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Disease management shapes genotype-by-environment interactions in European winter wheat

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Key Message: Disease management by fungicide application shapes genotype-by-environment interactions more strongly than nitrogen fertilization levels. Integrated factor analytic models improve interaction interpretation and prediction, while stability patterns depend on metric choice.

Abstract

Genotype-by-environment interactions (GEI) remain a major challenge for plant breeding, limiting accurate prediction across target populations of environments (TPE). To determine how GEI are influenced by contrasting crop management, we analysed 227 winter wheat genotypes representing over 50 years of European breeding. The genotypes were previously evaluated across 25 environments in Germany under contrasting fungicide and nitrogen treatments. Genome-wide marker effects for grain yield were assessed using genotype data from genome-wide single-nucleotide polymorphism (SNP) markers. Across environments, correlations between marker effects remained high across treatments (r = 0.71–0.94), indicating a stable genetic basis despite stronger fungicide than nitrogen treatment effects. Localized reductions in marker-effect correlations were primarily observed in the A and D subgenomes. Subsequently, integrated factor analytic models (IFA) were used to partition additive GEI into components associated with environmental covariates and latent factors. The selected IFA4 model captured 91.5% of the additive GEI variance. Measured environmental covariates accounted for 10.3% of this variance. Temperature-related covariates showed the strongest associations with the latent factors, while precipitation explained comparatively little variation. While genotype performance generally improved with breeding progress over time, temporal trends in environmental stability through breeding depended on how stability was quantified. The IFA4 model linked part of the observed GEI to measured environmental covariates while enabling prediction of genotype performance across environments. Our results show that both environmental conditions and management treatments contribute to GEI in European winter wheat.

Introduction

Genotype-by-environment interactions (GEI) determine phenotypic responses across environments and influence grain yield and stability (Falconer and Mackay 2009; Smith et al. 2021). Consequently, GEI affects crop adaptability, thereby influencing agricultural productivity and global food security (Snowdon et al. 2021). European winter wheat breeding has achieved substantial genetic gain over the past five decades under contrasting agrochemical input levels (Voss-Fels et al. 2019). However, it remains largely unknown how breeding influences the interplay between performance and stability of crop varieties. In particular, the relative contributions of climatic variation, fungicide treatment, and nitrogen fertilization to additive GEI remain poorly understood. Because crop performance reflects the combined effects of genotype, environment, and management (Cooper et al. 2021), disentangling GEI is essential for understanding adaptation and long-term breeding progress.

Identifying the environmental variables underlying GEI has therefore become a major objective in quantitative genetics and plant breeding (Heslot et al. 2014). Measured environmental covariates provide valuable biological information but typically explain only part of the observed GEI, as important environmental variables may remain unmeasured or cannot be adequately characterized (Jarquín et al. 2014). Early applications of environmental regression in plant breeding date back to Yates and Cochran (1938) and were later extended through genotype-specific and random regression models (Finlay and Wilkinson 1963; Laird and Ware 1982; Heslot et al. 2014). Factor analytic linear mixed models that parsimoniously decompose GEI into a small number of latent factors (Piepho 1997; Smith et al. 2001) have since become one of the most widely adopted frameworks for analysing GEI. They have been successfully implemented using both pedigree and genomic data and are now routinely applied in multi-environment trials (Smith et al. 2001; Burgueño et al. 2008; Tolhurst et al. 2019).

Non-crossover interactions are generally less relevant for selection because genotype rankings remain largely unchanged across environments (Allard and Bradshaw 1964). In contrast, crossover interactions alter genotype rankings among environments and therefore complicate selection decisions, particularly when genotypes with only moderate average performance outperform broadly adapted cultivars under specific environmental conditions (Smith and Cullis 2018). However, higher-order latent factors effectively capture these crossover interactions and facilitate the identification of environment-specific adaptation patterns. Earlier approaches interpreted latent factors after model fitting, for example by examining their relationships with measured environmental variables or by comparing the response patterns of selected genotypes across environments (Mathews et al. 2011; Oliveira et al. 2020). More recently, environmental covariates have been incorporated directly into factor analytic models, enabling both biological interpretation of latent factors and prediction in previously untested environments (Tolhurst et al. 2022). Recent studies further demonstrated that environmental covariates can be associated to latent factors, improving the characterization of target environments and the interpretation of GEI patterns (Fradgley et al. 2025).

