

Carbon isotope discrimination may predict grain yield in durum wheat under Mediterranean conditions

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Abstract

Carbon isotope discrimination (Δ) has been proposed as a criterion for the indirect selection to improve transpiration efficiency and grain yield in bread wheat and barley. Less interest has been devoted to durum wheat (*Triticum durum* Desf.) despite its economic importance in the Mediterranean basin. The Δ genetic variation and its relationship with productivity in durum wheat is investigated in this study. For this purpose, field experiments were conducted under Mediterranean conditions (South of France) on 144 durum wheat accessions, during three consecutive years with contrasting climatic conditions. Grain yield (GY), above-ground biomass (AGB), harvest index (HI) and carbon isotope discrimination of flag leaf (Δ_L) and kernel (Δ_G) were measured. Differences among years were noted for Δ_L and Δ_G , which were probably related to the variation in water availability between years. A large genotypic variation was also noticed for Δ_L and Δ_G . The two traits were found positively correlated with GY within and across years, which confirms the interest of Δ for selection for grain yield improvement under Mediterranean conditions. Δ_G and Δ_L correlated better with HI than with GY, suggesting that Δ could reflect the efficiency of carbon partitioning to the grain. The lack of correlation between Δ_L and both HI and GY in the favourable water conditions (1996) was probably due to the difference in water availability between the period until flag leaves sampling (favourable conditions) and the strong water stress which accompanied the grain filling. Δ_G correlated better with both HI and GY than Δ_L . Moreover, higher broad-sense heritability (h^2) was obtained for Δ_G than for Δ_L . As a result, Δ_G appeared to be a better predictive criterion for efficiency of the carbon partitioning to the kernel (harvest index) and hence for grain yield than Δ_L .

■ **Key words:** carbon isotope discrimination, durum wheat, dry matter partitioning, grain yield, Mediterranean conditions, harvest index.

■ Introduction

Durum wheat is probably one of the oldest cultivated plants in the world. This species is mainly grown under rainfed conditions in the Mediterranean regions, where the annual amount of precipitation varies between 200 to 800 mm (Baldy, 1986; Loss and Siddique, 1994). In these regions, water is the major resource limiting durum wheat production. Therefore, drought tolerance improvement of durum wheat varieties is a major objective for all breeders in the Mediterranean countries (Monneveux and Belhassen, 1996; Merah et al., 1999a). Several morphophysiological traits have been proposed as screening criteria for drought tolerance (Turner, 1997; Merah, 2001a; Blum, 2009). Transpiration efficiency (TE: the ratio of dry matter produced to water transpired) is an interesting attribute for plant growth in dry areas. However, its use has been limited by the lack of related screening criteria since its direct measurement is challenging, especially in field trials. Now, its indirect determination using the carbon isotope discrimination (Δ) allows to introduce TE in breeding programs.

During photosynthesis, plants discriminate against the heavy isotope of carbon (^{13}C) which leads to a depletion of the plant dry matter in ^{13}C . Carbon isotope discrimination is a measure of the $^{13}\text{C}/^{12}\text{C}$ ratio in plant dry matter compared with the value of the same ratio in the atmosphere (Farquhar and Richards 1984). In C_3 species, including bread wheat and barley, Δ was found to be positively correlated with C_i/C_a (i.e., the ratio of internal leaf CO_2 concentration to ambient CO_2 concentration) and negatively associated with TE. (Farquhar and Richards, 1984; Ehdai et al., 1991; Johnson and Bassett, 1991; Read et al., 1991; Acevedo, 1993; Monneveux et al., 2006). Δ values appear to provide a useful integration of TE of C_3 crop species and therefore has been proposed as a potential criterion for TE (Farquhar et al., 1989; Merah et al., 2001a).

