

Effect of drought on leaf gas exchange, carbon isotope discrimination, transpiration efficiency and productivity in field grown durum wheat genotypes

Philippe Monneveux^a, Djamila Rekika^a, Edmundo Acevedo^b, Othmane Merah^{a,*}

^a UMR Diversité et Génome des Plantes Cultivées, ENSA-INRA, 2 place Viala, F-34060 Montpellier Cedex 1, France

^b Facultad de Ciencias Agronómicas, Universidad de Chile, Casilla 1004, Santiago, Chile

Abstract

Under drought prone conditions, wheat productivity is strongly related to photosynthetic activity and transpiration efficiency. In the present study, photosynthesis related traits were assessed at anthesis under rainfed and irrigated conditions on five durum wheat (*Triticum durum* Desf.) cultivars grown under Mediterranean conditions. Carbon isotope discrimination was also evaluated in flag leaf at anthesis (ΔL_a) and grain at maturity (ΔG_m). Under rainfed conditions, highly significant correlations were found between both ΔL_a and ΔG_m , and leaf CO₂ exchange rate (CER), stomatal conductance (g_s) and internal to ambient CO₂ concentration ratio (C_i/C_a). ΔG_m was correlated negatively with transpiration efficiency (measured as CER/ g_s) under rainfed conditions, and positively under irrigated conditions. Under both conditions, ΔG_m was positively associated with grain yield. No significant correlation was observed between mesophyll conductance and CER. In contrast, the latter trait was positively related to g_s under irrigated conditions suggesting that CER was driven by stomatal limitations. No correlation was found between ΔL_a and grain yield. It is concluded that breeding for high ΔG_m would lead, under Mediterranean drought conditions, to higher stomatal conductance, lower transpiration efficiency and higher grain yield.

Keywords: Durum wheat; Drought; Carbon isotope discrimination; Intrinsic photosynthetic capacity; Stomatal conductance; Transpiration efficiency

1. Introduction

Transpiration efficiency (TE) can be evaluated at the leaf level as the ratio of leaf CO₂ exchange rate (CER) to stomatal conductance (g_s) [1,2]. In wheat, variation in TE was found to be related to the variation in the ratio of biomass production to water transpired of potted plants, suggesting that leaf gas exchange techniques may provide an assessment of the

transpiration efficiency of the whole plant [3]. However, under field conditions, the variation of environmental factors makes highly difficult to reveal genetic variation. Measuring gas exchange parameters and CER/ g_s in controlled conditions may considerably limit the effect of environmental variation [4–6], but the extent to which studies carried out in pots and controlled conditions are representative of field conditions is not clear [6,7]. Isotopic methods could represent another alternative to overcome these difficulties. In several species, carbon isotope discrimination (Δ) was correlated negatively with TE [2,8,7]. Thus, Δ may permit an integrated measure of TE during the entire period in which the sample tissue is growing. This represents a real advantage over the short-term data obtained from gas exchange studies. The physiological basis for Δ variation in C₃ plants is related to the variation in the internal CO₂ concentration (C_i) to ambient CO₂ concentration (C_a) ratio. High Δ values resulting from high C_i/C_a would lead to low TE [5,10,11]. Thus, many authors have suggested that Δ could be also related to grain yield (GY) and water use

Abbreviations: BIOM, above-ground biomass; CER, leaf CO₂ exchange rate; C_i/C_a , the ratio of internal CO₂ concentration to ambient CO₂ concentration; DH, days to heading; g_m , apparent mesophyll conductance; g_s , stomatal conductance; ΔG_m , carbon isotope discrimination of the grain at maturity; GY, grain yield; ΔL_a , carbon isotope discrimination of the leaf at anthesis; TE, transpiration efficiency; WUE, water use efficiency

* Corresponding author. Present address: IUT Paul Sabatier, Département de Génie Biologique, 24 rue d'Embaquès, F-32000 Auch, France.
Tel.: +33 5 62 61 63 12; fax: +33 5 62 61 63 01.

