RESEARCH ARTICLE **(Open Access)**

Evaluation of water deficiency at the post anthesis and source limitation during grain filling on grain yield, yield formation, some morphological and phonological traits and gas exchange bread wheat cultivar

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Abstract:

This paper attempts to determine the effect of post-anthesis water deficiency at the early and late grain growth periods separately and also the roles of main ear (spike) and leaves photosynthesis in yield production of wheat. The experiment was laid out in a randomized complete block design (RCBD) in a factorial arrangement with three replications. It comprised of source limitations i.e., control, defoliation of all leaves except the flag leaf and shaded ear and two water stress treatments i.e., well water or control (Irrigation in all stages of plant growth normally), water stress (post-anthesis water deficiency with withholding of irrigation). The results showed that the averages of grain yield and thousand grain weight of different treatments in controlled condition were 0.92 g spike^{-1} and 22.6 g respectively, while under water deficiency stress these values significantly reduced to 0.55 g spike^{-1} and 15.2 g respectively. Grain yield had the highest decrease percent under drought stress condition that it was probably due to reduce thousand grains weight under drought stress. The photosynthesis of all leaves except the flag leaf made significant contributions to the growing grains about 19% and ear photosynthesis makes a significant contribution to thousand grain weight of bread wheat, 18.6% in the absence of stress, and 23.3% under water deficit. Water deficiency at the post-anthesis significantly reduced net photosynthetic rate, stomatal conductance and transpiration rate. Net photosynthesis rate generally decreased with chlorophyll content and also this was paralleled by a lower stomatal conductance. Ear photosynthesis might represent a “buffer” to maintain grain yield under source limitations (e.g. defoliation, water stress conditions), and could have an important role even without stress, because an incipient ‘source’ limitation might be emerging in modern cultivars of bread wheat.

Keywords: Water deficiency, Flag leaf, Grain filling, Photosynthesis, Grain yield, Wheat.

Abbreviations: net photosynthetic rate (Pn), stomata conductance (gs), transpiration rate (E), days after anthesis (DAA).

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most important crops in world, which plays a special role in people’s nutrition. Also, Wheat provides over 20% of calories needed by the world's population [14]. Wheat are exposed to various environmental stresses during the course of their life cycle. Among these are drought, temperature, salinity and cold stress etc [13]. But unfortunately abiotic stresses, such as drought, decrease wheat growth and productivity by reducing water uptake and cause nutrient disorders and ion toxicity in this region. Water stress results in stomatal closure and reduced transpiration rates and net potosynthesis rate [43], a decrease in the water potential of plant tissues, accumulation of abscisic acid (ABA), proline, mannitol, sorbitol, formation of radical scavenging compounds (ascorbate, glutathione, α-tocopherol etc.), and synthesis of new proteins [29, 55].

The carbohydrates that are needed for grain growth are provided from two sources (1) during grain filling via leaves and spike [34, 45, 51] and (2) excess carbohydrates that are produced after and before anthesis, stored in the stem and remobilized to the grains during grain filling stage [20]. The primary signs of leaf senescence are the breakdown of chlorophyll and the decline of photosynthetic activity [25, 58]. It is generally accepted that genotypes that are able to sustain photosynthesis in the flag leaf for a longer time tend to yield more.

Although there are several physiological studies of leavs and ear photosynthesis [33, 45, 52], its actual contribution to yield is not well understood. The

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(Accepted for publication 30 March 2013)
***ISSN**: 2218-2020, © Agricultural University of Tirana*

