An assessment of wheat yield sensitivity and breeding gains in hot environments

Sharon M. Gourdji1,2, Ky L. Mathews3, Matthew Reynolds3, José Crossa3 and David B. Lobell1,2

1Department of Environmental Earth System Science, Stanford University, Stanford, CA 94305, USA
2Center on Food Security and the Environment, Stanford University, Stanford, CA 94305, USA
3International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

Genetic improvements in heat tolerance of wheat provide a potential adaptation response to long-term warming trends, and may also boost yields in wheat-growing areas already subject to heat stress. Yet there have been few assessments of recent progress in breeding wheat for hot environments. Here, data from 25 years of wheat trials in 76 countries from the International Maize and Wheat Improvement Center (CIMMYT) are used to empirically model the response of wheat to environmental variation and assess the genetic gains over time in different environments and for different breeding strategies. Wheat yields exhibited the most sensitivity to warming during the grain-filling stage, typically the hottest part of the season. Sites with high vapour pressure deficit (VPD) exhibited a less negative response to temperatures during this period, probably associated with increased transpirational cooling. Genetic improvements were assessed by using the empirical model to correct observed yield growth for changes in environmental conditions and management over time. These ‘climate-corrected’ yield trends showed that most of the genetic gains in the high-yield-potential Elite Spring Wheat Yield Trial (ESWYT) were made at cooler temperatures, close to the physiological optimum, with no evidence for genetic gains at the hottest temperatures. In contrast, the Semi-Arid Wheat Yield Trial (SAWYT), a lower-yielding nursery targeted at maintaining yields under stressed conditions, showed the strongest genetic gains at the hottest temperatures. These results imply that targeted breeding efforts help us to ensure progress in building heat tolerance, and that intensified (and possibly new) approaches are needed to improve the yield potential of wheat in hot environments in order to maintain global food security in a warmer climate.

1. Introduction

Wheat is the most widely grown crop in the world in terms of total harvested area [1], and currently provides an average of about 20 per cent of human calorie consumption [2]. Improvements in yield are essential to keep pace with population growth and increased demand, yet long-term climate trends threaten to reduce wheat yields, or at least slow yield growth, in many regions. Spring wheat is already grown in many tropical and sub-tropical environments near or past the optimal temperatures for wheat [3], particularly during the later grain-filling portion of the season [4–6]. Modelling studies have shown that even with adaptive agronomic changes to planting date and cultivar, projected warming will still have a negative impact on wheat yields around the globe [7]. Although elevated CO2 levels associated with warming may impart benefits, which in many regions could outweigh the negative impacts of warming for the next few decades [8], a warming climate still represents an important adaptation challenge to the maintenance of past productivity gains.
Beyond relatively straightforward agronomic changes, an often cited adaptation strategy is to breed new wheat varieties that combine improved heat tolerance with other desirable traits, such as disease resistance and high yield potential. The International Maize and Wheat Improvement Center (CIMMYT), based in Mexico, has been a leader in breeding and disseminating improved varieties of wheat in developing countries since its inception in 1943, funded by the Rockefeller Foundation and the government of Mexico. In the 1990s, it was estimated that 90 per cent of bread wheat releases in developing countries contained ancestry from one or more CIMMYT varieties [9], and today, more than 75 per cent of the area planted to modern wheat varieties in developing countries uses varieties developed by CIMMYT or its national-level partners (http://www.cimmyt.org/en/about-us/who-we-are). Recent studies assessing long-term genetic gains of wheat lines released by the CIMMYT Global Wheat Program show a continuous yield increase of approximately 0.7 per cent per year in both low-yielding areas, and well-irrigated and high-rainfall areas [10,11].

Given the major role of CIMMYT in international wheat improvement, and the evidence of widespread warming in major wheat growing regions in the past few decades [6,12], a relevant issue is the relative performance of CIMMYT lines under different temperature conditions. A related question is whether nurseries that focus on breeding for targeted drought or heat stress show evidence of more rapid yield gains at high temperatures than the more standard approach of breeding for high yield potential under optimal management, since this knowledge could help us to guide future efforts.