The relation between Δ (and TE) and plant productivity is less clear. Some studies have shown a negative correlation between dry matter production and Δ indicating that high TE may be important for high productivity (Johnson and Bassett, 1991). However, Δ has been found frequently to be positively associated with grain yield in bread wheat (Condon et al., 1987; Morgan et al., 1993; Sayre et al., 1995; Merah et al., 1999b, 2001b, 2002; Hafsi et al., 2001) and barley (Craufurd et al., 1991; Acevedo, 1993; Voltas et al., 1998; Atanassov et al., 1999; Teulat et al., 2001) under both irrigated and droughted conditions. Most of these studies have been carried out using a limited number of genotypes or under controlled growing conditions or both. Positive correlations were also reported between Δ and harvest index in peanut (Wright et al., 1993), bread wheat (Ehdaie and Waines, 1993), durum wheat (Merah et al., 2001c), lentil (Johnson et al., 1995) and cowpea (Menendez and Hall, 1996), suggesting that increased TE may also result in reduced dry matter partitioning to grain (Merah et al. 2001a). The relationships between Δ , grain or biomass production and harvest index are poorly documented in durum wheat under Mediterranean conditions. The objectives of this study were to determine how Δ is related to grain yield, biomass production and harvest index under water contrasted field conditions

Materials and methods

Plant material

A total of 144 durum wheat accessions (*Triticum durum* Desf.), constituting the CIMMYT/ICARDA Durum Wheat Core Collection, were used. The collection included landraces (66) originating from 18 countries, improved varieties (53) and CIMMYT/ICARDA advanced breeding lines (25).

Site and crop management

Trials were carried out under rainfed conditions at Montpellier, France during three successive years (1994/95, 1995/96, 1996/97). The soil was a sandy-loam (organic matter content 2.1%, pH 7.8) with a depth of about 0.6 m. A randomised complete block design was used, with two replicates per genotype. Seeds were sown in two 1.5 m rows per plot with 25 cm row spacing and 3 cm inter-plant spacing. Sowings were

done on 24, 17 and 8 November, respectively. Anthesis occurred between the last week of April and the beginning of May, and plants matured end of June.

Climatic conditions

Cumulative rainfall during the cropping cycle (November to June) was 285 mm in 1994/95, 933 mm in 1995/96 and 744 mm in 1996/97. More than 60% of the total rainfall occurred during the first three months of the cropping cycle (Table 1). 1995 was characterised by a drought period from February until the end of the growth cycle. A pronounced terminal water stress was noted in 1996. The ratio between rainfall and Penman evapotranspiration was very low in May to June. In contrast, a period of drought was observed from February to May in 1997, whereas, the terminal water stress was less pronounced in this year (Table 1). The three years could be then characterised as 3 different environments corresponding to an intensive and early water stress (1995 hereafter referred as M95), a mild terminal water stress (1996, M96) and a moderate intermittent water stress (1997, M97). More detailed informations on rainfall, evapotranspiration, radiation, and air relative humidity are reported elsewhere by Merah et al. (1999a).

Table 1. Monthly averages of mean temperature (T), Penman evapotranspiration (Penman ET), and rainfall during the three cropping seasons at Montpellier.

	1994 - 1995			1995 - 1996			1996 - 1997		
Month	T (°C)	Penman ET (mm)	Rainfall (mm)	T (°C)	Penman ET (mm)	Rainfall (mm)	T (°C)	Penman ET (mm)	Rainfall (mm)
November	14.3	16	108	11.5	18	90	11.1	15	106
December	9.6	8	51	8.8	7	192	9.1	7	259
January	8.0	18	27	10.4	6	271	8.1	8	185
February	11.2	29	8	7.3	26	126	10.5	25	8
March	10.5	66	12	10.1	47	103	13.8	68	14
April	14.4	85	50	14.2	73	76	14.2	90	21
May	16.9	114	29	17.1	104	46	17.9	98	34
June	21.5	152	2	22.3	136	31	20.2	97	119
Mean	13.3	61	36	12.7	52	117	13.1	51	93
Sum	-	486	285	-	417	933	-	406	744

Measurements

Specific leaf dry weight

At anthesis, four flag leaves (per genotype) were excised and immediately brought to the laboratory. The leaf area (LA, in cm²) was determined using an area meter (LI-3000, Li-Cor, Lambda Instruments Co., USA). The flag leaf dry weight (DW) was obtained by weighing after oven drying at 80°C during 48 hours. The specific leaf weight (SLDW) was then calculated as $SLDW = DW/LA$.

