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Photosynthetic and antioxidative upregulation in drought-stressed sesame (*Sesamum indicum* L.) subjected to foliar-applied salicylic acid

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Abstract

Insufficient attention has been paid to the physiological responses of sesame to drought and it is unclear if exogenous plant growth regulators are beneficial to drought-stressed sesame. Thus, a field study was conducted on seven *Sesamum indicum* genotypes affected by two levels of irrigation (60 and 80% depletions in available soil water) and by foliar-applied salicylic acid (SA; 0 and 0.6 mM). Water deficit led to depressions in net photosynthetic rate, stomatal conductance, leaf area index, chlorophyll *a*, *b*, and total chlorophyll contents, maximum quantum efficiency of PSII, and plant dry matter and seed yield, despite increases in carotenoid concentration, superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase activities. SA was found beneficial in ameliorating the depressions in all of the above characteristics, indicating that it could be applied for lessening the harmful effects of the drought stress.

Additional key words: antioxidant enzyme; gas exchange; oilseed; plant growth regulation.

Introduction

Difficulty in supplying the roots with sufficient water and a staggered transpiration rate are experienced frequently in the arid and semiarid environments during ontogeny of crop plants, resulting in drought stress (Ghobadi *et al.* 2013). Water scarcity and the subsequent drought is a major issue of the future climate change. Adoption and development of survival strategies in order to increase tolerance in the rapidly changing habitats seems to be crucial. Drought is a prominent environmental constraint that influences a wide range of physiological responses at molecular, cellular, and whole plant levels (Zhang *et al.* 2015). In addition to the direct effects of drought, secondary damages (*i.e.* oxidative stress) are imposed to the drought-stricken plants. Structural and functional disorders in chloroplasts are commonly observed during extended drought events (Leufen *et al.* 2016). All components of the photosynthetic apparatus, including leaf area (Hussain *et al.* 2009), pigments (Miao *et al.* 2015), stomatal opening and conductance (Ghobadi *et al.* 2013), thylakoid-bound electron transfer complexes, quantum efficiency of PSII (F_v/F_m) (dos Santos *et al.* 2013), and stromal-based enzymatic functions are reported to be negatively affected by drought. Evolutionary adaptations have brought about defensive mechanisms that help plants to overcome injuries of the photosynthetic apparatus. To address the water scarcity and improve water productivity, adopting drought-resistant species and genotypes is one of the pioneering strategies at least for maintaining an economically feasible agricultural productivity in the marginal environments. Utilization of drought-tolerant species and genotypes would contribute to the food security in the arid and semiarid parts of the world, which are characterized by serious drought episodes.

Some of the less-studied ancient crop species are gaining prominence nowadays, as they constitute the genetic source for combating harsh environmental circumstances (Mirjahanmardi and Ehsanzadeh 2016). *Sesamum indicum* is an orphan, though ancient, warm-season oilseed species. The seeds possess a great economic potential for pharmaceutical and cosmetic industry, yet greater economic interest lies in its oil content, which is used in the production of high quality edible oil. *Sesamum indicum*

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Abbreviations: APX – ascorbate peroxidase; ASW – available soil water; CAT – catalase; Car – carotenoids; Chl – chlorophyll; C_i – substomatal CO_2 concentration; F_0 – minimum fluorescence; F_m – maximum fluorescence; F_v/F_m – maximal quantum efficiency of PSII; g_s – stomatal conductance to the CO_2; LAI – leaf area index; LSD – least significant difference; MSI – membrane stability index; NBT – nitroblue tetrazolium; OY – oil yield; PGRs – plant growth regulators; P_N – net photosynthetic rate; POX – peroxidase; ROS – reactive oxygen species; SA – salicylic acid; SDM – plant aboveground dry mass; SOD – superoxide dismutase; SY – seed yield.
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is said to be partially resistant to some environmental constraints (Bazrafshan and Ehsanzadeh 2014). But its exposure to environmental stresses (*e.g.* drought) may result in alterations in plant dry mass and superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) activities (Fazeli *et al.* 2007). As such, understanding the physiological responses to drought stress is fundamental for use of this ancient crop instead of, or along with, the rather well-studied oilseed species.

Plant growth regulators could be employed to influence agriculturally important aspects of plant growth and development. Contrasting responses, *i.e.* from the field-grown plant, to the exogenous application of plant growth regulators could be observed, as plant responsiveness to uptake and translocation of such a substance could vary greatly and is not independent from the environmental conditions (Oswalt *et al.* 2014). SA is a naturally occurring plant growth regulator in higher plants, known to take part in signal transducing functions in response to biotic and abiotic stresses (Horvath *et al.* 2007). Its exogenous application may elicit an array of growth and physiological responses to drought stress. The SA-initiated alleviation of damaging effects of drought stress is brought about, mainly, by changing endogenous phytohormones. Applying SA has shown promoting effects on photosynthetic characteristics, *e.g.* stomatal conductance (g_s), chlorophyll (Chl) content, and leaf area of contrasting plant species, such as sunflower (*Helianthus annuus* L.) (Hussain *et al.* 2009), fennel (*Foeniculum vulgare* Mill.) (Askari and Ehsanzadeh 2015c), and barley (*Hordeum vulgare* L.) (Habibi 2012). Such information is lacking for *S. indicum*. The SA-induced tolerance in plants to various stresses is believed to be elicited by an enhanced antioxidative capacity (Horwath *et al.* 2007). Though, the efficacy of exogenously-supplied SA in alleviating stresses varies with plant species, developmental stage of the target plant, and its endogenous concentration.

The present study was carried out in an attempt to understand the physiological mechanism of SA-induced drought tolerance in *S. indicum*. Since limited information is available on the impacts of drought on the photosynthetic and antioxidative components of *S. indicum*, an integrated approach comprising of leaf area, gas exchange, Chl concentration, and fluorescence characteristics along with the antioxidative measures was attempted in seven *S. indicum* genotypes.

Materials and methods

Plant material and experiment set up: Seeds of seven *S. indicum* genotypes, 'Dashtestan', 'Isfahan', 'Naz-Takshakhe', 'Varamin', 'Yekta', 'Shiraz', and 'Oltan' were sown in the Lavark Research Farm of the Isfahan University of Technology, located in Najaf Abad (32º32´N, 51º23´E, 1,630 m a. s. l., 14.5°C is mean annual temperature and 140 mm is mean annual precipitation), central Iran, during 2014–2015. These genotypes were chosen mainly because they are used for sesame oil production in different areas of the country and some previous studies (*e.g.*, Bazrafshan and Ehsanzadeh 2014) have reported on differential responses of these genotypes to certain environmental constraints. The plants were exposed to 60 and 80% depletion of available soil water at the presence of SA (0.0 and 0.6 mM). The mean daily maximum and minimum air temperatures, mean relative humidity, evaporation rate, and monthly precipitations during the growing seasons in 2014 and 2015 are shown in the table.

