



The contribution of the awns of bread wheat (*Triticum aestivum* L.) to grain filling: Responses to water deficit and the effects of awns on ear temperature and hydraulic conductance

M.L. Maydup, M. Antonietta, C. Graciano, J.J. Guamet, E.A. Tambussi*

Instituto de Fisiología Vegetal (INFIVE), Universidad Nacional de La Plata—CONICET, cc 327, Diagonal 113 y 61, 1900 La Plata, Buenos Aires, Argentina

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ABSTRACT

The awns of the ear have been reported as important sources of assimilates in wheat. However, their actual importance in grain filling is not well known. We examined several aspects of the awns and their role in the grain filling, and the objectives of this work were: (i) to study their photosynthetic activity during grain filling, comparing flag leaf, ear body and awns in two cultivars differing in ear contribution to grain filling, (ii) to estimate the influence of awns on the temperature and the hydraulic conductance of the ear, (iii) to analyze the response of the flag leaf versus awns to water deficit, particularly regarding relative water content and photosynthetic activity, (iv) to analyze if there is a correlation between awn size versus ear and awn contribution to the grain filling in six modern Argentinean cultivars, and, (v) to explore if awn size and awn contribution have changed during the past century, analyzing old and modern Argentinean cultivars. In this paper we show that: (1) during late grain filling, ear parts (particularly the body of the ear) maintained a higher photosynthetic activity than the flag leaf, (2) awns showed some 'tolerance' to water deficit, maintaining a higher relative water content and electron transport rate than the flag leaf under drought, (3) awns increase water conductance of the ear (particularly in the cv. K. Escudo), decrease the ear temperature during the morning, but increase ear temperature after midday (4) there is a moderately positive relationship between awn size and contribution of the ear to grain filling, and (5) in the retrospective analysis we did not find a clear tendency in awn size and awn contribution to grain filling along the years. However, in general terms modern cultivars seem to have a higher awn contribution (and higher awns size) than old ones.

In summary, awns may have positive (increased photosynthetic area and activity, tolerance to drought) and negative (increased ear temperature) effects on grain filling, and their final impact on yield will depend on the interaction between these effects and prevailing environmental conditions.

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1. Introduction

In winter cereals (e.g. wheat, barley) three main sources of assimilates contribute to grain filling (i) the photosynthesis of the flag leaf (ii) retranslocation of pre-anthesis assimilates, mainly fructans accumulated in the stem and (iii) photosynthesis of the green parts of the ear (Araus et al., 1993; Maydup et al., 2010) such as bracts (glumes, lemmas) and the green layer of the pericarp. The relative importance of each of these sources of assimilates is not completely known, but there is evidences that it varies depending on the species, the cultivar and the environment (see Tambussi

et al., 2007). For instance, barley (*Hordeum* sp.) has small flag leaves compared with wheat, and presumably their relative contribution to grain filling might be lower. On the other hand, under stressful conditions (e.g. post anthesis water deficit), when leaf photosynthesis declines, retranslocation is a relevant mechanism to cope with the environmental restriction (e.g. Blum, 1998; Ehdaie et al., 2006). The quantitative role of ear photosynthesis in grain filling is less known, but several studies indicate that it is important in conditions of decreased leaf photosynthesis (e.g. Maydup et al., 2010; see references in Tambussi et al., 2007) and it seems to have increased in modern cultivars of Argentinean wheat (Maydup et al., 2012). It is widely accepted that source limitations are not present in old cultivars of wheat (Kruk et al., 1997; Borrás et al., 2004). In modern germplasm, however, source limitation could be emerging (e.g. Álvaro et al., 2008). In this context, assimilates fixed by green organs of the ear (e.g. awns) may become more relevant to sustain grain

* Corresponding author. Tel.: +54 221 4236618; fax: +54 221 4233698.
E-mail address: tambussi35@yahoo.es (E.A. Tambussi).

filling. There are several apparent advantages of the ear as a photosynthetic organ. For example, ear photosynthesis is tolerant to water deficit (e.g. Tambussi et al., 2005, 2007), and although the mechanistic basis for this is not clear, ear parts are able to keep a higher capacity for osmotic adjustment, and a higher relative water content than leaves under drought.

Awns, filiform and sclerophyllous prolongations of the lemmas, have been reported as important sources of assimilates in winter cereals (e.g. in barley, Biscoe et al., 1973; Bort et al., 1994; in wheat, Li et al., 2006). The contribution of awns to total ear net photosynthesis is high, reaching 50% or more in some cases (see Tambussi et al., 2007 and references cited therein). In general, awns seem to be more important in *Hordeum* than *Triticum*, and in durum (*Triticum turgidum* var. *durum*) than bread (*Triticum aestivum*) wheat (Blum, 1985). In barley (with long awns), awn photosynthesis may account for 90% of total ear net photosynthesis (Biscoe et al., 1973; Ziegler-Jöns, 1989). Hexaploid bread wheat has shorter awns than tetraploid durum wheat (Blum, 1985), thus, increasing awn size might be particularly relevant in bread wheat to increase the ear contribution to grain filling.

Because of the peculiar structure of the awn, its photosynthetic activity has been little studied (e.g. Lu and Lu, 2004). Modern techniques such as modulated chlorophyll fluorescence are useful to assess indirectly the photosynthetic activity during grain filling. In this study we used chlorophyll fluorescence to compare the photosynthetic activity of awns, the body of the ear and the flag leaf during the grain filling in well watered *versus* water stressed plants.

Besides their photosynthetic contribution, awns may influence ear temperature. In addition to general physiological effects (e.g. on photorespiration or senescence), ear temperature could have a direct impact on grain filling. It is well known that above 15 °C, each °C extra is deleterious in terms of grain weight in winter cereals such as barley and wheat (e.g. Savin, 2010). There is contradictory data in the literature regarding the influence of awns on ear temperature, since the presence of awns has been reported either to increase ear temperature (Panozzo et al., 1999) or to cool the canopy (Motzo and Giunta, 2002). The reason for the discrepancies between these studies is unknown, although these could be accounted for by environmental differences or methodological aspects. In the present work, we measured the ear temperature in intact and de-awned ears during the course of the day, to evaluate whether the influence of the awn on ear temperature is dependent on time of the day and solar angle. Hydraulic influences of the awn (possibly linked with the potential transpiration rate and thus, with cooling effects) over the ear have not been previously studied.

The actual impact of the presence/absence of awns (or the importance of awn length) in grain filling is controversial (see Tambussi et al., 2007). In fact, positive (Martin et al., 2003; Motzo and Giunta, 2002; Weyhrich et al., 1994), neutral (depending on the genotype, Martin et al., 2003) or even negative (McKenzie, 1972) effects on grain yield has been reported. Also, there are no studies analyzing the correlation between awn size and their contribution to grain filling. In addition, the issue of whether breeding affected the contribution of the awns to grain filling has not received attention.

In summary, the objectives of this work were: (i) to study the photosynthetic activity (*i.e.* photosynthetic electron transport rate, ETR, measured by modulated chlorophyll fluorescence) of the flag leaf, ear body (*i.e.* glumes) and awns in two cultivars differing in ear contributions to grain filling, (ii) to estimate the influence of the presence/absence of awns on the hydraulic conductance and the temperature of the body of the ear; (iii) to analyze the response of the flag leaf *versus* awns to water deficit (iv) to determine if awn size correlates with awn/ear contribution to grain filling in six modern cultivars of Argentinean wheat differing in this trait and (v) to explore if awn size and awn contribution to grain filling

were affected by breeding during the past century (retrospective study).

