agriculture

MDPI

Article

Wheat Under Warmer Nights: Shifting of Sowing Dates for Managing Impacts of Thermal Stress

Roshan Subedi [1,2,*], Mani Naiker [1], Yash Chauhan [3], S. V. Krishna Jagadish [4] and Surya P. Bhattarai [1]

[1] Institute of Future Farming Systems, School of Health, Medical and Applied Sciences, Central Queensland University, Rockhampton, QLD 4701, Australia; s.bhattarai@cqu.edu.au (S.P.B.)
[2] Institute of Agriculture and Animal Science, Tribhuvan University, Kirtipur 44600, Nepal
[3] Department of Primary Industries, Kingaroy, QLD 4610, Australia
[4] Department of Plant and Soil Science, Texas Tech University, Lubbock, TX 79409, USA
* Correspondence: r.subedi3@cqu.edu.au

Abstract

High nighttime temperature (HNT) due to asymmetric diurnal warming threatens wheat productivity. This study evaluated the effect of HNT on wheat phenology, physiology, and yield through field and controlled environment experiments in Central Queensland, Australia. Two wheat genotypes, Faraday and AVT#6, were assessed under three sowing dates—1 May (Early), 15 June (Mid), and 1 August (Late)—within the recommended sowing window for the region. In a parallel growth chamber study, the plants were exposed to two nighttime temperature regimes, of 15 °C (normal) and 20 °C (high), with consistent daytime conditions from booting to maturity. Late sowing resulted in shortened vegetative growth and grain filling periods and increased exposure to HNT during the reproductive phase. This resulted in elevated floret sterility, lower grain weight, and up to 40% yield loss. AVT#6 exhibited greater sensitivity to HNT despite maturing earlier. Leaf gas exchange analysis revealed increased nighttime respiration (Rn) and reduced assimilation (A), resulting in higher Rn/A ratio for late-sown crops. The results from controlled environment chambers resembled trends of the field experiment, producing lower grain yield and biomass under HNT. Cumulative nighttime hours above 20 °C correlated more strongly with yield losses than daytime heat. These findings highlight the need for HNT-tolerant genotypes and optimized sowing schedules under future climate scenarios.

Keywords: grain filling period; high nighttime temperature; phenology; respiration to photosynthesis (Rn/A) ratio; wheat

check for updates

Academic Editor: Ming Chen

Received: 1 July 2025
Revised: 25 July 2025
Accepted: 1 August 2025
Published: 5 August 2025

Citation: Subedi, R.; Naiker, M.; Chauhan, Y.; Jagadish, S.V.K.; Bhattarai, S.P. Wheat Under Warmer Nights: Shifting of Sowing Dates for Managing Impacts of Thermal Stress. *Agriculture* **2025**, *15*, 1687. https://doi.org/10.3390/agriculture15151687

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Wheat is the second most important cereal globally [1], contributing 20% of total dietary calories and protein [2]. Global predictions indicate that the food demand would rise by 35–56% by 2050 [3], thus requiring an annual increase of 2% to meet the growing population [4]. Moreover, this increase must be met within the context of a changing climate characterized by an increasing frequency of short- or long-term abiotic stress events [1].

As a cool-season annual, even a small rise in temperature poses a risk to wheat due to impacts on carbon and water balance [5]. The vegetative growth period in wheat exhibits more resilience to heat due to higher overall recovery potential [6] during these stages, maintaining grain yield [7]. However, anthesis and grain filling stages are sensitive to heat stress [8] as heat stress can drastically reduce the grain number and weight [9], impacting overall yield [10]. High temperatures during these critical stages also effect the grain quality

prominently, reducing starch and protein content [11]. The ideal temperature during the grain filling period for most wheat varieties ranges from 12 to 22 °C [12,13]. A temperature range of 30–34 °C, with a nighttime temperature of 20–25 °C, is reported to be the maximum threshold temperature for wheat [14,15]. Prasad, et al. [16] have reported a negative effect of HNT above 20 °C on spikelet fertility and size of wheat grains.

Diurnal asymmetry in rise of temperature is a feature of the changing climate and global warming, with most models predicting increases in nighttime temperature being more pronounced than increases in daytime temperature [1]. High nighttime temperature (HNT) alone can have similar impacts on grain and biomass productivity as high daytime temperature stress [17] due to reduced vegetative growth period [18], grain filling duration [17], and spikelet fertility [16]. Furthermore, HNT are reportedly associated with increased night respiration (Rn) leading to carbon loss, one major reason for decline in biomass [19]. HNT alone can stop starch accumulation in grains, providing more opportunities for protein and lipid accumulation [20], altering seed quality, and increasing the protein fraction while reducing the starch [18]. Furthermore, wheat yields exhibit a stronger correlation with nighttime temperatures than daytime maximum temperatures, with decreasing nighttime temperatures associated with higher yields [21]. Therefore, HNT is emerging as a critical factor affecting wheat production [20].

A number of studies have been conducted to evaluate the impact of HNT in wheat crops. However, these studies are concentrated either at plant levels in controlled environment glasshouses [15,16,22,23] or using specialized structures in field trials to raise the nighttime temperature with or without external heat sources [4,17,24–26]. These field trials have contrasting results, showing negative effects on wheat yield [4,17] when the rate of increase in nighttime temperature was ~4 °C, while in harsher winter conditions with a lower temperature rise, increased nighttime temperature favored growth and yield in wheat [25].

The HNT effect varies depending on the stages of exposure [24,27], suggesting that crops sown on different dates will respond differently to the existing ambient nighttime temperature regime. Crops implement different mechanisms to cope with heat stress that are regulated at the molecular level, and thermotolerance is acquired as a result of active processes that divert resources to functional and structural maintenance [28]. Furthermore, pre-anthesis exposure to HNT improves post-anthesis thermal acclimation during the critical periods [29], thereby creating early sowing options for HNT resilience under warmer nights during post-anthesis period in the Australian tropics.

The previous studies assessed the magnitude and amplitude of HNT effects in wheat, but there are very few studies conducted on ambient temperature regime with natural diurnal temperature amplitude maintained. Since the high daytime and high nighttime temperatures have similar impacts on physiology, biochemical, growth, and yield traits, they accumulate and aggravate their impacts [15]. Modeling studies have projected that wheat Australia will face heat stress, and the relative importance of heat stress is steadily increasing [30]. Night warming is evident in all seasons over most of Australia, exceeding the rate of rise in maximum temperature [31]. This study, therefore, aimed to investigate the effect of HNT at both the plant and crop levels through a parallel controlled environment experiment and a field trial conducted with different sowing dates to expose the crop to varying nighttime temperatures. The key questions the study addresses are as follows: (a) Does wheat crop sown at varying dates in tropical winter season experience HNT impacting yield; (b) Do the HNT impact at the plant level reflect similarly at the crop level; and (c) What are the underlying physiological and phenological bases underpinning HNT tolerance in wheat genotypes.

2. Materials and Methods

2.1. Experimental Site

Two independent experiments were conducted from May to December 2024 in CQIRP, Rockhampton (23.32° S, 150.51° E), QLD, Australia, to evaluate the effects of elevated nighttime temperatures on wheat growth and yield performance. Experiment-I encompassed a field trial sown at different sowing dates from May to November, while Experiment-II constituted a controlled environment plant growth chamber trial carried out from September to December.

2.2. Experimental Design

The field trial (Experiment-I) was carried out on 24 garden raised bed structures (Birdies, Australia: https://birdiesgardenproducts.com.au/raised-garden-beds-pots-and-planters/select-a-size-122cm-wide/ accessed 24 July 2025). This experiment comprised three sowing dates (Early: 1 May, Mid: 15 June, and Late: 1 August) within the recommended sowing window for wheat in Central Queensland, aimed at subjecting two wheat genotypes (Faraday and AVT#6) to contrasting nighttime temperature regimes during the critical growth period in open-field conditions. Faraday (commonly DS Faraday) is a high yielding variety comparable to other Australian Prime Hard (APH) varieties, commonly cultivated in Central Queensland for its grain dormancy and triple (leaf, stem, and stripe) rust resistance. AVT#6, on the other hand, is a short duration wheat line being developed to be cultivated in low moisture environments. The experiment was laid out in a randomized block design under split plot arrangement with 4 replicates, using sowing dates as the main-plot and genotypes as the sub-plot factor. During seed sowing, the seeds were manually sown with continuous sowing in three rows in each raised bed (treatment), spaced 25 cm apart. Each individual row was thinned after a week of emergence to maintain a plant population of 60 plants per row. The trial beds were irrigated with a surface drip system to supplement rainfall.

In Experiment-II, a total of 24 pots (12 for each genotype), 15 cm in diameter and 15 cm deep, were filled with 1.8 kg of the same black cracking Vertisol clay as in Experiment-I. Four seeds of the two wheat genotypes (Faraday and AVT #6) were hand sown in pots at a depth of 5 cm on 3 August 2024. After emergence, all pots were thinned to one plant per pot and maintained until maturity. Each pot received 5 g of controlled-release fertilizer: Scotts Osmocote All Purpose (21:0.5:6% ratio) (Evergreen Garden Care, Bella Vista, Australia). All pots were kept at ambient environment until the booting stage (Zadok-43) (https://www.agric.wa.gov.au/grains/zadoks-growth-scale accessed 24 July 2025). On the onset of booting, the pots were sprayed with Aphidex (ADAMA, St Leonards, Australia) @ 3 g/L to avoid aphids in the growth chambers. In the growth chambers, the two genotypes were replicated six times in each temperature treatment. The experiment utilized two indoor CLIMATRON growth chambers (Thermoline, Wetherill Park, Australia: https://www.thermoline.com.au/hubfs/User%20Manuals/Climatron/TM-025-UM%20Climatron.pdf accessed 24 July 2025) set at two different nighttime temperatures: 15 °C (low nighttime temperature-LNT) and 20 °C (high nighttime temperature-HNT). The daytime temperature and relative humidity in both chambers were consistently maintained at 28 °C and 65%, respectively. The nighttime condition was regulated from 18:30 to 06:00 h, and the daytime condition from 06:30 to 18:00 h, with a 30-min transition period for gradual temperature adjustments. Light in the chambers was supplied for 12 h (06:00 to 18:00 h), providing a PPDF of 400 µmol m^{-2} s^{-1}. Air temperature in both chambers was continuously monitored every 30 min using a Hobo Pendant data logger (LI-COR, MacArthur Blvd., Bourne, MA, USA). In the chambers, the pots were placed in a plastic trough maintained with 1 cm water to prevent any potential water stress.

2.3. Data Collection

In both the experiments, plant phenological, physiological, growth and development, and yield traits were assessed. Key phenological parameters included duration to heading (Zadok-59), anthesis (Zadok-65), and physiological maturity (Zadok-91). Crop physiological parameters were assessed by daytime and nighttime leaf level gas exchange traits. Additionally, biomass and grain yield data were collected at maturity in both the experiments.

The gas exchange traits were measured on fully expanded flag leaf. In Experiment-I, leaf level gas exchange measurements—specifically photosynthesis, respiration, stomatal conductance, transpiration, and maximum quantum efficiency—were measured from three random plants in the central row of each plot during anthesis and grain filling (two weeks after anthesis) using the LI-COR 6800 portable photosynthesis system (LI-COR, Lincoln, NE, USA). The photosynthesis measurements were taken between 10:00 to 12:00 h, and the respiration measurements were taken between 20:00 to 22:00 h at ambient temperature and relative humidity conditions. The photosynthesis system was operated at 7000 rpm, maintaining a flow rate of 500 μmol s^{-1}, and the CO_2 concentration within the leaf cuvette was set at 400 μmol mol^{-1}. The internal light source was configured at 1500 μmol m^{-2} s^{-1} for photosynthesis and 0 μmol m^{-2} s^{-1} for night respiration. In Experiment-II, the gas exchange traits were measured on the day before transferring the pots into the growth chambers and, subsequently, at one, two, and three weeks after temperature treatment at their respective growth temperature.

