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## Assessment of atmospheric and soil water stress impact on a tropical crop: the case of *Theobroma cacao* under Harmattan conditions in eastern Ghana.

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### Abstract

In West Africa, Harmattan-induced atmospheric and soil droughts represent seasonally recurring hazards for *Theobroma cacao* L. agro-ecosystems. Under the influence of the Harmattan winds, precipitation is impaired and air humidity and temperature reach stressful levels. Climate change is causing an increase in temperature that will drive up the evaporative power of the atmosphere, risking to harshen both the soil and atmospheric stress. This would further threaten the viability of cacao cultivation in this region. To characterize the response of cacao trees to atmospheric and soil drought, we monitored two sub-plots, with and without irrigation, throughout one Harmattan season (November 2019 - March 2020) in the Eastern region in Ghana. For both treatments we recorded: sap flow velocity, photosynthetic active radiation (PAR) above and below the canopy, soil moisture, temperature, air humidity and daily precipitation. Leaf area index (LAI) was estimated from PAR measurements. To characterize drought responses of mature cocoa trees during the day and at the seasonal scale, we developed two boosted regression trees models (BRT)

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with the environmental variables measured. The atmospheric component of Harmattan-induced drought was found to affect the canopy to a similar extent as soil water stress, both causing a decline in LAI of 33%. This study confirmed the importance of soil drought but highlighted as well the crucial role of atmospheric drought for this species' transpiration control. Soil and atmospheric water stresses did not have a synergistic effect on transpiration under the studied conditions. The BRT models identified LAI as one of the most influential drivers for sap velocity, which, in turn was sensitive to the interactive effect of both atmospheric and soil drought. Our results highlight that not only reduced precipitation but also increasing atmospheric drought is likely to negatively impact on cacao production in West Africa under increasingly dry conditions imposed by the influence of the Harmattan winds.

*Keywords:* cacao, physiology, canopy, drought, sap velocity, boosted regression trees

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## 1 1. Introduction

2 The global climate has changed over the past century and is projected to  
3 continue to change in the next decades at a higher pace than in the past [1].  
4 Global general circulation models (GCMs) agree that, except for an unlikely low  
5 emissions scenario, by the end of this century, global mean temperatures will rise  
6 by at least another 1.5°C and precipitation regimes over large areas worldwide  
7 will experience profound changes. In the tropical band (23°3'N-23°3'S), climate  
8 change is expected to have a negative impact on agriculture, ultimately threat-  
9 ening the economic stability of countries that rely heavily on this sector. This is  
10 particularly true for West Africa where agricultural systems are among the most  
11 vulnerable worldwide due to the economic constraints limiting access to agricul-  
12 tural technological advances, among other reasons [2, 3, 4]. West Africa's most  
13 famous exported crop, cacao (*Theobroma cacao* L.), will experience a severe  
14 reduction of its agro-pedo-climatic zone of cultivation [5, 6, 7]. Recent model  
15 predictions based on the SRES-A2 greenhouse gas emission scenario [8] project  
16 a continued rise in mean temperatures over the West African cocoa belt in the  
17 future and, while cumulative annual precipitations are not expected to change  
18 significantly, their distribution over the course of the year is. The period with  
19 no precipitations whatsoever may slightly shorten or remain unchanged in the  
20 coming decades across West Africa but, due to the aforementioned increase in  
21 temperatures, this region is expected to experience longer periods under greater  
22 evaporative demand. Ultimately, this will result into increased frequency, sever-  
23 ity and duration of episodes of both soil and atmospheric water stress at the  
24 plant level. Consequently, a large share of cocoa-producing regions in West  
25 Africa will become unsuitable for production in the future [5, 6, 7], leaving mil-  
26 lions of smallholder farmers without a reliable source of income [9].  
27 The West African long dry season is characterized by the co-occurrence of low  
28 precipitation and a dry wind, the Harmattan. The Harmattan is a north-easterly  
29 trade wind blowing over North Africa that results from the continental-scale  
30 pressure gradient between the subtropical subsidence zone and the Intertropical

31 Convergence Zone (ITCZ) [10]. During the West African dry season, corre-  
32 sponding to the boreal winter, the Harmattan advances to the southern part  
33 of West Africa conveying a dry air mass from the Sahara to the south which  
34 lingers around the northern edge of the cacao belt, along the Gulf of Guinea  
35 [10]. The presence of the Harmattan hinders moist convection and suppresses  
36 any chance of precipitations, only allowing for sporadic weak rains for hundreds  
37 of kilometers south of the Intertropical Front, that marks the southern Harmat-  
38 tan extent at ground level [11]. The Harmattan further enhances soil and air  
39 water stress as the evaporative demand increases due to higher wind speed and  
40 reduced air humidity, ultimately leading to wide temperature differentials from  
41 day to night. Hence, under the influence of the Harmattan, soil water content  
42 decreases due to the lack of precipitation together with increased evaporative  
43 demand at the leaf level.

44 Cacao is original from the Amazon basin, where water limitation is virtually in-  
45 existent [12, 13, 14]. The morphological traits of cacao are not adapted to deal  
46 with water limitation: for example, cacao has large, broad leaves with minimal  
47 waxing and high stomatal density that cause strong transpiration and evapo-  
48 ration rates under high irradiance or high vapor pressure deficit (VPD) [15].  
49 The hydraulic system of cacao is also poorly adapted to low water availability:  
50 the main stem has wide xylem vessels [16] to pump water more efficiently from  
51 the soil to the leaves, but this implies a greater risk of functionality loss due to  
52 cavitation under water stress [17]. Moreover, the cacao root system is relatively  
53 shallow, with high density of fine roots in the top 0.2-0.6 m of the soil, and hence  
54 it cannot access deep water [18, 19]. The physiological performance of cacao is  
55 also adapted to its native climatic conditions. Cacao optimum growth temper-  
56 ature is 24°C at night and 30°C during the day [20]. Cacao photosynthetic  
57 efficiency starts declining at temperatures above 33°C, while night tempera-  
58 tures below 15.8°C suffice to observe a decline in photosynthesis and stomatal  
59 conductance [17]. Additionally, for cacao trees of the Amelonado family, genet-  
60 ically the most representative in West Africa, the reported base temperature  
61 for vegetative growth is 19.7°C [21]. In West Africa, during the dry season and

62 under the influence of the Harmattan, air humidity is not sufficient to buffer  
63 large daily thermal oscillations and air temperature can reach values as high as  
64 44°C [22, 23] and as low as 12-14°C at night [24, 25]. These large daily temper-  
65 ature oscillations strongly inhibit the net growth and physiological performance  
66 of cacao [20]. In addition, reduced air humidity due to the influence of the Har-  
67 mattan has a direct, negative effect on growth and physiological performance.  
68 Indeed, in tropical environments it has been shown that 60% is the air humidity  
69 threshold below which tree physiological performance starts to decrease and be-  
70 low 40%, in combination with high temperatures, it is considered that trees are  
71 exposed to high atmospheric water stress [26, 27]. It can be assumed that such  
72 conditions would be stressful for cacao as well, in line with [28]. Overall, it is  
73 clear that cacao lacks high tolerance to drought or extreme temperatures. Thus,  
74 the viability of cultivation of this crop outside its native range, in West Africa,  
75 is severely threatened by future climate change. The future threats to cacao  
76 cultivation are further exacerbated in full sun or lightly shaded monocultural  
77 systems, preferred by farmers across West Africa for the higher yields in the  
78 short term but more exposed to atmospheric stress [23].

79 Both soil and atmospheric drought impact negatively on plant growth and pro-  
80 ductivity [29, 30]. Plants first respond to increasing vapour pressure deficit  
81 (VPD) by closing their pores on their leaf surfaces, the stomata, to reduce tran-  
82 spiration water loss, but this also entails a reduction in  $CO_2$  uptake to supply  
83 photosynthesis and, eventually, reduced growth and production of reproductive  
84 structures [31, 32]. On the other hand, soil drought reduces the conductivity  
85 of the soil-plant-atmosphere continuum, ultimately inducing stomatal closure  
86 to protect the hydraulic system of the plant from embolism [33, 34]. Beyond  
87 stomatal closure, high VPD also increases non-stomatal water losses, for exam-  
88 ple through the cuticle, further increasing risk of hydraulic failure [14, 16, 35].  
89 Besides reducing photosynthesis, soil drought also reduces xylem and phloem  
90 transport and, hence, export of carbohydrates from the leaves to reproductive  
91 organs for flower and fruit production [36, 30].

92 Several authors have already highlighted the need to better investigate the water

93 relations of cacao under field conditions [37], but we still lack a detailed char-  
94 acterization of how drought stress influences cacao physiology and reproduction  
95 [17]. The effects of relative humidity [28] and temperature have been addressed  
96 [20, 38, 21] and a few field trials have addressed soil drought stress but, to our  
97 knowledge, no previous study has assessed the simultaneous effect of soil and  
98 atmospheric drought, and their interaction [18, 19, 23]. The reduction of tran-  
99 spiration in response to soil water stress has been characterized in Brazil [13]  
100 and Indonesia [18, 19], but in these locations VPD and air temperature rarely  
101 reach stressful conditions for the trees. Such effects have not been addressed in  
102 the West African cacao belt, where radically different atmospheric conditions  
103 due to the influence of the Harmattan will likely impose drought stress levels  
104 beyond those previously studied. The objective of this study is to clarify the  
105 effects of atmospheric and soil water stress on cacao tree transpiration during  
106 the dry Harmattan season and shed light on the drivers of transpiration under  
107 such circumstances. Our hypothesis is that cacao trees will respond strongly to  
108 both types of stresses but we expect VPD to be more influential, due to the ex-  
109 tremely low relative humidities and large temperature oscillations experienced  
110 under the influence of the Harmattan.

