Chlorophyll fluorescence, yield and yield components of bread wheat affected by phosphate bio-fertilizer, zinc and boron under late-season heat stress

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Abstract

We examined effects of late-season heat stress (L-SHS) on chlorophyll (Chl) fluorescence parameters and yield of bread wheat as well as roles of phosphate bio-fertilizer (PB-F) and Zn and B to compensate for the likely effects of heat stress. Factors were planting date (21 November and 5 January to coincide with grain filling to L-SHS) as the main factor, no inoculation (control) and inoculation of the seeds with PB-F as the sub-factor, and foliar application of water (control), Zn, B, and Zn + B as 3 L ha^{-1} as sub-sub factor. Results revealed that L-SHS reduced maximal quantum yield of PSII photochemistry, effective quantum yield of PSII photochemistry, efficiency of PSII in the light-adapted state, and the grain yield. Moreover, L-SHS increased the nonphotochemical quenching. The PB-F mitigated the effects of L-SHS on Chl fluorescence, yield, and yield components. Among nutrients, the combined Zn + B was more effective in reducing the effects of L-SHS than that of Zn and B alone. Nevertheless, there was an interaction between foliar nutrients application and PB-F, suggesting that Zn application alone had a profound influence on improving Chl fluorescence parameters and increased yield in combination with PB-F.

Additional key words: photosynthesis; plant nutrition; *Triticum aestivum* L.

Introduction

Wheat (*Triticum aestivum* L.), as a major source of human food, is grown in a vast area of cultivated lands mostly located at altitudes from a few meters to more than 3,000 m a. s. l. (Ahmed and Farooq 2013). High temperature and drought are two major environmental factors limiting the growth and productivity of wheat (Prasad *et al.* 2011). Heat stress affects many cellular processes in plants, resulting in physiological, morphological, and biochemical changes (Zhang *et al.* 2016). Terminal or late heat stress during the last phases of wheat development, especially in booting, heading, anthesis and grain filling stages of the spring, is considered one of the major environmental constraints that drastically reduces grain yield and yield components of wheat in Khouzestan province and other warm and dry regions of Iran (Modhej *et al.* 2008). For optimum growth and yield, wheat plants need phosphorus (P) as a macronutrient and its role irreplaceable (Mohammadi 2012). Phosphate biofertilizers (PB-F), bacteria, such as *Bacillus* and *Pseudomonas*, increase soil soluble P by secreting organic acids and phosphatase enzyme (Ehteshami *et al.* 2007). The supply of P promotes the development of roots, flowers, and fruits formation, the rate of plant maturation, the efficiency and quality of crops, and the resistance to both biotic and abiotic environmental factors (Mohammadi 2012). Most of the Iranian soils, have a high pH and calcareous nature (Abdoli *et al.* 2014) and micronutrients solubility in these soils is low (Mousavi *et al.* 2007). It is believed that micronutrients foliar application is more effective in controlling deficiency problem than soil application (Torun *et al.* 2001). Micronutrients significantly affect dry matter, grain yield, and straw yield in wheat (Asad and Rafique 2000). Zinc is a ubiquitous micronutrient. It is required as a structural and functional component of many enzymes and proteins, and increases the yield and yield components of wheat (Jafari Moghadam *et al.* 2012). Boron is essential for pollen viability, flowering, fruiting, and seed production. As a micronutrient, it plays

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Abbreviations: Chl – chlorophyll; FA – foliar application of Zn and B; F_v/F_m – maximal quantum yield of PSII photochemistry; F_v'/F_m' – efficiency of PSII in the light-adapted state; LPD – late planting date; L-SHS – late-season heat stress; N-HS – no heat stress; NPQ – nonphotochemical quenching; OPD – optimum planting date; PB-F – phosphate bio-fertilizer; ROS – reactive oxygen species; Φ_{PSII} – effective quantum yield of PSII photochemistry.

a vital role in nitrogen metabolism, hormonal action, and cell division (BARI 2006). Boron foliar application at reproductive stage improves the grain yield of wheat (Ali *et al.* 2009). Boron can increase antioxidant activities of plants, thereby alleviating reactive oxygen species (ROS) damage induced by heat stress (Waraich *et al.* 2011). The role of B in regulation of the gene expression or regulation of the activity of certain antioxidant enzymes, *e.g.*, superoxide dismutase and catalase, has been proved (Keles *et al*. 2011).

