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Contribution of Different Organs to Grain Filling in Durum Wheat under Mediterranean Conditions I. Contribution of Post-Anthesis Photosynthesis and Remobilization

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Keywords

carbon isotope discrimination; grain filling; photosynthesis; remobilization; source sink manipulations; *Triticum turgidum* var. *durum*

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Abstract

Under Mediterranean conditions, drought affects cereals production principally through a limitation of grain filling. In this study, the respective role of post anthesis photosynthesis and carbon remobilization and the contribution of flag leaf, stem, chaff and awns to grain filling were evaluated under Mediterranean conditions in durum wheat (*Triticum turgidum* var. *durum*) cultivars. For the purpose, we examined the effects of shading and excision of different parts of the plant and compared carbon isotope discrimination (Δ) in dry matter of flag leaf, stem, chaff, awns and grain at maturity and in sap of stem, flag leaf, chaff and awns, this last measurement providing information on photosynthesis during a short period preceding sampling. Source sink manipulations and isotopic imprints of different organs on final isotope composition of the grain confirmed the high contribution of both carbons assimilated by ears and remobilized from stems to grain filling, and the relatively low contribution of leaves to grain filling. Grain Δ was highly and significantly associated with grain yield across treatments, suggesting the utilization of this trait as an indicator of source sink manipulations effects on grain yield. Chaff and awns Δ were better correlated with grain Δ than stem and leaf Δ , indicating that chaff were more involved in grain filling than other organs. Moreover, in chaff, sap Δ was highly significantly correlated with dry matter Δ . These results suggest the use of Δ for a rapid and non destructive estimation of the variation in the contribution of different organs to grain filling.

Introduction

Under Mediterranean climates, rainfall decreases and evaporative demand increases during grain filling of winter cereals (Oweis et al. 1998). These crops consequently suffer a post anthesis water stress that can considerably limit grain filling and ultimately grain yield (Monneveux et al. 2006). Grain growth depends on the supply of carbon products provided by two main sources, *that is* current assimilation by photosynthetic organs and remobilization of stored assimilates. Many authors have attempted to determine the respective role of these two sources in grain filling (Hafsi et al. 2001, Yang and Zhang 2006, Zhu et al. 2010).

Under optimal conditions, the major source of assimilates is considered to be the flag leaf (Austin and Edrich

1975, Evans et al. 1980, Araus and Tapia 1987). Under drought conditions, a large body of experiments however suggests a crucial role of ear (spike and awns) photosynthesis. Sanchez Bragado et al. (2014) reported a higher contribution of ear to grain filling in landraces than in modern cultivars. Shading the ear leads to a strong reduction in grain weight and yield (Saghir et al. 1968, Hannachi et al. 1996). Estimates of the relative contribution of ear photosynthesis to final grain weight vary between 10 % and 76 % of final grain weight (Gebbing and Schnyder 2001, Tambussi et al. 2007, Aranjuelo et al. 2011), awns having a particular importance (Yang and Zhang 2006, Zhu et al. 2010). Awne genotypes tend to maintain higher kernel weight and yield under stress (Atkins and Norris 1955). Evans et al. (1972) reported a proportion of assimilates

contributed by ear photosynthesis to grain filling of 24 % in awnless and 43 % in awned cultivars. Shading or excising the awns leads to a significant decrease of grain weight and yield (Hannachi et al. 1996).

Post anthesis water stress reduces more CO₂ assimilation than remobilization of carbon products to the grain (Yang and Zhang 2006, Xu et al. 2007). As a consequence, the contribution to grain filling of the remobilization of photosynthates stored in vegetative parts increases under drought conditions (Bidingier et al. 1977). These reserves, constituted by non structural carbohydrates including low molecular weight fructans and starch (Blacklow et al. 1984), are mainly stored in the upper internodes of the stem (Seidel 1996), with the peduncle being probably the main contributor (Hafsi et al. 2001). When water stress becomes more intense, grain growth on the main stem is increasingly supported by a transfer of assimilates from tillers (Palta et al. 1994, Xu and Zhou 2005).

