

Water and radiation use efficiency in different developmental stages in four bread wheat cultivars under moisture stress conditions

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Abstract

This research was conducted in Toroq Experimental field station, Mashhad, Iran, for two successive cropping seasons (2000-2002), using split plot experimental design based on complete randomized blocks with three replications. Moisture stress treatments (at seven levels) were assigned to main plots, including: D₁ (full irrigation), D₂ (no irrigation from one-leaf to double ridge stage, and in other treatments, no irrigation and preventing rainfall as: D₃ (from one-leaf to floral initiation stage), D₄ (from floral initiation to the commencement of stem elongation or Terminal spikelet), D₅ (from commencement of stem elongation to flag leaf emergence), D₆ (from flag leaf emergence to anthesis) and D₇ (from anthesis to the soft dough), and four wheat cultivars, namely: Roshan, Qods, Marvdasht and Chamran, were sown in sub plots. The results of combined analysis of variance showed that the effect of moisture stress was significant. Applying D₅, D₆ and D₇ treatments reduced the grain yield in comparison with control (D₁) by 36.7, 22.8 and 45.6, respectively. Severe moisture stress treatments (D₅ and D₇) caused a reduction in water use efficiency (WUE) and radiation use efficiency (RUE), due mainly to reduction of dry matter. Based on these results, grain filling (D₇) and fast growing (D₅) stages of wheat were more sensitive to moisture stress. Genotypic differences were also observed with respect to concerned characteristics. Chamran had a higher moisture tolerance, therefore, greater grain yield as compared with the other cultivars.

Keywords: Moisture stress; Developmental Stages; Water Use Efficiency; Radiation Use Efficiency; Grain yield

1. Introduction

Wheat is one of the oldest and most valuable crop plants on the earth. It is widely grown, occupying the vastest production area among crop plants. Moisture stress is one of the main limiting factors in wheat producing areas. It is estimated that almost 33% of all wheat growing areas in the world and 55% of wheat growing areas in developing countries, including Iran, are to some extent affected by moisture stress. The results of many a researches have demonstrated that moisture stress in different wheat growing stages cause

significant reductions in total dry matter yield (biomass) as well as in grain yield. Furthermore, the effects of moisture stress have been reported to be different, considering the severity of stress and the developmental stage in which the plant faces moisture stress (Araus et al., 2003, Zarea and Ghodsi, 2004). Passioura (1996) has developed the following relationship for estimation of grain yield under moisture stressed conditions:

$$GY = W \times WUE \times HI \dots \quad (1)$$

Where:

- GY: grain yield
- W: amount of water used up by the crop
- WUE: Water Use Efficiency

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- HI: Harvest Index

Water use efficiency is the capability of the crop to produce dry matter (biomass) in return for the evaporated and transpired water. It has been expressed by Richards (1991), as per following:

$$WUE = TE / [1 + (Es/T)] \dots\dots (2)$$

Where:

- TE: Transpiration Efficiency (the ratio of above ground dry matter to the amount of water lost as transpiration from plant surfaces)
- Es: the amount of water lost as evaporation from soil surface
- T: the amount of water lost as transpiration by the plant.

According to the above relationships developed by Passioura (1996) and Richards (1991), to increase the grain yield in stress prevailing environments, the concerned characteristics should be improved through:

- ◆ Improving crop water use
- ◆ Enhancing water use efficiency
- ◆ Improving the ability of crop plants in allocating dry matter to grains, i.e. HI

In equation (2), it is shown that WUE can be improved either by increasing TE or through decreasing Es components. This can be realized through breeding as well as through field management practices. In addition, the grain yield of a particular crop (e.g. wheat) through a certain period is determined as:

$$GY = RAD \times RI \times RUE \times HI \dots (3)$$

Where:

- RAD: total incident solar Radiation Absorbed by the crop during its growth period
- RI: fraction of RAD absorbed by the canopy of crop (Radiation Interception Percentage)
- RUE: Radiation Use Efficiency
- HI: Harvest Index

Hence, it becomes evident that grain yield is closely associated with canopy photosynthesis during the growth period (Villegase et al., 2001).

