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# Stage-specific genotype-by-environment interactions determine yield components in wheat

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In cereal crops, environmental fluctuations affect different physiological processes during various developmental phases associated with the formation of yield components. Because these effects are coupled with cultivar-specific phenology, studies investigating environmental responses in different cultivars can give contradictory results regarding key phases impacting yield performance. To dissect how genotype-by-environment interactions affect grain yield in winter wheat, we estimated the sensitivities of yield components to variation in global radiation, temperature and precipitation in 220 cultivars across 81 time-windows ranging from double ridge to seed desiccation. Environmental sensitivity responses were prominent in the short-term physiological subphases of spike and kernel development, causing phenologically dependent, stage-specific genotype-by-environment interactions. Here we reconcile contradicting findings from previous studies and show previously undetected effects; for example, the positive impact of global radiation on kernel weight during canopy senescence. This deep insight into the three-way interactions between phenology, yield formation and environmental fluctuations provides comprehensive new information for breeding and modelling cereal crops.

Wheat grain yield is an integrated outcome of different physiological processes during the vegetative and grain-filling phases[1–3]. Under field conditions, unpredictable natural fluctuations in environmental variables can lead to yield losses and threaten food security[4–6]. For example, enhanced climatic variability during European summers in recent decades shows increasingly negative impacts on yields[6–8]. This is partly due to unpredictable short-term (day-to-day) fluctuations in environmental variables during specific physiological phases. For example, heat during anthesis contributes to a gap between potential and actual yields in wheat and other grain crops[9,10]. Reductions in yield potential caused by deficits in specific yield formation processes—for example, kernel setting—may be due to fluctuations in a key

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environmental variable within a relatively narrow time-window[2,11,12]. For instance, high temperature stress at the pre- and post-anthesis phases causes vegetative and reproductive growth cessation in wheat by reducing photosynthetic activities and increasing floret abortion[13,14], whereas a reduced kernel number can be compensated for by high levels of solar radiation during the grain-filling stage[15]. Therefore, understanding the impacts of short-term environmental fluctuations in specific phenological subphases on grain yield and discovering genetic variation in phase-specific sensitivities to relevant environmental variables might provide new avenues for crop design[16]. However, experimental studies of short-term environmental impacts on the formation of yield components under field conditions have, to date, been limited to just a few levels of environmental variables investigated in low numbers of genotypes at specific developmental phases. More comprehensive studies have been restricted by the difficulty in obtaining detailed phenological data for a large number of genotypes. To overcome this deficit, alternative methods to examine the effects of fluctuating environmental variables on yield components during multiple developmental subphases are required.

## Results

### Sensitivity of yield components is cultivar-specific

To identify cultivar- and subphase-specific sensitivities of yield components in response to short-term fluctuations in different environmental variables, we decipher the impact of variations in global radiation (GR), precipitation (PR) and temperature, across 81 developmental time-windows, on the yield components of 220 winter wheat cultivars[17] (Supplementary Table 1) grown in field experiments that spanned contrasting cropping regimes in three consecutive growing seasons at six locations across Germany (Supplementary Tables 2 and 3). Because the management intensities strongly affected phenology[18], this experimental design resulted in 48 contrasting environmental conditions between treatments, locations and years during the period before and after the individually recorded heading date of each cultivar (Supplementary Figs. 1 and 2 and Supplementary Table 4). A large degree of variation in GR (maximal difference of 27.9 MJ $m^{-2}$ $d^{-1}$), daily minimal, mean and maximal temperature ($T_{min}$, $T_{mean}$ and $T_{max}$, ranging between −2.6 and 22.6 °C, 0.7 and 29.4 °C, and 2.81 and 39.6 °C, respectively) and PR (ranging between 0 and 25.6 mm $d^{-1}$) allowed us to determine the effects of mean environmental variables within a time-window of 50 °Cd on the kernel number per spike (KpS), spike number (Sno) and thousand kernel weight (TKW) of each cultivar, by comparing the models with and without the influence of an environmental variable (models M2 (equation (2)) and M1 (equation (1)), respectively; Methods). Analyses of variance (ANOVA) $-\ln(P_{value})$ of all the comparisons were used to quantify the significance of an environmental effect on yield components in 81 time-windows ranging from the double-ridge stage to grain desiccation. In total, 17,820 comparisons were conducted (220 cultivars × 81 time-windows) per combination of traits and environmental variables (Fig. 1a). Including environmental variables in M2 increased the explanatory power of the model ($P < 0.05$, $-\ln(P_{value}) = 3.00$), which is indicative of the effects of short-term environmental variations, or the interactive effects of environmental variable and treatment, on the formation of yield components. For example, 99% of the studied cultivars showed significant responses of TKW and KpS to GR (Table 1), indicated by 1,049 and 1,899 significant differences between M1 and M2 (6% and 11% of total comparison), respectively. This suggested that for most cultivars in the study TKW and KpS were sensitive to GR at multiple time-windows, whereas for 99% of the cultivars the yield components were affected by environmental variables in at least one specific time-window (Table 1).

We mapped the tested time-windows to corresponding periods of physiological subphases in spike and kernel development reported in literature[16,17,19,20], including seven pre-heading subphases ranging from the double-ridge stage, terminal spikelet development, white anther stage, green anther stage, yellow anther stage and tipping to heading, and five post-heading subphases ranging from anthesis, pre-grain filling, grain filling and 50% of canopy senescence (referred to as green canopy duration) to grain desiccation. By plotting the $-\ln(P_{value})$ of all cultivars with respect to time-windows, the responses of each yield component to the environmental variables from double ridge to grain desiccation were visualized to identify sensitive periods (Fig. 1). For example, the effects of GR on KpS were significant in most cultivars in three time-windows: −100 to −50 °Cd, 220 to 270 °Cd and 420 to 470 °Cd from heading (Fig. 1a). These three periods match the physiological subphases between yellow anther and tipping, shortly before pre-grain filling and beginning of grain filling[16,21,22], respectively. Interestingly, two groups of cultivars showed differences in their phenology and their sensitive time-windows of KpS to GR (Fig. 1b). In early-flowering cultivars (~23% of the test panel), the sensitive period before anthesis was closer to the heading date in comparison with the late-flowering cultivars, indicating shorter durations of pre-heading subphases in early-flowering cultivars than in late-flowering cultivars[22] (Fig. 1b). For example, sensitivity of KpS to GR in early-flowering cultivar 'Cajeme 71' was greatest at time-window 0 to 50 °Cd, whereas the most sensitive period of a late-flowering cultivar 'Kometus' was at −100 to −50 °Cd (Supplementary Fig. 3). The responses of all cultivars to all studied environmental variables are shown in Supplementary Fig. 4.

### Sensitivity of yield components is stage-specific

Coefficients $\beta$ in M2 (equation (2)) characterize the absolute effects of an environmental variable on yield components in a given time-window (Fig. 1c,d and Supplementary Fig. 4). A positive or negative value of $\beta$ indicates an increase or decrease in a yield component, respectively, per unit change of the environmental variable in a time-window. For example, the per unit increase in GR during yellow anther (−100 to −50 °Cd) and around the end of anthesis to the beginning of pre-grain filling (220 to 270 °Cd) improved by 0.50 and 0.60 KpS, respectively (Fig. 1c). By contrast, the per unit increase in GR during the grain-filling phase (420 to 470 °Cd) reduced by 0.59 KpS.

