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LETTER

Site conditions determine heat and drought induced yield losses in wheat and rye in Germany

Ludwig Riedesel[1,*], Markus Möller[2], Hans-Peter Piepho[3], Dirk Rentel[4], Carolin Lichthardt[4], Burkhard Golla[1], Timo Kautz[5] and Til Feike[1]

[1] Julius Kuehn Institute (JKI)—Federal Research Centre for Cultivated Plants, Institute for Strategies and Technology Assessment, Stahnsdorfer Damm 81, 14532 Kleinmachnow, Germany
[2] Julius Kuehn Institute (JKI)—Federal Research Centre for Cultivated Plants, Institute for Crop and Soil Science, Bundesallee 58, 38116 Braunschweig, Germany
[3] University of Hohenheim, Institute of Crop Science, Biostatistics Unit, Fruwirthstrasse 23, 70599 Stuttgart, Germany
[4] Bundessortenamt, Osterfelddamm 80, 30627 Hannover, Germany
[5] Humboldt University of Berlin, Thaer-Institute of Agricultural and Horticultural Sciences, Unter den Linden 6, 10099 Berlin, Germany
[*] Author to whom any correspondence should be addressed.

E-mail: ludwig.riedesel@julius-kuehn.de

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Abstract

Heat and drought are major abiotic stressors threatening cereal yields, but little is known about the spatio-temporal yield effect of these stressors. In this study, we assess genotype (G) × environment (E) × management (M) specific weather-yield relations utilizing spatially explicit weather indices (WIs) and variety trial yield data of winter wheat (*Triticum aestivum*) and winter rye (*Secale cereale*) for all German cereal growing regions and the period 1993–2021. The objectives of this study are to determine the explanatory power of different heat and drought WIs in wheat and rye, to quantify their site-specific yield effects, and to examine the development of stress tolerance from old to new varieties. We use mixed linear models with G × E × M specific covariates as fixed and random factors. We find for both crops that combined heat and drought WIs have the strongest explanatory power during the reproductive phase. Furthermore, our results strongly emphasize the importance of site conditions regarding climate resilience, where poor sites reveal two to three times higher yield losses than sites with high soil quality and high annual precipitation in both crops. Finally, our analysis reveals significantly higher stress-induced absolute yield losses in modern vs. older varieties for both crops, while relative losses also significantly increased in wheat but did not change in rye. Our findings highlight the importance of site conditions and the value of high-yielding locations for global food security. They further underscore the need to integrate site-specific considerations more effectively into agricultural strategies and breeding programs.

1. Introduction

Crop yields and the respective yield formation processes are complex and influenced by a combination of genetic (G) and management (M) factors, as well as the local environmental conditions (E) in which the crops are grown [1, 2]. As global warming continues, heat and drought stress are increasingly affecting yields and their variability globally [3–6], in Europe [7–9], and in Germany [10–12].

In particular, high temperatures reduce photosynthetic rates, increase respiration and accelerate leaf senescence, while they also impede fertilization during anthesis leading to a decrease in grain number [13–15]. Drought stress interferes with nutrient uptake and reduces transpiration, leaf growth and photosynthetic rates [16, 17]. In addition, heat and drought stress can be mutually reinforcing, and mostly more severe than those from either stress alone [5].

Winter wheat (*Triticum aestivum*) and winter rye (*Secale cereale*) are important staple crops in many world regions. While wheat is the most relevant crop for global food security [18], rye is increasingly

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important under climate change due to its superior properties against abiotic stress (i.e. climate resilience) [19] and its lower carbon footprint (i.e. climate mitigation) [20] compared to wheat. While their genetic differences and their plant physiological reaction to heat and drought stress have been well studied for wheat and rye in greenhouse experiments [19, 21], there is still high uncertainty regarding the site-specific effects of adverse weather on wheat and rye yields [22–25]. Different studies found diverging yield responses to heat and drought stress in different regions [7, 11].

Therefore, high-resolution G × E × M data are essential to disentangle influencing factors and analyze site-specific weather effects on crop yields [11]. In addition, crop-specific phenology data are a fundamental prerequisite to comprehend these confounding factors and achieve a thorough understanding of local weather effects on crops [26–28]. To our knowledge, no study has used such an extensive dataset to analyze the site-specific effects of combined heat and drought stress in wheat vs. rye.

Thus, we integrate wheat and rye variety trial data with gridded weather and phenological data at the national level for Germany from1993 to 2021. We aim to (1) describe the trend of heat and drought weather indices (WIs) over 29 years in Germany; (2) analyze the explanatory power of combined heat and drought WIs in wheat and rye; (3) identify and compare the effect size of combined heat and drought WIs on specific site clusters; and to (4) assess the genetic development towards stress tolerance of released varieties.

2. Material and methods

2.1. Study design

Figure 1 illustrates the study design along with the different data integration steps following Riedesel *et al* [11]: (1) we collect yield data, weather data, and phenological data (section 2.2). (2) We use site-specific phenological data from the model PHASE as well as trial-specific observations from the trial data. (3) We integrate phenological data with weather data and derive a set of spatio-dynamic WIs [29] based on the resulting nationwide 1 km^2 grid database. (4) We position the variety trial locations in the 1 km^2 grids corresponding to their coordinates and match the gridded WI with the yield data from each variety trial (section 2.3). (5) We statistically analyze the resulting data using a mixed model approach (section 2.4). Note: the input data, represent the best Germany-wide database, but are characterized by different geometric and semantic resolutions and thus by different scale-specific explanatory power, which may be a limitation to the scale-specific representativeness of the input data [30].

2.2. Data

2.2.1. Yield data

We conduct an analysis of yield data from German pre-registration variety trials, kindly provided by the Federal Plant Variety Office (Bundessortenamt) (table 1). In Europe, varieties need to proof additional value for cultivation and use (VCU) to be registered to a national list. In order to describe the VCU for wheat and rye, varieties submitted to be registered in Germany are tested in field trails at multiple sites representing all typical growing regions within Germany for three testing years. Our analysis focuses only on wheat and rye varieties that were finally approved and released for commercial production. In addition to yield characteristics, the dataset includes G × E × M specific information listed in table A in the appendix. Further information on the structure of the dataset can be found in previous studies for example by Laidig *et al* [31–33], Hadasch *et al* [34], or Hartung *et al* [35].

2.2.2. Soil data

We utilize two distinct datasets that describe soil quality to maximize the robustness of statements regarding soil quality. The parameter ‘soil quality’ is known as ‘Ackerzahl’ and based on a method for assessing the quality of arable land on a scale from 0–100 points that has been used in Germany since the 19th century and is provided for each trial in the variety trial dataset. Additionally, we use the soil quality rating (SQR) soil map to describe the yield potential of the trial sites with external data [36]. The SQR globally classifies soils according to their suitability for agricultural land use and yield potential, with the final score ranging from 0 to 102 points. The SQR map is available at a resolution of 250 m^2 on a scale of 1:1000 000 [37].

