



Assessing drought tolerance in field-grown sunflower hybrids by chlorophyll fluorescence kinetics

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Abstract

Drought is one of the most damaging abiotic stress factors commonly experienced by plants, resulting in a significant loss of crop yield worldwide. The aim of the study was to assess drought tolerance of sunflower (*Helianthus annuus*) hybrids and find out potentially underlying photobiological traits. Experiment was conducted in the agricultural field of Eastern Mediterranean Agricultural Research Institute in Adana. To evaluate the drought tolerance of twenty-six sunflower hybrids polyphasic chlorophyll fluorescence measurements were performed at the three growth stages named as vegetative, head formation and milky seed (stress 1, S1; stress 2, S2; stress 3, S3, respectively). The hybrids were classified from drought tolerant to drought sensitive based on their drought factor index (DFI) values calculated from photosynthetic performance index. 9444 A X 9947 R and 9444 A X 8129 R were determined as the most tolerant hybrids, whereas 2453 A X 8129 R and 7751 A X TT 135 R were determined as the most sensitive hybrids. Severe drought stress (S2) inhibited severely both the donor and the acceptor sides of photosystem II in sensitive hybrids. Photosynthetic structures of drought-tolerant hybrids were less damaged by drought stress, consequently these hybrids could maintain their photosynthetic performances (minor changes in φ_{Po} , ψ_o , δ_{Ro} , specific and/or phenomenological energy fluxes) approximately control levels under severe drought condition. As a result, results, 9444 A X 9947 R and 9444 A X 8129 R hybrids could be recommended to be used in the breeding programs and further studies as genetic material and to be grown in drought-prone areas.

Keywords *Helianthus annuus* · JIP test · OJIP fluorescence transient · Photochemical activity · Water stress

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1 Introduction

Sunflower (*Helianthus annuus*) is one of the most important oilseed crops in the world. Seeds of sunflower have 40–50% oil and, 17–20% protein, which have a potential to close the gap between production and consumption of edible oil and animal feed around the world (Hussain et al. 2018). It has been reported that approximately 47 million tons of sunflower seeds were produced in 2016 (FAOSTAT 2018). Sunflower, the second largest hybrid crop and the fifth largest oilseed crop, is grown globally and performs well in the most temperate climates (Seiler et al. 2017). Climate change and its impacts on life are among the most popular research topics. According to climate scenario, it is predicted that the crop production and yield will be limited and continue to decrease in the future (Hussain et al. 2018).

Abiotic environmental stresses affect almost every aspect of plant physiology and metabolism. Drought stress is among the most detrimental abiotic stress factors commonly experienced by plants, resulting in a significant loss of crop yield worldwide. Therefore, the identification/selection of tolerant plant species to water shortage conditions is a primary requisite. Searching out the physiological mechanisms underlying the response of plants to drought stress and discovering the traits that are giving drought tolerance provide new and powerful tools in breeding programs (Farooq et al. 2009; Osakabe et al. 2014; Fracasso et al. 2016).

Plants perceive the drought, one of the most detrimental environmental factors on plant growth and productivity, and generate some physiological, metabolic and molecular responses. These responses include decline in shoot elongation, decrease in photosynthetic activity, change in osmotic adjustment, carbohydrate status and antioxidant systems, accumulation of compatible solutes and, regulation in hormonal signaling (such as abscisic acid) and gene expression (Ekmekçi et al. 2005; Chaves et al. 2009; Pinheiro and Chaves 2011). The acclimation responses to drought stress are cultivar dependent and related to plant developmental stage (Flexas and Medrano 2002; Zivcak et al. 2013). Acclimation responses are also related with severity and intensity of drought and exposure time to the stress (Chaves et al. 2009; Pinheiro and Chaves 2011). Effects of drought on photosynthetic activity of plants can be observed directly or indirectly (Zivcak et al. 2013). Drought causes stomata closure (direct effect) leading to decline in carbon assimilation and/or net photosynthetic rate (Reddy et al. 2004; Sperdoui and Moustakas 2014). Non-stomatal effects (indirect effect) influence photosynthetic process by down-regulating electron transport, decreasing rubisco synthesis, inhibiting rubisco activity, reducing ATP synthesis, decreasing in Ribulose 1,5-bisphosphate (RuBP) regeneration and chlorophyll synthesis (Reddy et al. 2004; Zivcak et al. 2013). Plants respond

