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Awn contribution to gas exchanges of barley ears

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Abstract

The effects of awn removal on ear gas exchange in four barley lines (Morex, Harrington, Steptoe, and TR306) were studied under a controlled environment using a Before-After Control-Impact Paired (BACIP) experimental design. From ear emergence to grain maturity, plants were grown in pots at either 60 or 90 % of soil water holding capacity. Gas-exchange measurements of ears were made 9 and 10 d after anthesis (DAA). On 11 DAA, awn removal was performed on half of the ears in each pot, followed by measurements on both intact and de-awned ears on 12 and 13 DAA. Net photosynthetic (P_N) and transpiration (E) rates decreased significantly with awn removal, but dark respiration (R_D) rate was not affected. We estimated for each ear a temperature-adjusted respiration rate (R_a) from R_D. When we corrected P_N with R_a, we found that rates of spikelet photosynthesis were largely underestimated. Moderate water stress had minimal effect on gas exchange of bracts and awns of the barley ear. Barley lines did not differ for any individual gas-exchange parameter.

Additional key words: BACIP design; *Hordeum*; net photosynthetic rate; respiration rate; transpiration.

Introduction

Ears of C_3 cereals are photosynthetically active and play an important role in providing saccharides during grain filling (Blum 1985). In barley, ear carbon exchange, transpiration, and respiration rates peak near anthesis, begin to decline 9 to 12 d after anthesis (DDA), and cease about 30 DDA (Kjack and Witters 1974). Estimates of the contribution made by ear photosynthesis to final grain mass of barley vary from as little as 13 % (Biscoe *et al.* 1973) to as much as 70 % (Thorne 1963). Thus, ear metabolism makes a critical contribution to world food production of C_3 cereals and should not be ignored. However, few physiological studies have been conducted on ears and bracts in the last five years (Wechsung *et al.* 2000, Tambussi *et al.* 2005). Furthermore, these essential parts of the cereal plants are ignored in current studies of functional genomics that solely focus on effects of biotic or abiotic stresses on cereal leaves (Wilson *et al.* 2004).

Studies of ear carbon assimilation rates are scarce for three reasons. First, a volumetric chamber is required to enclose the whole ear (Kjack and Witters 1974). Second, it is problematical to report gas exchanges per unit area, as done with leaf rates, because total ear area is very difficult to assess (Wechsung *et al.* 2000). Third, underestimation of ear photosynthesis has plagued many studies, because high rates of gross photosynthesis (P_G) may be matched by equally high caryopsis respiration during grain filling (Knoppik *et al.* 1986, Araus *et al.* 1993). Thus, low P_N reported for ears were misleading, allowing many investigators to conclude that ear photosynthesis was not worthy of further investigation.

Awned lines of C_3 cereals have more stable yields under warm and dry climatic conditions (Derera and Stoy 1973). Awns can photosynthesize throughout grain filling (Johnson *et al.* 1974). Barley awns account for as much as 90 % of gas exchanges of ears (Ziegler-Jons 1989a) and are the most photosynthetically active ear part of wheat and oats (Ziegler-Jons 1989b). Different ear gas exchanges of barley lines are closely related to their amount of awn tissue (Biscoe *et al.* 1973, Johnson *et al.* 1975, Blum 1985).

Awn contribution to gas exchange of barley ears has been investigated using isogenic lines differing in the

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Abbreviations: BACIP = Before-After Control-Impact Paired; DAA = days after anthesis; E = transpiration rate; *i*WUE = instantaneous water-use efficiency; P_N = net photosynthetic rate; P_G = gross photosynthetic rate; PPFD = photosynthetic photon flux density; R_a = temperature-adjusted respiration rate; R_D = dark respiration rate.

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presence or length of awns (Bort *et al.* 1994) or by simply removing awns (Biscoe *et al.* 1973, Paluska 1981, Ziegler-Jons 1989a). Awn clipping is the easiest method to study the contribution of awns to final grain mass (Paluska 1981).

