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Photosynthetic and growth responses of *Theobroma cacao* L. clones to waterlogging

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Abstract

Six high yielding cacao clones (CCN-10, CP-49, CP-06, CEPEC-2007, CEPEC-2008, and PS-1319) were evaluated for photosynthetic performance, growth, and leaf nutrient concentration in response to 45 days of root waterlogging. Submergence reduced net CO_2 assimilation (*A*). The highest *A* value (6.8 mmol CO_2 $m^{-2}{\cdot}s^{-1}$) was observed in the control plants of CCN-10 at 15 days after submergence, and CEPEC-2007 and PS-1319 30 at days of submergence. Stomatal conductances (*gs*) were 115 and 102 mmol H_2O $m^{-2}{\cdot}s^{-1}$ for CP-49 and CCN-10, respectively. Fifteen days of submergence increased the leaf intercellular (*Ci*) to atmospheric CO_2 concentration (*Ca*) ratio (*Ci/Ca*) and decreased *gs* with CEPEC-2008 and PS-1319 being the most sensitive clones. CCN-10, CP-49, and CP-06 had relatively higher mean values of *A* and *gs* after waterlogging than other clones. All CEPEC-2008 and PS-1319 plants died after 35 days of waterlogging. The surviving clones had lower root, leaf and total plant dry weight, leaf area, leaf biomass ratio, relative growth rate, and leaf number, with the exception of clones CP-06 and CEPEC-2007. Waterlogging also decreased leaf concentrations of N, P, K, and Mg in all clones, except N in CEPEC-2007. The CCN-10 clone was the most tolerant to waterlogging with the least effects of waterlogging on leaf gas exchange. Clones CP-49, CP-06, and CEPEC-2007 showed intermediate tolerance, while CEPEC-2008 and PS-1319 were highly sensitive.

Keywords: Cacao, Leaf gas exchange; Macronutrients, Stomatal conductance, Submergence.

Introduction

Waterlogging is common in some cacao growing regions of southern Bahia, Brazil, due to high rainfall and poorly drained soils (Almeida and Valle, 2007). Frequent flooding may reduce the productivity of many tree crop species, which makes it essential to identify or develop flood-tolerant cultivars (Schaffer, 1998; Almeida and Valle, 2007). Plant tolerance to waterlogging, however, varies depending on species, duration of inundation, stage of plant development, and environmental conditions. Continuous flooding often leads to changes in plant morphology including adventitious root formation or development of aerenchyma and hypertrophic stem lenticels, which assist the plant to cope with anaerobic conditions (Kozlowski, 1997).

Anoxia in waterlogged soils may affect plant survival, growth, and productivity. Waterlogging also reduces leaf gas exchange and nutrient absorption due to impaired root metabolism and root mortality, alters partitioning and translocation of photosynthates, and induces production of endogenous hormones such as ethylene (Kozlowski, 1997; Pezeshki, 2001). Carbon assimilation is one of the main processes affected by waterlogging. Reduction in net CO_2 assimilation (*A*) following submergence can be due to closure of stomata or decreased Rubisco activity (Kozlowski, 1997; Pezeshki, 2001). However, such information is not

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readily available for the major cacao (*Theobroma cacao* L.) clones of southern Bahia, Brazil. The purpose of this study was to compare the effects of root waterlogging on leaf gas exchange, nutrient content, and plant growth of six different cacao clones and to determine whether interclonal variability to waterlogging exists in this species.

Materials and Methods

The experiment was performed at the Universidade Estadual de Santa Cruz, in Ilhéus, BA, Brazil (14º48'53"S/39º02'01"W) from 05 January 2008 to 20 November 2008. Young plants of six high yielding cacao clones (CCN-10, CP-49, CP-06, CEPEC-2007, CEPEC-2008, and PS-1319) were obtained by rooting 16 cm plagiotropic cuttings, including the apical bud collected from 5 to 10 year-old field-grown plants. Each cutting had three axillary buds. About ¾ of the leaf area was removed and the cut stem bases (3 cm) were dipped in a mixture of 4 g indole-3-butyric acid (IBA) per kg of talc before planting in individual black plastic conical containers (290 cm^3) filled with turf + milled *Pinus* cortex and coconut fiber in 1:1 proportion. All essential nutrients were supplied as per the crop requirement. The conical containers were placed in plastic trays (54 per tray) and transported to a greenhouse with 50% incident radiation, where they were irrigated with an automated mist system for 120 days. During the first 60 days in the nursery, the cuttings were irrigated at five min intervals for 30 seconds to promote adventitious root formation; afterwards irrigation was scheduled at 10 min intervals (20 $L{\cdot}h^{-1}$).

