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The contribution of ear photosynthesis to grain filling in bread wheat (*Triticum aestivum* L.)

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ABSTRACT

The contribution of ear photosynthesis to grain filling in wheat (*Triticum aestivum* L.) is not well known. The main objective of this work was to evaluate this contribution through three different experimental approaches: (1) ear photosynthesis was reduced by removing awns or shading the ears (in combination with a defoliation treatment), (2) grain weight per ear was compared in an 'all shaded' crop versus plants where only the vegetative parts were shaded ('ear emerging'), and (3) ear photosynthesis was reduced with DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea), a specific inhibitor of photosystem II.

In field experiments in La Plata (Argentina), cultivars Klein Escudo and BioINTA 3000 were subjected to awn removal and ear shading treatments, with or without severe defoliation, and to 'all canopy shaded' versus 'ear emerging' treatments. Although the estimated contribution of ear photosynthesis to grain yield differed depending on the experimental approach used (from about 12–42%), in general cv. Klein Escudo (with the largest awns) showed a greater contribution of ear photosynthesis. In both cultivars, the percentage contribution of ear photosynthesis was larger for defoliated plants. The magnitude of this contribution was positively associated with the length of awns of each cultivar. Awn removal had a non-significant ($p \leq 0.05$) effect on grain weight per ear (GW_{ear}) in the short-awned cv. BioINTA 3000. In cv. Klein Escudo, the effects of de-awning were larger, reaching values of ca. 15 and 19% decrease of GW_{ear} in non-defoliated and defoliated plants respectively. In both cultivars, grains in a distal position within the spikelet (G3) were most affected by the decrease of the photosynthetic source. The photosynthetic rate of the ear was higher in cv. Klein Escudo than in cv. BioINTA 3000.

We analyzed the contribution of remobilization of pre anthesis assimilates (stem plus sheaths). Comparing both cultivars, dry matter translocation from the stem showed the opposite pattern to the contribution of ear photosynthesis, i.e. it was higher in cv. BioINTA 3000 than in Klein Escudo.

In Bordenave, Argentina, ear shading treatments revealed an important contribution of ear photosynthesis to grain yield in cv. Huenpan (a long awned, water-deficit tolerant genotype), either under water deficit or irrigation, whereas in cv. Baguette Premiun 11 (short awns) there was apparently no effect of ear photosynthesis on yield.

Finally, inhibition of ear photosynthesis with DCMU reduced grain weight per ear to a similar extent as ear shading.

Ear photosynthesis might represent a "buffer" to maintain grain yield under source limitations (e.g. defoliation, water stress conditions), and could have an important role even without stress, because an incipient 'source' limitation might be emerging in modern cultivars of bread wheat.

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1. Introduction

In C_3 cereals, such as wheat and barley, grain filling is sustained by current photosynthesis of the upper parts of the plant, i.e. the flag and penultimate leaves plus the ear (see Tambussi et al., 2007 and references cited therein) and by redistribution of assimilates

stored in the stem (Blum, 1998; Foulkes et al., 2007; Ehdaie et al., 2008; Álvaro et al., 2008a). Although several studies analyzed ear photosynthesis from a physiological viewpoint (see references in Tambussi et al., 2007), its contribution to grain filling is not clear. In fact, compared with other sources of assimilates, the photosynthetic contribution of green parts of the ear (glumes, lemmas, awns and pericarp) has been less studied.

Grain yield of wheat is often limited by the strength of the sink rather by the availability of assimilates (i.e. the 'source', Slafer and Savin, 1994). Although this limitation due to sink capacity depends

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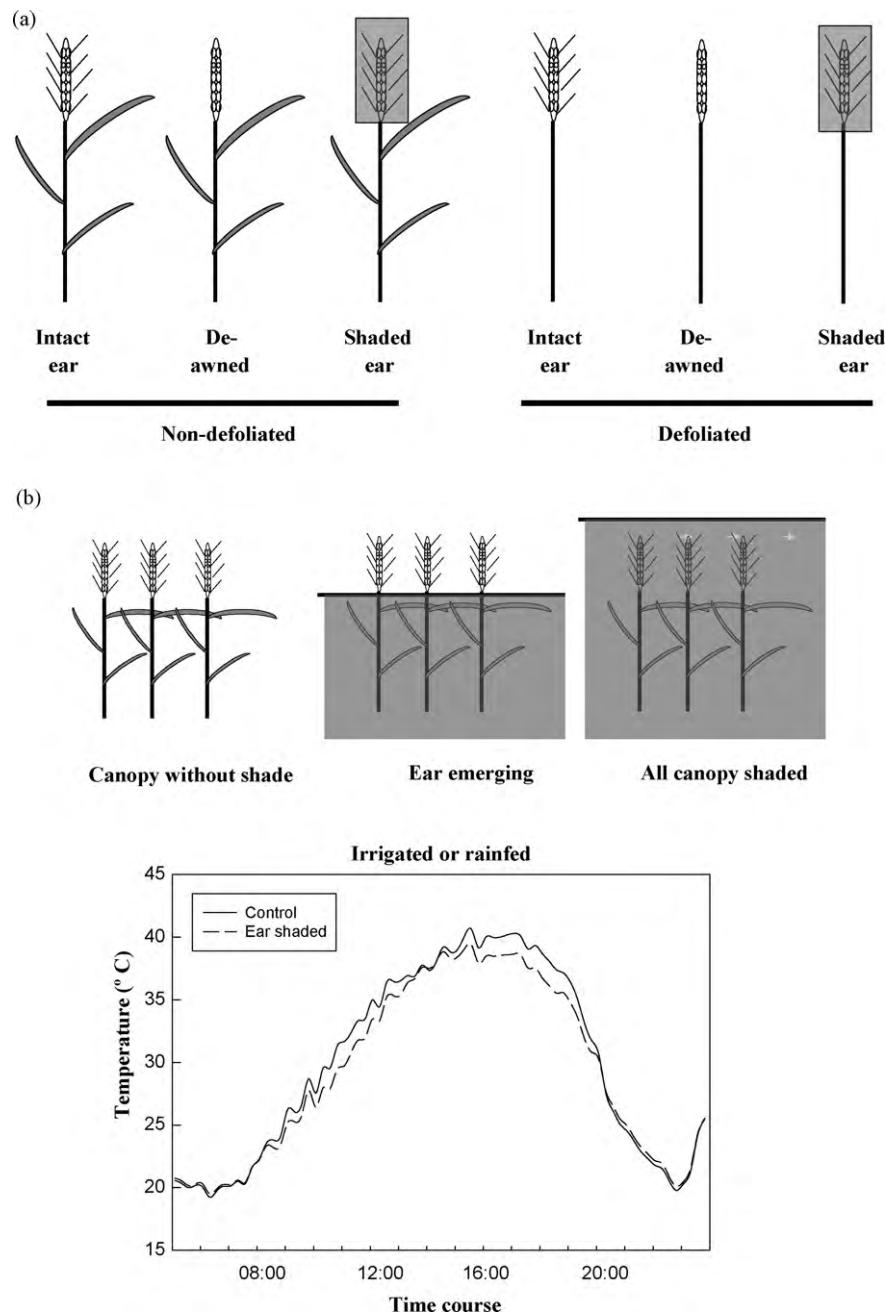


Fig. 1. Diagrams showing the experimental set-up for the awn removal, ear shading, defoliation (panel a) and the crop shading (panel b) experiments. All the treatments in both experiments were imposed five–seven days after anthesis. Shading of the ear (upper diagram) was made with a perforated aluminum foil. The shade in the second experiment had a transmittance ca. 10%. Panel c. Diurnal course of temperature of control (i.e. non-shaded) ears, and ears shaded with aluminum foil. Temperature was measured every fifteen minutes with thermocouple sensors placed beneath the glumes. Each line is the mean of eight ears per treatment.

on the environment (Blade and Baker, 1991), if there is an excess of assimilates during grain filling (Borrás et al., 2004), the photosynthesis of ear parts could be of minor importance. However, recent evidences indicate that some limitation by source could be emerging in modern cultivars of wheat (e.g. Álvaro et al., 2008a).

