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Full Length Article

Foliage Applied Selenium Improves Photosynthetic Efficiency, Antioxidant Potential and Wheat Productivity under Drought Stress

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Abstract

Selenium (Se) has been extensively reported to alleviate negative effects of abiotic stresses, including drought on several economic plants. This study was conducted to evaluate the effects of foliar application of Se with three levels (0 (Se_0), 25 (Se_{25}), and 50 (Se_{50}) m*M*) on water status, photosynthetic efficiency, antioxidative defense apparatus, and productivity of wheat sown under three deficit irrigation (DI) levels *i.e.*, DI_0, DI_{20}, and DI_{40} of crop evapotranspiration (ETc) during 2017–18 and 2018–19. DI_0, DI_{20}, and DI_{40} referred to 100, 80 and 60% of ETc, respectively. Foliar application of Se_{25} and Se_{50}, under normal and drought conditions, significantly increased the leaf tissue's succulency, chlorophyll contents, photosynthetic efficiency, antioxidant defense system components and osmoprotectants. Maximum grain yield and related attributes of wheat were recorded when Se was applied under normal and drought stress conditions. The highest grain yield was recorded when Se_{50} and Se_{25} were applied under normal condition (DI_0) in both seasons, respectively, while under drought stress conditions, the highest grain yield was obtained when Se_{25} or Se_{50} combined with DI_{20} level in both seasons. $DI_{40} \times Se_{25}$ compared to $DI_0 \times Se_0$ recorded the best results of water use efficiency (WUE) based on grain yield, exceed by 80.8 and 74.7% in both seasons, respectively. In conclusion, drought stress impaired the wheat productivity while foliar application of Se (25 or 50 m*M*) considerably improved wheat yield and WUE of wheat due to notable expansion in gas exchange traits and anti-oxidant potential of wheat subjected to drought stress. © 2020 Friends Science Publishers

Keywords: Wheat; Deficit irrigation; Selenium; Grain yield; Antioxidant defense system

Introduction

Wheat (*Triticum aestivum* L.) is an extremely significant cereal crop widely grown as a staple food, supplying about one-fifth of human calories for more than 35% of the world's population (FAO 2011). Globally, the harvested area in 2017 estimates by 2.19×10^8 ha produced close to 7.72×10^8 tons (FAO 2019). However, water scarcity due to recurrent droughts occurring by unexpected climate change is one of the main abiotic constraints limiting crops production including, wheat and has become a focus of interest of scientists at global scale (Farooq *et al*. 2015; Hussain *et al*. 2018). Drought stress exerts serious impacts on physio-biochemical and molecular processes and thus, reduces photosynthetic activity, limiting crop growth and its final economic yield including wheat (Farooq *et al*. 2014, 2015). Moreover, oxidative stress as a secondary stress is often co-occurring with drought-induced stress due to overproduction of reactive oxygen species (ROS) in the chloroplast such as superoxide anion ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), hydroxylic free radical ($OH^{\bullet}$), and malondialdehyde (MDA), which are harmful to plant cell biological activities (Nawaz *et al*. 2015; Farooq *et al*. 2019). Under prolonged drought conditions, ROS substantially impairs lipids and proteins in cellular membranes, destroys nucleic acids, oxidizes carbohydrates, degrades photosynthetic pigments, and ultimately deteriorations of enzymatic activities (Farooq *et al*. 2014). Thence, antioxidant capacity in drought-stressed wheat plants depends on their ROS-scavenging ability by enhancing concentrations of antioxidant metabolites as well as upgrading enzymatic and non-enzymatic antioxidants activities (Farooq *et al*. 2014). Several exogenous organic and inorganic substances (*i.e*., melatonin, silicon, brassinolide, polyamine, *etc*.) have been and are being still used as alternative strategies by investigators to enhance plant's tolerance to various abiotic environmental stressors (Sattar *et al*. 2019).

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Among the stress alleviating substances, selenium (Se) has displayed beneficial roles in enhancing drought tolerance in several crops by bettering bio-activities of non-enzymatic and/or enzymatic antioxidants in their plant cells and also keeping cell membrane integrity associated with photosynthetic apparatus (Nawaz *et al*. 2015; Ahmad *et al*. 2016). In this regard, Peng *et al*. (2001) indicated that the threshold concentration of Se as a foliar application for beneficial influences is ~ 1 mg L^{-1} and for harmful influences ~ 5 mg L^{-1} in wheat plants grown hydroponically. However, a number of studies on various crops, including wheat, published in the latest years showed that foliar application of Se at low concentrations (~ 1 mg L^{-1}) has beneficial physiological roles for plants grown in stressed and non-stressed environments (Nawaz *et al*. 2015; Ahmad *et al*. 2016; Ashraf *et al*. 2018). For instance, Se applied exogenously plays a substantial role in circumventing the harmful influences of toxic heavy metal ions (Feng *et al*. 2013), Ultraviolet-B irradiation (Yao *et al*. 2013), heat and cold stresses (Djanaguiraman *et al*. 2010), salt stress (Ashraf *et al*. 2018) and drought stress (Sattar *et al*. 2019).