Nowadays, Chl fluorescence has been used as an indicator of the level of stress. The advantage of this technique over many other techniques is that it provides rapid and nondestructive measures. Graham and McDonald (2001) showed that the decline in maximal quantum yield of PSII photochemistry (F_v/F_m) due to high temperature can be reduced by elevated Zn fertilization, at least in a Zn-inefficient wheat genotype. High temperature reduces effective quantum yield of PSII photochemistry (Φ_{PSII}) and nonphotochemical quenching (NPQ) (Hassan 2006). The Φ_{PSII} reflects the fraction of radiation absorbed by PSII that is used in photochemistry (Demmig-Adams and Adams 1992) and it is a good indicator of the effects of environmental stress on photosynthesis. PSII plays an important role in the response of plants to environmental stresses and it is a very sensitive component of the photosynthetic apparatus (Yordanov *et al.* 2000). Chl fluorescence parameters, such as minimal (F_0'), maximal (F_m'), variable (F_v'), and steady-state (F_s) fluorescence yields, F_v/F_m, F_v'/F_m', Φ_{PSII}, and NPQ serve as indicators of plant stress and have been utilized to assess the plant nutrient status and health (Netto *et al.* 2005). Under stress conditions, such as nutrient stress, decline in CO_2 assimilation also reduces the consumption of the chemical energy created in the light reaction of photosynthesis, which leads to the over-excitation of PSII reaction center due to continuing photon absorption by Chl molecules (Singh and Reddy 2016). This excess energy must be dissipated for optimum performance of photosystems and to avoid photoinhibition. Plants possess mechanisms to dissipate the excess excitation energy as heat, re-emite as Chl fluorescence or by nonradiative mechanisms (Ivanov *et al.* 2008). Singh and Reddy (2016) suggested the decrease in Chl concentration as a mechanism to avoid excessive light harvesting to protect PSII from photodamage under P deficiency. Graham and McDonald (2001) revealed that the decline in F_v/F_m due to high temperature can be lowered by elevated Zn fertilization, at least in a Zn-inefficient wheat genotype. In addition, Guidi *et al.* (2011) reported an increase in Chl fluorescence parameters, such as F_v/F_m, Φ_{PSII}, and NPQ, as a result of boron application. The aim of this study was to evaluate the effect of PB-F and foliar application of Zn and B to reduce the harmful effects of L-SHS on Chl fluorescence parameters, yield, and yield components of common bread wheat.

Materials and methods

Experimental site: A field experiment was performed during 2015–2016 in Ramhormoz city, Khouzestan province, Iran. Site altitude was 160 m above sea level (31°16' N, 49°37' E). Farm soil was silty clay and alkaline (pH 7.64) with 0.92% organic carbon, 18.6 mg(available P) kg^{-1}, and 140 mg(available K) kg^{-1}. Soil physical and chemical properties of experimental location are shown in the table:

B [mg kg^{-1}]	Zn [mg kg^{-1}]	Fe [mg kg^{-1}]	Cu [mg kg^{-1}]	Soil texture	Clay [%]	Silt [%]	Sand [%]	K [mg kg^{-1}]	P [mg kg^{-1}]	O.C [%]	pH	E.C [ds m^{-1}]
0.71	0.63	2.8	0.9	Silty clay	47	42	11	140	18.6	0.92	7.6	5.8

The available P and K were determined according to Olsen *et al*. (1954) and normal and neutral ammonium acetate methods, respectively (Page *et al*. 1982). The available B was determined by the azomethine-H method (Wolf 1974), and the available Zn, Cu, and Fe were determined by extraction method with diethylenetriamine pentaacetic acid (DTPA) (Sparks *et al*. 1996). The amounts of K and other available nutrients were determined before adding any fertilizer to the soil. Temperature, precipitation and relative humidity during the experimental period are shown in the table:

Month	Mean of air temperature [°C] Maximum	Minimum	Average	Precipitation [mm]	RH [%]
November	31.5	17.2	24.3	20.7	42
December	25.3	11.1	18.2	64.4	59
January	18.1	8.8	13.4	57.7	67
February	19.3	9.1	14.2	49.7	62
March	24.7	12.2	19.8	40.4	52
April	32.5	16.7	24.6	29.4	43
May	38.1	23.2	30.6	29.6	43

The average minimum and maximum temperature at the test site during the grain filling period for optimum and late planting dates were 18 and 32°C, and 22 and 38°C, respectively. During the grain filling and maturity stages, the mean of the canopy temperature depression for the LPD in all applied treatments decreased by about 3 and 5°C compared to the OPD, respectively.

Experimental design, treatments and plant material: The field experiment was arranged in a split-plot factorial design based on randomized complete blocks with 16 treatments and 3 replications. Experimental treatments included optimum planting date (OPD) (21 November) and the late planting date (LPD) (5 January) to coincide with the grain filling stage to L-SHS (Radmehr 1997) as the main factor, PB-F [no inoculation (control) and inoculation of the seeds with PB-F] as the sub-factor, and four levels of foliar application of water (control), Zn [3 L ha^{-1} of liquid Zn-EDTA chelate from *ZARAFSHAN Co*., containing 7.5% of Zn; as 3:1,000 (v/v) in water], B [3 L ha^{-1} of boric acid from *ZARAFSHAN Co*., containing 5% of B, as 3:1,000 (v/v) in water], and Zn (3 L ha^{-1}) + B (3 L ha^{-1}), as sub-sub factor. Total applied Zn and B in foliar application was 675 g(pure Zn) ha^{-1} and 450 g(pure B) ha^{-1}. This amount of fertilizers was sprayed three times at tillering, booting, and anthesis stages to the wheat plants. Treatments were applied to Aflak wheat cultivar (Debeira) which was recommended for planting in warm and dry areas such as the site of our experiment.

