South African Journal of Botany 117 (2018) 17–25

Contents lists available at ScienceDirect

South African Journal of Botany

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

Water relations and photo-protection mechanisms during drought stress in four coffee (*Coffea arabica*) cultivars from southwestern Saudi Arabia

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ARTICLE INFO

Article history:
Received 5 January 2018
Received in revised form 16 April 2018
Accepted 26 April 2018
Available online xxxx

Edited by V Kumar

Keywords:
Osmotic adjustment
Avoidance strategy
Tolerance
Photoinhibition
Water stress
Photoprotection

ABSTRACT

This study investigated for the first time the effect of drought on water relations, gas exchange, osmotic adjustment, and photoprotection mechanisms of local Arabica coffee cultivars namely, Dawairi, Tufahi, Kholani and Tessawi grown in Southwestern Saudi Arabia. Two-year-old plants growing in pots were subjected to water stress by withholding watering for four weeks. Water relations and gas exchange measurements revealed that the severity of the stress varied among cultivars. The most contrasting behavior was between the two cultivars Dawairi (drought-tolerant) and Kholani (drought-sensitive). Tufahi and Tessawi, however, showed intermediate tolerance. Under drought stress, Dawairi trees were able to maintain higher leaf water content (WC), plant turgor potential (Ψ_p) and net photosynthetic assimilation rate (A_{net}) at a given predawn leaf water potential (Ψ_{pd}) than the other three cultivars. Irreversible wilting (turgor loss) occurred at leaf Ψ_{pd} of about −2.5 MPa for Kholani and about −3.5 MPa or lower for the other cultivars. The drought tolerant cultivar also showed the highest increase in instantaneous water-use efficiency (*i*WUE) under drought stress. All coffee cultivars were able to slow the onset of water stress by controlling transpiration (avoidance). But they did vary in their ability to avoid tissue dehydration under such stress. The reduction in A_{net}, transpiration rate (E) and stomatal conductance (g_s) with decreasing Ψ_{pd} was earlier and more marked in Kholani and Tufahi than in Dawairi and Tessawi. Besides, the fluctuations in Ψ_{pd} and Ψ_{mid} revealed a contrasting behavior among the four cultivars. Under drought stress, Dawairi maintained the highest diurnal range of $\Delta\Psi_{pd\text{-}mid}$ and showed the highest daily re-saturation capability. Moreover, it had a greater capacity for osmotic adjustment through solute accumulation. In contrast, in Kholani and Tufahi the drought-induced accumulation of solutes was mainly passive due to dehydration of the leaves. Moreover, Dawairi and Tessawi accumulated more proline in their leaves than the two other cultivars under stress. Drought stress considerably altered total soluble sugar (TSS) concentration in most cultivars. Surprisingly, the decrease in TSS content was more pronounced in drought tolerant cultivars. Photoinhibition occurred in all four cultivars when subjected to drought stress albeit with variable severity. Moderate stress decreased the quantum efficiency of PSII (Φ_{PSII}), photochemical fluorescence quenching (qP) and electron transport rate (ETR), and increased the non-photochemical quenching (NPQ); this implies dynamic photoinhibition in all cultivars. However, when drought became severe towards the end of the experiment, the decrease in Φ_{PSII}, qP and ETR was accompanied by a decline in Fv/Fm indicating the occurrence of chronic photoinhibition in most cultivars. Still photoinhibition was more obvious in Kholani and Tufahi. Interesting genetic differences in drought tolerance appear to exist among these four economically important Arabica coffee cultivars.

1. Introduction

Coffee is one of the most important commodities in international trade, creating more than 90 billion dollars of income each year and over 120 million people depend on it for their livelihoods (FAO, 2003). Its production forms the main economic activity in many countries in Africa and Latin America. Among some 90 known species of the *Coffea* genus, *Coffea arabica* L.(Arabica coffee) and *Coffea canephora* L. Linden (Robusta coffee) account for 62% and 38%, respectively, of world coffee production (Willson, 1999).

