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in

Royo C. (ed.), Nachit M. (ed.), Di Fonzo N. (ed.), Araus J.L. (ed.).
Durum wheat improvement in the Mediterranean region: New challenges

Zaragoza : CIHEAM
Options Méditerranéennes : Série A. Séminaires Méditerranéens; n. 40

2000
pages 233-238

Photosynthetic water use efficiency of old and modern durum wheat genotypes from southeastern Anatolia, Turkey

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SUMMARY – The purpose of this experiment was to determine whether genotypic differences in photosynthetically water use efficiency (WUEg) and other gas exchange traits exist in 12 durum wheat genotypes, including six local cultivars from South-eastern Anatolia. Flag leaf gas-exchange measurements were performed on well-watered and fertilized field grown plants, which were planted after vernalization. Weather conditions during measurement were suitable for high transpiration. At anthesis no genotypic variation was observed for water use efficiency, calculated using leaf conductance ($WUEg_s$). Ten days later, most of the local cultivars showed higher $WUEg_s$ than the modern cultivars (18.0 vs 24.0 µmol CO_2/mol H_2O). Although differences were not significant under all of the measurement conditions $WUEg_s$ was more highly associated with leaf conductance (r = -0.892**) than net photosynthetic rate (r = -0.276**). The results indicate that measurements for WUEg should be performed during development under different environmental conditions to partially overcome difficulties caused by developmentally and environmentally induced variation.

Key words: Photosynthesis, water use efficiency, durum wheat, local cultivar.

RESUME – *"Efficacité photosynthétique de l'utilisation de l'eau chez des génotypes anciens et modernes de blé dur du Sud-Est de l'Anatolie, Turquie". Le propos de cette expérience était de déterminer si les différences génotypiques de l'efficacité photosynthétique en matière d'utilisation de l'eau (WUEg) et d'autres caractères d'échanges de gaz existent chez 12 génotypes de blé dur, y compris six cultivars locaux du SE de l'Anatolie. Des mesures d'échange de gaz sur des feuilles-drapeau furent enregistrées sur des plantes cultivées aux champs bien irriguées et fertilisées, qui furent plantées après vernalisation. Les conditions météorologiques pendant les mesures furent adéquates pour une forte transpiration. A l'anthèse aucune variation génotypique ne fut observée concernant l'efficacité de l'utilisation de l'eau, calculée en employant la conductance des feuilles ($WUEg_s$). Dix jours plus tard les génotypes montraient une variation significative de $WUEg_s$. La plupart des cultivars locaux montraient des $WUEg_s$ plus élevées que les cultivars modernes (18,0 vs 24,0 µmol CO_2/mol H_2O). $WUEg_s$ était plus fortement associée à la conductance des feuilles (r = -0,892 **) qu'au taux photosynthétique net (r = -0,276**). Les résultats indiquent que les mesures de WUEg devraient être menées pendant le développement sous différentes conditions environnementales pour surmonter partiellement les difficultés causées par la variation induite par le développement et l'environnement.*

Mots-clés : *Photosynthèse, efficacité de l'utilisation de l'eau, blé dur, cultivar local.*

Introduction

Durum wheat (*Triticum turgidum* L. var. *durum*) is grown widely in stressful environments. In these production areas drought and high temperatures often limit the grain yield. Under stressed conditions, the maintenance of high leaf net CO_2-exchange rates and higher water use efficiency was associated with higher wheat yields (Austin, 1987). On the other hand single leaf water use efficiency, defined as the ratio of leaf photosynthesis to transpiration (or stomatal conductance) has received considerable scrutiny with respect to its postulated adaptive significance for plants growing in drought prone environments (Heitholt, 1989; Morgan and LeCain, 1991). Numerous studies of plant gas exchange have been conducted over past decades. Most of these studies have focused on interspecific differences or (even not sufficient) genotypic differences in *T. aestivum* wheat. Studies on genotypic differences in durum wheat are limited.

Local durum wheat genotypes of South-eastern Anatolia have evolved in stressful environments. Thus they could provide a useful source for drought tolerance. The purpose of this experiment was to determine whether genotypic differences in photosynthetically water use efficiency (WUEg) and related traits exist in 12 durum wheat genotypes, including six local, three modern cultivars and three advanced selected lines.

