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ORIGINAL PAPER

Effect of elevated CO_2, high temperature, and water deficit on growth, photosynthesis, and whole plant water use efficiency of cocoa (*Theobroma cacao* L.)

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Abstract
In this study, the response of 6-month-old cocoa (*Theobroma cacao* L.) seedlings to elevated CO_2 concentration [ECO_2], elevated temperature [ET], and their interaction with water deficit stress was studied in an open top chamber (OTC). Each OTC was maintained at chamber control (400 ppm CO_2), [ECO_2] 550 ppm, [ECO_2] 700 ppm, ET 3 °C above chamber control, and ET 3 °C + [ECO_2] 550 ppm. Inside each OTC, a set of plants received moisture at 100% FC, while the other set was at 50% FC, which was the water deficit stress treatment. Increasing the CO_2 concentration in cocoa increased photosynthesis (Pn) by 27%, which resulted in high biomass accumulation, thus improving the whole plant water use efficiency (WUE). The impact of high temperature (T_{max}), around 39 °C in ET treatment against 36 °C in chamber control, is quite severe on Pn, leaf Ψ, and biomass accumulation. Similarly, water deficit at 50% FC resulted in the leaf Ψ reducing to − 14.06 bars at which Pn, leaf area, and biomass were significantly reduced. [ECO_2] could ameliorate the negative effect of high temperature and water deficit stress to certain extent. However, the relative response of cocoa seedlings to [ECO_2] in improving Pn, leaf Ψ, biomass, and WUE was greater under 50% FC compared to plants at 100% FC suggested additional advantage of [ECO_2] to cocoa under water limited conditions.

Keywords Climate change · Cocoa · Elevated carbon dioxide · Elevated temperature · Water deficit · Interaction effects · Water use efficiency

Introduction

Cocoa (*Theobroma cacao* L.) is an important commercial crop cultivated worldwide in the humid tropics within 20° North and South of the equator. Its production is mostly concentrated in West Africa, where more than 70% of cocoa is produced, followed by South-East Asia and Latin America (Lahive et al. 2019). Since 2008, a steady annual increase of 3% in the production of cocoa has been seen and is predicted to continue increasing further (WCF 2014). To strike a balance between future supply and demand, there remains a need to increase production either through increased productivity or through increased land cultivation area. However, if model projections are correct, then increasing the productivity of existing cocoa farming areas may be a challenge, as most of the cultivated areas, especially in Western Africa, are projected to be unsuitable for production in future due to climate change (Läderach et al. 2013; Schroth et al. 2016; Medina and Laliberte 2017). Hence, it may prove to be a great challenge to increase expected production levels unless adaptive measures to the predicted threat of climate change are implemented.

In India, cocoa is mostly grown in the South Indian states of Karnataka, Kerala, Andhra Pradesh, and Tamil Nadu. On the west coast of Karnataka and Kerala, the annual rainfall is > 2000 mm and cocoa is grown at a

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T_{max} (maximum temperature) of 34 to 36 °C, while on east coast of Andhra Pradesh and Tamil Nadu, the rainfall is low (around 1000 to 1200 mm) and T_{max} reaches as high as 40 to 42 °C in some of the cocoa growing regions (Apshara et al. 2018). Based on climate change projections, temperatures are likely to increase in these regions from 1.1 to 2.6 °C under RCP 4.5, 1.4 to 3.1 °C under RCP 6.0, and 2.6 to 4.8 °C under RCP 8.5, with a corresponding increase of CO_2 550, 750, and 1200 ppm by the end of the twenty-first century (2081–2100), relative to 1986–2005 (IPCC 2014). It is expected that precipitation levels may also change. Yet efforts to understand the impact and adaptive strategies of cocoa to climate change are very much limited (Lahive et al. 2019).

Among the many climatic factors that influence cocoa crop performance, temperature, rainfall, and carbon dioxide (CO_2) play vital roles in seedling establishment and productivity. Earlier studies have shown the beneficial effect of an increase in atmospheric CO_2 to cocoa growth and productivity. [ECO_2] have resulted in enhanced photosynthetic rates both in instantaneous exposure studies and more long-term growth studies (Baligar et al. 2008; Lahive et al. 2018). However, the additional benefit of decrease in stomatal aperture and resulting decrease in transpiration under high CO_2 as seen in other crops (Ainsworth and Rogers 2007) is contradictory in cocoa. Baligar et al. (2008) measured a 65% reduction in gs while Lahive et al. (2018) could not observe any change in gs at around 700 ppm CO_2. This reduction in gs should lead to enhanced WUE, i.e., the amount of biomass produced per unit of water transpired, and could be important for future climate scenarios in which water supplies are projected to be limited.

Additionally, the benefits observed with [ECO2] may be expected to significantly decrease with the increase in global temperatures, altered distribution of precipitation, and the intensification of drought in arid and semiarid areas (Wigley and Raper 2001; IPCC 2014). Photosynthesis in cocoa has been found to have an optimum temperature of 31 to 33 °C (Balasimha et al. 1991) and found to decline above mean monthly temperature of 34 °C during dry season. Yapp (1992) reported an optimum temperature of 33 to 35 °C. Similarly, soil water deficit decreases the growth and yield of cocoa; however, rainfall between 1400 and 2000 mm $year^{-1}$ is sufficient to support growth of cocoa and less than 1200 mm $year^{-1}$ results in soil water deficit (Alvim 1977).

Although high temperatures and water deficits reduce growth and yield of crops, its interaction with [ECO2] in most of the crops resulted in higher WUE and thus alleviated these effects to large extent (Tezara et al. 2002; Allen et al. 2003). Consequently, the measured growth responses to elevated CO_2 have often been inconsistent because of the factors that interact with CO_2, such as water availability and temperature (Van der Sleen et al. 2015; Korner 2006; Ainsworth et al. 2003; Prasad et al. 2006). In coconut, the benefits of elevated CO_2 on growth and yield decrease with increasing temperatures (Hebbar et al. 2016).