In winter cereals, e.g. wheat, water deficit is a common abiotic stress that reduces grain yield (Araus et al., 2002). Water stress decreases photosynthetic rate (e.g. Lawlor, 2002) and accelerates leaf senescence (Martinez et al., 2003). Compared with the flag leaf, the photosynthetic rate of the ear parts is reduced to a lesser extent under water stress in durum (Tambussi et al., 2005) and bread wheat (Martinez et al., 2003). Although the apparent drought ‘tolerance’ of ear photosynthesis is not completely understood, it seems

to be associated with the ability to maintain a higher relative water content in glumes, lemmas and awns (Tambussi et al., 2005). Moreover, ear bracts and the kernel pericarp can refix the CO₂ emitted by growing grains (Bort et al., 1994; Gebbing and Schnyder, 2001). Under drought conditions, the ear may become the main source of photosynthates for grain filling in barley (Bort et al., 1994; Sánchez-Díaz et al., 2002) and durum wheat (Araus et al., 1993; see also references in Tambussi et al., 2007).

In bread wheat the contribution of ear photosynthesis to grain yield is poorly understood. One reason for this is that the photosynthetic contribution of the ear is not easy to measure, in particular in field trials. The main objective of this work was to assess the contribution of ear photosynthesis to grain yield of bread wheat (using

several experimental approaches) under relatively non-limiting and stress conditions (e.g. defoliation, drought).

2. Materials and methods

2.1. Experiment 1. Defoliation/de-awning/ear-shading

Seeds of bread wheat cvs. BioINTA 3000 and Klein Escudo were planted on June 29, 2007, 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) under rainfed conditions. These cultivars were chosen because of their contrasting ear morphology (awn length) and very similar phenology (days to anthesis). These cultivars were planted in plots (1 m × 3.4 m per plot; five rows, 20 cm apart). Sowing density was 260 plants per m². Plots were arranged in randomized blocks with three replicates. The soil was a typic argiudol (USDA classification). Fertilization was applied as 100 kg ha⁻¹ diammonium phosphate immediately after sowing, and urea (250 kg ha⁻¹) 75 days after sowing, near tillering. Emergence took place on July 17.

Near anthesis (GS65, Zadoks et al., 1974), six treatments were imposed in the three central rows of each plot. These treatments were the result of combinations of defoliation, awn removal, and ear shading (Fig. 1, panel a). Defoliation consisted of the removal of all leaves of the culms in 1 m sections of the rows. De-awning involved the removal of all awns of an ear with scissors, and ears were shaded by wrapping each ear in aluminum foil. In order to prevent the accumulation of ethylene and to allow for convective heat flux, several holes were made in the aluminum foil covers. De-awning and ear shading were imposed at random on 10 ears from different rows within each plot.

Weather conditions are shown in Fig. 2 (upper panel). Seasonal rainfall from sowing to harvest was 407 mm, and temperature was moderate (mean temperature ca. 16 °C) throughout the grain filling period (November and the first half of December).

The daily course of temperature in control (i.e. non-shaded) and shaded ears was measured with copper-constantan thermocouples T¹ TC1047A (Microchip Inc.) and the data were recorded with a TC-Logger 16 (www.cavadevices.com). Thermocouples were inserted underneath the glumes. Eight replicate ears were measured in each treatment.

At maturity, number of kernels per ear, total (per ear) and average grain weight were measured. The average weight of grains from specific positions within the spikelet (G1–G3, from the proximal to the distal kernel, Kruk et al., 1997) was also determined.

We calculated the ear contribution to grain filling as:

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

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

2.2. Experiment 2. Ear shading under irrigated versus rainfed conditions

Seeds of bread wheat (*Triticum aestivum* L.) cvs. Huenpan and Baguette Premium 11 were planted on July 3, 2007, in the Experimental Field of Instituto Nacional de Tecnología Agropecuaria (INTA) Bordenave (37° 50' 55"S; 63° 01' 20"W, Argentina). These two cultivars are characterized by similar dates of anthesis but contrasting drought tolerance. In addition cv. Huenpan has longer awns than cv. B. Premium 11. These cultivars were planted in plots (1.4 m × 11 m per plot in seven rows, with 20 cm spacing between rows). Sowing density was 250 plants per m². The experimental design consisted of randomized blocks with four (B. Premium 11) and three (cv. Huenpan) replicates. Fertilization was carried out as above. Emergence took place on August 4, 2007. Plants were

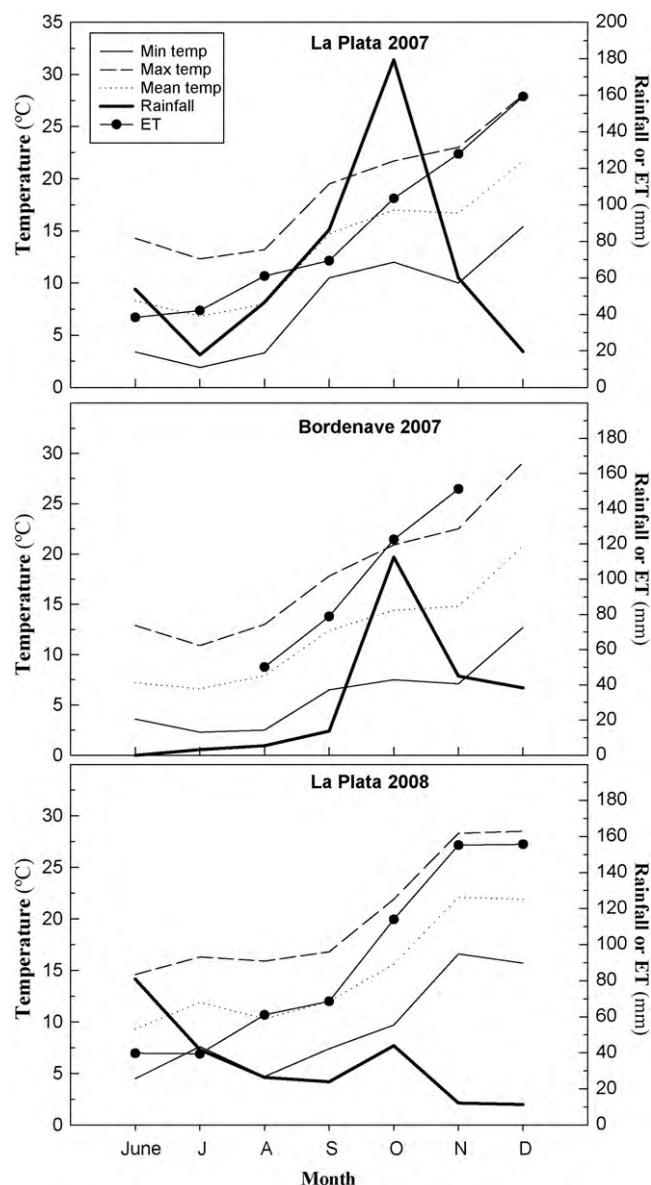


Fig. 2. Rainfall, and minimum, maximum and average temperatures recorded during Experiment 1 (La Plata, 2007; upper panel), Experiment 2 (Bordenave, 2007; medium panel) and Experiment 3 (La Plata, 2008; lower panel). Potential evapotranspiration is also shown.

grown under rainfed conditions until anthesis, thereafter half of the plots were irrigated as needed while the remaining half of the plots was maintained under rainfed conditions. Weather conditions are shown in Fig. 2 (middle panel). Rainfall from sowing to harvest was 306 mm. Additional 50 mm of water were applied during the grain filling period by drip irrigation. Temperature was moderate (mean temperature ca. 15 °C) throughout the grain filling period (November and the first half of December).