E-mail address: othmane.merah@iut-tlse3.fr (O. Merah).

efficiency (WUE), the dry matter production to water consumption ratio [7,8,11–14]. Consequently, Δ was proposed as a physiological tool to evaluate a large number of genotypes for GY and WUE under field conditions. Indeed, sampling for Δ is easy. Plant tissue is harvested, oven-dried, ground and analysed by isotopic mass spectrometry. As a matter of fact, grain yield was found to be positively associated with grain Δ under terminal drought [12,15–18]. Considering that water availability is rather similar for all genotypes, the association between Δ and grain yield suggests that Δ is positively correlated with WUE.

Due to some confusion between the transpiration efficiency at the leaf or plant level (TE) and the water use efficiency of the crop, some authors consider as contradictory the negative correlation between Δ and TE and the positive correlation between Δ and WUE. Some of them express doubts about the possibility to use Δ as a confident criterion to select for yield under drought conditions [19], while others consider that transpiration efficiency and Δ may be positively correlated under some conditions [11–20].

Comparison of instantaneous transpiration efficiency (evaluated from gas exchange measurements) and long-term transpiration efficiency (estimated by Δ analysis) may contribute to a better understanding of the relationships between transpiration efficiency, grain yield and Δ . Relationships between Δ and gas exchange parameters have been mainly studied under controlled conditions [4,7,8]. The main objective of the current study was to determine, under Mediterranean field conditions, the relationships between gas exchange parameters, transpiration efficiency, leaf and grain carbon isotope discrimination and yield.

2. Materials and methods

2.1. Plant material

Five durum wheat (*Triticum durum* Desf.) cultivars differing for yield potential and drought tolerance were used in this study. Oued Zenati and Jennah Khetifa are two landraces originating from Algeria and Tunisia, respectively. They are adapted to severe drought, but have low yield potential. Cham 1, Korifla and Kabir are three improved high yielding varieties from the CIMMYT/ICARDA Durum Wheat program. Cham 1 is characterized by high drought tolerance and yield stability, while Kabir and Korifla are more susceptible to drought [21].

2.2. Experimental conditions

Trials were carried out in Montpellier, France (4°29'East, 48°46'North, elevation 45 m). Sowing was on 24th of November 1994. The soil was a sandy-loam (organic matter content 2.1%, pH 7.8) with a depth of about 0.6 m. The growth season was characterized by a total low rainfall (285 mm). The Penman evaporation (PET) was 486 mm during the same period, i.e. 170% higher than rainfall. More than 65% of the total rainfall occurred during the first 3 months of the cropping cycle with a rainfall to evapotranspiration ratio (R/PET) of

5.06, which exceeded the crop demand during this period. Then, progressive drought developed until the end of the plant cycle (R/PET decreased strongly to 0.26 at anthesis). Strong terminal water stress occurred during the grain filling stage. Indeed, only 31 mm of rainfall were registered in May and June, whereas PET reached 266 mm (R/PET = 0.13). Total radiation during the cycle was about 2917 MJ m⁻². Monthly detailed information on rainfall, temperatures, radiation and relative air humidity are reported elsewhere by Merah et al. [22]. These conditions are representative of the Mediterranean climate which concerns around 50% of the wheat cultivated under drought worldwide [23].

The field experiment involved irrigated and rainfed conditions. Two replicates of a randomized complete block design were used under both conditions. Seeds were sown in four 1.50 m rows per plot (25 cm between rows and 3 cm inter-plant spacing). For the irrigated environment, 200 mm of water was applied with sprinklers in ten times from February until maturity. Anthesis occurred the last week of April and maturity at the end of June.

2.3. Physiological measurements

2.3.1. Gas exchange measurements

Gas exchange measurements were replicated 16 times for each genotype in each water treatment. Leaf CER, g_s and internal CO₂ concentration to ambient CO₂ concentration ratio (C_i/C_a) were measured on the flag leaf at anthesis by using a portable photosynthesis system LI-6200 (Li-Cor, Lincoln, NE, USA) and a 1143 cm³ leaf chamber. Leaf temperature was approximately 26 °C. In irrigated plots, measurements were carried out 1 day after irrigation. Leaf area was determined by multiplying the length by the average width of the leaf portion enclosed in the chamber. Leaf gas exchange rates were automatically calculated from slopes of CO₂ depletion and H₂O increase in the system in 30 s sampling periods. Apparent mesophyll conductance (g_M) was estimated as CER/ C_i . The instantaneous TE at the leaf level was calculated as CER/ g_s [6].