In Experiment-I, all the growth and yield parameters were measured from the central row in each raised bed, whereas in Experiment-II, each individual plant was treated as a separate experimental unit. Plant height at harvest and the length of panicle exertion was measured from the ground to the tip of the plant and from the flag leaf sheath to the base of spike, respectively. The central row was harvested, and the spikes were subsequently separated. Ten spikes were randomly selected for measurement of spike length. Following that, individual florets in the sampled spikes were checked for grain by pressing the floret between the thumb and finger. Floret fertility percentage was determined as the ratio of florets with grain to the total number of florets. The stem and leaves were dried at 60 °C for four days, and the spikes were sun-dried for four days, then oven-dried at 40 °C until constant weight. The biomass and grain yield from the central row and individual pots were measured in Experiment-I and -II, respectively. The harvest index was calculated as the ratio of grain yield to the total aboveground biomass.

2.4. Data Analysis

All the collected data were analyzed using R (Version 4.2.3). The data from Experiment-I were analyzed using analysis of variance (ANOVA) for split-plot design with sowing date as the main-plot and genotypes as the sub-plot factor. Type III sums of squares were used to test fixed effects, and assumptions of normality and homogeneity of variance were tested using diagnostic plots. Post-hoc analysis was done using LSD test at 5% level of significance ($\alpha = 0.05$) using "emmeans" and "multcompView" packages. The regression analysis, including the polynomial models, was conducted to examine the relationships between thermal stress variables and yield, with model fit assessed by r2 values, while Pearson's correlation coefficient was calculated to evaluate associations among traits. This was completed using "corrplot", "ggpmisc", and "Hmisc" packages. The graphical representations were generated using "ggplot2" package.

3. Results

3.1. Weather Conditions During Field Trial

During the wheat growing season, the average temperature declined from mid-June to early July, with a brief spike occurring mid-July, before decreasing again by the end of the month. The maximum temperature began to rise in mid-August; however, the increase in nighttime minimum temperature was noted only after early November. Rainfall was limited throughout the season, resulting in a cumulative precipitation of approximately 600 mm between May to December. Figure 1 illustrates the temperature and rainfall conditions observed during the field trials.

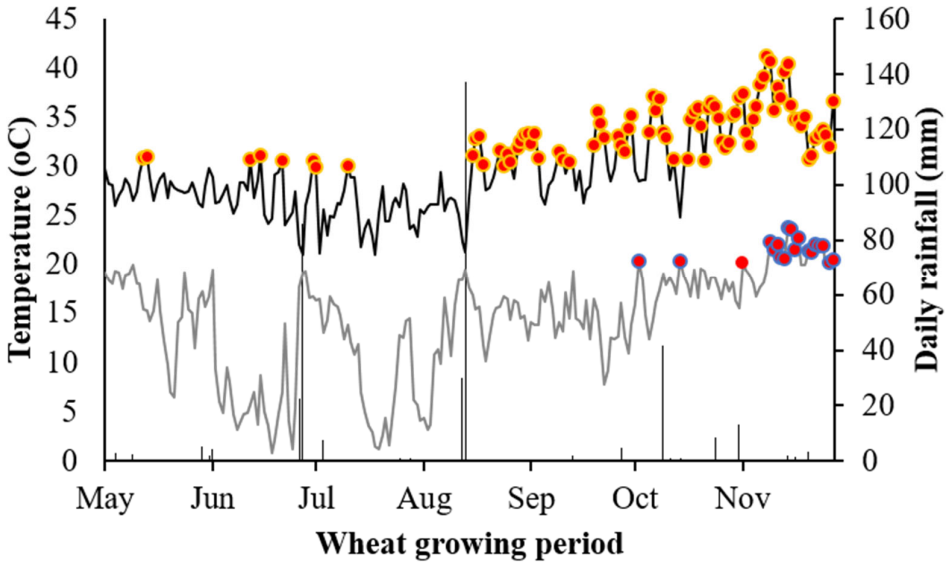


Figure 1. Daily weather condition during the wheat growing season in Rockhampton. The black and gray lines show the daily maximum and minimum temperatures, respectively. The orange and red dots in the lines indicate days with maximum and minimum temperature exceeding 30 and 20 °C, respectively. The bars show the daily rainfall recorded.

Additional insights into the weather patterns, particularly regarding the average daytime and nighttime temperatures as well as the duration of day and night above the threshold temperature of 30 and 20 °C, respectively, provided a more comprehensive understanding of thermal amplitudes. The average daytime temperature remained consistently below 30 °C for a long period until late September, after which the average daytime temperature almost constantly remained above 30 °C. Similarly, nighttime averages were below 20 °C from early June to mid-September; this pattern shifted as nighttime temperature subsequently rose above 20 °C. Notably, there were no recorded night hours above 20 °C in mid-June, the second fortnight in July, or early August. In contrast, the early period in May experienced prolonged night hours (~6 h) with temperature exceeding 20 °C despite the minimum temperature remaining below 20 °C. Prolonged night hours of temperature above 20 °C was common in October. By November, nighttime temperature consistently remained above 20 °C (Figure 2).

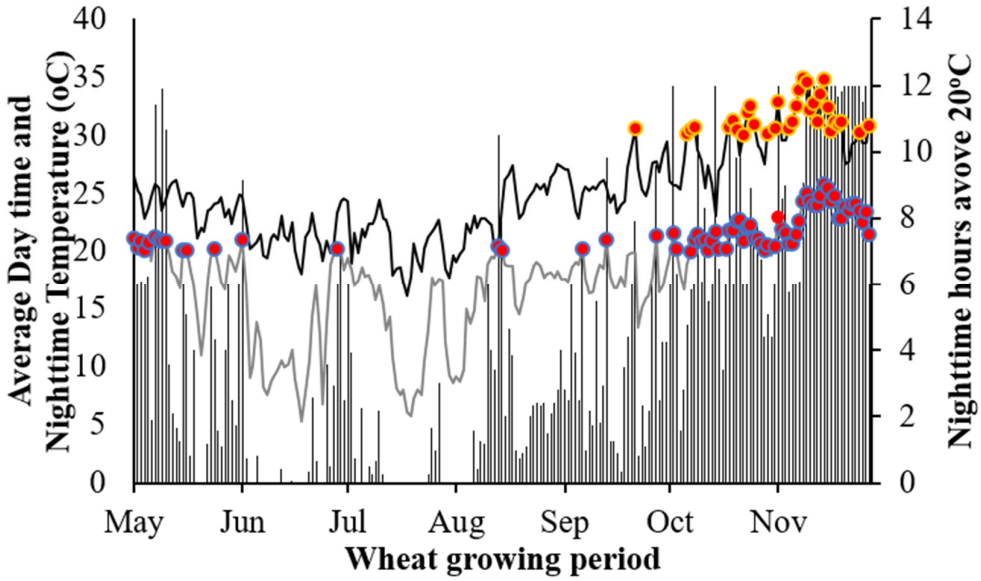


Figure 2. Average daily temperature regime throughout the wheat growing season in Rockhampton. The black and gray line indicate the daily mean daytime and nighttime temperature, respectively. The orange red dots indicate the days with average daytime and nighttime temperature exceeding 30 and 20 °C, respectively. The bars indicate the nighttime hours exceeding 20 °C.

The diurnal temperature recorded in the growth chambers in Experiment-II are listed in Table 1.

Table 1. Observed temperature in the CLIMATRON chambers.

Temperature Treatment Chamber	Temperature (°C)	
	Daytime	Nighttime
1: Low nighttime temperature (LNT)	28.2 ± 0.8	15.3 ± 0.5
2: High nighttime temperature (HNT)	28.6 ± 0.6	19.9 ± 0.8

3.2. Analysis of Variance of Observed Traits

In the field trial, measured vegetative and reproductive traits were significantly influenced by the sowing date, genotypes, and their interaction (Table 2). Most of the measured parameters were significantly affected by the genotype; however, grain yield and some yield attributing traits, like proportion of non-effective tillers, threshing percentage, and harvest index, did not significantly vary between the genotypes. All other observed plant parameters were influenced by sowing date. The interaction effect between sowing date and genotypes remained comparable, with only a few parameters, such as duration of vegetative and grain filling stages, harvest index, and 1000-grain weight, affected significantly by the interaction of sowing dates and genotypes.

In the controlled environment (Experiment-II), most of the observed plant growth and yield traits were influenced by genotype and nighttime temperature in isolation; however, the interaction had no significant effect on any of the observed parameters. The number of florets and grains per spike, grain yield and 1000-grain weight were not influenced by the genotype. On the other hand, nighttime temperature did not affect plant height, productive tillers, spike length, or the number of florets and grains per spike. The specific details of the influence of nighttime temperature are provided in Table 3.

Table 2. Analysis of variance of different phenological and biometrical observations in the field trial (Experiment-I).

Observed Parameters	Probability—Among the Factors			CV1 (%)	CV2 (%)	Mean
	Sowing Date	Genotype	Interaction			
Plant height (cm)	***	***	**	3	3.4	71.6
Panicle exertion length (cm)	***	*	NS	5.6	9.8	13.5
Days to heading (days)	***	***	NS	3.2	3.1	73.8
Days to flowering (days)	***	***	NS	2.1	2.4	79.9
Days to maturity (days)	***	***	**	2.1	1.5	116.2
Vegetative phase (days)	***	***	*	3.6	2.8	67.4
Grain filling duration (days)	***	***	*	5.3	2.6	36.3
Tillers (m^{-2})	NS	***	NS	14.2	9.4	280.3
Spikes (m^{-2})	NS	***	NS	13.2	12.1	210.2
Non-effective tillers (%)	**	NS	NS	11	29.3	25.1
Spike length (cm)	***	***	NS	4	4.2	7.97
Spikelets per spike (#)	NS	*	NS	7.7	8.8	22.4
Florets per spike (#)	NS	***	NS	8	8.8	52.8
Grains per spike (#)	***	**	NS	6.6	10.8	38.05
Floret Sterility (%)	***	*	NS	4.9	12.7	28.3
Spike yield (g m^{-2})	***	NS	NS	13.7	17.4	298.05
Grain yield (g m^{-2})	***	NS	NS	15.4	17.7	220
Straw yield (g m^{-2})	***	*	NS	12.8	14.9	217.04
Threshing %	**	NS	*	2.6	2	73.3
Harvest index (ratio)	*	NS	*	6.5	6.2	0.43
1000-grain weight (g)	**	***	**	4.2	2.7	41.2

*, **, and *** indicate statistical significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively; NS indicates no significant difference.

Table 3. Analysis of variance of different phenological and biometrical observations in the controlled environment experiment (Experiment-II).

Source of Variation	PH	TP	SP	SL	FPS	GPS	SP	TGW	GY	SY
Factor A: Genotype	**	**	**	**	NS	NS	**	NS	NS	**
Factor B: Nighttime temperatures	NS	**	NS	NS	NS	NS	**	*	**	NS
Interaction ($F_A \times F_B$)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
CV%	8.99	19.5	29.8	7.47	13.01	16.71	17.66	14.33	18.77	21.9

* and ** indicate statistical significance at $p < 0.05$ and $p < 0.01$, respectively; NS indicates no significant difference; PH—Plant height at harvest; TP—Tillers per plant; SP—Spikes per plant; SL—Spike length; FPS—Florets per spike; GPS—Grains per spike; SP—Sterility percentage; TGW—1000-grain weight; GY—Grain yield per plant; SY—Straw biomass per plant.