After anthesis (GS65, Zadoks et al., 1974), two treatments: (i) intact ear and (ii) ear shading, (as detailed for Experiment 1) were imposed randomly on individual ears in each plot. At maturity, total (per ear) and average grain weight were measured.

2.3. Experiment 3. Crop shading

Seeds of bread wheat (*T. aestivum* L.) cvs. BioINTA 3000 and Klein Escudo were planted on July 10, 2008, in La Plata, in 1.4 m × 7.5 m plots with seven rows, and 20 cm between rows. Sowing den-

sity was 260 plants per m². Emergence took place on July 25. The experimental design consisted of randomized blocks with three replicates per treatment (rainfed *versus* supplementary irrigation from anthesis to the end of grain filling). At anthesis, irrigated plots were watered by drip irrigation and watering continued regularly until maturity. Weather conditions are shown in the Fig. 2 (lower panel). Rainfall from sowing to harvest was 121 mm in the rainfed treatment. Irrigated plots received additional 75 mm of water distributed evenly during grain filling. Compared to 2007, temperature was higher (mean temperature *ca.* 20 °C) throughout the grain filling period (November and the first half of December).

Fertilization was carried out as indicated above (Experiment 1). Seven days after anthesis (GS69, Zadoks et al., 1974), two shade (gray 'Premium', 1 m × 1.4 m, transmittance *ca.* 10%) treatments were setup at random in each plot. In one of these treatments, the shades covered only the vegetative parts of the plants, while the ears emerged through the shade into full sunlight (see Fig. 1, panel b). In the other treatment, shades covered the whole crop (i.e. including the ears). One part of each plot was maintained without any shade as control. Only the three central rows of each plot were used to sample ears. At least eight ears per treatment (from the main stem or primary tillers) were analyzed. At the time shades were setup in the field, five samples (i.e. culms) per plot of each cultivar were taken in order to determine dry weight of each internode.

At maturity, total grain weight per ear, grain number and average grain weight were determined, as well as dry weight of each internode (six culms per treatment).

In this approach we calculated the ear contribution to grain filling as:

$$\left[\frac{(\text{GW}_{\text{ear of 'ear emerging'}} - \text{GW}_{\text{ear of 'all canopy shaded'}}) \times 100}{\text{GW}_{\text{ear of 'canopy without shade'}}} \right]$$

Dry matter translocation (DMT) was calculated as the decrease of stem (*plus* leaf sheaths) dry weight between anthesis and the end of grain filling, as an indicator of C remobilization to the grains. Dry matter translocation efficiency (DMT_e, %) and the contribution of preanthesis stem assimilates to grain yield (CPA) were calculated as in [Álvarez et al. \(2008a\)](#):

$$\text{DMT}_e = \left(\frac{\text{DMT}}{\text{DM}_{\text{anthesis}}} \right) \times 100$$

$$\text{CPA} = \left(\frac{\text{DMT}}{\text{GW}_{\text{ear}}} \right) \times 100$$

where DM_{anthesis} was the dry weight of the stem at anthesis and GW_{ear} was the total grain weight per ear.

2.4. Measurement of ear photosynthesis

In a field experiment during 2009 in La Plata, with crop management conditions identical to Experiment 3, we measured the net photosynthetic rate of the ear in cvs. BioINTA 3000 and Klein Escudo. This experiment was carried out under rainfed conditions (rainfall 423 mm) during the wheat growing season. Gas exchange measurements were made with an air-tight Plexiglass chamber (1.5 L) connected to an IRGA (Portable Photosynthesis System CIRAS 2, PP Systems). Temperature within the chamber was maintained at *ca.* 30 °C with a Peltier cooler inside the chamber. The chamber was illuminated from one side with two dichroic lamps (500 W). Photosynthetically active photon flux density was 850 μmol m⁻² s⁻¹ and CO₂ concentration in the chamber was *ca.* 360 ppm. Measurements were made between 11:00 and 16:00 h. Measurements were alternated between cultivars to reduce the bias due to time of mea-

surement. Four ears per cultivar were measured at 3, 17 and 24 days after anthesis.

2.5. Experiment 4. Inhibition of photosynthetic electron transport with DCMU

Plants (cv. Arriero) were grown in a greenhouse in La Plata, in 5 L pots filled with soil and well-watered during the whole plant cycle. Seven days after anthesis, ears were sprayed with 100 μM of DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea, 10 ml ear⁻¹) added with 0.1% (v/v) of Tween 20 as surfactant. DCMU is a specific inhibitor of photosynthetic electron transport ([Allen and Holmes, 1986](#)). Control ears were sprayed with a solution of the surfactant at the same concentration. In order to avoid spilling DCMU on the flag leaf, applications of DCMU were made with the ear enclosed in a plastic bag tied around the ear peduncle. The actual inhibition of photosynthesis in the ear (glumes and awns) and flag leaf was monitored by modulated chlorophyll fluorescence (FMSII, Hansatech, UK). Five measurements per organ and treatment were made at midday on sunny days, 1, 4 and 14 days after application. Quantum yield of photosystem II was measured and photosynthetic electron transport rate (ETR) was calculated as in [Rosenqvist and van Kooten \(2003\)](#). At maturity, ears were harvested and grain weight per ear was measured.

2.6. Statistical analysis

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

3. Results

3.1. Experiment 1. Defoliation/de-awning/ear-shading

In this experiment, defoliation was used to reduce the photosynthetic capacity of the canopy and, thereby, mimic the source limitations imposed by different kinds of stress, e.g. herbivory, drought, etc. Defoliation reduced grain weight per ear (GW_{ear}) *ca.* 26% in both cultivars (Fig. 3, right panels), where GW_{ear} represents the total amount of assimilates available for grain filling. In the cultivar with small awns (BioINTA 3000; awns FW = 13.2 mg ear⁻¹) de-awning did not decrease grain weight or grain number. In the cultivar with long awns (Klein Escudo; awns FW = 23.2 mg ear⁻¹) de-awning did not alter grain number, but it decreased grain weight (GW_{ear}) by 15% and 19% in intact (non-defoliated) and defoliated plants, respectively (Fig. 3). Shading the ear reduced GW_{ear} in both cultivars; this decrease was larger in cv. Klein Escudo than in BioINTA 3000. In cv. BioINTA 3000, GW_{ear} decreased by 25% and 41% in intact and defoliated plants, respectively. In cv. Klein Escudo, this decrease was 33% and 49% respectively. There was no interaction between defoliation and ear treatments (shading or de-awning) in any cultivar (data not shown). Kernel number per ear was only slightly or not affected by shading treatments (see Fig. 3, left panels).

We analyzed the changes of individual kernel weight at specific positions within the ear. In both cultivars, grains in a distal position within the spikelet (G3 in cv. BioINTA 3000, G3 and in some cases G2 in cv. Klein Escudo) were most affected by the decrease of the photosynthetic source (Table 1). For instance, the weight of the G3 kernels (mainly in basal and central spikelets) in cv. BioINTA 3000 was reduced strongly in the defoliation/shaded ear treatment, compared to control plants (Table 1, upper panel). Smaller, but significant decreases (*p* ≤ 0.05) were found in the G3 (central spikelets) and G2 (basal and apical spikelets) grains of cv. Klein Escudo (see lower panel in Table 1).