Coffee cultivation is confined to the intertropical zone, due to its temperature and humidity requirements. However, although coffee production is strongly affected by drought, most of the world's coffee has been cropped in drought-prone regions improper for its growth and production (DaMatta and Ramalho, 2006). Furthermore, water

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https://doi.org/10.1016/j.sajb.2018.04.022
0254-6299/

limitation to coffee production is expected to increase in several major coffee-growing regions due to climate change (DaMatta and Ramalho, 2006). In this context, selection of cultivars that can survive severe drought spells and still give economic yields under drought conditions is of greatest importance. However, so far coffee breeding has been largely empirical as relatively little is known about the physiological drought resistance mechanism used by the species (DaMatta, 2004; DaMatta and Ramalho, 2006). Furthermore, studying the effect of ambient factors on plant growth is crucial in order to be able to project plant's response to the changing environment.

Several studies on the ecophysiology of Arabica coffee have been undertaken (Barros et al., 1995; Maestri et al., 1995; Barros et al., 1997; Carr, 2001; DaMatta, 2004; DaMatta and Ramalho, 2006), but most of them were dedicated to modern cultivars used in large coffee plantations, whereas older cultivars originating from the Arabian Peninsula were not included in these studies. It is important to remember that Arabica coffee has been cultivated in Saudi Arabia and Yemen for the last 4 to 5 centuries on the terraced mountain slopes and narrow valleys at altitudes ranging from 1200 to 1800 m a.s.l. (Tounekti et al., 2017). Trees of more than 100 years of age can still be found in traditional coffee gardens in Jazan, Asir and Al-Baha districts. These cultivars represent a highly valuable genetic pool for modern plant breeding because of their presumed water stress tolerance since they grow and provide good yields in an area often inflicted by severe droughts.

Plants subjected to drought regulate their tissue water status by using several morphological, anatomical and physiological adaptations in order to control water loss and enhance water uptake. Under water-deficit conditions, either osmotic adjustment or increased cell wall elasticity, or both, may improve turgor maintenance, allowing physiological activity to be maintained for extended periods of drought (Kramer and Boyer, 1995; Turner, 1997). Osmotic adjustment allows leaf water potential (Ψ_w) to decrease without an accompanying decrease in leaf turgor which would affect turgor-dependent processes such as tissue metabolic activity and cell enlargement (Morgan, 1984). Such adaptation has been shown to help maintain photosynthetic activity and stomatal conductance (g_s) at low leaf Ψ_w and to delay leaf senescence under water-limited conditions. Plants osmotically adjust by actively accumulating inorganic and organic solutes in their cells in response to decreasing Ψ_w. As a result, their osmotic potential (Ψ_π) becomes more negative thus acting as a driving force for water uptake into the roots and other organs (Taiz and Zeiger, 2002; Ennajeh et al., 2009). In the case of Arabica coffee, the key component of the differential adaptation among cultivars seems to be stomatal control of water loss and/or efficiency of extraction of soil water (DaMatta and Ramalho, 2006). However, traits that increase water-use efficiency (*i*WUE) may conflict with those related with growth and productivity (Jones, 1998). Therefore, the identification of cultivars combining satisfactory growth and production and high *i*WUE would be of great relevance for drought-prone areas.

Previous studies demonstrated that drought-tolerant coffee genotypes are better able to maintain high tissue Ψ_w than drought-sensitive ones under drought conditions (DaMatta, 2004). This is not necessarily associated with the extent of osmotic and elastic adjustments, however (DaMatta et al., 1993). Despite this information, many questions about the morphological and physiological bases of drought tolerance in coffee remain unanswered. A better understanding of the mechanisms of adaptation to drought may provide new insights into factors controlling plant productivity and survival in drought-prone regions. In this study, we investigated the effect of severe drought stress on four Arabica coffee cultivars widely grown in southwestern Saudi Arabia. As a shade-adapted plant, coffee has a very low saturating irradiance for leaf photosynthesis and exposition to high irradiance during drought stress can seriously impact on plant performance. Therefore, the photosynthetic performance and the role of thermal energy dissipation (NPQ) in photoprotection and photoinhibition were also examined under the typical atmospheric conditions of southwestern Saudi Arabia.