111 **2. Materials and methods**

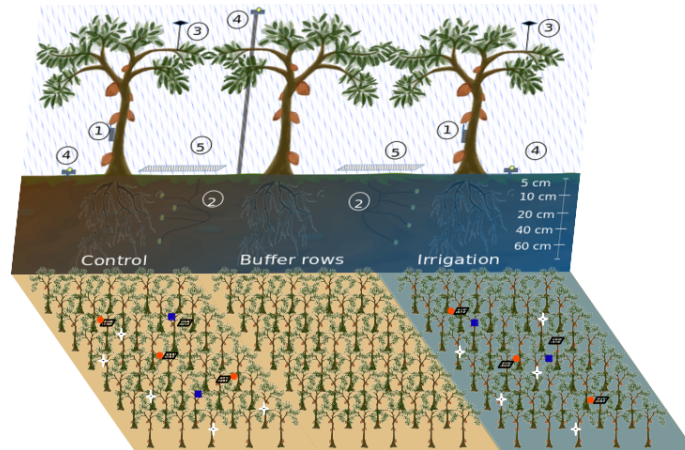


Figure 1: Schematic representation of the field experimental plan with an overview of the measurements taken. The experiment compared an irrigated plot (5 rows of 8 trees) to a control rain-fed one. The experimental plots were separated by a buffer of ten rows of trees. In each plot we measured 1) sap velocity (crosses), 2) soil moisture (squares), 3) temperature and air relative humidity (dots), 4) photosynthetically active radiation (PAR) above and below the canopy (dots) and 5) litterfall production (hatched parallelograms). The position of the sensors reflects their real position in the field experiment. Graphics by Pietro Della Sala, drawing of the cacao tree by Estelle Ribeyre.

112 *2.1. Study site and experimental design*

113 Two plots of cacao trees, with and without irrigation, were monitored through-  
114 out the duration of the experiment (3<sup>rd</sup> December 2019 to 16<sup>th</sup> March 2020)  
115 and their response to climate tracked closely by means of various sensors. The  
116 measured environmental variables were: soil volumetric water content at four  
117 depths from 10 to 60 cm, air temperature, air relative humidity and photosyn-  
118 thetically active radiation (Fig. 1).

119 The study was conducted at the experimental station of the Cacao Research In-  
120 stitute of Ghana (CRIG) located in New Tafo Akyem, Eastern Region, Ghana  
121 (6°13'53.7"N; 0°21'01.6"W; 203 m a.s.l.). At this location, the climate is warm  
122 and humid all year round except for two dry seasons. The main dry season has



123 its core between December and February, but the onset can be as early as mid  
124 November and lasts until sometime in March. The second dry season occurs  
125 between the second half of July and the beginning of September and is typically  
126 much less severe than the main dry season.

127 Throughout the year, temperature in Tafo oscillates between a monthly average  
128 minimum of 20 to 22°C and a monthly average maximum of 29 to 33°C [39].  
129 Annual rainfall ranges between 1150 and 1800 mm with a mean value of 1565  
130 mm per year [39, 40].

131 At the study site, a 2 ha cacao plantation was established in June 2013. Cacao  
132 trees (*Theobroma cacao* L.), of homogeneous genetic origin, were planted with  
133 a 2.5 x 2.5 m spacing (1600 trees ha<sup>-1</sup>), underneath *Gliricidia sepium* Jacq.  
134 previously planted at a density of 10 trees ha<sup>-1</sup>. The plantation consisted of  
135 four blocks with 10 plots each. Each plot contained 40 trees planted in five rows  
136 with eight trees per row. In November 2019, two plots of 40 hybrid Amelonado  
137 trees with mean canopy height of 3 meters were selected for the study. The se-  
138 lected plots were located at least 20 m away from the nearest shading tree and,  
139 therefore, were considered as a "typical West African full sun system". The two  
140 study plots were separated by ten rows of cacao trees to avoid any edge effect or  
141 interaction between the two (Fig. 1). From the 26<sup>th</sup> of November 2019 to the  
142 16<sup>th</sup> of March 2020, trees in one plot (irrigation treatment) were irrigated with  
143 60 L per tree (equivalent to approximately 9.6 mm per tree) on alternating dates  
144 using a hose, whereas trees in the second plot (control) only received ambient  
145 precipitation. The irrigation was evenly applied within 50 cm from the trunk,  
146 where most of the roots were believed to be distributed [37]. Irrigation close to  
147 the trunk was not reduced by losses due to canopy interception, thus its efficacy  
148 was higher than a rainfall of 9.6 mm.

## 149 2.2. Soil properties

150 According to a soil analysis of the experimental site conducted in March  
151 2020, the upper soil (0-15 cm) was a eutric fluvisol with sandy-loam texture  
152 and below 15 cm of depth the soil texture was sandy clay loam. The pH was 6.5

153 across the entire profile. The upper soil was poor: organic matter content was  
154 1.36%, magnesium was  $2.06 \text{ me} * 100\text{g}^{-1}$ , total nitrogen was 0.15 %, ammonium  
155 was 14.2 ppm, phosphorus was 12.96 ppm, potassium was  $0.049 \text{ me} * 100\text{g}^{-1}$   
156 and exchangeable calcium was  $3.72 \text{ me} * 100\text{g}^{-1}$ . Based on the soil texture at  
157 a depth of 30 cm, the bulk density (BD), field capacity (FC) and permanent  
158 wilting point (PWP) were estimated in  $1.45 \text{ g} * \text{cm}^{-3}$ , 34% and 13%, respectively.  
159 Below 30 cm, the values of BD, FC and PWP were  $1.55 \text{ g} * \text{cm}^{-3}$ , 35 and 16%,  
160 respectively.

### 161 *2.3. Transpiration measurements*

162 For the entire duration of the experiment, tree transpiration was estimated  
163 from measurements of sap velocity using the Heat Ratio Method (HRM: [41]).  
164 Five trees in each plot were selected, with mean $\pm$ sd diameters (measured 20  
165 cm below the main branch) of  $11.31 \pm 1.84$  and  $12.23 \pm 1.34$  cm in the control  
166 and irrigated plots, respectively (Fig. 1, (1)). Within each plot, the trees were  
167 selected based on a visual scoring system of overall condition (canopy density,  
168 leaf greenness, number and diameter of jorquette branches etc.) and avoiding  
169 spatial clustering of monitored trees. In November 2019, we installed one heat  
170 probe sensor (SF-3, East30sensors, USA) on each selected tree. Each sensor  
171 consisted of three probes, 35 mm in length, 1.3 mm in diameter, and 6 mm  
172 axial distance apart. The central probe contained an evanohm heater, and the  
173 lateral two probes, one upstream and one downstream with respect to the heater,  
174 contained 3 thermistors placed at 5 mm, 17.5 mm, and 30 mm from the sensor  
175 tip to monitor sap flow across the entire depth of the sapwood. The thermistor  
176 temperature sensor consisted of a 10K precision resistor and a 10K thermistor  
177 wired through a three wire half bridge connected to a datalogger per irrigation  
178 treatment ( CR800, Campbell Scientific, Logan, UT, USA). The accuracy of the  
179 thermistors was  $\pm 0.2$  °C, and the resolution was 0.001 °C. The central needle  
180 was heated by a 12V pulse of 3 seconds powered by the datalogger and reduced  
181 to 5V through a heat control board (East30sensors, USA).  
182 Sensors were installed on the trunk following the xylem direction, at a minimum

183 distance of 20 cm from any node or branching and at a minimum height from  
184 the soil of 50 cm. Bark thickness was  $0.3\pm 0.15$  cm ( $n = 10$  trees) and was kept  
185 in place to protect the wound from dryness and fungal attacks. The probes were  
186 programmed in accordance with the Dual Method Approach (DMA: [42]). The  
187 DMA combines the traditional approach to calculate sap velocity from heat  
188 pulse velocity [41] with the Tmax Method [43]. The latter allows to capture  
189 high and low flow rates both upward and downward along the stem [42]. Three  
190 values of heat pulse velocity were recorded every 30 minutes per sensor. Each  
191 value was calculated from the temperature difference between each pair of up-  
192 and down-flow thermistors located at three depths within the sapwood (5, 17.5  
193 and 30 mm from the bark). Sap velocity was calculated for each of the three  
194 positions and then upscaled to an integrated value of sap flux for each tree  
195 through a weighted sum based on the sapwood area, estimated through wood  
196 coring, associated to the specific radial position [42]. Before upscaling to a single  
197 value per tree, each couple of thermocouples was calibrated to have the zero for  
198 sap velocity when night potential evapotranspiration was zero (S. 2.6) [44, 45].  
199 In this study it was assumed that during the three months of dry season the  
200 sapwood area increment is negligible, therefore, changes in transpiration are  
201 approximated to variations in sap flux.

#### 202 2.4. Soil VWC

203 Soil volumetric water content (VWC) was monitored in two flat locations per  
204 plot, equidistant (170 cm) to all surrounding trees, at four depths (10, 20, 40,  
205 and 60 cm), with TEROS 10 capacitance probes (METER group, Pullman, WA,  
206 USA) (Fig. 1, (2)). The chosen distance allowed to capture the average VWC  
207 of both the irrigated and the non-irrigated plots, avoiding potential biases due  
208 to uneven irrigation in the former. Despite their distance from the trees, the  
209 locations for VWC monitoring were shaded by the plots' closed canopy, effec-  
210 tively limiting quick evaporation of water after a watering event, be it rainfall  
211 or irrigation. The TEROS 10 sensors estimate soil VWC from measurements of  
212 the apparent dielectric permittivity in the 430 mL of surrounding medium. For

213 this study, the manufacturer’s calibration for a generic mineral soil was used.  
214 A value of soil VWC per probe was recorded on a CR800 datalogger every 30  
215 minutes from November 26<sup>th</sup> 2019 to March 16<sup>th</sup> 2020. In one instance, the soil  
216 VWC was transformed into water potential to compare our results with other  
217 reported results. To obtain the pedotransfer function it was adopted the model  
218 by Van Genuchten [46]. The parametrization of the model was done with the  
219 R package *soilphysics 4.0* [47] and the soil properties measured with the soil  
220 analysis.

