









Decoupling of impact factors reveals the response of German winter wheat yields to climatic changes

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Abstract

Yield development of agricultural crops over time is not merely the result of genetic and agronomic factors, but also the outcome of a complex interaction between climatic and site-specific soil conditions. However, the influence of past climatic changes on yield trends remains unclear, particularly under consideration of different soil conditions. In this study, we determine the effects of single agrometeorological factors on the evolution of German winter wheat yields between 1958 and 2015 from 298 published nitrogen (N)-fertilization experiments. For this purpose, we separate climatic from genetic and agronomic yield effects using linear mixed effect models and estimate the climatic influence based on a coefficient of determination for these models. We found earlier occurrence of wheat growth stages, and shortened development phases except for the phase of stem elongation. Agrometeorological factors are defined as climate covariates related to the growth of winter wheat. Our results indicate a general and strong effect of agroclimatic changes on yield development, in particular due to increasing mean temperatures and heat stress events during the grain-filling period. Except for heat stress days with more than 31°C, yields at sites with higher yield potential were less prone to adverse weather effects than at sites with lower yield potential. Our data furthermore reveal that a potential yield levelling, as found for many West-European countries, predominantly occurred at sites with relatively low yield potential and about one decade earlier (mid-1980s) compared to averaged yield data for the whole of Germany. Interestingly, effects related to high precipitation events were less relevant than temperature-related effects and became relevant particularly during the vegetative growth phase. Overall, this study emphasizes the sensitivity of yield productivity to past climatic conditions, under consideration of regional differences, and underlines the necessity of finding adaptation strategies for food production under ongoing and expected climate change.

KEYWORDS

climate change impact, climate trend, long-term yield development, phenology trend, R^2 for mixed effect models, soil yield potential, weather extremes, Winter wheat

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1 | INTRODUCTION

Historical climate change, and first and foremost rising temperatures during the second half of the 20th century, contributed to profound changes in yield in many major wheat-producing regions globally and in Western Europe in particular (Alexander et al., 2006; Asseng et al., 2014; Frich et al., 2002; Lobell, Schlenker, & Costa-Roberts, 2011). For instance, an estimated net loss of 4% in wheat yield, coinciding with increasing temperature and decreasing precipitation between 1980 and 2008, has been found for France (Lobell et al., 2011). Wheat has been found to be very sensitive to high temperatures, and its response to heat stress varies at different phenological stages (Farooq, Bramley, Palta, & Siddique, 2011; Slafer & Rawson, 1994). High temperatures are presumed to be more harmful to grain yield during the reproductive growth phase than during the vegetative phase (VP; Wollenweber, Porter, & Schellberg, 2003). Heat stress around anthesis mainly leads to a reduction in photosynthesis rate, increased respiration, accelerated leaf senescence and enhanced evapotranspiration, which finally results in reduced grain numbers (Porter & Gawith, 1999; Reyer et al., 2013; Wheeler et al., 1996; Wollenweber et al., 2003). Exposed to drought stress during reproduction, grain yields of wheat are negatively affected due to a hampered uptake of nutrients, and in combination with a diminished surface cooling (induced by reduced transpiration) crop canopy temperatures increase and lead to further decrease in photosynthetic rates (Mäkinen et al., 2018; Porter & Semenov, 2005). During stem elongation, water is needed for expansive growth processes that bring up the spike to the top of the canopy through the unfolding leaf, as well as for spike growth and cell expansion, pollen ripening or grain growth and filling (Farooq et al., 2011). With enhanced climate variability during summer across Europe, encompassing a higher risk of heatwaves, droughts and heavy precipitation events, negative impacts on yields are likely to increase (Mäkinen et al., 2018; Meehl & Tebaldi, 2004; Porter & Semenov, 2005).

Besides environmental factors, quality and quantity of grain yields are determined by the crop genetic yield potential and by agronomic measures of crop management that aim to reduce environmental limitations. Despite the ongoing advancement in breeding for higher grain yields since the 1960s, the use of nitrogen fertilizers, irrigation or pesticides, the steady increase of winter wheat (*Triticum aestivum* L.) yields during the second half of the 20th century has slowed down since the 1990s in several regions of the globe (Brisson et al., 2010; Calderini & Slafer, 1998; Chen, Zhou, & Pang, 2015; Grassini, Eskridge, & Cassman, 2013; Laidig, Piepho, Drobek, & Meyer, 2014). For instance, historical yield records reveal that winter wheat yields almost simultaneously reached a plateau at about 7–8.5 t/ha in many West European high-yield countries between 1991 and 2000 (Brisson et al., 2010; Grassini et al., 2013). For Germany, yield data from the National Statistical Office show an increase of winter wheat yields from approximately 3 t/ha in 1960 up to 7.5 t/ha in the year 1999 (Wiesmeier, Hübner, & Kögel-Knabner, 2015), but thereafter, no further increase has been documented. A number of causes for the stagnation of grain yield have

been discussed. Besides aspects of climatic change (e.g. increasing temperatures, high precipitation events or drought stress) or the genetic and agronomic progress (expansion of wheat to sites with lower productivity, increasing shares of 'second wheat' in crop rotation), socio-economic incentives and/or constraints (e.g. world market price for wheat grain or general production factors; expansion of organic production systems; legal limitations to fertilization; political subsidies, price influences from climate events) were in the focus of research (Brisson et al., 2010; Grassini et al., 2013; Himanen, Hakala, & Kahiluoto, 2013; Laidig et al., 2017; Olesen et al., 2012; Reidsma, Oude Lansink, & Ewert, 2008; Trnka et al., 2019).

Many studies only account for the effect of one single impact factor and only take yield data from official statistics that represent annual averages at national or global scale, which result from diverse crop management of a multitude of farmers acting under diverse production conditions (Brisson et al., 2010; Calderini & Slafer, 1998; Hafner, 2003; Lobell & Field, 2007; Wiesmeier et al., 2015). However, the response of crop yields to climate variability might be enhanced or diminished depending on certain site conditions (Moot, Henderson, Porter, & Semenov, 1996; Porter & Gawith, 1999; Porter & Semenov, 2005). As a consequence, national data do not sufficiently consider regional diversity—both environmental and agronomical (Evans, 1996; Schlenker, 2010; van Ittersum et al., 2013). Similarly, studies building on a single experiment or using historical yield and fertilization data from only one location are limited in their explanatory power due to the restricted number of years, locations and used cultivars. Hence, a set-up combining multiple locations over a long period is preferable to compensate for these limitations.

In this study, we aim at examining the importance of a range of individual agroclimatic factors affecting winter wheat yields. However, since also other factors affecting yield development changed over time, it is necessary to disentangle the effects of climate change from those of genetic progress, and of all other agronomic factors that changed over time (e.g. socio-economic incentives and constraints). In order to dissect these factors, mixed-effect models were used, which allow attributing yield variability to randomly distributed independent effects. These models serve to analyse data sets—including unbalanced ones—and to dissect various impact factors by means of fixed regression terms and random residuals (Laidig, Drobek, & Meyer, 2008; Laidig et al., 2017; Mackay et al., 2011; Piepho, Laidig, Drobek, & Meyer, 2014). Moreover, statistical models do not depend on field calibration data for many driving variables as required for process-oriented models, and model uncertainties can be assessed in a more transparent way (Lobell & Burke, 2010b). Mixed-effect models can further take into account the influence of regional diversity, for instance, regarding soil type and quality. In this study, we make use of historical field trial records found in 34 publications that provide data on winter wheat yields, N-fertilization levels and cultivars from a total of 298 N-fertilization experiments over a long period of time and with a large geographic spread across Germany. The amount of nitrogen fertilizer applied is the agronomic factor, which usually has the strongest impact on yield and quality traits and features large regional and inter-annual variation (Basso,

Ritchie, Cammarano, & Sartori, 2011; Delogu et al., 1998; Whitfield & Smith, 1992). In order to exclude limiting effects of the factor 'N-fertilization', using data from optimum N-fertilization levels has been proven a useful approach (Basso et al., 2011; Raun et al., 2002). Specifically, experiments with multiple N-levels allow calculating the maximum of the nitrogen supply–yield relationship under standardized and predefined conditions.

We analyse the yield development of winter wheat over the last 60 years in Germany based on published data from wheat-N fertilization experiments. We identify the underlying causes of the observed trends by considering agronomic, genetic, inter-annual and geographic differences. Based on responses described in the literature, this study considers climatic factors linked to important winter wheat crop growth stages and phases. To estimate the explanatory value of an individual agroclimatic factor, we use a novel approach (Piepho, 2019) that compares the total variance estimates between two mixed-effect models—one that includes the climate variable of interest and one that does not, and employs the calculation of a coefficient of determination for such models (Section 2). First, we run the analysis over all experiment data across all study sites. In order to understand the impact and specify the significance of soil factors we then split the data into groups of experimental sites differing in yield potential and soil type. Understanding the interactive effects of climatic changes and genetic adaptation (i.e. genetic improvement through plant breeding) on yield productivity development is crucial

for developing viable crop adaptation strategies to future climate change.

2 | MATERIALS AND METHODS

2.1 | Study design

In order to assess the impact of climatic changes on winter wheat yield development, we applied several processing steps from raw data to final data analysis. As illustrated in Figure 1, we first gathered specific crop data including yields, N-fertilization amounts, cultivar choice and year of release (YOR). Furthermore, for every experimental site we gathered winter wheat phenology data (i.e. beginning of phenological stages), climatic data and site-specific soil information including soil type and soil rating (*Ackerzahl*) henceforth called 'soil yield potential'. In the second stage, we processed the experimental data to derive the optimal N-fertilization amounts and maximum yields. We used the climatic and phenological information to derive crop-specific agroclimatic conditions throughout the observation period. Third, for all time-series data, trend analyses were performed using simple linear regression models followed by segmented regression analysis. Additionally, linear plateau analyses were carried out for the yield and nitrogen data. Fourth, we used a data set with all data combined to decouple individual agroclimatic conditions from

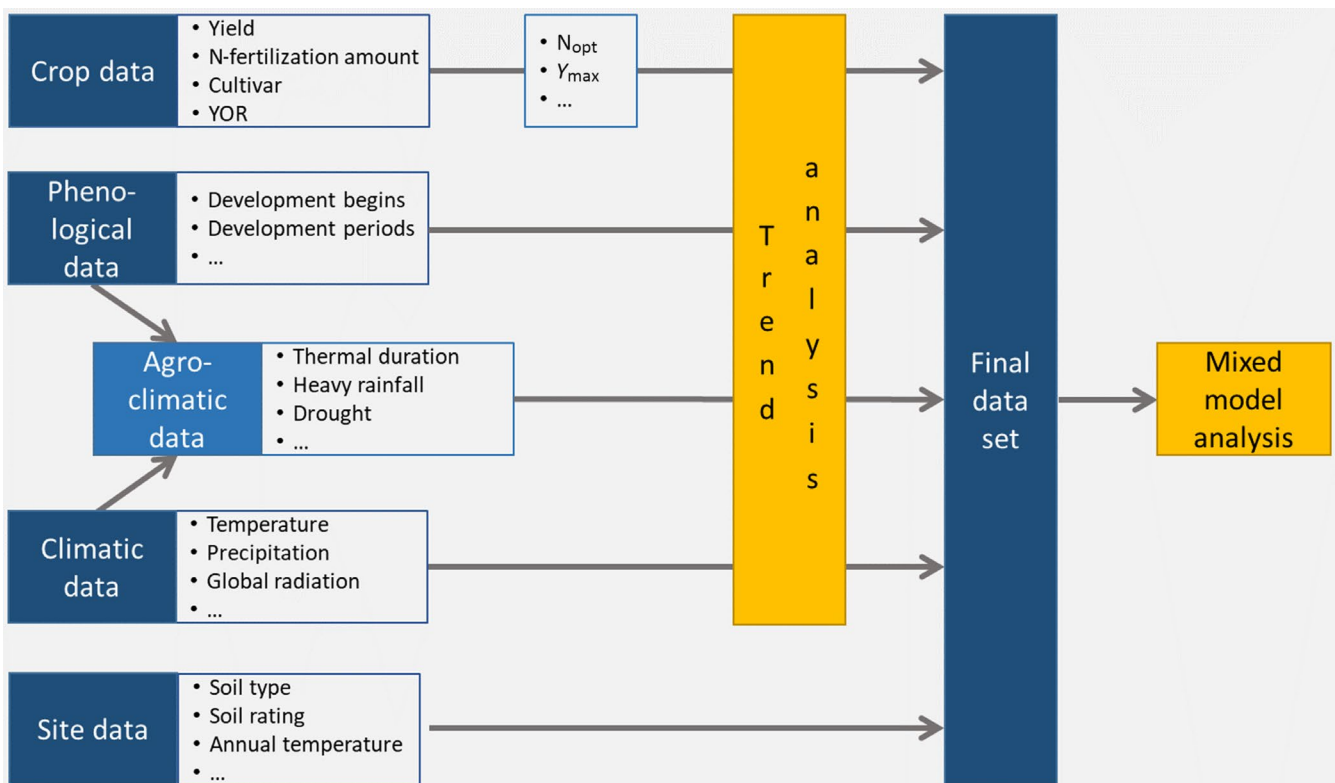


FIGURE 1 Data processing scheme from raw data to final data analysis. Crop, phenological, climatic, agroclimatic and site-specific data were collected in the first place and analysed for their trends. All data were combined into a data set from which individual agroclimatic variables were decoupled from all other influential factors using statistical mixed-effect models. Finally, the intensity of each variable was estimated by computing the coefficient of determination (R^2) for generalized linear mixed models as introduced by Piepho (2019)

all other influential crop parameters to finally assess the intensity of these individual factors by computing the coefficient of determination (R^2) for generalized linear mixed models as introduced by Piepho (2019).

