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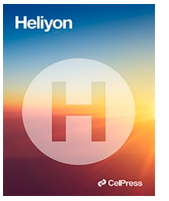

Contributions of glume and awn to photosynthesis, ^{14}C assimilates and grain weight in wheat ears under drought stress

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ABSTRACT

Ear photosynthesis plays a key role in wheat photosynthesis during the grain filling stage, particularly under drought stress. Thus, dissecting the responsibilities of the glume and awn in photosynthetic carbon fixation and assimilates transportation during the grain filling stage in spikes is imperative. In this study, the detachment of the glume (DG) and awn (DA) of a wheat variety (Pubing143) was used to estimate their influences on ear photosynthesis and dry matter distribution. Radioactive carbon-14 (^{14}C) isotope was detected by a multifunctional liquid scintillation counting system. The accumulation of ^{14}C assimilates and their contributions to grain weight were then calculated. Under well-watered conditions, ear photosynthesis was reduced by 16.8 % and 46.2 % 25 d after anthesis (DAA) in the de-glumed control (DGC) and de-awned control (DAC) treatments, respectively, compared with the intact ear control (IEC). Under drought stress, ear photosynthesis was reduced by 46 % and 74.2 % at 25 DAA after removing the glume and awn, respectively. Under normal conditions, the number of ^{14}C assimilates of DGC, and DAC was reduced by 14.6 % and 20.9 % in grains at 25 DAA, respectively, compared with the IEC. Compared with IED, the ^{14}C assimilates of DGD, and DAD declined by 17.2 % and 27 %, respectively, in grains at 25 DAA under drought conditions. Under well-watered conditions, the grain weight per pot was reduced by 11.2 % and 25.4 % in the de-glumed control (DGC) and de-awned control (DAC) treatments, respectively, compared with the intact ear control (IEC). The grain weight per pot was further reduced after removing the glume and awn (16 % and 32.2 %, respectively) under drought stress. Furthermore, the awn contribution to grain weight was twice that of the glume. Our results suggest that the glume and awn of ears play prominent roles during grain filling in wheat, especially under drought stress, and that the awn is more crucial than the glume.

1. Introduction

Wheat (*Triticum aestivum* L.) is the most important food crop in arid and semiarid regions of northern China [1–3]. The principal

Abbreviations: DA, de-awned ear; DAA, days after anthesis; DAC, de-awned ear control; DAD, de-awned ear + drought stress; DG, de-glumed ear; DGC, de-glumed ear control; DGD, de-glumed ear + drought stress; IE, intact ear; IEC, intact ear control; IED, intact ear + drought stress; Pn, net photosynthetic rate; RWC, relative water content; Tr, transpiration rate.

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abiotic stress limiting wheat yield is drought, which restricts photosynthesis, induces early senescence and eventually reduces plant yield [4,5]. Photosynthesis is a key process in drought stress response [6,7]. Drought stress perturbs physiological processes within plants, such as reducing chlorophyll content and enhancing canopy temperature, leading to a reduction in photosynthesis and other metabolic activities [8]. In addition, drought stress triggers the production of ROS, which results in the deterioration of membrane integrity, causing a reduction in the relative water content of leaves [9]. Inefficient physiological processes trigger metabolic activity, leading to low agronomic yields in terms of grain number, weight and plant biomass [8].

Generally, the flag leaf is considered the principal photosynthetic assimilation organ in wheat [10,11]. However, studies have suggested that ear photosynthesis is a key photoassimilate process that sustains grain filling [12–15]. According to the natural abundance of carbon isotope ($\delta^{13}C$) in wheat organs, carbon assimilates from flag leaves in wheat are mostly used for shoot growth [16], and a larger fraction of the assimilates stored in grains is derived from ears [17]. When wheat plants are labeled with $^{14}CO_2$ in the middle grain filling phase, a greater portion of the ^{14}C assimilates is allocated to the ears, and most of the ^{14}C assimilates from the ears are transferred to the grains [18,19]. Based on gene expression and physiological evidence, ears perform better than flag leaves under

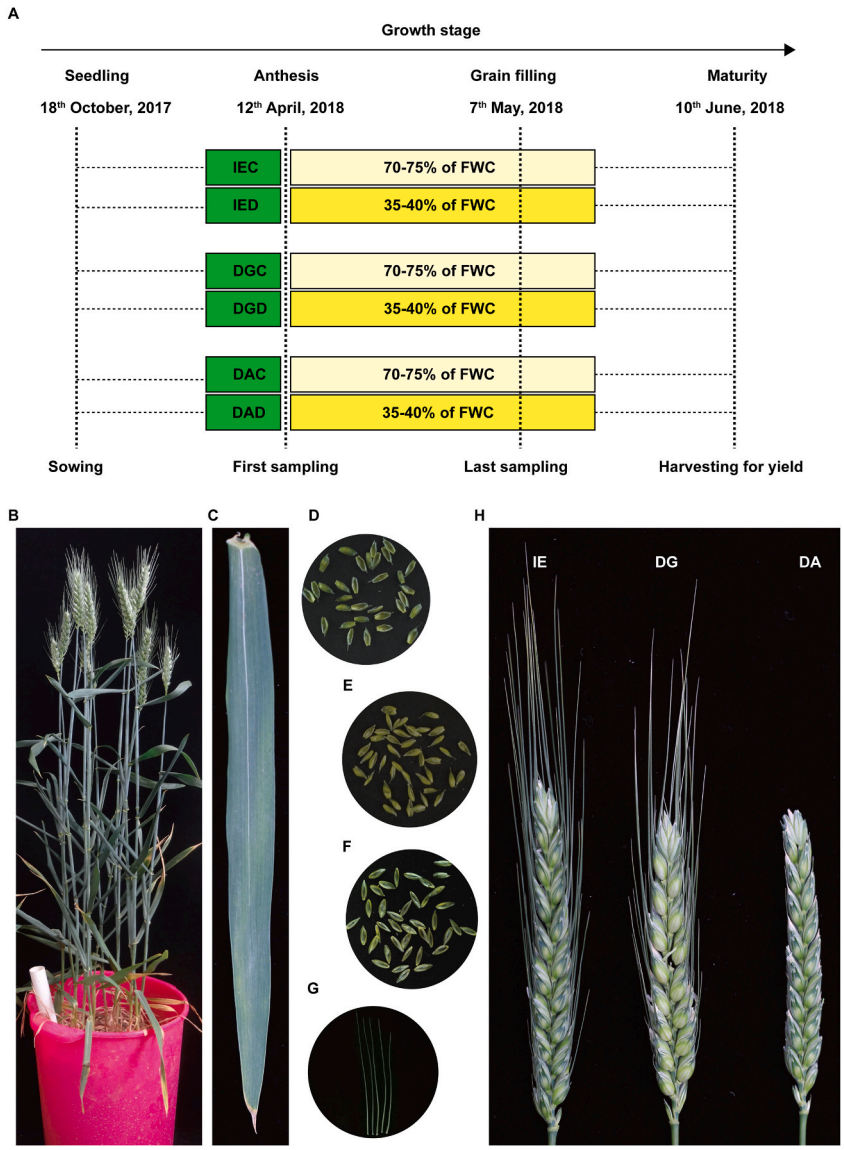

Fig. 1. An overview of the experimental design and treatments. **(A)** Glumes and awns of the ears were removed with scissors at 0 DAA. The soil water content of the control and drought stress treatments was maintained at 70%–75 % and 35%–40 % of field capacity, respectively. Six treatments were included: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress. The sampling or harvesting time is indicated in figure. **(B)** A pot experiment with wheat at anthesis. Flag leaf **(C)**, glume **(D)**, lemma **(E)**, palea **(F)**, and awn **(G)** of wheat. **(H)** The phenotypes of the intact ear (IE), de-glumed ear (DG), and de-awned ear (DA) treatments.

drought stress in durum wheat [6]. The major organs of the ear are the awns and glumes. The awn, filiform, and sclerophyllous prolongations of the lemma doubles the net photosynthetic rate of ears during grain filling under irrigated conditions, and the proportion of ear-contributed photosynthesis increases from 13% to 24 % in awnless ears, and from 34% to 43 % in awned ears under drought [20]. Glume is the closest organ to the grain and has a particular cellular and chloroplast allocation associated with its specific metabolism and sustained grain maturity [21–23]. It can contribute to nutrient distribution and photoassimilate conservation, which are transported to developing grains [24].

