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Review

Post-Anthesis Heat Influences Grain Yield, Physical and Nutritional Quality in Wheat: A Review

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Abstract: Climate change threatens to impact wheat productivity, quality and global food security. Maintaining crop productivity under abiotic stresses such as high temperature is therefore imperative to managing the nutritional needs of a growing global population. The article covers the current knowledge on the impact of post-anthesis heat on grain yield and quality of wheat crops. The objectives of the current article were to review (1) the effect of post-anthesis heat stress events (above 30.0 °C) on wheat grain yield, (2) the effect of heat stress on both the physical and chemical quality of wheat grain during grain development, (3) identify wheat cultivars that display resilience to heat stress and (4) address gaps within the literature and provide a direction for future research. Heat stress events at the post-anthesis stage impacted wheat grain yield mostly at the grain filling stage, whilst the effect on physical and chemical quality was varied. The overall effect of post-anthesis heat on wheat yield and quality was genotype-specific. Additionally, heat tolerance mechanisms were identified that may explain variations in yield and quality data obtained between studies.

Keywords: climate change; food security; nutrition; wheat; thermotolerance; abiotic stress

1. Introduction

In the context of climate change, various abiotic stresses including rising temperatures are significantly impacting the growth and development of crops. Since 1910, atmospheric temperature in Australia has risen by an average of 1.4 ± 0.24 °C, along with an increased frequency of extreme heat events across the continent [1]. For instance, Australia experienced 43 extreme heat days in 2019, three times more than in any given year prior to 2000 [2]. Additionally, climate modelling using data published by the Intergovernmental Panel on Climate Change (IPCC) forecasts global mean temperatures to rise by between 2.0–4.9 °C by the end of this century [3]. Increased global mean temperatures and frequency of extreme heat days pose a significant risk to the productivity of wheat cropping systems [4] that rely on optimal conditions between 12.0–22.0 °C for favourable growth and development [5]. This review examined the current literature to identify the effect of climate-change induced post-anthesis heat on wheat yield and quality. The objectives of this review were to firstly identify the effect of heat stress (above 30.0 °C) at anthesis and post-anthesis on wheat yield, before examining the effect of post-anthesis heat stress on the chemical and physical quality of wheat grain. The review also aimed to identify marker traits of the wheat cultivars in the literature that display resilience to heat stress and may be used in future breeding programs to respond to the impact of climate-induced heat stress. In this review, crop heat tolerance is the ability of a crop plant to cope with excessively high temperatures and crop heat resilience is the ability of a crop plant to resist and recover from excessively high temperatures (e.g., heat waves).

1.1. Wheat Grain Yield

Wheat is the third-largest cereal crop (by volume), and it is considered as one of the most important food crops for supplying the nutritional requirements of over 4 billion people [6,7]. Whilst the global population is forecast to increase to 9.8 billion by 2050, demand for food is expected to rise by 77.0% over the same period [8,9]. To adequately supply the global population in 2050, the Food and Agriculture Organisation predicts that an additional 900 million tonnes of cereals will be required to meet the demand [10].

Wheat cropping regions such as Australia, China and India are already experiencing high temperatures during the growing season; causing reduced grain yield [11,12]. Global wheat production is projected to decrease by up to 6.0% for each 1.0 °C increase above the optimum range of 12.0–22.0 °C [5,13]. The growth stage at which heat stress events occur has a significant impact on wheat grain yield [14]. Djanaguirama et al. [14] found that heat stress at 32.0 °C reduced yield per plant by 29.0% and 44.0% at anthesis and during the grain filling period, respectively. Due to the threat of food insecurity, there is a growing imperative to identify high-yielding wheat cultivars that display resilience to the impacts of rising temperatures and maintain nutritional and end-use quality.

1.2. Wheat Grain Quality

High temperature is well reported in the literature as among the significant factors, affecting the physical and chemical quality of wheat grains. Quality parameters, including grain number, size, grain weight, hardness and the composition of protein and carbohydrates determine the nutritional and end use value of wheat grain.

For example, grain weight and size are the important indicators of milling potential, where less flour may be extracted from smaller, more compact grains. Likewise, grain hardness is defined as the ability of grain kernels to resist mechanical force and is generally dictated by starch and protein composition within the endosperm. It is an important indicator of flour particle size and end use suitability, particularly as bread making generally requires harder wheat flour compared to biscuit and cake making [15].

Heat stress occurring at anthesis had a significant impact on grain number. Narayanan et al. [16] observed a reduction in grain number (17.0%) under a 7-d heat stress treatment at 15.0/35.0 °C, and similar results were obtained by Djanaguiraman et al. [14] when examining the cultivar Seri82 under heat stress at 32.0 °C. Grain weight is also susceptible to heat, particularly during post-anthesis period. Wang et al. [17] observed a significant reduction in mean grain weight of 20.7% across 38 diverse cultivars subjected to 37.0 °C for 3 day/night cycles at 12 days post-anthesis.

Additionally, grain protein content plays an important role in the end-use quality of wheat flour and high temperature, particularly during grain filling, and can significantly alter the quality and concentrations of grain proteins. Proteins constitute 8.0–20.0% of wheat grain, and these are divided into storage proteins (gluten) and metabolic (non-gluten) proteins. The high molecular weight gluten protein fractions gliadin and glutenin make up ~80.0% of total wheat protein [18,19]. The gliadin fraction of gluten protein provides cohesiveness and extensibility in the dough, whilst glutenins (which are further fractionalised into low and high molecular weight subunits) provide an important contribution to dough strength and elasticity [20,21]. The functionality of gluten properties, however, is dependent on the ratio of glutenin and gliadin which is found to be impacted by heat stress in the reproductive phase [22,23]. Barutcular et al. [24] reported a mean increase of 39.6% in protein content across all the tested genotypes at 36.3 °C, whilst multiple studies have found that heat stress can also have a significant impact on the composition of protein fractions in wheat flour [23,25,26].

Starch is also an important constituent of grain, comprising 60.0–75.0% of wheat yield [24]. The functional properties of starch are influenced by the ratio of amylose/amylopectin which can be negatively impacted by heat [27,28]. In normal starch, amylose content typically ranges between

20–30% [29]. A reduction in the ratio of amylose/amylopectin (from 0.22 to 0.20) was observed in the heat-tolerant cultivar Hubara-3*2/Shuha-4 when subjected to 37.0 °C temperature [27].

Empirical research into the effect of high temperature on wheat grain yield and quality is therefore important to securing reliable wheat yield and quality in the future climate. Identifying stable cultivars can minimise the disruption to desirable physical and chemical quality traits that govern the potential use of wheat flour in final food products. Various studies have identified a strong genotype-dependent response to post-anthesis heat in wheat. For instance, Poudel et al. [11] observed variation in yield between cultivars subjected to 30.0 °C; a cultivar Bhrikuti retained the highest yield of 3279 kg ha^{-1} (a 25.5% reduction from the control at 10.0/25.0 °C (day and night temperature), whilst yield in cultivar NL 1412 was reduced by 77.1% to 754.5 kg ha^{-1}. Additionally, Hernández et al. [30] identified a considerable genotypic effect for protein content and gluten strength amongst 54 spring wheat cultivars under heat stress. Moreover, of 28 selected wheat lines from the International Maize and Wheat Improvement Centre (CIMMYT) in Mexico, Borlaug 100 displayed a significant tolerance to heat, producing an 8.0% higher yield compared to control cultivars Roelfs F2007 and Vorobey [31].