In cocoa, however, there are few studies to show its responses to individual climate variables, but how these variables interact to influence growth and productivity is very much limited. In this study, in addition to the effect of individual climate change variables, we made an attempt to quantify the interaction effect between [ECO_2] and high temperatures with water deficit on growth, photosynthesis, and WUE of cocoa seedlings under controlled environmental conditions.

Materials and methods

Growth conditions

The research was conducted in an open top chamber (OTC) at ICAR-Central Plantation Crop Research Institute (CPCRI), Kasaragod Kerala, India. The CPCRI is located at 12° 18′ N latitude and 75° E longitudes, and at an altitude of 10.7 m above mean sea level. The average rainfall for this region is approximately 3400 mm, mainly received during the months of June to September. The average maximum temperature (T_{max}) in summer is about 33.5 °C and winter 31.2 °C. The average relative humidity of this region is about 88% and the soil type is sandy loam with a 4.3–5.5 pH.

Five OTCs, with dimension 4 m × 4 m × 4 m, were used for this study. The chamber was fabricated with galvanized iron (GI) pipe covered with a polyvinyl chloride (PVC) sheet of 120-μm gauge, designed to allow more than 90% of the light transmit through it. At a height of 2.4 m, a frustum with an angle 0.6 m towards the inside was maintained to reduce the dilution effect of the air current within the chamber. The upper portion of the chamber was kept open to maintain near-natural conditions of temperature and relative humidity. The further structural details of OTC were described in Vanaja et al. (2006). The gas flow and temperature in the OTC was controlled by a computer program interface with the supervisory control and data acquisition system (SCADA; Neogenesis, India). The set levels of CO_2 in the OTCs were attained by injecting air enriched with commercial-grade CO_2 and monitored with the help of SCADA linked infrared gas analyzer (IRGA) (Roger et al. 1983). All of the OTCs were equipped with temperature sensors (MST 10R, Muesen, Germany), and the air temperature of OTCs under ET treatment was raised to a set temperature with respect to a reference temperature of a control chamber by blowing hot air and was controlled by the SCADA system (Samol et al. 2015).

Plant growth and treatments

Six-month-old nursery grown seedlings of the cocoa variety VTLCC1 were transplanted to large 55-cm height by 32-cm diameter plastic pots, with 60 kg dry soil capacity. The pots were painted black on the outside to prevent light penetration and holes were placed at the bottom of the pots to drain out the excess water. Soil mixed with vermicompost at a 3:1 ratio was filled, leaving 5 cm space between the soil and the top in all of the pots. The soil was sandy loam in nature with sand:silt:clay at 76%, 1.92%, and 22%, respectively. Seedlings of similar heights and growth were transplanted to the pot on 23 June 2013, and a single plant was maintained in each pot. Pots with seedlings were then placed underneath coconut trees for 15 days with sufficient irrigation. After 15 days of initial establishment, nine pots with seedlings were moved to each OTC. The following were the climatic variable treatments of the study: (i) chamber control (ambient conditions in the chamber; 400 ppm CO_2), (ii) elevated CO_2 [ECO_2] 550 ppm, (iii) [ECO_2] 700 ppm, (iv) elevated temperature, ET (3 °C above chamber control), and (v) ET+ [ECO_2]; 3 °C + 550 ppm CO_2. The plants were exposed to above climate variables from 8 am to 5 pm daily throughout the experimental period (8 July 2013 to 31 May 2014).

With the cessation of the monsoon rains, water deficit treatments were imposed on 15 November 2013. Out of the nine seedlings in each OTC, three seedlings were uprooted to collect the initial biomass. The remaining six seedlings were randomly grouped into two sets with three replications. One set, T_1, had the soil moisture maintained at 100% field capacity (FC) and the other, T_2, was maintained at 50% FC. The 100% FC treatment was imposed as follows: 1 day before imposition of the stress treatment (14 November 2013), the soil in the pots was saturated with water, and the excess moisture was allowed to drain for 12 h. The moisture retained in the soil was determined using a PR2 profile probe (Delta T devices, UK), which was combined with the dedicated DL6 soil moisture logger for continuous soil moisture monitoring. The moisture content was found to be approximately 20% for the sandy loam soil, which we had used in our experiment. This moisture is equivalent to soil moisture in the field capacity. Daily, before irrigating the T_1 pots, soil moisture was determined and the amount of water added to attain 100% FC was recorded, whereas T_2 received 50% of the water applied to T_1. An additional pot of the same size, containing same amount of soil but without a seedling planted in it, was kept in each OTC to check the evaporative loss of water. It received the equal amount of water added to T_1. The excess water that drained out was then collected and quantified. The difference between the water applied and the drained water collected is the water loss through evaporation. All of the pots received the recommended dose of fertilizer at the rate of 0.5 kg, 0.32 kg, and 1.2 kg N:P:K per pot applied through urea, single super phosphate, and muriate of potash. The above experiment was continued until 31 May 2014.

Morphological and physiological traits

Prior to the termination of the experiment, morphological and physiological observations were recorded across different treatments. Plant height was recorded from the ground level to the highest point in the canopy. The number of plants jorquetted and the number of side branches at the jorquette also were recorded. Leaf sizes showed a large variation at different positions in the canopy. Therefore, in order to determine the leaf area, length and breadth of few representative leaves in different position of canopy was measured and its dry weight was recorded from each plant in each treatment. An area (length × breadth) to weight relation was established and was used to derive the leaf area from the total leaf dry biomass based on its specific position in the canopy. The leaf area of each position was pooled to obtain the total plant leaf area. The leaf Ψ of the topmost, fully hardened leaf was measured using a Scholandar Pressure Bomb (WESCOR). Additionally, the process parameters photosynthesis, stomatal conductance, and transpiration were measured using a portable photosynthesis system (LI-COR 6400XT, LI-COR, Lincoln, NE, USA). Measurements were made in triplicate with respect to the CO_2 concentration of treatments at a fixed light intensity of 1000 μmol m^{-2} s^{-1} (Jaimez et al. 2018) which is saturating for cocoa. Chlorophyll fluorescence indices of the same leaf were measured after dark adaption for 30 min, using a chlorophyll fluorescence meter (OS30p, OptiSciences, Hudson, MH, USA). All measurements were made in the topmost, fully hardened leaf around 10 am on clear, sunny days. The chlorophyll content of the topmost, fully hardened leaf was measured using dimethylsulfoxide (DMSO) as per the methodology described by Arnon (1949).