The experiment was designed as a three replicate split-plot factorial randomized complete block, in which main plots consisted of two irrigation levels and subplots consisted of seven *S. indicum* genotypes and two SA concentrations.

Month	Days	2014					2015				
		T_{max} [ºC]	T_{min} [ºC]	RH-mean [%]	Evaporation [mm]	Precipitation [mm]	T_{max} [ºC]	T_{min} [ºC]	RH-mean [%]	Evaporation [mm]	Precipitation [mm]
May	1–15	27.5	13.1	35.4	9.3	15.9	27.2	13.8	36.8	6.0	4.3
	15–31	29.0	14.7	37.6	9.4	17.3	31.0	16.6	23.7	9.2	0
June	1–15	33.0	17.8	24.0	11.7	0	36.0	20.5	22.5	10.2	0
	15–30	36.7	19.7	20.0	12.4	0	36.8	21.7	17.8	12.2	0
July	1–15	37.2	22.0	21.6	12.3	0	37.3	21.8	18.0	10.2	0
	15–31	38.5	22.0	21.8	13.0	0	34.5	20.0	30.6	9.9	5.4
August	1–15	38.0	21.0	21.9	12.5	2.6	35.1	19.3	22.0	9.9	0
	15–31	34.0	18.6	25.8	9.8	0	36.0	19.2	19.2	10.6	0
September	1–15	34.0	17.0	20.6	8.4	0	31.4	17.7	30.4	8.4	0
	15–30	32.6	16.2	21.6	8.5	0	28.8	13.6	33.1	6.5	0.7
October	1–15	27.7	11.9	28.3	6.1	0	29.2	14.0	28.6	7.1	0
	15–31	22.5	8.7	42.3	4.1	10.5	23.8	10.9	46.0	5.0	15.4

Before planting, the seeds were disinfected with fungicides to avoid fungal diseases and were seeded into the field plots in late May in 2014 and early May in 2015. Each experimental unit (subplot) consisted of five 2 m long rows with 0.5-m spacing between rows and 0.07-m spacing between plants in the same row. Therefore, the plants were sown at an approximate planting rate of 28 plants m^{-2} in each plot. The soil was a fine loam typical Haplargid, with N, P, K of 450, 21.6, and 222 mg kg^{-1}, respectively, EC = 1.6 dS m^{-1}, pH = 7.4, and bulk density = 1.34 g cm^{-3}. Based on the soil analysis, a fertilizer containing 46% of N was given uniformly at a 100 kg(urea) ha^{-1} to the soil prior to sowing in both years.

Irrigation regimes: The plots were irrigated uniformly when 60% of available soil water (ASW) was depleted at the beginning of the experiment, then at the onset of flowering stage (*i.e.*, when plants were 40 d old) irrigation treatments were applied and continued to nearly 70% of physiological maturity, *i.e.*, early October 2014 and late September 2015. The ASW is known as a content of soil water in the root zone between field capacity (–0.03 MPa) and the permanent wilting point (–1.5 MPa). Watering regimes were selected according to maximum allowable depletion percentage of ASW (*i.e.*, between –0.03 to –1.5 MPa) (Kramer and Boyer 1995), where 60 and 80% depletions of ASW were considered as control and drought-stressed levels, respectively. The 60% depletion of ASW was chosen as control (no drought stress) mainly because previous studies on sesame genotypes (Bazrafshan and Ehsanzadeh 2014, Kadkhodaie *et al.* 2014) have indicated that this crop could withstand mild osmotic stress and typical soil water depletion that brings about mild drought stress for some other crops. The ASW was calculated based on Eq. 1 (Allen *et al.* 1998):

$$ASW = (\theta_{FC} - \theta_{PWP}) \times Bd \times V \quad (1)$$

where θ_{FC} is the gravimetric soil-water content [%] at field capacity, θ_{PWP} is the gravimetric soil-water content [%] at permanent wilting point, Bd is the bulk density of the soil [g cm^{-3}], and V is the volume of soil layer in the root zone [m^3]. The gravimetric method was used to determine soil moisture content and irrigation time. The volume of irrigation water (V_{irrg}) for increase the soil water content to field capacity in root zone was calculated based on Eq. 2 (Allen *et al.* 1998):

$$V_{irrg} = (ASW \times f)/E_a \quad (2)$$

where f is the fraction of ASW depletion (60 and 80%) from the root zone and E_a is the percentage of irrigation efficiency.

SA treatment: Three weeks after a flowering stage (*i.e.*, when plants were 60 d old), SA (2-hydroxybenzoic acid, molecular mass of 138.1, *Sigma*) was dissolved in distilled water and sprayed on plants twice in a five-day interval. The SA solution was sprayed on plants to run-off and control plants were sprayed with distilled water.

Leaf gas exchange, Chl fluorescence, Chl and carotenoids (Car): Net photosynthetic rate (P_N), stomatal conductance to CO_2 (g_s), and substomatal CO_2 concentration (C_i) were measured three weeks after application of SA on three youngest fully expanded top leaves per plot with a calibrated portable gas-exchange system (*LCi, ADC Bioscientific Ltd.,* UK) between 09:30 to 13:00 h, where temprature ranged between 27 and 33ºC and photosynthetic photon flux density was 1200–1650 µmol m^{-2} s^{-1}. A mean of the three measurements for each attribute was used for each plot.

For Chl fluorescence measurements, three youngest fully expanded top leaves per plot were chosen, dark-adapted for 20 min, and maximum fluorescence (F_m), minimum fluorescence (F_0) and F_v/F_m were measured after three weeks of SA application between 09:00 to 14:00 h, using a portable Chl fluorometer (*Opti-Sciences, Inc., Hudson,* NH, USA). The mean of the three measurements was calculated and used for each experimental unit.

Leaf Chl and Car concentrations of the sesame genotypes were determined four weeks after SA treatment. Samples of 0.3 g from fully expanded healthy leaves were ground and extracted with 10 mL of 80% (v/v) acetone. The slurry was filtered and absorbance was measured at 470, 646, and 663 nm, using a UV-visible spectrophotometer (*HITACHI, U 1800,* Japan) to quantify Car, Chl *a* and Chl *b* concentrations, respectively, and then Chl (*a*+*b*) according to Lichtenthaler and Wellburn (1983).

Antioxidant enzyme activities

Enzyme extraction was done as described in Tabatabaei and Ehsanzadeh (2016), using fresh leaf samples that were taken three weeks after the application of SA. The enzyme extract was used to assay the following antioxidant enzyme activities and protein content. Activities were assayed spectrophotometrically (*U-1800 UV/VIS, Hitachi*, Japan).

Enzyme assay: The activity of catalase (CAT, EC 1.11.1.6) was determined by measuring the conversion rate of hydrogen peroxide (extinction coefficient = 39.4 mM^{-1} cm^{-1}) to water and oxygen molecules at 240 nm for 1 min. Details of the preparation of the mixture has been explained in a previous study (Tabatabaei and Ehsanzadeh 2016). The decrease in absorbance was quantified spectrophotometrically. CAT activity was expressed as unit per milligram of protein (Chance and Maehly 1955). The amount of CAT required to decompose 1.0 µM of H_2O_2 per min was defined as one unit of CAT activity.