2.3.2. Carbon isotope discrimination

Carbon isotope discrimination (Δ) was determined for flag leaves at anthesis and grains at maturity. For each genotype, 20 flag leaves were randomly detached at anthesis and immediately oven-dried at 80 °C for 48 h. At maturity, a 10 g grain sample was collected. Leaf and kernel samples were ground to a fine powder. Carbon isotope composition was determined with a mass spectrometer (Micromass, Villeurbanne, France) as: $\delta^{13}C$ (‰) = [($R_{\text{sample}}/R_{\text{reference}} - 1$) × 1000], R being the ¹³C/¹²C ratio. The discrimination (Δ) was calculated using the following formula [24]: Δ (‰) = [($\delta_a - \delta_p$)/(1 + δ_p)] × 1000, where δ_p is the $\delta^{13}C$ of the samples and δ_a , the $\delta^{13}C$ of the atmospheric CO₂, -8‰. Carbon isotope discrimination measurements were performed in the Institut de Biotechnologie des Plantes, Laboratoire Structure et Métabolisme des Plantes, Université Paris Sud (France). Carbon discrimination of the grain and the leaf was denoted ΔG_m and ΔL_a , respectively.

2.3.3. Agronomical traits

Earliness was expressed as the number of days from sowing to heading date (days to heading), when about half of the spikes had emerged. Above-ground biomass (BIOM) and GY were recorded at maturity on the two central rows of each plot.

2.4. Statistical analyses

All the data were subjected to variance analysis using the GLM procedure of SAS (SAS Institute, 1987, Cary, NC, USA). The mean pair wise comparisons were based on the Duncan test. Correlation analysis was performed to determine the relationship between the traits using the SAS CORR procedure.

3. Results

In both water treatments, there were significant genotypic differences in yield, leaf and grain carbon isotope discrimination (Table 1). Leaf gas exchange parameters also differed among genotypes except g_s under irrigated conditions. Rainfed conditions induced lower values in CER and g_s of 24%, and in C_i/C_a of nearly 15%. Carbon isotope discrimination of leaf (ΔL_a) and grain (ΔG_m) were also lower under rainfed than under irrigated conditions (−5.0 and −9.2%, respectively). Under rainfed conditions, Cham 1 had significantly higher CER, g_s and C_i/C_a values than the other genotypes. The lower CER and g_s values were noted in the landraces Oued Zenati and Jennah Khetifa. These genotypes exhibited the highest TE values. The highest Δ and grain yield were found in Cham 1 and the lowest in Oued Zenati and Jennah Khetifa (Table 1).

Significant correlations were found between CER and g_s under both rainfed and irrigated conditions (Table 2). Even under irrigated conditions, CER was stronger correlated with g_s than with mesophyll conductance (g_m) (Fig. 1). Under both conditions, CER and g_s were significantly correlated with grain

Table 2

Correlations between CO₂ exchange rate (CER), stomatal conductance (g_s), internal CO₂ concentration to ambient CO₂ concentration ratio (C_i/C_a), carbon isotope discrimination of leaf at anthesis (ΔL_a) and grain at maturity (ΔG_m), and grain yield (GY) under rainfed and irrigated field conditions

	CER	g_s	C_i/C_a	ΔL_a	ΔG_m	GY
Rainfed conditions						
g_s	0.99***					
C_i/C_a	0.96**	0.93**				
ΔL_a	0.88*	0.83*	0.96**			
ΔG_m	0.99***	0.98***	0.94**	0.90*		
GY	0.87*	0.90*	0.75ns	0.57ns	0.81*	
Biom	0.82*	0.84*	0.71ns	0.53ns	0.76ns	0.98***
Irrigated conditions						
g_s	0.84*					
C_i/C_a	−0.81*	−0.70ns				
ΔL_a	−0.36ns	0.00ns	0.16			
ΔG_m	0.91*	0.72ns	−0.90*	−0.13ns		
GY	0.86*	0.98***	−0.76ns	0.10ns	0.82*	
Biom	0.91*	0.97**	−0.74ns	0.25ns	0.74ns	0.92**