The current study addresses these questions using historical datasets from three different spring bread wheat nurseries at CIMMYT with different breeding goals: the Elite Spring Wheat Yield Trial (ESWYT), which contains the highest-yielding varieties under ideal environmental and management conditions; the Semi-Arid Wheat Yield Trial (SAWYT), where wheat is specifically bred to maintain yields under dry conditions that are frequently accompanied by heat stress; and the High Temperature Wheat Yield Trial (HTWYT), where wheat is bred for high temperature, irrigated environments. Data from these nurseries are first used in regression analysis to define the sensitivity of wheat yields to temperature and other environmental parameters. These regressions are then used to adjust observed yields for changes in the locations and environmental conditions of trials over time, a step necessary in order to assess true genetic gains under theoretically constant conditions. Inferred genetic gains are then compared across a range of cool to hot temperatures in the grain-filling stage, in order to determine the relative rate of gains in hot environments.

2. Methods

(a) Datasets

For each year and breeding nursery, a new set of varieties is sent annually by CIMMYT to a network of international collaborators (called the International Wheat Improvement Network, IWIN), who grow this common germplasm under a range of environmental conditions. For example, seasonal average temperatures vary in the database between 7°C and 27°C (see figure S1 in the electronic supplementary material). The IWIN serves primarily to distribute improved germplasm globally, but the data returned from these trials provide a valuable resource to assess genotype × environment (G × E) interactions and long-term trends in breeding. IWIN trial datasets have been used in studies to help us understand the impact of breeding nurseries such as the ESWYT [10,13], SAWYT [11,14] and HTWYT [15], among others.

All trials in this dataset were generally requested to be well managed in terms of water and fertilizer application, with trials affected by lodging or disease filtered out. One exception is in the SAWYT nursery, where collaborators were encouraged to apply only enough irrigation to achieve germination, with final yields being largely dependent on in-season rainfall and/or stored soil moisture. As might be expected in this 76-country, 25-year dataset, the implementation of management instructions most probably varied across trials within the database, as evidenced by the wide range of yields in the database (from approx. 1 to approx. 10 tonnes ha⁻¹ grown with the same varieties in any given year; figure 1). However, among international agricultural datasets, this one contains a relatively...
minimal amount of confounding factors, along with a wide range of environmental conditions, thereby enabling us to empirically assess relationships between wheat yield and environmental parameters throughout the crop life cycle. Such an empirical analysis can both confirm current understanding and elucidate mechanisms for future prediction of crop yields in a changing climate.

Yield data in this study represent means across genotypes and replications for a given trial location, sowing date and nursery. The trial means were calculated using only the subset of genotypes within a nursery each year that had similar phenology (i.e. ±3.5 days of the mean trial heading date) in high-yielding (i.e. more than 5 tonnes ha$^{-1}$) environments, in order to exclude the confounding effects of large maturity ranges in stress environments. However, mean yields for the selected genotypes were calculated for all trials, and included in the empirical model regardless of yield level.

Yield data were paired with reconstructed daily weather data, as described in the detailed methods section in the electronic supplementary material. In short, daily temperature data were obtained by combining high-spatial-resolution climatologies with interpolation of anomalies from nearby station data, while daily relative humidity and radiation were obtained from satellite-based datasets. While water was assumed not to be a limiting factor for the irrigated trials, unfortunately little information was available regarding timing and amount of irrigation water, nor were suitable soil moisture datasets available.

Yield data were paired with reconstructed daily weather data, as described in the detailed methods section in the electronic supplementary material. In short, daily temperature data were obtained by combining high-spatial-resolution climatologies with interpolation of anomalies from nearby station data, while daily relative humidity and radiation were obtained from satellite-based datasets. While water was assumed not to be a limiting factor for the irrigated trials, unfortunately little information was available regarding timing and amount of irrigation water, nor were suitable soil moisture datasets available.

(b) Empirical model
Mean yields from a total of 1353 trials, pooled across nurseries and planted from 1980 to 2009 in 349 unique locations (figure 1), were paired with weather data in a panel regression: $y = c_i + a_n + (y_e \times \text{year}) + (\beta \times W) + \epsilon$, where $c_i$ are country fixed effects, $a_n$ are nursery fixed effects, $y_e$ are yield trends by nursery, $W$ is a set of environmental variables defined by growth stage and $\beta$ are the coefficients on these variables.