Attempts to estimate the contribution of different organs to post anthesis photosynthesis and remobilization processes were mainly based of source sink manipulations, *that is* by shading or excising different organs of the plant. During the last decades new techniques have been developed and have enabled to better determine the origin of carbon products used in grain filling. Among them, the use of carbon stable isotopes is probably the most promising (Hafsi et al. 2001, Merah et al. 2002). Assessment of the discrimination (Δ) against the naturally occurring stable isotope ¹³C during photosynthetic CO₂ fixation provides an integrated measure of photosynthetic gas exchange components. Carbon isotope discrimination permits an integrated measure of transpiration efficiency during the entire period in which the sample tissue is growing (Farquhar et al. 1989, Monneveux et al. 2006). In addition, Δ values of different plant tissues formed along the growth cycle may reflect the variation of plant water status during the season, and the isotopic imprints of different organs on final isotope composition of the grain may inform on their contribution to grain filling (Araus et al. 1993, Hannachi et al. 1996).

This study aims to estimate the contribution of different organs to final yield by both manipulating sink source relationships and assessing Δ in dry matter and sap of different organs. The sink source manipulating consisted in shading or excising different organs of the plant.

Materials and Methods

Plant material

The six durum wheat (*Triticum turgidum* var. *durum*) cultivars including four landraces and two advanced lines were used in this study. They were chosen from the CIMMYT/

ICARDA durum wheat core collection involving a total of 144 genotypes as representing a large range of flag leaf and grain Δ variation (Merah et al. 2001, 2002).

Experimental conditions

Experiments were carried out in the ENSA INRA Montpellier experimental fields (south of France), during two successive years (1995–96, season 1 and 1996–97, season 2). These two seasons were characterized by different climatic conditions, particularly during grain filling. During the plant cycle duration, cumulative rainfall was 933 and 744 mm, and R/ET (rainfall:evapotranspiration ratio) was 1.75 and 0.46 in season 1 and 2, respectively. From heading to maturity (including grain filling period), cumulative rainfall was 78 and 152 mm, and R/ET was 0.33 and 0.77 in season 1 and 2, respectively. Temperatures were quite similar during the cropping seasons. Indeed, mean temperature values were 13.1 °C and 12.8 °C in 1996 and 1997, respectively. During grain filling, temperature was 19.7 °C and 19.1 °C in season 1 and season 2, respectively. Therefore, the two cropping seasons could then be considered as slightly contrasted corresponding to a mild terminal water stress (1995–96) and moderate intermittent water stress (1996–97). The six cultivars were cultivated under rainfed conditions. A randomized complete block design was used for the two trials, with four replicates *per* genotype. Seeds were sown in plots of 18 m² (6 m long × 3 m wide; 25 cm spacing row and 3 cm interplant spacing). Sowings were performed at 17th and 8th of November in season 1 and 2, respectively. Fertilizer was applied before sowing at 90 kg N ha⁻¹, 90 kg P ha⁻¹ and 30 kg K ha⁻¹. The trials were top dressed at the onset jointing and the beginning of heading with 70 and 20 kg N ha⁻¹. Pests and diseases were chemically controlled.

Treatments and measurements

The respective role of photosynthesis and remobilization processes was investigated by applying 16 different treatments consisting in excising or shading different organs, one week after anthesis (Fig. 1). The global contribution of flag leaf and awns to grain yield was evaluated by excising awns or flag leaves, or both (treatments 5, 9 and 13, respectively). Decrease in yield produced by leaf excision may be due not only to the elimination of a photosynthetic function of this organ, but also to the disappearance of a potential intermediate reserve. The role of whole plant, ears and stem photosynthesis was examined by covering them with aluminium sheet (treatments 4, 2 and 3, respectively). The sheet was holed to prevent accumulation of ethylene and water vapour. Plants of each treatment were harvested at maturity. For each treatment, yield components such as

grain yield per plant (GY), number of filled grains per spike (NFGS) and thousand kernel weight (TKW) were determined and average values across seasons and genotypes were also calculated. The average contribution of stem, flag leaf, chaff and awns photosynthesis and remobilization to grain yield was estimated from different treatments (Table 1). There were 10 rows of plants per plot. The plants were sampled within the eight internal rows to avoid edge effects. Two plants at the same developmental stage were sampled by treatment within each plot.