2.2.3. Weather and soil moisture data

The German Weather Service (DWD) supplies daily meteorological data, which includes daily maximum temperature readings from an extensive network of weather stations. This data is interpolated to a 1 km^2 grid resolution [38]. Additionally, the DWD offers soil moisture data, sourced from the statistical model AMBAV [39]. The AMBAV model integrates daily weather data, soil type, evaporation, and crop-specific phenological stages to generate daily soil moisture insights. This model also provides data on a 1 km^2 grid resolution. For further details, refer to Friesland and Löpmeier [40], Herbst *et al* [41], and appendix section context-A.

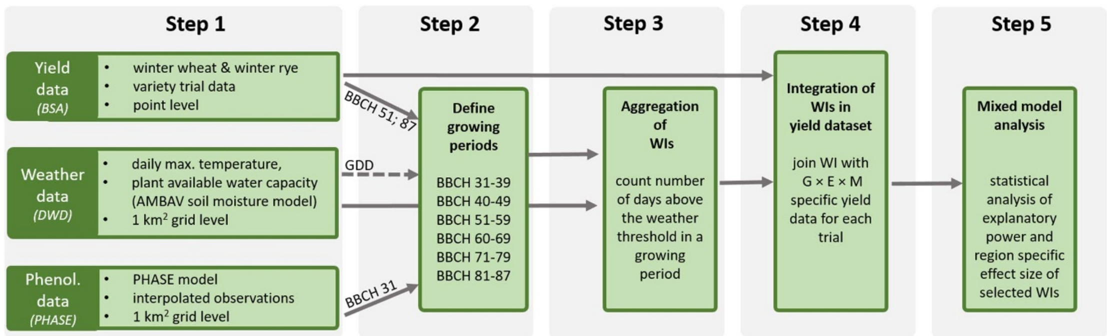

Figure 1. Overview of the study design and respective four working steps from 'Step 1' listing the data sets used, 'Step 2' defining phenological growing periods from different data sets, 'Step 3' aggregation of spatiotemporal weather indices (WIs), 'Step 4' integration of all data into one comprehensive dataset and 'Step 5' statistical analysis.

Table 1. Description of variety trial dataset for wheat and rye trials.

	Wheat	Rye
No. of variety trial sites	89	85
Average yield (t/ha)	9.8	8.8
No. of varieties (hybrid/population)	403	93 (77/23)
No. of trials (year × variety × site × trial series)	28 187	10 290

2.2.4. Phenological data

To achieve the highest possible crop-specific and spatio-temporal accuracy of the phenological stages, we use gridded (PHASE model [29, 42, 43]) and trial specific (variety trial data) phenological data (table 2). Additionally, we supplement the missing phenological stages in the data (i.e. booting, anthesis, milk ripening, and dough ripening) by employing a growing-degree-day approach according to McMaster and Wilhelm [44]. We calculate those stages for each trial using the reported trial specific day of year of the stage heading as starting point (table 2). We report the stages by a uniform decimal code according to Lancashire *et al* [45] and form phenological growing periods shown in figure 2.

2.3. WI configuration

To configure the WIs in this study, we follow the procedure outlined in Riedesel *et al* [11] and specify the WIs using site-specific phenological data. We blend the growing periods with gridded meteorological data from the DWD [49] including gridded daily data on plant available water (PAW) as percentage of plant available water capacity (PAWC) from the AMBAV model [39] to calculate combined heat and drought WIs. We account WIs as the cumulative number of days with daily maximum temperatures above 27 °C (i.e. moderate intensity), 29 °C (i.e. severe intensity), and 31 °C (i.e. extreme intensity) and PAW below 50% (i.e. moderate intensity), 30% (i.e. severe intensity), and 10% (i.e. extreme intensity) of PAWC.

2.4. Statistical analysis

2.4.1. Basic model

We use a linear mixed model with factors genotype, site, trial series and year according to Hartung *et al* [35] given by:

$$y_{ijkl} = \mu + G_i + Y_k + L_j + (LY)_{jk} + (LYT)_{jkl} + (GL)_{ij} + (GY)_{ik} + (GLY)_{ijk} + \varepsilon_{ijkl} \quad (1)$$

where y_{ijkl} is the mean yield of the ith genotype in the jth site and kth year within the lth trial series, μ is the overall mean, G_i is the main effect of the ith genotype, L_j is the main effect of the jth site, and Y_k is the main effect of the kth year. The effects $(LY)_{jk}$, $(GL)_{ij}$, $(GY)_{ik}$, and $(GLY)_{ijk}$ are the interaction effects of the corresponding main effects, ε_{ijkl} is the residual. In the trial data, each year starts a new testing cycle comprising a series of three test years (i.e. (T); S1, S2, S3). As in some sites, more than one cycle may be represented by a different series, we include $(LYT)_{jkl}$ as the main trial effect of the lth trial series, nested within the kth years and lth sites. All effects except μ, are assumed to be random and independent with constant variance for each effect.

We integrate time trends for genetic G_i and non-genetic Y_k as fixed regression components into the model:

$$G_i = \beta r_i + H_i \quad (2)$$

where β is the fixed regression coefficient for the genetic trend, is the first year in trial (FYT) for the ith cultivar, and H_i is the random deviation of G_i from the genetic trend line.

We model the non-genetic time trend as:

$$Y_k = \gamma t_k + Z_k \quad (3)$$

where γ is the fixed regression coefficient for the non-genetic trend, t_k is the continuous covariate for the harvest year and Z_k is a random residual. The time effect predominantly represents the effect of climatic changes, as time variable management effects are considered within the term $(LY)_{jk}$.

Table 2. Description of different calculation approaches to obtain the trial specific phenological stage entries of wheat (ww) and rye (wr). Note: GDD values are estimated based on different sources and expert knowledge.