2. Materials and Methods

The current review examined articles that investigated the impact of heat stress on plant yield and quality. The review outlined any contradictions in the literature and identified heat resilient cultivars that may be commercialised, used in breeding programs, or for future studies. The literature search process used Google Scholar, Scopus, and the University of Sydney library to identify relevant articles. The following keywords were used to find articles: "quality", "post-anthesis", "yield", "heat stress", "starch", "protein", "carbohydrate", "genotype", "weight", "micronutrient", "antinutritional factors", "baking quality", "dietary fibre" and "hardness".

3. Classification of Wheat Cultivars

Various wheat cultivars (*Triticum aestivum* L. and *Triticum durum* L.) were identified within the current literature that displayed a range of yield tolerance to heat. For instance, a Nepalese wheat variety Bhrikuti retained the greatest mean yield (amongst 20 spring wheat genotypes) of 3279 kg ha^{-1} under a 1-month heat treatment (max temp 35.0 °C) during anthesis, though, experiencing a 25.5% reduction from the control treatment at 10/25.0 °C [11]. Additionally, an Indian cultivar Raj 3765 displayed the greatest yield thermotolerance (37.5% reduction) amongst 30 different genotypes where the mean yield reduction was 59.5% with heat (35.0 °C) coinciding with the post-anthesis period [32]. Other significant genotypes that displayed tolerance to high temperatures included the high yielding Borlaug 100 (sourced from the CIMMYT in Mexico), and the Serbian/Bulgarian cultivar Pobeda [31,33].

Other cultivars that retained thousand kernel weight (TKW) under heat stress included the Mexican cultivar Cirno C2008 (pedigree: Sooty-9/Rascon-37//Camayo) and the Indian cultivar HD 2967 [23,28,32]. Cirno C2008, sown in February, retained the highest TKW of 41.6 g under heat stress at a max temperature between 35.0–36.0 °C during the grain filling period in May (a 21.5% reduction from the control at a maximum temperature of 32.0 °C) [23]. Similarly, HD 2967 retained the highest mean TKW of 30.7 g amongst 30 genotypes sown in mid-December and exposed to heat stress at 35.0 °C during post-anthesis (a 3.3% reduction from samples sown in optimum conditions in mid-November) [32].

Raj 4083 is a new thermotolerant wheat variety developed in Durgapura, India (pedigree: PBW 343/UP 2442//WR 258/UP 2425) that retained a TKW of 33.1 g at temperatures > 35.5 °C when sown in mid-December and exposed to post-anthesis heat, reducing by 21.4% compared to a mean TKW reduction of 31.2% across all cultivars [34,35]. Late sown Indian wheat HD 2985 retained higher TKW (23.0 g) under heat stress at 22.0/40.0 °C, 3.7 g above the mean of all genotypes compared to the control (36.6 g) at 18.0/30.0 °C, averaged across two separate growing seasons [36]. Moreover, PBW 621 increased in TKW by 5.9%, from 37.3 to 39.5 g at a temperature between 24.0–36.0 °C for 3 days in a controlled growth chamber [37]. Cultivars that could retain chemical quality under heat stress were also identified in the current literature.

4. The Effect of Heat Stress on Wheat Grain Yield

Heat Stress at Anthesis and Post-Anthesis have Varied Impacts on Wheat Grain Yield

The severity of grain yield depletion in wheat crops is highly dependent on the growth stage at which heat stress occurs. Whilst all growth stages are susceptible to some extent, heat stress during the reproductive phase (anthesis and grain filling) is particularly detrimental to grain development, which can cause reproductive sterility and significantly reduce grain number and yield [33,38,39].

The effect of heat stress on wheat grain yield is summarised in Table 1. Heat stress at anthesis had the greatest effect on grain number per plant. Mirosavljevic et al. [33] found that heat (25.0/35.0 °C) led to the cultivar Renesansa showing the highest reduction of 185 grains per plant, from 395 grains per plant at the control temperature of 16.0/24.0 °C. They concluded that the effect on grain number was likely due to flower abortion and pollen sterility at anthesis. Within the same study, the cultivar Pobeda displayed resilience to heat stress (28.0/38.0 °C) at grain filling, showing higher grain yield per plant (9 g) amongst the cultivars compared with the plants under optimum temperature (19 g) [32].

Similarly, Prasad and Djanaguiraman [40] identified the growth stages most sensitive to high temperature on the heat-sensitive cultivar Chinese Spring. Exposure to 5-d heat (26.0/36.0 °C) at 0–5 days pre-anthesis caused a maximum reduction in floret fertility (correlated to grain number) i.e., heat-stressed plants having ~25% fertility compared to the control (~80%) at 15.0/25.0 °C. Whilst heat stress during the period between 5–15 days pre-anthesis also had a significant impact on floret fertility, it had no significant impact on thousand kernel weight (TKW). In contrast, TKW was significantly decreased when 5-d heat (26/36.0 °C) was applied between 10 and 30 days post-anthesis; floret fertility was not impacted when heat was applied during this period, remaining at ~80%. In summary, heat stress at anthesis mainly lowers grain yield by reducing grain number per plant whereas heat stress post-anthesis (at grain filling) mainly lowers grain yield by reducing TKW and grain size.

Table 1. The effect of heat stress on wheat grain yield at anthesis and post-anthesis.