Our objectives in this study were (*a*) to assess the contribution of awns to net and gross values of ear gas exchanges at early stages of grain filling, (*b*) to assess the effect of a moderate water stress on ear gas exchanges, and (*c*) to test for differences in response to awn removal among genetic lines in ear gas exchange.

Materials and methods

Plants: Four barley (*Hordeum vulgare* L.) lines were tested: six-rowed types Morex and Steptoe, and two-rowed types Harrington and TR306. They are parental lines to double haploid mapping populations available from the North American Barley Genome Program. Seeds were sown in plastic square pots (20 × 20 × 20 cm). Four pots were planted for each line. The soil was composed of 50 % composted bark, 40 % fine pumice, and 10 % Canadian Sphagnum (peat moss). Two weeks after emergence, 0.5 g of slow-release fertilizer (*Osmocote*, 19-12-16 of N-P-K, *Scotts Co*., Marysville, OH, USA) was added to each pot. For each line, two pots were randomly assigned to 90 and 60 % of water holding capacity with approximate soil water potentials of –0.01 and –0.05 MPa, respectively. The soil water holding capacity for each pot was determined gravimetrically by adding a known volume of water and measuring the volume of water that was retained after drainage. From planting until ear emergence, plants were grown in an environmentally controlled greenhouse located at Utah State University (Logan, UT, USA). Greenhouse air temperatures were set at 28/22 ºC (day/night). At ear emergence the pots were moved to an environmentally controlled growth chamber (*Conviron, CMP 3023, Controlled Environments***,** Winnipeg, Manitoba, Canada). Temperature was set at 28/12 °C (day/night), photoperiod at 16/8 h (light/dark), irradiance at 500 µmol m^{-2} s^{-1}, and relative humidity at 30 %. Soil was watered daily to the assigned water holding capacity. Seven days after emergence, all seedlings except the most vigorous one were removed from each pot.

In our greenhouse conditions, Steptoe showed abnormally late heading and small ears. Other semi-winter types of spring barley (such as Steptoe) had similar delayed development in short photoperiods (Reid and Wiebe 1968). Therefore, we decided not to include Steptoe data in analyses of gas exchange.

Gas exchange: Two to four ears, similar in size and stage of development, were measured in each pot. A portable photosynthesis system (*LI-6400*, *Li-Cor*, Lincoln, NE, USA) was used to measure gas exchange on attached ears using a custom-made *Plexiglas* chamber with a volume of 475 cm^3, in line to the open gas-exchange system. Peltier coolers and heaters in the apparatus head were used to control the temperature of air blown through the measuring chamber. Flow rate was maintained at 600 µmol s^{-1}. An experimental CO_2 concentration of 400 µmol mol^{-1} was maintained by a built-in gas mixing device. Data were recorded when gas-exchange parameters became stable. Gas exchange measurements were made on 9 and 10 DAA. On 11 DAA, awns were clipped on half of the ears selected for measurement in each pot. Subsequently, measurements were made on 12 and 13 DAA, on both intact and de-awned ears.

Computation of temperature-adjusted respiration (*R*$_a$): Measurements of ear dark respiration (R_D) were conducted in the last two hours of the 'artificial night' as regulated by the growth chamber. A temperature-response curve for R_D for each ear was established by varying air temperature in the measuring ear chamber between 15 and 35 °C in 2 ºC increments (data not shown). Hence, for the temperature at which ear gas exchange was measured in the presence of light, we were able to compute an adjusted respiration (R_a).

Other gas exchange measurements were done after the light had been on for at least 30 min. Instantaneous differences in CO_2 and water vapor concentrations, air temperature, relative humidity, and photosynthetic photon flux density (PPFD) were recorded simultaneously during the measurements. Values for P_N and transpiration rate (*E*) were calculated using the equations of Caemmerer and Farquhar (1981). P_G was computed as the sum of P_N and R_a. Instantaneous water-use efficiencies $i\mathrm{WUE}_N$ and $i\mathrm{WUE}_G$ were calculated as the ratios of P_N and P_G, respectively, to *E* (Condon *et al.* 2002). WUE of the awns alone for individual spikelets was calculated with both net and gross rates (Bort *et al.* 1994) comparing awned and de-awned ears.

