Night temperature determines nearly half of wheat yield variation globally

Abstract

Daily minimum temperature (Tmin) is increasing faster than maximum temperature. However its impact on the physiology of crop yield and adaptation is barely studied. Using 42 years of annual yield trials at 255 sites representing most spring wheat production regions, the effects of environmental covariates were examined. During grainfilling, average Tmin explained 40% of yield variation, and 52% considering radiation; generally an increase of 1 degree C reduces yield ~0.5 t/ha. The relation between yield was linear over a 14 degree C range. An average increase of 1.2 degree C at the test sites reduced yield by more than 10%. A shortened grainfilling period is part of the explanation; nocturnal rates of dark respiration are also likely factors. Improvement of adaptation to warmer nights could generate a step-change in wheat yield, the most widely-grown crop globally, covering more than 220 million ha, and providing 20% of human calories and protein.

Introduction

Climate change has increased the frequency and intensity of hot weather events[1], and led to a relatively sharper increase in nighttime (Tn) than daytime temperature[2]. Importantly, the effects of global warming differ by region[3]; hence, one cannot expect identical changes in temperatures across all wheat production regions. Further, a review paper by Ullah et al.[4] concluded that the effects of extreme temperatures on grain yield of wheat are variable. One contributing factor is that irrigated wheat can cool its canopy up to 8ºC during the day in semi-arid regions[5], partially mitigating the effects of high daytime temperatures. To quantify the effect of global warming on historic and future wheat yields, crop simulation models take weather, as well as soil and cultivar effects into account [6,7,8]. Nevertheless, assessing the plausibility of the simulated impact of climate change on wheat production is challenging, since the simulation results depend on many inputs, such as climate scenarios, and the response of wheat to warming nighttime temperatures is still not fully understood. This is of major concern as crop productivity is negatively coupled to night temperature[9,10], for yet unknown reasons.

Wheat evolved in the Fertile Crescent, where it is exposed to cool temperatures during the winter months and high temperatures, as well as dry and sunny conditions during the grainfilling period, which coincides with the end of the rainy season in the spring. During the roughly three week period from heading, which coincides with the end of leaf growth, until the beginning of grain filling, organ growth is minimal and assimilates are stored in the form of water soluble carbohydrates and starch, to be subsequently remobilized for grain growth and maintenance respiration, especially under drought conditions[11–13]. This capacity to buffer adverse environmental conditions makes it challenging to quantify the effects of temperature and solar radiation on grain yield. As Evans et al.[14] pointed out, measured responses to heat can change across time and scale, i.e., from biochemical kinetics to a biome. Thermal acclimation of dark respiration to nighttime temperatures can greatly alter the net biomass accumulation, leading to discrepancies between results obtained under artificial conditions and in the field[15–17].

CIMMYT has been sending out its advanced nursery lines for testing by its partners across all major wheat production regions on Earth since the 1970's. In return, they share back key observations and measurements, such as yield. The lack of daily weather data has limited the analyses, but recent advances in reconstructing historic weather data to hourly and daily timesteps allow for thorough analyses of the effects of weather on yield[18]. Based on a global data set spanning more than 40 years, the objective was to identify environmental variables with global impact on yield. Results enable identification of lines and genomes with adaptation to Tn and other environmental conditions. This will provide 'model genotypes' to guide research and as sources for breeding.

Results

Our data set consists of 850 site-years. It spans a period of 42 years and represents most of the important spring wheat growing areas on Earth (Fig.1). We tested the effects of temperature, solar radiation, and vapor pressure deficit on grain yield during three cardinal growth periods: 1) sowing to heading minus 10 days when the canopy is established; 2) heading +/-10 days when grain-set is determined; and 3) grain filling. The analysis showed that weather conditions during the grain-filling period have the strongest association with yield variation: average daily minimum temperature during this period ranked first, followed by average daily solar radiation (Supplementary Fig. 1). These two parameters were followed by the minimum temperature during the heading period. The prediction powers of average daily minimum and maximum temperature, as well as solar radiation during grainfilling for grain yield are shown in Supplementary Fig. 2.

The locations with the coolest nights or lowest minimum temperatures, during the grainfilling period, are located in Egypt and Chile. These locations coincide with those that have the highest grain yields[19]. The Yaqui Valley in northwest Mexico also has high solar radiation, but slightly warmer minimum temperatures. Sudan, Nigeria, and several countries in South Asia had the warmest nighttime temperatures. The lowest yields were recorded in Laos and Thailand, where warm nights coincide with low solar radiation during the grain-filling period.