Each plot had seven rows of planting. The row spacing was 20 cm, and row length was 3 m. The seeds were sown at a depth of 3 cm by hand with a planting density of 400 plants m^{-2}. Before planting, seed inoculation was performed with the package content of 100 g of bio-fertilizer (*Barvar 2*) containing phosphate solubilizing bacteria such as *Bacillus* and *Pseudomonas*. *Barvar 2* is a phosphate bio-fertilizer designed for all agricultural purpose, all types of crops and trees that reduce the need for phosphate chemical fertilizer for at least 50%. Weeds were manually controlled in all treatments (Ehteshami *et al.* 2007). Fertilizer recommendations based on soil analysis results were applied including 300 kg(sulfur) ha^{-1}, 150 kg(potassium sulfate) ha^{-1}, and 350 kg(urea) ha^{-1}. Sulfur, potassium, and one-third of urea fertilizers were applied at sowing and the remaining part was applied during the beginning of stem elongation and flowering stages. Irrigation, fertilization, and weeds, pests, and diseases control were performed regularly to avoid any stress except the L-SHS. The water requirement for irrigation estimated about 550 mm using equation 1 (Gholinezhad *et al*. 2009), which supplied about 230 and 140 mm of it for OPD and LPD by rainfall, respectively.

$$V = [(FC - \theta m) \times \rho m \times D_{root} \times A]/IE \quad (1)$$

where, V is irrigation water volume (mm); FC is field capacity; θm is soil mass moisture percentage; ρm is soil external specific density (g cm^{-3}); D_{root} is root development depth (m); A irrigated area (m^2); and IE is irrigation efficiency. Irrigation was carried out by surface (furrow) method and at germination, emergence, tillering, stemming, heading, flowering, and seed filling stages and when the average soil moisture reached less than 50% of the available moisture content. For determining soil moisture, samples were taken from depth of 0–30 and 30–60 cm. Then moisture percentage was determined by pressure plate (armfield CAT.REF: FEL13B-1 Serial Number: 6353 A 24S98) (Gholinezhad *et al.* 2015). The harvesting time for OPD and LPD were 21 April and 7 May, respectively. During this period of about 17 d, the air temperature increased by about 6°C. It was also observed that from the grain filling stage to the maturity, the number of days with a temperature higher than 32°C at LPD was about 17 d; it was about 1 d during OPD.

Chl fluorescence: Chl fluorescence was measured with a portable photosynthetic efficiency analyser (*PEA*, *Hansantech Instrumental*, Hardwick, Norfolk, UK). Flag leaves were dark-adapted for 30 min in leaf clips before measurements. Chl fluorescence parameters, such as F_v/F_m, Φ_{PSII}, F_v'/F_m', and NPQ were calculated according to van Kooten and Snel (1990) and using the following equations:

$$F_v/F_m = (F_m - F_0)/F_m \quad (2)$$

$$\Phi_{PSII} = (F_m - F_t)/F_m' \quad (3)$$

$$F_v'/F_m' = (F_m' - F_0')/F_m' \quad (4)$$

$$NPQ = (F_m - F_m')/F_m' \quad (5)$$

where, F_v/F_m is the maximum quantum efficiency of PSII in the dark-adapted state; F_m is the maximum fluorescence (in the dark-adapted leaf); F_0 is the minimum fluorescence (dark); F_v is the variable fluorescence (dark) ($F_m - F_0$); Φ_{PSII} is the quantum efficiency of PSII; F_t is the fluorescence emitted by the leaves adapted to light; F_m' is the maximum fluorescence (light); F_v'/F_m' is the maximum quantum efficiency of PSII in the light-adapted state; F_0' is the minimum fluorescence (light); F_v' is the variable fluorescence (light) ($F_m' - F_0'$); and NPQ is the nonphotochemical quenching. Measurements were taken between 10:00–14:00 h from 10 flag leaves at the grain filling stage. During the measurement of Chl fluorescence parameters, the air temperature for optimum and late dates were 28 and 37°C, respectively.

Grain yield and yield components: The inner two rows of each plot were harvested to estimate the grain yield at maturity, and a sample of one square meter was obtained to determine the number of spikes m^{-2}, number of grain per spike, 1,000-grain mass, and grain yield.

Statistical analysis: Analysis of variance (*ANOVA*) was performed using general linear model (GLM) procedure of statistical analysis system (*SAS version: 9.1*). The means were analyzed using the least significant difference (LSD) method at *P*=0.05 (LSD 0.05).

Results

Grain yield and its compoments

Number of spikes per area: L-SHS, PB-F, and foliar application treatments had significant effects on the number of spikes m^{-2} (Table 1). L-SHS significantly reduced the number of spikes by 13% compared to N-HS. However, seed inoculation with PB-F and foliar application of Zn and B significantly reduced the harmful effects of L-SHS on the number of spikes by 5.9 and 5%, respectively, compared with control (Tables 1, 2). The maximum and minimum values were obtained after the combined treatments, namely PB-F + Zn foliar application under N-HS, and non-inoculation of the seeds with PB-F + water foliar application under L-SHS (Table 2).