Ascorbate peroxidase (APX, EC 1.11.1.11) activity was quantified by measuring the oxidation of ascorbate (extinction coefficient = 2.8 mM^{-1} cm^{-1}) to dehydroascorbate at 290 nm, spectrophotometrically, as described by Nakano and Asada (1981) and detailed by Tabatabaei and Ehsanzadeh (2016). APX activity was expressed as

unit per milligram of protein. One unit of APX activity was defined as the amount of enzyme necessary for the oxidation of 1 μmol of ascorbate per min.

The activity of peroxidase (POX, EC 1.11.1.7) was determined with guaiacol (extinction coefficient = 26.61 mM^{-1} cm^{-1}) as an electron donor. Details of the preparation of the mixture has been described in a previous document (Tabatabaei and Ehsanzadeh 2016). The increase in absorbance at 470 nm was monitored for 2 min spectrophotometrically. POX activity was expressed as unit per milligram of protein (Herzog and Fahimi 1973). One unit of POX activity indicates the amount of enzyme that catalyses the oxidation of 1.0 μM of guaiacol in 1 min.

The activity of SOD (EC 1.15.1.1) was assayed by measuring its ability to inhibit the photoreduction of nitro-blue tetrazolium (NBT) using the method of Giannopolitis and Ries (1977) and the criterion explained by Askari and Ehsanzadeh (2015a). The absorbance at 560 nm was measured spectrophotometrically. The amount of enzyme that inhibited 50% of NBT photoreduction was expressed as one unit of SOD activity.

Total protein content of leaf samples was determined using the method described by Bradford (1976).

Membrane stability index and growth parameters: For measuring membrane stability index (MSI), three weeks after SA application, leaf discs of at least 100 mg were cut with scissors and placed in two series of tubes containing 10 mL of double-distilled water. Then the first series of tubes were transferred to a hot water bath at 40°C for 30 min and the second series were kept at 100°C for 10 min. Later, the electrical conductivity of samples was measured with EC meter (*Model Cyberscan,* Singapore). The MSI was calculated as described by Bajji *et al.* (2002).

Leaf area index (LAI) at early pod filling stage was calculated after measuring total leaf area of three plants in each plot, using an *OSK 9875* area meter (*GA-5,* Japan).

At 70% of physiological maturity, plant aboveground dry mass (SDM) and seed yield (SY) were determined from the central 1.5 m^2 portion in each plot. The seed yield was adjusted to 10% moisture content and presented as kg ha^{-1}.

Determination of oil yield: After harvest at 70% physiological maturity, the seeds were air dried for 10 d and subsequently, seed oil was extracted using a crushed 5–6 g sample of each experimental unit according to Jensen (2007) by the petroleum ether and Soxhlet extractor. The oil yield (OY) was obtained by multiplying the SY in seed oil concentration.

Statistical analysis: The data were analyzed using a *Statistical Analysis Software* (*SAS Institute Inc., Version 9.1,* Cary, North Carolina, USA). The means were separated using *Fisher*'s protected least significant differences (LSD). Differences were considered significant at 0.05 level of probability. *Pearson*'s correlation coefficients were calculated for nonstressed and drought-stressed plants.

Results

Analysis of variance (*ANOVA*) revealed that the irrigation regime, genotype, and SA application had significant effects on all measured traits (Table 1). The irrigation × genotype interaction effects were significant for MSI, LAI, Chl *b*, P_N, g_s, C_i, CAT, APX, POX, and SOD activities and SDM, SY, and OY. The SA × irrigation interaction effects were significant for Chl *a*, Chl *b*, Chl (*a*+*b*) concentrations and F_m. The SA × genotype interaction effects were significant for Chl *a*, Chl (*a*+*b*), and Car concentrations, CAT, APX, POX, and SOD activities and SDM, SY, and OY.

The MSI of the drought-stressed plants decreased significantly in all studied genotypes. However, the magnitude of the decreases were different between genotypes, with genotypes 'Dashtestan' (33%) and 'Yekta' (23%) indicating the greatest and smallest decreases, respectively (Table 2). LAI of the water-stressed *S. indicum* genotypes declined significantly, though with different extents, relative to the control plants. Genotypes 'Oltan' (26%) and 'Varamin' (20%) indicated the greatest and smallest decreases in LAI, respectively. Water deficit significantly reduced P_N and g_s, but it substantially increased C_i of all seven genotypes, compared with the control conditions. The extent of the drought-associated decreases in P_N and g_s and increases in C_i differed between genotypes; genotypes 'Varamin' (35%) and 'Dashtestan' (32%) indicated the greatest and smallest decreases in P_N, while 'Naz-Takshakhe' (63%) and 'Yekta' (48%) indicated the greatest and smallest decreases in g_s, respectively. The greatest and smallest drought-initiated increases in C_i were observed in genotypes 'Yekta' (62%) and 'Naz-Takshakhe' (32%), respectively. Chl *b* concentration decreased in all genotypes in response to water limitation, however, the extent of the decline was smaller in the genotype 'Yekta'. Antioxidative responses of all genotypes to water deprivation were consistent; CAT, APX, POX, and SOD activities of all genotypes increased when they were water stressed. SDM, SY, and OY in drought-stressed plants of all studied genotypes were lowered, albeit in different magnitudes, in comparison to the nonstressed plants. The greatest and smallest stress-induced decreases in SDM were observed in the genotypes 'Varamin' (23%) and 'Yekta' (9%), respectively. The greatest and smallest drought-induced decreases in SY and OY were observed in genotypes 'Naz-Takshakhe' (49.3% and 50.0%, respectively) and 'Yekta' (9.6% and 19.0%, respectively), respectively. Exogenous SA led to enhancement in Chl *a*,

Table 1. Analysis of variance (mean squares) for membrane stability index (MSI), leaf area index (LAI), net CO_2 fixation rate (P_N), stomatal conductance (g_s), substomatal CO_2 concentration (C_i), chlorophyll (Chl) *a* concentration, Chl *b*, total Chl concentration [Chl (*a*+*b*)], minimum fluorescence (F_0), maximum fluorescence (F_m), maximal efficiency of PSII (F_v/F_m), leaf carotenoid concentration (Car), catalase activity (CAT), ascorbate peroxidase activity (APX), peroxidase activity (POX), superoxide dismutase activity (SOD), plant above ground dry mass (SDM), seed yield (SY), and oil yield (OY) of seven sesame genotypes evaluated at two levels of irrigation and two concentrations of salicylic acid (SA) in three replications. df – degrees of freedom *R* – replication; I – irrigation; G – genotype; ns – not significant; Error – within group variance; * – $P \leq 0.05$; ** – $P \leq 0.01$.

