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Research Article

Physiological responses of wheat (*Triticum aestivum* L.) to deficit irrigation and sowing density

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ABSTRACT- To evaluate the effect of sowing density (300, 400, 500, 600 and 700 plants/m^2) on the growth of wheat under deficit irrigation (100, 75 and 50% crop water requirement, I_{100}, I_{75} and I_{50}, respectively), an experiment was carried out during 2009 and 2010. In both years, deficit irrigation resulted in a considerable reduction in yield, yield components, leaf area index (LAI) and leaf water potential (Ψ_w). In contrast, the canopy temperature (CT) significantly increased under deficit irrigation. Furthermore, increasing of sowing density from 300 to 600 plants/m^2 resulted in a significant increase in grain yield under I_{100} and I_{75}. Maximum grain yield as 525.9 and 564.2 g/m^2 was obtained in the first and the second years, respectively in sowing density of 600 plants/m^2 and I_{100}. This sowing density was also the proper density in I_{75} and I_{50} irrigation regimes. Increasing of sowing density reduced 1000-grain weight and grain number per spike and increased spike number per square meter. In the first year, increasing of sowing density from 300 to 600 plants/m^2 caused a significant increase in LAI in all irrigation regimes, while in the second year, maximum LAI was observed in 700 plants/m^2 sowing density. It was found that increasing of sowing density significantly reduced the Ψ_w and the CT in both well-watered and deficit irrigation. In conclusion, the results suggest that 600 plants/m^2 would be the optimal sowing density under different water conditions. Alleviation of water stress by the increasing sowing density was found to be associated partly with enhanced LAI and reduced CT.

INTRODUCTION

Undoubtedly, wheat (*Triticum aestivum* L.) is one of the world's vital food crops. However, its optimum productivity cannot be achieved due to being exposed to several stressful cues such as heat, salinity and drought (Sinclair, 2011). Although all abiotic stresses adversely affect the wheat growth and production, water scarcity raises major concerns (Shi et al., 2017). In many regions of the world, shortage of water is the premier factor in wheat productivity decline (Costa et al., 2011). Under semi-arid climate conditions, wheat is usually exposed to drought stress during the growing season (Gonzalez et al., 2010). In fact, water scarcity adversely affects all phases of growth, and the most striking effect of this stress has been noted at the reproductive phase and grain filling, leading to less number of grains with small size in cereal crops including wheat. Impaired assimilate partitioning and the activities of vital enzymes taking part in the synthetic processes of key carbohydrates including starch and sucrose result in reduced grain filling (Guttieri et al., 2001; Erocli et al., 2007; Wang et al., 2013). Drought stress is also believed to affect the uptake, transport and accumulation of key inorganic nutrients in plants (Sinclair, 2011). Water stress as the most important abiotic stress which resulted from irrigation water shortage and modified in precipitation patterns and insufficient rainfall reduces the production and yield of plants (Toker et al., 2007). Drought-induced yield reduction in wheat, which has been shown to be dependent upon the duration of the stress period and severity, has been reported by many authors (Guttieri et al., 2001; Mary et al., 2001; Gonzalez et al., 2010; Maghsoudi et al., 2016a).

Optimizing plant density is a key factor influencing many aspects of crop management including susceptibility to pathogens, water and fertilizer requirements as well as yield (Dai et al., 2014; Jin et al., 2017). Enhancement of growth and grain yield of wheat requires sowing at an appropriate density since it directly affects the spike number per unit area. As a consequence, other yield components such as individual grain weight and the number of grains per spike are also affected (Saeys et al., 2009; Jin et al., 2017). Previous studies on winter wheat indicated that the plant density was related to the accumulated dry matter, the green fraction and the yield (Ozturk et al., 2006; Hiltbrunner et al., 2007). Hiltbrunner et al. (2007) reported that the number of spikelet per spike of wheat changes under different planting densities. Wheat grain yield was improved with increasing plant density as a result of the increased number of spikelet (HuiJuan et al., 2009). Yoshida (1981) also found that dense planting maximizes the leaf area index, ensuring that plant photosynthesis meets the high yield requirements. Furthermore, it was reported that in forage rice dense planting increases the 1000-grain weight, the percentage of filled spikelet, and the grain yield (Nakano et al., 2012). However, some studies have reported that dense planting does not necessarily increase the grain yield (Takeda and Hirota, 1971; Gendua et al., 2009).

Reducing plant density in this way can minimize the effects of climatological drought and neutralize soil drought (Honda et al., 2019). Plant distribution patterns and plant densities can practically affect the utilization of environmental resources to the extent that inter- and intra-plant competitions are influenced to a great degree. As a result, plant density is considered a vital factor when setting the aim to reach higher grain yield (Caterina et al., 2013). Plant density is not, however, the only factor that influences competition for water. Water uptake by plant communities is also related to their above-ground biomass (Toillon et al., 2013; Caterina et al., 2013), which increases over time up to a maximum level dictated by the environmental carrying capacity (Toillon et al., 2013). Since biomass increment over time in tree plantations is influenced by initial density, closer spacing results in higher carbon fixation rates (Toillon et al., 2013; Hakamada et al., 2017). Where water is scarce, however, the greater water uptake promoted by denser stands can lead to early exhaustion of available water, which, in turn, leads to decreased productivity or even death of the most sensitive individuals or species in the stand (Hakamada et al., 2017). Quantifying plant competition for soil water, therefore, is important not only for physiological plant ecologists, but also for ecological applications, such as ecological restoration and conservation management. Knowing the relationship between planting density and the community response to soil water competition can be an important tool to aid restoration planning and to support management decisions (Honda et al., 2019).

Although, it has been shown that proper plant density of wheat can effectively promote the grain yield (Maertens et al., 2003; Ozturk et al., 2006; Hiltbrunner et al., 2007; HuiJuan et al., 2009; Jin et al., 2017), the existing literature does not show much information on the role of increasing plant density in alleviating the drought-induced injurious effects on plants. Therefore, in the current investigation, the effects of plant density on wheat growth and grain yield under water deficit irrigation were studied.

MATERIALS AND METHODS

Experimental Site

To evaluate the effect of sowing density on yield and yield components of wheat (Shiraz cultivar) under deficit irrigation conditions, this study was carried out at the Research Station of College of Agriculture, Shiraz University, Shiraz, Iran, located 16 km north of Shiraz (29º 36′ N, 52º 32′ E, 1810 m above the sea level) during the two growing seasons in 2009 and 2010. The climate of the study area is semi-arid with a mean annual rainfall of about 386 mm. The soil texture is clay loam. Averaged soil physical properties and some of the atmospheric parameters of the experimental site for two years are shown in Table 1 and Table 2, respectively.

Experimental Design and Procedure

This study was carried out as a factorial experiment based on complete randomized block design with three replicates. Experimental treatments included irrigation regimes (100, 75 and 50% of crop water requirement, as I_{100}, I_{75} and I_{50}) and sowing density (300, 400, 500, 600 and 700 plants/m^2). The experimental area was divided into 45 plots. The dimension of each plot was 4 m wide and 4 m long, that led to 16 rows in each plot with 25 cm between rows. Distance between experimental plots was considered 1 m apart to avoid water movement.

