Journal of Plant Physiology and Breeding
2016, 6(1): 23-34 ISSN: 2008-5168

Agronomic and Photosynthetic Characteristics of Different Maize Hybrids in Response to Water Deficit Stress at Different Phenological Stages

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Received: October 3, 2015 Accepted: April 19, 2016

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Abstract

The aim of present study was to evaluate the effects of drought stress on net photosynthesis rate (Pn), stomatal resistance, water use efficiency (WUE) and biomass (BM) of six maize (*Zea mays* L.) hybrids. Drought stress applied by withholding water supply at 4-5 leaf stage (S1, vegetative stage), anthesis (S2, reproductive stage), and dual stress condition (S3, combination of vegetative and reproductive stages). Results showed that all of the traits changed differently among hybrids under water stress but recovered close to initial values after re-watering. S3 affected leaf gas exchange and agronomic traits more severely than S1 and S2 treatments. Pn decreased due to imposed drought but more slowly in hybrids SC647 and SC704. In addition, SC700, SC704 and SC647 had the maximum BM and plant height. But, WUE decreased during the water stress period especially in hybrids SC260 and SC370 in which the decrease was remarkable. It can be concluded that SC704 and SC647 were the most tolerant and SC260 and SC370 were the least tolerant hybrids to water stress. The variation observed amongst the evaluated hybrids suggests the existence of valuable genetic resources for crop improvement in relation to drought tolerance.

Keywords: Dry weight; Drought; Gas exchange; Re-watering; Water use efficiency

Abbreviations: Net photosynthesis rate (Pn), Stomatal resistance (Rs), Water use efficiency (WUE), Biomass (BM), Field capacity (FC), Total water use (WU), Photosynthetically active radiation (PAR), Analysis of variance (ANOVA), Plant dry weight (PDW), Plant height (PH)

Introduction

Maize (*Zea mays* L.) is the most important C_4 crop (Baldochi *et al.* 2010) and is extensively cultivated throughout the world. But, its production is limited by drought stress worldwide especially in drought prone areas. Drought stress affects many physiological and molecular aspects of plants, such as gas exchange, water use efficiency (WUE) and biomass production (Chalapathi Rao and Reddy 2008). Stomatal closure is the primary and important response to water stress and is assumed to be the main cause of impaired photosynthesis under drought stress condition, because stomatal closure limits CO_2 availability to chloroplast of the mesophyll cells (Flexas *et al.* 2004; Grassi and Magnai 2005; Zlatev and Lidon 2012). On the other hand, the amount of soil water content accessible to plant roots can be crucial for growth and development and eventually crop yield (David *et al.* 2007). Also, physiological characteristics of plant are correlated with soil and plant water potential (Allahmoradi *et al.* 2013). Different growth and development related processes depend on the interplay of intercellular organelles (Saibo *et al.* 2009; Rahnama *et al.* 2010). Several researchers explained numerous effects of water deficit on plant growth parameters (Ohashi *et al.* 2000; Yao *et al.* 2009; Allahmoradi *et al.* 2013), photosynthesis (Chen *et al.* 2011; Saeidi and Abdoli 2015), stomatal conductance (Flexas *et al.* 2004; Zlatev and Lidon 2012), and crop yield (Gholinezhad *et al.* 2013). However, studies concerning the effects of drought stress on photosynthetic apparatus and WUE of C_4 crops are less than that of C_3 (Niinemets *et al.* 2009), despite C_4 crops can successfully maintain photosynthetic activity (Sairam *et al.* 2005; Saeed Rauf and Sadagat 2008) and shoot growth (Nayyar 2003; Ashraf 2010) under low soil water potentials at which the C_3 plants cannot with-stand. Some studies showed the stomatal closure for the restrain of C_4 photosynthesis under water stress while others deduced that non-stomatal factors have the major rule. The effects of drought on photosynthesis can be attributed directly to the stomatal limitations for diffusion of gases, which ultimately alters photosynthesis and the assimilate metabolism (Parida *et al.* 2007; Chaves *et al.* 2009).