Selenium can play defensive roles against various environmental stressors, including drought and salinity, through strengthening the antioxidant defense mechanization mainly by activation enzymatic antioxidants (Nawaz *et al*. 2015; Sattar *et al*. 2019). Further, Se can activate non-enzymatic antioxidants such as ascorbate (AsA), glutathione (GSH), α-tocopherol, flavonoids, and other polyphenols to counteract various plant stressors (Hajiboland *et al*. 2015; Nawaz *et al*. 2015; Shahzadi *et al*. 2017). Both enzymatic and non-enzymatic antioxidants can efficiently regulate and scavenge the high levels of toxic ROS to improve plant tolerance to oxidative stress induced by abiotic stressors, including drought and salinity (Hussain *et al*. 2018). These organic compatible solutes not only maintenance of cellular osmoregulation but also stabilize cellular membrane, complex proteins, and structure of enzymes as well as act as a ROS quencher and a cytoplasmic pH regulator in plants exposed to various abiotic stressors including drought (Feng *et al*. 2013; Farooq *et al*. 2009). Further, Se plays an affirmative role in alleviating drought stress by adjusting water status in plant tissues *via* enhancing root water absorption (Tadina *et al*. 2007; Bocchini *et al*. 2018), and improving leaf water potential plus stomatal conductance without lowering the transpiration rate from plant's canopy (Nawaz *et al*. 2016; Sattar *et al*. 2019).

Relatively little is known about the selenium's protective role, sprayed exogenously, in the alleviation of the drought-induced negative effects in wheat. Therefore, the present work aimed to study the potential positive roles of Se in modulating drought-induced oxidative stress by increasing the antioxidant defense system activity, and improving gas exchange traits, yield related traits and water use efficiency of wheat under drought conditions. Our study hypothesis was that Se supplementation would positively affect the performance of drought-stressed wheat plants.

Materials and Methods

Experimental site, layout and crop growth conditions

This two-year field experiment was done during the 2017–18 and 2018–19 winter seasons at the experimental farm (located at 29°17′N latitude; 30°53′E longitude) of the Faculty of Agriculture, Fayoum University, Southeast Fayoum province, Egypt. Climatic data of this region during growing seasons are given in Table 1. Pre-sowing soil physio-chemical data is given in Table 2 which indicated that the tested soil is a moderate saline soil (4.94 dS m^{-1}) according to the classification reported by Dahnke and Whitney (1988).

Wheat was sown under three DI levels [DI_0, DI_{20}, and DI_{40} of ETc (100, 80 and 60% of ETc, respectively taken as DI_0, DI_{20}, and DI_{40})] subjected to foliar application of Se at 25 (Se_{25}) and 50 (Se_{50}) m*M* while 0 (Se_0) m*M* was taken as control. Each rate of Se in sodium selenite (Na_2SeO_4, Sigma-Aldrich, MO state, U.S.A.) form was sprayed two times at 20 days' intervals commencing from 40 days from planting (DFP) to a second application. The experiment was laid following randomized complete block design (RCBD) under split-plot arrangement keeping irrigation levels in main while Se levels in sub-plots. The total experiment was replicated three times with net plot size of subplots of 5 m × 4 m. To control against irrigation treatment's border effects, an external border of 2 m a wide were utilized to separate main plots.

Seeds of bread wheat cv. 'Misr 1' were obtained from the Field Crops Research Institute, Agricultural Research Center, Egypt and were planting on Nov 18 and 25 and harvested on April 15 and 21 in both winter seasons, respectively. According to recommendations agronomical practices particularizing for bread wheat cultivars in Egypt, the tested soil received 62 kg P_2O_5 ha^{-1} (*i.e*., 400 kg calcium monophosphate; 15.5% P_2O_5) and 72 kg K_2O ha^{-1} (*i.e*., 150 kg potassium sulfate; 48% K_2O) during land preparation. Also, 200 kg N ha^{-1} (*i.e*., 600 kg ammonium-nitrate; 33.5% N) was applied broadcasting in three doses (1/5 at planting, 2/5 before the 1st irrigation and 2/5 before the 2nd irrigation). Wheat plants were irrigated every 15-days in all irrigation treatments utilizing the surface watering method. As per the subsequent equation described by Allen *et al*. (1998), the required ET_c for irrigation periods was calculated using the wheat crop coefficient in each growth stage and climate data for Fayoum region.

$$ETc = Kc \times Epan \times Kpan$$

Where: ET_c = crop water requirements (mm d^{-1}), K_c = crop coefficient, E_{pan} = evaporation from the Class-A pan (mm d^{-1}), and K_{pan} = the pan evaporation coefficient.

