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Effect of Water Deficit Imposed during the Early Developmental Phase on Photosynthesis of Cocoa (*Theobroma cacao* L.)

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Abstract

A greenhouse study was carried out at Cocoa Research Institute of Nigeria, Ibadan to study the effect of water stress on the four popular cocoa genotypes at the institute. F_3 Amazon, T_1, T_7 and Amelonado were raised under different water regimes (daily, 3-day interval, 5-day interval and 7-day interval) at 100%, 50% and 25% field capacities. Data were collected on the height, leaf area, root length, stomata conductance, photosynthetic rate and water use efficiency of the plants. Results showed that plant performances showed genotypic variation in their response to water stress. Generally, there were linear and positive relationships between water level and values in both physiological and morphological responses of cocoa genotypes.

Keywords

Cocoa, Water Stress, Photosynthesis, Growth

1. Introduction

For highest level of successful establishment of most tree crop plantations to be guaranteed, a lot of work must be put in place before the field operation is actually set in motion. One of such activities is the selection of appropriate materials which will be raised for a specific period of time in the nursery. Response of cocoa to drought and/or other stress conditions varies considerably [1]. Such variations are mostly due to adjustments in their morphological parameters like leaf area, number and thickness of leaves as well as other features that are

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generated by phylogeny and adaptations [2]. Aside its morphological adjustment, several studies have shown that plant tolerance or sensitivity to water stress depends on their physiological characteristics [3]. Many physiological mechanisms displayed by plants across different agro-ecological zones are not only related to environmental parameters but also genetic dependant [4]. Consequently, the genetic, morphological and environmental factors that influence plants survival and growth during stress are inter-dependent.

Plant species or genotypes with better tolerance abilities to drought are different morphologically and/or physiologically from other species of the same crop due to variability in their mechanisms for survival and growth under limited water supply. When compared with other tree crops, cocoa is less efficient in the control of water loss [5] and does not tolerate periods of long water stress [6] while ability for osmotic adjustment during water stress varies in cocoa [7]. According to [8], ability to identify the genotypes that combine the traits for good growth and high yield with efficient WUE is an essential mechanism for breeding crops for drought-prone areas. Also, [9] positioned that traits which favour drought tolerance in plants include greater allocation of biomass to root than above ground parts, lower evaporative surface (leaf area) and thicker leaves.

The limited drought tolerance ability of the crop is a growing concern in the cocoa production areas mainly due to the inconsistent rainfall patterns [10]. While [11] explained that many research findings had already reported evidences of decline annual rainfall in the cocoa grown areas of Ghana. In Nigeria, a lot of the newly transplanted cocoa seedlings and/or cuttings die during the “longer-than usual” dry spell in the cocoa production area of the country.

Increase in the length of dry seasons and high potential of expansion of cocoa production to many marginal environments in Nigeria demand the identification and selection of drought tolerance cocoa genotypes. According to [12], it is now paramount to study the water requirement of cocoa and breed for new genotypes that are more tolerant to environmental stress which is currently being experienced in the crop’s production areas. This work, therefore, presents a greenhouse experiment that studied the effect of water stress conditions on some morphological and physiological parameters in the growth and early development of four genotypes of cocoa in Nigeria.

2. Materials and Methods

The study was carried out in the greenhouse of Cocoa Research Institute of Nigeria, Ibadan, with the daylight and temperature during the growth season varied from 14 h to 17 h and 22˚C to 30˚C, respectively. Four cocoa varieties (F_3 Amazon, T_1, T_7 and Amelonado) were sown at the rate of 4 seeds per pot which were previously filled with about 3 kg soil and thinned to 2 seedlings per pot at 4 weeks after sown (WAS). T_1 and T_7 were selected randomly from the CRIN’s newest release (T_1, T_2, T_3, T_4, T_5, T_6, T_7 and T_8 cocoa genotypes) which were also known as CRIN Seed Garden or 18-month Cocoa Varieties. While F_3 Amazonis described as the 3rd filial generation of the Upper Amazonian variety released by CRIN, Ibadan, Tsimply means *Theobroma*. Both F_3Amazon and Seed Garden are high yielding and early bearing cocoa varieties. However, the latter was the newest release of CRIN and has an advantage of earlier fruit production, about 18-month after planting. F_3 Amazon starts fruit bearing around 24 months old. Unlike the first two varieties, Amelonado cocoa, also known as West African Amelonado, is less efficient in terms of time and quantity of fruits production.

