Journal of Agronomy and Crop Science

WILEY

Journal of Agronomy and Crop Science

ORIGINAL ARTICLE OPEN ACCESS

Drought Stress

Physiological Contribution of Awns to Grain Yield and Quality in Bread and Durum Wheat Under Water-Limited Mediterranean Conditions

Volkan Yeşil | Recep Karakoç | Özgür Tatar

Department of Field Crops, Faculty of Agriculture, Ege University, İzmir, Turkey

Correspondence: Özgür Tatar (ozgur.tatar@ege.edu.tr)

Received: 27 December 2025 | **Revised:** 12 April 2026 | **Accepted:** 27 April 2026

Keywords: source–sink relationships | terminal drought | *Triticum aestivum* L. | *Triticum turgidum* subsp. *durum* (Desf.) Husn. | water use efficiency | wheat

ABSTRACT

Terminal drought is a primary constraint to wheat production in Mediterranean environments, often severely reducing grain weight and quality. This study evaluated the physiological contribution of awns to yield formation, water use efficiency (WUE), and grain quality traits in bread wheat [*Triticum aestivum* L.] and durum wheat [*Triticum turgidum* subsp. *durum* (Desf.) Husn.]. Two field experiments were conducted in Izmir, Turkey, over the 2018–2019 and 2022–2023 growing seasons under rainfed and supplemental irrigation conditions. Treatments consisted of intact spikes and manually de-awned spikes to assess the net photosynthetic and metabolic contribution of awns. De-awning significantly reduced grain yield and thousand-grain weight in both species, though the magnitude of loss was influenced by water availability. In durum wheat, a significant Awn × Irrigation interaction ($p < 0.01$) for yield suggested that awns play a more critical compensatory role in durum cultivars under water stress compared to bread wheat. Physiologically, awns contributed to maintaining higher WUE and, in bread wheat, supported grain protein accumulation. However, the presence of awns tended to reduce the concentration of essential amino acids, likely due to the dilution effect resulting from increased carbohydrate accumulation. Awn removal reduced protein content in *T. aestivum* but not *T. durum*, yet increased essential amino acid concentrations in both species, likely reflecting a concentration effect due to reduced yield. These findings confirm that awns serve as a vital photosynthetic organ during terminal drought, playing a decisive role in sustaining yield and regulating the carbon-nitrogen balance in Mediterranean wheat cultivation.

1 | Introduction

Wheat (*Triticum* spp.) remains a fundamental pillar of global food security; however, its productivity is increasingly threatened by environmental fluctuations, specifically water scarcity during reproductive stages (Demirhan 2020; Reynolds et al. 2005; Demirhan and Bayraktar 2025). In Mediterranean climates, crops frequently encounter 'terminal drought', a phenomenon where water stress intensifies during grain filling (İlker et al. 2011). Although the timing and severity of terminal drought fluctuate, prolonged exposure has been reported to cause yield reductions reaching 92% (Dhanda and Sethi 2002; Farooq et al. 2014). Under these conditions, physiological processes are severely disrupted: accelerated leaf senescence, oxidative stress in chloroplasts, and stomatal closure collectively diminish the capacity of the flag leaf to sustain carbon fixation (Asada 2006; Yang et al. 2003; Plaut et al. 2004). Consequently, the availability of current photoassimilates becomes a limiting factor for grain sink strength and final yield (Liang et al. 2001). In wheat, grain filling relies largely on post-anthesis photosynthesis originating mainly from the flag leaf, whereas remobilization from vegetative

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Journal of Agronomy and Crop Science* published by Wiley-VCH GmbH.

Key Points

- Terminal drought severely limits Mediterranean wheat production.
- We examined physiological effects of awn removal in two species.
- Awn removal reduced grain yield and water use efficiency.
- Durum wheat showed higher awn dependency than bread wheat.
- Awns are vital for sustaining yield and quality under water stress.

tissues provides an additional source; in our previous study, post-anthesis photosynthesis accounted for 68.2%–72.6% of grain dry matter formation depending on water regime (Tatar et al. 2016).

Given the rapid decline in leaf photosynthesis under drought, the physiological contribution of the wheat ear (spike) has emerged as a critical compensatory mechanism (Abbad et al. 2004; Tambussi et al. 2007). Recent research confirms that the ear, and specifically the awns, plays a pivotal role in grain filling, acting as a major source of assimilates when leaf function is compromised (Sanchez-Bragado et al. 2014; Martinez-Pena et al. 2023; Li et al. 2023). Unlike leaves, the spike exhibits 'stay-green' traits and possesses distinct xeromorphic adaptations that allow it to maintain higher water potential and photosynthetic electron transport rates during water deficit (Blum 1985; Tambussi et al. 2005). Furthermore, molecular evidence suggests that the spike plays a superior role in drought tolerance compared to the flag leaf, potentially through the activation of secondary metabolic pathways such as the phenylpropanoid pathway (Li et al. 2020).

The awns, as long slender extensions of the lemma, are the primary drivers of this ear-based photosynthesis (Blum 1985). Morphologically, awns can increase the total photosynthetic surface area of the spike by 59%, significantly enhancing radiation interception (Motzo and Giunta 2002). This morphological advantage translates into physiological gains; ear photosynthesis has been shown to contribute 13%–43% of grain assimilates under drought conditions, largely driven by the presence of awns (Evans et al. 1972; Maydup et al. 2014). However, the role of awns is not limited to carbon fixation. As highlighted by Tambussi et al. (2007), the ear possesses a unique metabolic capacity to refix respiratory CO_2 and ammonium, allowing it to function as a stable physiological buffer when leaf activity declines. Consequently, enzymes of ammonia metabolism in the ear remain highly active during grain development, facilitating nitrogen assimilation even when soil uptake is limited (Maheswari et al. 1992). Sanchez-Bragado et al. (2006) further demonstrated that this mechanism allows ear components (glumes and awns) to act as a substantial source of nitrogen for the developing grain, specifically under water deficit. This interaction is particularly relevant for grain quality, as drought-induced reductions in starch deposition often lead to higher protein concentrations via the 'dilution effect' (Gooding et al. 2003; Ozturk and Aydin 2004; Triboi et al. 2003).

Despite these physiological benefits, the agronomic value of awns remains a subject of debate due to potential trade-offs. Although awns serve as a source of assimilates, they also constitute a sink cost during their formation and can alter the crop's interaction with the environment (Rebetzke et al. 2016; Blum 1985). For instance, recent research by Faizan et al. (2025) on cereal head morphology highlights that larger spikes and complex awn structures can significantly alter aerodynamic drag, potentially influencing crop stability. This complexity is reflected in conflicting yield reports: while some studies suggest awns provide a yield advantage in winter wheat (Patterson et al. 1962; Bruening 2019), others indicate that awnless variants may achieve higher water use efficiency (WUE) or similar yields due to trade-offs between grain number and grain size (Rebetzke et al. 2016; Sanchez-Bragado et al. 2020; Hosseini et al. 2012).

These contradictions suggest that the net benefit of awns is highly context-dependent, varying significantly between genotypes (e.g., bread vs. durum wheat) and water regimes. Few studies have simultaneously evaluated these factors under controlled field conditions. Therefore, the main objective of this study was to investigate the specific contribution of awns to grain filling, final yield components, and quality parameters in bread wheat [*Triticum aestivum* L.] and durum wheat [*Triticum turgidum* subsp. *durum* (Desf.) Husn.]. By comparing intact and de-awned spikes under supplemental irrigation and rainfed Mediterranean conditions, this research aims to clarify the physiological value of awns as a trait for drought adaptation.

2 | Materials and Methods

2.1 | Plant Material

Two distinct spring wheat cultivars widely cultivated in the west-coastal region of Türkiye were utilized in this study: a bread wheat [*T. aestivum* L.] cultivar, 'EGE 99', and a durum wheat [*T. turgidum* subsp. *durum* (Desf.) Husn.] cultivar, 'Şölen'. The experiment compared these cultivars based on awn condition, specifically evaluating intact awns versus manually removed awns.