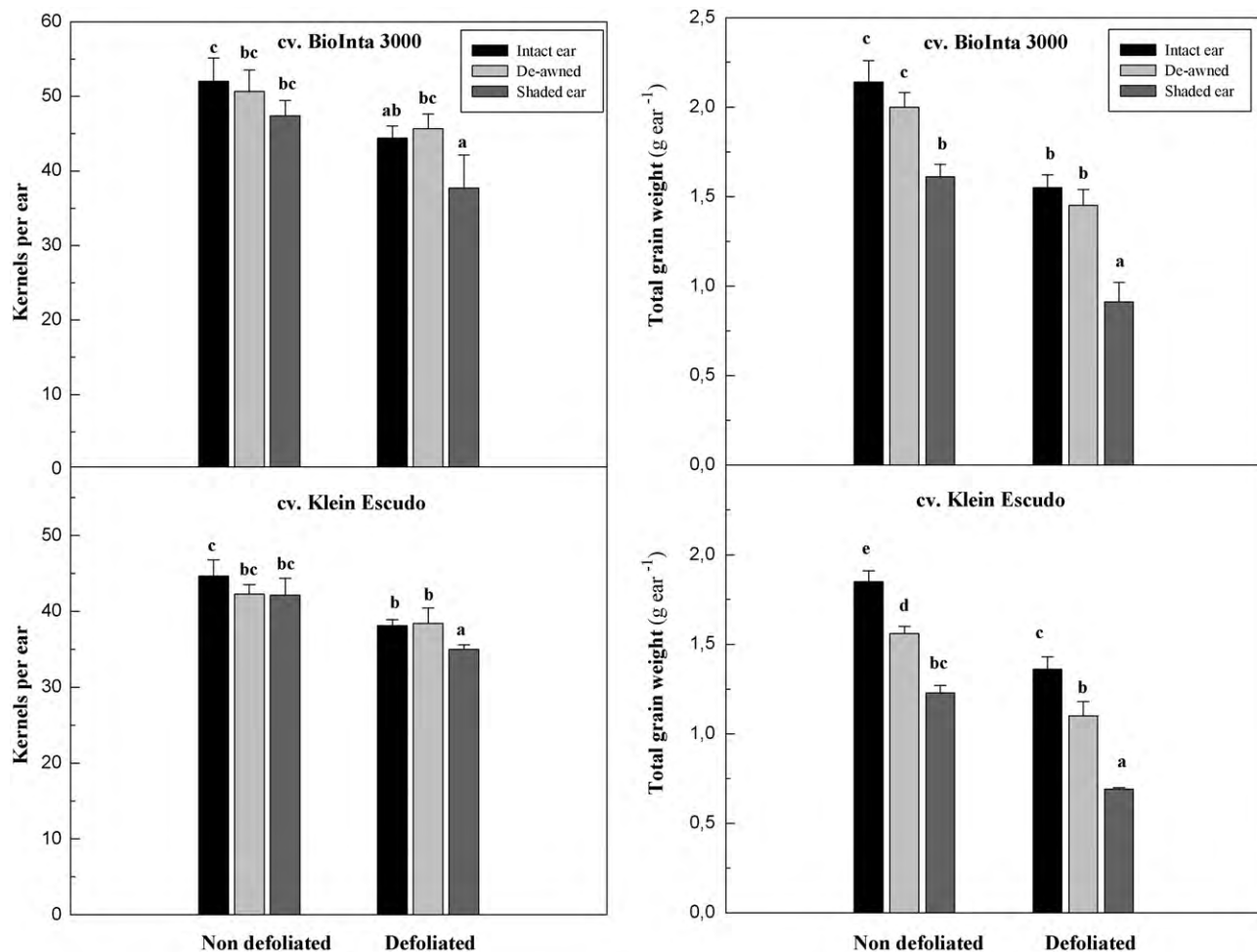


Fig. 3. Kernel number (left panels) and total grain weight per ear (right panels) in Experiment 1. Upper panel: cultivar BioINTA 3000; lower panel: cv. Klein Escudo. In each panel, bars correspond to intact (left bars) and defoliated (right bars) plants. Each value represents the mean $\pm$ s.e. of three replicates (=plots) per treatment. In each plot, eight ears were analyzed and averaged. For each cultivar, different letters indicate significant differences between treatments ($p \leq 0.05$) according to the LSD test. For more details of the treatments see Fig. 1 (upper diagram).

Table 1
Individual grain weight (mg) at specific positions in the ear of the bread wheat cultivars BioINTA 3000 and Klein Escudo in the defoliated/de-awning/ear-shading experiment (Experiment 1 in La Plata, 2007). Grain positions are referred to as in Section 2. The first part of treatment abbreviation designates the leaf treatment (C = control, intact leaves versus D = defoliated). The second part is the ear treatment (C, control intact ears; de-awn, de-awned ears and shade, shaded ears). Analysis of variance was performed separately for each spikelet position, considering the leaf treatment (control or defoliated), spike treatment (control, de-awned or shaded) and grain position (G1, G2 or G3) as main factors. For a given spikelet and grain positions, means followed by the same letters are not significantly different ($p \leq 0.05$) according to LSD test.

	Basal spikelets			Central spikelets			Apical spikelets	
	G1	G2	G3	G1	G2	G3	G1	G2
cv. BioINTA 3000								
C/C	45.1 hi	49.1 i	36.3 defg	50.2 j	50.0 ij	34.2 efgh	38.0 g	36.7 fg
C/de-awn	38.2 fgh	43.6 g-i	24.0 c	43.9 hij	45.5 hij	23.1 bcde	35.3 efg	30.7 cdef
C/shade	39.2 fgh	39.6 fgh	23.9 c	41.1 ghij	42.5 ghij	19.2 bcd	31.1 defg	23.9 bc
D/C	34.8 def	37.5 efgh	12.5 b	43.3 ghij	43.1 ghij	10.5 b	32.5 defg	28.6 bcde
D/de-awn	34.2 def	39.2 fgh	12.0 b	36.6 fghi	39.5 ghij	16.5 bc	30.2 cdf	27.7 bcd
D/shade	29.3 cd	29.9 cde	0.5 a	30.4 defg	25.9 cdef	1.1 a	23.0 b	13.9 a
	Basal spikelets			Central spikelets			Apical spikelets	
	G1	G2		G1	G2	G3	G1	G2
cv. Klein Escudo								
C/C	36.3 def	41.0 f	49.3 ij	54.3 j	33.0 ef	43.3 e	39.4 de	
C/de-awn	37.7 ef	40.9 f	43.7 ghi	43.4 ghi	25.4 cde	37.2 de	35.8 cde	
C/shade	32.3 de	31.4 cde	39.4 fgh	38.3 fgh	23.3 bcd	28.3 abc	27.1 ab	
D/C	37.9 ef	35.9 def	46.8 hij	50.5 ij	22.2 bc	31.1 bcd	37.9 de	
D/de-awn	24.0 abc	29.3 bcd	32.2 def	34.4 efg	14.9 ab	26.1 ab	23.4 ab	
D/shade	18.4 a	22.9 ab	25.6 cde	26.9 cde	11.6 a	20.7 a	20.7 a	

