Physiological response of cocoa (*Theobroma cacao* L.) genotypes to drought

M. Suchithra*, B. Suma, J.S. Minimol, Deepu Mathew¹ and A.V. Santhosh Kumar²

Cocoa Research Center, Kerala Agricultural University, Thrissur-680 656, Kerala, India ¹Centre for Plant Biotechnology and Molecular Biology, Kerala Agricultural University, Thrissur- 680 656, Kerala, India ²Department of Forest Biology and Tree Improvement, College of Forestry, Kerala Agricultural University, Thrissur-680 656, Kerala, India

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Abstract

Drought is one of the major environmental stresses affecting crop productivity worldwide. Climate change is expected to result in a rise in the number and intensity of drought events in the coming decades, so climate-resilient crops that can withstand this stress are in high demand. There are few genotypes in cocoa where it can tolerate water deficit conditions. The objective of the current investigation was to evaluate the effect of drought stress on the photosynthetic and physiological parameters of six cocoa genotypes (*Theobroma cacao* L.) with two irrigation regimes (100% field capacity and 40% field capacity) under greenhouse conditions at Cocoa Research Station, Kerala Agricultural University, Thrissur. The effect of water deficit conditions on gas exchange and physiological parameters such as relative water content, membrane stability index, chlorophyll stability index, and chlorophyll content, chlorophyll stability and membrane stability. All genotypes revealed significant differences for most parameters with two irrigation regimes. Among the cocoa genotypes, P.IV 19.9, which is classified as a highly tolerant genotype, recorded better results for all the parameters studied under water deficit conditions at 40 per cent FC. The findings of this study support the classification of these genotypes as highly tolerant, tolerant, and susceptible. These parameters may be used as the most promising indicators to screen for drought tolerance in cocoa. The results of the study revealed that photosynthetic and physiological parameters have a significant role in imparting drought stress tolerance to cocoa. Furthermore, these selected drought-tolerant genotypes can be used in future crop improvement programmes in cocoa.

Keywords: Cell membrane stability, chlorophyll content, cocoa, genotypes, parameters, photosynthetic, physiological response

Introduction

Cacao (*Theobroma cacao* L.) is a species that has significant economic importance worldwide because of its beans, which are a major ingredient in chocolate production (Lahive *et al.*, 2019). Due to its significance and higher requirements, cocoa is currently grown in nearly all tropical areas, particularly West Africa, which produces over 70 per cent of the world's cocoa annually (ICCO, 2013). Globally, around 5 million farmers depend on cocoa for their livelihood, which in turn supports

In India, cocoa is cultivated predominantly in four southern states, Kerala, Karnataka, Tamil Nadu and Andhra Pradesh. It occupies an area of 97563 ha with a production of 27072.15 MT and with national productivity of 669 kg dry beans ha⁻¹. Kerala leads in cocoa with a production of 9647.40 MT from an area of 17366 ha (DCCD, 2021). In Kerala and Karnataka, cocoa is grown as a mixed cropping system under coconut and arecanut.

⁴⁰⁻⁵⁰ million people to survive on cocoa cultivation (WCF, 2012).

^{*} Corresponding Author: suchithramss@gmail.com

In these traditional zones, during the dry period of 4-6 months, cocoa survives with supplemental irrigation. Moreover, cocoa is spreading to nontraditional areas like Andhra Pradesh, where water scarcity is a major concern during the dry seasons. High temperatures prevailing in this area demand a continuous supply of moisture to the root zone for the survival of this crop.

Climate change and water shortages are the major key barriers to cocoa production worldwide as it is sensitive to stress (Amitha *et al.*, 2018). The ability of plants to withstand drought stress varies throughout species and sometimes even within species (Jaleel *et al.*, 2009).