2.2 | Study Site & Growth Conditions

The research was conducted in Izmir Province, Türkiye (38°27′06″ N, 27°13′34″ E), under Mediterranean climate conditions. The experiment spanned two growing seasons: in the first year (2018–2019), plants were sown on December 9, 2018, and harvested on June 13, 2019; in the second year (2022–2023), sowing was performed on December 28, 2022, with harvest on June 16, 2023. Meteorological data during the sowing-to-harvest periods were obtained from a nearby official meteorological station (Figure 1). For context, the long-term (1938-present) average annual rainfall and temperature at the site are 407 mm and 17.1°C, respectively.

The soil texture at the experimental site was identified as clay-loam, with a moderately alkaline pH of approximately 7.9.

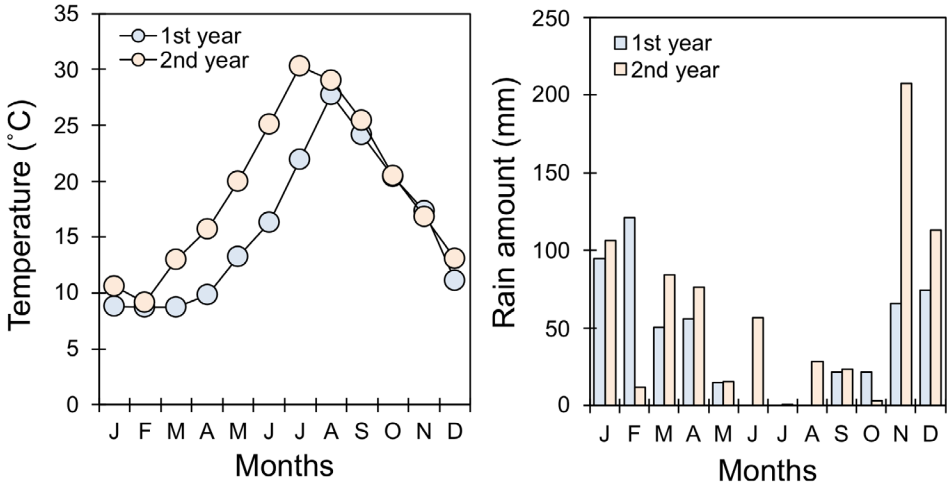


FIGURE 1 | Monthly average temperature (°C) and total rain amount (mm) at the experimental sites during 1st year (2019) and 2nd year (2023).

Fertilization was applied in two stages to meet crop requirements. Initially, 70 kg ha^{-1} of nitrogen was applied at sowing using a composite fertilizer (15-15-15) containing nitrogen (N), phosphorus (P_2O_5) and potassium (K_2O). Subsequently, an additional 70 kg ha^{-1} of nitrogen was applied at the onset of stem elongation using ammonium sulphate (21% N and 24% S).

Meteorological conditions varied between the two experimental years. During the growing period in the 2018–2019 season (Year 1), total natural rainfall was 370 mm. In the 2022–2023 season (Year 2), total natural rainfall was 440 mm. In the irrigated treatments, water was delivered via a drip irrigation system featuring lateral pipes spaced 36 cm apart and drippers (nozzles) positioned at 20 cm intervals. A water meter was installed in the system to precisely record the irrigation volume.

Throughout the growing seasons, weed control was managed by manual removal, and no herbicides were used. Furthermore, no disease symptoms were observed on the plants; consequently, no fungicides or pesticides were applied.

Grain development stages of wheat plants were determined according to Zadok's scale and grain moisture content patterns.

2.3 | Experimental Design & Treatments

The experiment was arranged in a randomized complete block design (RCBD) with a split-plot arrangement and four replications. The irrigation treatments (water regimes) were assigned to the main plots, whereas the wheat genotypes were assigned to the sub-plots. The water regimes consisted of rainfed conditions, where plants depended solely on natural precipitation, and supplemental irrigation, where water was applied from the heading stage to harvest.

To establish the different water availability treatments, natural rainfall was supplemented with irrigation in the well-watered plots. In the first year (2018–2019), 150 mm of supplementary irrigation was applied, resulting in total water inputs of 370 mm for the rainfed treatment and 520 mm for the irrigated treatment. In the second year (2022–2023), 100 mm of supplementary irrigation was applied, bringing the total water inputs to 440 and 540 mm for the rainfed and irrigated treatments, respectively. Irrigation timing and amount were determined empirically based on soil moisture, crop condition, and weather observations to avoid severe water limitation after heading. The volume of applied irrigation water was precisely quantified using a volumetric water meter installed on the main irrigation line. The amounts were manually recorded in cubic meters (m^3) during each irrigation event and subsequently converted to millimetres (mm) based on the specific surface area of the irrigated plots. Irrigation timing and volume were adjusted according to plant phenological stages.

Sowing was performed manually in marker-made rows to achieve a target density of 500 plants m^{-2}, calculated using the thousand-kernel weight for each cultivar. Plots measured 3.5 × 2.4 m with an inter-row spacing of 18 cm.

To establish the awn treatments within the sub-plots, 110 spikes per plot were randomly selected at the onset of heading and carefully de-awned using scissors. Simultaneously, 110 intact (awned) spikes within the same plots were tagged as controls to ensure a homogenous comparison.

2.4 | Measurements

2.4.1 | Agronomic Traits & Yield Components

At harvest maturity, data were collected after border rows were removed to minimize edge effects. Grain yield (GY) was determined by harvesting the central area of each plot, threshing the spikes, and weighing the grain, with values adjusted to 12% moisture content following standard CIMMYT protocols (Pask et al. 2012). Thousand-grain weight (TGW) was assessed by counting and weighing 1000 randomly selected grains from the harvested lot. Water use efficiency was calculated to evaluate the productivity of water input in relation to yield, using the following equation:

$$\text{WUE}\left(\text{kg m}^{-3}\right) = \text{Yield (kg)} / \text{total water input}\left(\text{m}^3\right)$$

Note: Total water input includes both rainfall and irrigation.

2.4.2 | Ear Physiological Measurement

Physiological monitoring of the ear components performed only in the first year. Sampling commenced 144 days after sowing (DAS). Ten main stem ears from each treatment (bread and durum wheat; awned and awnless) were sampled independently at weekly intervals, corresponding to 144, 151, 158, 165, 172 and 179 DAS. In the second year, sampling was restricted to the final period of grain filling.

Sampled ears were dissected into grains, rachis and awns. The remaining floral parts (lemmas, paleas and glumes) were pooled and classified as 'spikelet bracts'. Fresh weights of these separated components were recorded immediately upon sampling. Subsequently, samples were oven-dried at 60°C for 72 h to determine dry matter content. Relative water content (RWC) for each component was calculated based on the relationship between the fresh weight at the sampling date and the final dry weight.

2.4.3 | Grain Quality Analysis

In the second year of the study, detailed quality analyses were conducted using near-infrared spectroscopy (NIR). Whole grain samples were cleaned and scanned using a SubNIR-2700 spectrometer calibrated for wheat analysis (FPI NIR Analysis Software). Spectral data were acquired in reflectance mode to quantify major quality parameters including crude protein, starch, crude fibre and fat content.

Additionally, the concentrations of essential amino acids were estimated via the NIR calibration curves. These included lysine, methionin, cystine, threonine and tryptophan. All measurements were performed in triplicate, and results were expressed on a dry matter basis.

2.5 | Statistical Analysis

Statistical analyses were performed using R version 4.5.0. For agronomic traits and grain quality analysis, data were subjected to analysis of variance (ANOVA) suitable for the split-plot design to determine the main and interaction effects of irrigation and genotype. For the ear physiological measurements, Student's *t*-tests were performed to compare means between treatments at specific sampling dates. Statistical significance was defined at probability levels of $p < 0.05$ and $p < 0.01$.