The entire quota of water per subplot was conveyed from the field's waterway across a plastic pipe (spile) of 2-inch diameter after calculated according to the next equation reported by Israelsen and Hansen (1962).

Table 1: Weather data during the whole course of study at El-Fayoum region, Egypt

Months	2017–2018						2018–2019					
	Mean temperatures (°C)		Mean relative humidity (%)	U_2 (m s^{-1})	E_p	Precipitation	Mean temperatures (°C)		Mean relative humidity (%)	U_2 (m s^{-1})	E_p	Precipitation
	Day	Night			(mm d^{-1})		Day	Night			(mm d^{-1})	
Nov.	27.70	15.70	41.0	2.0	2.2	0.24	28.10	15.60	42.0	1.9	2.1	0.18
Dec.	22.20	9.20	43.0	1.6	1.8	0.03	21.00	9.50	42.0	1.7	1.5	0.24
Jan.	20.50	8.50	43.0	2.1	1.5	0.35	20.50	8.50	42.6	2.2	1.6	0.03
Feb.	24.60	9.50	41.0	1.6	2.7	0.15	22.00	8.50	42.0	1.9	2.8	0.10
Mar.	28.00	13.40	36.0	2.2	4.0	0.02	28.30	12.60	36.6	2.2	3.9	0.12

U_2= Average of wind speed, E_P= Averaged measured pan evaporation Class-A
Source: Fayoum Agricultural Research Station, Fayoum province, Egypt

Table 2: Pre-sowing physical and chemical analysis of soil

Soil depth (cm)	Particle size distribution				Bulk density (g cm^{-3})	K_{sat} (cm h^{-1})	Soil moisture contents at			pH	ECe (dS m^{-1})	$CaCO_3$ (%)	OM (%)
	Sand (%)	Silt (%)	Clay (%)	Textural class			FC (%)	WP (%)	AW (%)				
0–30	74.12	15.19	10.69	SL	1.53	2.21	20.76	10.19	10.57	7.72	4.77	7.8	1.22
30–60	73.31	13.51	13.18	SL	1.58	1.79	21.71	12.05	9.66	7.63	5.10	8.6	0.95

S = Sandy loam, FC=Field capacity, WP= Wilting point, AW= Available water, K_{sat}= Hydraulic conductivity, OM= Organic matter

$$Q = CA\sqrt{2gh} \times 10^{-3}$$

Where: Q is the discharge (L s^{-1}), C is the coefficient of discharge, A is the area of pipe (cm^2), g is gravity acceleration (cm s^{-2}) and h is the effective head of water (cm). The rest required agricultural practices (*i.e.*, agronomic, crop disease, and pests, *etc.*) were managed according to the local guidance for wheat crop production.

Sampling and measurements

Leaf tissue's succulency, total chlorophyll content and photosynthetic efficiency: After excluding margins and leaf midrib, 10-discs of 2 cm-diameters were taken from five completely-extended fresh leaves from each treatment for measuring relative water content (RWC). These discs were weighed for recording fresh weight (FW) and later submerged, instantly; in distilled water in a dim place for 24 h. Water-drenched discs were taken out and wiped with tissue paper from adhering water drizzles for recording turgid weight (TW). The dry weight (DW) was recorded by weighing the discs after dried for 48 h at 70 ± 5°C. The leaf RWC% was computed through the next equation:

$$RWC\ (\%) = [(FW - DW)/(TW - DW)] \times 100$$

After excluding margins and leaf midribs, 200 mg sample of fresh leaf tissue was taken, parted to small pieces, and placed in 10 mL distilled water in boiling tubes for the determination of membrane stability index (MSI %) following the method outlined in Premchandra *et al*. (1990). At 40°C, these samples were then heated for 1/2 h using a water bath and a solution's electrical conductivity (EC_1) was measured by using a conductivity meter. At 100°C, a second sample for the same treatment was heated for 10 min and the solution's electrical conductivity (EC_2) was also recorded. The leaf MSI % was computed through the next equation:

$$MSI\ (\%) = [1 - (EC_1/EC_2)] \times 100$$

The 2nd and 3rd completely-extended top leaves were utilized to measure total leaf chlorophyll concentration by utilizing a SPAD-502 chlorophyll meter (KONICA MINOLTA, Tokyo, Japan). At a similar time on other leaves of the same plants in 2 different sunny days, chlorophyll fluorescence (F_v/F_m) along with photosynthetic performance index (PI) based on the similar absorption were measured as outlined in Maxwell and Johnson (2000) and Clark *et al*. (2000), respectively by utilizing a portable Handy-PEA fluorometer (Hansatech Instruments Ltd., Kings Lynn, U.K.).