Carbon isotope discrimination analysis was carried out on the same plants that have been used for the determination of yield components. Thus, grain, stems, chaff, flag

leaves and awns (if not excised) were separated. All samples (including sap samples) were oven dried at 80 °C for 48 h and grounded to a fine powder. In season 2 only, two plants per plot of each treatment were sampled to determine carbon isotope discrimination in cell sap. Chaff, awns, flag leaves (if not excised) and stems were sampled two weeks after anthesis, a stage which corresponds to the onset of the linear phase of grain filling (Carr and Wardlaw 1965). The cell sap was obtained by pressing the organ in a plastic syringe. Carbon isotope composition of samples was performed with an elemental analyser (Carlo Erba, Courtaboeuf, France) coupled to an isotope mass spectrometer (Micromass, Villeurbanne, France) operating in continuous

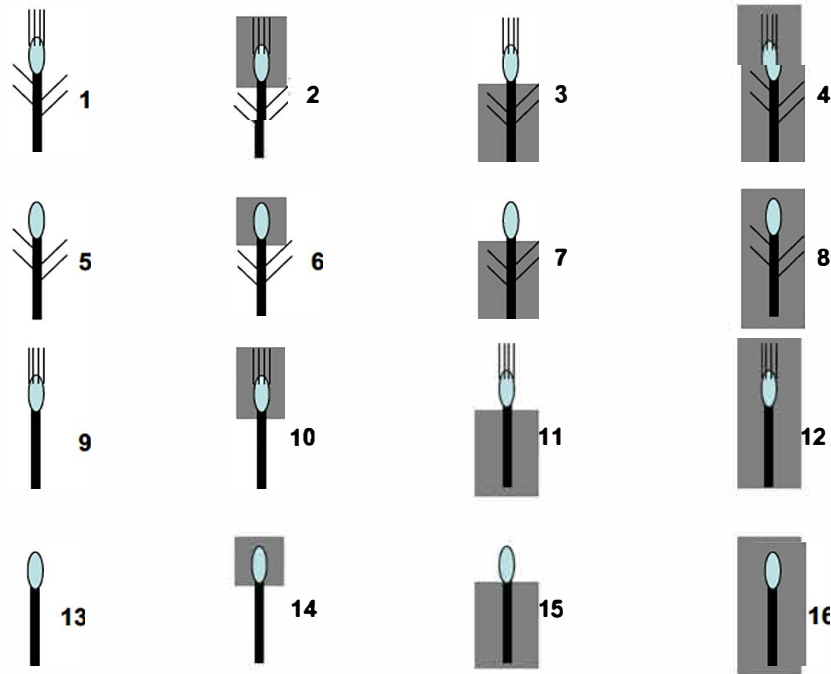


Fig. 1 The different excision and/or shading treatments used to study sink source relations on six durum wheat genotypes grown under field Mediterranean conditions.

Table 1 Relative contribution of photosynthesis and remobilization of the different organs of durum wheat to the grain filling. Numbers in column at right are the treatments (see Fig. 1 for the detail)