Stage	BBCH	Approach	Source
Stem elongation	31	Interpolated observations (1 km^2)	PHASE model
Booting	41	Heading −200 GDD (base: 0 °C)	Alquadah *et al* [46]
Heading	51	Trial-specific observations	Variety trial data
Anthesis	60	Heading + 200 GDD (base: 0 °C)	Alquadah *et al* [46], Miller *et al* [47]
Milk ripening	71	Heading + 450/500 GDD (ww/wr; base: 0 °C)	Ercoli *et al* [48], Miller *et al* [47]
Dough ripening	80	Heading + 650/700 GDD (ww/wr; base: 0 °C)	Ercoli *et al* [48], Miller *et al* [47]
Yellow ripening	87	Trial specific observations	Variety trial data

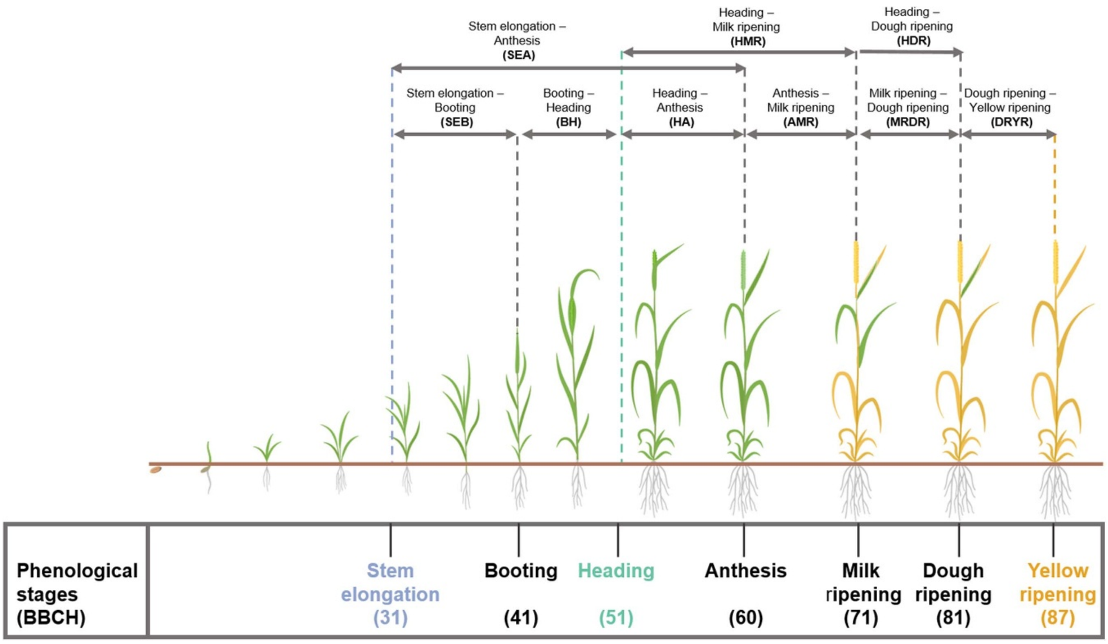

Figure 2. Overview of phenological stages with BBCH code from the PHASE model (stem elongation), the trial dataset (heading; yellow ripening) and GDD calculations (booting; anthesis; milk ripening; dough ripening) as well as respective stage-to-stage and cross-stage growing periods for WI calculations. Stage-to-stage growing periods are displayed as: stem elongation—booting (SEB; BBCH: 31–39); booting—heading (BH; BBCH: 41–49); heading-anthesis (HA; BBCH: 51–59); anthesis—milk ripening (AMR; BBCH: 60–69); milk ripening—dough ripening (MRDR; BBCH: 71–79); dough ripening—yellow ripening (DRYR; BBCH: 81–87). Cross-stage growing periods are displayed as: stem elongation—anthesis (SEA; BBCH: 31–59); heading—milk ripening (HMR; BBCH: 51–69); heading—dough ripening (HDR; BBCH: 51–79).

We additionally adjust for time-constant environmental (E) covariates to account for location differences between the trial sites as:

$$L_j = \delta u_j + S_j \quad (4)$$

where L_j is the main effect of the jth site, δ is the fixed regression coefficient for the respective E covariate, u_j is its specific value for the jth site and S_j is the random deviation from the trend. All E covariates (u_j) tested in the model are listed in table A in the appendix.

We further include time-variable management (M) covariates to control for the varying farming practices between sites and trials as:

$$(LYT)_{jkl} = \varphi m_{jkl} + R_{jkl} \quad (5)$$

where $(LYT)_{jkl}$ is the main effect of the jth site, kth year and lth trial series, φ is the fixed regression coefficient for the respective M covariate, m is the specific value of the M covariate and R_{jkl} the is the random deviation from the trend. In this study we used data from crops grown under optimum N-fertilization levels and full crop protection, limiting the selection options of M attributes. All M covariates (m_{jkl}) tested in the model are listed in table A in the appendix.

The WIs represent time-variable weather extremes that cause adverse yield effects and are included as:

$$(LY)_{jk} = \alpha s_{jk} + C_{jk} \quad (6)$$

where α is the fixed regression coefficient for the respective WI covariate, s_{jk} is the specific value of the covariate for the kth year and the jth site and C_{jk} is a random residual. We list all WI covariates in table 2.

Table 3. Site clusters (N) with its cluster group (m), defined cluster threshold and respective share of trials per cluster group for wheat and rye.

site cluster	cluster group	cluster threshold	Share trials wheat	No. trials rye
Precipitation	Precipitation +	>650 mm	45.18%	61.47%
	Precipitation −	⩽650 mm	54.82%	38.53%
Soil quality	Soil quality+	>50 points	86.90%	35.30%
	Soil quality−	⩽50 points	13.10%	64.7%
Soil type	Soil type +	Loam	90.22%	48.77%
	Soil type −	Sand	9.78%	51.23%
Soil quality rating	sqr +	>60 points	77.89%	52.35%
	sqr −	⩽60 points	22.11%	47.65%

The final model can be described as:

$$y_{ijkl} = \mu + \beta r_i + H_i + \gamma t_k + Z_k + \delta u_j + S_j + \varphi m_{jkl} + R_{jkl} + \alpha s_{jk} + C_{jk} + (GL)_{ij} + (GY)_{ik} + (GLY)_{ijk} + \varepsilon_{ijkl}. \quad (7)$$

2.4.2. Explanatory power
Following Riedesel *et al* [11], we use the method of variance reduction for the selection of the E and M covariates, as well as for decoupling the explanatory power of the individual and combined heat and drought WIs.

Therefore, we quantify the variance reduction (VR—$\%\mathrm{Var}_y$) of each covariate by estimating the coefficient of determination (R^2) for mixed models following Piepho [50]:

$$\%\mathrm{Var}_y = \frac{\mathrm{Var}_{y(M-x)} - \mathrm{Var}_{y(M+x)}}{\mathrm{Var}_{y(M-x)}} \times 100. \quad (8)$$

In this regard, we analyze the marginal variance of the random effects of equation (1) (M) twice—first without ($\mathrm{Var}_{y(M-x)}$) and second with ($\mathrm{Var}_{y(M+x)}$) the covariate under assessment. Next, we derive the VR between both models as described in equation (8).

For selecting *E* and *M* covariates, we apply a forward selection procedure, where we add the covariates sequentially, one at a time to our baseline model. In this context, we select a covariate when the VR of was at least −0.5% compared to the baseline model ($\mathrm{Var}_{y(M-x)}$). The list covariates is displayed in appendix table A and the VR of the selected variables is listed in appendix table B.