ns: not significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

yield and biomass. No significant effect of earliness was noted on these relationships (data not shown). C_i/C_a correlated positively with CER and ΔG under rainfed conditions and negatively under irrigated conditions. Under rainfed conditions, C_i/C_a was positively associated with g_s and ΔL_a . Significant correlations were noted between CER and g_s and both ΔL_a and ΔG_m . ΔL_a and ΔG_m were correlated under rainfed conditions, but not under irrigated conditions. TE was negatively correlated with ΔG_m under rainfed conditions and positively under irrigated conditions (Fig. 2). A positive association was noted between ΔG_m and grain yield in both treatments (Table 2). No significant correlation was noted between biomass and ΔG_m .

Table 1

Genotypic variation in CO₂ exchange rate (CER), stomatal conductance (g_s), internal CO₂ concentration to ambient CO₂ concentration ratio (C_i/C_a), instantaneous transpiration efficiency (TE), carbon isotope discrimination of leaf at anthesis (ΔL_a) and grain at maturity (ΔG_m), grain yield (GY) and biomass production (BIOM) under rainfed and irrigated field conditions

Genotype	CER ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	C_i/C_a	TE ($\mu\text{mol mol}^{-1}$)	ΔL_a (‰)	ΔG_m (‰)	GY (t ha^{-1})	BIOM (t ha^{-1})
Rainfed conditions								
Oued Zenati	12.6 ^C	0.18 ^C	0.58 ^D	75.6 ^A	18.4 ^C	14.8 ^D	3.60 ^D	15.80 ^B
Jennah Khetifa	12.6 ^C	0.18 ^C	0.60 ^{CD}	71.5 ^{AB}	18.5 ^{BC}	14.6 ^E	3.80 ^D	16.00 ^B
Cham 1	19.9 ^A	0.34 ^A	0.67 ^A	59.0 ^D	19.4 ^A	16.1 ^A	7.52 ^A	21.84 ^A
Korifla	17.6 ^B	0.29 ^B	0.65 ^{AB}	62.0 ^{CD}	19.3 ^A	15.8 ^B	4.76 ^C	16.60 ^B
Kabir	16.8 ^B	0.29 ^B	0.62 ^{BC}	67.5 ^{BC}	18.6 ^B	15.5 ^C	6.76 ^B	19.84 ^{AB}
F	33.26 ^{***}	36.67 ^{***}	7.72 ^{**}	9.94 ^{**}	132.58 ^{***}	188.58 ^{***}	267.13 ^{***}	6.92 [*]
Irrigated conditions								
Oued Zenati	19.72 ^{BC}	0.32 ^{AB}	0.79 ^A	37.7 ^B	19.6 ^B	16.3 ^D	6.76 ^B	18.20 ^B
Jennah Khetifa	18.50 ^C	0.33 ^{AB}	0.76 ^A	42.0 ^B	20.3 ^A	16.1 ^E	7.08 ^B	19.16 ^B
Cham 1	23.00 ^A	0.37 ^A	0.70 ^B	53.1 ^A	20.1 ^A	17.6 ^A	8.56 ^A	37.16 ^A
Korifla	20.95 ^{ABC}	0.33 ^{AB}	0.70 ^B	54.1 ^A	20.0 ^A	17.4 ^B	7.38 ^{AB}	21.08 ^B
Kabir	22.30 ^{AB}	0.35 ^{AB}	0.69 ^B	54.7 ^A	19.2 ^C	17.2 ^C	7.68 ^{AB}	33.40 ^A
F	4.84 [*]	1.44ns	7.35 ^{**}	7.22 ^{**}	32.69 ^{**}	189.33 ^{***}	3.79 [*]	16.83 ^{**}

Within each trial, means followed by a different letter are significantly different by Duncan's multiple range test at $P = 0.05$; ns: not significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