To completely identify the roles of ear organs, researchers have most often used the detachment of some wheat organ, such as stem defoliation and awn removal at the anthesis stage [13,25], the inhibition of photosynthesis by shading [12,13,25,26] and application of herbicides [27,28]. However, the vital roles of the glume and awn remain unclear. The ear makes outstanding photosynthetic contributions, the study of which might improve the understanding of how to enhance photosynthetic ability under drought conditions [29]. The importance of glumes and awns has been observed in their contributions to grain yield [20,25,30]. The detachment approach and carbon isotope traces have been used to analyze the respective photosynthesis contributions of wheat organs, such as the flag leaf and ear [19,25].

In this study, we combine the detachment of organs with carbon isotope traces to simultaneously illuminate their specific functions and the percentages of organ contributions to photosynthesis and assimilate translocation. The study provides valuable evidence regarding ear traits that could be regarded as vital indicators for breeding new material for dryland wheat and lays a theoretical foundation for exploring the capacity of yield increases in wheat.

2. Materials and methods

2.1. Plant material and experimental setup

A pot experiment was conducted in a waterproof greenhouse. The wheat variety Pubing 143 was used. The soil field capacity was 29.2 %. Twenty seeds were sown in each pot and thinned to 14 seedlings per pot at the three-leaf stage. The tillers were removed before the jointing stage. The experimental design is shown in Fig. 1A. Wheat plants that bloomed on the same day were marked with tags. The glumes and awns of the ears were removed with scissors at 0 d after anthesis (DAA). The soil water content of the control and drought stress treatments was maintained at 70%–75 % and 35%–40 % of the soil field capacity, respectively. The pots were weighed and supplemented with water to the standard daily.

We used six treatments: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress. The sampling and harvesting times are indicated in Fig. 1. Twelve replicate pots were prepared for each treatment group. The flag leaf and ear organs (glume, lemma, palea, and awn) of wheat are shown in Fig. 1B–G. The phenotypes of the intact (IE), de-glumed (DG), and de-awned (DA) ears are shown in Fig. 1H.

2.2. Analysis of net photosynthetic rate (P_n) and transpiration rate (T_r) of flag leaf and ear

The P_n and T_r values of flag leaves were directly measured by a portable gas-exchange photosynthesis system (LI-6400 XT, LiCor, USA). The P_n and T_r of the ears were determined using a special cylindrical chamber connected to a portable photosynthetic system, as in Ding [11,31]. All measurements were performed 0, 6, 18, and 25 DAA. The ear surface area was calculated according to the equation of Zhang [32]. Six biological replicates were analyzed.

2.3. Determination of relative water content (RWC)

Ear organs (glume, lemma, palea, and awn) and flag leaves were collected at 6, 18, and 25 DAA. RWC was determined according to the method of Nemati [33]. Six biological replicates were analyzed.

2.4. Assay of radioactive carbon isotope ^{14}C labeling of assimilates

Twelve representative ears per treatment that flowered on the same day were randomly selected and labeled with $^{14}CO_2$ on a sunny day at 6 DAA. Each ear was placed in a polyethylene plastic bag (100 mL) and sealed. Five milliliters of $^{14}CO_2$ with 81.77×10^4 Bq L^{-1} CO_2 intensity was injected by syringe into the bag according to the method of Jia [19]. The ears and flag leaves of labeled plants were harvested at 6 DAA after 1 h of labeling, 18 DAA, and 25 DAA. Radioactive carbon isotopes were detected using a multifunctional liquid scintillation counting system (LS-6500, Beckman, USA) and expressed as counts per minute (cpm). Disintegrations per minute (dpm) were corrected using counting efficiency and quench correction. The ^{14}C-assimilate distribution ratio (%) in different organs was calculated using the following equation: ^{14}C assimilate distribution ratio (%) = radioactivity of the organ (dpm)/total radioactivity (dpm) × 100. Four biological replicates were analyzed.

2.5. Determination of dry matter accumulation of ears

Ears were sampled at 6, 18, and 25 DAA and immediately separated into glume, lemma, palea, awn, and grain. Dry matter accumulation was determined according to the method of Jia [19]. Six biological replicates were analyzed.

2.6. Analysis of grain weight and organ contribution

Grain weight was determined from wheat ears harvested at maturity. Agronomic traits, including aboveground biomass per pot, fertile spikelets, infertile spikelets, 1000-grain weight, and grain weight per pot, were obtained. Five pots were analyzed per treatment.

The photosynthetic contributions of the glume and awn of the ear to grain filling (organ contribution) were calculated based on the equations of Maydup [13] and Sanchez-Bragado [28], with some modifications under normal and drought conditions.

Glume contribution (%) = [1-GW_{ear} of DA ear/GW_{ear} of IE] × 100

Awn contribution (%) = [1-GW_{ear} of DA ear/GW_{ear} of IE] × 100, where GW_{ear} is the grain weight per ear.

2.7. Statistical analysis

Data analyses were performed using Microsoft Excel 2016. Duncan's multiple range analysis at $P<0.05$ was used to detect significant differences by using SPSS statistical software. Figures were created using GraphPad Prism 7.0 and further processed using Adobe Illustrator CC software. The error bars represent standard error (SE).

3. Results

3.1. P_n and T_r of the flag leaf and ear

The P_n of the flag leaf decreased during the grain filling period (Fig. 2A). The P_n of the ear increased at 6 DAA and then decreased during the grain filling phase (Fig. 2C). The P_n values of the flag leaf and ear decreased under drought stress. Compared with intact wheat, the removal of glumes and awns caused significant reductions in the P_n of the ear but did not effect on the P_n of the flag leaf. In addition, the P_n of the DG ears decreased less than that of the DA ears. Compared with the control (IEC, DGC, and DAC treatments), the P_n of the ear decreased by 15.1 %, 17.5 %, and 25.5 % at 18 DAA in the IED, DGD, and DAD treatments, respectively. The trend of T_r was consistent with that of P_n. During the grain filling phase, the T_r of the flag leaf was always reduced (Fig. 2B), and the T_r of the ear

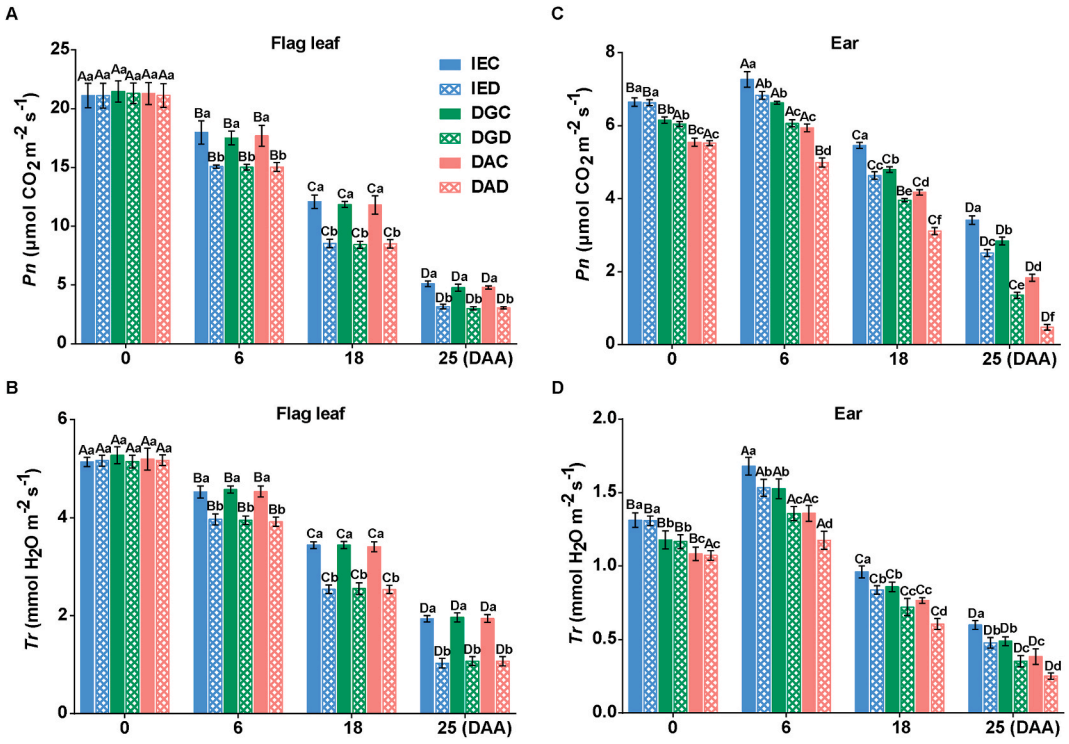

Fig. 2. The P_n and T_r of the flag leaf **(A, B)** and ear **(C, D)** in de-glumed and de-awned ears under drought stress. Capital letters indicate significance at $P < 0.05$ among different DAA under the same treatment. Lowercase letters represent significance at $P < 0.05$ among different treatments simultaneously. Six treatments were included: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress. P_n-net photosynthetic rate; T_r-transpiration rate; DAA: day after anthesis.

was first increased and then decreased (Fig. 2D). Compared with the control, the T_r of the flag leaf and ear declined. The T_r of the DG and DA ears was significantly lower than that of the intact ear. The decline in the DA ear was greater than that in the DG ear.