The environmental variables in $W$ include: air temperature (both linear and squared terms), diurnal temperature range (DTR), shortwave radiation, day length, vapour pressure deficit (VPD), and interaction terms between VPD and temperature (linear and quadratic). Vapour pressure deficit was calculated as the difference between saturation and actual vapour pressures, which were derived from daily minimum and maximum temperatures and relative humidity data. Each environmental variable included in the regression was averaged for three stages throughout the growing season [16]: vegetative (from sowing to 300 growing degree-days, GDD, before heading), reproductive (from 300 GDD before heading to 100 GDD after) and grain-filling (from 100 GDD after heading to harvest).

The linear and quadratic temperature terms allowed the model to choose an ‘optimal’ temperature per growth stage, while DTR allowed for a differential response to day-versus-night-time temperatures. Radiation and day length affect photosynthesis and development rates, respectively, and while radiation tends to covary with temperature (especially in the vegetative stage), day length, along with temperature, is also an important determinant of phenology. VPD interacts with air temperature through its impact on transpiration and, hence, canopy temperatures. A number of alternative models were also tested (e.g. excluding day length and/or DTR, excluding the temperature quadratic terms, or additionally including stage length terms and their interaction with temperature). The results using these alternative models confirmed that the main conclusions of the study were not sensitive to model formulation.

Country fixed effects in the model accounted for average differences in management or soil type by country, after accounting for variability explained by the weather-based predictors in the regression. We assumed that any remaining variations in management or soil type within countries were not correlated with weather, and therefore did not bias our regression estimates.

Trials were pooled across nurseries into a single model in order to increase statistical power, and because of large differences in the number of trials per nursery (959 from ESWYT versus 259 from SAWYT and 135 from HTWYT). However, structural differences exist in germplasm, environment and management between the nurseries (e.g. irrigation in ESWYT and HTWYT, but none in SAWYT). Nursery fixed effects and nursery-specific year trends, corresponding to varying levels of genetic yield growth, help us to account for these differences. As a sensitivity test, we also ran three separate nursery-specific regression models.

(c) Assessment of genetic gains by nursery and temperature bins
Genetic gains were assessed by using the regression model to correct observed yield trends for changing environmental and management conditions over time. (Here, ‘genetic gains’ refers to the relative performance of the changing germplasm in the trial means over the lifetime of the nurseries.) Specifically, the regression model was used to predict yield changes in the dataset caused by changes in environmental variables and country effects over time, and these partial fitted values are then subtracted from the observed yields. Linear time trends are finally fitted to the residuals to assess ‘climate-corrected’ yield trends, or inferred genetic gains. Time trends in residuals can also be assessed for subsets of the data (e.g. by nursery and/or temperature ranges). For this analysis, four temperature bins were defined based on average temperature quartiles during the grain-filling period, typically the hottest portion of the season. Genetic gains were not analysed for HTWYT, given the short life-span (1993–2004) and lack of significant observed yield trends in this nursery. (Regardless, the HTWYT trials were retained in the empirical model in order to help increase statistical power.)

Trends in environmental variables in the database primarily reflect the changing mix of sites over time, rather than the climatic trends at the sites themselves. For example, there was a strong warming trend across trials in the grain-filling stage, which rose from an average daily temperature of 19°C in 1983 to 24°C in 2009. However, the annual average global warming trend in the station database compiled for this study was only approximately 0.8°C over this same period. There was also a significantly positive trend in radiation (by about 7%) in the grain-filling stage over the period. These strong trends in temperature and radiation in the trial dataset were probably because of the growing proportion of trials in India, which rose from 5 per cent in the earliest decade (1983–1992) to 30 per cent in the last decade (2000–2009). India has some of the highest average temperatures in the grain-filling stage (26°C versus a mean of 21.9°C), which may have depressed overall observed yield trends in recent years, although the higher radiation would have had an opposing effect. Our method for assessing genetic gains should correct for any trends in environmental variables and country makeup in the database, regardless of their source.

