



Short communication

Photosynthetic acclimation of sweet sorghum under progressive water stress



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ABSTRACT

This study addressed photosynthetic acclimation of sweet sorghum under progressive soil drying at different growth stages: (i) three fully expanded leaves (D1); (ii) growing point differentiation (D2); (iii) booting (D3); (iv) half-blooming (D4). Soil water potential (SWP), photosynthetic traits and soluble sugars accumulation were determined. Under progressive drought stress, D1 and D2 photosynthesized until 20 days after stress imposition (SWP ≈ -3.5 MPa), while, D3 and D4 were photosynthetically inactive 12 days after irrigation suspension (SWP ≈ -1.5 MPa). Photoprotection mechanisms also changed with plant age: in mature plants, electron transport rate per cross section (ET_o/CS_m), and silent PSII reaction centers (RCs) drastically declined at SWP of -1.0 MPa, while remained unchanged in young plants until -1.5 MPa. As water stress increased (SWP < -1.8 MPa), the light energy absorption (ABS/CS_m), the trap energy flux (TR_o/CS_m) and ET_o/CS_m dramatically decreased in mature plants (-70% compared to control). Soluble sugars significantly correlated with thermal energy dissipation (DI_o/CS_m) and density of active reaction centers (RC_o/CS_m) at young stages. The acceptor side of Photosystem I (PSI) was affected by plant age resulting in a lower efficiency than donor side of PSII.

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1. Introduction

Drought stress effects were found to negatively affect the ability to convert or dissipate the absorbed radiation (Ott et al., 1999; Srivastava and Strasser, 1997) and to modify the size of light-harvesting antenna (Govindjee, 2002). Common mechanisms undertaken by plants to counteract water stress are the thermal dissipation by xanthophylls cycle (Xiong et al., 2012) and cycling electrons transport around photosystem I and II (Heber and Walker, 1992), the latter providing complementary and reliable information on drought-related mechanisms, e.g., PSI resulted in higher tolerance to heat than PSII in sweet sorghum (Yan et al., 2013). The reduction of the acceptor side of the PSII and re-reduction of plastocyanin and P700+ in the PSI (I–P phase) of the Kautsky curve (O–J and J–P phases, respectively) are other effective indicators of photochemical changes (Ceppi et al., 2012; Stirbet and Govindjee, 2011). Soluble sugars were also supposed to play an antagonistic role with reactive oxygen species (ROS) as protective solutes against the photodamage of PSI (Rajagopal and Carpentier, 2003) and PSII (Zegada-Lizarazu and Monti, 2012); Peshev and Van den

Ende (2013), for example, showed antioxidant activities of soluble sugars as true ROS scavengers.

Sweet sorghum has a peculiar ability to counteract drought stress; however, its photosynthetic acclimation mechanisms at different developmental stages are still greatly unknown. In the present study, we analyzed the ability of young and mature sorghum plants to down-regulate the linear electron transport under increasing levels of drought.

2. Materials and methods

Twenty 1-m³ rhizotrons were filled with sandy loam soil (pH of 7.9) and randomly arranged under a prefabricated structure as previously described by Zegada-Lizarazu and Monti (2012). During the experiment, air temperature and RH% were 25 ± 4 °C, and $60 \pm 13\%$, respectively. Water stress (interruption of irrigation until plant death) was imposed at 4 developmental stages: D1, 3rd-leaf collar completely developed; D2, 7th-leaf collar developed (growing point of differentiation); D3, booting (head extended into flag leaf sheath); and D4, half-bloom. Control plants were maintained at field water capacity (25% v/v; $\Psi = -36$ KPa). Leaf gas exchange and fluorescence were measured from 10.00 to 12.00 am on the adaxial face of the youngest fully expanded leaves (4 plants per treatment) every other day, starting from the suspension of irrigation until

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plant physiological death (net photosynthesis (P_n) approx. zero for three consecutive measurements). The JIP-test was calculated as given by Strasser et al. (2000) to evaluate indicative PSII electron transport events from fluorescence data. The time marks were 0.05, 2, 30 and 300 ms, i.e., O–J–I–P steps (F_o to F_m), respectively. Leaf soluble sugars (glucose, sucrose and fructose) were determined by high-performance liquid chromatography. Sugars were quantified prior calibration curve obtained by commercial standard solutions (D(+) glucose anhydrous, fructose pure and sucrose).

3. Results

Young plants (D1 and D2) did not change photosynthetic rates (P_n) until 6 days from stress imposition, thereafter they continued to photosynthesize for about 20 days until soil water potential of about -3.5 MPa (Fig. 1). On the other hand, mature plants (D3 and D4) decreased P_n only 3 days after irrigation suspension, and they were photosynthetically inactive after 12 days from stress imposition (SWP ≈ -1.5 MPa) (Fig. 1). PSII traits (PI_{ABS} and ϕP_o)