The experimental soil was a top-soil of a Sandy loam Alfisol, Olorunda Series (USDA Soil Classification). The soil was moderately rich in organic content and collected within 0 - 15 cm depths with a soil auger from a virgin forest in the nearby Onigbambari Forest Reserve. The soil was air-dried before and passed through 10mm sieve to remove stones, roots and any other debris. All pots were circular and of equal size while weather parameters like light intensity and duration, temperature and relative humidity were same for all treatments.

All pots were watered at 2-day interval till 4WAS when different water regimes were imposed on the plants. After the determination of the rate of water loss from cocoa seedlings, appropriate quantities of water were applied at 4 different frequencies (daily, 3-day, 5-day and 7-day intervals) till 28WAS. Field capacity of the soil was determined using the modified [13] and applied to the plants at 100%, 50% and 25%. There were 4 cocoa genotypes, 3 field capacities (100%, 50% and 25%), 4 watering frequencies (daily, 3-day, 5-day and 7-day intervals), 3 replications and 2 stands per genotype per replicate of cocoa plants totalling 288 experimental pots arranged in Completely Randomised Design (CRD). All cocoa plants were sampled for data collection.

Data was collected at 8WAS, 12WAS, 16WAS, 20WAS, 24WAS and 28WAS on some of the morphological parameters (plant height, leaf area and root length) and gas exchange characteristics (stomatal conductance, photosynthetic rate and water use efficiency) of the cocoa plants. Plant height was measured non-destructively in-situ while the leaf area was measured destructively with portable Leaf Area Meter AM 300 (ADC Bio Scientific Ltd). The plant total harvest was conducted twice at 14 WAS and 28 WAS to study the effect of variation in water regimes on the root length of the plants while a portable infra-red gas analyser (ADC Bio Scientific, United Kingdom) was used to measure stomatal conductance as well as the transpiration and photosynthetic rates. Water use efficiency was a ratio between the photosynthetic rate and transpiration or the photosynthetic rate and stomatal conductance, as the case may be.

Measurements on gas exchange characteristics were collected between 12:00 pm and 3: 30 pm during each sampling day in order to obtain an accurate indication of cocoa response to environmental stress [14]. However, the plants were sometimes moved out of the greenhouse to the open place in order to get ≥300 μmol·m^{-2}·s^{-1} of sunshine needed for optimum performance of the cocoa. Genstat (VSN International Limited) 13th edition was used to analyse the data by means of analysis of variance with significant means were determined by least significant difference (LSD) at P = 0.05 value.

3. Results

3.1. Soil Analysis

The physico-chemical analyses of the soil (**Table 1**) showed that it was slightly acidic (pH (H_2O) = 6.66) and quite suitable for optimum cocoa production [15]. The values of nitrogen (5.7 g·kg^{-1}) and phosphorus (4.77 mg·kg^{-1}) of the soil were above their critical levels of 1.8 g·kg^{-1} and 0.13 mg·kg^{-1} respectively, while potassium value (0.25 cmol·kg^{-1}) was below its critical level of 1.2 cmol·kg^{-1} for raising cocoa [16]. The soil can be described as sandy loam while both calcium and magnesium values (0.41 cmol·kg^{-1} and 0.24 cmol·kg^{-1}) were also above their critical levels of0.3 cmol·kg^{-1} and 0.2 cmol·kg^{-1}, respectively [16].