2. Material and methods

2.1. Experiment 1. Photosynthetic activity of the flag leaf, body of the ear and awns

Seeds of bread wheat cvs. BioINTA 3000 and Klein Escudo (named simply as 'K. Escudo') were planted on June 29 2008 in La Plata, (34°54'24"S; 57°55'56"W, Argentina) in the Experimental Field of Facultad de Ciencias Agrarias y Forestales (Universidad Nacional de La Plata). These cultivars were chosen because of their contrasting ear morphology (awn length), and similar phenology (days to anthesis). In addition, we found that the photosynthetic contribution of the ear (including awns) to grain filling is higher in cv. Klein Escudo than in cv. BioInta 3000 (Maydup et al., 2010). The cultivars were planted in plots (1 × 3.4 m per plot; five rows, 20 cm apart). Sowing density was ca. 260 plants per m². Plots were arranged in randomized blocks with three replicates. The soil was a Typic Argiudoll (USDA classification). Fertilization was applied as 100 kg ha⁻¹ of diammonium phosphate immediately after sowing and as urea (250 kg ha⁻¹) 75 days after sowing, near tillering. Emergence took place on July 17. This experiment was carried out under rainfed conditions during the wheat growing season. Rainfall from April to June was 120 mm. Rainfall from sowing to harvest was 121 mm.

2.1.1. Modulated chlorophyll fluorescence: Electron transport rate (ETR)

Modulated chlorophyll fluorescence of the flag leaf, ear body (mainly glumes and non-covered areas of the lemmas) and awns was measured with a fluorimeter (FMSII, Hansatech, UK). For each cultivar and plot, four ears and their respective flag leaves were measured at 3, 17 and 24 days after anthesis. Measurements were made at midday on sunny days at *in situ* photosynthetically active photon flux density (PPFD) conditions in the normal position of each organ, between 11:00 and 15:00 h, alternating between cultivars to avoid the bias due to time of measurement. In the case of awns, several awns of each ear were placed in the clip of the fluorimeter. In all cases, measurements were taken after reaching a steady-state value of basal fluorescence. Effective quantum yield of photosystem II was measured by the saturating pulse method and photosynthetic electron transport rate (ETR) was calculated as in Rosenqvist and van Kooten (2003).

2.2. Experiment 2. Analysis of daily thermal patterns in the ear: Role of awns

2.2.1. Thermal daily pattern in intact and de-awned ears

The daily course of temperature in control (intact) and de-awned ears was measured in 2011 in an experimental setup very similar to Experiment 1 (rainfall from April to June was 242 mm and rainfall from July (sowing) to harvest was 376 mm). Measurements were made with copper-constantan thermocouples 'T' TC1047A (Microchip Inc.) and the data were recorded with a TC-Logger 16 (www.cavadevices.com). Thermocouples were inserted underneath the glumes in central spikelets of the ear of cv. Klein Escudo and cv. BioInta 3000. De-awning was performed with scissors. Four replicate (ears) were measured in each treatment and cultivar. In order to avoid a spatial bias, the sensors were placed in pairs, *i.e.* in two ears close to each other, comprising one intact and one de-awned ear in each pair. The daily pattern of temperature was recorded during several days.

2.2.2. Hydraulic conductance of intact and de-awned ears

Hydraulic conductance (K) of ears was measured with the low-pressure steady-state flow meter (SSFM) method, which uses the drop in pressure across a tube of known conductance to measure the flow rate into the ear, and, together with the pressure at the peduncle insertion point, to calculate K ($\text{kg of water h}^{-1} \text{MPa}^{-1}$) (Brodrick and Feild, 2000). In brief, it consists of a hydraulic head (near 0.005 MPa) filled with de-gassed distilled water, a tube of known resistance and a pressure sensor that allows to calculate the flow of water through the ear. The peduncle was cut under water leaving 3 cm length and was fitted to the system with a silicon tube. Water enters through the peduncle, moves along the ear and passes to the atmosphere through the stomata. First, K of the intact ear was measured. Then all the awns were cut and K of the de-awned ear was measured. Five ears of each cultivar (Klein Escudo and BioInta 3000) were analyzed. In order to permit stomata opening, the ears were irradiated with $300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (dichroic lamp) during the measurements. Measurements were recorded after flow was stable at least for 5 min. Finally, the ears were dried to constant weight. Total dry mass of the ear was used to analyze if differences in K between cultivars covaried with the size of the ear. It is important to note that this measurement reflects the capacity of the organ to move water along it. The movement of water from the hydraulic head source to the ear starts immediately after the spike is connected to the system due to the negative potential of the tissues that demand water. As the stomata are open, after a short time a constant flux is achieved and the tissue is stabilized at a certain water potential. If the transpiration rate is higher than the capacity of the tissue to conduct water, the tissue will stabilize at a lower water potential, but the calculation of K will not be affected. Therefore, the conductance (K) represents the amount of water that passes through the spike by each unit of time and unit of pressure gradient between the input point and the organ. If the transpiring area is reduced, probably the conductance will be also reduced, because the water will have fewer pathways to exit the ear, therefore water movement will be impaired.

2.3. Experiment 3. Flag leaf versus awns under water deficit

Seeds of cv. Buck Chambergro were grown in 6-l plastic pots (one plant per pot) filled with soil (Typic Argiudoll; USDA classification). We used the cultivar Chambergro in the water stress experiment, because we had previously obtained (for this cultivar; unpublished results) the relationship between ETR (fluorescence) and net assimilation rate (IRGA) of the flag leaf in well watered and water stressed plants (IRGA LI-COR 6400 system, LI-COR Inc., Lincoln, NB, USA, with the standard cuvette LI 6400-02) (see Tambussi et al., 2005 for more methodological details).

Plants were grown in a greenhouse in La Plata. Mean day/night temperatures and maximum photosynthetically active photon flux density (PPFD) during post-anthesis were ca. $28^\circ\text{C}/20^\circ\text{C}$ and $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The soil water content (SWC) in the containers was maintained at close to field capacity until anthesis, when drought treatments started. In water-stressed (WS) plants, every day the water content of the substrate was determined gravimetrically and maintained by irrigation at ca. 30% of container soil field capacity. Well-watered (WW) plants were maintained close to soil field capacity throughout the experiment, until 15 days after anthesis when water status (relative water content and water potential) and electron transport rate (ETR) were measured.

2.3.1. Water status

Relative water content (RWC) was measured in the awns and flag leaf blades of WW and WS plants 15 days after anthesis. Leaf blade segments or awns were weighed (w_i), floated on distilled water at 4°C overnight, weighed again (w_f), and dried at 60°C for

48 h, after which, dry mass was determined (w_d). Relative water content was calculated as:

$$\text{RWC} = \frac{(w_i - w_d)}{(w_f - w_d)} \times 100.$$

Water potential was measured in the flag leaf of WW and WS plants. Regarding awns, only the water potential of WW plants could be measured, since in WS plants the pressure needed to balance tension in the xylem exceeded the limit of the equipment (ca. 4 MPa). Measurements were taken at midday, 15 days after anthesis (about mid-grain filling) using a pressure chamber (Biocontrol, Argentina) plus a binocular microscope, with a damp piece of paper at the bottom of the chamber to avoid plant material desiccation.