Various morphological, physiological, and biochemical adaptive mechanisms are exhibited by cocoa for survival and growth under water deficit conditions (Raja-Harun and Hardwick, 1988) which includes a reduction in chlorophyll content, photosynthetic rate, and transpiration rate (Carvalho et al., 2019). In maize, photosynthetic activity was significantly reduced under prolonged and severe drought stress (Qi et al., 2021). Balasimha et al. (2013) and Apshara et al. (2013) studied morphophysiological, biochemical, and photosynthetic changes in cocoa under drought stress. They confirmed that a few gas exchange parameters could be utilised as a measure to study the response of plants under water deficit conditions. In addition, plants use physiological traits to acclimate to conditions under water stress by retaining a high water status regardless of the moisture content in the soil (Zhang et al., 2018). Relative water content (RWC) is a vital indicator of the level of hydration in cells and tissues, which is essential for normal physiological activities and growth. Several studies have found that maintaining a high RWC during stress conditions indicates drought tolerance (Silva et al., 2007). Relative water content (RWC), cell membrane stability index and chlorophyll content are appropriate tools to measure drought stress tolerance in many plants (More et al., 2019). These physiological parameters contribute to a major role in maintaining plant vitality and survival during drought stress.

Changes in climatic conditions and the expansion of the crop to non-traditional areas necessitate screening for drought-tolerant genotypes. Developing these genotypes is a prerequisite for cocoa crop improvement. Therefore, in this investigation, the changes in photosynthesis and physiological parameters of six cocoa genotypes under two irrigation regimes were evaluated to identify the drought-tolerant genotypes.

Materials and methods

Plant material and water stress imposition

This experiment trial was conducted during the period 2020 to 2022 at Cocoa Research Centre, Kerala Agricultural University, Thrissur, with a latitude of 10°322 N, 76°172 E in a greenhouse. The selected six cocoa genotypes, namely, P.IV 19.9, P.II 12.11, P.IV 59.8, and VSD.I 11.11, VSD.I 3.4 and VSD.I 29.9 were budded on the six-month-old rootstock of seedlings raised from polyclonal gardens. GIV 18.5 (CCRP 5) (progeny of pods from Nileshwar), which is a highly susceptible genotype as reported by Binimol (2005) used as a check in the experiment. The treatments were imposed on six-month-old budded plants with two irrigation regimes - 100 per cent field capacity and 40 per cent field capacity based on the gravimetric method (Souza et al., 2000). The earlier reports stated that cocoa could not withstand water stress when field capacity is less than 40 per cent FC (CCRP report, 2015; Juby et al., 2021). Hence, these plants were selected to maintain 40 per cent FC for one week. By visual observation, the percentage of leaves retained was recorded after one week of stress imposition. The morphological classification was undertaken based on a standardised score chart depicted by Juby et al. (2021). These cocoa genotypes were categorised as highly tolerant (>70%), tolerant (40.1-70%), susceptible (10.1-40%) and highly susceptible (0-10%) according to the score chart. The percentage of leaves retained after stress imposition was calculated by recording the total number of leaves before stress imposition and the retained leaves after one week and expressed in percentage. Daily readings of temperature and humidity in the greenhouse were taken using a whirling psychrometer.

Photosynthetic and physiological parameters

Photosynthetic parameters such as net photosynthetic rate (Pn: μ mol CO₂ m⁻²s⁻¹), transpiration rate (E: mmol H₂O m⁻²s⁻¹), and leaf

temperature (°C) were recorded using a portable photosynthesis system LI-6400 (LICOR, USA). Readings were recorded at a PAR of 1000 μ mol m²s⁻¹ and ambient CO₂ concentration (380-400 μ mol CO₂ mol⁻¹ air) between 10.00 and 12.00 h on the fully expanded third leaf from the top in six plants in control and water stress imposed plants including check. Along with the above parameters, chlorophyll content (SPAD 502), chlorophyll stability index (CSI), relative water content (RWC) and cell membrane stability (CMS) were also determined.

All the collected data were statistically analysed at a level of significance of 0.05 probability to differentiate different treatment means. The correlation was studied in order to find out the degree of association of these physiological characteristics with drought stress.

Results and discussions

Percentage of leaves retained

After one week of stress imposition, the percentage of retained leaves was calculated using visual observation of these selected six cocoa genotypes along with check variety and categorised as highly tolerant, tolerant, susceptible and highly susceptible according to the standardised score chart. The genotypes are classified according to the score chart and presented in Table 1.