In both years (2009 and 2010), the wheat seeds (Shiraz cultivar) were sown on 28th October. For plant nutrition, 100 kg ha^{-1} ammonium phosphate fertilizer was uniformly mixed with the soil during field preparation. Also the soil was fertilized with 200 kg ha^{-1} of urea at two different times, i.e., half at sowing time and the rest at mid tillering stage. The irrigation interval was about 7-10 days. Before each irrigation event, soil water content at different depths (0.3, 0.6, 0.9, 1.2 and 1.5 m) was measured with the neutron scattering method. Because during wheat growth period it was rainfall in the region soil water content was measured up to 1.5 m to deep percolation. Soil water content in the root zone was used to determine the amount of net irrigation water as calculated by the following equation:

$$d = \frac{\left(Fc - \theta_V\right) * R_Z}{100} \qquad (1)$$

Where d is the irrigation water depth (m), Fc and Θv are the volumetric soil water content at field capacity and before irrigation, respectively (m^3 m^{-3}), and Rz is the depth of root.

Depth of root was determined by using following equation (Borg and Grimes, 1986):

$$z_r = R_{DM}\left[0.5 + 0.5 sin\left(\frac{3.03 D_{as}}{D_{tm}} - 1.47\right)\right] \qquad (2)$$

Where Z_r is the root depth (m), R_{DM} is the maximum root depth (1.8m). D_{as} is the number of days after planting, and D_{tm} is the number of days for maximum root depth.

In this region, most rainfall occurs in winter and at this time of year, the soil surface is usually wet and it can be assumed that the soil water content reduction is equal to reference evapotranspiration (ET_0) (Farshi et al., 1987). ET_0 was estimated by the Penman-Monteith equation (Allen et al., 1998) which was calibrated for semi-arid environments in the study area (Razzaghi and Sepaskhah, 2012). Figs 1 and 2 show the amounts of ET_0 and irrigation water applied for each irrigation regimes under different sowing densities. The total amount of rainfall was 127 and 187.5 mm for the first and second years, respectively.

Measurement of Plant Parameters

A 25 × 20 cm^2 area within each treatment was harvested and leaf area index (LAI) was calculated from leaf areas measured with WINDIAS leaf area meter (Delta-T Devices). LAI was determined at 125, 150, 175, 200, 225 and 250 days after planting in both years of study. Leaf water potential was measured using a pressure chamber technique (PMS instrument company, ALBANY Oregon 97322) at 167, 182, 190, 203 and 220 days after planting in the second year. Canopy temperature was measured using an infrared thermometer (Model 5500, KYORISU) in the first and second years of this research, at 166, 178, 188 and 213 days after planting.

Table 1. Averaged soil physical properties of the experimental site for two years

Physical properties	Soil depth (cm)				
	0-30	30-54	54-112	112-158	158-180
pH	8.0	8.2	8.0	8.1	8.4
Electrical Conductivity (EC,dS m^{-1})	0.59	0.40	0.52	0.50	0.56
Organic matter (%)	2.0	-	1.0	-	1.0
Sand (%)	35	23	21	27	33
Silt (%)	35	38	39	48	51
Clay (%)	30	39	40	25	16
Soil texture	Loam	Clay loam	Clay loam	Clay loam	Clay loam
	Soil depth (cm)				
	0-15	15-30	30-60	60-90	
Field capacity (cm^3 cm^{-3})	0.33	0.33	0.34	0.35	
Bulk density (kg m^{-3})	1430	1720	1830	-	

Table 2. Mean monthly maximum, minimum and average temperature, relative humidity, rain and pan evaporation in the two experimental years

		Temperature (C^o)			Relative humidity (%)			Rain	E (Pan)
Year	Month	Max	Min	Avg	Max	Min	Avg	mm	mm/day
First	September	27.05	4.53	15.79	68.30	12.43	40.40	0.00	5.90
	October	23.00	-0.31	11.34	67.43	13.11	40.70	0.00	3.80
	November	15.60	-2.38	6.61	-	-	48.20	18.00	3.37
	December	7.20	-4.27	1.46	-	-	68.00	76.00	2.95
	January	11.62	-4.23	3.70	-	-	53.90	29.50	5.01
	February	19.55	-1.34	8.99	51.00	10.67	29.20	0.00	6.15
	March	23.90	4.00	13.95	62.1	16.35	39.24	3.50	5.69
	April	27.83	6.75	17.29	58.93	15.41	37.17	0.00	7.37
	May	34.08	10.75	22.42	56.77	13.22	35.00	0.00	9.68
	June	35.60	14.52	25.06	53.29	16.29	34.79	0.00	10.68
Second	September	28.58	5.053	16.42	86.46	14.80	50.63	0.00	5.03
	October	19.13	3.21	11.17	86.63	27.40	57.01	42.00	2.03
	November	13.58	-3.35	5.11	86.30	26.46	56.38	12.50	3.23
	December	12.84	-5.78	3.52	80.73	24.51	53.51	20.50	1.55
	January	12.80	-2.66	5.07	84.70	23.53	54.11	31.50	1.98
	February	16.74	1.50	9.11	80.85	24.88	52.87	23.00	4.18
	March	17.68	3.06	10.37	87.06	30.09	58.58	58.00	4.59
	April	27.29	7.74	17.514	75.41	17.16	46.29	0.00	7.69
	May	32.47	10.66	21.56	56.48	16.87	36.67	0.00	10.38
	June	35.91	13.50	24.71	57.00	17.25	37.12	0.00	10.90