WUE is considered as one of the important factors for determination of crop yield under drought stress and even as a component of crop drought resistance. This trait is used to imply that plant production in dryland condition can be increased per unit water used (Niinemets *et al.* 2009). Most of the maize world production is derived from high yielding hybrids. Physiological variability among hybrids will be useful for the selection of drought tolerant traits/hybrids and will contribute to the understanding of drought stress effects and responses in C_4 plants. Generally, grain filling period is crucial for determination of final grain yield. Any environmental adversities during this period could obviously reduce grain yield and biomass (Ahmad *et al.* 2007; Gholinezhad *et al.* 2013). Decreased yield in response to drought stress during the reproductive and grain filling stages has been reported in several studies (Pradhan *et al.* 2012; Azhand *et al.* 2015), whilst the effects of drought stress during the vegetative period on yield and physiological traits remain unclear.

In the present study effects of drought stress on the agronomic traits associated with the biomass of different maize hybrids were evaluated. Also, physiological characteristics (such as gas exchange variables) of plant response to drought stress at different stages, which may be crucial for selecting/breeding resistant crop genotypes, were studied.

Materials and Methods

Experimental procedure and design

A pot experiment was conducted during the spring and summer seasons of 2012 in the greenhouse of Razi University, Kermanshah, Iran (47º, 9′/E; 34º, 21′/N, 1319 m above sea level). The experiment was laid out as factorial using randomized complete block design with four replications. The treatments included four irrigation regimes and six maize hybrids. The irrigation regimes were as follows: control (C) for which the plants were irrigated every day to 90 ± 5% FC from the date of sowing to maturity; early water shortage (S1) i.e., withholding irrigation at 4-5 leaf stage (vegetative stage) for three weeks and re-watering thereafter; late water shortage (S2) i.e., withholding irrigation at anthesis (reproductive stage) for three weeks and re-watering thereafter, and dual stress (S3) i.e., withholding irrigation at both vegetative and reproductive stages each of which for three weeks and re-watering thereafter to 50 ± 5% FC for all drought treatments. The maize hybrids were SC704, SC700, SC647, SC500, SC370 and SC260. All hybrids were grouped into three sets based on the length of their grow period (Table 1).

Soil water holding capacity was determined (Mckim *et al.* 1980) after sowing and the amount of water applied to the pots was adjusted at 90% and 50% of FC for normal (control) and water stressed pots, respectively. During the growth period pots were weighted every two days using an electronic balance (RADIN 1204, precision = 1 g) and irrigated up to their initial weight to maintain the growing condition constant.

The maize hybrids were grown in plastic pots (50 cm × 70 cm) with 15.5 kg of silty-clay soil. The physico-chemical characteristics of the soil used in the experiment were presented in Table 2. Five seed were sown in each pot on 20th May 2012 and the number of seedlings was reduced to two per pot two weeks after their emergence. During planting, 17 g CH_4N_2O (urea), 0.86 g P_2O_5 and 13 g K_2O were added into the soil and thereafter, another 0.13 g N per pot was added as top-dressing at 5-6 leaf stage. Water stress treatments were started at 18 (vegetative stage) and 72 (reproductive stage) days after sowing, and the plants were harvested 118 days after sowing.

Table 1. Classification of the hybrids based on their growth period

Maize hybrids	Time of maturity
SC704 and SC700	Late
SC647 and SC500	Medium
SC370 and SC260	Early

SC: Single cross.

Table 2. Physico-chemical characteristics of the soil used in the pot experiment

Soil type	pH	†OC	K	Ca	Mg	P	As	Cd	Pb
		(%)	(mg kg^{-1})						
Silty-clay	6.8	1.2	221	5717	200	131	17.8	0.414	29.1

†OC: Organic carbon. Note: Available nutrients were determined in extracts obtained by Mehlich III procedure (Zbíral 2000).

Gas exchange parameters

Gas exchange characters i.e., net photosynthetic rate (Pn) and stomatal resistance (Rs) were measured on stressed and non-stressed plants around mid-day between 09:00 to 12:00 in the three youngest plant leaves at every stage. These measurements were made on 2×6 cm of leaf area using a portable photosynthesis system LI-6400

(LI-COR Biosciences Inc., Nebraska, USA) with 6400-11 Narrow Leaf Chamber under ambient CO_2 concentration of 370-400 µmol mol^{-1} and photosynthetically active radiation (PAR) of 1200 µmol (photon)m^{-2} s^{-1}.