Trait	*R*	I	*R*(I)	G	SA	SA × G	I × G	SA × I	SA × G× I	Error
df	2	1	2	6	1	6	6	1	6	52
MSI	76.64	11229.84**	5.15	374.80**	180.86**	4.12^{ns}	14.88*	0.22^{ns}	1.51^{ns}	6.36
LAI	0.058	5.34*	0.08	0.36**	0.21**	0.003^{ns}	0.02**	0.008^{ns}	0.001^{ns}	0.003
P_N	0.19	918.72**	0.25	22.91**	65.54**	0.65*	0.83**	0.11^{ns}	0.16^{ns}	0.25
g_s ($\times 10^4$)	4.79	2050.29**	2.90	68.36**	44.29**	0.18^{ns}	1.21*	0.10^{ns}	0.41^{ns}	0.42
C_i	601.07	97036.01**	215.03	2903.55*	107.44*	1.38^{ns}	157.66**	1.19^{ns}	0.49^{ns}	23.30
Chl *a*	0.006	1.68**	0.002	0.03**	0.04**	0.005*	0.002^{ns}	0.017**	2.03^{ns}	0.001
Chl *b*	0.0001	0.20**	0.0004	0.002**	0.01**	0.0003^{ns}	0.0007**	0.008**	0.0002^{ns}	0.0002
Chl *a*+*b*	0.0071	3.06**	0.0041	0.047**	0.10**	0.0046*	0.0040^{ns}	0.049**	0.0041^{ns}	0.0018
F_0	6.48	1833.58**	2.10	4.81^{ns}	868.72**	12.84^{ns}	2.20^{ns}	29.48^{ns}	14.37^{ns}	8.53
F_m	4.75	18098.67**	0.10	684.45**	540.1**	10.27**	38.123**	152.01**	2.51^{ns}	1.49
F_v/F_m ($\times 10^4$)	0.33	368.76**	0.15	1.42*	86.01**	1.03^{ns}	0.19^{ns}	1.71^{ns}	1.15^{ns}	0.62
Car ($\times 10^4$)	1.15	953.44**	0.44	59.35**	109.71**	6.26*	3.11^{ns}	2.33^{ns}	1.84^{ns}	1.97
CAT ($\times 10^5$)	2.76	64067**	0.408	78330.8**	6396**	652.4**	1196**	0.386^{ns}	0.305^{ns}	35.4
APX	0.98	148.01**	0.007	49.36**	20.65**	0.54**	8.64**	0.000003^{ns}	0.016^{ns}	0.089
POX	0.189	4573.1**	0.00002	401.27**	186.36**	6.88**	101.89**	0.000^{ns}	0.00003^{ns}	0.062
SOD	0.26	5303.7**	0.01	304.51**	247.16**	12.104**	114.99**	0.05^{ns}	0.124^{ns}	0.104
SDM ($\times 10^{-5}$)	1.71	448.28**	2.57	204.53**	107.54**	0.68^{ns}	5.74**	0.0007^{ns}	0.23^{ns}	0.97
SY ($\times 10^{-4}$)	0.077	397.04**	0.39	103.88**	161.10**	6.42**	8.80**	0.70^{ns}	0.11^{ns}	0.42
OY ($\times 10^{-2}$)	8.18	13555.74**	11.99	3567.76**	4140.97**	168**	148.08**	32.76	5.18	12.46

Chl *b*, and Chl (*a*+*b*) concentrations under both stressed and nonstressed conditions, but the extent of the increase was greater under the drought-stress condition (Table 3).

Foliar-applied SA affected leaf Chl concentration in a genotype-dependent manner, *i.e.* Chl *a* concentration in genotypes 'Yekta', 'Shiraz', and 'Naz-Takshakhe' increased and that of the remaining genotypes indicated no significant changes after application of 0.6 mM of SA (Table 4). Foliar application of SA induced the greatest and smallest increases in leaf Car concentration in the genotypes 'Yekta' (23%) and 'Dashtestan' (5%), respectively (Table 4). Differences in the extents of SA-induced alterations in the defensive enzymes of the examined genotypes gave rise to the significant interaction of SA × genotype. In contrary to the CAT activity, where it decreased significantly in the SA-treated plants of all genotypes, APX, POX and SOD activities of the SA-treated plants of all genotypes increased compared with the nontreated plants (Table 5). In contrast to the lack of evidence for differential responses of the examined genotypes to SA in terms of g_s and C_i, SA-driven enhancement of P_N in all genotypes was evident, albeit to different extents (Table 4). The SA-induced increases in P_N ranged from 7% in genotype 'Naz-Takshakhe' to 14% in 'Yekta'. The SA treatment increased the SY and OY in all studied genotypes (Table 4) in the same manner, though the extent of these increases varied with the genotype. The SA-induced increases in SY and OY ranged from 3–4% in 'Naz-Takshakhe' to 35–36% in 'Dashtestan'.

Discussion

From the data in Table 2, it is obvious that the stressed plants of seven *S. indicum* genotypes shared, more or less, the same decreasing trend in leaf Chl concentrations. The decrease in leaf Chl concentration could occur due to an upregulation of chlorophyllase activity and, hence, Chl degradation and a stagnation of the biosynthesis of this pivotal photosynthetic pigment (Singh and Dubey 1995). The decrease in Chl concentration of the stressed plants

Table 2. Mean comparisons of interaction effect of soil moisture × genotypes on membrane stability index (MSI), leaf area index (LAI), net CO_2 fixation rate (P_N), stomatal conductance (g_s), substomatal CO_2 concentration (C_i), chlorophyll *b* (Chl *b*) concentration maximal efficiency of PSII (F_v/F_m), catalase activity (CAT), ascorbate peroxidase activity (APX), peroxidase activity (POX), superoxide dismutase activity (SOD), plant aboveground dry mass (SDM), seed yield (SY), and oil yield (OY) of sesame; LSD – least significant difference. In each column, means followed by *the same letter* are not significantly different according to LSD at $P \leq 0.05$.