3 | Results

Grain yield was significantly influenced by awn presence, irrigation regime and growing season (Table 1). In *T. aestivum* (TA), the removal of awns led to a grain yield reduction of 1.1 t/ha, corresponding to an 11.3% decrease (Figure 2). Supplemental irrigation applied after the booting stage enhanced grain yield by 8%, increasing from 8.8 to 9.5 t/ha compared to rainfed conditions. Year-to-year variability also played a role: the average grain yield in the first year was 9.9 t/ha, whereas it declined by 14% to 8.8 t/ha in the second year. A similar trend was observed in *T. turgidum* subsp. *durum* (Desf.) Husn. (TD), where grain yield decreased from 12.7 to 10.5 t/ha (17.3%). In TD plants, awn detachment under irrigated conditions resulted in a 14.5% yield reduction, whereas under rainfed conditions, the effect of awn removal was not statistically significant.

Awn removal also had a clear impact on thousand grain weight (TGW), particularly in TA (Figure 2). In TA, TGW decreased by 7.4%, from 43.2 to 40.0 g, when awns were detached. Irrigation significantly improved TGW in TA, resulting in a 14.7% increase from 38.7 g under rainfed conditions to 44.4 g with supplemental watering. In TD, the influence of awn removal on TGW was more pronounced under irrigated conditions, where TGW declined by 14.3% (from 52.5 to 45.0 g). Under rainfed conditions, the reduction was limited to 3.1%, with TGW decreasing from 44.5 to 43.2 g following awn removal.

Water use efficiency was reduced by 11.6% in TA when awns were removed, decreasing from 21.6 to 19.1 mg/g (Figure 2). In the same species, irrigation caused a 14.2% decrease in WUE. In both species, lower WUE values were recorded in the second year compared to the first, with reductions of 23.8% in TA and 27.2% in TD. In irrigated TD plants, awn removal led to a 14.4% decrease in WUE, whereas no significant change was observed under rainfed conditions.

In both species, the milky stage occurred between 128 and 148 days after sowing (DAS), followed by the dough stage from 148 to 161 DAS. Physiological maturity was reached between 161 and 172 DAS, and full maturity occurred between 172 and 182 DAS. During grain filling, a continuous decline in water content was observed in all ear components up to physiological maturity (Figure 3).

In TA, slightly lower bract water content was recorded in rainfed plants with intact awns during the full maturity stage (Figure 3). Conversely, grain water content at physiological maturity (165 DAS) was slightly higher in these same treatments. In TD, similar patterns were observed, with relatively higher RWC in rainfed plants with intact awns during full maturity. Additionally, rachis water content in TD was higher under rainfed conditions when awns were not removed.

In TA, the dry weight of all spike components, including bracts, rachis and grains, increased progressively until physiological maturity (165 DAS), followed by a decline during the full maturity stage (Figure 4). Among these components, grain dry weight showed the least reduction after physiological maturity. In contrast, TD did not exhibit a consistent increase–decrease trend across all spike components; only grain dry weight followed a similar temporal pattern.

Treatment effects were most pronounced in grain dry weight during the full maturity stage in both species (Figure 4). In general, plants with intact awns maintained higher dry weights after physiological maturity, regardless of irrigation regime. In TA, the removal of awns led to reduced grain dry weight under rainfed conditions compared to irrigated ones. However, this difference between irrigation regimes was not observed in TD following awn removal.

TABLE 1 | *p*-values and significance levels of the effects of awn presence (A), irrigation regime (IR), year (Y), and their interactions on agronomic traits (grain yield, thousand grain weight [TGW], water use efficiency [WUE]) and grain quality parameters [protein, starch, fibre, fat and amino acid contents] in two wheat species [*Triticum aestivum* L. and *Triticum turgidum* subsp. *durum* (Desf.) Husn.].

	Triticum aestivum							***Triticum turgidum* subsp. *durum***						
Traits	**Awn (A)**	**Irrigation (IR)**	**Year (Y)**	**AxIR**	**AxY**	**IRxY**	**AxIRxY**	**Awn (A)**	**Irrigation (IR)**	**Year (Y)**	**AxIR**	**AxY**	**IRxY**	**AxIRxY**
Grain yield	$<0.001^{***}$	0.005^{**}	$<0.001^{***}$	0.698^{ns}	0.896^{ns}	0.062^{ns}	0.604^{ns}	0.014^{*}	0.007^{**}	$<0.001^{***}$	0.006^{**}	0.701^{ns}	0.620^{ns}	0.751^{ns}
TGW	0.003^{**}	$<0.000^{***}$	0.899^{ns}	0.244^{ns}	0.139^{ns}	0.374^{ns}	0.854^{ns}	$<0.001^{***}$	$<0.001^{***}$	0.114^{ns}	0.007^{**}	0.678^{ns}	0.268^{ns}	0.061^{ns}
WUE	$<0.001^{***}$	$<0.001^{***}$	$<0.001^{***}$	0.344^{ns}	0.800^{ns}	0.621^{ns}	0.521^{ns}	0.029^{*}	$<0.001^{***}$	$<0.001^{***}$	0.011^{*}	0.802^{ns}	0.092^{ns}	0.891^{ns}
Protein	0.092^{ns}	0.437^{ns}	—	0.028^{*}	—	—	—	0.939^{ns}	0.946^{ns}	—	0.743^{ns}	—	—	—
Strach	0.148^{ns}	0.387^{ns}	—	0.807^{ns}	—	—	—	0.071^{ns}	0.268^{ns}	—	0.689^{ns}	—	—	—
Fibre	0.964^{ns}	0.751^{ns}	—	0.039^{*}	—	—	—	0.313^{ns}	0.286^{ns}	—	0.171^{ns}	—	—	—
Fat	0.158^{ns}	0.295^{ns}	—	0.333^{ns}	—	—	—	0.306^{ns}	0.762^{ns}	—	0.615^{ns}	—	—	—
Lysine	0.302^{ns}	0.763^{ns}	—	0.032^{*}	—	—	—	0.725^{ns}	0.131^{ns}	—	0.052^{*}	—	—	—
Methionin	0.682^{ns}	0.682^{ns}	—	0.682^{ns}	—	—	—	0.640^{ns}	0.175^{ns}	—	0.175^{ns}	—	—	—
Cystine	0.205^{ns}	0.205^{ns}	—	0.205^{ns}	—	—	—	0.266^{ns}	0.819^{ns}	—	0.012^{*}	—	—	—
Threonine	0.536^{ns}	0.358^{ns}	—	0.056^{*}	—	—	—	0.668^{ns}	0.212^{ns}	—	0.022^{*}	—	—	—
Tryptophan	0.724^{ns}	0.724^{ns}	—	0.013^{*}	—	—	—	0.663^{ns}	0.663^{ns}	—	0.205^{ns}	—	—	—

Note: Significance levels are indicated as follows: $^{*}p<0.05$, $^{**}p<0.01$, $^{**}p<0.001$.
Abbreviations: —, not applicable (no year factor in grain composition data); ns, not significant. Gray-shaded cells indicate statistically significant effects.