Statistical analyses: The experiment was run twice (October 2002–January 2003; January–April 2003). These two sets of results were analyzed separately. A Before-After Control-Impact Paired (BACIP) experimental design was used for gas-exchange measurement. This design is used in environmental impact assessments when the time of a pending impact or activity is known (Smith 2002). The approach is based on comparing control experimental units (here, intact ears) to impacted experimental units (here, de-awned ears) measured before and after the impact (here, awn removal). In the control group, ears are intact in both before and after periods; in the impacted group, ears are intact in the before period and are de-awned in the after period. The control group serves as a temporal control. Measured variables should be similar for both control and impacted groups in the before period, prior to the implementation of the impact. Effects of the impact are assessed as deviations of the impacted group from the control group during the after period. We illustrate two possible outcomes using data generated by Exp. 1 (Fig. 1*A*,*B*). Mean P_N (Fig. 1*A*) for the de-awned group was similar to mean P_N for the control group prior to de-awning, but deviated dramatically from the control following de-awning, indicating an effect of de-awning. Mean temperature-adjusted respiration (Fig. 1*B*) tended to decrease from 9 to 13 DAA for both control and de-awned groups, but the decrease was similar for both groups, indicating little effect of de-awning.

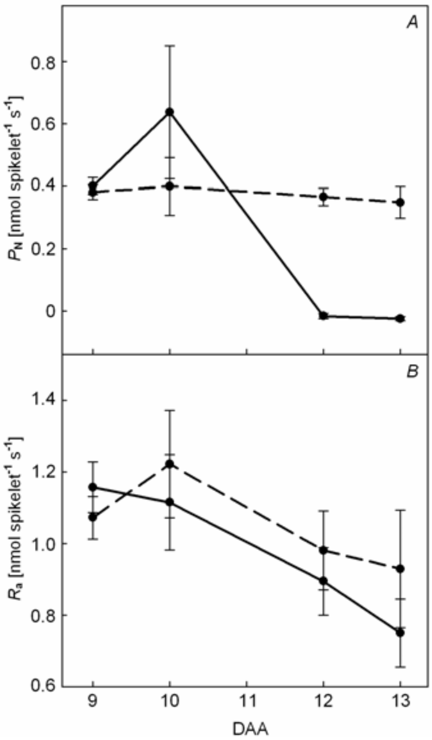

Fig. 1. Effect of awn removal on (*A*) net photosynthesis (P_n) and (*B*) temperature-adjusted dark respiration (R_a) of barley individual spikelet pooled over lines and water levels. *Solid and dashed lines* denote responses for de-awned and intact ears, respectively. Awns were removed from 'de-awned' ears at 11 DAA. Means of two experiments. *Error bars* represent two standard errors based on variability among a total of 24 pots.

Two-rowed lines (*e.g*. Harrington, TR306) have a smaller number of fertile spikelets per ear than does six-rowed Morex (data not shown), in accordance with multiple reports (Hochhalter and Horsley 2004). Therefore, rather than considering an interpretation at the whole ear level, we chose to analyze gas-exchange rates at the individual spikelet level by dividing the whole-ear gas exchange by the number of fertile spikelets recorded for that ear.

Data for temperature-adjusted R_a, *E*, P_N, P_G, and instantaneous water use efficiency (iWUE) were analyzed using analyses of variance of a four-way factorial in a mixed model design. Cultivar, water level, treatment (intact or clipped awns), and period (before or after awn clipping) were incorporated as fixed-effects factors. Using pot as a random-effects factor, total variance was partitioned into variability among pots, variability among treatment units within pots, variability among repeated measures within pots, and residual variability. Data from each experiment were analyzed separately. Means over multiple spikes receiving the same treatment in a pot were computed, and then these means were averaged over both days in each period for a pot to obtain the numerical values used as data in the analyses. Computations were obtained using *Proc MIXED* in *SAS for Windows 9.1.2*.

