



Research article

Superoxide dismutase and ascorbate peroxidase improve the recovery of photosynthesis in sugarcane plants subjected to water deficit and low substrate temperature



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ABSTRACT

The physiological responses of C₄ species to simultaneous water deficit and low substrate temperature are poorly understood, as well as the recovery capacity. This study investigated whether the effect of these abiotic stressors is cultivar-dependent. The differential responses of drought-resistant (IACSP94-2094) and drought-sensitive (IACSP97-7065) sugarcane cultivars were characterized to assess the relationship between photosynthesis and antioxidant protection by APX and SOD isoforms under stress conditions. Our results show that drought alone or combined with low root temperature led to excessive energetic pressure at the PSII level. Heat dissipation was increased in both genotypes, but the high antioxidant capacity due to higher SOD and APX activities was genotype-dependent and it operated better in the drought-resistant genotype. High SOD and APX activities were associated with a rapid recovery of photosynthesis in IACSP94-2094 plants after drought and low substrate temperature alone or simultaneously.

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1. Introduction

Drought is the most important stress factor limiting crop production worldwide, especially in tropical and subtropical regions [1]. Low soil temperature is another restrictive condition that limits plant growth [2]. While studies involving drought as a single stress factor have been abundantly reported for several crops, little research has addressed the combination of drought and low

temperature [3]. To the best of our knowledge, studies on the combination of drought and low temperatures at the root medium associated with high air temperature, a common situation under field conditions, are scarce. These combined stressors can trigger a synergic effect on plant photosynthesis because cooling of the root may also contribute to water deficit in the leaves [4]. A low substrate temperature may decrease root hydraulic conductivity and cause stomatal closure and biochemical limitations to photosynthesis [5,6]. Under such conditions and high light intensity, drought stress might be aggravated and an energetic unbalance may be induced, that has consequences for photosynthesis and antioxidant metabolism [7].

Impairment in the photosynthetic electron consumption by the CO₂ assimilation reactions may generate an over-reduction of electron carriers at the thylakoid membrane [8]. One fraction of this electron excess must be dissipated around photosystem I (PSI) and stroma by water–water and ascorbate–glutathione cycles involving both chloroplast Cu/Zn- and Fe-SOD isoforms which catalyze the transference of electrons to superoxide radicals to produce hydrogen peroxide (H₂O₂). H₂O₂ is converted to H₂O by the thylakoid and stromal ascorbate-peroxidase (APX) isoenzymes [9].

Abbreviations: APX, ascorbate-peroxidase; C, cold treatment; CAT, catalase; CD, cold + drought treatment; D, drought treatment; dag, days after germination; E, transpiration; ETR, apparent electron transport rate; ETR/P_N, ratio between the apparent electron transport rate and leaf CO₂ assimilation; EXC, relative excessive photosynthetic photon flux density; F_v/F_m, maximum quantum yield of PSII; g_s, stomatal conductance; H₂O₂, hydrogen peroxide; NPQ, non-photochemical quenching; PET, photosynthetic electron transport; PPFD, photosynthetic photon flux density; P_N, leaf CO₂ assimilation; PSII, photosystem II; R, reference treatment; SOD, superoxide dismutase; SDM, shoot dry matter; RDM, root dry matter; ROS, reactive oxygen species; TBARS, thiobarbituric acid-reactive substances; TDM, total dry matter; Ψ_w, leaf water potential; ΔF/F_m, actual quantum yield of PSII.

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These cycles are essential to avoiding an over-reduction in the photosystems and accumulation of reactive oxygen species (ROS). Without them, photoinhibition and photooxidative stress can occur under stressful conditions [8]. As photorespiration is nearly absent in C_4 plants [10], the excessive light energy at the photosystem II (PSII) level must be drained to alternative electron sinks or dissipated as heat [8]. Although the chloroplast SOD and APX activities may consume the electron excess from the photosynthetic electron transport (PET) chain, ROS accumulation can arise and cause oxidative damage under acute water deficit, which can cause damage to the chloroplasts and trigger changes in signaling [11]. Light capture, photochemical and biochemical activities, and chloroplast SOD and APX activities must therefore operate in a balanced way to cope with drought and cold stress conditions [12].

The differential response of sugarcane genotypes to water stress has already been reported; a resistant genotype has a higher photosynthetic performance under drought and no impairment in plant growth [13,14]. Effective antioxidant protection may be involved in drought tolerance response in sugarcane [15]; however, no data concerning the effectiveness of antioxidant protection in maintaining plant growth are available for plants facing multiple stressors. In this study, we tested the hypothesis that low substrate temperature aggravates the effects of water deficit in sugarcane plants in a cultivar-dependent manner. The drought-resistant sugarcane cultivar IACSP94-2094 [14] and the drought-sensitive cultivar IACSP97-7065 [16] were exposed to water deficit, low substrate temperature and both factors simultaneously. Our data revealed that drought and the combination of cold + drought cause significant impairment in leaf gas exchange and photochemical activity, with the antioxidant response being cultivar-dependent. The drought-resistant genotype IACSP94-2094 presented a more effective APX–SOD antioxidant system, which lead to an improvement in the recovery of photosynthesis after stressful conditions. The mechanisms behind such improvement and the balance among CO_2 assimilation, PSII activity, and antioxidant protection are discussed.