Whole plant water use efficiency

The whole plant water use efficiency (WUE) was calculated by determining the dry biomass produced by the plant per unit of water consumed. The initial biomass at the start of treatment and the final biomass at the termination of the experiment were determined. The soil in the pot was washed off with a jet of water to pull out the plants with intact roots. Leaf, stem, and root parts were separated, oven dried at 65 °C for 2 days, and their dry weights were recorded. The total biomass increase during the experiment was estimated as difference between the whole plant dry weight at the beginning and at the end of the experiment. Plant water consumed over the experimental period was estimated as follows:

Plant water consumed = Sum of quantity of water irrigated + Rain water − Evaporation

The whole plant WUE was determined using the following equation and expressed as g biomass L^{-1} water.

WUE = Δ biomass (final biomass−initial biomass)/Amount of water consumed

Data analyses

All observations were analyzed in triplicate in a two factorial, completely randomized design using the ANOVA procedure in SAS Ver.9.3 (SAS Institute Inc. 2011). There were five OTCs with CO_2 and ET treatment as climatic factor and water deficit stress as second factors. Treatment means were separated using Tukey's multiple comparison tests.

Results

Climatic variables

Climate conditions of the experimental site that prevailed during the experimental period are listed in Table 1. During that period, T_{max} ranged from between 25.8 and 34.8 °C, with a higher T_{max} in the months of April and May. T_{min} ranged from between18.7 and 28.7 °C. Rainfall during the experimental period was minimal, and the same was taken into account when calculating the water consumption of a plant. Figure 1 depicts the typical diurnal CO_2 concentration and temperature of an OTC set at different levels during November 2013. Figure 1a shows the CO_2 concentration at 700 and 550 ppm in comparison to chamber control around 400 ppm. In both elevated CO_2 concentrations, the actual concentration in an OTC was around ± 20 to 40 ppm of the target concentration for most of the period from 10 am until 4 pm, while higher fluctuations were recorded for the rest of the period. There was an overall average daily increase in air temperature in the OTCs, as compared to outside temperatures by 2–3 °C. Figure 1b presents the variation in temperature between chamber control and OTC with ET treatments. At noon, T_{max} inside the chamber control reached to 36 °C as compared to 33.8 °C outside (T_{max} of November), while in [ET] treatment, it reached 38 °C. The overall average daily increase in air temperature in the OTCs with ET treatment as compared to chamber control was 2–3 °C. The average midday (11 am until 3 pm) temperature increase was around 2–2.5 °C as compared to ambient temperatures.

Alterations in morphological traits

Climate change variables had a significant effect on plant height ($p < .0001$), the number of plants jorquetted ($p < .0001$), the number of branches at jorquette ($p < .0001$), leaf area ($p = .0008$), and biomass ($p < .0001$), as indicated in Table 2. Pot-grown 1-year-old cocoa seedlings had grown to a height of 1.4 m in chamber control. Plants grown under [ECO_2] were taller and attained a height of 1.64 m and 1.71 m at 550 and 700 ppm respectively. Plant height in ET treatment was on par with ambient control, but it was significantly higher in ET + ECO_2 treatments compared to ambient control. Among the three plants, only one plant jorquetted under 700 ppm CO_2, as compared to two from chamber control and all the three from ET treatment. Moreover, the number of branches at jorquette was significantly lower with [ECO_2] treatment (3.3) as compared to chamber control (4.0) and ET (4.3) ($p < .0001$). Water deficit at 50% FC significantly reduced the plant height ($p < .0001$) and number of plants jorquetted ($p = .04$), but the number of branches at jorquette were on par with 100% FC. Plant height at 50% FC was reduced by 6%, 19%, 11%, 14%, and 22% under chamber

Table 1 Monthly minimum and maximum temperatures (mean and range) and rainfall data of the experimental station at CPCRI Kasaragod during the experimental period of 2013–2014

Year	Month	Maximum temperature (°C)			Minimum temperature (°C)			Rainfall (mm)
		Mean	Range		Mean	Range		
2013	October	30.15	28.2	31.2	25.34	24.1	26.5	174
	November	32.19	30.0	33.8	24.74	23.0	26.2	48
	December	32.10	30.6	34.3	22.01	19.8	25.8	9
2014	January	31.54	30.5	34.2	21.99	18.7	24.1	0
	February	31.55	30.3	33.0	22.28	19.7	25.0	0
	March	32.39	30.5	33.5	23.84	20.1	25.4	0
	April	33.57	32.3	34.8	26.31	23.4	28.7	15
	May	34.85	25.8	34.6	24.98	22.1	27.4	290