3.2. Influence of drought stress on RWC in wheat

The RWCs of the glume, lemma, palea, awn, and flag leaves decreased from 6 to 25 DAA during the grain filling phase. The RWCs of the remaining organs (glume, palea, awn, and flag leaf) remarkably decreased in the IED, DGD, and DAD treatments after drought

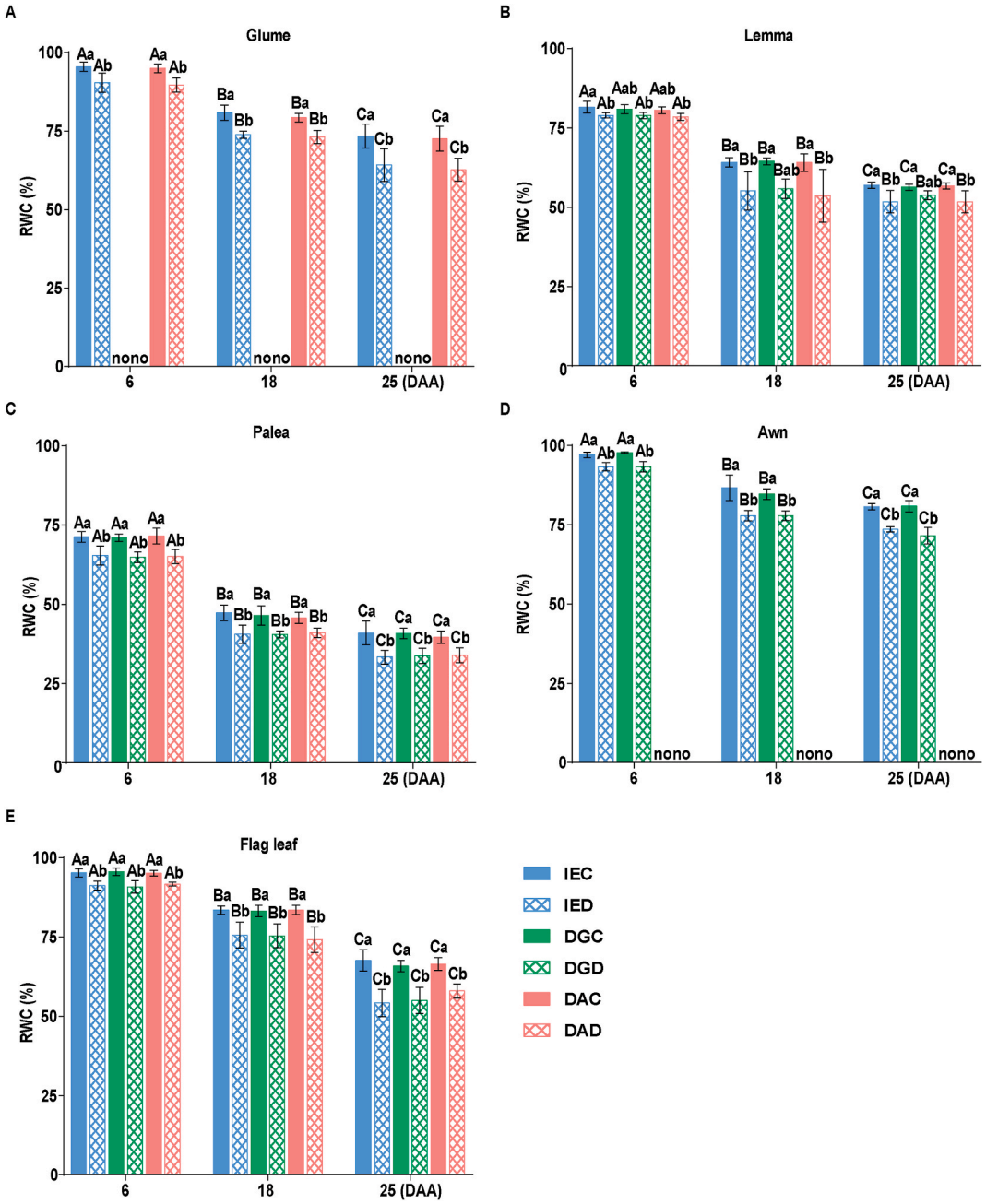

Fig. 3. RWC of the ear organs and flag leaf in the de-glumed and de-awned ears under drought stress. **(A)** Glume, **(B)** Lemma, **(C)** Palea, **(D)** Awn, and **(E)** Flag leaf. Capital letters indicate significance at $P < 0.05$ among different DAA under the same treatment. Lowercase letters represent significance at $P < 0.05$ among different treatments simultaneously. Six treatments were included: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress. RWC-relative water content. DAA: day after anthesis.

stress compared with those in the IEC, DGC, and DAC treatments (Fig. 3A–E). The RWCs of the glume, lemma, palea, awn, and flag leaves decreased by 12.6 %, 9.2 %, 18.6 %, 8.8 %, and 19.8 %, respectively, in the IED treatment at 25 DAA, compared with IEC. After removal of the glume, the RWCs of the lemma, palea, awn, and flag leaves were reduced by 4.5 %, 17.4 %, 11.5 %, and 16.4 %, respectively, in the DGD treatment at 25 DAA, when compared with the DGC treatment. After detachment of the awn, the RWCs of the glume, lemma, palea, and flag leaves decreased by 13.6 %, 8.8 %, 14.4 %, and 12.7 %, respectively, in the DAD treatment at 25 DAA, compared with DAC. The RWCs of the remaining organs showed no significant changes after the glume and awn removal treatments compared with those of the intact ear.

3.3. Differences in radioactivity and distribution ratio of ^{14}C assimilates

The $^{14}CO_2$ tracer test showed that the radioactivity of ^{14}C assimilates and that the distribution ratio of ^{14}C assimilates of grains was elevated from 6 to 25 DAA but declined in the glume, lemma, palea, and awn during the grain filling phase. In the awn, the content of ^{14}C assimilates and the partition ratio of ^{14}C assimilates were significantly higher than those in the glume, lemma, and palea. A small amount of ^{14}C was assimilated into the flag leaves.

The radioactivity of ^{14}C assimilates decreased by 28 %, 30.2 %, and 33.6 % in grains in IED, DGD, and DAD, respectively, 25 DAA after drought treatment **(Table 1)**. Compared with the IEC, the partition ratio increased significantly in lemma (7.3 %), palea (1.3 %), awn (2.4 %), and grain (3 %) in the DGC treatment. Moreover, the ratio was higher in the glume (4.7 %), lemma (3.6 %), palea (2.9 %), and grain (6 %) in the DAC treatment at 6 DAA than that in the IEC. Under drought stress, the distribution ratio of ^{14}C assimilates was elevated in the glume, lemma, and awn (but not in the palea) and decreased in the grain in the IED, DGD, and DAD treatments. During the grain filling phase (6–25 DAA), the ^{14}C assimilates from the glume, lemma, palea, and awn were withdrawn and transported into the grains. The distribution ratio of ^{14}C assimilates in the grain increased from 48.1%-54.1 % to 74.4%–81.2 % **(Table 2)**.