While most studies have primarily focused on climatic drivers of GEI, management factors also represent a major source of GEI (Cooper et al. 2021). In European winter wheat production, nitrogen fertilization and fungicide application are among the most influential management treatments because they strongly affect resource availability, disease pressure, yield formation,

and resource-use efficiency (Heier et al. 2005; Caldelas et al. 2023). Evaluating genotype performance across year-by-location environments under contrasting management regimes therefore provides an opportunity to disentangle GEI and to better characterize genotype adaptation and yield stability. Using grain yield and environmental data from 227 winter wheat genotypes evaluated across 25 year-by-location environments, the objectives of this study were (i) to quantify GEI in a European winter wheat panel representing over 50 years of breeding history under contrasting fungicide treatment and nitrogen fertilization, (ii) to evaluate the relative contributions of known and latent environmental covariates to additive GEI, (iii) to assess prediction accuracy across heterogeneous environments using known and latent environmental variables, and (iv) to identify stable and management-sensitive genomic regions associated with grain yield.

Materials and methods

Experimental material

The study included 227 winter wheat (*Triticum aestivum* L.) cultivars released from 1963 to 2016. These cultivars were evaluated in multi-environment trials (MET) at six locations in Germany between 2015 and 2020. The subsequent analyses were based on the MET dataset described by Wang et al. (2025), which builds upon the winter wheat MET originally reported in Voss-Fels et al. (2019).

Multi-environment trials

Briefly, field experiments were established at six locations in Germany (Gross-Gerau, Hannover, Kiel, Klein Altendorf, Quedlinburg, and Rauischholzhausen). In total, 25 location-year combinations were evaluated across six growing seasons (Wang et al. 2025). The experiments followed a two-phase design, comprising a randomized complete block design during Phase I (2015–2017) and a full treatment-factorial design during Phase II (2018–2020). Three treatment combinations representing contrasting crop management intensities were analysed in the study, namely high nitrogen with fungicide application (HiN_HiF; 220 kg N ha^{-1}), high nitrogen without fungicide application (HiN_NoF; 220 kg N ha^{-1}), and low nitrogen without fungicide application (LoN_NoF; 110 kg N ha^{-1}). Herbicides, insecticides, and growth regulators were applied according to local standard management practices across treatments. An overview of the locations and the distribution of treatment combinations across environments is provided in Figure 1. Phenotypic data included grain yield measurements obtained from Wang et al. (2025). Detailed descriptions of field protocols, sampling procedures, and yield determination are provided by Voss-Fels et al. (2019). Summary statistics for each environment, including the number of genotypes, mean grain yield, standard deviation, and yield range, are provided in Supplementary Table S1.

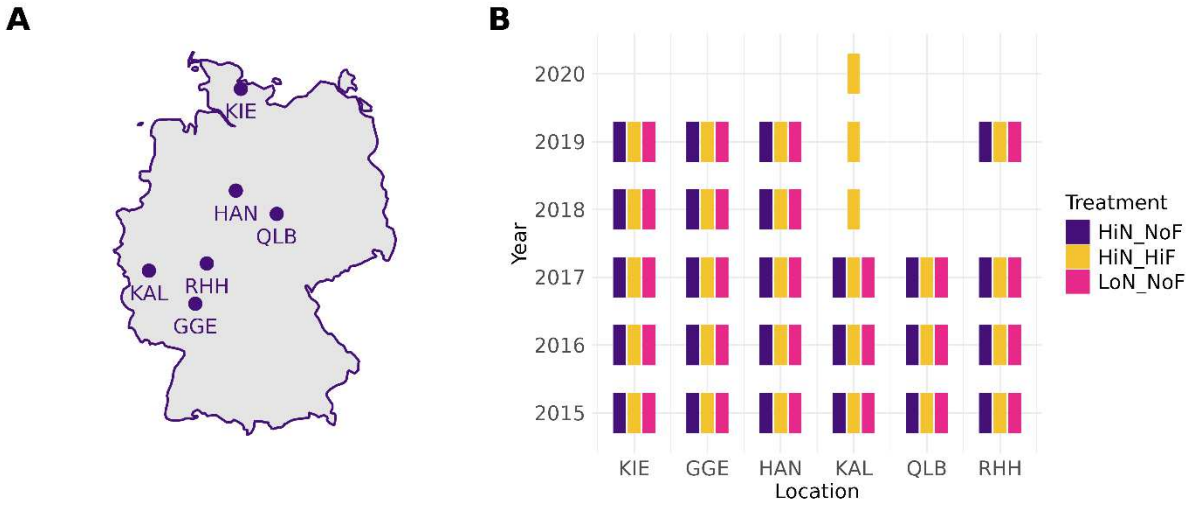


Figure 1 | Overview of the MET dataset. (A) Map showing the six field trial locations in Gross Gerau (GGE), Hannover (HAN), Kiel (KIE), Klein Altendorf (KAL), Quedlinburg (QLB), and Rauischholzhausen (RHH), Germany. (B) Distribution of treatment combinations across locations and years. Treatments comprised high nitrogen with fungicide application (HiN_HiF), high nitrogen without fungicide application (HiN_NoF), and low nitrogen without fungicide application (LoN_NoF). Colors indicate treatment combinations.

