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Association between water use efficiency components and stomatal conductance in some Iranian wheat cultivars

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Abstract
Wheat is a pivotal crop plant in Iran. However, it is mostly grown in drought prone areas of Iran. On the other hand, the trend of global warming is increasing. Therefore, in order to better use the limited water sources, it is needed to improve wheat yield by studying the mechanisms of enhancing water use efficiency (WUE). This study was conducted to determine the effect of stomatal conductance (g_s) on water use efficiency and its components in wheat (*Triticum aestivum* L.). Seven bread wheat cultivars (Marvdasht, B.C.Roshan, Darab2, Vee/Nac, Shiraz, Chamran, Maroon) were grown in pots under well-watered conditions. The pattern of variation for WUE and its components was different for cultivars. Stomatal conductance showed a positive correlation with total water use, transpiration efficiency and grain yield. A path analysis revealed that transpiration efficiency had a higher direct effect on grain yield (0.91) than did harvest index (0.40). Although g_s showed a direct effect of almost zero on grain yield, but imposed its effect indirectly via transpiration efficiency (0.47).

Keywords: Cereals; Drought resistance; Harvest Index; Stomata; Transpiration Efficiency; *Triticum aestivum* L.; Water use efficiency.

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Introduction

Water-use efficiency (the ratio of grain yield to crop water use) is considered as an important component of adaptation to drought stress in wheat (*Triticum aestivum* L.). Therefore, the breeding of wheat genotypes with higher water use efficiency and tolerant to drought is regarded as an important criterion for increasing yield in the environments encountered with drought stress. Passioura (1977) introduced an equation about factors that affect yield (Y) under drought stress condition:

$$Y = TWU \times TE \times HI \qquad [1]$$

where, total water use (TWU) is the amount of water used in the growth season, transpiration efficiency (TE) is the biomass produced per unit evapotranspiration (transpiration + soil evaporation) and harvest index (HI) is the ratio of harvested yield to total aboveground biomass. Also, TE and HI are the two primary components of WUE, which are defined as follows:

$$WUE = TE \times HI \qquad [2]$$

The Eq. [1] has been extensively utilized to increase the grain yield of winter cereals under water deficit stress (Acevedo 1987; Richards 1987; Turner 2004). Increasing each of these WUE components could improve the grain yield because these components are largely independent of each other. The improvement of WUE for grain in modern wheat cultivars as compared to old varieties, is associated with higher harvest index (Siddique *et al.* 1990). Although the use of dwarfing genes for the reduction of plant height and improved lodging resistance has increased the genetic gain of grain yield and resulted in “Green Revolution", but increasing of the TE level can be regarded as a significant factor in grain yield improvement under drought condition (Condon *et al*. 2004; Chen *et al*. 2013). Wheat genotypes have shown considerable variation in TE (Fischer *et al.* 1998; Condon *et al.* 2004). Chowdhry *et al*. (2000) reported the positive correlation of grain yield with total dry matter, TE, HI and WUE in wheat. Furthermore, TE and WUE showed maximum positive indirect effects of 0.7382 and 0.4079, respectively, on grain yield via total dry matter. In addition, a positive correlation has been obtained between TE and leaf g_s, a physiological trait with potential to improve crop yield, in many wheat genotypes (Richards *et al.* 2002). g_s is involved in the diffusion of CO_2 into the leaf in photosynthesis and also in water loss in the transpiration process. Although lowering g_s often will decrease the photosynthesis rate and TE because of the reduced rate of CO_2 diffusion into the leaf (Chaves *et al.* 2002), in most plant species more than 90% of the water loss occurs through stomata via transpiration for CO_2 exchange (Schroeder *et al.* 2001). Because of this dual role, it can be stated that the leaf gas exchange regulation of stomata can be in charge of plant adaptation to specific environments (Jones 1987; Chaves *et al.* 2002). The aim of this study was to investigate the relationship of g_s with grain yield and WUE of wheat cultivars grown in a glasshouse pot experiment.

Materials and Methods

Seven bread wheat cultivars (Marvdasht, B.C.Roshan, Darab2, Vee/Nac, Shiraz, Chamran, Maroon) were grown in pots under well-watered condition. Pots were filled with 10 kg of soil composed of 51% sand, 31% silt and 18% clay with water holding capacity of 24% by weight and fertilized once using granular N:P:K (3:1:1, respectively). Fifteen seeds were sown in each pot and after two weeks, 10 seedlings were retained in each pot. Pots were arranged in a randomized complete block design with three replications in an unheated water-cooled glasshouse of University of Zanjan, Iran.

Pots were weighted every two days and amounts of water loss from field capacity in weight were added. Cultivars received different amounts of water because of genotypic differences in maturity. Plants were harvested as they dried up. The total amount of water used was calculated as the difference between final and initial pot weight and the amount of water supplied to each pot. Thus, the total water used included both transpired and evaporated water. Stomatal conductance (g_s, mmol m^{-2} s^{-1}) was measured with a hand porometer (AP4, Delta-t, Devices, England) and corresponded to Zadoks stages 45-50.