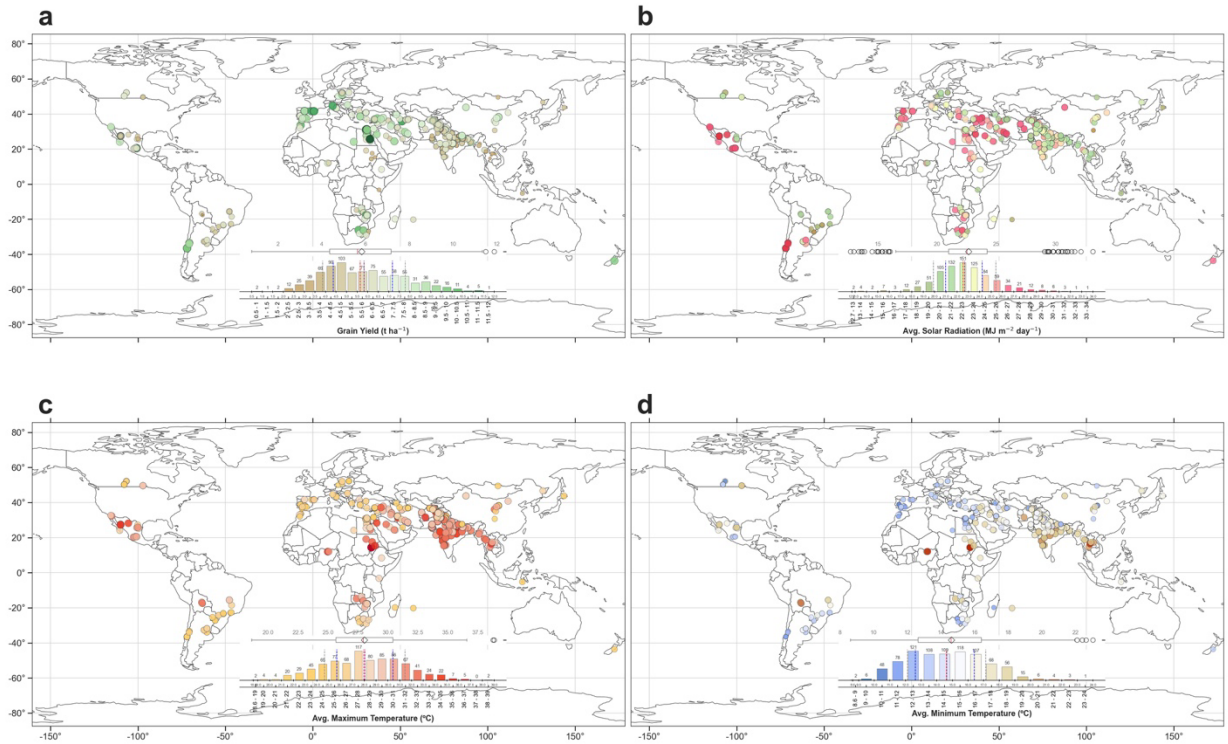

Figure 1: a) *Grain yield, and* ***b)*** *average daily solar radiation,* ***c)*** *maximum and* ***d)*** *minimum temperatures during grainfilling at 255 test sites for the Elite Spring Wheat Yield Trial (ESWYT) nurseries grown between 1979 and 2021.*

Combined minimum temperature and solar radiation during grain filling can explain 52% of the variability of grain yield at sites across the globe, with a root mean square error of 1.38 t/ha (Fig. 2). Our data set which encompasses the majority of spring wheat production regions, shows that the yield response to average nighttime temperature is linear within the observed range from 8ºC to 22ºC. An increase of 1ºC of average nighttime temperature reduces yield by 0.5 t/ha. The results also show that high solar radiation can help plants compensate for warm nighttime temperatures: even under warm average nighttime temperatures of e.g., 18ºC, yields increased from 2.6 t/ha to 5.9 t/ha when average daily solar radiation increased from 15 to 31 MJ/m2/day. Notably, the interaction between nighttime temperature and solar radiation was not significant;

hence, the effect of solar radiation is constant over the entire range of minimum temperatures. The combination of low radiation and warm nighttime temperature causes the lowest yields, or vice versa, cool nights in high radiation environments such as in Egypt or the Yaqui Valley in Mexico, result in the highest yields. The capacity of wheat to take advantage of high solar radiation levels can presumably be traced back to its origins in the Fertile Crescent, which helped it propagate under conditions of limited and erratic water supply combined with high temperatures and solar radiation during grain filling. This study shows that high solar radiation helps wheat tolerate warm nights.