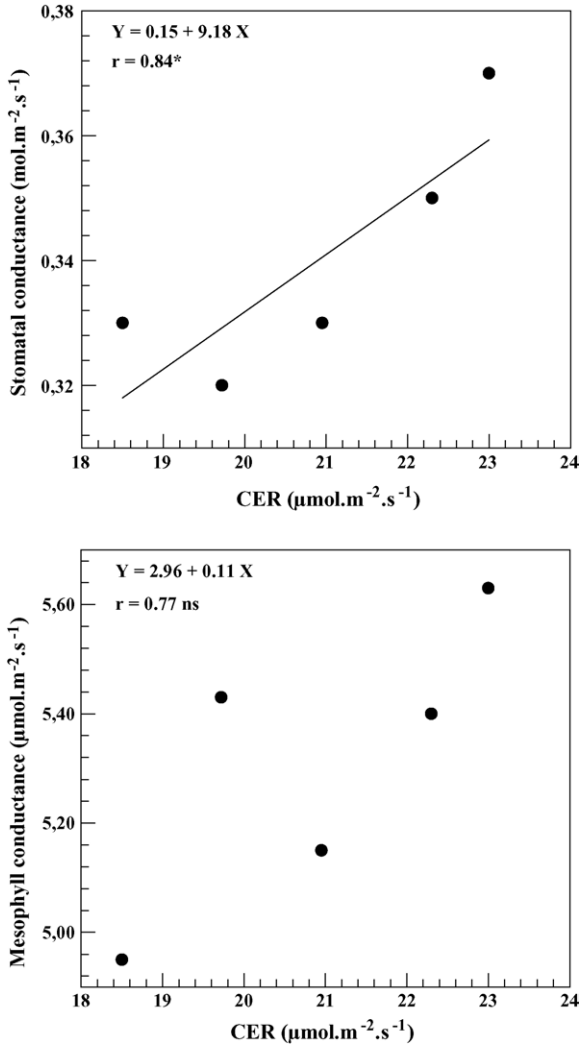


Fig. 1. Relationship between CO₂ exchange rate (CER), and stomatal (g_s) and mesophyll conductance (g_m) under irrigated field conditions.

4. Discussion

4.1. Relationships among leaf gas exchange parameters

CER and g_s values were strongly lower under drought conditions. Highly significant correlations noted between CER and g_s under rainfed conditions (Table 2) are in agreement with results reported by, Gutiérrez-Rodríguez et al. [1], Xue et al. [2] and Kalapos et al. [5]. These authors suggested that the positive correlation between CER and C_i/C_a could be due to a stomatal limitation on both traits. Negative correlation between these traits, as observed under irrigated conditions (Table 1), has been less reported. The value of C_i/C_a is determined by the balance between stomatal conductance and intrinsic photosynthetic capacity of leaves [25]. Under irrigated conditions, the association between CER and g_s is much weaker than under rainfed conditions. High stomatal aperture was reached in all genotypes, with g_s values comprised between 0.32 and 0.37 mol m⁻² s⁻¹. Under such conditions, CER could depend both on stomatal conductance and intrinsic photosynthetic activity that tends to reduce C_i . Data show, however, that CER

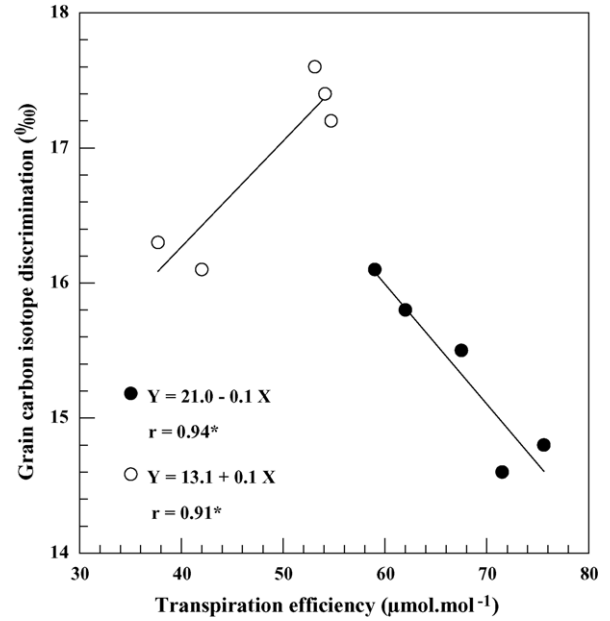


Fig. 2. Relationship between transpiration efficiency (measured as CER/ g_s) and grain carbon isotope discrimination (ΔG_m) under rainfed (black circles) and irrigated (white circles) field conditions.

correlated stronger with stomatal conductance than with mesophyll conductance (Fig. 1).