3.4. Effects of drought stress on dry matter accumulation in ears

Dry matter accumulation in the glumes, lemmas, paleae, and awns gradually decreased from 6 to 25 DAA (Fig. 4A–E and Table 3). Dry matter content decreased under drought stress. Compared with the IEC, the dry matter of the glume and awn were elevated by 2.8 % and 3.6 % at 25 DAA in the DAC and DGC treatments, respectively. However, drought counteracted the rising effect and reduced the dry matter. Compared with that in IEC, the dry matter of the lemma increased by 18.8 % in DGC but declined by 2.6 % in DAC at 25 DAA. Under drought conditions, dry matter increased by 16.9 % and decrease by 11.6 % in DGD and DAD, respectively, compared with the lemma in IED at 25 DAA. There were no significant differences in the dry matter of the palea among the IE, DG, and DA treatments. Compared with that of IED, the grain dry matter of DGD and DAD was reduced by 16.4 % and 31.6 %, respectively, at 25 DAA under drought stress. As shown in Table 3, the tendency of dry matter accumulation was consistent with that of the dry matter.

Table 1
Radioactivity of^{14}C assimilates (dpm value) in DG and DA ears under drought stress.

Treatments	Flag leaf	Glume	Lemma	Palea	Awn	Grain
6 DAA						
IEC	20.19 ± 1.09 Aa	196.31 ± 10.79 Aa	150.51 ± 7.27 Ac	123.39 ± 4.55 Aa	243.22 ± 8.45 Aa	680.43 ± 14.98 Ca
IED	18.79 ± 0.38 Ab	168.50 ± 2.19 Ab	124.60 ± 6.91 Ad	95.01 ± 4.63 Ab	217.95 ± 5.54 Ab	490.01 ± 11.29 Cd
DGC	17.36 ± 0.88 Ac	no	220.10 ± 9.33 Aa	122.73 ± 4.74 Aa	240.53 ± 7.83 Aa	627.77 ± 13.48 Cb
DGD	15.36 ± 0.67 Bde	no	172.48 ± 2.49 Ab	94.43 ± 4.77 Ab	217.60 ± 2.96 Ab	443.22 ± 7.48 Ce
DAC	15.71 ± 0.51 Ad	196.73 ± 9.41 Aa	150.23 ± 5.19 Ac	122.84 ± 6.67 Aa	no	571.71 ± 9.77 *Cc*
DAG	14.29 ± 0.66 Ae	168.21 ± 4.91 Ab	124.42 ± 5.01 Ad	94.39 ± 5.50 Ab	no	409.64 ± 7.84 Cf
18 DAA						
IEC	20.96 ± 1.38 Aa	127.98 ± 3.41 Ba	97.34 ± 4.75 Bb	87.16 ± 2.82 Ba	150.37 ± 5.82 Ba	928.51 ± 18.65 Ba
IED	19.54 ± 0.48 Ab	115.31 ± 4.03 Bb	83.36 ± 7.49 Bc	75.61 ± 3.91 Bb	128.30 ± 2.44 Bb	636.50 ± 14.19 Bd
DGC	18.86 ± 0.27 Ab	no	117.12 ± 4.03 Ba	86.62 ± 3.16 Ba	147.31 ± 3.04 Ba	806.35 ± 17.54 Bb
DGD	17.36 ± 0.67 Ac	no	86.38 ± 3.79 Bc	68.42 ± 2.56 Bc	126.67 ± 2.26 Bb	545.33 ± 8.46 Be
DAC	15.66 ± 0.48 Ad	119.81 ± 1.89 Bb	96.81 ± 4.52 Bb	85.36 ± 2.37 Ba	no	735.51 ± 3.12 Bc
DAG	14.02 ± 0.30 Ae	95.58 ± 1.67 Bc	82.47 ± 2.58 Bc	64.67 ± 0.74 Bc	no	479.14 ± 5.41 Bf
25 DAA						
IEC	20.71 ± 1.02 Aa	83.39 ± 4.17 Ca	66.84 ± 3.42 Cbc	55.59 ± 3.37 Ca	94.50 ± 5.86 Ca	1079.08 ± 17.69 Aa
IED	19.04 ± 0.43 Ab	68.13 ± 3.42 Cb	54.23 ± 3.30 Cd	45.92 ± 5.57 Cb	79.30 ± 2.45 Cb	776.69 ± 19.51 Ad
DGC	18.61 ± 0.99 Ab	no	85.28 ± 2.53 Ca	55.05 ± 2.46 Ca	84.82 ± 2.04 Cb	921.33 ± 12.48 Ab
DGD	16.36 ± 0.91 ABc	no	71.26 ± 3.25 Cb	44.63 ± 1.30 Cb	67.93 ± 1.06 *Cc*	643.33 ± 14.97 Ae
DAC	15.41 ± 0.80 Ac	66.05 ± 3.09 Cb	63.83 ± 1.97 *Cc*	52.82 ± 1.40 Ca	no	853.98 ± 14.45 Ac
DAG	13.52 ± 0.86 Ad	51.43 ± 2.42 *Cc*	51.75 ± .3.44 Cd	41.92 ± 2.86 Cb	no	567.26 ± 16.76 Af

Six treatments were included: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress. DAA: day after anthesis. Capital letters indicate significance at $P < 0.05$ among different DAA under the same treatment. Lowercase letters represent significance at $P < 0.05$ among different treatments simultaneously.

Table 2
Distribution ratio of ^{14}C assimilates in DG and DA ears under drought stress.

Treatments	Flag leaf (%)	Glume (%)	Lemma (%)	Palea (%)	Awn (%)	Grain (%)
6 DAA						
IEC	1.43 ± 0.08 Ac	13.88 ± 0.72 Ad	10.64 ± 0.58 Ad	8.73 ± 0.37 Ac	17.20 ± 0.58 Ac	48.12 ± 0.75 *Cc*
IED	1.69 ± 0.06 Bab	15.11 ± 0.27 Ac	11.18 ± 0.47 Ad	8.52 ± 0.27 Ac	19.55 ± 0.21 Ab	43.95 ± 0.46 Cd
DGC	1.41 ± 0.05 Bc	no	17.92 ± 0.51 Aa	9.99 ± 0.29 Ab	19.58 ± 0.83 Ab	51.10 ± 0.76 Cb
DGD	1.63 ± 0.08 Bb	no	18.29 ± 0.43 Aa	10.01 ± 0.44 Ab	23.07 ± 0.32 Aa	47.00 ± 0.43 *Cc*
DAC	1.49 ± 0.06 Ac	18.61 ± 0.77 Ab	14.21 ± 0.39 Ac	11.62 ± 0.62 Aa	no	54.08 ± 1.02 Ca
DAG	1.76 ± 0.08 Aa	20.74 ± 0.25 Aa	15.34 ± 0.27 Ab	11.64 ± 0.35 Aa	no	50.51 ± 0.50 Cb
18 DAA						
IEC	1.48 ± 0.09 Ad	9.06 ± 0.16 Bd	6.89 ± 0.33 Be	6.17 ± 0.21 Bd	10.65 ± 0.53 Bc	65.74 ± 0.60 Bc
IED	1.85 ± 0.08 Ab	10.89 ± 0.22 Bc	7.91 ± 0.60 Bd	7.14 ± 0.36 Bd	12.12 ± 0.24 Bb	60.10 ± 0.57 Be
DGC	1.60 ± 0.04 Ac	no	9.96 ± 0.44 Bb	7.36 ± 0.24 Bc	12.53 ± 0.30 Bb	68.54 ± 0.56 Bb
DGD	2.06 ± 0.06 Aa	no	10.23 ± 0.36 Bb	8.10 ± 0.24 Bb	15.01 ± 0.43 Ba	64.60 ± 0.15 Bd
DAC	1.49 ± 0.05 Ad	11.38 ± 0.10 Bb	9.19 ± 0.36 Bc	8.11 ± 0.28 Bb	no	69.84 ± 0.20 Ba
DAG	1.91 ± 0.05 Ab	12.99 ± 0.22 Ba	11.21 ± 0.35 Ba	8.79 ± 0.12 Ba	no	65.11 ± 0.53 Bcd
25 DAA						
IEC	1.48 ± 0.06 Ab	5.99 ± 0.22 Cb	4.77 ± 0.27 Cd	3.97 ± 0.19 Ce	6.75 ± 0.45 *Cc*	77.04 ± 0.53 Ac
IED	1.83 ± 0.05 Aa	6.54 ± 0.43 Cab	5.20 ± 0.30 Cd	4.40 ± 0.54 Cde	7.60 ± 0.27 Cab	74.44 ± 0.67 Ad
DGC	1.60 ± 0.10 Ab	no	7.32 ± 0.26 Cb	4.73 ± 0.22 Ccd	7.28 ± 0.14 Cb	79.08 ± 0.30 Ab
DGD	1.94 ± 0.08 Aa	no	8.45 ± 0.37 Ca	5.29 ± 0.16 Cab	8.06 ± 0.17 Ca	76.26 ± 0.53 Ac
DAC	1.46 ± 0.05 Ab	6.28 ± 0.31 Cb	6.07 ± 0.09 Cc	5.02 ± 0.09 Cbc	no	81.17 ± 0.32 Aa
DAG	1.86 ± 0.12 Aa	7.09 ± 0.36 Ca	7.13 ± 0.51 Cb	5.78 ± 0.31 Ca	no	78.15 ± 1.08 Ab

Six treatments were included: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress. DAA: day after anthesis. Capital letters indicate significance at $P < 0.05$ among different DAA under the same treatment. Lowercase letters represent significance at $P < 0.05$ among different treatments simultaneously.