Table 1. Analysis of variance for yield, yield components and chlorophyll fluorescence parameters, such as F_v/F_m – maximal quantum yield of PSII photochemistry; Φ_{PSII} – effective quantum yield of PSII photochemistry; F_v'/F_m' – efficiency of PSII in the light-adapted state; and NPQ – nonphotochemical quenching of bread wheat affected by PB-F – phosphate bio-fertilizer and FA of Zn and B – foliar application of zinc and boron under L-SHS – late-season heat stress. ns, * , and ** – not significant, significance at the 0.05 and 0.01 probability level, respectively.

Sources Changes	DF	Number of spikes [m^{-2}]	Number of grain $spike^{-1}$	1,000- grain mass	Grain yield	F_v/F_m	Φ_{PSII}	F_v'/F_m'	NPQ
Block	2	4.32^{ns}	0.092^{ns}	0.672^{ns}	234.3^{ns}	3×10^{-6ns}	4×10^{-6ns}	3×10^{-6ns}	2×10^{-6ns}
L-SHS	1	$50,659.81^{**}$	108.76^{**}	276.73^{**}	$9,629,107.66^{**}$	$33\times10^{-4**}$	$99\times10^{-4**}$	$49\times10^{-4**}$	0.1264^{**}
Error a	2	6.67	0.347	0.673	3,345.48	6×10^{-6}	6×10^{-6}	5×10^{-6}	6×10^{-6}
PB-F	1	$21,792.59^{**}$	29.98^{**}	38.36^{**}	$4,548,470.47^{**}$	$51\times10^{-4**}$	$63\times10^{-4**}$	$58\times10^{-4**}$	$10\times10^{-4**}$
FA (Zn and B)	3	$8,884.07^{**}$	138.92^{**}	61.37^{**}	$1,28,3540.14^{**}$	$36\times10^{-5**}$	$19\times10^{-4**}$	$19\times10^{-5**}$	$5\times10^{-5**}$
L-SHS×PB-F	1	141.53^{**}	2.31^{*}	0.027^{ns}	$167,825.58^{**}$	$2\times10^{-5*}$	$4\times10^{-5**}$	$24\times10^{-6*}$	$1\times10^{-5*}$
L-SHS×FA (Zn, B)	3	$14,401.76^{**}$	41.36^{**}	7.32^{**}	$1,848,486.96^{*}$	$1\times10^{-5*}$	$3\times10^{-5**}$	$2\times10^{-5*}$	4×10^{-6ns}
PB-F×FA (Zn, B)	3	111.87^{*}	27.2^{ns}	4.31^{**}	$638,874.08^{**}$	$52\times10^{-5**}$	$15\times10^{-4**}$	$74\times10^{-5**}$	$7\times10^{-5**}$
-SHS ×PB- ×FA (Zn, B)	3	154.06^{**}	12.33^{**}	0.743^{ns}	$16,518.91^{*}$	$14\times10^{-6**}$	$1\times10^{-5**}$	$16\times10^{-6**}$	$8\times10^{-6*}$
Error b	28	19.32	0.632	0.415	6,936.45	7×10^{-5}	8×10^{-5}	8×10^{-5}	6×10^{-5}

Table 2. Mean values for yield, yield components and chlorophyll fluorescence parameters, such as F_v/F_m – maximal quantum yield of PSII photochemistry; Φ_{PSII} – effective quantum yield of PSII photochemistry; F_v'/F_m' – efficiency of PSII in the light-adapted state; and NPQ – nonphotochemical quenching of bread wheat affected by PB-F – phosphate bio-fertilizer and FA of Zn and B – foliar application of zinc and boron under L-SHS – late-season heat stress; in a split-plot factorial design with three replications. Column means followed by *the same letter* are not significantly different at 0.05 probability level using LS means of *SAS*.