Genotypic data

Previously published SNP marker data for all 227 accessions were obtained from two genotyping platforms, the 15K Illumina Infinium iSelect SNP array (Voss-Fels et al. 2019) and the 135K Affymetrix TGWEXCAP array comprising 136,780 SNP markers (Lichthardt et al. 2020). SNPs with more than 10% missing data and a minor allele frequency below 5% were filtered, resulting in a final dataset of 50,518 SNP markers. Missing marker data were imputed using BEAGLE v5.4 (Browning and Browning 2007; Browning et al. 2018). The genomic relationship matrix was constructed following VanRaden (2008) as:

$$\boldsymbol{G}_g = \frac{\boldsymbol{M}\boldsymbol{M}'}{2\sum p_i(1-p_i)} \quad (1)$$

The entries of $\boldsymbol{Z}$ are represented by $(0-2p_i)$ for homozygous allele A, $(1-2p_i)$ for the heterozygous state and $(2-2p_i)$ for homozygous allele B, with p_i being the allele frequency of the B allele.

Environmental data

Weather data were obtained from meteorological stations located near each experimental site. Environmental conditions across all environments are summarized in Supplementary Figure S1, which presents thermal time profiles of global radiation, precipitation, relative humidity, air temperature, and wind speed throughout each growing season. Thermal time was calculated as cumulative growing degree days (°Cd), using a base temperature of 0 °C to align environmental conditions across environments according to crop development rather than calendar date. Prior to analysis, environmental covariates were centred and scaled.

Linear mixed model

The MET dataset was analysed through a parsimonious decomposition of the additive genetic covariance structure (Kelly et al. 2007) using the linear mixed model described by Tolhurst et al. (2022):

$$\boldsymbol{y} = \boldsymbol{X}\boldsymbol{\tau} + \boldsymbol{Z}\boldsymbol{u} + \boldsymbol{Z}_p\boldsymbol{u}_p + \boldsymbol{e}, \quad (2)$$

where $\boldsymbol{\tau}$ denotes the vector of fixed effects, including location-year environment and management main effects, $\boldsymbol{u}$ represents the random additive genotype-by-environment (GE) effects, $\boldsymbol{u}_p$ comprises random non-genetic trial design effects, and $\boldsymbol{e}$ is the vector of residual errors. The design matrices $\boldsymbol{X}$, $\boldsymbol{Z}$, and $\boldsymbol{Z}_p$ relate observations to their corresponding effects.

The additive GE effects were assumed to follow:

$$\boldsymbol{u} \sim N(\mathbf{0}, \boldsymbol{G}_E \otimes \boldsymbol{G}_g), \quad (3)$$

where $\mathbf{G}_E$describes the genetic covariance matrix among environments and $\mathbf{G}_g$the genomic relationship matrix. The matrix $\mathbf{G}_E$was modelled using either a diagonal variance structure (DIAG) or reduced-rank factor-analytic (FA) structures with one to five factors (FA1–FA5; Smith et al. 2001; Kelly et al. 2007).

Non-genetic random effects included environment-specific replicate and incomplete-block effects. Random row and column effects were additionally fitted when valid field-layout information was available. Environment-specific residual variances were modelled using a block-diagonal residual structure. Variance components were estimated in ASReml-R by residual maximum likelihood (REML; Patterson and Thompson 1971) using the average information algorithm (Gilmour et al. 1997).

Model for genotype by environment effects

GE effects were modelled within a FA linear mixed model framework (Smith et al. 2001). The FA model represents the covariance structure of GE effects through a reduced number of latent factors (Kelly et al. 2007). Hence, the vector of GE effects was expressed as:

$$\boldsymbol{u} = (\boldsymbol{\Lambda} \otimes \boldsymbol{I}_v)\boldsymbol{f} + \boldsymbol{\delta}, \quad (4)$$

where $\boldsymbol{\Lambda}$ defines the matrix of environment-specific factor loadings, $\boldsymbol{I}_v$ is an identity matrix of dimension v, $\boldsymbol{f}$ is the vector of genotype scores across latent factors, and $\boldsymbol{\delta}$ represents environment-specific residual GE effects.