Materials and methods

Genotypes were grown in field under well watered conditions, at the experimental farm of the Faculty of Agriculture, University of Çukurova in Adana (36º 59' N and 35º 18' E, 21 m above sea level)/Turkey. The field experiment was conducted in randomized block design with four replications on a sandy loam soil. Twelve durum wheat (*Triticum turgidum* L. var. *durum)* genotypes were used: (i) local cultivars Bağacak, Beyaziye, Devedişi, Hacıhalil, Iskenderi and Sorgül; (ii) advanced lines – Bintepe, VK.85.17, VK.85.18; and (iii) modern cultivars – Kunduru, Cham.1, Diyarbakır.81. The seeds were vernalized during 4 weeks at 1 ± 0.5ºC, to minimize the developmental differences between genotypes. Genotypes were planted on 13 February 1997 into 1.0 by 1.2 m plots with a 0.20 m row spacing. Planting density was 100 plants/m^2. The late sowing time was chosen to perform the measurements on leaves with a high transpiration rate. P (80 kg/ha P_20_5) was applied prior to seeding. Nitrogen was top dressed 80, 40 and 40 kg/ha at the Zadoks growth stages 2.0, 3.0 and 5.5, respectively. Flood irrigation was applied when needed. No pesticide was used to prevent possible genotype x pesticide interaction effects. Weeds were removed by hand.

Crop development was scored after Zadoks Growth Stages (GS) as described in Bell and Fisher (1994). Flag leaf gas-exchange measurements were made with an open system using a portable ADC infrared gas analyser (LCA-3, Analytical Development Co., Hoddeston, England). For a given measurement, measurements were repeated across the experiment several times for greater accuracy. Measurements were made on 10 May (129 days after planting, GS of latest genotype was 6.0, see Table 1) and ten days later on 20 May between 10:00 and 14:00 h (solar time). The middle part of the main stem flag leaf blade exposed to sunlight, with the leaf chamber positioned to the sun to give a proper light intensity. Photosynthetic photon-flux density (PPFD) incident on the leaf was 1000 μmol/m^2/s at the first; and 1000 μmol/m^2/s and 1300 μmol/m^2/s at the second measurement. Mean air temperature during measurements was 36 ± 1ºC and 36 ± 3ºC on 10 May and on 20 May, respectively. Measurements were taken under ambient CO_2 concentrations 355 ± 5 μl/L and 348 ± 8 μl/L. Relative humidity inside the photosynthesis chamber averaged 40 ± 3% for measurements on 10 May and 39 ± 5% for measurements on 20 May. Net CO_2 exchange rate (CER), leaf conductance to water vapour (g) and internal CO_2 concentration (Ci) were measured simultaneously. WUEg was determined by dividing micromolar CER by molar g, considering the suggestion of Morgan and LeCain (1991).

The area of flag leaf-blades of randomly selected five main stems in each plot were measured with the area meter AAM-5 (Hayashi-Denko, Tokyo). After the measurement on 20 May. Flag leaf-blade dry weights were determined after drying to constant weight in a forced air oven at 70ºC. Specific leaf dry weight was then calculated.

Results and discussion

Flag leaf gas exchange measurements were undertaken under very similar measurement conditions. Thus differences between two measurements for leaf gas exchange traits to be thought due to the genotype related differences. However, an important additional source of phenotypic variation as stated by Araus *et al.* (1989) must also be considered.

Leaf gas exchange traits

Significant differences occurred among genotypes for CER measured on 10 May (Table 1). Beyaziye had the highest and VK.85.18 the lowest rates of flag leaf photosynthesis. Bağacak, VK.85.17, Bintepe and Kunduru showed also quite high CER at this stage. Beyaziye and Bağacak, in an earlier investigation comparing most of the genotypes studied here, also showed higher CER (Koç, 1993).

No significant differences were observed at 10 May for g and for Ci, in spite of genotypes with higher CER tending to have lower Ci and higher g (Table 1). This indicates that genotypic differences for CER observed at 10 May were not related to the differences in stomatal conductance to CO_2. However the higher values of CER seem a result of higher biochemical activity of flag leaves. The maintenance of high CER at a low Ci is indicative of high photosynthetic capacity of the mesophyll tissue (Morgan and LeCain, 1991).