Forty 120 days-old plants (~40 cm tall) of each clone were transplanted in 3 L perforated plastic bags filled with the rooting substrate described above and grown in a greenhouse with 50% incident radiation, ambient temperature of 28 ± 1°C, and relative humidity of 80 ± 3% for two months. Thereafter, four plants of each clone (six months-old) were placed in 25 L plastic buckets and with 10 to 20 cm column of standing water (waterlogged treatment) for 45 days. Control plants were placed in similar buckets with drainage holes and irrigated daily for 45 days to maintain the water content close to field capacity. The experiment was laid out in a complete randomized design with five replications.

At the beginning and end of the experimental period, root (RDW), stem (SDW) and leaf (LDW) dry weights, number of leaves, and leaf area per plant were determined on five plants. For dry weight determinations, the plant materials were dried in a circulating air oven at 75ºC until constant weights. Leaf area was measured with a LI-3100 area meter (Li-Cor Inc., Lincoln, Nebraska, USA) on five plants. Mean relative growth rate (RGR), the leaf area ratio (LAR), leaf (LDWR), stem (SDWR), and root (RDWR) dry weight ratios were calculated following Hunt (1990). Leaf concentrations of phosphorus (P), magnesium (Mg), nitrogen (N), and potassium (K) were determined after digestion of 0.2 g of dried plant tissue (five samples per clone) in nitric and perchloric acids (5:1): total P by colorimetry (Golterman et al., 1978), Mg by atomic absorption spectrometry, N by Kjeldahl method (Jackson, 1958), and K by flame photometry (Isaac and Kerber, 1971).

Leaf gas exchange measurements

Net photosynthetic rate per unit of leaf area (*A*) and stomatal conductance of water vapor (*gs*) were measured on one mature, fully expanded leaf per clone 15, 30, and 45 days after imposing the waterlogging treatment. Leaf gas exchange was measured between 07:30 to 12:30 with a portable photosynthesis system LI-6400 (Li-Cor, Lincoln, Nebraska, USA) equipped with an artificial light source (6400-02B RedBlue), when photosynthetic photon flux density and air temperature in the cuvette remained at 800 $mmol{\cdot}m^{-2}{\cdot}s^{-1}$ and 27ºC, respectively. Leaf intercellular CO_2 concentration (*Ci*) was calculated and the atmospheric CO_2 concentration (*Ca*) was measured, from which the *Ci*/*Ca* ratio was computed. Mean atmospheric CO_2 concentration, air temperature, and ambient vapor pressure deficit during the leaf gas exchange measurements were 386 ± 0.4 $\mu mol\ mol^{-1}$, 32.1 ± 0.3ºC and 2.26 ± 0.04 kPa, respectively.

The experimental data were analyzed following two way analysis of variance and Tukey's mean separation test. Gas exchanges data were analyzed separately for each measurement date.

Results and Discussion

All clones developed hypertrophic stem lenticels and adventitious roots at the base of the stems after 15 days of waterlogging. Two clones (CEPEC-2008 and PS-1319) died after 35 days of flooding, and the surviving plants exhibited weak flushes, chlorosis, and premature leaf senescence. Waterlogging also resulted in significant (p<0.01) reductions in stomatal conductance (*gs*), net CO_2 assimilation (*A*), and internal to external CO_2 concentration ratios (*Ci/Ca*) in all clones (Table 1). As the duration of waterlogging increased, the magnitude of such reductions also increased. Reductions in *A* values following waterlogging may be due to limitations in CO_2 uptake owing to stomatal closure (Gomes and Kozlowski, 1986), biochemical changes associated with the photosynthetic reactions (Schaffer, 1998), and decreases in Rubisco concentrations (Pezeshki, 2001). Hypertrophic stem lenticels as observed in the present study may serve as openings through which toxic compounds associated with anaerobiosis in the roots are released, thus preventing its translocation to leaves (Gomes and Kozlowski, 1986). These authors also reported that production of adventitious roots may compensate for the loss of original roots and maintain water absorption.