differently to the stress conditions depending on the adaptation mechanisms. The responses of plants to drought vary widely not only among species, but also among the genotypes of a given species. Genotypes grown under drought stress can be screened and classified by measuring photosynthetic performance. Chlorophyll *a* fluorescence measurement is one of the methods for measuring photosynthetic efficiencies in stressed or non-stressed plants (Oukarroum et al. 2007; Goltsev et al. 2012, 2016; Kalaji et al. 2016a, b) and has been used to investigate the effects of various abiotic stress factors, such as drought or excess amounts of water, salt stress, mineral nutrient deficiency and toxicity and temperature stress (low or high). (Naumann et al. 2008; Ceppi et al. 2012; Öz et al. 2014; Brestic et al. 2016; Kan et al. 2017; Askri et al. 2018; Çiçek et al. 2018; Kalaji et al. 2018a, b). This rapid and nondestructive technique measures photosynthetic electron transport rate and gives insight into light energy utilization (Oukarroum et al. 2018; Stirbet et al. 2018 and references therein). Illuminating dark-adapted photosynthetic samples exhibit polyphasic fluorescence transients (OJIP transient) which can be plotted on logarithmic scale. Besides, the shape of the OJIP fluorescence transient curves under different environmental conditions could change because of physiological situation of the sample. Strasser and Strasser (1995) introduced the JIP test to analyze the OJIP transients and it provides information related to structural and functional parameters that quantify the efficiency of photosynthetic apparatus (Yusuf et al. 2010). JIP test depends strongly on the assumption that F_O-F_M rise reflects the reduction in Q_A (Kalaji et al. 2014). The rise from F_O to F_M has several phases, like O–J–I–P, and these phases are related to the functionality of PSII acceptor and donor sides (Goltsev et al. 2016). The O–J represents the reduction in the acceptor side of PSII (and also gives information on the connectivity between the PSII photosynthetic units), the J–I relates to the partial reduction in the PQ pool and the I–P reflects the reduction in the acceptor side of PSI (Yusuf et al. 2010; Ripoll et al. 2016). Many parameters can be calculated from the data obtained by measurements: (1) efficiencies and quantum yields; i.e., maximum quantum yield of primary PSII photochemistry (F_v/F_M), efficiency with which a PSII-trapped electron is transferred from Q_A^- to PQ (ψ_o), quantum yield for electron transport (φ_{Eo}) and the quantum yield for the reduction in PSI end electron acceptors per photon absorbed (φ_{Ro}); (2) specific fluxes; i.e., the absorption/antenna size (ABS/RC), maximum trapping (TRo/RC), electrons transferred (ETo/RC) and dissipation (Dio/RC) per active PSII. (3) Phenomenological energy fluxes; i.e., the absorption (ABS/CSo), maximum trapping (TRo/CSo), electron fluxes transferred (ETo/CSo) and amount of active PSII RCs (RC/CSo) per cross section. (4) The most sensitive JIP parameters, performance indexes (PI_{ABS} and PI_{Total}) (Strasser et al. 2000, 2010; Hermans et al. 2003; Oukarroum et al. 2007; Zivcak et al. 2008; Boureima et al. 2012; Chen

et al. 2016; Banks 2018; Kalaji et al. 2018b). In addition to that some JIP parameters give information about the PSII donor side; i.e., the fraction of the active OEC centers and, inactivation and damage of OEC (V_K/V_J).

This study was a part of National Sunflower Hybrid Breeding Project carried out by Trakya Agriculture Research Institute (TARI, Republic of Turkey Ministry of Food, Agriculture and Livestock), which is the only local supplier of the Turkey's sunflower. Firstly, fifty main and restorer lines were tested under drought conditions and drought-tolerant lines were determined (Pekcan et al. 2015; Kaya et al. 2016). Later, test hybrids were developed from drought-tolerant parent lines in 2015. Finally, this study was carried out in 2016. The purpose of the study was to investigate the drought tolerance of sunflower hybrids by polyphasic fluorescence kinetics, screen the hybrids and find out potential underlying mechanisms in terms of photosynthetic process.

2 Materials and methods

Experimental setup – Experiment was established in the agricultural field of Eastern Mediterranean Agricultural Research Institute in Adana, Turkey. The soil properties of the experiment field and some climatic characteristics during growth period in Adana are given in Tables 1 and 2, respectively. Twenty-six sunflower hybrids (*Helianthus annuus*) were used in the study (Table 3). Seeds of hybrids were sown on March 24, 2016, and plants were harvested on August 23, 2016, in the experimental plot. There were four rows in a plot which had 7.5 m long and, the distances in each row and between rows were 30 × 70 cm. Five seeds were sown in each row. The experiment was conducted under a randomized complete

block design with three replicates. Seedlings were separated into groups: control and drought stress treatments. When control plants were irrigated regularly and soil moisture was maintained approximately 404.49 mm, stressed plants were not irrigated and were left to natural conditions. Soil moisture was determined by gravimetric method (Delibaş 1994; Robock et al. 2000). The values of soil moisture are given in Table 2.

Measurements – To ascertain the drought effects on the photochemical efficiency, chlorophyll a fluorescence measurements were performed. Polyphasic chlorophyll, a fluorescence measurement, was carried out on the fully developed leaves in each treatment by the Handy-PEA fluorimeter (Plant Efficiency Analyzer, Hansatech Instruments Ltd, Kings Lynn, UK) as described previously (Strasser and Strasser 1995; Strasser et al. 2010; Ouarrroum et al. 2015). Measurements were made at three different growth stages; R-3 [vegetative, stress 1 (S1)], R5-1 [head formation, stress 2 (S2)] and R-6 [milky seed, stress 3 (S3)]. After at least 30 min adaptation to darkness, leaves were illuminated with three light emitting diodes providing a pulse of saturating light intensity of 3000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Data, recorded between 10 μs and 1 s, were used to calculate some JIP test parameters. As mentioned before, JIP test is based on a proposed theory of energy fluxes in biomembranes (Strasser 1978; Strasser et al. 2000) and can be utilized to screen many samples quickly and to provide information about the structure, conformation and function of their photosynthetic apparatus (Strasser and Strasser 1995). The equations and calculations for specific energy fluxes (per reaction center, RC) and phenomenological energy fluxes (per excited cross section, CS), as well as for flux ratios or yields, are given in Table 4. In addition, the drought factor index (DFI) was calculated by utilizing photosynthetic performance index (PI_{ABS}) according to Ouarrroum et al. (2007) and Boureima et al. (2012) with minor modifications.