2.2 | Data set compilation

2.2.1 | Crop data

Winter wheat field experiment data were gathered from multiple sources including peer-reviewed articles, dissertation theses, habilitation theses, conference papers and N-fertilization experiment reports from state authorities. Germany was selected as study region, as it represents a specific breeding region and ensures a sufficient number of well-documented experiments. All considered experiments investigated the response of grain yield of one or several cultivars to varied levels of N-fertilization (suboptimal, optimal, supraoptimal). In rainfed experiments with optimal plant protection, grain yields are supposed to be defined by the site-specific soil and climate conditions and limited by the genetic yield potential of the selected cultivar and the applied N rates. To be included in the study data set, the following criteria had to be fulfilled by an experiment: at least three levels of total rates of mineral N-fertilization (sum of all applications within one growing season [GS]) are represented, plant protection excluded biotic stress and the experiment was not irrigated. Moreover, site- and year-specific grain yields at defined dry matter content (either 86% or 100% dry matter) had to be available for each N-fertilization level. To make data comparable, all analyses were carried out by converting data to 100% dry matter, expressed in tons dry matter per hectare (t DM/ha). The exact location of each experimental site had to be given. A final data set was derived from 34 publications comprising 43 individual experimental sites between 1958 and 2015 and a total of 59 individual cultivars (Bönecke et al., 2020). The duration of the individual experiments ranged from 1 to 6 years. Information about

the YOR of the corresponding cultivars was retrieved from databases of the Federal Plant Variety Office and from GRIS (Genetic Resources Information System for Wheat and Triticale, CIMMYT).

Calculation of Y_{\max} and N_{\max}

N-fertilization experiments provide the opportunity to estimate the yield maxima (Y_{\max}) for each experiment, which then represent the environmental and agronomic limits in an experimental year and of a region. Y_{\max} can then be used to compare the yield variation between different locations and years. To derive potential grain yields under non-N-limited conditions for each experimental year, site and cultivar, data on dry matter grain yield at individual N-fertilization levels were used to calculate Y_{\max} and the corresponding maximum N-fertilization level (N_{\max}). Most trials implemented suboptimal, close to optimal and supraoptimal N-levels in equal quantity steps (e.g. 50, 100, 150 kg N/ha). We fitted a quadratic yield response function.

$$Y = a + bN + cN^2, \quad (1)$$

to the data of each individual N-fertilization response trial, where N is the applied N-level and Y is the observed yield (Equation 1; Figure 2), using the statistical software R (R Development Core Team, 2008). Values of Y_{\max} and N_{\max} were obtained from the coefficients of these functions by setting their first derivatives to 0 and solving for N :

$$N_{\max} = -b/2c, \quad (2)$$

$$Y_{\max} = a + bN_{\max} + cN_{\max}^2, \quad (3)$$

where a , b , and c are the model parameters.

When fitting quadratic functions to the trial data, several scenarios need to be considered for interpreting the derived yield as Y_{\max} under the given site and climatic conditions: the derived Y_{\max} value may lie (a) beyond the highest observed N-level, and (b) it may be higher or lower than a measured Y_{\max} value. To deal with these issues,

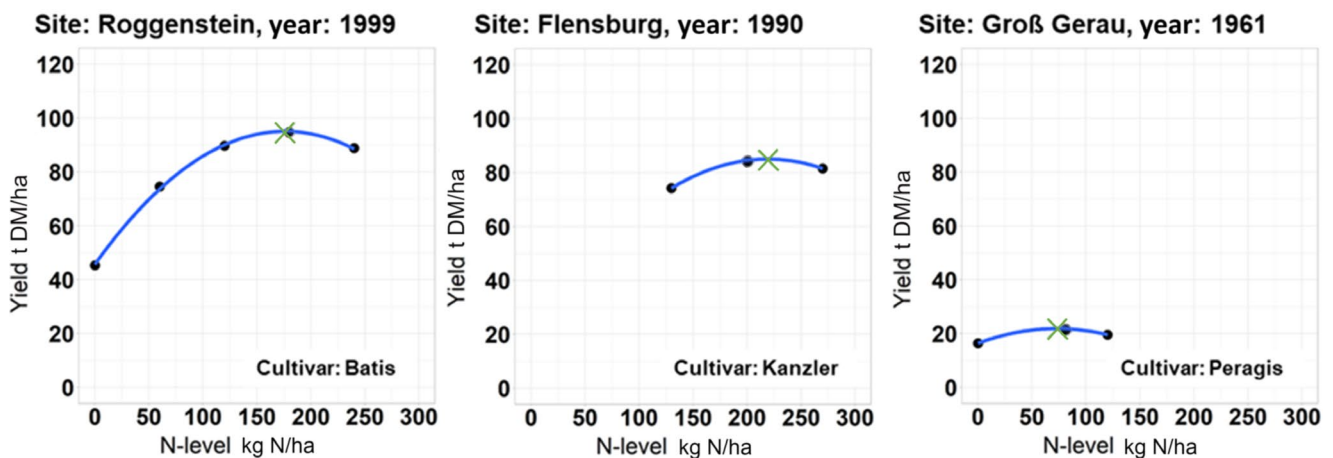


FIGURE 2 Examples for the yield response curves to nitrogen fertilizer level and derived maximum yields and corresponding nitrogen values of three fertilization experiments. The green crosses mark the maximum achievable winter wheat yields as derived from a quadratic linear function and its corresponding nitrogen level

certain thresholds were set: When the derived Y_{\max} was not reached within the observed range of N-levels, an upper threshold was set for acceptance of a study. Specifically, we determined the mean width of the N-level increments. The threshold was computed as the largest N-level tested in the study, plus the mean increment. A study was accepted only if Y_{\max} was estimated to occur at an N-level below that threshold. For instance, in an 80–120–160 kg N/ha trial, the mean increment of the N-fertilization levels is 40 kg N/ha and when Y_{\max} was estimated at 210 kg N/ha, the trial was then excluded from the data set, whereas when Y_{\max} was derived below or equal to 200 kg N/ha, the trial was included. Moreover, Y_{\max} values below 50 kg N/ha were excluded from further analysis and considered as unrealistic under conditions present in Germany. When the derived Y_{\max} value was below the highest yield measured by more than 5%, the measured yield was taken as Y_{\max} . Yet, when the derived Y_{\max} was greater than 5% of the highest measured yield, the derived Y_{\max} was chosen to reflect the maximum yield achievable. In any case, experiments outside these defined thresholds were excluded from the data set. About 11.2% of the data were removed from further analysis due to decreasing yield functions and coefficients of determination below 0.5. Following these plausibility tests, 324 out of 331 individual trials remained within the data set. The correlations between Y_{\max} and the corresponding N_{\max} , the intercept and the linear coefficient of the quadratic regression model were 0.51, 0.62 and 0.33 respectively. Correlations between N_{\max} , the intercept, and the slope factors of the quadratic regression model ranged between -0.1 and 0.52.

National yield data

The national average winter wheat yield data were obtained from FAO statistics (<http://www.fao.org>) and from the Federal Statistical Office (German: Statistisches Bundesamt, shortened DESTATIS), Wiesbaden.

2.2.2 | Phenological data

None of the publications from which yield data were retrieved provided precise information about phenological stages and phases. Therefore, data on the beginning of the individual phenological stages of winter wheat were retrieved from the phenological observation database on arable cropping systems (ftp://ftp-cdc.dwd.de/pub/CDC/observations_germany/phenology/) from the German Weather Service (Deutscher Wetterdienst, DWD). Phenological dates were recorded from voluntary observers within a radius of 1.5–2 km and not more than 50 m in altitude from the mean altitude of the observation site covering a period from 1951 to 2015 (as at November 2017). Cultivars used in the fertilization experiments may differ from those underlying the phenological records of the DWD. For this study, the beginning of sowing, emergence, stem elongation, heading, hard dough and harvest were recorded on an annual basis for all sites where experiments were conducted. In order to estimate the start dates of the aforementioned phenological stages, all DWD observation

sites within a radius of 30 km of each experiment site were selected using the ArcGIS Desktop software by Esri (version 10.5.1). To eliminate errors and incorrectly recorded single values, data records were processed by an automated selection process. As suggested in Menzel (2003), only observation sites with relatively complete data records of more than 20 or 30 years should be considered as meaningful for reliable predictions because trend analysis strongly depends on the number of years included in the linear regression. In this study, 30 years was set as minimum record length to ensure a certain degree of temporal stability of the resulting trends. Even then, a small uncertainty remained because part of the variation in trends might be caused by differing start and end years. With respect to topography and altitude (m a.s.l.), all stations with more than 50 m difference in altitude from the experimental sites were removed to avoid misinterpretation due to vertical thermal differences and their influence on stage initiation. Mean values and standard deviation for each year of the dates were calculated and potential outliers removed when they fell outside the range of the mean value \pm two times the standard deviation as suggested in Siebert and Ewert (2012). After applying the filtering process, the total number of observations obtained for the 43 sites across the study regions was 15,238. Moreover, the duration of the whole GS, the generative phase (GP) and the VP was calculated, and in addition VP was subdivided into the leaf development and tillering phase (LP) and the stem elongation and booting phase (SP). As shown in Figure 3, the length of the VP was defined as the time between emergence and heading and the GP as the time between heading and hard dough. The LP and SP were separated at the beginning of the stem elongation.

2.2.3 | Climatic data

As for phenology, high-resolution weather data that allow calculating agrometeorological variables was scarcely provided within the publications. For this reason and to investigate long-term climate trends for the crop growth phases outlined above at each respective experimental site, we obtained information from several databases providing climate data. The daily mean temperature ($^{\circ}\text{C}$), precipitation (mm) and relative air humidity (%) were obtained from the hydrological raster (HYRAS) data set ($5 \times 5 \text{ km}^2$) of the DWD for the period 1951–2015 (Frick et al., 2014). The interpolation of the gridded HYRAS data set is based on a combination of multiple linear regression and inverse distance weights and described in detail in Rauthe, Steiner, Riediger, Mazurkiewicz, and Gratzki (2013). Data on minimum and maximum temperature were obtained from the European Climate Assessment & Dataset (ECA&D) database and are available for the period between 1950 and 2017 (Haylock et al., 2008). Data about the surface solar radiation income (global radiation, $\text{W}^{-1} \text{ m}^{-2}$) were available for the period 1983 and 2017 (Huld, Müller, & Gambardella, 2012) from the Satellite Application Facility on Climate Monitoring (CMSAF) database of the European Organisation for the Exploitation of Meteorological Satellites (EUMETSAT).