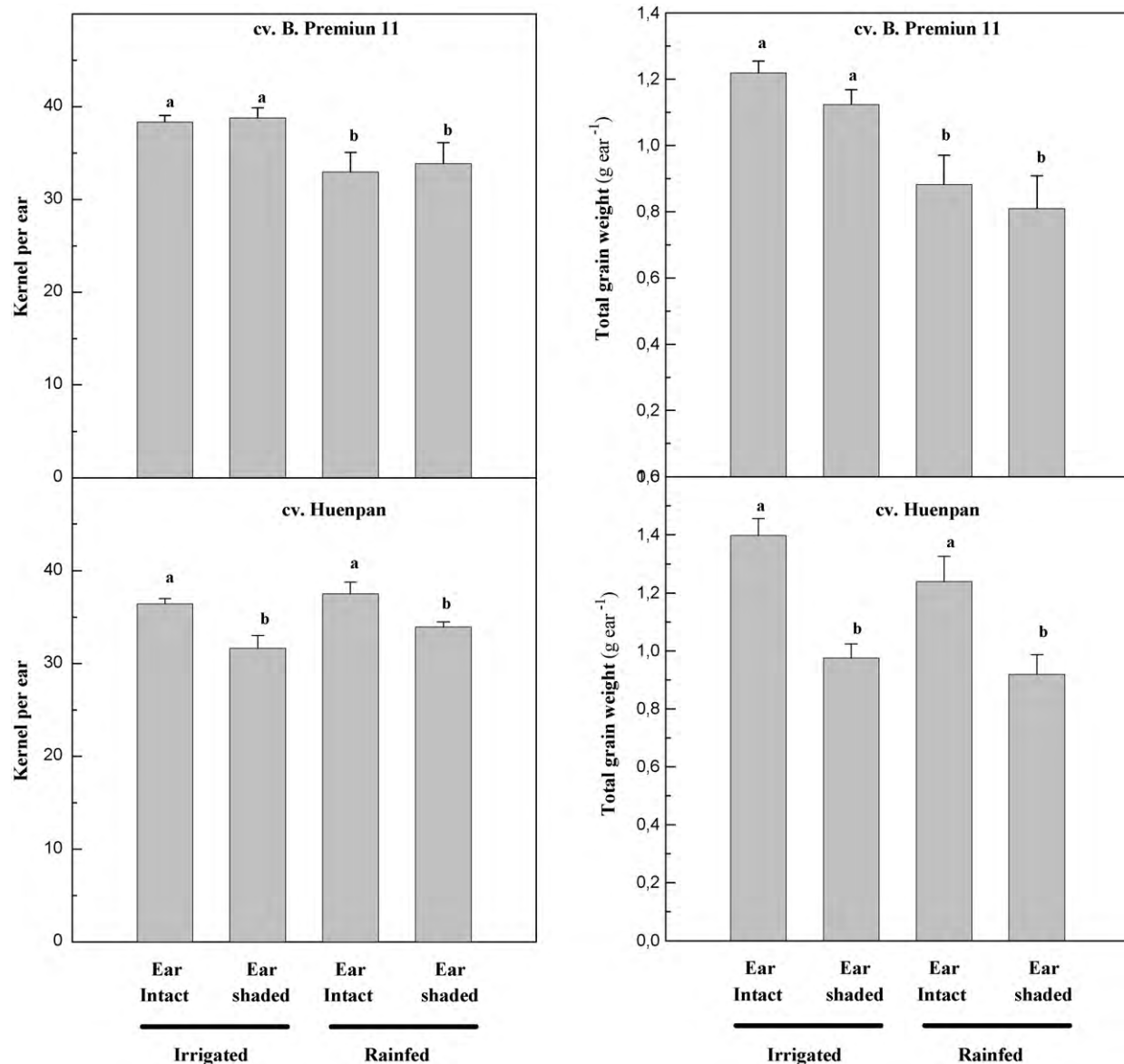


Fig. 4. Kernel number (left panels) and total grain weight per ear (GW_{ear}) (right panels) in the irrigation versus rainfed (Experiment 2) carried out in Bordenave (year 2007) with cultivars Baguette Premium 11 (upper panel) and Huenpan (lower panel). Bars correspond to irrigated (left bars) and rainfed (right bars) conditions. Each value represents the mean $\pm$ s.e. of four replicates per treatment (=plots). In each plot, eight ears were analyzed. For each cultivar, different letters indicate significant differences between treatments ($p \leq 0.05$) according to the LSD test.

Table 2 shows the estimated photosynthetic contribution of ears to grain filling in cultivars BioINTA 3000 and Klein Escudo. In Experiment 1 (i.e. the defoliation/de-awning/ear-shading) ear contribution was higher in cv. Klein Escudo than in cv. BioINTA 3000 in intact (non-defoliated) plants. In defoliated plants, the ear contribution was similar in both cultivars (Table 2). In cv. BioINTA 3000 (which has a smaller awns $FW \text{ ear}^{-1}$), awns contributed ca. 6% to grain filling, irrespective of the defoliation treatment; however, this was not statistically significant ($p \leq 0.05$). In cv. Klein Escudo, with larger awns, the contribution of awns to grain filling was 15.8% and 17.6% in intact and defoliated plants, respectively (data not shown).

3.2. Experiment 2. Ear shading under irrigated versus rainfed conditions

Fig. 4 shows GW_{ear} in two cultivars of bread wheat grown under irrigated versus rainfed conditions during the grain filling period. Water deficit in the rainfed plots reduced grain weight by 25% and

Table 2

Contribution of the ear to the grain filling in cultivars BioINTA 3000 and cv. Klein Escudo in Experiment 1 (defoliation and ear shading approach) and Experiment 3 (canopy shading approach). The ear contributions to grain filling (expressed as percentage) in each experimental approach were calculated as detailed in Section 2. For each experiment, means followed by the same letters are not significantly different ($p \leq 0.05$) according to LSD test.

Treatment	Ear contribution to grain filling (%)	
	BioINTA 3000	Klein Escudo
Experiment 1		
Non-defoliated	22.6 a	33.5 b
Defoliated	42.3 bc	45.2 c
Experiment 3		
Irrigated	12.9 a	30.5 b
Rainfed	22.4 ab	36.3 b