Photosynthetic parameters

In the present investigation, the photosynthetic rate of six genotypes and check variety recorded significant differences among genotypes in both 100 per cent and 40 per cent field capacity (Table 2). P.IV 19.9 highly tolerant genotype recorded the highest photosynthetic rate (2.74 μ mol CO₂ m⁻²s⁻¹). It was closely followed by P.IV 59.8 (2.70 µmol CO₂ m⁻²s⁻¹) with respect to check variety, CCRP 5 recorded the lowest photosynthetic rate (1.32 µmol CO₂ m⁻²s⁻¹, 0.78 µmol CO₂ m⁻²s⁻¹) at 100 per cent and 40 per cent field capacity, respectively. It was found that the photosynthetic rate was higher under 100 per cent field capacity when compared to the water deficit condition of 40 per cent field capacity. P.IV 19.9 (2.74 µmol CO, m⁻² s⁻¹), P.IV 59.8 (2.70 µmol CO₂ m⁻² s⁻¹), VSD.I ²3.4 (2.04 µmol CO₂ m⁻² s⁻¹),

VSD.I 11.11 (1.92 µmol CO, m⁻²s⁻¹), and VSD.I 29.9 (1.89 μ mol CO, m⁻² s⁻¹) showed a higher photosynthetic rate at 100 per cent field capacity. At 40 per cent field capacity of water deficit condition, these five genotypes had higher photosynthetic rates than check variety, revealing the drought tolerant ability of these genotypes. Reduction in chlorophyll content, photosynthesis rate and transpiration are one of the initial physiological responses in plants (Carvalho et al., 2019). Reduced photosynthesis in drought-stressed plants can be related to both stomatal (stomatal closure) and non-stomatal (impairment of metabolic activities) aspects. Under mild to moderate stress, stomatal closure and the consequent CO₂ shortage in the chloroplasts are the primary reasons for impaired photosynthesis (Mafakheri et al., 2010). Balasimha et al. (1991) studied drought tolerance in cocoa and identified five tolerant clones, and observed a 25 per cent reduction in daily photosynthesis of stressed plants when compared to non-stressed plants. They also reported that a higher photosynthetic rate was recorded in tolerant clones than susceptible ones in cocoa genotypes. These results are in accordance with the studies of Ayegboyin et al. (2016), Amitha et al. (2018) and Janani et al. (2019) in cocoa, chickpea (Mafakheri et al., 2010), soybean (Li et al., 2020) and amaranthus (Jamaluddin et al., 2021).

The transpiration rate also followed the same trend as the photosynthetic rate between the genotypes. In this study, the transpiration rate showed significant variation between genotypes at both field capacity levels. The selected cocoa genotypes recorded a higher transpiration rate at 100 per cent field capacity than in plants under conditions of water deficit condition of 40 per cent field capacity (Table 1) when compared with check variety, P.IV 19.9 (2.89 m mol H₂O m⁻² s⁻¹) recorded highest transpiration rate at 100 per cent FC followed by P.IV 59.8 (2.64 mmol $H_2O m^{-2} s^{-1}$), VSD.I 3.4 (1.73 mmol H₂O m⁻² s⁻¹), VSD.I 11.11 (1.70 mmol H₂O m⁻² s⁻¹), VSD.I 29.9 (1.63 mmol H₂O m⁻²s⁻¹) and P.II 12.11 (1.48 mmol H₂O m⁻²s⁻¹). At 40 per cent field capacity, there was a reduction in the transpiration rate of all these genotypes. P.IV 19.9 (0.29 mmol $H_2O m^{-2} s^{-1}$) recorded the least transpiration rate, followed by P.IV 59.8 (0.32 mmol H₂O m⁻² s⁻¹), VSD.I 29.9 (0.57 mmol H₂O m⁻² s⁻¹), VSD.I 11.11 (0.62 mmol H₂O m⁻² s⁻¹), VSD.I 3.4 $(0.64 \text{ mmol H}_{2}\text{O} \text{ m}^{-2}\text{s}^{-1})$ compared to check variety $(1.87 \text{ mmol H}_{2}^{\circ}\text{O} \text{ m}^{-2}\text{s}^{-1})$; this implies their droughttolerant potential. Check variety recorded the highest transpiration rate under 40 per cent FC water stress, which was attributed to its high susceptibility to water deficit conditions. The highly tolerant and tolerant group of genotypes showed lower transpiration and photosynthetic rates without much reduction. Compared to plants receiving irrigation, the transpiration rate of three cocoa accessions under stress conditions decreased by 54 to 59 per cent (Balasimha et al., 1988). Compared to the other rainforest tree species, cocoa was inefficient at controlling transpiration loss under drought conditions (Baligar et al., 2008). Stomatal regulation is one of the primary systems engaged in water conservation during times of water scarcity. However, stomatal closure can also restrict carbon intake for photosynthesis (Lahive et al., 2019). Similar findings were observed in crops like cashew (Latha, 1998), grape (Tombesi et al., 2018), chickpea (Mafakheri et al., 2010), soybean (Li et al., 2020) and cocoa (Zakhariya and Indradewa, 2018).