Such management practices as changing the sowing dates or opting for breeding approaches to change the plant life cycle (e.g. phenological variations, increasing stress tolerance and leaf surface durability) can influence RI. The level of RI can be increased by early ground cover (i.e. early growth vigor) within a shorter period of time (e.g. development of tolerant cultivars adapted to stressful environments). Radiation Use Efficiency can also be improved by increasing absorption of

Photosynthesis Active Radiation (PAR) by leaves as well as by improving the overall plant photosynthesis rate in stressful conditions. In addition to increasing the absorption of radiation during the growth period, improving the rate of dry matter production per unit of used radiation (i.e. RUE) by the crop is an important and practical measure in evaluating the production of biomass in the crop. Thus, dry matter production under normal conditions is a function of time, PAR, absorbed PAR and RUE (Tollennar and Aguilera, 1992). Monteith (1972) reported that RUE can be relatively constant. He has reported that RUE is about 1.4 g/MJ for field crops. In contrast, other researchers have shown that RUE is variant for different cultivars (Jast and Cathren, 2000). Calderini et al. (1997) in a study on the impact of wheat breeding research on biomass, radiation interception and RUE, concluded that; although RUE in the pre- anthesis phase in new and old cultivars was the same, RUE and crop growth rate (CGR) were clearly higher in the new cultivars, during the post anthesis phase, in comparison with old cultivars. Many studies have demonstrated that moisture stress affects leaf growth and canopy development earlier than photosynthesis (Passioura 1996). To optimize for photosynthesis efficiency under stress prone conditions, the balance between maximum level of photosynthesis in the critical growth stages (under the optimum conditions) and the destructive effects of additional radiation incidence in stress prone environments must be taken into consideration. On this basis, stress conditions (the intensity and timing of stress incidence) should be considered in selecting for the concerned desirable characteristics. The main objective of this study was therefore to investigate the effects of moisture stress, in different growth stages, on grain yield, water use efficiency (WUE) and radiation use efficiency (RUE) in wheat cultivars.

2. Materials and Methods

The research was carried out as a field experiment, using split plot arrangement in a randomized complete blocks design with three replications in fields of Toroq Experimental Station, Mashhad, Iran with a latitude of 36° 13' N and an altitude of 59° 40' E (985 m above sea level), in two successive cropping seasons (2000-2002). Soil was of Fine-loamy over Sandy-Skeletal, Mixed, Mesic type. Moisture stress treatments were applied in seven phases (as main plots) of D₁ (Full irrigation); D₂ (No irrigation from one-leaf to double ridge stage, 11-23 of Zadoks scale, and in other treatments, No

irrigation and preventing rainfall as: D₃ (from one-leaf to double ridge stage); D₄ (from double ridge to the commencement of stem elongation/ Terminal spikelet, 23-31 of Zadoks scale); D₅ (from the commencement of stem elongation to flag leaf emergence, stages 31-41 of Zadoks scale); D₆ (from flag leaf emergence to anthesis, 41-65 of Zadoks) and D₇ (from anthesis to soft dough stage, 65-85 of Zadoks). Four spring bread wheat cultivars, C₁: Roshan (an old cultivar with wide adaptation to different environments), C₂: Qods (a high yield potential cultivar and susceptible to moisture deficit), C₃: Marvdasht (an improved cultivar with high yield potential but unknown response to moisture stress) and C₄: Chamran (an improved cultivar with high yield potential and tolerant to terminal drought) were sown in sub-plots of 3×2.4=7.2 m². Each cultivar was planted in 12 rows with 20 cm row spacings. In order to prevent moisture interference through infiltration, a distance of 2.4 meters was left out between main plots. Sowing date was late October, and the seeding rate calculated based upon 400 seeds per square meter taking into account 1000 kernel weight. The seeds having been treated with fungicide, Carboxin-Tiram (Vitavax) were planted at 5 cm depths.