Agronomic traits

For measuring the plant height and plant dry weight (biomass), 10 plants were harvested at physiological maturity for each treatment (five pots).

Water use efficiency

The amount of water utilized by each plant was determined by weighting each single plant in the pot. On the basis of these measurements aboveground biomass (BM) as well as total water used (WU) were utilized to calculate water use efficiency based on the following equations (Kaminski *et al.* 2014):

$$\text{WUE (g L}^{-1}\text{)} = [\text{BDM (g plant}^{-1}\text{)}] / [\text{WU (L plant}^{-1}\text{)}]$$

Statistical analysis

All data were subjected to the one-way analysis of variance. Means were compared using Duncan's multiple range test ($P \leq 0.05$). For this purpose, the MSTAT-C (version 1.42, Michigan State University) software was used. The Figures were drawn using Excel software (version 10.0).

Results

Table 3 showed significant differences among hybrids, drought stress levels and their interaction for all of the traits under study.

Table 3. Analysis of variance of the effect of hybrids and drought stress on agronomic and photosynthetic characters

Source of variation	df	Mean squares				
		Net photosynthesis rate	Stomatal resistance	Plant height	Plant dry weight	Water use efficiency
Hybrids (H)	5	**	**	**	**	*
Drought stress (D)	3	**	**	**	**	**
H × D	15	**	**	*	**	*
CV (%)	-	11.2	12.5	12.3	11.5	10.6

ns, * and **: Non-significant and significant at 5% and 1% probability levels, respectively.

Photosynthetic activity and stomatal resistance

All plants subjected to drought stress demonstrated a significantly reduced photosynthetic activity, as compared to the control plants (Figure 1). In general, drought stress at vegetative growth stage (S1), reproductive stage (S2) and the combination of both stages (S3) significantly decreased net photosynthesis rate (Pn) and rate of CO_2 exchange in sub-stomata chamber of leaves (Figure 1A) in all maize hybrids. But, the effect of combination of water stress at both stages (S3) was far greater than other water treatments. The SC260 was the most sensitive genotype followed by SC370 in terms of the foregoing trait. The results showed that Pn of SC704 and SC700 were recovered after re-watering and the former hybrid maintained the highest Pn among the hybrids after re-watering.

Figure 1B shows the effects of drought stress on leaf stomatal resistance (Rs) of maize hybrids. Rs of stressed-plants were higher than the control. There were also significant differences among the hybrids. Generally, Rs of the hybrids ranged from 100.4 to 129.9 and 197.8 to 314.8 m^2 s mol^{-1} under control and drought stress conditions, respectively. Even under water stress and re-watering condition, there was diversity for Rs between different growth stages (i.e., vegetative and reproductive stage). A negative strong relationship between Pn and Rs under drought stress at the vegetative stage (R^2 = -0.71**) and the reproductive stage (R^2 = -0.66**) was observed (Table 4).