contribution of leaves and spike photosynthesis and carbohydrate remobilization from stem affect the final grain weight. Traditionally, the flag leaf has been considered as the main photosynthetic organ in grain yield formation [22] but Aggarwal et al. [3] and Ahmadi et al. [4] reported that defoliation at anthesis had only small effects on grain yield of wheat, and they stated that the yield of cultivars used under those conditions was more controlled by sink than source strength. Recently, Maydup et al. [34] have indicated that the defoliation significantly reduced the total grain weight per spike about 25% in two wheat cultivars. There is evidence that when a photosynthesis organ of plant is detached, the compensations in the remaining photosynthesis tissues or remobilization may occur and diminish the photo assimilate reduction [15]. Thus, the source limitation of grain yield in previous works [4] may be because of the fact that the photosynthetic role of spike was neglected. The contribution role of ear photosynthesis in grain yield formation in wheat and barley has been reported from 10% to 76%, respectively [11, 44]. A recent study by Maydup et al. [34] showed that the ear photosynthesis makes a significant contribution to grain yield of wheat from 13% to 33% in control and 22% to 45% under water deficiency conditions. So far, there is no report about the source manipulation when defoliation and inhibition of ear photosynthesis are practiced at the beginning of grain filling stage of grain growth and simultaneously in irrigated and drought stress conditions. Moreover, there has been little evidence about application of these treatments in semiarid region such as Iran, where the wheat grain growth takes place under high temperature and high radiation conditions. The objectives of this research were to determine the role of ear and leaf photosynthesis to the grain filling stage. In addition, it was also attempted to evaluate the roles of net photosynthetic rate of bread wheat cultivar in grain yield production under controlled and post anthesis water deficit treatments.

2. Materials and Methods

2.1. Plant material and treatments

The experiments during the growing season from 2011 to 2012 in the greenhouse of Campus of Agricultural and Natural Resource, Razi University in Kermanshah state in the west of Iran (47º, 9′/E; 34º, 21′/ N), with 1319 meter elevated from sea level. This DN-11 wheat cultivar was chosen because it has the highest area under cultivation in the Kermanshah province and it is new modern cultivar with unknown physiological characteristics. And also, according to the Abdoli and Saeidi [2] results, cultivation of DN-11 cultivar in such regions is associated with lower risk. The experiment was laid out in a randomized complete block design (RCBD) in a factorial arrangement with three replications. It comprised of source limitations i.e., control, defoliation of all leaves except the flag leaf and shaded ear and two water stress treatments i.e., well water or control (Irrigation in all stages of plant growth normally), water stress (post anthesis water deficiency with withholding of irrigation). Shading of the ear (upper diagram) was made with a perforated aluminum foil. In order to prevent the accumulation of ethylene and to allow for convective heat flux, several holes were made in the aluminum foil covers [34]. Pots with a diameter of 20 cm and height of 30 cm were each containing 1:1:1 clay, sand and manure. Date of anthesis was determined from middle rows in each pot when 50% of the spikes had extruded anthers [18, 19].

2.2. Grain yield and its components

In the measuring grain yield and its components such as: thousand grain weight, number of grains per spike, number of fertile and infertile spikelet's, biomass and plant height, 10 plants randomly selected and measurements were performed. Harvest index was measured by dividing grain yield to biomass production. Taking notes during the growing season to estimate the grain filling period was performed.

2.3. Gas exchange

The net photosynthetic rate (Pn), stomata conductance (gs) and transpiration rate (E) were measured with a portable photosynthesis system LI-6400 (LI-COR, Lincoln, USA) on the flag leaves on 0, 7, 14, 21, 28 and 35 DAA. Photo-synthetically active radiation (PAR) of 1800 μmol m^{-2} s^{-1} was provided at each measurement by the 6400 light source.

2.4. Chlorophyll content (SPAD)

Leaf chlorophyll content was obtained by portable chlorophyll meter (SPAD-502, Minolta, Japan) from five individual flag leaves per pots on the flag leaves on 0, 7, 14, 21, 28 and 35 DAA.

2.5. Statistical analyses

Statistical analyses were performed using EXCEL and SAS 9.1software. Differences were analyzed by ANOVA. Means were compared by the LSD test ($p < 0.05$).