Carbon isotope discrimination

For each genotype, 20 flag leaves were randomly detached at anthesis and immediately oven-dried for 48 h at 80°C. At maturity, a 10g grain sample was collected. Leaf and kernel samples were ground to a fine powder. Carbon isotope composition ($\delta^{13}C$) was then determined with an isotope mass spectrometer (Micromass, Villeurbanne, France) and calculated as: $\delta^{13}C$ (‰) = $[(R \text{ sample}/R \text{ reference}-1) \times 1000]$, with R being $^{13}C/^{12}C$ ratio. Carbon isotope discrimination (Δ) was calculated using the following formula (Farquhar et al., 1989): Δ (‰) = $[(\delta a - \delta p) / (1 + \delta p)] \times 1000$, where δp is the $\delta^{13}C$ of the leaves and δa is the $\delta^{13}C$ of the atmospheric CO₂ (-8‰).

Agronomical traits

The number of days from sowing to heading (HD) was recorded when 50% of the plants (for a given genotype) were at this stage. At maturity, above-ground biomass (AGB) and grain yield per plant (GY) were also recorded. Harvest index (HI = GY / AGB) was then calculated.

Statistical analysis

Data were analysed using SAS, version 6.10 (SAS Institute, 1987, Cary, NC, USA) software. Differences between either genotypes or year for the traits measured were tested using two-ways analysis of variance. Year means were compared by Duncan's least significant difference at $P < 0.05$. Linear correlation analysis was used to determine the relationships between the traits using the CORR SAS procedure. A set of adjusted means was obtained using the number of days from sowing to heading (HD) as a covariate and by fixing this effect. Components of variance were computed using the mean-squares expectation obtained from the VARCOMP SAS procedure. Estimates of the variance components $\delta^2 g$ (genotypic variance) and $\delta^2 e$ (error variance) allowed the calculation of the broad sense heritabilities of the mean of genotypes (h^2) for all the traits as $h^2 = \delta^2 g / (\delta^2 g + \delta^2 e/k)$, where k is the number of replicates per accession ($k = 2$ in our case).

Results

The analysis of variance revealed significant differences among genotypes for grain yield (GY), harvest index (HI), above-ground biomass (AGB), carbon isotope discrimination of flag leaf (ΔL) and of kernel (ΔG), specific leaf dry weight (SLDW) (Table 2). Significant differences were also observed among years (hereafter referred to as environments) for all the measured traits (Table 2). The average mean GY for all the genotypes was higher in 1996 (161%) and in 1997 (106%) than in 1995. Similar range of variation among the three years was also noted for AGB. Harvest index differed significantly among the three years, with the lowest values obtained in 1995 (M95) and the highest values in 1996 (M96). A high range of variation was also noted for SLDW among years (Table 2). ΔL was nearly 2‰ higher in M96 than in M95 and M97. Mean ΔG in M95 was 2.5‰ and 0.7‰ lower than in M96 and M97, respectively. The greatest difference for ΔL between extreme genotypes (3.9‰) was observed in M97, a year characterised by intermediate water availability. The greatest genotype difference for ΔG (3.4‰) was found in M95, the driest year in our study (Table 1). The smallest ranges of values for ΔL and ΔG were observed in M96, the wettest year.

A negative correlation was obtained between SLDW and ΔL in M96 (Table 3). When calculated from the adjusted means (HD effect fixed) over the three years, genotypical correlation between SLDW and ΔL was negative and significant ($r = -0.221$, $P < 0.01$). No significant correlation was found between ΔG and SLDW.