Table 1. Flag leaf CO_2 exchange rate (CER), stomatal CO_2 conductance (Gc) and intercellular CO_2 concentration (Ci) at beginning of grain filling period of 12 durum wheat genotypes

	CER (µmol $CO_2/m^2/s$)			g (mol $H_2O/m^2/s$)			Ci (CO_2 mol/l)		
	1000†	1300	Mean	1000	1300	Mean	1000	1300	Mean
10 May 1997									
Bağacak	16.1	–	–	0.477	–	–	211	–	–
Beyaziye	17.8	–	–	0.545	–	–	212	–	–
Devedişi	14.4	–	–	0.470	–	–	220	–	–
Hacıhalil	14.1	–	–	0.435	–	–	218	–	–
Iskenderi	15.4	–	–	0.472	–	–	219	–	–
Sorgül	14.4	–	–	0.450	–	–	220	–	–
Kunduru	15.7	–	–	0.448	–	–	213	–	–
VK.85.17	15.9	–	–	0.505	–	–	212	–	–
VK.85.18	13.4	–	–	0.385	–	–	219	–	–
Bintepe	15.9	–	–	0.508	–	–	208	–	–
Cham.1	15.5	–	–	0.548	–	–	214	–	–
Diyarbakır.81	14.4	–	–	0.445	–	–	216	–	–
Mean	15.2	–	–	0.474	–	–	215	–	–
LSD (0.05)	2.206	–	–	ns	–	–	ns	–	–
20 May 1997									
Bağacak	15.8	17.6	16.7	0.697	0.815	0.756	227	222	224
Beyaziye	15.7	17.3	16.5	0.540	0.728	0.634	221	222	221
Devedişi	15.3	16.5	15.9	0.627	0.842	0.735	219	222	220
Hacıhalil	16.2	18.7	17.5	0.638	0.823	0.731	220	214	217
Iskenderi	18.4	18.9	18.6	0.998	1.325	1.162	222	230	226
Sorgül	16.6	18.2	17.4	0.777	1.055	0.916	227	226	227
Kunduru	15.9	17.2	16.5	0.700	0.943	0.822	226	226	226
VK.85.17	16.0	17.7	16.8	0.845	1.343	1.094	223	225	224
VK.85.18	14.8	16.6	15.7	0.715	1.000	0.858	225	224	225
Bintepe	16.2	17.8	17.0	0.972	1.330	1.151	230	229	229
Cham.1	16.1	17.4	16.7	0.775	1.172	0.974	231	232	231
Diyarbakır.81	14.9	16.4	15.7	0.873	1.215	1.044	228	226	227
Mean	15.99	17.5	–	0.763	1.049	–	225	225	–
LSD (0.05)	ns	ns	ns	ns	ns	0.304	ns	ns	7.815

†PPFD: µmol/m^2/s.

Flag leaf photosynthesis rates of genotypes were not different at 20 May measured at the same PPFD as 10 May for any background (Table 1). The average CER of flag leaves was 16.0 µmol $CO_2/m^2/s$ and similar (not significantly different) to mean rate (15.2 µmol $CO_2/m^2/s$) measured at 10 May. There was no significant genotype by measurement-day interaction if the combined data of both measurements analysed (data not shown). This indicated, that flag leaf senescence had not yet started and thus provided measurement of flag leaf photosynthesis over a period of highest rates.

Increasing PPFD from 1000 µmol/m^2/s to 1300 µmol/m^2/s on 20 May resulted in an increase of CER (Table 1). Genotype by light level interaction was not significant (data not presented here). The average increase was only 9.4% indicating that 1300 µmol/m^2/s was still near saturating levels and consistent with previous reports showing saturating densities about these levels (Winzeler and Nösberger, 1980; Teramura *et al.,* 1990; Kebede *et al.,* 1992) for wheat.

The g and Ci values were significantly higher at the measurement on 20 May than that on 10 May, while no significant differences were observed between genotypes. Similar CER at either stage in spite of different g and Ci values suggest that factors internal to the leaf were involved in net photosynthesis during early grain filling period.