2.3.2. Modulated chlorophyll fluorescence

Modulated chlorophyll fluorescence of photosystem II of the flag leaf and awns was measured with a fluorimeter (FMSII, Hansatech, UK). Five measurements per organ and treatment were made at midday on sunny days at *in situ* photosynthetically active photon flux density (PPFD). In the case of awns, several awns attached to one ear were placed in the clip of the fluorimeter and measurements were made at three positions (i) vertical (normal) position on the side of the ear exposed to lower PPFD; (ii) vertical position, on the side exposed to higher PPFD and (iii) on a horizontal position. In all cases, measurements were taken after reaching a steady-state value of basal fluorescence. Quantum yield of photosystem II was measured and photosynthetic electron transport rate (ETR) was calculated as in Rosenqvist and van Kooten (2003).

2.4. Experiment 4. Awn and ear contribution to grain filling in six modern cultivars differing in awn size

2.4.1. Plant material

In a set of twenty six modern cultivars of bread wheat cropped at present in Argentina ('Red de Ensayos Territoriales'; Epoca de Siembra 1; <http://www.inase.gov.ar>), we analyzed awn size of each cultivar (i.e., fresh weight, FW, of awns per spikelet). To increase the chance of finding variability in the size of awns, cultivars from different breeding companies/institutions in Argentina were included (i.e., Klein, Buck, Asociación de Cooperativas Argentinas, INTA and Don Mario). The cultivars used were: (1) Baguette Premium11; (2) Baguette 10; (3) B. Malevo (4); Baguette 19; (5) B. Norteño (6) BioInta 3003 (7) B. Ranquel (8) K. Guerrero (9) BioInta 3000 (10) ACA 304; (11) ACA 303; (12) B. Baqueano; (13) BioInta 3004; (14) ACA 315; (15) B. Guatimozin; (16) K. Capricornio; (17) K. Jabalí; (18) K. Gavilán; (19) B. Arriero; (20) INIA Torcaza; (21) D.M. Themix L; (22) ProInta Puntal; (23) ProInta Huenpan; (24) ACA 201; (25) Cooperación Liqueu; (26) B. Guapo (acronyms ACA, B., D.M. and K. in the name of each cultivar indicate the breeding companies Asociación de Cooperativas Argentinas, Buck, Don Mario and Klein, respectively).

To determine the relationship between awn size and contribution to the grain filling, we chose six cultivars covering the range of variation of awn size, (i.e., FW of awns per spikelet). The cultivars were: Baguette Premium 11, Baguette 19, ACA 304, K. Gavilán, B. Puntal and B. Guapo.

2.4.2. Experimental set-up

Seeds of the six wheat cultivars chosen (see above) were planted on July 17 2008 in La Plata, ($34^\circ 54' 24''\text{S}$; $57^\circ 55' 56''\text{W}$, Argentina) in the Experimental Field of Facultad de Ciencias Agrarias y Forestales (Universidad Nacional de La Plata) under rainfed and irrigated conditions. The cultivars were planted in plots ($1 \times 3.4 \text{ m}$ per plot; five rows, 20 cm apart). Sowing density was 260 plants per m^2 . Plots were arranged in randomized blocks with three replicates. The soil was a Typic Argiudoll (USDA classification). Fertilization

was applied as 100 kg ha⁻¹ of diammonium phosphate immediately after sowing and urea (250 kg ha⁻¹) 75 days after sowing, near tillering. Emergence took place ca. 15 days after sowing. Rainfall data are mentioned in Experiment 1.

Seasonal rainfall from sowing to harvest was 148 mm, and mean temperature was ca. 16 °C throughout the grain filling period. Irrigated plot received additional 75 mm of water distributed evenly from heading until maturity.

Near anthesis (GS65, Zadoks et al., 1974), three treatments were imposed in the central rows of each plot: intact ears, de-awned and shaded ears. De-awning was performed with scissors, and ears were shaded by covering with aluminum foil. In order to prevent the accumulation of ethylene and to allow for convective heat flux, the aluminum foil covers had several holes (diameter ca. 5 mm). De-awning and ear shading treatments were imposed at random on ca. 20 ears from different rows within each plot. We have previously demonstrated (Maydup et al., 2010) that this methodology does not produce effects on ear temperature; i.e. the effects of the ear shading treatment were not due to artifactual changes in temperature.

2.4.3. Quantification of awn and ear contribution to grain filling

The awn contribution to grain filling was calculated as:

$$= \left[\frac{(\text{GW}_{\text{ear}} \text{ of intact ear} - \text{GW}_{\text{ear}} \text{ of de-awned ear}) \times 100}{\text{GW}_{\text{ear}} \text{ of intact ear}} \right]$$

Ear contribution to grain filling was calculated as in Maydup et al. (2010, 2012):

$$= \left[\frac{(\text{GW}_{\text{ear}} \text{ of intact ear} - \text{GW}_{\text{ear}} \text{ of shaded ear}) \times 100}{\text{GW}_{\text{ear}} \text{ of intact ear}} \right]$$

where GW_{ear} is total grain weight per ear.

2.5. Experiment 5. Analysis of changes in awn size and awn contribution in a retrospective study

2.5.1. Plant material

Eight cultivars of bread wheat (*T. aestivum* L.) released in different years from 1932 to the present were used in this work. The cultivars used were: Klein 32 (1932), Klein Cometa (1942), Klein Rendidor (1954), Klein Toledo (1969), Klein Chamaco (1979), Buck Pucará (1980), Klein Cacique (1992) and Buck Taita (2008). This historical series includes cultivars released before and after the introduction of dwarfism alleles. In a previous paper (Maydup et al., 2012) we reported that ear contribution increased with year of release in this historical series (Maydup et al., 2012; note that two of the cultivars of that historical series are awnless, and were therefore excluded from the analysis in the present study).

2.5.2. Experimental setup

Seeds of the eight cultivars were planted on July 7 2009 as in experiment 4. Emergence took place 15 days after. Rainfall from April to June was 88.4 mm. Seasonal rainfall from sowing to harvest was higher than 400 mm and mean temperature ca. 16 °C throughout the grain filling period. Quantification of awn contribution to grain filling was done as in the experiment 4 (see above). A group of plants in one of the three central rows of each plot was completely defoliated 7 d after anthesis to impose a condition of source limitation.

2.6. Statistical analysis

Statistical analyses were carried out using the Statistica 5.1 software (StatSoft, Inc.). Differences in RWC and ETR were analyzed by ANOVA. Means were compared by the LSD test ($p < 0.05$).

3. Results

3.1. Photosynthesis of the flag leaf, body of the ear and awns (Experiment 1)

We measured the photosynthetic electron transport rate (ETR) of the flag leaf, the body of the ear (i.e. the photosynthetic activity of the glumes and lemmas) and the awns at three times during the grain filling period of cv. K. Escudo and cv. BioInta 3000 (middle panel in Fig. 1). Although initially, at 3 days after anthesis, ETR was higher in the flag leaf than in the ear parts, later in grain filling (around 24 days after anthesis) this relationship was reversed, with ETR of the ear body being higher than ETR of the flag leaf. Comparing ear parts, the ETR of the ear body was higher than that of the awns during the entire grain filling period. Due to their vertical position, both parts, i.e. body of the ear and awns received similar PPFD during the measurements (for instance, ca. 800 μmol photons m⁻² s⁻¹ on day 17 after anthesis; top panel in Fig. 1). This behavior was observed in both cultivars (i.e. cv. BioInta 3000 and cv. K. Escudo; Fig. 1, leaf and right panels, respectively), thus the body of the ears maintained a higher photosynthetic activity than the awns. During the whole of the grain filling phase, ETR of the awns of cv. K. Escudo was always higher than that of cv. BioInta 3000 (compare triangles in left and right middle panels in Fig. 1, respectively). Note that the quantum yield of the body of the ear was higher than that of the awns for both cultivars (lower panel in Fig. 1), even though both organs intercepted similar PPFD (upper panels in Fig. 1). Thus, differences in ETR between both ear parts (awns and body) are explained by different quantum yields and not simply by the incident PPFD.