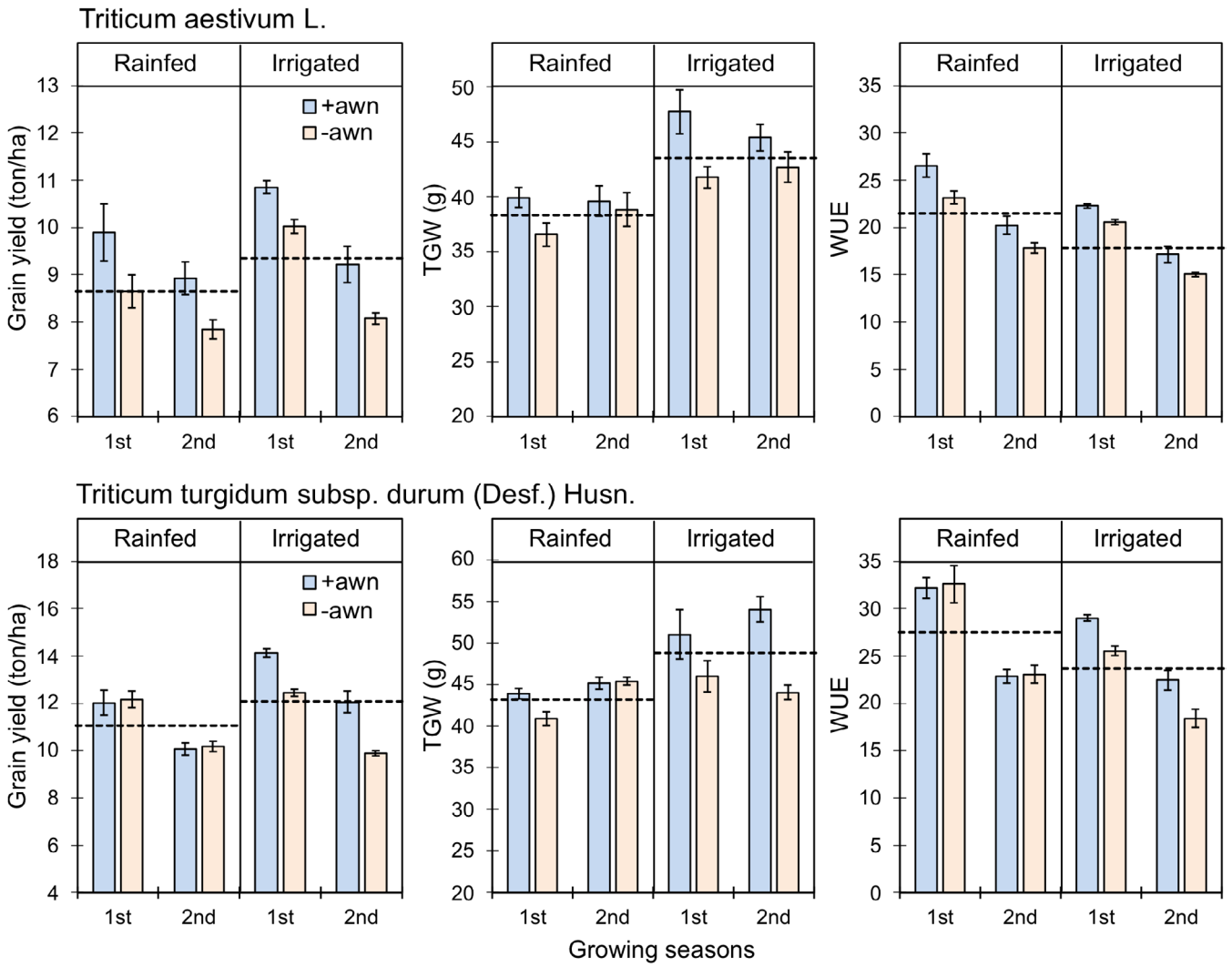


FIGURE 2 | Grain yield (ton/ha), thousand grain weight-TGW (g), and water use efficiency-WUE (mg/g) of two wheat species, *Triticum aestivum* L. and *Triticum turgidum* subsp. *durum* (Desf.) Husn., grown under irrigated (Ir) and rainfed (Rf) conditions. Bars are grouped to compare intact awns (+awn) versus removed awns (−awn) across two growing seasons. Dotted lines indicate the mean values of Ir and Rf conditions. Error bars represent the standard deviation (±SD).

The removal of awns in TA resulted in a slight but significant reduction in grain protein and starch content. Protein content decreased from 10.2% to 9.7%, whereas starch content declined from 51.1% to 50.3% (Figure 5). In contrast, fibre and fat contents in TA grains were not affected by awn removal or irrigation, with average values of 4.0% and 5.3%, respectively.

In TD, none of the grain components, protein, starch, fibre or fat were significantly influenced by either awn presence or irrigation regime. Although durum wheat often shows higher grain protein content than bread wheat, this pattern is not consistent across all cultivars and environments. The average values recorded in TD grains were 10.6% for protein, 52.3% for starch, 4.6% for fibre and 5.1% for fat.

In TA, awn removal under rainfed conditions resulted in a 17% increase in grain lysine content, rising from 0.22% to 0.26% (Figure 6). A slight increase (2.2%) in threonine content was also observed under rainfed conditions. Additionally, tryptophan content increased in awn-removed plants grown without irrigation. In contrast, methionine and cystine contents remained unaffected by treatments, with average values of 0.22% and 0.24%, respectively.

In TD, irrigation was associated with a slight increase in lysine content (0.23%), and this effect was more pronounced when awns were removed (Figure 6). A similar pattern was observed for cystine and threonine, where awn removal under irrigated conditions led to an increase in their content. Methionine and tryptophan levels in TD grains were not influenced by either awn removal or irrigation, with mean values of 0.23% and 0.16%, respectively.

4 | Discussion

The removal of awns led to substantial grain yield reductions in both TA and TD, with a more pronounced effect under irrigated

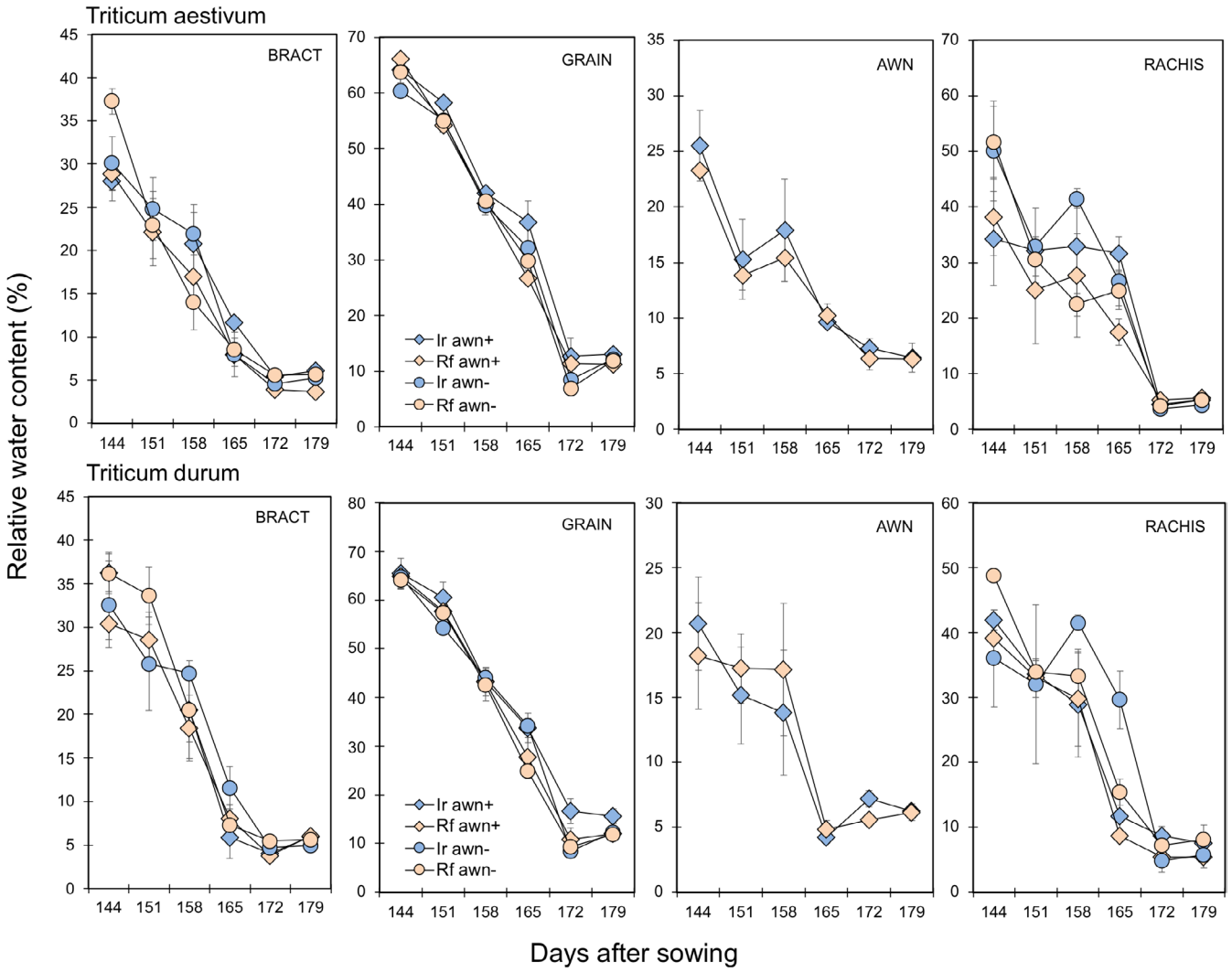


FIGURE 3 | Changes in relative water content (%) of spike components—bract, grain, awn and rachis—of two wheat species, *Triticum aestivum* L. and *Triticum turgidum* subsp. *durum* (Desf.) Husn., grown under irrigated (Ir) and rainfed (Rf) conditions, with two awn treatments: Awns intact (+awn) and awns removed (−awn). Samples were collected at six time points during grain development: 144, 151, 158, 165, 172 and 179 days after sowing (DAS). Error bars represent the standard deviation (±SD).