Table 1 Soil properties of the field which sunflower hybrids were grown

Soil depth (cm)	Saturation (%)	Total salinity (%)	pH	CaCO ₃ (%)	P ₂ O ₅ (kg ha ⁻¹)	K ₂ O (kg ha ⁻¹)	Organic matter (%)
0–20	55	0.04	7.78	14.20	0.56	9.01	1.28
20–40	58	0.05	7.75	13.43	0.63	8.92	1.10

Table 2 Some climatic data during growth period in Adana and the moisture of field soil which were left to natural conditions

Months	Max. average temp. (°C)	Min. average temp. (°C)	Average temp. (°C)	Average humidity (%)	Rainfall (mm)	Soil moisture (mm)
March	27.6	4.6	14.1	73.4	97.5	366.74
April	31.7	6.4	18.4	70.3	5.0	347.36
May	33.2	9.8	19.8	81.1	71.0	324.71
June	31.2	17.1	22.9	83.1	5.0	267.38
July	35.3	18.9	29.0	88.9	0	169.53
August	39.8	19.7	29.0	67.6	9.9	206.62

Table 3 Sunflower hybrids were used in the study

Genotype number	Genotypes	DFI	Order
25	9444 A × 9947 R	0.02	1
26	9444 A × 8129 R	-0.02	2
24	9444 A × TT 135 R	-0.49	3
23	9444 A × CL 217 R	-0.75	4
3	P 64 G 46	-0.76	5
20	9814 A × CL 217 R	-0.77	6
1	TUNCA	-0.83	7
18	7751 A × 9947 R	-1.04	8
11	9209 A × TT 135 R	-1.07	9
2	BOSFORA	-1.08	10
19	9814 A × TT 135 R	-1.32	11
10	2453 A × CL 217 R	-1.59	12
13	9209 A × 8129 R	-1.64	13
6	2453 A × TT 135 R	-1.74	14
16	7751 A × CL 217 R	-1.76	15
21	9814 A × 9947 R	-1.84	16
17	7751 A × 9979 R	-1.85	17
8	2453 A × 9979 R	-1.91	18
4	LG 5485	-1.94	19
12	9209 A × 9947 R	-2.02	20
15	7751 A × 8129 R	-2.03	21
5	CORAL	-2.03	22
22	9814 A × 9979 R	-2.11	23
7	2453 A × 9947 R	-2.20	24
9	2453 A × 8129 R	-2.22	25
14	7751 A × TT 135 R	-2.98	26

Bold were selected the most tolerant and sensitive hybrids according to their drought factor indexes

Hybrids were screened and ranked according to their Drought Factor Indexes (DFI, its equation and calculation was explained in material and methods section)

$$DFI = \log A + 4 \log B + 2 \log C$$

where A is the relative PI_{ABS} measured at the R-3 (vegetative stage-S1), B the relative PI_{ABS} measured at the R5-1 (head formation-S2) and C the relative PI_{ABS} measured at the R-6 (milky seed-S3). The relative PI_{ABS} for each treatment was calculated as PI_{ABS} drought stressed/ PI_{ABS} control. It has been seen that the minimum rainfalls were about in June–July, having looked at Table 2, and hybrids were exposed to severe drought stress during S2 period. Therefore, this is the reason why four factors for B are given in formulae. DFI is a reliable indicator used for evaluating and categorizing the drought tolerance of many plants, as well as sunflower (Boureima et al. 2012; Kaya et al. 2016).

Statistical analysis – The study was conducted in a completely randomized block design with three replicates.

Analysis of variance (ANOVA) of the data (five replicates of each measurement) was performed using SPSS 20.0 software (IBM SPSS Statistics), and the significance of differences between treatments and hybrids was compared with LSD's test at $P < 0.05$. The four rows plots were 7.5 m long with the 70 × 30 cm plant spacing.

3 Results and discussion

Photosynthesis is one of the primary processes for growth, development and biomass production of plants. The efficiency of this process depends on the environmental conditions, as well as plant's genetic code. Environmental stresses may influence all the steps from light energy absorption to electron transfer to final acceptors (Ripoll et al. 2016) and, drought is the major stress factor that cause destructive effects on photosynthetic performance of plants. The sunflower, which is the most important source of edible oil, is a moderately drought-tolerant crop (Hussain et al. 2018). However, most of the hybrids examined in the present study have been negatively affected by drought (Fig. 1). The state of the photosynthetic processes in sunflower hybrids subjected to different drought conditions was analyzed by means of measuring chlorophyll a fluorescence and applying JIP test. Performance index (PI_{ABS}) of hybrids, an indicator of plant vitality and usually used to evaluate physiological state of the sample, was adversely affected from stress treatments, except 9444 A × 9947 R (25) and 9444 A × 8129 R (26) hybrids (Fig. 1). Strauss et al. (2006) and Oukarroum et al. (2007) reported that the PI_{ABS} can be a sensitive parameter for assessing a large number of hybrids for stress tolerance. The hybrids were sorted from drought tolerant to drought sensitive based on their DFI values calculated from PI_{ABS} and, 9444 A × 9947 R and 9444 A × 8129 R hybrids exhibited better performance (highest DFI, 0.02 to -0.02) under drought conditions, whereas 2453 A × 8129 R and 7751 A × TT 135 R hybrids exhibited lower performance (lowest DFI, -2.22 to -2.98) (Table 3). Meanwhile, the relative deviation of PI_{ABS} values [$\Delta PI_{ABS} = ((PI_{ABS} \text{ control} - PI_{ABS} \text{ stress}) / PI_{ABS} \text{ control}) \times 100$] for each genotype was examined to reveal the hybrids' responses to severe water deficit conditions (stress 2 period, Fig. 2). Two groups of hybrids can be seen in Fig. 2: (1) $\Delta PI_{ABS} < 0$, including 9444 A × 9947 R and 9444 A × 8129 R (-5.35 to -10.02, tolerant hybrids), and (2) $\Delta PI_{ABS} > 0$, 2453 A × 8129 R and 7751 A × TT 135 R (67.32–75.12, sensitive hybrids). According to Boureima et al. (2012), if relative deviation of PI_{ABS} of sample is lower than zero ($\Delta PI_{ABS} < 0$), hybrids perform better than control under stress condition, and if ΔPI_{ABS} of sample is higher than zero ($\Delta PI_{ABS} > 0$), hybrids perform worse under stress condition.