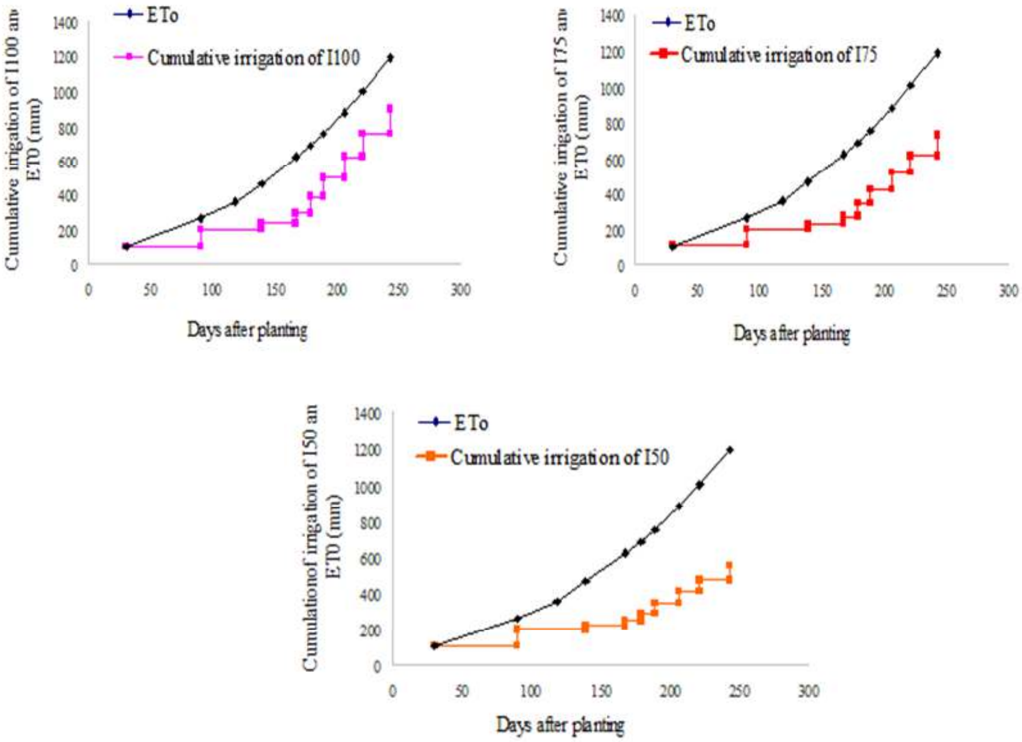


Fig. 1. Cumulative reference evapotranspiration (ET_0) and applied irrigation water (I_{100}, I_{75} and I_{50}) in the first year (2009) of this study.

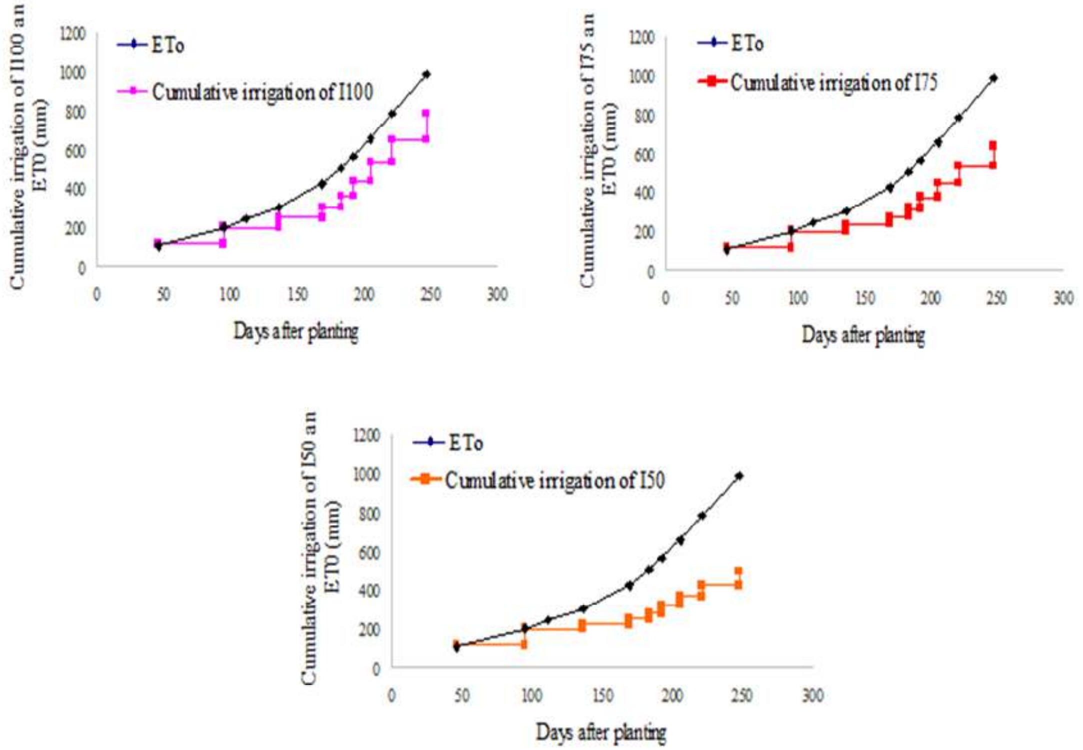


Fig. 2. Cumulative reference evapotranspiration (ET_0) and applied irrigation water (I_{100}, I_{75} and I_{50}) in the second year (2010) of this study.

These measurements were focused to 5:1 meter and at afternoon cloudless periods (12:00 to 15:00 hours). As similar to the method of Otoole and Real (1986), the data for each plot were the mean of four readings, taken from the same side of each plot at an angle of approximately 30° to the horizontal in a range of directions such that they covered different regions of the plot and integrated many leaves. At maturity (June 30 and July 5 in the first and the second years, respectively), plants in 1.0 m^2 area from each plot were harvested and grain yield, 1000-grain weight, spike number per unit area and the number of grains per spike were determined.

Data Analysis

The data for each parameter were analyzed using the SAS v.9.1 software to work out analysis of variance. The significant differences among the mean values were compared using the Duncan's Multiple Range test ($P \leq 0.05$).

RESULTS

Yield and Yield Components

The interaction of growing season and irrigation treatment and sowing density was significant (Data are not shown). Therefore, the results of the first and the second years of this study were analyzed separately. In the first and the second years, deficit irrigation (I_{75} and I_{50}) significantly reduced the grain yield of Shiraz cultivar. In contrast, increasing of sowing density from 300 plants/m^2 to 600 plants/m^2 resulted in a significant increase in grain yield under I_{100} and I_{75}. Furthermore, maximum grain yield in the first year (525.9 g/m^2) and the second year (564.2 g/m^2) was obtained in the sowing density of 600 plants/m^2 and I_{100}, while minimum grain yield was shown in I_{50}. However, there was no significant difference among the different sowing densities under I_{50} conditions in the first year of study. In the second year, the sowing density of 400 plants/m^2 significantly increased grain yield in I_{50} density (Table 3). Mean grain yield in the second year (434.6 g/m^2) was higher than that (405 g/m^2) in the first year. This may be due to higher precipitation in the second year (187.5 mm) compared with the first year (127 mm).

In both years, relative to the full irrigation regime, I_{75} and I_{50} irrigation regimes significantly reduced the 1000-grain weight of Shiraz cultivar and the effect of I_{50} was more severe than the other irrigation regimes. Furthermore, in both years, maximum 1000-grain weight was obtained in 300 and 400 plants/m^2 sowing density under I_{100} treatment. Generally, increasing of sowing density resulted in reduction in 1000-grain weight (Table 3). In both years, under I_{100}, I_{75} and I_{50} irrigation regimes, increasing of sowing density from 300 plants/m^2 to 700 plants/m^2 resulted in significant increase in spike number per unit area. In contrast, deficit irrigation significantly reduced the spike number per unit area and the effect of I_{50} was more severe than the other irrigation regimes (Table 3). In addition, in both years, there was a significant difference ($P \leq 0.05$) in the grain number per spike between the different irrigation regimes and different sowing densities. However, minimum grain number per spike was observed in 700 plants/m^2 sowing density (21.5 in the first year and 23.0 in the second year) under the I_{50} irrigation regime, while maximum grain number per spike (32.0) was shown in 300 plants/m^2 with full irrigation (Table 3).