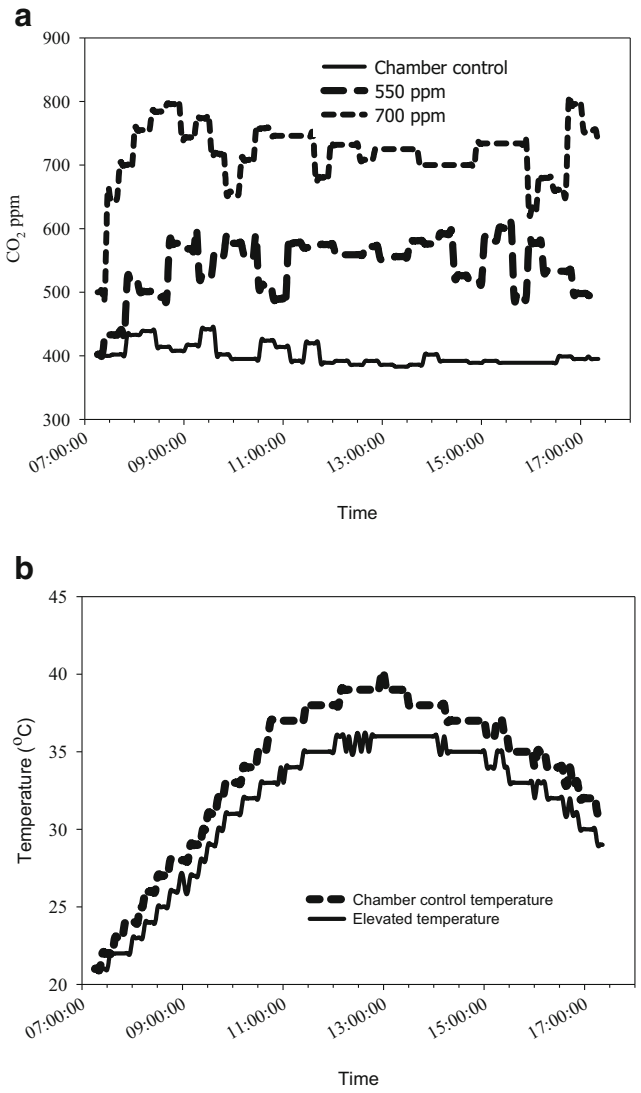

Fig. 1 A representative diurnal record of CO_2 concentration in the open top chambers - ambient, 550 ppm and 700 ppm (a) and temperature of the ambient and ambient + 3 °C set chambers during November 2013

control, 550 ppm CO_2, 700 ppm CO_2, ET and ET + CO_2 treatments respectively from 100% FC. However, there was a significant interaction effect ($p = .03$) of water deficit and climate change variables on plant height. Plants under 50% FC with 700 ppm CO_2 could grow 8% taller than the plants grown under 100% FC in chamber control.

Leaf area (LA) marginally increased with [ECO_2], but the difference was not significant. Significant decline could be observed under ET treatment. It was 2.59 m^2 with ET against 3.25 m^2 at chamber control (Table 2). The ET + CO_2 treatment leaf area (2.90 m^2) was on par with the ambient chamber (Table 1). 50% FC significantly ($p = 0.001$) reduced LA to 2.36 m^2 from 3.01 m^2 of the 100% FC plants. However, the interaction effect of water deficit with climatic variables (temperature, CO_2) was not significant (Figs. 2 and 3).

Table 2 Plant height, number of plants jorquetted, number of branches at jorquette, leaf area, dry weight of leaf, shoot, root, and total biomass of cocoa seedlings with climate change variables and water deficit. Data are mean value of three replicates. NS denotes no significance at 5% level. Mean with the same letter represents non-significance while different letter represents significance. Significance levels of each factor are indicated by p values and standard error of mean (SEm) is given

Treatments	Plant height (cm)	No. of plants jorquetted	No of branches at jorquette	Leaf area (m^2)	Leaf wt (g)	Shoot wt (g)	Root wt (g)	Biomass (g)	WUE (g biom. L^{-1} H_2O)
Climatic variables (CV)									
Chamber control	140^{c}	2.0^{b}	3.67^{ab}	3.25^{ab}	66.83^{bc}	217.67^{c}	110.33c	395.00^{c}	2.15^{c}
550 PPM CO_2	164^{ab}	1.8^{b}	3.33^{b}	3.28^{ab}	74.33^{b}	236.67^{b}	116.67^{bc}	428.00^{b}	2.33^{b}
700 PPM CO_2	171^{a}	1.0^{c}	2.33^{c}	3.45^{a}	93.00^{a}	282.00^{a}	135.67^{a}	510.67^{a}	2.78^{a}
ET	144^{c}	3.0^{a}	4.33^{a}	2.13^{c}	64.66c	148.33^{e}	76.17^{d}	289.17^{d}	1.57^{d}
ET + 550 PPM CO_2	159^{b}	3.0^{a}	4.00^{ab}	3.03^{a}	67.83^{bc}	175.33^{d}	126.33^{b}	369.33^{c}	2.01^{c}
Moisture factors (MF)									
100% FC	155^{a}	2.3^{a}	3.53	3.01^{a}	74.20^{a}	212.60^{a}	112.96^{a}	398.43^{a}	2.165^{b}
50% FC	132^{b}	1.9^{b}	3.13	2.36^{b}	55.70^{b}	156.66^{b}	106.20^{a}	317.06^{b}	3.446^{a}
SEm									
Climate	2.71 ($p < .0001$)	0.17 ($p < .0001$)	0.27 ($p < .0001$)	0.13 ($p = .0008$)	2.85 ($p = .001$)	4.90 ($p < .0001$)	3.22 ($p < .0001$)	9.25 ($p < .0001$)	0.07 ($p < .0001$)
Moisture	1.69 ($p < .0001$)	0.10 ($p \leq .04$)	NS ($p = .117$)	0.10 ($p = .001$)	1.79 ($p < .0001$)	3.09 ($p < .0001$)	NS ($p = .064$)	5.85 ($p < .0001$)	0.05 ($p < .0001$)
Climate × moisture	4.07 ($p = .03$)	NS ($p = .075$)	0.38 ($p = .02$)	NS ($p = .981$)	NS ($p = .135$)	6.93 ($p < .0001$)	NS ($p = .244$)	13.08 ($p = 0.004$)	0.08 ($p = 0.04$)

Seedlings accumulated significantly higher dry biomass ($p < .0001$) with [ECO_2] (428 and 511 g at 550 and 700 ppm CO_2), in comparison with chamber control (395 g) (Table 1). This corresponds to increase of 8% and 29%. ET treatment significantly reduced biomass to 312.08 g while in ET+ [ECO_2], which was on par with chamber control. Both below and aboveground plant parts contributed to the accumulation of high biomass. At 700 ppm, leaf, shoot, and root weight were 93 g, 282 g, and 136 g, in comparison to 69 g, 218 g, and 110 g respectively of those grown in the ambient chamber. Root biomass was the least with ET treatment (76 g) while in all the other treatments, it was significantly higher from chamber control (110 g). However, the fractionation of biomass partitioned towards different parts of the leaves, shoots, and roots remained almost same at 0.17 g, 0.55 g, and 0.27 g respectively across all treatments.