In a BACIP design, the effect of treatment is observed as deviation of treatment response from control one during the after-treatment (impact) period. Consequently, only interaction effects including both treatment and period factors are of interest and are presented in Table 1.

Correlations were analyzed with *Sigmaplot 2001* software (*SPSS*, Chicago, IL, USA). Scattered plots were made first. Then, different functions were attempted to obtain the best-fit curves including *Sigmaploid* (3 parameters) and inverse first order in *Polynomial*.

Results and discussion

We emphasize here only effects that were significant in both experiments, while also noting that Exp. 2 has less statistical power due to fewer R_D measurements, and consequently fewer degrees of freedom for tests of P_G, R_a, and gross rates of water-use efficiency (*i*WUE$_G$) (Table 1). Figs. 2–5 present results of Exp. 1 only.

Effect of awn removal on R_D of whole spikelet: The originality of this study is in the systematic measurement of R_D for each ear (see Materials and methods) along a temperature gradient. The increase of respiration as a function of temperature is usually estimated by a Q_{10} calculation, in which respiration rate is expected to double with an increase of 10 ºC (Amthor 1989) (Fig. 2). We found that the increase of R_D was lower than expected. For the 20–30 ºC range, calculated Q_{10} values were 1.58 and 1.49 for intact and de-awned ears, respectively (data not shown). These Q_{10} values are appreciably lower than 2 and may provide a more realistic estimation of ear respiration. The response to a temperature increase remained higher with awned ears than de-awned ones (Fig. 2). It indicates that awns react quicker to a temperature increase than the remainder of the ear. Nevertheless, awn removal did not seem to significantly affect ear respiration analyzed with values of R_a (Table 1). Previous reports indicate that glumelles, and especially the caryo-

Table 1. Observed significance levels (*p*-values) for interactive effects between water level (WL), barley line (GL), treatment (TR), and period (PE) from analyses of variance for gas-exchange parameters at the individual spikelet level for temperature-adjusted respiration (R_a), transpiration (E), net photosynthesis (P_N), gross photosynthesis (P_G), and instantaneous water-use efficiency based on rates of net photosynthesis (iWUE$_N$) and gross photosynthesis (iWUE$_G$) in Exp. 1 (*top line*) and Exp. 2 (*bottom line*). **Bold values** are *p*-values considered significant ($p<0.10$) in both experiments. df indicates the number of degrees of freedom.

Effect	Num	R_a		E		P_N		P_G		iWUE$_N$		iWUE$_G$	
	df	*p*	den df	*p*	den df	*p*	den df	*p*	den df	*p*	den df	*p*	den df
TR PE	1	0.117	6	**<0.001**	6	**<0.001**	6	0.017	6	**<0.001**	6	**<0.001**	6
	1	0.616	1	**<0.001**	6	**<0.001**	6	0.174	1	**<0.001**	6	**0.061**	1
WL TR PE	1	0.924	6	**0.005**	6	**<0.001**	6	0.216	6	0.143	6	0.284	6
	1	0.713	1	**0.093**	6	**<0.007**	6	0.425	1	0.057	6	0.208	1
GL TR PE	2	0.322	6	0.289	6	0.002	6	0.974	6	**0.005**	6	**0.093**	6
	2	9.494	1	0.630	6	0.145	6	0.523	1	**0.031**	6	**0.098**	1
WL GL TR PE	2	0.429	6	0.567	6	0.307	6	0.515	6	0.983	6	0.221	6
	2	0.962	1	0.147	6	0.048	6	0.781	1	0.180	6	0.090	1