Fertilizer need was determined based upon soil test and applied using (120-90-50 kg/ha) N-P-K per hectare formula. The whole phosphorous and potassium fertilizers as well as one third of nitrogen fertilizer were applied at sowing time while the rest of nitrogen fertilizer being applied at two stages of: commencement of stem elongation and beginning of spike emergence. Trial was sown using seed plotter (Winter Stieger) and the first irrigation was applied on the 11th of November. The experimental field was weeded once or twice during the growing season. During the 2nd year, climatic conditions were favorable for the incidence of diseases, and when the first symptoms of yellow rust were observed on some susceptible cultivars (e.g. Roshan and Qods), fungicide (Tilt) with a dose of 0.75 per thousand was applied to control the disease. Moisture stress treatments in different growth stages were also applied as no irrigation accompanied by prevention of rainfall. A mobile rain shelter was employed in each sub-plot to prevent rainfall. The rain shelters had been constructed out of frame beams and white greenhouse poly-ethylene plastics of 95% light transparency rate. The shelters were mobile and their heights adjustable. These plastic shelters were spread over the field only whenever there was rain. In the full irrigation treatment as well as other treatments, after application of moisture stress treatments in the concerned growth stages the required volume of

water for each plot as well as and timing of irrigation was determined following weighing method soil moisture measurements. Irrigation was applied through furrows. In order to measure water use in each irrigation interval, prior to applying the next irrigation, soil samples (up to 60 cm depth) were taken. The samples were placed in the oven at 105°C for 24 hours. The dry weight of samples was found out and the percent moisture for soil samples calculated. Forty eight hours after irrigation and at the threshold of Field Capacity (FC), sampling was repeated and volume of water reserved at depth of 60 cm (the depth sufficient for root development) calculated using the following equation:

$$(\theta w_1 - \theta w_2) \times Bd \times r/100 = R \quad \dots \quad (4)$$

Where

θw_1 : percent soil moisture after irrigation

θw_2 : percent soil moisture before irrigation

Bd: bulk density (apparent specific gravity gr/cm³)

R: depth of wheat root development

R: depth of reserved moisture in centimeters

The volume of irrigation water (V) was calculated using the following equation (5):

$$V \text{ (m}^3\text{)} = (R/100) \times 10000 \text{ m}^2$$

Based on 50% soil moisture depletion (from field capacity level) irrigation was applied up to root development depth. Partial Flume type IV was employed to measure the volume of water into and out of each plot to control water use based on the volume needed as calculated for each treatment. The amount of water use was calculated based on water column needed for saturation of soil profile at the maximum root development depth, in cubic meters. Soil sampling demonstrated that soil moisture percentages at threshold of F.C. and Permanent Wilting Point (PWP) were 18% and 8%, respectively. Soil moisture percentages in more severe moisture stress treatments; i.e. D₅ and D₇ were 12% and 10%, respectively. Finally, water use efficiency (kg / mm), which is the ratio of seed yield (kg/ha) to the amount of water used, was determined based on the estimated water use for each treatment. By knowing the required amount of water and after recording the level of water in column in Partial Flume, the exact timing for irrigation intervals were calculated. In fact, the amount of required water to realize field capacity for each experimental plot was controlled through Partial Flume, based on soil depth into which roots develop, and the amount of water allocated to each plot.

The level of radiation incidence was measured using a radiation meter device equipped with a 1-meter sensor, located in lower and higher halves of canopy. Radiation level was recorded at solar noon (with one hour difference) and with a clear sky. The radiation sensor was placed horizontally, above the plants, in each sub-plot and the incoming radiation recorded as incident radiation (I₀). The radiation at the lower canopy was measured in three different directions, and the average considered as transmitted radiation (I) through canopy. Then, the percentage of intercepted radiation (IR%) and extinction coefficient (K) were calculated as follows:

$$RI\% = [1 - (I / I_0) \times 100 \dots \quad (6)$$

$$K = [\ln (I / I_0)] / LAI \dots \quad (7)$$

Equation (6) was used by Fischer (2001). LAI is the leaf area index. Using the daily radiation data (from a meteorological station near the experimental field) and the following relationships, the values for daily and cumulative radiation were calculated:

$$PAR_0 = 0.48 RG_0 \dots \quad (8)$$

$$PAR_a = 0.95 \times PAR_0 [1 - \exp(-k \times GLAI)] \dots \quad (9)$$

Where:

PAR₀ is the active photosynthesis radiation in the higher canopy

RG₀ is the incoming radiation

PAR_a is the intercepted PAR

LAI values for different growing stages (6 stages: one leaf, double ridge, terminal spikelet, booting, anthesis and soft dough) were measured using leaf area meter. Radiation Use Efficiency (RUE) was calculated using the following equation:

$$RUE = (W_n - W_{n-1}) / (cPAR_a_n - cPAR_a_{n-1}) \dots \quad (10)$$

Where:

W_n and W_{n-1} are the dry matter weights (biomass) of above ground plant parts in nth and n-1 (th) days, respectively. cPAR_{a_n} and cPAR_{a_n-1} are intercepted PAR in nth and n-1(th) days, respectively.

In order to determine the growing phases for application of moisture stress treatments, five plants were randomly taken from each plot and by dissection of shoot apex, double ridge and terminal spikelet, different stages were determined using binocular. Other growing stages were identified as: emergence of more than 50% of flag

leaf (booting), emergence of more than 50% of anthers (anthesis), and 50% of grains in soft dough (soft dough stage). To avoid marginal effects, six rows (three rows from each side) and one meter from the top and bottom ends of each plot were discarded. Six central rows covering on area of 1.2 square meters were harvested, using sickle, and then threshed. Grain yield was assessed and recorded for each plot. SAS and MSTATc softwares were employed to analyze the data. Bartlett homogeneity test was performed on the concerned variances. Combined analysis of variance was then performed.

3. Results and Discussion

Results indicated that the highest and the lowest grain yields belonged to D₂ and D₇, respectively. Significant decrease in grain yield was observed in D₇, D₅ and D₆ treatments, in comparison with D₁ as control. The average grain yield in these treatments, as compared to D₁, decreased by 45.6, 36.7 and 22.8%, respectively (Fig. 1). Meanwhile, moisture stress in initial growth phases (D₂, D₃ and D₄ treatments) did not result in a significant decrease in grain yield. There are many other reports on the effects of moisture stress in various growth stages of wheat that confirm these results.

Besides different effects of moisture stress on grain yield, cultivars responded differently to various treatments. In general, among the tested cultivars, Roshan showed a very low grain yield potential. Grain yield of Roshan and Chamran cultivars under D₅ treatment decreased by 23.5 and 30.2%, respectively, in comparison with their grain yield in control treatment (D₁). Grain yield of Qods and Marvdasht cultivars under the same treatments decreased by 46.5 and 41.7%, respectively (Fig. 1). Furthermore, under the severe moisture stress conditions (D₇ treatment), grain yield in Roshan, Chamran, Qods and Marvdasht cultivars decreased by 41.1, 34.1, 54.5, and 50.6%, respectively, as compared with control (D₁) (Fig. 1).

Naderi et al. (2000), reported that Roshan and Chamran wheat cultivars had a relatively higher tolerance threshold to moisture stress, their findings being in agreement with the results in this research. The results also demonstrated that grain yield of Qods and Marvdasht cultivars significantly decreased, in all moisture stress treatments. This means that these cultivars have high grain yield potential under optimum irrigation conditions, but slight moisture stress would adversely influence their grain yield (Fig. 1). Researchers believe that there are genotypic variations in wheat cultivars regarding their

threshold of tolerance to moisture stress conditions. Usually, cultivars with high grain yields under optimum conditions, are more

tolerant to moisture stress, and produce reasonable grain yield under these conditions.