### 221 2.5. Leaf area index

222 Leaf Area Index (LAI) was estimated from measurements of photosyntheti-  
223 cally active radiation (PAR) above ( $I$ ) and below ( $I_0$ ) the canopy (Fig. 1, (4))  
224 in an inverted form of Beer’s law (Eq. (1)). Measurements of PAR were col-  
225 lected from November 26<sup>th</sup> 2019 to March 16<sup>th</sup> 2020, with a brief interruption  
226 from December 27<sup>th</sup> 2019 to January 8<sup>th</sup> 2020. Incoming photosynthetic active  
227 radiation (PAR;  $\mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$ ) above the canopy was measured every 30  
228 minutes at one position in the irrigated plot. The PAR sensor (SQ110, Apogee  
229 instruments, Santa Monica, CA, USA) was mounted on top of a 5 m levelled  
230 iron pipe planted in the soil, i.e., 2 m above the canopy. Additionally, PAR was  
231 monitored under the canopy at three locations in each plot with three sensors  
232 mounted on levelled poles at 20 cm height. The extinction coefficient (K), nec-  
233 essary to calculate LAI from PAR data (Eq. (1)), depends on the solar angle ( $\phi$ )  
234 and a leaf angle distribution coefficient ( $x$ ) and was calculated applying Eq. (2)  
235 [48]. The parameter  $x$  was calculated as the ratio of vertical to horizontal pro-  
236 jections of the canopy [48]. Based on field measurements,  $x$  was evaluated at 1.2,  
237 corresponding to an ellipsoid leaf angle distribution. A reliable estimation of K  
238 is possible only when the solar angle is close to the zenith [49, 50], therefore,  
239 we estimated LAI from PAR measurements collected between 10:30 and 14:30  
240 (solar time). Furthermore, to avoid overestimation of LAI due to excess direct  
241 radiation reaching the sensors under the canopy, data from each sensor were  
242 smoothed and interpolated with the *Daniell* modified Fourier method [51, 52]

243 and the three resulting curves averaged to get a final LAI value for the entire  
244 plot.

$$\frac{I}{I_0} = e^{-K*LAI} \quad (1)$$

$$K = \frac{\sqrt{x^2 + 1/\tan^2\phi}}{1.47 + 0.45x + 0.1223x^2 - 0.013x^3 + 0.000509x^4} \quad (2)$$

245 LAI change due to defoliation was also monitored through the same monitor-  
246 ing period with a set of four litter traps per treatment (Fig. 1, (5)). Each trap  
247 consisted on a suspended fine net of 1.2 m<sup>2</sup> that was positioned in randomized  
248 locations within each plot. The litter production was collected every 15 days  
249 and oven-dried at 100 °C for 36 hours to obtain the dry weight. To convert the  
250 leaf dry weight in LAI, in the beginning of the experiment the mean specific leaf  
251 area (SLA cm<sup>2</sup> \* g[dryleaf]<sup>-1</sup>) was calculated. A sample of 30 leaves (10 from  
252 the lower, middle and top canopy) for each treatment plot was scanned on a  
253 reference surface (an A4 sheet). The total area was estimated as the percentage  
254 of the images that was not white with ImageJ 1.53a [53]. To obtain the SLA,  
255 the average leaf area was divided by its oven-dry weight.

## 256 2.6. Atmospheric conditions

257 Air temperature and relative humidity were logged hourly in each plot, with  
258 with two iButtons (DS1923-F5: Hygrochron, iButtonLink LLC, Whitewater,  
259 WI,USA) above the canopy at c.a. 5 m height. To protect the sensors from  
260 direct radiation and precipitation, these were installed facing the ground, glued  
261 to the internal part of bottle caps (Fig. 1, (3)). As temperature and relative  
262 humidity were logged hourly and as they represent continuous variables, a linear  
263 interpolation was applied in order to obtain half-hourly time series that matched  
264 those of the other measured variables in the data set. The vapour pressure  
265 deficit (VPD) and night-time potential evapotranspiration (required to calibrate  
266 the zero point for sap velocity) were calculated following the FAO-56 Penman-  
267 Monteith method [54] by means of the Python package *'opencroplib=0.1.5'*  
268 [55]. The calculation of the night-time potential evapotranspiration used a wind

269 velocity above the canopy of  $0.77 \text{ m} * \text{s}^{-1}$  at 5 m height, in compliance with the  
270 average night-time value from a weather station at less than 1 km from the site.  
271 Daily precipitation data between October 1<sup>st</sup>, 2019 and March 16<sup>th</sup>, 2020 were  
272 retrieved from the Unified Gauge-Based Analysis of Daily Precipitation of the  
273 NOAA Climate Prediction Center (CPC; [40]).

## 274 *2.7. Statistical analysis*

275 Prior to analysis, we checked for sensor glitches, numerical artefacts of the  
276 sensor raw signal and measurement errors caused by faulty sensors. All mea-  
277 sured variables but sap velocity were treated as continuous, with the hypothesis  
278 that they cannot abruptly change over half an hour. For this reason, it was  
279 decided to study the evolution of their first derivative in time and consider as  
280 outliers the points whose absolute value lied outside the two standard deviations  
281 confidence interval. A graphical evaluation of the data points flagged as outliers  
282 was carried out before they were discarded.

### 283 *2.7.1. GAMM analysis*

284 A generalized additive mixed model (GAMM) was used to model and as-  
285 sess the differences between the irrigated and non-irrigated plot dynamics of  
286 LAI over time. The GAM family of models was chosen primarily because LAI  
287 was expected to exhibit a complex non-linear relationship with the environ-  
288 ment. Secondly, it was necessary to use a GAMM because LAI measurements  
289 in time were not completely independent as they were taken by the same sen-  
290 sors. Lastly, the choice to use a GAMM was dictated by the fact that for each  
291 date we had only few points for LAI, thus large variance. It would have been  
292 difficult to appreciate the difference without the GAMM model capturing the  
293 time evolution of LAI. The built GAMM model fitted a gaussian distribution  
294 for LAI (continuous variable) using the treatment (irrigated or control) as fixed  
295 effects and taking into account the random sensor-to-sensor variability. The  
296 effect of time was fitted by a smooth term using Duchon splines, allowing the  
297 the predictions to take into account the differential in water availability due to

298 irrigation. The GAMM-modeled LAI for both watering treatments was plotted  
299 and we interpreted non-overlapping 95% confidence intervals as a significant  
300 difference between treatment levels for a given period. All these analyses were  
301 performed in the R environment v3.6.1 [56] using packages plyr [57], tidyverse  
302 v1.3.0 [58], mgcv [59] and itsadug v2.3 [60].

### 303 *2.7.2. Boosted Regression Tree analysis*

304 We used Boosted Regression Trees analysis (BRT) modelling to predict tran-  
305 spiration from climatic variables [61]. BRT uses two algorithms: regression tree  
306 and boosting. Tree-based regression models, described for use in ecology by  
307 [62], partition the solutions space with a set of rules, identifying the most ho-  
308 mogeneous regions in terms of response to predictors. They then fit a constant  
309 to each region, fitting the average response in that region with the assumption  
310 of normally distributed errors. With each iteration the tree grows by repeat-  
311 edly applying the analysis of the predictors space to its own output until a  
312 user-defined stopping criterion is reached. Tree-based models are intuitive, easy  
313 to visualize and are fairly insensitive to outliers, missing data and data types  
314 (numeric, binary, categorical etc.) but they lack the accuracy of other methods,  
315 such as GLM and GAMM. To compensate for this downside it is convenient  
316 to combine tree-based models with boosting. The idea behind the boosting  
317 methods is that it is more probable to find many rules of thumb, than to find  
318 a single, highly accurate prediction rule [63]. It is, therefore, more convenient  
319 to approximate the solution by averaging the results of a large number of rules  
320 of thumb rather than aiming for a unique highly accurate one. The BRT uses  
321 boosting as a way to evaluate the gradient of the predictors space by focusing  
322 on the variation in the response not explained yet by the model at a given step  
323 and fitting a new tree to its residuals [64]. Through boosting, decision trees are  
324 fitted iteratively to the training data, increasingly emphasising the still poorly  
325 modelled observations. As the boosting process is stage-wise, existing trees are  
326 left unchanged as the model is enlarged but the fitted value is estimated at each  
327 step to reflect the contribution of the newly added tree. The final BRT model

328 is a linear regression model where each term is a tree.  
329 In order to ensure the stability of the models' results and avert over-fitting,  
330 the evaluation looked at the difference between the training data coefficient of  
331 correlation and the coefficient of correlation for the 100-fold cross-validation.  
332 The skill of the models, instead, was assessed by plotting the predicted values  
333 against the measured ones [61, 64].  
334 The BRT analyses were carried out using R v3.6.1 [56] and the gbm [65] and  
335 dismo [66] packages. The parameterization of the two models can be found in  
336 Tab. C.3.