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Impact	Reference
38 different cultivars.	Spring *Triticum aestivum* L.	17.0/37.0	12 days post-anthesis.	Reduced grain filling duration by 2–9 days. The greatest reduction in grain filling duration was in the Chinese Spring variety, from a mean of 40.5 days at ambient temperature to 30 days at 37.0 °C (26.0% reduction). BJY/COC//PRL/BOW/3/Bloyka-1 had the lowest reduction from 39 days at ambient temperature to 33 days at 37.0 °C (14.8% reduction).	[17]
Karl 92 (USA) (Hard red winter) Ventnor (Australia) (Hard white winter)	*Triticum aestivum* L.	15.0/35.0	7 days at anthesis.	16.0% mean reduction across both varieties. Ventnor had no significant yield reduction. Karl 92 had a significant mean reduction in yield per plant (g), decreasing from 10.0 g at optimum temperature (15.0/25.0 °C) to 6.0 g at 35.0 °C.	[16]
Renesansa (Serbia) Pobeda (Serbia/Bulgaria) Simonida (Serbia) Gladius (Australia)	Winter *Triticum aestivum* L.	25.0/35.0 for all cultivars. 28.0/38.0 for all cultivars.	7 days at anthesis. Mid-grain filling 14 days post-anthesis.	The significant mean reduction in grain yield per plant for all cultivars. Pobeda retained the highest mean grain yield per plant under all treatments; 19.0 g at the control temperature (16.0/24.0 °C), 11.0 g with heat stress at anthesis, and 9.0 g with heat stress during post-anthesis. The lowest mean grain yield per plant was observed in Renesansa; 11.0 g at the control temperature, 5.0 g with heat stress at anthesis, and 5.0 g with heat stress during post-anthesis.	[33]
Bhrikuti (Nepal) Gautum (Nepal) 3 × Bhairahawa lines (Nepal) 15 × Nepal lines (Nepal)	Spring *Triticum aestivum* L.	15.0/30.0	At grain filling.	47.6% mean yield reduction across all cultivars. The greatest mean yield at 30.0 °C was observed in Bhrikuti (3279.0 kg ha^{-1}); a 25.5% reduction compared to the control at 10.0/25.0 °C. The lowest mean yield at 30.0 °C was observed in NL 1412 (754.5 kg ha^{-1}); the mean yield was reduced by 77.1% compared to the control (4144 kg ha^{-1}) at 10.0/25.0 °C.	[11]
11 released varieties (India, Pakistan) 17 breeding lines (India, Pakistan) Chirya 3, BAZ (China)	*Triticum aestivum* L.	6.0/35.0	Post-anthesis.	59.5% mean yield reduction across all cultivars. The highest yielding (g/plant) genotypes during late sown heat stress were HD 2967 (5.7 g), BRW 3797 (5.4 g), and SW 129 (5.3 g) at 35.0 °C. The yield was reduced by 58.5%, 54.1%, and 47.7% for each cultivar, respectively. Raj 3765 displayed the greatest yield thermotolerance, reducing by 37.4% at temperatures up to 35.0 °C during post-anthesis.	[32]

Table 1. *Cont.*

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Impact	Reference
28 lines from International Maize and Wheat Improvement Centre (CIMMYT Mexico)	*Triticum aestivum* L.	8.0/35.0	Vegetative and grain filling.	50.0% reduction in yield from combined heat and drought stress. Borlaug 100 displayed stability, with a mean yield 8.0% higher than the control cultivars Roelfs F2007 and Vorobey.	[31]
Yangmai16 (China) Xumai30 (China)	Winter *Triticum aestivum* L.	21.0/31.0 25.0/35.0 29.0/39.0 33.0/43.0	At anthesis and grain filling.	1.5–1.6% yield reduction per increase in heat degree days (above 30.0 °C) at anthesis, averaged across all treatments. 1.0–1.3% yield reduction per increase in heat degree days (above 30.0 °C) at grain filling, averaged across all treatments.	[41]
Seri82 (CIMMYT Mexico)	*Triticum aestivum* L.	22.0/32.0	14 days at anthesis. 14 days during grain filling.	Grain yield per plant was reduced by 29.0% (from 3.5 g at the control temperature of 14.0/24.0 °C to 2.5 g at 22.0/32.0 °C) during anthesis. Grain yield per plant was reduced by 44.0% (from 3.5 g at the control temperature to 1.95 g at 22.0/32.0 °C) during grain filling.	[14]
Almansor, Antequera, Bancal, Estero, Nabão, Pata Negra, and Roxo (Portugal)	*Triticum aestivum* L.	20.0/40.0	10 days after anthesis.	Bancal was the least affected variety, recording no significant difference in grains per the first spike between the control temperature (20.0/25.0 °C) and heat stress treatment (20.0/40.0 °C). Antequera was the most affected variety, recording a significant decrease in grains per the first spike, decreasing from 12 to 7 grains at the control and heat stress treatment, respectively.	[42]

5. The Effect of Post-Anthesis Heat Stress on the Physical Quality of Wheat Grain

The effect of post-anthesis heat stress on the physical quality of wheat has been extensively covered in the current literature (Table 2). Grain kernel number and TKW are the two major physical components that are closely correlated to wheat grain yield. Grain numbers are typically determined in the anthesis phase whilst TKW is highly dependent on the rate and duration of grain filling post-anthesis [43]. For wheat crops, a temperature above 30 °C can induce pollen sterility, interfere with grain fill, and alter grain weight and yield [44]. The reduction in grain fill duration has been attributed to leaf senescence caused by disruption to photosynthetic processes including chlorophyll degradation [44]. Consequently, the measurement of kernel number and TKW is of particular importance in empirical research for identifying thermotolerant cultivars for use in future studies and breeding programs.

The current literature reports mixed findings on the effect of heat stress on grain number. Thomason et al. [45] found no significant effect of post-anthesis heat (35.0 °C) on grain numbers of six USA cultivars. However, grain numbers are highly sensitive to high temperatures at anthesis. For example, Narayanan et al. [16] found a 17% reduction in grain number per main spike in response to 7-d heat stress (15.0/35.0 °C) at anthesis. Similarly, Djanaguiraman et al. [14] also observed a 36.0% reduction in grain number in response to 14-d heat stress (22.0/32.0 °C) at anthesis stage.

Moreover, the current literature also identifies that post-anthesis heat significantly affects grain weight. Wang et al. [17] showed a mean grain weight reduction of 20.7% across two growing seasons with temperatures reaching 37.0 °C. Similarly, Guzman et al. [23] found that TKW was reduced by 27.0% when comparing six durum cultivars. In a study testing the effect of 32.0 °C temperature on wheat cultivar Seri82, Djanaguiraman et al. [14] found that heat stress applied at anthesis had a negligible impact on grain weight, however, when applied during grain filling, the grain weight was reduced by 39.0%. These findings were in agreement with Mirosavljevic et al. [33] who reported no significant change in grain weight at anthesis, however, a significant reduction at the grain filling stage was observed when subjected to temperatures exceeding 35.0 °C. Therefore, the current literature on grain number and grain weight suggests that the developmental stage at which heat stress normally occurs is significant.

Grain hardness (also referred to as endosperm texture) and size are also important physical quality parameters, however, this is less studied within the current literature. Measuring grain hardness in the context of post-anthesis heat is important as it impacts milling properties and the end-use potential of wheat flour for baking [46]. Kernels with higher protein content are generally regarded as harder wheat, producing a strong gluten structure, ideal for breadmaking [47,48]. Singh et al. [49] found that the grain hardness index (which correlates to resistance to fracture from mechanical stress in grain) of 16 Indian wheat lines showed a general increase of 4.06 in heat-stressed samples when compared to timely sown samples. In the same study, mean protein content increased by 2.2%, which could explain the hardness increase. Additionally, Aktar and Islam [50] identified that a temperature > 30.0 °C may cause the shrinking of grains due to structural changes in grain endosperm. Li et al. [27] reported a decrease in grain width for cultivars subjected to heat stress at 37.0 °C, and similar results were obtained by Singh et al. [49] whereby grain width decreased to 2.78 mm from 3.05 mm. The decrease in grain width within this study was attributed to shortened grain filling.

Table 2. The effect of post-anthesis heat stress on the physical quality of wheat grain.