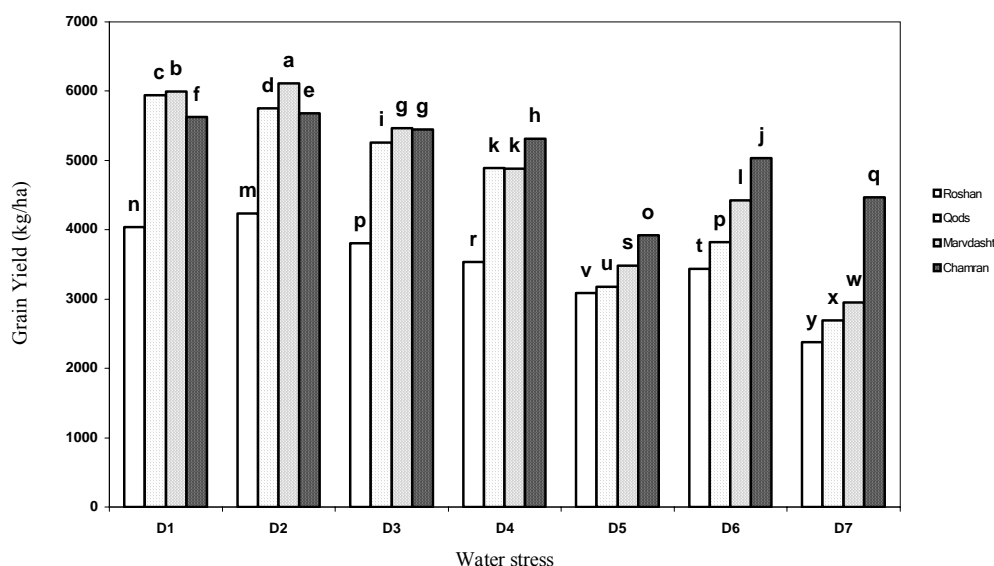


Fig. 1. The interaction of moisture stress and cultivar on grain yield

Precipitation, evaporation from class A evaporation pan, water use, and water use efficiency using grain yield (WUEG) in different moisture stress treatments over 2 years are presented in Table 1. Due to higher precipitation levels during the second year (2001-2002), water use (including effective rainfall) was greater than that in the first year (2000 – 2001). Water use in

control (D₁, full irrigation) and D₂ (No irrigation from one-leaf to double ridge stage except rainfall) treatments were almost similar; 467.9 and 528.1 mm in the first and second years, respectively. Evaporation from class A pan at the beginning of growth stages in the second year was higher than that in the first year (Table 1).

Table 1. Precipitation, evaporation from class A pan, water use and water use efficiency (WUE) in different moisture stress treatments

Moisture stress treatments	Growing Seasons	Precipitation (mm)	Water use plus effective rainfall (mm)	Evaporation from class A pan (mm)	Grain yield (Kg.ha ⁻¹)	WUEG (Kg.ha ⁻¹ .mm ⁻¹)	Mean of 2 years WUEG (Kg.ha ⁻¹ .mm ⁻¹)
D ₁	First	58.1	467.9	0	4763	10.18	10.805
	Second	76.6	528.1	21	6038	11.43	
D ₂	First	58.1	467.9	0	4827	10.32	10.900
	Second	76.6	528.1	21	6065	11.48	
D ₃	First	58.1	409.8	0	4653	11.35	11.580
	Second	76.6	451.5	21	5333	11.81	
D ₄	First	18.7	449.2	0	4321	9.62	9.725
	Second	21.0	507.1	0	4981	9.83	
D ₅	First	18.3	456.6	81.3	3700	8.10	7.180
	Second	26.5	501.6	83.2	3138	6.26	
D ₆	First	2.9	465.0	79.5	4216	9.07	8.645
	Second	25.4	502.7	80.1	4132	8.22	
D ₇	First	7.6	460.3	228.9	3103	6.74	6.245
	Second	47.3	480.8	165.6	2767	5.75	

Results obtained on the basis of water use efficiency using grain yield (WUE_G) revealed that in the first year, in all moisture stress treatments, WUE_G was higher than that during the second year (Table 1). Application of lower moisture stress treatments (D₃ and D₄ treatments) relatively increased WUE_G, whereas, application of higher moisture stress treatments (D₅, D₆ and D₇

treatments) increased WUE_G, in either year. The average WUE_G showed that application of D₃ treatment, relatively increased water use efficiency (WUE_G), but D₅, D₆ and D₇ treatments decreased WUE_G by 8kg.mm⁻³ (Table 1). Although the amount of water use is almost the same in D₁ and D₇ treatments, grain yield in severe moisture stress treatments (D₇)

significantly decreased in comparison with control treatment (D₁) and consequently, had considerable effect on reducing WUEG in D₇ treatment. This is mainly due to reduction of WUEG under more severe moisture stress treatments (No irrigation) in critical growth phases (e. g. grain filling).