337 Two BRT models were built using 75% of the dataset to explain the relative  
338 importance of the potential drivers of transpiration during the dry Harmattan  
339 season. The remaining 25% was used to fit the models and evaluate them  
340 against the measured values. The two BRT models considered soil volumetric  
341 water content (VWC), photosynthetic active radiation above the canopy (PAR)  
342 and the vapour pressure deficit of the atmosphere (VPD) as environmental  
343 predictors, the leaf area index (LAI) of the two plots as indicator of the general  
344 state of the canopy and the diameter of individual trees as a proxy for their  
345 dimension. The first model (model 1) used the half-hourly daytime data (PAR  
346  $> 15 \mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$ ) to investigate the importance of each aforementioned  
347 predictors in determining the daily daytime cycle of sap velocity. The second  
348 model (model 2) investigated the role of the same predictors at the time scale  
349 of one day; for this, the input variables as well as sap velocity were averaged  
350 over the period of the day with a PAR above  $15 \mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$ .

351 To avoid possible co-variations due to a common daily cycle, for the first  
352 model it was decided to remove the daily pattern from the vapor pressure deficit  
353 and radiation, maintaining only the effects due to the variation from the average  
354 daily cycle. The global daily pattern was maintained as a separate variable, i.e.,  
355 the hour of the day (Hour), and included among the predictors.  
356 The two models were based on the assumption of a normal distribution of the  
357 data (family = "Gaussian") and parameterized to avoid over-fitting (Tab. C.3)  
358 [61, 64].



359 **3. Results**

360 *3.1. Climatic conditions*

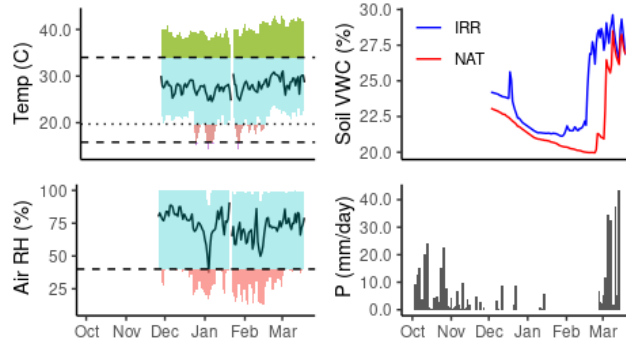


Figure 2: Climatic conditions during the study period. Left top: mean daily air temperature (solid black line), the thresholds for photosynthetic decline (34 and 15.8°C) and observed base temperature for vegetative growth (19.7°C) [17] (dashed lines) and the range of values (shaded area) are depicted. Left bottom: mean daily relative air humidity (solid black line) with the threshold of 40% (dashed line) and its range of observed values (shaded area). Right top: average soil VWC for the entire profile (10 to 60 cm) for the irrigated (blue line) and non irrigated (red line) plots. Right bottom: daily precipitation.

361 The average daily temperature during the experiment (26<sup>th</sup> of November,  
362 2019 -18<sup>th</sup> of March, 2020) was  $27.8 \pm 1.5$  °C, and the maximum and minimum  
363 recorded temperatures were 43.1 °C and 13.6 °C respectively (Fig. 2). Between  
364 January and February, the site experienced the hottest temperatures and the  
365 largest daily thermal oscillations, surpassing both the upper and lower thresh-  
366 olds for maintaining photosynthesis for several hours. Temperatures above the  
367 threshold at which photosynthesis declines (34 °C), were recorded throughout  
368 the entire period under analysis on average for  $6.5 \pm 1.5$  hours a day (Fig. A.1).  
369 Temperatures below the lower threshold for photosynthetic efficiency (19.7 °C),  
370 instead, occurred only in January and February when the Harmattan winds  
371 reached the site. Relative humidity fell below 40% for the first time in early De-  
372 cember and, from late December until March, the site experience several hours  
373 with RH below 40% almost daily (Fig. A.1), reaching up to fifteen hours per

374 day below 40% in January. During our study period, the total precipitation  
 375 was 116 mm, of which 92 mm fell in March while the remaining 24 mm were  
 376 distributed in sporadic events from December to February. Prior to the onset of  
 377 our study, in October and November 2019, the site received 222 mm of precip-  
 378 itation. The average soil VWC across the entire 10 - 60 cm profile was always  
 379 higher in the irrigated treatment than in the control throughout the experiment.  
 380 Soil VWC was above 21% in January and February in the irrigated plot, while  
 381 in the non-irrigated (control) plot, VWC continued to decline below 20% over  
 382 the same period. VWC quickly recovered in both treatments in March, when  
 383 rains resumed.

384

### 385 3.2. Leaf area index (LAI)

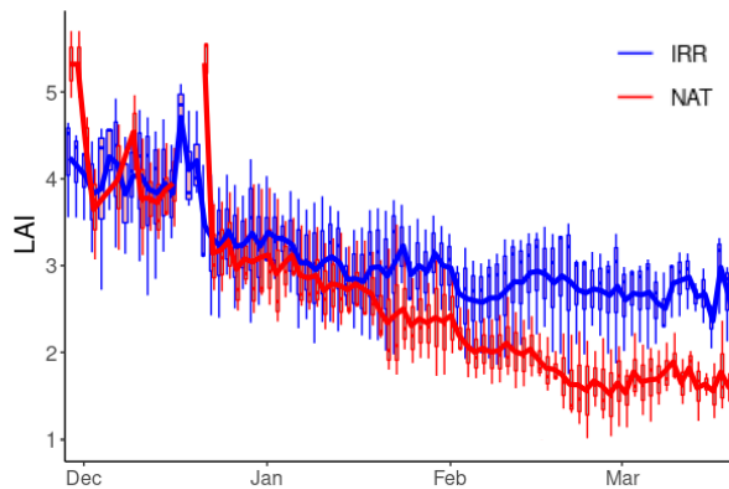


Figure 3: Leaf area index (LAI:  $m^2[leaf]*m^{-2}[soil]$ ) in the two watering treatments: irrigated (blue) and control (red), throughout the observed dry season. The lines represent the three day-moving averages of the LAI times series. Box-plots represent the variability between the three sensors in each plot for every date.

386 Overall, LAI declined steadily throughout the experiment both in the irri-  
 387 gated and in the control plot. Throughout December, the LAI remained con-  
 388 stant and started to decrease in January, in both treatment plots, at the same

389 time as the number of days with  $RH < 40\%$  started to increase (Fig. 3, Fig. A.1).  
390 In February, LAI continued to decrease, faster in the non-irrigated (control) plot  
391 than in the irrigated one. At the end of the study, the estimated LAI was 2.7  
392  $m^2[leaf] * m^{-2}[soil]$  at the irrigated plot and 1.5  $m^2[leaf] * m^{-2}[soil]$  at the  
393 non-irrigated plot compared to an estimated 4  $m^2[leaf] * m^{-2}[soil]$  in the be-  
394 ginning of the study for both treatments (Fig. 3). The LAI, thus, dropped by  
395 approximately 32.5% in the irrigated plot and by approximately 62.5% in the  
396 control. According to the GAMM, from mid-February onwards, LAI in the ir-  
397 rigated plot was significantly higher than in the control plot (Fig. B.1).  
398 The total litter collected throughout the entire experiment was greater in the  
399 control (309  $g[dry] * m^{-2}$ ) than in the irrigated (247  $g[dry] * m^{-2}$ ) treatment.  
400 Most of the shedding appears to have occurred in late December for both treat-  
401 ments, while in March, with the resumption of rain, the litterfall went to zero  
402 (Fig. B.2). The average litterfall was lower in the irrigated plot, notably in the  
403 first week of January (Fig. B.2), when air humidity dropped below 40% for the  
404 first time. (Fig. 2). This is in agreement with the results of LAI dynamic that  
405 evidenced a difference in LAI between plots at the end of the season resulting  
406 from a steadily larger foliage loss in the non-irrigated plot (Fig. 3, Fig. B.2).

407

### 408 3.3. Sub-daily patterns of sap velocity in response to climatic drivers

409 Figure 4 shows the response of sap velocity to VPD under different levels of  
410 PAR above the canopy in the two treatments. At low VPD values ( $< 1 kPa$ )  
411 trees in the control plot seem to have transpired more than those in the irrigated  
412 plot. Under high VPD ( $> 4 kPa$ ), measurements of sap flow velocity from trees  
413 from both treatments presented a high dispersion regardless of the PAR level.  
414 Under intermediate VPD (2-4  $kPa$ ), sap velocity appeared to respond more to  
415 PAR in trees from the irrigated plot. Figure 5 shows the average daily cycle  
416 of sap velocity during the 25% most and least stressing days over the study  
417 period. Sap velocity at low VPD followed the same cycle in the two plots  
418 without significant differences except in the early morning when the control

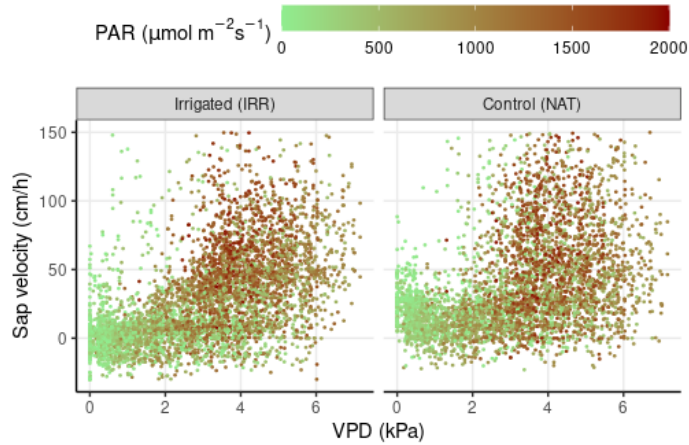


Figure 4: Sub-daily daytime measurements of cacao trees sap velocity in response to varying VPD: in the irrigated plot (left) and in the control plot (right) during the dry Harmattan season. Symbol colours depict PAR levels measured above the canopy (in  $\mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$ ).