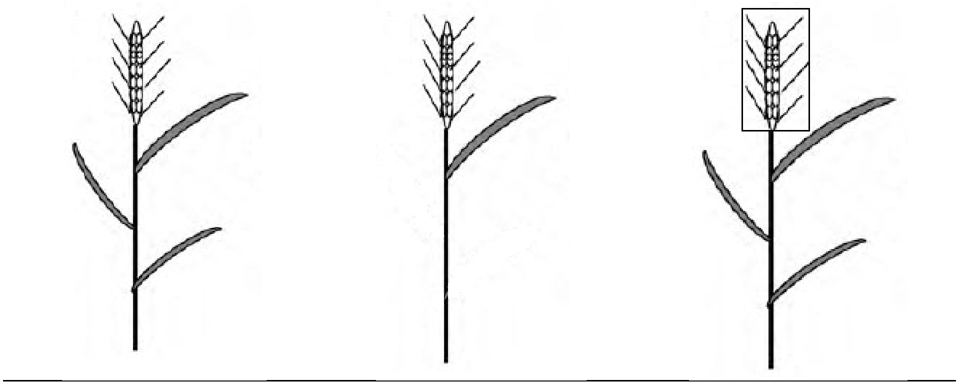

Figure 1. Diagrams showing the experimental set-up for the defoliation and ear shading, all the treatments in both experiments were imposed three-five days after anthesis. Shading of the ear (upper diagram) was made with a perforated aluminum foil.

3. Results and Discussion

3.1. Grain yield and its components

3.1.1. Grain yield:

For treatments, grain yield was reduced significantly under water deficits (Table 1); the reduction percentage in shaded ear (37.7%) was higher than Defoliated (28.5%) under stress condition. In this case, Maydupa et al. [34] and Saeidi et al. [44] reported that role of photosynthesis spike on the grain yield is more than photosynthesis of leavs. Birsin [10] and Khaliq et al. [28] reported that flag leaf removal also resulted in significant reduction in the yield attributes like number of grains per spike, grain weight per spike and 1000 grain weight. The averages of grain yield and thousand grains weight of different treatments in controlled condition were 0.92 g spike^{-1} and 22.6 g respectively, while under water deficiency stress these values significantly reduced to 0.55 g spike^{-1} and 15.2 g respectively (Table 1). The decrease in grain yield, 1000 grain weight and biomass under water deficit stress was probably because the assimilate produced by photosynthesis was lower under drought stress and this lower amount of assimilate was consumed and/or stored in sources (i.e. leaves and spike); hence, the growth of cobs as the main influencing factor of final grain yield, which should develop at this stage, was not realized under drought stress. The results showed that the water deficit stress treatments led to the decrease in grain yield which was in agreement with Saeidi et al. [45].

About the roles of current photosynthesis in grain yield production Aggarwal et al. (1990) and Ahmadi et al. [4] reported that defoliation at anthesis had only small effects on grain yield of wheat and stated that the yield of cultivars used under those conditions was more controlled by sink than source strength. Recently, Maydup et al. [34] have indicated that defoliation significantly reduced total grain weight per spike (about 25%) in wheat cultivars. Also, we found that inhibition of leaves except the flag leaf and ear photosynthesis at grain filling stage caused 19% and 28.3% reduction in grain yield, respectively (Table 1). There is evidence that when a photosynthesis part of a plant is inhibited, the compensations in the remaining photosynthesis tissues such as spike or remobilization may occur and diminish the photo assimilates [15]. Thus, the lack of source limitation of grain yield in previous works may be the result of the fact that the photosynthetic role of spike was neglected [3, 4].

The inhibition of ear photosynthesis reduced grain yield of two conditions. For wheat and barley, the contribution roles of spike photosynthesis in grain yield formation have been reported from 10% to 76% [11]. Maydup et al. [34] recently have reported that blockage of ear photosynthesis with shading near anthesis stage makes a significant contribution to grain yield of wheat from 13% to 33% in control and 22% to 45% under water deficiency conditions. However, the findings of the current study do not support the previous research by Maydup et al. [34] and showed that under control treatment, inhibition of ear photosynthesis at early grain filling caused more reduction in grain yield than water deficiency condition.