Re-watering of treatments following termination of moisture stress did not have any significant effect on grain yield, however, it was considered in calculations of water use. This was true for all moisture stress treatments. Anderson (1992) reported that under severe moisture stress treatments, wheat water use efficiency decreased, because stress treatments were applied in critical growth stages (e.g. double ridge, commencement of stem elongation, and anthesis) and had adverse effects on dry matter accumulation. His findings confirm the results of this research.

Furthermore, water use, effective precipitation, grain yield, and water use efficiency of different wheat cultivars under different moisture stress treatments, over two years, are presented in Table 2. The intensity of environmental stress (SI) for each environment (stress treatment) was calculated and it was determined that grain yield under D₃, D₄, D₅, D₆ and D₇ treatments decreased by 7.5, 13.8, 36.6, 22.7, and 45.6%, respectively, as compared to full irrigation treatment (D₁). Under D₅ and D₇ treatments, stress was more severe and subsequently, the environmental severity was more than in the other treatments (Table 2). Acevedo et al. (2002) reported that water use efficiency in wheat under moisture stress treatments in growth phases before anthesis and grain filling stages were 14.6, 12.4 and 15.2, respectively. They reported WUE of 16.8 kg.mm⁻³ for control treatment (D₁). They concluded that moisture stress in critical growth stages (anthesis and grain filling stages) significantly decreased water use efficiency, which confirms the results of this research.

In the first year, the highest WUEG under D₁, D₂ and D₃ treatments belonged to Qods and Marvdasht cultivars, however, under D₄, D₅, D₆ and D₇ treatments, the highest WUEG belonged to Chamran cultivar. On the other hand, Roshan had the lowest WUEG under all moisture stress treatments, in both growing seasons. Under D₁ to D₅ treatments, Qods, Marvdasht, and Chamran cultivars had almost the same WUEG, while under severe moisture stress treatments (D₆ and D₇), Chamran cultivar had the highest WUEG (Table 2). Nakhjavani Moqaddam and Qahraman (2004) studied the effect of moisture stress on grain yield, agronomical characteristics and water use efficiency in different growth stages for Tous a facultative wheat cultivar. They concluded that

there is a significant difference in WUEG between

moisture stress treatments and control treatment (D₁), particularly in tillering, stem elongation and anthesis stages. Nakhjavani Moqaddam and Qahraman (2004) also reported that ceasing of irrigation in each growth phase caused some variations in grain yield and water use, thus, combined effects of these two parameters, changed water use efficiency. They also concluded that differences in water use under moisture stress treatments as compared to control, depended on grain yield and water use differences.

These differences imply the likely differences in sensitivity of wheat at different growth stages to water deficit. These results also are in match with the results of the present research. Variations in WUEG between different cultivars and moisture stress treatments are due mainly to differences in grain yield of cultivars. Passioura (1996) believes that under circumstances where water use for different wheat cultivars is similar, the cultivars that produce higher grain yield under optimum (no stress) conditions would have greater water use efficiency under stress conditions too. This is in agreement with the findings in this study in which the lowest and the highest water use efficiency (as averaged over two growing seasons (2000-2002)) were obtained for Roshan and Chamran, respectively (Table 2).

Radiation Use Efficiency (RUE) is the ratio of produced dry matter to cumulative intercepted photosynthesis active radiation (cPARa) (Fig. 2). It is clearly shown that RUE increases with time and growth stage progression. This is due mainly to expansion of leaf area (increase in leaf area index) which leads to an increase in green active photosynthetic area for interception of more incident radiation. Potential radiation use efficiency depends on the following factors (Acevedo et al., 2002): sufficient

Sufficient moisture for maximum stomata conductance and CO₂ transfer to the leaves; relative vertical arrangement of leaves to facilitate the penetration of solar radiation through canopy; sufficient nourishment of leaves to support photosynthesis; and enough canopy for interception of CO₂ and dissemination of extra heat.

