.
- 788 Vargas G., G., Brodrigg, T. J., Dupuy, J. M., González-M., R., Hulshof, C. M., Medvigy, D., Allerton, T. A. P.,
789 Pizano, C., Salgado-Negret, B., Schwartz, N. B., Van Bloem, S. J., Waring, B. G., and Powers, J. S.: Beyond leaf
790 habit: generalities in plant function across 97 tropical dry forest tree species, *New Phytologist*, 232, 148–161,
791 <https://doi.org/10.1111/nph.17584>, 2021.
- 792 Wang, R., Goll, D., Balkanski, Y., Hauglustaine, D., Boucher, O., Ciais, P., Janssens, I., Penuelas, J., Guenet, B.,
793 Sardans, J., Bopp, L., Vuichard, N., Zhou, F., Li, B., Piao, S., Peng, S., Huang, Y., and Tao, S.: Global forest carbon
794 uptake due to nitrogen and phosphorus deposition from 1850 to 2100, *Global Change Biology*, 23, 4854–4872,
795 <https://doi.org/10.1111/gcb.13766>, 2017.
- 796 Waring, B. G., Gei, M. G., Rosenthal, L., and Powers, J. S.: Plant–microbe interactions along a gradient of soil
797 fertility in tropical dry forest, *Journal of Tropical Ecology*, 32, 314–323,
798 <https://doi.org/10.1017/S0266467416000286>, 2016.
- 799 Waring, B. G., Pérez-Aviles, D., Murray, J. G., and Powers, J. S.: Plant community responses to stand-level nutrient
800 fertilization in a secondary tropical dry forest, *Ecology*, 100, e02691, <https://doi.org/10.1002/ecy.2691>, 2019.
- 801 Waring, B. G., Guzman, M. E. D., Du, D. V., Dupuy, J. M., Gei, M., Gutknecht, J., Hulshof, C., Jelinski, N.,
802 Margenot, A. J., Medvigy, D., Pizano, C., Salgado-Negret, B., Schwartz, N. B., Trierweiler, A. M., Bloem, S. J. V.,
803 Vargas G., G., and Powers, J. S.: Soil biogeochemistry across Central and South American tropical dry forests,
804 *Ecological Monographs*, 91, e01453, <https://doi.org/10.1002/ecm.1453>, 2021.
- 805 Werden, L. K., Becknell, J. M., and Powers, J. S.: Edaphic factors, successional status and functional traits drive
806 habitat associations of trees in naturally regenerating tropical dry forests, *Functional Ecology*, 32, 2766–2776,
807 <https://doi.org/10.1111/1365-2435.13206>, 2018a.