The correlations between ΔL and both GY and

HI were positive and significant in M95 and M97 but not significant in M96 (Table 3).

In contrast, ΔL and AGB were positively and significantly correlated in favourable conditions of M96 only (Table 3). Genotypical correlations (calculated from the means of the genotypes averaged over the three years) between ΔL and both GY and HI were positive and significant, whereas not significant relationship between ΔL and AGB was found (Table 3). The correlations between ΔL and both GY and HI improved when adjusted means were used (Fig. 1a,c).

High significant and positive correlations were noted between ΔG and both GY and HI within and across environments (Table 3) and after subtracting for HD effect on these traits (Fig. 1). A significant positive correlation was also found between ΔG and AGB in M96 and in M97. In M95, these two traits were negatively related. Genotypical correlation (across environments) between ΔG and AGB was not significant (Table 3).

Broad-sense heritabilities (h^2) of flag leaf and grain Δ , AGB, GY and HI were calculated. Harvest index, above-ground biomass and grain yield showed lower h^2 than Δ . ΔG showed higher h^2 than ΔL (Table 4).

Table 2: Carbon isotope discrimination of flag leaf (ΔL) and of grain (ΔG), specific leaf dry weight (SLDW), above-ground biomass (AGB), grain yield (GY) and harvest index (HI) of durum wheat cultivated during three consecutive years (contrasted for their water regimes) at Montpellier (South of France).

Trait	1995		1996		1997		LSD	Source of variation		
	Mean	SD	Mean	SD	Mean	SD		Mean square		
								Year (df=2)	Genotype (df=143)	HD (df=1)
ΔL (‰)	18.21 ^C	0.65	20.30 ^A	0.59	18.68 ^B	0.65	0.14	466.47***	2.21***	1.02
ΔG (‰)	15.75 ^C	0.64	18.28 ^A	0.53	16.76 ^B	0.68	0.11	997.16***	2.90***	0.16
SLDW (g m ⁻²)	61.61 ^A	3.97	58.64 ^B	6.79	58.85 ^B	4.99	1.49	395.17***	2.80**	8.46*
AGB (g m ⁻²)	176.15 ^C	33.26	257.87 ^A	92.75	208.75 ^B	47.30	13.62	70.66***	1.46**	58.84***
GY (g m ⁻²)	50.87 ^C	12.72	81.84 ^A	38.48	66.19 ^B	21.09	5.89	53.64***	1.97**	66.58**
HI	0.29 ^B	0.07	0.32 ^A	0.09	0.31 ^A	0.08	0.016	4.36**	1.93***	0.10
HD (days)	128.70 ^C	5.78	134.24 ^A	4.20	133.38 ^B	5.75	0.49	289.13***	16.98***	---

For each year, values presented are means and standard deviation of 144 genotypes. For each parameter, degrees of freedom (df) and mean square of the environmental and genotypical effects, as well as the covariant effect of the number of days from sowing to heading (HD). LSD: Least significant difference (at $P < 0.05$) of the Duncan comparison test. Means of each trait with the same letter are not significantly different. * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Fig. 1. Relationships between grain yield and carbon isotope discrimination of flag leaves sampled at anthesis (a) and mature kernels (b) and between harvest index and ΔFL (c) and ΔK (d). Each point represents the adjusted mean (HD effect fixed) of an individual genotype over the three environments where the durum wheat collection was grown.