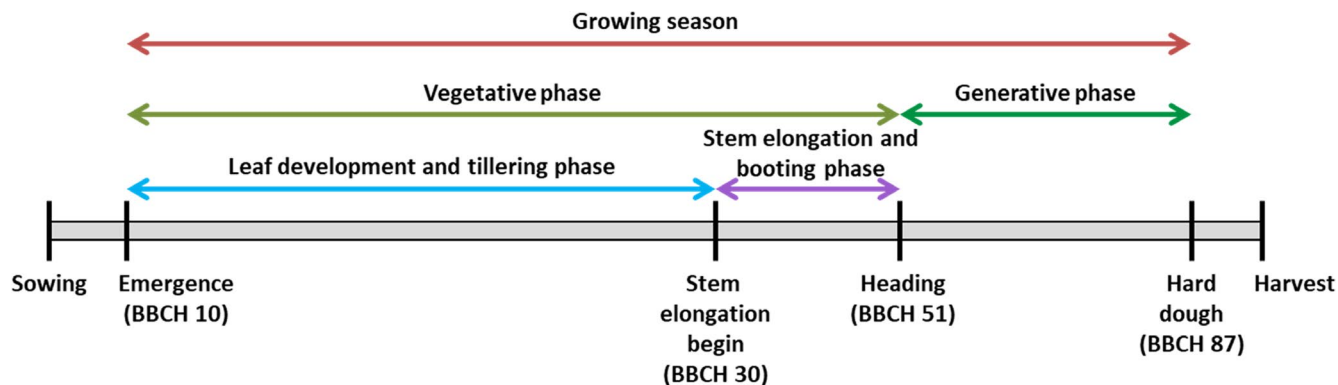


FIGURE 3 Development stages (black vertical bars), phases (coloured) and reference values according to the plant developmental BBCH-scale (Meier, 1997) similar to the Zadoks scale (Zadoks, Chang, & Konzak, 1974) for winter wheat along the whole vegetation period

2.2.4 | Agrometeorological variables

Obtained climate variables were evaluated for the long-term changes in accordance with the duration of the phenological phases of winter wheat. This was done for individual sites and the overall mean across all study sites. In addition, the long-term trend was estimated for the normal calendar year as well as for the periods of the defined hydrological winter (1 November to 30 April) and summer (1 May to 31 October). This was intended to provide information on the weather conditions independent of crop phenology.

Crop and drought parameters

To assess crop-related and site-specific developments during the observation period, additional climatic and hydrological variables were calculated from the available meteorological data sets. First of all, the thermal duration (TD, °Cd) for each phenological phase was calculated after McMaster and Wilhelm (1997; formula described in the Supporting Information). The potential evapotranspiration (PET, mm) for winter wheat crops was calculated after Haude (1954). The formula and the data processing are described in the Supporting Information. Moreover, the climatic water balance (CWB, mm) as a drought indicator differs largely within Germany and was calculated to estimate the available water supply. It is defined as the difference between the precipitation height and the amount of the PET.

Adverse weather conditions

Moreover, we accounted the occurrence of adverse weather events in order to evaluate their impact on the yield potential. Due to limitations in the climate projection as daily values based on the available DWD data, we counted the frequency of those days with high precipitation events, those days with potential heat stress impact, and those days with negative CWB and calculated their cumulative numbers for each crop developmental phase and each individual site. We defined high precipitation events in two ways in order to account for all days that may have caused water logging and lodging even in short phases such as SP or GP in the first place and in particular for those precipitation events that cause severe logging and lodging effects in

particular during summer months. Thus, we considered those days with a minimum rainfall of 20 mm in 24 hr as reported and analysed in Gömann et al. (2015) and the number of days, which had more than 40 mm of daily rainfall as high rainfall events (Mäkinen et al., 2018; Trnka et al., 2014). We used 27°C as upper temperature threshold with considerable impact on yield losses due to sterilization of grains of wheat around anthesis (Mitchell, Mitchell, Driscoll, Franklin, & Lawlor, 1993; Tashiro & Wardlaw, 1989), and 31°C as threshold for large detrimental effects around anthesis (Porter & Gawith, 1999; Wheeler et al., 1996).

2.2.5 | Site-specific characteristics

Climate conditions

In order to obtain additional site-specific information of each trial site, the long-term mean annual temperature, precipitation and CWB were calculated using the HYRAS data set based on the 30 year (1961–1990) reference period (Figure S7). Mean annual temperatures ranged from 7.8 to 10.6°C at the sites of this study. The average was at 8.9°C and the median at 8.8°C. Mean annual precipitation at the sites varied between 580 and 1,110 mm. The average was 774 mm and the median 744 mm. As for the mean annual CWB, the minimum was 198 mm, the maximum 822 mm, the average 465 mm and the median was at 431 mm.

Each site can be determined by the mean number of stress events during a specific growth phase. For example, based on the number of heat stress days during the GP—detected over the entire observation period—the number of these stress events for each site varied between 1.6 and 3.6 days and was 2.4 days in average.

Soil type

Soil types differ in water and nutrient availability and thus have an impact on the yield potential. Therefore, the soil type was retrieved from the publications at the level of the soil type group according to the German soil classification system—KA5 (Ad-hoc-AG Boden, 2005). If not available in the publication, soil type data were obtained from the soil type classification map of the Federal Institute

for Geosciences and Natural Resources (BGR) in Germany (Düwel, Siebner, Utermann, & Krone, 2007). Four soil type groups were identified for the experimental sites in this study: 8 loamy sands, 12 sandy loams, 13 loams and 10 clayey silts. Locations with loamy soils (loam and sandy loam) are dominant within the data set over the experimental years from 1958 until 2015, whereas silty soils (clayey silt) and sandy soils (loamy sand) were predominant in the early and mid-1980s (Figure 4a).

Soil yield potential

The suitability of a site under agricultural land use and its estimated yield potential is an indicator for the annual productivity of grain yields. Thus, we retrieved soil yield potential for all sites in this study based on the Muencheberg Soil Quality Rating (MSQR) developed

by the Leibniz Centre for Agricultural Landscape Research (ZALF) at a global scale (Mueller et al., 2010). In brief, this approach evaluates a set of soil describing properties, such as the substrate, rooting depth, topsoil structure or soil compaction in combination with potential yield effecting hazardous factors that are critical for farming and limit the overall soil quality, such as drought risk, soil depth above solid rock, flooding or extreme waterlogging regimes. The final scores range from about 0 to 102 points and are displayed on a map that shows the MSQR for cropland in Germany based on the land use stratified soil map of Germany at scale 1:1,000,000. The MSQR for the 43 sites in this study ranged from 31 to 99 points, with a median at 69 and a mean of 67.9 points. In order to divide the research area in relatively poor and relatively good soils, the data set was split at a soil yield potential of 70 points.

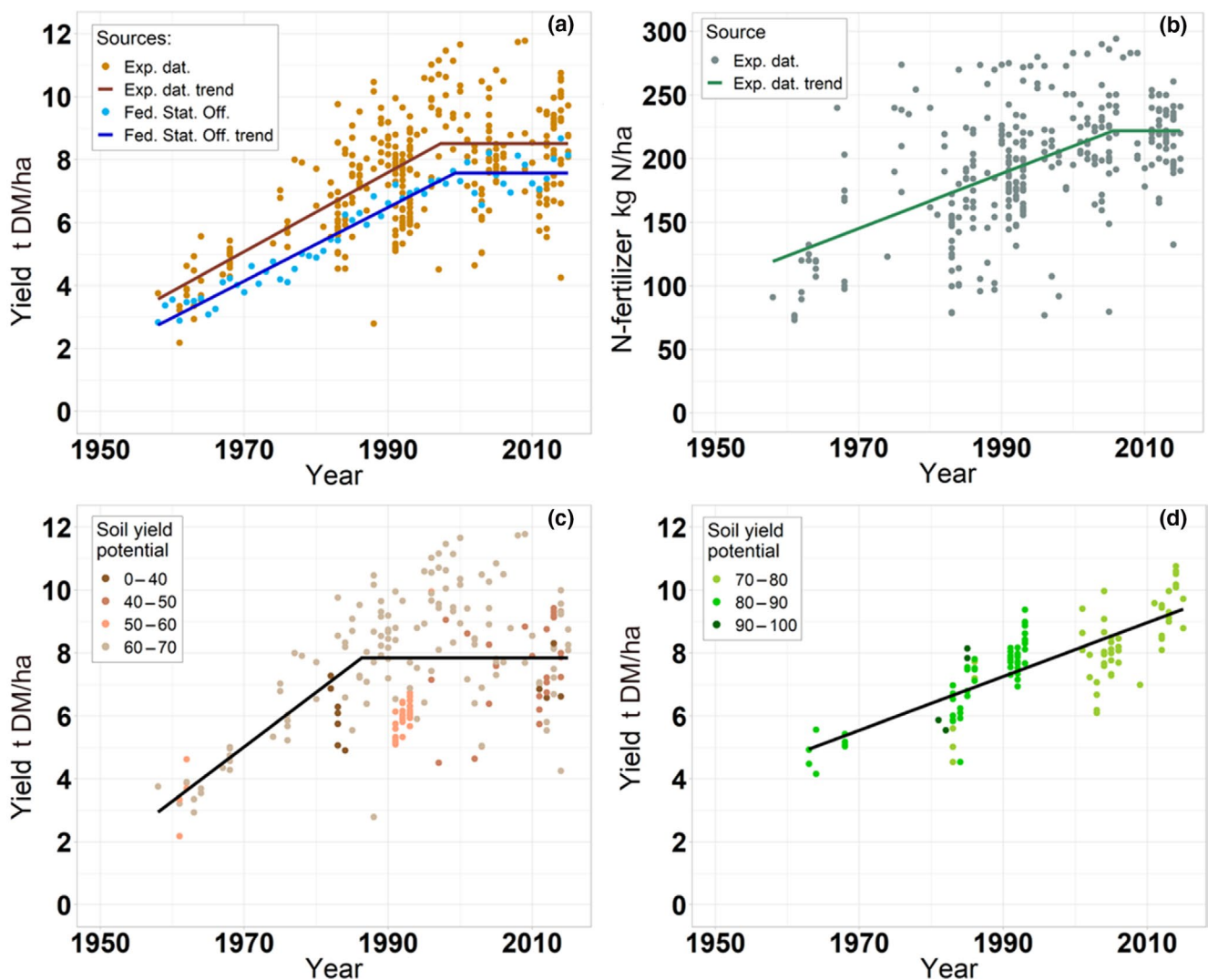


FIGURE 4 Grain yield development (as dry matter content) of winter wheat and nitrogen (N)-fertilization dosages across the study sites in Germany between 1949 and 2016. (a) Overall grain yield development. Data points refer to the derived experimental values (Exp. dat.) as described in Section 2 and to mean values of the Federal Statistical Office of Germany (Fed. Stat. Off.) The blue line visualizes the development of the official statistical data and the brown line shows the yield development of the experimental data. (b) Development of N-fertilization dosages. (c) Yield development of sites with yield potential lower than 70 points. (d) Yield development of sites with a yield potential of more than 70 points. The yield potential classification of the sites is based on the Muencheberg Soil Quality Rating (MSQR; Mueller et al., 2010; Section 2)

2.3 | Statistical methods and models

2.3.1 | General trend analysis—Linear and segmented

In order to analyse the development of all obtained phenological, climatic and agroclimatic time series, data were fitted with ordinary linear regression models (Equation 4) in the first place and depicted using the statistical software R (R Development Core Team, 2008). Linear trends and point data were then analysed visually and when trend changes were obvious within the point data, the data were analysed again by segmented piecewise linear regressions (Equation 5) to obtain more detailed information about these potential trend changes (Piepho & Ogutu, 2003; Schabenberger & Pierce, 2001).

$$E(y) = a + bx, \quad (4)$$

$$E(y) = \begin{cases} a_1 + b_1x; & \text{if } x < x_0 \\ a_2 + b_2x; & \text{if } x > x_0 \end{cases}, \quad (5)$$

where the parameters of the model are a_1 , a_2 , b_1 , b_2 and x_0 .

There is an implicit constraint that the regression lines must intersect at $x = x_0$. This can be done by removing one parameter and explicitly introduce x_0 as a parameter:

$$a_1 + b_1x_0 = a_2 + b_2x_0, \quad (6)$$

which can be transformed into:

$$a_2 = a_1 + b_1x_0 - b_2x_0, \quad (7)$$

and allows removing a_2 from the list of parameters to be estimated, leaving the parameters a_1 , b_1 , b_2 and x_0 .

2.3.2 | Segmented plateau analysis for maximum yield and nitrogen development

To test whether the yield and nitrogen development result in any kind of levelling, data were plotted against year using linear regressions with an upper plateau (Equation 7)—graphically depicted as a rising line or curve followed by a plateau. The 'linear plateau' model corresponds to a special case of the segmentation approach with $b_2 = 0$.

The segmentation analysis is based on an iterative approach where a breakpoint value is estimated based on nonlinear least squares (Muggeo, 2003, 2008). The initial parameters were derived from values of a pre-fitted ordinary linear model. The advantage of this type of fit is that it can estimate the year of change or transition to plateau. The significances of these trends were calculated using the t test. Only those phenological and climatic changes with significant trends were chosen for the final discussion.

2.3.3 | General decoupling—Dissecting genetic from nongenetic sources

Here we explicitly point out that the data set used for this analysis differs from the data set used to investigate phenology and climate trends (Figure 1). A subset of years with experimental data, which include cultivar information, was established. Next, all data on the beginning of the phenological stages, the duration of phenological phases and the agroclimatic variables were attached for those experimental years where it was possible to obtain this information. However, this data set faces certain limitations. First, the true phenology of the cultivars used in the fertilization trials may differ from the phenological information obtained from the DWD. Second, agroclimatic information was only available for those years where weather and phenological data were available and adverse weather events occurred. Moreover, effects of individual agroclimatic conditions are considered to occur only when they vary in their variability and error. It also needs to be considered that cultivars largely vary in occurrence, duration over time, and in location. Also, the applied N-levels vary between experiments, over time and in location.