With respect to leaf temperature, almost similar results were observed in all the genotypes under both water regimes (Table 1). Since no significant variation was observed, it cannot be considered a reliable indicator for drought tolerance in cocoa. However, Surendar *et al.* (2013) revealed that a temperature rise was recorded for the droughtstressed plants than for well-watered plants in banana. Similarly, in sugarcane, all genotypes recorded an increase in leaf temperature, regardless

Table 1. Morphological classification of cocoa genotypes towards drought stress

1. P			
	P.IV 19.9	81.81	Highly tolerant
2. P	P.II 12.11	20.83	Susceptible
3. P	P.IV 59.8	66.66	Tolerant
4. V	VSD.I 11.11	47.06	Tolerant
5. V	VSD.I 3.4	52.94	Tolerant
6. V	VSD.I 29.9	66.67	Tolerant
7. C	CCRP 5 Check	9.09	Highly susceptible

of tolerance or susceptibility under drought stress (Silva *et al.*, 2007).

Physiological parameters

Relative water content (RWC) has been a very effective index for measuring the water status of a plant; it also indicates the ability of a plant to tolerate water deficit conditions (Torres et al., 2019; Xing et al., 2021). In the study, six cocoa genotypes along with check variety exhibited significant variation for all the physiological parameters under water deficit condition of 40 per cent FC (Table 3). All the genotypes, along with check variety, did not show a significant difference for relative water content at 100 per cent FC. The genotype, P.IV 19.9 (84.04%), followed by P.IV 59.8 (82.02%), VSD.I 29.9 (80.09%), VSD.I 3.4 (78.30%), and VSD.I 11.11(73.96%) recorded higher relative water content under water stress conditions, which could be attributed to their ability to overcome drought impact. In contrast, the check variety (42.97%) and P.II 12.11 (60%) recorded the least relative water content when subjected to drought stress conditions at 40 per cent FC. Relative water content and water potential are highly correlated in plant tissue. A similar study in cocoa revealed that, under normal watering conditions, no significant variations were recorded among the clones (Zakhariya and Indradewa, 2018). Balasimha (1984) stated that higher RWC was recorded in tolerant clones than susceptible ones under drought stress. In another study, an increased water stress resulted in a decline in RWC in barley (Yuan et al., 2005) and peanut (Meher et al., 2018).

In the current investigation, it was found that all the cocoa genotypes recorded higher chlorophyll content at the optimum condition of 100 per cent field capacity (Table 3). SPAD index is a reliable and non-destructive method of measuring chlorophyll content which is sensitive and readily measurable. The genotype, P.IV 19.9 (39.55), recorded a higher SPAD index; the least was recorded in check variety (30.00). A decline in the SPAD index was seen in plants exposed to 40 per cent FC (Table 2), in which chlorophyll degradation resulted in photoinhibition and photobleaching at water stress conditions, as stated by (Silva *et al.*, 2007). This parameter can be used appropriately to determine drought tolerance in cocoa genotypes.