3.5. Differences in grain weight and organ contribution

Compared with the control plants, the aboveground biomass per pot, 1000-grain weight, grain weight per pot, and number of fertile and infertile spikelets declined in the IED, DGD, and DAD treatments under drought stress (Fig. 5A–D). The aboveground biomass was reduced by approximately 25.7%–26.7 % in the IED, DGD, and DAD treatments under drought stress. The 1000-grain weight decreased by 27.9 %, 31 %, and 36 %, in the IED, DGD, and DAD treatments, respectively. The change in grain weight per pot was in accordance with the aboveground biomass and 1000-grain weight. With a normal water supply, the grain weight per ear decreased by 11.2 % and 25.4 % when glumes and awns were removed, respectively. When wheat was exposed to adverse drought conditions, the decrease was exacerbated, and the reductions were 16 % and 32.2 %, respectively, in DGD and DAD wheat compared with IED. The numbers of fertile and infertile sipkelets decreased and increased, respectively, in IED, DGD, and DAD wheat under drought stress. Compared with intact ear wheat, the removal of glumes and awns decreased the number of fertile sipkelets by approximately 6.9 % under normal conditions and by approximately 4.8%–5.6 % under drought conditions. The detachment of the glumes and awns increased the number of infertile sipkelets by approximately 21.2%–52 % under normal conditions, and approximately 23.2%–26.8 % under drought conditions, compared with intact ear wheat. As shown in Fig. 6, the awn contribution was 2.3 times more than the glume contribution under normal conditions. Under drought stress, the contribution of awn was twice that of glume.

4. Discussion

Reports have clarified the contribution of ear photosynthesis to grain yield and the higher drought tolerance in plants [6,13,32,34]. In this study, the RWC results indicated that the glume and awn possessed a better capacity to endure drought (Fig. 3A–E). This finding supports the finding in the literature that the awn of bread wheat was able to maintain a higher RWC than the flag leaf under drought stress [34]. The awn also had the most marked sclerenchymatous structure among the plant organs studied, which endows it with tolerance to drought stress [15].

We also found that the decreases in P_n and T_r in the ears were lower than those in the flag leaves under drought conditions (Fig. 2A–D). These findings suggest a smaller reduction in photosynthesis in the ear than in the flag leaf of stressed wheat. These results are consistent with findings in the literature that the ear was not as sensitive to drought as the flag leaf in wheat [6,10,31]. In this context, the rate of decline in P_n indicated that the contribution of the awn to ear photosynthesis was greater than that of the glume after the removal of the glumes and awns (Fig. 2C). The importance of the awn was similar to the finding that awns, particularly in awned cultivars, possess a strong capacity for photosynthesize [30,34]. Ear organs that play key roles in the grain filling phase have been observed in other Poaceae species, such as barely. Comparative transcriptional profiling also showed that the barely awn was the major photosynthetic organ of ears [35]. Metabolic and transcriptional transitions revealed that the barley glume functioned as a transitory resource buffer during endosperm filling [23].

Carbon isotope ^{14}C labeling can reflect ^{14}C assimilates in the early grain filling phase (6 DAA) and the distribution of those assimilates from the ear organs to the grains. ^{14}C assimilates in ears were transported to grains from 6 to 25 DAA during the grain filling period (Tables 1 and 2). Several studies have highlighted the importance of photosynthesis in the ear. The contribution of ear

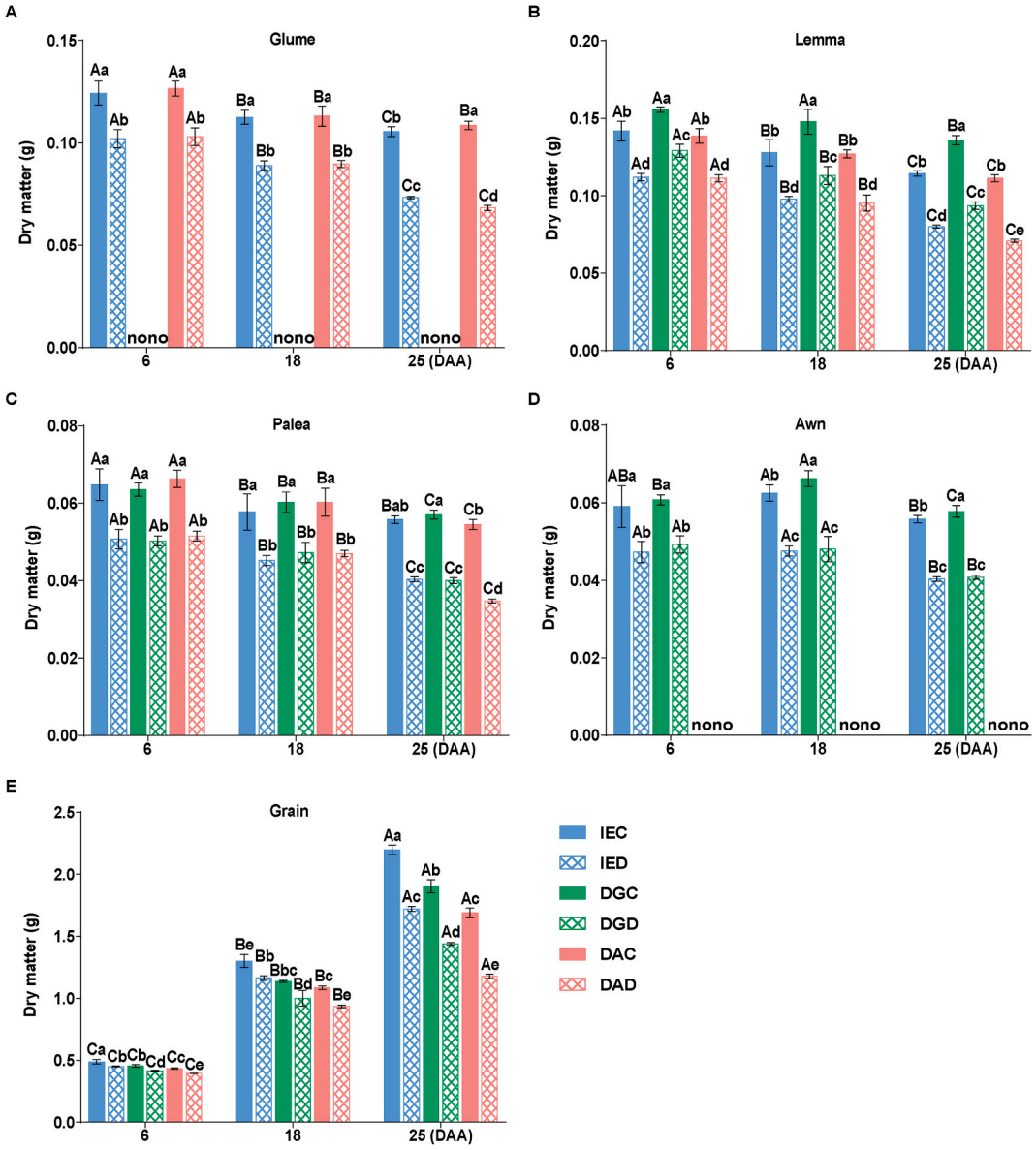

Fig. 4. Dry matter of the de-glumed and de-awned ears under drought stress. **(A)** Glume, **(B)** Lemma, **(C)** Palea, **(D)** Awn, and **(E)** Grain. Capital letters indicate significance at $P < 0.05$ among different DAA under the same treatment. Lowercase letters represent significance at $P < 0.05$ among different treatments simultaneously. Six treatments were included: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress. DAA: day after anthesis.

photosynthesis to grain filling has been shown to increase with a decrease in water supply [14,15,28].