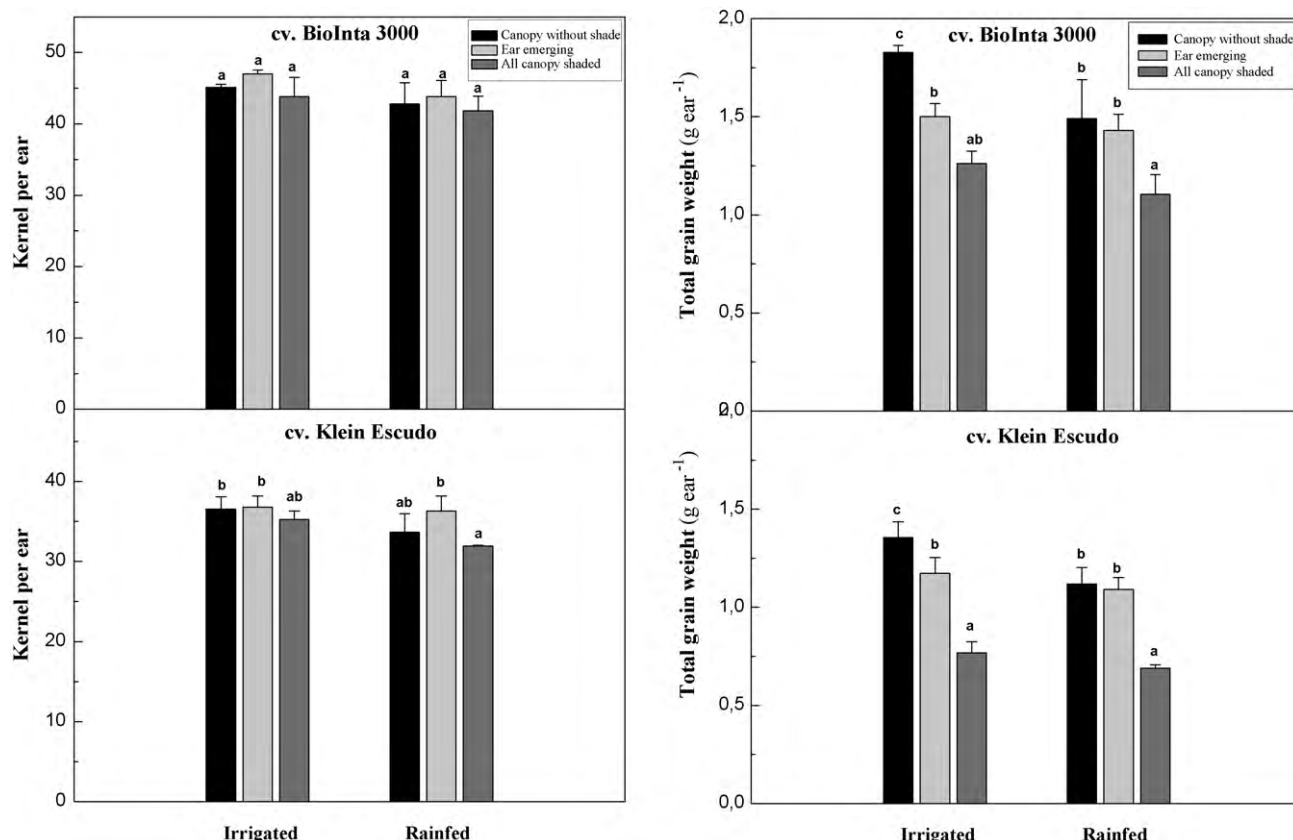


Fig. 5. Kernel number (left panels) and total grain weight per ear (right panels) in the crop shading approach (Experiment 3). Upper panel: cultivar BioINTA 3000; lower panel: cv. Klein Escudo. Bars correspond to irrigated (left bars) and rainfed (right bars) conditions. Each value represents the mean $\pm$ s.e. of three replicates per treatment (=plots). In each plot, eight ears were analyzed. For each cultivar, different letters indicate significant differences between treatments ($p \leq 0.05$) according to the LSD test. For more details of the experimental set-up see Fig. 1b.

11% in cv. Baguette Premium 11 and Huenpan, respectively, compared to plants that received additional 50 mm of irrigation water during grain filling. Thus, water stress was not severe. In the short awned cultivar Baguette Premium 11 (awns FW = 8.24 mg ear⁻¹), ear shading reduced GW_{ear} ca. 10% (non-significant; $p \leq 0.05$), whereas in cv. Huenpan (awns FW = 18.9 mg ear⁻¹) GW_{ear} was strongly reduced by shading the ear (28 and 26.6% in irrigated and rainfed conditions, respectively). Kernel number was not affected by shading treatments (Fig. 4, left panels).

3.3. Experiment 3. Crop shading

In an alternative approach to assess the contribution of ear photosynthesis, grain yield was compared in plants where the whole canopy (including the ear) or only the leaves were shaded (Fig. 1, panel b), thus leaving the ear as the main photosynthetically active organ of the plant. In this experiment, water-deficit reduced grain yield in both cultivars (Fig. 5). The decrease of total grain yield (rainfed compared to irrigation) was 17% and 20% in cvs. Klein Escudo and BioINTA 3000 respectively, thus, water stress was not severe. Under rainfed conditions GW_{ear} in the 'ear emerging' treatment was near identical to control (i.e. non-shaded) plants, irrespective of the cultivar. Thus, under rainfed conditions, photosynthesis of the ear seemed enough to compensate for the decrease of assimilation by the leaves. However, under irrigation, the GW_{ear} of 'ear emerging' treatment was lower, and statistically different ($p \leq 0.05$) from control plants. In either cultivar, GW_{ear} of the 'ear emerging' treatments under irrigation versus rainfed conditions (see gray bars in Fig. 5), were identical. Shading treatment did not cause a decrease of kernel number in any of the cultivars (Fig. 5, left panels).

We calculated the photosynthetic contribution of the ear to grain filling in this experiment (Table 2). As in Experiment 1, cultivar Klein Escudo showed a larger contribution of the ear, although this was significantly ($p \leq 0.05$) different from cv. BioINTA 3000 only under irrigated conditions. In both cultivars, this contribution appeared to be higher under rainfed conditions, but this difference was not statistically significant ($p \leq 0.05$).

Table 3 shows the decrease of stem dry weight between anthesis and the end of grain filling, dry matter translocation efficiency (DMT_e) and the contribution of preanthesis assimilates (CPA) to grain filling. In our study, DMT_e was ca. 23% and 15% in cvs. BioINTA 3000 and Klein Escudo, respectively, regardless of the irrigation regime (Table 3). The contribution of preanthesis stem assimilates

Table 3

Decrease of total stem dry weight during grain filling, dry matter stem retranslocation efficiency (DMT_e) and contribution of preanthesis assimilates of the stem to grain yield (CPA) in two cultivars of bread wheat under rainfed and irrigated conditions. Data of stem weight reduction are expressed as the difference in weight (mg) between seven days after anthesis and the end of grain filling. Dry matter stem retranslocation efficiency (DMT_e) and the contribution of preanthesis assimilates of the stem to grain yield (CPA) were calculated as described in Section 2. Means followed by the same letters are not significantly different ($p \leq 0.05$) according to LSD test.

Treatment	Stem weight reduction (mg culm ⁻¹)	DMT_e (%)	CPA (%)
cv. BioINTA 3000			
Rainfed	368 b	22.5 b	27.9 b
Irrigated	417 b	25.0 b	22.2 b
cv. K. Escudo			
Rainfed	138 a	15.0 a	13.0 a
Irrigated	144 a	13.3 a	10.9 a

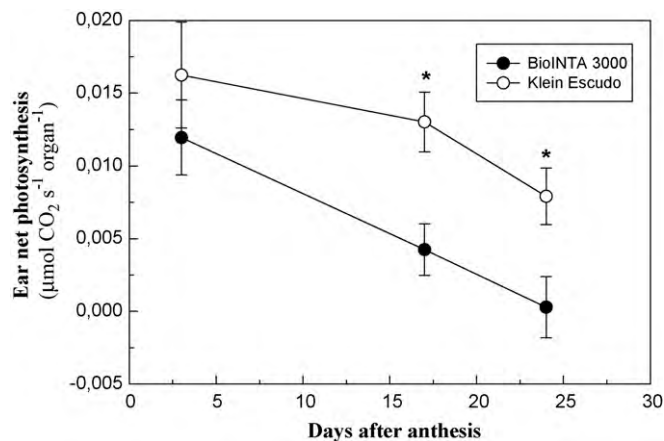


Fig. 6. Net photosynthetic rate of the ear during grain filling of cvs BioINTA 3000 and Klein Escudo. Each value represents the mean $\pm$ s.e. of four measurements. Significant differences ($p \leq 0.05$) between cultivars according to the LSD test are indicated with an asterisk.

to grain yield was unaffected by the water regime. CPA, i.e. the ratio of stem mobilized reserves to GW_{ear} , was 10.9% and 13.0% in cv. Klein Escudo under irrigated and rainfed conditions, respectively. In cv. BioINTA 3000 stem reserves accounted for 22.0 and 27.9% of GW_{ear} under irrigated and rainfed conditions, respectively.

3.4. Ear photosynthesis

Fig. 6 shows the net photosynthetic rate of the ear in cvs. Klein Escudo and BioINTA 3000 during the grain filling period. The photosynthetic rate was always higher in cv. Klein Escudo than in BioINTA 3000, although three days after anthesis this difference was not statistically significant ($p \leq 0.05$). Later in grain filling (17 days after anthesis) the photosynthetic rate of ears of cv. Klein Escudo was 3-fold higher than in cv. BioINTA 3000, and at 24 days after anthesis the difference between both cultivars was even higher.

3.5. Experiment 4. Inhibition of ear photosynthesis with DCMU

All previous experiments manipulated ear photosynthesis by reducing irradiance. In a different approach, we analyzed the contribution of ear assimilation to grain filling by inhibiting ear photosynthesis with DCMU. Photosynthetic electron transport rate (ETR; calculated from modulated chlorophyll fluorescence measurements, see Section 2) of glumes and awns was severely reduced in ears treated with DCMU, whereas flag leaf ETR was not affected (Fig. 7, panel a). Thus, DCMU was not translocated outside the ear, or spilled over the leaves during application. In the ear, the inhibition of ETR persisted (glumes) or even increased (awns) during grain filling, at least until fourteen days after the application of DCMU (Fig. 7, panel a). Consistently with the inhibition of photosynthesis in ear parts, GW_{ear} was reduced to a similar extent by shading or DCMU treatment (Fig. 7, panel b). Number of kernels per ear was not affected by DCMU (data not shown).