Leaf Area Index (LAI)

In the first and second years of study, deficit irrigation reduced the average leaf area index (LAI) of Shiraz cultivar. There was a significant difference in average LAI among the different irrigation regimes, and this reduction was higher in I_{50} as compared with that in I_{75}. In contrast, the negative impact of deficit irrigation on average LAI was alleviated by increasing of sowing density (Table 4). Furthermore, in the first year, under all irrigation regimes, increasing of sowing density from 300 plants/m^2 to 600 plants/m^2 resulted in significant increase in average LAI, while in the second year, the maximum value of the average LAI was observed in 700 plants/m^2 sowing density under all irrigation regimes. However, increasing of sowing density improved average LAI under well-watered and deficit irrigation conditions, and the effect of increasing of sowing density being pronounced under deficit irrigation conditions (Table 4). Furthermore, average LAI in the second year was higher than that in the first year (Table 4). This may be due to higher precipitation in the second year compared with the first year. In addition, in all irrigation regimes under different sowing densities, LAI has risen over timer to its peak. Then LAI decreased due to leaf senescence (Figs 3 and 4).

Leaf Water Potential (Ψ_w)

At all measurements, deficit irrigation treatments resulted in marked decrease in leaf water potential (Ψ_w); however, the influence of I_{50} on Ψ_w was higher compared to I_{75} irrigation regime. In addition, the Ψ_w was significantly reduced by increasing of sowing density, under well-watered and deficit irrigation conditions. Considering the trend of Ψ_w during the growing period, the minimum Ψ_w (3.33 -MPa), was found at 220 days after planting (Table 5). In 700 plants/m^2 sowing density, Ψ_w at 220 days after planting compared with 167 days after planting decreased 37, 40 and 42% in I_{100}, I_{75} and I_{50} irrigation regimes, respectively (Table 5). In other words, the negative effect of increasing the sowing density on Ψ_w under deficit irrigation conditions was higher than full irrigation.

Table 3. The effect of plant density on yield and yield components of wheat (Shiraz cultivar) under deficit irrigation conditions in the two experimental years.

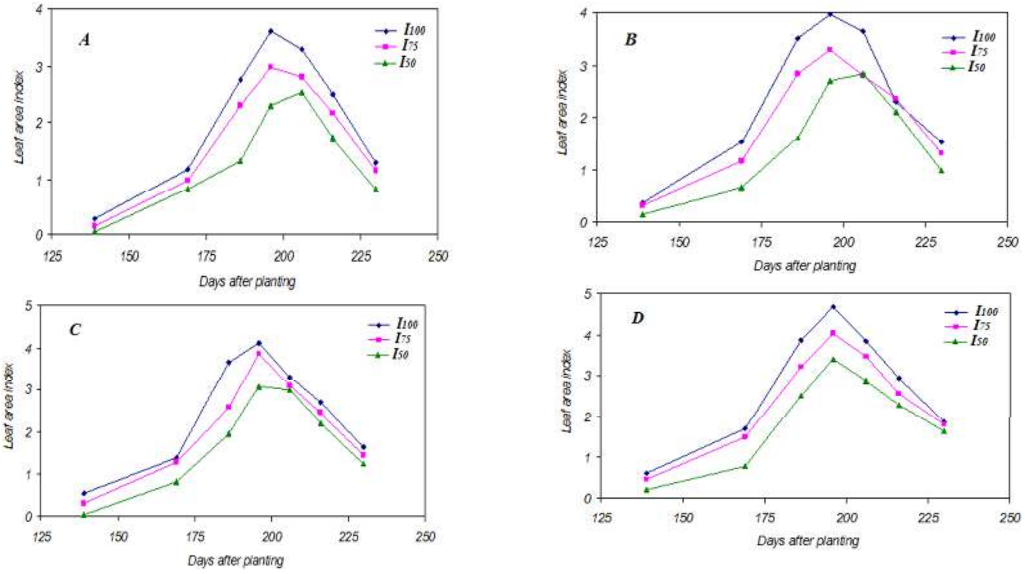
	Plant density	Grain yield (g m^{-2})		1000-Grain weight (g)		Spike number per square meter (-m^{-2})		Grain number per spike (-$spike^{-1}$)	
Crop water requirement (%)	(plants/m^2)	First Year	Second Year	First Year	Second Year	First Year	Second Year	First Year	Second Year
100	300	453.01^{bcd}	444.13^{def}	40.10^{a}	38.80^{a}	573.30^{def}	620.70^{def}	30.70^{a}	32.00^{a}
	400	463.64^{bc}	468.46^{de}	39.90^{a}	38.40^{ab}	6350^{bc}	655.00^{bcd}	29.30^{ab}	31.00^{ab}
	500	484.82^{b}	508.33^{bc}	39.30^{b}	37.90^{cd}	601.30^{bcde}	694.70^{ab}	28.00^{bcd}	29.00^{bcd}
	600	525.94^{a}	564.16^{a}	39.10^{bc}	38.20^{bc}	683.30^{a}	722.00^{a}	27.30^{cde}	28.00^{cde}
	700	453.29^{bcd}	532.10^{ab}	38.90^{cd}	37.70^{cd}	638.30^{bc}	688.70^{abc}	26.60^{def}	28.60^{bcd}
75	300	377.96^{fg}	358.40^{g}	38.80^{cd}	36.80^{fg}	540.70^{f}	594.30^{ef}	28.60^{bc}	29.60^{abc}
	400	364.35^{gh}	418.80^{f}	38.60^{de}	37.80^{cd}	586.70^{def}	600.00^{ef}	26.30^{defg}	27.30^{cdef}
	500	414.14^{def}	408.80^{f}	38.70^{d}	37.40^{de}	613.30^{bcd}	641.30^{cde}	26.00^{efgh}	26.60^{defg}
	600	441.83^{cde}	477.53^{cd}	38.50^{de}	37.00^{ef}	641.70^{ab}	677.30^{abc}	25.30^{fghi}	26.00^{efgh}
	700	411.74^{ef}	459.00^{de}	38.30^{de}	36.90^{ef}	610.00^{bcd}	646.00^{bcde}	24.40^{hij}	24.30^{ghi}
50	300	315.61^{i}	298.03^{h}	37.80^{f}	36.10^{h}	477.70^{g}	528.30^{g}	26.60^{def}	27.30^{cdef}
	400	327.95^{hi}	354.37^{g}	37.60^{fg}	36.10^{h}	558.30^{ef}	575.70^{f}	24.70^{ghi}	26.00^{efgh}
	500	338.66^{ghi}	374.23^{fg}	37.40^{g}	36.40^{gh}	566.70^{def}	612.70^{def}	23.80^{ij}	25.30^{fghi}
	600	347.96^{ghi}	435.30^{ef}	37.20^{g}	36.40^{gh}	590.70^{cde}	621.30^{def}	22.70^{jk}	24.00^{hi}
	700	353.98^{ghi}	417.33^{f}	37.30^{g}	36.10^{h}	567.70^{def}	615.00^{def}	21.50^{k}	23.00^{i}

Means with the same letters in each column are not significantly different (Duncan's multiple range test, $P \leq 0.05$ level)

Table 4. The effect of plant density on average leaf area index of wheat (Shiraz cultivar) under deficit irrigation conditions in the two experimental years.