Treatments			Number of spikes m^{-2}	Number of grain $spike^{-1}$	Grain yield [kg h^{-1}]	F_v/F_m	Φ_{PSII}	F_v'/F_m'	NPQ
L-SHS	PB-F	FA							
N-HS	NPB-F	WFA	424^{g}	37.6^{g}	$4,730.67^{g}$	0.817^{def}	0.772^{fg}	0.803^{defg}	0.347^{c}
(OPD)		ZnFA	426^{g}	43.3^{de}	$5,388.21^{f}$	0.821^{de}	0.766^{gh}	0.796^{fghi}	0.348^{c}
		BFA	456^{f}	34.3^{i}	$5,379.82^{f}$	0.823^{de}	0.777^{efg}	0.809^{cdef}	0.349^{c}
		Zn+BFA	481^{d}	44.3^{cd}	$5,779.46^{e}$	0.830^{bcd}	0.803^{bc}	0.813^{cde}	0.352^{c}
	PB-F	WFA	532^{b}	45.3^{bc}	$5,925.53^{d}$	0.841^{abc}	0.793^{cd}	0.819^{bc}	0.357^{c}
		ZnFA	593^{a}	48.7^{a}	$7,751.55^{a}$	0.854^{a}	0.823^{a}	0.836^{a}	0.359^{c}
		BFA	483^{d}	36.3^{h}	$6,117.66^{c}$	0.832^{bcd}	0.786^{def}	0.817^{bcd}	0.353^{c}
		Zn+BFA	497^{c}	45.6^{b}	$6,474.06^{b}$	0.841^{abc}	0.815^{ab}	0.831^{ab}	0.359^{c}
HS	NPB-F	WFA	369^{k}	35.6^{h}	$3,464.39^{k}$	0.801^{g}	0.753^{hi}	0.785^{ij}	0.448^{b}
(LPD)		ZnFA	370^{k}	40.3^{f}	3977.68^{j}	0.802^{fg}	0.735^{j}	0.773^{j}	0.449^{b}
		BFA	383^{j}	38.6^{g}	3916.34^{j}	0.805^{fg}	0.747^{ij}	0.786^{hij}	0.451^{ab}
		Zn+BFA	412^{h}	41.1^{f}	3978.42^{j}	0.811^{efg}	0.775^{efg}	0.790^{ghi}	0.454^{ab}
	PB-F	WFA	392^{i}	42.3^{e}	4193.78^{i}	0.826^{cde}	0.763^{gh}	0.801^{efgh}	0.462^{ab}
		ZnFA	472^{e}	43.3^{de}	5843.53^{de}	0.843^{ab}	0.790^{cde}	0.822^{abc}	0.466^{a}
		BFA	$419g^{h}$	38.2^{g}	4344.33^{h}	0.812^{efg}	0.755^{hi}	0.797^{fghi}	0.454^{ab}
		Zn+BFA	423^{g}	44.1^{d}	4672.48^{g}	0.825^{de}	0.786^{def}	0.807^{cdef}	0.461^{ab}

Number of grains per spike: L-SHS, PB-F, and foliar application treatments significantly affected the number of grains per spike (Table 1). L-SHS reduced the number of grains by 5.3% compared to N-HS. Nonetheless, seed inoculation with PB-F and foliar application of Zn and B significantly reduced the harmful effects of L-SHS on the number of grains by 15.8 and 11%, respectively, compared with control (Tables 1, 2). The maximum and minimum values were obtained after the combined treatments, namely PB-F + Zn foliar application under N-HS, and NPB-F + B foliar application under N-HS (Table 2).

1,000-grain mass: L-SHS significantly reduced the 1,000-grain mass by 12.2% (Fig. 1*A*). Seed inoculation with PB-F significantly increased this parameter by 6.3% (Fig. 1*B*). In addition, Zn and B foliar application significantly increased the 1,000-grain mass (Fig. 1*C*). Among the interactions of L-SHS and nutrients foliar application, the maximum and minimum 1,000-grain mass were observed after the combined treatments of N-HS + B foliar application, and L-SHS + Zn + B foliar application (Fig. 1*D*). As well as, among the interactions of PB-F and nutrients foliar application, the maximum and minimum 1,000-grain mass were obtained in the combined treatments of PB-F + B foliar application, and NPB-F + Zn + B foliar application (Fig. 1*E*).

Grain yield: L-SHS, PB-F, and foliar application treatments significantly affected the grain yield. L-SHS significantly reduced the grain yield by 26.8% compared to N-HS. However, seed inoculation with PB-F and foliar application of Zn and B significantly reduced the harmful effects of L-SHS on the grain yield by 17.4 and 12.5%, respectively, compared with control (Tables 1, 2). The maximum and minimum grain yield were obtained in the combined treatments namely PB-F + Zn under N-HS, and NPB-F + water foliar application under L-SHS (Table 2).