3.1.2. Thousand grains weight:

Means comparison showed that the treatment of control had the highest thousand grain weight (21.7 g) which was higher than that under the treatments of defoliated and shaded ear by 17.7 and 17.3 g, respectively (Table 1). Ear photosynthesis makes a significant contribution to thousand grain weight of bread wheat, 18.6% in the absence of stress, and 23.3% under water deficit. The decrease in thousand grain weight under irrigation stop treatments could be related to the lower level of carbohydrates stored in vegetative organs before pollination and to the decrease in leaf area duration which resulted in shortened grain-filling period. The results of current study confirm the results of the earlier studies in which it has been suggested that drought stress decreased the source potential and available assimilates level and hence, decreases grain weight [12]. Decreasing of grain weight under post-anthesis water deficit also has been elucidated by many reports as the main factor in determination of yield [24, 42]. Water deficit may act through reduction in photo assimilate production and enzyme activity in growing grains to reduce the grain weight. Defoliation of all leaves except the flag leaf treatment was due to increase of grain yield (2.1%), thousand grain weight (2.2%) and harvest index (16.9%) under water stress condition (Table 1). No decrease of some traits under effect source limitation such as grain yield and thousand grain weight in water stress condition, perchance throught increase of photosynthesis of other plant parts [15, 35] and/or cause a increase remobilization of store mater in stem to grain supply is being developed [27, 38].

3.1.3. Harvest index:

The results obtained from mean comparison analysis of grain yield and its components are shown in Table 1. Showed that post anthesis water deficiency stress caused 24.8 percent reduction in harvest index. Defoliation of all leaves except the flag leaf did not decrease harvest index but shaded ear reduced harvest index by 23.5% and 17.7% in the well water and water deficiency at the post anthesis, respectively (Table 1). Yang et al. [56, 57] showed that mild water deficiency increased the harvest index through increasing the carbohydrate remobilization from stems to the growing grains but severe water deficiency reduced the harvest index [7, 21]. Austin [8] suggested that high harvest index may be due to improved resistance to drought by making the plants much shorter along with enhancing the supply of nutrient substances to kernels.

3.1.4. Biomass and number of grain per spike:

Defoliation of all leaves except the flag leaf reduced biomass in the both conditions; this decrease was larger in drought stress condition (Table 1). Number of grain per spike was only slightly or not affected by shading treatments. The irrigation significantly affected morphological traits include biomass and number of grain per spike (Table 1). Means comparison showed that biomass under no-water stress irrigation treatment (2.32 g plant^{-1}) and under water stress (1.86 g plant^{-1}). It appears that water deficit stress decelerated yield growth rate and therefore, the decrease in assimilate during growth season led to the decrease in dry matter accumulation in stem intercalary meristem and consequently, the decrease in biomass. In addition, since the stress at final growth stages may decrease assimilate build-up; the plant resorted to the remobilization of stem storages for filling the grains which led to the decrease in biomass. Also, biological yield was reduced under stress condition that it was probably related to the lower spike weight and grain yield due to drought stress (Table 1). The results showed that the water deficit stress treatments led to the decrease in biomass which was in agreement with Abdoli and Saeidi [2].

3.1.5. Fertile spikelet and infertile spikelet:

In the control and drought stress conditions and source limitations (defoliation of all leaves except the flag leaf and shaded ear) did not decrease fertile spikelet and infertile spikelet but post-anthesis water deficiency stress caused 31.2 percent increase in infertile spikelet (Table 1).

3.2. Morphological and phonological traits

3.2.1. Plant height:

Results showed that, plant height was no significantly affected by water deficit after anthesis stage (Despite of insignificant reduction in the length of the plant) (Figure 2). Shaded ear had no significant effect on plant height but defoliation of all leaves except the flag leaf were significant differences between well water and drought stress conditions for this trait (Figure 2). Richards et al. [41] have reported that one of the major effects of water stress is to decrease plant height, which also caused a reduction in dry matter accumulation and subsequently plant production. Malik and Hassan [32] have earlier reported that stem length of guar (*Cyamopsiste tragonaloba* L.) genotypes significantly reduced under water stress.

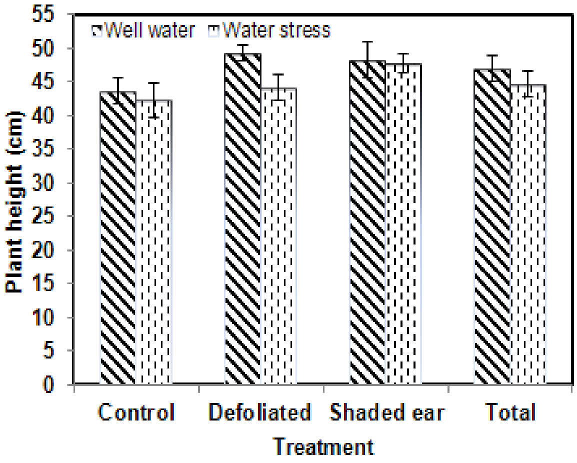

Figure 2. Effect of different water treatment (well watered and water stress from anthesis to maturity) and source limitation (control, defoliated and shaded ear) on the plant height in DN-11 wheat cultivar. Vertical bars represent ± SE of the mean (n=3) Data are means ± SE of three independent samples.