- 808 Werden, L. K., Alvarado, P., Zarges, S., Calderón M., E., Schilling, E. M., Gutiérrez L., M., and Powers, J. S.:
809 Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of
810 degraded Vertisols, *Journal of Applied Ecology*, 55, 1019–1028, <https://doi.org/10.1111/1365-2664.12998>, 2018b.
- 811 Werden, L. K., Calderón-Morales, E., J, P. A., L, M. G., Nedveck, D. A., and Powers, J. S.: Using large-scale
812 tropical dry forest restoration to test successional theory, *Ecological Applications*, 30, e02116,
813 <https://doi.org/10.1002/eap.2116>, 2020.
- 814 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry,
815 L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P.,
816 Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., and Yutani, H.: Welcome to the Tidyverse, *Journal of*
817 *Open Source Software*, 4, 1686, <https://doi.org/10.21105/joss.01686>, 2019.
- 818 Witt, C., Gaunt, J. L., Galicia, C. C., Ottow, J. C. G., and Neue, H.-U.: A rapid chloroform-fumigation extraction
819 method for measuring soil microbial biomass carbon and nitrogen in flooded rice soils, *Biology and Fertility of*
820 *Soils*, 30, 510–519, <https://doi.org/10.1007/s003740050030>, 2000.
- 821 Wood, S. N.: Stable and Efficient Multiple Smoothing Parameter Estimation for Generalized Additive Models,
822 *Journal of the American Statistical Association*, 99, 673–686, <https://doi.org/10.1198/016214504000000980>, 2004.
- 823 Wood, S. N.: Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric
824 generalized linear models, *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73, 3–36,
825 <https://doi.org/10.1111/j.1467-9868.2010.00749.x>, 2011.
- 826 Wright, S. J.: Tropical forests in a changing environment, *Trends in Ecology & Evolution*, 20, 553–560,
827 <https://doi.org/10.1016/j.tree.2005.07.009>, 2005.
- 828 Wright, S. J., Yavitt, J. B., Wurzburger, N., Turner, B. L., Tanner, E. V. J., Sayer, E. J., Santiago, L. S., Kaspari, M.,
829 Hedin, L. O., Harms, K. E., Garcia, M. N., and Corre, M. D.: Potassium, phosphorus, or nitrogen limit root
830 allocation, tree growth, or litter production in a lowland tropical forest, *Ecology*, 92, 1616–1625,
831 <https://doi.org/10.1890/10-1558.1>, 2011.
- 832 Wright, S. J., Turner, B. L., Yavitt, J. B., Harms, K. E., Kaspari, M., Tanner, E. V. J., Bujan, J., Griffin, E. A.,
833 Mayor, J. R., Pasquini, S. C., Sheldrake, M., and Garcia, M. N.: Plant responses to fertilization experiments in
834 lowland, species-rich, tropical forests, *Ecology*, 99, 1129–1138, <https://doi.org/10.1002/ecy.2193>, 2018.
- 835 Wu, D., Vargas G., G., Powers, J. S., McDowell, N. G., Becknell, J. M., Pérez-Aviles, D., Medvigy, D., Liu, Y.,
836 Katul, G. G., Calvo-Alvarado, J. C., Calvo-Obando, A., Sanchez-Azofeifa, A., and Xu, X.: Reduced ecosystem
837 resilience quantifies fine-scale heterogeneity in tropical forest mortality responses to drought, *Global Change*
838 *Biology*, 28, 2081–2094, <https://doi.org/10.1111/gcb.16046>, 2022.
- 839 Wurzburger, N. and Miniati, C. F.: Drought enhances symbiotic dinitrogen fixation and competitive ability of a
840 temperate forest tree, *Oecologia*, 174, 1117–1126, <https://doi.org/10.1007/s00442-013-2851-0>, 2014.
- 841 Xu, L., Saatchi, S. S., Yang, Y., Yu, Y., Pongratz, J., Bloom, A. A., Bowman, K., Worden, J., Liu, J., Yin, Y.,
842 Domke, G., McRoberts, R. E., Woodall, C., Nabuurs, G.-J., de-Miguel, S., Keller, M., Harris, N., Maxwell, S., and
843 Schimel, D.: Changes in global terrestrial live biomass over the 21st century, *Sci. Adv.*, 7, eabe9829,
844 <https://doi.org/10.1126/sciadv.abe9829>, 2021.



845 Xu, X., Medvigy, D., Powers, J. S., Becknell, J. M., and Guan, K.: Diversity in plant hydraulic traits explains
846 seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests, *New Phytologist*, 212,
847 80–95, <https://doi.org/10.1111/nph.14009>, 2016.

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849 TABLES AND FIGURE CAPTIONS

850 **Table 1.** Focal tree species present in the experimental manipulations and their functional and hydraulic traits
851 measured in other studies (Data from Powers and Tiffin, 2010; Powers et al, 2020). Here we present species leaf
852 habit (LH), nitrogen fixation (NF), specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$), wood density (WD, g cm^{-3}), water potential at
853 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}
Bignoniaceae	<i>Handroanthus impetiginosus</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

854



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

858

859 **Figure 2.** Volumetric soil moisture records at two depths for plots with a throughfall exclusion structure and plots
860 without it. **a)** Temporal variability at a weekly resolution median volumetric soil moisture with its associated 75 and
861 25 percentiles, where the dashed vertical line represents the date when the structures were established. **b)** Histogram
862 distribution of the percent difference between soil moisture during the experiment (SM_{Exp}) and the soil moisture
863 preceding the experimental treatments (SM_{Pre}) for each depth during the dry season and the wet season, where the
864 vertical lines represent the median $SM_{Exp} - SM_{Pre}$ percent value for plots with a throughfall exclusion structure
865 (dashed) and plots without it (continuous). Reported results from a linear mixed effect model comparing weekly
866 $SM_{Exp} - SM_{Pre}$ percent values for each depth during the dry season and the wet season.