Contribution	Organ	Estimation
Photosynthesis	Flag leaf	[(1 3) (9 11)]; [(5 7) (13 15)]
	Ear	(3 4); (11 12); [(1 10) (1 9)]; [(1 12) (1 11)]
	Spike	(7 8); (15 16); [(1 6) (1 5)]; [(1 8) (1 7)]; [(1 14) (1 13)]; [(1 16) (1 15)]
	Awns	[(3 4) (7 8)]; [(11 12) (15 16)]; [(11 15) (12 16)]; [(1 4) (1 3)].
	Stem	(9 11); (13 15); [(1 11) (1 9)]; [(1 12) (1 10)]; [(1 15) (1 13)]; [(1 16) (1 14)]
	Flag leaf	(3 11); (7 15); 8 16; (4 12); [(2 4) (10 12)]; [(6 8) (14 16)]
Remobilization	Ear	(1 2); (9 10)
	Spike	(5 6); (13 14)
	Awns	(2 6); (4 8); (12 16); [(2 14) (2 10)]; [(1 2) (5 6)]; [(9 10) (13 14)]
	Stem	(10 12); (14 16)

flow mode allowing the determination of the isotopic ratio $^{13}\text{C}/^{12}\text{C}$ of the same samples as:

$$\delta^{13}\text{C} (\text{‰}) = [(R \text{ sample}/R \text{ reference} - 1) \times 1000],$$

R being $^{13}\text{C}/^{12}\text{C}$ ratio.

The standard error was 0.1‰. Carbon isotope discrimination (Δ) was calculated using the following formula (Farquhar et al. 1989):

$$\Delta (\text{‰}) = [(\delta a - \delta p) / (1 + \delta p)] \times 1000,$$

where δp is the carbon isotope composition ($\delta^{13}\text{C}$) of the samples and δa , the $\delta^{13}\text{C}$ of the atmospheric CO_2 , -8‰ . Carbon isotope discrimination values in dry matter of stem, flag leaf, chaff, awns and grain were thereafter referred to as ΔS_m , ΔL_m , ΔC_m , ΔA_m and ΔG_m , respectively. Carbon isotope discrimination values in sap (Δ_s) of stem, flag leaf, chaff and awns were referred to as ΔS_s , ΔL_s , ΔC_s and ΔA_s , respectively.

Statistical analysis

All data were subjected to analysis of variance using GLM procedure of SAS. Comparison between different combinations of control, shading and excision was performed using Duncan test at 5 % probability level. The relationships between traits were analysed by single correlation using CORR procedure of SAS.

Results

The results presented hereafter are the mean values of six genotypes and two cropping seasons except for carbon isotope discrimination in cell sap which was measured only in the season 2. There was a broad variation for both grain yield (GY) and thousand kernel weight (TKW) across treatments and a very strong effect of shading and excising treatments on these traits (Table 2). The effect of shading and excision on the number of filled grains per spike (NFGS) was significant, but much lower. TKW was affected more by ear shading than by stem shading (Fig. 2a). GY and TKW were affected more by flag leaf excision than by

awns excision (Fig. 2). The contribution (in per cent of the control, treatment 1) of the different organs to photosynthesis and remobilization, calculated from different treatments, led to different values (Table 3). For example, spike photosynthesis estimated as the difference between treatments 13 (flag leaf and awns excised) and 14 (flag leaf and awns excised and spike shaded) led to a value of 15.3 %, while the estimation based on the difference between treatments 7 (stem and flag leaf shaded, and awns excised) and 8 (whole plant shaded and awns excised) led to a value of 29.7 %. Table 3 shows the ranges obtained for the contribution of each organ. Some ranges were very broad (e.g. photosynthesis of stem, remobilization from flag leaf), but other were quite narrow (e.g. remobilization from stem and spike). By adding the median value of the obtained ranges, we found a total participation (photosynthesis and remobilization) of stem, flag leaf, spike and awns close to 100 % (108.5 %), validating the mode of calculation retained in this study. The major contribution to grain filling came from stem and spike that participated in average (both through photosynthesis and remobilization) for more than 70 % to final grain weight. The participation of the ear (spike and awns) was also very high (more than 60 %). Spike participated more than awns, however, particularly in photosynthesis. The participation of flag leaf (both through photosynthesis and remobilization) was lower than the participation of awns.