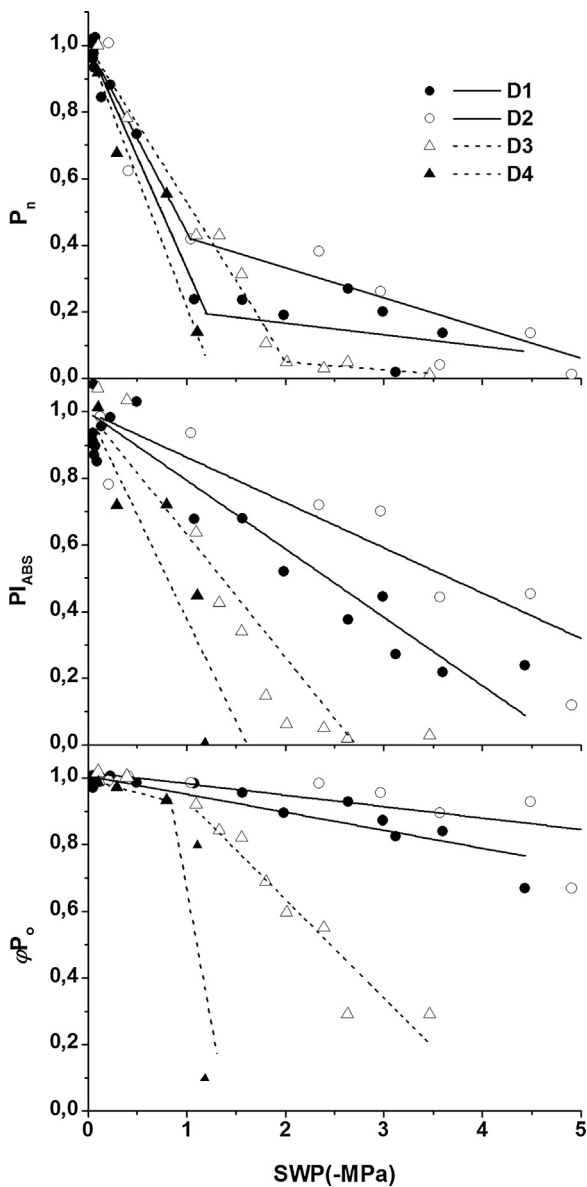


Fig. 1. Net photosynthesis (P_n), absolute performance index (PI_{ABS}), and maximum quantum yield (ϕP_o) expressed as ratio to control under progressive soil drying at different developmental stages (D1–D4, see methods).

were generally ineffective to predict P_n loss: in young plants, P_n decreased earlier than PI_{ABS} and ϕP_o , whereas in mature plants PI_{ABS} showed similar pathways to P_n (Fig. 1). In young plants, significant reductions of energy flux, electron transport per cross section (ET_o/CS_m ; dark gray arrows in Fig. 2) and number of silent RCs (closed circles, Fig. 2) were observed when SWP approximated -1.5 MPa, while thermal energy dissipation (DI_o/CS_m ; black arrows, Fig. 2) progressively increased. In mature plants (D3), ET_o/CS_m and RCs were considerably compromised already at SWP of -1 MPa (Fig. 2). Under severe water stress (SWP < -1.8 MPa, RWC $< 70\%$), light energy absorption (ABS/CS_m), trap energy flux (TR_o/CS_m) and linear electron transport (ET_o/CS_m) decreased up to 70% compared to control plants. In D4 plants, all the photosynthetic indicators significantly declined soon after the suspension of irrigation (Fig. 2). Young and mature plants showed a different normalized variable fluorescence ($\Delta V_{OJ}/\Delta V_{IP}$) pathway: $\Delta V_{OJ}/\Delta V_{IP}$ declined soon after irrigation suspension in D3 and D4, whereas D1 and D2 showed an initial rise followed by a decrease when SWP reached -2 MPa (Fig. 3). In D1 and D2 leaves, glucose and sucrose increased with drought by about 40% and 30%, respectively. Both sugars positively correlated with DI_o/CS_m ($r=0.66^{**}$ and $r=0.83^{**}$, respectively), while negatively correlated with RC_o/CS_m ($r=0.59^*$ and $r=0.77^{**}$; data not shown). Sugar concentration did not change in mature plants.

4. Discussion

Literature is lacking of information on quantitative estimations of the alterations of the photosynthetic activity at PSI and PSII levels in young and mature sorghum plants, especially when the drought increased progressively until reaching the lethal level. We showed that energy absorption, electron transport, RC closure, and energy dissipation, were all controlled more efficiently in young than mature plants. Young plants were able to keep high photosynthetic rates for about ten-more days than mature plants, and until a considerable lower SWP (≈ -3.5 MPa compared to ≈ -1.5 MPa of mature plants). Furthermore, in the young plants, the balance between photo-induced inactivation of PSII complex and the repair mechanism, such as degradation and re-synthesis of D1 protein, was not changed until a severe drought stress; young plants were able to enhance the PSII down-regulation through the activation of dissipative mechanisms of excess energy (DI_o/CS_m) and by closing RCs, where xanthophyll and lutein cycles are thought to be involved as a consequence of *trans*-thylacoid lumen acidification (Demmig-Adams and Adams, 1994). In contrast, such self-alleviation capacity against the deleterious oxidative stress was inhibited at reproductive stages, as evidenced by the steeply decrease in energy dissipation capacity; thus, the formation of ROS (Fig. 2). Therefore, a conclusion of this study is that, under prolonged and severe drought stress, young plants had the capacity to minimize or retard the inactivation of D1 proteins through a more efficient dissipation mechanism of excess energy, and most probably by ROS scavenging.

The differential response on the donor/acceptor side of PSII and PSI in young and mature plants was also supported by the of $\Delta V_{OJ}/\Delta V_{IP}$ ratio (Fig. 3) that revealed that the electron acceptor side of PSI at mature stages was reduced; thus, prolonged severe drought stress irretrievably damaged the PSI reaction centers (Huang et al., 2013). At young stages, however, the effects of such drought levels were not that clear (indicated by the changes in the I–P phase contribution to fluorescence transient), suggesting that PSI of young plants is less sensitive to drought than PSII. The greater amplitude of the I–P than O–J curves (Fig. 3) in young leaves indicates that the reduction of the Calvin–Benson cycle had more marked effect on sustaining an efficient electron transport toward PSI, possibly as a consequence of the inactivation of

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