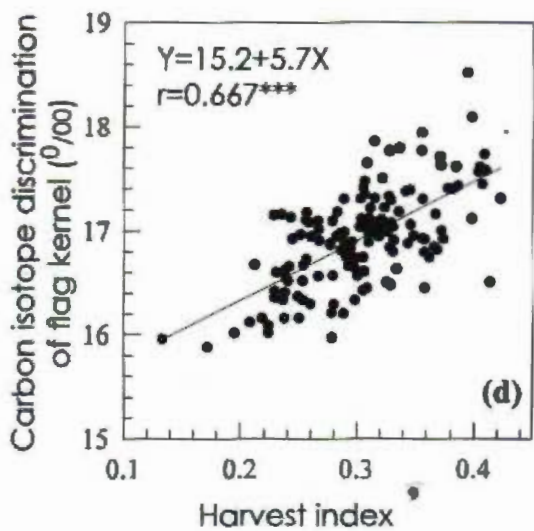
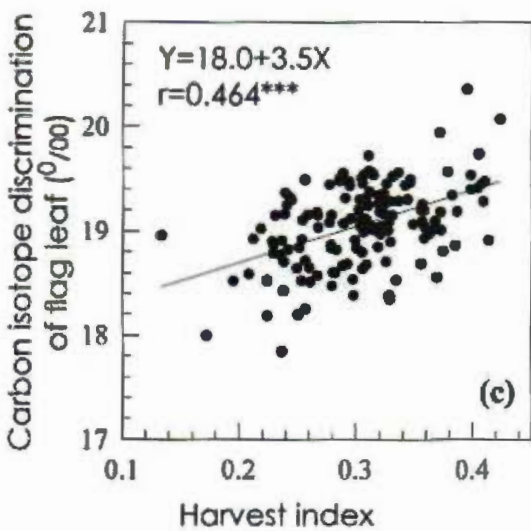
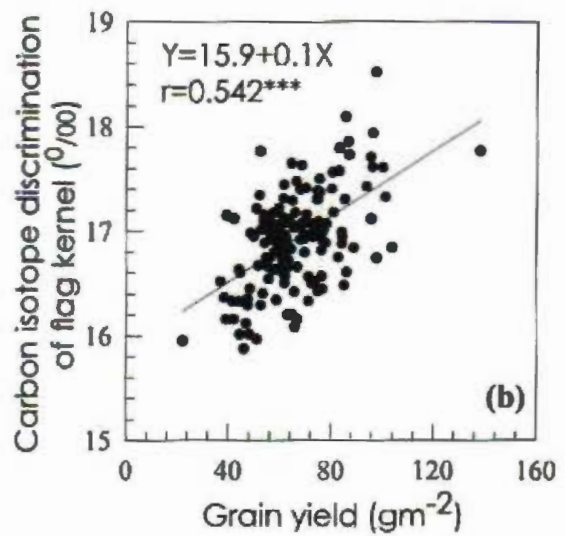
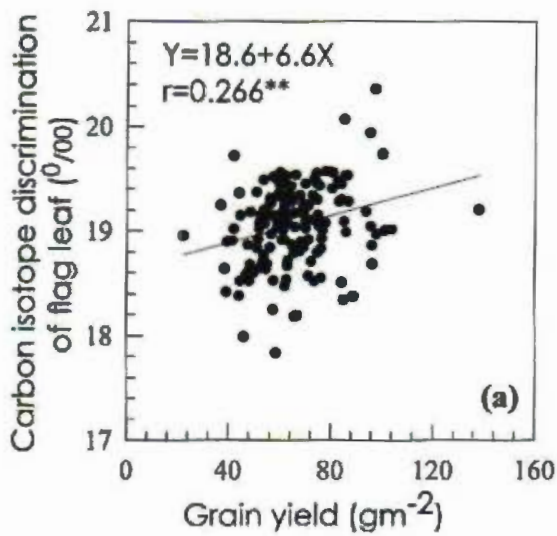


Table 3: Correlation coefficients of the relationships between carbon isotope discrimination of flag leaf (Δ_L) and of grain (Δ_G) and days from sowing to heading (HD), specific leaf dry weight (SLDW), above-ground biomass (AGB), grain yield (GY) and harvest index (HI) within and across years.

Table 4. Means values (\pm standard deviation) of broad sense heritabilities of carbon isotope discrimination of flag leaves (Δ_{FL}) and of kernels (Δ_K), grain yield (GY), above-ground biomass (AGB), and harvest index (HI).