Table 4 Definitions, explanations and calculations of the JIP test parameters used in the present study (Tsimilli-Michael and Strasser 2008; Goltsev et al. 2016; Ripoll et al. 2016; Stirbet et al. 2018)

Technical fluorescence parameters	Definition
F_o	Initial fluorescence intensity, when all PSII RCs are open
F_{300}	Fluorescence intensity at 300 μ s
F_J	Fluorescence intensity at the J-step (at 2 ms)
F_I	Fluorescence intensity at the I-step (at 30 ms)
F_M	Maximal fluorescence intensity, when all PSII RCs are closed
V_J	$(F_{2ms} - F_o)/(F_M - F_o)$, relative variable fluorescence at the J-step (2 ms)
V_I	$(F_{30ms} - F_o)/(F_M - F_o)$, relative variable fluorescence at the I-step (30 ms)
V_K	$(F_{300\mu s} - F_o)/(F_M - F_o)$, relative variable fluorescence at the K-step (300 μ s)
Mo or $(dV/dt)_o$	$4(F_{300\mu s} - F_o)/(F_M - F_o)$, initial slope (in ms^{-1}) of the O–J fluorescence rise
Sm	$Area/(F_M - F_o)$, normalized area between the OJIP curve and the line $F = F_M$, which is a proxy of the number of electron carriers per electron transport chain
OEC	$[1 - (V_K/V_J)]_{treated}/[1 - (V_K/V_J)]_{control}$, fraction of oxygen-evolving complexes (OEC)
V_K/V_J	Limitation/inactivation and possibly damage of the oxygen-evolving complex
<i>Efficiencies and quantum yields</i>	
$TRo/ABS = \varphi_{P_0}$	F_V/F_M , maximum quantum yield of primary PSII photochemistry
$ETo/ABS = \varphi_{E_0}$	$\varphi_{P_0} \times \Psi_o$, quantum yield for electron transport from Q_A^- to PQ
$ETo/TRo = \Psi_o$	$1 - V_J$, efficiency with which a PSII-trapped electron is transferred from Q_A^- to PQ
$\varphi_{D_0} = 1 - \varphi_{P_0}$	F_o/F_M , the quantum efficiency of energy dissipation
$RE/ETo = \delta_{R_0}$	$(1 - V_I)/(1 - V_J)$, the efficiency with which an electron from PQH_2 is transferred to final PSI acceptors
$REo/ABS = \varphi_{R_0}$	$\varphi_{P_0} \times \Psi_o \times \delta_{R_0}$, the quantum yield of electron transport from Q_A^- to the PSI end electron acceptors
$RC/ABS = \gamma_{RC}/(1 - \gamma_{RC})$	Q_A reducing RCs per PSII antenna chlorophyll (reciprocal of ABS/RC)
<i>Specific fluxes (per active PSII)</i>	
ABS/RC	$(Mo/V_J)/\varphi_{P_0}$, apparent antenna size of an active PSII
TRo/RC	Mo/V_J , maximum trapped exciton flux per active PSII
ETo/RC	$(Mo/V_J) \times \Psi_o$, the flux of electrons transferred from Q_A^- to PQ per active PSII
DIo/RC	$ABS/RC - TRo/RC$, the flux of energy dissipated in processes other than trapping per active PSII
<i>Phenomenological energy fluxes (per CS)</i>	
$ABS/CS \approx F_o$	Absorbed photon flux per CS
TRo/CS	$(TRo/ABS) \times (ABS/CS)$, maximum trapped exciton flux per CS
ETo/CS	$(ETo/ABS) \times (ABS/CS)$, the flux of electrons from Q_A^- to PQ per CS
RC/CS	$\varphi_{P_0} \times (V_J/Mo) \times F_o$, amount of active PSII RCs per CS
<i>Performance indexes</i>	
PI_{ABS}	$(RC/ABS) \times [\varphi_{P_0}/(1 - \varphi_{P_0})] \times [\Psi_o/(1 - \Psi_o)]$
SFI	$(RC/ABS) \times \varphi_{P_0} \times \Psi_o$, an indicator of PSII 'structure and functioning'
PI_{Total}	$(RC/ABS) \times (\varphi_{P_0}/(1 - \varphi_{P_0})) \times (\Psi_o/(1 - \Psi_o)) \times (\delta_{R_0}/(1 - \delta_{R_0}))$, Performance index (potential) for energy conservation from photons absorbed by PSII to the reduction in PSI end acceptors

To clarify and evaluate the drought stress effect on sunflower plant, some JIP test parameters of four hybrids [with two lowest DFI values, 2453 A \times 8129 R and 7751 A \times TT 135 R (sensitive) and two highest DFI values, 9444 A \times 9947 R and 9444 A \times 8129 R (tolerant)] suffered from severe drought condition were analyzed. The maximum quantum yield of PSII (F_V/F_M , φ_{P_0}), one of the PI_{Total} components, significantly decreased in 2453 A \times 8129 R and 7751 A \times TT 135 R under severe drought condition (Fig. 3). While the efficiency with which a PSII-trapped electron is transferred from Q_A^- to PQ (ψ_o), another PI_{Total} component, similarly to F_V/F_M , decreased same hybrids; Q_A reducing RCs per

PSII antenna chlorophyll (RC/ABS), other component of the parameter, significantly increased under severe drought stress (Fig. 3). The efficiency with which an electron from PQH_2 is transferred to final PSI acceptors, (δ_{R_0}) final component of PI_{Total} , declined markedly in sensitive hybrids and increased significantly in 9444 A \times 8129 R (Fig. 3). As a result, PI_{ABS} and PI_{Total} , which provide valuable information about plant performance and vitality, decreased significantly in drought-stressed leaves in sensitive sunflower hybrids (2453 A \times 8129 R and 7751 A \times TT 135 R), when those parameters in stressed conditions exhibited closer values to control levels in tolerant hybrids (9444 A \times 9947