SI. No.	Genotype	Photosynthetic rate (µmol CO, m ⁻² s ⁻¹)		Transpiration rate (mmol H ₂ O m ⁻² s ⁻¹)		Leaf temperature (°C)	
		100% FC	40% FC	100% FC	40% FC	100% FC	40% FC
1.	P.IV 19.9	2.74	1.63	2.89	0.29	34.62	37.75
2.	P.II 12.11	1.48	0.80	1.48	1.62	31.99	36.06
3.	P.IV 59.8	2.70	1.34	2.64	0.32	32.76	36.99
4.	VSD.I 11.11	1.92	1.07	1.70	0.62	32.83	37.31
5.	VSD.I 3.4	2.04	1.14	1.73	0.64	32.74	36.77
6.	VSD.I 29.9	1.89	0.98	1.63	0.57	32.23	36.78
7.	CCRP 5 Check	1.32	0.78	1.24	1.87	31.84	35.67
	CD (5%)	0.235	0.14	0.227	0.123	NS	NS
	SE (m)	0.077	0.046	0.074	0.04	1.037	1.379
	CV (%)	6.617	7.178	6.746	8.19	5.49	6.495

Table 2. Effect of water deficit condition at both 100 per cent FC and 40 per cent FC for photosynthetic parameters of cocoa genotypes

Table 3. Effect of water deficit condition of 100 per cent FC and 40 per cent FC for physiological parameters of cocoa genotypes

SI. No.	Genotype	RWC (%)		Chlorophyll content (SPAD unit)		Chlorophyll stability index (%)	
		100% FC	40% FC	100% FC	40% FC	100% FC	40% FC
1.	P.IV 19.9	86.68	84.04	39.55	34.70	93.86	87.14
2.	P.II 12.11	82.98	60.00	32.50	28.39	81.72	67.94
3.	P.IV 59.8	84.56	82.02	38.58	30.67	90.84	83.28
4.	VSD.I 11.11	83.95	73.96	34.82	32.58	87.52	78.89
5.	VSD.I 3.4	84.63	78.30	34.24	32.88	88.42	77.29
6.	VSD.I 29.9	85.97	80.09	32.04	29.70	85.49	78.98
7.	CCRP 5 Check	82.91	42.97	30.00	26.22	77.06	49.02
	CD (5%)	NS	5.794	3.995	2.71	9.368	6.812
	SE (m)	2.314	1.892	1.304	0.882	3.059	2.224
	CV (%)	4.742	4.575	6.543	4.968	6.131	5.161

In cocoa, chlorophyll content and photosynthesis are affected under water deficit stress due to damage to membranes and photosynthetic apparatus (Janani *et al.*, 2019). Reduction in chlorophyll content under drought stress has been studied in crops like sugarcane (Silva *et al.*, 2007), peanut (Meher *et al.*, 2018), taro (More *et al.*, 2019) and wheat (Khayatnezhad and Gholamin, 2020).

A similar trend was observed in the chlorophyll stability index under water stress conditions (Table 3). In the current investigation, among the six genotypes which were screened for drought tolerance compared with check, a higher chlorophyll stability index was found in P.IV 19.9 (93.86%), and the least was recorded in check (77.06%). Under drought

stress of 40 per cent FC, higher chlorophyll stability was recorded in P.IV 59.8 (83.28%), followed by VSD.I 29.9 (78.98%), VSD.I 11.11 (78.89%) and VSD.I 3.4 (77.29%) indicated that these genotypes could tolerate drought stress at 40 per cent FC. Chlorophyll stability is reduced mostly due to chloroplast destruction, protein complex instability, and an increase in chlorophyllase enzymes (Dutta *et al.*, 2016). The results were in agreement with Janani *et al.* (2019) and More *et al.* (2019).

Figure 1 depicts the effect of water stress on cell membrane stability of six cocoa genotypes along with check variety. All the genotypes exhibited higher membrane stability compared to checks under both water regimes. The genotype,

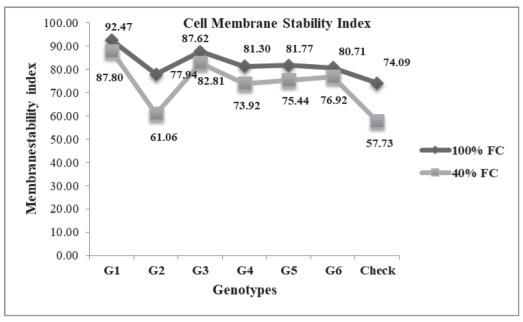


Fig. 1. Effect of water deficit condition of 100 per cent FC and 40 per cent FC for cell membrane stability index of cocoa genotypes

* G1: P.IV 19.9; G2: P.II 12.11; G3: P.IV 59.8; G4: VSD.I 11.11; G5: VSD.I 3.4; G6: VSD.I 29.9 FC: Field capacity

P.IV 19.9 (87.80%), recorded higher membrane stability under water deficit of 40 per cent FC and the least was observed in check variety (57.73%) and in P.II 12.11 (61.06%), which was screened as a susceptible genotype. The membrane stability index measures the extent of membrane damage and indicates the ability to survive drought stress (More *et al.*, 2019). The decline in membrane stability is mainly attributed to lipid peroxidation and oxidative damage caused by ROS. It can be stated that the higher CSI and CMS are desirable characters for screening drought stress tolerance genotypes in cocoa.