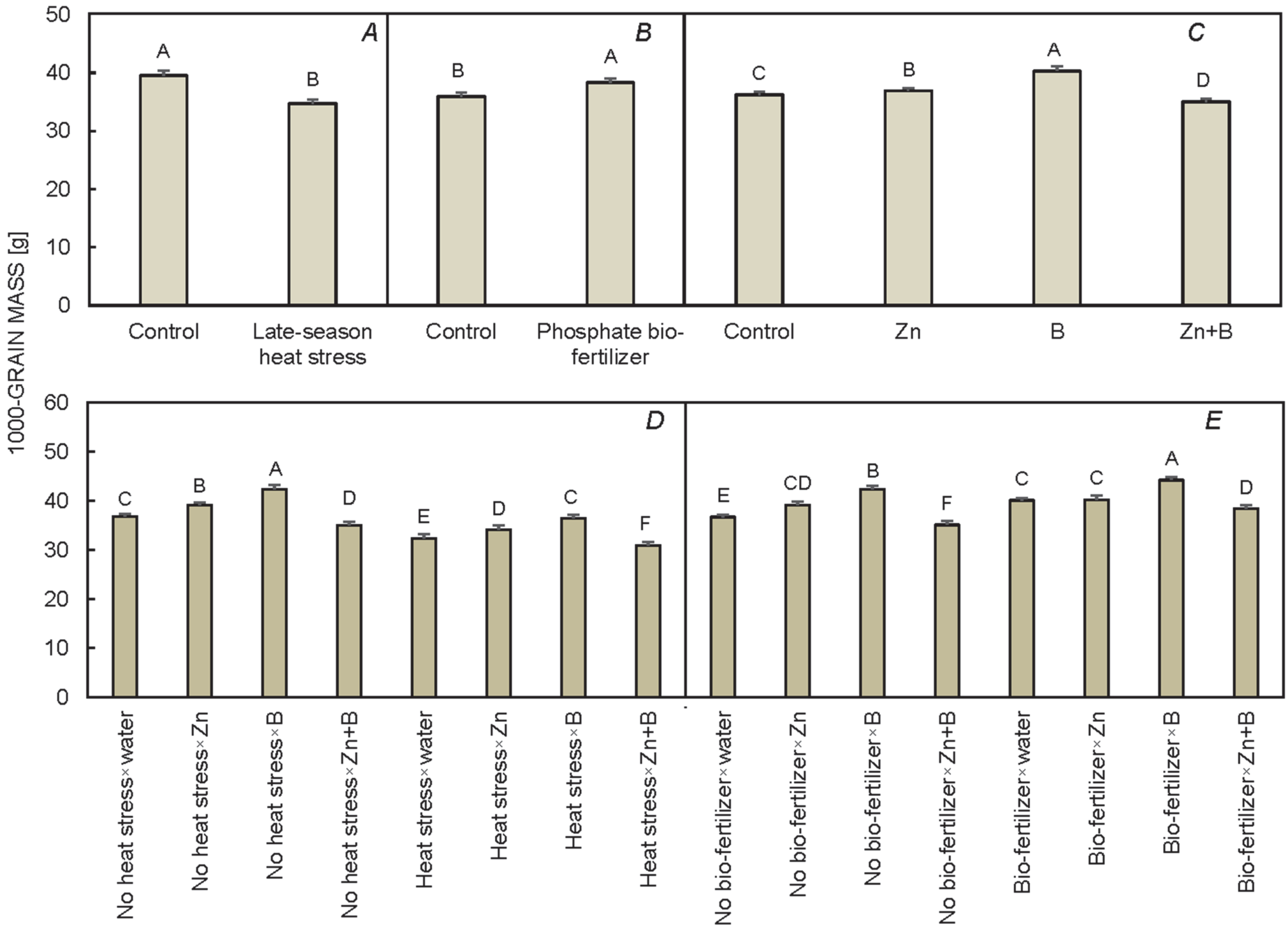

Fig. 1. Effect of LSHS (*A*), PBF (*B*), Zn and B foliar application (*C*), interaction of LSHS with foliar application of Zn and B (*D*) and interaction of PBF with foliar application of Zn and B (*E*) on 1000-grain mass of bread wheat.

Chl fluorescence parameters

F_v/F_m: L-SHS significantly reduced the F_v/F_m by 2%. However, seed inoculation with PB-F and application of Zn and B enhanced F_v/F_m under L-SHS (Table 2). The maximum and minimum of F_v/F_m was obtained in the combined treatments, namely PB-F + Zn foliar application under N-HS, and NPB-F + water foliar application under L-SHS (Table 2).

Φ_{PSII}: L-SHS significantly reduced Φ_{PSII}. However, seed inoculation with PB-F mitigated the effects of L-SHS on the Φ_{PSII} by 1.3%, but Zn and B application was not effective (Tables 1, 2). The maximum and minimum Φ_{PSII} was obtained in the combined treatments namely PB-F + Zn foliar application under N-HS, and NPB-F + Zn foliar application under L-SHS (Table 2).

F_v'/F_m': L-SHS significantly reduced F_v'/F_m'. However, seed inoculation with PB-F improved F_v'/F_m' by 2% under L-SHS, but Zn and B was not effective in reducing the harmful effects of L-SHS on F_v'/F_m' (Tables 1, 2). The maximum and minimum F_v'/F_m' was obtained in the combined treatments, namely PB-F + Zn foliar application under N-HS, and NPB-F + Zn foliar application under L-SHS (Table 2).

NPQ: L-SHS increased the value of NPQ by 22.5%. Nonetheless, seed inoculation with PB-F and Zn and B foliar application increased NPQ under L-SHS conditions (Table 2). The maximum and minimum value of NPQ was obtained in the combined treatments, namely PB-F and Zn foliar application under L-SHS, and NPB-F + water foliar application under N-HS (Table 2).