Because the mean values of yield components differ greatly between the studied cultivars[17,18], $\beta$ of the $i$th cultivar was normalized by the mean values ($\mu_i$) of the yield components across all environments (location, year and treatment) to represent the relative effects of an environmental variable on yield components (Fig. 2b). In any given time-window, the normalized $\beta$ (%)—referred to as genotypic sensitivity—is only meaningful if $-\ln(P_{value})$ indicates significant differences between model 1 and model 2 (Fig. 2a). For each yield component, we showed the top 5% most-sensitive time-windows (Fig. 2c–e) and grouped them into physiological subphases. For example, the effects of $T_{min}$ on KpS can be grouped into two subphases: (1) from the end of anthesis (positive effects up to 4.76% per °C between 180 and 220 °Cd) to pre-grain filling (increase by 4.45% and 4.99% per °C at 240 and 260 °Cd, respectively); and (2) white anther (increase up to 3.53% per °C between −260 and −280 °Cd; Fig. 2c). Variations in $T_{mean}$ affected KpS similarly to $T_{min}$ around the end of anthesis, with positive effects up to 3.22% per °C (from 200 to 240 °Cd). However, they showed a negative effect up to −2.36% per °C at the beginning of grain filling (460 and 480 °Cd), probably because of the positive correlation between $T_{mean}$ and $T_{max}$ (Supplementary Fig. 2i), which showed similar negative effects (from −1.53% to −1.77% per °C) on KpS at grain filling (from 440 to 500 °Cd). Interestingly, positive effects (2.14% per °C) of $T_{max}$ on KpS were found at pre-grain filling (240 °Cd), similar to the effect of GR on KpS in this period (1.59% per unit of GR). Furthermore, KpS was also affected positively by GR (1.33% per unit of GR) at yellow anther (−100 °Cd) and negatively by PR (from −1.45% to −1.98% per unit of PR) at grain filling (520 and 540 °Cd). Based on these results, environmental variables at four physiological subphases (yellow anther, anthesis, pre-grain filling and grain filling) were identified as the most sensitive subphases for kernel development, both in early and late cultivars (Supplementary Fig. 5).

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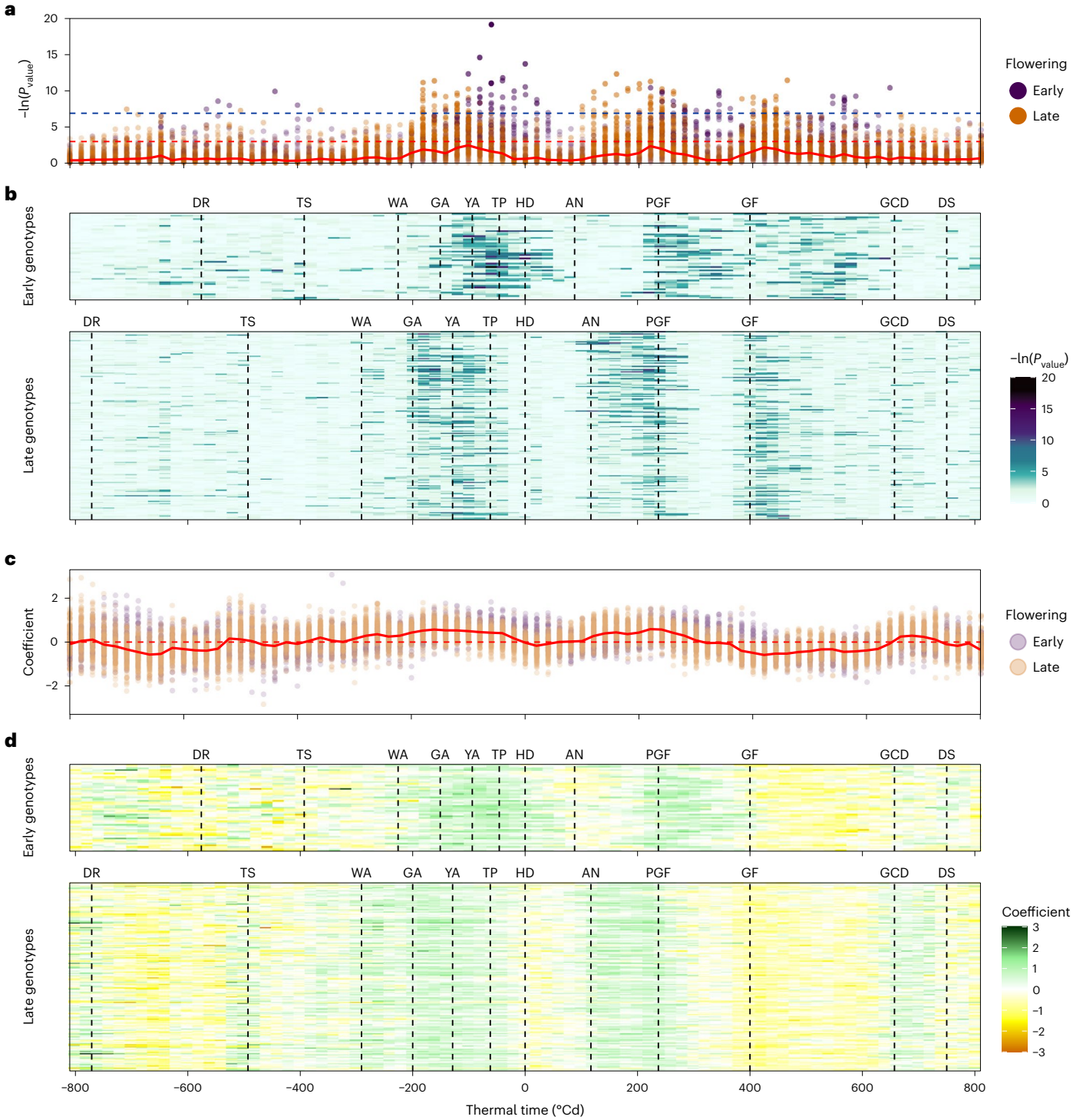


**Fig. 1 | Effects of GR in 81 time-windows before and after heading (thermal time = 0 °Cd) on KpS.** Cultivars were classified as 'late' or 'early' based on their flowering time[17]. **a**, Overview of 17,820 ANOVA $-\ln(P_{values})$ comparing model 1 and model 2, with 169 late (orange) and 51 early (purple) heading cultivars. The solid red line represents the median $-\ln(P_{value})$ of 220 cultivars at each time-window. The dotted red and blue lines indicate $-\ln(P_{value}) = 3.00$ ($P < 0.05$) and 6.91 ($P < 0.001$), respectively. **b**, Cultivar-specific $-\ln(P_{value})$ in 81 time-windows. **c**, Coefficients $\beta$ (KpS (MJ m$^{-2}$ d$^{-1}$)) in model 2 showing the sensitivity of KpS to GR in 220 cultivars. Solid red lines represent median coefficient of all cultivars and dotted red line indicates $\beta = 0$. **d**, Cultivar-specific coefficients $\beta$ in model 2 showing positive (green) and negative (yellow and red) effects of GR on KpS. Different physiological subphases before flowering of photoperiod-sensitive (late flowering) cultivars are shown by vertical black dotted lines[22]. AN, anthesis; DR, double-ridge stage; DS, desiccation; GA, green anther stage; GCD, green canopy duration characterized by 50% canopy senescence; GF, grain filling; HD, heading stage; PGF, pre-grain filling; TS, terminal spikelet stage; WA, white anther stage; YA, yellow anther stage.