2. Materials and methods

2.1. Plant material and experimental design

Two-year-old coffee plants were used in this study. Seedlings of coffee cultivars “Dawairi”, “Kholani”, “Tessawi” and “Tufahi” (Tounekti et al., 2017) were transplanted into 8-L pots filled with a mixture of sandy soil (85% coarse- to fine-grained sand, 15% silt) and vermiculite (4:1; *v*/v). The plants were 70–80 cm high and had comparable leaf biomass. The pots were covered with aluminum foil to reduce evaporation from the soil surface and to minimize solar heating. Plants were kept in a lath house covered with a shade net which lets in 50% photosynthetic photon flux density (PPFD) at the Centre for Environmental Research and Studies (Jazan, Saudi Arabia). Temperature under the lath house was 25–32 °C and PPFD was about 1000 μmol m^{-2} s^{-1}. The trees were watered weekly, alternately, with tap water and a modified Hoagland nutrient solution. Drought stress was applied by withholding water from 15 plants of each cultivar for 28 days. At 5-day intervals during the drought treatment, water relations and gas exchange parameters were measured on three plants of each cultivar selected for similarity in predawn leaf water potential (Ψ_{pd}). Soil water potential (Ψ_{soil}) in the pots was measured with thermocouple psychrometers (PST-55-15-SF, connected to a HR-33T Dew Point Microvoltmeter, Wescor) placed in the pots at 10-cm depth.

2.2. Plant water relations

Plant water status was evaluated by measuring predawn (Ψ_{pd}) and midday (Ψ_{mid}) leaf water potentials and leaf water content (WC; WC = (FM − DM) / DM, where FM is fresh mass, and DM is dry mass of the leaf). Coffee leaves were weighed immediately upon harvest to determine FM. Later, these leaves were oven-dried at 80 °C for 48 h to determine DM. On each sampling date, Ψ measurements were taken on the terminal twigs of selected plants and monitored at midday (Ψ_{mid}) and the following predawn (Ψ_{pd}) on the uppermost fully expanded leaves. The measurements were made on three plants per cultivar. Because the short petioles of coffee leaves did not protrude beyond the rubber seal of the pressure bomb, we used whole small shoots bearing 2 leaves instead of single leaves in order to standardize the measurements. The terminal part of a branch was enclosed in an aluminum bag for at least 2 h before measurement to prevent leaf water loss and thus allow leaf and xylem water potentials to equilibrate. The measurements were done with a Scholander pressure chamber (PMS instrument Company, Albany, OR). Osmotic potential (Ψ_π) was measured on the same samples used to measure Ψ_{pd} and Ψ_{mid}. Plant tissue samples were stored at −80 °C for 12 h. Frozen tissues were then equilibrated at 20 °C for 15 min, then cell content was collected by vacuum extraction (Bollard, 1953) and Ψ_π was measured on 10-μl aliquots with a thermocouple psychrometer (Wescor C-52 sample chamber connected to a HR-33T Dew Point Microvoltmeter, Wescor, UT, USA). Turgor potential (Ψ_p) was calculated as: $\Psi_{pd} - \Psi_\pi$.

2.3. Gas exchange measurements

Net photosynthetic assimilation rate (A_{net}), transpiration rate (E) and stomatal conductance (g_s) were measured on fully expanded leaves in actively growing shoots. Three coffee trees per cultivar were selected for measurements and four measurements were made on each tree. The measurements were carried out in situ between 9 a.m. and 11 a.m. at PPFD of 1000 to 1200 μmol m^{-2} s^{-1} and air temperature ranging from 29 °C to 33 °C. These parameters were measured with a CIRAS-2 Portable Photosynthesis System (PP system, USA). Instantaneous water use efficiency (*i*WUE) was calculated by the following formula: *i*WUE = A_{net} / E.