Effect of phenology on Δ and productivity

In this study, the number of days from sowing to heading (HD) differed, within each trial, by more than 2 weeks between extreme genotypes, which may result in differences in Δ and grain yield (Acevedo, 1993; Annichiarico and Pecetti, 1998). An analysis of variance, where HD was used as covariate, was performed in order to test if HD could be at the origin of Δ variation. No significant HD effect on both Δ_G and Δ_L was noted. Even when HD effect was significant on SLDW, AGB and GY, differences between genotypes remained highly significant (Table 2). Adjusted means were generated by fixing the HD effect to overcome the influence of HD on SLDW, AGB and GY. Therefore, it appears that the genotypic variability in durum wheat for Δ ,

SLDW, GY and AGB is not only attributable to difference in phenology as reported for barley and bread wheat (Acevedo, 1993; Sayre et al., 1995).

Relationships between Δ and productivity

Grain yield was positively correlated to both Δ_G and Δ_L within and through environments. Our results agreed with those reported for bread wheat and barley under both water stressed and well watered conditions (Condon et al., 1987; Craufurd et al., 1991; Ehdai et al., 1991; Acevedo, 1993; Morgan et al., 1993; Sayre et al., 1995; Voltas et al., 1998; Merah et al., 2001d, 2001e, 2001f, 2002). The positive association between Δ_L and Δ_G and GY suggests that variation in water used for transpiration determines genotypes differences in Δ and GY (Morgan et al., 1993, Merah et al., 1999b, 2001g). Higher Δ is caused by a higher ratio of intercellular to atmospheric concentrations of CO₂ due to a larger stomatal conductance, leading to higher photosynthetic rates and, higher yield (Ehleringer, 1990; Morgan et al., 1993; Monneveux et al., 2006). The not significant correlation between SLDW and both Δ_L and Δ_G noted in M95 and M97 also supports this explanation. Indeed, Δ variation may result from differences in stomatal conductance and / or in photosynthetic capacity (Condon et al., 1987). SLDW has been proposed as good indicator of photosynthetic capacity and hence of Δ (Wright et al. 1993).

Trait	Environment	HD	SLDW	AGB	GY	HI
Δ	1995	-0.483***	-0.163	-0.150	0.421***	0.609***
	1996	0.528***	-0.307***	0.236**	0.106	-0.090
	1997	-0.156	0.006	0.148	0.264**	0.203*
	Mean across years	-0.144	-0.113	-0.003	0.255**	0.399***
Δ_G	1995	-0.307***	-0.123	-0.179*	0.511***	0.749***
	1996	-0.274**	0.039	0.217**	0.480***	0.546***
	1997	-0.058	0.052	0.439***	0.476***	0.273**
	Mean across years	-0.277**	0.082	0.091	0.541***	0.650***

* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

	Δ_{FL}	Δ_K	GY	AGB	HI
h^2	0.756 ± 0.06	0.854 ± 0.01	0.314 ± 0.08	0.403 ± 0.09	0.371 ± 0.08

Nevertheless, Craufurd et al. (1991) found a negative correlation between Δ and GY in barley, under irrigated conditions. Under those conditions, stomatal limitation was lower for all genotypes and the differences for stomatal conductance could then partly disappear. Simultaneously, the genetic variation in internal photosynthetic activity would be more highly expressed leading to a high assimilation per unit area and thus a negative correlation between Δ and GY. Significant and negative correlation was noted between ΔL and SLDW in M96, the leaves with high SLDW exhibiting the lowest discrimination (Table 2). In this year, water supply was not limited during vegetative stages (Table 1) and stomatal conductance was then likely to be high in all accessions. Thus, variation in ΔL would reflect differences in the photosynthetic capacity of different genotypes (Craufurd et al., 1991, Monneveux et al., 2006).