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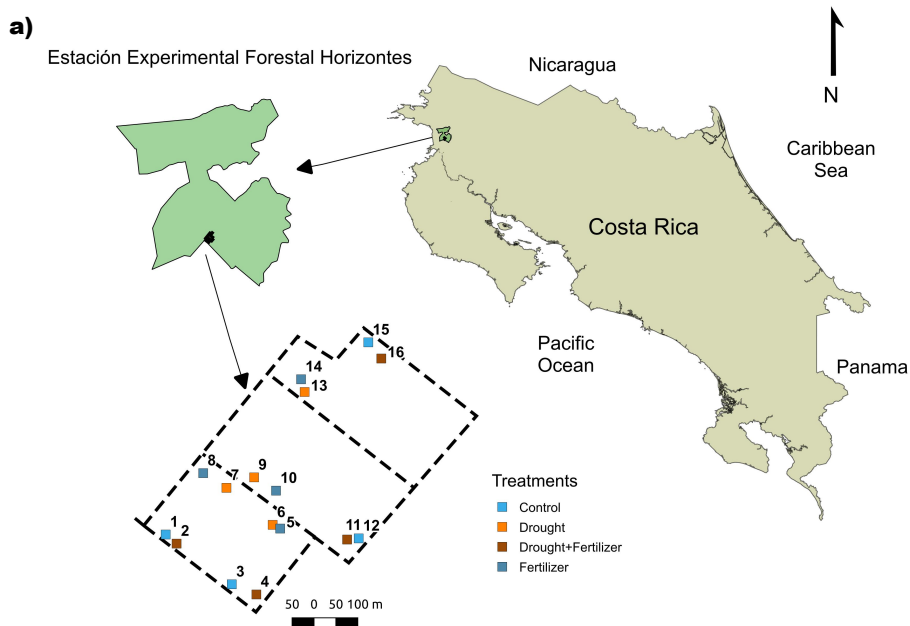
868 **Figure 3.** Relative growth rate responses (RGR_{DBH}) of plantation (panel a) and understory (panel b) trees to
869 fertilization (F), drought (D), and drought plus fertilization (D + F) over a period of four years (2016-2020). Bar
870 plots showing the media with the associated standard error (error bars) were obtained from a total of 194 plantation
871 trees and 462 understory trees in 16 experimental plots. Lowercase letters stand for multiple comparisons among
872 experimental treatments from a Post-Hoc Tukey's honest significance difference test.