Taking logarithms of the Eq. [1] yielded the following equation:

$$\text{Log}(Y) = \log(TWU) + \log(TE) + \log(HI). \quad [3]$$

The direct and indirect effects of each component on WUE were assessed by path analysis according to the method described by Dewey and Lu (1959) and Ehdaie and Waines (1993). Statistical analysis was performed using SPSS software. For mean comparisons, Duncan’s multiple range test was used at the probability level of 5%.

Results and Discussion

Cultivar means for TE ranged from 2.041 g kg^{-1} for B.C.Roshan to 1.36 g kg^{-1} for Vee/Nac; the latter was the shortest cultivar and showed the highest HI (Table 1). The variation pattern for TE and for HI was different for cultivars, and they were arranged into three distinct groups. The first group, Chamran and Shiraz, had higher yield and TE, with acceptable HI. There was a balance between components of WUE in these cultivars. High WUE in Vee/Nac resulted in high HI but very low TE. B.C.Roshan was placed in the third group with high TE and low HI that caused reduction of WUE in this cultivar. Siddique *et al.* (1990) reported higher WUE of improved wheat cultivars was higher than landraces grown in the field under the Mediterranean environment of Western Australia. Ehdaie and Waines (1993) observed significant genotypic variation for WUE and its components in wheat cultivars. They also reported relatively higher TE but much lower HI in old tall varieties, on average, had relatively higher TE as compared with new semi-dwarf and dwarf cultivars.

Cultivars differed ($p \leq 0.05$) in g_s. Table 1 shows a strong increase of stomatal conductance in more recently released cultivars, such as

Table 1. Means of grain yield (Y), water-use efficiency (WUE), transpiration efficiency (TE), harvest index (HI) and stomatal conductance (g_s) of wheat cultivars grown in a well-watered pot experiment.

Cultivar	Y (g)	WUE (g kg^{-1})	TE (g kg^{-1})	HI	g_s (mmol m^{-2} s^{-1})
Marvdasht	4.57^{bc}	0.38^{ab}	1.69^{a}	0.23^{b}	103.8^{bc}
B.C.Roshan	3.28^{cd}	0.28^{b}	2.01^{a}	0.14^{c}	65.8^{cd}
Darab2	4.62^{bc}	0.41^{ab}	1.52^{bc}	0.26^{b}	165.3^{a}
Vee/Nac	5.63^{ab}	0.52^{a}	1.36^{c}	0.37^{a}	122.3^{ab}
Shiraz	5.30^{ab}	0.44^{a}	1.83^{ab}	0.24^{b}	104.2^{bc}
Chamran	6.27^{a}	0.55^{a}	2.08^{ab}	0.26^{b}	99.1^{bc}
Maroon	5.13^{ab}	0.43^{a}	1.80^{ab}	0.24^{b}	67.1^{cd}

Values with the same letter are not significantly different at the 0.05 probability level using Duncan's multiple range test.

Darab2 (165.3 mmol m^{-2} s^{-1}), in comparison with the old cultivars, such as B.C.Roshan (65.8 mmol m^{-2} s^{-1}). Recent research at CIMMYT has shown that increased yield of CIMMYT bread wheats over the last 30 years reflects proportional increases in g_s (Fischer *et al.* 1998). The correlation coefficients between stomatal conductance and Y, and between TWU and TE were significant (Table 2), indicating that these characters are associated. The positive relationship of grain yield with g_s has been mentioned in the studies about semi dwarf spring wheat cultivars (Fischer *et al.* 1998; Del Blanco *et al.* 2000; Rebetzke *et al.* 2001). Greater g_s has the alternative potential for increasing yields of crops grown in environments where water is plentiful and has been linked to increased yield of soybean (*Glycine max* L.) (Morrison *et al.* 1999) and pima cotton (*Gossypium barbadense* L.) (Lu *et al.* 1998) and variation in yield among

Table 2. Simple correlation coefficients of stomatal conductance (g_s), grain yield (Y), total water use (TWU), transpiration efficiency and harvest index (HI) of wheat cultivars.

	g_s	Y	TWU	TE
g_s				
Y	0.485**			
TWU	0.641**	0.863**		
TE	0.524*	0.917**	0.955**	
HI	0.026	0.426**	-0.003	0.029

*, **significant at 0.05 and 0.01 probability levels, respectively.

wheat varieties grown in warm environments (Reynolds *et al.* 1994; Lu *et al.* 1998).

The results of path analysis for the direct and indirect effects of g_s, log TWU, log TE and log HI on grain yield (Y) are presented in Table 3. TE had a higher positive direct effect (0.91) on Y than HI (0.40). The same results were obtained by Ehdaie and Waines (1993), but they showed that selection for TE alone might result in reduced harvest index because there is a negative correlation between TE and HI. On the other hand, high TE in some genotypes has shown a close relationship with high biomass production capacity (Morgan and LeCain 1991; Hussain *et al.* 1999; Condon *et al.* 2002). In view of the fact that most wheat plants with higher TE have higher grain yield under drought condition (Condon *et al.* 2002), it is believed that TE can be an advantage in some elite lines for improving crop yield in drought-prone areas.

