Agricultural Water Management 171 (2016) 80–88

Contents lists available at ScienceDirect

Agricultural Water Management

journal homepage: www.elsevier.com/locate/agwat

Physiological responses to drought and experimental water deficit and waterlogging of four clones of cacao (*Theobroma cacao* L.) selected for cultivation in Venezuela

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ARTICLE INFO

Article history:
Received 24 November 2015
Received in revised form 5 February 2016
Accepted 16 March 2016

Keywords:
Cocoa
Waterlogging
Lenticels
Photosynthesis
Water deficit

ABSTRACT

Cocoa is sensitive to both water deficit (WD) and waterlogging (WL), especially during the juvenile stage. The aim of this study was to compare in four cocoa clones the water status, gas exchange and photochemical activity of PSII of adult trees subjected to natural drought in the field, and young individuals in the greenhouse subjected to either WD or WL. In the greenhouse, pots in which eight-month-old saplings were growing were placed in 8-L plastic buckets and either weekly watered (control, C), left without watering (WD), or filled with tap water up to 1 cm above soil surface (WL). In the field, drought affected clones differently in their water relations and photosynthetic responses. In the greenhouse, after 35 days of treatment, the four clones showed decreases in water potential which were stronger under WD than WL. Photosynthetic rate (P_N) decreased on average 86% due to WD and 60% due to WL, clone 415 being the most susceptible to both stresses. On average, P_N reached 100% of control values 7 d after re-watering but only 74% after drainage. Stomatal closure with maintenance of leaf water was the general response to WD. Clone 439, with highest relative lenticel area, was the one in which P_N recovered most from WL. Lenticel hypertrophy, particularly in clone 439, apparently was one of the mechanisms of acclimation to WL. Chronic photoinhibition occurred in no case. We conclude that all clones are adequate for growth in the field, although 415 is the one with lower P_N during the rainy season. Saplings of all clones are suitable for cultivation in drought-prone areas for dry periods of at least a month, and clone 439 is the one best suited for soils under short-term WL .

1. Introduction

Cocoa (*Theobroma cacao* L., Malvaceae) is a tropical woody species that normally grows in the understory of tropical forests in areas of high annual rainfall (1500-2000 mm; Carr and Lockwood, 2011). It is cultivated by approximately six million smallholder farmers (Baligar et al., 2008). Cocoa plants are sensitive to WD (Wood and Lass, 2001; Carr and Lockwood, 2011) and WL (Wood and Lass, 2001), therefore requiring well-drained irrigated soils. Most research on cocoa has been carried out under greenhouse conditions and been directed toward the identification and development of drought-tolerant genotypes (e.g. Bae et al., 2008), and the need to do more studies under field conditions has been highlighted (Carr and Lockwood, 2011).

Almeida et al. (2002) classified cultivars as tolerant to WD based on higher xylem water potential (ψ), lower g_s and the occurrence of osmotic adjustment. In a Criollo cultivar growing in the field in Venezuela, a significant decrease in P_N and g_s took place as drought progressed; osmotic adjustment and increased water use efficiency (WUE) were observed (Rada et al., 2005), similar to the responses observed in two Criollo cultivars in an agroforestry system also in Venezuela (Araque et al., 2012). Xylem water potential decreased in cocoa subjected to WD in the laboratory (Joly and Hahn, 1989) and the field (Balasimha et al., 1991), whereas it remained unchanged

Abbreviations: C_a, ambient CO_2 concentration; C_i, intercellular CO_2 concentration; CE, carboxylation efficiency; E, transpiration rate; Φ_{PSII}, relative quantum yield of PSII; F_0, minimum fluorescence in dark-adapted leaves; F_v/F_m, maximum quantum yield of photosystem II; Γ, CO_2 compensation concentration; g_s, stomatal conductance; k_L, leaf-specific hydraulic conductivity; P_N, photosynthetic rate; PPFD, photosynthetic photon flux density; q_N, nonphotochemical quenching of fluorescence; ψ, xylem water potential; ψ_{dawn}, dawn ψ, ψ_{noon}, noon ψ, ψs, leaf osmotic potential; $\psi_{substrate}$, substrate water potential; ψ_T, turgor potential; RLA, relative lenticel area; WUE, water use efficiency.

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http://dx.doi.org/10.1016/j.agwat.2016.03.012
0378-3774/

between the rainy and the dry season in several cultivars growing in Venezuela (Araque et al., 2012).

A decrease due to WD in P_N may be caused by lower g_s. If the mechanisms of photoprotection operate, a diminution in relative quantum yield of PSII (Φ_{PSII}) but not in maximum quantum efficiency of PSII (F_v/F_m) is observed (Baker, 2008). Drought has been previously shown to reduce Φ_{PSII} and F_v/F_m in cocoa cultivars under drought (Ávila-Lovera et al., 2016; Bae et al., 2008).

Waterlogging is common in some cocoa growing regions due to high rainfall and poor drainage of soils (Almeida and Valle, 2007). Cocoa trees can withstand WL but stagnant water causes their death after a few days (Wood and Lass, 2001).

The first physiological response to WL and flooding is a reduction in g_s, which may occur as early as a few hours after the stress is imposed, paralleled by a reduction in P_N (Kreuzwieser and Renhenberg, 2014), suggesting an increase in stomatal limitation of photosynthesis. In a flood-susceptible cocoa clone, WL caused a decrease in F_v/F_m, oxidative stress and chlorosis, all of which was interpreted as evidence of nonstomatal limitation of photosynthesis (Bertolde et al., 2012). In contrast, the decline in cocoa of P_N under WL was attributed to increased stomatal limitation (Balasimha et al., 1991).