3.3. Crop Phenology

The two genotypes tested exhibited differences in their phenological development, as measured by the days to heading, flowering, and maturity. Genotype AVT #6 was identified as a short-duration crop and, compared to Faraday, it demonstrated a significantly shorter duration for each of the developmental stages across all sowing dates. Sowing date also had a significant impact on wheat phenology. Delaying sowing within the designated window resulted in a progressive shortening of the crop period (Figure 3). The early-sown crops required 133 days to mature, which was significantly longer than the mid-window-sown crops maturing in 114 days. The late-sown crops showed a further shrink in crop period, maturing in a significantly shorter duration of 101 days. This variation in phenology is a result of truncation in both vegetative and grain filling periods. Both the vegetative and grain filling stages were longer for the Faraday genotype compared to AVT#6. The sowing date also influenced these stages, with the early-sown crops demonstrating significantly

longer duration for both vegetative growth and grain filling than the late-sown crops. However, mid-sown crops had a longer vegetative phase, but the grain filling duration was comparable to that of the late-sown crops.

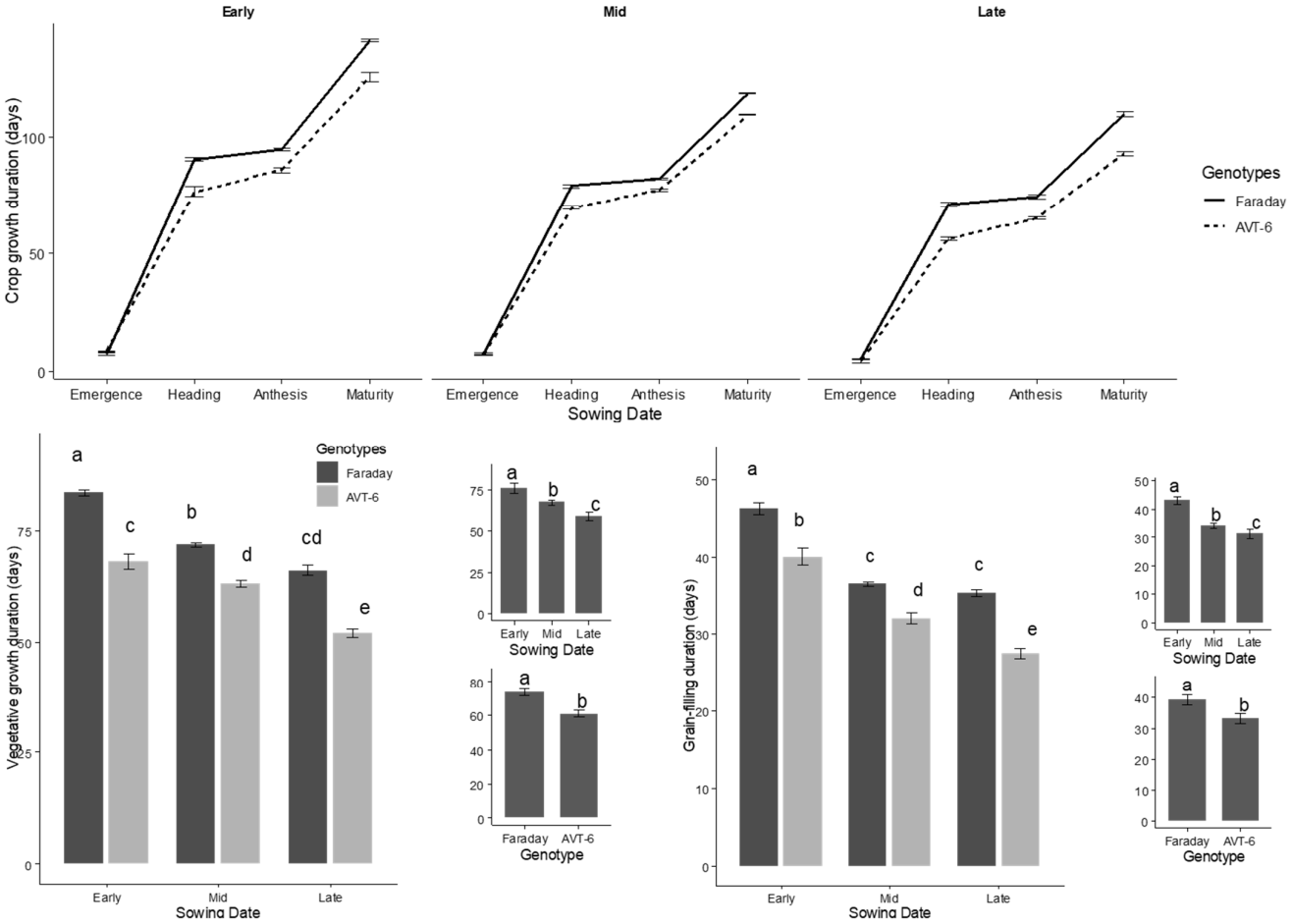


Figure 3. Crop phenology of two tested wheat genotypes exhibited as the duration to different crop stages (**Above**), and effect of sowing dates, genotypes and their interaction on the vegetative growth (**Below left**) and grain filling duration (**Below right**) in Experiment-I. Same letters suggest no statistical significance between the treatments.

In the controlled environment (Experiment-II), the crop phenology exhibited similarities with the field trials. AVT#6 matured earlier than Faraday wheat. Similarly, high nighttime temperature induced the wheat plants to mature quicker, with HNT treatment with 20 °C nighttime temperature forcing maturity a week earlier than the LNT treatment with 15 °C nighttime temperature.

3.4. Growth and Yield Attributes

Plant height at harvest differed significantly between genotypes, with Faraday recording greater height than AVT#6 across all sowing dates. Plant height reduced significantly for mid and late planting, irrespective of genotypes (Figure 4). Similarly, the length of spike exertion above the flag leaf also declined progressively with delay in sowing. Overall, Faraday recorded longer panicle exertion compared to AVT#6 (Figure 4).

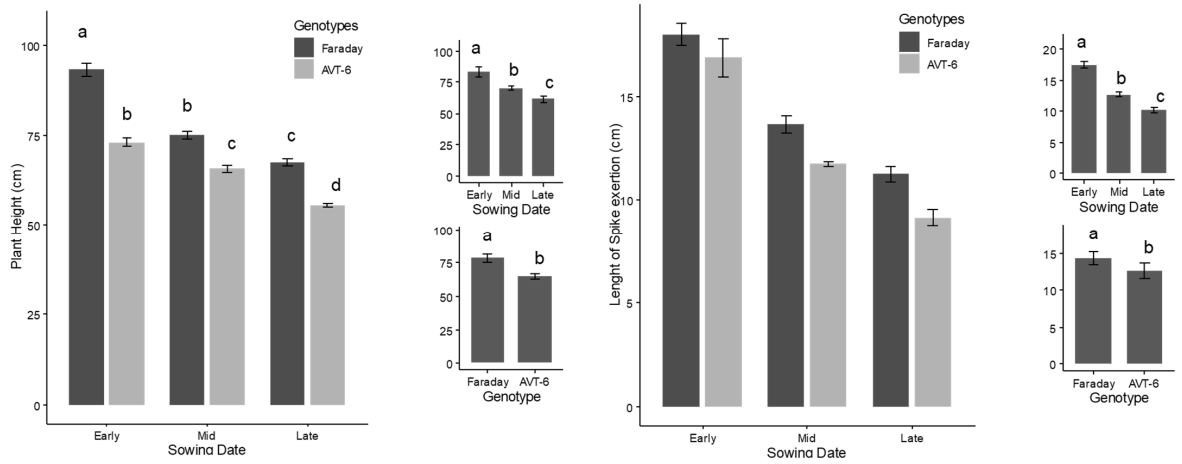


Figure 4. Effect of sowing date, genotypes, and their interaction on Plant height at harvest (**left**), and Length of spike exertion (**right**) in Experiment-I. The bars represent the mean, and the vertical line represents the s.e.m. Same letters suggest no statistical significance between the treatments.

In the controlled environment (Experiment-II), plant height at harvest in general was much shorter than that in the open-field trials, probably due to limited rooting volume associated with pots in the chambers compared to the open-field condition. The plant height varied between genotypes, with Faraday recording significantly taller height than the AVT#6 plants. However, the nighttime temperature had no effects on the plant height, with comparable plant height at harvest between the LNT and HNT treatments (Table 3).

Tillering in wheat represents another critical crop growth parameter impacting both grain and straw yield. Observations were conducted on both total tillers and productive tillers, quantified as number of spikes per unit area. The tillering behavior in wheat was unaffected by sowing dates (Table 2). Consequently, a reduction in spike production relative to total tillering ability in the late-sown crops was noticed; thus, a significantly higher proportion of non-productive tillers were produced in late-sown crops compared to mid and early sowings. Overall, the proportion of non-productive tillers remained between 20–30% in the field trials. Among the genotypes, Faraday exhibited more profuse tillering ability, and the initial phyllochron development produced significantly more tillers and spikes per plant than AVT#6 (Table 4). However, the proportion of unproductive tillers were not significantly different between the genotypes (Table 4).

Table 4. Effect of sowing date, genotypes, and their interaction on tillering behavior of wheat.

Treatments	Tillers (# m^{-2})	Spikes (# m^{-2})	Proportion of Non-Effective Tillers (%)
Sowing date			
Early-sown	273 ± 12.7	212 ± 11.5	22.5 ± 1.6 a
Mid-sown	290 ± 18.5	223 ± 19.4	23.4 ± 2.88 a
Late-sown	278 ± 23.2	196 ± 16.1	29.4 ± 1.66 b
LSD	61.2 (ns)	42.5 (ns)	4.25 **
Genotype			
Faraday	309 ± 14.7 a	236 ± 13.8 a	23.8 ± 1.96
AVT#6	251 ± 9.1 b	184 ± 5.8 b	26.4 ± 1.84
LSD	24.2 ***	23.6 ***	6.78 ns
Interaction	ns	Ns	ns
CV%	14.2	13.2	11
Grand-mean	280.3	210.2	25.1

** and *** indicate statistical significance at $p < 0.01$ and $p < 0.001$, respectively; ns indicates no significant difference. Same letters suggest no statistical significance between the treatments.

Considering the tillering ability in individual plants in the controlled environment (Experiment-II), the two genotypes studied varied considerably in the production of tillers and spikes per plant, as observed in the field trials. Similar to the field trials, Faraday also produced more tillers and spikes than AVT#6 in Experiment-II. The nighttime temperature treatments, however, influenced only the number of tillers produced, not the spikes per plant (Figure 5). Lower nighttime temperature did induce higher tiller count than high nighttime temperature, but the number of spikes per plant was indifferent, suggesting that tiller development continued under low nighttime temperature regimes, considerably enhancing late tiller development, which failed to produce spikes until the spikes in the main and primary culm matured under the abundant moisture environment in the growth chamber.