3.2. Hydraulic conductance and daily variations in ear temperature: The role of awns (Experiment 2)

The daily courses of temperature in the body of intact (early in the grain filling period, thus ears with green awns) and de-awned ears are shown in Fig. 2. In cv. K. Escudo (long awned cultivar), intact ears were slightly cooler than de-awned ears during the morning (the difference reached 1.5 °C in some measurements). However, during the afternoon the temperature was sensibly higher (ca. 4 °C) in intact than in de-awned ears, with a crossover point at ca. midday (Fig. 2, upper panel). In cv. BioInta 3000 (short awned cultivar), differences between intact versus de-awned ears were lower ($\Delta T_{(\text{intact-de-awned})}$ ca. -0.5 and +2 °C in the morning and the afternoon, respectively; Fig. 2, lower panel). In cloudy days, by contrast, we did not find any difference in temperature between intact and de-awned ears (data not shown).

Intact ears of cv. K. Escudo had higher hydraulic conductance than ears of cv. BioInta 3000. Nevertheless, when ears of cv. K. Escudo were de-awned, the conductance decreased to values similar to cv. BioInta 3000, which had similar conductance with or without awns (Fig. 3). Therefore, in cv. K. Escudo awns are important in channeling water from the ear to the atmosphere.

3.3. Flag leaf versus awns under water deficit (Experiment 3)

The relative water content (RWC) of the awns was similar in water stressed (WS) and well watered (WW) plants (Fig. 4). By contrast, the flag leaf showed a strong reduction in the RWC in WS plants (ca. 12% less in WS compared to WW plants). Measurements of water potential (not shown) with a pressure chamber showed that the awns had a lower water potential than the flag leaf in WW plants at midday (near -4 MPa and -1.2 MPa in awn and flag leaf, respectively); as mentioned above, we could not measure the water potential in the awns of WS plants. At pre-dawn and fully-hydrated awns had higher values of water potential (-3.13 and -3.38 MPa,

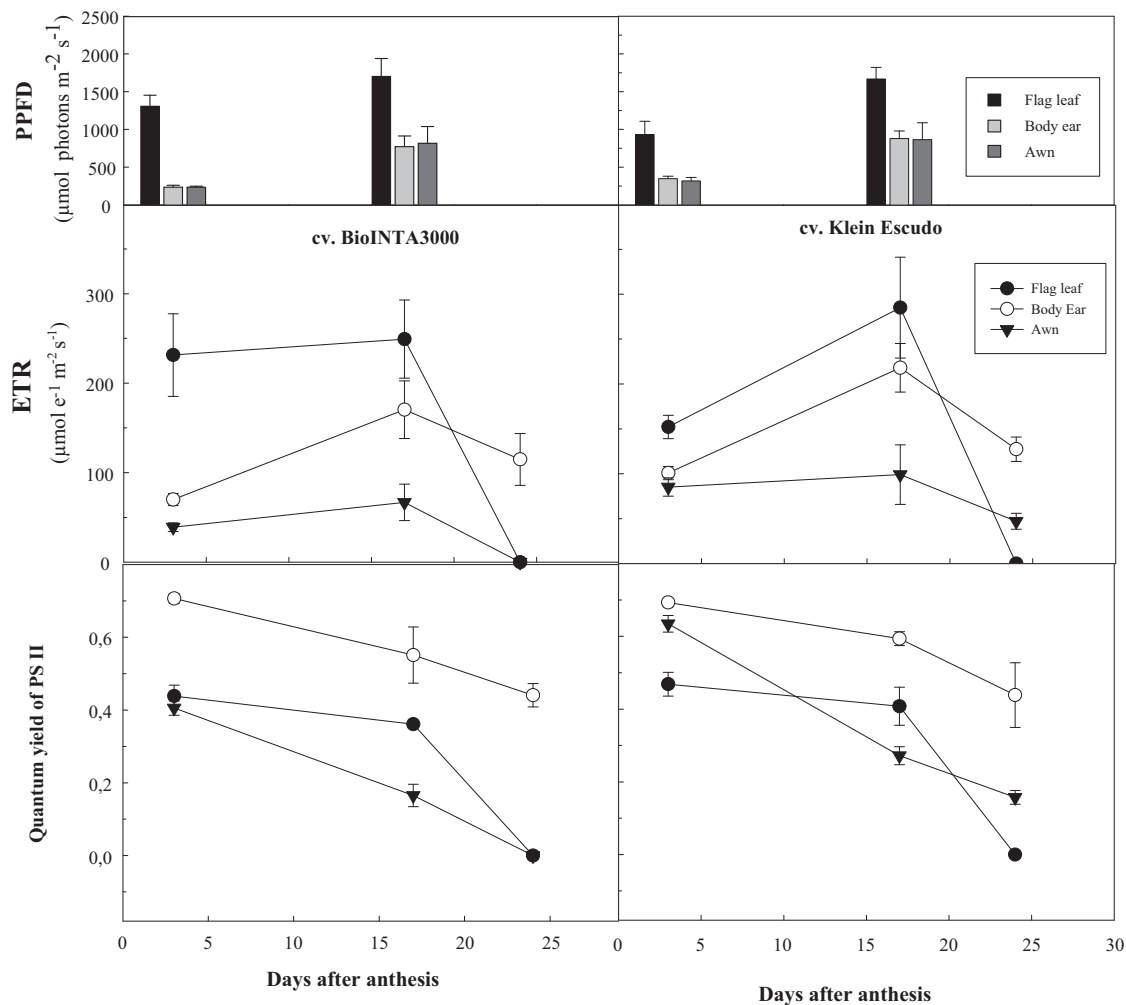


Fig. 1. Photosynthetically active photon flux density (PPFD) in the normal position of each organ at the time of measurement (Upper panel). Middle and lower panels, Photosynthetic electron transport rate (ETR) and Quantum yield of PSII, respectively, of the flag leaf (closed circles), glumes (body of the ear; open circles) and awns (triangles) in bread wheat cultivars BioInta 3000 (left panels) and K. Escudo (right panels) during grain filling (Experiment 1). Day 0 indicates anthesis. Measurements of ETR were performed at midday in sunny days with a portable modulated fluorimeter (for more details see Section 2). Values are the means of five measurements $\pm$ s.e.

respectively) compared with midday, although still sensibly lower than typical non-stressed leaves of wheat (*ca.* -1 MPa; see above).

