

The contribution of green plant parts to grain filling of durum wheat under water deficit

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Abstract

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The grain developing and filling are considered as key step for durum wheat yield (*Triticum turgidum*), under water deficit. The present work aimed to evaluate the contribution of green organs to grain filling. Excision and shading the green organs were performed on five genotypes contrasted for their reaction for the water deficit. The experiment was conducted under three water treatments, 100%, 60% and 30% of field capacity. The contribution of current photosynthesis and reserves remobilization in the grain filling, were obtained by excision and shading of plant organs. The results showed that the contribution of each green organ to grain filling was dependent greatly on genotype and also the water supply. The photosynthetic activity of ear and reserves re-mobilization, contributed the largest rates in grain filling. This contribution, mainly the remobilization, increased more in most genotypes under the water deficit. The contribution rate of the current photosynthesis of the flag leaf and awns proved more effective in well-watered conditions. The reserves translocation resulting from the photosynthetic activity of the spike's neck for grain filling were greatly dependent on the genotypes where it was higher in ACSAD1361 and Waha. However, it rose with increasing water deficit.

Keywords: *Triticum turgidum* var. *durum*; grain filling; genetic variation; water supply; photosynthesis; remobilization

Introduction

Drought is one the main abiotic stress that affects the agricultural production in many world regions. In many areas of the Mediterranean region, grain yield of durum wheat is greatly reduced under drought (Giunta et al., 1993; Adda et al., 2005; Tigkas & Tsakiris, 2015). Post-anthesis phase and grain filling period are known as very sensitive to water availability. The occurrence of water deficit during this period reduces greatly the final grain weight by reducing grain

weight (i.e. thousand grains weight). Indeed, water deficit reduces the longevity and organs activity involved in the elaboration of the photo-assimilates necessary for the grain filling (Cruz-Aguado et al., 2000; Foulkes et al., 2007). Availability of assimilates necessary for the grain filling draws their origin from two sources, current photoassimilates produced by green organs and the remobilization of carbohydrates from senescent tissues rises (Cruz-Aguado et al., 1999). The current photosynthesis is mainly provided by the organs located above the last node (Ehdaie et al., 2008; Álvaro et al., 2008).

The implication of the two processes depends on the water supply and genotype (Haberle et al., 2008; Harcha & Calderini, 2014). Under optimal water supply, grain is mostly filled by current photoassimilates provided by green organs. While under drought conditions, grain is mainly filled by remobilized components (Davies & Gan, 2012). The involvement of the organs responsible for these processes include essentially their proximity to the grain, their photosynthetic yield, their longevity and the hydraulic resistance of the conductive tissues to insure the flow of sap (Bijanazadeh & Emam, 2012). The current photosynthesis comes mainly from the organs located above the upper node, such as spike's neck, awns, flag leaf and grain envelopes (Sanchez-Bragado et al., 2014).

Assimilate translocation, mainly fructose throughout the post-anthesis period, is done from accumulated reserves in the stem (Álvaro et al., 2008). Among these organs, the flag leaf occupies an important part, which by its active period during the grain filling; it determines its quality (Khaliq et al., 2008). The involvement of the spike, the spike's neck and the awns in the grain formation was already demonstrated (Araus et al., 1993; Maydup et al., 2010). However, the relative contribution of these organs depends on the conditions of water supply. Under water deficit and high temperature, the relative contribution of ear (spike and awns) photosynthesis to final grain weight is important and varies between 10% and 76% (Araus et al., 2002). Under optimal water conditions, the flag acquires a major role in grain formation and filling (Khaliq et al., 2008).

These studies did not emphasize the environmental and genotype effects on the contribution of different organs to grain filling. Indeed, except the study of Merah et al. (2018), most of these works have been carried out on a reduced number of genotypes and often under uncontrolled water supply conditions. In the present work, these effects were considered. The relative contribution of different plant organs to grain filling was studied in five durum wheat genotypes under three water supply levels (100%FC, 60%FC, 30%FC). Genotypes of different origins were chosen according to their morphological characteristics different and their contrast degrees of behavior under drought conditions.