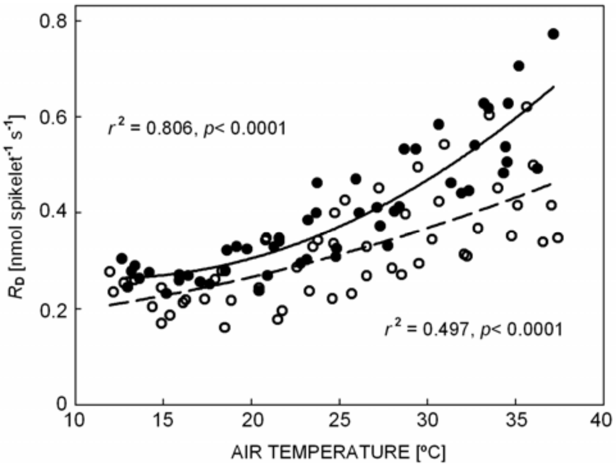

Fig. 2. Ear dark respiration (R_D) as a function of temperature for awned and de-awned ears. Results are presented on an individual spikelet basis. All measurements were performed during the 'after' period on intact ears (*solid circles*) and de-awned ears (*empty circles*). *Solid and dashed lines* denote responses for intact and de-awned ears, respectively.

psis, actively contribute to ear respiration (Knoppik *et al.* 1986). Minor awn contributions to ear respiration are consistent with reports made on barley (Biscoe *et al.* 1973, Johnson *et al.* 1975) and durum wheat (Araus *et al.* 1993).

Effect of awn removal on *E* of whole spikelet: Awn removal significantly impacted ear E in both experiments (Table 1). We also found that soil water content influenced the effect of awn removal. We present effects of awn removal on E for two water levels by combining data from all lines (Fig. 3*A,B*). Upon awn removal, there was a pronounced decrease (*ca*. 60–70 %) in E, indicating a significant awn contribution. The decrease was greater for well-watered ears [*ca*. 0.167 μmol(H_2O) spikelet^{-1} s^{-1}] than for water-stressed ears [*ca*. 0.125 μmol(H_2O) spikelet^{-1} s^{-1}]. This proportional reduction is much higher than that reported by Blum (1985) (10 %) but is comparable to that found by Biscoe *et al.* (1973) (73 %).

Effect of awn removal on P_N and P_G of whole spikelet: Same-scale representation of both P_N and P_G for both periods and both treatments clearly indicated a considerable underestimation of photosynthetic rates when measured as P_N (Fig. 4*A,B*), with respiration rates per spikelet (*i.e.* R_a) dwarfing net photosynthetic rates (Fig. 4*A,B*). It is likely that a large release of CO_2 by the caryopsis in formation was occurring at 12–13 DAA (after period) in both intact and de-awned ears. For wheat ear, Knoppick *et al.* (1986) reported that maintenance respiration of bracts and respiration of kernels were large components of ear respiration with the latter contributing about twice as much as the former one.

Awn removal reduced P_N (Table 1); in fact, P_N for de-awned ears was close to zero. There was no statistical evidence of an effect of awn removal on P_G (Table 1). Hence, P_G would provide a smaller estimation of awn relative contribution (Fig. 4*A,B*). The use of P_N to assess awn contribution may lead to a relative overestimation of that contribution.

Gas exchange of plants is usually reported per unit surface area. For grass ears this approach is complicated by the complexity in the shapes of glumelles, awns, and rachis. An alternative method based on digital imaging has been recently suggested and may be helpful in some studies (Wechsung *et al.* 2000). A few researchers have emphasized that P_N values for whole ears of barley or wheat during grain filling are misleading (Knoppik *et al.* 1986, Araus *et al.* 1993, Bort *et al.* 1996, Tambussi *et al.* 2005) due to high respiratory rates of the caryopsis in formation. Indeed, it is not the grain area, but the grain mass and its relative stage of filling that have the largest antagonistic influence on rates of ear P_N. In this study, since we opted to report gas exchange rates per fertile spikelet, respiratory contribution of each grain during filling is better accounted for. There are no previous examples of reporting ear gas exchanges per fertile spikelet. This experimental approach is particularly helpful in the comparative study of two and six-rowed barley ears.