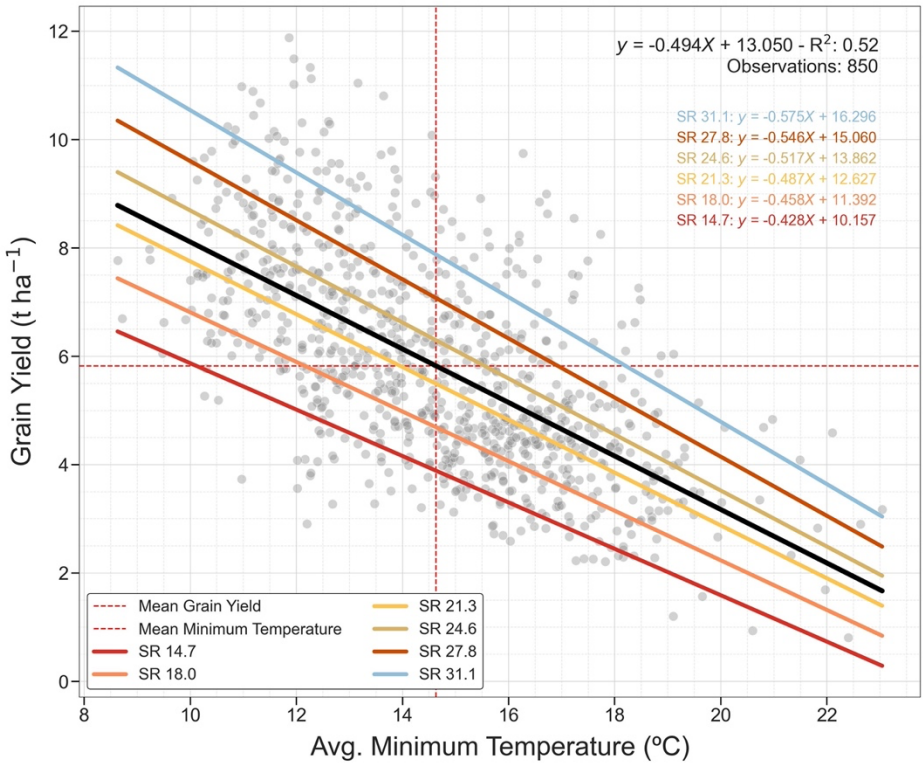

Figure 2: *Effect of average minimum temperatures and solar radiation during the grain filling period on the average yield obtained at 850 nursery-site-years. The non-significant interaction effects of different levels of solar radiation (SR) are overlaid.*

As shown in Fig. 3, there is a large regional variability in the increase in nighttime temperatures during grain filling over the period from 1980 to 2021. The largest increases were observed for the Mediterranean basin. They were generally above 1.5ºC. Central Europe, Sudan, Mesopotamia, and Western China experienced similar temperature increases. In the other parts of the world, the temperature increases were generally below 1.5ºC. The lowest increases were observed for Chile, Argentina, and the Canadian Prairies, as well as north-east China. These are important spring wheat-

producing regions. Interestingly, in India and Pakistan, the warming trend was higher at sites in the Indo-Gangetic Plain than at those further south.

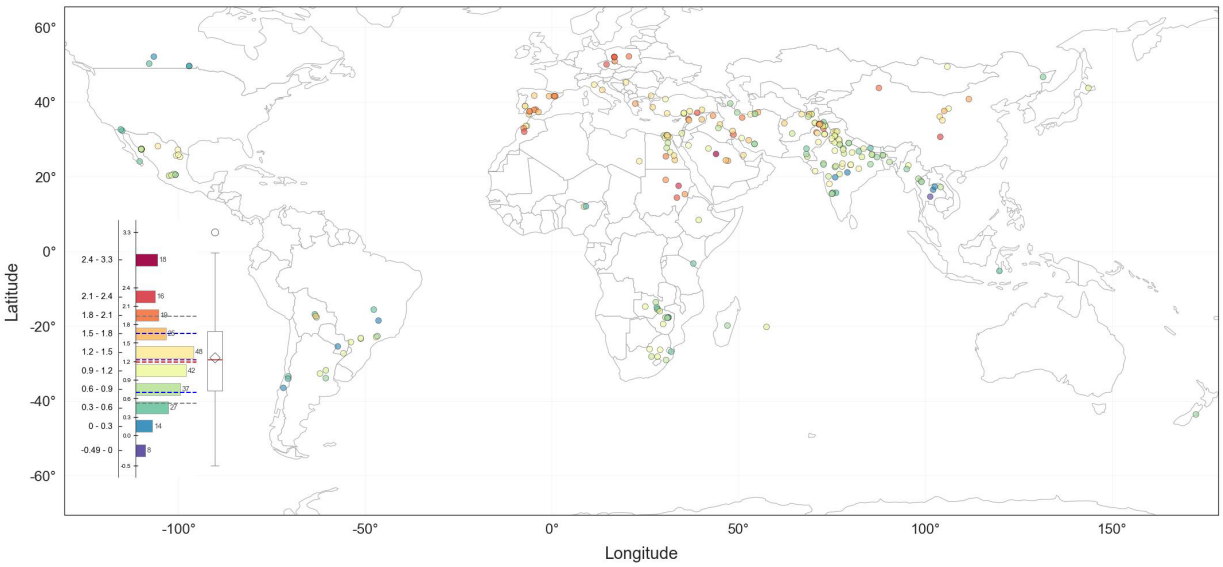

Figure 3: *Change in minimum temperature (ºC) at 255 nursery test sites of spring wheat between 1979 and 2021 during the grain filling period.*

Based on the trends in changes of nighttime temperatures, we calculated their impact on yield, using the estimated value of a yield loss of 0.5 t/ha for an increase by 1ºC. The yield declines over the past 42 years, expressed in percent of the reported yields (Supplementary Fig. 3), tended to be larger in locations that are already low yielding, such as Sudan, where the average minimum temperatures during the grain filling are higher than 20ºC (Fig. 4). In that country, the yield loss at three out of 4 locations exceeded more than 40%. Yield declines of more than 20% percent were estimated for Morocco, Central Europe, Mongolia, and five out of 19 locations in Pakistan. The majority of sites in Spain, Portugal, Iran, Syria, Türkiye, Afghanistan, and China had yield losses of 10 to 20%. In India, Iran, Mexico, and Türkiye, the yield losses hovered at around 10%. Slightly lower yield losses were observed for Brazil. In southern Africa, yield losses were below 10% in Zambia, Zimbabwe and South Africa. Relatively small yield losses were also observed for Argentina, Chile and Canada. It is noteworthy that in Chile, the country with the highest reported average yield, yield losses were close to zero (Supplementary Table 1).