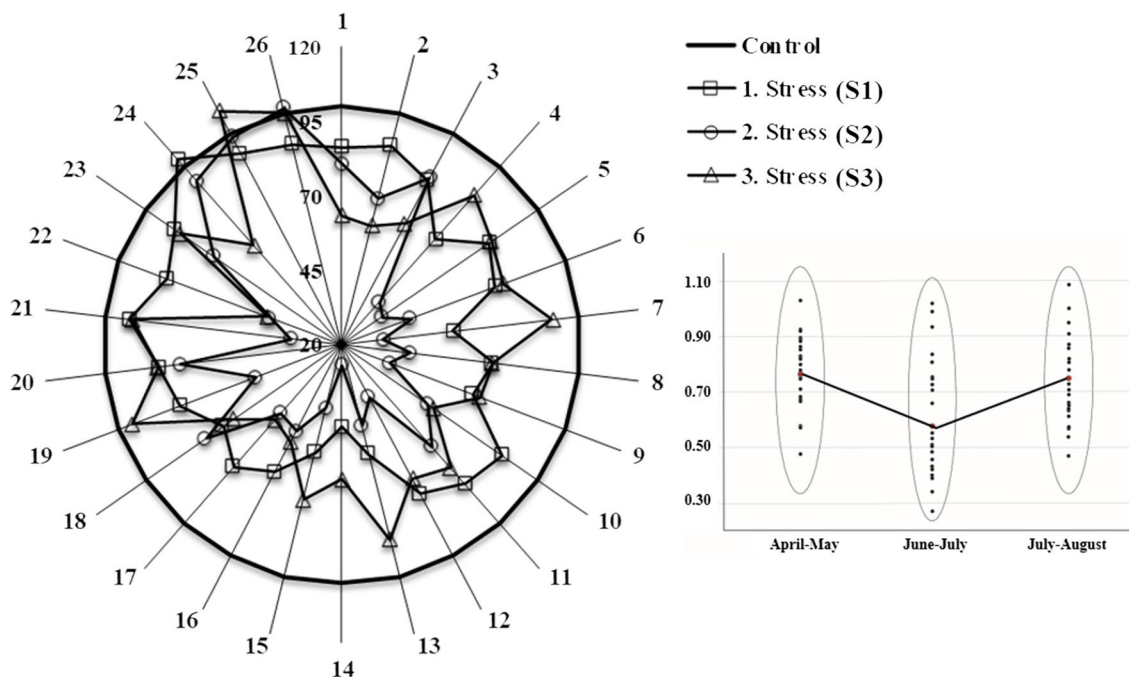


Fig. 1 Changes in the photosynthetic performance indexes (PI_{ABS}) of 26 sunflower hybrids exposed to drought stress. The inset: normalized values of PI_{ABS} and their mean (line) of hybrids at the three measurement times (i.e., drought stress periods). June–July received the lowest precipitation, and therefore, this period has been accepted as severe drought stress

R and 9444 A \times 8129 R). These results are consistent with previous studies' results, in which better performer plants under stress conditions have higher indexes values than others (Oukarroum et al. 2007, 2009; Boureima et al. 2012; Çiçek et al. 2015; Umar and Siddiqui 2018). Consequently, tolerant hybrids succeeded to sustain photosynthetic electron transport under drought compared to sensitive hybrids (Fig. 3). These results are verified with DFI results (Table 3).

Specific fluxes and parameters related to PSII donor side are presented in Fig. 4. Specific energy flux per RC for absorption (ABS/RC) exhibited an increase in sensitive sunflower hybrids, whereas tolerant hybrids maintained the absorption value at the control levels. According to Strasser et al. (1999), the change in the ABS/RC might indicate a change in the number of LHC complexes per PSII reaction center or could also be the result of changes in the relative amount of inactive RCs. The significant increase in sensitive hybrids might point out a decrease in the effective antenna size and could result from PSII inactivation. The flux of excitation energy trapped per RC (TRo/RC), the electron flux transferred per RC (ETo/RC) and the energy dissipation per RC (Dio/RC) also increased significantly in sensitive hybrids under severe stress condition (Fig. 4). Increase in energy dissipation implies the loss of absorbed excitation energy as heat and fluorescence and energy transfer to other systems rather than electron transport/photochemistry.

Moreover, an increase in the Dio/RC might also mean the loss of connectivity between PSII units.

Amplitude of relative variable fluorescence of I–P, ΔV_{IP} (one of semiquantitative indicator for changes in the PSI content) and capacity of the intersystem pool to accept electron until full reduction in Q_A . Sm (the number of electron carriers), increased significantly in 9444 A \times 8129 R, while they decreased in other three hybrids (Fig. 4). On the contrary, the quantum efficiency of energy dissipation (ϕ_{Do}) significantly increased in 2453 A \times 8129 R and 7751 A \times TT 135 R hybrids under severe drought conditions (Fig. 4). Previous studies have demonstrated that the I–P amplitude of the OJIP transient is sensitive to stress treatments including drought (Oukarroum et al. 2009; Ceppi et al. 2012; Çiçek et al. 2015, 2018; Jedmowski et al. 2015). Schansker et al. (2005) observed that the I–P phase is a reflection of electron transfer through PSI in the presence of an inactive PSI acceptor side. For drought stress, it was shown that a loss of I–P amplitude correlates with the maximum light inducible 820 nm change (Oukarroum et al. 2009; Ceppi et al. 2012). However, since we did not do 820 measurements here, we cannot not exclude that the decreased I–P amplitude is not only due to a loss of PSI but could also be due to loss of ferredoxin or maybe even more likely, a combination of both. Some conditions have been described in which no correlation between I–P amplitude and PSI content was observed. Zivcak et al. (2015) gave ninety 300 ms

Fig. 2 Relative deviation of PI_{ABS} in percent of control of each sunflower hybrids exposed to severe drought (S2) condition [ΔPI_{ABS} was calculated according to Boureima et al. (2012)]