Integrated factor analytic model (IFAk)

To investigate whether environmental variation across trials could be partly explained by measured environmental covariates, the selected FA4 model was extended to an integrated factor analytic model (IFA4) as described by Tolhurst et al. (2022). As a first step, the estimated environment-specific effects were decomposed into contributions explained by measured environmental covariates and residual latent environmental variables:

$$\boldsymbol{\tau} = \mathbf{1}_p\mu + \boldsymbol{S}\boldsymbol{\tau}_S + \boldsymbol{\omega}, \quad (5)$$

where μ represents the overall mean, $\boldsymbol{S}$ contains the matrix of environmental covariates, $\boldsymbol{\tau}$ is the vector of regression coefficients describing the contribution of each environmental covariate to the environmental means, and $\boldsymbol{\omega}$ represents residual environmental deviations not explained by the measured covariates.

Following the IFA framework of Tolhurst et al. (2022), the estimated factor loadings of the fitted FA4 model were expressed as a linear combination of observed environmental covariates and residual latent environmental effects:

$$\boldsymbol{\Lambda} = \boldsymbol{S}\boldsymbol{\Lambda}_s + \boldsymbol{\Lambda}_r, \quad (6)$$

where $\boldsymbol{S}$ is the p x q matrix of the known environmental covariates, $\boldsymbol{\Lambda}_s$contains the contribution of observed environmental covariates to the factor loadings and $\boldsymbol{\Lambda}_r$represents the contribution of the latent covariates to the factor loadings which is not explained by environmental covariates.

Substituting this decomposition into the fitted FA4 model yields its IFA4 representation:

$$\boldsymbol{u} = ([S\boldsymbol{\Lambda}_s + \boldsymbol{\Lambda}_r] \otimes \boldsymbol{I}_v)\boldsymbol{f} + \boldsymbol{\delta}, \quad (7)$$

This specification enables the joint modelling of observed and unobserved environmental sources underlying GE interactions. Random effects were assumed to follow a multivariate normal distribution, with latent factor variances and environment-specific residual variances estimated from the data.

Model estimation, selection, and predictive assessment

The DIAG and FA linear mixed models were fitted in R (version 4.3.3; R Core Team 2024) using ASReml-R (version 4.2.0.355) based on restricted maximum likelihood (REML) estimation (The VSNi Team 2023). Model performance was evaluated using Akaike's Information Criterion (AIC), Bayesian Information Criterion (BIC), and log-likelihood. The optimal number of latent factors in the FA models was selected based on a combination of model fit, prediction accuracy, and the proportion of additive GE variance explained (Tolhurst et al. 2022).

As described by Smith et al. (2021), a principal component rotation was applied to the estimated factor loadings and genotype scores. The rotation was performed such that the first factor accounted for the largest proportion of common GE variation, while subsequent factors explained progressively smaller proportions and remained orthogonal to one another. Further details on the rotation procedure and the calculation of variance explained are provided by Tolhurst et al. (2022). Factor analytic selection tools (FAST; Smith and Cullis 2018) were used to quantify overall performance and stability. Overall performance was derived from the first latent factor, which captured the predominant pattern of genotype performance across environments.

Prediction accuracy was evaluated by sequentially omitting each environment in a leave-one-environment-out cross-validation scheme (Tolhurst et al. 2022). In each iteration, the FA4 model was fitted to the remaining $p - 1$ environments and subsequently transformed into its IFA4 representation before predicting additive GE effects for the omitted environment. Prediction accuracy, r_j, was calculated by correlating the observed genotype means in environment, $\bar{y}_{ij}$, with the predicted additive GE effects, $\hat{u}_{ij}$. The resulting $r_j$values were summarized across each location by calculating the minimum, mean, and maximum across years.

Marker effect correlations across management treatments

Genome-wide SNP marker effects for grain yield were derived from the additive GE effects jointly estimated for all environment-treatment combinations using the selected FA4 model. These effects were reconstructed from the rotated factor loadings and genotype scores and then averaged across environments within each treatment combination. Treatment-specific marker

effects $\boldsymbol{b}$ were back solved by applying the Moore-Penrose pseudoinverse of the marker matrix to the corresponding averaged genetic effects as

$$\boldsymbol{b} = \frac{1}{2\sum p_i(1-p_i)} M'\boldsymbol{G}_g\boldsymbol{u}. \quad (8)$$

Pairwise correlations between treatment-specific marker effects were calculated to assess their similarity across nitrogen and fungicide treatments. Higher correlations indicate more consistent marker effects between treatments, whereas lower correlations indicate stronger treatment-dependent changes. To examine variation along chromosomes, correlations were calculated within sliding windows of 50 consecutive SNPs and subsequently smoothed using a rolling mean with a window size of 900.