	First year			Second year		
Plant density (plants/m^2)	Crop water requirement (%)			Crop water requirement (%)		
	100	75	50	100	75	50
300	2.14^{c}	1.80^{f}	1.37^{h}	1.99^{g}	1.72^{i}	1.42^{j}
400	2.41^{b}	2.01^{d}	1.58^{g}	2.36^{e}	2.02^{g}	1.68^{i}
500	2.48^{b}	2.14^{c}	1.75^{f}	2.65^{d}	2.35^{e}	1.91^{h}
600	2.79^{a}	2.44^{b}	1.97^{de}	3.03^{b}	2.58^{d}	2.19^{f}
700	2.73^{a}	2.44^{b}	1.92^{e}	3.24^{a}	2.79^{c}	2.41^{e}

Means with the same letters in each column are not significantly different (Duncan's multiple range test, $P \leq 0.05$ level).



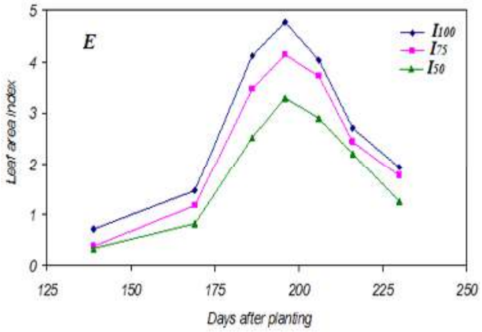


Fig. 3. The trend of changes in the leaf area index during the growing season in the first year (2009) of this study. A, B, C, D and E are plant densities of 300, 400, 500, 600 and 700 plants/m^2, respectively.

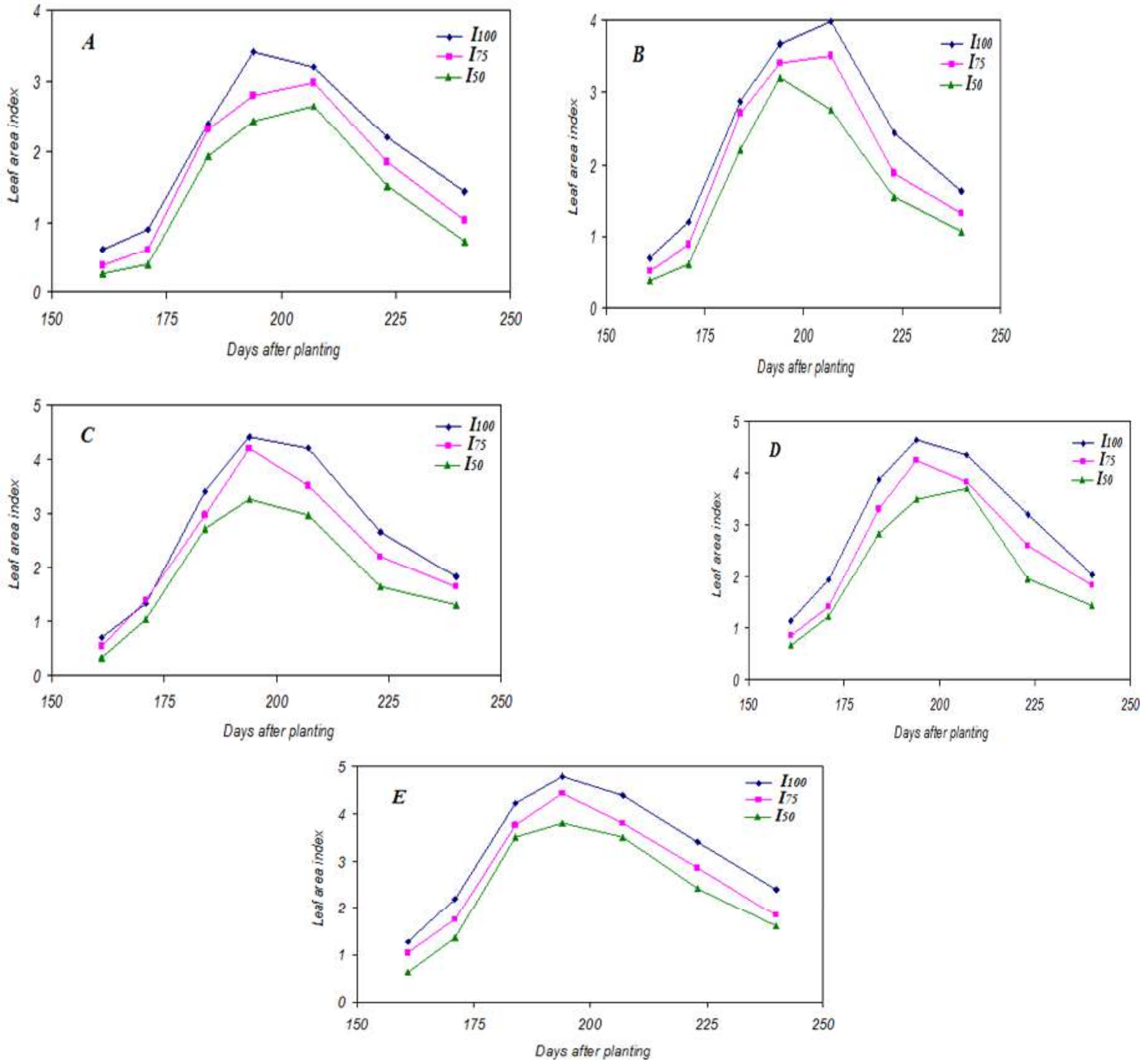


Fig. 4. The trend of changes in the leaf area index during the growing season in the second year (2010) of this study. A, B, C, D and E are plant densities of 300, 400, 500, 600 and 700 plants/m^2, respectively.

Table 5. The effect of plant density on leaf water potential (-MPa) of wheat (Shiraz cultivar) under deficit irrigation conditions at different days after planting in the second year.

Crop water requirement (%)	Plant density (plants/m^2)	Days after planting 167	182	190	203	220
100	300	1.53 ^{h}	1.87 ^{j}	2.36 ^{efg}	2.30 ^{g}	2.67 ^{i}
	400	1.68 ^{fg}	1.93 ^{ij}	2.23 ^{g}	2.45 ^{f}	2.72 ^{hi}
	500	1.65 ^{fg}	2.02 ^{ghi}	2.32 ^{fg}	2.57 ^{ef}	2.80 ^{ghi}
	600	1.73 ^{efg}	2.08 ^{fgh}	2.30 ^{fg}	2.47 ^{f}	2.87 ^{fgh}
	700	1.83 ^{bcde}	2.03 ^{ghi}	2.37 ^{efg}	2.65 ^{de}	2.93 ^{efg}
75	300	1.75 ^{def}	1.97 ^{hij}	2.42 ^{def}	2.62 ^{de}	2.87 ^{fgh}
	400	1.63 ^{gh}	2.07 ^{fgh}	2.33 ^{efg}	2.77 ^{abcd}	2.97 ^{efg}
	500	1.77 ^{def}	2.17 ^{def}	2.52 ^{bcd}	2.70 ^{bcde}	3.00 ^{def}
	600	1.83 ^{bcde}	2.25 ^{bcde}	2.57 ^{bc}	2.67 ^{cde}	3.10 ^{bcde}
	700	1.93 ^{ab}	2.28 ^{bcd}	2.47 ^{cde}	2.75 ^{bcd}	3.22 ^{abc}
50	300	1.85 ^{abcd}	2.18 ^{cdef}	2.53 ^{bcd}	2.82 ^{abc}	3.03 ^{cdef}
	400	1.75 ^{def}	2.13 ^{efg}	2.60 ^{abc}	2.70 ^{bcde}	3.17 ^{abcd}
	500	1.82 ^{cde}	2.30 ^{bc}	2.73 ^{a}	2.90 ^{a}	3.23 ^{ab}
	600	1.95 ^{a}	2.35 ^{b}	2.62 ^{ab}	2.73 ^{bcd}	3.23 ^{ab}
	700	1.92 ^{abc}	2.53 ^{a}	2.63 ^{ab}	2.83 ^{ab}	3.33 ^{a}