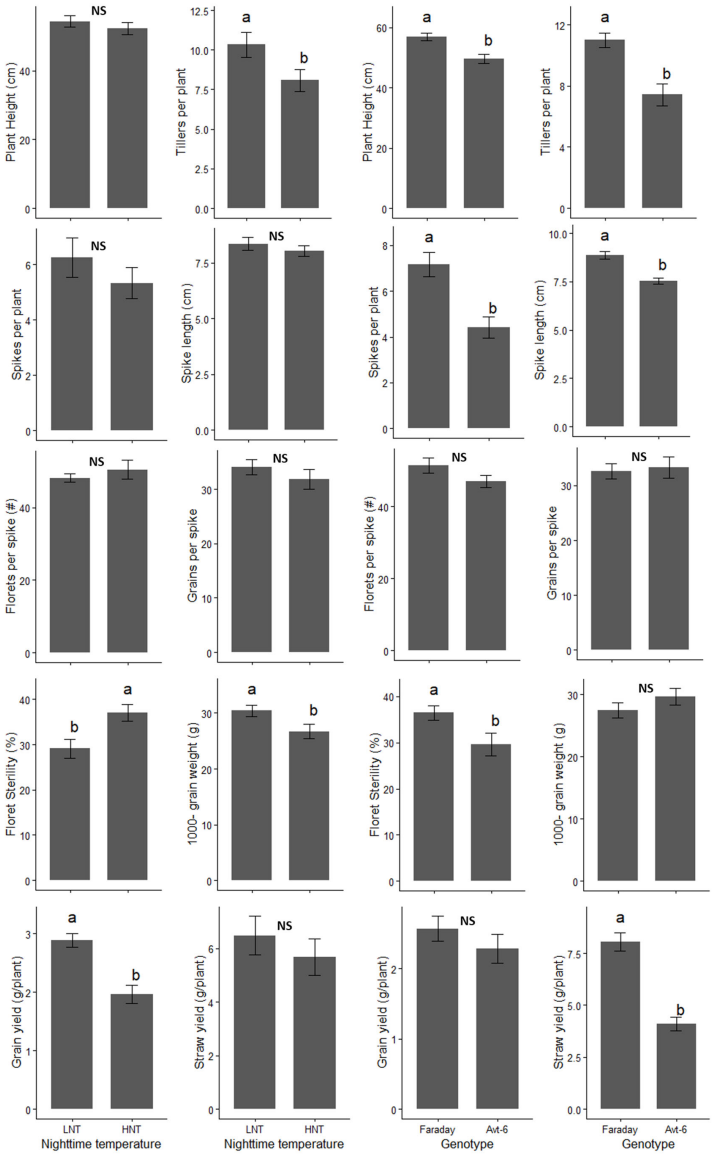


Figure 5. Effect of nighttime temperatures (two columns on left) and genotype (two columns on right on Plant height at harvest, Tillers per plant, Spikes per plant, Spike length, Florets per spike, Grains per spike, Floret sterility, 1000-grain weight, Grain yield per plant, and Straw yield per plant in Experiment-II. LNT and HNT represent low and high nighttime temperature, respectively. The bars represent the mean, and the vertical lines represent the s.e.m. Same letters suggest no statistical significance between the treatments and NS means non-significant difference between the treatments.

Spike and grain traits, specifically spike length, number of spikelets, florets, and grains per spike, floret sterility percent, and 1000-grain weight were recorded. All these traits differed significantly between the genotypes, while the sowing date influenced all parameters except for the number of spikelets and florets per spike. Faraday exhibited longer panicles compared to AVT#6, thereby bearing more spikelets and florets in individual spikes. Furthermore, floret sterility was comparatively lower in Faraday, resulting in more grains per spike. Late sowing produced significantly shorter spikes than the two earlier sowing dates, with spikes measuring less than 7.5 cm in length; this affected both genotypes (Table 5).

Table 5. Effect of sowing date, genotypes, and their interaction on spike traits of wheat.

Treatments	Spike Length (cm)	Spikelets per Spike (#)	Florets per Spike (#)	Grains per Spike (#)	Floret Sterility (%)
Sowing date					
Early-sown	8.52 ± 0.28 a	23.4 ± 0.93	54.5 ± 2.57	42.5 ± 2.22 a	22.1 ± 1 a
Mid-sown	8.07 ± 0.25 a	22.9 ± 0.99	54.2 ± 2.47	39.9 ± 2.22 a	26.6 ± 1.45 b
Late-sown	7.32 ± 0.13 b	22.1 ± 0.48	49.8 ± 1.28	31.8 ± 1.2 b	36.3 ± 1.49 c
LSD	0.49 ***	2.7 ns	6.5 ns	3.8 ***	2.14 ***
Genotype					
Faraday	8.47 ± 0.23 a	23.7 ± 0.77 a	56.3 ± 1.83 a	41.8 ± 2.08 a	26.1 ± 1.85 a
AVT#6	7.48 ± 0.12 b	21.2 ± 0.42 b	49.4 ± 1.18 b	34.3 ± 1.3 b	30.6 ± 2.06 b
LSD	0.31 ***	1.8 *	4.28 ***	3.80 **	3.32 *
Interaction	ns	ns	ns	ns	ns
CV%	4	7.7	8	6.6	4.9
Grand-mean	7.97	22.4	52.8	38.05	28.3

*, **, and *** indicate statistical significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively; ns indicates no significant difference. Same letters suggest no statistical significance between the treatments.

The number of spikelets and florets varied significantly between genotypes and was less influenced by time of sowing. Despite the reduced spike length in late-sown crops, the number of spikelets and florets per spikes was not compromised for early and mid-sowings. However, the number of grains per panicle reduced across time of sowing, suggesting low pollen viability in late-sown crops. Late sowing led to an increased floret sterility, which rose to over 35%, resulting in a correspondingly lower number of grains per spike, significantly lower than that produced in earlier sowing dates.

In the controlled environment experiment (Experiment-II), similar observations as in the field trial were observed among the genotypes in terms of the spike length, with Faraday producing longer spikes than AVT#6. In contrast to the open-field condition, the number of florets and grains per spike were similar in both the genotypes. On the other hand, HNT reduced the number of grains per spike due to reduced floret fertility, despite having no such influence on the length of spike and the number of florets per spike.

3.5. Leaf Gas Exchange Parameters

The leaf gas exchange parameters measured during anthesis and grain filling (two weeks after anthesis) showed considerable effect due to sowing date, while there were no comparable differences among the genotypes. Table 6 provides the details of the effects of sowing dates, genotypes, and their interaction on different gas exchange traits.

The CO_2 assimilation (A) during the daytime and respiration (Rn) rates during the nighttime did not vary significantly due to genotypes and sowing date x genotype interaction. However, sowing date significantly impacted the respiration (Rn) during anthesis, as well as both A and Rn rates during grain-fill. Photosynthesis (A) rate during grain filling

diminished for late-sown crops compared to early-sown crops, while the mid-sowing exhibited intermediate but similar rates. In contrast, the R_N during anthesis was significantly higher for both early- and late-sown compared to mid-sown, whereas during the grain fill, Rn was significantly higher for late-sown compared to both prior-sown crops.

Table 6. Effect of treatment on leaf level gas exchange and photosynthetic efficiency observed during anthesis and grain filling stage in Experiment-I.

Treatments	Anthesis		Grain Fill	
	A (μmol m^{-2} s^{-1})	R_N (μmol m^{-2} s^{-1})	A (μmol m^{-2} s^{-1})	R_N (μmol m^{-2} s^{-1})
Sowing date				
Early-sown	11.1 ± 0.73	1.62 ± 0.12 a	11.8 ± 0.79 a	0.5 ± 0.044 b
Mid-sown	9.5 ± 0.67	0.32 ± 0.02 b	10.2 ± 0.58 ab	0.76 ± 0.045 b
Late-sown	12.6 ± 0.55	1.32 ± 0.05 a	9.47 ± 0.86 b	2.18 ± 0.1 a
LSD	4.1 (ns)	0.46 ***	2.27 *	0.26 ***
Genotype				
Faraday	11.2 ± 0.67	1.13 ± 0.18	11 ± 0.55	1.09 ± 0.21
AVT#6	10.9 ± 0.57	1.05 ± 0.17	10 ± 0.75	1.2 ± 0.24
LSD	1.3 (ns)	0.18 (ns)	1.97 (ns)	0.2 (ns)
Interaction	ns	ns	ns	ns
CV%	13.2	18	20.3	19.1
Grand-mean	11.05	1.09	10.5	1.15

* and *** indicate statistical significance at $p < 0.05$ and $p < 0.001$, respectively; ns indicates no significant difference. Same letters suggest no statistical significance between the treatments.

The maximum quantum efficiency (Fv/Fm) showed a different trend, with the genotype, sowing dates, and their interaction having no effect on Fv/Fm during the anthesis. However, during the grain filling stage, Fv/Fm differed between the genotypes in the mid-sown crops, with mid-sown AVT#6 exhibiting significantly higher photosynthetic efficiency than mid-sown Faraday.

Similarly, the respiration to photosynthesis (Rn/A) ratio during anthesis was significantly lower in mid-sown crops for both the genotypes that saw a slight increase during grain fill. The early-sown crops recorded higher Rn/A ratio, despite the ratio remaining below 0.2 during the developmental stage, and reduced significantly below 0.05 during grain fill. In contrast, the Rn/A ratio in the late-sown crops was comparable to that of early-sown during anthesis, but it peaked exponentially during the grain fill (Figure 6), indicating a substantial amount of photosynthates diverted for respirational demand during the grain fill.

The gas exchange traits in Experiment-II showed a different view of plant acclimation in altered environment. In the ambient environment, the individual potted plants of both genotypes exhibited a fair amount of photosynthesis and a considerably lower respiration. However, after the plants were transferred to the growth cabinets with different nighttime temperatures, the photosynthesis rate was compromised in both the cabinets, showing a significant drop, probably due to much lower light intensities in the cabinet compared to the ambient environment that had existed for the well-developed photosystem until the first week of transfer to the chambers. Simultaneously, the nighttime respiration rate rose in both the chambers, with HNT treatment having a significantly higher Rn than the LNT treatment. The photosynthesis rate did not recover in either chamber until three weeks of treatment in both genotypes, while photosynthesis in AVT#6 tended to recover at the end of three weeks of treatment. Similarly, respiration rate in both the genotypes in LNT tended to lower down to the level of treatment initiation after three weeks of treatment, which was not achieved under HNT (Figure 7).