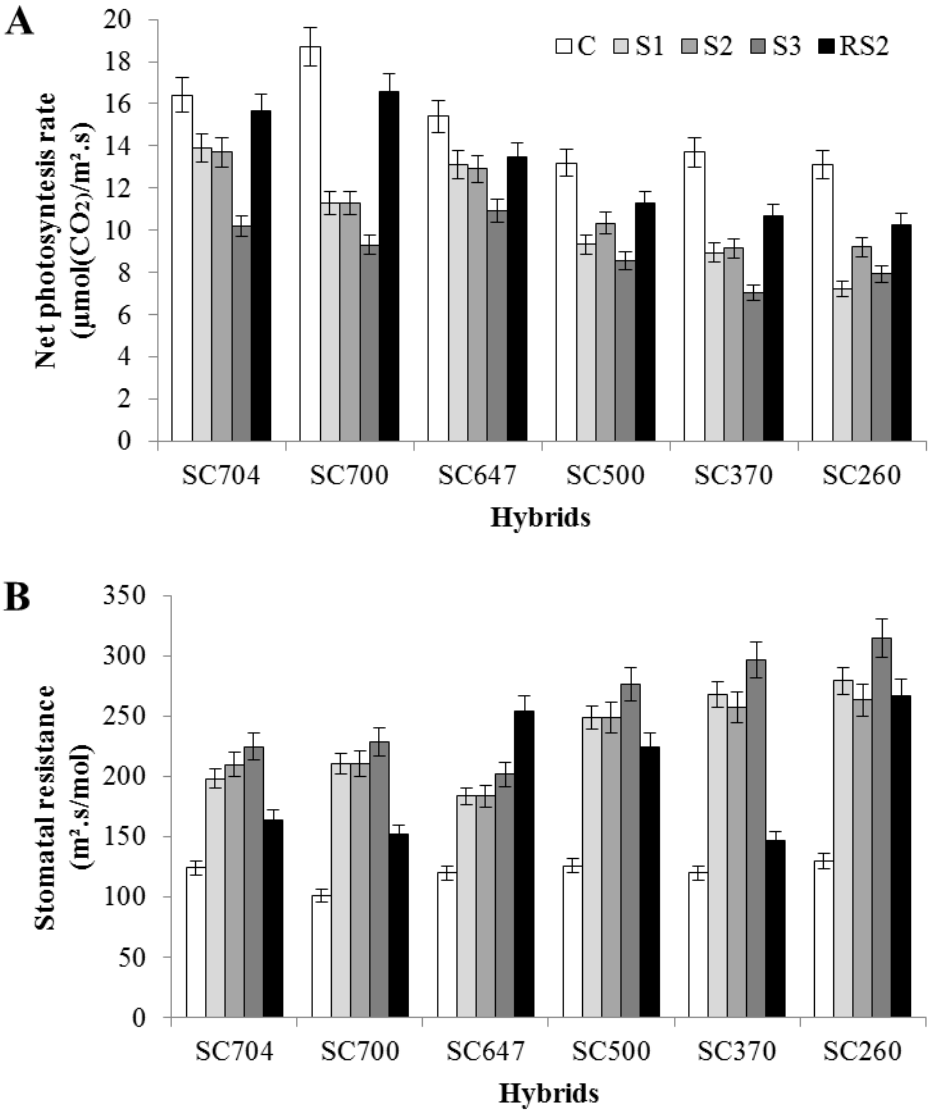

Figure 1. Effects of drought stress and re-watering on net photosynthesis rate (A) and stomatal resistance (B) in maize hybrids during vegetative growth stage, reproductive stage and combination of both stages; C: control (90% FC), S1: 50% FC at the vegetative stage, S2: 50% FC at the reproductive stage, S3: 50% FC at both vegetative and reproductive stages, and RS2: re-watered S2 after 3 weeks. The values are mean ± SE (n = 4).

Agronomic traits

Agronomic traits such as plant height and dry weight of plants were decreased in the water-stressed plants of maize hybrids (Figures 2A, B). Under drought stress condition, plant dry weight and plant height decreased by 27.7 and 24.1

percent, respectively, in comparison to their respective plants under well-watered conditions. The results showed that the highest plant height and plant dry weight belong to SC704, SC700 and SC647 at the water stress condition, but SC370 and SC260 hybrids had the lowest values for these traits at the same environment (Figures 2A, B). There was a positive and significant correlation between biomass and photosynthetic activity under drought stress (Table 4).

Table 4. Correlation among agronomic and photosynthetic characters in maize hybrids under drought stress during vegetative and reproductive growth stages

Traits	Drought at the stage of	PDW	PH	Pn	Rs	WUE
Plant dry weight (PDW)	Vegetative	1				
	Reproductive	1				
Plant height (PH)	Vegetative	0.79**	1			
	Reproductive	0.62**	1			
Net photosynthesis rate (Pn)	Vegetative	0.63**	0.75**	1		
	Reproductive	0.70**	0.67**	1		
Stomatal resistance (Rs)	Vegetative	-0.59**	-0.61**	-0.71**	1	
	Reproductive	-0.51**	-0.55*	-0.66**	1	
Water use efficiency (WUE)	Vegetative	0.53*	0.59**	0.61**	-0.57**	1
	Reproductive	0.58*	0.63**	0.59	-0.60**	1

* and **: significant at 5% and 1% levels of probability, respectively.