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Grain Weight/Thousand Kernel Weight (TKW)	Grain Number	Grain Hardness/Grain Size	Reference
38 cultivars of different thermotoler-ance (China).	Spring *Triticum aestivum* L.	17.0/37.0	Post-anthesis.	Mean grain weight reduction of 20.7%. Hubara-3*2/Shuha-4–5 was the most thermotolerant, with a mean TKW reduction of 2.7 g. Zemamra-5/Zemamra-5–2 was the least thermotolerant, with a mean TKW reduction of 13.1 g.	N/A	N/A	[17]
KSG103, KSG1191, KSG1194, KSG1201, KSG1203, KSG132, KSG199, KSG41, Seri82, Nacozari76, Pavon76	Spring *Triticum aestivum* L.	16.0/34.0	At anthesis.	A significant decrease in main spike single kernel weight was observed. This was highest in KSG1191 (26.0%), Seri 82 (21.9%), KSG41 (17.9%), KSG1194 (15.6%), and Pavon76 (15.0%). The least affected was Nacozari76, experiencing a 6.7% increase in main spike single kernel weight.	KSG1201 had the highest reduction (17.0%). KSG1194, KSG1203, KSG41, and Seri82 were not affected.	N/A	[51]
Karl 92 (USA) (Hard red winter) Ventnor (Australia) (Hard white winter)	*Triticum aestivum* L.	15.0/35.0	7 days at anthesis.	Not significant as the heat was applied just after anthesis but before grain filling.	Grain number per the main spike reduced by a mean of 17.0%.	N/A	[16]
6 Durum cultivars: Mexicali C75, Yavaros C79, Altar C84, Atil C2000, Jupare C2001 and Cirno C2008 (Mexico)	*Triticum durum* L.	35.0–36.0 max	At grain filling.	TKW was reduced by a mean of 27.0% across all cultivars. Cirno C2008 showed the highest mean TKW of 41.6 g at 35.0–36.0 °C (a 21.5% reduction from the control at a max temperature of 32.0 °C). Mexicali C75 showed the lowest mean TKW of 32.6 g (36.0% reduction from the control).			[23]
14 cultivars: HD2733, HD2888, HD2967, HD2985, HD2987, HD3043, HD3070, HD3076, HD3086, HD3093, PBW-17, DL-788-2, GW-322, GW-366	*Triticum aestivum* L.	22.0/40.0	Post-anthesis.	Mean TKW was 19.3 g under heat stress, compared to 36.6g under control treatment. TKW at 40.0 °C was greatest for HD2985 (23.0 g), HD2967 (22.0 g), HD2733 (21.9), GW366 (20.0). Reductions compared to the control (at 18.0/30.0 °C) were 33.3%, 40.0%, 37.6% and 50.9%, respectively. TKW at 40.0 °C was lowest for HD3043 (15.7 g), reduced by 54.1%.	N/A	N/A	[36]

Table 2. *Cont.*

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Grain Weight/Thousand Kernel Weight (TKW)	Grain Number	Grain Hardness/Grain Size	Reference
5 cultivars: Safi-1/Zemamra-1, Hubara-3*2/Shuha-4, Tinamou-2/Tevee-1/Shuha-6, Karawan-1/Tallo 3/Jadida-2 (ICARDA, Egypt), Chinese spring	*Triticum aestivum* L.	17.0/37.0	At grain filling.	Karawan-1/Tallo 3/Jadida-2, Tinamou-2/Tevee-1 and Chinese spring significantly decreased in TKW at 37.0 °C, by 16.0%, 17.5% and 21.4%, respectively compared to the control at 17.0/24.0 °C. Safi-1/Zemamra-1 increased in TKW by 1.7% (from 40.06 to 40.74g) at 37.0 °C. Hubara-3*2/Shuha-4 was also identified as a heat-tolerant line, with a reduction in TKW of 4.9% (from 45.15 to 42.94 g).	N/A	Decrease in grain width. Findings correlate width to the reduction in grain weight.	[27]
Renesansa (Serbia) Pobeda (Serbia/Bulgaria) Simonida (Serbia) Gladius (Australia)	Winter *Triticum aestivum* L.	25.0/35.0 28.0/38.0	7 days at anthesis. Mid-grain filling 14 days post-anthesis.	At anthesis, no reduction in grain weight, but significantly reduced at grain filling.	Pobeda had the highest grain number per plant of 530 at the control temperature (16.0/24.0 °C), 310 with heat stress during anthesis, and 450 with heat stress during grain filling. Renesansa had the lowest grain number per plant, with 395 at the control temperature, 210 and 284 with heat stress during anthesis and during grain filling, respectively.		[27]
11 released varieties (India, Pakistan) 17 breeding lines (India, Pakistan) Chirya 3, BAZ (China)	*Triticum aestivum* L.	6.0/35.0	Post-anthesis.	Significant reduction in TKW by a mean of 29.6% across all cultivars. Mean TKW was highest for HD2967 (30.66 g), and lowest for BRW3807 (20.0 g). Reduction in TKW at 35.0 °C was 3.3% and 39.4% for HD2967 and BRW3807, respectively.	N/A	N/A	[32]
28 lines from International Maize and Wheat Improvement Centre (CIMMYT Mexico)	*Triticum aestivum* L.	8.0/35.0	Vegetative and grain filling.	TKW significantly reduced. Mean TKW of 32.2g.	N/A	N/A	[31]
Raj 4083, Raj 4037, PBW 373 and PBW 590	*Triticum aestivum* L.	17.9/35.5	Post-anthesis.	TKW declined by a mean of 31.2%. The smallest mean TKW reduction was in heat-tolerant Raj4083 (21.4%), the highest in PBW590 (46.4%). Mean TKW for late sown Raj4083 and PBW590 was 33.1 g and 18.8 g, respectively.	N/A	N/A	[35]