419 trees transpired significantly more than the irrigated ones (Fig. 5 B). In days  
 420 when VPD was high the average sap velocity peaked around 70 cm/h for both  
 421 treatments, but the irrigated plot presented on average a sap velocity higher  
 422 than the control during the late mornings while the control tended to maintain  
 423 a higher sap velocity in the late afternoon (Fig. 5 A). In the morning the  
 424 control presented a peak in sap velocity around 6 a.m. (20 cm/h), regardless  
 425 of the level of VPD. An early morning peak in sap velocity was also found for  
 426 the irrigated plot in days when VPD was high. Both Figure 4 and 5 hinted to  
 427 some behaviours that were not always easy to grasp, thus the importance of the  
 428 study with the two BRT models.

429 The main drivers of half-hourly variations in sap velocity during the day were  
 430 identified by means of a BRT model (model 1) (Fig. 6). The model averted over-  
 431 fitting and was considered to be stable (training data correlation = 0.885; cross-  
 432 validation correlation coefficient = 0.741). A regression analysis of predicted  
 433 against measured values for the test data set showed that model 1, at low values  
 434 (up to  $30 \text{ cm} * \text{h}^{-1}$ ), slightly overestimated half-hourly sap velocity, otherwise  
 435 it underestimated sap velocity (Fig. C.1). The "fitted function" in Figure 6

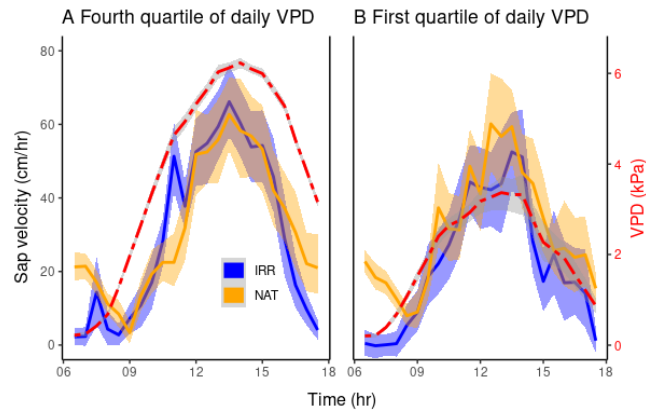


Figure 5: Sap velocity average daily cycle for cacao trees under high (A) and low (B) VPD conditions. The dashed line represents the average VPD cycle. The average cycles for sap velocity and VPD were obtained using the data from the 25% most and least stressing days of the dry Harmattan season 2019/2020. The shadings depict the the 95% confidence interval.

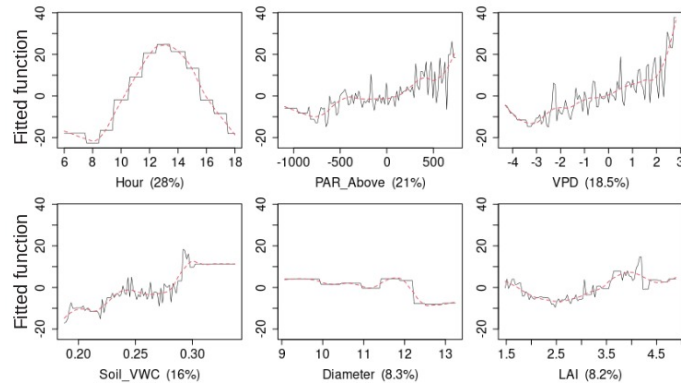


Figure 6: Overview of daytime sap velocity response to the main environmental drivers as identified with a BRT model (model 1). The responses are calculated on half-hourly data during the entire period of this study. Functional shapes of the response of sap velocity to the environmental variables: Hour, VPD, PAR, Soil VWC, LAI and tree diameter. PAR and VPD were expressed as variations from the respective daytime cycle. Each variable was presented with the relative weight of its variation in that of sap velocity within parentheses. The red dotted lines represent the LOESS smoothing for each response function.

436 represents the partial dependency of sap velocity to the different variables and  
 437 it is obtained by averaging out the effects of all the variables in the model except

438 one, and then plot the average fitted value with respect to the one variable left.  
 439 Furthermore, it was chosen to plot a smoothing of the BRT functions using a  
 440 LOESS smoothing - the smoothed functions are shown in red (Fig. 6). Once  
 441 the effect of the daily cycle (Hour), which has a relative influence of 28.0%  
 442 in explaining sap velocity, was removed, the prevalent environmental variables  
 443 explaining the variability in sap velocity were PAR above the canopy (21.0%)  
 444 and VPD (18.5%), followed by soil VWC (16.0%). The evolution of LAI over  
 445 the season in the two plots explained 8.2% of the variability, while tree diameter,  
 446 proxy for the different trees, accounted for 8.3% of the total variability.  
 447 Sap velocity responded linearly to the variations of VPD around its mean daily  
 448 cycle ( $\Delta$  VPD) up to 2 *kPa*. Beyond this point, the BRT model suggests  
 449 an increase in the slope of this relationship. The variability in PAR above  
 450 the canopy was a key driver of sap velocity. When PAR was above-average  
 451 compared to its mean daily cycle ( $\Delta$  PAR > 0), sap velocity increased with PAR  
 452 in a linear fashion. For below-average PAR ( $\Delta$  PAR < 0), sap velocity remained  
 453 relatively stable until  $\Delta$  PAR reached  $-500 \mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$ . Beyond this point,  
 454 the response of sap flow to PAR declined and then stabilized. Sap velocity  
 455 increased with soil VWC up to  $0.24 \text{ m}^3 * \text{m}^{-3}$  and plateaued until it reached  
 456 a threshold value of  $0.27 \text{ m}^3 * \text{m}^{-3}$ . Beyond this value, sap velocity increased  
 457 steeply until VWC reached a value of  $0.29 \text{ m}^3 * \text{m}^{-3}$ . At a VWC above 0.29  
 458  $\text{m}^3 * \text{m}^{-3}$  the response of sap velocity flattened out until field capacity ( $0.34$   
 459  $\text{m}^3 * \text{m}^{-3}$ )(Figure 6). The LAI and tree diameter showed a rather flat relation  
 460 with sap velocity and were negligible drivers of sap velocity at the sub-daily  
 461 timescale.

462 In the sub-daily model, the interactions between VPD and PAR and VPD  
 463 and LAI were more important than the other interactions (Tab. 1) which means  
 464 that VPD modified the sap velocity response to both LAI and PAR significantly.  
 465 When VPD and PAR were low compared to the average daily cycle, sap velocity  
 466 was very low (Fig. 7). When VPD was high, the sap velocity was very high,  
 467 for any value of PAR. Similarly, when PAR was high, sap velocity was high  
 468 and stable whatever the value of VPD, except when VPD was very high, where

	Hour	Diameter	VPD	PAR_Above	LAI	Soil_VWC
Hour	0	15532.81	43578.24	40167	8701.57	13663.24
Diameter	0	0	23831.45	12599.22	10280.22	25915.23
VPD	0	0	0	<b>82788.32</b>	<b>71754.54</b>	59080.78
PAR_Above	0	0	0	0	35495.65	23574.91
LAI	0	0	0	0	0	27616.26
Soil_VWC	0	0	0	0	0	0

Table 1: Interactions between the variables considered in the BRT Model 1 in explaining cacao sap velocity at a sub-daily timescale. For each pair of variables, the table reports the mean value of the residuals, which represents the strength of the interaction. In bold: the interactions considered strong, thus significant, by the model.

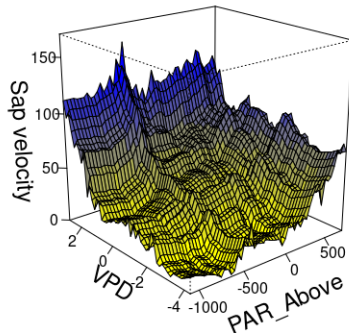


Figure 7: Three-dimensional partial dependence plots for the interaction between VPD ( $\Delta kPa$ ) and PAR ( $\Delta \mu mol * s^{-1} * m^{-2}$ ) variations from the mean daily cycle in the BRT model 1 for half-hourly sap velocity ( $cm * h^{-1}$ ) in cacao trees. All variables except those plotted are held constant at their mean values.

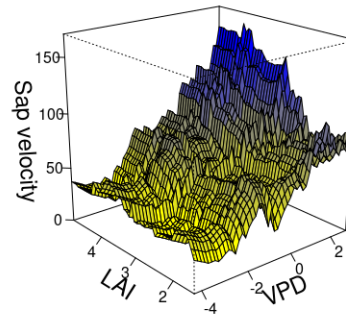


Figure 8: Three-dimensional partial dependence plots for the interaction between LAI ( $m^2[leaf] * m^{-2}[soil]$ ) and VPD ( $\Delta kPa$ ) variation from the mean daily cycle in the BRT model 1 for half-hourly sap velocity ( $cm * h^{-1}$ ) in cacao trees. All variables except those plotted are held constant at their mean values.

469 sap velocity was very high. When VPD and LAI were low, the sap flow was  
470 also very low (Fig. 8). When VPD was low, the sap velocity remained low,  
471 whatever the value of LAI. When LAI was low ( $<2.5$ ), sap velocity increased  
472 with the VPD anomaly with the same evolution and reached similar high values  
473 for positive VPD anomalies. But, when both LAI and VPD were high (LAI $>2.5$ ;  
474 VPD anomaly  $>0$ ), the response of sap velocity was characterized by a steeper

475 slope, indicating a possible positive synergistic effect on sap velocity between  
476 VPD and LAI. This synergy meant that the positive response of sap velocity to  
477 positive VPD anomalies (Fig. 6) was amplified by the canopy density when LAI  
478 was above 2.5 (Fig. 8). If the LAI alone was not able to sensibly change the  
479 sap velocity (Fig. 6), at high values (LAI>2.5) its importance was inflated by  
480 positive VPD anomalies (Fig. 8). Ultimately, the sap velocity of trees with an  
481 LAI above 2.5 under a stronger pulling force from the atmosphere (positive VPD  
482 anomalies) resulted to be higher than the single responses to each of the two  
483 predictors alone. Conversely, the potentially interesting interaction between  
484 VPD and soil VWC was not found strong enough to be considered relevant  
485 according to model 1 (Tab. 1).