Results

The MET encompassed substantial environmental variation, both across years and across locations. Within individual locations, mean grain yield varied considerably between years due to pronounced variation in temperature, precipitation, radiation, relative humidity and wind speed at each of the six locations (Supplementary Figure S1). For example, mean yield at GGE increased from 52.1 dt ha^{-1} in 2016 to 67.1 dt ha^{-1} in 2017, while at HAN it varied from 73.7 dt ha^{-1} in 2015 to 59.2 dt ha^{-1} in 2019. At KAL, mean yield increased from 75.8 dt ha^{-1} in 2016 to 92.0 dt ha^{-1} in 2017 (Supplementary Table S1). Across all 25 environments, mean grain yield ranged from 45.3 dt ha^{-1} in QLB_2015 to 92.0 dt ha^{-1} in KAL_2017.

Model selection

Linear mixed models were fitted using a DIAG variance structure and reduced-rank factor analytic (FA1–FA5) structures. Model fit improved substantially when moving from the DIAG model to factor analytic models, as indicated by lower AIC values and higher log-likelihoods. Within the FA models, model fit continued to improve with increasing factor order, whereas BIC increased beyond FA2. The proportion of additive GE variance explained also increased with factor order but only marginally between FA4 and FA5. Given the small gain in model fit and explained variance relative to the additional model complexity, FA4 was selected for subsequent analyses (Table 1).

Table 1 | Summary of factor analytic linear mixed models fitted to the MET dataset. For each model, the number of estimated genetic variance parameters, the number of coefficients, Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), residual log-likelihood (LogLik), and the percentage of additive GE variance explained are presented. The model selected for subsequent analyses is highlighted in bold.

Model	Parameters	Coefficients	AIC	BIC	LogLik	% var
DIAG	148	12648	157727.2	158959.8	-78715.6	-
FA1	198	18550	154705.6	156146.5	-77179.8	78.33
FA2	223	18777	154287.1	155927.9	-76946.6	85.36
FA3	248	19004	154118.3	155950.6	-76839.2	88.65
FA4	**273**	**19231**	**154041.0**	**156056.5**	**-76778.5**	**91.49**
FA5	298	19458	154013.1	156203.5	-76743.5	93.12

Integrated factor analytic linear mixed model

To identify the biological contribution to the additive GE effects, loadings from the selected FA4 model were projected onto measured environmental covariates using the IFA framework of Tolhurst et al. (2022). The first factor explained most of the additive GE variance (73.4%), whereas Factors 2–4 contributed progressively smaller proportions. The variance explained by measured environmental covariates increased from 14.1% to more than 50% for Factors 3 and 4 (Table 2).

Table 2 | Variance explained by the four latent factors of the IFA4 model and the corresponding contribution of known environmental covariates derived from the IFA4 projection.

Factor	Total variance (%)	Known EC variance (%)	% factor explained by EC
FA1	73.4	3.13	14.11
FA2	11.37	3.36	21.6
FA3	3.91	2.26	58.72
FA4	2.82	1.52	54.05
Overall	**91.49**	**10.27**	**37.12**

Additive genetic variance ranged from 8.08 to 75.23 across environments, with an overall mean of 22.50. The proportion of additive genetic variance explained by the four common factors ranged from 63.9% to 100.0%, averaging 91.5%, whereas environment-specific variance averaged 8.5% (Supplementary Table S2). The first latent factor accounted for 73.4% of the additive GE variance represented by the model and showed consistently positive loadings across environments. In contrast, Factors 2–4 explained substantially smaller proportions of the variance and displayed both positive and negative loadings (Figure 2A; Supplementary Table S2).

Measured environmental covariates accounted for 10.27% of the additive genetic variance represented by the IFA4 model. Their contribution differed among latent factors, increasing from 14.1% for Factor 1 to 54.1–58.7% for Factors 3 and 4 (Table 2). Among the individual environmental covariates, mean temperature contributed most strongly to Factors 1–3, whereas global radiation explained the largest proportion of covariance associated with Factor 4 (Figure 2B; Supplementary Table S3).