Table 2. *Cont.*

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Grain Weight/Thousand Kernel Weight (TKW)	Grain Number	Grain Hardness/Grain Size	Reference
16 wheat lines: CL3870, CL3884, CL3899, CL3922, CL3929, CL3942, CL3949, CL3950, CL3952, QBP17-15, QBP17-16, QBP17-17, QBP17-18, QBP17-19, QBP17-20 and HD2932 (India)	*Triticum aestivum* L.	17.0/30.0	At grain filling.	TKW range was 24.7–37.5g. Mean TKW was 32.5 g across all cultivars under heat stress at 30 °C. The lowest TKW was observed in CL3899 (24.7 g), reducing by 32.7% at 30 °C compared to the control at 9.0/23.2 °C. The highest TKW was observed in QBP17-16 (37.4 g), decreasing by 12.6% at 30 °C compared to the control at 9.0/23.2 °C.		Mean grain width was 2.78 mm for heat stress, reduced from 3.05 mm at the control. The grain hardness index increased from 85.1 to 89.2 under heat stress.	[49]
Axe (Australia) Janz (Australia) Bolac (Australia)	*Triticum aestivum* L.	Max daily temperatures above thresholds of 26.0, 28.0, 30.0, 32.0 or 35.0.	At anthesis and grain filling.	Grain weight declined by 4.0% on average per decade since 1985.	Decrease of 1.0% on average per decade for grain number.	N/A	[1]
Seri82 (CIMMYT Mexico)	*Triticum aestevium* L.	22.0/32.0	14 days at anthesis. 14 days during grain filling.	Grain weight was not significantly affected at anthesis. Grain weight was reduced by 37.5% at grain filling from 0.04 g per seed at the control temp of 14.0/22.0 °C to 0.025 g per seed at 22.0/32.0 °C.	The number of grains decreased by 36.0% with heat stress at anthesis.	N/A	[14]
Ventnor, CB208 (VA12W72), CB210 (LA03200E2), CB213 (LA06027EP7), CB205 (AGS2000), and CB202 (USG3120) (USA)	*Triticum aestivum* L.	28.0/35.0	10 days post-anthesis.	The greatest mean grain weight reduction was observed in Ventnor (54.1%), significantly different from all other cultivars. CB202 and CB208 had the lowest mean reduction in great weight of 26.8% and 27.9%, respectively at 35.0 °C.	No effect on grain number.	N/A	[45]
DBW14, Halna, HD2733, HD2987, NW1012 and Raj4238 (India)	*Triticum aestivum* L.	33.0 max	At grain filling.	TKW was 12.0–34.0 g with heat stress at grain filling. Halna and DBW14 retained the highest TKW (reduced by 14.5% and 16.6%, respectively).	N/A	N/A	[28]
PBW 343, PBW 550 (stress susceptible), PBW 621, PBW 175 (drought tolerant), C 306, HD 2967 (heat tolerant) (India)	*Triticum aestivum* L.	24.0/36.0	At grain filling.	PBW550 had highest reduction in TKW (44.8%), from 39.0 g to 21.5 g at 24.0/36.0 °C. PBW 621 increased in TKW by 5.9%, from 37.3 g to 39.5 g at 24.0/36.0 °C. C 306 had lowest reduction in TKW (2.5%), from 40.0 g to 39.0 g at 24.0/36.0 °C.	N/A	N/A	[37]

6. Effect of Post-Anthesis Heat on Chemical Quality of Wheat Grains

Wheat plays an important role in diets for both human and monogastric animals. The chemical quality of wheat grain is explored extensively within the literature, measuring the content and composition of protein and carbohydrates in response to post-anthesis heat stress. Table 3 provides a summary that compares the effect of heat stress at various development stages on the chemical quality of wheat grain. Wheat grain protein content is a vital determinant of nutritional quality and the end-use potential of wheat flour. The protein content is affected by heat stress, particularly during the grain filling period where it is reported to increase [52].

Furthermore, carbohydrate concentration and composition is a critical measure of grain chemical quality and has important implications for the functionality of wheat flour. Starch is the main carbon reserve in wheat and it is composed of linear amylose and branched amylopectin polymers that comprise up to 75.0% of total grain dry weight [24]. Various studies indicate that post-anthesis heat can inhibit the efficiency of starch biosynthetic enzymes, affecting starch deposition in developing grains. Post-anthesis heat also alters the amylose and amylopectin ratio in grains, which may influence the pasting properties of wheat flour [53,54].

Additionally, wheat is an important source of dietary fibre within the human diet. The main constituents of dietary fibre within wheat are the non-starch polysaccharides arabinoxylan and beta-glucan which provide significant health benefits; this includes reduced risk of coronary atherosclerosis. The current literature on the effect of post-anthesis heat on dietary fibre is limited, however, Rakszegi et al. [55] have identified that heat stress at heading (just prior to anthesis) has a significant effect on the content and composition of arabinoxylan and beta-glucan in wheat grains.

Following corn, wheat is the second dominant grain in the animal feeding industry globally. In a typical wheat-soybean meal-based diet is used for pigs and poultry, where wheat starch is the primary source of energy. Soluble non-starch polysaccharides were reported to increase gut viscosity, compromise amino acid digestion, and energy utilisation in poultry [56] and non-starch polysaccharide-degrading enzymes, especially xylanase, were reported to significantly improve apparent metabolisable energy and growth performance in poultry [57]. Nowadays, xylanase is routinely included in the diets for pigs and poultry, and such an implication has shown to minimise variations in wheat quality [58] to gain consistent growth performance in animals. The potential impact of climate on concentrations and properties of non-starch polysaccharides and protein in wheat is important for both human food and animal feeding industries and a detailed review of these potential impacts is discussed below.

Table 3. The effect of post-anthesis heat stress on protein and carbohydrate quality of wheat grain.

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Protein Content and Quality	Carbohydrate Content	Reference
Yangmai 16 and Xumai 30 (China)	Winter *Triticum aestivum* L.	17.0/27.0 21.0/31.0 25.0/35.0 29.0/39.0 33.0/43.0	At anthesis. At grain filling.	Yangmai 16 increased in protein content by a mean of 0.79% and 0.82% at anthesis and grain filling, respectively, for every unit increase in heat degree days above 30.0 °C. Xumai 30 increased in protein content by a mean of 0.51% and 0.78% at anthesis and grain filling, respectively for every unit increase in heat degree days above 30.0 °C.	N/A	[41]
Gaoyou 2018 and Zhongmai 8 (China)	Winter *Triticum aestivum* L.	15.0/38.0	At grain filling.	Protein content increased by 5.0% and 2.7% in Gaoyou 2018 and Zhongmai, respectively, at 38.0 °C. Glutenin/gliadin ratio increased for both cultivars.	Significant mean starch reduction of 11.0% in Gauyou 2018 and 6.6% in Zhongmai.	[22]
16 Genotypes Adana-99, Balatilla, Cemre, Cumakalesi, Genc-99, Karacadag-98, Meta-2002, Ozkan (Turkey), Cham-6, Siete Cerros (Syria), Colfiorito (Italy), Dariel, Galil (Israel), Inqilab-91, V-3010 (Pakistan), Mane Nick (Spain)	Spring *Triticum aestivum* L.	36.0	Post-anthesis.	39.6% mean increase across all genotypes.	7.0% mean starch reduction across all genotypes. Inqilab-91, Cham-6 and Adana-99 showed highest starch content (62.5%, 62.5% and 61.9%, respectively).	[24]
KSG103, KSG1191, KSG1194, KSG1201, KSG1203, KSG132, KSG199, KSG41, Seri82, Nacozari76, Pavon76	Spring *Triticum aestivum* L.	16.0/34.0	At anthesis.	21.0% mean reduction in protein content at 34.0 °C.	Mean starch reduction of 25.0% at 34.0 °C. The highest mean starch reduction was observed in KSG1201 (38.0%). The lowest mean starch reduction was observed in Seri82 (18.8%).	[51]