2. Results

2.1. Leaf water potential

Drought reduced the leaf water potential (Ψ_w) after 11 days of withholding water only in IACSP94-2094. The cold treatment did not affect Ψ_w . Both genotypes presented a reduction in Ψ_w under the simultaneous occurrence of cold + drought, with the lowest values being found in IACSP94-2094 (Fig. 1A). Regardless of the presence of stressful conditions, both genotypes presented a Ψ_w similar to the reference plants after the recovery period (Fig. 1B).

2.2. Plant growth

Shoot (SDM), root (RDM) and total (TDM) dry matter production in IACSP94-2094 were not affected by drought, cold and their combination (Table 1). IACSP97-7065 showed reductions in SDM, RDM and TDM when subjected to water deficit either alone or combined with low temperature. As there was more dry matter present in the shoots, the measure of TDM correlated with changes in SDM. Compared to the reference condition, the combination of cold + drought reduced the TDM in IACSP97-7065 by ~37% (Table 1). In a comparison of the genotypes, IACSP94-2094 presented higher SDM and TDM than IACSP97-7065 under cold and cold + drought conditions (Table 1). While IACSP94-2094 had a higher RDM than IACSP97-7065 under drought and cold + drought conditions, the latter genotype presented a higher RDM under low temperature alone.

2.3. Leaf gas exchange and photochemistry

The stomatal conductance (g_s), CO_2 assimilation (P_N) and transpiration (E) in both sugarcane genotypes were similarly affected by water deficit, either alone or combined with cold (Fig. 2). Compared to the reference plants (R), g_s , P_N and E were reduced between 82% and 87% in IACSP94-2094 and between 77% and 95% in IACSP97-7065. Low temperature affected the leaf gas exchange only in IACSP94-2094 (Fig. 2A, C and E).

After four days under recovery conditions, both genotypes showed recovery of leaf gas exchange after being subjected to drought or cold. When plants faced the simultaneous occurrence of cold + drought, g_s and E in both genotypes were not fully recovered to the reference levels. IACSP94-2094 demonstrated a full recovery of P_N , even with low g_s and E . This was not observed in IACSP97-7065, which did not recover P_N after the combination of cold and drought (Fig. 2B, D and F). Such a differential response led to higher intrinsic water use efficiency (P_N/g_s) in IACSP94-2094 (~185 $\mu\text{mol mol}^{-1}$) compared to IACSP97-7065 (~135 $\mu\text{mol mol}^{-1}$) after the recovery period.

The cold + drought treatment reduced (–10%) the maximum quantum yield of PSII (F_v/F_M) in both genotypes. The drought condition alone caused a reduction in F_v/F_M only in IACSP97-7065 (Fig. 3A). In response to drought alone or drought combined with cold, the actual quantum yield of PSII ($\Delta F/F_M'$) and the apparent electron transport rate (ETR) were reduced similarly in both genotypes. When the effects of low temperature were evaluated, IACSP97-7065 presented a reduction in $\Delta F/F_M'$ and ETR, whereas IACSP94-2094 was insensitive to this condition (Fig. 3C and E). We believe that the F_v/F_M variation around 0.8 following the recovery period did not reveal any difference between treatments from a biological point of view; rather, it represents a full recovery in all treatments (Fig. 3B). While IACSP97-7065 did not recover $\Delta F/F_M'$ and ETR values following drought and cold + drought treatments, IACSP94-2094 presented a full recovery of these photochemical variables (Fig. 3D).

The relative excessive PPFD (EXC) increased to a similar degree in both IACSP94-2094 (+18%) and IACSP97-7065 (+25%) due to drought and cold + drought treatments. Only IACSP97-7065 presented an increase in EXC (+7%) under low temperature alone (Fig. 4A). After the recovery period, IACSP94-2094 presented a full recovery of EXC; in IACSP97-7065, this parameter remained high in plants that had undergone drought and cold + drought treatments (Fig. 4B). The increase in the non-photochemical quenching (NPQ) in IACSP94-2094 and IACSP97-7065 was similar under drought and cold + drought treatments (Fig. 4C). However, only IACSP97-7065 presented increases (+36%) in NPQ under low temperature alone (Fig. 4C). Even after the recovery period, NPQ remained high in plants that faced simultaneous cold and drought; this measurement was approximately 79% higher compared to reference plants (Fig. 4D). The ratio between the apparent electron transport rate and leaf CO_2 assimilation (ETR/ P_N) increased more than ten times in IACSP94-2094 under the cold + drought treatment, being higher in IACSP94-2094 as compared to IACSP97-7065 (Fig. 4E). The rehydration and warming led to a complete recovery of ETR/ P_N in all plants, with both genotypes presenting similar values around 7 $\mu\text{mol mol}^{-1}$ (Fig. 4F).

2.4. Oxidative damage and antioxidant responses

The thiobarbituric acid-reactive substances (TBARS) concentration, an index of lipid peroxidation, increased in IACSP94-2094 in response to drought and cold + drought treatment. IACSP97-7065 showed increases in TBARS in response to all stressful conditions (Fig. 5A). Under the cold + drought treatment, TBARS in IACSP97-7065 was 79% higher compared to reference plants and 29%

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