2.4.3. Estimating site-specific effect size of heat and drought WI
For evaluating the different site-specific impact on weather-induced yield losses, we derive five binary variables (i.e. site clusters) and model the interaction of each cluster with the combined heat and drought WI terms (table 3). Each site cluster has two groups. We define the groups of the site clusters annual soil quality, SQR, and annual precipitation sum, according to the 50% quantile of the full variety trial dataset (i.e. all crop × genotype × year × site × trial series combinations). Further, we define the levels of the site cluster soil type as sand (clay: ⩽ 17%) and loam (clay: >17% and <45%; silt: < 50%) for each trial site. The selected site clusters help to classify the trial sites into high/low yield potential sites.

In the model, we extend the $(LY)_{jkm}$ term from equation (1) as follows:

$$(LY)_{jkm} = \alpha s_{jk} + \psi_{c(j)} s_{jk} + C_{jk} + D_{jkm} \quad (9)$$

where we add WI × site cluster interaction term with $\psi_{c(j)}$ as the fixed regression term for the *c*th cluster, where $c(j)$ is the cluster to which site j is assigned, and D_{jkm} as its random residual.

2.4.4. Estimating breeding progress for absolute and relative stress tolerance
To examine the influence of breeding progress regarding abiotic stress tolerance,

we model the interaction of the WI term with the genetic trend. Therefore, we identify the absolute stress tolerance (i.e. absolute yield change due to stress per FYT) by extending the term $+(GLY)_{ijk}$ in equation (1):

$$GLY_{ijk} = \theta s_{jk} r_i + E_{ijk} \quad (10)$$

where θ is the fixed regression coefficient of the WI (s_{jk}) × FYT (r_i) interaction term for the *k*th year, *j*th site and *i*th genotype and E_{ijk} is the random residual.

Moreover, to derive the relative stress tolerance (i.e., percentage yield change due to stress per FYT), we additionally take the logarithm of the dependent variable. In that regard, let a linear regression of $\log Y$ on continuous time *t* in years be given by

$$\log Y_t = \alpha + \beta t. \quad (11)$$

Then

$$\log Y_{t+1} - \log Y_t = \beta \text{ and } Y_{t+1}; Y_t = \exp(\beta). \quad (12)$$

Thus, the relative rate of change over one year is

$$\rho = \frac{Y_{t+1} - Y_t}{Y_t} = \exp(\beta) - 1. \quad (13)$$

For small β ($|\beta| < 0.05$, say), we have by a first-order Taylor-series expansion of $\exp(\beta)$ around zero [51, p 880]:

$$\rho = \frac{Y_{t+1} - Y_t}{Y_t} = \exp(\beta) - 1 \approx \beta. \qquad (14)$$

To express this approximation of ρ as a percentage change, the estimate of β need to be multiplied by 100%.

3. Results and discussion

3.1. Development of heat and drought stress from 1993 to 2021

While there is no significant change in WI occurrence from 1993 to 2021 for wheat and rye from stem elongation to heading, the occurrence of combined heat and drought stress increases in wheat from heading and in rye from anthesis to yellow ripening across all intensities (increase in direct stress). We observe the strongest increase in wheat from milk ripening to dough ripening and in rye from dough ripening to yellow ripening (DRYR) across all intensities (figure 3).

The assessment of the median stage entries (figure 4(A)) shows that rye enters the stages stem elongation (−8 d) and heading (−20 d) earlier than wheat. However, both crops reach the yellow ripening stage at about the same time. Consequently, wheat has a median of 49 d from heading to yellow ripening while rye needs a median of 67 d. We confirm this trend by comparing the timings of heading and yellow ripening using phenology data from the PHASE model (figure A-appendix). Comparing the development of stage entry from 1993 to 2021 (figure 4(B)), we observe that stem elongation and yellow ripening both shift significantly by about −8 to −10 d over time. In comparison, heading occurs only slightly and not significantly earlier over time in both crops. This also explains the lengthening of the growing periods from stem elongation to heading and the concurrent shortening of the growing periods from anthesis to yellow ripening (figure 5). Several studies explain the shortening of the growing periods in the reproductive and generative phase as a result of increasing abiotic stress [19, 52].

With the acceleration of phenological development and respective shortening of growing periods the relative stress (i.e., the proportion of days above the threshold in a specific growing period) increases even stronger from 1993 to 2021. In addition to the direct yield losses due to heat and drought stress, there are also indirect yield losses due to the above-described heat and drought stress-induced acceleration of phenological development, which reduces the time for photosynthesis and corresponding biomass accumulation [13, 53, 54]. Consequently, these findings are in line with previous studies, which also find agricultural yields being under increasing pressure due to increasing direct and indirect effects of heat and drought stress [5, 52, 55–59].

3.2. Strongest explanatory power for combined heat and drought WIs during HDR

In wheat, the growing period from heading to anthesis is the most significant phase for explaining stress induced yield effects in all stage-to-stage growing periods. That way, the cross-stage growing periods from stem elongation to flowering and from heading to dough ripening (HDR) are both particularly influential. In rye, the stage-to-stage growing period anthesis to milk ripening (AMR) shows the greatest variance reduction in all intensities, with the cross-stage growing period HDR being especially impactful. Kottmann *et al* [19] emphasize that rye is particularly sensitive to heat and drought before anthesis as the number of ears per square meter and kernels per ear are formed. Notably, combined heat and drought is almost non-existent in rye during the growing periods before anthesis, likely due to its earlier start of the stem elongation phase and rapid progress towards the heading stage (figure 4(A)). Hence, the most significant stress takes place during AMR, which is reflected in our results (figure 6).

Rye and wheat face similar stress during the generative growth phase, as they both reach the yellow ripening stage simultaneously (figure 4(A)). However, rye has a longer duration from DRYR. Interestingly, we find no significant impact, and often a positive effect, during the DRYR phase in both crops, as this growing period involves grain ripening where heat and drought stress do not harm yield. These findings confirm previous research of Riedesel *et al* [11] which shows that the reproductive phases (HDR) within the generative phase offers the best explanatory power. Accordingly, we focus on the growing period HDR in the following WI analysis.

3.3. Yield losses due to heat and drought stress are highest on marginal sites

Looking at the variance distribution of the random effects (figure 7), we find the highest proportion (35.0/44.2%) in the combined site × year effect and in the single site effect (26.1/28.1%) for wheat and rye. The site effect covers regional variation and the year effect mainly represents inter-annual climatic changes, as genetic changes are controlled for. In addition, changes in agronomic practices play a minor role, as the crops in the variety trials are generally grown under good local agronomic practice with optimal N fertilization and full crop protection [33]. Thus, in our study, site-specific climatic changes predominantly explain the yield development during the study period 1993–2021.