Table 3. *Cont.*

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Protein Content and Quality	Carbohydrate Content	Reference
38 thermotolerant cultivars (China)	Spring *Triticum aestivum* L.	17.0/37.0	Post-anthesis.	Mean increase in protein content of 28.3% across all cultivars in late sown conditions experiencing heat stress at max 37.0 °C. The highest increase in protein content was observed in Karawan-1/Tallo 3//Jadida-2-2 (39.1%), increasing from 14.1% to 19.6% at early sown and late sown conditions, respectively. The lowest increase in protein content was observed in Chinese Spring (11.0%), increasing from 15.4% to 17.14% at early sown and late sown conditions, respectively.	N/A	[17]
6 Durum cultivars: Mexicali C75, Yavaros C79, Altar C84, Atil C2000, Jupare C2001 and Cirno C2008 (Mexico)	*Triticum durum* L.	35.0–36.0 max	At grain filling.	All cultivars had significantly higher grain protein content. The genotype Cirno C2008 had the highest mean protein content of 17.8% and the highest increase of 35.7% at 35.0–36.0 °C. The genotypes Mexicali C75 and Jupare C 2001 had the lowest mean protein content of 16.1%, increasing by 27.8% and 22.2% at 35.0–36.0 °C, respectively. All cultivars had the same glutenin content.	N/A	[23]
5 cultivars: Safi-1/Zemamra-1, Hubara-3*2/Shuha-4, Tinamou-2/Tevee-1/Shuha-6, Karawan-1/Tallo 3/Jadida-2 (ICARDA, Egypt), Chinese spring	*Triticum aestivum* L.	17.0/37.0	At grain filling.	N/A	Amylose/amylopectin ratio significantly increased for Tinamou-2/Tevee-1/Shuha-6 (0.27 to 0.33) and significantly decreased for all heat-tolerant lines, including Hubara-3*2/Shuha-4 (0.22 to 0.20).	[27]

Table 3. *Cont.*

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Protein Content and Quality	Carbohydrate Content	Reference
6 durum wheat cultivars: MexicaliC75, YavarosC79, AltarC84, AtilC2000, JupareC2001 and CirnoC2008	*Triticum durum* L.	35.0–36.0 max	At grain filling.	Gliadin fraction was significantly influenced by genotype. Glutenin fraction was significantly reduced by heat stress. Cirno C2008 had the lowest mean high molecular weight glutenin content at 3.2%. Altar C84 had the highest mean low molecular weight glutenin content at 75.1%.	N/A	[25]
Duzi and Kariega	*Triticum aestivum* L.	15.0/32.0	Post-anthesis.	Mean protein content increased by 8.3% and 10.5% in Kariega and Duzi, respectively, at 15.0/32.0 °C when compared the control treatment at 15.0/22.0 °C. The mean protein content of Kariega and Duzi was 19.34% and 19.62%, respectively, under the heat stress treatment. Gliadin content increased for both cultivars by 3.6% when exposed to temperatures up to 32.0 °C. Glutenin decreased for both cultivars by 4.6% when exposed to temperatures up to 32.0 °C.	N/A	[26]
54 cultivars (CIMMYT, Mexico)	Spring *Triticum aestivum* L.	35.0–39.0 max	At grain filling.	The highest mean protein content was observed in the cultivar Pfau/Weaver, increasing by 31.5%, from 13.0% to 17.1% under heat stress conditions at 35.0–39.0 °C. The lowest mean protein content was observed in the cultivar Pfau/Seri.1B//AM, increasing by 15.0%, from 11.3% to 13.0% under heat stress conditions at 35.0–39.0 °C.	N/A	[30]
16 wheat lines: CL3870, CL3884, CL3899, CL3922, CL3929, CL3942, CL3949, CL3950, CL3952, QBP17-15, QBP17-16, QBP17-17, QBP17-18, QBP17-19, QBP17-20 and HD2932 (India)	*Triticum aestivum* L.	17.0/30.0	At grain filling.	The mean protein content was 13.7% for delayed sown wheat, compared to 11.5% for timely sown wheat across all cultivars. CL3942 showed the highest increase in mean protein content of 48.4%, increasing from 9.1% under the timely sown treatment to 13.5% under the delayed sown treatment experiencing heat stress at 30.0 °C. The highest mean protein content was 15.0%, observed under heat stress at 30.0 °C in the cultivars CL3870, QBP17-15 and CL3899 which increased by 41.5%, 13.6% and 45.6%, respectively, compared to the control treatment. The lowest mean protein content was 11.4%, observed under heat stress at 30.0 °C in the cultivar CL3952; this was a 7.5% increase from the control treatment.	Lowered starch synthesis and reduced arabinoxylan content.	[49]

Table 3. *Cont.*

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Protein Content and Quality	Carbohydrate Content	Reference
Almansor, Antequera, Bancal, Estero, Nabão, Pata Negra, and Roxo (Portugal)	*Triticum aestivum* L.	20.0/40.0	10 days after anthesis.	Protein content decreased significantly for Antequera (16.3% to 13.4%) and Pata Negra (14.7% to 13.7%) at 40.0 °C.	Increase in starch content for Nabão and Roxo.	[42]
Triso (Germany)	Spring *Triticum aestivum* L.	32.0 max	Post-anthesis.	Protein content increased from 12.0% under the control treatment (maximum of 21.7 °C) to 14.0% under the heat stress treatment (maximum of 32.0 °C). Increased gliadin and glutenin content by 23.9% and 24.6%, respectively.	N/A	[52]
DBW14, Halna, HD2733, HD2987, NW1012 and Raj4238 (India)	*Triticum aestivum* L.	33.0 max	At anthesis.	N/A	Late sown (December) and very late sown (January) cultivars decreased in starch accumulation by 2.6% and 4.2%, respectively. Halna and HD2733 maintained relatively high starch content when compared to other cultivars. Mean reduction of 27.9% and 26.6%, respectively.	[28]
10 cultivars: Zhongmai 895, Shimai 15, ShiU 09-4366, Hengguan 35, Zhongmai 875, Shiyou 17, Zhongmai 175, Heng08guan 29, Zhongmai 162, Zhongmai 816 (China)	*Triticum aestivum* L.	2.2 higher than optimum	Post-anthesis.	Mean protein content significantly increased (13.6% to 13.8%).	Mean starch content decreased significantly (from 57.3% to 55.8%).	[53]

Table 3. *Cont.*

Cultivar and Origin	Type	Heat Stress (min/max °C)	Growth Stage	Protein Content and Quality	Carbohydrate Content	Reference
Plainsman V, Mv Magma and Fatima 2	Winter *Triticum aestivum* L.	20.0/35.0	12th day after heading.	N/A	Reduction in Beta-glucan content by 15.8–16.6% and increase in arabinoxylan content by 9.5–26.8%.	[55]

6.1. Protein Content and Quality

Various studies within the current literature report that post-anthesis heat stress alters protein content in wheat. A study conducted on two winter wheat varieties (Yangmai16 and Xumai30) showed that a temperature > 30 °C can significantly increase grain protein content. The cultivars Yangmai16 and Xumai30 experienced a 0.82% and 0.78% increase in their respective grain protein content for every unit increase in heat degree days above 30.0 °C during the trial [41]. In a similar study, Tao et al. [22] compared the response of two wheat cultivars of different gluten types (strong gluten Gaoyou 2018 and medium gluten Zhongmai 8) to high-temperature (20 days post-anthesis) and found that exposure to a 2-d heat treatment (38.0 °C) increased total protein content by 5.0% and 2.7% for Gaoyou 2018 and Zhongmai 8, respectively, when compared to the control treatment at ambient temperatures. Barutcular et al. [24] reported a similar increase in protein content in 16 spring wheat genotypes subjected to post-anthesis heat stress > 36.0 °C, observing an average of 5.5% increase. Whilst the literature reports total protein increasing under heat stress, the composition of protein fractions is also affected.