Effect of awn removal on *i*WUE of whole spikelet: For intact ears, values of *i*WUE$_N$ were about 1.5 µmol(CO_2) mmol^{-1}(H_2O) on average (Fig. 5*A*). This value is similar to those observed previously for awned ears of barley at 5 and 10 DDA (Bort *et al*. 1994). Mean awn *i*WUE$_N$, calculated as indicated above, is of the order of 3 µmol(CO_2) mmol(H_2O) (Exp. 1, $\overline{\chi}$ = 2.640±0.317; Exp. 2, $\overline{\chi}$ = 3.242±0.200). These values are 50 to 100 % higher than those reported by Bort *et al.* (1994) at 5 and 10 DDA. Calculation of the mean awn *i*WUE$_G$ using gross rates of photosynthesis generates similar results (Exp. 1, $\overline{\chi}$ = 1.958±0.960; Exp. 2, $\overline{\chi}$ = 3.089±0.404). Nevertheless, *i*WUE$_G$ for the whole ear (*i.e.* individual

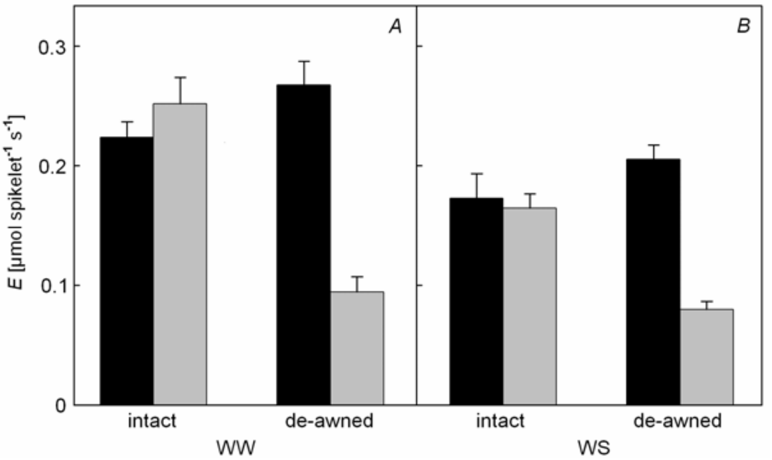

Fig. 3. Effect of awn removal on ear transpiration rate, *E* for intact ear and de-awned ears pooled over lines at two water levels (WW: well-watered, *A*; WS: water-stressed, *B*). *Black and gray bars* represent values for before (9–10 DAA) and after (12–13 DAA) periods, respectively. Results are from Exp. 1. *Error bars* represent two standard errors based on variability among 6 pots.