The relative increase in CER resulting from an increase of PPFD from 1000 µmol/m^2/s to 1300 µmol/m^2/s on 20 May, was much less than that in g (9.6% versus 37.5%), whereas Ci remained constant. It follows that the apparent mesophyll conductance (CER/Ci) also increased in high PPFD.

Leaf water use efficiency

According to the suggestion of Morgan and LeCain (1991) flag leaf WUEg was determined as the ratio of CER to stomatal conductance (gs).

In spite of large variations in the values at first measurement on 10 May 1997, no significant differences were observed between genotypes for WUEg (Fig. 1). The mean WUEg was 33.6 µmol CO_2/mol H_2O. At second measurement on 20 May the mean WUEg was decreased to 22.9 µmol CO_2/mol H_2O. The decrease was a result of an increase of g. Increase in leaf g (occurred in all genotypes) was not associated with the environmental factors during the measurements, because of the similar conditions during both measurements. This increase in stomatal conductance could be related to adaptation to high temperatures occurred between two measurement days as reported previously by Araus *et al.* (1986), quoted in Araus *et al.* (1989) in well watered wheat. Such large fluctuations as a result of temporal changes in leaf conductance were also reported in previous studies (Heitholt, 1989; Morgan and LeCain, 1991; Frederick and Camberato, 1994; Rudorff *et al.,* 1996; Frederick, 1997).

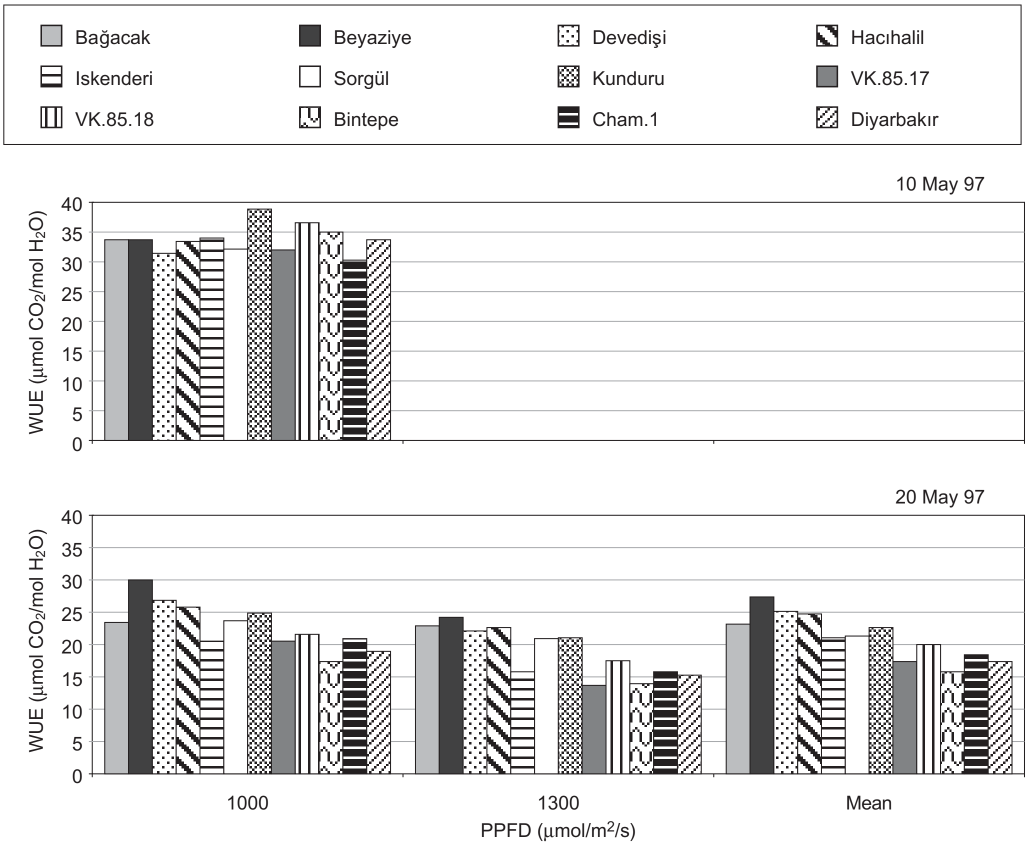

Fig. 1. WUEg on flag leaves at beginning of grain filling period of 12 durum wheat genotypes.

