



## Drought tolerance of sugarcane is improved by previous exposure to water deficit



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### ARTICLE INFO

#### Keywords:

Drought  
Photosynthesis  
Recovery  
ROS  
*Saccharum*

### ABSTRACT

Under field conditions, plants are exposed to cycles of dehydration and rehydration during their lifespan. In this study, we hypothesized that sugarcane plants previously exposed to cycles of water deficits will perform better than plants that have never faced water deficits when both are subjected to low water availability. Sugarcane plants were grown in a nutrient solution and exposed to one (1WD), two (2WD) or three (3WD) water deficit cycles. As the reference, plants were grown in a nutrient solution without adding polyethylene glycol. Under water deficits, leaf gas exchange was significantly reduced in 1WD and 2WD plants. However, 3WD plants showed similar CO<sub>2</sub> assimilation and lower stomatal conductance compared to the reference plants, with increases in intrinsic water-use efficiency. Abscisic acid concentrations were lower in 3WD plants than in 1WD plants. Our data revealed root H<sub>2</sub>O<sub>2</sub> concentration as an important chemical signal, with the highest root H<sub>2</sub>O<sub>2</sub> concentrations found in 3WD plants. These plants presented higher root dry matter and root:shoot ratios compared to the reference plants, as well as higher biomass production when water was available. Our data suggest that sugarcane plants were able to store information from previous stressful events, with plant performance improving under water deficits. In addition, our findings provide a new perspective for increasing drought tolerance in sugarcane plants under nursery conditions.

### 1. Introduction

Plants close stomata to avoid losing water through transpiration under water limiting conditions (Chaves, 1991), a physiological response that is related to either hydraulic or chemical signals (Davies and Zhang, 1991; Christmann et al., 2007). Plant acclimation to water deficits involves morphological changes that regulate water balance, with plants showing decreases in leaf area and shoot/root ratio (Pimentel, 2004). Cell osmoregulation by solutes such as sugars, glycine-betaine, and proline is another response to water deficits, allowing the maintenance of water content and protecting cellular structures (Verlues et al., 2006). Rapid stomatal response to changes in water availability is an important feature in sugarcane (*Saccharum* spp.), preventing excessive loss of leaf turgor and further decreases in leaf water content (Ribeiro et al., 2013). However, it is well-known that

stomatal closure causes low CO<sub>2</sub> availability for photosynthetic enzymes (Du et al., 1996; Chaves et al., 2009; Machado et al., 2013) and then an imbalance between photochemical and biochemical reactions in the leaves. Therefore, production of reactive oxygen species (ROS) is enhanced under drought conditions, and plants should be able to control such deleterious molecules through their antioxidant system. This protective system consists of several enzymatic and non-enzymatic compounds, which prevent oxidative damage by scavenging ROS inside cells (Mittler, 2002). For instance, increases in superoxide dismutase and ascorbate peroxidase activities were associated with rapid recovery of leaf gas exchange in sugarcane plants after rehydration (Sales et al., 2013).

These reported plant responses to a single drought event are quite common; however, plants are exposed to recurrent cycles of drought and rehydration in nature, and the consequences of such repetitive

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drought events are less understood (Walter et al., 2011). Plants can acclimate to varying water conditions through morphological and physiological changes, which favor the maintenance of plant growth or survival under stressful conditions (Chaves et al., 2002). Some changes during an acclimation period can allow faster responses and enhanced plant performances during the next stressful event. In fact, an experimental design with repeated cycles of droughts is a more realistic approach when considering plants in their natural environment, with improved plant performances under limiting conditions being found in several species when there was previous exposure to stressful conditions. While *Trifolium alexandrinum* was able to maintain high leaf water potential and relative water content after a second drought event (Iannucci et al., 2000), *Quercus ilex* exhibited reductions in leaf water potential and transpiration accompanied by osmotic adjustment after hardening (Villar-Salvador et al., 2004). Seedlings of *Moringa oleifera* that had previously been subjected to osmotic stress experienced increased drought tolerance, with plants showing higher water-use efficiency, higher photosynthesis and increases in activity of antioxidant enzymes under water deficit conditions (Rivas et al., 2013). However, most of these studies compared plants of differing ages under varying stress intensities and environmental conditions, which makes the study of stress memory difficult.

As a semi-perennial crop grown in rainfed areas, sugarcane may experience seasonal variations in water availability and unexpected dry periods. In addition, new areas cultivated with sugarcane are located in marginal regions, where water availability is an important issue (MAPA, 2009; Smith et al., 2009). In this study, we used a fine experimental design to understand how sugarcane performance under water limiting conditions is affected by previous exposure to water deficits. We hypothesized that sugarcane plants subjected to previous droughts will exhibit improved performance, which would be achieved through changes in sugarcane physiology, biochemistry and morphology, under water deficit.