3. Results and discussion
(a) Results from empirical model
The regression results exhibited a clear influence of temperature on trial mean yields, with significant interactions between temperature and VPD. Nearly half of all yield variability was captured by the regression model (adjusted
The importance of temperature (linear and quadratic terms), VPD, and the interactions of temperature and VPD were less significant than in the vegetative or reproductive stage, most probably because of faster development and lower potential grain number associated with longer photoperiod [21]. Although day- and night-time temperatures have been shown to have differential impacts on grain yield in previous studies [22], results here did not show a significant relationship between diurnal temperature range (DTR) and yield in any of the three growth stages.

\[ r^2 = 0.44 \], with weather providing a substantial fraction of the explanatory power (i.e. the adjusted \( r^2 = 0.23 \) for a model with only weather and no country fixed effects). The country fixed effects showed a substantial and significant variation across countries, with countries such as Zimbabwe and Canada having a strong yield benefit (approx. 3 tonnes ha\(^{-1}\)) relative to what is predicted by weather alone, and Nepal and Algeria having a significant yield penalty (approx. \(-1\) tonnes ha\(^{-1}\)).

Figure 2 shows the inferred yield response to temperature from the regression model for each growth stage under both high and low VPD conditions. These curves represent the average temperatures by growth stage \(\left( ^{\circ}C \right)\) at optimal temperatures of approximately \(12^\circ C\). In the reproductive stage, warming had a negative impact on yields across the full range of temperatures in the database. Given the higher average air temperatures during grain-filling relative to those earlier in the season (see the electronic supplementary material, figure S2), it may be that canopy temperatures in this growth stage (especially in humid conditions) often reached physiological limits in terms of plant metabolism [20].

The regression results also allowed us to infer relationships between the ancillary variables and yield, in addition to temperature (results not shown). For example, we saw a very positive and significant relationship between radiation and yield during the grain-filling stage with an inferred coefficient of 0.1 tonnes ha\(^{-1}\) (MJ m\(^{-2}\) day\(^{-1}\))\(^{-1}\). Coefficients on radiation were negative, but insignificant, during the vegetative and reproductive stage, most probably because of their correlation with other variables and/or processes counteracting what would otherwise be a positive association. Day length has a significantly negative coefficient in the vegetative stage, most probably because of faster development and lower potential grain number associated with longer photoperiod [21]. Although day- and night-time temperatures have been shown to have differential impacts on grain yield in previous studies [22], results here did not show a significant relationship between diurnal temperature range (DTR) and yield in any of the three growth stages.

(b) Inferred response to \(+2^\circ C\) warming

As an overall summary of the regression results, figure 3 displays the estimated yield loss (or gain) in tonnes ha\(^{-1}\) from \(+2^\circ C\) warming throughout the growing season for trials in the 1990s and 2000s. The projected yield changes owing to warming were calculated by comparing the actual fitted values from the regression with recomputed fitted values that reflect historical temperatures \(+2^\circ C\) across stages, along with associated changes in VPD and DTR. Radiation and relative humidity values were assumed to stay constant. Radiation trends are primarily affected by trends in air pollution and aerosol-cloud feedback effects [23,24], whereas relative humidity is projected to stay constant on a global basis with greenhouse-gas-induced warming [25,26].

The model predicted that 95 per cent of trials would have a lower mean yield from a \(+2^\circ C\) warming, with a mean loss of approximately 0.3 tonnes ha\(^{-1}\), and a range of 0.3 tonnes ha\(^{-1}\) gain to 1.4 tonnes ha\(^{-1}\) loss. This translated into an average loss of approximately 11 per cent of current yields across the globe. In general, the regions that were most subject to warming-related losses already had high seasonal average temperatures (see the electronic supplementary material, figure S2).
material, figure S4)), such as in Sudan, Myanmar and Paraguay, where projected losses average approximately 61, 58 and 35 per cent, respectively, of current yields. Humidity also played a role, with regions such as the Nile basin in Egypt, Iran and northwest Mexico showing only modest projected losses for relatively high current seasonal temperatures, because of their dry, high VPD conditions. Overall, the Mediterranean basin showed the least amount of losses from warming, and in some cases slight gains, owing to low humidity and lower temperatures associated with winter planting in the region.