Grain carbon isotope discrimination (ΔG_m) varied across treatments and decreased in shading and excision treatments (Table 4). Shading and excision also decreased dry matter Δ in stem and chaff, as well as in awns and flag leaf when present. All what follows has been calculated on the means of 2 seasons. Except for grain, Δ of sap was more affected by shading and excision in sap than in dry matter (Table 4). There was a very strong correlation between GY and TKW ($r = 0.989^{***}$) and a highly significant correlation between ΔG_m and GY across treatments (Table 5). There was also a highly significant correlation between ΔG_m and carbon isotope discrimination in sap of awns

Table 2 F values of the effect of source-sink manipulations on yield and yield components (means of two years and six genotypes). Mean values for each season are also displayed

Year/variation	Effect	Trait		
		Grain yield (g plant ⁻¹)	Thousand kernel weight (g)	Number of filled grains per spike
Season 1		6.38	31.93	37.19
Season 2		6.09	32.76	39.26
Range of variation		2.75 10.49	14.62 46.21	27.42 40.80
Source of variation	Shading effect (S)	362.5**	437.0**	7.0*
	Excision effect (E)	1069.5**	1469.9**	14.6*
	S × E	19.0**	10.1**	5.6**

*P < 0.05, significant at P = 0.05.

**P < 0.001 significant at P = 0.001.

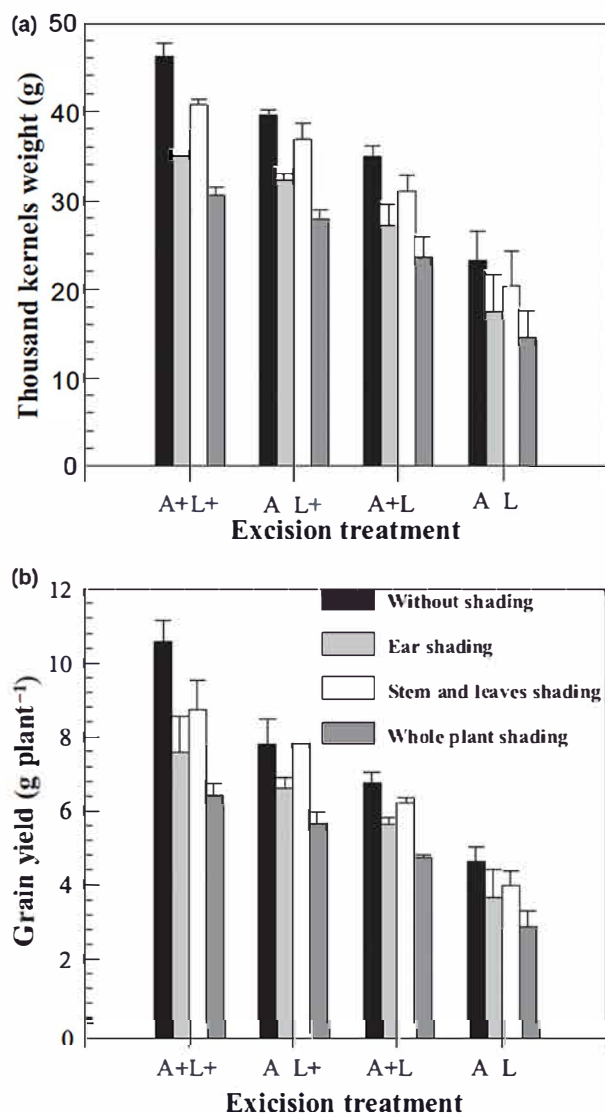


Fig. 2 The mean values of thousand kernel weight (a) and grain yield (b) obtained for each of the sixteen treatments. Average values of six genotypes and two growing seasons under Mediterranean conditions. Vertical bars are standard error. A+ and A are treatments without and with awns excision, respectively. L+ and L are treatments without and with leaves excision, respectively.