The photosynthetic electron transport rate (ETR) of the flag leaf around midday was *ca.* 20% lower in WS plants (Fig. 5), a response consistent with what had been observed for RWC. A correlation between ETR (measured by chlorophyll fluorescence) and net assimilation rate (An) in the flag leaf of the same cultivar, showed that a decrease of 20% in ETR corresponds to a reduction of *ca.* 50% in An (data not shown). We measured ETR in the awns in three ways because of their erect position. On vertical positions (both on the side under low PPFD as on the side intercepting a high PPFD), ETR was lower in the awns than the flag leaf, but there were not differences between WW and WS plants. In a horizontal position (considered as a measurement of photosynthetic capacity of the awns, *i.e.* photosynthesis at saturating PPFD), ETR was higher in the awns than in the flag leaf, both in WW as in WS plants. Again, no significant differences were recorded between ETR of awns in WW and WS plants.

3.4. Ear and awn contributions in modern cultivars differing in awn size (Experiment 4)

Of the cultivars of Argentinean bread wheat examined, only one was awnless (not shown in Fig. 6) and we observed some variability

in awn size between the other, awned cultivars (Fig. 6A). To study the role of awns in relation to the photosynthetic contribution of the ear to grain filling, we chose six modern cultivars differing in awn size (awn FW *per* spikelet), trying to cover the whole range of variability for this character in the set of 26 varieties (Fig. 6A). We analyzed the ear and awn contribution to grain filling in each cultivar under irrigated and rainfed conditions, and we contrasted this contribution with awn size (Fig. 6B) **see also Supplementary Fig. S1**. The correlations between awn size *versus* ear/awn contribution were high ($r^2 = 0.67$ and 0.81 , respectively) in irrigated conditions (Fig. 6B, upper panel); under rainfed conditions, however, the correlations were lower compared with irrigated conditions, in particular for ear contribution ($r^2 = 0.24$ and 0.60 for ear and awn contribution, respectively; Fig. 6B, lower panel).

3.5. Breeding effects on awn size and awn contribution to grain filling (retrospective study, Experiment 5)

There was not a clear trend in awn size in this historical series, although in general terms modern cultivars have greater awn size than older ones (Fig. 7). Awn contribution to grain filling (inset in Fig. 7) also seemed to be higher in modern cultivars (for instance, compare awn contribution before and after 1980), but there was

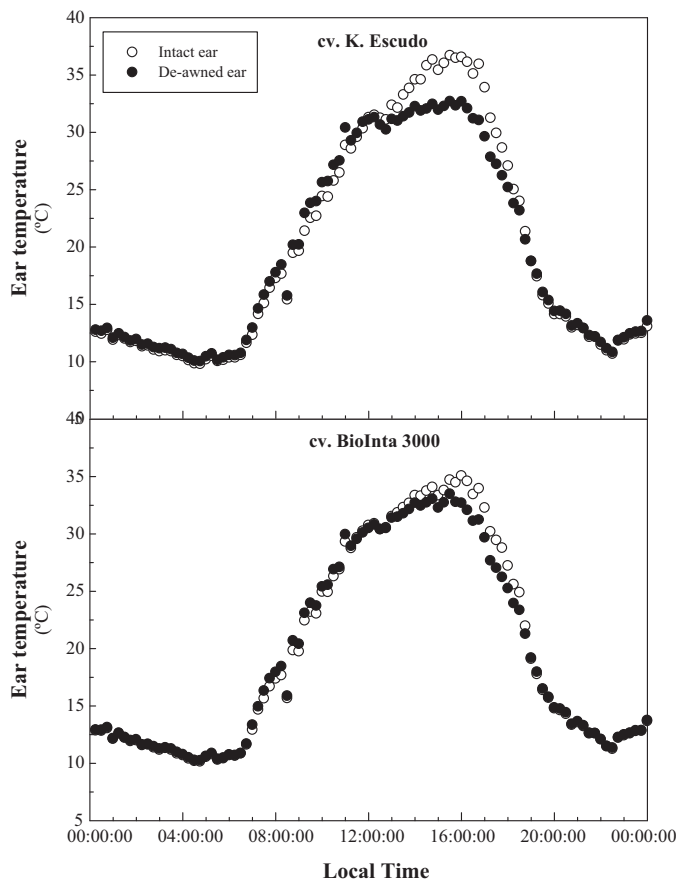


Fig. 2. Diurnal course of temperature of control (*i.e.* intact, open circles) and de-awned (closed circles) ears of cv. K. Escudo (upper panel) and cv. BioInta 3000 (lower panel). Temperature was measured every 15 min with copper-constantan thermocouple sensors placed beneath the glumes and recorded with a data logger (Experiment 2). Each line is the mean of four ears per treatment and cultivar. For more details see Section 2.

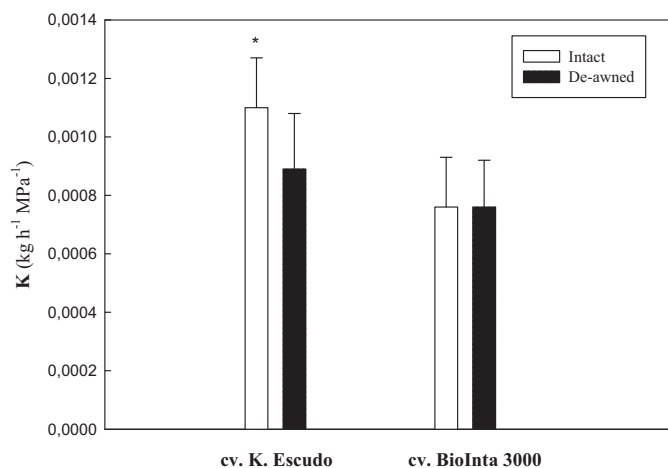


Fig. 3. Hydraulic conductance (K) of intact (open bars) and de-awned (closed bars) ears of cultivars Klein Escudo and BioInta 3000 (left and right, respectively). Hydraulic conductance was measured with a pressure steady-state flow meter (SSFM) method. Values are the means of five/six measurements $\pm$ s.e. Asterisk indicates significant differences between treatments ($p \leq 0.05$) according to the LSD test. For more details see Section 2.

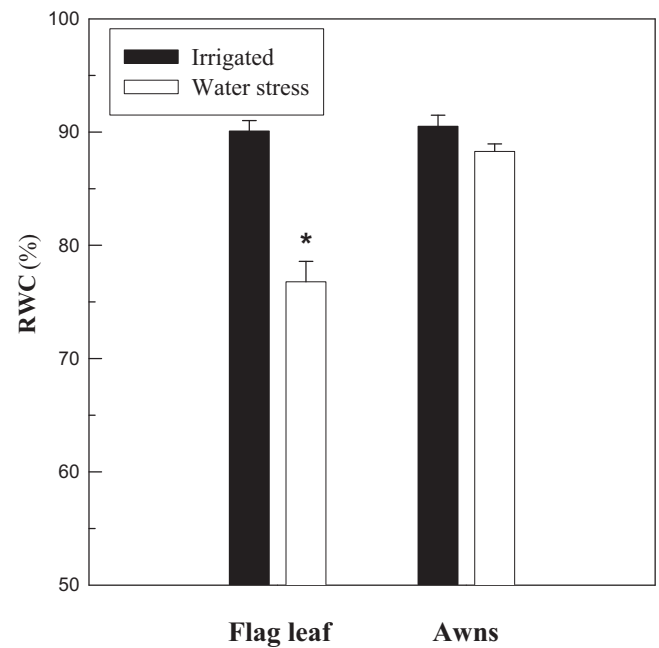


Fig. 4. Relative water content (RWC) of flag leaf and awns in control (irrigated, closed bars) and water stressed (open bars) plants of Experiment 3. Values are the means of five measurements $\pm$ s.e. Plants of bread wheat (cv. Chambergro) were grown in a glasshouse. For more details of the treatments see Section 2. Asterisk indicates significant differences between treatments ($p \leq 0.05$) according to the LSD test.