3.2. Morphological Parameters

Most of the morphological traits measured varied between clones. Plant heights ranged from 69.9 cm for F_3 Amason watered 3-day interval at 50% field capacity to 10.2 cm for Amelonado watered 7-day interval at 25% field capacity (**Table 2**). Differences in the leaf area ranged from 252.3 cm^2 for T_1 watered daily at 50% field capacity to 99.0 cm^2 for Amelonado watered 7-day interval at 25% field capacity (**Table 3**). The root length ranged from 39.4 cm for T_1 watered 3-day interval at 50% field capacity to 22.3 cm for Amelonado watered 7-day interval at 50% field capacity with most plants watered 3-day interval at 100% and 50% FC having longer

Table 1. The physico-chemical property of the experimental soil before planting.

Property	Value
pH (H_2O)	6.66
Organic Carbon (g·kg^{-1})	25.4
Total Nitrogen (g·kg^{-1})	5.7
Available Phosphorus (mg·kg^{-1})	4.77
Calcium (cmol·kg^{-1})	0.41
Magnesium(cmol·kg^{-1})	0.24
Potassium (cmol·kg^{-1})	0.25
Manganese (mg·kg^{-1})	70.5
Iron (mg·kg^{-1})	2.88
Zinc (mg·kg^{-1})	3.7
Boron (mg·kg^{-1})	6.9
Sand (g·kg^{-1})	809
Silt (g·kg^{-1})	164
Clay (g·kg^{-1})	117

Table 2. Plant height (cm) of cocoa under different field capacities and water frequencies.

Cocoa genotype	Field capacity (%)	Daily (cm)	3-d interval (cm)	5-d interval (cm)	7-d interval (cm)
F_3 Amazon	100	67.1	69.8	68.6	69.5
	50	66.9	69.9	59.8	56.0
	25	65.0	55.0	45.0	40.6
T_1	100	68.9	66.7	61.4	66.3
	50	66.5	66.5	46.5	56.0
	25	64.2	53.8	45.7	42.2
T_7	100	68.3	66.1	67.6	68.0
	50	69.2	69.3	63.2	63.1
	25	61.6	58.4	48.6	38.6
Amelonado	100	69.2	70.1	64.2	64.2
	50	67.5	67.1	53.5	47.5
	25	68.9	44.0	28.9	10.2
LSD genotype		NS	8.8	7.8	20.6
LSD genotype * field capacity		NS	9.2	7.3	11.6

Values represent the means of 3 replicates measured 6 times at 8, 12, 16, 20, 24 and 28 weeks after sowing.

Table 3. Mean leaf area (cm^2) of cocoa under different field capacities and water frequencies.

Cocoa genotype	Field capacity (%)	Daily (cm)	3-d interval (cm)	5-d interval (cm)	7-d interval (cm)
F_3 Amazon	100	227.7	238.1	209.0	199.3
	50	216.0	230.0	199.4	186.4
	25	215.9	200.0	178.3	140.3
T_1	100	219.9	238.9	203.1	198.1
	50	252.3	240.2	194.9	176.0
	25	217.0	196.1	173.8	134.6
T_7	100	238.2	217.7	215.0	179.0
	50	219.2	210.5	197.9	178.1
	25	223.5	187.5	174.3	141.0
Amelonado	100	252.0	231.6	102.9	174.9
	50	229.4	209.5	180.9	150.0
	25	202.7	170.5	158.5	99.0
LSD genotype		NS	57.1	42.7	39.4
LSD genotype * field capacity		NS	38.9	21.1	32.6

Values represent the means of 3 replicates measured 6 times at 8, 12, 16, 20, 24 and 28 weeks after sowing.

roots than their counterparts which were watered daily (**Table 4**).

3.3. Variation in Stomatal Conductance, Photosynthesis and Water Use Efficiency (WUE) between Cocoa Clones

The stomatal conductance, photosynthetic rate and WUE varied significantly between cocoa clones ($P < 0.01$). The highest stomatal conductance of 0.099 mol $m^{-2} \cdot s^{-1}$ was produced by T_3 Amazon watered 3-day interval at

100% field capacity while the lowest stomatal conductance value was 0.007 mol $m^{-2} \cdot s^{-1}$ from Amelonado watered 7-day interval at 25% field capacity (**Table 5**). Average photosynthetic rate ranged from 4.671 μmol (CO_2) $m^{-2} \cdot s^{-1}$ for F_3 Amazon watered daily at 50% field capacity and 1.021 μmol (CO_2) $m^{-2} \cdot s^{-1}$ for Amelonado watered 7-day interval of Amelonado at 25% field capacity (**Table 6**).