Enzymatic and non-enzymatic antioxidant activities

The method of Bradford (1976) was applied for preparing the extraction from the plant tissues for utilizing as a crude enzyme extract for determination the enzymatic and non-enzymatic antioxidant activities. The nitro blue tetrazolium (NBT) procedure outlined in Giannopolitis and Ries (1977) was followed to assay the SOD (EC 1.15.1.1) activity, determining its Units as the amount of enzyme needed to inhibit 50% of the rate of NBT reduction as recorded at 560 nm. Assay of CAT (EC 1.11.1.6) activity was done according to Aebi (1983) method using potassium phosphate (pH 7) as a buffer in addition to H_2O_2 as a substrate. A decrease in absorbance rate at 240 nm as an outcome of H_2O_2 decomposition indicates the enzyme activity. Assay of APX (EC 1.11.1.11) activity was made as detailed in method of Rao *et al*. (1996) by measuring the optical density at 290 nm. The cellular activity of GR (EC 1.6.4.1) was assayed as described also by Rao *et al*. (1996) after monitoring GSH-dependent oxidation of NADPH for three absorbance times recorded at 340 nm. Nonetheless, the methods detailed by Mukherjee and Choudhuri (1983) and Griffith (1980) were applied for quantification of reduced glutathione (GSH) and ascorbic acid (AsA) contents, respectively, in fresh wheat leaf's tissues.

Osmoprotectants contents

The methods outlined in Bates *et al*. (1973) and Irigoyen *et al*. (1992) were applied for extraction and quantification of free proline (FP) and total soluble sugars (TSS) contents (mg g^{-1} DW), respectively, in fresh wheat leaf's tissues. Also, total soluble proteins (TSP) and total free amino acids (TFAA) were determined by adhering to the methods suggested by Bradford (1976).

Yield and related traits, and irrigation water use efficiency

At harvest, 10 plants $subplot^{-1}$ were randomly selected and carefully removed to determined grain yield components of wheat such plant height (cm), number of tillers $plant^{-1}$, spike length (cm), number of grains $spike^{-1}$ and 1000-grain weight (g). All the rest wheat plants of each subplot were harvested to estimate grain yield (t ha^{-1}), straw yield (t ha^{-1}) and biological yield (t ha^{-1}). Harvest index was calculated as ratio of the grain yield weight to biological yield expressed in percentage while irrigation water-use efficiency based on grain yield (G-IWUE) or straw yield (S-IWUE) was calculated according to the following both equations described by Jensen (1983).

$$G-IWUE = \text{Grain yield } (Kg\ ha^{-1})/\text{water applied } (m^3\ ha^{-1})$$

$$S-IWUE = \text{Straw yield } (Kg\ ha^{-1})/\text{water applied } (m^3\ ha^{-1})$$

Statistical analysis

The obtained data for each variable were subjected to two-way analysis of variance (ANOVA) using GenStat statistical package (12^{th} Ed., VSN International Ltd., Oxford, U.K.). In case of significant effects, the treatments means were separated using Duncan's new multiple range test at $P \leq 0.05$ probability level. Interaction between irrigation levels and Se levels was significant for all traits; there only interactions results are given.

Results

Leaf tissue's succulency, total chlorophyll content and photosynthetic efficiency

Interaction between DI and Se foliar application (DI × Se) had significant effect on leaf tissue's succulency (*i.e*., RWC and MSI), SPAD chlorophyll value, and photosynthetic efficiency indices (*i.e*., F_v/F_m and PI) of wheat in both years of study (Table 3). The combined application of Se_{25} or Se_{50} with DI_0 or DI_{20} contributed to produce more leaf tissue succulence, higher chlorophyll contents, and thereby better photosynthetic efficiency in both years of study (Table 3). The DI_0 × Se_{50} combination had resulted significantly higher SPAD chlorophyll and PI but it was at par with DI_{20} × Se_{50} during 1^{st} year while DI_0 × Se_{50} in the second season resulted higher RWC and Fv/Fm (Table 3). The highest MSI was obtained in DI_0 × Se_{25} in the first season and DI_0 × Se_{50} in the second season of study (Table 3). Moreover, no significant differences were found in RWC, SPAD chlorophyll, Fv/Fm, and PI between DI_0 × Se_{50} and DI_{20} × Se_{50} in both years. However, the lowest values of all parameters mentioned above were recorded in DI_{40} × Se_0 combination in both years of trial (Table 3).

Enzymatic and non-enzymatic antioxidant activities and osmoprotectants

Interaction between DI and Se foliar application (DI × Se) had significant effect on the activity of enzymatic (CAT, GR, SOD and APX), non-enzymatic (GSH and AsA) antioxidants, and accumulated osmoprotectants (TSS, TSP, TFAA and FP) of wheat during 2018–19 (Table 4). Wheat plants grown under severe drought (DI_{40}) with exogenous supplementation of Se_{50} compared to normal control (DI_0 × Se_0) significantly increased activities of CAT by 36%, GR by 306%, SOD by 140%, APX by 71%, GSH by 308, AsA by 71%, TSS by 78%, TSP by 96%, FP by 268%, and TFAA by 270% (Table 4).