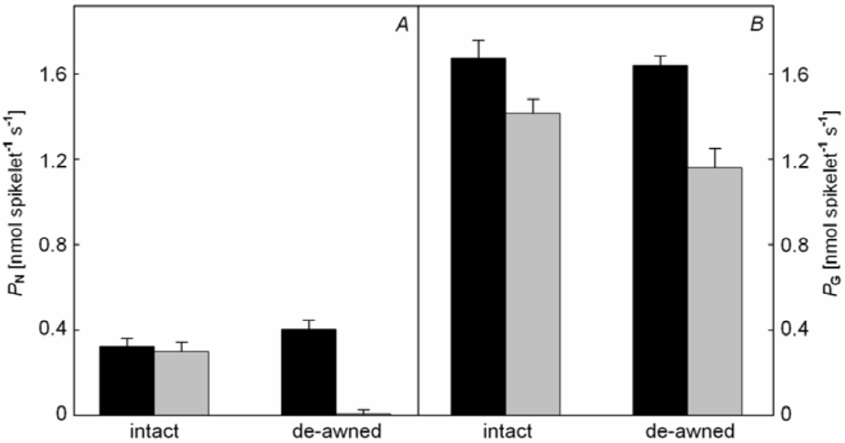

Fig. 4. Effect of awn removal on (*A*) net (P_N) and (*B*) gross (P_G) photosynthetic rates per spikelet for intact and de-awned ears pooled over lines and water levels. *Black and gray bars* represent values for before (9–10 DAA) and after (12–13 DAA) periods, respectively. *Equal vertical axis scaling* emphasizes the discrepancy between P_N and P_G values. Results are from Exp. 1. *Error bars* represent two standard errors based on variability among 12 pots.

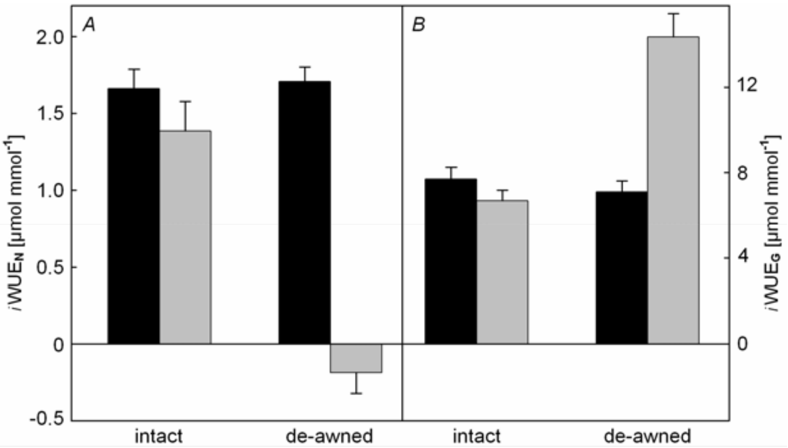

Fig. 5. Effect of awn removal on net water-use efficiency (*i*WUE$_N$) (*A*) and gross water-use efficiency (*i*WUE$_G$) (*B*) for intact and de-awned ears pooled over lines and water levels. *Black and gray bars* represent values for before (9–10 DAA) and after (12–13 DAA) periods, respectively. Results are from Exp. 1. *Error bars* represent two standard errors based on variability among 12 pots.

spikelet in our study) is four-fold higher than that of *i*WUE$_N$ (Fig. 5*A*,*B*). A difference of similar (three-fold) magnitude between *i*WUE$_N$ and *i*WUE$_G$ for whole ears of durum wheat was previously reported (Araus *et al.* 1993), though with no attempt at interpretation. Awn removal had a strong effect on both evaluations of *i*WUE (Table 1). However, the effect of awn removal on spikelet WUE could be interpreted quite differently depending on whether we look at *i*WUE$_N$ or *i*WUE$_G$. With the former, we would conclude that awns have a high specific WUE because their removal coincided with a decrease in WUE of the de-awned spikelet (Fig. 5*A*). On the contrary, the use of *i*WUE$_G$ would lead to the conclusion that awn WUE is being overestimated (Fig. 5*B*). The effect of awn removal is not the same for all lines (Table 1). Unfortunately, though these interactive effects were found in both experiments, the ranking of genetic lines for both estimated values of *i*WUE differed between the two experiments. Hence, it is difficult to conclude to what extent the three genetic lines tested in this study differed in their respective awn contribution to whole ear WUE.

In conclusion, at 11 DAA we clipped the awns to assess their relative contribution to gas exchange of individual spikelets. We found that awn removal had little effect on respiration rates but it caused a drastic reduction in transpiration, especially in well-watered conditions. Evaluation of awn contribution to photosynthetic gas exchange was rendered difficult by the large release of respiratory CO_2 from the filling caryopsis. When photosynthetic rates were not corrected for respiration, we found concurrent underestimation of photosynthetic rates and overestimation of awn relative contribution.

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