Nursery-specific models fitted to only ESWYT or SAWYT trials showed that SAWYT germplasm is more resilient than ESWYT to warming up to approximately 21°C, when both models began to converge in terms of their negative response to future warming (see the electronic supplementary material, figure S4b). Finally, we note that higher atmospheric CO$_2$ should offset some of the temperature-related declines in yield shown here for wheat, a C3 crop sensitive to CO$_2$ fertilization. However, the magnitude of CO$_2$ fertilization in field conditions, with associated interactions between nutrient, water and temperature limitations, is still subject to debate [27–29].

(c) Estimated genetic gains by nursery and temperature bins

Both the observed and climate-corrected yield trends in ESWYT were positive in all of the grain-filling temperature bins since 1983 (figure 4a), although trends were only significant in the two coolest bins, closer to the optimal temperature for wheat yields [30–32]. Inferred genetic gains in the warmer bins were insignificant after accounting for trends in environment and location (i.e. country effects). The environmental trends since 1983 had small net effects in ESWYT on average, with negative impacts of a warming environment and location (i.e. country effects). The warmer bins were insignificant after accounting for trends for wheat yields [30–32]. Inferred genetic gains in the two coolest bins, closer to the optimal temperature in the SAWYT nursery, where relatively flat yield trends mask much stronger genetic gains evident in this breeding programme. Moreover, the significant genetic gains at high temperatures in SAWYT, but not ESWYT, indicate that a targeted breeding programme helps one to ensure success in breeding for heat tolerance. It should be noted that these results can also be explained by the environments in Mexico, in which new varieties were sown and selected for the two nurseries. For example, the median seasonal temperature across ESWYT trials in Mexico is 17.9°C, whereas that for SAWYT is 20.1°C, with most probable even higher canopy temperatures owing to drought conditions and a lack of evaporative cooling.

Figure 3. Map of trial locations since 1990 with estimated loss/gain from +2°C warming; multiple years and sites clustered within a 100 km distance are averaged for illustration purposes.
CO₂ fertilization has also probably played a role in the inferred 'genetic' gains shown here for both nurseries, given a 45 ppm rise in atmospheric CO₂ from 1983 to 2009 (as measured at Mauna Loa, HI). Rising atmospheric CO₂ may have especially promoted yield gains in SAWYT, because of decreased stomatal conductance and increased water savings at higher CO₂ under drought conditions [33]. However, given the covariance between variety improvement and increasing atmospheric CO₂ in recent years, it is difficult to statistically identify the CO₂ effect in this study.

Understanding the underlying mechanisms behind the differential yield progress for ESWYT and SAWYT at hot temperatures is beyond the scope of this paper. However, we offer a few observations. First, one strategy to withstand hotter temperatures while maintaining similar growth durations would be to lengthen the accumulated temperature (or GDD) requirements for development. In the CIMMYT database, both ESWYT and SAWYT showed positive trends for GDD in the vegetative stage. Consistent with the greater inferred genetic gains for SAWYT versus ESWYT at hot temperatures in the grain-filling stage, the positive trend in vegetative GDD requirements was more than two times higher for SAWYT than for ESWYT over a common time-frame (1993–2009, 13 versus 5 degree-days per year). GDD requirements for the vegetative stage increased by 23 per cent in SAWYT over the lifetime of the nursery, which was enough to maintain a constant duration of this period, despite significant warming because of a combination of climate trends and a changing mix of sites. Since the potential grain number is positively associated with both vegetative duration [21,34] and yields, the increased GDD requirements in this period have probably played a role in maintaining yield performance in hot conditions.