Yield and related traits and irrigation water use efficiency (G-IWUE and S-IWUE)

Interaction between DI and Se foliar application (DI × Se) had significant effect on entire yield related traits and water use efficiency (WUE) wheat during both study years (Tables 5 and 6). The DI_0 × Se_{25} combination recorded the highest plant height, number of tillers $plant^{-1}$, spike length, number of grains $spike^{-1}$, 1000-grain weight and harvest index but it was at par with DI_{20} × Se_{25} combination for most of above said traits. However, the lower values of the abovementioned traits were recorded under DI_{40} × Se_0 (Table 5). The best result for biological, grain and straw yields was obtained in wheat plants supplied by Se_{50} and Se_{25} under normal irrigation (DI_0) conditions in both seasons. There were non-significant differences in grain yield among DI_0 × Se_{50}, DI_0 × Se_{25}, DI_{20} × Se_{25}, and DI_{20} × Se_{50} combinations in the first season, straw yield among DI_0 × Se_{25}, DI_0 × Se_{50}, and DI_{20} × Se_{50} combinations in both seasons and biological yield among DI_0 × Se_{25}, DI_0 × Se_{50}, and DI_{20} × Se_{50} combinations in the first season (Table 6). Moreover, DI_{40} × Se_{25} combination compared to DI_0 × Se_0 recorded more WUE, surpassed by 81 and 757% for G-IWUE in both seasons, respectively, while DI_{40} × Se_{25} surpassed DI_0 × Se_0 by 92% in the first season and DI_{40} × Se_{50} surpassed DI_0 × Se_0 by 90% in the second year of study for S-IWUE (Table 6).

Discussion

In this two-year field study, deficit irrigation (DI) resulted in reduced growth and productivity of wheat plants while

Table 3: Effect of deficit irrigation and selenium foliar application on leaf relative water contents, membrane stability index, SPAD chlorophyll, chlorophyll fluorescence and photosynthetic performance index of wheat plants

Deficit irrigation (DI)	Selenium (Se) levels (Mm)	RWC (%)		MSI (%)		SPAD chlorophyll		F_v/F_m		PI	
		2017–18	2018–19	2017–18	2018–19	2017–18	2018–19	2017–18	2018–19	2017–18	2018–19
	Se_0 (tap water)	86.8bc	85.8c	47.8cd	49.9ce	43.4ac	42.6bc	0.80ab	0.81bd	2.2d	3.2bd
DI_0	Se_{25}	88.6ab	88.6b	67.8ab	67.9ab	45.8ab	45.5ab	0.82a	0.82ac	4.3bc	4.4b
	Se_{50}	90.0a	93.0a	78.3a	74.7a	49.7a	48.3a	0.81a	0.83a	5.9a	6.1a
	Se_0 (tap water)	86.0cd	82.3de	44.1d	41.5ef	38.3cd	39.6cd	0.78bc	0.80cd	2.5d	2.7cd
DI_{20}	Se_{25}	82.4ef	83.5cd	57.9bc	56.9bd	41.6bc	41.1bd	0.81a	0.81a–d	4.2bc	3.9bc
	Se_{50}	90.5a	91.5a	66.2b	59.7bc	47.1ab	45.2ab	0.82a	0.83ab	5.0ab	6.0a
	Se_0 (tap water)	77.2g	78.9f	32.5e	34.5f	28.8e	26.1e	0.73d	0.73e	2.5d	2.0d
DI_{40}	Se_{25}	81.3f	80.5ef	44.2d	46.5df	34.4de	37.9d	0.75c	0.79d	3.5c	2.9cd
	Se_{50}	84.4de	82.3de	51.2cd	55.3cd	38.5cd	38.3cd	0.81a	0.80cd	3.5c	3.6bc

Means followed by the same letter in each column are not significantly different according to Duncan's test ($P \leq 0.05$)
DI_0, DI_{20}, and DI_{40} refer to 100%, 80% and 60% of ET_c, respectively, Se_0= tap water, Se_{25}= 25 m*M* Se, and Se_{50}= 50 m*M* Se, RWC= Relative water content, MSI= Membrane stability index, F_v/F_m= Efficiency of PSII maximal quantum, PI= Performance index of photosynthesis

Table 4: Effect of deficit irrigation and selenium foliar application on the activity of enzymatic and non-enzymatic antioxidants and osmoprotectants of wheat