To overcome the uncertainty of such unbalanced data sets, we used well established statistical mixed-effect models, which take the large number of environmental and nonenvironmental covariates into account. These models include a predetermined number of independent factors treated as random effects. Moreover, to disentangle the main effects that influence the evolution of winter wheat yields and to quantify the impact of an individual agroclimatic factor, a varying number of fixed effects can be included in these models.

Grain yield is a function of genetic and nongenetic conditions and thus, a standard three-way model after Laidig et al. (2008) was established:

$$Y_{ijk} = \mu + G_i + L_j + Y_k + LY_{jk} + GL_{ij} + GY_{ik} + GLY'_{ijk}, \quad (8)$$

where Y_{ijk} represents the mean yield of the i th genotype in the j th location and the k th year, μ is the overall mean, G_i is the main effect of the i th genotype, L_j is the main effect of the j th location, Y_k is the main effect of the k th year, LY_{jk} is the jk th location \times year interaction effect, GL_{ij} is the ij th genotype \times location interaction effect, GY_{ik} is the ik th genotype \times year interaction effect, GLY'_{ijk} is the residual of the ijk th genotype \times location \times year interaction effect and error of the mean. As in Piepho et al. (2014), we assume that all effects except μ , G_i and Y_k are random and independent with constant variance, following a normal distribution. Thus, we integrated genetic and nongenetic time trends as fixed regression components into the model. G_i was then estimated as the following regression term based on the YOR:

$$G_i = \beta r_i + H_i, \quad (9)$$

where β is the fixed regression coefficient for the genetic trend, r_i is the first year of testing (YOR) for the i th cultivar, and H_i is the random deviation of G_i from the genetic trend line. If there was a linear nongenetic time trend, we modelled Y_k as:

$$Y_k = \gamma t_k + Z_k, \quad (10)$$

where γ is the fixed regression coefficient for the nongenetic trend, t_k is the continuous covariate for the experimental year and Z_k is a random residual. Both, β and γ quantify the genetic and nongenetic trends per year in the same units as y_{ijk} .

In this study, we made use of data from crops grown under optimum N-fertilization levels and full crop protection. Hence, changes in agronomic practices can be considered to play a minor role and the time effect predominantly represents the effect of climatic changes. To evaluate whether the overall climate change has to be accounted for as linear or nonlinear regression terms in the mixed model, a pre-analysis was carried out, modelling the time effect first with a linear relationship and second with a quadratic relationship. The latter should account for the potential yield levelling. While the linear relationship was significant ($p < .001$) in the pretest, the quadratic was not ($p = .69$). Hence, the time trend was included as a linear function and a potential yield levelling cannot be traced back to climate change only.

2.3.4 | Specific decoupling—Dissecting individual agroclimatic trends

We further investigated whether an agronomic variable has a specific impact on winter wheat yield development. While we assume that γ in Equation (10) represents all climatic changes over time combined, we assume that Z_k in Equation (10) neither represents the interyear variability of a single agroclimatic variable appropriately nor does it account for the effect of a climatic factor at a specific location. Thus, in order to simultaneously model interyear and interlocation variation due to climatic or agronomic variables, we modified the model by regressing LY_{jk} on these variables:

$$LY_{jk} = \alpha s_{jk} + C_{jk}, \quad (11)$$

where α is the fixed regression coefficient for the respective climatic or agronomic covariate, s_{jk} is the specific value of the covariate for the k th year and the j th location and C_{jk} is a random residual location \times year interaction.

Crop growth and yields not merely depend on weather effects during the GS, but also on the site and soil conditions, which, hence, should be considered more explicitly. To account for such disparities among the experimental sites, the variance estimates were additionally adjusted for their location attributes (L_j) yield potential and soil type, and each tested within separate models as:

$$L_j = \delta u_j + S_j, \quad (12)$$

where L_j is the main effect of the j th location, δ is the fixed regression coefficient for the respective spatial attribute or site condition (e.g. yield potential), u_j is the specific value of the attribute for the j th location and S_j is the random deviation from the trend.

2.3.5 | Estimating the intensity of individual agroclimatic variables on yield variation

For each independent variable assessed, the total variance, defined as the sum of variance components of all random effects, was estimated twice: once without and once with the agroclimatic variable included. The model without the factor is henceforth called M_{-x} and the model with the specific factor is called M_{+x} , where M is the model, x describes the specific factor and '-' and '+' refer to the absence or presence of the factor respectively. In both models, trend components in G_p , Y_k and L_j were modelled using regression Equations (9), (10), and (12) respectively. In M_{+x} , however, the spatio-temporal covariate s_{jk} was modelled additionally as per Equation (11). The sum of all variance components estimated in M_{+x} ($\text{Var}_y(M_{+x})$) was subtracted from the corresponding sum estimated in M_{-x} and expressed as a percentage of that of M_{-x} ($\text{Var}_y(M_{-x})$) (Equation 13), describing the impact of a single climatic or agronomic factor on the overall yield development. This corresponds to the coefficient of determination (R^2) for generalized linear mixed models as introduced by Piepho (2019):

$$\% \text{Var}_y = \frac{\text{Var}_y(M_{-x}) - \text{Var}_y(M_{+x})}{\text{Var}_y(M_{-x})} \times 100. \quad (13)$$

In order to assess the impact of climatic or agronomic factors on yield development under different site-specific conditions, this procedure was repeated for subsets of two groups of soil type and two groups of soil yield potential. For this purpose, soils of sandy loam and loamy sand were combined and addressed as sandy soils, and loams and clayey silts were addressed as loamy soils. The threshold for the two groups of different yield potential was the median yield potential (70) across the study sites. For further analysis, the agroclimatic variables were also tested for interaction with the time effect.

2.3.6 | Adjusting trends of agroclimatic covariates

To compare the slope for an agroclimatic variable (α) with the overall time trend (γ) and the genetic time trend (β), α was multiplied by the covariate's slope in an ordinary regression on time over the entire observation period (b , from Equation 4) to yield an adjustment climate trend:

$$\alpha_{\text{adj}} = \alpha \times b. \quad (14)$$

3 | RESULTS

3.1 | Yield development as a result of soil type and site-specific yield potential

Over all the trials analysed in this study, between 1958 and 1997 the annual yield of winter wheat increased on average by 0.12 t DM ha⁻¹ year⁻¹ and reached a plateau at 8.35 t DM/ha (Figure 4a; equation coefficients in Table 1). This corresponds to average wheat yields in Germany recorded by the Federal Statistical Office which also show increases beginning in the late 1950s until the end of the

TABLE 1 Regression coefficients of winter wheat yield (t DM/ha) and N-fertilization (kg N/ha) trends estimated by segmented regression line analysis and simple linear models (Equations 4–7). Heavy soils refer to loams and clayey silts and light soils to sandy loams and loamy sands (Section 2). Low yield potential soils are soils with MSQR below 70 points and high yield potential soils are those with MSQR above 70 points (Section 2). SE describes the standard error of the fitted parameter

Dependent variable	Subset	n	Term	Estimate	SE	t	p
Winter wheat yield	All experimental sites	328	Intercept	-231	0.12	-11.43	<.001
			Trend	0.12	0.01	11.77	<.001
			Breakpoint	1,997.6	1.7	1,179.9	<.001
	Low yield potential	211	Intercept	-336.2	50.7	-6.6	<.001
			Trend	0.17	0.03	6.75	<.001
			Breakpoint	1,986.3	2.3	846.5	<.001
	High yield potential	117	Intercept	-163	12.5	-13	<.001
			Trend	0.08	0.01	13.6	<.001
			Breakpoint	1,996.5	1.4	1,350.9	<.001
	Heavy soils	151	Intercept	-258.5	17.4	-14.9	<.001
			Trend	1.34	0.01	15.24	<.001
			Breakpoint	1,996.5	1.4	1,350.9	<.001
	Light soils	177	Intercept	-396.3	104.3	-3.8	<.001
			Trend	0.2	0.05	3.86	<.001
			Breakpoint	1983	3.	601.4	<.001
	Federal Statistic Office	67	Intercept	-226.1	10.5	-21.6	<.001
			Trend	0.12	0.005	22.1	<.001
			Breakpoint	1,999.3	1.41	1,421.7	<.001
Nitrogen fertilization	All sites	328	Intercept	-4,104.4	438.9	-9.4	<.001
			Trend	2.16	0.22	9.78	<.001
			Breakpoint	2,005.6	3	667.4	<.001
	Heavy soils	151	Intercept	-4,235.5	441.6	-9.6	<.001
			Trend	2.22	0.22	10	<.001
			Breakpoint	2,007.6	3.6	557.3	<.001
	Light soils	177	Intercept	-3,877.3	960.3	-4	<.001
			Trend	2.04	0.48	4.24	<.001
			Breakpoint	2,002.3	4.7	429.1	<.001
	Low yield potential	211	Intercept	-3,815.7	632.9	-6	<.001
			Trend	2.01	0.32	6.33	<.001
			Breakpoint	2,003.5	4.2	472.4	<.001
	High yield potential	117	Intercept	-7,144.1	825	-8.7	<.001
			Trend	3.68	0.41	8.87	<.001
			Breakpoint	1,997.2	1.9	1,025.6	<.001

1990s. From around 1997 onwards, no further yield increase was observed in our trial data, which also corresponds with the official data and with other studies which point out a yield levelling beginning in the late 1990s (Brisson et al., 2010; Grassini et al., 2013). In parallel, the optimal nitrogen fertilizer dosage increased by about 2 kg N ha⁻¹ year⁻¹ between 1958 and 2006 (Figure 4b) with no further increase after 2006.

At sites with relatively low yield potential (<70 quality points, Section 2), yield levelling occurred about a decade earlier compared to the average of all sites (Figure 4c), while for sites with relatively high yield potential no stagnation was revealed. Still, our data indicate that yield levelling occurred at sites with light

soils (sandy loams and loamy sands) as well as at sites with heavy soils (clayey silts and loams; Figure S1). The optimal nitrogen dosage showed a levelling for all soils and both yield potential groups (Figure S2a–d).

3.2 | Earlier occurrence of wheat growth stages and shortened development phases except for stem elongation

Besides agronomic and soil factors, weather conditions during the whole GS and the occurrence of severe weather events during

sensitive crop growth phases significantly affected crop development and yields. Altogether, between 1951 and 1968 the sowing dates of winter wheat shifted to nearly 7 days later, while for the period 1969 until 2015 a shift towards earlier dates by 12.6 days is documented (Figure 5a; equation coefficients in Table 2). Yet, there was a strong geographical heterogeneity, and sowing tended to shift to earlier dates by up to 6 days per decade at North German sites, whereas South German sites showed inconsistent patterns of sowing dates (± 2 days per decade) during the same period (Figure S3). A similar pattern as for the overall trend in sowing was found for the dates of emergence ($r^2 = .88$ between sowing and emergence dates) and of heading ($r^2 = .34$ between sowing and heading dates). For both stages, the change from later dates towards earlier dates occurred around 1970. Harvest dates shifted to 26 days later between 1951 and 1961. Afterwards and until 2015, a shift towards earlier harvests by approximately 17 days occurred. Between 1961 and 2015, the onset of stem elongation changed by 24 days towards earlier dates and the estimated hard dough occurred 21 days earlier in 2015 than in 1979. The growth duration of winter wheat was shortened by more than 2 weeks, which almost equally affected the vegetative and GP (Figure 5b). Within the VP, contrasting patterns were revealed for individual development stages. While the LP was shortened by 16 days between 1951 and 1974, the SP was prolonged by nearly 2 weeks (3.7 days per decade) between 1951 and 1987. Beyond 1974 and 1987, no further changes in the duration of leaf development and stem extension, respectively, were detected. Expressed in TD (Section 2), the VP of winter wheat was extended by 81°Cd during

the entire 55 years of observation time, whereas the GP was reduced by 72°Cd (Figure 5c). The SP was prolonged by 134°Cd in the period from 1951 to 1999, whereas it was reduced by 85°Cd between 1999 and 2006. From 1952 to 1979, the LP was reduced by 126°Cd .

3.3 | Increasing temperatures during the vegetative growth period

Across the trial locations, the annual mean temperature increased on average by $0.024^\circ\text{C}/\text{year}$ and was nearly 1.3°C higher in 2006 than in 1951 (Figure S4; equation coefficients in Table 3). The same trend was found for the mean annual minimum and maximum temperatures. The temperature increase was accompanied by an increase of the mean annual potential evapotranspiration by 1.6 mm per year, summing up to 85 mm over the entire observation period of 55 years. However, mean annual precipitation and mean annual CWB did not change significantly, even though the latter showed a negative trend indicating dryer conditions.