Genotypes	Irrigation regimes	MSI [%]	LAI	P_N [µmol CO_2 m^{-2} s^{-1}]	g_s [µmol CO_2 m^{-2} s^{-1}]	C_i [µmol CO_2 m^{-2} s^{-1}]	Chl *b* [mg g^{-1} (FM)]	F_v/F_m	CAT mg^{-1}protein	APX mg^{-1}protein	POX mg^{-1}protein	SOD mg^{-1}protein	SDM [kg ha^{-1}]	SY [kg ha^{-1}]	OY [kg ha^{-1}]
Dashtestan	Control	78.90^{b}	2.15^{d}	20.36^{c}	0.20^{b}	153.2^{j}	0.78^{a}	0.81^{ab}	0.33^{f}	5.49^{d}	8.44^{j}	11.64^{h}	7306.2^{e}	1558.8^{e}	859.6^{c}
	Stress	53.08^{gh}	1.62^{i}	13.81^{h}	0.09^{h}	220.9^{d}	0.69^{c}	0.77^{c}	0.52^{e}	7.66^{c}	26.56^{d}	31.73^{c}	5717.2^{k}	1025.4^{k}	507.4^{h}
Isfahan	Control	80.60^{b}	2.01^{e}	19.64^{d}	0.18^{c}	162.9^{i}	0.77^{a}	0.81^{ab}	0.20^{h}	2.58^{h}	9.17^{i}	7.98^{k}	6342.3^{h}	1311.0^{i}	670.6^{ef}
	Stress	55.05^{g}	1.56^{ij}	13.21^{i}	0.08^{i}	229.2^{c}	0.68^{cd}	0.77^{c}	0.34^{f}	3.64^{g}	20.42^{e}	21.66^{e}	4462.0^{m}	779.8^{m}	376.4^{i}
Oltan	Control	83.56^{a}	2.33^{b}	21.02^{b}	0.20^{b}	146.1^{k}	0.77^{a}	0.81^{a}	0.56^{d}	4.37^{f}	10.93^{h}	11.64^{h}	8238.7^{c}	1635.4^{d}	776.2^{d}
	Stress	59.63^{f}	1.73^{h}	14.16^{h}	0.10^{g}	217.1^{de}	0.65^{e}	0.77^{c}	0.78^{b}	8.52^{b}	30.07^{c}	32.17^{b}	7184.2^{f}	1284.6^{j}	610.8^{g}
Shiraz	Control	84.70^{a}	2.25^{c}	19.10^{de}	0.17^{d}	169.3^{h}	0.78^{a}	0.81^{ab}	0.56^{d}	4.88^{e}	10.73^{h}	9.15^{j}	7719.3^{d}	1740.0^{b}	908.5^{b}
	Stress	62.50^{f}	1.69^{h}	12.56^{j}	0.08^{i}	234.8^{c}	0.67^{d}	0.77^{c}	0.79^{b}	8.33^{b}	30.40^{b}	28.39^{d}	6293.7^{i}	1463.6^{f}	708.9^{e}
Naz-Takshakhe	Control	72.10^{d}	2.44^{a}	17.72^{f}	0.16^{e}	187.8^{f}	0.77^{a}	0.80^{b}	0.12^{i}	1.38^{i}	4.19^{k}	6.82^{m}	5958.6^{j}	1365.4^{h}	646.7^{fg}
	Stress	49.85^{i}	1.82^{g}	11.91^{k}	0.06^{k}	247.3^{a}	0.65^{e}	0.76^{c}	0.20^{h}	2.27^{h}	10.71^{h}	14.14^{g}	3961.3^{n}	692.9^{n}	322.8^{j}
Varamin	Control	74.51^{c}	1.84^{g}	18.81^{e}	0.16^{e}	177.1^{g}	0.77^{a}	0.81^{ab}	0.13^{i}	3.41^{g}	4.38^{k}	7.26^{l}	6683.5^{g}	1395.0^{g}	652.3^{f}
	Stress	51.75^{hi}	1.47^{k}	12.26^{jk}	0.07^{j}	240.6^{b}	0.67^{d}	0.76^{c}	0.25^{g}	4.93^{e}	12.82^{f}	15.37^{f}	5157.3^{l}	896.8^{l}	414.7^{i}
Yekta	Control	85.90^{a}	1.91^{f}	22.69^{a}	0.23^{a}	132.4^{l}	0.78^{a}	0.81^{a}	0.65^{c}	4.12^{f}	11.24^{g}	10.78^{i}	9034.6^{a}	1892.2^{a}	1062.6^{a}
	Stress	66.55^{e}	1.51^{jk}	15.12^{g}	0.12^{f}	214.8^{e}	0.72^{b}	0.77^{c}	0.89^{a}	9.47^{a}	31.39^{a}	33.05^{a}	8279.9^{b}	1711.0^{c}	857.1^{c}
LSD (0.05)		2.92	0.06	0.58	0.007	5.59	0.016	0.009	0.021	0.35	0.29	0.37	362.2	75.7	40.9

Table 3. Mean comparisons of interaction effects of soil moisture × salicylic acid on chlorophyll (Chl) *a*, Chl *b*, and total Chl concentrations, and maximum fluorescence of sesame genotypes. F_m – maximum fluorescence; LSD – least significant difference. In each column, means followed by the same letter are not significantly different according to LSD at $P \leq 0.05$.

Irrigation regimes	Salicylic acid [mM]	Chl *a* [mg g^{-1}(FM)]	Chl *b* [mg g^{-1}(FM)]	Chl (*a*+*b*) [mg g^{-1}(FM)]	F_m
Control	0.0	2.03^{b}	0.77^{b}	2.81^{a}	378.5^{b}
	0.6	2.05^{a}	0.78^{a}	2.83^{a}	386.2^{a}
Water stress	0.0	1.72^{d}	0.65^{d}	2.38^{c}	351.8^{d}
	0.6	1.79^{c}	0.70^{c}	2.49^{b}	354.2^{c}
LSD (0.05)		0.02	0.008	0.03	0.8

might be seen as an adaptive strategy to avoid oxidative stress by reducing the amount of light intercepted and, hence, amounts of ROS generated by chloroplasts. Contrarily, it is quite likely that overproduction of chloroplast-associated ROS in the stressed plants led to photosynthetic pigment destruction. Decreases in Chl concentration of stress-stricken plants have been reported in many plant species including *Artemisia annua* L. (Aftab *et al.* 2011), *S. indicum* (Bazrafshan and Ehsanzadeh 2014), *Foeniculum vulgare* Mill. (Askari and Ehsanzadeh 2015b), and *Triticum dicoccum* L. (Tabatabaei and Ehsanzadeh 2016). The decrease in the leaf Chl concentration of the present genotypes might contribute to the reduction in their photosynthetic activity under the water stress. Interestingly, photosynthetic activity of the drought-stressed plants was suppressed, *i.e.*, in almost the same proportion to the reduction in the LAI, Chl concentration, SDM, SY and OY. Correlative associations among the above traits (Table 5) conform to the above notion.

It is not surprising that water deficit led to declines of g_s in the *S. indicum* plants, as it is well-established that stressful environments in general and water shortage in particular inhibit stomatal opening (Venora and Calgacno 1991). The reduction in P_N in drought-stressed *S. indicum* plants could be, partially, ascribed to a reduced CO_2 supply due to a decreased stomatal opening (Table 2). A decline of P_N associated with an increase in C_i has been frequently interpreted as a direct effect of the stressor factor on the photosynthetic capacity, rather than on the diffusional limitations (Zhang *et al.* 2015). Such changes in the photosynthetic capacity that are not proportional to diffusional limitations are, perhaps, related to either changes in the concentration and/or efficiency of operation of the photosynthetic machinery (Seemann and Critchley 1985). It is, therefore, tempting to summarize that an inhibition of photosynthetic activity at the biochemical level, *i.e.*, a decreased mesophyll conductance, has contributed to the lowered photosynthetic performance, SDM, SY, and OY of the stressed plant of *S. indicum* genotypes. The phenomenon of photosynthesis-associated yield depression in drought-stressed plants has been confirmed in different crop species (Miao *et al.* 2015). The fact that genotype 'Yekta' out-yielded the remaining genotypes could be explained in the context of the outstanding performance of its photosynthetic components (Table 3). An intimate association between SDM and g_s and P_N of the examined genotypes (*e.g.*, the high positive correlations presented in Table 5), in general, and of this genotype, in particular, supports the notion that it took advantage of the sustained photosynthetic areas (*i.e.*, reflected in a greater mean LAI shown in Table 2) and gas-exchange capacity under stress condition. We, hence, can propose with confidence that the greater SDM (*i.e.*, and the consequent SY and OY) of the genotype 'Yekta', which reached 110% of SDM of 'Oltan' and 140% of SDM of 'Naz-Takshakhe', was attributable to maintaining a greater LAI and g_s under both drought-stressed and nonstressed conditions.