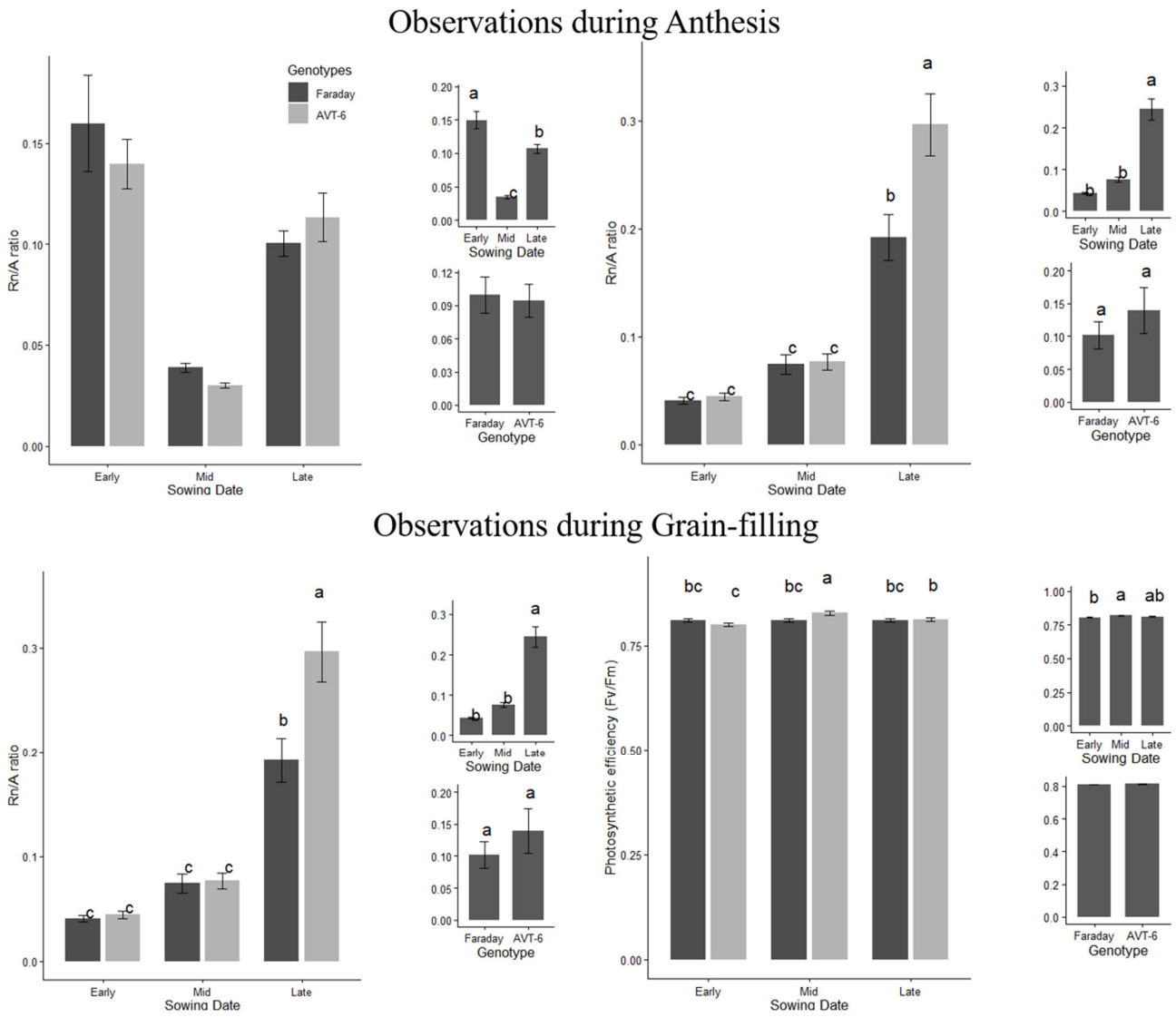


Figure 6. Effect of sowing date, genotypes, and their interaction on Respiration to photosynthesis (Rn/A) ratio and Maximum quantum efficiency of PSII (Fv/Fm) during anthesis (**top**) and grain filling stages (**bottom**). The bar represents the mean, and the vertical lines represent the s.e.m. Same letters suggest no statistical significance between the treatments.

3.6. Grain Weight and Yield Traits

Thousand-grain weight varied significantly due to sowing dates, genotypes, and their interaction. Early and mid-sown wheat produced heavier grains compared to the late-sown crops. Similarly, 1000-grain weight was greater for AVT#6 than for Faraday. The interaction effects were significant due to lower 1000-grain weight of AVT#6 in the late-sown crops, whereas Faraday exhibited declining 1000-grain weight with successive delays in sowing (Figure 9). Further, HNT also reduced the 1000-grain weight compared to LNT (Figure 5).

Sowing date influenced both grain and straw yield in wheat, while the genotype differed only in their straw yield (Figure 8). Harvest index was influenced by sowing date and the interaction with genotypes, but not exclusively by genotype alone. Significant decline in grain yield, up to 40%, was recorded for late-sown crops compared to earlier sowing dates. The straw yield was much reduced, by almost 50% in the late-sown crops compared to early, and among the genotypes, Faraday produced greater straw yield than AVT#6. This indicates that the vegetative biomass is driven primarily by growing duration, plant height, and tillering ability in wheat.

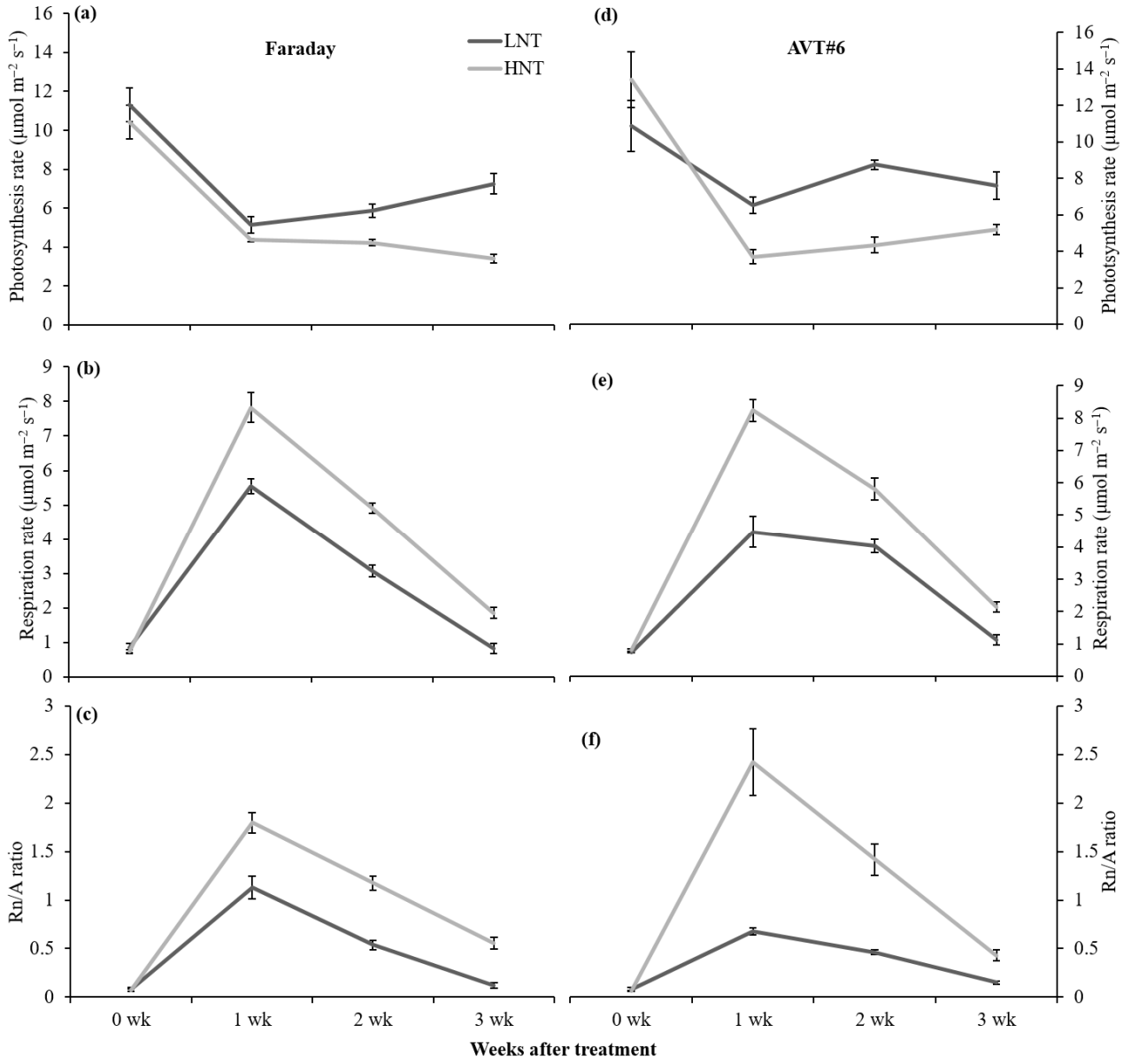


Figure 7. Net photosynthesis (**a**,**d**), nighttime respiration rate (**b**,**e**), and respiration to photosynthesis ratio (**c**,**f**) of two wheat genotypes: Faraday (**left**) and AVT#6 (**right**) under low nighttime temperature (LNT) and high nighttime temperature (HNT) in the controlled environment growth chambers in Experiment-II.

The harvest index (HI) did not differ significantly between the genotypes but varied for sowing date with mid-sown crops recording significantly higher HI compared to early- and late-sown crops. The mid-sown crops recorded low straw yield without proportionate reduction of grain yield unlike the early crops, while late-sown crops exhibited low HI associated with low grain and straw yield. The interaction effects suggested that HI of Faraday remained unaffected across the sowing dates, whereas AVT#6 recorded a significantly higher HI for mid-sown compared to early- and late-sown crops, as the lower straw yield in mid-sowing was more prominent in AVT#6 than in Faraday.

In the controlled environment trial (Experiment-II), similar to the open field condition, the grain yield per plant between the genotypes did not vary significantly, but the above-ground biomass at harvest was significantly higher for Faraday, indicating more straw production. Nighttime temperature showed substantial impact on both grain and straw produced. HNT significantly lowered the grain yield and above-ground biomass compared

to LNT, indicating that high nighttime temperature penalizes both grain and vegetative biomass at plant level.

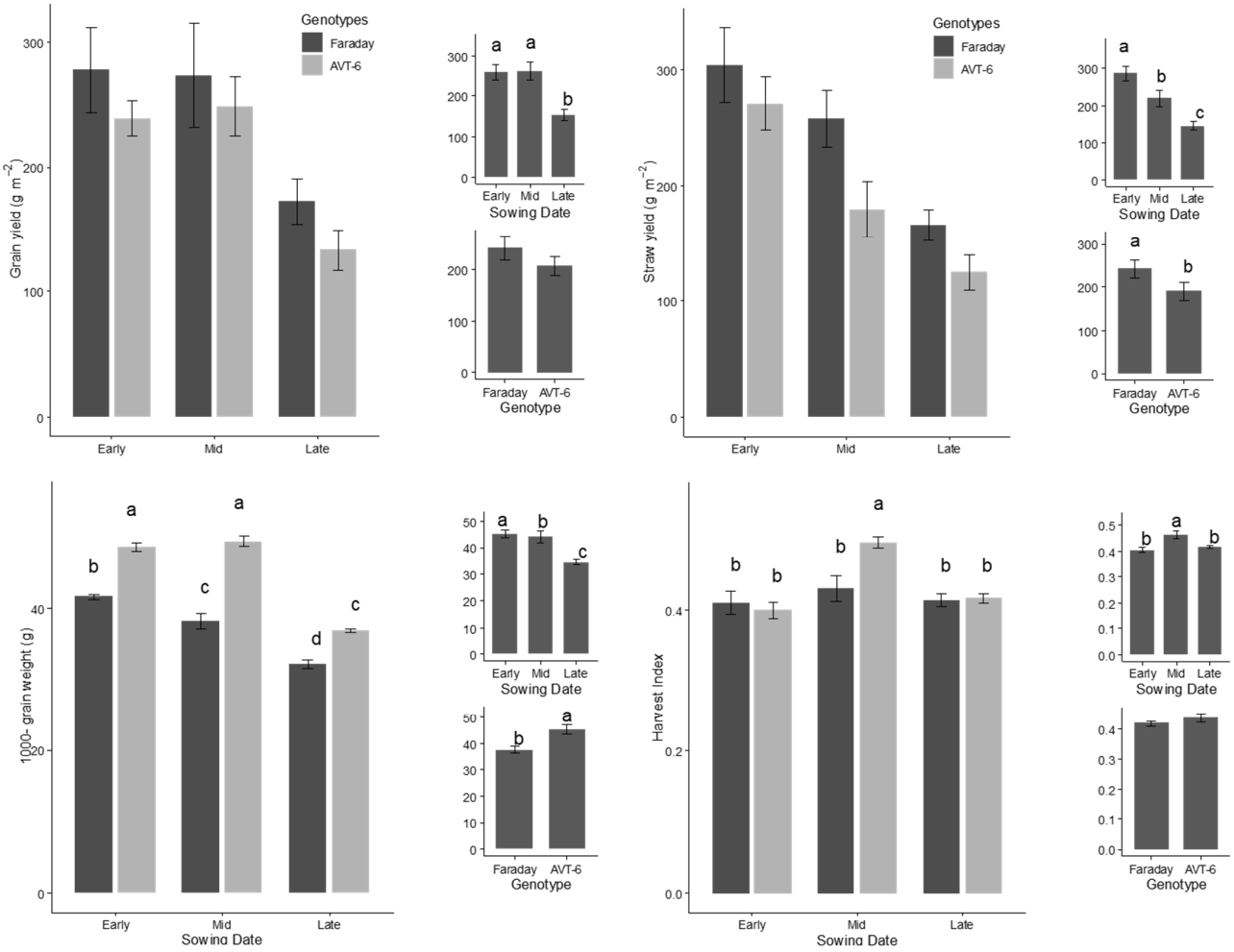


Figure 8. Effect of sowing date, genotypes, and their interaction on: Grain yield (**top left**), Straw yield (**top right**), 1000-grain weight (**bottom left**), and Harvest index (**bottom right**). The bars represent the mean, and the vertical lines represent the s.e.m. Same letters suggest no statistical significance between the treatments.