The direct effect of g_s on yield was nearly zero, but its positive indirect effects, mainly via TE, on grain yield showed that this physiological trait is suitable for indirect selection (Table 3). There are many reports about positive yield-g_s correlations in wheat cultivars. Lack of direct effect of g_s on yield showed that the closure of the stomata could reduce internal CO_2 concentration and assimilation rate (Chaves and Oliveira 2004). It was suggested that g_s is a primary factor limiting photosynthesis rate in wheat. At physiological and biochemical levels, TE presumably associated with three major components: rate of photosynthesis, carbon use efficiency (the ratio of the amount of carbon incorporated into plant biomass to the amount of carbon fixed through photosynthesis) and stomatal conductance. The rates of photosynthesis and carbon use efficiency are engaged in the biomass production rate per unit of photosynthetic leaf area (Xue *et al.* 2006).

Conclusions

Genetic approaches in plant breeding activities have almost doubled grain yield in cereals in the last century. However, this achievement has not been accompanied by the change in photosynthesis rate per unit leaf area. On the other hand, increase in the leaf area, daily duration of photosynthesis, or stay green has enhanced total photosynthesis. Photosynthesis improvement gained by breeding programs may have also come from indirect means. One approach is selection for a high and sustained stomatal conductance. Reports have shown that the correlation between yield and g_s was the strongest among the relationship of photosynthetic characteristics with yield (Richards *et al*. 2000). Our investigation showed that the direct effect of g_s on yield was nearly zero (Table 3), but there are strong evidences that the increase in maximum photosynthetic rate is associated with enhancements in g_s; therefore, high stomatal conductance leads to an increase in total above-ground biomass and transpiration efficiency. Thus, its indirect effect on yield via TE can be used for indirect selection under favorable conditions (Del Blanco *et al.* 2000).

Stomatal conductance has a higher heritability. Its measurement is very simple and less expensive (Rebetzke *et al.* 2001). A hand-held instrument has been developed for the rapid assessment of stomatal conductance in plants. It is much faster, smaller and can be operated by one person. Therefore, it increases the efficiency of selection for grain yield indirectly via TE.

Table 3. Direct and indirect effects of factors influencing grain yield in wheat cultivars using the model:
Log (Y) = log (TWU) + log (TE) + log (HI).

Pathway of association	
Log (TWU) on log (Y)	
Direct effect	0.000
Indirect effect via log (TE)	0.864
Indirect effect via log (HI)	-0.001
Indirect effect via g_s	0.000
Total correlation	0.863**
Log (TE) on log (Y)	
Direct effect	0.905
Indirect effect via log (TWU)	0.000
Indirect effect via log (HI)	0.012
Indirect effect via g_s	0.000
Total correlation	0.917**
Log (HI) on log (Y)	
Direct effect	0.400
Indirect effect via log (TWU)	0.000
Indirect effect via log (TE)	0.026
Indirect effect via g_s	0.000
Total correlation	0.426**
g_s on log (Y)	
Direct effect	0.000
Indirect effect via TWU	0.000
Indirect effect via TE	0.474
Indirect effect via HI	0.011
Total correlation	0.485**

**significant at the 0.01 probability level; Y: grain yield; TWU: total water use; TE: transpiration efficiency; HI: harvest index

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رابطه بین اجزای کارایی مصرف آب و هدایت روزنه‌ای در برخی از ارقام ایرانی گندم

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چکیده

با وجود نقش محوری گندم، کشت آن در ایران اغلب به صورت دیم است. از طرف دیگر روند گرم شدن جهانی به صورت افزایشی است. برای استفاده بهینه از منابع محدود آب، اصلاح عملکرد گندم از طریق مطالعه سازوکارهای افزایش کارائی مصرف آب، امری ضروری است. در این مطالعه اثر هدایت روزنه‌ای (g_s) بر روی کارایی مصرف آب (WUE) و اجزای آن در گندم نان (*Triticum aestivum* L.) مورد مطالعه قرار گرفت. هفت کولتیوار گندم نان (مرودشت، روشن B.C.، داراب ۲، Vee/Nac، شیراز، چمران، مارون) در گلدان تحت شرایط آبیاری نرمال کشت شدند. الگوی تغییرات برای WUE و اجزای آن در کولتیوارهای مختلف، متفاوت بود. هدایت روزنه‌ای همبستگی مثبت با کارایی مصرف آب کل، کارایی تعرق و عملکرد دانه داشت. تجزیه ضرایب مسیر نشان داد که اثر مستقیم کارایی تعرق بر عملکرد دانه (۰/۹۱) بیشتر از اثر مستقیم HI (۰/۴۰) بود. اگر چه g_s اثر مستقیم نزدیک به صفر روی عملکرد دانه داشت، ولی اثر خود را به طور غیرمستقیم از طریق کارایی تعرق (۰/۴۷) اعمال نمود.

واژه‌های کلیدی: شاخص برداشت؛ کارایی تعرق، کارایی مصرف آب؛ هدایت روزنه‌ای؛ *Triticum aestivum* L.