Waterlogging x clones interaction effects for *gs* were significant at the early stage (Table 1), implying interclonal differences in the early response to waterlogging. As can be seen from Table 2, 15 days after the treatments were imposed, net CO_2 assimilation (*A*) of the waterlogged plants was only 24 to76% of the control for five clones, while it was similar for CP-06 in both waterlogged and control plants. Likewise, *gs* was lower in the waterlogged plots than in the control (50 to 70% of control values) for four clones; but CCN-10 and CP-49 had similar *gs* values for both treatments. A decrease in *gs* is a common response to soil flooding, although in specific cases, after a few weeks of water-logging, *gs* values in tolerant plants have a tendency to recover (Kozlowski, 1997).

Long periods of flooding resulted in wilting, growth impairment of shoots and roots, and death of the CEPEC-2008 and PS-1319 clones. These two clones had more severe and earlier reduction in gas exchanges following waterlogging, compared with the surviving clones. Low tolerance to waterlogging was probably due to the large decrease in *A* and *gs* values which impaired its growth.

Table 1. Stomatal conductance to water vapor (*gs*), net CO_2 assimilation (*A*) and ratio between internal to external CO_2 concentrations (*Ci/Ca*) of six *Theobroma cacao* clones during different time periods under waterlogged and non-waterlogged (control) conditions.

Variable	Time (days)	Control	Waterlogged	ANOVA		
				Waterlogging	Clone	W x C
gs (mmol H_2O $m^{-2}{\cdot}s^{-1}$)	15[1]	73.8 ± 5.40	56.8 ± 7.23	**	**	**
	30[1]	61.7 ± 3.56	19.3 ± 1.65	**	*	ns
	45[2]	51.5 ± 3.35	13.3 ± 0.97	**	ns	ns
A (mmol CO_2 $m^{-2}{\cdot}s^{-1}$)	15[1]	6.03 ± 0.19	3.49 ± 0.33	**	**	**
	30[1]	6.44 ± 0.16	1.58 ± 0.19	**	**	**
	45[2]	5.46 ± 0.26	1.02 ± 0.10	**	*	ns
Ci/Ca	15[1]	0.58 ± 0.02	0.66 ± 0.03	**	**	**
	30[1]	0.50 ± 0.02	0.65 ± 0.03	**	**	**
	45[2]	0.49 ± 0.02	0.63 ± 0.03	**	**	ns

[1] Clones CCN-10, CP-49, CP-06, CEPEC-2007, CEPEC-2008, PS-1319 (df clone = 5; df waterlogging = 1). Means of 30 replications (five replications per six clones per treatment) ± SE.
[2] Clones CCN-10, CP-49, CP-06, CEPEC-2007 (df: clone = 3; waterlogging = 1). Means of 20 replications ± SE.

Table 2. Effects of waterlogging on stomatal conductance, net CO_2 assimilation and ratio between internal to external CO_2 concentrations in six *Theobroma cacao* clones of Brazil.