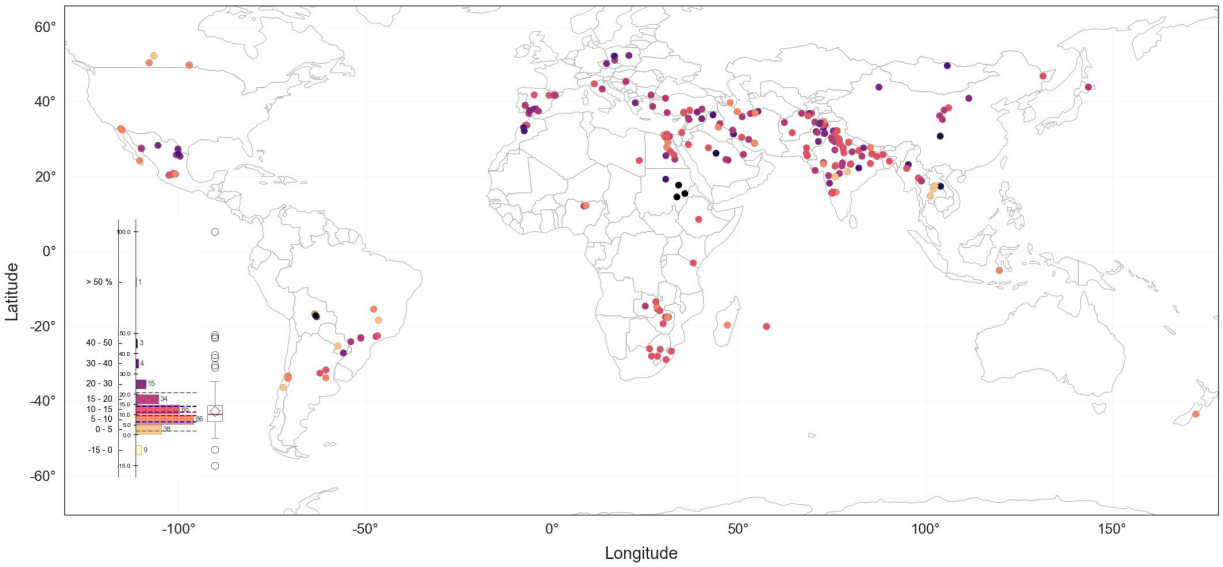

Figure 4: Yield losses in percent of average reported yield caused by changes in daily minimum temperatures during the grain filling period at 255 nursery test sites for spring wheat.

Discussion

Our study is based on a set of global multilocation elite-wheat field trials, spanning 42 years and representative of most spring wheat production regions. The finding that nighttime temperatures control grain yield to a much larger extent than generally assumed is in line with a large meta-analysis[20]. The authors of that study[20] also emphasized that results from field studies differ from those obtained under controlled conditions.

In a recent review, Amthor[21] hypothesized that the warming effects on truncating the duration of grainfilling[22], and thus grain yield, may override the effects of warming *per se* on specific rates of photosynthesis and respiration, i.e, yield declines are mostly due to a change in phenology. We had records of observed days to maturity for 262 site-years. As shown in Supplementary Fig. 4, grainfilling duration indeed was shortened by warmer nighttime temperatures. Each increase by one degree C accounted for a shortening by 1.6 days. However, the prediction accuracy was not very high, with an R^2 of 0.27 and RMSE of 6.4 days. In order to quantify the relative importance of the two factors, we calculated the Variable Importance Index, that reflects the relative contribution of a factor alone, not in combination with other factors. Using the dependent resampled inputs options, the report revealed that the main effect of nighttime temperature on yield was 0.56, while it was 0.44 for duration of grainfilling.

Hence the shortened duration of grain filling is important. However, the direct effect of nighttime temperatures on other processes carried even more weight.

We did not measure the rates of photosynthesis and respiration; however, the observed grain yield is a function of these two metabolic processes. Daytime temperature has a strong effect on the rate of photosynthesis, i.e., the production of ATP and NADPH (energy and reducing power) to synthesize sugars like glucose, while nighttime temperatures primarily stimulate dark respiration rates[23,24], the process that produces ATP for cellular maintenance and plant growth. It is noteworthy that higher dark respiration rates can create a larger sink for photosynthates, leading to higher photosynthesis rates under sink-limited conditions[23,24]. A key process that is likely accelerated by night warming is nocturnal protein turnover [22] – which increases demand for respiratory ATP and the rate of respiratory CO_2 release in darkness [22]. Another is the effect of night warming on membrane fluidity, with negative consequences for the efficiency of respiratory ATP synthesis and the scale of nocturnal respiratory CO_2 release[25,26] The loss of carbon by respiration matters, as even under optimal conditions whole-plant respiration releases 30–60% of the carbon fixed by photosynthesis each day[27,28,29,30] with approximately half of the CO_2 released by whole-plant respiration coming from leaves during the night[31,32]. High rates of leaf respiraton during warm nights thus have the potential to play an important role in controlling daily carbon gain, with consequences for plant growth and yield.