Means with the same letters in each column are not significantly different (Duncan's multiple range test, $P \leq 0.05$ level).

Canopy Temperature (CT)

The results showed that, in both years, the canopy temperature (CT) significantly increased under deficit irrigation conditions. Also, I_{50}-treated plants had greater CT than that in the plants grown in the I_{75} regime. This trend of change was similar in all plant densities. It was found that increasing of sowing density significantly reduced the CT in both well-watered and deficit irrigation regimes. At different sampling times, the maximum CT, was observed at 213 days after planting (Tables 6 and 7). Furthermore, there was a negative correlation between CT and grain yield of wheat in the first (R^2 =0.83) and second (R^2 =0.77) years (Fig 5).

DISCUSSION

The results of this study showed that when deficit irrigation was imposed, the grain yield of wheat (Shiraz cultivar) was strongly reduced (Table 3). It has been reported that deficit irrigation regimes affect the physiological responses and growth of almost all crops including wheat (Yao et al., 2009; Maghsoudi et al., 2015; Maghsoudi et al., 2016a; Maghsoudi et al., 2016b; Srivastava et al., 2016; Maghsoudi et al., 2018; Maghsoudi et al., 2019). Indeed, the importance of water availability in yield formation of bread wheat, an important staple food crop of the world, was demonstrated here. Generally, drought especially during anthesis and grain filling could lead to small-sized grains and lower yield (Guttieri et al., 2001; Erocli et al., 2007; Sinclair, 2011). The impaired grain filling caused be attributed to reduced partitioning of assimilates and activities of key enzymes involved in sucrose and starch synthesis (Sinclair, 2011). Grain filling in cereals is a process of starch biosynthesis from simple carbohydrates (Mary et al., 2001). Gonzalez et al. (2010) reported that the decline activity of sucrose synthase caused a reduction in the rate of grain growth, while in the water-stressed wheat inactivation of adenosine diphosphate glucose pyrophosphorylase caused cessation of growth.

However, under deficit irrigation regimes, grain yield reduction in Shiraz cultivar was lower in the dense planting than that in the 300 plants/m^2 plant density. Therefore, dense planting could improve grain yield under water and non-water stress conditions. Maximum grain yield in the first year (525.9 g/m^2) and the second year (564.2 g/m^2) was obtained in the sowing density of 600 plants/m^2 and I_{100} irrigation regime (Table 3). Similarly, it has been reported that the increasing sowing density of wheat can effectively promote the enhancement of grain yield (Maertens et al., 2003; Ozturk et al., 2006; Hiltbrunner et al., 2007; HuiJuan et al., 2009; Dai et al., 2014; Jin et al., 2017). In this study, the number of grains per spike and 1000-grain weight reduced with the increasing sowing density (Table 3). Li et al. (2016) and Xu et al. (2015) also reported that the grain number at the 3rd and 4th grain positions and the 1st and 2nd grain positions of the basal and top spikelets decreased under dense planting. Furthermore, Ferrante et al. (2015) and Guo et al. (2007) reported that the differences in the number of grains per spike in wheat under different sowing density conditions were significant.

In the present investigation, it was observed that the spike number per unit area increased with the increasing sowing density (Table 3). HuiJuan et al. (2009) also found that spike number per unit area increases in very high sowing density in wheat cultivation. Spike number per unit area is determined by the number of tillers. The total number of tillers are affected by the sowing density as well as the number of tillers produced from a single seed. Li et al. (2016) reported that as the density increases, tillers produced by a single grain become less. There is considerable compensation by the crops grown at low densities, which was in agreement with Whaley et al. (2000) findings. The ratio of wheat grain yield in 75% (I_{75}) and 50% crop water requirement (I_{50}) to full irrigation (I_{100}) under different sowing densities in the first and second years is shown in Fig 6. In both years, the wheat grain yield in I_{75}/I_{100} \was higher than that in the I_{50}/I_{100} in all sowing densities. In the other words, increasing the severity of deficit irrigation resulted in reduction in grain yield and the negative effect of I_{50} was more severe than the I_{75}. In the first year, increase of sowing density from 300 plants/m^2 to 600 and 700 plants/m^2 resulted in a remarkable increase in the ratio of I_{75}/I_{100}. In other words, increasing the sowing density (600 and 700 plants/m^2) has reduced the negative effect of deficit irrigation. Furthermore, under I_{50} irrigation regime, the negative impact of deficit irrigation on grain yield was alleviated by increasing of sowing density from 300 plants/m^2 to 700 plants/m^2 and I_{50}/I_{100} was increased. In the second year, the maximum I_{75}/I_{100} and I_{50}/I_{100} values, were observed at 400 plants/m^2 sowing density. The highest yield was achieved via optimum cultivation density which is in effect synonymous with the consistent distribution of plants.

Leaf water potential (Ψ_w) is one of the potential indicators used for determining plant water status and it plays an important role in enhancing plant photosynthetic capacity (Endres et al., 2010). In the present investigation, drought stress significantly decreased Ψ_w in wheat cultivar examined (Table 5). Under water stress conditions, shoots with the ability to maintain a relatively high amount of water may increase plant performance (Morgan, 1996). This process is a significant adaptation mechanism under scarce water regimes (Rontein et al., 2002; Hummel et al., 2010). Osmotic adjustment is a very common phenomenon that occurs in plants exposed to drought or salinity stress. The maintenance of a high amount of water by the shoots may occur mainly due to the accumulation of organic osmotica, a process which is referred to as osmotic adjustment (Reddy et al., 2004; Zhu et al., 2005). It is believed to maintain water status with the plant body under the condition when the water potential is low. The results of this study showed that the increasing sowing density reduced the Ψ_w parameter under deficit irrigation conditions. In leaves of the stressed plants, was observed that the Ψ_w value was lower under dense planting (Table 5).