(ΔA_s) and chaff (ΔC_s) (Table 5). As a consequence of the association between ΔG_m , GY and TKW, ΔA_s and ΔC_s were also correlated with GY and TKW. Significant but weaker

associations were also noted between carbon isotope discrimination in stem sap (ΔS_s) and ΔG_m and GY. In all organs, carbon isotope discrimination in sap (Δ_s) highly differed from ΔG_m , particularly when Δ was low, *that is* when organs were shaded or excised. In chaff, a significant correlation was found between Δ in sap (ΔC_s) and in dry matter (ΔC_m) (Fig. 3). The relationship was, however, not linear. $\Delta C_m/\Delta C_s$ ratio was maximal in control plants and decreased as Δ decreased.

Discussion

As expected, source sink manipulations performed at anthesis greatly affected TKW and GY (Fig. 2). Significant effect on NFGS (Table 2) indicated, however, that shading or excision can also lead to the abortion of grains, as previously reported by Aggarwal et al. (1990). The respective contribution of photosynthesis and remobilization to grain yield showed a very large variation according to the mode of estimation, as a consequence of the intrusive nature of the treatments as well as physiological compensations that might increase the contribution to grain filling of unaffected photosynthetic organs or of pre anthesis reserves (Aggarwal et al. 1990, Zhu et al. 2004). This evidenced the difficulty to reach a precise evaluation of the contribution of different organs or physiological processes such as photosynthesis and remobilization from source sink manipulations, which deeply modify the plant metabolism (Hannachi et al. 1996, Zhang et al. 2011).

Remobilization of assimilates stored in stem and flag leaf before anthesis accounted for 19.4–29.9 % to final grain yield. In previous studies, pre anthesis assimilate contribution to yield was found to vary from 20 % (Thorne 1982) to 43 % (Gallagher et al. 1976). By estimating this contribution from ^{14}C data, Bidinger et al. (1977) reported values comprised between 12 % and 27 %. Estimations from these authors included, however, the participation of all leaves. Although our experimental conditions did not permit to directly evaluate the contribution of stem to remobilization, our indirect calculation led to a narrow range of value (18.3–21.5 %) and confirmed that stem is the main source of remobilization as suggested by Palta et al. (1994), Seidel (1996) and Zhang et al. (2011). According to these authors, stem reserves could account for 8–25 % of yield. The participation of stem in whole plant photosynthesis

Table 3 Range of variation and median value (between parenthesis) of the contribution (in % of control) of stems, leaves, spikes, and awns and of photosynthesis and remobilization to thousand kernel weight (means of two seasons), calculated from the shading and excision of different organs as presented in table 1

Component	Stem	Leaves	Spike	Awns
Photosynthesis	6.1 21.5 (13.8)	4.1 6.1 (5.5)	15.3 29.7 (22.5)	4.0 13.9 (9.0)
Remobilization	18.3 21.5 (19.9)	1.1 8.4 (4.8)	15.3 19.5 (17.4)	7.8 14.9 (11.4)

Table 4 Mean values of carbon isotope discrimination (Δ) measured in dry matter (average of two seasons and six genotypes) and in cell sap (in season 2, average of six genotypes) of grain (ΔG), stem (ΔS), flag leaf (ΔL), chaff (ΔC) and awns (ΔA) of durum wheat grown under rainfed Mediterranean conditions

Treatment	Dry matter			Cell sap		
	Control	Shading	Excision	Control	Shading	Excision
ΔG (‰)	17.7	16.1	16.2	16.7	15.4	15.5
ΔS (‰)	19.9	19.6	19.6	18.0	17.5	17.5
ΔL (‰)	19.9	19.8	20.0	17.7	17.4	17.3
ΔC (‰)	18.8	18.3	18.5	17.1	16.4	16.6
ΔA (‰)	18.8	18.5	18.6	17.0	16.6	16.6

Table 5 Correlation between grain carbon isotope discrimination, grain yield, thousand kernel weight and sap carbon isotope discrimination of stem, flag leaf, chaff and awns. These traits were measured on six durum wheat genotypes grown under rainfed conditions in Montpellier (south of France) during the cropping season 2 (1996–97). Correlations were calculated across treatments