3.2.2. Grain filling period:

It was found that post-anthesis water deficit significant effect on the grain filling period (Figure 3). Simane et al. [47] and Villegas et al. [53] reported that the positive relationship between grain yield and morphological and phonological traits under water deficit condition indicate that low growth rate of plants is one of the limiting factors of yield under water deficit conditions. Water stress induced shortening of grain filling duration with smaller kernels at maturity was earlier reported [54]. Donaldson [17] and Nazeri [36] have reported that water deficit after anthesis stage decreased grain filling period, kernel weight and crop production.

Better light reception and air circulation and optimized phonological pattern will increase the total assimilates available for spike growth, thereby increasing the potential for grain filling and permitting the maximum partitioning of the available assimilates to the spikes [40].

3.3. Gas exchange

Figure 4 shows the net photosynthetic rate, stomatal conductance and transpiration rate of the flag leaf in source limitation and different water treatment. The photosynthetic rate was always higher in control treatment (Without limitation of photosynthetic resources) and well water condition (Figure 4). There were no significant differences in the rate of photosynthesis, stomatal conductance and transpiration rate among control and defoliation of all leaves except the flag leaf treatments under well water, but shaded ear was used to reduce the photosynthetic capacity of the canopy.

Net photosynthesis rate generally decreased with chlorophyll content and also this was paralleled by a lower stomatal conductance (Figure 4 and 5). Several researchers have published convincing evidence showing that photosynthetic carbon metabolism is affected by reduced plant water potentials [26, 30].

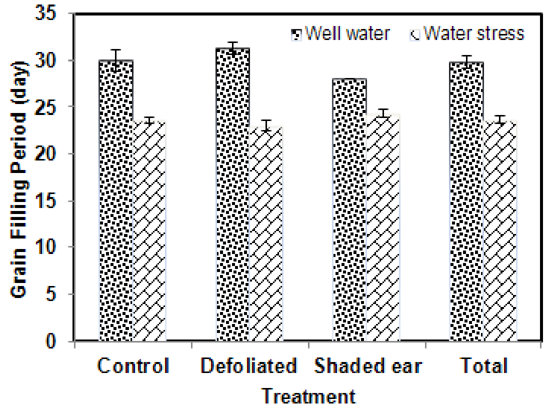

Figure 3. Effect of different water treatment (well watered and water stress from anthesis to maturity) and source limitation (control, defoliated and shaded ear) on grain filling period in DN-11 wheat cultivar. Vertical bars represent ± SE of the mean (n=3) Data are means ± SE of three independent samples.

Many studies have concluded that the reduction in photosynthesis in response to drought stress is to some extent the result of reduced stomatal conductance and, consequently, restriction of the availability of CO_2 for carboxylation [16, 30]. Reduction in transpiration rate under drought stress is another evidence for interference of water deficiency to stomatal conductance. Although reduction of photosynthesis by water deficiency is partly due to a reduced stomatal conductance, non-stomatal inhibition of photosynthesis, caused by direct effects of water stress on the photosynthetic apparatus, has been reported for some species [48, 49].