4.2. Relationships between leaf gas exchange parameters and carbon isotope discrimination

The positive association observed under rainfed conditions between C_i/C_a and both ΔG_m and ΔL_a (Table 2) is in agreement with theory [24]. It also agrees with results obtained in experiments in which variation in C_i/C_a was due to physiological treatments [26] or genotypic effects [11,20]. Correlations noted under rainfed conditions between ΔL_a , ΔG_m , CER and g_s (Table 2) suggest that higher g_s could lead to higher C_i/C_a , Δ and CER, and consequently to higher yield [6]. GY effectively correlated with CER, g_s and ΔG_m (Table 2).

Under irrigated conditions, the lack of correlation between C_i/C_a and Δ , may be explained by differences between the instantaneous measurement of gas exchange parameters and the long-term measurement of Δ in plant dry matter [4,12]. Indeed, gas exchange parameters were assessed on well-watered plants, which suffered small stomatal limitation, as revealed by high g_s values (Table 1). Although irrigated, the crop should have experimented further intermittent drought stress related to very low R/PET ratio, particularly during grain filling.

4.3. Gas exchange parameters and carbon isotope discrimination genotypic variation

Under rainfed conditions lowest CER were found in the two landraces Oued Zenati and Jennah Khetifa, while the highest g_s and CER values were noted in Cham 1. High g_s in Cham 1 was largely confirmed by its ΔL_a and ΔG_m values (Table 1). Moreover, the ranking among varieties noted here for gas

exchange parameters and Δ is the same that this registered for osmotic adjustment by Rekika et al. [27]. This leads to consider Δ as a good indicator of leaf water status under moisture stressed conditions, as already postulated by Monneveux et al. [18] and Merah et al. [28]. Under irrigated conditions, the high CER of the improved varieties Cham 1, Korifla and Kabir allowed them to attain higher yield. Their lower C_i/C_a and higher g_M values suggest a high intrinsic photosynthetic capacity (Table 1). Physiological and yield data obtained under rainfed and irrigated conditions show that these genotypes (and particularly Cham 1) combine high productivity and drought tolerance and confirm observations previously made on these varieties [21,22].

4.4. Relationships between carbon isotope discrimination, transpiration efficiency and yield

The negative correlation observed under rainfed conditions between TE and Δ is quite general in literature [29]. The significant correlation between ΔG_m and grain yield agrees with results obtained under Mediterranean-type environments [9,14,15,17]. This correlation was found to be higher under rainfed conditions, as already noted by Merah et al. [30]. Different hypothesis can explain the association between ΔG_m and GY under terminal drought conditions. First, high ΔG_m and GY could result from high Δ values at early stage of growth. In this case high Δ may reflect faster growth rate throughout crop development [20]. In the present study, ΔG_m and ΔL_a are significantly correlated. However, no significant correlation was found between grain yield and ΔL_a (Table 2). In an experiment under similar conditions, Merah et al. [31] found a weak correlation between grain yield and ΔL_a . Strong positive correlation was found between grain yield and ΔL_a only under very severe conditions [32]. Thus, the higher grain yield of genotypes with high grain Δ is probably poorly explained by a faster growth rate which was confirmed by results observed in cotton and rice [7,33]. This is not surprising since under Mediterranean conditions, consistent winter rainfall maintains a high soil water status so that there is little limitation from water supply on early growth. Secondly, high grain Δ could characterize genotypes with high leaf Δ that are more dependent on pre-anthesis stem reserves for grain filling. Grain Δ may be higher if a large proportion of starch originates from stem reserves, accumulated when plants are less stressed and have high Δ values. This hypothesis implies a close correlation between leaf and grain Δ . As mentioned above, this condition is satisfied in the present study (Table 2). ΔL_a and ΔG_m were also found to correlate significantly in a 3-year experiment carried out in the same location with another set of genotypes [30]. Moreover, in this last study the correlation between ΔL_a and ΔG_m was stronger as the water-stress increased. Thirdly, high ΔG_m can be the consequence of earlier flowering [34], or greater access to soil moisture during grain filling because of deeper rooting and better water extraction [12]. In this study, earliness was not found to have significant effect on Δ (data not shown). Rooting patterns were not examined, but Ali Dib and