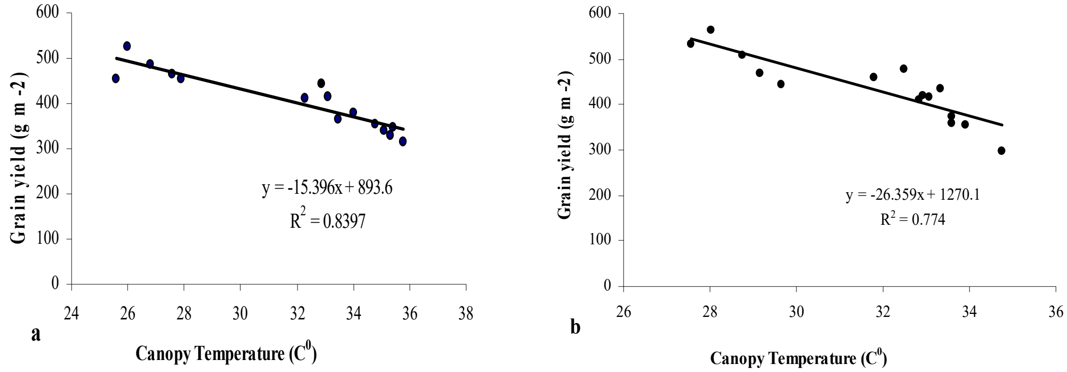


Fig. 5. Correlation between grain yield and canopy temperature (213 days after planting) of wheat in the first (a) and second (b) years.

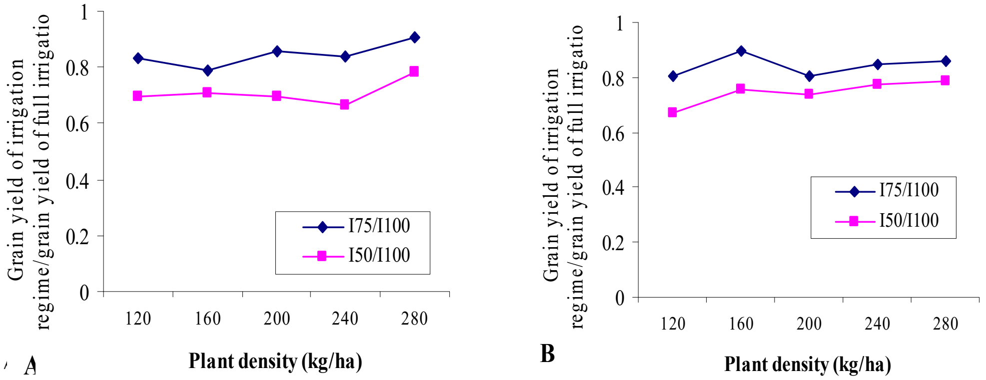


Fig. 6. Ratio of wheat grain yield in 75% (I_{75}) and 50% (I_{50}) crop water requirement to full irrigation (I_{100}) under different plant densities in the first (A) and the second year (B) of this study

Table 6. The effect of plant density on average canopy temperature (C^{o}) of wheat (Shiraz cultivar) under deficit irrigation conditions at different days after planting in the first year. (e.g. n=3).

	Days after planting											
Plant density (plants/m^2)	213			188			178			166		
	Crop water requirement (%)			Crop water requirement (%)			Crop water requirement (%)			Crop water requirement (%)		
	50	75	100	50	75	100	50	75	100	50	75	100
300	35.80^{a}	34.00^{b}	27.90^{e}	28.14^{a}	26.55^{c}	24.60^{e}	31.50^{a}	29.70^{c}	27.00^{ef}	25.00^{a}	23.14^{d}	22.00^{e}
400	35.34^{a}	33.45^{c}	27.60^{e}	27.78^{a}	26.10^{c}	24.24^{e}	30.74^{ab}	29.30^{c}	26.24^{f}	24.60^{a}	22.84^{bc}	21.00^{ef}
500	35.10^{ab}	33.10^{c}	26.80^{f}	27.27^{b}	25.87^{d}	23.67^{f}	30.23^{ab}	28.90^{d}	26.00^{g}	24.46^{ab}	22.90^{bc}	20.9^{e}
600	35.44^{a}	32.86^{d}	26.00^{f}	27.63^{ab}	25.94^{d}	23.00^{f}	30.10^{b}	28.85^{d}	25.14^{gh}	24.14^{b}	22.84^{bc}	19.67^{gh}
700	34.77^{b}	32.30^{d}	25.57^{fg}	27.37^{b}	25.74^{d}	22.16^{g}	29.65^{c}	27.94^{e}	26.00^{g}	23.93^{bc}	21.90^{e}	20.24^{g}

Means with the same letters in each column are not significantly different (Duncan's multiple range test, $P \leq 0.05$ level).

Table 7. The effect of plant density on average canopy temperature (C^{o}) of wheat (Shiraz cultivar) under deficit irrigation conditions at different days after planting in the second year.

	Days after planting											
Plant density (plants/m^2)	213			188			178			166		
	Crop water requirement (%)			Crop water requirement (%)			Crop water requirement (%)			Crop water requirement (%)		
	50	75	100	50	75	100	50	75	100	50	75	100
300	34.76a	33.60b	29.66e	32.03a	31.16b	27.50de	27.96a	26.93b	24.16d	23.30a	22.03b	9.13e
400	33.90ab	32.93c	29.16e	31.83a	31.00bc	27.03e	28.06a	26.36bc	23.76de	23.03a	21.83bc	8.93ef
500	33.60b	32.83c	28.76ef	31.20b	29.96c	26.83ef	27.30ab	26.56b	23.06e	22.76ab	21.66bc	8.46f
600	33.34b	32.50c	28.03f	31.70ab	29.20c	25.80f	26.80b	25.76c	22.56ef	22.06b	21.03c	8.10f
700	33.06b	31.80d	27.56fg	32.10a	28.26d	25.56f	26.40b	25.46c	22.06f	21.83a	20.90d	7.70g

Means with the same letters in each column are not significantly different (Duncan's multiple range test, $P \leq 0.05$ level).

It was reported that crop production strategies are usually designed to maximize light interception by achieving complete ground cover through promoting rapid leaf expansion and growth as well as manipulating the sowing density and spatial arrangement (Hovenden et al., 2004). Increased leaf area during vegetative growth is important in terms of optimizing dry matter production. The leaf area of plants in a community may be expressed as the leaf area index (LAI) or the leaf area per unit land area. The process of leaf expansion is partly controlled by the genetic constitution, as well as affected by the environmental conditions during leaf growth (Aspelmeier and Leuschner, 2006). Harrington et al., (2001) reported that besides water availability, radiation, temperature and nitrogen supply are environmental factors that are known to influence leaf expansion. The majority of studies reported a positive relationship between precipitation or soil water availability and LAI (Eamus, 2003; Hovenden et al., 2004; Prior et al., 2005; Aspelmeier and Leuschner, 2006). Similarly, in this research, leaf growth (as measured by LAI) was greatly reduced under deficit irrigation conditions (Table 4), thereby reduced the grain yield of wheat. Water stress through accelerating leaf senescence, as well as decreasing leaf area caused a considerable reduction in production of dry matter and biomass of crops (Hovenden et al., 2004). Prior et al. (2005) also reported that reduction in leaf growth had caused a reduced amount of light intercepted and hence limited the capability of crops to carry out photosynthesis. Leaf area reduction is a common response to soil water shortage (Pedrol et al., 2000; Otieno et al., 2005), thereby reducing the transpiring surface area and avoiding severe decreases in cell water potential and turgor (Hovenden and Vander Schoor, 2004). The results of this research showed that, although, deficit irrigation significantly reduced the LAI; however, dense planting enhanced this parameter as well as grain yield under water stress and non-water stress conditions (Table 4). Similarly, Yoshida (1981) have observed earlier that dense planting maximizes the LAI, ensuring that plant photosynthesis meets the high yield requirements. Tetio-Kagho and Gardner (1988) also reported that increasing sowing density increases leaf area and consequently leaf area index. sowing density through alteration in architecture and patterns of growth and development of crops, as well as influence on production and partitioning of carbohydrate, thereby influence on yield (Ozturk et al., 2006; HuiJuan et al., 2009).