The second physiological response to WL and flooding is a decrease in ψ in many intolerant species (Kreuzwieser and Renhenberg, 2014); in tolerant tropical trees, on the contrary, annual flooding produced an increase in ψ with a decrease in osmotic potential (ψ_s), suggesting the occurrence of osmotic adjustment (Herrera, 2013). Decreased ψ under WL is caused by reduced water absorption, which in turn may be due to a decrease in root hydraulic conductivity, believed to be the result of deficient operation of aquaporins (Kreuzwieser and Renhenberg, 2014).

In plants of *Prioria copaifera*, a species not normally subjected to flooding, WL for 45 d produced a decrease in g_s and P_N, the latter resuming control values after another 45 d of WL, and this recovery was attributed to the presence of large lenticels from the beginning of the experiment (Lopez and Kursar, 1999). The occurrence of hypertrophied lenticels has been associated to increased O_2 availability to tissues which, in turn, may cause an increase in root hydraulic conductivity (Kreuzwieser and Renhenberg, 2014).

The main objective of this study was to compare the physiological performance of four clones recently planted in an agroforestry system in Venezuela with the aim of selection for large-scale production. Changes in physiological variables (water status, gas exchange and photochemical activity of PSII) due to seasonal changes in water availability in the field and experimental WD and WL in the greenhouse were examined. We hypothesized that P_N would decrease under water deficit or WL due to stomatal closure and under, in the particular case of WL, stomatal closure would be due to decreased leaf-specific hydraulic conductivity, k_L, measured instead of root hydraulic conductivity.

2. Materials and methods

2.1. Plant material and growth conditions

The four cocoa clones used in this study were obtained at the Padrón-INIA Experimental Station, Estado Miranda, by hybridization; cuttings, un-grafted on rootstock except for clone 415, were planted in the field at the Experimental Station. Cuttings of clone 415 were grafted on a IMC67 rootstock. Saplings used for greenhouse experiments were obtained from cuttings of adult trees, all grafted on IMC67 rootstock. The clones were selected for their productivity and/or their resistance to *Phytophthora palmivora* (brown spot disease). Clones were 415, a hybrid with Forastero characteristics selected for its high productivity and widely used in commercial plantations around the area of study; 439, a hybrid of Criollo and Forastero, selected for an incidence of brown spot disease lower than 25%; 443, a hybrid of a modern Criollo and a Forastero and resistant to brown spot, and 447, a combination of hybrid and Forastero with an incidence of brown spot greater than 25% but with a high yield.

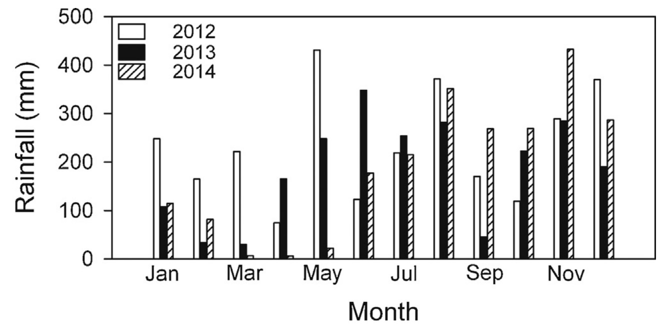

Fig. 1. Rainfall during 2012–2014 in the Padrón-INIA Experimental Station. Year indicated in the insert.

2.1.1. Field conditions

The field study was conducted in a 1-ha plot in the Experimental Station, located in a wet evergreen forest at 10° 13′ N–66° 18′ W and 38 m. Rainfall is rather erratic, as evidenced by the large yearly variability (2534 ± 214 mm yr^{-1} for 2008–2014), with two drier periods in Jan.-Mar. and Sep.-Oct. and two wetter periods in May–Aug. and Nov.–Dec. (Fig. 1). Measurements were made in between Nov. 2012, Feb. 2013 and May 2014 during rainy and wet seasons in mature fully expanded leaves of four to six seven-year-old adult trees of each clone similar in foliage and height. During the period of study, no waterlogging events, which are known to occur in the area, took place to allow the evaluation of their effects on physiological variables.

2.1.2. Greenhouse

Controlled WD and WL were undertaken in a greenhouse at the Instituto de Biología Experimental in Caracas, 10° 24′ N–67° 36′ W and 1100 m. Eight-month-old plants of the four clones, similar in foliage and height (approximately 50 cm), were subjected during Nov.–Dec. 2014 to a month of WD or WL (six plants per treatment) in a 10-m^2 area shaded to 20% of sun exposure with the use of neutral polythene sheets. Pots containing 5 kg of a 1:1 mixture of field-site soil and soil bought at a nursery and plants were introduced in 8-L buckets regardless of treatment. All plants were fertilized with N:P:K 15:15:15 one week before starting the experiments. For the WD experiment, irrigation was suspended and resumed 35 d later to assess the potential recovery. For the WL experiment, buckets were filled with tap water to 1 cm above the pot ground, maintained waterlogged for 35 d, and then drained to assess the potential recovery. Periodic physiological measurements were made in fully expanded leaves. Control plants were placed in the same conditions without waterlogging and watered every other day.

2.2. Microclimatic variables

The PPFD was measured with a 190-S quantum sensor connected to a LI-185 meter (LI-COR Inc., Lincoln, NE). Values of air temperature and relative humidity at the field site were obtained from a weather station, some 300 m from the cocoa trees. In the greenhouse, these variables were measured with two HOBO Pro V2 loggers and data dumped with a HOBO Waterproof Shuttle (Onset Computer Corporation, Pocasset, MA).