Our study, at the biome level, helps better understand how temperature and solar radiation affect these two metabolic processes: photosynthesis and nocturnal respiration. The fact that nighttime temperatures are more closely related to yield than daytime temperatures emphasizes the important role of nocturnal dark respiration, a process which has received much less attention than photosynthesis. While both photosynthesis and respiration matter, growth rates of wild and crop plants are often much more strongly correlated with dark respiration than with photosynthesis[33]. The importance of respiration for growth and yield was further highlighted by the finding that low-respiring ryegrass lines exhibited the highest yield[34]. Our study, which found that increasing night temperatures reduce yields, complements these findings, emphasizing the importance of nocturnal rates of dark respiration.

One factor that likely influences the extent to which warm-night mediated increases in respiratory CO_2 release influence yield is whether respiration acclimates to sustained increases in night temperature. Acclimation to high growth temperatures often results in reduced rates of leaf dark respiration at any given temperature[35], potentially reducing the stimulatory effect of warm nights on respiration rates. For wheat, this can result in homeostatic rates of whole-plant respiratory CO_2 release in plants experiencing both warm days and nights, compared to those grown under cooler days/nights, when each

(i.e. cool and warm grown plants) are measured at their respective growth temperatures[27]. However, in a recent study assessing the impact of warm nights *per se* on leaf respiration and growth in wheat, no acclimation of leaf respiratory CO_2 release was observed[36]. As a result, warm nights stimulated respiratory CO_2 loss and reduced plant growth. If similar patterns of minimal acclimation responses to warm nights occur at the field sites used in our study (particularly during grain filling), it would explain why warm nights were associated with reduced yields. Looking forward, improvements in yield under warm nights may be possible through screening for genotypic variability in thermal acclimation potential, building on the recent observations that leaf dark respiration is partially under genetic control[37] and that there is genotypic variation in the extent of acclimation of wheat respiration to warmer nights[38]. A better understanding of dark respiration in combination with targeted breeding efforts may help limit yield losses caused by global warming, which creates a sharp increase in nighttime temperatures.

Our estimated yield losses tend to be larger than the forecasts generated by ensembles of crop simulation models in conjunction with climate change scenarios[7,8]. These two papers cover different periods: while the paper by Asseng et al.[7] focused on hot spots of yield decline for irrigated spring wheat for the period from 2030 to 2041, Jägermeyr et al.[8] covered most current and potential wheat production regions on Earth between 1980 and 2100. Unlike these studies, our study did not account for the contested effects of CO_2 fertilization[39]. A recent meta-analysis[39] concluded that rising temperatures can negate the effects of CO2 fertilization. Nevertheless, one would expect similar regional trends, even when our study focuses on the past. Asseng et al.[7] forecast yield declines in all regions, which matches our analyses: Our studies agree on small yield declines for Egypt, and strong yield declines for Sudan, Saudi Arabia, and Western China. However, for India and Pakistan, our model estimates the largest relative yield losses for the regions with the highest production levels: Punjab in Pakistan and India, and Haryana in India, and smaller losses for the regions further south and east, which is the opposite pattern predicted by the multimodel ensemble. We also estimate relatively larger yield declines for Mesopotamia. The global study by Jägermeyr et al. agrees with our estimate of largest declines in Sudan and Saudi Arabia, and intermediate declines in Mexico. We estimate only small declines for Chile and Canada, whereas Jägermeyr estimates yield increases for these countries by 2100. The largest discrepancies between our nighttime temperature based model and Jägermeyr et al. are observed for the Mediterranean, the Middle East and Western China, for which we estimate a yield decline since 1980 by 10 to 20%, whereas Jägermeyr estimates a slight increase in yield by 2100 in the Mediterranean and a strong yield increase for the Middle East, Central Asia and all of China. While our model is empirical, based on daily minimum temperature and solar radiation and was developed with measured yield data, the crop simulations rely on several assumptions. Our observations show much bleaker trends

for wheat production in these regions. Unlike the crop simulation models, we do not take rainfall into account. Given the fact that rainfall amounts have shown a declining trend and have become more erratic over the past four decades in Mesopotamia and Türkiye[40,41], it is unrealistic to foresee an increase in wheat yields in this region, where wheat is the most important staple crop.

Our study shows that the warming trends vary greatly among wheat production regions. Some of them, such as those in the Mediterranean basin and Mesopotamia, are much more affected by global warming than those located south of the equator. Our results, which are representative for most of the important spring wheat production regions on Earth, also indicate that the effects of warming on grain yield of wheat are more severe than forecasted by ensembles of crop simulation models or in meta-analyses[20,42].

Conclusions

Our study, based on field-grown wheat representing most of the spring wheat production regions globally, demonstrates that increases in nighttime, and not maximum temperatures, have limited the grain yield of wheat. This is partly due to a shortening of the grainfilling period, but to a larger extent caused by the impact of warmer temperatures on a multitude of respiratory processes collectively referred to as maintenance respiration. High solar radiation appears to mitigate the negative effects of warm nights.