Clone	Treatments	Stomatal conductance (*gs*) (mmol H_2O $m^{-2} \cdot s^{-1}$)	Net CO_2 assimilation (*A*) (mmol CO_2 $m^{-2} \cdot s^{-1}$)		Ratio between internal to external CO_2 concentrations (*Ci/Ca*)	
		Day 15	Day 15	Day 30	Day 15	Day 30
CCN-10	Control	102[1]± 6^{Aac}	6.8 ± 0.5^{Aab}	6.4 ± 0.5^{Aab}	0.7 ± 0.01^{Babc}	0.5 ± 0.06^{Aabc}
	Waterlogged	122 ± 11^{Aa}	5.1 ± 0.5^{Bab}	3.0 ± 0.5^{Bab}	0.8 ± 0.02^{Aa}	0.5 ± 0.05^{Ac}
	% of control	140	76	47	117	113
CP-49	Control	115 ± 12^{Aa}	5.7 ± 0.4^{Aa}	6.3 ± 0.3^{Aa}	0.8 ± 0.02^{Aab}	0.6 ± 0.04^{Babc}
	Waterlogged	75 ± 14^{Bbc}	3.5 ± 0.5^{Bab}	1.8 ± 0.2^{Bab}	0.7 ± 0.06^{Aa}	0.4 ± 0.05^{Abc}
	% of control	73	62	28	96	33
CP-06	Control	60 ± 9^{Aab}	5.7 ± 0.4^{Aa}	6.4 ± 0.4^{Aab}	0.5 ± 0.03^{Abc}	0.5 ± 0.05^{Aac}
	Waterlogged	62 ± 11^{Abcd}	5.4 ± 0.7^{Aab}	1.8 ± 0.3^{Bab}	0.6 ± 0.02^{Ab}	0.6 ± 0.04^{Aabc}
	% of control	117	98	29	105	116
CEPEC-2007	Control	51 ± 5^{Ab}	5.5 ± 0.4^{Aa}	6.8 ± 0.6^{Aab}	0.5 ± 0.03^{Ac}	0.6 ± 0.02^{Aa}
	Waterlogged	27 ± 5^{Bd}	2.9 ± 0.4^{Bb}	1.8 ± 0.2^{Bab}	0.5 ± 0.03^{Ab}	0.5 ± 0.06^{Ac}
	% of control	60	54	26	98	93
CEPEC-2008	Control	51 ± 4^{Abd}	6.0 ± 0.3^{Aab}	6.0 ± 0.3^{Aa}	0.4 ± 0.05^{Ac}	0.5 ± 0.02^{Ba}
	Waterlogged	21 ± 2^{Bd}	2.3 ± 0.4^{Bb}	0.4 ± 0.1^{Bb}	0.6 ± 0.10^{Ab}	0.9 ± 0.10^{Aabc}
	% of control	60	35	7	145	183
PS-1319	Control	64 ± 5^{Abcd}	6.6 ± 0.6^{Aab}	6.8 ± 0.4^{Aab}	0.5 ± 0.04^{Bc}	0.5 ± 0.04^{Babc}
	Waterlogged	33 ± 3^{Bcd}	1.6 ± 0.6^{Bb}	0.7 ± 0.2^{Bb}	0.8 ± 0.06^{Aa}	0.7 ± 0.06^{Aabc}
	% of control	50	24	10	151	157

[1]Means of five replications ± SE. Means compared using Tukey test ($p < 0.05$). For each variable lower case letters indicate comparisons between clones and capital case comparisons between treatments.

The *Ci/Ca* initially was 117 and 151% more in CCN-10 and PS-1319 clones, respectively in the waterlogged treatment compared to the control (Table 2). On the 30th day of flooding, *Ci/Ca* of CEPEC-2008 and PS-1319 were higher in the waterlogged than in the control plants (157 to 183% higher). The CP-49 clone had a significantly lower *Ci/Ca* ratio (33% of the control values) than the other waterlogged clones. Low *Ci/Ca* values imply high stomatal limitations to photosynthesis and increased water conservation. Intercellular CO_2 concentration in the leaf (*Ci*), however, was not affected by waterlogging on the 45th day of flooding, although all clones had higher *Ci/Ca* values in the waterlogged than the control plots. The relatively higher *Ci/Ca* for the waterlogged cacao clone PS-1319 may indicate that this clone is non-conservative in relation to water use, similar to many other woody species in the humid tropical forests (Mielke et al., 2003).

Significant reductions in root, stem, leaf, and total dry weights, total leaf area, relative growth rate, and the number of leaves were recorded for all clones after 45 days of waterlogging and for leaf area ratio and leaf dry weight ratios in four clones (Table 3). There was, however, an increase in stem dry weight ratios and a decrease in the root dry weight ratios for the waterlogged plants of clone CCN-10 compared to control. However, there was no effect of waterlogging on SDWR of the other clones (data not shown). Waterlogging caused a 71% reduction in TDW of CEPEC-2007, 29% for CP-4, and 40% for CP-06 (Table 4).