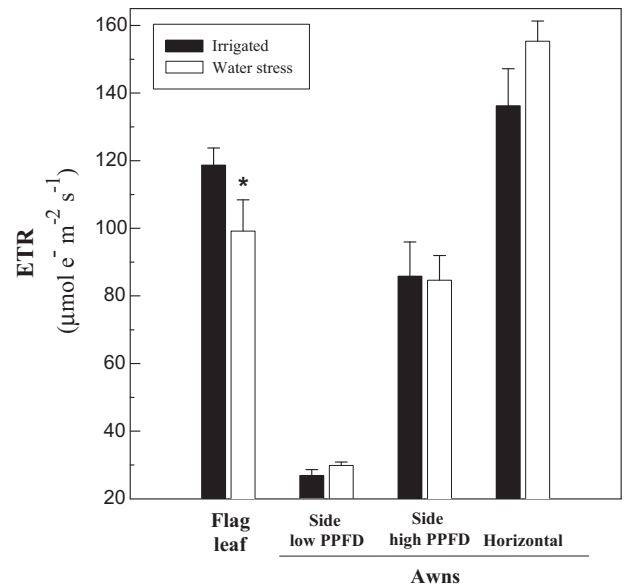


Fig. 5. Electron transport rate (ETR) of the flag leaf and awns of bread wheat in control (irrigated, closed bars) and water stressed (open bars) plants. Measurements of ETR were performed at midday in sunny days (15 days after anthesis) with a portable modulated fluorimeter. In the case of awns, several awns of each ear were placed in the clip of the fluorimeter and measurements were made in three different ways: (i) in a vertical (normal) position, on side of lower PPFD (named as 'side low PPFD'), (ii) in a vertical position, on the side of higher PPFD (named as 'side high PPFD') and (iii) in a horizontal position. In all cases, the measurements were taken after reaching a steady-state value of basal fluorescence (for more details see Section 2). Plants of bread wheat (cv. Chambergro) were grown in a glasshouse in 6 l pots (Experiment 3). Values are the means of five measurements $\pm$ s.e. Asterisk indicates significant differences between treatments ($p \leq 0.05$) according to the LSD test.

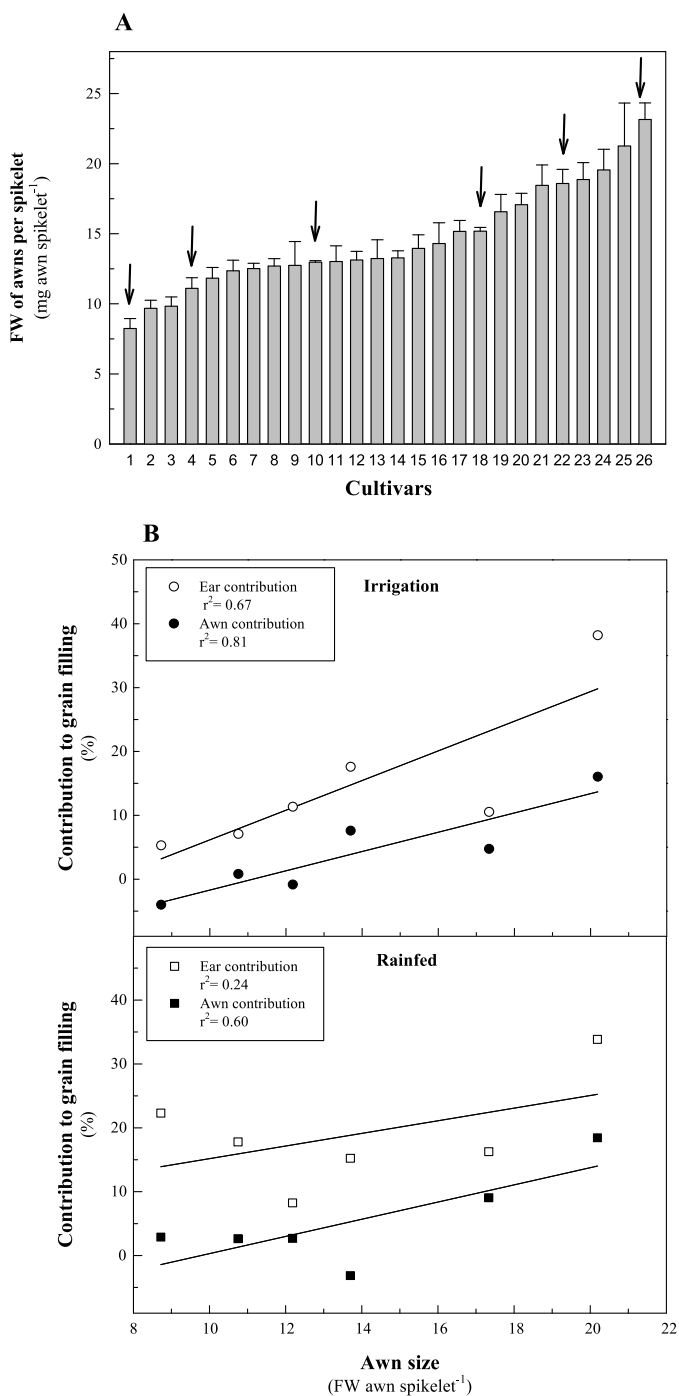


Fig. 6. Panel (A) awn size of several commercial cultivars (numbered from 1 to 26) of bread wheat planted in Argentina. Each bar represents the mean $\pm$ s.e. of five ears (main stem). Awn size was quantified as fresh weight (mg) per spikelet. Arrows show the six cultivars chosen for subsequent study. Panel (B) relationship between awn size (mg awn FW spikelet⁻¹) versus ear contribution (open symbols) or awn contribution (closed symbols) to grain filling in the six cultivars shown in panel A. Values of irrigated (upper panel, circles) and rainfed (lower panel, squares) plots are shown (Experiment 4). For more details see Section 2.

no correlation between awn size and the contribution of awns to grain filling (not shown).

4. Discussion

If we consider only the net assimilation of external (atmospheric) CO₂, awns contribute about 40–50% of ear photosynthesis

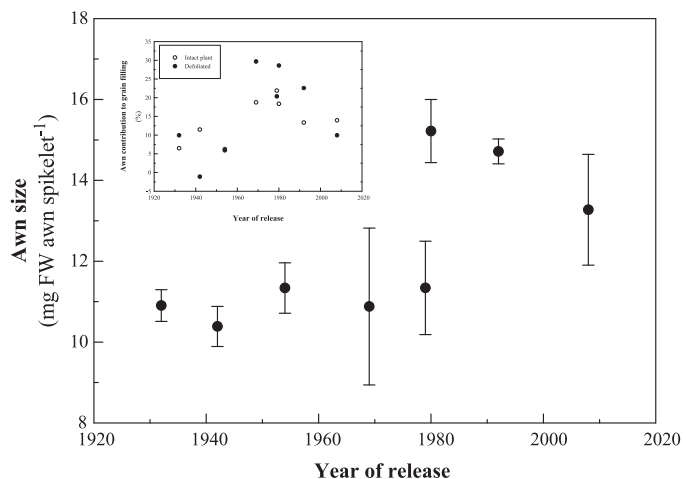


Fig. 7. Awn size (expressed as mg awn FW spikelet⁻¹; main panel of the figure) and awn contribution to grain filling (expressed as percentage; inset) versus year of release in the eight cultivars of the retrospective study (Experiment 5). Awn contribution was evaluated as described in Section 2. The cultivars set is a historical series including varieties released from 1932 to 2008 in Argentina. In the inset, the values of awn contribution in intact (open symbols) and defoliated (closed symbols) plants are shown.