Instantaneous water use efficiency (defined as the ratio of photosynthetic rate to transpiration rate) varied between 4.9 mmol (CO_2) $mmol^{-1}$ (H_2O) and 3.0 mmol (CO_2) $mmol^{-1}$ (H_2O) while genotypic differences in the

Table 4. Mean root length (cm) of cocoa under different field capacities and water frequencies.

Cocoa genotype	Field capacity (%)	Daily (cm)	3-d interval (cm)	5-d interval (cm)	7-d interval (cm)
F_3 Amazon	100	33.3	38.3	39.0	39.3
	50	35.4	39.2	37.1	32.5
	25	31.0	29.9	28.4	29.8
T_1	100	31.5	38.8	35.5	39.1
	50	32.3	39.4	34.5	32.6
	25	27.0	28.0	25.2	27.4
T_7	100	38.1	37.4	38.2	39.2
	50	33.4	37.9	37.5	28.6
	25	27.0	29.7	25.8	29.7
Amelonado	100	35.0	35.6	37.6	34.7
	50	34.4	34.5	27.2	22.3
	25	26.5	25.3	24.0	22.5
LSD genotype		NS	3.1	7.2	10.1
LSD genotype * field capacity		10.2	11.5	10.1	12.6

Values represent the means of 3 replicates measured 6 times at 8, 12, 16, 20, 24 and 28 weeks after sowing.

Table 5. Mean stomatal conductance (mol $m^{-2} \cdot s^{-1}$) of cocoa under different field capacities and water frequencies.

Cocoa genotype	Field capacity (%)	Daily (mol $m^{-2} \cdot s^{-1}$)	3-d interval (mol $m^{-2} \cdot s^{-1}$)	5-d interval (mol $m^{-2} \cdot s^{-1}$)	7-d interval (mol $m^{-2} \cdot s^{-1}$)
F_3 Amazon	100	0.081	0.099	0.067	0.061
	50	0.098	0.081	0.056	0.048
	25	0.051	0.062	0.043	0.014
T_1	100	0.089	0.091	0.071	0.067
	50	0.075	0.092	0.069	0.051
	25	0.026	0.067	0.042	0.017
T_7	100	0.078	0.088	0.097	0.067
	50	0.077	0.087	0.073	0.045
	25	0.067	0.080	0.055	0.019
Amelonado	100	0.088	0.087	0.068	0.059
	50	0.081	0.082	0.067	0.060
	25	0.068	0.077	0.056	0.048
LSD genotype		0.011	0.013	0.009	0.007
LSD genotype * field capacity		0.034	0.025	0.041	0.021

Values represent the means of 3 replicates measured 6 times at 8, 12, 16, 20, 24 and 28 weeks after sowing.

Table 6. Mean photosynthetic rate (μmol·$m^{-2}s^{-1}$) of cocoa under different field capacities and water frequencies.

Cocoa genotype	Field capacity (%)	Daily (μmol $m^{-2}\cdot s^{-1}$)	3-d interval (μmol $m^{-2}\cdot s^{-1}$)	5-d interval (μmol $m^{-2}\cdot s^{-1}$)	7-d interval (μmol $m^{-2}\cdot s^{-1}$)
F_3 Amazon	100	4.321	4.331	3.671	3.045
	50	4.671	3.491	2.901	2.962
	25	3.123	2.011	2.491	1.050
T_1	100	4.034	4.201	3.718	3.041
	50	3.982	4.067	3.541	3.011
	25	3.171	2.902	2.703	1.034
T_7	100	3.901	4.067	3.785	2.991
	50	4.272	3.552	2.890	2.091
	25	4.001	3.078	2.744	1.072
Amelonado	100	4.098	4.051	2.901	2.078
	50	4.321	3.908	2.090	2.045
	25	4.671	2.891	1.997	1.021
LSD genotype		1.034	1.012	1.007	1.008
LSD genotype*field capacity		NS	1.051	1.257	1.061