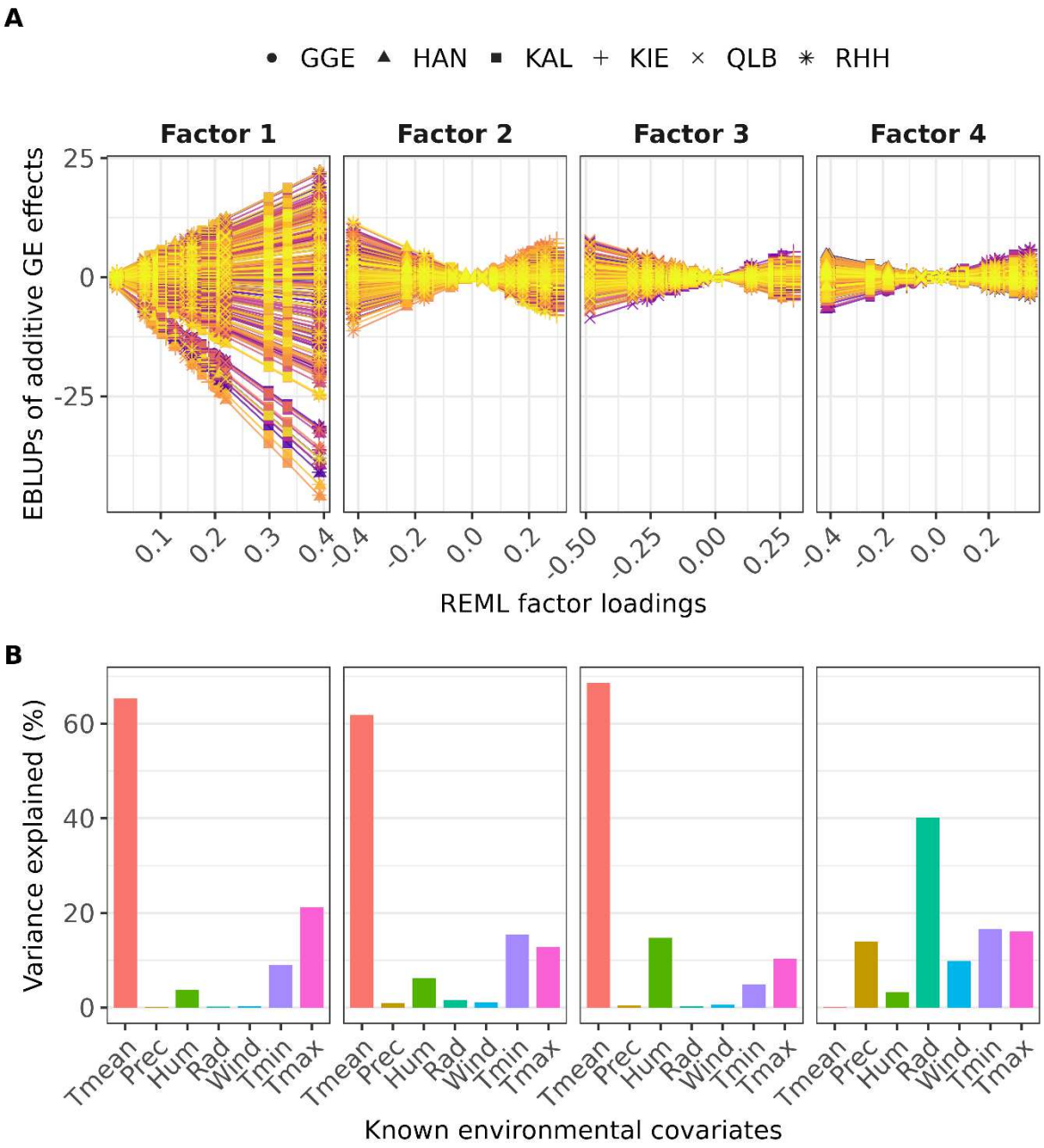


Figure 2 | (A) Regression plots for all genotypes based on the four joint factors. Different marker shapes indicate distinct environments. (B) Proportion of the additive genetic variance in each factor explained collectively by the known covariates. Tmean, mean temperature; Prec, precipitation; Hum, relative humidity; Rad, global radiation; Wind, wind speed; Tmin, minimum temperature; Tmax, maximum temperature.

Genotype performance and stability

Overall performance and stability varied substantially among the 227 wheat genotypes. Overall performance ranged from approximately −21 to 10, while RMSD values ranged from 0 to 6.4. Several genotypes showed high overall performance together with low RMSD. Genotypes with high RMSD, in contrast, showed stronger environment-specific variation in performance. No clear trade-off was observed between overall performance and stability, indicating that high-performing genotypes were not necessarily less stable. More recently released cultivars tended to occupy the upper part of the overall performance distribution, suggesting a general breeding

trend towards overall performance. In contrast, RMSD showed no apparent relationship with release year (Figure 3).