in C₃ cereals, depending on genus (*Triticum* vs. *Hordeum*), species (*T. aestivum* vs. *T. turgidum*) and cultivar (e.g., long vs. short awned) (Blum, 1985). First, awns increase the green area of the ear by 30–50%, depending on the genotype (see Ali et al., 2010 and references cited therein). One advantage of awns, compared with the flag leaf, is that their chloroplasts remain intact and active during the grain filling period. By contrast, chloroplasts in flag leaves are almost completely degraded at the dough and ripening development stages (Li et al., 2006). Our measurements of photosynthetic activity estimated by chlorophyll fluorescence support this idea. A delayed senescence has been reported also for other organs of the ear (Martinez et al., 2003). However, it has been suggested that in some conditions (e.g. hot wind; Motzo and Giunta, 2002), awns can senesce prematurely and in this scenario, their contribution to grain filling could be lower. In our results, for instance, the awns of cv. Biointa 3000 had a lower ETR than awns of cv. K. Escudo during the grain filling period (see Fig. 1). We reported in a previous work that the contribution of awns in Biointa 3000 (a ‘short awned’ cultivar) is lower than in cv. K. Escudo (a ‘long awned’ cultivar; Maydup et al., 2010); the ETR data presented here indicate that differences in ear contribution to grain filling between K. Escudo and Biointa 3000 are due to differences in, both, awn size and photosynthetic activity. Data for cv. K. Escudo, where the awns maintained photosynthetic activity late in the grain filling period (compared with flag leaf) are in agreement with oxygen evolution measurements in awns by Li et al. (2006).

On the other hand, assimilation by the ‘body’ of the ear (e.g. glumes, lemmas; including both fixation of atmospheric CO₂ and re-assimilation of respired CO₂) seems to be a quantitatively important process (e.g. Gebbing and Schnyder, 2001). In fact, ETR was higher in the ear body than in the awns in both cultivars (see Fig. 1, both panels), which supports this point of view. At mid grain filling (i.e. around 15 days after anthesis) differences between photosynthetic activity of awns and body of the ear could also be explained by re-assimilation (refixation) of respired CO₂ near the grain, a well documented process in wheat (Bort et al., 1996; Gebbing and Schnyder, 2001; Kriedemann, 1966). It has been postulated that bracts surrounding the grain (glumes, lemmas and internally, the paleas) conform an ‘closed box’, in which CO₂ released from the kernels is re-assimilated in neighboring photosynthetic tissues (see Tambussi et al., 2007 and references therein). In short, despite the

importance of awns as photosynthetic organs, the relevance of green parts in the body of the ear cannot be minimized; photosynthesis of bracts in the ear body could be even more important than awn photosynthesis. In cv. K. Escudo, for instance, we found that awn contribution to grain filling was around 15% (calculated from data of Fig. 3 in Maydup et al., 2010), representing less than half of the total photosynthetic contribution of the ear.

4.1. Awns under water deficit

In wheat, there are progressive ontogenic changes in photosynthetic structures, with organs of late phenology having lower water contents and a more sclerophyllous structure (Tambussi et al., 2005). In this context, awns have the most markedly sclerenchymatous structure (e.g. Li et al., 2006) which seems to endow this organ with some tolerance to water deficit (e.g. Tambussi et al., 2005). Deposition of silica (SiO₂) in awns has been also pointed out as a relevant trait in drought tolerance (Peleg et al., 2010 and references cited therein), probably decreasing water loss through the cuticle (Ma, 2001). Compared with other organs (flag leaf, glumes, and blade of lemmas), awns have the lowest percentage of water content in their tissues (Tambussi et al., 2005). In this work we showed that awns of bread wheat are able to keep a higher RWC than the flag leaf under water deficit. In addition, compared with the flag leaf, a higher photosynthetic activity (in particular electron transport rate, ETR) is also observed in awns of water stressed plants. Surprisingly, compared with the flag leaf, water potential of awns is very low (ranging ca. –3 to –4 MPa) even in well watered plants. Measurements at pre-dawn (i.e., under non-transpiring conditions) and in fully hydrated awns also showed low values of water potential. Thus, the awn seems to be pre-adapted to low tissue water potentials, even under well hydration conditions.

4.2. Awns and their possible role influencing ear temperature

In the present study, the presence of awns clearly increased the temperature of the ear after midday, mainly in the long awned cultivar K. Escudo (see Fig. 2); by contrast, in the morning, intact (i.e. awned) ears were slightly cooler than de-awned ears. This apparent contradictory role of awns (cooling in the morning and warming in the afternoon) could be explained by stomatal closure at midday in the awns, although we do not have data in this regards; thus, transpirational (i.e. latent) loss of heat taking place during the morning could be abolished after midday when stomata close, a well known process in leaves (e.g. Monneveux et al., 2003). On the other hand, light scattering/shading and the increase of energy inputs (awns increase the interception of radiation in the ear; Motzo and Giunta, 2002) and changes in convective losses of heat (i.e. latent heat) could be involved in the cooling and warming effects, respectively. In durum wheat (*T. turgidum* L. var. *durum*), Motzo and Giunta (2002) reported that the canopy of awned ears maintains a lower temperature than the canopy of awnless ears. By contrast, Panozzo et al. (1999) found that awned cultivars had higher temperatures than awnless ones. In fact, we observed by thermal images of the ear that at midday the awns are warmer than the ear body (unpublished results). In the two cultivars analyzed, the ear has different resistance to water movement: the long-awned cultivar (cv. K. Escudo) offers less resistance to water movement compared with the short-awned cultivar (cv. BioInta 3000). Additionally, the high hydraulic conductance of the ear of cv. K. Escudo is due to its awns, because de-awned ears have similar conductance to the short-awned cultivar (see Fig. 3). In short, our data could reconcile the results of previous studies, suggesting a dual action of the awns, cooling or warming the ear depending on time of the day.

The effect of awns on ear temperature could have several, relevant consequences. First, a negative (i.e. deleterious) relationship

between canopy temperature during grain filling (above 15 °C) and kernel weight is well characterized for winter cereals (e.g. Ayeneh et al., 2002; Savin, 2010). Changes in grain filling rate (Dias and Lidon, 2009), duration of grain filling period and senescence of photosynthetic tissue are implicated (Savin, 2010) in these responses to temperature. Second, a higher temperature is related with higher photo-respiration (von Caemmerer, 2000), therefore possibly reducing net assimilation of CO₂ in the green parts of the ears. The impact of these negative effects in grain weight might counteract (at least partially) the beneficial effects of the presence of awns, such as the increase of photosynthetic area and total CO₂ assimilated in the ear. Thus, in spite of the higher photosynthetic activity in the awns (see Fig. 1) of cv. K. Escudo (compared to cv. BioInta 3000), the presence of larger awns could also be detrimental. Clearly, considering the higher contribution to the grain filling of cv. K. Escudo awns (compared with cv. BioInta 3000; Maydup et al., 2010), positive effect of long awns in photosynthesis seems to outweigh the negative impact of the awns on ear temperature.