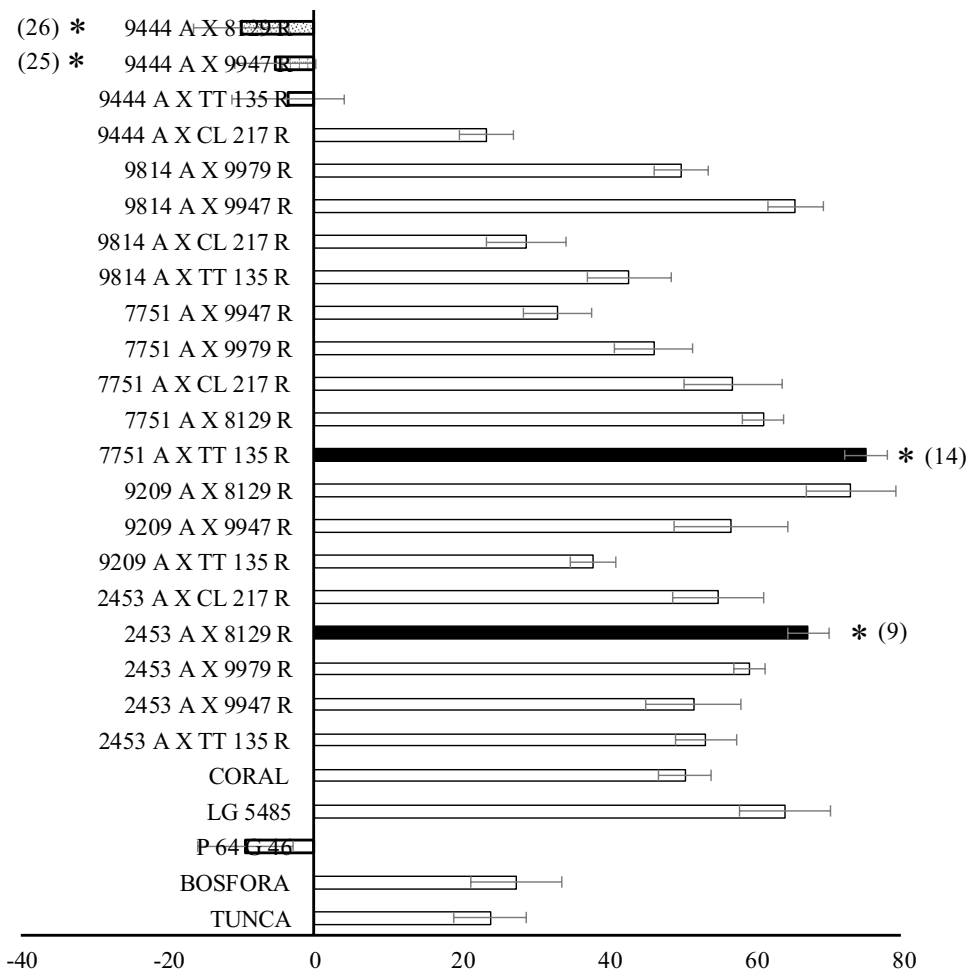
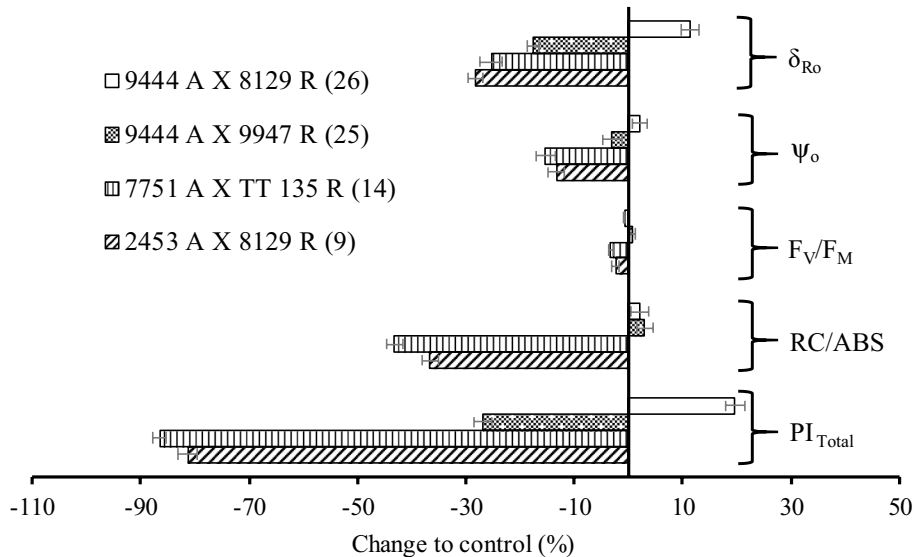