It is equally important to consider the effect of post-anthesis heat on wheat grain protein quality. The composition and ratio of monomeric gliadins and polymeric glutenins regulate dough strength and extensibility. Labuschagne and Biljon [26] reported that heat stress (32.0 °C) has a significant impact on protein composition in two hard red spring wheat varieties, Duzi and Kariega. Soluble large monomeric proteins increased, whilst small polymeric proteins decreased under heat stress for both cultivars. Barak et al. [21] identified an inverse relationship between the gliadin and gluten ratio and rheological properties of wheat dough in a separate article. Furthermore, Zhang et al. [52] studied the effect of post-anthesis heat stress on the quantity and quality of protein in wheat, finding that the gliadin and glutenin ratio decreased in the samples subjected to heat stress.

Gluten proteins are the major determinants of the baking quality of wheat flour. In breadmaking, for example, gluten proteins allow the formation of a viscoelastic dough when mixed with water; this dough can hold gas formed during the fermentation process. Whilst a high protein content is linearly associated with superior breadmaking performance, genetic variation between cultivars suggests that protein quality is equally as important in determining the functionality of wheat flour. Variation in viscosity and dough strength arises from the ratio of gliadin to glutenin subunits, whilst a high level of aggregation of larger glutenin subunits is associated with superior breadmaking performance [59].

The effect of heat stress on baking quality has previously been tested. Li et al. [60] found that post-anthesis heat (temperature > 30.0 °C) led to a mean increase in alveograph extensibility (from 100.7 mm to 106.8 mm) and loaf volume (from 797.8 cm^3 to 841.3 cm^3). Conversely, peak mixograph time decreased by 0.3 min on average, indicating a slight decrease in gluten strength when examining 15 common wheat cultivars. The change in gluten strength was primarily attributed to a decrease in the amount of polymeric glutenin. Whilst the response of each cultivar to heat stress varied, those containing stronger gluten and extensibility may lower the impact of heat stress, and therefore retain a good baking quality for breadmaking. This is supported by Guzman et al. [23] who also found an association between severe heat (maximum temperature of 36.0 °C) and reduced gluten strength in six durum wheat cultivars. Additionally, Hernández-Espinosa et al. [30] reported a dominant genotype effect for cultivars subjected to 39.0 °C. The genotypes Kachu #1, Misr1 and Kanchan exhibited superior values for gluten strength and extensibility which led to higher loaf volumes when comparing 54 diverse wheat lines. Labuschagne et al. [61] found a reduction in polymeric and an increase in monomeric proteins in response to severe heat stress, agreeing with previous evidence that gluten strength increases with a temperature up to 30.0 °C before decreasing at temperatures > 30.0 °C.

6.2. Carbohydrate Content

Carbohydrates are an important component in wheat grain that, like protein, impact the nutritional quality and end-use functionality of wheat grain. Bala et al. [37] conducted a crop trial in the semi-tropical region of Punjab, India to study the heat stress (36.0 °C) response on six wheat cultivars. They found that the starch biosynthesis was severely impeded by post-anthesis heat due to the reduced activity of key starch synthesis enzymes. High temperature prematurely ceased starch deposition thus decreasing total starch content in grain samples exposed to a 3-d heat treatment at 15 days post-anthesis. Additionally, heat stress significantly reduced amylopectin content without impacting the amylose content of the grains. Poudel and Poudel [54] noted that high temperatures can increase grain amylose content, however, exposure to extreme heat stress (i.e., 40.0 °C) can significantly hinder starch deposition resulting in a decline in soluble starch synthase activity. Moreover, Tao et al. [22] reported a significant mean reduction in starch content of 11.0% and 6.6% for the winter wheat cultivars Gaoyou 2018 and Zhongmai 8, respectively. Additionally, Aiqing et al. [51] identified a mean reduction in starch content of 25% for grain samples subjected to heat stress at anthesis stage.

Dietary fibre is an important constituent of carbohydrate composition within the wheat grain, however, there is a lack of studies that explore the effect of post-anthesis heat stress on dietary fibre within the current literature. Dietary fibre in wheat grain is primarily made up of plant cell wall polysaccharides beta-glucan and arabinoxylan; these contribute 20.0% and 70.0% of the total polysaccharide content in the endosperm, respectively. Rakszegi et al. [55] suggested that exposure to 35.0 °C at 12 days post flowering significantly decreased beta-glucan content (15.8–16.6% reduction) of three wheat cultivars whilst arabinoxylan content increased in the range of 9.5–26.8%. Given the human health benefits of dietary fibre in wheat, further attention could be given to the impact of heat stress on dietary fibre content in future studies.

The pasting properties of wheat flour are also impacted by the genotype and environmental interaction. Wang et al. [53] studied 10 bread wheat cultivars, finding that heat stress (between 25.0–35.0 °C during the growing season) reduced peak viscosity and breakdown of wheat flour, however, minor effects were observed on other pasting properties. Genetic variation among the tested cultivars was the primary explanation for the variation in peak viscosity values, followed by the treatment effect. Additionally, a previous study by Li et al. [60] observed a decrease in peak viscosity of wheat starch as well, particularly at a temperature exceeding 30.0 °C. At a temperature below 30 °C, the viscosity was not affected. Liu et al. [62] also observed a reduction in peak viscosity, breakdown and setback for the cultivars Yangmai 9 and Yangmai 12 when exposed to heat stress above 30 °C, 6–8 days post-anthesis.

7. Effect of Heat Stress on Micronutrient and Antinutritional Properties

Malnutrition presents a major challenge for countries that rely on cereal-based food [63]. It is estimated that up to 2 billion people experience zinc and iron deficiency in the diet; therefore, maintaining the nutritional content of wheat, despite an increase in the prevalence of severe heat stress is paramount [64]. Breeding for high zinc and iron content in wheat is a challenge that requires consideration of the complexity of the trait and the interaction between genotype and the environment [32]. Velu et al. [64] observed an increase in mean zinc value in 54 bread wheat varieties exposed to temperatures exceeding 35.0 °C during grain filling. Mean zinc content rose by 27.1%, increasing from 35 mg kg^{-1} to 44.5 mg kg^{-1} attributed primarily to a reduction in grain size and number under heat stress. Conversely, mean iron content decreased moderately, from 32.5 mg kg^{-1} in the non-stressed environment to 31.5 mg kg^{-1} in heat stress conditions. Narendra et al. [32] reported varied zinc and iron concentrations in response to temperatures up to 35.0 °C amongst 30 diverse bread wheat cultivars. A significant difference in zinc content was observed in SW 139 and HUW 468, which increased by 17.7% (from 25.78 ppm to 30.34 ppm) and 14.9% (from 26.28 to 30.30 ppm), respectively. Iron content was insignificant, except for the cultivar BAZ which increased by 5.6% under heat stress conditions.