Trait	Δ_s Chaff (n 16)	Δ_s Stem (n 16)	Δ_s Flag leaf (n 8)	Δ_s Awns (n 8)	ΔG_m (n 16)
Δ Grain	0.86***	0.59*	0.37 ns	0.96***	
Thousand kernel weight	0.80***	0.50 ns	0.51 ns	0.92**	0.88***
Grain yield	0.78***	0.52*	0.47 ns	0.93***	0.90***

*, ** and ***, significance at 0.05, 0.01 and 0.001 probability level, respectively. ns, non significant.

has been scarcely considered. According to Hannachi et al. (1996), it could reach 44 %. In the present study, stem photosynthesis was found to contribute in the range 6.1–21.5 % to grain yield. This evaluation has to be carefully considered, being calculated on plants without leaves. It is possible that photosynthesis and remobilization of stem become more efficient when leaves are removed, thus over estimating the real participation of stem in intact plants. Moreover, Zhang et al. (2011) observed that, under water stressed conditions, ear and peduncle contributed for more than 73 % of grain weight.

Spike and awns were found to have an important participation in photosynthesis (Table 3). In the present experiment, ear shading led to a decrease in grain yield of around 60 %, very similar to that observed by Araus et al. (1993) in durum wheat under Mediterranean conditions (59.0 %). Spike and awns photosynthesis contributed more than flag leaf photosynthesis to grain yield (around 30 % vs. 5 %). Flag leaf photosynthesis is known to decline from anthesis onward, while ear photosynthesis increases up to 15 days after anthesis, the approximate time of onset of the linear phase of grain filling (Martinez et al. 2003). In addition, wheat spike occupies a favourable position for providing photosynthates to the growing grains. Spikes are located near the top of the canopy where light is plentiful and the transport route for carbon products to the grain is short (Kramer and Didden 1981). In the present conditions, the contribution of spike to photosynthesis was much higher than the participation of awns (Table 3). The total participation of awns (photosynthesis and remobilization) was however important (median value of 20.8 %).

Excision of awns was found by Saghir et al. (1968) to result in a 20.8 % yield decrease. In the current experiment, a higher proportion of awns contribution was attributable to remobilization (Table 3).

Similarly to Aggarwal et al. (1990), we observed a remarkably small contribution of flag leaf to final yield. Flag leaf shading resulted in a slight reduction in TKW (around 5 %) compared to data from Araus et al. (1993) and Hannachi et al. (1996) (22.4 % and 30 %, respectively). This discrepancy is probably attributable to differences in environment and genotypes as reported by Sanchez Bragado et al. (2014) who highlighted differences in relative contribution of ear and flag leaf to grain filling. Zhang et al. (2011) showed for example that irrigation affects slightly the contribution of flag leaf to grain yield, and Hannachi et al. (1996) studied mostly non awned bread wheats. In the present study, less than half of the contribution of flag leaf to grain filling was due to remobilization.

The strong correlation across treatments between grain yield and grain carbon isotope discrimination, also reported by Hannachi et al. (1996), suggests the utilization of Δ as an indicator of source sink manipulations effects on grain yield. In control plants, the highest Δ values were found in flag leaf and stem and the lowest in chaff, awns and grain as previously reported in different cereals (Hannachi et al. 1996, Merah et al. 2002, Maydup et al. 2010, Zhu et al. 2010). The ^{13}C enrichment (lower Δ) of ear organs may be attributed to the gradual increase in evaporative demand occurring at the end of the growing cycle under Mediterranean climate, inducing a partial closure of