Materials and Methods

Plant material

Five genotypes of durum wheat (*Triticum durum* Desf.) provided by the Technical Institute of Cereals of Tiaret (Algeria). Two of them, Oued Zenati and Langlois are landraces, while the three others, Waha, Acsad 1361, Mexicali 75, have been introduced from ICARDA, ACSAD and CIMMYT, respectively. Morphological traits are presented in Table 1.

These genotypes were reported as contrasted for their reaction to water deficit (Merah et al., 2001; Adda, 2006).

Experimentation conditions

The experimentation was conducted in a greenhouse on the Faculty of Agronomy of the University of Tiaret (34°04' North and 1°33' East) at 450 km West of Algiers. Disinfected grains sowing and pre-sprouted was carried in PVC cylinders 120 cm long and 25 cm of diameter, filled with homogeneous substrate made up of sand, soil and compost (8:3:1). Each cylinder contained seven plants. Temperature of the greenhouse was been maintained around 25°C (diurnal) and 15°C (nocturnal) and relative humidity at 70%. From the planting until anthesis stage, all the cylinders have been supplied daily with 300 ml of water. The irrigation water has been replaced each week by a commercial nutrient solution type Activeg (Angibaud, La Rochelle, France). At anthesis, irrigation regimes have been separated in three treatments. For the control treatment, the cylinders moisture was maintained at the field capacity (100% FC) until ripening, the two others lots have been conducted at 60% (60% FC) and 30% of field capacity (30% FC) which correspond to a moderate and severe stressed conditions. At each water treatment, each genotype is repeated five times, which makes a total of 25 cylinders per water treatment.

Plants of each water treatment were placed in the same conditions. Sink source relations were modified according the scheme developed by Merah (1999) and Merah et al. (2015). Figure 1 summaries the treatments operated on plants. Excision or shading or both were applied. Excisions were made

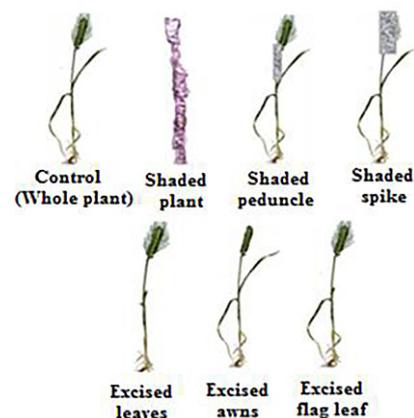


Fig. 1. Sink-source modification scheme used by shading of the photosynthetic organs with aluminum sheet (the peduncle, the ear and shaded plant) and or by excision of vegetative organs (the spike, the flag leaf and the excised leaves)

by cutting flag leaf, all leaves or awns. Shading was done by covering ear neck, spike, or whole plant by aluminum sheet finely perforated in order to alleviate fermentation.

Measurements

At anthesis, plant height, the peduncle, spike, the upper node, the ear lengths were measured as well as the flag leaf area. At maturity the grain diameter, number of kernels per ear and average grain weight were measured.

The contribution rates of excised and shaded organs in the grain filling, has been determined by the method of Maydup et al. (2010) and Merah et al. (2018), Rate of contribution of organs:

$$= \left[\frac{(\text{G}^{\text{Wear of control plant}} - \text{G}^{\text{Wear excised or shaded organ}}) \times 100}{\text{G}^{\text{Wear of control plant}}} \right]$$

Statistical analysis

The results of the measurements were analyzed using Statistica 8.0 software (StatSoft, Inc.). Differences in all measured parameters were determined by ANOVA. Mean comparison were released by using Duncan test at 0.05 probability level.

Results

Variation of morphological traits of tested genotypes

The morphological traits of the used genotypes are presented in Table 1. The results obtained show the height of the plant, the length of the upper internode, the peduncle length,

the length of the ear, flag leaf surface and the length of the spike are significantly different between the studied genotypes (Table 1). Langlois was the tallest genotype and ACSAD 1361 and Mexicali were the shortest ones. The longest upper internode and spike's neck were recorded by Waha and shortest ones by Langlois.