**Table 1 | Significant cases of ANOVA comparing model 1 and model 2. These numbers represent cases of yield components sensitive to environmental variables in 81 time-windows in 220 winter wheat cultivars, from a total of 17,820 comparisons per trait per environmental variable. The numbers of cultivars sensitive to the environmental variables in at least at one time-window are shown**

| Yield components | Environmental variables | No. of significant ANOVA comparisons | No. of significant cultivars |
|---|---|---|---|
| KpS | GR | 1,899 | 218 |
| KpS | $T_{max}$ | 2,062 | 217 |
| KpS | $T_{mean}$ | 2,303 | 215 |
| KpS | $T_{min}$ | 1,854 | 218 |
| KpS | PR | 1,431 | 219 |
| Sno | GR | 1,102 | 217 |
| Sno | $T_{max}$ | 1,724 | 215 |
| Sno | $T_{mean}$ | 1,652 | 211 |
| Sno | $T_{min}$ | 1,248 | 217 |
| Sno | PR | 1,073 | 218 |
| TKW | GR | 1,049 | 218 |
| TKW | $T_{max}$ | 424 | 157 |
| TKW | $T_{mean}$ | 656 | 202 |
| TKW | $T_{min}$ | 1,235 | 219 |
| TKW | PR | 1,339 | 220 |

In comparison with KpS and TKW, Sno showed lower environmental sensitivity (Fig. 2d). The most significant environmental effects on Sno were the negative effects of $T_{mean}$ and $T_{max}$ after anthesis (up to −2.44% per °C $T_{mean}$ or $T_{max}$ between 140 and 200 °Cd). Variations in $T_{mean}$ and $T_{max}$ also showed effects during pre-grain filling (positive effect up to 1.78% per °C from 320 to 380 °Cd) and during the white anther stage (negative effect up to 1.23% per °C from −300 to −240 °Cd). Furthermore, Sno was also affected positively by $T_{min}$ at the start of grain filling (2.04% per °C at 400 °Cd) and by PR (1.85% per unit of PR) at the end of green canopy duration (680 °Cd). Thus, four physiological subphases were identified as being most strongly influenced by environmental variables for spike formation (Fig. 2d). Interestingly, environment affected Sno after anthesis more strongly in late than in early cultivars (Supplementary Fig. 5).

TKW was affected positively by GR (up to 1.74% per unit of GR), particularly in the period from 50% of canopy senescence to seed desiccation (from 640 to 780 °Cd). Also, the effects of $T_{min}$ on TKW were identified between double ridge and development of the terminal spikelet (up to 4.65% per °C at −600 and −580 °Cd, similar to $T_{mean}$) as well as the white anther stage (up to 2.71% per °C between −260 and −240 °Cd). Contrasting effects of PR on TKW were detected before the white anther stage (up to −2.73% per unit of PR at −300 and −320 °Cd), at the green anther stage (up to 4.77% per unit of PR at −200 and −180 °Cd) and at the yellow anther stage (−2.64% per unit of PR at −120 °Cd). To summarize, in the set of cultivars analysed, the strongest influence of environmental variables on TKW was detected during four pre-heading stages (after double ridge, before white anther, at green and yellow anther) and the canopy senescence stage (Fig. 2e).

### Additive effects of environmental variables

Our results suggested that significant effects of an environmental variable on a yield component could be due to the close relationship of this environmental variable with another (for example, $T_{max}$ and GR; Supplementary Fig. 2). Therefore, a third model (M3 (equation (3))) extending M2 (equation (2)) to two environmental variables at time window $t$ ($E_1(t)$ and $E_2(t)$) was used to test whether two environmental variables could have additive effects, by comparing the explanatory power of M3 with M2 of $E_1(t)$. Interestingly, although no temperature effect on KpS at heading was observed from M2 (Fig. 2a), combining $T_{min}$ and $T_{mean}$ better explained the variation in KpS (median of $-\ln(P_{value})$ up to 2.77; Fig. 3), especially in late-flowering cultivars (Supplementary Figs. 7a and 8a). Similarly, combining $T_{min}$ with $T_{mean}$ or $T_{max}$ during spikelet differentiation (around −600 °Cd with $-\ln(P_{value})$ up to 2.52) improved the prediction of KpS (Fig. 3), similar to the improvement observed in Sno at green canopy duration (Supplementary Fig. 6a). An interesting additive effect of $T_{min}$ and GR on TKW was observed around −600 °Cd ($-\ln(P_{value})$ up to 3.74; Supplementary Fig. 6b). These time-windows overlapped with the time at which additive effects of $T_{min}$ and $T_{mean}$ on KpS were observed, implying that $T_{min}$, $T_{mean}$ and GR could collectively mediate the potential pleiotropic effects between KpS and TKW during spikelet differentiation. Also, although temperature effects on TKW were not significant at anthesis in M2, combining $T_{min}$ with $T_{mean}$ and $T_{max}$ in M3 showed significant effects of temperature ($-\ln(P_{value})$ up to 3.65; Supplementary Fig. 6b).

## Discussion

### Merits of standardized large-scale field experiments

Impacts of environmental fluctuations on yield formation in crop plants depend on the physiological subphases of the plant during which they occur[23]. Here, we identified the sensitive subphases of winter wheat subjected to five environmental variables and quantified cultivar-specific sensitivities. In comparison with previous studies on the formation of yield components, we provide a far more comprehensive temporal and physiological view of the processes involved, in a broad genetic context spanning strongly contrasting plant responses. For example, literatures suggest that increased (but lower than optimal) temperature during the early booting stages (from white to yellow anther) improves floret development and increases KpS[24] because low temperatures (15/12 °C day/night temperature) can cause abnormal pollen development[25,26], a reduced instantaneous photosynthetic rate[27], smaller leaf area and less dry matter accumulation[28]. Our data show strong effects of night temperature ($T_{min}$), lesser effects of $T_{mean}$ and no effect of $T_{max}$ on KpS during the early booting stage (Fig. 2a), therefore suggesting that night temperature is more critical for pollen development (sink development) than day temperature in these subphases. By contrast, the positive effects of GR on KpS occur later (after yellow anther; Fig. 2c), probably because of the impact of GR on photosynthetic supplies and floret survival (source strength)[12,29,30]. Positive effects of $T_{min}$ and $T_{max}$ on KpS at anthesis (Fig. 2c) were not consistent with previous findings[31–33], probably because $T_{min}$ and $T_{max}$ at our experimental locations during anthesis were below the critical threshold for heat stress (≥22–25 and ≥32–35 °C, respectively; Supplementary Figs. 1d and 2e). Our results show that $T_{max}$ during grain filling reduced kernel number (Fig. 2b) without significant effects on TKW, indicating that the effects of warm temperature on grain abortion during grain filling are more important than its effects on shortening the duration of grain-filling phase[34]. Recent studies suggest that not only grain filling, but also spike development limits TKW[35–39].