Our nighttime-based model shows an alarming trend, with the potential yield generally declining by 10% or more over the past four decades. More efforts and resources are needed to intensify breeding efforts for lines that are more tolerant of high nighttime temperatures. These efforts need to be complemented by better agronomic practices, such as conservation agriculture, that improve soil health and can buffer surface soil temperature from weather anomalies where crop residue retention is practiced and thus foster yields[43,44]. Most of the low-hanging fruits, such as improved harvest index, have been exploited. New breeding tools, such as genomic selection and gene editing, offer new paths to accelerate breeding gains, but we first need to better understand the mechanisms of how nighttime temperature and nighttime physiology in general control key physiological processes, including dark respiration.

Our results are of immense importance to food security and commerce. However, they also fill a gap in fundamental research by showing that growth is tightly coupled to a relatively wide range of night temperatures. Hence, a significant improvement of adaptation to warmer nights has the potential to generate a step change in yield over the majority of current wheat-growing environments. Similarly, contributors to increased

respiratory costs for cellular maintenance - which include protein turnover and maintenance of ion gradients across membranes- along with the energy costs of starch synthesis in growing spikes, will need to be studied for genetic variation and potential to improve efficiency. For example, starch synthase is well known to be heat-labile. Genetic variation in diurnal cycles and temperature thresholds may help to identify the genetic bases of components of maintenance respiration. Differences in varietal response to warming nighttime temperatures identified by this study can be used in crossing strategies almost immediately.

Material and Methods

We used a data set derived from the Elite Spring Wheat Yield Trials (ESWYT) for this analysis. Under the umbrella of the International Wheat Improvement Network (IWIN), CIMMYT sends out different nurseries consisting of 30 to 50 advanced lines for testing by its partners across all the major wheat production regions on Earth (Fig. 1). In return for getting access to advanced genetic material, the partners record many parameters, such as sowing date, days to heading and maturity, plant height, disease incidence levels and yield. However, some of the returned data sets have missing values. Days to heading was available for 92% of the records, while days to maturity was reported for 32%. Missing phenological data were gap-filled. The data set was quality controlled, resulting in 850 site-year combinations. For each combination and line, we calculated the best linear unbiased estimation (BLUE) yield. Each nursery year consists mostly of new lines, and only a few are retained for more than one year. All in all, 1402 lines were tested. We extracted the daily weather parameters from AgERA5[18] and calculated weather related parameters for the following three periods: 1) sowing to heading minus 10 days, 2) heading minus 10 days to heading plus 10 days, and 3) heading plus 10 days to maturity. The last period will be referred to as grain filling. The first period covers the establishment of the plants and tiller growth, the second one lasts from booting to the beginning of grainfilling, the period around anthesis, during which organ growth is minimal, and the last one coincides with grainfilling. For each period, we calculated average daily minimum and maximum temperature, solar radiation, vapor pressure deficit (VPD), number of days on which daily maximum temperature is exceeding 30ºC and daily minimum temperature is exceeding 25ºC, and vapor pressure deficit VPD exceeding 4 kPa. For ease of understanding, we will refer to daily minimum temperature as nighttime temperature, although they are not precisely the same.

Statistical analyses were conducted with JMP V18.2 (www.jmp.com). First, we identified the variables with the largest prediction power for yield, using the Predictor Screening Platform. For each response, it builds a bootstrap forest model using 100 decision trees.

Average daily minimum temperature and solar radiation during the grainfilling period had the largest prediction power (Supplementary Fig. 1). We then used the Neural Network platform to model the response and interactions between the 2 parameters. We also used JMP to calculate the variable importance index, which reflects the relative contribution of a factor alone, not in combination with other factors.

In order to quantify and visualize the changes in minimum daily temperatures during the grainfilling period, we calculated the average minimum temperature for each site-year-occurrence combination, between the start and end day of the year for all 42 years. Next, we fit a linear regression of harvest year versus all average minimum temperatures to estimate the change in minimum temperatures during grain filling at a given location. In a last step, we used the finding of this study that an increase in average minimum daily temperatures by 1ºC decreases yield by 0.5 t/ha to estimate the yield loss, using the average of the reported yields at a given location as a reference.

Data availability

The nursery data together with the environmental covariables can be accessed at: https://doi.org/10.71682/10549387
The AgERA5 agrometeorological indicators from 1979 to present derived from reanalysis, can be downloaded from: https://doi.org/10.24381/cds.6c68c9bb

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Author contributions

US, MPR and SS conceptualized the study. US conducted the data analysis.
US, OA and MPR wrote the initial draft and EG wrote the software for data analysis and visualization. SS was was responsible for funding acquisition and project administration.
All authors contributed suggestions and reviewed and refined the text.