Values represent the means of 3 replicates measured 6 times at 8, 12, 16, 20, 24 and 28 weeks after sowing.

ratio of intrinsic water use efficiency (defined as the ratio of photosynthetic rate to stomatal conductance) were also significant ($P < 0.01$) with mean values ranged from 67.4 μmol (CO_2) $mmol^{-1}$ (H_2O) for F_3 Amazon to 42.3 μmol (CO_2) $mmol^{-1}$ (H_2O) for Amelonado (**Table 7**). A large proportion of the observed variation between cocoa genotypes in light-saturated photosynthetic rate across all water regimes and watering frequencies could be explained by variation in stomatal conductance (**Figure 1**).

4. Discussion

In the present work, most of the morphological parameters (especially, plant height and leaf area) had linear and positive relationships with the quantities of water supplied. In Ghana, [17] similarly found that cocoa plants that received smaller quantities of water, in terms of water volume and/or frequency, produced shorter and thinner plants. The study showed that water deficit also resulted in the reduction in leaf cell sizes which invariably led to declined leaf areas. Leaf growth is one of the first physiological processes affected by changes in plant water status under drought since a decrease in leaf expansion rate usually precedes any reduction in stomatal conductance or photosynthesis [18]. In cocoa, although growth and leaf expansion are controlled by endogenous mechanisms, the effects of environment override such influence [19].

Relationships between vegetative growth and photosynthesis are important in determining yield while availability of enough water to create non-water stress environment increase the proliferation of the plant root. Reduction in leaf area is considered as one of the earliest adaptation mechanisms to water deficits. The work of [20] discovered that in cocoa, leaf size is more sensitive to water stress than stomatal conductance and CO_2 assimilation. Persistence water stress leads to reduction in the leaf area and consequent lower net assimilation per unit leaf area and the harvestable yield of cocoa [21]. Ability to specifically diminish above-ground biomass and maintain good root system will afford cocoa the opportunity to exploit the limited water resources, to some extent, during drought. The significant differences ($P = 0.05$) that existed in the plant height, leaf area and root length of plants confirmed similar results of early genotypic variation in the morphological attributes of cocoa [22]. The results of the present work show that cocoa leaf area, stomatal conductance and photosynthetic rate had linear and positive relationships with the quantities of water supplied in agreement with [1].

The observed high correlation between plant photosynthetic rate and stomatal conductance showed that water potential has a serious impact on the growth and development of cocoa [23]. Decrease in photosynthetic rate

Table 7. Mean water use efficiency (WUE) traits of the four cocoa genotypes with standard error in brackets.

Genotype	$WUE_{INSTANTANEOUS}$ mmol (CO_2) $mmol^{-1}$ (H_2O)	$WUE_{INTRINSIC}$ µmol (CO_2) $mmol^{-1}$ (H_2O)
F_3 Amazon	4.9 (0.2)	67.4 (4.4)
$Theobroma_1$	4.1 (0.2)	67.0 (3.9)
$Theobroma_7$	4.8 (0.2)	66.9 (4.7)
Amelonado	3.0 (0.1)	42.3 (3.2)