4. Discussion

4.1. Contribution of ear photosynthesis to grain filling: estimation through different experimental approaches

Although there are several physiological studies of ear photosynthesis (Ziegler-Jöns, 1989; Wang et al., 2001; Martinez et al., 2003; Tambussi et al., 2005), its actual contribution to yield is not well understood. The classical methodology to measure the contribution of ear photosynthesis to grain filling (i.e. shading with

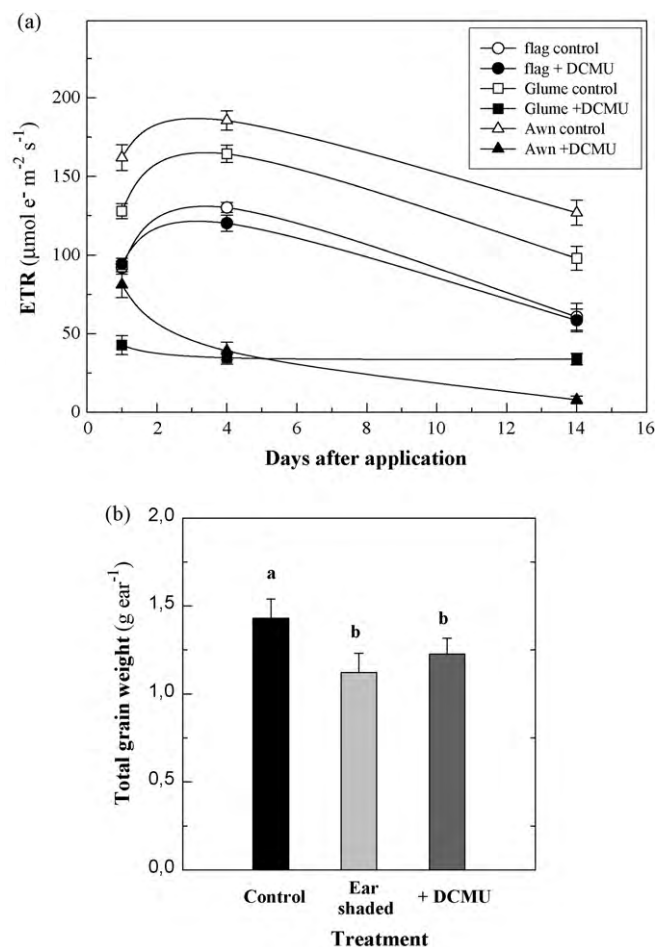


Fig. 7. Inhibition of ear photosynthesis with DCMU in Experiment 4 (greenhouse, cv. Arriero). *Panel a.* Electron transport rate (ETR) of the flag leaf, glumes (body of the ear) and awns in control and treated ears (+DCMU) during two weeks after DCMU application. Day 0 indicates the day of DCMU application. 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. *Panel b.* Grain weight per ear (GW_{ear}) in control, shaded and DCMU-treated ears. Values are the mean $\pm$ s.e. of five measurements. Different letters indicate significant differences between treatments ($p \leq 0.05$) according to the LSD test. For more details see panel a.

aluminum foil; e.g. Araus et al., 1993) has been criticized because ear temperature could be altered by this treatment, thereby hypothetically affecting grain weight through physiological processes other than photosynthesis (see a discussion of this issue in Tambussi et al., 2007). In wheat, temperatures above 15 °C during grain filling cause a decrease of final grain weight of 3–5% per °C (Wardlaw and Wrigley, 1994). We measured the temperature of control and shaded ears throughout the day with thermocouples inserted underneath the glumes, and did not find significant differences in temperature between control and shaded ears (Fig. 1, panel c), indicating that the effects of the ear shading treatment were not due to changes in temperature.

In addition to shading individual ears with aluminum foil, we analyzed the ear contribution through the use of shades covering the whole crop, or only the leaves with ears emerging through the shades. Although there were minor differences in the apparent contribution of ear photosynthesis estimated in this way compared to 'shading' with aluminum foil, the estimated relative contribution of the ear was similar and consistent with both experimental approaches, i.e. cv. Klein Escudo showed a higher ear contribution than cv. BioINTA 3000 (Table 2). Consistent with this difference between cultivars in their responses to ear shading, the actual

photosynthetic rate of the ears measured by IRGA was substantially higher in cv. Klein Escudo than in cv. BioINTA 3000.

Finally, instead of reducing irradiance, in Experiment 4 ear photosynthesis was inhibited with DCMU, a specific inhibitor of photosystem II and, thus, of photosynthetic electron transport (e.g. Allen and Holmes, 1986). The decrease of grain weight in ears treated with DCMU is further evidence for an important contribution of ear photosynthesis to grain filling. DCMU reduced GW_{ear} to the same extent as ear shading (Fig. 7, panel b), i.e. decreasing ear photosynthesis reduced grain weight irrespective of the experimental approach used to reduce photosynthesis. As far as we know, this is the first report where different, independent experimental approaches were used to assess the contribution of ear photosynthesis to grain filling.

4.2. Source limitation in modern germoplasm of wheat: the role of ear photosynthesis

Several evidences indicate that source limitation (or at least source-sink co-limitation) is emerging in modern cultivars of wheat. While in older Argentinean cultivars of bread wheat, for instance, grain weight is relatively insensitive to defoliation, i.e. yield is not limited by source activity, in modern cultivars with larger ears there are larger decreases of grain weight under defoliation treatments (Kruk et al., 1997). More recently it has been reported (Álvarez et al., 2008a, b) that modern Spanish and Italian cultivars of durum wheat are more responsive to defoliation and de-graining treatments (i.e. manipulations of source-sink ratio). Thus, assimilate availability may limit grain filling in modern cultivars, which have more grains per unit area and less vegetative biomass due to the presence of dwarfing genes (Álvarez et al., 2008a, b). Therefore, the potential contribution of ear photosynthesis to grain filling could be relevant in modern cultivars, even in the absence of abiotic stresses. In our study, defoliation reduced total grain weight per ear (GW_{ear}) around 25% in both cultivars. Shading of the ear reduced GW_{ear} even under non-stressful conditions (e.g. cv. Huenpan under irrigated conditions; see Fig. 4, lower panel), thus, grain filling could not be fully supported only by leaf photosynthesis and dry mass redistribution from vegetative structures. Moreover, when leaf and ear photosynthesis were eliminated simultaneously (defoliation *plus* shaded ear), the decrease of GW_{ear} was 57% and 63%, compared to intact plants in cv. BioINTA 3000 and Klein Escudo, respectively. The apparent lack of 'source limitation' of grain yield in previous works may be partly due to the fact that the photosynthetic role of the ear was not considered (e.g. Kruk et al., 1997; Ahmadi et al., 2009). The interpretation of source manipulation treatments must take into account compensatory mechanisms that may occur in the remaining photosynthetic tissues. There is evidence that when a photosynthetic source is detached, compensations in the remaining organs can occur (e.g. Chanishvili et al., 2005). Thus, photosynthetic rate is increased, compensating for the decrease of the photosynthetic area. The actual decrease of assimilate availability for grain filling cannot be simply predicted from the reduction of green leaf area, as in some earlier work (see references above). If such compensations occur in our case (e.g. if leaf photosynthesis increases to compensate for ear shading), this might mean that calculated contributions of ear photosynthesis are conservative, i.e. they could be even higher.