Table 1. Effect of different water treatment (well watered and water stress from anthesis to maturity) and source limitation (control, defoliated and shaded ear) on the grain yield, its components in DN-11 wheat cultivar

Condition	Treatment	Grain yield (g spike^{-1})	D* (%)	Biomass (g plant^{-1})	D (%)	Harvest Index (%)	D (%)	thousand grain weight (g)	D (%)	Number of grains per spike	D (%)	Fertile Spikelet	D (%)	Infertile Spikelet	D (%)
WW††		0.92±0.07†		2.32±0.10		39.5±2.6		22.6±0.5		40.6±2.7		15.3±0.3		1.48±0.19	
WS		0.55±0.08	-39.0	1.86±0.12	-19.6	29.6±2.8	-24.8	15.2±2.3	-31.4	36.6±1.8	-8.7	15.0±0.3	-2.0	1.84±0.12	31.2
	Control	0.87±0.09		2.27±0.09		37.3±3.0		21.7±1.9		39.6±2.4		15.0±0.4		1.61±0.13	
	Defoliated	0.71±0.08	-19.0	1.88±0.10	-17.1	37.1±2.5	-0.4	17.7±1.4	-18.5	39.7±1.8	0.2	15.4±0.1	2.3	1.74±0.17	8.1
	Shaded ear	0.63±0.07	-28.3	2.11±0.15	-7.2	29.4±2.6	-21.2	17.3±0.9	-20.4	36.5±2.6	-7.8	15.2±0.3	1.1	1.64±0.16	2.1
WW	**Control**	1.17±0.08		2.60±0.10		44.8±1.8		27.1±0.5		43.1±2.7		15.4±0.5		1.28±0.20	
	Defoliated	0.82±0.07		2.09±0.05		39.5±3.1		18.7±0.3		44.0±3.3		15.6±0.1		1.32±0.19	
	Shaded ear	0.77±0.07		2.27±0.16		34.3±3.0		22.1±0.6		34.9±2.2		14.9±0.3		1.83±0.17	
Relative decrease (%) (1)		-29.5		-19.9		-11.8		-31.0		2.2		1.3		3.1	
Relative decrease (%) (2)		-34.0		-13.0		-23.5		-18.6		-19.0		-3.3		43.5	
WS	**Control**	0.58±0.09	-50.6	1.94±0.07	-25.4	29.7±4.2	-33.6	16.3±3.3	-39.9	36.2±2.1	-16.0	14.6±0.4	-5.6	1.93±0.07	51.3
	Defoliated	0.59±0.08	-28.5	1.68±0.15	-19.4	34.7±1.9	-12.1	16.7±2.4	-10.9	35.4±0.2	-19.6	15.1±0.2	-3.7	2.15±0.14	63.4
	Shaded ear	0.48±0.07	-37.7	1.95±0.14	-13.9	24.5±2.3	-28.6	12.5±1.2	-43.3	38.2±3.1	9.5	15.4±0.4	3.3	1.44±0.15	-21.2
Relative decrease (%) (1)		2.1		-13.4		16.9		2.2		-2.2		3.4		11.4	
Relative decrease (%) (2)		-16.7		0.5		-17.7		-23.3		5.6		5.8		-25.3	

†† WW: Irrigation in all stages of plant growth normally and WS: post anthesis water deficiency with withholding of irrigation.
†Data were means ± SE (n=3).
In each column, compared to the 5% level of LSD method is used.
D* (%): Percentage decrease down control when water deficiency was applied at post anthesis.
(1) and (2): Percentage decrease down control when Photosynthesis inhibition treatments were applied only on leaves and ears, respectively.

Water deficiency at the post-anthesis significantly reduced net photosynthetic rate, stomatal conductance and transpiration rate (Figure 4). The results in this experiment confirmed several previous studies showing that water deficit stress significantly affects gas exchange, water relations and physiology in wheat, tomato and other plant [37, 39, 43, 50]. Source limitations (defoliation of all leaves except the flag leaf and shaded ear) significantly increase net photosynthetic rate, stomatal conductance and transpiration rate in water deficiency condition (Figure 4). Makunga et al. [31] reported that most of the carbon in mature wheat grains comes from leaf photosynthetic CO_2 assimilation during the grain filling period and the flag leaf assimilates are the most important contributor to the dry weight accumulation in grains.