We also found a negative effect of PR on TKW during the white and yellow anther stages (Fig. 2e), which potentially contributes to the negative effects of high PR events on yield[6]. Effects of PR on KpS and Sno were insignificant (Figs. 2c,d), so its effect on TKW was not a compensation effect between grain number and grain size. Because the effects of PR are difficult to interpret, the soil water content of experimental sites was simulated using the dynamic crop growth modelling environment HUME model[40,41]. By applying M2 (equation (2)) to the simulated water content, negative effects water content in top soil layers (0–40 cm) on TKW during the white and yellow anther stages

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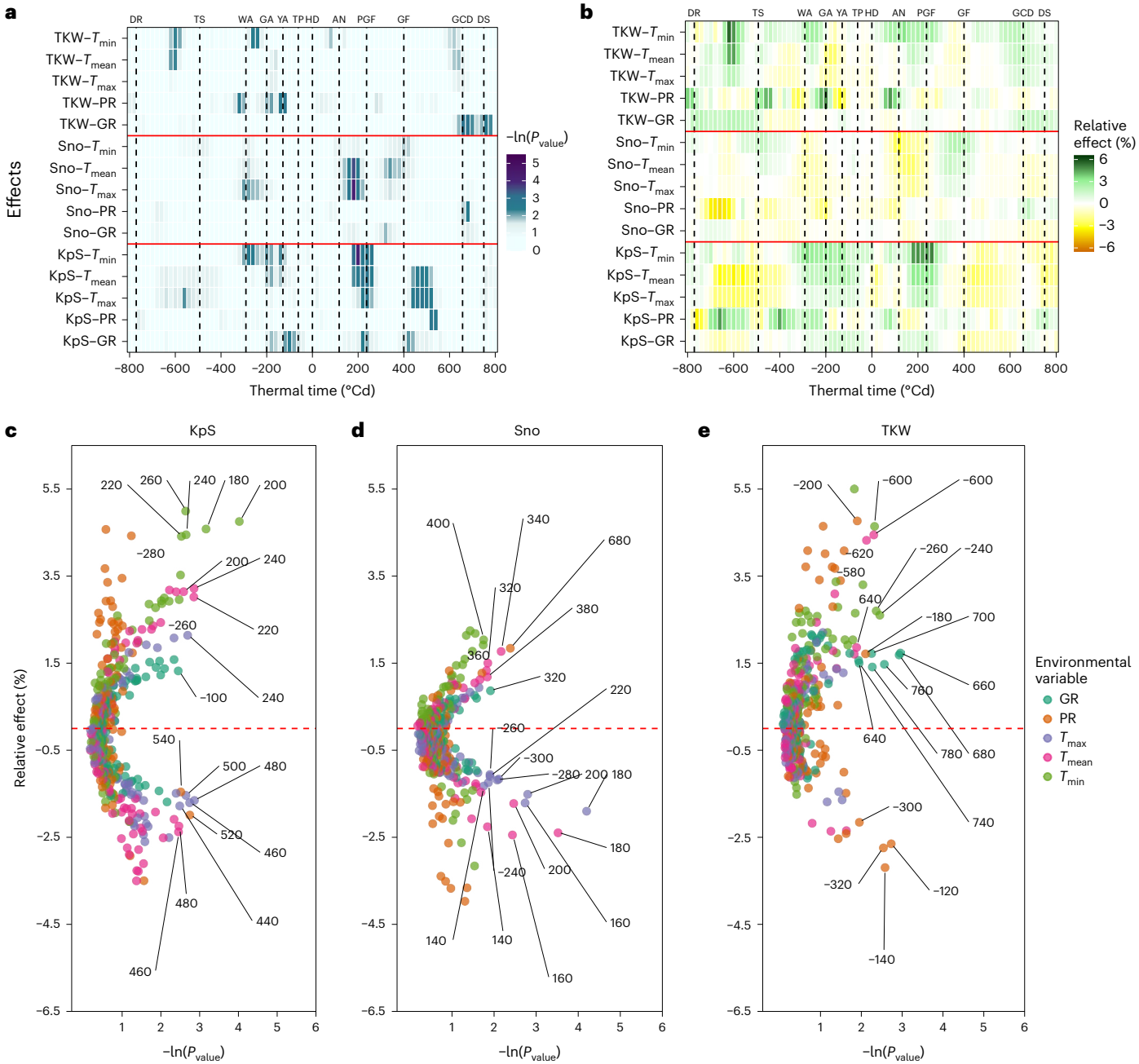


**Fig. 2 | Identification of time-windows of yield components (KpS, Sno and TKW) sensitive to variations in environmental variables (GR, $T_{max}$, $T_{mean}$, $T_{min}$ and PR). a**, Significance (median −ln($P_{values}$) of 220 cultivars solid red line in Fig. 1a and Supplementary Fig. 4a) of environment effects on yield components. **b**, Sensitivity (median of normalized $\beta$ in model 2 of 220 cultivars (%)) of yield components to environmental variables. Positive and negative effects are shown in green and yellow, respectively. Three yield traits are separated by two solid red lines (**a**,**b**). Different physiological subphases around the flowering of photoperiod-sensitive (late flowering) cultivars are shown by vertical black dotted lines[22]. **c**–**e**, Relationships between significance and genotypic sensitivities to environmental variables in KpS (**c**), Sno (**d**) and TKW (**e**). The top 5% of significant time-windows are marked with the thermal time (°Cd) at the beginning of the time-windows (**c**–**e**). Results for early- and late-flowering cultivars are presented separately in Supplementary Fig. 5.

were detected (Supplementary Figs. 8 and 9). Therefore, the observed effect on TKW may be associated with the potential for short-term waterlogging during this period (Supplementary Fig. 9), which can affect the capacity of kernels to grow during the grain-filling period by reducing the size of ovaries in developing florets[42] or increasing the risk of *Fusarium* infection.

Four particularly novel findings emerged from our study: (1) GR has a positive effect on TKW before seed desiccation (Fig. 2e), a period coinciding with maximum grain expansion (grain width, length, volume and height) and flag leaf senescence[43]; (2) $T_{min}$ has a positive effect on TKW during spikelet development and between the white and green anther stages (Fig. 2e), suggesting a potential link between $T_{min}$ and grain development such as cell size; (3) PR and soil water have a positive effect on Sno between canopy senescence and seed desiccation (Supplementary Fig. 6), probably caused by the delayed asynchronized development of ears from tillers that have no direct contribution to yield; and (4) PR has a negative effect on KpS during grain filling. Towards further understanding the complex interactions between