Effect of water supply and sink-source modification on final grain weight and grain filling

The results show that the final grain weight depends on genotypes, water supply and the treatment shading-excision (Table 2). In the control treatment and under optimal water supply (100% FC), the range of variation between extreme genotypes was about 11mg which represented nearly $\frac{1}{4}$ of the average grain weight of all genotypes (Table 3). For the same treatment leads to 60%FC, the grain weight decreases significantly with values ranging from 9% (Langlois) to 18% (Oued Zenati). This reduction is more marked at 30%FC where the highest value was recorded by Oued Zenati with 39% compared with well-watered conditions (100%FC). In the same water conditions, the lowest value was found in ACSAD 1361 with 21%.

The excision or shading of plant organs through the different treatments led to significant decrease of the final grain weight (Table 3). However, this reduction depends on the cultivars and the water supply levels. Among all treatments, the spike and whole plant shaded caused the largest reductions of grain weight in all water conditions (Table 3). This indicates that spike photosynthesis and reserves re-mobiliza-

Table 1. The main morphological traits of the five studied genotypes of durum wheat cultivated under three water conditions

Genotypes	PH	UIL	PL	SL	FLA, cm ²	AL
ACSAD 1361	85.65 ^a	40.59 ^a	21.65 ^a	8.82 ^b	34.94 ^c	10.86 ^a
Langlois	148.07 ^c	44.28 ^a	18.20 ^b	9.98 ^c	46.57 ^d	16.26 ^c
Mexical 75	87.84 ^a	40.25 ^a	22.43 ^b	8.35 ^a	37.62 ^a	12.66 ^b
Oued Zenati	147.51 ^c	43.80 ^b	22.32 ^b	8.33 ^a	39.71 ^b	13.27 ^b
Waha	94.68 ^b	40.33 ^b	22.67 ^b	8.47 ^a	38.39 ^{ab}	10.58 ^a
F values	656.97***	12.44***	10.87***	93.16***	58.17***	36.35***

PH: plant height, UIL: length of the upper internode, PL: peduncle length, AL: awns length, FLA: Flag leaf surface, SL: Spike length. Means followed by a different letter are significantly different by Duncan's test at $p < 0.05$

Table 2. Effect of genotypes, water supply and treatments (shading and/or excision) on the final grain weight and the relative contribution of different organs on the grain filling

	Cultivar	Water supply	Treatment	Cultivar x water supply	Cultivar x treatment
Final kernel weight	972.3***	2764.9***	2386.6***	32.2***	25.5***
Relative contribution	196.16***	4.03**	3209.02***	26.26***	46.87***

*** Significant at 0.001 of probability; ** Significant at 0.01; * not significant

Table 3. The average grain weight (mg) obtained in the different treatments (shading/excision) and under three water supplies (100%FC, 60%FC, 30% FC) of five tested genotypes

Cultivars	WS	SSP	SS	EA	SP	EFL	EL	CP
	30%FC	27.15	17.86	34.14	17.73	29.50	28.61	36.05
ACSAD1361	60%FC	31.59	19.78	35.98	19.30	31.14	31.01	39.29
	100%FC	37.06	29.31	36.63	25.29	35.22	34.65	45.48
	30%FC	25.80	14.31	29.80	17.54	29.99	27.21	36.01
Waha	60%FC	30.08	26.20	34.01	20.69	33.56	30.38	40.86
	100%FC	42.70	32.06	41.15	24.12	37.94	34.26	47.46
	30%FC	24.83	16.61	27.14	12.87	26.28	25.63	32.11
Oued Zenati	60%FC	41.28	23.94	35.18	15.20	32.68	33.61	43.27
	100%FC	51.12	30.39	39.40	15.35	36.57	36.22	52.73
	30%FC	36.77	26.26	36.75	23.92	39.66	36.72	41.75
Langlois	60%FC	45.48	34.36	46.32	29.18	41.75	40.62	51.11
	100%FC	52.72	38.02	54.10	31.42	45.03	42.93	56.43
	30%FC	29.55	21.85	29.35	11.98	27.46	26.99	33.43
Mexicali75	60%FC	38.05	23.08	37.84	16.08	34.77	33.00	42.84
	100%FC	44.12	25.23	44.95	22.37	37.84	36.72	47.82