At the measurement on 20 May most of the local genotypes and Kunduru tended to be generally more water-use efficient in CO_2 assimilation than modern genotypes. As noted above, the values of WUEg were variable and this undoubtedly contributed to the failure of the analysis of variance to detect highly significant differences between genotypes. Differences were greater (significant only at $p = 0.08$) if the genotypes compared at 1300 µmol/m²/s PPFD and even significantly higher if the pooled data of both measurements (1000 µmol/m²/s and 1300 µmol/m²/s) were analysed. Although the differences in the WUEg were significant only at the $p = 0.08$ level, the result of the combined analysis indicates that accepting this level of significance is reasonable. Greater WUE was associated with lower g, while CER was maintained at similar levels.

Leaf traits related to WUEg

At the end of anthesis the genotypes exhibited significant variation in flag leaf area and flag leaf width (Table 2). With the exception of Bağacak and Devedişi flag leaf area of the old genotypes and from old material selected lines tended to be smaller than that of modern genotypes. Most of the old genotypes and Kunduru showed lower flag leaf width than modern genotypes. Specific flag leaf weight (SLW) did not vary significantly between genotypes.

Table 2. Individual flag leaf area, leaf width and specific leaf weight at the beginning of grain filling period of 12 durum wheat genotypes

Genotype	Leaf area (cm^2)	Leaf width (mm)		Specific leaf dry weight (g/m^2)
		10 May	20 May	
Bağacak	23.5	15.2	15.9	77.8
Beyaziye	16.3	14.0	14.1	76.2
Devedişi	21.8	16.2	15.9	75.3
Hacıhalil	17.6	15.4	15.2	81.2
Iskenderi	19.0	14.9	14.6	66.8
Sorgül	17.0	14.6	13.8	77.9
Kunduru	20.9	14.4	14.6	77.0
VK.85.17	19.1	16.5	16.6	72.8
VK.85.18	17.9	16.4	16.8	87.9
Bintepe	20.9	16.1	16.0	63.6
Cham.1	23.8	15.9	15.3	67.2
Diyarbakır.81	22.9	16.8	16.8	64.9
Mean	20.1	15.5	15.4	74.0
LSD (0.05)	4.796	1.209	1.280	ns

Simple correlation coefficient indicated that WUEg was negatively correlated with g (and as a consequence with Ci) not only at this measurement day, but also at the measurement on 10 May and averaged across all dates (Table 3). Leaf width was the only structural leaf trait to show a significant correlation with WUEg. WUEg was negatively correlated with leaf width. Flag leaf area and SLW showed no correlation with WUEg.

Although one of two gas exchange measurements indicated that most of the studied old cultivars might be more water use efficient than modern cultivars, increased water use efficiency at the whole plant level must also be studied.

It is also suggested that these features of old cultivars may confer the ability to adapt to low levels of water supply under drought conditions. While low WUEg may be an important trait in selecting genotypes for drought prone environments the underlying physiological mechanisms need to be better understood before selection for these traits can be routinely used in breeding programme. Because, as Araus *et al.* (1989) point out, high WUE in wheat may benefit productivity under condition of limited water supply, but a lower WUE due to high g, can result in maximum carbon assimilation when water supply is adequate. Recently, Fischer *et al.* (1998) reported a genetically determined positive association between grain yield, photosynthetic rate, and gs in irrigated semidwarf spring wheats.

Table 3. Simple correlations among WUEg and photosynthetic and morphological traits of flag leaf at the beginning of grain filling period of 12 durum wheat genotypes

	10 May	20 May			10 + 20 May
	1000[†]	1000	1300	Mean	1000
CER	-0.061	-0.217**	-0.164	-0.276**	-0.232*
g	-0.872**	-0.900	-0.919**	-0.892**	-0.891**
Ci	-0.838**	-0.741	-0.648**	-0.661**	-0.826**
Leaf wide	-0.140	-0.443**	-0.510**	-0.457**	-0.117
Leaf area	-0.006	-0.158	-0.005	-0.079	-0.064
SLW	0.059	0.123	0.000	0.060	0.071

[†]PPFD: μmol/m^2/s.

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Thus further research is needed on these genotypes to clarify the changes of WUEg during the development and what adaptive significance of higher WUE may confer.

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