Flag leaves sampled around anthesis represent the photosynthesis functioning over the time that the dry matter was laid down. In M96, the flag leaf formation (February to April) was accompanied with favourable water conditions according to a rainfall to Penman evapotranspiration ratio of 2.69 (Table 1). This ratio was clearly lower during grain formation and filling (May to June) reaching a value of 0.33 (Table 1). These conditions have probably lead to high stomatal limitation on transpiration during grain filling and thus influences ΔG and grain yield. This could also explain the absence of significant correlation between ΔL and grain yield (Merah et al., 2002).

Relationship between Δ and harvest index

Harvest index (HI) was found to be strongly correlated with ΔG in the three environments, whereas ΔL and HI were correlated only in M95 and M97 (Table 3). The genotypical correlations between Δ traits and HI were also higher even after subtracting the HD effect on these traits (Fig 1). Moreover, the coefficients of correlation between HI and Δ traits were higher than those found between Δ and GY (Table 3).

A positive association between Δ and HI was found in peanut (Wright et al., 1993), lentil (Johnson et al., 1995) and cowpea (Menendez and Hall, 1996). In cereals, the relationship between Δ and HI has been scarcely studied. Ehdai and Waines (1993) have found a positive correlation between Δ and HI in bread wheat,

suggesting that higher water use efficiency values may result in reduced dry matter partitioning to grain (Ehdai and Waines, 1993). Our results suggest that genotypes which were able to maintain higher transpiration losses (and thus high Δ) were more efficient in carbon partitioning to the grain. Voltas et al. (1998) and Merah et al. (1999a,b, 2001c) have observed a negative relationship between kernel ash content and both ΔG and grain yield in barley and durum wheat. This correlation is more marked in stressed conditions. According to Loss and Siddique (1994), photosynthesis is more affected by drought than translocation. Therefore, genotypes unable to maintain high rates of stomatal conductance and photosynthesis during grain filling (i.e., with a lower ΔG) would fill their kernels through retranslocation of photoassimilates from preanthesis reserves, and of minerals from early senescent vegetative tissues (Wardlaw, 1990; Merah et al., 2001c,f). The ash concentration in mature grain could indicate the importance of the retranslocation processes during kernel filling (Merah et al. 1999b; Merah, 2001b). These results suggest that kernel ash content is higher (ΔG being thus lower) in genotypes more affected by drought during grain filling. Therefore, it is suggested that higher ΔG values represent a greater efficiency of carbon partitioning to the kernel.

Interest for durum wheat improvement.

A broad genotypic variation in both flag leaf and mature kernel Δ was found in the durum wheat core collection which is not only attributable to differences in phenology. Both grain yield and harvest index were positively correlated to Δ traits, especially under water stressed conditions, suggesting that these traits are strongly dependent on stomatal conductance. The positive correlation between grain yield and both ΔL and ΔG observed in this study is well documented elsewhere for barley and bread wheat under both irrigation and drought conditions. Our results confirm that Δ is a good indicator of grain yield in durum wheat under Mediterranean conditions. However, the relationship between Δ and HI has been undocumented. The positive correlation observed, in our study, between HI and Δ suggests that the genotypes which sustain greater transpiration losses (and thus high Δ) during grain filling are more efficient in dry matter partitioning to the grain,

and therefore can produce higher yield in a wide range of contrasted environments. This study provides evidence of positive relationship between Δ and harvest index in durum wheat.

The higher values of broad-sense heritability for Δ confirmed those reported for bread wheat and barley (Ehdaie et al., 1991; Acevedo, 1993; Voltas et al., 1998; Merah et al., 2001d), which confirms that Δ is a highly heritable trait. Carbon isotope discrimination measured in mature kernel showed a higher broad sense heritability and better correlations with both grain yield and harvest index than in Δ_L , suggesting that a better assessment of durum wheat yield and harvest index variation among genotypes could be obtained by using Δ values from mature kernel. This was not surprising; because Δ_G provides more information on events during grain filling than Δ_L (sampling of flag leaves was done around anthesis).

The extent to which kernel Δ may be useful as a selection criterion in durum wheat breeding depends upon the consistency of the ranking of genotypes for Δ and correlation with other desirable and undesirable traits.

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