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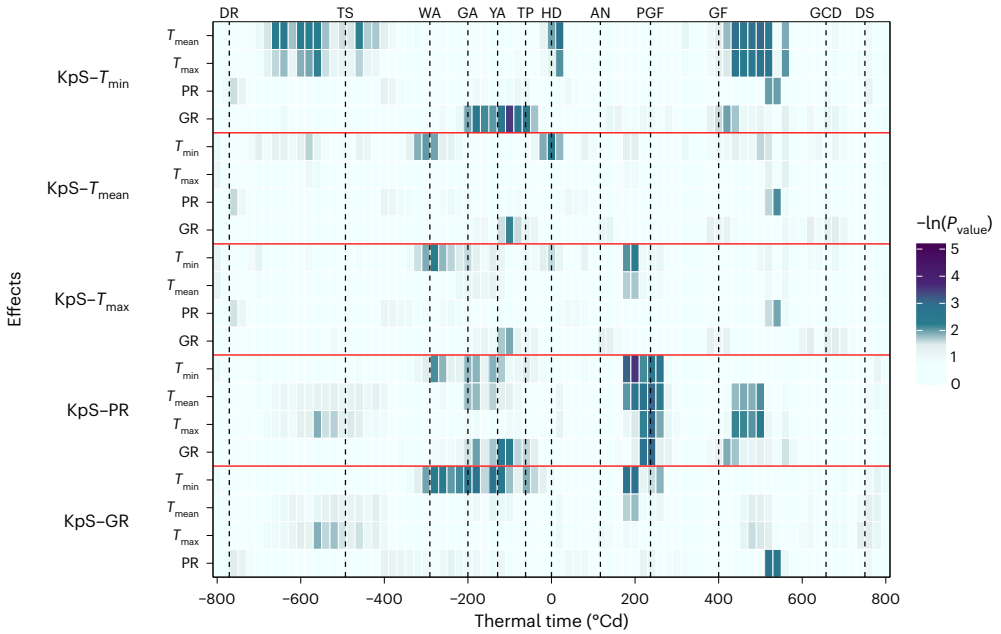


**Fig. 3 | Time-windows of KpS that showed significant synergistic effects of two environmental variables on its formation.** The colour represents median −ln($P_{values}$) of ANOVA comparisons between M3 (two environmental variables) and M2 (one environmental variable) of 220 cultivars. Figure labels are the same as in Fig. 2a. The environmental variable in M2 was the first variable in the labels. Results for TKW and Sno can be found in Supplementary Fig. 6. Results for early- and late-flowering cultivars are presented in Supplementary Figs. 7 and 8, separately.

short-term environmental fluctuations and the formation of yield components, these findings may be used to formulate new hypotheses to be tested experimentally.

## Triple interactions determining yield components

We showed that combined effects of short-term environmental fluctuations, phenology and genotype-specific sensitivities determine yield components. Different studies deliver seemingly contradictory findings about environmental effects on yield components[8,11,30]. Our detailed analysis suggests that many findings in the literature are not directly comparable because different genotypes are used, plants are exposed to environmental treatments for extended periods (8–20 days) across several subphases and detailed developmental subphases are often not recorded. This also explains the reported differences in the sensitivity of KpS to $T_{mean}$ and $T_{max}$ at the beginning of grain filling[44] and the different effects of temperature on Sno[45]. Furthermore, because agricultural management (for example, application of growth regulators) affects phenology in a genotype-specific manner[18], meta-analyses for studying environmental effects on the formation of yield component are not reliable.

Understanding complex genotype × environment × management (G × E × M) interactions in yield formation can help during selection in breeding programmes to mitigate the effects of climate variability[46,47]. Here we quantify the magnitude of G × E interaction effects using the regression coefficient $\beta$ in M2 (equation (2)) or M3 (equation (3)), an alternative to the environment-dependent allelic effects shown by the quantitative genetics[23,48]. Also, we show that the formation of yield components is determined by genotypic sensitivity (G) to short-term, mostly unpredictable, environmental fluctuations (E) in concordance with physiological processes associated with phenological subphases. Phenology per se is the outcome of G × E × M and we highlight that its concordance with G and E adds a feedback in the G × E × M interactions. Phenology can be considered as the duration of developmental subphases associated with physiological events and the duration of genotype-specific developmental subphases. For example, alleles of the wheat *Ppd-D1* locus on chromosome 2D affect photoperiod sensitivity and the duration of pre-anthesis subphases[32,35,36]. This explains the clear shifts in pre-anthesis-sensitive time-windows between early- and late-flowering cultivars (Fig. 1). Although we did not find *Ppd-D1*-specific durations of post-anthesis subphase and could not map them differently for early- and late-flowering cultivars (Supplementary Figs. 5, 7 and 8), a clear post-anthesis shift suggests regulation of *Ppd-D1* in post-anthesis phenology. Taken together, subphase-specific responses of yield components to short-term fluctuations in environmental variables may be a mechanistic explanation for the pleiotropic effects of flowering genes on the formation of reproductive structures.

## Studying the formation of yield components in detail

In contrast to labour-intensive experimental manipulation of environmental variables, we demonstrate that comprehensive field phenotyping with standardized protocols in multi-environmental field experiments can reveal the patterns of hundreds of cultivars in response to environmental fluctuations. The prerequisites of our approach are: (1) phenotypic and meteorological data collected using standardized protocols across experimental sites; (2) substantial variation in environmental variables across experimental sites and years, as observed in our data (Supplementary Fig. 1); and (3) weak correlations between environmental variables at different subphases to ensure that the detected effect of one variable on a trait during a subphase is not a result of spurious relationships between another environmental variable at other subphases. In our dataset, the strongest spurious relationships of environmental variables at different subphases were observed between: (1) GR at anthesis and GR at the white anther stage (with the highest coefficient of determination $R^2$ of 0.67); and (2) $T_{max}$ before terminal spikelet and $T_{max}$ after grain filling (with the highest $R^2$ of 0.67, Supplementary Fig. 10). Because the significance (Fig. 2a) and coefficient (Fig. 2b) of all yield components between these periods did not show any similarity, it is unlikely that our main findings were subjected to the potential spurious relationships. Furthermore, our results should be interpreted within the values of environmental variables (Supplementary Fig. 1) and within the linear phase of dosage–response

curves[49,50] between environment and phenotypes. The detected effects indicate statistical associations and not necessarily causal relationships. These associations could be used to derive new hypotheses to be proved by sophisticated experiments under controlled environments. In addition, it would be valuable to experimentally investigate whether the environmental effects from multiple time-windows contribute to yield formation in an additive or multiplicative manner.

Using a sliding time-window for regression analyses has the potential to identify the most critical time points showing the strongest evidence of environmental effects on biological traits[51,52]. Assuming that a physiological event in response to an environmental variable is associated with a specific phenological subphase, further statistical analyses of the significance (peak detection in Supplementary Fig. 3) would provide a new way to define cultivar-specific phenological duration, which normally requires labour-intensive measurements[22]. If peaks are detected, $\beta$ in M2 or M3 at the peak representing a physiological event can be a quantitative trait for genome-wide association studies, the first step towards marker-assisted selection in breeding. Combining environmental variables in the environment-sensitive subphases with markers of sensitivity in genomic prediction could improve accuracy. For cereal breeders, it remains to be tested whether selecting environment-insensitive genotypes could improve yield stability or stress tolerance. Our results can be used to refine crop models by introducing subphase- and genotype-specific stress factors of environmental variables during formation of the yield component. This integration has the potential to improve prediction of cultivar performance under a G × E interaction in a wide range of environmental scenarios[23,48].