Water use efficiency

Figure 3 shows the effects of withholding irrigation on WUE in maize hybrids. WUE of all the hybrids decreased under drought stress. In addition, in all treatments the WUE value for S3 condition was significantly lower than that of the control.

Discussion

The physiology of plant response to drought stress at the whole plant level is highly complex and involves deleterious and/or adaptive replacement. This complexity is due to some factors such as species and variety of plant, the dynamics, duration and intensity of soil water reduction, as well as plant growth stage at which drought stress is developed. Exposure to drought stress inhibits plant growth in maize hybrids, as is observed in other plants species (Liu and Stutzel 2004; Degu *et al.* 2008).

In this study, decrease in net photosynthetic rate (Pn) and increased stomatal resistance (Rs) in response to drought stress treatments (S1, S2 and S3) was observed in all hybrids (Figures 1 A, B). This is in line with the findings of Wentworth *et al.* (2006) and Saeidi and Abdoli (2015) in wheat. In addition, in all treatments the Pn value for S3 condition was significantly lower than that of the control. Furthermore, the S3 condition affected leaf gas exchange more severely than S1 and S2 treatments. This could be partially ascribed to the combined effect of water stress at vegetative and reproductive stages, as compared to the one stage alone. In addition, Pn decreased to a less extent in SC704 and SC647 than other hybrids under the same stress environment, indicating that these two hybrids were more tolerant to the water stress in contrast to others (Figure 1 A). The decrease in Pn under water stress could be due mainly to enhanced

Rs, while non-stomatal limitation on Pn might have also occurred in leaves under stressful conditions. For instance, the lowered CO_2 of intracellular and/or increase Rs in the stressed leaves might have contributed to the decrease of Pn. Similar findings have been reported in wild soybean species (Kao *et al.* 2003), ryegrass (Cartes *et al.* 2010), tobacco (Bacelar *et al.* 2006) and bread wheat (Saeidi and Abdoli 2015) under drought stress. According to Flexas *et al.* (2004), Pn reduction in salt or drought stressed plants is mainly due to stomatal closure and mesophyll damage.

The results of many experiments have revealed that Pn drops when Rs increases (Mansurifar *et al.* 2012). Therefore, it might be thought that Pn severely decrease because stomata close before the leaf water potential drop probably by the signals from roots. These results showed that the rate of photosynthesis was significantly influenced by the stomatal closure due to a soil water deficiency at different growth stage of maize plants.

The changes in photosynthetic apparatus activity at severe water stress and consequent re-watering can be related to the abnormalities in an internal structure of chloroplasts (such as damage to thylakoid and destruction of plasma membrane). Our results showed the limitation level of recovery of photosynthetic activity from drought stress. However, based on the results of Rios *et al.* (2009) chloroplasts sub-structures such as thylakoids were not disordered under moderate water deficit and they were damaged only under severe stress conditions in maize. Figures 1A, B showed the recovery of Pn and Rs by re-watering. When re-watered after three weeks, Rs of some hybrids such as SC704, SC647 and SC700 became similar to that of the control plants. Some experiments have stated the recovery of the photosynthesis activity and improvement of physiologic traits after re-watering (Srivastava *et al.* 2009; Goodarzian-Ghahfarokhi *et al.* 2015).

In the present study, significant decrease in the photosynthetic rate was associated with a significant reduction in plant growth. Also a strong relationship between biomass production and Pn under drought stress was observed (Table 4). Down-regulation of photosynthesis may depend more on the availability of CO_2 in the chloroplast rather than on leaf water content or water potential (Flexas *et al.* 2004; Saibo *et al.* 2009; Galmés *et al.* 2011).

In our study, genotypic differences were observed among the hybrids. SC260 was more sensitive to water stress as compared to other hybrids. For example, biomass of this hybrid was reduced 1.79 fold more than that of SC647 (Figure 2 B). Rosales-Serna *et al.* (2004) and Goodarzian-Ghahfarokhi *et al.* (2015) also reported similar results in common bean and maize, respectively. They observed that overall yield reduction was greater in the susceptible genotypes than in the tolerant genotypes under drought stress condition.