#### 486 3.4. Daily variations of sap velocity in response to climatic drivers

487 The BRT model based on the daily averages of sap flow velocity rendered  
488 a strong training data correlation (0.944), a good cross-validation correlation  
489 (0.803). Thus, the model was found to be stable and reliable. An evaluation  
490 of predicted against measured values on the test data showed that model 2  
491 predicted well sap velocity despite a slight underestimation at high daily aver-  
492 age sap velocities (above  $57 \text{ cm} * \text{h}^{-1}$ ) (Fig. C.2). Furthermore, when scaling  
493 up from the half-hourly to the daily analysis, the weight of the predictors on  
494 sap velocity changed (Fig. 9). The variability in daily sap velocity was mostly  
495 explained by LAI (27.2%) and soil VWC (21.4%). The relative importance of  
496 radiation (PAR) and VPD decreased to 18.1% and 17.0% respectively. 16.3%  
497 of the variability in sap velocity was explained by variations in trunk diameter.

498  
499 The shape of the response curves of daily sap velocity to the considered  
500 variables was different to that observed for half-hourly values (Fig. 6, 9). Sap  
501 velocity increased nearly linearly with LAI above  $3.5 \text{ m}^2[\text{leaf}] * \text{m}^{-2}[\text{soil}]$ . Sap  
502 velocity was insensitive to LAI, for values between 2 and  $3.5 \text{ m}^2[\text{leaf}] * \text{m}^{-2}[\text{soil}]$ .  
503 Below  $2 \text{ m}^2[\text{leaf}] * \text{m}^{-2}[\text{soil}]$  and down to  $1.5 \text{ m}^2[\text{leaf}] * \text{m}^{-2}[\text{soil}]$  (minimum  
504 value measured in our study), sap flow velocity also responded to changes in



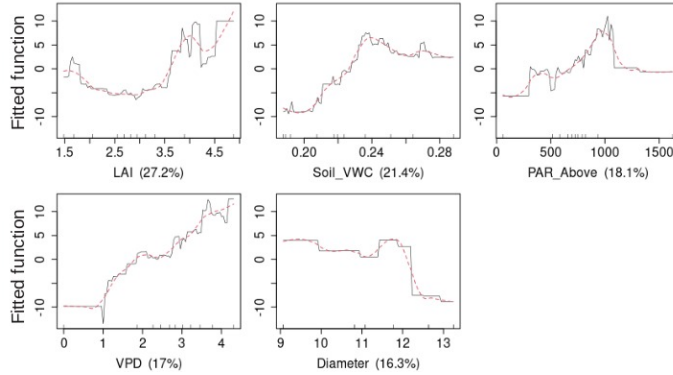


Figure 9: Overview of cacao's daily sap velocity response to the main environmental drivers according to a BRT model (model 2). The responses are calculated for daily averages during the entire period of this study. Functional shapes of the response of sap velocity to the environmental variables: VPD, PAR, Soil VWC, LAI and tree diameter. Each variable is presented with the relative importance of its variation on that of sap velocity within parentheses. The red dotted lines represent the LOESS smoothing for each response function.

505 LAI, increasing as LAI was lower. Sap flow velocity increased linearly with  
 506 soil VWC until a threshold level of  $0.24 \text{ m}^3 * \text{m}^{-3}$  (approximately  $-0.16 \text{ MPa}$   
 507 for our soil), past which it plateaued. The shape of the response curve of sap  
 508 velocity to mean daily PAR was almost linear in the range from 0 to 1100  
 509  $\mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$ . Beyond this value, the response of sap velocity captured by  
 510 the BRT model leaned on few points, thus was not considered reliable. Finally,  
 511 the mean daily sap velocity increased linearly with daily average VPD in a sim-  
 512 ilar fashion to that observed in the half-hourly model 1 (Fig. 6, 9).

513

514 A significant interaction was found between LAI and soil VWC and, to a  
 515 lesser extent, between VPD and PAR (Tab. 2). When LAI was low, sap velocity  
 516 increased slightly with soil VWC (Fig. 10). But when LAI reached the value of  
 517  $3 \text{ m}^2 * \text{m}^{-2}$ , the increase with soil VWC became much more important and sap  
 518 velocity reached very high values. The interaction between average daily VPD  
 519 and PAR, although less pronounced, showed that the increase in VPD and PAR  
 520 may have a synergistic effect on sap velocity (Fig. 11). As PAR increased (up

	PAR_Above	LAI	Soil_VWC	VPD	Diameter
PAR_Above	0	2692.77	340.99	<b>5507.51</b>	4970.65
LAI	0	0	<b>19350.06</b>	5019.99	5275.63
Soil_VWC	0	0	0	510.93	1408.86
VPD	0	0	0	0	2304.21
Diameter	0	0	0	0	0

Table 2: Interactions between the variables considered in the BRT Model 2 in explaining cacao sap velocity at a sub-daily timescale. For each pair of variables, the table reports the mean value of the residuals, which represents the strength of the interaction. In bold: the interactions considered strong, thus significant, by the model.

521 to  $1100 \mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$ ), sap velocity responded more readily to daily average  
522 VPD and vice versa. Few PAR values were recorded above  $1100 \mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$   
523 and the apparent decrease in sap velocity after this value was not interpretable.  
524 At the one-day time scale, no interaction between mean soil VWC and VPD  
525 was detected by model 2 (Tab. 2), similarly to what was found at the sub-daily  
526 timescale (Tab. 1).

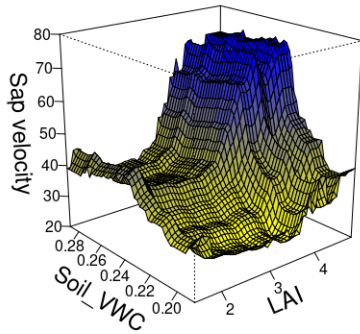


Figure 10: Three-dimensional partial dependence plots for the interaction between soil VWC ( $\text{m}^3 * \text{m}^{-3}$ ) and LAI ( $\text{m}^2[\text{leaf}] * \text{m}^{-2}[\text{soil}]$ ) in the BRT model 2 for daily average sap velocity ( $\text{cm} * \text{h}^{-1}$ ) in cacao trees. All variables except those plotted are held constant at their mean values.

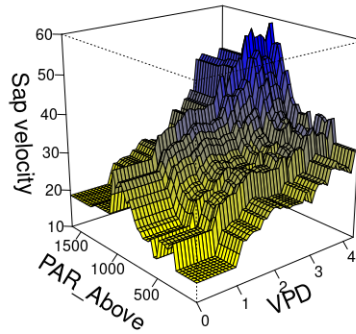


Figure 11: Three-dimensional partial dependence plots for the interaction between PAR ( $\mu\text{mol} * \text{s}^{-1} * \text{m}^{-2}$ ) and VPD ( $\text{kPa}$ ) in the BRT model 2 for daily average sap velocity ( $\text{cm} * \text{h}^{-1}$ ) in cacao trees. All variables except those plotted are held constant at their mean values.

## 527 4. Discussion

### 528 4.1. Climate

529 The measured climate of the 2019-2020 dry season (Fig. 2) was representative  
530 for the conditions experienced by cacao during this time of the year in the  
531 Eastern region of Ghana. As soil VWC approached the wilting point in the  
532 control plot, air humidity dropped even below 20% and temperatures were sub-  
533 optimal (Fig. 2, Fig. A.1), on a daily basis, the measured conditions were found  
534 to be stressful according to the definitions given for soil and atmospheric stresses  
535 (see Section 1).

### 536 4.2. Canopy

537 Despite the occurrence of high temperatures, the trees were able to cope  
538 with the climate in December. We argue so because we did not observe any  
539 decline in LAI in either watering treatment, in line with previous studies with  
540 no atmospheric stress [67, 19]. Leaf shedding is a common response to drought of  
541 tropical and subtropical species [68, 69], as it allows trees to reduce transpiration  
542 rates and, hence, avoid hydraulic failure. In line with the idea that cacao trees  
543 apply this drought-coping strategy, during the more severe part of the dry season  
544 (from January onwards), LAI decreased in both watering treatments, although  
545 at a faster rate in the control plot (Fig. 3), supporting the idea that leaf shedding  
546 helps cacao to cope with soil drought. However, given that LAI also decreased  
547 in the irrigated plot throughout the experimental period, it is likely that trees  
548 in the irrigated plot also suffered from water stress. It could be argued that the  
549 irrigation level (60 L/tree on alternate days, equivalent to approximately 9.6 mm  
550 of rain) was not sufficient to completely mitigate soil drought (Fig. 2), despite  
551 being in line with the water requirement of a mature tree found in literature  
552 [37].

553 Alternatively, it can be interpreted as the atmospheric drought having con-  
554 tributed to leaf shedding. This latter interpretation is supported by the more  
555 abundant litter production observed in December, when the soil VWC was sig-  
556 nificantly higher in the irrigated plot than in the control but air humidity and

557 temperature reached values above stressful thresholds (Fig. A.1, B.2). The tim-  
558 ing of the drop in LAI suggests that the key atmospheric condition impacting  
559 the canopy was the extremely low air humidity to which cacao leaves might not  
560 be adapted, especially considering that cacao developed under very high relative  
561 air humidity [70].