## Methods

### Plant material and field experiments

Multiple environment field trials were conducted in three seasons (2014–2015, 2015–2016 and 2016–2017) at six different locations using 220 wheat cultivars[17,18] (Supplementary Table 1). The collection consisted of 191 cultivars, registered in Europe between 1966 and 2013, and 29 international genotypes, obtained from the German gene bank (https://gbis.ipk-gatersleben.de). The experimental sites were Gross Gerau, Hannover, Klein Altendorf, Kiel, Quedlinburg and Rauischholzhausen, which are situated throughout Germany and have diverse environmental conditions (Supplementary Fig. 1 and Supplementary Tables 2 and 3). Field trials were conducted in yield plots (4.5–12.0 $m^2$) depending on site-specific sowing and harvesting machinery[17,18]. All 220 cultivars were sown in plots with 300–330 viable seeds per $m^2$. Following standard agrochemical applications in Germany, full-intensity insecticides and growth regulators were applied. Applications were conducted on all plots when most cultivars reached the relevant stage for application and they were all treated once. The experiment had a randomized block design with two replications and management intensities: HiN/HiF, HiN/NoF and LoN/NoF[18], where HiN and LoN indicate optimal and reduced nitrogen supply (soil mineral nitrogen plus nitrogen fertilization) of 220 and 110 kg N $ha^{-1}$, respectively, and HiF and NoF represent full and no application of fungicides. HiN/HiF represents standard conditions for high-intensity wheat production in Western Europe. Within a management intensity, cultivars were randomized within four subgroups according to the flowering time and plant height (early and short; early and tall; late and short; late and tall) based on previous knowledge. Full details are shown in Supplementary Table 3.

Temperature, PR and GR were recorded at hourly resolution by weather stations close to each study site. Soil water potential and soil water content were simulated using the dynamic crop growth modelling environment HUME[41], where the actual water status is the result of PR and evapotranspiration in the context of a layer-based soil model[40]. Variable inputs for environments were weather and soil type at the experimental sites. Sno (spikes $m^{-2}$), TKW (g) and KpS were determined[17,18]. Full details of all field trials, phenotypic measurements, weather data processing and related scientific papers are provided in Supplementary Table 4. Heading date was recorded for all cultivars for three treatments in one replication per year (Supplementary Table 1 and Supplementary Data). Thermal time ($t$, °Cd) was calculated as the accumulated daily mean temperature for each location, starting from sowing date with a base temperature of 0 °C (ref. 49). For early- and later-flowering cultivars, subphase durations from double ridge to anthesis were defined according to their photoperiod sensitivity (insensitive and sensitive alleles at the *Ppd-D1* locus on chromosome 2D, respectively) reported in the literature[22] with the following thermal time onset for each subphase: double ridge, −576 and −771 °Cd; terminal spikelet, −393 and −493 °Cd; white anther, −226 and −291 °Cd; green anther, −151 and −200 °Cd; yellow anther, −94 and −129 °Cd; tipping, −46 and −62 °Cd; heading, 0 °Cd; and anthesis, 88 and 117 °Cd. Post-anthesis subphases were not mapped differently between cultivars because of the data availability. Subphases of pre-grain filling and grain filling began at 237 °Cd (ref. 43) and 400 °Cd (refs. 19,43), respectively. The thermal time for green canopy duration (657 °Cd), characterizing 50% of canopy senescence, was inferred from the 220 investigated cultivars[17,18], whereas seed desiccation was assumed to start at 750 °Cd (ref. 43). Given that all cultivars were presumably vernalized at the beginning of the vegetation period and there is a lack of literature specifically addressing the effects of vernalization requirements on subphase duration, we did not group the cultivars based on their vernalization requirements.

### Statistical analyses and models

The effects of an environmental variable within a time-window $t$ ($E(t)$) on the yield components was identified by comparing model 1 (M1, equation (1)) and model 2 (M2, equation (2)):

$$Y_{ijkl} = \mu_i + \alpha_{ij}T + \varepsilon_{ij} \quad (1)$$

$$Y_{ijkl} = \mu_i + \alpha_{ij}T + \beta(t)_i E(t)_{ijkl} + \gamma(t)_{ij} E(t)_{ijkl} \times T + \varepsilon_{ijkl} \quad (2)$$

where $Y_{ijkl}$ is the phenotypic observation of a yield component of the $i$th cultivar in $j$th treatment, $k$th year and $l$th location, $\mu_i$ is mean of the $i$th cultivar, $\alpha_{ij}$ is the effect of treatment on cultivar $i$th, $T$ is the factorial level of treatment and $\beta(t)_i$ is the regression coefficient considered as the sensitivity of the $i$th cultivar in response to an environmental variable ($E(t)_{ijkl}$) during the time-window $t$. Genotype-specific interactions between treatment and $E(t)_{ijkl}$ are represented by $\gamma(t)_{ij}$, whereas $\varepsilon_{ijkl}$ is the residual error. Our data show that location and year are confounding effects with $E(t)_{ijkl}$ in 99% of the regressions. This means that the variations in $E(t)_{ijkl}$ were largely contributed by year, location and their interactions (Supplementary Fig. 11). Therefore, year, location and their interactions were intentionally not included in M1 and M2 to avoid artifactitious partition of variances between year, location and $E(t)_{ijkl}$. A sliding time-window ($t$ in M2) with a window duration of 50 °Cd (2–4 days) and an overlap of 20 °Cd was used to extract data for six environmental variables: GR (MJ $m^{-2}$ $d^{-1}$), daily mean temperature ($T_{mean}$, °C), maximal temperature ($T_{max}$, °C), minimal temperature ($T_{min}$, °C), (mm $d^{-1}$), water potential (hPa) and soil water content (vol%) during a period ranging across 800 °Cd (~40 days) before and after the observed heading date ($t$ = 0 °Cd) of individual cultivars in each treatment, year and location ($E(t)_{ijkl}$). M2 was then fitted repeatedly with all time-windows within this time range, which covers the main developmental phases of yield components, from the double-ridge stage (−771 °Cd) to seed desiccation (750 °Cd)[16,17,19,43]. To identify the explanatory power of both models, M1 and M2 were further compared by ANOVA and the $-\ln(P_{value})$ of all comparisons was used to quantify the significance of an environmental effect, at time $t$, on yield components.

To explore the additive effects of two environmental variables and their interactions on a yield component, model 3 (M3 (equation

(3))), including two environmental variables ($E_1(t)$ and $E_2(t)$) and their full interactions with treatments, was tested:

$$Y_{ijkl} = \mu_i + \alpha_{ij}T + \beta_1(t)_i E_1(t)_{ijkl} + \beta_2(t)_i E_2(t)_{ijkl} + \gamma_1(t)_{ij} E_1(t)_{ijkl} \times T + \gamma_2(t)_{ij} E_2(t)_{ijkl} \times T + \varepsilon_{ijkl} \quad (3)$$

during the time-window $t$, the sensitivities of genotype $i$ to the two environmental variables tested ($E_1(t), E_2(t)$) were represented by their coefficients $\beta_1(t)_i$ and $\beta_2(t)_i$ and their interactions ($\gamma_1(t)_{ij}$, $\gamma_1(t)_{ij}$). The explanatory power of M3 was compared with M2 of $E_1(t)$, similar to the comparison between M2 and M1. In cases in which heading dates were not recorded in all treatments in an experiment (~4.7% of the complete dataset, that is GGE), heading dates of the cultivars were imputed from the mean heading dates of the cultivar in other treatments in the same experiment. Overall, 36–45 data points (on average, 44.7 points) were available for fitting the linear models. All linear models were fitted with lm() function, and ANOVA was conducted with anova() function in the R environment[53].