A second potential mechanism relates to grain-filling rates. The grain-filling period became significantly shorter in SAWYT over time owing to rising temperatures in this growth stage (i.e. 12 days shorter for a 4.5°C average rise from 1993 to 2009, with no evidence of increasing thermal requirements in this final growth stage). Yet grain weight data, available for only approximately 20 per cent of the records in the database, show a 4 per cent increase for SAWYT. A higher grain weight, together with a shorter grain-filling period, implies an increased grain-filling rate per day (perhaps to a small extent owing to temperature [35], but probably owing to variety improvement). The data support a significant increase in grain-filling rates for both ESWYT and SAWYT of 0.004 and 0.008 mg (kernel × day)⁻¹ year⁻¹, respectively.

Thus, increased thermal time to flowering and higher grain-filling rates appear to be two sources of yield...
maintenance and growth at high temperatures in the SAWYT database. Increased water savings at higher atmospheric CO₂ may also play a role, given increased evaporative demand at higher temperatures. However, it should be noted that increasing GDD requirements, faster grain-filling rates and reduced stomatal conductance at higher atmospheric CO₂ will not prevent irreversible damage from extreme heat episodes [36], particularly during the reproductive period. Therefore, other breeding strategies, such as speeding development to force flowering earlier in the season, may be beneficial in some environments and for risk-averse farmers [20].

4. Conclusions

Decades of wheat breeding efforts at CIMMYT have resulted in an extensive trial database of wheat yields under varying environmental conditions. This database provides a valuable means of empirically assessing the response of wheat to environmental variation, and also the genetic gains over time and in different environments that are associated with different breeding strategies. Consistent with previous studies, our empirical model showed the most negative response to high temperatures in the grain-filling phase under low VPD, or humid conditions. Assuming sufficient water supply, higher VPD for a given temperature leads to more transpiration cooling, lower canopy temperatures and a less negative response to warming. A negative response to warming was also seen during the reproductive phase at average temperatures above 13°C, but a higher sensitivity to water stress during this phase reduced the relative advantage of high VPD trials.

With current breeding strategies, projected future climate change will probably put a drag on growth in global spring wheat yields, and may even depress them, especially in locations where wheat is already grown in hot conditions (particularly in south Asia, and also parts of sub-Saharan Africa, the Middle East and Latin America). Agronomic changes (e.g. shifts in planting dates or locations, and improved access to inputs) in combination with CO₂ fertilization, can potentially help to mitigate these losses. However, new varieties of wheat with high yield potential in hot environments are required in order to adequately prepare for projected temperature rises of approximately 2°C by 2050.

ESWYT and SAWYT epitomize two different breeding strategies, to develop wheat varieties that are (i) high-yielding in irrigated and high rainfall conditions, but potentially sensitive to abiotic stresses, and (ii) tolerant to drought and heat stress under rain-fed conditions, but with lower yield potential. This study finds that most progress in ESWYT to date has been achieved at the cooler temperatures in the grain-filling phase, closest to the optimal temperatures for wheat production. In contrast, progress has been made in SAWYT across temperature bins, but most significantly in the hottest bin, thereby building greater amounts of heat tolerance into the germplasm. Two potential mechanisms for the relatively higher genetic gains in SAWYT at high temperatures relate to longer vegetative GDD requirements and faster grain-filling rates. It will also be imperative to build resilience to extreme heat into future germplasm, especially during the reproductive phase, in order to avoid the risk of complete crop failure with more frequent heat waves.

The lack of yield increase to date for the highest-yielding varieties under hot conditions, as shown in this study, indicates the need for new and intensified efforts to achieve these gains. This will require a combined effort, using genetic diversity with physiological and molecular breeding, and bioinformatic technologies, along with the adoption of improved agronomic practices by farmers. Although many trade-offs exist between high yield potential and stress adaptation, in our view it should be feasible to achieve both goals as long as hot environments are systematically included in the selection process for a breeding strategy like ESWYT. Given that disease resistance, pest resistance and maintaining grain quality will also continue to be priorities, additional resources may be needed to simultaneously achieve all of these targets.

We gratefully acknowledge Mateo Vargas, who prepared much of the data for analysis in this study, and Thomas Payne, who contributed valuable interpretation of the results. This work was supported by a grant from the Rockefeller Foundation. The data associated with this study are deposited in the Dryad Repository: http://dx.doi.org/10.5061/dryad.525vm.

References