Antinutritional factors are compounds that affect the bioavailability of nutrients for digestion. Phytate is one antinutritional factor that constitutes approximately 85% of the total phosphorus content in wheat grains and impedes human digestion of zinc and iron [65]. Phytic acid affects the bioavailability of minerals due to its ability to bind to positively charged ions and form insoluble salts which inhibit digestion [66]. Significant variation in phytic acid content between genotypes has been observed in previous literature examining the wheat genome, however, there is limited information on phytic acid concentration in response to heat stress [67]. One study conducted by Singh et al. [66], however, reported an increase in phytate content for late sown wheat exposed to a mean maximum temperature of 29.4 °C across two growing seasons. Timely sown PBW 343 produced a mean phytate content of 8.24 mg g^{-1}, whilst late sown PBW 343 produced a mean phytate content of 9.79 mg g^{-1}.

8. Heat Tolerance Mechanisms in Wheat

With the frequency of extreme heat stress events likely to increase in the future climate, wheat breeding programs are critical to ensuring a stable yield and quality. Various thermotolerant traits have been identified in the current literature that may be useful to prevent disruptions to crop development from abiotic stress within the growing season. Stay green and the high prevalence of heat shock proteins have been identified as characteristics that are present in thermotolerant wheat varieties. Stay-green is identified as the ability of wheat to retain chlorophyll, photosynthetic capacity (i.e., leaf greenness), and subsequently yield, aiding the plant's ability to manage development under heat stress [68]. Ullah and Chenu [44] found a significant genotype effect when studying the effect of post-anthesis heat stress above 32.0 °C on the cultivars SB062 and SB003. SB062 showed no significant variation in the rate of leaf senescence, displaying a stay green characteristic greater than SB003. SB003 experienced leaf senescence to varying degrees which was dependent on the timing of heat stress at the post-anthesis stage. Similarly, Latif et al. [68] conducted a study in Pakistan on 123 diverse bread wheat cultivars, concluding that heat stress at 36.0 °C had a significant genotype effect. Cultivars that exhibited a greater ability to stay-green showed higher maximum yield than non-stay green cultivars. Genotypes with superior assimilation supply through photosynthesis during grain-filling could ensure grain development under hot environments, and these traits should be considered in the future wheat breeding programs [69].

Moreover, genotypes that exhibit more heat shock proteins are desirable candidates for breeding thermotolerant wheat crops. Heat shock proteins occur in response to high temperatures, and they are categorised based on their molecular weight [70]. Heat shock proteins play a specific role under heat stress, binding to denatured proteins as protection from aggregation, before facilitating their reformation after high temperature ceases [71]. They exist as molecular chaperones (aiding protein folding) differing from other protein fractions in wheat grain (e.g., glutenin and gliadin) [72]. Upregulation of heat shock (Hsp70s) and cytoskeletal proteins in pollen tissues is linked with fertility restoration under hot environments [73]. In a study comparing 10 different bread wheat cultivars at 4 different temperature regimes, Katakpara et al. [74] attributed the accumulation of heat shock proteins to increases in protein content for high-temperature treatment. Additionally, in a study comparing 4 bread wheat varieties under heat stress (38.0 °C) during the grain filling stage, Kumar et al. [75] found the expression of heat shock proteins to be genotype specific. The thermotolerant cultivar Halna showed significant expression of heat shock proteins when compared to the PBW343 and HD2329. Where heat shock proteins are not expressed, yield components such as TKW decreased which was found for the cultivar PBW343 by Bala et al. [37].

Several other heat tolerance mechanisms are reviewed in detail. For example, antioxidant defense system is one such example that is covered by Farooq et al. [76]. Heat stress can trigger the production and buildup of reactive oxygen species, however, in thermotolerant wheat, the activities of both enzymatic (including catalase and ascorbate peroxidase) and non-enzymatic (ascorbate, glutathione and tocopherols) antioxidants are increased to provide protection from heat induced oxidative damage. Additionally, Sarkar et al. [77]

reviewed canopy temperature depression as an important physiological mechanism for sustaining grain yield after exposure to heat stress. In high temperature and low humidity conditions, thermotolerant cultivars expressed more efficient transpirational cooling, owing to greater stomatal conductance of the leaf. Other heat tolerance mechanisms reviewed include membrane thermostability and photoassimilate translocation. Likewise, soluble starch synthase activity under heat stressed conditions has been considered an important indication of heat stress tolerance in wheat [77].

9. Gaps in the Current Literature

The impact of post-anthesis heat stress on wheat yield has been studied extensively, however, there is scope to further study the impact of post-anthesis heat stress on quality parameters such as grain hardness and size. Further attention could also be given to micronutrient content (particularly, vitamin content), antinutritional factors and baking quality. There is also a lack of studies that examine the effect of heat stress on dietary fibre content, which has important implications for human nutrition. Additionally, since heat stress affects the traits important to the marketability of wheat (including protein and starch), future studies could utilise the thermotolerant cultivars identified in the current literature to examine the impact of heat stress on the quality of final food products.

10. Conclusions

The current literature extensively covers the effect of post-anthesis heat on wheat yield and quality. Given future climate projections, there is a growing imperative to identify wheat cultivars that display resilience to heat stress throughout the growing season so that productivity may be maintained to facilitate the energy needs of a growing population. Studies have found that heat stress at different stages of crop development impacts the yield potential of wheat grain (Table 1). Heat at the pre-anthesis stage has a significant impact on grain number, reducing yield, whilst the grain filling period is shortened by post-anthesis heat.

Additionally, the impact of post-anthesis hot events on the physical and chemical quality of grain is examined within the current literature. Physical parameters which are highly correlated to yield include grain number and weight which decreased under heat stress at anthesis and post-anthesis (Table 2), whilst grain hardness and size were less covered in the current literature. The composition and quality of wheat grain protein are important in governing viscoelastic properties in the wheat dough, and subsequently the end-use potential for food products. Findings from empirical research suggested that heat stress impacted total protein content to varying degrees (Table 3). Similarly, the composition of gliadin and glutenin fractions was affected by heat stress with a strong genotype effect identified (Table 3). Whilst starch content and composition are also covered extensively in the literature, less attention is given to dietary fibre which could form a basis for future research.

A limitation of the current review is the ability to make comparisons between cultivars within previous studies that have used different experimental designs, including a diverse range of heat stress treatments. Future studies could test the thermotolerant cultivars identified within the current review to determine the effect of post-anthesis heat stress more accurately on yield and quality amongst the different cultivars. Given the observed genotype specific response to heat stress identified in the previous literature, cultivars with traits such as stay green and heat shock proteins can provide viable options for wheat growers seeking greater productivity with the projected future climate.

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