Correlation studies on physiological parameters to drought stress

Correlation coefficients were estimated for different physiological parameters with respect to the percentage of leaves retained using Pearson's correlation was presented in Table 4. A decline in chlorophyll content under water deficit stress directly affects the photosynthetic mechanism in plants (Juby, 2019). In this study, the photosynthetic rate (0.860) exhibited a positive and significant correlation with the dependent variable. However, the transpiration rate (-0.960) had a negative and significant correlation with the percentage of leaves. This negative correlation in transpiration rate during water stress is an important mechanism for maintaining water balance in the plant system. Leaf temperature (0.755) had a non-significant association with the percentage of leaves retained. Among the physiological parameter studied, cell membrane stability (0.984) expressed a highly positive significant association with the dependent variable. So, it can be utilised as an indicator for measuring drought stress tolerance in cocoa. Cell membrane stability is an indicator of the degree of cell membrane injury. CSI (0.925) also had a significant positive correlation with the percentage of leaves retained. It measures the heat stability nature of plant pigments under stress conditions. Juby (2019) observed high chlorophyll stability index attributed to tolerant cocoa hybrids to withstand drought stress. Chlorophyll content (0.793) also expressed the same trend as CSI. Chen et al. (2016) and Allahverdiyev et al. (2015) noticed a correlation between chlorophyll content and drought adaptability in maize seedlings. Relative water content (0.952) was found to be high and

	V1	PN	TR	LT	RWC	CSI	CMS	SPAD
V1	1							
PN	0.860 *	1						
TR	-0.960 **	-0.823 *	1					
LT	0.755 NS	0.936 **	-0.692 *	1				
RWC	0.952 **	0.768 **	-0.968 **	0.648 NS	1			
CSI	0.925 **	0.791 *	-0.941 **	0.703 NS	0.980 **	1		
CMS	0.984 **	0.923 **	-0.970 **	0.808 **	0.937 **	0.923 **	1	
SPAD	0.793 **	0.829 **	-0.832 **	0.864 **	0.825 **	0.852 **	0.832 **	1

Table 4. Correlation matrix among drought tolerant contributing characters in cocoa genotypes

** Significant at 0.01 level *Significant at 0.05 level NS- Non significant

V1 -% Leaf retained, PN- Photosynthetic rate, TR -Transpiration rate

LT - Leaf temperature, CSI- Chlorophyll stability index, RWC- Relative water content

CMS - Cell membrane stability, SPAD - Chlorophyll content

significantly correlated with the dependent variable. Rodriguez *et al.* (2010) reported a positive correlation of RWC with drought stress in tomato. Photosynthetic rate expressed a positive and significant association with chlorophyll content (0.829). All the physiological parameters had a negative and significant association with transpiration rate. The results of correlation studies revealed that all the physiological parameters have a direct association with the drought-adaptive capability of cocoa. So, these parameters can be utilised as promising indicators for screening drought tolerance in cocoa.

Conclusion

In this investigation, P.IV 19.9 cocoa genotype, which is classified as highly tolerant, recorded higher values for Pn, RWC, CSI, CMS, and chlorophyll content under water deficit conditions at 40 per cent FC and also other tolerant genotypes (P.IV 59.8, VSD.I 11.11, VSD.I3.4 and VSD.I 29.9) recorded higher values for all these parameters than check variety under drought condition. This implies the role of these physiological parameters in screening drought tolerance in cocoa genotypes. This study could help to understand the role of photosynthetic and physiological parameters in the drought adaptive mechanism of cocoa. These can be utilised as the most promising tool or indicators to screen the drought tolerance in cocoa.

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