Climate change became apparent not only by enhanced annual mean temperatures but also by higher mean temperatures during the VP of winter wheat (Figure 6a; equation coefficients in Table 3). Temperatures in this phase were approximately 0.8°C higher in 2006 than in 1951. The VP reflects in the pattern of a shortened total duration in days (Figure 5b), but also of a prolongation of the TD (Figure 5c). The reduced duration of the GP (both, in days and thermal) and a reduced amount of total precipitation during that phase

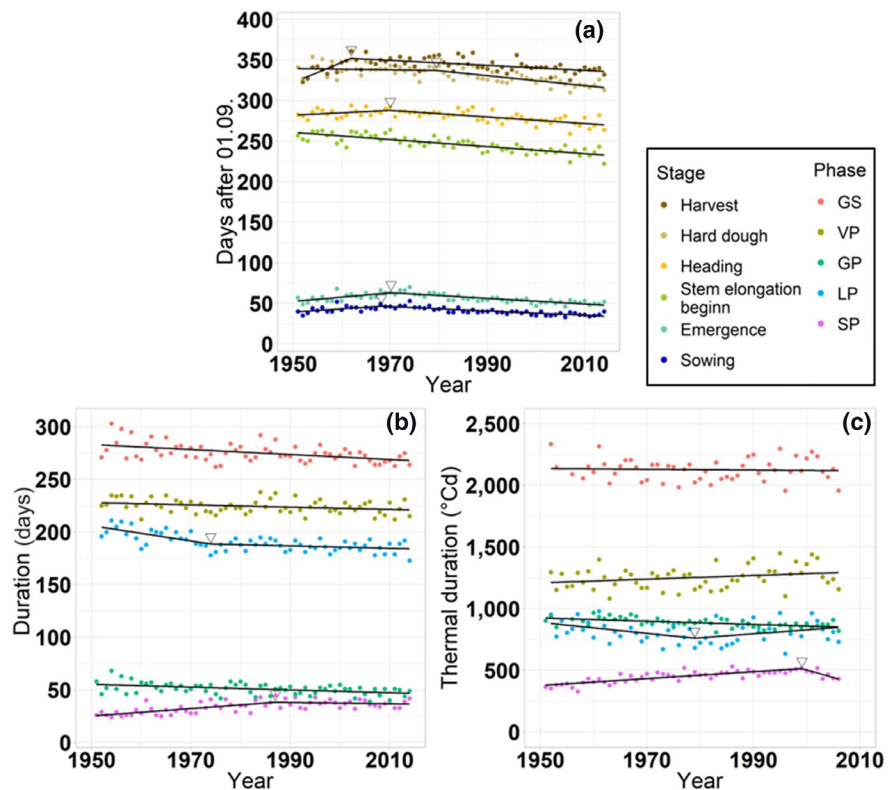


FIGURE 5 Estimated phenology trends of winter wheat across the study sites between 1951 and 2015. (a) Average days of sowing, harvest and the actual crop phenological stages (emergence, begin of stem elongation, heading and hard dough) after 1 September. Average duration (b) and thermal duration (c) of the entire growing season (GS) divided into the generative phase (GP) and vegetative phase (VP). The latter comprises the leaf development phase (LP) and the stem elongation phase (SP). Inverse triangles indicate trend changes

Stages and phases	Term	Estimates	SE	t	p
Sowing	Intercept	-743.6	245.1	-3.033	.004
	Trend part 1	0.401	0.125	3.209	.002
	Trend part 2	-0.668	0.129	-5.189	<.001
	Breakpoint	1,968.2	2.254	0	<.001
Emergence	Intercept	-991.5	252.8	-3.923	<.001
	Trend part 1	0.535	0.129	4.152	<.001
	Trend part 2	-0.886	0.135	-6.568	<.001
	Breakpoint	1,970.2	2	0	<.001
Stem elongation begin	Intercept	1,113.4	75.9	14.676	<.001
	Trend	-0.437	0.038	-11.426	<.001
Heading	Intercept	-296.5	403.4	-0.735	.465
	Trend part 1	0.297	0.206	1.442	.155
	Trend part 2	-0.703	0.215	-3.265	.002
	Breakpoint	1,970	3.995	0	.001
Hard dough	Intercept	500.9	295.7	1.694	.095
	Trend part 1	-0.083	0.15	-0.55	.584
	Trend part 2	-0.529	0.188	-2.807	.007
	Breakpoint	1,979.5	6.442	0	.008
Harvest	Intercept	-4,529.9	1,232.9	-3.674	.001
	Trend part 1	2.488	0.63	3.95	<.001
	Trend part 2	-2.797	0.633	-4.419	<.001
	Breakpoint	1,962	1.489	0	<.001
Growing Season	Intercept	746.5	106.8	6.99	<.001
	Trend	-0.238	0.054	-4.411	<.001
Leaf development	Intercept	1,654.3	246.4	6.713	<.001
	Trend part 1	-0.743	0.126	-5.916	<.001
	Trend part 2	0.640	0.138	4.650	<.001
	Breakpoint	1,974	3.241	0	<.001
Stem elongation	Intercept	-674.5	88.1	-7.656	<.001
	Trend part 1	0.359	0.045	8.017	<.001
	Trend part 2	-0.433	0.078	-5.555	<.001
	Breakpoint	1,987	3.178	0	<.001
Vegetative phase	Intercept	438.8	85.3	5.147	<.001
	Trend	-0.108	0.043	-2.513	.015
Generative phase	Intercept	316.2	64.7	4.888	<.001
	Trend	-0.134	0.033	-4.099	<.001

TABLE 2 Regression coefficients of the linear and segmented regression analysis of the phenological beginning (days after September 1) and duration (d) of winter wheat development

by approximately 52 mm (Figure 6b) may have had negative effects on the overall grain-filling period and consequently on winter wheat yields. Moreover, a change was observed for the potential evapotranspiration during this phase (Figure 6c) as well as for the CWB by 86 mm (Figure 6d). An increase of the potential evapotranspiration was additionally detected for the SP from 1951 onwards before it started to decrease between around 1992 and 2006. By contrast, the potential evapotranspiration during the LP decreased constantly throughout the entire observation period. The VP apparently, was dominated by the course of evapotranspiration during the SP. It is noteworthy that

between 1998 and 2006, TD during stem elongation decreased by about 40°Cd, and the trend of potential evapotranspiration turned from an increase to a decrease in 1992, which lasted until 2006.

3.4 | Climatic variation explained yield variability the most

Differentiating the results of the main influential factors on yield development from the specific agroclimatic effects, the general

TABLE 3 Regression coefficients for the linear and segmented trends of climatic factors during phenological phases of winter wheat. *p* values refer to the slope coefficient

Climate factor	Unit	Stages and phases	Period	Intercept	Trend	<i>p</i>
Thermal duration	°Cd	Growing season	1952–2006	2,735.9	-0.307	.711
		Vegetative phase	1952–2006	-1,742.5	1.504	.045
		Generative phase	1951–2006	3,485.8	-1.313	<.001
		Leaf development	1952–1979	9,999.9	-4.671	.011
			1979–2006	-6,214.4	3.522	.099
		Stem elongation	1951–1999	-5,055.1	2.786	<.001
	1999–2006	24,898.9	-12.198	.013		
Mean temperature	°C	Growing season	1952–2006	-4.8	0.006	.342
		Vegetative phase	1952–2006	-25.2	0.015	.024
		Generative phase	1951–2006	-8.4	0.013	.166
		Leaf development	1952–2006	-14.9	0.009	.218
		Stem elongation	1951–2006	13.5	0	.992
		Calendar year	1951–2006	-39.1	0.024	<.001
Maximum temperature	°C	Growing season	1952–2006	-7.2	0.009	.175
		Vegetative phase	1952–2006	-21.5	0.015	.023
		Generative phase	1951–2006	-13.5	0.018	.14
		Leaf development	1952–2006	-8.4	0.008	.309
		Stem elongation	1951–2006	16.8	0.001	.931
		Calendar year	1951–2006	-37.3	0.025	<.001
Minimum temperature	°C	Growing season	1952–2006	-10.9	0.007	.316
		Vegetative phase	1952–2006	-35.6	0.019	.013
		Generative phase	1951–2006	-0.3	0.006	.347
		Leaf development	1952–2006	-29.5	0.015	.078
		Stem elongation	1951–2006	8.1	0	.998
		Calendar year	1951–2006	-43.3	0.024	<.001
Precipitation	mm	Growing season	1952–2006	1,594.6	-0.516	.531
		Vegetative phase	1952–2006	-1,017.4	0.73	.245
		Generative phase	1951–2006	2,000.3	-0.937	.018
		Leaf development	1952–2006	-683.6	0.522	.347
		Stem elongation	1951–2006	-320.7	0.202	.393
		Calendar year	1951–2006	-859.8	0.815	.371
Potential evapotranspiration	mm	Growing season	1952–2006	-488.9	0.518	.214
		Vegetative phase	1952–1992	-486.9	0.399	.153
			1992–2006	4,979	-2.345	.041
		Generative phase	1951–2006	-1,003.6	0.631	.072
		Leaf development	1952–2006	1,687.4	-0.768	<.001
		Stem elongation	1951–1992	-2,571.6	1.371	<.001
1992–2006	4,678.5		-2.27	.024		
Calendar year	1951–2006	-4,719.1	2.758	<.001		
Climatic water balance	mm	Growing season	1952–2006	2,131.8	-1.06	.355
		Vegetative phase	1952–2006	-1,377.4	0.76	.277
		Generative phase	1951–2006	3,003.9	-1.567	.023
		Leaf development	1952–2006	-2,301.4	1.254	.034
		Stem elongation	1951–2006	935.1	-0.499	.14
		Calendar year	1951–2006	3,852.3	-1.939	.2

(Continues)

TABLE 3 (Continued)

Climate factor	Unit	Stages and phases	Period	Intercept	Trend	<i>p</i>
Global radiation sum	W/m ²	Growing season	1983–2015	-4,151.6	2.972	.352
		Vegetative phase	1983–2015	-78.7	0.599	.85
		Generative phase	1983–2015	-4,016.5	2.351	.271
		Leaf development	1983–2015	430.3	0.124	.967
		Stem elongation	1983–2015	-171.5	0.311	.898
		Calendar year	1951–2006	-19,682.9	11.179	.099

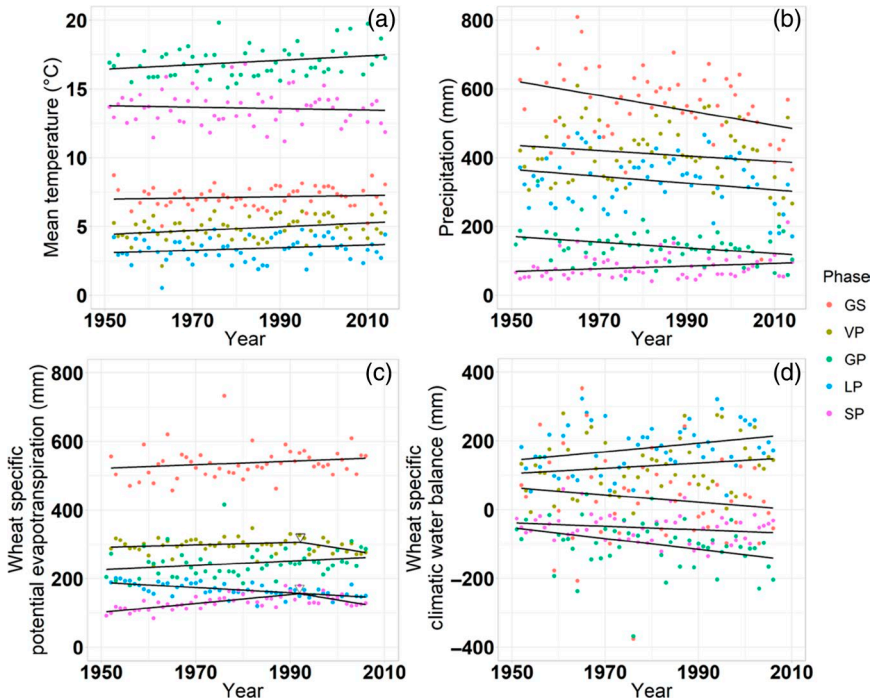


FIGURE 6 Climate trends within phenological growth phases of winter wheat across the study sites in Germany. Trends are shown for the growing season (GS), vegetative phase (VP), leaf development phase (LP), generative phase (GP) and stem elongation phase (SP). (a) Mean temperature between 1951 and 2014. (b) Precipitation between 1951 and 2014. (c) Wheat-specific potential evapotranspiration between 1951 and 2006. (d) Wheat-specific climatic water balance between 1951 and 2006