Monneveux [35] found a much deeper rooting in Algerian landraces than in Cham 1. Finally, ΔG_m could reflect a better ability to maintain stomata more open after anthesis [10,31]. This hypothesis is supported by the strong correlation between g_s and ΔG_m (Table 2). The close correlation observed between ΔG_m and GY could be explained by the fact that both traits strongly depend on g_s . It confirms that under Mediterranean conditions, ΔG_m is a good predictor of grain yield [16,17,32]. The negative correlation between ΔG_m and TE (Fig. 2) confirmed the negative association between Δ and the TE reported by Xue et al. [2] and Morgan et al. [10]. Many studies found an association between Δ and water use efficiency, WUE [8,14,24]. This would mean a negative association between TE and WUE and suggests that under water stress, gas exchange at the leaf and canopy levels are not correlated among genotypes [24]. A possible explanation is the influence of boundary layer resistance on transpirational water loss from field canopies [36]. More generally, any variation in the transpiration/evaporation ratio would modify the relationships between TE and WUE [11,13]. Thus, all traits modifying the transpiration/evaporation ratio, as earliness, early vigour, growth habit, leaf posture, access to water and seasonal pattern of water use may interfere in this relationship.

Under irrigated conditions, ΔG_m was found to correlate positively with TE (Table 2). In such conditions g_s was high and showed a little variation among genotypes. Thus, the positive correlation registered between ΔG_m and TE is likely to be due more to the association between ΔG_m and CER than between ΔG_m and g_s (Table 2). In most studies realized under well-watered conditions, no correlation was found between ΔG_m and TE [7,10,19]. Information is scarce concerning the relationship between Δ and grain yield under favourable or irrigated conditions. Grain yield of irrigated cereals was found to correlate positively with carbon isotope discrimination of the peduncle [12], grain [16] and flag leaf [18,32]. In all these experiments, however, the analysed organ was sampled at maturity, after the crop experienced a terminal water stress. Conversely, a negative correlation was observed between leaf Δ and the biomass of young bread wheat seedling cultivated in absence of water stress [20]. Under such conditions, stomatal conductance is likely to be high. Thus, higher photosynthetic capacity would induce lower C_i , leading to lower Δ values. In the present study, no correlation was found between ΔL_a and GY (Table 2). This suggests that, despite of the irrigation, the decrease in C_i associated with increased photosynthetic capacity was largely offset by the decrease in C_i caused by stomatal closure, leading to a lack of association between ΔL_a and GY. Subtle drought stress is likely to have occurred, since total water availability (485 mm rainfall and irrigation) was lower than PET. Moreover, CER was stronger related to g_s than to g_M (Fig. 1) and ΔL_a was higher than under drought conditions (Table 1), confirming that leaf Δ was more driven by stomatal limitations than intrinsic photosynthetic ones as also shown in soybean and cotton [13,33]. The difference between ΔL_a and ΔG_m reflected a strong decline in C_i , due to an important stomatal limitation during grain filling. As a consequence, ΔG_m was positively correlated with grain yield.

Productivity of wheat genotypes under terminal drought is related to their capacity to maintain their photosynthetic activity. Evaluation of photosynthetic traits under field conditions, when possible, may allow a better understanding of the behaviour of genotypes under stress. Under irrigated conditions, many factors as low variation in g_s , high intrinsic photosynthetic activity and increased role of time-scale differences between measurements were found to interfere in the relationship between Δ , gas exchange parameters and transpiration efficiency. Under terminal water stress, and due to its strong correlation with gas exchange parameters ΔG_m appeared, as already suggested by previous studies [28,31], as a good predictive criterion for transpiration efficiency and yield.

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