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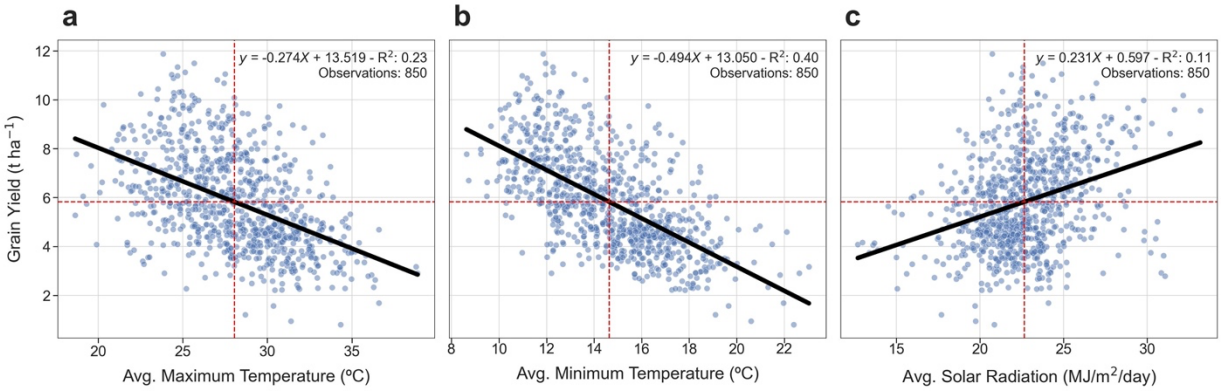
Supplementary Table 1: Average change in minimum temperature (Tmin) during grain filling at the ESWYT nurseries test sites. Yield data represent the average nursery yield reported within a country, and yield losses are expressed as a percentage of the reported yield. The data cover 42 years, from 1979 until 2021.

Country	Change in TMin grain filling (°C)	Yield (t/ha)	Yield loss (t/ha)	Yield loss (%)
Afghanistan	1.29	5.611	0.646	11.5
Argentina	0.83	5.234	0.416	7.9
Bangladesh	0.69	4.715	0.343	7.3
Bolivia (Plurinational State Of)	0.99	2.412	0.493	20.4
Brazil	0.73	4.563	0.364	8.0
Canada	0.09	4.830	0.043	0.9
Chile	0.18	8.964	0.091	1.0
China	1.81	6.126	0.903	14.7
Czechia	0.68	7.294	0.339	4.7
Egypt	1.36	8.020	0.681	8.5
Eswatini	0.34	2.726	0.168	6.1
Ethiopia	1.04	6.298	0.520	8.2
Greece	2.20	6.133	1.099	17.9
India	0.95	4.855	0.474	9.8
Iran (Islamic Republic Of)	1.35	6.599	0.677	10.3
Iraq	1.59	6.363	0.793	12.5
Israel	1.10	6.550	0.550	8.4
Italy	1.67	8.638	0.836	9.7
Japan	0.95	3.548	0.474	13.3
Libya	1.54	8.859	0.768	8.7
Madagascar	0.61	6.794	0.306	4.5
Mexico	1.02	5.828	0.510	8.8
Mongolia	1.36	2.907	0.680	23.4
Morocco	2.04	7.301	1.022	14.0
Myanmar	0.82	2.663	0.412	15.5
Nepal	0.68	5.278	0.338	6.4
New Zealand	0.60	9.422	0.301	3.2
Nigeria	0.87	5.158	0.433	8.4
Pakistan	1.53	4.713	0.765	16.2
Paraguay	0.57	3.890	0.285	7.3
Poland	2.48	6.486	1.239	19.1

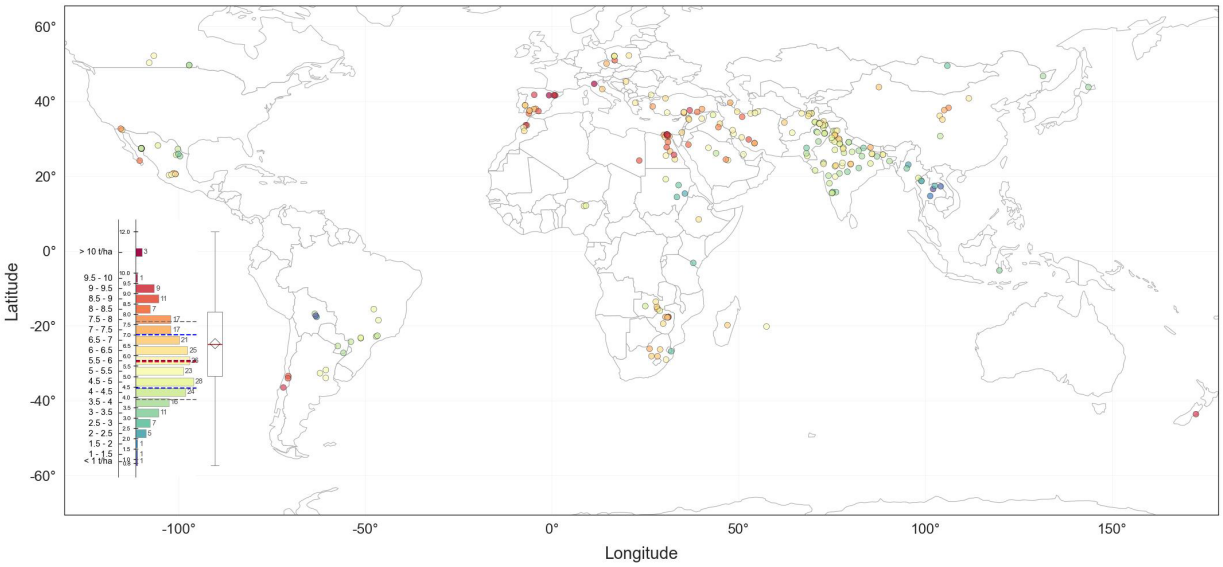
Portugal	1.68	6.815	0.838	12.3
Qatar	1.66	5.321	0.832	15.6
Saudi Arabia	1.94	6.257	0.969	15.5
Serbia	1.61	6.497	0.807	12.4
South Africa	1.05	6.747	0.527	7.8
Spain	2.14	8.155	1.070	13.1
Sudan	2.50	3.171	1.249	39.4
Syrian Arab Republic	2.09	6.263	1.046	16.7
Thailand	0.28	2.352	0.140	6.0
Türkiye	1.62	7.118	0.811	11.4
Zambia	0.73	6.012	0.363	6.0
Zimbabwe	0.66	7.161	0.332	4.6