In addition to the photosynthetic pigments, areas and enzymes, thylakoid membranes and PSII could be the subject of harmful stress effects. In fact, the stomatal limitations to photosynthesis under environmental stresses are associated with decreases in the rate of ATP and NADPH utilization for CO_2 assimilation. Therefore, under many environmental stresses plants are inhibited by utilizing much radiation energy for photosynthesis and may use some mechanisms to safely dissipate excess of light energy in order to avoid photoinhibition and photo-oxidation. The photoinhibition may be ameliorated by increasing the dissipation of excessive energy by non-photochemical quenching, *i.e.*, Chl fluorescence. In the present study, smaller Chl concentrations and lower photosynthetic activities (CO_2 assimilation) in the water-stressed sesame plants were associated with increased fluorescence intensity and lowered F_v/F_m of the plants (Tables 2, 5). We are, therefore, convinced that the perturbed photosynthetic metabolism induced by the water stress modified the fluorescence emission kinetics of the examined genotypes. The stress-induced decreases in F_v/F_m of the *S. indicum* plants of the present study appeared to be associated with increases in F_0 rather than with decreases in F_m values (Table 2). Increases in F_0 are suggestive of Chl breakdown or antenna reconfiguration and, hence, structural disorders in PSII (Pestana *et al.* 2011) and decreases in light absorption by the Chl antenna.

A common consequence of most abiotic and biotic stresses is production of ROS in plant cells (Alscher *et al.* 1997). The ROS produced through chloroplasts increased

Table 4. Mean comparisons of interaction effect of genotypes × salicylic acid on net CO_2 fixation rate (P_N), chlorophyll (Chl) *a* concentration, total Chl, maximum fluorescence (F_m), leaf carotenoids concentration (Car), catalase activity (CAT), ascorbate peroxidase activity (APX), peroxidase activity (POX), superoxide dismutase activity (SOD), seed yield (SY) and oil yield (OY) of sesame; LSD – least significant difference. In each row and within each factor, means followed by *the same letter* are not significantly different according to LSD at $P \leq 0.05$.

Genotypes	SA [mM]	P_N [µmol CO_2 m^{-2} s^{-1}]	Chl *a* [mg g^{-1}(FM)]	Chl (*a*+*b*) [mg g^{-1}(FM)]	F_m	F_v/F_m	Car [mg g^{-1}(FM)]	CAT [mg^{-1}protein]	APX [mg^{-1}protein]	POX [mg^{-1}protein]	SO [mg^{-1}protein]	SY [kg ha^{-1}]	OY [kg ha^{-1}]
Dashtestan	0	16.18^{e}	1.88^{ef}	2.60^{de}	361.0^{j}	0.78^{a}	0.20^{ghi}	0.437^{f}	6.01^{bc}	15.73^{f}	19.23^{de}	$1,097.9^{j}$	580.1^{fg}
	0.6	18.00^{c}	1.88^{ef}	2.64^{cd}	365.5^{h}	0.79^{a}	0.21^{def}	0.413^{g}	7.15^{a}	19.28^{c}	24.15^{b}	$1,486.4^{e}$	787.4^{d}
Isfahan	0	15.55^{f}	1.83^{g}	2.55^{fg}	367.1^{g}	0.78^{a}	0.21^{def}	0.285^{h}	2.83^{g}	13.76^{g}	13.82^{h}	979.0^{n}	488.9^{h}
	0.6	17.30^{d}	1.85^{fg}	2.59^{ef}	373.3^{d}	0.80^{a}	0.23^{bc}	0.264^{h}	3.40^{f}	15.84^{f}	15.83^{g}	$1,111.7^{i}$	558.1^{g}
Oltan	0	16.51^{e}	1.90^{de}	2.60^{de}	371.8^{e}	0.78^{a}	0.22^{cde}	0.705^{c}	5.72^{c}	18.53^{e}	19.42^{d}	$1,263.3^{h}$	606.2^{f}
	0.6	18.60^{b}	1.91^{cde}	2.65^{c}	378.5^{b}	0.80^{a}	0.24^{b}	0.647^{d}	7.19^{a}	22.48^{b}	24.40^{b}	$1,656.8^{c}$	780.6^{d}
Shiraz	0	15.09^{fg}	1.92^{cd}	2.64^{cd}	363.3^{i}	0.78^{a}	0.20^{fgh}	0.736^{b}	5.92^{bc}	18.46^{e}	16.77^{f}	$1,399.1^{f}$	702.6^{e}
	0.6	16.58^{e}	1.98^{b}	2.72^{b}	368.6^{f}	0.80^{a}	0.22^{cd}	0.620^{e}	7.30^{a}	22.68^{b}	20.78^{c}	$1,804.4^{b}$	914.8^{b}
Naz-Takshakhe	0	14.28^{h}	1.83^{g}	2.53^{g}	357.8^{l}	0.77^{a}	0.19^{hij}	0.171^{jk}	1.63^{i}	6.90^{j}	9.94^{k}	$1,014.3^{m}$	476.7^{h}
	0.6	15.35^{f}	1.92^{cd}	2.64^{cd}	359.6^{jk}	0.79^{a}	0.21^{efg}	0.152^{k}	2.03^{h}	8.00^{i}	11.02^{j}	$1,043.9^{k}$	492.9^{h}
Varamin	0	14.76^{gh}	1.85^{fg}	2.56^{efg}	359.1^{kl}	0.77^{a}	0.17^{j}	0.206^{i}	3.83^{e}	8.03^{i}	10.78^{j}	$1,019.3^{l}$	473.6^{h}
	0.6	16.31^{e}	1.86^{fg}	2.59^{ef}	363.0^{i}	0.80^{a}	0.18^{ij}	0.182^{j}	4.53^{d}	9.19^{h}	11.87^{i}	$1,272.6^{g}$	593.3^{fg}
Yekta	0	17.65^{cd}	1.94^{c}	2.68^{bc}	375.6^{c}	0.78^{a}	0.22^{cde}	0.842^{a}	6.15^{b}	18.92^{d}	18.95^{e}	$1,633.6^{d}$	867.9^{c}
	0.6	20.16^{a}	2.04^{a}	2.81^{a}	382.8^{a}	0.81^{a}	0.27^{a}	0.717^{bc}	7.44^{a}	23.72^{a}	24.88^{a}	$1,969.6^{a}$	$1,051.8^{a}$
LSD (0.05)		0.58	0.036	0.049	1.4	0.009	0.015	0.021	0.35	0.29	0.37	75.7	40.9