Figure 8 shows the site-specific yield losses due to combined heat and drought stress on wheat and rye variety trial sites. We divide these sites into high and low yield potential sites within the clusters of

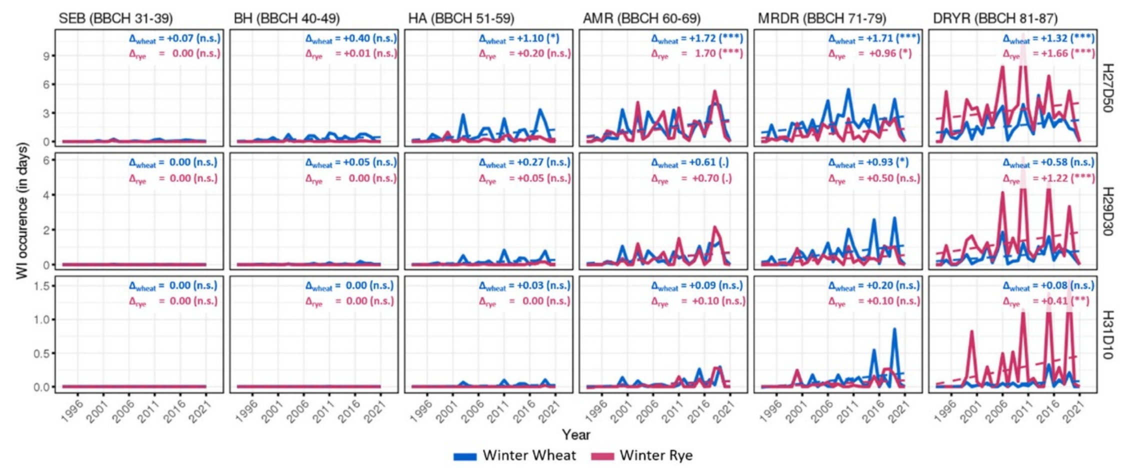

Figure 3. Development of the absolute number of days above the threshold for the WI H27D50 (top); H29D30 (middle); H31D10 (bottom) over the growing periods SEB (BBCH 31–39); BH (BBCH 41–49); HA (BBCH 51–59); AMR (BBCH 60–69); MRDR (BBCH 71–79); DRYR (BBCH 81–87) and in the observation period (1993–2021) for wheat (**blue**) and rye (**red**). Absolute trend (annual means) is displayed as solid line and statistic trend (linear regression) is displayed as dashed line. Values above the curves display the delta (Δ) in trend development and p values of the trend regression curves are given in brackets with $p < .001 = (***)$; $p < .01 = (**)$; $p < .05 = (*)$; $p < .1 = (.)$; $p > .1 =$ (n.s.). Wheat and rye varieties were mainly grown on different trial sites and are therefore not directly comparable in this study.

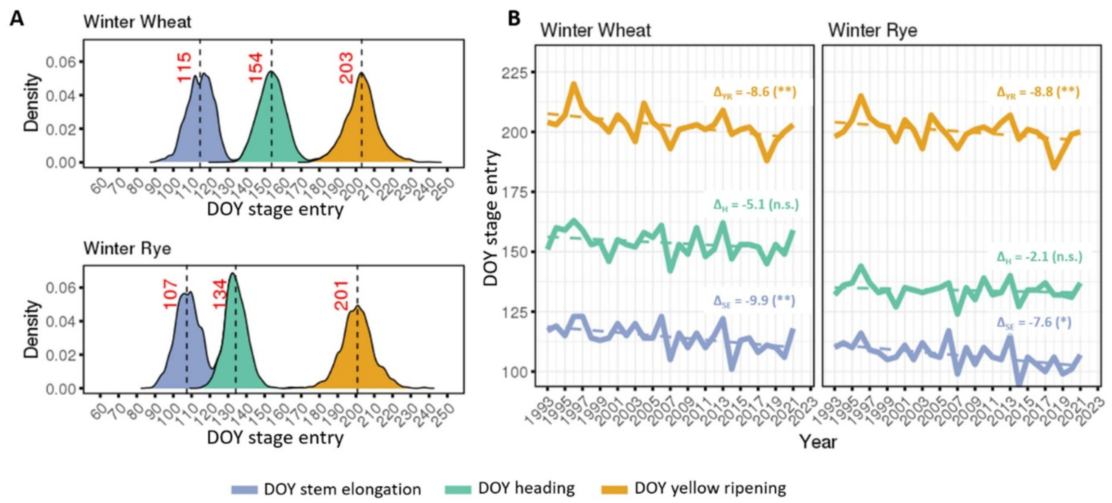

Figure 4. Entry date (day of year, DOY) of the phenological stages stem elongation (blue), heading (green), and yellow ripening (yellow) (A) distribution of observed stage entry (DOY) for winter wheat (top) and winter rye (bottom) over the whole observation period (1993–2021). Dashed lines represent median DOY values. (B) Trend development of stage entry (DOY) from 1993 to 2021 for winter wheat (left) and winter rye (right). Absolute trend (annual means) is displayed as solid line and statistic trend (linear regression) is displayed as dashed line. Values display delta (Δ) in absolute trend development and p values of the trend regression curves are given in brackets with $p < .001 = (***)$; $p < .01 = (**)$; $p < .05 = (*)$; $p < .1 = (.)$; $p > .1 =$ (n.s.). Values for trend development of stage entry (4B) are listed in table C in the appendix.

soil quality, SQR, soil type, and cumulated annual precipitation. The results show a clear pattern: low yield potential sites amplify yield losses from heat and drought stress across all intensities, whereas heat and drought stress-induced yield losses on high yield potential sites are about two to three times smaller and mostly insignificant. This is also in line with Bönecke *et al* [60], who report temperature-related wheat yield losses being on average about one sixth higher on sites with low yield potential. Furthermore, our results emphasize that drought is the driving force of yield losses, as for both crops yield losses on low yield potential sites are higher with increasing drought intensity compared to increasing heat intensity. Ribeiro *et al* [61], who also found drought as the most dominant driver of compound effects in wheat and barley, also support these findings.