4. Discussion

The seasonal weather conditions observed during the trial period indicated that wheat crops sown on different dates were subjected to varying temperature regimes at distinct stages of crop growth and development, including the critical periods for HNT impacts. Furthermore, a subtle difference in phenology, the exposure to thermal amplitudes and the responses by the two genotypes, has been captured.

Crops sown early experienced moderate temperatures during the vegetative growth phase and until tillering, following the period of low temperatures during heading and anthesis stages. Conversely, mid-sown crops experienced lower temperature during the vegetative growth phase (including tillering), continuing with both day and night temperatures remaining below the threshold of 28 and 20 °C, respectively, until anthesis and active grain fill (two weeks post-anthesis). During this period, nighttime temperatures were predominantly low, with the majority of nights below 20 °C. By far, late-sown crops thrived under favorable temperature conditions during the vegetative period until the heading stage, ensuring exposure to increasing day and nighttime temperatures during anthesis, and grain filling periods coinciding with high temperature exceeding the thresh-

olds. Additionally, the late-sown, longer duration genotype, Faraday, experienced an entire grain filling period under higher daytime and nighttime temperature.

Variation in sowing dates directly impacts the thermal environment experienced by the crops [32]. Temperature is the primary abiotic factor influencing flowering time and overall developmental rates; elevated ambient temperatures are associated with accelerated growth and development [33].

Heat stress can adversely affect wheat phenology, growth, and development. High temperature response on plant height is caused by reducing cell division and expansion, as well as hastening senescence [34]. The relationship between sowing date and plant height must be analyzed in context of several interrelated factors, including thermal accumulation and the physiological responses of specific genotypes to environmental conditions. Nonetheless, plant height is predominantly determined by the genetic and physiological response of wheat to varying sowing dates, and genetic variability among wheat genotypes can result in differing growth responses to these dates [35]. In our study, the plant height decreased with delays in sowing, aligning with a trend of shortened crop duration, which suggests that higher straw yield during extended crop periods is attributable to profuse tillering and taller plants.

The length of spike exertion—distance the spike extends from the flag leaf—is particularly significant during the flowering and grain filing stages. A well-exerted spike can enhance plant's exposure to sunlight and improve photosynthesis and carbon assimilation [36]. The longer spike exertion and taller plants in the two earlier sowings in the study are likely to also contribute to higher grain yield and biomass. Conversely, crops sown later experienced elevated temperatures throughout critical flowering and grain filling stages, which negatively impacted overall biomass accumulation [37,38].

Tillering in wheat is a critical physiological process influencing grain yield. Dueri, et al. [39] highlighted that early sowing is often associated with higher grain yield due to higher tillering in early-sown crops, regardless of the non-linearity of the relationship. However, under higher plant population, excessive tillering in early-sown crops seldom increases competition among the tillers for resources leading to higher tiller mortality and negative impacts on grain yield [39], particularly under well-fertilized condition [40]. The tillering ability is significantly governed by the genetic background which differentially respond to sowing dates [41] with some genotype exhibiting higher degree of susceptibility to the negative effects of excessive tillering. Arduini, et al. [42], in their study of durum wheat, emphasized that both main culm and tillers contribute to grain yield and sowing dates, determining not only the tillering capacity but also their contribution to grain yield, as was observed in our study. Cooler temperatures during early growth extend the vegetative phase, thereby promoting tillering [43], and elevated temperature suppress tiller formation and induce tiller mortality, and simultaneously divert resources away from tiller development [6]. In our field trials, we observed profuse tiller in the early and mid-sowing and a significant reduction in tillering in the late-sown crops.

The leaf level respiration differs as per developmental stages, as indicated by Pinto, et al. [44] in spring wheat, where Rn decreased as crop progressed from anthesis to grain filling. Their experiments exhibited the Rn during grain-fill below 1 μmol m^{-2} s^{-1} when the temperature remained below 20 °C. In our trial, the nighttime temperature was also below 20 °C during the early and mid-sowing, particularly in the early sowing, when the nighttime temperature dropped towards the reproductive stages and the respiration rates saw a declining trend. Respiration to photosynthesis (Rn/A) ratio increases towards the reproductive growth and with stress [45]. In our field trial, the trend of Rn/A ratio during the anthesis and grain filling stages suggest that Rn/A ratio in the grain filling stages exhibits some thermal stress in the late-sown crops (Figure 8). Additionally, in Experiment-II, despite constant daytime

temperature in the chambers, the A rate was lower under HNT treatment. Similar results, in which HNT not only increases the nighttime respiration (Rn) rates but also decreases the daytime photosynthesis (A) rate, thereby altering the carbon balance, have been reported by [16,46] under growth chambers and field conditions, respectively.

Since there are contrasting results showing unaffected maize yields under increased leaf level respiration (Rn) and lowered photosynthesis [46] against the ones exhibiting declined wheat under warmer nights without rise in Rn [17], we cannot casually relate grain yields and increased respiration rates under warmer nights. Consequently, the Rn/A ratio remained unchanged in cultivars experiencing no yield losses, while it increased in the cultivars that suffered yield loss [47], suggesting that it could be a better leaf level gas exchange trait to be utilized relating to HNT stress in crops. Moreover, rapid phenological development resulting in shortening of growth and grain filling periods are major drivers of grain yield and biomass, and they override the gas exchange traits [45].

The crop duration (phenology) exhibited a reduction with late sowing, characterized by diminished periods in both vegetative growth phase and grain filling period. Notably, the reduction in the period leading to heading was significantly more pronounced in late-sown crops, while the grain filling period remained comparable between mid-and late-sown crops, both of which were shorter than of early-sown crops. The consequences of this abbreviated phenology were reflected in the metrics of tillering, biomass accumulation, and grain yield. Conversely, extended crop durations were associated with increased tillering and enhanced biomass across both genotypes. Previous studies have indicated substantial reduction in grain yield due to increases in temperature, with estimates of 3–5% yield decline for every 1 °C rise in temperature above 15 °C [48]. Elevated temperature accelerates wheat development [49], but the timing and duration of heat stress are critical in determining impacts on grain yield. Riedesel, et al. [50] demonstrated that even moderate heat stress during the reproductive phase significantly penalizes grain yield. Furthermore, Fan, et al. [27] emphasized that high nighttime temperature (HNT) during vegetative growth phase had a positive impact on grain yield and biomass if HNT subsided following jointing. Conversely, their study indicated that the wheat yield failed to compensate when HNT occurred any time after jointing. HNT solely reduces grain yield by decreasing grains per spike due to increased floret sterility and decreased grain weight [16].

It is posited that the increase in floret sterility diminishes sink size, positively impacting seed size; however, the decline in 1000-grain weight observed in the late-sown crops, despite increased floret sterility, indicates that HNT consistent during the active grain filling period negatively affected the rate of grain fill. Additionally, the contraction of the grain filling duration attributable to shorter crop duration in late-sown crops further contributes to the observed decline in 1000-grain weight. The trends in threshing recovery can be ascribed to the combined effects of increased floret sterility and reduced seed weight for late-sown wheat, particularly the late-sown Faraday, which demonstrated a floret sterility of approximately 34%, while AVT#6 exhibited floret sterility levels as high as 39%. García, et al. [51] also showed increased floret sterility and reduced grain weight under HNT even when the treatment was applied after mid-anthesis. Grain fill is influenced by temperature, as high temperatures diminish sink strength, and concurrently, a lack of assimilate availability can accelerate grain maturation [52]. Late-sown crops exhibit shorter crop duration with reduced periods for both pre-anthesis and grain filling duration. The accelerated wheat development constricts the resource utilization window and diminishes the pre-anthesis biomass accumulation [12]. These are the sources for about 80% of carbohydrates utilized during grain filling and are related to grain number [16]. Therefore, the phenology is one important determinant for lowering biomass and grain yield under late-sown condition (Figure 9).

Faraday

	GF	*SPA*	*SL*	*GPS*	*FSP*	*TGW*	*GY*	*AGB*	*CHD*	*CHN*
SPA	−0.11									
SL	0.68*	0.43								
GPS	0.61*	0.42	0.93***							
FSP	−0.65*	−0.13	−0.64*	−0.83***						
TGW	0.77**	0.04	0.76**	0.81**	−0.80**					
GY	0.38	0.80**	0.78**	0.83***	−0.61*	0.50				
AGB	0.47	0.73**	0.84***	0.89***	−0.65*	0.62*	0.97***			
CHD	−0.72**	−0.19	−0.83***	−0.90***	0.90***	−0.94***	−0.64*	−0.71**		
CHN	−0.5239	−0.29	−0.77**	−0.88***	0.85***	−0.86***	−0.67*	−0.71**	0.96***	
CHS	−0.65*	−0.23	−0.81**	−0.90***	0.89***	−0.92***	−0.66*	−0.72**	0.99***	0.99***

AVT#6

	GF	*SPA*	*SL*	*GPS*	*FSP*	*TGW*	*GY*	*AGB*	*CHD*	*CHN*
SPA	0.46									
SL	0.78**	0.42								
GPS	0.62*	0.31	0.89***							
FSP	−0.83***	−0.52	−0.86***	−0.80**						
TGW	0.70*	0.37	0.79**	0.67*	−0.83***					
GY	0.63*	0.63*	0.72**	0.63*	−0.70*	0.87***				
AGB	0.77**	0.71*	0.81**	0.67*	−0.76**	0.80**	0.93***			
CHD	−0.90***	−0.45	−0.86***	−0.68*	0.92***	−0.92***	−0.79**	−0.84***		
CHN	−0.84***	−0.44	−0.84***	−0.68*	0.91***	−0.96***	−0.84***	−0.84***	0.99***	
CHS	−0.87***	−0.45	−0.85***	−0.68*	0.92***	−0.94***	−0.81**	−0.84***	0.99***	0.99***

Figure 9. Correlation among the observed parameters in two wheat genotypes in Experiment-I—Faraday (**top**) and AVT#6 (**bottom**); GF—Grain filling duration (days); SPA—Spikes per m^2; SL—Spike length; GPS—Grains per spike; FSP—Floret sterility percentage; TGW—1000-grain weight; GY—Grain yield; AGB—Above-ground biomass; CHD—Cumulative day hours above threshold temperature; CHN—Cumulative night hours above threshold temperature; CHS—Cumulative hours above threshold temperature; *, **, and *** representing significance at $p < 0.05$, $p < 0.01$, and $p < 0.01$, respectively; colors blue and red represent positive and negative correlation, respectively, with the higher color intensity suggesting stronger correlation.

The correlation between the observed crop growth and yield variables in relation to temperature extremes, as indicated by cumulative hours of high daytime, nighttime, and overall cumulative temperatures exceeding the 28/20 °C during the early period of reproductive stage (3 weeks of heading), demonstrate that all yield attributes, with the exception of spikes per unit area, negatively correlate with cumulated temperature. The number of spikes per unit area is dependent on the tillering ability of the plants and is primarily determined during the earlier growth phases, rather than during the reproductive phases. Moreover, cumulative nighttime hours exceeding the threshold temperature exhibited a stronger correlation with grain yield compared to cumulative daytime hours above the threshold temperature in both tested wheat genotypes. The magnitude of these differences was greater in AVT#6 than in Faraday. The crop traits correlating strongly with the grain yield are spikes per unit area, spike length, and grains per spike. The number of spikes or the productive tillers, and the grains per spike, are positively associated to grain yield, and thus are critical in determining sink strength. It is, therefore, evident that grain number and floret fertility is more important attributes than the duration of grain filling or the grain weight. Similarly, among the cumulative stress hours, the cumulative night hours above 20 °C during flowering and early grain filling exhibited high explanatory power (Figure 10), indicating pronounced sensitivity of wheat yield to HNT.