conditions, particularly in TD. Historically, the photosynthetic contribution of the ear has been debated. Teare et al. (1972) demonstrated that while awns provide a massive surface area for photosynthesis, the flag leaf in awnless lines often exhibits higher photosynthetic rates, suggesting a physiological attempt to compensate for the loss of ear components. Similarly, Olugbemi et al. (1976) suggested that flag leaves could compensate for awn removal. However, contradictions in the literature may stem from methodological differences, specifically whether awn effects were evaluated through manual de-awning (as in the present study) or by comparing near-isogenic awned and awnless lines. Compensatory mechanisms, such as enhanced flag leaf photosynthesis, may be constitutive genetic traits in naturally awnless lines rather than immediate induced responses in mechanically de-awned plants. Consequently, our de-awning results align more closely with Duwayri (1984) and Maydup et al. (2014), who reported significant yield penalties following de-awning. Under our field conditions, both species progressed through broadly similar grain-filling and maturity stages in terms of days after sowing, suggesting that the contrasting responses between TA and TD were not primarily due to major differences in overall phenological timing. However, the distinct patterns of spike dry matter accumulation observed between the species indicate that assimilate deposition and remobilization during grain filling may have differed, which could partly explain their different responses to awn removal.

Furthermore, studies on the contribution of different organs confirm that under Mediterranean conditions, the ear, and specifically the awns, play a pivotal role in grain filling, acting as a major source of assimilates when leaf photosynthesis is compromised (Sanchez-Bragado et al. 2014). This suggests that under favourable conditions, the awn serves as a critical 'boost' to the source-sink balance that the flag leaf cannot fully replace.

Conversely, some authors have argued that awns do not consistently improve yield, proposing instead that their primary role influences the trade-off between grain number and grain size (Rebetzke et al. 2016; Motzo and Giunta 2002). Our data supports this 'trade-off' hypothesis: while yield declined, the most

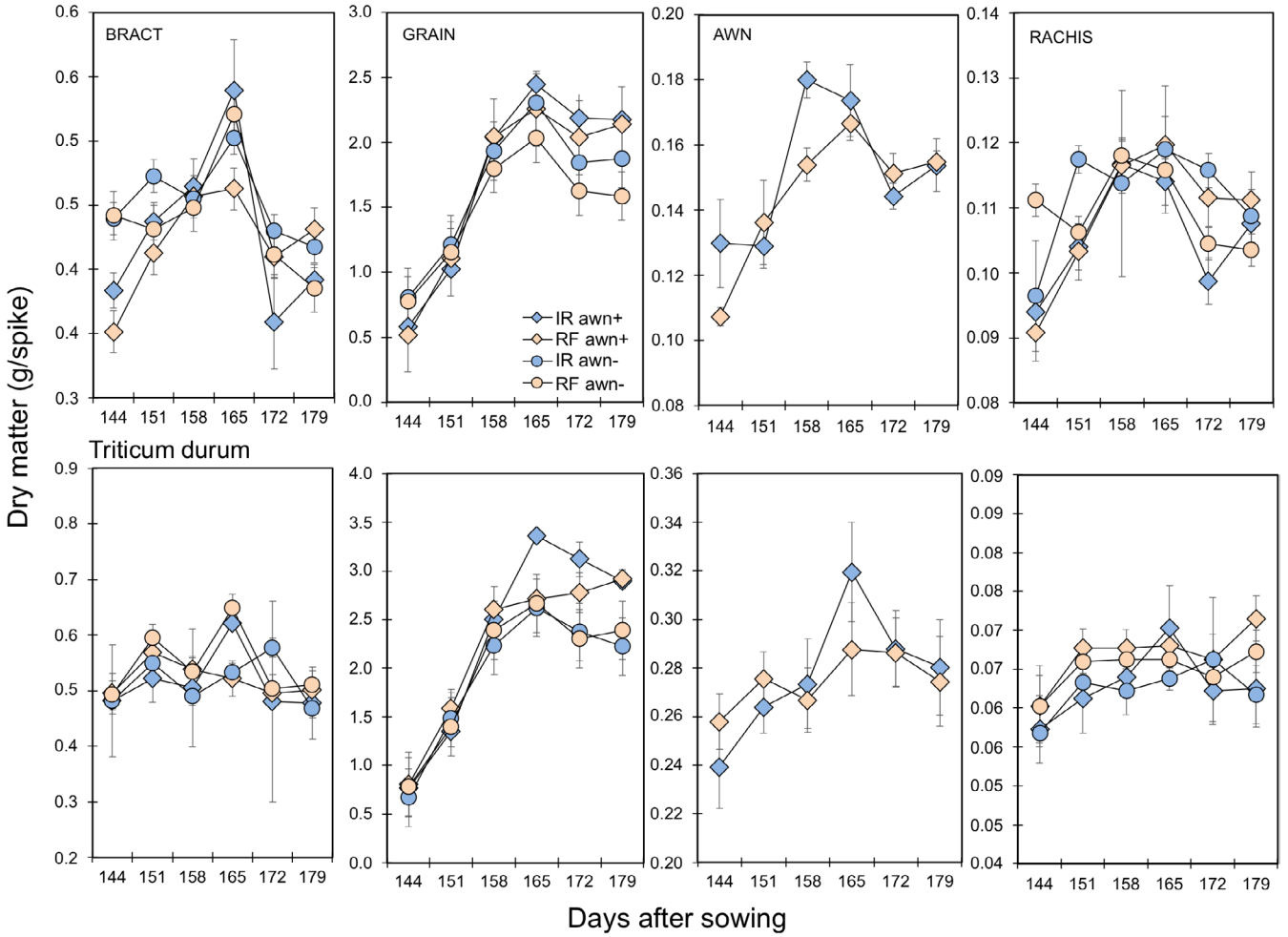


FIGURE 4 | Changes in dry matter (g) of spike components—bract, grain, awn and rachis—of two wheat species, *Triticum aestivum* L. and *Triticum turgidum* subsp. *durum* (Desf.) Husn., grown under irrigated (Ir) and rainfed (Rf) conditions, with two awn treatments: Awns intact (+awn) and awns removed (−awn). Samples were collected at six time points during grain development: 144, 151, 158, 165, 172 and 179 days after sowing (DAS). Error bars represent the standard deviation (±SD).

significant impact of awn removal was on TGW, confirming that awn-derived assimilates are preferentially allocated to grain filling rather than grain setting.

A critical finding of this study is the divergence between TA and TD. We observed that TD (a tetraploid species) exhibited a much higher dependency on awns under irrigated conditions than TA (hexaploid). This observation is strongly supported by Motzo and Giunta (2002), who established that modern durum cultivars have been bred for larger awns that can contribute significantly to the spike's total photosynthetic area and grain yield. However, under rainfed conditions, the yield penalty of removing awns in TD was negligible in our study. This points to a hydraulic and morphological cost–benefit analysis: while large awns provide photosynthates, they are also significant sources of transpiration.