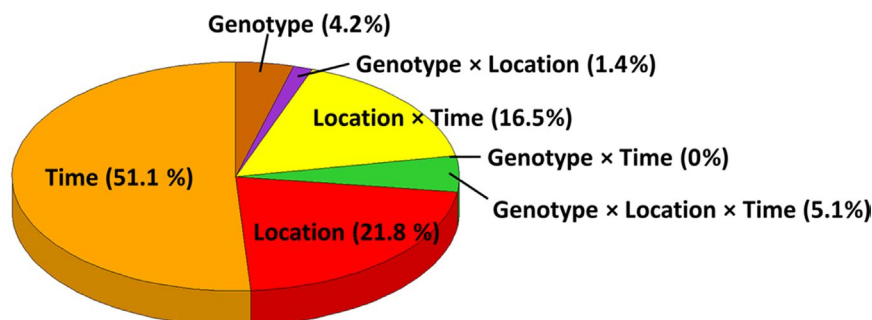


FIGURE 7 Proportions of variance explained by the main influential factors (genotype, location and time) and their interactions in German long-term yield data. Results indicate a relative strong variance of all factors that changes along the timeline (time effect) except those caused by altering genotypes, which were relatively low. Moderate variabilities were only found for the location effect and the location × time interaction. Other interaction effects were rather low with no effect for the genotype × time interaction

findings are discussed first and the individual climatic factors thereafter. The effect of the three main influential factors—'genotype' (genetic variation over time), 'location' (covering all regional variation) and 'time' (comprising all changes along the timeline except

those caused by altering genotypes; Section 2)—as well as their interactions highlight that the genotype effect explained about 4% of the variability of the yield development and therefore was comparatively low (Figure 7). The effect of the location on crop

yield explained about 22% of the total variance. Nearly 17% of the variance was explained by the location \times time interaction, whereas the genotype \times time interaction and the genotype \times location interaction either had no or a very low impact of about 1%. The three-way genotype \times location \times time interaction accounted for 5% of the total variance. However, the variability of the long-term yield development was predominantly explained by more than 50% of the total of the factors summarized as time effect. Changes in agronomic practices only play a minor role since data from crops grown under optimum N-fertilization levels and full crop protection were considered. Thus, the time effect mainly represents climatic changes.

3.5 | Elevated temperatures, heat stress and drought-affected yield development

In order to quantify the influence of an individual agroclimatic factor in terms of explained variance on yield development, we modified our model by including a fixed regression term for that particular agroclimatic variable (Section 2). The estimated variances explain the importance of a tested variable on yield development and can be considered as a 'coefficient of determination' for mixed-effect models (Piepho, 2019; Section 2).

The increase of the mean temperature during the GP explained about 16% of the yield variance over all locations (Figure 8; Table 4). Higher temperatures are presumed to have led to enhanced evapotranspiration rates during that phase, which also had an effect of about 16%. The number of days with maximum temperatures above 27 or 31°C during the GP explained about 25% and 17%, respectively, of the variance. While the effect of the mean global radiation on yield variation was relatively low during the entire GS (<2%), it was more pronounced during the phase of leaf development (6%) and stem elongation (4%). Heat stress and temperature effects were less pronounced when the influence of the soil yield potential or the soil type was removed from the random effects (Table S3).

The trend of the agroclimatic factors on yield development (Table 5), however, may vary from their magnitude of the explained variance. As for the genetic and nongenetic (time) effects, the trends were positively related to yield development at all sites combined and increased in average by about 0.044 and 0.049 t ha⁻¹ year⁻¹ respectively. The individual agroclimatic variables, however, were mainly negatively associated with yield (except for the mean global radiation during the SP). For instance, while the mean temperature during the GP (°C) reduced yields by about -0.278 t ha⁻¹ °C⁻¹ temperature increase, the effect over time was comparatively low with -0.004 t ha⁻¹ year⁻¹.

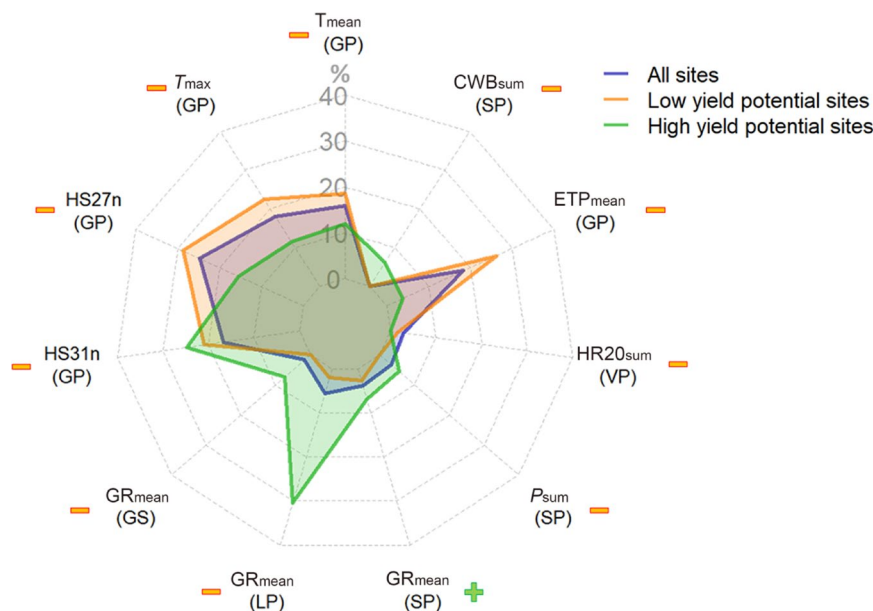


FIGURE 8 Effect of selected agroclimatic variables on winter wheat yield development. Each break represents an agroclimatic variable and the stretches of the coloured areas shows their influence in percentages, described as 'coefficient of determination for mixed effect-models' (Section 2). Low yield potential sites refer to sites with quality points between 0 and less than 70, while high yield potential sites refer to quality points between 70 and 100. The classification is based on the Muencheberg Soil Quality Rating (MSQR; Mueller et al., 2010; Section 2). T_{mean} is the average temperature (°C), T_{max} is the maximum temperature (°C), HS27n is defined as the number of heat stress days above 27°C, HS31n is defined as the number of heat stress days above 31°C, GRmean is the average global radiation (W/m²), Psum is the total precipitation amount (mm), HR20sum is the total amount of precipitation of days with minimum 20 mm precipitation (mm), ETPmean is the average winter wheat-specific potential evapotranspiration (mm), and CWBsum is the wheat-specific climatic water balance (mm). All climate variables are related to wheat-specific growth stages: the entire growing season (GS), the vegetative phase (VP), the generative phase (GP), the leaf developmental phase (LP) and the shooting phase (SP; Section 2). The mathematical symbol '+' describes a positive relationship to yield development and the '-' a negative relationship (Table 2)

TABLE 4 Estimated explained variance (%) of the agroclimatic variables (units in parentheses) on winter wheat yield development between 1958 and 2006 across the study sites in Germany. All explained variances are estimated after accounting for the genetic and nongenetic time trends. Low yield potential sites refer to sites with quality points between 0 and less than 70, while high yield potential sites refer to quality points between 70 and 100. (Section 2)

Phenological phase or stage	Agroclimatic variable	Description	Sites					
			Explained variance (%)			n		
			All	Low yield potential	High yield potential	All	Low yield potential	High yield potential
Growing season	GS_HS27_n	Number of heat stress days with $T_{\max} > 27^{\circ}\text{C}$	22	24.7	16.1	236	141	95
	GS_HS31_n	Number of heat stress days with $T_{\max} > 31^{\circ}\text{C}$	13.1	15.3	22.3	236	141	95
	GS_HS27_Tm_n	Number of heat stress days with $T_{\text{mean}} > 27^{\circ}\text{C}$	4.3	3.7	2.1	236	141	95
	GS_HS27_sum	Cumulative heat stress temperature with $T_{\max} > 27^{\circ}\text{C}$ ($^{\circ}\text{C}$)	22.6	25.2	17.4	236	141	95
	GS_HS31_sum	Cumulative heat stress temperature with $T_{\max} > 31^{\circ}\text{C}$ ($^{\circ}\text{C}$)	13.4	15.4	23.3	236	141	95
	GS_HS27_Tm_sum	Cumulative heat stress temperature with $T_{\text{mean}} > 27^{\circ}\text{C}$ ($^{\circ}\text{C}$)	4.2	3.6	2.1	236	141	95
	GS_GR_mean	Daily global radiation mean (W/m^2)	–	–	7.4	–	–	87
	GS_ETPm	Daily potential evapotranspiration mean (mm)	12.2	13.7	5.3	231	136	95
	GS_ETPs	Total potential evapotranspiration sum (mm)	11.1	15.8	3.2	231	136	95
	GS_CWBneg_n	Number of days with negative climatic water balance	2.4	1.8	–	236	141	–
	GS_CWBm	Daily climatic water balance mean (mm)	2.7	5.1	–	231	136	–
	GS_CWBs	Total climatic water balance sum (mm)	2.9	5.3	–	231	136	–
	GS_TD	Thermal duration ($^{\circ}\text{C}\text{d}$)	2.3	4.5	–	231	136	–
	GS	Duration (d)	6.3	8.7	–	233	138	–
Generative phase	GP_T_mean	Mean temperature ($^{\circ}\text{C}$)	15.9	18.6	12	229	134	95
	GP_T_max	Maximum temperature ($^{\circ}\text{C}$)	18	22.5	11.4	232	137	95
	GP_HS27_n	Number of heat stress days with $T_{\max} > 27^{\circ}\text{C}$	24.8	28.8	15.5	236	141	95
	GP_HS31_n	Number of heat stress days with $T_{\max} > 31^{\circ}\text{C}$	16.7	21	24.8	236	141	95
	GP_HS27_Tm_n	Number of heat stress days with $T_{\text{mean}} > 27^{\circ}\text{C}$	4.3	3.7	2.1	236	141	95
	GP_HS27_sum	Cumulative heat stress temperature with $T_{\max} > 27^{\circ}\text{C}$ ($^{\circ}\text{C}$)	25.5	29.5	17.1	236	141	95
	GP_HS31_sum	Cumulative heat stress temperature with $T_{\max} > 31^{\circ}\text{C}$ ($^{\circ}\text{C}$)	16.9	21.1	25.7	236	141	95
	GP_HS27_Tm_sum	Cumulative heat stress temperature with $T_{\text{mean}} > 27^{\circ}\text{C}$ ($^{\circ}\text{C}$)	4.2	3.6	2.1	236	141	95
	GP_GR_sum	Total global radiation sum (W/m^2)	–	1.2	4.7	–	108	87
	GP_ETPm	Daily potential evapotranspiration mean (mm)	18.2	26.1	3.8	229	–	95
	GP_ETPs	Total potential evapotranspiration sum (mm)	11.1	16.4	6	229	–	95
	GP_CWBm	Daily climatic water balance mean (mm)	2.9	7.5	–	229	–	–
	GP_CWBs	Total climatic water balance sum (mm)	–	3.1	–	–	134	–
	GP_TD	Thermal duration ($^{\circ}\text{C}\text{d}$)	–	–	2.9	–	95	–
	GP	Duration (d)	4.3	11	–	232	137	–

(Continues)

TABLE 4 (Continued)