873

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

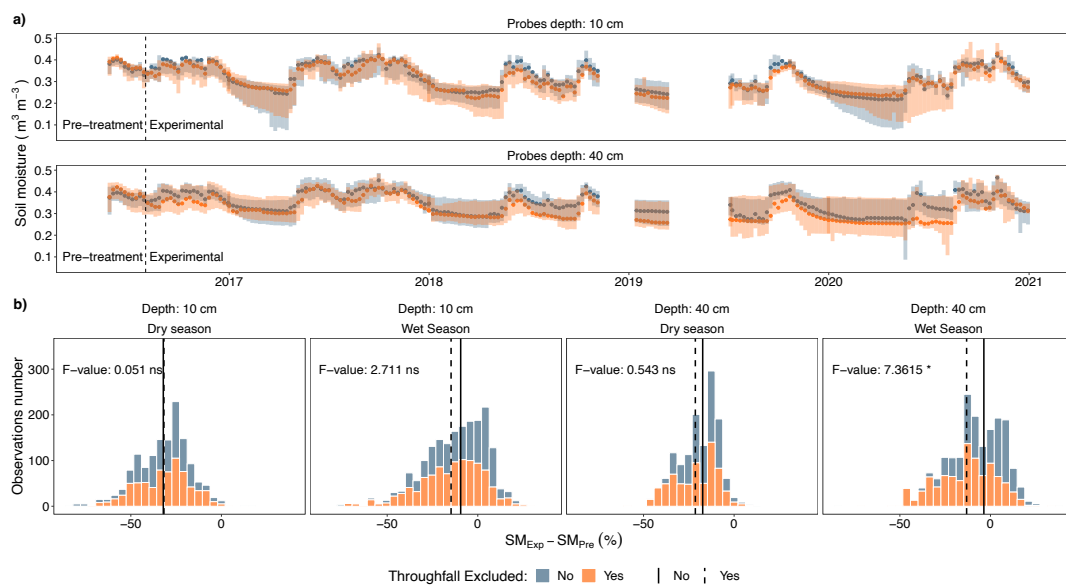
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881 **Figure 5.** Responses of ecosystem net primary productivity (NPP), aboveground net primary productivity (ANPP),
882 and aboveground to belowground ratios to fertilization (F), drought (D), and drought plus fertilization (D + F) over a
883 period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



887

888 **Figure 1**



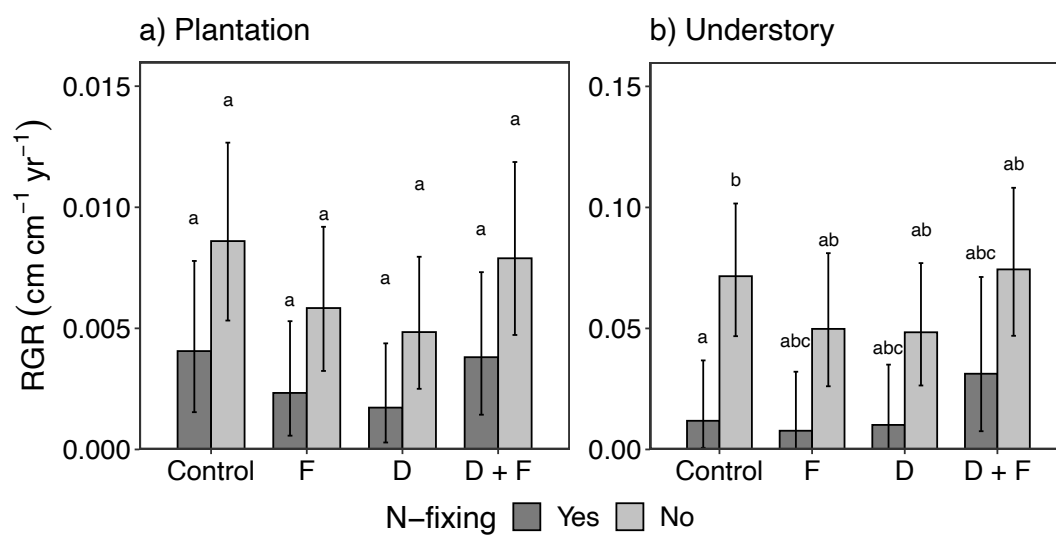
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890 **Figure 2**