(SSP: shaded peduncle; SS: shaded spike; EA: excised awns; SP: shaded plant; EFL: excised flag leaf; EL: excised leaves; CP: control plant)

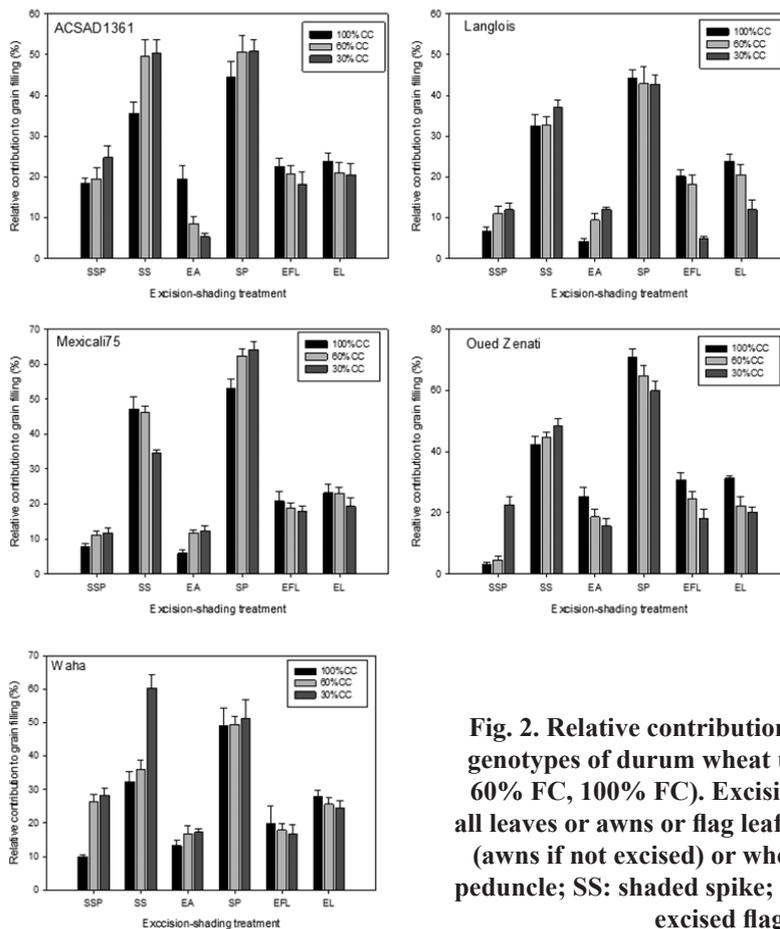


Fig. 2. Relative contribution of different organs to grain filling of five genotypes of durum wheat under three water supply levels (30% FC, 60% FC, 100% FC). Excision treatments were performed by cutting all leaves or awns or flag leaf. Shading was done by darkening of spikes (awns if not excised) or whole plant or spike peduncle. (SSP: shaded peduncle; SS: shaded spike; EA: excised awns; SP: shaded plant; EFL: excised flag leaf; EL: excised leaves)

tion is the main sources of grain filling. Its respective average contribution at 100% FC was respectively 38% and 52.36%. These rates are more accentuated at 60% FC and 30% FC to reach respectively the values of 41.8%, 54% and 46.1%, 53.7%. The contribution of these two pathways in grain filling also differs among genotypes and particularly in water supply of 30% CC. Thus, the contribution of spike photosynthetic activity (Figure 2) varies between 34.7% (Mexicali 75) and 60.2% (Waha) and reserves re-mobilization values are between 42.7% (Langlois) and 64.1% (Mexicali 75).