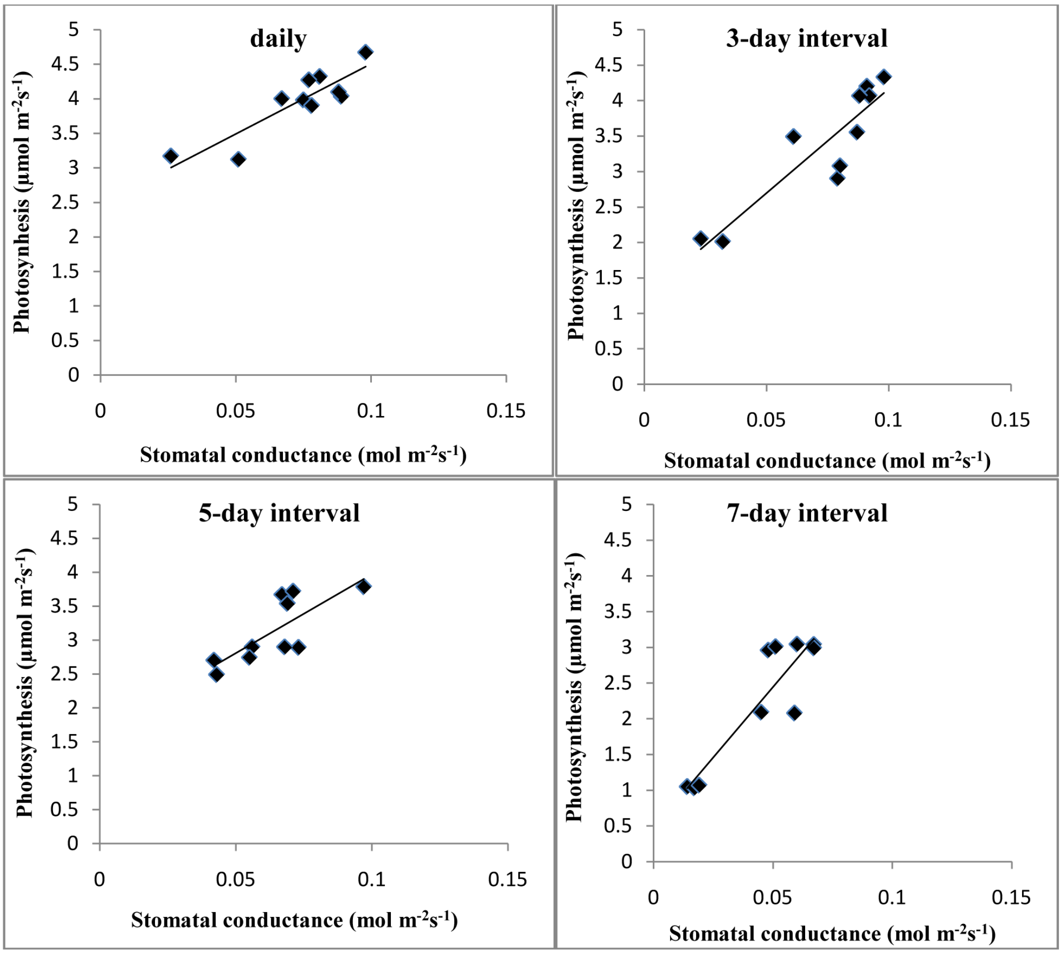

Figure 1. The relationships between stomatal conductance and light saturated photosynthesis of cocoa at different watering frequencies.

occurs as a consequence of stomatal closure and decreased CO_2 uptake. However, extreme stomatal closure usually results in degradation of photosynthetic pigments leading to the losses of activity of the Calvin's cycle enzymes, such as the ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco) [24] which probably led into the death of most Amelonado watered 7-day interval at 25% field capacity at 28WAS.However,water applied more frequently at 100% field capacity to refill the root zone, in the present study, did not transform to better growth. Consequently, achievement of highest possible WUE and other water-stress traits in cocoa can be harnessed in breeding for more marginal growing areas where rainfall is less consistent.

Plants have developed physiological responses as well as ecological strategies to cope with soil water shortage, either by stress avoidance or stress tolerance [25]. Mechanisms developed by cocoa plants to survive water deficits in the present study mainly involve avoidance of tissue water stress which includes stomatal closure and reduction in leaf area, among other factors.

5. Conclusion

Water deficit adversely affected development and growth of cocoa directly by dehydration of the photosynthetic apparatus or indirectly through stomatal closure. There was an evidence of genotypic variation in response of cocoa to water stress and considerable intra-specific variation in the photosynthetic performance and growth of cocoa. Therefore, ability for higher photosynthetic activity during water deficit may be an important step for enhancing cocoa cultivation and a factor for consideration in breeding of cocoa. The results of the experiment showed that F_3 Amazon, T_1 any T_7 performed better than Amelonado during water stress.

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