Moreover, the 'cost' of awns may extend beyond water use. Recent research by Faizan et al. (2025) on cereal head morphology highlights that larger spikes and complex awn structures can significantly alter aerodynamic drag. In addition to mechanical drag, the presence of awns increases canopy surface roughness, which decreases aerodynamic resistance. This reduction in resistance facilitates water vapour flux, thereby driving up transpiration rates. Although our study focused on hydraulic balance, it is plausible that the 'optimality' of awn size is also constrained by such physical factors, where excessive awn development could predispose plants to mechanical stress or lodging, alongside the transpiration penalties noted under severe drought. In our rainfed conditions, it is likely that the transpirational cost of the large durum awns negated their photosynthetic benefit. In contrast, TA, with its inherently smaller awn biomass, may have maintained a more favourable hydraulic balance.

The reduction in WUE following awn removal (11.6% in TA and 14.4% in irrigated TD) strongly supports the view that awns are highly water-use efficient organs. This aligns with findings by Bort et al. (1994), who demonstrated that intact awns significantly improve the overall gas exchange efficiency of the ear, allowing for greater biomass accumulation per unit of water transpired. Previous studies have further attributed this to the xeromorphic traits of awns, which allow them to maintain higher water potential and photosynthetic electron transport rates than leaves during drought (Blum 1985; Tambussi et al. 2005; Sanchez-Bragado et al. 2014). Our results regarding RWC confirm this; plants with intact awns maintained higher

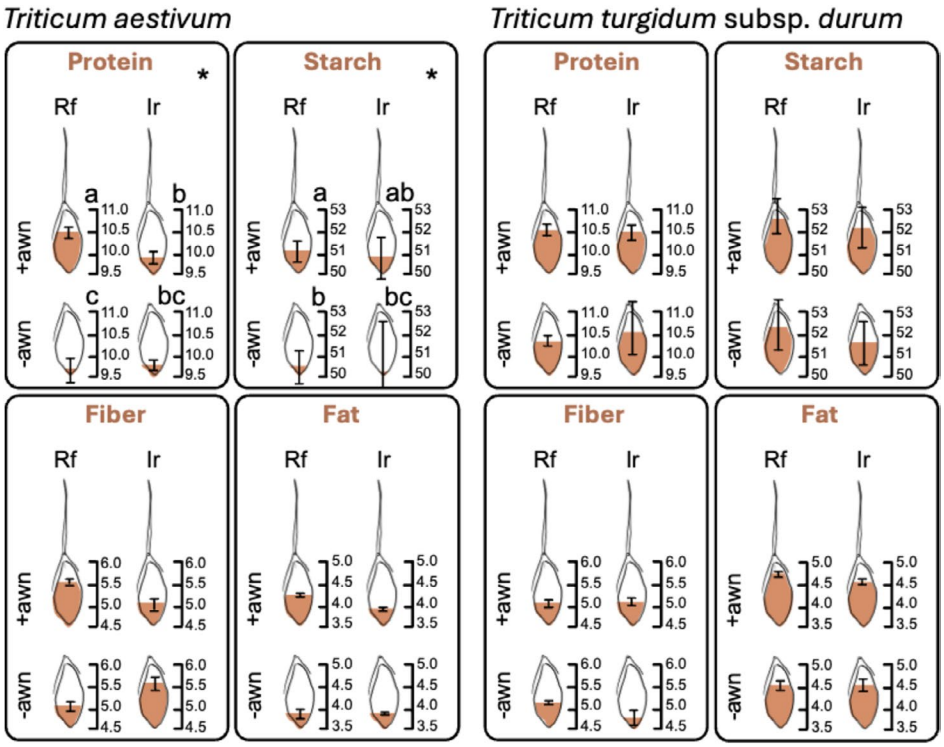


FIGURE 5 | Protein, starch, fibre and fat content (%) of grain of two wheat species, *Triticum aestivum* L. and *Triticum turgidum* subsp. *durum* (Desf.) Husn., grown under irrigated (Ir) and rainfed (Rf) conditions, with two awn treatments: Awns intact (+awn) and awns removed (−awn). Different lowercase letters indicate statistically significant differences among treatment means based on LSD test at $p \leq 0.05$. Asterisks represent significance levels from two-way ANOVA: $^{*}p \leq 0.05$. Error bars represent the standard deviation (±SD).

moisture levels in the rachis and bracts during late maturity. This 'stay-green' effect likely facilitates a longer duration of assimilate transport to the grain, acting as a hydraulic buffer.

Although the role of awns in yield formation is well documented, their influence on specific nutritional traits such as amino acid composition remains less well understood. In the present study, awn removal decreased both protein and starch content in TA. The relatively high standard deviation observed for starch content, especially in the de-awned treatment, may reflect biological variability among replicates as well as the sensitivity of starch deposition to changes in assimilate availability during grain filling. These results support the view that awns contribute to late-season source activity. Recent studies have shown that wheat ear organs remain metabolically more stable than leaf tissues under water stress and maintain important pools of carbon- and nitrogen-related metabolites during grain filling, thereby contributing to assimilate supply for the developing grain (Martinez-Pena et al. 2023). Similarly, Li et al. (2023) demonstrated that glumes and awns make a substantial contribution to ear photosynthesis, assimilate accumulation, and final grain weight under drought stress. In this context, the reduction in protein content observed after awn removal in our study likely reflects a weakening of localized ear function during grain filling including processes related to carbon assimilation and nitrogen metabolism. Although durum wheat often shows higher grain protein content than bread wheat, this pattern is not consistent across all cultivars and environments. Thus, the similar protein and starch values observed here in the awned treatments likely reflect cultivar-specific responses under the shared environmental and fertilization conditions of this experiment (Guinta et al. 2019).

Interestingly, we observed a significant increase in specific amino acids (lysine and threonine) in awn-removed plants under rainfed conditions. This inverse relationship is likely a 'concentration effect' resulting from the reduction in starch accumulation (smaller grains). When grain filling is inhibited (as seen in our de-awned plants), the total starch mass decreases more than the nitrogen accumulation, leading to an apparent increase in the concentration of certain amino acids. This aligns with general findings on drought stress and quality, where stress-induced reductions in grain size often result in higher protein or amino acid concentrations due to the 'dilution effect' of starch being compromised (Gooding et al. 2003; Ozturk and Aydin 2004; Triboi et al. 2003). Our findings suggest that while awns are essential for maximizing total starch yield, their absence can paradoxically enhance the density of specific nutritional components.

5 | Conclusion

This study demonstrates that awns are critical functional organs contributing significantly to grain yield and quality in both TA and TD, acting as a vital source of photosynthates preferentially allocated to grain filling rather than grain setting.

A key synthesis of our findings reveals a divergent response between the hexaploid and tetraploid species. TD exhibited a higher