## 2. Materials and methods

### 2.1. Plant material and growth conditions

Sugarcane (*Saccharum* spp.) variety IACSP94-2094 was used in this study due to its reasonable yield under low water availability and its drought tolerance (Machado et al., 2009; Ribeiro et al., 2013). Plants were propagated using mini-stalks (with one bud) obtained from adult plants, which were planted in trays containing a commercial substrate composed of sphagnum peat, expanded vermiculite, limestone dolomite, gypsum and NPK fertilizer (Carolina Soil of Brazil, Vera Cruz RS, Brazil). Thirty-five days after planting (DAP), the plants were moved to plastic boxes (12 L) containing modified Sarruge (1975) nutrient solution (15 mmol L<sup>-1</sup> N [7% as NH<sub>4</sub><sup>+</sup>]; 4.8 mmol L<sup>-1</sup> K; 5.0 mmol L<sup>-1</sup> Ca; 2.0 mmol L<sup>-1</sup> Mg; 1.0 mmol L<sup>-1</sup> P; 1.2 mmol L<sup>-1</sup> S; 28.0 μmol L<sup>-1</sup> B; 54.0 μmol L<sup>-1</sup> Fe; 5.5 μmol L<sup>-1</sup> Mn; 2.1 μmol L<sup>-1</sup> Zn; 1.1 μmol L<sup>-1</sup> Cu and 0.01 μmol L<sup>-1</sup> Mo). To avoid osmotic shock, we diluted the nutrient solution, and the initial ionic force was 25%. Then, the ionic force was increased to 50% in the second week and to 100% in the following week. The electrical conductivity of the nutrient solution was monitored with a conductivity probe (Tec-4MPp, Tecnopon, Piracicaba SP, Brazil) and maintained at approximately 1.5 mS cm<sup>-1</sup> by replacing the solution once a week. The pH of the nutrient solution was 5.4 ± 0.6 and it was monitored with a pHmeter (Tec-3MPp, Tecnopon, Piracicaba SP, Brazil). The osmotic potential of the nutrient solution was measured with a C-52 chamber (Wescor Inc., Logan UT, USA) attached to a microvoltmeter HR-33T (Wescor Inc., Logan UT, USA). The nutrient solution with a 100% ionic force presented an osmotic potential of -0.12 MPa. After being moved to the nutrient solution, plants were placed in a growth chamber (PGR14, Conviron, Winnipeg MB, Canada) under 30/20 °C (day/night), 80% air relative humidity, a 12-h photoperiod (7:00 to 19:00 h) and a photosynthetic photon flux density

(PPFD) of 800 μmol m<sup>-2</sup> s<sup>-1</sup>.

### 2.2. Water deficit treatments

Fifty-five day-old plants were subjected to water deficit cycles by adding polyethylene glycol (Carbowax™ PEG-8000, Dow Chemical Comp, Midland MI, USA) to the nutrient solution. To prevent osmotic shock, PEG-8000 was added to the nutrient solution to cause a gradual decrease in its osmotic potential as follows: -0.27 MPa the first day and -0.56 MPa the second day. These values were based on previous experiments with sugarcane (Silveira et al., 2016, 2017). Then, an osmotic potential of -0.56 MPa was maintained by replacing the solution with a new one with the same amount of PEG-8000.

Four groups of plants were formed according to the exposure to water deficit: plants grown under well-watered conditions, i.e. not exposed to water deficit (Reference); plants that faced water deficit once (1WD); plants that faced water deficit twice (2WD); and plants that faced water deficit three times (3WD). The water deficit cycles were similar in intensity and duration, and plants were the same age at the end of the experiment, as shown in Supplementary Material Fig. S1. Each water deficit cycle was five days in the nutrient solution with -0.56 MPa and other three days of recovery in nutrient solution with -0.12 MPa. During the experimental phase (Fig. S1), five plants of each treatment were collected at midday, leaves and roots were immediately frozen in liquid nitrogen, and then this material was stored at -80 °C for further analyses. This procedure was done on the fifth day of the water deficit cycle, i.e., the maximum water deficit.

### 2.3. Leaf gas exchange and photochemistry

Leaf gas exchange and photochemistry were measured daily with an infrared gas analyzer (LI-6400, LICOR, Lincoln NE, USA) coupled to a modulated fluorometer (6400-40 LCF, LICOR, Lincoln NE, USA) throughout the experimental period. The measurements were performed between 10:00 and 13:00 h under PPFD of 2000 μmol m<sup>-2</sup> s<sup>-1</sup> and an air CO<sub>2</sub> concentration of 380 μmol mol<sup>-1</sup>. We measured leaf CO<sub>2</sub> assimilation (*A*), stomatal conductance (*g<sub>s</sub>*), intercellular CO<sub>2</sub> concentration (*C<sub>i</sub>*) and transpiration (*E*), with the intrinsic water-use efficiency (*A/g<sub>s</sub>*) and the instantaneous carboxylation efficiency (*k = A/C<sub>i</sub>*) calculated according to Machado et al. (2009). The chlorophyll fluorescence was measured simultaneously with the leaf gas exchange and the apparent electron transport rate estimated as  $ETR = \phi_{PSII} \times PPFD \times 0.85 \times 0.4$ , in which  $\phi_{PSII}$  is the effective quantum efficiency of photosystem II (PSII), 0.85 is the light absorption and 0.4 is the fraction of light energy partitioned to PSII in C4 plants (Edwards and Baker, 1993; Baker, 2008). The *A* and *E* values were integrated during the experimental period to estimate the total CO<sub>2</sub> gain (*A<sub>i</sub>*), the total water vapor loss (*E<sub>i</sub>*), and the water-use efficiency (*A<sub>i</sub>/E<sub>i</sub>*) in each treatment. The integrated values were estimated assuming that the values measured between 10:00 and 13:00 h were constant during the 12 h of the photoperiod. In the experimental phase (Fig. S1) and after plant rehydration, the relative recoveries of *A* and *g<sub>s</sub>* were evaluated daily, considering the values of the reference plants as 100%.

### 2.4. Leaf water potential and relative water content

In the experimental phase, predawn leaf water potential ( $\psi$ ) was evaluated with a pressure chamber model 3005 (Soilmoisture Equipment Corp., Santa Barbara CA, USA). The leaf relative water content (RWC) was calculated using fresh (FW), turgid (TW) and dry (DW) weight of leaf discs according to Weatherley (1950):  $RWC = 100 \times [(FW - DW)/(TW - DW)]$ . Both variables were measured on the fifth day of the water deficit cycle and at the third day of recovery.

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