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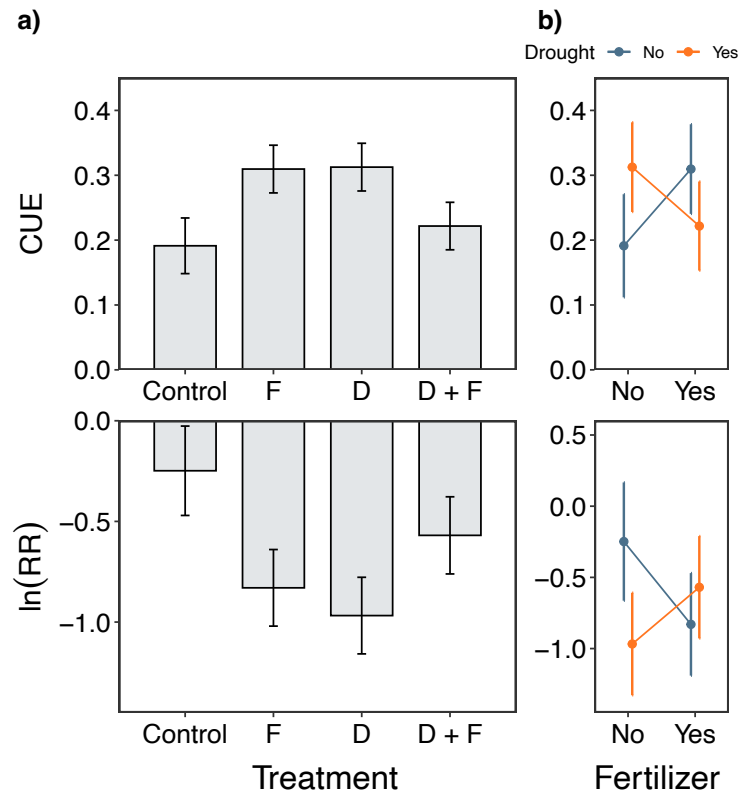
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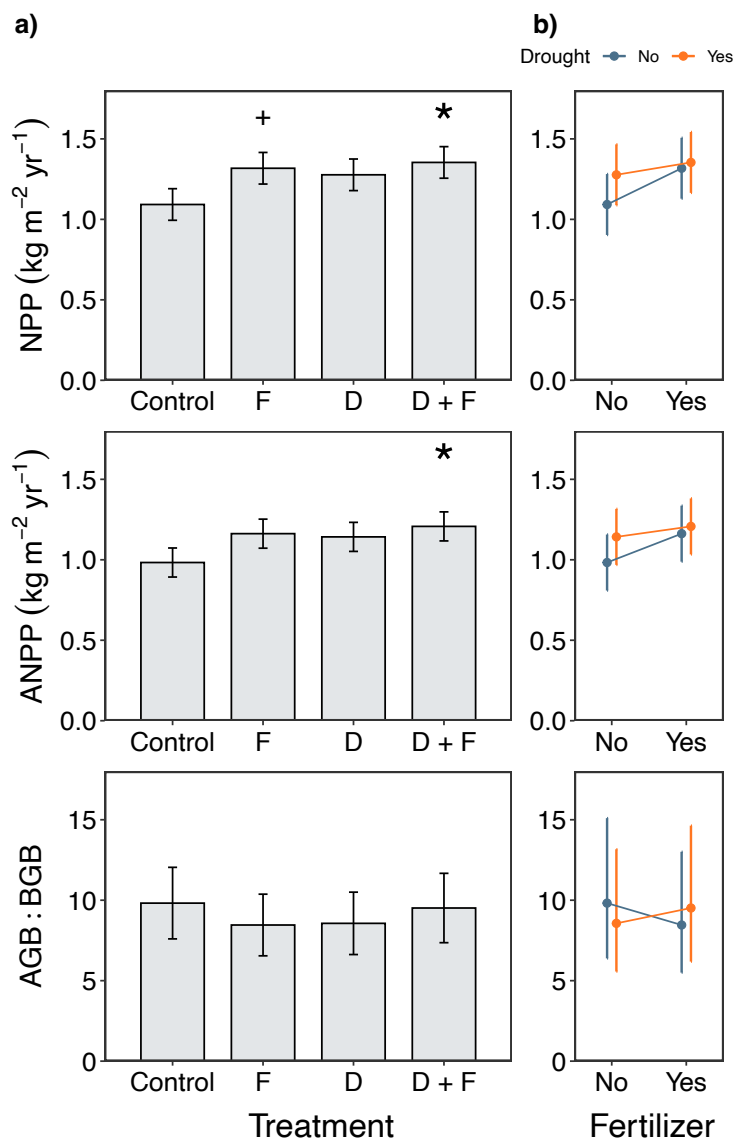
894 **Figure 3**

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897 Figure 4



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 899 **Figure 5**