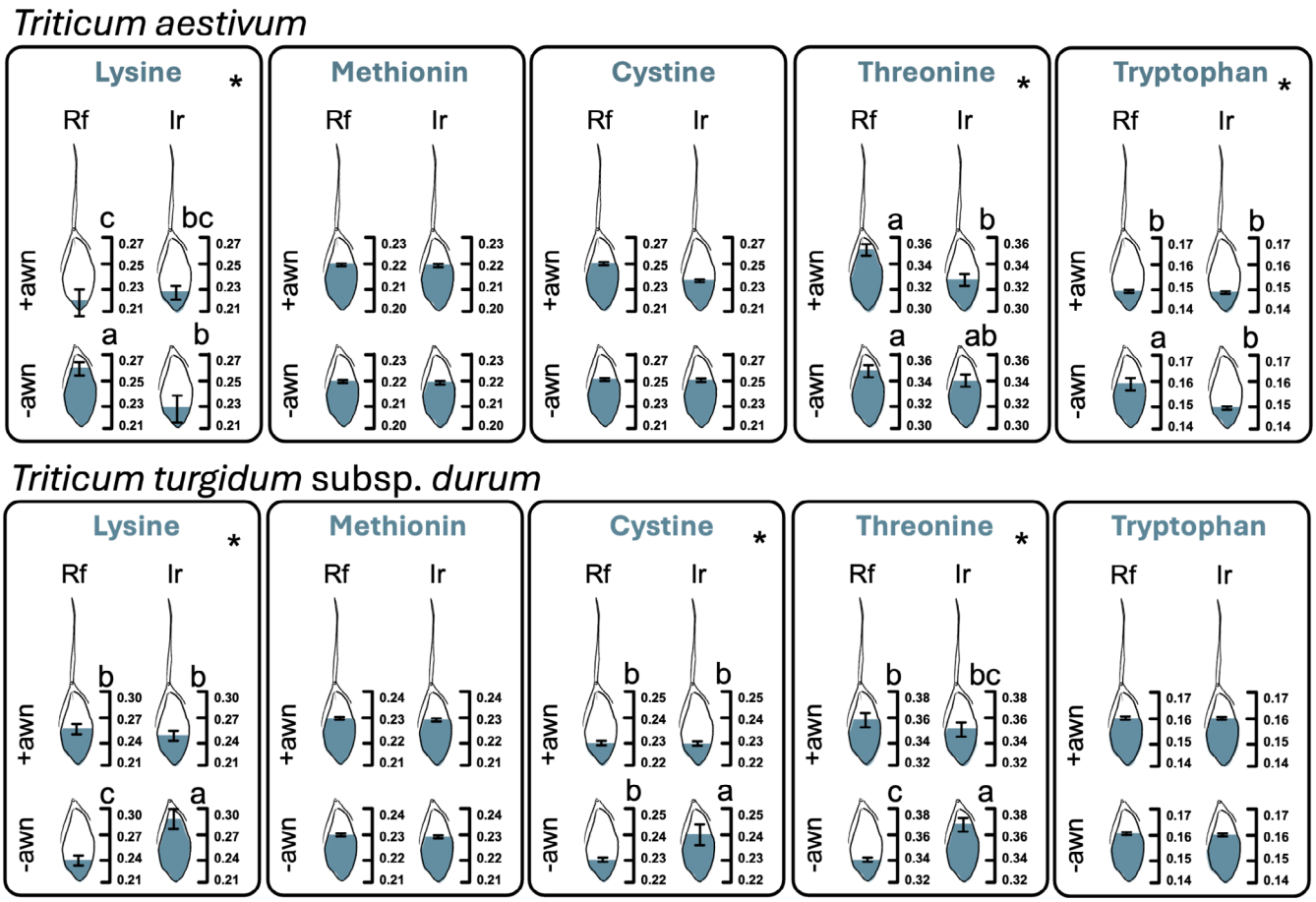


FIGURE 6 | Lysine, methionin, cystine, threonine and tryptophan content (%) of grain of two wheat species, *Triticum aestivum* L. and *Triticum turgidum* subsp. *durum* (Desf.) Husn., grown under irrigated (Ir) and rainfed (Rf) conditions, with two awn treatments: Awns intact (+awn) and awns removed (−awn). Different lowercase letters indicate statistically significant differences among treatment means based on LSD test at $p \leq 0.05$. Asterisks represent significance levels from two-way ANOVA: $^{*}p \leq 0.05$. Error bars represent the standard deviation (±SD).

dependency on awns under irrigated conditions, likely due to modern breeding efforts that maximize photosynthetic surface area. However, under rainfed conditions, this advantage was neutralized, suggesting that the transpirational cost of large awns, alongside potential physical constraints such as aerodynamic drag, offsets their photosynthetic benefits when water is limiting. In contrast, TA, with its smaller awn biomass, maintains a more favourable hydraulic balance across different moisture regimes.

Physiologically, our data indicate that awns possess xeromorphic traits that assist in maintaining ear water status during late maturity. Regarding nutritional quality, while awn removal reduced total starch and protein accumulation, highlighting the ear's role in late-season remobilization, it paradoxically increased the concentration of specific amino acids due to a 'concentration effect' caused by compromised starch accumulation.

In summary, while awns are generally beneficial for maximizing yield potential, their value is environmentally context-dependent. Future breeding programs should consider the trade-offs between the photosynthetic capacity of large awns and their hydraulic and physical costs, tailoring overall spike architecture particularly for cultivars targeted for rainfed or drought-prone environments.

Author Contributions

Recep Karakoç: investigation, validation, formal analysis, data curation, software. **Volkan Yeşil:** data curation, investigation, formal analysis, validation, writing – original draft. **Özgür Tatar:** conceptualization, validation, supervision, writing – original draft, writing – review and editing, visualization, methodology.

Acknowledgements

The authors acknowledge that the first year of data collected for this study belongs to the Master's thesis of Recep Karakoç, conducted at the Ege University Graduate School of Natural and Applied Sciences (Thesis ID: 651683).

Funding

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Abbad, H., S. El Jaafari, J. Bort, and J. L. Araus. 2004. "Comparison of Flag Leaf and Ear Photosynthesis With Biomass and Grain Yield of Durum Wheat Under Various Water Conditions and Genotypes." *Agronomie* 24: 19–28. https://doi.org/10.1051/agro:2003056.

Asada, K. 2006. "Production and Scavenging of Reactive Oxygen Species in Chloroplasts and Their Functions." *Plant Physiology* 141, no. 2: 391–396. https://doi.org/10.1104/pp.106.082040.

Blum, A. 1985. "Photosynthesis and Transpiration in Leaves and Ears of Wheat and Barley Varieties." *Journal of Experimental Botany* 36, no. 3: 432–440. https://doi.org/10.1093/jxb/36.3.432.

Bort, J., A. Febrero, T. Amaro, and J. L. Araus. 1994. "Role of Awns in Ear Water Use Efficiency and Grain Weight in Barley." *Agronomie* 14: 133–139. https://doi.org/10.1051/agro:19940209.

Bruening, P. W. 2019. "Effects of Awns on Wheat Yield and Agronomic Characteristics Evaluated in Variety Trials." *Journal of Crop Variety Testing* 2: 1–5.

Demirhan, A. A., and S. S. Bayraktar. 2025. "The Impact of Temperature and Precipitation on Wheat Production in Türkiye." *Central Bank Review* 25, no. 1: 100191. https://doi.org/10.1016/j.cbrev.2025.100191.

Demirhan, H. 2020. "Impact of Increasing Temperature Anomalies and Carbon Dioxide Emissions on Wheat Production." *Science of the Total Environment* 741: 139616. https://doi.org/10.1016/j.scitotenv.2020.139616.

Dhanda, S. S., and G. S. Sethi. 2002. "Tolerance to Drought Stress Among Selected Indian Wheat Cultivars." *Journal of Agricultural Science* 139, no. 3: 319–326. https://doi.org/10.1017/S0021859602002526.

Duwayri, M. A. 1984. "Effect of Flag Leaf and Awn Removal on Grain Yield and Yield Components of Wheat Grown Under Dryland Conditions." *Field Crops Research* 8: 307–313. https://doi.org/10.1016/0378-4290(84)90077-7.

Evans, L. T., J. Bingham, P. Jackson, and J. Sutherland. 1972. "Effect of Awns and Drought on the Supply of Photosynthate and Its Distribution Within Wheat Ears." *Annals of Applied Biology* 70, no. 1: 67–76. https://doi.org/10.1111/j.1744-7348.1972.tb04689.x.

Faizan, M., N. Freidoonimehr, M. Tucker, and M. Arjomandi. 2025. "Drag Measurement of Barley (*Hordeum vulgare* L.) Heads With Varying Morphology." *Journal of Agronomy and Crop Science* 211, no. 4: e70106. https://doi.org/10.1111/jac.70106.

Farooq, M., M. Hussain, and K. H. M. Siddique. 2014. "Drought Stress in Wheat During Flowering and Grain-Filling Periods." *Critical Reviews in Plant Sciences* 33, no. 4: 331–349. https://doi.org/10.1080/07352689.2014.875291.

Gooding, M. J., R. H. Ellis, P. R. Shewry, and J. D. Schofield. 2003. "Effects of Restricted Water Availability and Increased Temperature on the Grain Filling, Drying and Quality of Winter Wheat." *Journal of Cereal Science* 37, no. 3: 295–309. https://doi.org/10.1006/jcrs.2002.0501.

Guinta, F., G. Pruneddu, M. Zuddas, and R. Motzo. 2019. "Bread and Durum Wheat: Intra- and Inter-Specific Variation in Grain Yield and Protein Concentration of Modern Italian Cultivars." *European Journal of Agronomy* 105: 119–128. https://doi.org/10.1016/j.eja.2019.02.011.