There were some differences among moisture stress treatments in RUE. D₁, D₂ and D₃ treatments exhibited the highest RUE, however, the lowest RUE belonged to D₅ and D₆ treatments (Fig. 2).

Table 2. The calculated water use and water use efficiency for four wheat cultivars under different moisture stress treatments

Growing season		1379-80 (2000-01)			1380-81 (2001-02)			Mean of two years	
Water stress	Cultivar	Water use (mm)	Grain yield (kg.ha ⁻¹)	WUE _G (Kg.ha ⁻¹ .mm ⁻¹)	Water use (mm)	Grain yield (kg.ha ⁻¹)	WUE _G (Kg.ha ⁻¹ .mm ⁻¹)	Mean of grain yield (kg.ha ⁻¹)	WUE _G (Kg.ha ⁻¹ .mm ⁻¹)
D1	Roshan	467.9	3753	8.021	528.1	4323	8.186	4040	8.112
	Qods	467.9	4960	10.601	528.1	6927	13.117	5940	11.928
	Marvdasht	467.9	5250	11.220	528.1	6733	12.749	5990	12.028
	Chamran	467.9	5087	10.872	528.1	6167	11.678	5630	11.305
D2	Roshan	467.9	3777	8.072	528.1	4700	8.900	4240	8.514
	Qods	467.9	5100	10.900	528.1	6403	12.125	5750	11.546
	Marvdasht	467.9	5593	11.953	528.1	6633	12.560	6110	12.269
	Chamran	467.9	4837	10.338	528.1	6523	12.352	5680	11.406
D3	Roshan	409.8	3533	8.621	451.5	4077	9.030	3810	8.847
	Qods	409.8	4767	11.633	451.5	5743	12.720	5260	12.214
	Marvdasht	409.8	5357	13.072	451.5	5567	12.330	5460	12.679
	Chamran	409.8	4953	12.086	451.5	5947	13.172	5450	12.655
D4	Roshan	449.2	3290	7.324	507.1	3777	7.448	3530	7.383
	Qods	449.2	4500	10.018	507.1	5277	10.406	4890	10.227
	Marvdasht	449.2	4617	10.278	507.1	5143	10.142	4880	10.206
	Chamran	449.2	4877	10.857	507.1	5740	11.319	5310	11.105
D5	Roshan	456.6	3350	7.337	501.6	2833	5.648	3090	6.450
	Qods	456.6	3450	7.556	501.6	2900	5.781	3180	6.637
	Marvdasht	456.6	3540	7.753	501.6	3430	6.838	3490	7.284
	Chamran	456.6	4460	9.768	501.6	3390	6.758	3930	8.203
D6	Roshan	465	3563	7.662	502.7	3317	6.598	3440	7.110
	Qods	465	3493	7.512	502.7	4147	8.249	3820	7.895
	Marvdasht	465	4403	9.469	502.7	4447	8.846	4430	9.156
	Chamran	465	5403	11.619	502.7	4617	9.184	5010	10.354
D7	Roshan	460.3	2400	5.214	480.8	2357	4.902	2380	5.058
	Qods	460.3	2690	5.844	480.8	2700	5.616	2700	5.738
	Marvdasht	460.3	3433	7.458	480.8	2477	5.152	2960	6.291
	Chamran	460.3	3887	8.444	480.8	3533	7.348	3710	7.884