In the intact ear, the number and partition ratio of ^{14}C assimilates in the awn were the highest, followed by those in the glume, lemma, and palea. This finding proves that awns play an important role in ear photosynthesis, followed by glume. The literature has demonstrated that awns possess a strong capacity to provide assimilation products to grain mass during the grain filling phase in awned cultivars [30].

The contributions of flag leaf, stem, chaff, and awn to grain filling were evaluated under Mediterranean conditions in durum wheat. The results indicated the importance of spike and awns as providers of carbon products by photosynthesis and the modest contribution of flag leaf to final grain yield [25]. Different experimental setups have been used to quantify the contribution of the ear to grain filling by removing awns and shading the entire ear in bread wheat [13]. The findings have demonstrated the contribution of ear photosynthesis is vital to resource limitation. The relative contribution of ears to grain filling, particularly under drought stress, was further confirmed by our experimental data. The content of radioactive ^{14}C assimilates significantly decreased in the grains after detaching the glumes and awns because of a reduction in ear photosynthesis. The extent of the descent was greater in the DA treatment than in the DG

Table 3
Dry matter accumulation in the DG and DA ears under drought stress.

Treatments	Glume (%)	Lemma (%)	Palea (%)	Awn (%)	Grain (%)
6 DAA					
IEC	14.15 ± 0.28 Ac	16.15 ± 0.33 Ae	7.37 ± 0.30 Ac	6.71 ± 0.29 Ac	55.62 ± 0.78 Ce
IED	13.39 ± 0.29 Ad	14.70 ± 0.18 Af	6.66 ± 0.17 Ad	6.20 ± 0.21 Ad	59.05 ± 0.59 Cc
DGC	no	21.21 ± 0.27 Aa	8.66 ± 0.08 Aa	8.29 ± 0.18 Aa	61.84 ± 0.38 Cb
DGD	no	20.06 ± 0.41 Ab	7.81 ± 0.13 Ab	7.66 ± 0.27 Ab	64.47 ± 0.56 Ca
DAC	16.55 ± 0.24 Aa	18.12 ± 0.42 Ac	8.67 ± 0.16 Aa	no	56.66 ± 0.54 Cd
DAG	15.60 ± 0.46 Ab	16.85 ± 0.19 Ad	7.80 ± 0.19 Ab	no	59.75 ± 0.34 Cc
18 DAA					
IEC	6.78 ± 0.23 Bc	7.69 ± 0.27 Bc	3.47 ± 0.15 Bd	3.76 ± 0.09 Bb	78.30 ± 0.23 Bc
IED	6.17 ± 0.06 Bd	6.77 ± 0.17 Bd	3.13 ± 0.05 Be	3.29 ± 0.08 Bc	80.63 ± 0.17 Bb
DGC	no	10.48 ± 0.49 Ba	4.27 ± 0.16 Bab	4.70 ± 0.12 Ba	80.55 ± 0.47 Bb
DGD	no	9.36 ± 0.13 Bb	3.92 ± 0.26 Bc	3.98 ± 0.25 Bb	82.74 ± 0.52 Ba
DAC	8.15 ± 0.32 Ba	9.16 ± 0.15 Bb	4.35 ± 0.19 Ba	no	78.34 ± 0.17 Bc
DAG	7.69 ± 0.17 Bb	8.16 ± 0.31 Bc	4.03 ± 0.02 Bbc	no	80.12 ± 0.29 Bb
25 DAA					
IEC	4.17 ± 0.04 Cc	4.52 ± 0.02 Ce	2.21 ± 0.03 Ce	2.21 ± 0.01 Cc	86.90 ± 0.06 Ae
IED	3.75 ± 0.02 Cd	4.09 ± 0.01 Cf	2.07± 0.02 Cf	2.07 ± 0.02 Cd	88.02 ± 0.07 Ac
DGC	no	6.30 ± 0.05 Ca	2.65 ± 0.02 Cb	2.68 ± 0.01 Ca	88.37 ± 0.06 Ab
DGD	no	5.80 ± 0.09 Cb	2.49 ± 0.05 Cd	2.53 ± 0.02 Cb	89.19 ± 0.09 Aa
DAC	5.51 ± 0.03 Ca	5.66 ± 0.03 Cc	2.77 ± 0.01 Ca	no	86.03 ± 0.04 Af
DAG	5.05 ± 0.02 Cb	5.23 ± 0.02 Cd	2.57 ± 0.03 Cc	no	87.14 ± 0.04 Ad

Six treatments were included: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress. DAA: day after anthesis. Capital letters indicate significance at $P < 0.05$ among different DAA under the same treatment. Lowercase letters represent significance at $P < 0.05$ among different treatments simultaneously.

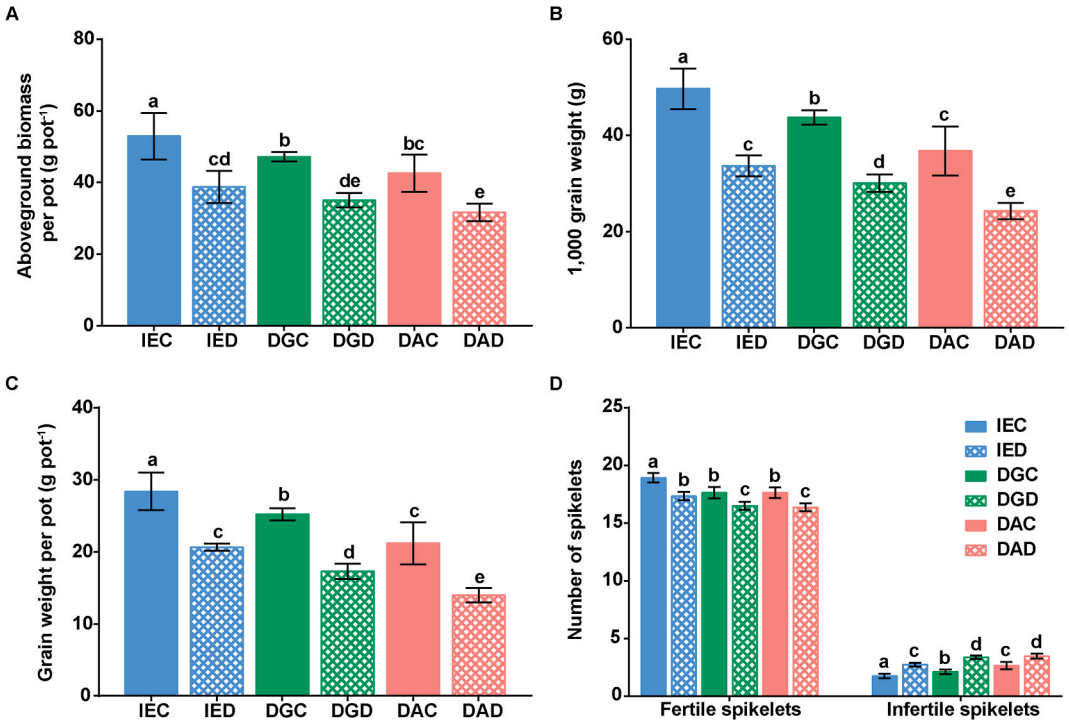

Fig. 5. The grain weight and numbers of fertile and infertile spikelets in the de-glumed and de-awned ears under drought stress. **(A)** Aboveground biomass per pot, **(B)** 1000-grain weight, **(C)** Grain weight per pot, and **(D)** The numbers of fertile and infertile spikelets. Different letters indicate significance at $P < 0.05$ among all treatments. Six treatments were included: IEC: Intact ear control; IED: Intact ear + drought stress; DGC: De-glumed ear control; DGD: De-glumed ear + drought stress; DAC: De-awned ear control; DAD: De-awned ear + drought stress.