Discussion

The results in the current study have showed that the L-SHS, as a result of a delay in planting, significantly reduced the number of spikes, number of grains, 1,000-grain mass, and grain yield of bread wheat. In wheat, high temperature stress during reproductive development is a primary constraint to its production. Accumulation of ROS as a result of high temperature stress is a major cause of loss of crop productivity globally (Khan and Sing 2008, Gill *et al.* 2010). Formation of ROS is related to ethylene production and lipid peroxidation and results in membrane fluidity (Weckx *et al.* 1989). Increased ethylene has been shown in mature wheat plants to shorten the grain filling period, reduce 1,000-grain mass, hasten maturity, trigger premature senescence, and finally reduce the grain yield (Beltrano *et al.* 1999). Therefore, the cause of reduced yield and yield components of bread wheat under L-SHS can be due to the formation of ROS and subsequently ethylene production. Moreover, other researchers reported that grain filling period coincided with L-SHS due to delay in planting; resulting in decreasing yield and yield components of wheat (Ayeneh *et al.* 2002, Moshatati *et al.* 2012), which confirms the results of this experiment. Xiao *et al.* (2009) showed that if the temperature rises by 0.5–2.5ºC, the yield of spring wheat decreases by 16.5–18.5%. Moreover, it was reported that when the temperature increased by 1.0–2.5°C, the number of grains per spike and 1,000-grain mass decreased in spring wheat by 1.0–5.0, and 1.3–8.8 g, respectively (Zhang and Deng 2008). It can be due to negative effects of L-SHS causing shorter growth period, which leads to reduced dry matter accumulation and transfer, and decreases bread wheat yield. In addition, the L-SHS reduced the values of Chl fluorescence parameters, such as F_v/F_m, Φ_{PSII}, F_v'/F_m', indicating that a structural and functional disorder of the photosynthetic apparatus and damage to the PSII had occurred (Pereira *et al.* 2000, Murkowski 2001). Reductions in the F_v/F_m, Φ_{PSII}, and F_v'/F_m' under L-SHS suggested that an important portion of the PSII reaction centre was damaged under L-SHS. These damages were associated with structural modifications on PSII, especially in D1 protein, which under conditions of heat stress was phosphorylated and degraded afterwards (Asada *et al.* 1998). Furthermore, reduction in the F_v/F_m, Φ_{PSII}, and F_v'/F_m' also suggested the occurrence of photoinhibition and photodamage (Colom and Vazzana 2003). When this occurs, accumulation of reduced electron acceptors may increase the generation of ROS, which can induce oxidative injuries (Souza *et al.* 2004). These oxidative injuries could enhance Chl degradation or the inhibition of its biosynthesis (Papadakis *et al.* 2004), damage PSII components (Souza *et al.* 2004), inactivate many chloroplast enzymes, especially, those participating in CO_2 assimilation (Dekov *et al.* 2000). It could further explain the reductions in F_v/F_m, Φ_{PSII}, and F_v'/F_m' in the high temperature-stressed wheat plant in the present study. It was also observed that the L-SHS increased the value of NPQ. It seems that such an increase in NPQ may be a mechanism to downregulate photosynthetic electron transport so that production of ATP and NADPH would be in equilibrium with the decreased demand in the Calvin cycle in heat-treated leaves and to also avoid over-reduction of Q_A (Bukhov *et al.* 1998). Lu and Zhang (2000) showed that under heat-stress conditions, the decrease in F_v'/F_m' and Φ_{PSII} was associated with a decrease in F_v/F_m, and the decrease in F_v/F_m occurred due to a decrease in the OEC activity and an inhibition of electron transport at the PSII acceptor side. Increase in NPQ results in a decrease in F_v'/F_m' (Demmig-Adams *et al.* 1996). Therefore, the decrease in F_v/F_m, Φ_{PSII}, F_v'/F_m' under L-SHS was a result of the increased nonphotochemical dissipation of excitation energy. Seed inoculation with PB-F significantly increased the number of spikes, number of grains per spike, 1,000-grain mass, yield and yield components of bread wheat under both N-HS and L-SHS conditions.

It was observed that seed inoculation with PB-F increased the number of grains per spike by 17 and 15.8%

in both N-HS and L-SHS conditions, respectively, which could be the main reason for increase in wheat yield in this study. P is a component of nucleic acids and cellular membranes, and essential for metabolic processes and photosynthesis (Vance *et al.* 2003) and also for its role in reduction of ROS during environmental stresses (Wu *et al.* 2005, Behl *et al.* 2003). Therefore, increasing wheat yield is expected due to the using PB-F under L-SHS conditions. Decreases in plant yield due to nutrient stress including P have been previously reported in other crops and can be attributed to the limited availability of the plant resources such as phosphorus and decreased overall photosynthesis (Singh *et al.* 2013). Nezarat and Gholami (2009) attributed the increase in grain yield to bacteria existing in PB-F, such as *Bacillus* and *Pseudomonas*, which are able to enhance P solubility of rock phosphate and increase its availability for wheat by oxidizing P and decrease soil pH. Moreover, seed inoculation with PB-F increased the values of Chl fluorescence parameters, such as F_v/F_m, Φ_{PSII}, F_v'/F_m', and NPQ, which might be related to the regulatory role of P in CO_2 assimilation pathway, increase in the amount and activity of Rubisco, and ribulose-1,5-bisphosphate (RuBP) regeneration capacity (Fleisher *et al.* 2012). Shool and Shamshiri (2014) reported that the use of bio-fertilizer containing phosphate-solubilizing bacteria increased the values of Chl fluorescence parameters, such as F_v/F_m, Φ_{PSII}, and F_v'/F_m'. Xu *et al.* (2007) showed that the NPQ decreased in plants under P deficiency conditions. Severe decrease of Chl fluorescence parameters, such as F_v/F_m, F_v'/F_m', Φ_{PSII}, and electron transport rate (J_F) under P deficiency suggested the occurrences of excess energy dissipation by NPQ or non-radiative mechanisms in the PSII reaction center (Singh and Reddy 2015). Photosynthetic processes are dependent on the phosphate precursors, inorganic phosphate or phosphorylated intermediates, such as ADP, ATP, NADP(H) and sugar phosphates, essential for energy transfer. Therefore, P deficiency affects plant photosynthetic capacity due to its direct effect on the tissue P status and especially phosphorus homeostasis in the cytosol and chloroplasts (Warren 2011). Among nutrients foliar application treatments, the combined Zn + B was more effective to reduce harmful effects of L-SHS. However, among the combined application nutrients FA + PB-F, Zn separate application influenced more improvement of Chl fluorescence parameters and increase of yield and yield components of bread wheat under L-SHS.