The recorded reduction in plant height probably is associated with a decline in cell enlargement and division, and increased leaf senescence under water deficit (Bhatt and Srinivasa Rao 2005). Oktem (2008), Payero *et al.* (2009) and Kabiri and Naghizadeh (2015) reported that drought stress decreased dry matter, plant height and grain yield in maize and barley plants. It is important to consider that both the time and degree of stress are important and effective in determining the final crop yield (Nayyar 2003).

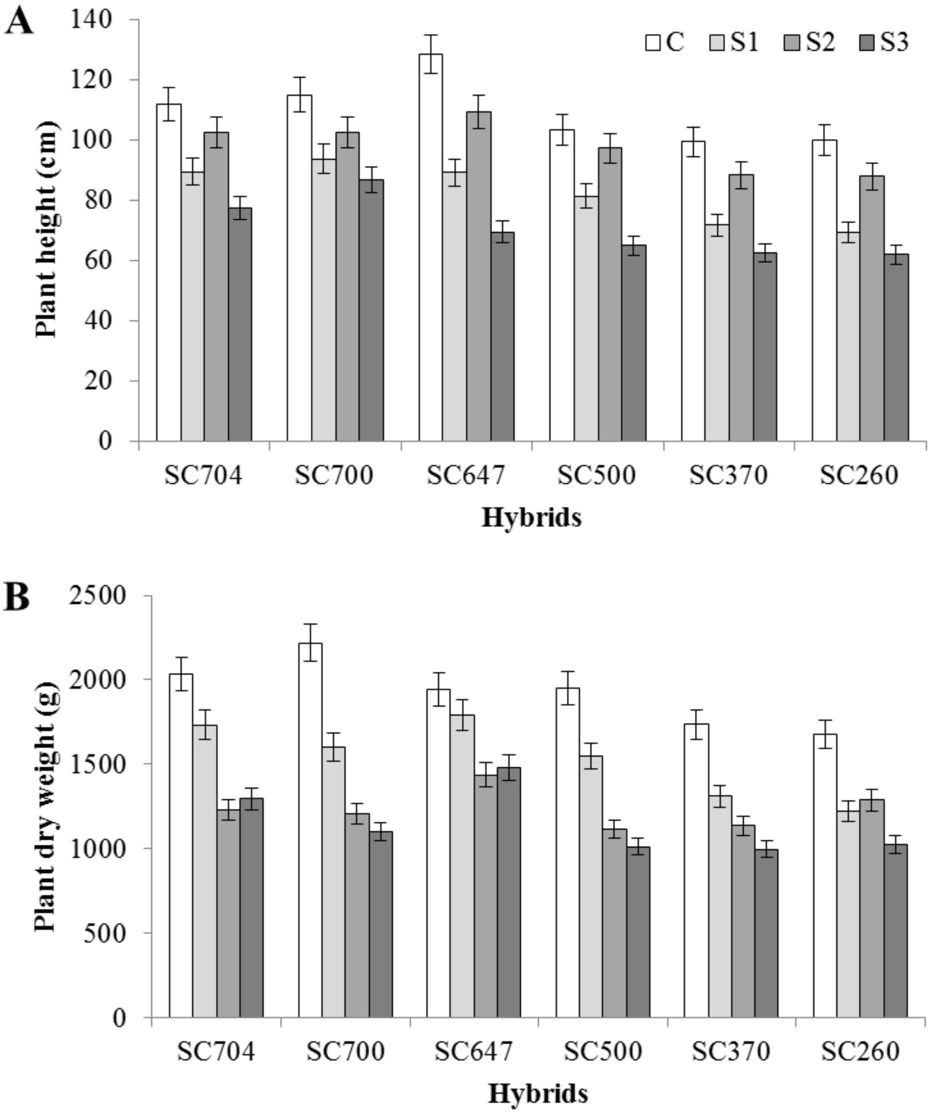

Figure 2. Effects of drought stress on plant height (A) and plant dry weight (B) in maize hybrids during the vegetative growth stage, reproductive stage and combination of both stages; C: control (90% FC), S1: 50% FC at the vegetative stage, S2: 50% FC at the reproductive stage, S3: 50% FC at combination of vegetative and reproductive stages. The values are mean ± SE (n = 4).