treatment (Table 1). It also proved that the awn and glume are the curial parts of ear organs during ear photosynthesis. However, the partitioning of ^{14}C was higher in the grains of the DG and DA plants than in those of IE plants (Table 2). The main reason this finding was observed was that the detachments of the glume and awn decreased the total dry matter of the ear, eventually leading to a higher

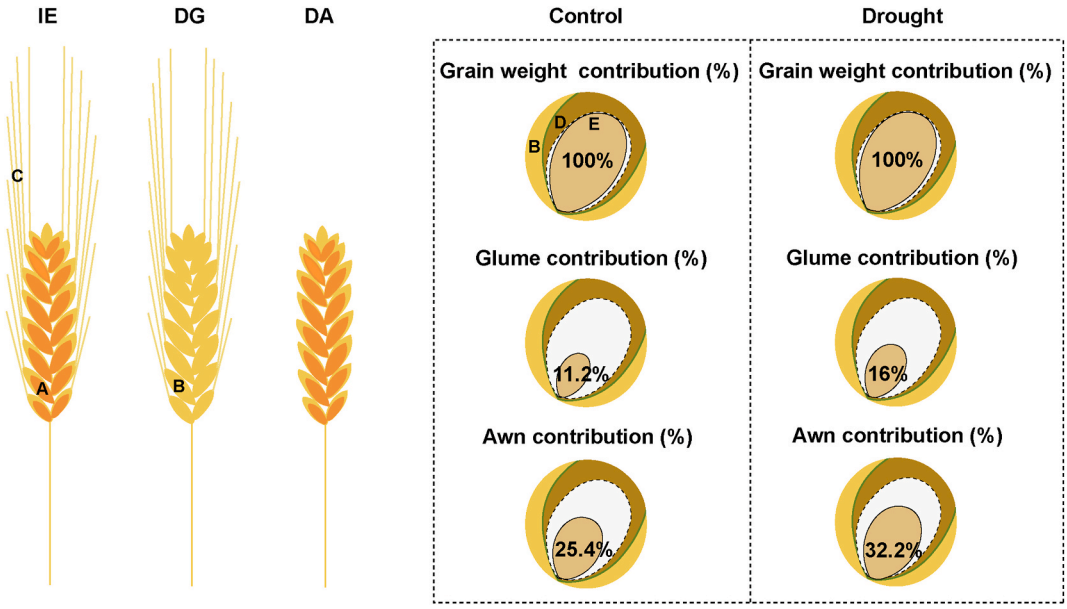

Fig. 6. Illustration of a wheat plant showing the relative photosynthetic contribution of the glume and awn to grain filling as estimated with detached organ treatments. The contributions (%) of the glume and awn were calculated relative to that in the control. IE, DG, and DA represent the intact ear, de-glumed and de-awned ears, respectively. Capital letters **(A–E)** represent glume, lemma, awn, palea, and grain, respectively.

ratio in the grains. These results suggest that awns and glumes are the major photosynthetic organs in the ears. Moreover, the photosynthetic function of awns ie more important than that of glumes.

Dry matter partitioning is the result of processes that affect the distribution of dry matter among plant organs [36]. Decreases in partitioning to the ear organs can be targeted to favor partitioning to the grain [37,38]. In this study, dry matter and dry matter accumulation were reduced in the glume, lemma, palea, and awn from 6 to 25 DAA (Fig. 4A–E and Table 3). Dry matter accumulation was also reduced in the ear organs under drought stress, possibly because of the low photosynthesis and water state of wheat. During the grain filling phase, dry matter accumulation was significantly higher in the grains than in the other ear organs. The main reason for this finding is that the dry matter in the ear organs was withdrawn, transported, and assimilated into to the grains during the grain filling phase. This tendency was consistent with several findings in the literature [13,19].

As expected, source-sink manipulations conducted at anthesis (6 DAA) greatly affected the aboveground biomass per pot, 1000-grain weight, and grain weight per pot (Fig. 5A–C). The significant effect on the number of fertile and infertile spikelets (Fig. 5D) indicated that organs detachment could also lead to grain infertile, as reported by Merah and Monneveux [25]. In this study, glume and awn detachment led to decreases in grain weight per pot of approximately 11.2 % and 25.4 %, respectively, under normal conditions. All yield components are negatively affected by drought [39]. When wheat was exposed to adverse drought stress, the grain weight per pot decreased by 16 % and 32.2 %. Notably, we also observed large contributions from the glume and awn to the final yield (Fig. 6). The awn contribution was approximately 2–2.3 times that of the glume. These results indicate that assimilates produced by the glume and awn of the ear during the grain filling phase are key factors in sustaining grain weight. Moreover, awn photosynthesis contributed more to grain weight than glume photosynthesis did. This result is similar to the finding that awn and glume have vital functions in ear photosynthesis and grain yield [23,25,26,34,35]. In this study, we focused on the contributions of the glume and awn to ear photosynthesis, assimilates and grain weight. The potential effects of detaching the glume and awn on enzyme activities and the expression of genes involved in sugar transportation should also be considered and require further investigation.

In conclusion, glume or awn removal treatments may decrease ear photosynthesis and ^{14}C assimilation, leading to a decline in the grain weight of ears under normal and drought conditions. These findings indicate that the glume and awn play crucial roles during grain filling in wheat, especially under drought conditions, and that the contribution of the awn is greater than that of the glume. Our findings provide valuable information on ear traits that can be used as essential indicators for breeding new material for dry land wheat and lay a theoretical foundation for exploring the potential yield increase in wheat.

Author contribution statement

Xiaorui Li: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Yan Tang, Chunju Zhou: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data.

Jinyin Lv: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data.

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Data availability statement

Data included in article/supplementary material/referenced in article.
No additional information is available for this paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