In general, the clones evaluated had increased SDW in response to waterlogging, with the exception of CP-06 and CEPEC-2007. According to Akilan et al. (1997), waterlogged clones of *Eucalyptus camaldulensis* formed adventitious roots and produced a significant

Table 3. Growth variables and leaf nutrient contents of six *Theobroma cacao* clones of Brazil during 45 day period of waterlogged and non-waterlogged (control) conditions.

			ANOVA		
Variable	Control	Waterlogged	Waterlogging	Clone	W x C
RDW ($g{\cdot}plant^{-1}$)	4.28 ± 0.29	2.36 ± 0.20	**	ns	ns
SDW ($g{\cdot}plant^{-1}$)	5.66 ± 0.33	5.20 ± 0.25	Ns	**	**
LDW ($g{\cdot}plant^{-1}$)	11.5 ± 0.79	5.93 ± 0.47	**	**	**
TDW ($g{\cdot}plant^{-1}$)	21.4 ± 1.28	13.5 ± 0.82	**	**	**
TLA ($cm^2{\cdot}plant^{-1}$)	22.9 ± 1.52	9.96 ± 0.76	**	**	**
LN	33.0 ± 2.57	13.7 ± 1.16	**	**	**
RDWR	0.21 ± 0.01	0.18 ± 0.01	**	**	ns
SDWR	0.27 ± 0.01	0.40 ± 0.01	**	ns	ns
LDWR	0.53 ± 0.01	0.42 ± 0.01	**	**	ns
LAR ($cm^2{\cdot}g^{-1}$)	1.06± 0.03	0.72 ± 0.02	**	**	ns
RGR ($mg{\cdot}g^{-1}{\cdot}day^{-1}$)	15.4 ± 1.23	5.16 ± 1.21	**	**	*
N ($g{\cdot}kg^{-1}$)	23.7 ± 0.84	20.0 ± 0.41	**	**	**
P ($g{\cdot}kg^{-1}$)	4.02 ± 0.16	3.28 ± 0.13	**	**	ns
K ($g{\cdot}kg^{-1}$)	26.5 ± 0.76	22.6 ± 0.79	**	ns	ns
Mg ($g{\cdot}kg^{-1}$)	5.56 ± 0.09	4.60 ± 0.23	**	**	**

Root (RDW), stem (SDW), leaf (LDW) and total dry weight (TDW), total leaf area (TLA), leaf number (LN), root (RDWR), stem (SDWR) and leaf (LDWR) dry weight ratios, leaf area ratio (LAR) relative growth ratio (RGR) and nitrogen (N), phosphorus (P), potassium (K) and magnesium (Mg) concentrations of leaves (df: clone = 3; waterlogging = 1). Means of 20 replications (five replications per treatment per four clones) ± SE.

amount of stem dry mass. In the present study also clones of CCN-10, CP-49, CEPEC-2008, and PS-1319 showed increases in SDW. Decreases in LN and total leaf area were correlated. The two cacao clones tolerant to substrate waterlogging (CCN-10 and CP-49) had low LAR values (data not shown), which according to Almeida and Valle (1988) would favour high photosynthetic rates. Waterlogging, in general, increased the relative proportion of stem dry matter (0.40 ± 0.01 vs. 0.27 ± 0.01), and decreased allocation to leaves (0.42 ± 0.01 vs. 0.53 ± 0.01) and roots (0.18 ± 0.01 vs. 0.21 ± 0.01). Decreases in root and leaf dry weight and leaf area in cacao clones in response to waterlogging were also reported by Gomes and Kozlowski (1986). Leaf N, P, K and Mg concentrations in the four surviving clones declined substantatially after 45 days of waterlogging (Table 3). There was a 48 to 50% reduction in the number of leaves in the waterlogged plants compared to control plants of clones CCN-10 and CP-49 and a 63-65% reduction in clones CP-06 and CEPEC-2007 (Table 4).

On the whole, all surviving clones showed lower leaf area and leaf number. Waterlogging reduced leaf nutrient (N, P, K, Mg) concentrations, *gs* and *A*, and increased *Ci/Ca*. The most tolerant clone to waterlogging with least effect of waterlogging on gas exchange was CCN-10. Clones CP-49, CP-06, CEPEC-2007 showed intermediate tolerance while CEPEC-2008 and PS-1319 were sensitive to waterlogging.