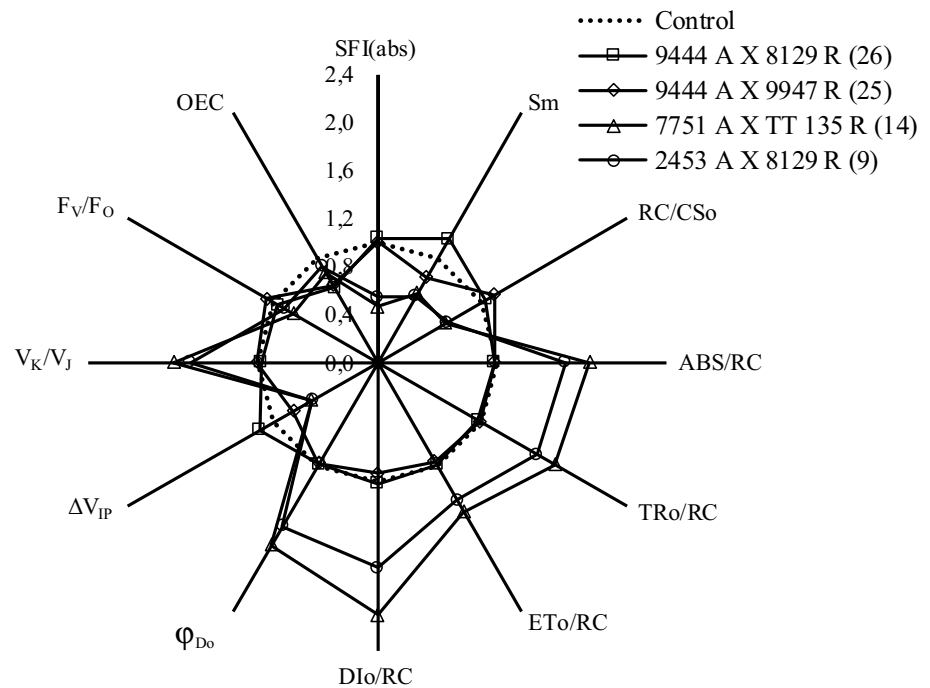
Fig. 3 Effect of severe drought stress (S2) on the total performance index (PI_{Total}) and its partial components of two drought sensitive (7751 A X TT 135 R and 2453 A X 8129 R) and two drought-tolerant sunflower hybrids (9444 A X 9947 R and 9444 A X 8129 R) according to DFI value



pulses of $15,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ spaced 10 s apart which caused damage to PSI (and as well to PSII) and did not observe an effect on VIP. In the case of severe salt stress

the relationship between the I-P and PSI content is also lost (Çiçek et al. 2018). Higher energy dissipation and lower I-P amplitude in 2453 A X 8129 R and 7751 A X TT 135 R

Fig. 4 Some selected JIP test parameters quantifying the behavior of PSII in four sunflower hybrids exposed to severe drought (S2) condition



hybrids suggest that these hybrids did not adequately protect their photosynthetic apparatus from drought and did not sustain their photosynthetic capability, whereas other two hybrids had better performance under the same condition.

Drought stress inhibited the donor side of PSII (OEC, V_K/V_J , F_V/F_O), especially in sensitive hybrids (Fig. 4). V_K/V_J , associated with possible damage and inactivation of the oxygen-evolving complex, significantly increased in 2453 A × 8129 R and 7751 A × TT 135 R under drought condition. OEC, fraction of oxygen-evolving complexes, also decreased in same hybrids (Fig. 4). Results of V_K/V_J represent inactivation in OEC. Drought-tolerant 9444 A × 9947 R and 9444 A × 8129 R hybrids achieved to maintain the value near the control levels. Brestic et al. (2012) determined a significant increase in V_K/V_J in wheat under higher temperatures. Some other studies can be found in the literature showing increased values of V_K/V_J under various stresses. Lu and Zhang (1999) and Oukarroum et al. (2009) demonstrated that F_K/F_J , associated parameter with V_K/V_J , was increased by high temperature and drought. It has been supposed that an increase in F_K/F_J (in other words, the decrease in the ratio of J-step/K-step) is a quantitative indicator which reflects the inactivation of PSII donor side (Oukarroum et al. 2009). A similar result was obtained from the study with UV-B and Scot pine, which UV-B treatment caused the increase in V_K/V_J of Scot pine (Çiçek N, Kalaji HM and Ekmekçi Y, under review). In contrast to V_K/V_J , F_V/F_O , characterized the changes in water-splitting complex in PSII, significantly decreased in sensitive sunflower hybrids. It has been considered that the water-splitting complex is a very sensitive part

of the photosynthetic electron transport chain (Pereira et al. 2000; Goltsev et al. 2016). The last parameter of Fig. 4 is structure–function indexes; SFI(abs), structural and functional information about the strength of the influence of internal factors promoting the reactions in PSII, remained at their control levels in tolerant hybrids, while it significantly decreased in sensitive hybrids under severe drought stress (stress 2). Oukarroum et al. (2015) stated that changes in electron transport reactions (both donor and acceptor sides of photosystems) induce an increase in ROS formation.

Figure 5 demonstrates the energy pipeline leaf model of phenomenological fluxes (per cross section, CS) of drought sensitive and tolerant sunflower hybrids. Each relative value is expressed by the appropriate adjustment of the width of the corresponding arrow. Decrease in PSII efficiencies has been seen in sensitive hybrids under drought condition. They had somewhat high number of energy dissipation (DIo/CSO) and low electron transport (ETo/CSO), as well as high inactive reaction centers (the black points) compared to the corresponding controls. However, phenomenological energy fluxes per excited cross sections of the leaves of tolerant hybrids achieved to maintain the control levels (Fig. 5). Kalaji et al. (2011) suggested that the accumulation of inactive reaction centers might be associated with the increase in heat dissipation of excitation energy under salt stress. In the present study, drought stress also caused the inactivation of reaction centers in sensitive sunflower hybrids and thus the absorbed energy was dissipated as heat (higher values of ϕ_{Do} , DIo/RC, DIo/CSO). However, tolerant hybrids were