Kong *et al.* (2003) and Li-Ping *et al.* (2006) showed that soil water deficit during vegetative development of maize decreases vegetative growth, impairs the development of reproductive structures, and decrease grain yield ultimately. Grain filling of maize can be reduced by drought stress due to decreases in carbon exchange rates (photosynthesis) and/or the duration of grain filling. In this case, Li-Ping *et al.* (2006) indicated that when drought stress occurred at the reproductive phase, the supply of photo-assimilate for the subsequent grain filling is limited. Blum

(2009) pointed out that source limitation (decrease of photosynthesis) was the cause of lower grain weight and reduction of grain yield depended on the severity of soil moisture deficiency.

Drought stress at different growth stage showed negative effects on WUE of different maize hybrids (Figure 3) and there was positive correlation between WUE and BDM (Table 4). Many reports have pointed out the linear relationship between WUE and yield in wheat, maize and other plants (Munns 2002; Li *et al.* 2003; Gao *et al.* 2004). WUE and dry matter are related closely up to the redox state in plants. Plants complete transportation and conversion of photosynthetic products earlier (Gao *et al.* 2004).

The positive correlation between agronomic traits and photosynthetic activity suggests that the reduction in biomass at the drought stress condition may be due to factors affecting stomatal closure and damage of photosynthetic apparatus (Table 4). In addition, increase in the photosynthetic activity after water stress (during re-watering stage) showed that stomata are the main limiting factors to carbon uptake (Boussadia *et al.* 2008). However, degree and intensity of recovery of photosynthesis and stomatal resistance after re-watering has not been fully clarified.

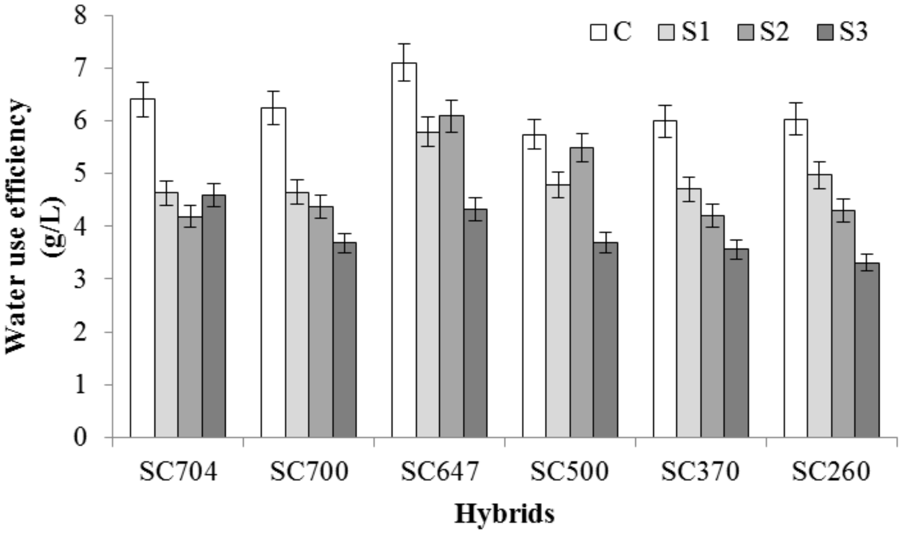

Figure 3. Effects of drought stress on water use efficiency in maize hybrids during the vegetative growth stage, reproductive stage and combination of both stages; C: control (90% FC), S1: 50% FC at the vegetative stage, S2: 50% FC at the reproductive stage, S3: 50% FC at combination of vegetative and reproductive stages. The values are mean ± SE (n = 4).

Conclusion

Drought stress impaired physiological function and biomass production. Significant reductions in the water use efficiency and biomass are due to a reduced leaf size and leaf area affecting carbon assimilation, as well as decreased net photosynthesis rate and stomatal conductance. In general, our findings suggest that the capacity of a plant to induce lower photosynthetic activity in response to drought stress may greatly connect to its ability to sustain growth. Furthermore, among the hybrids, SC647 had the maximum plant growth and photosynthetic activity, followed by SC704. The variation observed amongst the evaluated hybrids suggests the existence of valuable genetic diversity for crop improvement in relation to drought tolerance.

Acknowledgements

The authors are thankful for the support of the colleagues in Agricultural and Natural Resources, Razi University, Kermanshah, Iran, who helped us to conduct the experiment.

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