The contribution of the spike peduncle varies significantly among genotypes and water situations. Its contribution increases progressively with the decrease of the water supply level, it records values of 9.2%, 14.5% and 19.8% in the water treatments of 100% FC, 60% FC and 30% FC, respectively. In this water treatment (30% FC), the highest value of this contribution is recorded at Waha with 28.3%. A contrary tendency has been noted of the awns contribution in the grain filling. Thus, it decreases with the water deficit increase. It records average values of 13.6%, 12.9% and 10.9% respectively at the level of the water treatments of 100% CC, 60% CC and 30% CC.

Finally, the different foliage stages have contribution rates ranging from 14% to 27%. Among all leaves, the flag leaf holds shares varying between 80% and 90%. The values of its involvement in the grain filling vary, through different water treatments (Figure 2), between 14.7% (100% FC) and 27.1% (30% FC).

Discussion

Filling determines the development of grain weight and quality in durum wheat. However, it's frequently subjected to environmental constraints especially to drought. Water deficit prevailing during post-anthesis phases could affect negatively the grain filling processes. The grain weight could be significantly reduced if the wheat plants are exposed to a short period of water deficit (Nezhad et al., 2012; Farooq et al., 2014). This trait (thousand kernels weight) has been reported as the most sensitive yield component to water supply variations at the post-anthesis stage, in durum wheat (Ivanova & Tsenov, 2011). These studies confirm the results recorded here, which showed that the increase in the water deficit was accompanied by a significant reduction in the thousand kernel weight at maturity.

However, this effect was related to genotypes effect. Indeed, the application of the moderate water deficit (60% FC) caused a decrease in the TKW and reached 9% in Langlois and twice more marked in Oued Zenati genotype (Figure 2). The accentuation of the water deficit (30% FC) reduced

more TKW that fluctuated between the values of 39% (Oued Zenati) and 21% (ACSAD1361). The water deficit effect on the final grain weight is mainly explained by a reduction in its size and a disruption of reserves migration. So, drought and high temperatures greatly reduce the size of the durum wheat grain. This effect is explained by an inhibition of cell division and the organization of the reserve accumulation tissue (Schnyder & Baum, 1992; Calderini et al., 2000). After the differentiation of the seed reserve parenchyma, the water deficit effect on its filling depends on the availability of assimilates and their migration to the grain. This process therefore depends on the activity and longevity of the provider organs that are involved in photoassimilates production and storing. The remobilization of the stem reserves presents the ultimate way for the grain filling. Its relative contribution holds values ranging from 44.05% up to 70.49%. Variations in these values were dependent on water supply and genotypes tested. For example, for Oued Zenati, the relative contribution of stem to grain filling increases with the decrease of water supply (Figure 2).

For the other genotypes, they held high values but whatever the water regimes. The role of stem re-mobilization in grain filling has been reported by several studies (Cruz-Aguado et al., 2000; Tambussi et al., 2007), that Ehdaie et al. (2008), have shown that the rate of this contribution varies between 10% and 50%, according to the genotype and the water supply. Other studies have noticed that stem contributes more to grain filling under drought conditions (Monneveux et al., 2006; Lopes et al., 2006). Our results did not find a relationship between the plant height and the ability of stem reserves re-mobilization for grain filling as already. The same relations were described by Tatar et al. (2016).

The ear shading caused a significant decrease in TKW (Figure 2). This is explained by its important relative contribution in the grain filling, which hold the second position after that ensured by the stem reserves re-mobilization. This contribution is justified by its photosynthetic activity ensured during the grain formation and filling and its proximity to grain. The spike contribution was observed in all three water conditions. However, in ACSAD1361, Langlois and Waha, the relative contribution of the spike increases with the decrease of water availability.

Thus, in the Waha genotype it recorded values of 32.37%, 35.91% and 60.21% in 100%, 60% and 30% FC, respectively. The role of the spike is explained by its longevity (photosynthesis activity duration), particularly under drought conditions. Indeed, Mohammady et al. (2009) show that grain envelopes are less sensitive to the drought effects, thanks to their higher osmotic adjustment capacity than other organs. Arous et al. (1993) have demonstrated that in triticale, the

different spike parts ensure the availability of a large part of photosynthesis products, essential for the grain filling.