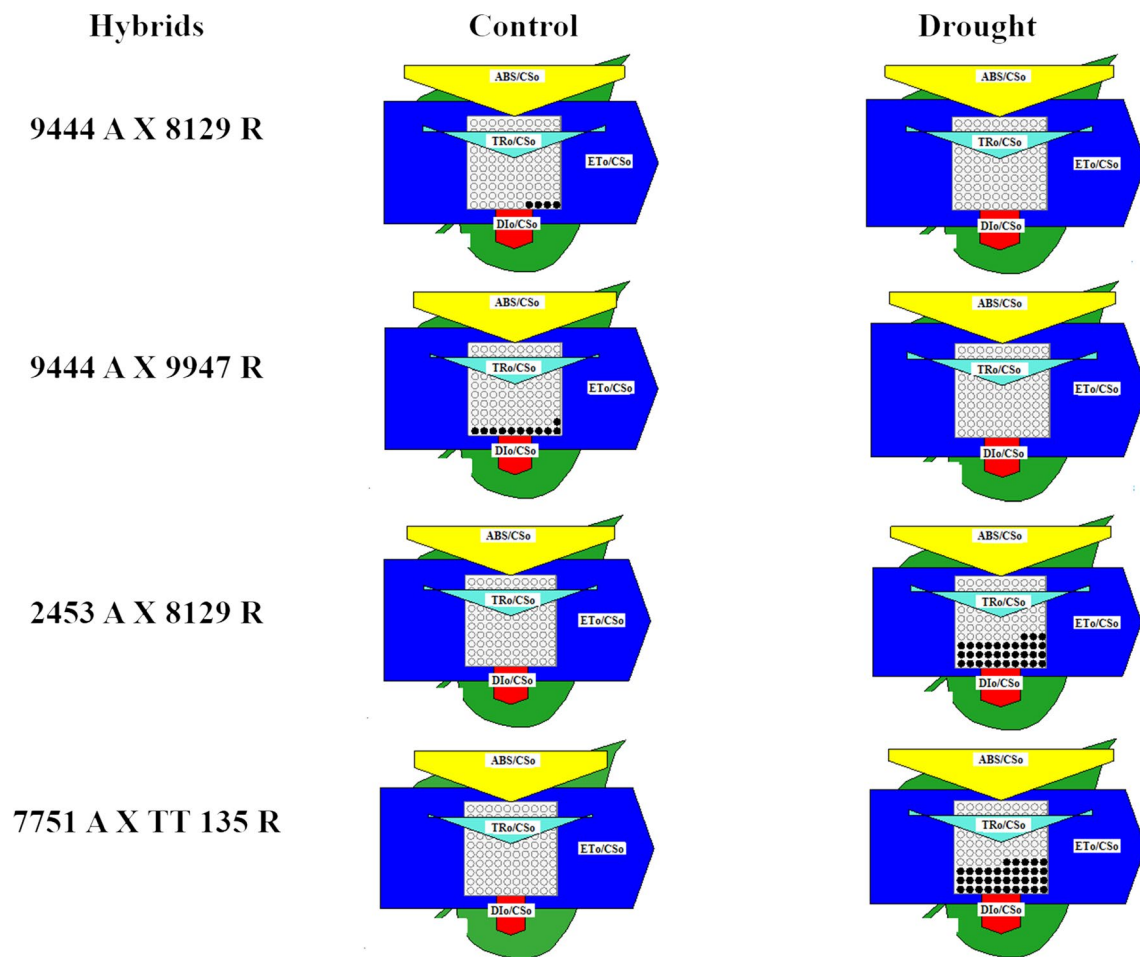


Fig. 5 Phenomenological leaf models based on calculations of parameters per excited leaf cross section (CSo) for control and severe drought (S2)-stressed sunflower hybrid leaves. Each relative value is drawn by the width of corresponding arrow, representing the value of a parameter. The value of absorbance (ABS/CSo), trapping flux (TR/CSo), electron transport (ET/CSo) or heat dissipation of excess light (DI/CSo), all expressed per leaf cross section. The black points represent the fraction of inactive reaction centers

able to actively direct the absorbed energy to the electron transport, therefore exhibited more efficient photosynthetic activity.

In nature, drought and high temperature are concurrent environmental factors which affect negatively plant metabolism. Psidova et al. (2018) have determined a tolerance to drought and high temperature in *Fagus sylvatica* and suggested that this tolerance was related to employ the alternative electron sinks to decrease the excitation pressure on photosystems as a photoprotective mechanism. In addition to that, Sperdouli and Moustakas (2012) have suggested that *Arabidopsis* young leaves achieved a drought tolerance by dissipating the excess excitation energy, consequently these leaves could protect their photosynthetic apparatus from possible photodamage. The sensitive genotypes exhibited lower photosynthetic capacity (low PI_{Total} , PI_{ABS} , ψ_o , δ_{Ro} and ΔV_{IP} and high V_K/V_J , dissipations), the tolerant genotypes showed better performance under drought condition in this study.

Tolerant sunflower genotypes might drive this type alternative pathway to maintain the photosynthetic apparatus and functionality.

Abiotic stress factors including drought induce the changes in structural and functional properties of the photosynthetic apparatus, affecting the electron transport and excitation energy utilization. In this study, the effects of drought stress on photosynthetic efficiency of sunflower hybrids were assessed using polyphasic chlorophyll a fluorescence and JIP test. Fluorescence results have indicated that drought caused a decrease in the number of electron carriers (lower Sm), dissociation of the OEC from PSII, and lower phenomenological energy fluxes in sensitive hybrids. However, tolerant hybrids exhibited minor changes in their photosynthetic structure, electron transport efficiency and energy utilization. Consequently, the drought-tolerant hybrids (9444 A × 9947 R and 9444 A × 8129 R) which were identified in this study could be utilized in breeding

programs/practices and can further our understanding of genetic mechanisms under this drought-tolerant phenotype. Chlorophyll a fluorescence measurement allows the assessment of photosynthetic efficiency which is one of the main metabolic processes of plant life. We believe this technique can be utilized in breeding programs along with molecular techniques, a large number of hybrids in the field condition.

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Authors' contributions VP and YK designed the study and ANÇ and VŞ carried out the field experiment. ÖA, ŞÇE and ASBN performed the chlorophyll fluorescence measurements. NÇ and YE analyzed the data and wrote the manuscript. We attest to the fact that all authors listed on the title page have contributed significantly to the work, have read the manuscript, attest to the validity and legitimacy of the data and its interpretation and agree to its submission to Brazilian Journal of Botany.

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