562 By the end of the dry season, the control plot had lost two thirds of its  
563 foliage, twice the loss in the irrigated plot. In light of the lack of interaction  
564 between VPD and soil VWC in explaining sap velocity (Tab. 1, 2) it could  
565 be assumed that the effects of atmospheric and soil stress on LAI were inde-  
566 pendent. If this assumption is accepted, the difference in LAI drop between  
567 the two plots must have been driven by the difference in soil VWC (Fig. 2, 3).  
568 The fact that the net loss in LAI in the control relative to that in the irrigated  
569 treatment (-62.5% vs. -32.5% over the course of the experiment, respectively)  
570 was much larger than the difference in litterfall between the two treatments (309  
571  $g[dry] * m^{-2}$  and  $247 g[dry] * m^{-2}$ , respectively - a relative difference of 25%)  
572 suggests that some leaf flushing might have occurred in the irrigated treatment.  
573 This hypothetical leaf flushing in the irrigated treatment never sufficed to coun-  
574 terbalance the leaf shedding, possibly due to a limitation in carbon to invest in  
575 leaf production, resulting in a drop in LAI. Further, more specific, studies to  
576 investigate the effects of atmospheric and soil drought on leaf flushing dynamics  
577 would be needed in order to properly characterize such effects.

578 It is acknowledged that the irrigation might have been sub-optimal but, based  
579 on the above reasoning, the loss of canopy density in the irrigated plot was  
580 imputable mostly to the atmospheric stress. In the control treatment the ad-  
581 ditional loss was caused by the soil stress and the interaction between the two  
582 stresses, if present. Thus, our results on the LAI evolution and litterfall produc-  
583 tion show that the impact of atmospheric stress (VPD) on the canopy during  
584 the dry Harmattan season may be of similar magnitude, if not greater, than  
585 that of soil stress (soil VWC), regardless of the possible interaction between the  
586 two stresses (Fig. 3). If the two stresses were independent, then the depressing  
587 effects of soil and atmospheric stress were of the same magnitude, one third

588 of the initial canopy density each. Alternatively, the existence of an interac-  
589 tion between the two would mean that the soil stress impacted the canopy less  
590 than the atmospheric one. The major role found for the aerial stress is in line  
591 with Hutcheon et al. (1973) [71], who concluded that the beneficial effect of  
592 irrigation on cacao total biomass production was limited when in presence of  
593 atmospheric stress. Other authors reported the same [17, 37] but, to our knowl-  
594 edge, this was the first attempt to quantify the effects under field conditions in  
595 West Africa. Our results contrast with those from a study in which LAI did  
596 not change in response to a 73% reduction in precipitation over 13 months [19].  
597 It must be noted that the experimental conditions between this experimental  
598 site in Sulawesi, Indonesia and ours in eastern Ghana differ greatly. For the site  
599 in Sulawesi, it was suggested that the reduction in incoming precipitation was  
600 insufficient to impose stressful conditions due to the high mean annual rainfall  
601 (2,844 mm) [72]. Furthermore, at the Indonesian site, daily mean relative air  
602 humidity never dropped below 69%, in contrast to our study site, where relative  
603 air humidity often fell below 40%, and where we found a significant drop in LAI,  
604 irrespective of the irrigation regime.

#### 605 4.3. Sap velocity

606 The two models developed (half-hourly: BRT model 1, daily: BRT model 2)  
607 allowed us to obtain a good estimate of the environmental and climatic drivers of  
608 sap velocity on a half-hourly and daily scale. This allowed an effective investiga-  
609 tion of the impacts of atmospheric and soil water stress on cacao during Harmat-  
610 tan season. Up to now, in cacao, the response of transpiration to atmospheric  
611 drought stress had only been studied under controlled conditions, in young in-  
612 dividuals and never in combination with limited water availability [13, 14, 15].  
613 Previous studies addressing the effects of climatic factors (VPD, soil VWC and  
614 PAR mainly) on transpiration did not find clear patterns [13, 17]. Fraga et al.  
615 2020 [13] argued that large temporal and spatial heterogeneity, mainly in VPD  
616 and soil water, could account for some of the unexplained variability in transpi-  
617 ration. We argue that our approach of separating the instantaneous half-hourly

618 effect from the integrated daily effects allowed us to disentangle some of these  
619 patterns. Furthermore, to our knowledge, this is the first study that addressed  
620 the effect of the interactions among variables on sap velocity.  
621 Soil VWC and LAI did not change significantly at the time scale of one day.  
622 Despite their lack of variation at the sub-daily level, soil VWC and LAI varied  
623 over the season, setting different daily conditions for sap velocity variation in  
624 response to the variability of the remaining variables (PAR, VPD) (Fig. 4,5,6).  
625 The BRT model 1 showed that, of these two conditions, soil VWC mattered  
626 more than LAI (Fig. 6). This suggests that water availability matters more  
627 than the total leaf area available for transpiration in determining sap velocity.  
628 In cacao the transpiration is largely performed in the outer crown, while the  
629 shade leaves are far less active [17, 67]. The loss of foliage probably interested  
630 mostly sun leaves [67] but the trees were probably able to adapt the lower strata  
631 of the canopy to the new conditions [73, 74], minimizing the direct effect of LAI  
632 on sub-daily sap velocity. This was reflected in the flat response of sap velocity  
633 to LAI in model 1 (Fig. 6). Instead, the different soil VWC over the season  
634 appeared to matter more in determining the sub-daily sap velocity, possibly  
635 hinting that cacao might be more limited by its root water uptake and by the  
636 conductivity of the vascular system rather than by the canopy conductance, in  
637 line with [16].  
638 Within a day, sap velocity responded mainly to the variation of PAR and VPD  
639 and their synergistic effects (Fig. 7). At the sub-daily time scale, PAR was the  
640 principal driver for sap velocity, as long as VPD did not exceed the mean daily  
641 cycle by more than  $2\text{ kPa}$ . Beyond this value for the anomaly, it is possible  
642 that for most part of the day stomatal regulation was no longer effective in  
643 dealing with the high water demand from the atmosphere. This is supported  
644 by the fact that irrigation was not able to limit water loss when VPD was ex-  
645 tremely high and the irrigated trees ended up transpiring as much as the trees  
646 in the control plot (Fig. 5 A). Moreover, the observed peak in sap velocity up  
647 to  $20\text{ cm/h}$  in the morning cannot be explained by the extremely low values of  
648 VPD and PAR (Fig. 5 A, B). However, said peak may be explained as a phe-

649 nomenon of recovery from embolism [75]. It has been described in other plants  
650 that, following embolism due to hydraulic stress, the plant applies a positive  
651 root pressure to force the gas to dissolve. Such recovery strategy of embolism  
652 removal is often put in place concurrently to the start of transpiration in the  
653 morning [76, 77, 75]. The control trees, constantly stressed by the low VWC,  
654 may have had to adopt this strategy regardless of the VPD level, as the early  
655 morning peak in sap velocity suggests (Fig. 5 A,B). The irrigated trees did not  
656 present the same peak in the early morning in days with moderate-low average  
657 VPD but irrigation might have not prevented embolism when VPD was high,  
658 leading to an early morning sap velocity peak compatible with the refilling of  
659 vases (Fig. 5 A, B). This behaviour is congruent with the idea that irrigation  
660 is not sufficient when the atmospheric stress is too strong.

661 Cacao plants naturally occur in the understorey of tropical forests, where light  
662 is limited and VPD is rarely high [78]. Hence, we could expect that stomatal  
663 behavior is finely-tuned in cacao to respond to variations in light availability,  
664 to maximize photosynthesis [74, 79], but it might not be adapted to regulate  
665 water loss under increasing VPD, as we observed in our experiment (Fig. 4).  
666 Before this study, the atmospheric component of water stress had rarely been  
667 taken into account because such conditions are seldom met in most of the cacao-  
668 growing areas worldwide [18, 72]. Nonetheless, most of the West African cacao  
669 belt undergoes atmospheric stress on a quasi-seasonal basis under the influence  
670 of the Harmattan winds [23] and the chances of harsher atmospheric stress in  
671 the region will increase with climate change. Given that West Africa includes  
672 the two leaders of cacao production worldwide (Ivory Coast and Ghana) [80],  
673 our study highlights the importance of recognizing the due importance of the  
674 atmospheric stress.

675 At the seasonal time scale (effects on daily averages), the effects of PAR and  
676 VPD, as well as their interaction, were maintained. Together with PAR and  
677 VPD, at the seasonal time scale soil VWC played a major role as well (Fig. 9,  
678 11). The response curve of sap velocity to soil VWC in figure 9 highlights that,  
679 under our experimental conditions, the soil reached a critical soil VWC at which

680 cacao water extraction capacity was challenged ( $0.24 \text{ m}^3 * \text{m}^{-3}$ , approximately  
681  $-0.16 \text{ MPa}$  for our soil). A significantly lower critical value of soil water poten-  
682 tial for water extraction ( $-0.079 \text{ MPa}$ ) has previously been reported for young  
683 cacao plants under field conditions in Brazil [13]. The difference between the  
684 Brazilian study and ours is possibly related to the differences in genetics, age,  
685 and rooting depth considered in the two experiments. Here, we studied mature  
686 trees subject to water stress on a regular basis every year. These two elements  
687 (age and prevailing climate) imply that our trees would have had a more devel-  
688 oped rooting system, capable of exploring a larger soil volume.