Finally, an additional possible advantage of the ear as a photosynthetic organ is its proximity to the sink. In fact, 49% of the carbon assimilated by the flag leaf moved to the grain, compared to 80% for ear-derived photosynthates (Carr and Wardlaw, 1965). In addition to participating in grain filling, the flag leaf exported assimilates to other parts of the plant (e.g. roots) (Carr and Wardlaw, 1965).

Changes in individual grain weight showed that kernels at distal positions in each spikelet (mainly, G3) were most affected by source

manipulation (in particular defoliation and ear shading; Table 1). Sandaña et al. (2007) also found that distal kernels are the most affected by decreases in source activity. Genetic gains in wheat yield have been associated with the increase of ear dry weight and kernel number (Calderini et al., 1999). Future increases in grain yield should be paralleled by an increase of photosynthetic activity, including that of the green parts of the ear. For example, multiovary lines have 2–3 grains per floret and more grains per plant (Monneveux et al., 2004). However, these multiovary lines do not have a higher grain yield (Reynolds et al., 2005), which suggests limitation by assimilate availability. Obtaining a higher number of kernels, e.g. through the use of the multiovary trait, will probably not increase grain yield unless this is paralleled by higher photosynthetic activity of leaves and the ear.

4.3. Contribution of ear photosynthesis under drought

Compared with the flag leaf, net photosynthesis of durum and bread wheat ears seems to be maintained under drought (e.g. Martínez et al., 2003; Tambussi et al., 2005). A greater capacity for osmotic adjustment capacity in bracts (glumes, lemmas, awns; Tambussi et al., 2005) and a concomitant higher relative water content, compared to the flag leaf, may account for the maintenance of photosynthetic activity in ear parts of droughted plants (Wardlaw, 2002; Tambussi et al., 2005; Tambussi et al., 2007 and references cited therein). Secondly, ear parts, including the green pericarp, can recycle the carbon dioxide emitted by respiration of the growing grains and other heterotrophic tissues, a well documented process in C_3 cereals such as wheat and barley (Kriedemann, 1966; Bort et al., 1996; Gebbing and Schnyder, 2001). CO_2 refixation is completely independent of the external sources of carbon dioxide, and thus, it is much less affected by environmental (water) stress. Thirdly, the degradation of chloroplast components and the decline in photosynthetic competence are delayed in the ear compared to the flag leaf (Martínez et al., 2003), i.e. the ear is a 'stay-green' organ that can continue to assimilate CO_2 late in the grain filling period.

Experiment 2 was carried out in the sub-humid Argentinean Pampas (Bordenave), where post-anthesis water deficit is a common phenomenon (www.smn.gov.ar, see Fig. 2, medium panel). In this study, the photosynthetic contribution of the ear was significant in cv. Huenpan (with long awns), whereas in the French cultivar Baguette Premium 11 (with short awns) the contribution of the ear was low and non-significant. Drought reduced grain yield in cv. Baguette Premium 11 but not in Huenpan, suggesting that the C contribution of ear photosynthesis, e.g. in cv. Huenpan, could represent a 'buffer' for grain filling when source limitations are exacerbated by drought. However, our data also suggest that even under 'non-stressful' conditions, photosynthesis of the ear could make an important contribution to grain filling (e.g. cv. Huenpan under irrigation, Fig. 4).

4.4. Role of awns and their contribution to grain filling

The photosynthetic organs of the ear can fix atmospheric CO_2 (net fixation) or refix CO_2 respired by growing grains. Although it is clear that awns represent the main part of the ear involved in net fixation of atmospheric CO_2 (Thorne, 1965; Evans et al., 1972; Blum, 1985; Ziegler-Jöns, 1989), the role of awns in grain filling of cereals is still controversial (Tambussi et al., 2007). In fact, positive (Blum, 1985; Chhabra and Sethi, 1989; Motzo and Giunta, 2002); partially positive (Bort et al., 1994), neutral (e.g. Foulkes et al., 2007) or even negative effects (Mc Kenzie, 1972) of the presence of awns have been reported. In our study, awn removal caused the larger decrease of grain weight in cultivars with higher FW awns ear^{-1} , which is consistent with the idea that larger awns have a positive effect on grain filling. However, we are aware

that mechanistic (causal) conclusions cannot be drawn from our experiments.

Even when the effect of de-awning was small (as in cv. BioINTA 3000), the contribution of the body of the ear (i.e. green pericarp, glumes and lemmas without the awns) was important (see Table 2). Bremner and Rawson (1972), measuring $^{14}\text{CO}_2$ fixation, showed that lemmas (including awns) were the photosynthetically most active bracts in bread wheat. However, it should be noted that when considering overall photosynthesis, refixation of respired CO_2 is non-quantified by techniques using $^{14}\text{CO}_2$ labeling.

Unlike awns, which are mostly involved in net CO_2 fixation, glumes and lemmas can assimilate both atmospheric as well as respired CO_2 , i.e. both net photosynthesis and refixation take place in the body of the ear (Gebbing and Schnyder, 2001). These authors showed that ca. 70% of the sucrose accumulating in bracts may come from fixation of respired CO_2 . Thus, cultivar differences in the contribution of ear photosynthesis to grain filling cannot be accounted for only by net photosynthesis of awns: differences in refixation rate (body of the ear; Tambussi et al., 2007) could be also involved and further research is needed to elucidate this question.

4.5. Remobilization and ear photosynthesis

As discussed above, remobilization of assimilates stored before anthesis (mainly fructans in the stem; Blum, 1998) is an important source of C when current photosynthesis is reduced during grain filling. In bread and durum wheat, the contribution of remobilization of stem assimilates ranges from 10% to 50% of final kernel weight, depending on genotype and water regime (e.g. Blum, 1998; Plaut et al., 2004; Ehdaie et al., 2006a, b, 2008). In our work, grain yield per ear was partially maintained even when the photosynthetic source was severely reduced (for instance, in defoliated/ear shaded and in all canopy shaded treatments; see Figs. 3 and 5), reinforcing the importance of retranslocation of preanthesis assimilates. We measured the decrease of stem dry weight between anthesis and the end of grain filling. Because respiration rate is negligible compared with remobilization (see references in Cruz-Aguado et al., 2000), the change of stem dry weight is a good estimate of the amount of water-soluble carbohydrates retranslocated during grain filling (Ehdaie et al., 2008). In our study, dry matter translocation efficiency (DMT_e) and the contribution of pre-anthesis assimilates of the stem to grain yield (CPA) were higher in cv. BioINTA 3000 than cv. Klein Escudo. Both cultivars seemed to reach final grain weight through different strategies. Whereas in cv. BioINTA 3000 there was a small contribution from ear photosynthesis (Table 2) and a higher contribution from stem retranslocation (Table 3), cv. Klein Escudo showed the opposite behavior. More research is needed to determine if this is a coincidental association occurring in this particular pair of cultivars, or if there is a negative correlation between the contributions of ear photosynthesis and redistribution of stem carbohydrates to grain filling. A negative association between ear and stem contribution to grain filling could be caused by compensatory changes in assimilate movement to the sinks.

5. Concluding remarks

In summary, ear photosynthesis makes a significant contribution to grain yield of bread wheat, from 13% to 33% in the absence of stress, and up to 22–45% under source limitations (e.g. defoliation, water deficit). Moreover, the ear shows a higher stimulation of net photosynthesis (compared to the flag leaf) under high CO_2 atmospheric conditions (Wechsung et al., 2000). Thus, the contribution of the ear to grain filling is likely to increase in the future under higher CO_2 and drought conditions. In addition, future increases of

grain number per ear (and/or increases in kernel weight) by breeding, with the concomitant increase of 'sink' demand, will require an increased assimilate availability to fill the grains. The selection of cultivars with higher ear photosynthesis (for instance, ears with long awns) could help meet this need for assimilates.

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