Awns are one of the spike constituents whose relative contribution has been studied separately. Its involvement in grain filling remains relatively weak and depends greatly on genotypes and the water supply (Abbad et al., 2004; Merah & Monneveux, 2015; Merah et al., 2018).

The ear contribution depends on its surface and probably on its photosynthetic yields (Wang & Shangquan, 2015; Sanchez-Bragado et al., 2016; Ding et al., 2018). In fact the important contribution of the ear to grain filling would be ensured essentially by seeds and their envelopes.

Our results showed that the contribution of the flag leaf decreases with the decline of water supply levels (Figure 2). Indeed, the lowest contribution of flag leaf to grain filling was observed at 30%FC (Figure 2). This trend could be explained by the effect of the water deficit which decreases the longevity of this organ (Martinez et al., 2003; Merah et al., 2018).

The photosynthetic activity of the stem also ensures the availability of assimilates essential for the grain filling. Among, the different parts of the stem, the exposed peduncle (spike's neck) is of great interest because its contribution is accentuated in dry conditions. So, Lingan et al. (2010) had suggested that the exposed peduncle is a photosynthetically active organ that produces photosynthates and thereby makes a crucial contribution to grain growth, particularly during the late stages of grain-filling. Also, Takahashi et al. (2001) and Esmailpour – Jahromi et al. (2012) had reported that Assimilated carbon during vegetative and early reproductive growth in wheat is temporarily stored in stem internodes and leaf sheaths (LSs), and can later be remobilized and transported to developing grain.

Conclusion

The results obtained by the present work showed that the declaration of water deficit after the post-anthesis phase considerably reduces the grain final weight. The contributions of different organs with the current photosynthesis and re-mobilization depend on genetic factors and the water supply.

References

- Abbad, H., El Jaafari, S., Bort, J. & Araus, J. L. (2004). Comparison of flag leaf and ear photosynthesis with biomass and grain yield of durum wheat under various water conditions and genotypes. *Agronomie*, 24 (1), 19-28.
- Adda, A. (2006). Study of drought adaptation mechanisms in durum wheat (*Triticum durum* Desf.). Doctoral dissertation, Es-senia University of Oran Algeria.
- Adda, A., Mohamed, S., Meriem, K. H. & Merah, O. (2005). Impact of water deficit intensity on durum wheat seminal roots. *Comptes Rendus Biologies*, 328 (10), 918-927.
- Álvarez, F., Royo, C., Garcíadel Moral, L. F. & Villegas, D. (2008). Grain filling and dry matter translocation responses to source-sink modifications in a historical series of durum wheat. *Crop Science*, 48 (4), 1523-1531.
- Araus, J. L., Brown, H. R., Febrero, A., Bort, J. & Serret, M. D. (1993). Ear photosynthesis, carbon isotope discrimination and the contribution of respiratory CO₂ to differences in grain mass in durum wheat. *Plant Cell & Environment*, 16 (4), 383-392.
- Araus, J. L., Slafer, G. A., Reynolds, M. P. & Royo, C. (2002). Plant breeding and drought in C3 cereals: what should we breed for? *Annals of Botany*, 89 (7), 925-940.
- Bijanzadeh, E. & Emam, Y. (2012). Evaluation of assimilate remobilization and yield of wheat cultivars under different irrigation regimes in an arid climate. *Archives of Agronomy and Soil Science*, 58 (11), 1243-1259.
- Calderini, D. F., Abeledo, L. G. & Slafer, G. A. (2000). Physiological maturity in wheat based on kernel water and dry matter. *Agronomy Journal*, 92 (5), 895-901.
- Cruz-Aguado, J. A., Reyes, F., Rodes, R., Perez, I. & Dorado, M. (1999). Effect of Source-to-sink Ratio on Partitioning of Dry Matter and ¹⁴C-photoassimilates in Wheat during Grain Filling. *Annals of Botany*, 83 (6), 655-665.
- Cruz-Aguado, J. A., Rodés, R., Pérez, I. P. & Dorado, M. (2000). Morphological characteristics and yield components associated with accumulation and loss of dry mass in the internodes of wheat. *Field Crops Research*, 66 (2), 129-139.
- Davies, P. J. & Gan, S. (2012). Towards an integrated view of monocarpic plant senescence. *Russian Journal of Plant Physiology*, 59 (4), 467-478.
- Ding, H., Liu, D., Liu, X., Li, Y., Kang, J., Lv, J. & Wang, G. (2018). Photosynthetic and stomatal traits of spike and flag leaf of winter wheat (*Triticum aestivum* L.) under water deficit. *Photosynthetica*, 56 (2), 687-697.
- Ehdaie, B., Alloush, G. A. & Wainies, J. G. (2008). Genotypic variation in linear rate of grain growth and contribution of stem reserves to grain yield in wheat. *Field Crops Research*, 106 (1), 34-43.
- Esmailpour-Jahromi, M., Ahmadi, A., Lunn, J. E., Abbasi, A., Poustini, K. & Joudi, M. (2012). Variation in grain weight among Iranian wheat cultivars: the importance of stem carbohydrate reserves in determining final grain weight under source limited conditions. *Australian Journal of Crop Science*, 6 (11), 1508-1515.
- Farooq, M., Hussain, M. & Siddique, K. H. M. (2014). Drought stress in wheat during flowering and grain-filling periods. *Critical Reviews in Plant Sciences*, 33 (4), 331-349.
- Foulkes, M. J., Sylvester-Bradley, R., Weightman, R. & Snape, J. W. (2007). Identifying physiological traits associated with improved drought resistance in winter wheat. *Field Crops Research*, 103 (1), 11-24.
- Giunta, F., Motzo, R. & Deidda, M. (1993). Effect of drought on yield and yield components of durum wheat and triticale in