Biomass at 50% FC was significantly reduced ($p < .0001$) to 317 g from 399 g at 100% FC. The trend in biomass change at 50% FC was similar to that of 100% FC, 15% and 28% increase with 550 ppm and 700 ppm CO_2 and 7% decline in ET treatment as compared to the chamber control. There was a significant interaction effect ($p = .004$) between water deficit and climatic variables. In comparison to plants at 100% FC of chamber control, the biomass reduction of plants under 50% FC was 26% for chamber control, 15% for 550 ppm CO_2, 5% for 700 ppm CO_2, 32% for ET, and 20% for ET + CO_2. The relative increase in biomass in response to 550 ppm and 700 ppm CO_2 in 50% FC was 14% and 27% in comparison to 8% and 29% at 100% FC respectively from chamber control.

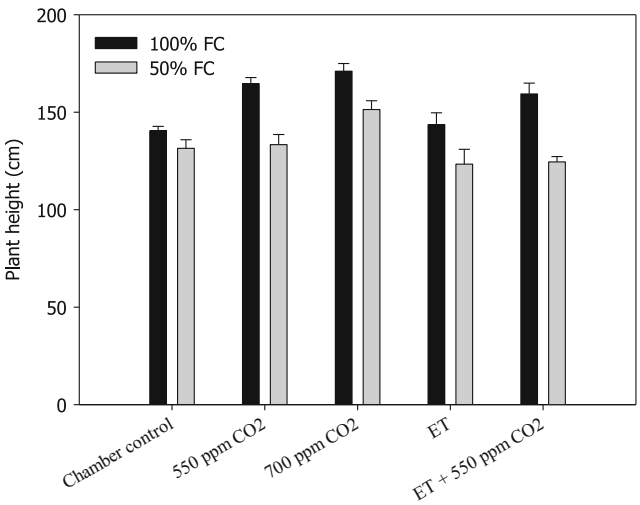

Fig. 2 Plant height of cocoa seedlings grown at ambient CO_2, elevated CO_2, and elevated temperature treatments in OTC with (50% FC) and without (100% FC) water deficit. Data are mean value of three replicates. Significance is indicated by p value (climate ($p < .0001$); moisture ($p < .0001$) and climate × moisture ($p = 0.03$)). Vertical lines represent standard error of the mean

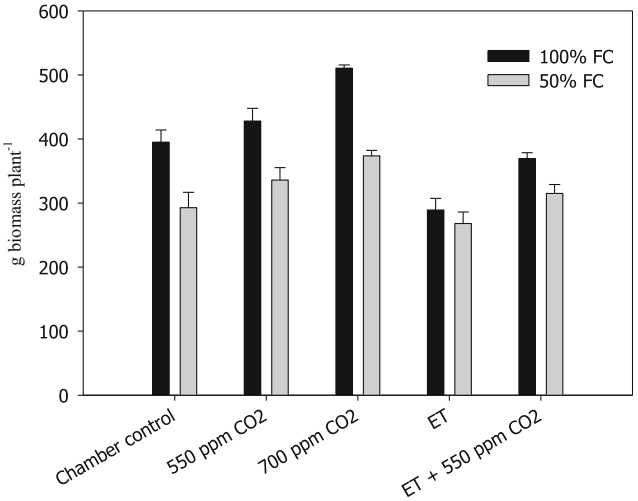

Fig. 3 Total dry biomass of cocoa seedlings grown at ambient CO_2, elevated CO_2, and elevated temperature treatments in OTC with (50% FC) and without (100% FC) water deficit. Data are mean value of three replicates. Significance is indicated by p value (climate ($p < .0001$); moisture ($p < .0001$) and climate × moisture ($p = 0.004$)). Vertical lines represent standard error of the mean

Modulations in physiological traits

Photosynthesis (Pn) of chamber control plants was 6.63 μmol m^{-2} s^{-1} (Table 3). It significantly ($p < .0001$) increased to 7.28 μmol m^{-2} s^{-1} at 550 ppm and 8.54 μmol m^{-2} s^{-1} at 700 ppm CO_2, which corresponds to a 10% and 29% increase, respectively. ET treatment significantly decreased Pn (4.68 μmol m^{-2} s^{-1}), while under ET + CO_2, it was on par to that of chamber control. Stomatal conductance (gs) on the other hand was significantly low in [ECO_2] treatment. Compared to 0.088 mol of chamber control, it was 0.067 mol m^{-2} s^{-1} and 0.074 mol m^{-2} s^{-1}, which is equivalent to a 24% and 16% decline at 700 and 550 ppm, respectively. In the rest of the treatments, it was on par with chamber control. However, even though transpiration had declined from 3.41 mmol in chamber control to 2.97 mmol m^{-2} s^{-1} at 700 ppm, the difference was not significant. Pn at 50% FC was significantly ($p < .0001$) reduced to 5.63 μmol m^{-2} s^{-1} as compared to 6.65 μmol m^{-2} s^{-1} of plants at 100% FC. Significant decline was also seen in gs ($p < .0001$) and Tr ($p = .003$). The decline in Pn, gs, and Tr was 15, 28, and 24% respectively. There was a positive interaction effect of water stress and [ECO_2] on Pn. Pn of 50% FC plants at 550 and 700 ppm CO_2 was 6.76 and 7.12 μmol m^{-2} s^{-1} which was on par with 100% FC plants of chamber control (6.63 μmol m^{-2} s^{-1}), whereas it was too low for 50% FC plants in chamber control (4.82 μmol m^{-2} s^{-1}) (Fig. 4). Pn was the least in ET with 50% FC (4.2 μmol m^{-2} s^{-1}). It was 5.5 μmol m^{-2} s^{-1} in ET + CO_2 with 50% FC. The relative increase in Pn, in response to 550 ppm and 700 ppm CO_2 in 50% FC, was 36% and 47% as compared to 9% and 28% at 100% FC respectively from chamber control.