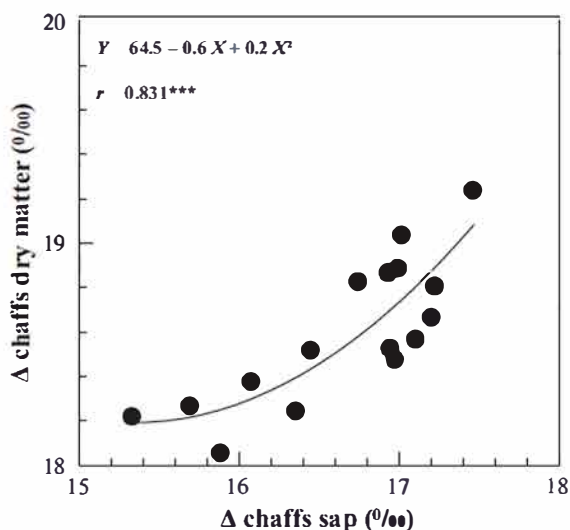


Fig. 3 The relationship between carbon isotope discrimination measured in chaff dry matter and chaff sap across the sixteen treatments of the season 2.

stomata. Stomatal conductance was effectively found by Zhang et al. (2011) to be much lower (and transpiration efficiency higher) in awns and chaff than in flag leaf. In addition to higher stomatal conductance, grain Δ may also reflect a higher dependence on pre anthesis reserves for grain filling. These assimilates were accumulated during periods of reduced stress and consequently have higher Δ . More generally, by considering that isotopic imprints of different organs on grain isotope composition inform on the participation of these organs in grain filling, the relative contribution of the different organs can be evaluated according to the similarity of their Δ value with grain Δ (Araus et al. 1993, Hannachi et al. 1996). The low difference registered in control plants at maturity between grain and chaff Δ compared with difference between grain and leaf Δ suggests that a larger part of the carbon used for grain filling was supplied by the ear than by the flag leaf.

While carbon isotope discrimination and water use efficiency values in dry matter are influenced by both long term stomatal conductance and remobilization (Xu and Zhou 2005, Monneveux et al. 2006, Wu and Bao 2012), determination of carbon isotope discrimination in sap provides information on stomatal conductance and photosynthesis during a short period preceding sampling. In fact, the extracted sap reflects the carbon present in cells corresponding then to recent photosynthetic activity and stomatal conductance (Ninou et al. 2013). In all organs, Δ assessed in sap decreased with shading treatments, as a result of photosynthesis decline (Xu and Ishii 1996). On the other hand, Δ of the different organs was lower, and consequently closer to ΔG_m , when assessed in sap at anthesis

than in dry matter at maturity (Table 4). As dry matter Δ , sap Δ was higher in leaf and stem than in ear organs, such as chaff and awns (Table 4). As chaff and awns represent almost the entire photosynthetic area of ears, the highly significant correlations across treatments between ΔG_m and ΔC_s and ΔA_s confirmed the preponderant role of ear photosynthesis in our experimental conditions (Table 5). They suggested that measuring Δ in the sap of chaff or awns two weeks after anthesis could provide a good estimation of treatments effects on grain yield. The significant association between sap and dry matter Δ in chaff (Fig. 3) indicated that dry matter Δ was highly determined by the photosynthetic activity of this organ. As expected, lower $\Delta C_m/\Delta C_s$ values were noted in treatments strongly affecting photosynthesis and promoting remobilization.

Conclusion

Both source sink manipulations and Δ analysis in different organs allowed estimation of the contribution of different organs to grain yield. Comparisons between shading and excision and between Δ analysis in dry matter and sap permitted to distinguish between carbon supply through photosynthesis and remobilization. Both approaches indicated the importance of spike and awns as providers of carbon products by photosynthesis and the modest contribution of flag leaf to final grain yield under Mediterranean conditions. The approach based on Δ analysis permitted to avoid destructive manipulations and subsequent artefacts and confirmed the major role of ears and awns under post anthesis water stress. It was not able, however, to quantitatively estimate the contribution of all organs. Determining the best tissues and/or compounds to be analysed and the optimal timing of sampling should improve considerably the capacity of this method to estimate the contribution of different organs to grain filling and final yield in durum wheat and other C_3 crops.

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