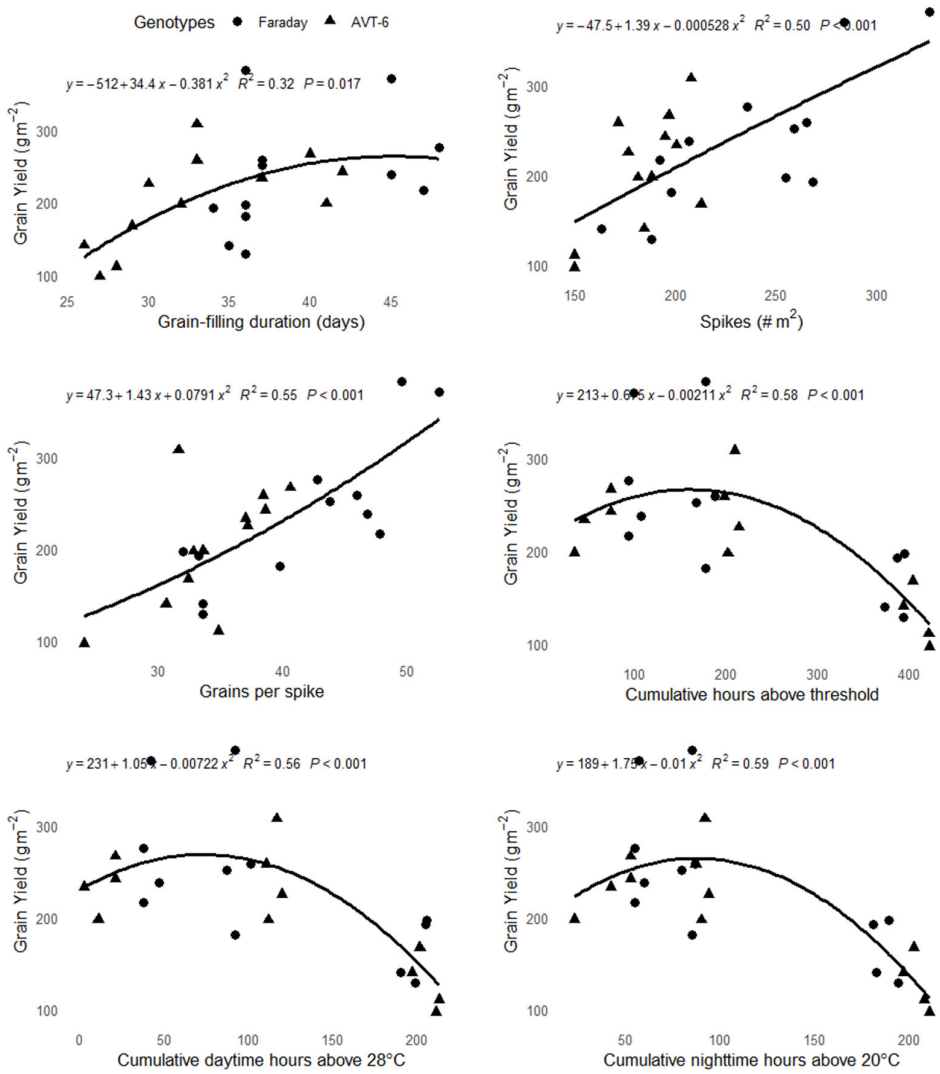


Figure 10. Relation between yield and various predictors in Experiment-I; Grain filling duration (days); Spikes per m^2; Grains per spike; Cumulative day hours above 28 °C; CHN—Cumulative night hours above 20 °C; CHS—Cumulative hours above daytime and nighttime threshold temperature.

The findings from this study support previous reports of HNT leading to wheat yield losses but in an Australian context, providing evidence of negative impact of HNT on wheat productivity at regional and global scales [4]. Due to changing global climate and the associated higher rate of increase in night temperatures compared to daytime maximum temperature, and since wheat grown in Australia is equally valuable to wheat grown in other regions of the world, this change is a serious challenge to global food security. Knowledge gained from these multiregional trials support the urgency in identifying locally adapted HNT-tolerant germplasm and the need to include resilient germplasm into wheat breeding programs, thereby ensuring minimal yield losses under future warming nights.

Unlike options such as developing short duration varieties to escape stress or improved transpiration cooling to adapt wheat to high daytime temperatures [53], addressing HNT impact would require genetic approaches. The ideal route involves identifying resilient germplasms, developing breeding populations to unravel stable genomic regions that control HNT tolerance, and utilizing advances in molecular marker technology to develop HNT-tolerant locally adapted cultivars. In addition, recent advances in CRISPR-Cas allows for gene editing to target specific candidate genes identified either through biparental or GWAS (Genome Wide Association Studies) analysis to confirm the functional relevance of

the candidate genes that can induce HNT tolerance [54]. Utilizing the functionally validated genes can be used to develop breeder-friendly KASP markers for developing HNT-tolerant wheat cultivars for target population of environments.

5. Conclusions

This study provides compelling evidence that high nighttime temperature (HNT), driven by asymmetric diurnal warming, poses a threat to wheat yields in the tropical Australian environment. Through a combination of field trials involving staggered sowing dates and controlled environment experiments involving constant day with normal and high nighttime temperatures, we demonstrated that HNT accelerates phenological development, particularly during reproductive stages, reduces the grain filling duration, increases floret sterility, and reduces grain yield. Genotypic differences were observed between the two tested genotypes, with AVT#6 showing greater sensitivity to HNT compared to Faraday. Both experiments confirmed that HNT increases nighttime respiration rates and reduces photosynthesis rates, altering carbon balance during grain filling. Cumulative nighttime hours above 20 °C showed strongest negative relationship with grain yield than the daytime hours or combined hours indicators. These findings explain the need for HNT resilient wheat genotypes and strategic sowing date adjustments to mitigate adversities relating to warming nights under changing climate scenarios.

Author Contributions: Conceptualization, R.S., S.P.B., M.N., Y.C. and S.V.K.J.; methodology, R.S. and S.P.B.; formal analysis, R.S.; investigation, R.S.; writing—original draft preparation, R.S.; writing—review and editing, S.P.B., M.N., Y.C. and S.V.K.J.; supervision, S.P.B., M.N., Y.C. and S.V.K.J.; funding acquisition, S.P.B. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by a CRCNA scholarship and the CQ University Elevate Scholarship.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Acknowledgments: We thank the CRCNA and CQ University Elevate scholarship program. We are also grateful to AgriVentis Ltd. for the provision of seed lines used in the trials and the CQU technical staffs who helped carry out the research. We deeply appreciate the initial guidance of QDAFF senior scientist Douglas Sands in the initial conceptualization and designing of the field experiment.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Jacott, C.N.; Boden, S.A. Feeling the heat: Developmental and molecular responses of wheat and barley to high ambient temperatures. *J. Exp. Bot.* **2020**, *71*, 5740–5751. [CrossRef]
2. Shiferaw, B.; Smale, M.; Braun, H.-J.; Duveiller, E.; Reynolds, M.; Muricho, G. Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. *Food Secur.* **2013**, *5*, 291–317. [CrossRef]
3. van Dijk, M.; Morley, T.; Rau, M.L.; Saghai, Y. A meta-analysis of projected global food demand and population at risk of hunger for the period 2010–2050. *Nat. Food* **2021**, *2*, 494–501. [CrossRef] [PubMed]
4. Hein, N.T.; Bheemanahalli, R.; Wagner, D.; Vennapusa, A.R.; Bustamante, C.; Ostmeyer, T.; Pokharel, M.; Chiluwal, A.; Fu, J.; Srikanthan, D.S.; et al. Improved cyber-physical system captured post-flowering high night temperature impact on yield and quality of field grown wheat. *Sci. Rep.* **2020**, *10*, 22213. [CrossRef] [PubMed]
5. Cossani, C.M.; Reynolds, M.P. Physiological traits for improving heat tolerance in wheat. *Plant Physiol.* **2012**, *160*, 1710–1718. [CrossRef]
6. Balla, K.; Karsai, I.; Bonis, P.; Kiss, T.; Berki, Z.; Horvath, A.; Mayer, M.; Bencze, S.; Veisz, O. Heat stress responses in a large set of winter wheat cultivars (*Triticum aestivum* L.) depend on the timing and duration of stress. *PLoS ONE* **2019**, *14*, e0222639. [CrossRef]