Table 3 Leaf Ψ, total chlorophyll (chl), Fv/Fm, photosynthesis (Pn), stomatal conductance (gs), and transpiration (Tr) of cocoa seedlings with climate change variables and water deficit. Data are mean value of three replicates. NS denotes no significance at 5% level. Mean with the same letter represents non-significance while different letter represents significance. Significance levels of each factor are indicated by p values and standard error of mean (SEm) is given

Treatments	Leaf Ψ (bars)	Total chl (mg g^{-1})	Fv/Fm (ratio)	Pn (μmol m^{-2} s^{-1})	gs (mol m^{-2} s^{-1})	Tr (mmol m^{-2} s^{-1})
Climatic variables						
Chamber control	-8.50^{bc}	1.31^{a}	0.73	6.63c	0.088^{a}	3.41
550 ppm CO_2	-7.83^{c}	1.34^{a}	0.69	7.28^{b}	0.077^{b}	3.42
700 ppm CO_2	-8.50^{bc}	1.03^{a}	0.65	8.54^{a}	0.067^{b}	2.97
ET	-12.17^{a}	0.41^{b}	0.73	4.68d	0.079^{a}	3.07
ET + 550 ppm CO_2	-9.54^{b}	0.85^{b}	0.69	6.23^{c}	0.081^{a}	3.04
Moisture level						
100% FC	-9.31^{b}	0.86^{b}	0.71^{a}	6.65^{a}	0.078^{a}	3.18^{a}
50% FC	-14.06^{a}	1.07^{a}	0.61^{b}	5.59^{b}	0.058^{b}	2.41^{b}
SEm						
Climate	0.46 ($p < .0001$)	0.07 ($p < .0001$)	NS ($p = .06$)	0.19 ($p < .0001$)	0.004 ($p < .01$)	NS ($p = .528$)
Moisture	0.29 ($p < .0001$)	0.04 ($p = .005$)	0.01 ($p < .0001$)	0.12 ($p < .0001$)	0.003 ($p < .0001$)	0.16 ($p = .003$)
Climate × moisture	0.65 ($p = .03$)	NS ($p = .423$)	NS ($p = .123$)	0.63 ($p = .01$)	NS ($p = .123$)	NS ($p = .931$)

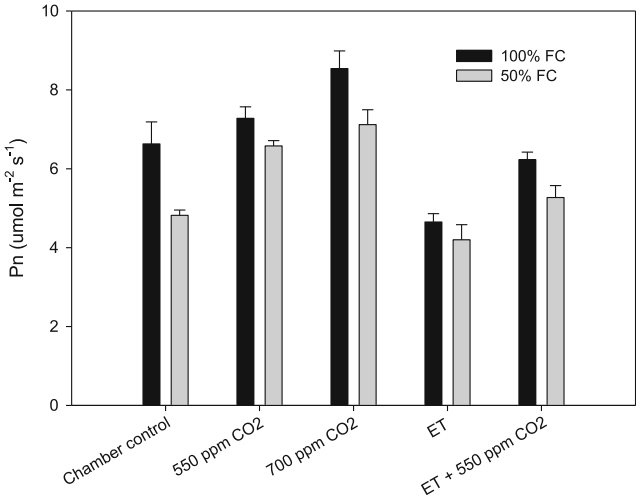

Fig. 4 Photosynthesis of cocoa seedlings grown at ambient CO_2, elevated CO_2, and elevated temperature treatments in OTC with (50% FC) and without (100% FC) water deficit. Data are mean value of 3 replicates. Significance is indicated by p value (climate ($p < .0001$); moisture ($p < .0001$) and climate × moisture ($p = 0.01$)). Vertical lines represent standard error of the mean

Climate change variables had a significant effect on leaf Ψ ($p < .0001$). At 550 and 700 ppm, CO_2 leaf Ψ was on par with control plants (−8.50 bars) (Table 3). ET treatment significantly reduced it to −12.17 and it was −9.54 in ET + CO_2. At 50% FC, WP was −14.06 bars in comparison to −9.31 bars at 100% FC. A significant positive interaction ($p < .03$) effect of [ECO_2] with water deficit was seen on WP. At 50% FC with 500 ppm and 700 ppm CO_2, WP reduced to only −11.06 bars and −11.4 bars in comparison to −15.13 bars for chamber control (Fig. 5). The relative improvement in leaf Ψ in response to 550 ppm and 700 ppm CO_2 in 50% FC was 27% and 25% in comparison to 7% and 0% at 100% FC respectively for chamber control.

Chlorophyll content did not show significant difference with variations in [ECO_2] but reduced in ET treatments compared to chamber control. Climate change variable effect was not significant on chlorophyll fluorescence (Table 3). However, both chlorophyll and chlorophyll fluorescence were significantly low in plants under 50% FC compared to that of plants at 100% FC.

Water use efficiency

Climate change variable had significant ($p < .0001$) effect on whole plant WUE (Table 1). It increased to 2.35 and 2.84 at 550 ppm and 700 ppm CO_2 respectively from 2.13 g/L water of chamber control. It corresponds to an 8% and a 29% increase respectively. On the other hand, in ET treatment, it significantly decreased by 30% (1.47). However, in the case of ET + 550 ppm CO_2, WUE was on par with chamber control. At 50% FC, WUE significantly ($p < .0001$) increased to

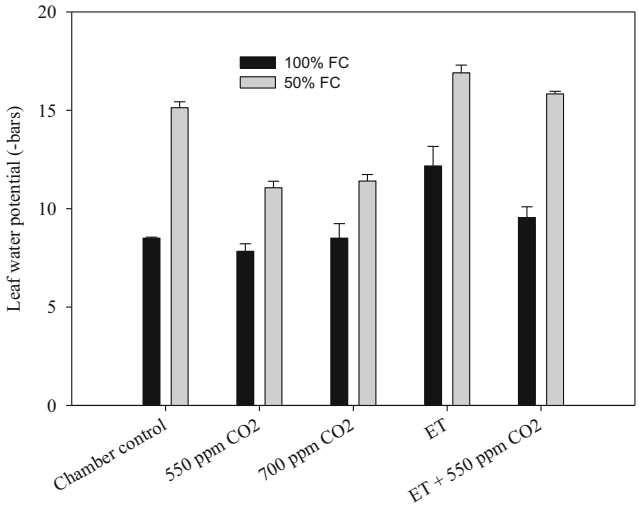

Fig. 5 Leaf Ψ of cocoa seedlings grown at ambient CO_2, elevated CO_2, and elevated temperature treatments in OTC with (50% FC) and without (100% FC) water deficit. Data are mean value of 3 replicates. Significance is indicated by p value (climate ($p < .0001$); moisture ($p < .0001$) and climate × moisture ($p = 0.01$)). Vertical lines represent standard error of the mean

3.446 against 2.165 at 100% FC (48% increase). A positive ($p < .004$) interaction effect with [ECO_2] was seen on WUE at 50% FC (Fig. 6). The WUE of plants grown at 50% FC under 550 ppm and 700 ppm CO_2 was3.65 g and 4.06 g l^{-1}, which was 14% and 28% higher than chamber control (3.18) and 74% and 97% higher than non-stress (100% FC) chamber control (2.15), respectively. The ET in interaction with 50% FC recorded the lowest WUE of 2.91 g while in ET + CO_2, it was 3.42 g l^{-1}.