Current study revealed that the combined application of Zn and B compared to Zn separate application increased number of spikes by 10.9% under L-SHS, however, combined application of PB-F + Zn was more effective for yield improvement. Also, the PB-F + Zn treatment induced the highest Chl fluorescence parameters, such as F_v/F_m, F_v'/F_m', Φ_{PSII}, and NPQ, under L-SHS and OPD conditions, which can justify the increase of the grain yield as a result of the combined application of these treatments compared to the combined application of Zn and B. Mohammadi (2017) reported that PB-F and Zn interaction could increase grain yield by increasing nutrient availability, leaf area index, Chl content, photosynthesis, growth hormones, and creating favorable growth conditions. As already mentioned, one of the main reasons for the loss of yield and damage to the photosynthetic apparatus under heat stress conditions is the accumulation of ROS. Therefore, any factor that reduces ROS damage can help to increase the yield and improve the Chl fluorescence parameters. Zn plays an important role in lowering ROS generation and defending cells against ROS attack, while Zn deficiency can induce higher contents of ROS causing plant damage (Cakmak 2000). It has been reported that the primary physiological role of Zn is activating antioxidative mechanisms of crops against biotic and abiotic stresses (Marschner 1995). Yavas and Unay (2016) reported that foliar application of Zn resulted in a significant increase in antioxidant enzyme activities in response to stress, which could be one of the main reasons for improving the Chl fluorescence parameters and increasing wheat yield by Zn application in this study. Furthermore, Chl synthesis is improved by Zn, which acts as a structural and catalytic component of proteins, enzymes, and as co-factor for normal development of pigment biosynthesis (Balashouri 1995). In addition, Zn is known to have a stabilizing and protective effect on biomembranes; improving the integrity of biomembranes may improve photosynthesis under stress conditions (Cakmak 2000). Furthermore, Zn exerts a key function in cell membrane by protecting sulfhydryl groups in membrane proteins from oxidation by free radical groups (Cakmak *et al.* 1996).

In this experiment, it was observed that B foliar application increased the grain yield by 12.1 and 11.5% under both N-HS and L-SHS conditions, respectively. The reason for this increase can be attributed to an increase of 7.0 and 3.7% in the number of spikes under both N-HS and L-SHS conditions, respectively. B is directly or indirectly involved in several physiological and biochemical processes during plant growth such as cell elongation, cell division, cell wall biosynthesis, membrane function, nitrogen metabolism, leaf photosynthesis, and uracil synthesis (Marschner 1995). B application induces changes in carbohydrate metabolism (Camacho-Cristobal and Gonzalez-Fontes 1999), which in turn is responsible for the decrease in concentration of phenolic compounds in leaves (Blevins and Lukaszewski 1998). The low content of these phenolics oxidized to derivatives such as quinones, reduce the production of extremely ROS and cause reduction in peroxidative damage to vital components of cell membrane such as lipids and proteins, which eventually leads to repair of several cellular functions (Cakmak and Römheld 1997, El-Shintinawy 1999), Therefore, B may also protect plasma membrane against peroxidative damage by toxic O_2 species. B nutrition improves sugar transport in the plant, which helps to improve seed germination and grain formation. This in turn improves the yield by improving the temperature stress (Waraich *et al.* 2011).

Many researchers have reported the positive effects of Zn and B foliar application on increase yield and yield component (Ali *et al.* 2009) and improve values of Chl fluorescence parameters such as F_v/F_m, Φ_{PSII}, F_v'/F_m', and NPQ under stress conditions (Graham and McDonald 2001, Wang and Jin 2007, Guidi *et al.* 2011). Generally, the results obtained by the above researchers were observed only in the combined application of these elements with PB-F but were not observed in the micronutrient separate application.

Conclusions: The results of the present study indicate that seed inoculation with PB-F rather than Zn and B foliar application was more effective in reducing the harmful effects of L-SHS on chlorophyll fluorescence, yield, and yield components of common bread wheat. Zn + B combined application, rather than their separate application, was more effective to improve chlorophyll fluorescence parameters, yield, and yield components of common bread wheat under both N-HS and L-SHS conditions. In general, it can be concluded that the optimum planting date (21 November), seed inoculation with PB-F and Zn + B combined application are three appropriate management strategies to improve the chlorophyll fluorescence parameters and increase yield and yield components of bread wheat (*Triticum aestivum* L.) in Mediterranean climates such as the southwestern part of Iran (Khouzestan province).

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