Deficit Irrigation (DI)	Selenium (Se) levels (Mm)	Enzymatic activity				Non-enzymatic activity		Osmoprotectants			
		CAT	GR	SOD	APX	GSH	AsA	TSS	TSP	TFAA	FP
		(μmol mg^{-1} protein)				(mmol g^{-1} DW)		(mg g^{-1} DW)			
DI_0	Se_0 (tap water)	0.152h	0.115h	0.223i	0.215h	0.149h	0.269g	0.126f	1.01i	0.167e	0.117h
	Se_{25}	0.157g	0.150f	0.243h	0.226g	0.195f	0.277f	0.146e	1.47g	0.183e	0.128g
	Se_{50}	0.175c	0.238e	0.333f	0.331d	0.308e	0.414c	0.173c	1.56d	0.220d	0.154f
DI_{20}	Se_0 (tap water)	0.161d	0.124g	0.262g	0.221gh	0.161g	0.283f	0.156d	1.40h	0.337c	0.236e
	Se_{25}	0.167f	0.239e	0.375d	0.318e	0.309e	0.398d	0.173c	1.50f	0.345c	0.242e
	Se_{50}	0.172e	0.267d	0.363e	0.339c	0.347d	0.423b	0.186b	1.55e	0.366c	0.256d
DI_{40}	Se_0 (tap water)	0.170d	0.277c	0.485c	0.273f	0.360c	0.342e	0.174c	1.95c	0.572b	0.395c
	Se_{25}	0.194b	0.286b	0.526b	0.354b	0.371b	0.454a	0.182b	1.96b	0.620a	0.415b
	Se_{50}	0.206a	0.467a	0.534a	0.367a	0.608a	0.459a	0.224a	1.98a	0.618a	0.430a

Means followed by the same letter in each column are not significantly different according to Duncan's test ($P \leq 0.05$)
DI_0, DI_{20}, and DI_{40} refer to 100%, 80% and 60% of ETc, respectively, Se_0= Tap water, Se_{25}= 25 m*M* Se, Se_{50}= 50 m*M* Se, CAT= Catalase, GR= Glutathione reductase, SOD= Superoxide dismutase, APX= Ascorbate peroxidase, AsA= Ascorbic acid, GSH= Glutathione, TSS= Total soluble sugars, TSP= Total soluble proteins, TFAA= Total free amino acids, FP= Free proline

foliar application of Se counteracted the negative effects of DI to a certain extent on wheat growth and yield. Drought stress, caused by DI, not only reduced leaf tissue's succulency which negatively affected health of leaf tissues but also deactivated photosynthetic efficiency and consequently reduced wheat yield (Tables 3–6). However, Se foliar application reduced the harmful effects of DI and increases resistance to drought in wheat plants through its regulatory role in photosynthetic efficiency, enzymatic and non-enzymatic anti-oxidants, and osmoprotectants accumulation (Tables 3 and 4).

Foliar Se-supplement found to be effective in increasing the wheat plant tolerance to drought stress induced by DI through improving RWC, MSI, SPAD chlorophyll, F_v/F_m, and PI (Nawaz *et al.* 2015; Sattar *et al.* 2019; Table 3). The sustentation of leaf tissue's succulency is viewed as a main defending mechanism against dehydration stress (Kaldenhoff *et al.* 2008). However, foliar application of Se_{25} or Se_{50} recovered DI-stressed wheat leaf tissues, improving their succulency in RWC and MSI terms. These positive results concerning leaf tissue's succulency might be attributed to the Se's role in regulating water status and reducing lipid peroxidation in drought-stressed wheat plants (Ahmad *et al.* 2016). It appears that this protective impact is owing to more active uptake of soil's water by the plant root system and maintenance of stabilities and integrity of cellular membranes, keeping the leaf tissues in a better healthiness state (Hartikainen *et al.* 2000; Mekdad and Shaaban 2020). Optimal exogenous supplementation of Se reduced the effect of DI stress and modulated the photosynthetic functions by reducing ROS production that partially accountable for photosynthetic pigments quenching (Feng *et al.* 2013) along with a maintenance of chloroplasts structure integrity from drought-induced destructive (Malik *et al.* 2012), causing increased chlorophyll pigment and its biosynthesizing enzymes activity in the plant tissues even under cases of excessive ROS production. Further, the Se-mediated up-regulation of many physio-biochemical and metabolic processes leads to F_v/F_m increment, total chlorophylls, and energizing of antioxidative machinery (Alyemeni *et al.* 2018), which reflect affirmatively in elevating photosynthesis efficiency in drought-stressed plants.