Table 5. Correlation coefficients among membrane stability index (MSI), leaf area index (LAI), net CO_2 fixation rate (P_N), stomatal conductance (g_s), substomatal CO_2 concentration (C_i), chlorophyll (Chl) *a*, Chl *b*, total Chl concentrations, minimum fluorescence (F_0), maximum fluorescence (F_m), maximal efficiency of PSII (F_v/F_m), leaf carotenoids concentration (Car), catalase activity (CAT), ascorbate peroxidase activity (APX), peroxidase activity (POX), superoxide dismutase activity (SOD), plant above ground dry mass (SDM), seed yield (SY) and oil yield (OY) of seven sesame genotypes under water deficit stress (lower triangle) and control conditions (upper triangle, bold type); ** – significant at $P \leq 0.01$.

Trait	MSI	LAI	P_N	g_s	C_i	Chl *a*	Chl *b*	Chl (*a*+*b*)	F_0	F_m	F_v/F_m	Car	CAT	APX	POX	SOD	SDM	SY	OY
MSI	1	**0.02**	**0.66****	**0.67****	**-0.67****	**0.50**	**0.43**	**0.52**	**-0.17**	**0.76****	**0.44**	**0.70****	**0.73****	**0.59****	**0.83****	**0.57**	**0.75****	**0.62****	**0.65****
LAI	-0.11	1	**-0.14**	**-0.10**	**0.20**	**-0.05**	**-0.24**	**-0.08**	**-0.12**	**-0.08**	**0.07**	**0.04**	**-0.01**	**0.007**	**0.09**	**0.2**	**-0.05**	**0.08**	**-0.04**
P_N	0.62**	-0.02	1	**0.89****	**-0.78****	**0.46**	**0.65****	**0.51**	**-0.33**	**0.86****	**0.62****	**0.76****	**0.54**	**0.58**	**0.77****	**0.80****	**0.82****	**0.75****	**0.77****
g_s	0.70**	-0.18	0.82**	1	**-0.89****	**0.45**	**0.62****	**0.50**	**-0.08**	**0.84****	**0.39**	**0.71****	**0.69****	**0.53**	**0.71****	**0.70****	**0.83****	**0.69****	**0.75****
C_i	-0.58	0.23	-0.72**	-0.82**	1	**-0.38**	**-0.49**	**-0.42**	**-0.04**	**-0.77****	**-0.26**	**-0.60****	**-0.69****	**-0.54**	**-0.67****	**-0.60****	**-0.71****	**-0.54**	**-0.62****
Chl *a*	0.66**	0.20	0.58	0.51	-0.32	1	**0.43**	**0.99****	**-0.09**	**0.41**	**0.24**	**0.41**	**0.63****	**0.40**	**0.47**	**0.31**	**0.61****	**0.61****	**0.65****
Chl *b*	0.44	-0.13	0.67**	0.59**	-0.44	0.45	1	**0.54**	**-0.33**	**0.47**	**0.46**	**0.45**	**0.44**	**0.62****	**0.56**	**0.58**	**0.66****	**0.66****	**0.79****
Chl (*a*+*b*)	0.68**	0.11	0.69**	0.60**	-0.40	0.95**	0.70**	1	**-0.13**	**0.45**	**0.29**	**0.44**	**0.65****	**0.46**	**0.51**	**0.37**	**0.66****	**0.65****	**0.71****
F_0	-0.11	-0.25	-0.43	-0.25	0.02	-0.32	-0.46	-0.41	1	**-0.19**	**-0.92****	**-0.26**	**0.15**	**-0.30**	**-0.30**	**-0.45**	**-0.23**	**-0.40**	**-0.31**
F_m	0.78**	-0.17	0.76**	0.84**	-0.77**	0.47	0.45	0.53	-0.09	1	**0.55**	**0.81****	**0.63****	**0.42**	**0.86****	**0.67****	**0.79****	**0.69****	**0.67****
F_v/F_m	0.30	0.19	0.60**	0.44	-0.22	0.41	0.54	0.52	-0.96**	0.34	1	**0.53**	**0.11**	**0.42**	**0.59****	**0.64****	**0.51**	**0.61****	**0.53**
Car	0.65**	0.13	0.74**	0.69**	-0.56	0.60**	0.44	0.63**	-0.16	0.78**	0.34	1	**0.51**	**0.39**	**0.79****	**0.66****	**0.66****	**0.63****	**0.66****
CAT	0.80**	-0.08	0.47	0.61**	-0.68**	0.50	0.19	0.47	0.13	0.70**	0.05	0.50	1	**0.52**	**0.67****	**0.41**	**0.81****	**0.66****	**0.65****
APX	0.77**	-0.13	0.66**	0.71**	-0.74**	0.58	0.40	0.60**	-0.12	0.65**	0.27	0.47	0.88**	1	**0.66****	**0.78****	**0.69****	**0.67****	**0.68****
POX	0.86**	-0.01	0.67**	0.72**	-0.77**	0.54	0.38	0.56	-0.13	0.72**	0.30	0.62**	0.90**	0.91**	1	**0.80****	**0.78****	**0.78****	**0.78****
SOD	0.71**	-0.004	0.75**	0.79**	0.83**	0.52	0.44	0.57	-0.16	0.70**	0.33	0.62**	0.82**	0.91**	0.96**	1	**0.72****	**0.78****	**0.74****
SDM	0.81**	-0.15	0.72**	0.80**	0.74**	0.63**	0.47	0.66**	-0.14	0.79**	0.34	0.59**	0.85**	0.92**	0.83**	0.82**	1	**0.84****	**0.83****
SY	0.87**	-0.06	0.66**	0.70**	-0.58	0.71**	0.52	0.75**	-0.21	0.70**	0.38	0.60**	0.81**	0.88**	0.83**	0.78**	0.90**	1	**0.94****
OY	0.87**	-0.08	0.68**	0.72**	-0.60**	0.71**	0.54	0.75**	-0.21	0.71**	0.37	0.61**	0.82**	0.88**	0.84**	0.80**	0.90**	0.99**	1

particularly in plants stricken by a set of adverse environmental conditions that impair photosynthesis (Mittler *et al.* 2004). An impaired photosynthesis leads to an increase in photoinhibition of PSII, potentiating the overproduction of superoxide radical and H_2O_2 (Foyer and Noctor 2005). As plant cell membranes are among the primary sites of stress injury, a notable decrease in MSI of the stressed sesame plants (Table 2) is indicative of severe damage to the membrane integrity. The observed impairment in plant membrane integrity might be a further confirmation of ROS-elicited injuries. ROS synthesized in plants are, normally, scavenged by a variety of antioxidant systems including enzymatic and nonenzymatic components. There are various enzymatic scavenging systems that are found, more or less, in different cell compartments. In this work, in addition to Car, the activities of POD, CAT, SOD, and APX were determined and the results showed that drought stress invariably increased the concentration of Car and stimulated the activities of these enzymes (Table 2). As it has been noted in different studies (Ghobadi *et al.* 2013, dos Santos *et al.* 2013), stress imposition on plants brings about increases in antioxidative defensive measures including nonenzyme (*e.g.*, Car) and enzymatic antioxidants (*e.g.*, CAT, SOD, POX and APX).