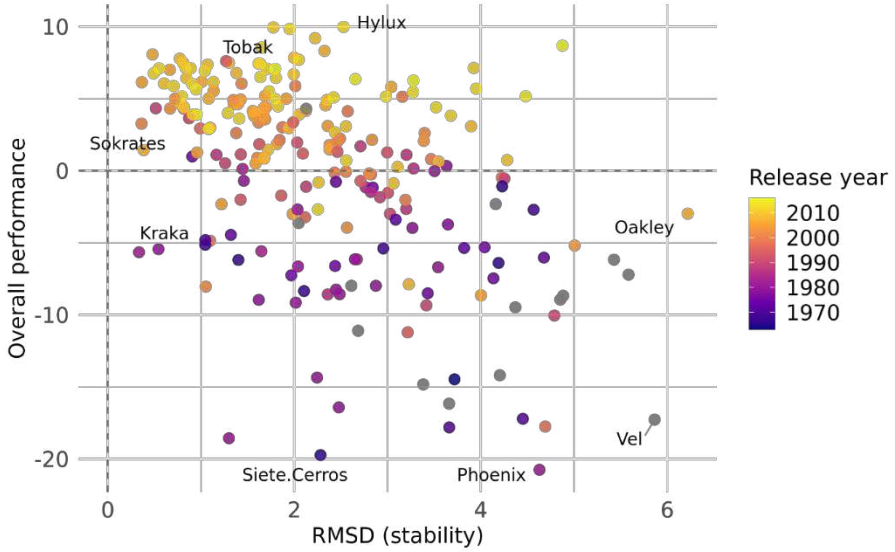


Figure 3 | Overall performance in relation to their respective root mean square deviation (RMSD) for the 227 wheat genotypes. Higher RMSD values indicate greater instability across environments. Release year refers to the registration year of the variety. Genotypes representing the upper and lower extremes of overall performance and RMSD were labelled for orientation.

Prediction accuracy

Prediction accuracy varied considerably among environments, ranging from 0.09 in KAL_2015 to 0.93 in KAL_2016, with an overall mean of 0.74 (Supplementary Table S4). At the location level, mean prediction accuracy was highest for HAN (0.85) and GGE (0.79), whereas the lowest means were observed for KAL and RHH (both 0.65; Table 3). Prediction accuracy was relatively consistent across years at QLB, RHH, and HAN, while substantially greater interannual variation was observed at GGE, KIE, and particularly KAL. The large variation at KAL was mainly driven by the exceptionally low prediction accuracy in KAL_2015; estimates for the remaining KAL environments ranged from 0.62 to 0.93 (Supplementary Table S4).

Table 3 | Summary of prediction accuracies obtained from leave-one-environment-out cross-validation of the IFA4 model. Values represent the minimum, mean, and maximum Pearson correlations (r_j) across the location-year environments available at each location. Prediction ability was calculated across genotypes as the correlation between observed genotype mean yields and predicted additive genetic effects for the omitted environment. Detailed results for all 25 environments are provided in Supplementary Table S4.

Location	Min	Mean	Max
GGE	0.49	0.79	0.90
HAN	0.77	0.85	0.92
KAL	0.09	0.65	0.93
KIE	0.41	0.75	0.87
QLB	0.64	0.69	0.74
RHH	0.60	0.65	0.73
Overall	**0.50**	**0.73**	**0.85**

Correlation of marker effects across treatments

Pairwise correlations were calculated to assess the consistency of genome-wide SNP marker effects for grain yield across the three management treatments. Genome-wide correlations were high for all treatment pairs, ranging from r = 0.71 to r = 0.94, indicating broadly similar patterns of additive marker effects across management regimes. The highest correlation was observed between the two nitrogen levels without fungicide application (HiN.NoF_LoN.NoF; r = 0.94), whereas the lowest correlation occurred between the high-nitrogen treatments differing in fungicide application (HiN.HiF_HiN.NoF; r = 0.71). The comparison between HiN.HiF and LoN.NoF showed an intermediate correlation (r = 0.82). Thus, marker effects were more similar between treatments differing only in nitrogen supply than between treatments differing in fungicide application (Figure 4).

Although genome-wide correlations were consistently high, local marker-effect correlations varied considerably along the chromosomes. The magnitude of these local fluctuations differed among treatment contrasts, with the largest deviations observed for comparisons involving fungicide application, whereas correlations between nitrogen treatments remained comparatively stable across most chromosomal regions. Overall, marker-effect correlations appeared more variable across the A and D subgenomes, whereas the B subgenome showed comparatively stable correlation profiles. The strongest local reduction in marker-effect correlations was observed on chromosome 5A, with additional pronounced fluctuations on chromosomes 1A, 2D, and 4D (Figure 4).