* SI: Stress Intensity

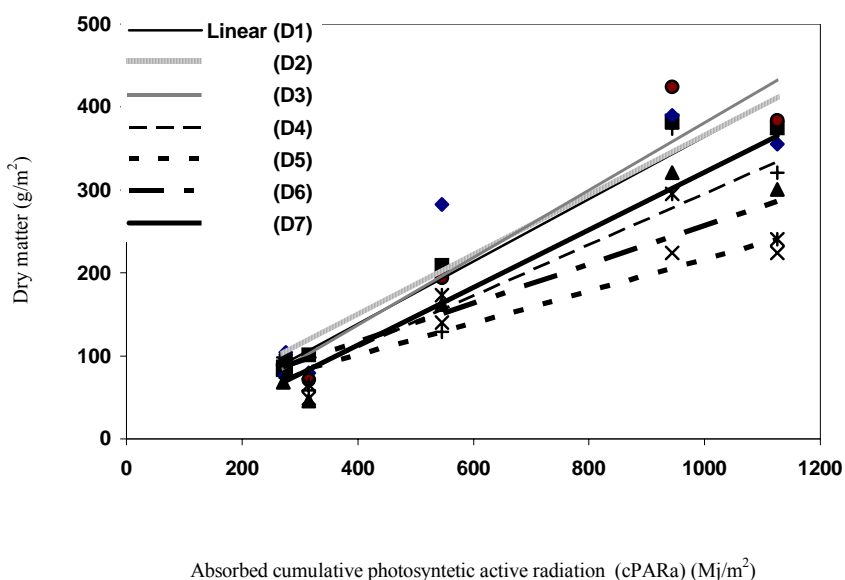


Fig. 2. Variation in Radiation Use Efficiency (RUE) in different moisture stress treatments

The trend of variations in RUE is similar to that of grain yield which was discussed earlier. Generally, in severe moisture stress treatments (D5, D6 and D7), reduction in leaf area index, green active photosynthetic areas as well as the

percentage of intercepted radiation decreased, hence, accumulated dry matter, grain yield and RUE decreased (Fig. 2). Montieth (1972) reported that RUE can be fairly constant. He defined this coefficient for different crops as 1.4 grams of dry

matter per each mega joules of absorbed solar radiation. Other researchers (Jost and Cothren, 2000) believe it would vary for different crops and genotypes. For instance, Acevedo, et al. (2002), reported RUE values for wheat as 3gMj^{-1} , which was calculated based upon the above ground dry matter and roots. They also believed that moisture stress had a slight effect on RUE; however, radiation intensity in a defined area influenced RUE. Calderini et al. (1997) studied RUE in wheat cultivars and reported that in newly bred cultivars, during post-anthesis stage, RUE and the crop growth rate were clearly greater than in old cultivars; however, RUE was similar in all cultivars, in the pre-anthesis stage. This is also in agreement accordance with the findings in this study. They also emphasized that in new cultivars, at anthesis stage, biomass was lower than in old cultivars, therefore, suggested that RUE must be taken into consideration for genetic improvement in wheat breeding programs as an important physiological attribute. Overall, improving crop photosynthesis under stress prone conditions requires a balance between maximum level of photosynthesis at critical growth stages (optimum conditions) and avoidance from destructive effect of surplus intercepted radiation in severe stress conditions. In these environments, selection for desired characteristics would be based on the definition and severity of stress conditions (i.e. timing as well as intensity).

4. Conclusion

The results of this study illustrated that imposing moisture stress in critical growth stages (Commencement of stem elongation, anthesis and grain filling) would significantly decrease grain yield; however, imposing moisture stress in initial growth stages would not have such a significant effect on grain yield. Furthermore, wheat cultivars reacted differently to different moisture stress treatments. Chamran cultivar had a higher grain yield and was more tolerant to moisture stress during critical growth stages. On the other hand, it was demonstrated that application of lower moisture stress treatments (D3 and D4) relatively increased water use efficiency (WUE), however, severe moisture stress treatments (D5, D6 and D7) decreased WUE. Genetic differences also played a significant role in variation in WUE among different cultivars. Roshan and Chamran cultivars exhibited the lowest and the highest WUE, respectively. It was also illustrated that there were some differences in moisture stress treatments for radiation use efficiency (RUE). D1, D2 and D3 treatments showed the highest RUE, while the lowest RUE belonged to D5 and D6 treatments.

This can be due mainly to significant reduction in leaf area index, radiation interception areas as well as to the percentage of intercepted radiation which led to reduction in dry matter, grain yield, and RUE.

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