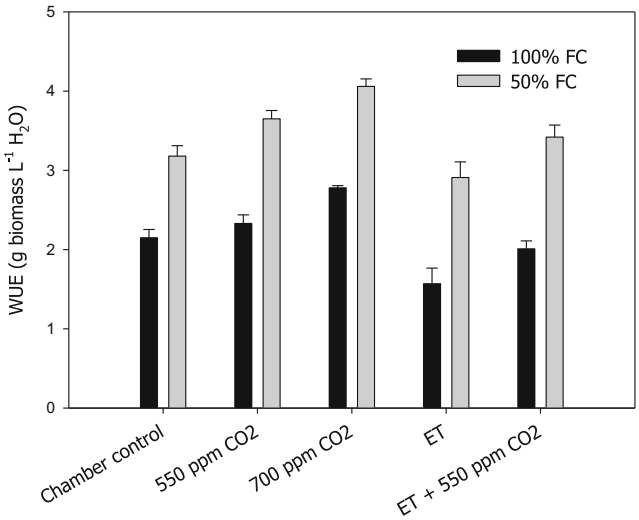

Fig. 6 Whole plant water use efficiency (g biomass liter^{-1} water) of cocoa seedlings grown at ambient CO_2, elevated CO_2, and elevated temperature treatments in OTC with (50% FC) and without (100% FC) water deficit. Data are mean value of 3 replicates. Significance is indicated by p value (climate ($p < .0001$); moisture ($p < .0001$) and climate × moisture ($p = 0.04$)). Vertical lines represent standard error of the mean

Discussion

In this study, we determined the response of cocoa seedlings to [ECO_2], ET, and their interaction with water deficit grown in OTC. There was a significant gain in biomass production and WUE of cocoa seedlings under elevated CO_2 conditions. However, there was a significant at high temperatures and water deficit stress. Increased CO_2, to a certain extent, ameliorated the negative effects of both high temperature and with water deficit stress. The following section discusses the response of cocoa seedlings to climate change variables like [ECO_2] and [ET] and their interaction with water deficit stress.

Elevated CO_2 effect

As expected, based on other C3 crop examples, in cocoa [ECO_2], there was a significant increase in biomass by 8% and 29% when the CO_2 concentration had increased from 400 ppm (chamber control) to 550 ppm and 700 ppm respectively. At 700 ppm, Pn increased by 29%, while there was no significant difference in leaf area in comparison to chamber control, suggesting Pn is the major contributor to biomass production. Earlier studies also showed an average increase in Pn by 28.5% with an increase in CO_2 concentration from 400 to 700 ppm (Lahive et al. 2017), and an increase in Pn in long-term studies of cocoa with increased CO_2 exposure (Baligar et al. 2005; Lahive et al. 2018). In addition to increased plant height, plants under [ECO_2] accumulated more biomass in their roots, shoots, and leaves, as compared to chamber control, but the proportion of increase was almost similar to different parts. In this study, we could measure only at 24% gs at 700 ppm than chamber control, which is too low for optimum levels measure (65%), as observed and reported by Baligar et al. (2008), which resulted in improved intrinsic WUE (iWUE). However, at the same concentration, Lahive et al. (2018) could not see any effect on the gs of juvenile plants of the Amelonado variety. Through transpiration, loss of water declined at 700 ppm, but it was not significant from chamber control. Thus, the increased whole plant WUE recorded in cocoa under elevated CO_2 could be due to increased biomass production through high Pn rather than reduced water loss through stomatal restriction. While measuring the iWUE of tropical trees using carbon isotope discrimination, Hietz et al. (2005) concluded that the increases in iWUE in recent decades were due to increases in assimilation rates rather than declines in gs.

High temperature effect

The overall average temperature T_{max} of the experimental site ranged from 31.2 to 34.6 °C during the experimental period. The months of March, April, and May are relatively hot and dry periods in this region. In the cocoa growing

regions of the west coast of Karnataka and Kerala, the T_{max} is 34 to 36 °C while on the east coast of Andhra Pradesh (AP) and Tamil Nadu (TN), the T_{max} reaches as high as 40–42 °C (Apshara et al. 2018). Compared to outside temperatures of around 33.8 °C in November, there was an increase in temperature inside the OTC by 2–2.5 °C and therefore T_{max} reached up to 36.5 °C in chamber control. Earlier, Norris et al. (2016) observed a similar rise in temperatures of around 2 °C inside the OTC during warm, clear, sunny days. During the same period, T_{max} inside the ET treatment chamber was higher by 2–3 °C from chamber control and reached as high as 39.5 °C. Although this elevation is higher than what is predicted in RCP 4.5 (1.1 to 2.6 °C) and RCP 6.0 (1.4 to 3.1 °C) with a corresponding increase of CO_2 550 and 750 ppm by the end of the twenty-first century (2081–2100) relative to 1986–2005 (IPCC 2014) in Karnataka and Kerala, it is close to what is common during the summer in AP, TN, and in other cocoa growing regions of Ghana (Abdulai et al. 2018).