The direct comparison between wheat and rye should be done with caution, as the variety trials are not always conducted at the same trial site, because they are selected individually for each crop according to its typical growing environment [32]. Hence, in our dataset rye varieties are grown under more marginal conditions than wheat varieties (table 3; figure 8). To the best of our knowledge, there is no study that directly compares the effects of heat and

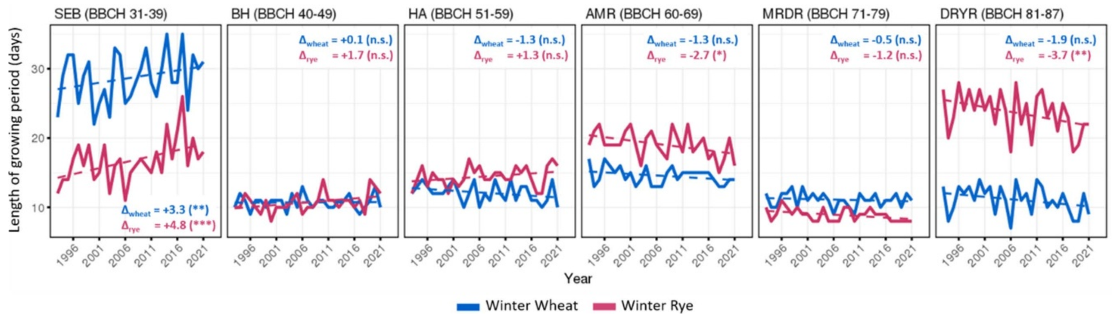

Figure 5. Lengths of the stage-to stage growing periods in the observation period 1993–2021 for wheat (blue) and rye (red). Investigated growing periods are: stem elongation—booting (SEB; BBCH 31–39); booting—heading (BH; BBCH 41–49); heading—anthesis (HA; BBCH 51–59); anthesis—milk ripening (AMR; BBCH 60–69); milk ripening—dough ripening (MRDR; BBCH 71–79); dough ripening—yellow ripening (DRYR; BBCH 81–87). Absolute trend (annual means) is displayed as solid line and statistic trend (linear regression) is displayed as dashed line. Values display delta (Δ) in absolute trend development and p values of the trend regression curves are given in brackets with $p < .001 = (^{***})$; $p < .01 = (^{**})$; $p < .05 = (^{*})$; $p < .1 = (.)$; $p > .1 =$ (n.s.). Wheat and rye varieties were mainly grown on different trial sites and are therefore not directly comparable in this study.

Figure 6. Variance reduction (VR) and effect size of combined heat and drought WI for wheat (left) and rye (right). Intensities of the WIs are arranged into three sections on the y-axis, each section representing moderate (Tmax > 27 °C), severe (Tmax > 29 °C) and extreme (Tmax > 31 °C) heat with moderate drought (50% PAWC; top section), severe drought (30% PAWC; middle section) and extreme drought (10% PAWC; bottom section). Growing periods of the WIs are displayed on the x-axis, where stage-to-stage periods are displayed left and cross-period are displayed after the gap on the right. Variance reduction is displayed as heat map where green colors indicate reduction of variance and red colors indicate increase in variance. VR is based on model output from equation (8). Black values at the bottom of each effect size indicate the absolute yield effect (MT ha^{-1}) due to one day above the threshold. Positive/negative effect size is displayed in blue/red. Effect size is red from the model output from equation (7). Significances of the effect size are given with $p < .001 = ^{***}$; $p < .01 = ^{**}$; $p < .05 = ^{*}$; $p < .1 = .$; $p \geqslant .1 =$ n.s. Wheat and rye varieties were mainly grown on different trial sites and are therefore not directly comparable in this study. VR values, model estimates and length of growing periods are displayed in table G (wheat) and table H (rye) in the appendix.

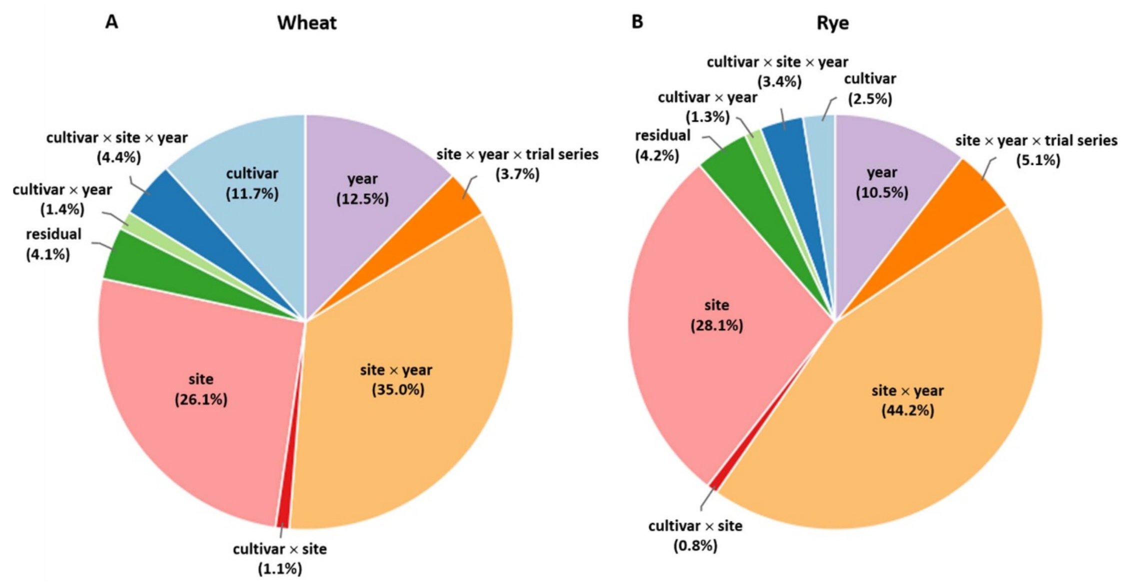

Figure 7. Proportion of variance of random effects in the model output of equation (1) for wheat and rye without WI as covariate.

drought between wheat and rye. Yet, there are some studies that attribute a higher tolerance to heat and drought in rye compared to wheat due to its phenological advantages and pronounced root system [19, 62–65]. We also find higher yield losses for wheat, if we only filter yield data those year × trial site combinations where both wheat and rye were cultivated simultaneously (appendix—figure B). However, it is important to note that the data available for these specific conditions are very limited, leading to none of these results being statistically significant.

If we compare heat and drought-induced yield losses between wheat and rye on weak soil quality (i.e. <50 points), SQR (i.e. <60 points) and soil type (i.e. sand) clusters, our results also reveal higher yield losses for wheat at extreme stress intensities (figure 8). However, if we look at the annual precipitation cluster, a clear pattern emerges for the low-precipitation sites: rye reveals higher yield losses than wheat across all stress intensities. This is because soil quality or soil type is not taken into account in this cluster. Hence, rye (i.e. cluster prec-: 60% sandy sites; ∅ soil quality: 40 points) is grown on significantly worse sites than wheat (i.e. cluster prec-: 15% sandy sites; ∅ soil quality: 74 points) in this cluster. These results indicate that as weather extremes increase, the site conditions are of higher relevance regarding stress induced yield losses than crop characteristics, which is in line with further studies like Anderson [66].