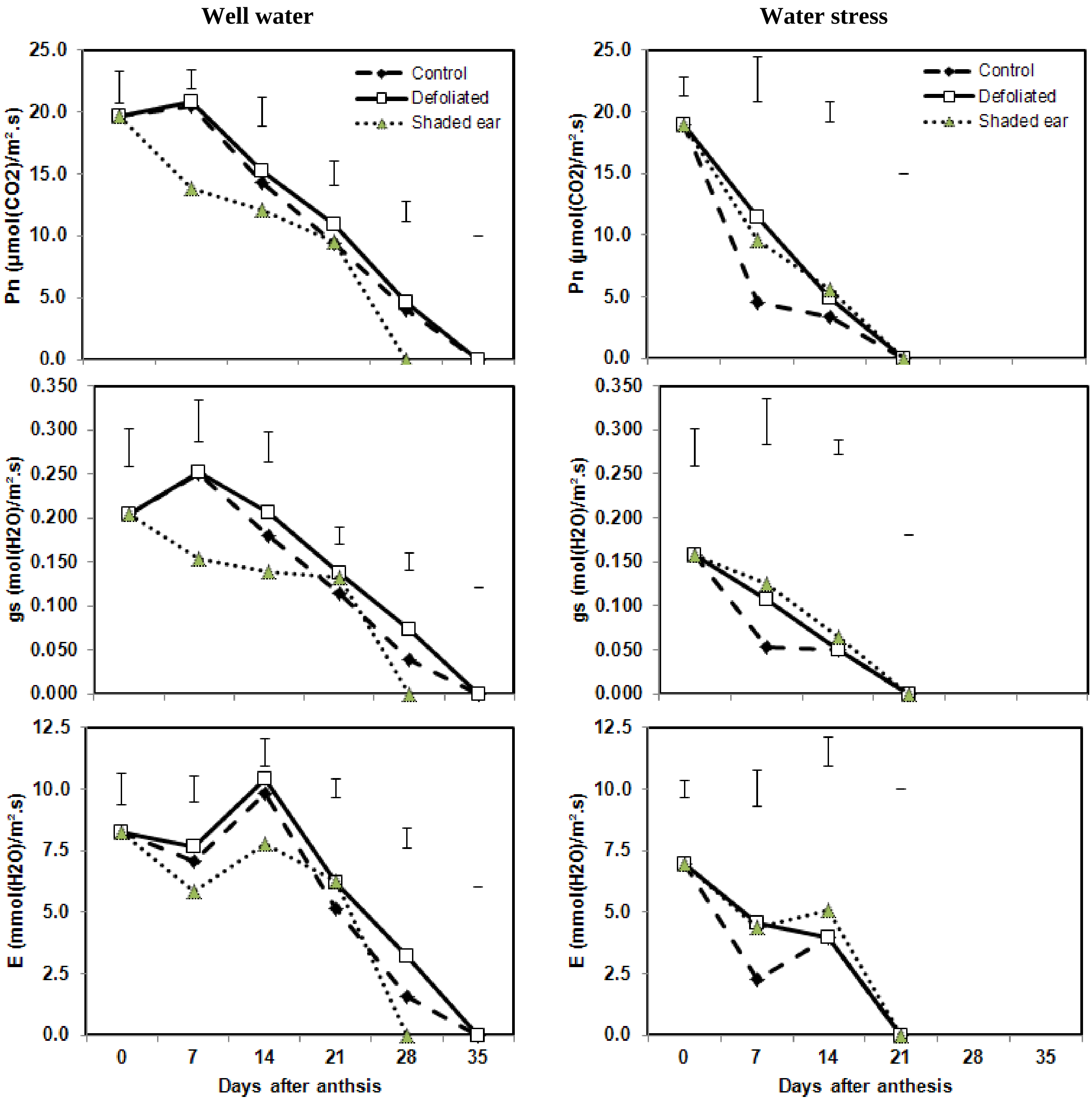

Figure 4. Changes in gas exchange flag leaves (Pn, gs and E) in well watered (WW) and water stress from anthesis to maturity (WS) and source limitation (control, defoliated and shaded ear) during grain filling in DN-11 wheat cultivar. Vertical bars represent ± SE of the mean (n=3) Data are means ± SE of three independent samples.

3.4. Chlorophyll content (SPAD)

In the well water and drought stress treatments, relevant differences were recorded in the SPAD throughout the experiment (Figure 5). SPAD decreased steadily in response to water deficit treatment and a significant change was found in the chlorophyll contents at 21 and 28 days after anthesis between treatments (Figure 5). Irrespective to water regime, the lower SPAD levels were measured in flag leaves of the shaded ear treatment during 0 to 14 days after anthesis. Drought stress imposed at anthesis contrast to control condition led to the senescence process started earlier in source limitation treatments (Figure 5).