4.3. Awn photosynthesis and contribution to grain filling

Although the photosynthetic role of awns of cereals has been studied for a long time (e.g. Jiang et al., 2006; Li et al., 2006; Olugbemi et al., 1976), their contribution to grain filling is not well known, and even controversial (e.g. McKenzie, 1972; see Tambussi et al., 2007 and references therein). The presence of long awns has been identified as part of the current wheat ideotype, in particular for drought conditions (Reynolds and Tuberosa, 2008), but as far as we know there is no clear evidence of a correlation (e.g. Maydup et al., 2010) between awn size and ear contribution to grain filling. Ali et al. (2010) found a decrease of total grain weight in de-awned ears, but there was no association between awn size of the cultivars and percentage ear contribution to grain filling. In fact, there are reports where the presence of awns has a positive effect on grain yield (Motzo and Giunta, 2002) and others where it is detrimental (McKenzie, 1972). In addition, the positive or neutral effect of the awns on the grain yield depends on the genetic background (Weyhrich et al., 1994). In the study presented here, although the correlation between awn size of the cultivars versus (total) ear contribution to grain filling was variable (depending on water availability, i.e., irrigation or rainfed), the correlation between awn size and awn contribution was high ($r^2 = 0.81$ and 0.6 for irrigation and rainfed conditions, respectively). Motzo and Giunta (2002) found that in durum wheat the presence of awns is positive for grain yield, but under drought conditions this effect could be irrelevant due to accelerated senescence. Thus, although awn photosynthesis seems to be tolerant to water stress in green tissues (see Figs. 4 and 5), it only can have a positive impact on grain yield if there is not premature degradation of photosynthetic components (see discussion of this topic above).

We are aware that the analysis of the effect of awns in near-isogenic lines could be better (*a priori*) than de-awning experiments with several cultivars. However, since the effects of the presence of awn depend on genetic background, and the suppression of awn presence could have pleiotropic effects (beyond their photosynthetic role), we think that data employing near-isogenic lines could be not conclusive either. In addition, we think that the correlation found in a set of cultivars (for instance, differing in awn length; e.g. Fig. 6) is relevant, in spite of differences in genetic background of these cultivars.

Summarizing the information mentioned above, the discrepancies (i.e. positive or negative effects on yield) between several studies could come from different causes: (i) the increase of photosynthetic area in the ear due to the presence of awns (e.g. Weyhrich et al., 1994) is, *per se*, a positive trait if grain filling is limited by availability of assimilates (i.e. limitation by source); (ii) the apparent

tolerance of awns to water deficit (in durum wheat, Tambussi et al., 2005, see Figs. 4 and 5) is also a positive trait; (iii) the presence of awns has been reported as both increasing (Panozzo et al., 1999), decreasing (Motzo and Giunta, 2002) or having both effects on ear temperature (depending on time of the day in the present work), with the corresponding effects on grain filling; (iv) premature senescence of the awns under some conditions (for instance, hot winds) has been pointed out as negative (Motzo and Giunta, 2002) and (v) there are some reports where the presence of awns is negative (deleterious) in terms of kernel number (e.g. in barley Bort et al., 1994; Teich, 1982 in bread wheat, Weyhrich et al., 1994). It has been argued that the development of the awns occurs in a critical phase for grain number determination, and it could have an adverse effect (e.g. a trade-off between awn size and floret fertility). The effect of the presence of awns on the yield is genotype dependent; i.e. the genetic background seems to be relevant (e.g. Weyhrich et al., 1994; Motzo and Giunta, 2002) although conclusive data in this sense are lacking. In our data, we did not find a significant relationship between awn size and grain number (data not shown). However, this issue has been hardly explored and should be researched further.

These effects mentioned above (some positive and some negative for grain yield) might interact in complex ways. Further research is needed (e.g. to clarify these possible interactions) in order to determine whether the presence of awns will be ultimately positive or deleterious to grain yield.

4.4. Awns in a retrospective analysis: Changes in their size and contribution to grain filling

As far as we know, there are no studies analyzing the changes in awn size and contribution to grain filling due to breeding. Although we did not observe a significant tendency in awn size along the years in this historical series, awn FW per spikelet seems to be higher in modern cultivars of wheat (see Fig. 7). In fact, old cultivars have an awn size lower than 12 mg of awns spikelet⁻¹, whereas, if we consider the set of 26 modern varieties analyzed in the present study (Fig. 6A), ca. 20 cultivars have values above this. Thus, although no progressive increase of awn size is observed in this historical series, awn size seems to be higher in modern cultivars of Argentinean bread wheat (see Fig. 7). In our previous retrospective study analyzing varieties released from 1920 (basically the same historical series presented here) we found an increase of total ear contribution to grain filling in modern Argentinean cultivars (Maydup et al., 2012). The correlation between awn size and ear (total) contribution was rather moderate in that historical series ($r^2 = 0.46$ and 0.42 for intact and defoliated plants, respectively; see Fig. 6 in Maydup et al., 2012). Although this could be explained by the limited range of variability of awn size in the set of cultivars employed in that study, the results presented here suggest that awn size would explain only marginally the increased ear contribution in modern varieties (Maydup et al., 2012). Breeding has altered other physiological traits related to C assimilation (e.g., the size of pre-anthesis stores of assimilates, the contribution of ear bracts, Maydup et al., 2012) which may mask changes in the contribution of awns. In short, although the size of the awns could have importance in total ear photosynthesis, the contribution of the awns to grain filling (although significant) explains only a minor part of total photosynthetic contribution of the ear. Differences in photosynthesis in the body of the ear (glumes, lemmas, green pericarp) between cultivars could explain a larger part of the variability in ear contribution. Further research (mainly focused in the study of refixation of respired CO₂) is needed to elucidate this question.

In accordance with the above considerations, the awns impact positively or negatively in the components of the yield. On the one hand, although awn contribution to grain filling is rather moderate

(ranging 10–15% as maximum), photosynthetic activity of the awns help to maintain of final grain size under some conditions (e.g. under water stress, in particular if a premature awn senescence is not induced). On the other, the possible penalty in grain number (an issue that should be more researched) could be deleterious if the assimilates availability is not critical (e.g. in sink limited cultivars).

5. Concluding remarks

In this paper we show that: (1) during late grain filling, ear parts (including awns, and particularly the body of the ear) can have a higher photosynthetic activity than the flag leaf; (2) the presence of awns could have favorable effects on ear temperature during the morning, but deleterious effects (i.e. increasing the temperature of the ear) after midday; (3) however, a positive characteristic of awns is some 'tolerance' to water deficit, maintaining a higher RWC and ETR than the flag leaf under drought; this positive effect could be abolished if premature senescence takes place (4) we found a moderately positive relationship between awn length and contribution of the ear to grain filling, and (5) in a retrospective analysis of Argentinean bread wheat we did not find a clear trend for awn size and awn contribution to grain filling in a historical series of cultivars.

In summary, the presence of awns could have positive (e.g. larger ear photosynthetic area, tolerance to water deficit) and negative (e.g. increased ear temperature after midday) influences on grain filling. The final effects on grain weight could result from the interactions between these partial influences of awns and the climate conditions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fcr.2014.07.012>.

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