Accordingly, the worse site conditions of rye outweigh its potential genetic advantages over wheat regarding abiotic stress tolerance. Rye in fact may suffer more from climate change than wheat being grown on worse sites, which is also in line with findings from Miedaner and Laidig [67]. However, due to the steady increase in wheat production area in Germany, wheat production expanded also to more marginal sites over the last decades [68]. Hence, our wheat data may not fully reflect the conditions in agricultural practice. Yet, in the face of increasing climate-related yield losses in many lower latitude regions [2, 69], it seems essential to maintain high productivity in the higher latitude regions, including Northwest Europe and Germany in particular. Site-optimized management and the identified high resilience of favored sites need to be utilized effectively to successfully address future food security challenges.

3.4. No increase of stress tolerance of wheat and rye varieties towards combined heat and drought stress

According to our model output from equation (1) (appendix tables E and F) we observe a continuously increasing yield trend for both crops, driven by breeding progress (genetic trend), which outweighs the negative annual trend (i.e. agronomic and climatic changes over time). This is in line with previous studies of Laidig *et al* [33] and Riedesel *et al* [20].

However, if we look at the analysis of breeding progress towards stress tolerance (figure 9), our results show a significant increase in heat and drought stress-induced yield losses for newer varieties (i.e. a decrease in absolute stress tolerance). In wheat, the increase in absolute yield loss is significant for all intensities, while in rye the absolute trend is significant with higher drought intensity (appendix table J). These results are in agreement with Tack *et al* [70], who also find that newer cultivars are less resistant to heat than older cultivars. Furthermore, Tack *et al* [70], find a trade-off between heat tolerance and mean yield in wheat, with high yielding cultivars featuring a lower heat tolerance.

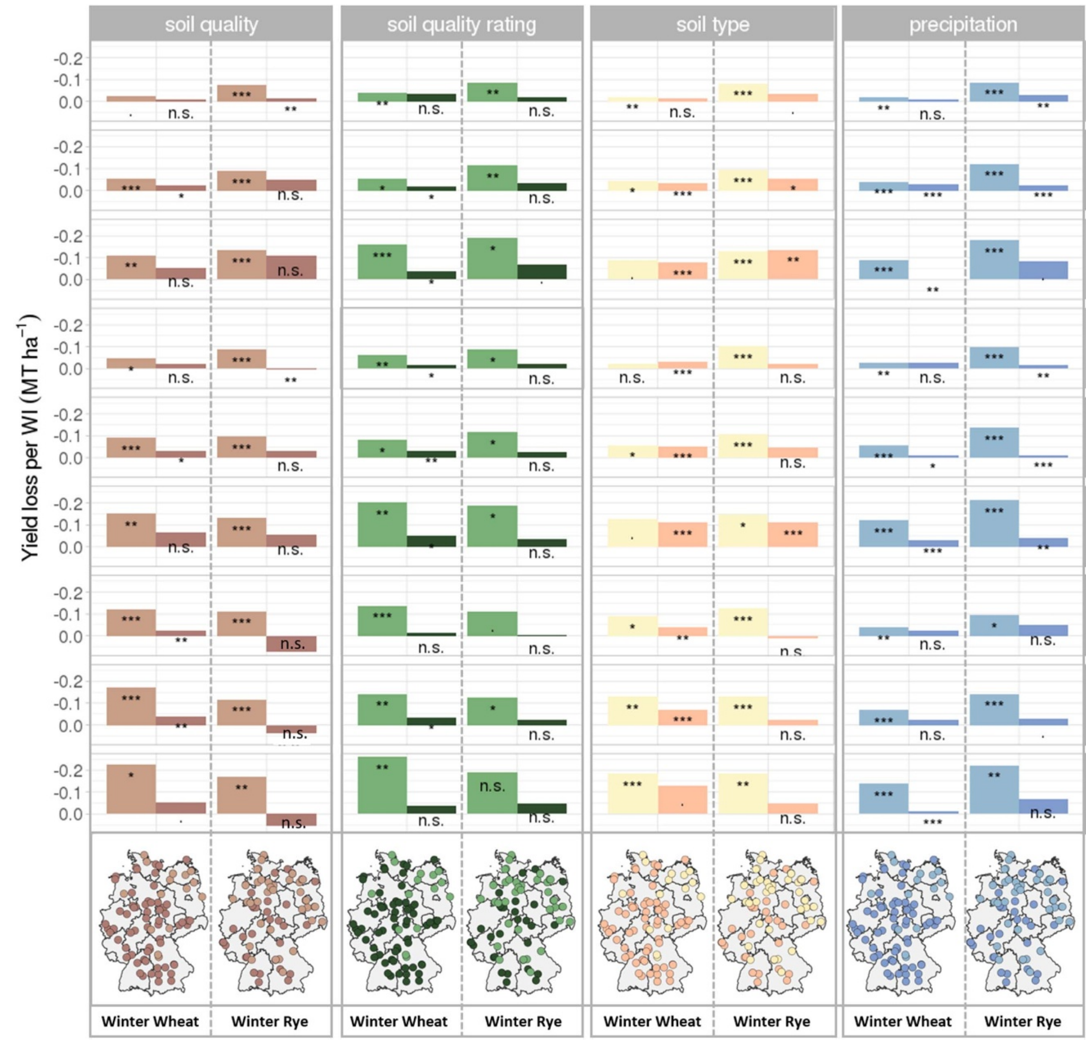

Figure 8. Estimated coefficients of combined heat and drought WIs during heading—dough ripening (HDR; BBCH 51–79) at high vs. low precipitation (prec+ = > 650 mm; prec− = < 650 mm), soil quality (soil+ = > 50 points; soil− = <50 points), soil type (loam; sand), soil quality rating (sqr+ = > 60 points; sqr− = < 60 points). The signs ± of a cluster group symbolize high/low yield potential of the site. Significances shown as $p < .001 = ***$; $p < .01 = **$; $p < .05 = *$; $p < .1 = .$; $p > .1 =$ n.s. Estimates, p values of the WI × cluster interaction is listed in table I in the appendix.

Therefore, we additionally consider the relative yield reduction due to abiotic stress in the genetic trend analysis (equation (9); change in relative stress tolerance). We still find a significant trend in wheat, but no significant trend in rye (figure 9). Hence, the observed yield increase with newer varieties results in absolutely but not relatively higher yield losses due to abiotic stress in rye, which may be explained by (1) a higher number of grains as well as larger grains are proportionally more damaged and (2) high yielding varieties suffer proportionally more, due to the higher water demand compared to older low yielding varieties. However, in wheat we observe also significant reductions in relative stress tolerance. Tack *et al* [70] also highlight genetic drawbacks of modern high-yielding wheat varieties, as newer varieties are characterized by longer grain filling periods, which increases their susceptibility to high temperatures during critical growth periods. Thus, we conclude that the ongoing efforts to improve tolerance to heat and drought stress through breeding have not yet yielded the hoped-for progress. Previous studies also explain this by insufficient understanding and consideration of site-specific effects (G × E), making it very difficult to identify useful markers for variety selection [71, 72]. Therefore, our results emphasize the importance of better understanding and characterizing site-specific effects (E) in order to consider them in variety breeding and in the adaptation of relevant traits under drought-limited growth conditions. Thus, the results of this study also support the conclusions of Miedaner and Laidig [67], who recommend to include sites with less rainfall or controlled drought experiments (i.e. rain-out shelters) in the selection environments of varieties.