Foulkes et al. [23] reported that longer green flag leaf area duration was related with the ability to maintain yield under drought. However, in drought conditions optimum flag leaf area is important for optimum photosynthetic activity as more area causes more transpiration losses [5].

Water deficiency at the post-anthesis significantly reduced in the SPAD during grain filling (Figure 4). The decrease in chlorophyll content under drought stress has been considered a typical symptom of oxidative stress and may be the result of photo-oxidation of photosynthetic pigments [6]. As result, chlorophyll concentration decreases under condition of stress by chlorophylls, peroxidase enzymes and phenolic components production [1]. Decreasing of chlorophyll content in plants such as wheat [43], bean [9] and also safflower [46] is reported under drought stress.

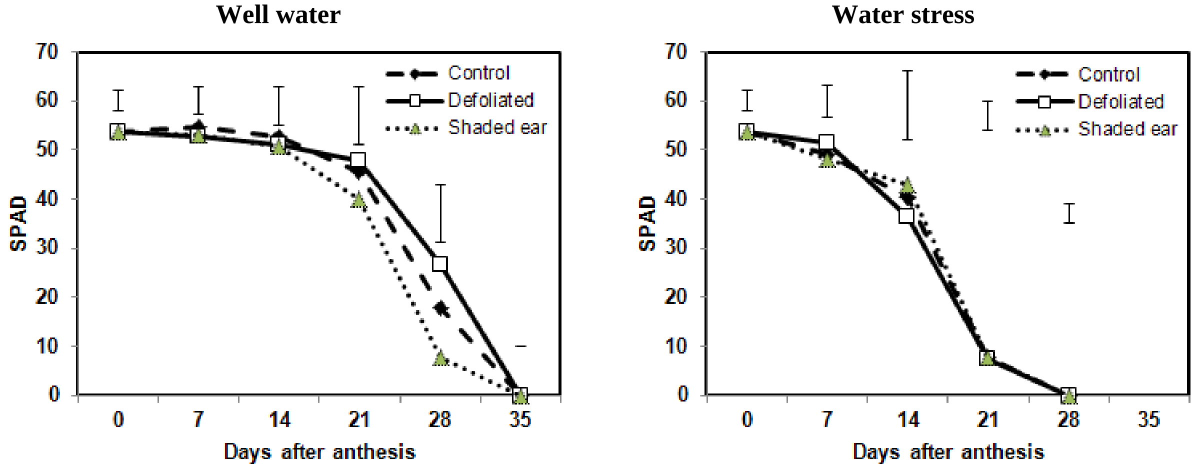

Figure 5. Changes in SPAD flag leaves in well watered (WW) and water stress from anthesis to maturity (WS) and source limitation (control, defoliated and shaded ear) during grain filling in DN-11 wheat cultivar. Vertical bars represent ± SE of the mean (n=3) Data are means ± SE of three independent samples.

4. Conclusion

It is concluded that water deficit stress at grain filling period can considerably decrease yield and its components of wheat. Grain yield had the highest decrease percent under drought stress condition that it was probably due to reduce thousand grains weight under drought stress. All leaves except the flag leaf and ear photosynthesis makes a significant contribution to grain yield of bread wheat 19% and 28.3% respectively, also 1000 grain weight 18.5% and 20.4% respectively. Water deficiency at the post-anthesis significantly reduced net photosynthetic rate, stomatal conductance and transpiration rate. Net photosynthesis rate generally decreased with chlorophyll content and also this was paralleled by a lower stomatal conductance. With respect to the future requirements for the production of wheat cultivar with higher grain yield, among the different sources of assimilates, spike (ear) photosynthesis had the main role in grain filling and should be more considered in future breeding programs.

5. Acknowledgments

The authors would like to thank their colleagues in Agricultural and Natural Resource, university of Razi, Kermanshah, Iran. Also, the authors are extremely thankful to Mrs. Shiva Ardalani for excellent technical assistance in some phases of this study.

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