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

The complete set of climate data and simulated soil data, yield components of all environments, and sensitivity and significance of yield components to all environmental variables of all genotypes and all time-windows are available in the Zenodo data repository[54].

## Code availability

No custom algorithm was used in this study. All code used to analyse the data is available from the authors. Please contact the first author or corresponding author (sabir@gem.uni-hannover.de or tsu-wei.chen@hu-berlin.de) in case of interest.

## References


1. Wang, E. et al. The uncertainty of crop yield projections is reduced by improved temperature response functions. *Nat. Plants* **3**, 17102 (2017).
2. Reynolds, M. et al. Raising yield potential in wheat. *J. Exp. Bot.* **60**, 1899–1918 (2009).
3. Reynolds, M. et al. Achieving yield gains in wheat. *Plant Cell Environ.* **35**, 1799–1823 (2012).
4. Raza, A. et al. Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. *Plants* **8**, 34 (2019).
5. Liu, B. et al. Global wheat production with 1.5 and 2.0 °C above pre-industrial warming. *Glob. Chang. Biol.* **25**, 1428–1444 (2018).
6. Bönecke, E. et al. Decoupling of impact factors reveals the response of German winter wheat yields to climatic changes. *Glob. Chang. Biol.* **26**, 3601–3626 (2020).
7. Mäkinen, H. et al. Sensitivity of European wheat to extreme weather. *Field Crops Res.* **222**, 209–217 (2018).
8. Porter, J. R. & Semenov, M. A. Crop responses to climatic variation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**, 2021–2035 (2005).
9. Zhang, X. et al. Contribution of cultivar, fertilizer and weather to yield variation of winter wheat over three decades: a case study in the North China Plain. *Eur. J. Agron.* **50**, 52–59 (2013).
10. Xu, J., Henry, A. & Sreenivasulu, N. Rice yield formation under high day and night temperatures – a prerequisite to ensure future food security. *Plant Cell Environ.* **43**, 1595–1608 (2020).
11. Abbate, P. E., Andrade, F. H., Culot, J. P. & Bindraban, P. S. Grain yield in wheat: effects of radiation during spike growth period. *Field Crops Res.* **54**, 245–257 (1997).
12. Fischer, R. A. Number of kernels in wheat crops and the influence of solar radiation and temperature. *J. Agric. Sci.* **105**, 447–461 (1985).
13. Cossani, C. M. & Reynolds, M. P. Physiological traits for improving heat tolerance in wheat. *Plant Physiol.* **160**, 1710–1718 (2012).
14. Wang, X. et al. Pre-anthesis high temperature acclimation alleviates the negative effects of post-anthesis heat stress on stem stored carbohydrates remobilization and grain starch accumulation in wheat. *J. Cereal Sci.* **55**, 331–336 (2012).
15. Villegas, D. et al. Daylength, temperature and solar radiation effects on the phenology and yield formation of spring durum wheat. *J. Agron. Crop Sci.* **202**, 203–216 (2016).
16. Guo, Z., Chen, D. & Schnurbusch, T. Plant and floret growth at distinct developmental stages during the stem elongation phase in wheat. *Front. Plant Sci.* **9**, 330 (2018).
17. Lichthardt, C., Chen, T.-W., Stahl, A. & Stützel, H. Co-evolution of sink and source in the recent breeding history of winter wheat in Germany. *Front. Plant Sci.* **10**, 1771 (2020).
18. Voss-Fels, K. P. et al. Breeding improves wheat productivity under contrasting agrochemical input levels. *Nat. Plants* **5**, 706–714 (2019).
19. Wu, X., Tang, Y., Li, C. & Wu, C. Characterization of the rate and duration of grain filling in wheat in Southwestern China. *Plant Prod. Sci.* **21**, 358–369 (2018).
20. Ferreira, M. S. et al. Physicochemical control of durum wheat grain filling and glutenin polymer assembly under different temperature regimes. *J. Cereal Sci.* **56**, 58–66 (2012).
21. Guo, Z., Chen, D. & Schnurbusch, T. Variance components, heritability and correlation analysis of anther and ovary size during the floral development of bread wheat. *J. Exp. Bot.* **66**, 3099–3111 (2015).
22. Guo, Z., Chen, D., Röder, M. S., Ganal, M. W. & Schnurbusch, T. Genetic dissection of pre-anthesis sub-phase durations during the reproductive spike development of wheat. *Plant J.* **95**, 909–918 (2018).
23. Tardieu, F., Simonneau, T. & Muller, B. The physiological basis of drought tolerance in crop plants: a scenario-dependent probabilistic approach. *Annu. Rev. Plant Biol.* **69**, 733–759 (2018).
24. Ji, H. et al. Effects of jointing and booting low temperature stresses on grain yield and yield components in wheat. *Agric. For. Meteorol.* **243**, 33–42 (2017).
25. Fernández-Gómez, J., Talle, B., Tidy, A. C. & Wilson, Z. A. Accurate staging of reproduction development in Cadenza wheat by non-destructive spike analysis. *J. Exp. Bot.* **71**, 3475–3484 (2020).
26. Fernández-Gómez, J., Talle, B. & Wilson, Z. A. Increased expression of the *MALE STERILITY 1* transcription factor gene results in temperature-sensitive male sterility in barley. *J. Exp. Bot.* **71**, 6328–6339 (2020).
27. Allen, D. J. & Ort, D. R. Impacts of chilling temperatures on photosynthesis in warm-climate plants. *Trends Plant Sci.* **6**, 36–42 (2001).
28. Valluru, R., Link, J. & Claupein, W. Consequences of early chilling stress in two *Triticum* species: plastic responses and adaptive significance. *Plant Biol. (Stuttg.)* **14**, 641–651 (2012).
29. González, F. G., Miralles, D. J. & Slafer, G. A. Wheat floret survival as related to pre-anthesis spike growth. *J. Exp. Bot.* **62**, 4889–4901 (2011).
30. Reynolds, M. P., Acevedo, E., Sayre, K. D. & Fischer, R. A. Yield potential in modern wheat varieties: its association with a less competitive ideotype. *Field Crops Res.* **37**, 149–160 (1994).
31. 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.* **201**, 206–218 (2015).
32. Marcela, H. et al. Effect of heat stress at anthesis on yield formation in winter wheat. *Plant Soil Environ.* **63**, 139–144 (2017).
33. 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.* **20**, 268–280 (2020).
34. Wheeler, T. R. et al. The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and $CO_2$. *J. Exp. Bot.* **47**, 623–630 (1996).
35. Distelfeld, A., Avni, R. & Fischer, A. M. Senescence, nutrient remobilization, and yield in wheat and barley. *J. Exp. Bot.* **65**, 3783–3798 (2014).
36. Fahy, B. et al. Final grain weight is not limited by the activity of key starch-synthesising enzymes during grain filling in wheat. *J. Exp. Bot.* **69**, 5461–5475 (2018).
37. Ugarte, C., Calderini, D. F. & Slafer, G. A. Grain weight and grain number responsiveness to pre-anthesis temperature in wheat, barley and triticale. *Field Crops Res.* **100**, 240–248 (2007).
38. Sinclair, T. R. & Jamieson, P. D. Grain number, wheat yield, and bottling beer: an analysis. *Field Crops Res.* **98**, 60–67 (2006).
39. Ma, Y.-Z., MacKown, C. T. & van Sanford, D. A. Sink manipulation in wheat: compensatory changes in kernel size. *Crop Sci.* **30**, 1099–1105 (1990).
40. Neukam, D., Ahrends, H., Luig, A., Manderscheid, R. & Kage, H. Integrating wheat canopy temperatures in crop system models. *Agronomy* **6**, 7 (2016).
41. Kage, H. & Stützel, H. In *Modelling Cropping Systems* (eds Donatelli, M. et al.) 299–300 (European Society of Agronomy, 1999).
42. Marti, J., Savin, R. & Slafer, G. A. Wheat yield as affected by length of exposure to waterlogging during stem elongation. *J. Agron. Crop Sci.* **201**, 473–486 (2015).
43. Xie, Q., Mayes, S. & Sparkes, D. L. Carpel size, grain filling, and morphology determine individual grain weight in wheat. *J. Exp. Bot.* **66**, 6715–6730 (2015).
44. Tomás, D., Rodrigues, J. C., Viegas, W. & Silva, M. Assessment of high temperature effects on grain yield and composition in bread wheat commercial varieties. *Agronomy* **10**, 499 (2020).
45. Fischer, R. A. & Maurer, O. R. Crop temperature modification and yield potential in a dwarf spring wheat. *Crop Sci.* **16**, 855–859 (1976).
46. Hatfield, J. L. & Walthall, C. L. Meeting global food needs: realizing the potential via genetics × environment × management interactions. *J. Agron.* **107**, 1215–1226 (2015).
47. Russell, K., Lee, C. & van Sanford, D. Interaction of genetics, environment, and management in determining soft red winter wheat yields. *J. Agron.* **109**, 2463–2473 (2017).
48. Millet, E. J. et al. Genomic prediction of maize yield across European environmental conditions. *Nat. Genet.* **51**, 952–956 (2019).
49. Parent, B., Millet, E. J. & Tardieu, F. The use of thermal time in plant studies has a sound theoretical basis provided that confounding effects are avoided. *J. Exp. Bot.* **70**, 2359–2370 (2019).
50. Arnold, P. A., Kruuk, L. E. B. & Nicotra, A. B. How to analyse plant phenotypic plasticity in response to a changing climate. *New Phytol.* **222**, 1235–1241 (2019).
51. Kahlen, K. & Stützel, H. Modelling photo-modulated internode elongation in growing glasshouse cucumber canopies. *New Phytol.* **190**, 697–708 (2011).
52. Kahlen, K. & Chen, T.-W. Predicting plant performance under simultaneously changing environmental conditions – the interplay between temperature, light, and internode growth. *Front. Plant Sci.* **6**, 1130 (2015).
53. R Core Team. R: A language and environment for statistical computing (R Foundation for Statistical Computing, 2014).
54. Sabir, K. et al. Stage-specific genotype-by-environment interactions determine yield components in wheat [Data set]. *Zenodo* https://doi.org/10.5281/zenodo.8248543 (2023).