Phenological phase or stage	Agroclimatic variable	Description	Sites					
			Explained variance (%)			n		
			All	Low yield potential	High yield potential	All	Low yield potential	High yield potential
Vegetative phase	VP_T_mean	Mean temperature (°C)	2	–	–	231	–	–
	VP_HR20_n	Number of days with precipitation >20 mm (mm)	2.3	–	–	236	–	–
	VP_HR20_sum	Cumulative rainfall amount of days with precipitation >20 mm (mm)	2.8	–	–	236	–	–
	VP_GR_mean	Daily global radiation mean (W/m ²)	–	1.1	–	–	108	–
	VP_CWBneg_n	Number of days with negative climatic water balance	3.7	–	–	236	–	–
	VP_TD	Thermal duration (°Cd)	2.1	–	3.6	231	–	95
Leaf development phase	LP_T_mean	Mean temperature (°C)	3	–	–	231	–	–
	LP_GR_mean	Daily global radiation mean (W/m ²)	5.6	2	30.4	195	108	87
	LP_GR_sum	Cumulative global radiation amount (W/m ²)	1.5	–	9.3	195	–	87
	LP_P_mean	Daily precipitation mean (mm)	2.9	–	–	231	–	–
	LP_CWBm	Daily climatic water balance mean (mm)	3.1	–	–	231	–	–
	LP_CWBneg_n	Number of days with negative climatic water balance	3.3	4.3	–	236	141	–
	LP_TD	Thermal duration (°Cd)	2.7	–	–	231	–	–
Stem elongation phase	LP	Duration (d)	2.6	3.8	–	233	138	–
	SP_HS27_n	Number of heat stress days with $T_{max} > 27^{\circ}\text{C}$	–	–	1.6	–	–	95
	SP_HS27_sum	Cumulative heat stress temperature with $T_{max} > 27^{\circ}\text{C}$ (°C)	–	–	1.8	–	–	59
	SP_GR_mean	Daily global radiation mean (W/m ²)	3.9	–	6.9	196	–	87
	SP_P_mean	Daily precipitation mean (mm)	–	–	2.5	–	–	95
	SP_P_sum	Total precipitation sum (mm)	3.3	–	5.5	231	–	95
	SP_HR20_n	Number of days with precipitation >20 mm	3.3	–	–	236	–	–
	SP_HR20_sum	Cumulative rainfall amount of days with precipitation >20 mm	3.5	–	–	236	–	–
	SP_CWBm	Daily climatic water balance mean (mm)	–	–	2.7	–	–	95
SP_CWBs	Total climatic water balance sum (mm)	–	–	6.1	–	–	95	
Sowing	SD	Day of year	9.1	11.2	6.1	233	138	95
Emergence	ED	Day of year	9	6.6	5	233	138	95
Hard dough	HDD	Day of year	4.4	9.7	–	234	139	–
Harvest	HVD	Day of year	2.8	8.9	–	233	138	–

3.6 | Sites with relatively low yield potential were particularly affected by temperature and heat stress events

After analysing the sensitivity of individual agroclimatic factors for the total of the sites represented, we separately examined those sites with relatively low (<70 quality points) and relatively high (>70 quality points) soil yield potential (Section 2). In comparison to the average of all locations, temperature-related effects were on average about one-sixth higher at sites with low yield potential (Figure 8 and Table 4).

There, the number of days with heat stress above 27°C during the GP explained nearly 30%, being the strongest effect of a single agroclimatic factor at the same time. Heat stress days above 31°C during the GP still explained up to 21%. The number of heat stress days above 31°C doubled within the whole observation period considered (Figure S6). Moreover, while the effect of the mean temperature during the GP increased to as much as 19%, the effect of maximum temperatures during the GP was even more pronounced and explained nearly 23% of the yield variation. As a consequence, the effect of the mean evapotranspiration during the GP also increased by more than one-third at

TABLE 5 Coefficient estimates of the fixed effects (genotype, time and selected agroclimatic variables as found in Figure 4) in the mixed-effect models on the yield development over time. *SE* denotes the standard error, *df* the degree of freedom, *n* the number of observations and *p* the significance of the estimates of each model. Values in parentheses describe the trend of the appropriate selected agroclimatic variable adjusted by its trend over time (Section 2). Low yield potential sites refer to sites with quality points between 0 and less than 70, while high yield potential sites refer to quality points between 70 and 100 (Section 2)

Sites	Model	<i>n</i>	Effect	Estimate	<i>SE</i>	<i>df</i>	<i>t</i>	<i>p</i>
All	1	229	Intercept	-70.674	17.689	53.5	-3.996	<.001
			Genotype	0.042	0.009	52.6	4.658	<.001
			Time	0.065	0.014	91.9	4.606	<.001
			Mean temperature during the generative phase (°C)	-0.278 (-0.004)	0.09	36.2	-3.1	.0037
	2	232	Intercept	-70.987	17.587	53.2	-4.036	<.001
			Genotype	0.042	0.009	52.4	4.721	<.001
			Time	0.064	0.014	97	4.617	<.001
			Maximum temperature during the generative phase (°C)	-0.228 (-0.004)	0.068	44.9	-3.329	.0017
	3	236	Intercept	-71.15	17.671	53.6	-4.026	<.001
			Genotype	0.04	0.009	53.6	4.472	<.001
			Time	0.066	0.014	99.4	4.793	<.001
			Number of days with $T_{max} > 27^{\circ}\text{C}$ during the generative phase	-0.098 (-0.0005)	0.021	66.2	-4.547	<.001
	4	236	Intercept	-67.226	17.787	56.3	-3.78	<.001
			Genotype	0.038	0.009	56.3	4.195	<.001
			Time	0.063	0.014	93.8	4.437	<.001
			Number of days with $T_{max} > 31^{\circ}\text{C}$ during the generative phase	-0.291 (-0.001)	0.074	77.9	-3.92	<.001
5	196	Intercept	-111.275	22.055	21.8	-5.045	<.001	
		Genotype	0.06	0.011	21.7	5.412	<.001	
		Time	0.065	0.027	51.9	2.44	.0181	
		Global radiation mean during the growing season (W/m^2)	-0.027 (-0.0006)	0.024	78.2	-1.141	.2572	
6	195	Intercept	-111.901	22.138	21.6	-5.055	<.001	
		Genotype	0.061	0.011	21.6	5.409	<.001	
		Time	0.057	0.026	43.2	2.217	.0319	
		Global radiation mean during the leaf development phase (W/m^2)	-0.037 (0.0031)	0.022	64.1	-1.671	.0996	
7	196	Intercept	-107.707	22.308	21.5	-4.828	<.001	
		Genotype	0.057	0.011	21.5	5.11	<.001	
		Time	0.038	0.027	42.1	1.404	.1678	
		Global radiation mean during the stem elongation phase (W/m^2)	0.006 (0.002)	0.005	67.6	1.196	.236	
8	231	Intercept	-67.273	17.884	55.1	-3.762	<.001	
		Genotype	0.038	0.009	55	4.213	<.001	
		Time	0.062	0.015	95.2	4.164	<.001	
		Cumulative precipitation amount during the stem elongation phase (mm)	-0.003 (-0.006)	0.002	88.6	-1.326	.1874	
9	133	Intercept	-68.859	17.779	55.7	-3.873	<.001	
		Genotype	0.027	0.011	39.9	2.447	.0189	
		Time	0.063	0.018	89.2	3.443	<.001	
		Cumulative precipitation amount of days with precipitation >20 mm during the vegetative phase (mm)	-0.013 (-0.0007)	0.005	54.3	-2.747	.0081	

(Continues)

TABLE 5 (Continued)

Sites	Model	n	Effect	Estimate	SE	df	t	p
	10	229	Intercept	-72.312	17.656	54.3	-4.096	<.001
			Genotype	0.04	0.009	52.9	4.44	<.001
			Time	0.06	0.015	87.7	4.107	<.001
			Mean potential evapotranspiration during the generative phase (mm)	-0.01 (-0.0063)	0.004	87.4	-2.325	.0224
	11	231	Intercept	-67.449	17.968	54.8	-3.754	<.001
			Genotype	0.038	0.01	54.6	4.234	<.001
			Time	0.062	0.015	92	4.14	<.001
			Climatic Water balance during the stem elongation phase (mm)	-0.06 (0.0299)	0.085	91	-0.704	.4832
Low yield potential	1	134	Intercept	-79.469	19.39	30.4	-4.098	<.001
			Genotype	0.0463	0.01	29.6	4.729	<.001
			Time	0.0638	0.018	71.2	3.489	<.001
			Mean temperature during the generative phase (°C)	-0.31 (-0.0039)	0.119	31.8	-2.606	.0138
	2	137	Intercept	-79.03	19.306	30.6	-4.094	.0003
			Genotype	0.0463	0.01	29.8	4.762	<.001
			Time	0.0609	0.018	79.9	3.48	<.001
			Maximum temperature during the generative phase (°C)	-0.261 (-0.0039)	0.091	37.8	-2.864	.0068
	3	141	Intercept	-79.858	19.323	32.6	-4.133	<.001
			Genotype	0.044	0.01	32.6	4.546	<.001
			Time	0.061	0.017	83.4	3.579	<.001
			Number of days with $T_{max} > 27^{\circ}\text{C}$ during the generative phase	-0.115 (-0.0055)	0.03	54.8	-3.846	<.001
	4	141	Intercept	-75.933	19.602	34.1	-3.874	<.001
			Genotype	0.042	0.01	34.1	4.257	<.001
			Time	0.062	0.018	87.6	3.551	<.001
			Number of days with $T_{max} > 31^{\circ}\text{C}$ during the generative phase	-0.36 (-0.0017)	0.105	56.6	-3.44	.0011
	5	109	Intercept	-140.762	19.185	8.6	-7.337	<.001
			Genotype	0.075	0.01	8.4	7.755	<.001
			Time	0.07	0.034	50.1	2.053	.0454
			Global radiation mean during the growing season (W/m^2)	-0.02 (-0.0001)	0.034	40.3	-0.588	.5596
	6	108	Intercept	-142.203	19.19	8.4	-7.41	<.001
			Genotype	0.076	0.01	8.4	7.818	<.001
			Time	0.059	0.035	49.9	1.708	.0939
			Global radiation mean during the leaf development phase (W/m^2)	-0.04 (0.0003)	0.029	39.1	-1.377	.1762
	7	109	Intercept	-139.277	19.93	8.9	-6.988	<.001
			Genotype	0.073	0.01	8.9	7.29	<.001
			Time	0.03	0.035	50.9	0.856	.3962
			Global radiation mean during the stem elongation phase (W/m^2)	0.01 (0.0036)	0.008	38.4	1.335	.1896

(Continues)

TABLE 5 (Continued)

Sites	Model	n	Effect	Estimate	SE	df	t	p
	8	141	Intercept	-76.159	19.703	33.1	-3.865	<.001
			Genotype	0.042	0.01	33.1	4.245	<.001
			Time	0.06	0.018	88.8	3.263	.0016
			Cumulative precipitation amount during the stem elongation phase (mm)	-0.004 (-0.0037)	0.003	54.8	-1.6	.1153
	9	141	Intercept	-78.441	19.483	33	-4.026	<.001
			Genotype	0.043	0.01	33	4.4	<.001
			Time	0.059	0.018	88.3	3.216	.0018
			Cumulative precipitation amount of days with precipitation >20 mm during the vegetative phase (mm)	-0.006 (-0.0015)	0.003	60.2	-1.805	.0762
	10	134	Intercept	-80.651	19.487	31	-4.139	<.001
			Genotype	0.045	0.01	30.9	4.612	<.001
			Time	0.065	0.018	71	3.586	<.001
			Mean potential evapotranspiration during the generative phase (mm)	-0.517 (-0.0116)	0.168	42.5	-3.077	.0036
	11	136	Intercept	-76.251	19.876	32.5	-3.836	<.001
			Genotype	0.042	0.01	32.5	4.178	<.001
			Time	0.059	0.019	78	3.127	.0025
			Climatic Water balance during the stem elongation phase (mm)	-0.004 (0.0002)	0.003	48.1	-1.244	.2197
High yield potential	1	134	Intercept	-79.469	19.39	30.4	-4.098	<.001
			Genotype	0.0463	0.01	29.6	4.729	<.001
			Time	0.0638	0.018	71.2	3.489	<.001
			Mean temperature during the generative phase (°C)	-0.31 (-0.0039)	0.119	31.8	-2.606	.0138
	2	137	Intercept	-79.03	19.306	30.6	-4.094	.0003
			Genotype	0.0463	0.01	29.8	4.762	<.001
			Time	0.0609	0.018	79.9	3.48	<.001
			Maximum temperature during the generative phase (°C)	-0.261 (-0.0039)	0.091	37.8	-2.864	.0068
	3	141	Intercept	-79.858	19.323	32.6	-4.133	<.001
			Genotype	0.044	0.01	32.6	4.546	<.001
			Time	0.061	0.017	83.4	3.579	<.001
			Number of days with $T_{max} > 27^{\circ}\text{C}$ during the generative phase	-0.115 (-0.0055)	0.03	54.8	-3.846	<.001
	4	141	Intercept	-75.933	19.602	34.1	-3.874	<.001
			Genotype	0.042	0.01	34.1	4.257	<.001
			Time	0.062	0.018	87.6	3.551	<.001
			Number of days with $T_{max} > 31^{\circ}\text{C}$ during the generative phase	-0.36 (-0.0017)	0.105	56.6	-3.44	.0011
	5	109	Intercept	-140.762	19.185	8.6	-7.337	<.001
			Genotype	0.075	0.01	8.4	7.755	<.001
			Time	0.07	0.034	50.1	2.053	.0454
			Global radiation mean during the growing season (W/m^2)	-0.02 (-0.0001)	0.034	40.3	-0.588	.5596

(Continues)

TABLE 5 (Continued)