- a Mediterranean environment. *Field Crops Research*, 33 (4), 399-409.
- Haberle, J., Svoboda, P. & Raimanov, I.** (2008). The effect of post-anthesis water supply on grain nitrogen concentration and grain nitrogen yield of winter wheat. *Plant, Soil and Environment*, 54 (7), 304-312.
- Harcha, C. I. & Calderini, D. F.** (2014). Dry matter and water dynamics of wheat grains in response to source reduction at different phases of grain filling. *Chilean Journal of Agriculture Research*, 74 (4), 380-390.
- Ivanova, N. & Tsenov, N.** (2011). Winter Wheat productivity under favorable and drought environments' an overall effect. *Bulgarian Journal of Agricultural Science*, 17 (6), 777-782.
- Khaliq, I., Irshad, A. & Ahsan, M.** (2008). Awns and flag leaf contribution towards grain yield in spring wheat (*Triticum aestivum* L.). *Cereal Research Communications*, 36 (1), 65-76.
- Lingan, K., Fahong, W., Bo, F., Shengdong, Li., Jisheng, S. & Bin, Z.** (2010). The structural and photosynthetic characteristics of the exposed peduncle of wheat (*Triticum aestivum* L.): an important photosynthate source for grain-filling. *BMC Plant Biology*, 10 (141), 1-10.
- Lopes, M. S., Cortadellas, N., Kichey, T., Dubois, F., Habash, D. Z. & Araus, J. L.** (2006). Wheat nitrogen metabolism during grain filling: comparative role of glumes and the flag leaf. *Planta*, 225 (1), 165-181.
- Martinez, D. E., Luquez, V. M., Bartoli, C. G. & Guiamét, J. J.** (2003). Persistence of photosynthetic components and photochemical efficiency in ears of water-stressed wheat (*Triticum aestivum*). *Physiologia Plantarum*, 119 (4), 519-525.
- Maydup, M. L., Antonietta, M., Guiamet, J. J., Graciano, C., López, J. R. & Tambussi, E. A.** (2010). The contribution of ear photosynthesis to grain filling in bread wheat (*Triticum aestivum* L.). *Field Crops Research*, 119 (1), 48-58.
- Merah, O.** (1999). Use of carbon isotope discrimination for drought tolerance improvement in durum wheat (*Triticum durum* Desf.) in Mediterranean regions. Doctoral dissertation, National Institute of Agronomic Sciences of Rennes, France.
- Merah, O., Deléens, E. & Monneveux, P.** (2001). Relationships between flag leaf carbon isotope discrimination and several morphophysiological traits in durum wheat under Mediterranean conditions. *Environmental and Experimental Botany*, 45 (1), 63-71.
- Merah, O. & Monneveux, P.** (2015). Contribution of different organs to grain filling in durum wheat under Mediterranean conditions. I-Contribution of post-anthesis photosynthesis and re-mobilization. *Journal of Agronomy and Crop Science*, 201 (5), 344-352.
- Merah, O., Evon, P. & Monneveux, P.** (2018). Participation of green organs to grain filling in *Triticum turgidum* var. durum grown under Mediterranean conditions. *International Journal of Molecular Sciences*, 19 (56), 1-14.