SOD converts the superoxide radical into H_2O_2 that is less toxic but still could harm the cell (Mirjahanmardi and Ehsanzadeh 2016). H_2O_2 has to be further detoxified by CAT and/or POD or APX through conversion to water and oxygen molecules (Shah *et al.* 2001). Detoxification of H_2O_2 prevents the oxidation of biological molecules and destruction of the cells (Liochev and Fridovich 1994). Stress-induced increase in H_2O_2 concentration plays a signaling role towards upregulation of expression of CAT. Thus, as far as our data are concerned, increase in CAT activity in the stressed plants (Table 2) was not far from our expectation. APX contributes, through the ascorbate-glutation cycle, to the elimination of cellular H_2O_2 (Bowler *et al.* 1992). During the conversion of H_2O_2 to H_2O by the APX, ascorbate is the main substrate. Thus, increase in the expression of the latter enzyme in response to environmental stresses (*e.g.*, drought stress in the present study) was expected (Caverzan *et al.* 2012).

Car are capable of downregulating the production of singlet oxygen in chloroplasts (Abogadallah 2010). Thus, capacity of the drought-stressed *S. indicum* plants for ROS detoxification might increased due to the notably increased Car concentrations, *i.e.*, 0.18 and 0.25 mg g^{-1} of Car in nonstressed and drought-stressed plants, respectively (data not shown). In the studied sesame genotypes the 50–175% increases in CAT, POX, APX, and SOD activities were concomitant to a nearly 40% increase in the Car concentration of the stressed plants (data not shown). Similar responses to drought, in terms of antioxidative enzymes activity and Car concentration, in seven *S. indicum* genotypes studied here is, perhaps, suggestive of benefiting from the same strategy in order to withstand the presumed drought-initiated oxidative stress. Positive correlative associations between the Car, SOD, APX, CAT, and POX on one hand, and photosynthetic attributes and SDM on the other (Table 5), confirmed the above proposition. Therefore, our findings led us to conclude that the examined genotypes rely mainly on their antioxidative enzymes and in a lesser extent on Car in order to withstand the ROS generation under water deficit conditions. Reliance of *S. indicum* genotypes (*i.e.*, genotype 'Yekta') on the enhanced antioxidative activities to combat the drought stress has been confirmed by an earlier study (Fazeli *et al.* 2007).

Plant growth regulators (PGRs) are capable of regulating several physiological functions and biochemical processes and, hence, may play a crucial role in inducing drought tolerance. Exogenous supply of PGRs may correct water relations of the drought-stricken plants, leading to an increased osmotic adjustment and the subsequent water intake and improved photosynthesis under water limitation (Hayat *et al.* 2012, Wu *et al.* 2012). SA, one of the endogenous PGRs that is ubiquitous in plants, has been found to initiate a wide range of metabolic and physiological functions and, therefore, to affect plant growth and productivity. SA-initiated responses are believed to be mediated by changes in the endogenous ethylene concentration. Ethylene is considered to have regulating role in plant growth and development. It acts as a signaling molecule in plant growth and photosynthetic functions both under stress and nonstress conditions (Khan *et al.* 2014). SA inhibits the conversion of 1-amino-cyclopropane-1,1-carboxylic acid to ethylene (Leslie and Romani 1986) and, thus, influences ethylene biosynthesis and plant growth. In the present study, promoting effects of SA were not limited to drought-stressed plants. Photosynthetic pigment biosynthesis along with photosynthetic activities appeared to be upregulated in the SA-treated plants, leaving aside water availability status (Table 4). Application of 0.6 mM of SA led to enhancement of various physiological attributes, including Chl concentration, P_N, g_s, and in a lesser extent F_v/F_m and, consequently, SDM, SY, and OY of the examined sesame genotypes. Some of these SA-elicited increases seemed to be more pronounced in the water-deprived plants (Tables 3, 5). SA-induced improvement in certain photosynthetic attributes of the stressed *S. indicum* plants could be ascribed to changes in the biochemical and physiological processes related to water maintaining and osmoregulatory capabilities (data not shown). In harmony to our findings, photosynthetic attributes such as P_N, C_i, g_s, water-use efficiency, and transpiration rate in *Brasica juncea* L. (Fariduddin *et al.* 2003), and *Z. mays* and *Glycine max* L. (Khan *et al.* 2003) increased due to the application of SA.

SA may affect defensive responses of plant, *e.g.*, antioxidative defense, to many abiotic stresses (Knorzer *et al.* 1999, Yang *et al.* 2003). Noticeably increased Car concentration and elevated APX, POX, and SOD activities of the SA-treated plants of all sesame genotypes (Table 4)

supported the notion that SA is capable of modifying the antioxidant system capacity (Ananieva *et al.* 2004). The SA-induced upregulations in the antioxidative system can lessen the damage to cell membrane and, therefore, improve cell membrane integrity (Cui *et al.* 2010). As it has been noticed in the present study, SA may, potentially, act as a signal molecule and improve the antioxidative mechanism through inhibiting CAT and stimulating POX enzymes (Rao *et al.* 1997). We propose that SA-associated resistance to drought originates at least partially from the antioxidative-related amelioration of the induced oxidative stress.

Considering the previously documented involvement of SA in improving osmoregulation and yield responses of different crop species to drought (Hussain *et al.* 2009, Saruhan *et al.* 2012, Askari and Ehsanzadeh 2015a), together to the above-mentioned findings of the present study, it is reasonable to deduce that SA is potent to improve the drought stress tolerance capability and SDM, SY, and OY of *S. indicum* either through correcting photosynthetic attributes or *via* mediating antioxidative responses of the plants.

Conclusions: Results of the present study showed that drought is potent to hamper all photosynthetic components and/or functions of *S. indicum*. Though, this oilseed crop seems to be able to cope with drought stress by a mechanism in which antioxidative defense plays a pivotal role, as it was evident from increases in the both enzymatic and nonenzymatic antioxidative defenses in drought-stressed plants of this species. SA seems to be potent to improve the drought-stress tolerance and, hence, productivity of *S. indicum* either through upregulating photosynthetic attributes or *via* mediating antioxidative responses. From seven *S. indicum* genotypes, 'Yekta' emerged as a higher yielding genotype under optimal and drought stress conditions.

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