689 Contrary to our initial expectations, our results from the BRT models did not  
690 clearly show an interactive effect between atmospheric and soil drought on ca-  
691 cao transpiration, represented in the models by VPD and soil VWC (Tab. 1,  
692 2). Yet, our results cannot completely rule out our initial hypothesis as, for  
693 example, Model 1 highlighted a not significant but strong link between VPD  
694 and soil VWC (Tab. 1). The BRT models could have failed at capturing such  
695 interaction because of the paucity of observations when atmospheric and soil  
696 drought co-occurred in the control plot, a key requirement to train the model.  
697 Furthermore, the provided level of irrigation might have not been sufficient to  
698 completely alleviate the soil stress in the irrigated part. If this was the case,  
699 the small  $\Delta \text{ VWC}$  between plots might have made more complicated for the  
700 model to capture an interaction between soil and atmospheric drought across  
701 treatments as well.

702 At the seasonal time-scale (daily average measurements), we found that the re-  
703 sponse of sap velocity to both atmospheric and soil drought was modulated by  
704 the interaction with LAI. We found that beyond certain threshold values of both  
705 VWC ( $0.24 \text{ m}^3 * \text{m}^{-3}$ ) and LAI ( $3.5 \text{ m}^2[\text{leaf}] * \text{m}^{-2}[\text{soil}]$ ), sap velocity did not  
706 respond to further increases in either variable. The daily average sap velocity  
707 measured under these conditions, high VWC and LAI( $76 \text{ cm} * \text{h}^{-1}$ ), could be  
708 the maximum supported by the root and vascular system of cacao, although  
709 this should be further tested in other climates. When soil VWC was below  $0.24$   
710  $\text{m}^3 * \text{m}^{-3}$ , sap velocity was strongly responsive to soil VWC variations, regard-



711 less of the LAI, whereas for a given soil VWC, the response of sap velocity to  
712 changes in LAI was less pronounced (Fig. 10). This behaviour is compatible  
713 with the higher importance of soil VWC over LAI found in model 1 (Fig. 6)  
714 and with the more dynamic shape for the response of sap velocity to soil VWC  
715 and flatter one for LAI in model 1 (Fig. 6) and for most of the range (1.5 to 3.5)  
716 in model 2 (Fig. 9). Furthermore, the irrigated trees only showed signs of prob-  
717 able embolism recovery in the mornings of days with a high VPD, suggesting  
718 that they were not able to uptake enough water from the soil to avoid embolism  
719 (Fig. 5 A), while in the control the morning peak in sap velocity, that we pro-  
720 posed as a sign of embolism recovery, was present with approximately the same  
721 magnitude under high and low VPD (Fig. 5 A,B). This suggests that the main  
722 limitation for water transportation in the soil-plant-atmosphere continuum was  
723 found in the ability of the plant to extract water from the soil. The results dis-  
724 cussed in this paragraph support the theory that cacao's transpiration is mostly  
725 limited by the root water uptake capacity rather than by the conductivity of  
726 the vascular system or the total leaf area, in line with [16].

## 727 5. Conclusions

728 For the first time, in this study, we assessed the effects of soil and atmo-  
729 spheric water stress on canopy transpiration of adult cocoa trees. We showed  
730 that under high soil and atmospheric water stress, irrigation decreased leaf shed-  
731 ding in response to limited water availability in the soil. Nonetheless, under a  
732 climate change scenario with harsher conditions experienced by cacao under the  
733 influence of the Harmattan winds, irrigation might not suffice to sustain cacao  
734 production. In fact, our study highlights that cacao transpiration increases with  
735 high VPD, which could further compromise soil water availability and eventu-  
736 ally aggravate soil stress. The use of shade nets or of shade trees with a deep  
737 rooting system, as previously suggested [81, 82], could be a key requirement for  
738 cacao farming in the future to partially alleviate atmospheric drought stress.  
739 Deep-rooted vegetation and/or shading nets diminish the detrimental impact

740 of increased atmospheric drought by buffering temperature and relative air hu-  
741 midity. This prevents stressful values for temperature and relative air humidity  
742 without adding competition for water extraction. Still, to predict the actual  
743 impact of increased drought severity under climate change on cacao production,  
744 it will be necessary to look beyond the effects of soil and atmospheric drought  
745 on transpiration and leaf area, and study how these conditions affect flower,  
746 fruit and seed production in the field. Furthermore, other similar studies are  
747 needed to validate and strengthen these conclusions, which rely on data with  
748 limited replicates that may limit the possibility of generalizing these findings for  
749 other situations. In any case, this study has confirmed in the field what previous  
750 studies had found in controlled environments and proposed new results that are  
751 in line with the behaviour in similar environments of cacao and other species.

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760 Walker for assistance with the data collection and maintenance of the field and  
761 instrumentation.

762 **Appendix A. Atmospheric stressors**

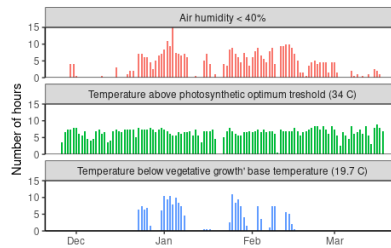


Figure A.1: Number of hours per day under stressful climatic conditions for cacao trees according to values reported in [17, 26, 27, 28, 21]; each bar is one day. Top: air humidity below 40%; middle: temperature above photosynthetic optimum threshold (34 °C); bottom: temperature below the base temperature for vegetative growth (19.7 °C).

763 **Appendix B. Leaf area index**

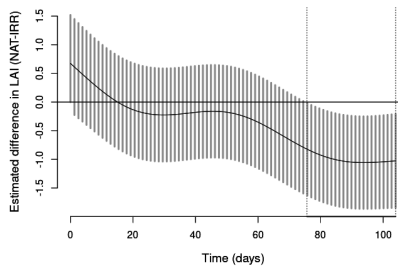


Figure B.1: Difference in estimated leaf area index (LAI) between the irrigated and the control plot. The fitted line is a generalized additive model and the shaded area is the 95% prediction interval. A shaded area non-overlapping with the zero-line indicates a significant difference between watering treatments.

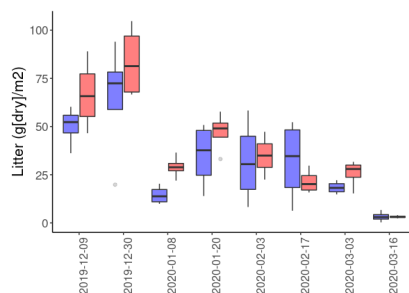


Figure B.2: Litter production of cacao trees during the dry Harmattan season, in presence (blue) and absence (red) of irrigation. Box-plots represent variations between the four litter traps per treatment and date. Bold lines represent means per plot and date.

## 764 Appendix C. Boosted Regression Trees analysis

### 765 Appendix C.1. parameterization of the models

	Step	Family	t1	bg	nt	tc	lr
Model 1	30 min	Gauss	0.01	0.75	100	3	0.1
Model 2	1 day	Gauss	0.001	0.75	100	3	0.05

Table C.3: Parametrization of the BRT models to predict the transpiration during the day at a 30-minute time interval (Model 1) and at a daily time step (Model 2). A BRT model requires the definition of a set of hyperparameters:

family - the type of statistical error distribution characterizing the data, in our case Gaussian; tolerance (t1) - the threshold in variance change under which to stop the model reiteration; bag fraction (bg) - the fraction of dataset to use for the training of each tree. The remaining data is used at each step to cross validate the set of relations found;

number of trees (nt) - the number of trees necessary for optimal prediction. It is determined based on t1 and bg;

tree complexity (tc) - the maximum level of interaction between variables to consider in a tree;

learning rate (lr) - determines the contribution of each tree to the growing model.

The seed number used was - 210920.

### 766 Appendix C.2. Evaluation of BRT models on the test data

767 To allow an independent evaluation of the BRT models, 25% of the field  
768 data was set aside to be used as a test subset of data and was not used at any

769 point in the training of the BRT models. This section of the appendix presents the evaluation of the models (Model 1, Model 2) on this test data subset.

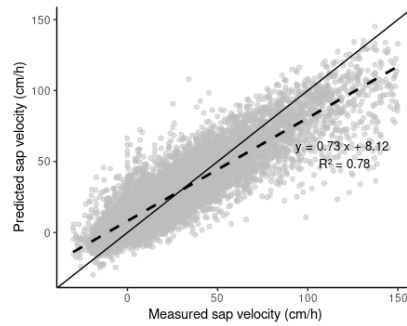


Figure C.1: Observed (abscissa) vs. predicted (ordinates) sap velocity, the corresponding linear regression (dashed line) and  $y=x$  line (full black line) for the BRT half-hourly model (model 1) test data.

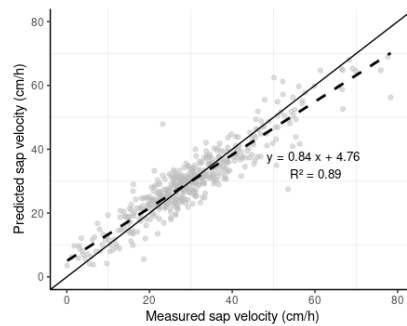


Figure C.2: Observed (abscissa) vs. predicted (ordinates) sap velocity, the corresponding linear regression (dashed line) and  $y=x$  line (full black line) for the BRT daily model (model 2) test data.

770

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## Highlights

**Assessment of atmospheric and soil water stress impact on a tropical crop: the case of *Theobroma cacao* under Harmattan conditions in eastern Ghana.**

Pietro Della Sala, Christian Cilas, Teresa E. Gimeno, Steven Wohl, Stephen Yaw Opoku, Alina Găinușă-Bogdan, Fabienne Ribeyre

- Soil and atmospheric water stresses' effect on cacao's transpiration are independent
- Atmospheric stress reduced the canopy density by one third regardless of irrigation
- An extra third of the canopy density was lost due to soil water stress in the control
- Soil moisture and air vapour pressure are the key drivers of cacao sap velocity
- Cacao transpiration appears more limited by root uptake than canopy conductivity