7. Zhai, H.; Jiang, C.; Zhao, Y.; Yang, S.; Li, Y.; Yan, K.; Wu, S.; Luo, B.; Du, Y.; Jin, H.; et al. Wheat heat tolerance is impaired by heightened deletions in the distal end of 4AL chromosomal arm. *Plant Biotechnol. J.* **2021**, *19*, 1038–1051. [CrossRef]
8. Farooq, M.; Bramley, H.; Palta, J.A.; Siddique, K.H.M. Heat Stress in Wheat During Reproductive and Grain-Filling Phases. *Crit. Rev. Plant Sci.* **2011**, *30*, 491–507. [CrossRef]
9. Prasad, P.V.V.; Djanaguiraman, M. Response of floret fertility and individual grain weight of wheat to high temperature stress: Sensitive stages and thresholds for temperature and duration. *Funct. Plant Biol.* **2014**, *41*, 1261–1269. [CrossRef]
10. Hein, N.T.; Wagner, D.; Bheemanahalli, R.; Sebela, D.; Bustamante, C.; Chiluwal, A.; Neilsen, M.L.; Jagadish, S.V.K. Integrating field-based heat tents and cyber-physical system technology to phenotype high night-time temperature impact on winter wheat. *Plant Methods* **2019**, *15*, 41. [CrossRef]
11. Aiqing, S.; Somayanda, I.; Sebastian, S.V.; Singh, K.; Gill, K.; Prasad, P.V.V.; Jagadish, S.V.K. Heat stress during flowering affects time of day of flowering, seed set, and grain quality in spring wheat. *Crop Sci.* **2018**, *58*, 380–392. [CrossRef]
12. Posch, B.C.; Kariyawasam, B.C.; Bramley, H.; Coast, O.; Richards, R.A.; Reynolds, M.P.; Trethowan, R.; Atkin, O.K. Exploring high temperature responses of photosynthesis and respiration to improve heat tolerance in wheat. *J. Exp. Bot.* **2019**, *70*, 5051–5069. [CrossRef] [PubMed]
13. Djanaguiraman, M.; Narayanan, S.; Erdayani, E.; Prasad, P.V.V. Effects of high temperature stress during anthesis and grain filling periods on photosynthesis, lipids and grain yield in wheat. *BMC Plant Biol.* **2020**, *20*, 268. [CrossRef]
14. Asseng, S.; Zhu, Y.; Wang, E.; Zhang, W. Crop modeling for climate change impact and adaptation. In *Crop Physiology*; Academic Press: Cambridge, MA, USA, 2015; pp. 505–546.
15. Narayanan, S.; Prasad, P.V.V.; Fritz, A.K.; Boyle, D.L.; Gill, B.S. Impact of high night-time and high daytime temperature stress on winter wheat. *J. Agron. Crop Sci.* **2015**, *201*, 206–218. [CrossRef]
16. Prasad, P.V.V.; Pisipati, S.R.; Ristic, Z.; Bukovnik, U.; Fritz, A.K. Impact of Nighttime Temperature on Physiology and Growth of Spring Wheat. *Crop Sci.* **2008**, *48*, 2372–2380. [CrossRef]
17. Garcia, G.A.; Dreccer, M.F.; Miralles, D.J.; Serrago, R.A. High night temperatures during grain number determination reduce wheat and barley grain yield: A field study. *Glob. Change Biol.* **2015**, *21*, 4153–4164. [CrossRef]
18. Li, D.; Xiao, Y.; Guo, L.; Shan, B.; Liu, X.; Duan, X.; Rehman, A.U.; Guo, C.; Zhang, W.; Li, H.; et al. Effect of High Nighttime Temperatures on Growth, Yield, and Quality of Two Wheat Cultivars During the Whole Growth Period. *Plants* **2024**, *13*, 3071. [CrossRef]
19. Sadok, W.; Jagadish, S.V.K. The Hidden Costs of Nighttime Warming on Yields. *Trends Plant Sci.* **2020**, *25*, 644–651. [CrossRef]
20. Impa, S.M.; Raju, B.; Hein, N.T.; Sandhu, J.; Prasad, P.V.V.; Walia, H.; Jagadish, S.V.K. High night temperature effects on wheat and rice: Current status and way forward. *Plant Cell Environ.* **2021**, *44*, 2049–2065. [CrossRef]
21. Dreccer, M.F.; Fainges, J.; Whish, J.; Ogbonnaya, F.C.; Sadras, V.O. Comparison of sensitive stages of wheat, barley, canola, chickpea and field pea to temperature and water stress across Australia. *Agric. For. Meteorol.* **2018**, *248*, 275–294. [CrossRef]
22. Impa, S.M.; Sunoj, V.S.J.; Krassovskaya, I.; Bheemanahalli, R.; Obata, T.; Jagadish, S.V.K. Carbon balance and source-sink metabolic changes in winter wheat exposed to high night-time temperature. *Plant Cell Environ.* **2019**, *42*, 1233–1246. [CrossRef]
23. Chunduri, V.; Kaur, A.; Kaur, S.; Kumar, A.; Sharma, S.; Sharma, N.; Singh, P.; Kapoor, P.; Kaur, S.; Kumari, A.; et al. Gene Expression and Proteomics Studies Suggest an Involvement of Multiple Pathways Under Day and Day-Night Combined Heat Stresses During Grain Filling in Wheat. *Front. Plant Sci.* **2021**, *12*, 660446. [CrossRef] [PubMed]
24. Mamrutha, H.M.; Rinki, K.; Venkatesh, K.; Gopalareddy, K.; Khan, H.; Mishra, C.N.; Kumar, S.; Kumar, Y.; Singh, G.; Singh, G.P. Impact of high night temperature stress on different growth stages of wheat. *Plant Physiol. Rep.* **2020**, *25*, 707–715. [CrossRef]
25. Fang, S.; Cammarano, D.; Zhou, G.; Tan, K.; Ren, S. Effects of increased day and night temperature with supplemental infrared heating on winter wheat growth in North China. *Eur. J. Agron.* **2015**, *64*, 67–77. [CrossRef]
26. Russell, K.; Van Sanford, D.A. Breeding Wheat for Resilience to Increasing Nighttime Temperatures. *Agronomy* **2020**, *10*, 531. [CrossRef]
27. Fan, Y.; Qin, B.; Yang, J.; Ma, L.; Cui, G.; He, W.; Tang, Y.; Zhang, W.; Ma, S.; Ma, C.; et al. Night warming increases wheat yield by improving pre-anthesis plant growth and post-anthesis grain starch biosynthesis. *J. Integr. Agric.* **2024**, *23*, 536–550. [CrossRef]
28. Wahid, A.; Gelani, S.; Ashraf, M.; Foolad, M. Heat tolerance in plants: An overview. *Environ. Exp. Bot.* **2007**, *61*, 199–223. [CrossRef]
29. Fan, Y.; Lv, Z.; Zhang, Y.; Ma, L.; Qin, B.; Liu, Q.; Zhang, W.; Ma, S.; Ma, C.; Huang, Z. Pre-anthesis night warming improves post-anthesis physiological activity and plant productivity to post-anthesis heat stress in winter wheat (*Triticum aestivum* L.). *Environ. Exp. Bot.* **2022**, *197*, 104819. [CrossRef]
30. Lobell, D.B.; Hammer, G.L.; Chenu, K.; Zheng, B.; McLean, G.; Chapman, S.C. The shifting influence of drought and heat stress for crops in northeast Australia. *Glob. Change Biol.* **2015**, *21*, 4115–4127. [CrossRef]
31. van Wijngaarden, W.A.; Mouraviev, A. Seasonal and Annual Trends in Australian Minimum/Maximum Daily Temperatures. *Open Atmos. Sci. J.* **2016**, *10*, 39–55. [CrossRef]

32. Spink, J.H.; Semere, T.; Sparkes, D.L.; Whaley, J.M.; Foulkes, M.J.; Clare, R.W.; Scott, R.K. Effect of sowing date on optimum plant density of winter wheat. *Ann. Appl. Biol.* **2000**, *137*, 179–188. [CrossRef]
33. Slafer, G.A.; Kantolic, A.G.; Appendino, M.L.; Tranquilli, G.; Miralles, D.J.; Savin, R. Genetic and environmental effects on crop development determining adaptation and yield. In *Crop Physiology*; Academic Press: Cambridge, MA, USA, 2015; pp. 285–319.
34. Kronenberg, L.; Yates, S.; Boer, M.P.; Kirchgessner, N.; Walter, A.; Hund, A. Temperature response of wheat affects final height and the timing of stem elongation under field conditions. *J. Exp. Bot.* **2021**, *72*, 700–717. [CrossRef] [PubMed]
35. Porker, K.; Straight, M.; Hunt, J.R. Evaluation of G × E × M Interactions to Increase Harvest Index and Yield of Early Sown Wheat. *Front. Plant Sci.* **2020**, *11*, 994. [CrossRef]
36. Wolde, G.M.; Mascher, M.; Schnurbusch, T. Genetic modification of spikelet arrangement in wheat increases grain number without significantly affecting grain weight. *Mol. Genet. Genom.* **2019**, *294*, 457–468. [CrossRef]
37. Ding, D.Y.; Feng, H.; Zhao, Y.; He, J.Q.; Zou, Y.F.; Jin, J.M. Modifying Winter Wheat Sowing Date as an Adaptation to Climate Change on the Loess Plateau. *Agron. J.* **2016**, *108*, 53–63. [CrossRef]
38. Jain, M.; Singh, B.; Srivastava, A.A.K.; Malik, R.K.; McDonald, A.J.; Lobell, D.B. Using satellite data to identify the causes of and potential solutions for yield gaps in India's Wheat Belt. *Environ. Res. Lett.* **2017**, *12*, 09401. [CrossRef]
39. Dueri, S.; Brown, H.; Asseng, S.; Ewert, F.; Webber, H.; George, M.; Craigie, R.; Guarin, J.R.; Pequeno, D.N.L.; Stella, T.; et al. Simulation of winter wheat response to variable sowing dates and densities in a high-yielding environment. *J. Exp. Bot.* **2022**, *73*, 5715–5729. [CrossRef]
40. Liang, Y.F.; Khan, S.; Ren, A.-x.; Lin, W.; Anwar, S.; Sun, M.; Gao, Z.-Q. Subsoiling and Sowing Time Influence Soil Water Content, Nitrogen Translocation and Yield of Dryland Winter Wheat. *Agronomy* **2019**, *9*, 37. [CrossRef]
41. Zou, J.; Semagn, K.; Iqbal, M.; N'Diaye, A.; Chen, H.; Asif, M.; Navabi, A.; Perez-Lara, E.; Pozniak, C.; Yang, R.C.; et al. Mapping QTLs Controlling Agronomic Traits in the 'Attila' × 'CDC Go' Spring Wheat Population Under Organic Management Using 90K SNP Array. *Crop Sci.* **2017**, *57*, 365–377. [CrossRef]
42. Arduini, I.; Pellegrino, E.; Ercoli, L. Contribution of main culm and tillers to grain yield of durum wheat: Influence of sowing date and plant traits. *Ital. J. Agron.* **2018**, *13*, 235–247. [CrossRef]
43. Lawlor, D.W.; Boyle, F.A.; Keys, A.J.; Kendall, A.C.; Young, A.T. Nitrate nutrition and temperature effects on wheat: A synthesis of plant growth and nitrogen uptake in relation to metabolic and physiological processes. *J. Exp. Bot.* **1988**, *39*, 329–343. [CrossRef]
44. Pinto, R.S.; Molero, G.; Reynolds, M.P. Identification of heat tolerant wheat lines showing genetic variation in leaf respiration and other physiological traits. *Euphytica* **2017**, *213*, 76. [CrossRef]
45. Amthor, J.S. After photosynthesis, what then: Importance of respiration to crop growth and yield. *Field Crops Res.* **2025**, *321*, 109638. [CrossRef]
46. Kettler, B.A.; Carrera, C.S.; Nalli Sonzogni, F.D.; Trachsel, S.; Andrade, F.H.; Neiff, N. High night temperature during maize post-flowering increases night respiration and reduces photosynthesis, growth and kernel number. *J. Agron. Crop Sci.* **2022**, *208*, 335–347. [CrossRef]
47. Bahuguna, R.N.; Solis, C.A.; Shi, W.; Jagadish, S.V.K. Post-flowering night respiration and altered sink activity account for high night temperature-induced grain yield and quality loss in rice (*Oryza sativa* L.). *Physiol. Plant.* **2017**, *159*, 59–73. [CrossRef] [PubMed]
48. Elbashier, E.M.; Elbashier, E.M.E.; Idris, S.E.; Tadesse, W.; Tahir, I.S.A.; Ibrahim, A.E.S.; Elhashimi, A.M.A.; Saad, S.I.; Idris, A.A.; Mustfa, H.M. Genetic variations, heritability, heat tolerance indices and correlations studies for traits of bread wheat genotypes under high temperature. *Int. J. Clim. Change Strateg. Manag.* **2019**, *11*, 672–686. [CrossRef]
49. Yang, J.; Feng, Y.; Chi, T.; Wen, Q.; Liang, P.; Wang, A.; Li, P. Mitigation of Elevated CO_2 Concentration on Warming-Induced Changes in Wheat Is Limited Under Extreme Temperature During the Grain Filling Period. *Agronomy* **2023**, *13*, 1379. [CrossRef]
50. Riedesel, L.; Moller, M.; Horney, P.; Golla, B.; Piepho, H.P.; Kautz, T.; Feike, T. Timing and intensity of heat and drought stress determine wheat yield losses in Germany. *PLoS ONE* **2023**, *18*, e0288202. [CrossRef]
51. García, G.A.; Serrago, R.A.; Fernanda Dreccer, M.; Miralles, D.J. Post-anthesis warm nights reduce grain weight in field-grown wheat and barley. *Field Crops Res.* **2016**, *195*, 50–59. [CrossRef]
52. White, J.W.; Kimball, B.A.; Wall, G.W.; Ottman, M.J.; Hunt, L.A. Responses of time of anthesis and maturity to sowing dates and infrared warming in spring wheat. *Field Crops Res.* **2011**, *124*, 213–222. [CrossRef]
53. Lal, M.K.; Tiwari, R.K.; Gahlaut, V.; Mangal, V.; Kumar, A.; Singh, M.P.; Paul, V.; Kumar, S.; Singh, B.; Zinta, G. Physiological and molecular insights on wheat responses to heat stress. *Plant Cell Rep.* **2022**, *41*, 501–518. [CrossRef]
54. Kumar Saini, D.; Hein, N.T.; Somayanda, I.; Bheemanahalli, R.; Ostmeyer, T.; Jagadish, S.V.K. Genetic mapping and haplotype analysis identify novel candidate genes for high night temperature tolerance in winter wheat. *Plant Genome* **2025**, *18*, e70075. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.