- Mohammady, S., Arminian, A., Khazaie, H. & Kozak, M.** (2009). Does water-use efficiency explain the relationship between carbon isotope discrimination and wheat grain yield. *Acta Agriculturae Scandinavica, section B-Soil & Plant Science*, 59 (4), 385-388.
- Monneveux, P., Rekika, D., Acevedo, A. & Merah, O.** (2006). Effect of drought on leaf gas exchange, carbon isotope discrimination, transpiration efficiency and productivity in field grown durum wheat genotypes. *Plant Science*, 170 (4), 867-872.
- Nezhad, K. Z., Weber, W. E., Röder, M., Sharma, S. S., Lohwasser, U., Meye, R. C., Saal, B. & Börner, A.** (2012). QTL analysis for thousand-grain weight under terminal drought stress in bread wheat (*Triticum aestivum* L.). *Euphytica*, 186 (1), 127-138.
- Sanchez-Bragado, R., Moleró, G., Reynolds, M. P. & Araus, J. L.** (2014). Relative contribution of shoot and ear photosynthesis to grain filling in wheat under good agronomical conditions assessed by differential organ $\delta^{13}\text{C}$. *Journal of Experimental Botany*, 65 (18), 5401-5413.
- Sanchez-Bragado, R., Moleró, G., Reynolds, M. P. & Araus, J. L.** (2016). Photosynthetic contribution of the ear to grain filling in wheat: a comparison of different methodologies for evaluation. *Journal of Experimental Botany*, 67 (9), 2787-2798.
- Schnyder, H. & Baum, U.** (1992). Growth of the grain of wheat (*Triticum aestivum* L.). The relationship between water content and dry matter accumulation. *European Journal of Agronomy*, 1 (2), 51-57.
- Takahashi, T., Chevalier, P. M. & Rupp, R. A.** (2001). Storage and remobilization of soluble carbohydrates after heading in different plant parts of a winter wheat cultivar. *Plant Production Science*, 4 (3), 160-165.
- Tambussi, E. A., Bort, J., Guiamet, J. J., Nogués, S. & Araus, J. L.** (2007). The photosynthetic role of ears in C3 cereals: metabolism, water use efficiency and contribution to grain yield. *Critical Reviews in Plant Sciences*, 26 (1), 1-16.
- Tatar, Ö., Brück, H. & Asch, F.** (2016). Photosynthesis and remobilization of dry matter in wheat as affected by progressive drought stress at stem elongation stage. *Journal of Agronomy and Crop Sciences*, 202 (4), 292-299.
- Tigkas, D. & Tsakiris, G.** (2015). Early estimation of drought impacts on rainfed wheat yield in Mediterranean climate. *Environmental Processes*, 2 (1), 97-114.
- Wang, L. & Shangguan, Z.** (2015). Photosynthetic rates and kernel-filling processes of big-spike wheat (*Triticum aestivum* L.) during the growth period. *New Zealand Journal of Crop and Horticultural Science*, 43 (3), 182-192.

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