Predictor	BLUE_YLD Contribution	Portion	Rank
avg_TMin_GrainFill	715.670	0.4120	1
avg_SolRad_GrainFill	278.766	0.1605	2
avg_TMin_Hminus10d-Hplus10d	194.766	0.1121	3
avg_SolRad_Hminus10d-Hplus10d	97.847	0.0563	4
avg_TMin_SHminus10d	95.936	0.0552	5
avg_TMax_SHminus10d	60.174	0.0346	6
avg_TMax_GrainFill	57.860	0.0333	7
avg_SolRad_SHminus10d	48.787	0.0281	8
avg_TMax_Hminus10d-Hplus10d	48.604	0.0280	9
avg_VPD_SHminus10d	43.096	0.0248	10
ndays_TMax_Hplus10dM	39.738	0.0229	11
avg_VPD_GrainFill	31.111	0.0179	12
ndays_TMax_gt32C_Hminus10d-Hplus10d	19.749	0.0114	13
ndays_TMax_gt32C_SHminus10d	4.675	0.0027	14
ndays_TMin_Hplus10dM	0.430	0.0002	15
ndays_VPD_gt4kPa_Hminus10d-Hplus10d	0.048	0.0000	16
ndays_VPD_gt4kPa_SHminus10d	0.000	0.0000	17
ndays_TMin_gt25C_SHminus10d	0.000	0.0000	18
ndays_TMin_gt25C_Hminus10d-Hplus10d	0.000	0.0000	19

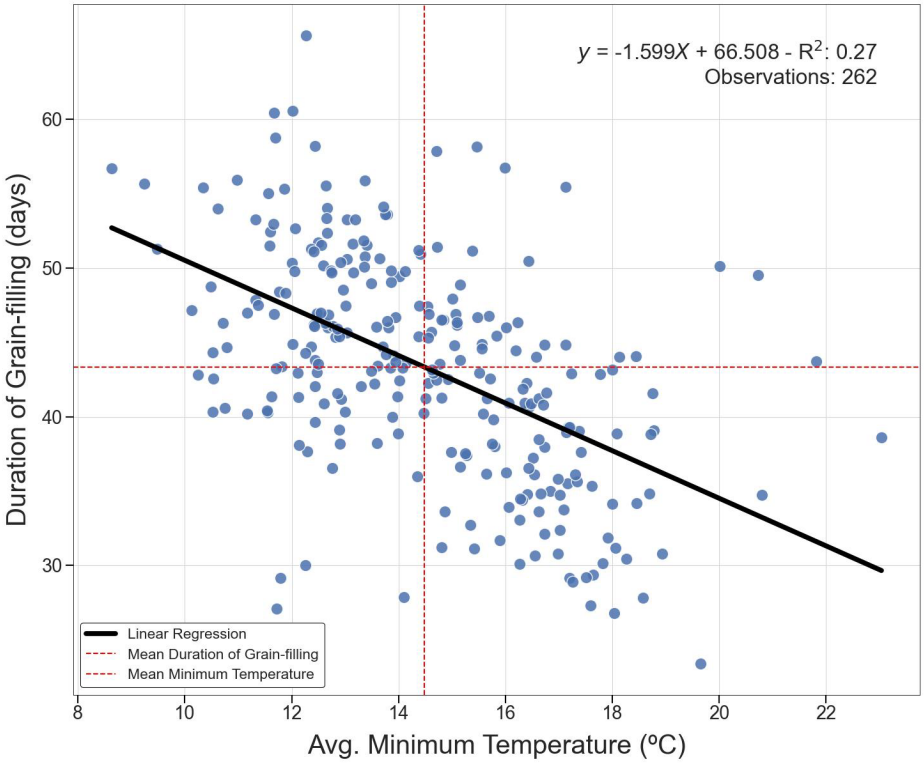
Supplementary Fig. 1*: Prediction power of environmental variables to estimate grain yield at 850 site-years. Variables represent three periods: 1) sowing to heading minus 10 days (SHMinus10d), 2) heading minus 10 days to heading plus 10 days (HMinus10d-Hplus10d), and 3) heading plus 10 days to maturity (Hplus10dM). The last period represents grain filling.*



Supplementary Fig. 2*: Prediction of yield at 850 site-years as a function of* ***a)*** *daily average maximum temperature,* ***b)*** *minimum temperature and* ***c)*** *solar radiation observed during the grainfilling period.*



***Supplementary Figure 3**: Observed average yield at 255 spring wheat nursery test sites.*



***Supplementary Figure 4:** Effect of minimum temperature during grainfilling on the number of reported days between heading and maturity at 262 site-years.*