[1] F. Feng, Y. Han, S. Wang, S. Yin, Z. Peng, M. Zhou, W. Gao, X. Wen, X. Qin, K.H.M. Siddique, The effect of grain position on genetic improvement of grain number and thousand grain weight in winter wheat in north China, Front. Plant Sci. 9 (2018) 1–9.
[2] Y.H. Fan, Z.Y. Lv, Y.X. Li, B.Y. Qin, Q.Y. Song, L.L. Ma, Q.Q. Wu, W.J. Zhang, S.Y. Ma, C.X. Ma, Z.L. Huang, Salicylic acid reduces wheat yield loss caused by high temperature stress by enhancing the photosynthetic performance of the flag leaves, Agronomy-Basel 12 (2022) 1–17.
[3] X. Li, Y. Tang, H. Li, W. Luo, C. Zhou, L. Zhang, J. Lv, A wheat R2R3 MYB gene *TaMpc1-D4* negatively regulates drought tolerance in transgenic *Arabidopsis* and wheat, Plant Sci. 299 (2020) 1–11.
[4] C. Zheng, Z. Yu, Y. Shi, S. Cui, D. Wang, Y. Zhang, J. Zhao, Effects of tillage practices on water consumption, water use efficiency and grain yield in wheat field, J. Integr. Agric. 13 (2014) 2378–2388.
[5] S.Z. Lv, K.W. Feng, S.F. Peng, J.Q. Wang, Y.F. Zhang, J.X. Bian, X.J. Nie, Comparative analysis of the transcriptional response of tolerant and sensitive wheat genotypes to drought stress in field conditions, Agronomy-Basel 8 (2018) 1–13.
[6] R. Vicente, O. Vergara-Díaz, S. Medina, F. Chairi, S.C. Kefauver, J. Bort, M.D. Serret, N. Aparicio, J.L. Araus, Durum wheat ears perform better than the flag leaves under water stress: gene expression and physiological evidence, Environ. Exp. Bot. 153 (2018) 271–285.
[7] D.S.M. Murtaza Shah, G. Shabbir, I.S. Malik, I.N. Raja, H.Z. Shah, M. Rauf, A.Y. Zahrani, F. Alghabari, H. Alsamadany, K. Shahzad, H.S. Yang, Delineation of physiological agronomic and genetic responses of different wheat genotypes under drought condition, Agronomy-Basel 12 (2022) 1–16.
[8] F. Morales, M. Ancin, D. Fakhet, J. Gonzalez-Torralba, A.L. Gamez, A. Seminario, D. Soba, S. Ben Mariem, M. Garriga, I. Aranjuelo, Photosynthetic metabolism under stressful growth conditions as a bases for crop breeding and yield improvement, Plants-Basel 9 (2020) 1–23.
[9] Z.H. Shah, H.M. Rehman, T. Akhtar, I. Daur, M.A. Nawaz, M.Q. Ahmad, I.A. Rana, R.M. Atif, S.H. Yang, G. Chung, Redox and ionic homeostasis regulations against oxidative, salinity and drought stress in wheat (A systems biology approach), Front. Genet. 8 (2017) 1–10.
[10] L. Lou, X. Li, J. Chen, Y. Li, Y. Tang, J. Lv, Photosynthetic and ascorbate-glutathione metabolism in the flag leaves as compared to spikes under drought stress of winter wheat (*Triticum aestivum* L.), PLoS One 13 (2018) 1–18.
[11] X. Li, X. Zhang, G. Liu, Y. Tang, C. Zhou, L. Zhang, J. Lv, The spike plays important roles in the drought tolerance as compared to the flag leaf through the phenylpropanoid pathway in wheat, Plant Physiol. Biochem. 152 (2020) 100–111.
[12] J.L. Araus, H.R. Brown, A. Febrero, J. Bort, M.D. Serret, Ear photosynthesis, carbon isotope discrimination and the contribution of respiratory CO_2 to differences in grain mass in durum wheat, Plant Cell Environ. 16 (1993) 383–392.
[13] M.L. Maydup, M. Antonietta, J.J. Guiamet, C. Graciano, J.R. López, E.A. Tambussi, The contribution of ear photosynthesis to grain filling in bread wheat (*Triticum aestivum* L.), Field Crop. Res. 119 (2010) 48–58.
[14] R. Sanchez-Bragado, A. Elazab, B. Zhou, M.D. Serret, J. Bort, M.T. Nieto-Taladriz, J.L. Araus, Contribution of the ear and the flag leaf to grain filling in durum wheat inferred from the carbon isotope signature: genotypic and growing conditions effects, J. Integr. Plant Biol. 56 (2014) 444–454.
[15] E.A. Tambussi, S. Nogues, J.L. Araus, Ear of durum wheat under water stress: water relations and photosynthetic metabolism, Planta 221 (2005) 446–458.
[16] I. Aranjuelo, L. Cabrera-Bosquet, R. Morcuende, J.C. Avice, S. Nogues, J.L. Araus, R. Martinez-Carrasco, P. Perez, Does ear C sink strength contribute to overcoming photosynthetic acclimation of wheat plants exposed to elevated CO_2? J. Exp. Bot. 62 (2011) 3957–3969.
[17] R. Sanchez-Bragado, G. Molero, M.P. Reynolds, J.L. Araus, Relative contribution of shoot and ear photosynthesis to grain filling in wheat under good agronomical conditions assessed by differential organ delta13C, J. Exp. Bot. 65 (2014) 5401–5413.
[18] M.P.N. Gent, R.K. Kiyomoto, Assimilation and distribution of photosynthate in winter wheat cultivars differing in harvest index, Crop Sci. 29 (1989) 120–125.
[19] S. Jia, J. Lv, S. Jiang, T. Liang, C. Liu, Z. Jing, Response of wheat ear photosynthesis and photosynthate carbon distribution to water deficit, Photosynthetica 53 (2015) 95–109.
[20] L.T. Evans, J. Bingham, P. Jackson, J. Sutherland, Effect of awns and drought on the supply of photosynthate and its distribution within wheat ears, Ann. Appl. Biol. 70 (1972) 67–76.
[21] S.P. Waters, M.B. Peoples, R.J. Simpson, M.J. Dalling, Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.) I. Peptide hydrolase activity and protein breakdown in the flag leaf, glumes and stem, Planta 148 (1980) 422–428.
[22] M.S. Lopes, N. Cortadellas, T. Kichey, F. Dubois, D.Z. Habash, J.L. Araus, Wheat nitrogen metabolism during grain filling: comparative role of glumes and the flag leaf, Planta 225 (2006) 165–181.
[23] S. Kohl, J. Hollmann, A. Erban, J. Kopka, D. Riewe, W. Weschke, H. Weber, Metabolic and transcriptional transitions in barley glumes reveal a role as transitory resource buffers during endosperm filling, J. Exp. Bot. 66 (2015) 1397–1411.
[24] Z. Wang, A. Wei, D. Zheng, Photosynthetic characteristics of non-leaf organs of winter wheat cultivars differing in ear type and their relationship with grain mass per ear, Photosynthetica 39 (2001) 239–244.
[25] O. Merah, P. Monneveux, Contribution of different organs to grain filling in durum wheat under mediterranean conditions I. contribution of post-anthesis photosynthesis and remobilization, J. Agron. Crop Sci. 201 (2015) 344–352.

[26] Q. Li, S. Zhong, S. Sun, S.A. Fatima, M. Zhang, W. Chen, Q. Huang, S. Tang, P. Luo, Differential effect of whole-ear shading after heading on the physiology, biochemistry and yield index of stay-green and non-stay-green wheat genotypes, PLoS One 12 (2017) 1–14.
[27] J.K. Jarmołkowicz, J. Olszewski, Gas exchange parameters in leaves and ears of winter wheat *Tricitum aestivum* L. and its productivity under fungcide control conditions, Acta Agrobot. 63 (2010) 135–147.
[28] R. Sanchez-Bragado, G. Molero, M.P. Reynolds, J.L. Araus, Photosynthetic contribution of the ear to grain filling in wheat: a comparison of different methodologies for evaluation, J. Exp. Bot. 67 (2016) 2787–2798.
[29] Y. Wang, W. Xi, Z. Wang, B. Wang, X. Xu, M. Han, S. Zhou, Y. Zhang, Contribution of ear photosynthesis to grain yield under rainfed and irrigation conditions for winter wheat cultivars released in the past 30 years in North China Plain, J. Integr. Agric. 15 (2016) 2247–2256.
[30] X. Li, H. Wang, H. Li, L. Zhang, N. Teng, Q. Lin, J. Wang, T. Kuang, Z. Li, B. Li, A. Zhang, J. Lin, Awns play a dominant role in carbohydrate production during the grain-filling stages in wheat (*Triticum aestivum*), Physiol. Plant. 127 (2006) 701–709.
[31] H. Ding, D. Liu, X. Liu, Y. Li, J. Kang, J. Lv, G. Wang, Photosynthetic and stomatal traits of spike and flag leaf of winter wheat (*Triticum aestivum* L.) under water deficit, Photosynthetica 56 (2017) 687–697.
[32] Y. Zhang, Y. Zhang, Z. Wang, Z. Wang, Characteristics of canopy structure and contributions of non-leaf organs to yield in winter wheat under different irrigated conditions, Field Crop. Res. 123 (2011) 187–195.
[33] F. Nemati, F. Ghanati, H.A. Gavlighi, M. Sharifi, Fructan dynamics and antioxidant capacity of 4-day-old seedlings of wheat (*Triticum aestivum*) cultivars during drought stress and recovery, Funct. Plant Biol. 45 (2018) 1–9.
[34] M.L. Maydup, M. Antonietta, C. Graciano, J.J. Guiamet, E.A. Tambussi, 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, Field Crop. Res. 167 (2014) 102–111.
[35] T. Abebe, R.P. Wise, R.W. Skadsen, Comparative transcriptional profiling established the awn as the major photosynthetic organ of the barley spike while the lemma and the palea primarily protect the seed, Plant Genome 2 (2014) 247–259.
[36] L.F.M. Marcelis, Sink strength as a determimant of dry matter partitioning in the whole plant, J. Exp. Bot. 47 (1996) 1281–1291.
[37] C. Rivera-Amado, E. Trujillo-Negrellos, G. Molero, M.P. Reynolds, R. Sylvester-Bradley, M.J. Foulkes, Optimizing dry-matter partitioning for increased spike growth, grain number and harvest index in spring wheat, Field Crop. Res. 240 (2019) 154–167.
[38] H. Zhang, K. Han, S. Gu, D. Wang, Effects of supplemental irrigation on the accumulation, distribution and transportation of 13C-photosynthate, yield and water use efficiency of winter wheat, Agric. Water Manage. 214 (2019) 1–8.
[39] N. Frantová, M. Rábek, P. Elzner, T. Streda, I. Jovanovic, L. Holková, P. Martinek, P. Smutná, T.I. Prášil, Different drought tolerance strategy of wheat varieties in spike architecture, Agronomy-Basel 12 (2022) 1–13.