Sites	Model	n	Effect	Estimate	SE	df	t	p
6	108	Intercept	-142.203	19.19	8.4	-7.41	<.001	
		Genotype	0.076	0.01	8.4	7.818	<.001	
		Time	0.059	0.035	49.9	1.708	.0939	
		Global radiation mean during the leaf development phase (W/m ²)	-0.04 (0.0003)	0.029	39.1	-1.377	.1762	
7	109	Intercept	-139.277	19.93	8.9	-6.988	<.001	
		Genotype	0.073	0.01	8.9	7.29	<.001	
		Time	0.03	0.035	50.9	0.856	.3962	
		Global radiation mean during the stem elongation phase (W/m ²)	0.01 (0.0036)	0.008	38.4	1.335	.1896	
8	141	Intercept	-76.159	19.703	33.1	-3.865	<.001	
		Genotype	0.042	0.01	33.1	4.245	<.001	
		Time	0.06	0.018	88.8	3.263	.0016	
		Cumulative precipitation amount during the stem elongation phase (mm)	-0.004 (-0.0037)	0.003	54.8	-1.6	.1153	
9	141	Intercept	-78.441	19.483	33	-4.026	<.001	
		Genotype	0.043	0.01	33	4.4	<.001	
		Time	0.059	0.018	88.3	3.216	.0018	
		Cumulative precipitation amount of days with precipitation >20 mm during the vegetative phase (mm)	-0.006 (-0.0015)	0.003	60.2	-1.805	.0762	
10	134	Intercept	-80.651	19.487	31	-4.139	<.001	
		Genotype	0.045	0.01	30.9	4.612	<.001	
		Time	0.065	0.018	71	3.586	<.001	
		Mean potential evapotranspiration during the generative phase (mm)	-0.517 (-0.0116)	0.168	42.5	-3.077	.0036	
11	136	Intercept	-76.251	19.876	32.5	-3.836	<.001	
		Genotype	0.042	0.01	32.5	4.178	<.001	
		Time	0.059	0.019	78	3.127	.0025	
		Climatic Water balance during the stem elongation phase (mm)	-0.004 (0.0002)	0.003	48.1	-1.244	.2197	

sites with light soils to 26% in comparison to the total of the sites considered. Similar effects were found for soils classified as light soils, which are shown in Table S6.

Except for the effect of days with maximum temperatures above 31°C during the GP, temperature and heat stress effects were less pronounced at sites with higher yield potential (Figure 8). Here the explained yield variance decreased to about 16% for the effect of days with maximum temperatures above 27°C during the GP. Yet, when stress events with maximum temperatures above 31°C occurred, the explained variance increased from 17% to 25%.

Regarding the exposure of wheat to heat stress events above 31°C during the GP along the overall time effect, sites with fewer heat stress events were less afflicted by high temperatures than sites with more stress events (Figure 9a). Winter wheat yields increased at sites of low yield potential and with an average of 1.6 heat stress days by 0.1 t DM ha⁻¹ year⁻¹, while at sites with an average of 3.6 heat stress days yields increased by about 0.088 t DM ha⁻¹ year⁻¹.

At sites with high yield potential and exposed to 1.9 heat stress days during the GP, yields increased by about 0.072 t DM ha⁻¹ year⁻¹ and by about 0.071 t DM ha⁻¹ year⁻¹ at sites with 3.0 heat stress days (Figure 9b).

3.7 | Negative effects due to high rainfall events and water deficit

Interestingly, our data reveal that effects related to high precipitation events (defined as days with more than 20 mm precipitation) became relevant during the VP (Figure 8). Here the total amount of precipitation through high rainfall events explained about 2.8% of the variance in winter wheat yields. The effect was strongest during the SP (3.5%), which still is inferior to temperature-related effects. Nevertheless, waterlogging might become more likely due to high precipitation events, leading to oxygen deficiency or enhanced

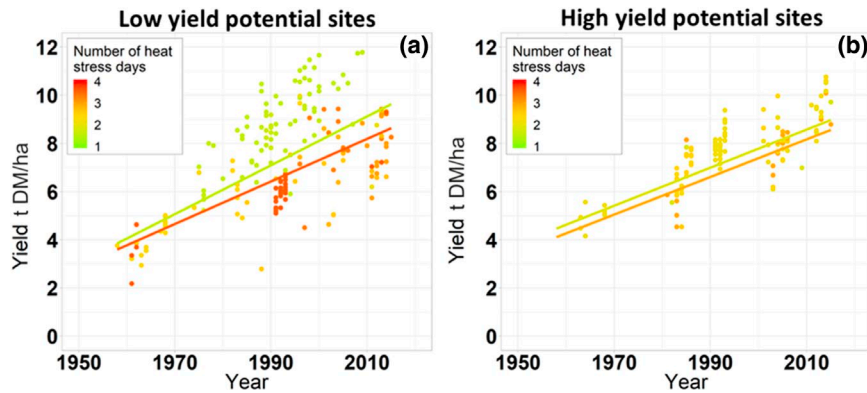


FIGURE 9 Grain yield evolution of winter wheat at sites with different heat stress conditions during the generative growth phase at sites with (a) low (0–70 quality points) and (b) high (70–100 quality points) yield potential (classified based on the Muncheberg Soil Quality Rating [MSQR; Mueller et al., 2010; Section 2]). The different colours depict the number of heat stress days during generative phase for each single site-year (points) and trend (lines) at the sites with the lowest (green lines [a] & [b]) and highest (red line [a]; orange line [b]) number of heat stress days

erosion processes, which causes nutrient losses accelerated by a reduced ground cover canopy in particular during the LP at sites with higher clay content (Malik, Colmer, Lambers, Setter, & Schortemeyer, 2002; Nearing et al., 2005). The effect of the overall precipitation amount during the SP was more than 1.5-fold stronger at sites of high yield potential (5.5%) as compared to all sites (3.3%). The magnitude of radiation effects increased at sites with higher yield potential, foremost during leaf development to up to 30%. The relatively large temperature and radiation effects are presumed to have resulted in an enhanced effect of the negative CWB in particular during stem elongation. This effect was not evident when considering the total of all sites or sites with low yield potential only. All climate effects are found in a similar way in soils classified as heavy (Table S7).

4 | DISCUSSION

For interpreting the results of the statistical models used for time-series analysis, several aspects need to be considered. First, these models tend to include collinearity effects between predictor variables (e.g. temperature and precipitation) and hence results do not stack up automatically to 100% (Lobell & Burke, 2010b). This means a single effect might be suppressed or intensified due to interdependencies or confounding effects with other variables. Moreover, they assume that past relationships will continue in future, even though, for example, management systems may have evolved or changed completely, and they may have low signal-to-noise ratios in yield or weather records in many locations (Lobell & Burke, 2010a).

In this meta-analysis, we found that many agroclimatic effects were negatively related to yield development except for the mean global radiation during SP. We assume that the prolongation of the SP was caused by breeding progress since the mean temperature during this phase did not change significantly and modelling revealed no effect. Moreover, the SP is known to be critical for yield development and has been proposed as a target trait to improve

yield and environmental adaptation of wheat in numerous studies (González, Slafer, & Miralles, 2003; Kronenberg, Yu, Walter, & Hund, 2017; Miralles, Richards, & Slafer, 2000). The prolongation of the SP may, however, also have been due to advanced sowing dates. The advanced sowing may have been a consequence of changed climates prior to sowing dates (Johnen, Boettcher, & Kage, 2012). The probability of a higher number of leaf primordia initiated between sowing and the double ridge stage is greater with earlier sowing and may lead to a delay in the appearance of the leaves that emerge until stem elongation and of the final flag leaf until heading (Johnen et al., 2012). However, the duration of the SP did not change significantly beyond 1988—nearly one decade before winter wheat yields, in general, started to level off (Figure 4a). Interestingly, the TD of the SP showed an ongoing increase by approximately 40°Cd between 1988 and 1997. This may indicate that in this period winter wheat continued to increase radiation uptake due to enhanced temperature and light use potential during stem elongation as well as due to increased nitrogen uptake from the continuous increase of fertilizer input (Loomis & Amthor, 1999).

The values presented in Figure 7 reflect the explained variance of the main effects (genotype, location, time) and their interactions. The results show that the variability of the time effects explained the variance of the winter wheat yields over time and across the study sites the most, followed by the variability of the location effect. However, a lower explained variance of the genotype effect does not automatically mean that this factor has a lower influence on yield development. The slopes of the specific covariates used in the fixed regression part of the mixed-effects model might, therefore, provide a more detailed assessment (Table 5). While most of the agroclimatic parameters had a negative impact on yield development, the effect of the genotype was always positive. However, the slopes of the agroclimatic covariates come in their own unit (e.g. °C) and in themselves have no time unit as the genetic and the overall time effect. Hence, an adjusted climate trend, which was obtained by multiplying the slope

of the covariate with the time trend of this specific covariate, was used for comparison with the two temporal trends (Section 2). We found that the trend of the genetic progress was, for example, about 100 times larger than the trend of the mean or maximum temperature during the GP at all study sites ($0.004 \text{ t ha}^{-1} \text{ year}^{-1}$)—as well as at sites with lower or greater yield potential. Moreover, the results indicate a high-temperature variability between the years and over the locations in this study.

This study uses the agronomic yield maxima for each experimental year and site as achieved by optimal N-fertilization dosage (estimated from fertilizer dose–yield response functions, Section 2) and optimal plant protection. In this way, the effect of variation of agronomic practices over time was minimized so that the overall time trend essentially reflects climatic effects (Figures 7 and 8). In practice, however, optimal agronomic management is often not realized on the farmers' fields (Figure 4a). In practical farming, socio-economic aspects have an important influence on the intensity of agronomic inputs, for example the fact that since the late 1990s subsidies from the European Union have been paid based on production area instead on yield, or that export subsidies were reduced (Himanen et al., 2013; Reidsma et al., 2008). Nevertheless, we also assume that the optimal amount of N fertilizer is a result of decreasing prices of nitrogen, comparable to, for example, decreasing prices of the crops and, additionally.

The increased potential evapotranspiration during stem elongation between 1951 and 1992 is very likely a result of the SP prolongation rather than a climatic change response, as for mean temperature and precipitation no significant changes were detected, and mixed-model analysis revealed no effects due to potential evapotranspiration. This prolongation is probably also the explanation of the increased number of days with negative CWB until 1997. Resulting water limitations, accompanied by an increased number of heat stress days during stem elongation (Figure S6) may have enhanced irreversible plant damage associated with yield losses in particular on shallow soils and/or in dry regions before maturity was reached (Farooq et al., 2011; Semenov, 2009).

Our data show that yield stagnation in German winter wheat occurred since the late 1990s for all sites combined, and since the late 1980s on soils with relatively low yield potential. Climate variation—spatial and temporal—explained most of the variability of the winter wheat yields (>50%), whereas genetic variation over time explained only 4%. Our results emphasize that except for heat stress days with more than 31°C , sites with higher yield potential were less prone to adverse weather effects than sites with lower yield potential. In general, elevated temperatures, heat stress during the GP and drought stress during the SP affected wheat development the most. Regarding the sole effect of the agroclimatic variables at all experimental sites combined, the mean temperature during the GP explained about 16% of the yield variability. Days with maximum temperatures above 27 or 31°C during the GP explained about 25% and 17% respectively. With respect to the winter wheat yield development of the entire observation period (1958–2015), the mean temperature during the GP reduced yields by about 0.23 t/ha in

total. At sites with higher yield potential, relatively large radiation effect during the leaf development (30%) and negative precipitation effects during stem elongation (5.5%) are presumed to have resulted in an enhanced effect of the negative CWB in particular during stem elongation. Hence, the response of yield productivity to past climatic conditions demonstrates the sensitivity of German wheat production to climatic variation and underlines the need of finding adaptation strategies for food production under expected ongoing climate change.

The analysis shows that German wheat production is continuously adjusting to climatic changes, both with regard to the genetic adjustment (i.e. respective cultivar/variety selection choice) as well as management adjustment, especially shift of sowing times. However, in the light of continuous climatic changes in the future, further cropping system adjustments might be required to support stable winter wheat production in Germany. As such, it might be necessary to employ additional measures such as irrigation, in particular at sites with light soils and high risk of drought induced yield losses. Furthermore, earlier sowing in combination with 'early' wheat genotypes might be suitable to escape drought stress.

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CONFLICT OF INTERESTS

The authors declare that there are no competing interests.


AUTHOR CONTRIBUTION

All authors contributed to the content of the manuscript, discussed the results and commented on the manuscript. E.B. and L.B. collected the data. E.B. carried out the statistical analysis and wrote the major part of the manuscript.

DATA AVAILABILITY STATEMENT

All data and sources used in this study are available at Bonares Datenzentrum (<https://doi.org/10.20387/bonares-YG6F-K61B>). Correspondence and requests for material should be addressed to E.B. and H.S.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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