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Table 4. Effect of waterlogging on stem (SDW), leaf (LDW), and total plant (TDW) dry weights, leaf area, leaf number, relative growth rate (RGR), and leaf nitrogen (N) and magnesium (Mg) concentrations in six *Theobroma cacao* clones of Brazil.

Variable	CCN-10			CP-49			CP-06			CEPEC-2007		
	Control	Waterlogged	% of control	Control	Waterlogged	% of control	Control	Waterlogged	% of control	Control	Waterlogged	% of control
SDW ($g \cdot plant^{-1}$)	$3.7^{1} \pm 0.18^{Ab}$	4.8 ± 0.63^{Aa}	130	4.8 ± 0.35^{Ab}	5.2 ± 0.26^{Aa}	108	7.2 ± 0.59^{Aa}	5.6 ± 0.64^{Ba}	78	6.9 ± 0.61^{Aa}	5.1 ± 0.41^{Ba}	74
LDW ($g \cdot plant^{-1}$)	6.2 ± 0.44^{Aab}	4.7 ± 0.62^{Aa}	76	9.3 ± 0.48^{Ab}	5.2 ± 0.42^{Ba}	56	15.9 ± 1.51^{Aa}	8.1 ± 1.31^{Ba}	51	14.6 ± 1.19^{Aa}	5.7 ± 0.88^{Ba}	39
TDW ($g \cdot plant^{-1}$)	13.8 ± 1.00^{Ab}	12.3 ± 1.77^{Aa}	89	17.5 ± 0.87^{Ab}	12.4 ± 0.68^{Ba}	71	27.4 ± 2.40^{Aa}	16.4 ± 2.22^{Ba}	60	31.2 ± 14.25^{Aa}	9.1 ± 0.31^{Ba}	29
TLA ($cm^2 \cdot plant^{-1}$)	13.8 ± 1.34^{Ab}	7.7 ± 1.01^{Ba}	56	17.6 ± 0.97^{Ab}	9.0 ± 0.66^{Ba}	51	31.8 ± 3.09^{Aa}	13.7 ± 2.08^{Ba}	43	28.5 ± 1.73^{Aa}	9.4 ± 1.43^{Ba}	33
LN	26.2 ± 2.55^{Abc}	13.5 ± 2.14^{Ba}	52	20.9 ± 3.32^{Ac}	10.4 ± 0.91^{Bac}	50	51.3 ± 5.24^{Aa}	18.8 ± 3.26^{Bac}	37	33.7 ± 3.35^{Abc}	11.9 ± 1.72^{Ba}	35
RGR ($mg \cdot g^{-1} \cdot day^{-1}$)	7.4 ± 1.49^{Ac}	3.4 ± 2.93^{Aab}	46	$12.7\ \ 1.18^{Abc}$	4.9 ± 1.18^{Babc}	39	19.6 ± 2.08	7.0 ± 3.10	36	$21{,}9 \pm 1.90^{Aab}$	5.3 ± 2.28^{Bac}	24
N ($g \cdot kg^{-1}$)	26.8 ± 0.40^{Aa}	19.6 ± 1.03^{Ba}	73	25.8 ± 0.69^{Aa}	21.5 ± 0.33^{Ba}	83	21.9 ± 1.55^{Ab}	18.5 ± 0.52^{Ba}	85	20.2 ± 1.12^{Ab}	20.4 ± 0.66^{Aa}	101
Mg ($g \cdot kg^{-1}$)	5.5 ± 0.10^{Aa}	5.3 ± 0.48^{Aa}	96	5.8 ± 0.15^{Aa}	5.5 ± 0.20^{Aa}	95	5.9 ± 0.07^{Aa}	3.9 ± 0.11^{Bb}	67	5.2 ± 0.09^{Aa}	3.7 ± 0.10^{Bb}	72

Means of five replications ± SE. Mean's comparison were done using the Tukey's studentized range test ($p \leq 0.05$). For each variable lower case letters indicate comparisons between clones and capital letters indicate differences between treatments.

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