Moreover, foliar-applied Se improved the activity of enzymatic and non-enzymatic antioxidants, namely CAT, GR, SOD, APX, GSH, and AsA along with the osmotic solutes, namely TSS, TSP, TFAA, and FP under drought stress (Nawaz *et al.* 2016; Jiang *et al.* 2017; Sattar *et al.* 2019; Table 4). The Se-mediated activated effect for

Table 5: Effect of deficit irrigation and selenium foliar application on plant height, yield related traits and harvest index of wheat

Deficit Irrigation (DI)	Selenium (Se) levels (Mm)	Plant height (cm)		Number of tillers plant^{-1}		Spike length (cm)		Number of grains spike^{-1}		1000-grain weight (g)		Harvest index (%)	
		2017–18	2018–19	2017–18	2018–19	2017–18	2018–19	2017–18	2018–19	2017–18	2018–19	2017–18	2018–19
DI_0	Se_0 (tap water)	97.2ab	92.0c	3.0ab	2.4bc	11.2cd	10.4de	43.4d	47.4bc	44.3cd	45.9a	0.30cd	0.31ab
	Se_{25}	102.0a	99.4a	3.0ab	3.4a	14.6a	14.6a	60.8a	58.2a	50.2a	47.8a	0.38ab	0.36a
	Se_{50}	99.6ab	99.4a	3.4a	3.2ab	13.2ab	13.0b	56.0b	52.8ab	47.2b	46.8a	0.39a	0.36a
DI_{20}	Se_0 (tap water)	89.0c	91.0c	3.0ab	2.2c	11.0cd	10.4de	43.6d	43.8cd	44.0d	42.6b	0.32cd	0.31ab
	Se_{25}	95.4abc	96.0b	2.6bc	2.8abc	12.2bc	11.8bcd	47.4cd	46.8bc	46.3bc	45.9a	0.36abc	0.34ab
	Se_{50}	97.4ab	96.0b	3.0ab	2.8abc	11.8cd	12.8bc	51.0c	49.2bc	45.9bcd	47.3a	0.34bcd	0.32ab
DI_{40}	Se_0 (tap water)	88.4c	85.8d	1.8d	2.0c	10.0d	9.8e	33.0e	37.6d	40.7e	41.9b	0.28d	0.28b
	Se_{25}	88.8c	92.2c	2.6bc	2.4bc	11.0cd	11.0de	44.2d	43.8bcd	44.8cd	43.6b	0.33cd	0.32ab
	Se_{50}	94.4bc	92.0c	2.2cd	2.4bc	12.0bc	11.4cd	45.0d	40.2cd	44.9cd	43.6b	0.31cd	0.30ab

Means followed by the same letter in each column are not significantly different according to Duncan's test ($P \leq 0.05$)
DI_0, DI_{20}, and DI_{40} refer to 100%, 80% and 60% of ETc, respectively, Se_0= Tap water, Se_{25}= 25 m*M* Se, Se_{50}= 50 m*M* Se

Table 6: Effect of deficit irrigation and selenium foliar application on grains, straw and biological yields, and irrigation use efficiency of wheat

Deficit Irrigation (DI)	Selenium (Se) levels (Mm)	Biological yield (t ha^{-1})		Grain yield (t ha^{-1})		Straw yield (t ha^{-1})		G-IWUE (kg m^{-3})		S-IWUE (kg m^{-3})	
		2017–18	2018–19	2017–18	2018–19	2017–18	2018–19	2017–18	2018–19	2017–18	2018–19
DI_0	Se_0 (tap water)	13.35d	14.03d	5.17bc	4.39d	8.18d	9.63b	0.99d	0.91d	1.56e	2.00e
	Se_{25}	18.89a	19.69a	6.87a	7.27a	12.03a	12.42a	1.31bc	1.51ab	2.30c	2.59cd
	Se_{50}	19.10a	18.21b	7.05a	6.51b	12.05a	11.70a	1.35bc	1.36b	2.30c	2.43d
DI_{20}	Se_0 (tap water)	12.62d	13.83d	4.45cd	4.49d	8.17cd	9.33b	1.02d	1.12c	1.88d	2.33d
	Se_{25}	16.21b	17.48b	6.65a	5.81c	9.56b	11.66a	1.53b	1.45ab	2.20c	2.92bc
	Se_{50}	18.19a	17.37b	6.45a	5.61c	11.74a	11.76a	1.49b	1.51ab	2.70b	2.94bc
DI_{40}	Se_0 (tap water)	10.86e	11.70e	3.86d	3.34e	6.99c	8.37b	1.24c	1.10c	2.24c	2.76cd
	Se_{25}	14.94c	14.63d	5.56b	4.85d	9.38bc	9.78b	1.79a	1.59a	3.00a	3.23b
	Se_{50}	13.07d	16.07c	4.35cd	4.59d	8.72bcd	11.49a	1.40bc	1.51ab	2.80ab	3.79a