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## Author contributions

T.-W.C. conceived the analyses. K.S. and T.-W.C. analysed the data. T.R. simulated the soil water content. B.W., A.S. and R.J.S. designed the experiments. T.-W.C., T.R., H.Z., A.B., F.O., J.L., H.K., H.S. and W.F. performed and supervised the experiments and provided data. K.S., H.S. and T.-W.C. wrote the paper.

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s41477-023-01516-8.

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| ☐ | ☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
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*Our web collection on statistics for biologists contains articles on many of the points above.*

## Software and code

Policy information about availability of computer code

| | |
|---|---|
| Data collection | No software was used for data collection. All data were collected from the field trails |
| Data analysis | All data analyses were conducted in open source R environment (version 4.0.3) |

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The complete set of 1) climate data and simulated soil data; 2) yield components of all environment and 3) sensitivity and significance of yield component to all environmental variables of all genotypes and all time-windows are available in an online ZENODO data repository (https://doi.org/10.5281/zenodo.718098)

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Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

| | |
|---|---|
| Reporting on sex and gender | n/a |
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| Population characteristics | n/a |
| Recruitment | n/a |
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# Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

| | |
|---|---|
| Study description | Field trials were conducted in three seasons (2014–2015, 2015–2016, and 2016–2017) at six different locations with 220 wheat cultivars. Field trials were conducted in yield plots (4.5–12 m2) depending on site-specific sowing and harvesting machinery. Experimental design was a randomized block design with two replications and management intensities. Full details are shown in Table S3.<br><br>In the statistics section above, items about Bayesian analysis, hierarchical complex design and effect sizes are not relevant in this study |
| Research sample | All yield components of winter wheat were sampled at maturity. Sample size per location, treatment and genotype = 2, corresponding the maximal capacity of the field experiments. |
| Sampling strategy | Yield components were determined by standarized agronomic approach. Shortly before harvesting the plots, a sample of one row (50 cm in length) was cut to determine numbers of spikes, thousand kernal weight and spikes per $m^2$ and grains per spike and $m^2$. |
| Data collection | Field assistant + PhD students + Postdoc of all locations collected the data. |
| Timing and spatial scale | There was only one harvest time (maturity) per year per field trails |
| Data exclusions | Unrealistic data points were excluded (e.g. thousand kernal weight = 100g, less than 0.1% of the whole dataset) |
| Reproducibility | Not applicable for field study. The analyses were reproducible by R-script |
| Randomization | Randomized block design |
| Blinding | not applicable |

Did the study involve field work? ☒ Yes ☐ No

## Field work, collection and transport

| | |
|---|---|
| Field conditions | Experimental fields included agronomic reseasrch stations in Gross Gerau, Hannover, Klein Altendorf, Kiel, Quedlinburg, Rauischholzhausen throughout Germany with diverse environmental conditions. Temperature, precipitation and global radiation were recorded with hourly resolution by weather stations close to each study site. |

| | |
|---|---|
| Location | Gross Gerau, Hannover, Klein Altendorf, Kiel, Quedlinburg, Rauischholzhausen in Germany |
| Access & import/export | not applicable |
| Disturbance | not applicable |

# Reporting for specific materials, systems and methods

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| n/a | Involved in the study |
|---|---|
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| ☒ | ☐ Palaeontology and archaeology |
| ☒ | ☐ Animals and other organisms |
| ☒ | ☐ Clinical data |
| ☒ | ☐ Dual use research of concern |
| ☐ | ☒ Plants |

## Methods

| n/a | Involved in the study |
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| ☒ | ☐ ChIP-seq |
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| ☒ | ☐ Demonstrate how to render a vaccine ineffective |
| ☒ | ☐ Confer resistance to therapeutically useful antibiotics or antiviral agents |
| ☒ | ☐ Enhance the virulence of a pathogen or render a nonpathogen virulent |
| ☒ | ☐ Increase transmissibility of a pathogen |
| ☒ | ☐ Alter the host range of a pathogen |
| ☒ | ☐ Enable evasion of diagnostic/detection modalities |
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