High temperatures are known to affect the growth and yield of cocoa; however, the effect of high temperatures on the physiology of cocoa is not yet well-understood (Lahive et al. 2019). In OTC, even under well-irrigated (100% FC) conditions, when T_{max} reaches to around 39 °C from 36 °C of chamber control, biomass production was significantly reduced. However, under field conditions of AP and TN, where summer temperatures climb above 40 °C, there are no reports to show if these high temperatures impacted the growth and yields of cocoa. As cocoa is grown as an understory crop, with either coconut or oil palm for shade, it might have gotten acclimatized to higher temperature. Both leaf area and Pn are sensitive to high temperature and cocoa has an optimum temperature requirement of 31–33 °C for Pn (Balasimha et al. 1991) and 33–35 °C (Yapp 1992). Temperatures above 34 °C under dry conditions decreased the Pn of field-grown plants (Balasimha et al. 1991). The Pn in cocoa might have been affected at the enzymatic level, but not at the electron transport chain level, as the photochemical quenching activity was still intact. In spite of no evidence of significant decline in both gs and transpiration, leaf Ψ was very low compared to chamber control. This suggests that cuticular transpiration might be a significant source of water loss from the leaf under drier temperature conditions (Baligar et al. 2008), or that water uptake might have been restricted as the root weight was the least under high temperature. Plants grown under higher temperatures lost apical dominance, which resulted in early jorquetting and more branch growth, as noticed by Sale (1968), while plants under [ECO_2] had more a pronounced effect of apical dominance, and thus took more time for jorquetting and produced fewer branches.

Water deficit

Although cocoa is mostly an irrigated crop in India, at some period during its life cycle, it was exposed to a soil moisture deficit. Similar dry season conditions are prevalent in Western Africa (Schroth et al. 2016), and juvenile cocoa is sensitive to soil moisture deficiencies and beyond a critical moisture level of plant water status, it would not recover (Lahive et al. 2019). In order to study the response of cocoa to water deficit, we created a soil moisture depletion by supplying only 50% of water added to the plants at 100% FC. At 50% FC, the leaf Ψ declined to − 14.06 bars from − 9.31 bars of 100% FC, which led to significant decline in plant height, leaf area, Pn, gs, Tr, leaf, and shoot dry weight and biomass. At leaf Ψ below − 15 bars, gs and Pn have been observed to decline significantly (Deng et al. 1990; Mohd Razi et al. 1992); however, root biomass was not affected, causing shifts in root/shoot ratios. Greater root biomass is a beneficial trait for conferring tolerance under water deficit by enabling greater access to the uptake of soil water.

Root growth and stomatal regulation are the key mechanisms involved in water conservation during periods of water deficit. Root growth was not a limitation to water deficit in cocoa but gs significantly declined thereby limiting both Tr and Pn. The higher decline in Tr (24%) than Pn (15%) could lead to greater iWUE (Farquhar and Sharkey 1982). Earlier workers also reported higher iWUE in cocoa under water deficit (Balasimha 1993; Rada et al. 2005). In our experiment, we saw an increase in whole plant WUE under water deficit conditions, which was mainly because of an increase in photosynthetic capacity and decrease in Tr and gs, in agreement with results from previous cocoa studies (Dos Santos et al. 2014), groundnut (Hebbar et al. 1994), and wheat (Shi et al. 2014; Guan et al. 2015).

Interaction effect

Increased CO_2 concentrations of 550 ppm could minimize the severity of the high temperature effect on Pn, leaf Ψ, and biomass accumulation, and the measures of these parameters were on par with chamber control thus mitigating the negative effect of high temperature. Similar response of less severe effect of high temperature with elevated CO_2 was seen in coffee (Rodrigues et al. 2016). Similarly, water deficit stress (50% FC) effect has been ameliorated by growth at [ECO_2] through various mechanisms like improved Pn, leaf Ψ maintenance by reduced gs, and Tr resulting in high WUE, greater root/shoot ratios. Wullschleger et al. (2002) could observe fine root production and improved iWUE under elevated CO_2 with water deficit stress. The greater relative increase in Pn and leaf Ψ observed in response to [ECO_2] under water deficit compared to well-watered plants at 100% FC could not contribute to an increase in biomass and WUE, which is in contrast to the

observation made by Bishop et al. (2014). In an OTC study, they reported a greater relative increase in biomass and yield in response to increased CO_2 in drier soil conditions. The WUE of well-watered and water-stressed plants increased to 2.78 g and 4.06 g l^{-1} at 700 ppm from 2.15 g and 3.18 g l^{-1}in chamber control, respectively, suggesting an additional advantage of [ECO_2] under water deficit stress. These results suggested that [ECO_2] enabled the plants to use water more efficiently under water deficit stress.

The impact of high temperatures on Pn, leaf Ψ, and biomass was more severe under water deficit in comparison to stress applied alone in cocoa. Earlier workers (Savin and Nicolas 1996; Pradhan et al. 2012) reported similar responses in other crops, where an increased CO_2 concentration of 550 ppm could not ameliorate the effect on leaf Ψ. To a certain extent, increased CO_2 concentrations improved the Pn thus resulted in higher biomass accumulation and WUE under water deficit with ET + 550 ppm CO_2, as compared to water deficit with ET.

Conclusions

In this study, we determined the response of cocoa seedlings to [ECO_2], ET, and their interaction with water deficit grown in OTC. There was a significant gain in biomass production and WUE under elevated CO_2, increased CO_2, to a certain extent ameliorated the negative effects of both high temperature and water deficit stress. This study, conducted on cocoa seedlings in an OTC with multiple climate variables and their interactions, gives an indication of how cocoa would respond to climate change variables under controlled conditions. However, the situation is much more complex in adult plants under field conditions, wherein the reproductive stage, especially during flowering, is more sensitive to both high temperatures and water deficit. Therefore, future studies should focus on studying the impact of climate change during the reproductive stage of cocoa. This will assist in the research on the development of climate resilient varieties that are more tolerant to drought, high temperatures, and low nutrients, and the adaptation of improved crop, soil, and water management practices will help minimize the impact of climate change on cocoa and help support future cocoa production in vulnerable areas.

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Author contribution statement KBH—conceived and designed the study; KBH, EA—performed the experiments; KPC, analyzed the data; KBH and PVVP wrote the manuscript and all the authors read and approved the manuscript.

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