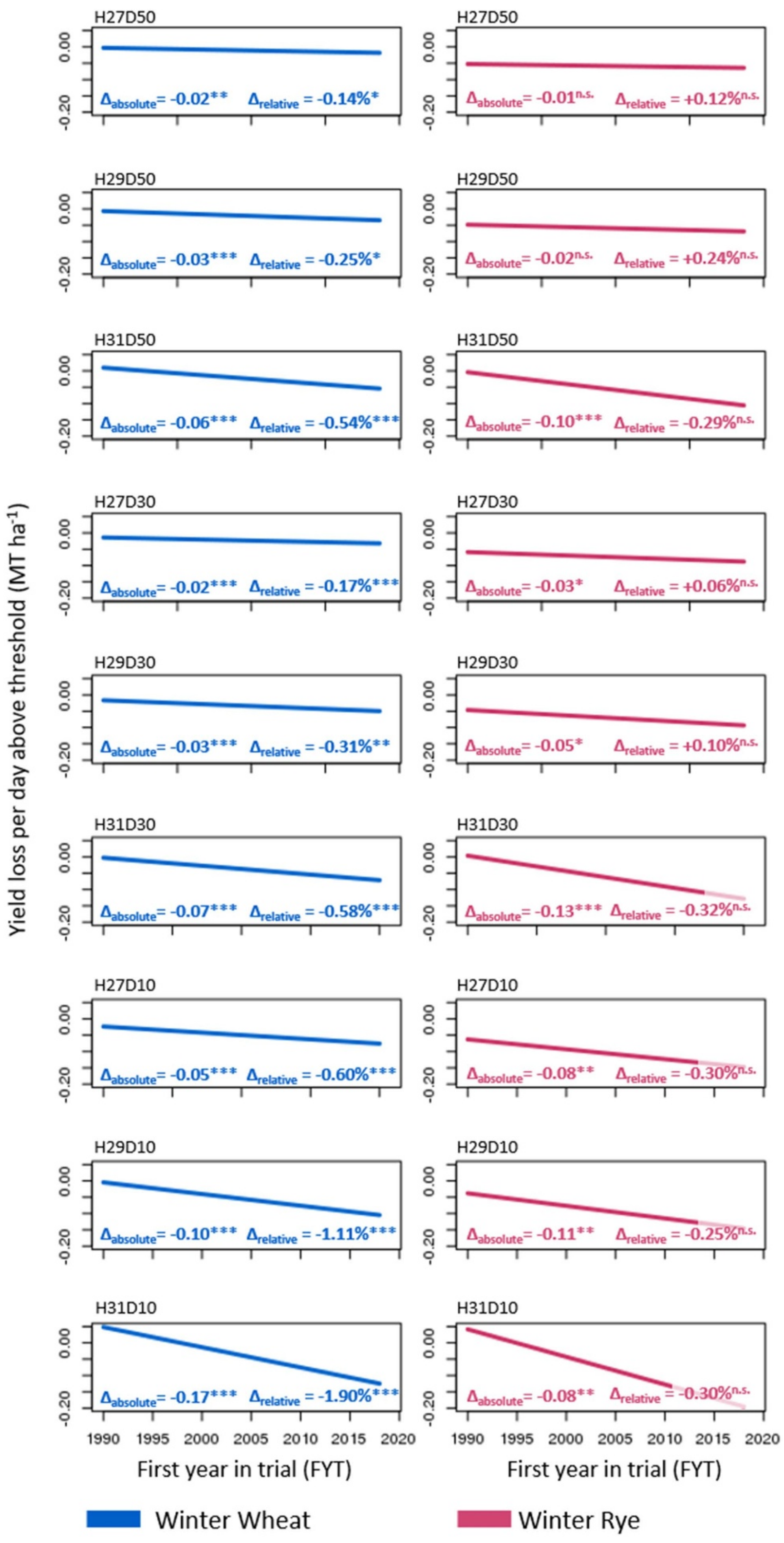

Figure 9. Estimated coefficients of combined heat and drought WIs during heading—dough ripening (HDR; BBCH 51–79) over first year in trial (FYT) for wheat (blue) and rye (red). Values above the curves display the delta (Δ) in trend development between FYT 2016 and FYT 1990 and p values of the trend regression curves are given in brackets with $p < .001 = (***)$; $p < .01 = (**)$; $p < .05 = (*)$; $p < .1 = (.)$; $p > .1 = (\text{n.s.})$. The displayed adjusted means are listed in table O (wheat) and table P (rye) and the underlying model outputs are displayed in the table J in the appendix.

4. Conclusion

This study uses WIs in combination with G × E × M specific yield data, representing the first comprehensive effort to analyze site-specific effects of heat and drought stress on wheat and rye. The results show that rye reaches anthesis much earlier than wheat, thus experiencing less pre-anthesis stress than wheat. However, post-anthesis stress significantly increased over time for both crops, increasing direct and indirect heat and drought pressure on both crops. Consequently, we find significant explanatory power for combined heat and drought WIs during the reproductive phase for both crops. Furthermore, we observe most substantial yield losses on sites with low rainfall, sandy soils and poor soil quality. We find that local site disadvantages outweigh genetic advantages, further emphasizing the critical role of understanding local site conditions in cropping systems design and climate change adaption. Interestingly, our study finds no significant improvements in stress tolerance for modern varieties compared to older ones in neither crop. In conclusion, this study underscores the necessity of better integrating site-specific considerations into agricultural strategies and breeding programs.

Data availability statement

Yield data were provided by the Federal Plant Variety Office for exclusive use in this study and are generally not publicly available. Reasonable requests may be addressed to the Federal Plant Variety Office, Hannover, Germany. All other data that support the findings of this study are included within the article (and any supplementary files).

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Conflict of interest

The authors have declared that no competing interests exist.

ORCID iDs

Ludwig Riedesel https://orcid.org/0000-0001-9505-6266
Markus Möller https://orcid.org/0000-0002-1918-7747
Hans-Peter Piepho https://orcid.org/0000-0001-7813-2992
Burkhard Golla https://orcid.org/0000-0003-3867-6076
Timo Kautz https://orcid.org/0000-0002-7906-8512
Til Feike https://orcid.org/0000-0002-1978-9473

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