Means followed by the same letter in each column are not significantly different according to Duncan's test ($P \leq 0.05$)
DI_0, DI_{20}, and DI_{40} refer to 100%, 80% and 60% of ETc, respectively, Se_0= Tap water, Se_{25}= 25 m*M* Se, and Se_{50}= 50 m*M* Se, G-IWUE= Irrigation use efficiency based on grain yield, S-IWUE= Irrigation use efficiency based on straw yield

enzymatic and non-enzymatic antioxidants might be attributed to selenium's vital role in stimulating the gene expression responsible for the antioxidant defense system, and thereby increased the SOD, CAT, and APX activities, finally leading to improved plant tolerance to drought stress (Jiang *et al*. 2017). Further, the activation of antioxidant defense system components under drought stress may also be ascribed to the substantially antagonistic influences of Se element due to ROS over-production by activating the determined enzymes that help in detoxification of $O_2^{\bullet-}$, H_2O_2, lipid peroxidation in MDA terms, and reduce the generation of a very toxic $OH^{\bullet}$ (Rady *et al*. 2020). Further, both AsA and GSH act a protective role versus oxidative stress along with lipid peroxidation prompted by abiotic stresses, including drought due to their antioxidative capacities (Rady *et al*. 2018; Agami *et al*. 2019). Therefore, increased GSH and AsA activities through the AsA-GSH cycle under drought stress may be involved in reducing ROS levels in droughted Se-treated wheat plants (Table 4). The incrementing concentrations of both AsA and GSH with Se addition indicate betterment in the AsA-GSH cycle, which acts against a redundant ROS and further controls H_2O_2 produced in stressed plant cells (Noctor and Foyer 1998). Increasing TSS in drought stressed Se-treated wheat plants may be related to Se's role in stimulating carbohydrates metabolism enzyme activities mainly fructose 1, 6-diphosphatase and carbonic anhydrase (CA) (Owusu-Sekyere *et al*. 2013), where CA is activated indirectly through enhancing FP content (Hayat *et al*. 2013). However, the improvement of biosynthesis and accumulation of TSP, TFAA, and FP in Se-treated plants was for altering cellular osmoregulation adjustment in water-stressed plants.

Deficit irrigation substantially decreased the wheat yield due to significant cut in entire yield related traits like population of productive tillers, and grains count and size (Hussain *et al*. 2016; Tables 5 and 6). Nonetheless, the deleterious effects of DI stress on the grain yield components were decreased by the exogenous suppling of Se (Tables 5 and 6) and similar trends were also noted by Tadina *et al*. (2007), Hajiboland *et al*. (2015), and Shahzadi *et al*. (2017) in wheat crop. These findings may indicate the simulative effect of Se application in improving elongation and activity of plant root, and consequently increased uptake and movability of water and nutrients from the soil to plant (Ashraf *et al*. 1998), which may positively be reflected in enhancing root cells division, its enlargement, and whole aerial parts growth (Yao *et al*. 2013).

Furthermore, the interaction between DI and Se showed that Se_{25} in most cases markedly improved wheat plant performance under normal (DI_0) and water deficit (DI_{20}) conditions. The betterment of growth and grain yield components may be due to that Se positively affected cells of leaf mesophyll and root as an adaptive response to drought conditions by maintaining stability and correct permeability of their membranes (Akladious 2012). Further, Se might helped to mitigate drought stress by supporting root growth, increasing chlorophyll and carotenoids pigments (Sharma *et al*. 2010; Lan *et al*. 2019), starch in chloroplasts (Malik *et al*. 2011), and mitochondrial respiration potential (Germ *et al*. 2007). It also promoted nutrients uptake (particularly K^+), which has a critical role in cellular osmoregulation, cell membrane polarization, and nitrate absorption (Shin 2014).

Results revealed marked increase in wheat yields in biological, grain and straw terms as well as G-IWUE and S-IWUE under DI conditions by foliar application of Se (Table 6). This might be due to the positive influences of Se on leaf tissue's succulency by keeping on cell turgor and cell membrane integrity (increases in RWC and MSI), total chlorophyll content (increase in SPAD chlorophyll), photosynthetic efficiency (increases in F_v/F_m and PI), which benefit wheat plants to yield more dry biomass under normal and DI stress conditions (Tables 3–6). Also, the boosted activity of the antioxidant defense machinery and compatible osmoprotectants might had induced nutrients uptake along with translocating of photo-assimilated products to shoot (Nawaz *et al*. 2015) to improve wheat productivity and WUE in terms of G-IWUE and S-IWUE (Nawaz *et al*. 2017; Shahzadi *et al*. 2017).

Conclusion

Higher photosynthetic efficiency and leaf tissue's succulency coupled with enzymatic and non-enzymatic antioxidants activity of Se-treated plants might be responsible for the enhanced growth and productivity of wheat plants under DI. The regulatory and protective role of Se may also be associated with enhancement of osmoprotectants *i.e*., TSS, TSP, TFAA, and FP, which together, increased G-IWUE and S-IWUE under DI. Se foliar application may therefore find in future a potential application as anti-abiotic stresses for improving plant growth and productivity under deficit irrigation by 20–40%.

Author Contributions

All authors contributed equally to this work.

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