Canopy temperature (CT) measurements made over a large area allow for spatiotemporal mapping of crop water stress and yield predictions (Peters and Evett 2008; O'Shaughnessy et al., 2011). Reynolds et al., (2001) reported that CT was affected by environmental and biological factors like plant metabolism, relative humidity, air temperature, water status of soil, wind, evapotranspiration, cloudiness, conduction systems, and continuous radiation. CT has been recognized as indicator of water status of plants and used for evaluation of plant responses to abiotic stress as a selection criterion to improve tolerance to drought and heat (Reynolds et al., 1998; Rashid et al., 1999; Brennan et al., 2007; O'Shaughnessy et al., 2011). In this research, the CT was recorded to be increased in wheat plants under deficit irrigation regimes (Tables 6 and 7).

Similar findings have been reported by Asemanrafat and Honar (2017) in red bean. Furthermore, in this study has been shown that the increasing sowing density significantly reduced the CT of water-stressed plants (I_{75} and I_{50}) and control plants (I_{100}) (Tables 6 and 7). Yang et al. (2014) also reported that under the moderate sowing density of hybrid cotton, there was a lower mean daily temperature attributing to a moderate mean canopy light transmittance. The results of this investigation showed that there was negative correlation between canopy temperature and grain yield of wheat in the first (R^2 =0.83) and second (R^2 =0.77) years (Fig. 5). Munjal and Rena (2003) have reported that one of important physiological characteristics for high temperature tolerance in wheat is a cool canopy, especially during the grain filling period. Under deficit irrigation conditions, the closure of stomata is the first response of plants to prevent water loss from plant tissues (Mansfield and Atkinson, 1990). The closure of stomata caused a reduction in turgor and water potential of a leaf as well as transpiration and thereby increasing canopy temperature (Maroco et al., 1997). However, stomatal closure is the main determinant to reduce photosynthesis and as a result decreasing yield (Yokota et al., 2002). In this research, there was a negative correlation between CT and Ψ_w of wheat (R^2 =0.83). So that with increasing the CT, Ψ_w decreased (Fig. 7), thereby negative influences on grain yield of wheat.

CONCLUSIONS

The results of this research suggest that irrigation and sowing density are the most important environmental factors that affect the grain yield and physiological responses of wheat. Furthermore, 600 plants/m^2 would be the optimal sowing density under water and non-water stress conditions. Alleviation of water stress by the increasing sowing density was found to be associated partly with enhanced LAI and reduced canopy temperature.

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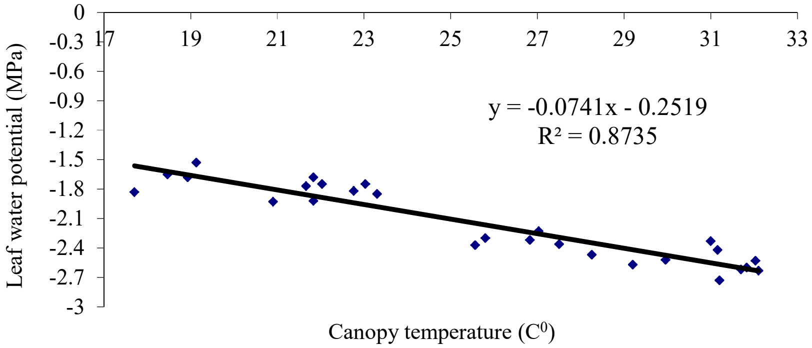

Fig. 7. Correlation between canopy temperature and leaf water potential of wheat Shiraz cultivar

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پاسخ‌های فیزیولوژیکی گندم (*Triticum aestivum* L.) تحت تأثیر کمبود آب و تراکم گیاه

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دمای کانوپی
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چکیده- به منظور بررسی تأثیر تراکم بوته (۳۰۰، ۴۰۰، ۵۰۰ ، ۶۰۰ و ۷۰۰ بوته در مترمربع) بر رشد و عملکرد گندم تحت شرایط کمبود آب (۱۰۰، ۷۵ و ۵۰ درصد نیاز آب زراعی: به ترتیب I_{100}، I_{75} و I_{50})، این مطالعه در طی سال‌های ۸۹-۱۳۸۸ انجام شد. در هر دو سال، کمبود آب منجر به کاهش معنی‌دار عملکرد، اجزای عملکرد، شاخص سطح برگ (LAI) و پتانسیل آب برگ (Ψw) گردید. در مقابل، دمای کانوپی (CT) به طور قابل توجهی در شرایط کمبود آب، افزایش یافت. همچنین افزایش تراکم بوته از ۳۰۰ به ۶۰۰ بوته در متر مربع، باعث افزایش معنی‌دار عملکرد دانه در تیمارهای I_{100} و I_{75} شد. بیشترین عملکرد دانه در سال اول و دوم، به ترتیب به میزان ۵۲۵/۹ و ۵۶۴/۲ گرم در متر مربع، در تراکم ۶۰۰ بوته در متر مربع و رژیم آبیاری I_{100} بدست آمد. همچنین این تراکم بوته در رژیم‌های آبیاری I_{75} و I_{50}، مناسب‌ترین تراکم گیاهی بود. افزایش تراکم بوته باعث کاهش وزن هزار دانه و تعداد دانه در سنبله و نیز موجب افزایش تعداد سنبله در متر مربع شد. در سال اول، افزایش تراکم بوته از ۳۰۰ به ۶۰۰ بوته در مترمربع باعث افزایش قابل توجه LAI در کلیه رژیم‌های آبیاری شد، در حالیکه در سال دوم، حداکثر LAI در تراکم ۷۰۰ بوته در متر مربع، مشاهده شد. مشخص گردید افزایش تراکم گیاه باعث کاهش Ψ_w و CT، در هر دو شرایط آبیاری مطلوب و تنش گردید. در نتیجه، بر اساس نتایج، تراکم ۶۰۰ بوته در متر مربع، تراکم بهینه گیاه در شرایط تنش و غیر تنش پیشنهاد می‌شود. می‌توان بیان داشت تعدیل تنش خشکی با افزایش تراکم گیاهی، در ارتباط با افزایش LAI و نیز کاهش CT بوده است.