Hosseini, S. M., K. Poustini, K. H. M. Siddique, and J. A. Palta. 2012. "Photosynthesis of Barley Awns Does Not Play a Significant Role in Grain Yield Under Terminal Drought." *Crop & Pasture Science* 63, no. 5: 489–499. https://doi.org/10.1071/CP11256.

İlker, E., Ö. Tatar, F. A. Tonk, and M. Tosun. 2011. "Determination of Tolerance Level of Some Wheat Genotypes to Post-Anthesis Drought." *Turkish Journal of Field Crops* 16, no. 1: 59–63.

Li, X., Y. Tang, C. Zhou, and J. Lv. 2023. "Contributions of Glume and Awn to Photosynthesis, ^{14}C Assimilates and Grain Weight in Wheat Ears Under Drought Stress." *Heliyon* 9: e21136. https://doi.org/10.1016/j.heliyon.2023.e21136.

Li, X., X. Zhang, G. Liu, et al. 2020. "The Spike Plays Important Roles in the Drought Tolerance as Compared to the Flag Leaf Through the Phenylpropanoid Pathway in Wheat." *Plant Physiology and Biochemistry* 152: 100–111. https://doi.org/10.1016/j.plaphy.2020.05.002.

Liang, J., J. Zhang, and X. Cao. 2001. "Grain Sink Strength May Be Related to the Poor Grain Filling of Indica-Japonica Rice (*Oryza sativa*) Hybrids." *Physiologia Plantarum* 112, no. 4: 470–477. https://doi.org/10.1034/j.1399-3054.2001.1120403.x.

Maheswari, M., T. V. R. Nair, and Y. P. Abrol. 1992. "Ammonia Metabolism in the Leaves and Ears of Wheat (*Triticum aestivum* L.) During Growth and Development." *Journal of Agronomy and Crop Science* 168, no. 5: 310–317. https://doi.org/10.1111/j.1439-037X.1992.tb01014.x.

Martinez-Pena, R., O. Vergara-Diaz, A. Schlereth, et al. 2023. "Analysis of Durum Wheat Photosynthetic Organs During Grain Filling Reveals the Ear as a Water Stress-Tolerant Organ and the Peduncle as the Largest Pool of Primary Metabolites." *Planta* 257: 81. https://doi.org/10.1007/s00425-023-04115-1.

Maydup, M. L., M. Antonietta, C. Graciano, J. J. Guiamet, and E. A. Tambussi. 2014. "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 Crops Research* 167: 102–111. https://doi.org/10.1016/j.fcr.2014.07.012.

Motzo, R., and F. Giunta. 2002. "Awnedness Affects Grain Yield and Kernel Weight in Near-Isogenic Lines of Durum Wheat." *Australian Journal of Agricultural Research* 53, no. 12: 1285–1293. https://doi.org/10.1071/AR02008.

Olugbemi, L. B., R. B. Austin, and J. Bingham. 1976. "Effects of Awns on the Photosynthesis and Yield of Wheat, *Triticum aestivum*." *Annals of Applied Biology* 84, no. 2: 241–250. https://doi.org/10.1111/j.1744-7348.1976.tb01753.x.

Ozturk, A., and F. Aydin. 2004. "Effect of Water Stress at Various Growth Stages on Some Quality Characteristics of Winter Wheat." *Journal of Agronomy and Crop Science* 190, no. 2: 93–99. https://doi.org/10.1046/j.1439-037X.2003.00080.x.

Pask, A. J., J. Pietragalla, D. M. Mullan, and M. P. Reynolds. 2012. *Physiological Breeding II: A Field Guide to Wheat Phenotyping*, 140. CIMMYT.

Patterson, F. L., L. E. Compton, R. M. Caldwell, and J. F. Schafer. 1962. "Effects of Awns on Yield, Test Weight and Kernel Weight of Soft Red Winter Wheats." *Crop Science* 2, no. 3: 199–200. https://doi.org/10.2135/cropsci1962.0011183X000200030006x.

Plaut, Z., B. J. Butow, C. S. Blumenthal, and C. W. Wrigley. 2004. "Transport of Dry Matter Into Developing Wheat Kernels and Its Contribution to Grain Yield Under Post-Anthesis Water Deficit and Elevated Temperature." *Field Crops Research* 86: 185–198. https://doi.org/10.1016/j.fcr.2003.08.005.

Rebetzke, G. J., D. G. Bonnett, and M. P. Reynolds. 2016. "Awns Reduce Grain Number to Increase Grain Size and Harvestable Yield in Irrigated and Rainfed Spring Wheat." *Journal of Experimental Botany* 67, no. 9: 2573–2586. https://doi.org/10.1093/jxb/erw081.

Reynolds, M. P., A. Mujeeb-Kazi, and M. Sawkins. 2005. "Prospects for Utilizing Plant-Adaptive Mechanisms to Improve Wheat and Other Crops in Drought and Salinity-Prone Environments." *Annals of Applied Biology* 146, no. 2: 239–259. https://doi.org/10.1111/j.1744-7348.2005.040058.x.

Sanchez-Bragado, R., A. Elazab, B. Zhou, et al. 2014. "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." *Journal of Integrative Plant Biology* 56, no. 5: 444–454. https://doi.org/10.1111/jipb.12106.

Sanchez-Bragado, R., J. W. Kim, C. Rivera-Amado, et al. 2020. "Are Awns Truly Relevant for Wheat Yields? A Study of Performance of Awned/Awnless Isogenic Lines and Their Response to Source–Sink Manipulations." *Field Crops Research* 254: 10782. https://doi.org/10.1016/j.fcr.2020.107827.

Sanchez-Bragado, R., M. D. Serret, and J. L. Araus. 2006. "The Nitrogen Contribution of Different Plant Parts to Wheat Grains: Exploring Genotype, Water and Nitrogen Effects." *Frontiers in Plant Science* 7: 1986. https://doi.org/10.3389/fpls.2016.01986.

Tambussi, E. A., J. Bort, J. J. Guiamet, S. Nogués, and J. L. Araus. 2007. "The Photosynthetic Role of Ears in C_3 Cereals: Metabolism, Water Use Efficiency and Contribution to Grain Yield." *Critical Reviews in Plant Sciences* 26, no. 1: 1–16. https://doi.org/10.1080/07352680601147901.

Tambussi, E. A., S. Nogués, and J. L. Araus. 2005. "Ear of Durum Wheat Under Water Stress: Water Relations and Photosynthetic Metabolism." *Planta* 221, no. 3: 446–458. https://doi.org/10.1007/s00425-004-1455-7.

Tatar, O., H. Brück, and F. Asch. 2016. "Photosynthesis and Remobilization of Dry Matter in Wheat as Affected by Progressive Drought Stress at Stem Elongation Stage." *Journal of Agronomy and Crop Science* 202: 292–299. https://doi.org/10.1111/jac.12160.

Teare, I. D., J. W. Sij, R. P. Waldren, and S. M. Goltz. 1972. "Comparative Data on the Rate of Photosynthesis, Respiration, and Transpiration of Different Organs in Awned and Awnless Isogenic Lines of Wheat." *Canadian Journal of Plant Science* 52, no. 6: 965–971. https://doi.org/10.4141/cjps72-165.

Triboi, E., P. Martre, and A. M. Triboi-Blondel. 2003. "Environmentally-Induced Changes in Protein Composition in Developing Grains of Wheat Are Related to Changes in Total Protein Content." *Journal of Experimental Botany* 54, no. 388: 1731–1742. https://doi.org/10.1093/jxb/erg183.

Yang, J., J. Zhang, Z. Wang, Q. Zhu, and L. Liu. 2003. "Involvement of Abscisic Acid and Cytokinins in the Senescence and Remobilization of Carbon Reserves in Wheat Subjected to Water Stress During Grain Filling." *Plant, Cell & Environment* 26, no. 10: 1621–1631. https://doi.org/10.1046/j.1365-3040.2003.01081.x.