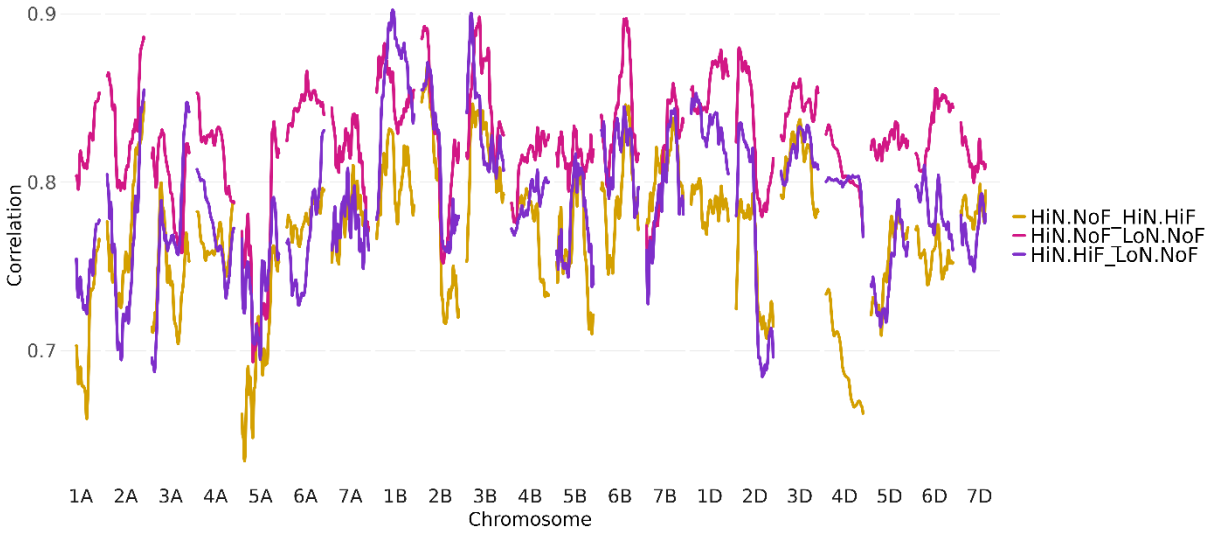


Figure 4 | Smoothed correlation of SNP marker effects along chromosomes. Grain yield (dt/ha) in 25 environments. Treatments differed in nitrogen level (HiN, LoN) and fungicide application (HiF, NoF); colors indicate treatment combinations. Lines represent locally smoothed correlations of SNP marker effects along the chromosomes; genome-wide correlations were calculated across all markers.

Discussion

The study applied an IFA model to investigate additive GEI for grain yield in a winter wheat MET conducted under contrasting fungicide treatment and nitrogen fertilization. Furthermore, the study evaluated overall performance and stability across more than 50 years of breeding history and compared genome-wide marker-effect correlations between contrasting fungicide treatments and nitrogen fertilizations. The MET showed substantial variation across years and locations. This broad environmental variation provided a suitable basis for the description and prediction of additive GE effects.

Measured environmental covariates capture only part of GEI

The selected IFA4 model captured 91.5% of the additive GE variance, indicating that four factors adequately described the genetic covariance across environments (Table 1). The first factor accounted for 73.4% of the additive GE variance and predominantly represented generalized genotype performance and non-crossover GEI, as indicated by the consistently positive factor loadings across environments (Figure 2A). The dominant contribution of the first factor reflects the fact that most environments shared a common genetic response pattern, with differences among genotypes largely corresponding to changes in the magnitude rather than the direction of their performance across environments. Consequently, the higher-order factors explained only 18.1% of the additive GE variance and primarily described environment-specific crossover interactions (Supplementary Table S2), consistent with previous reports using IFA models (Tolhurst et al. 2022).

Measured environmental covariates accounted for 10.3% of the additive genetic variance captured by the IFA4 model (Table 2). Their contribution was particularly small for Factor 1 (14.1%), whereas substantially larger proportions of Factors 2–4 were explained (21.6–58.7%). This suggests that the dominant pattern of additive GEI was largely driven by environmental processes that were not represented by the available weather variables. Rather than reflecting a single environmental gradient, the first latent factor likely captured the combined influence of multiple environmental and management processes that consistently affected genotype performance across environments. In contrast, the higher-order factors represented more specific environmental responses that were more closely associated with the measured environmental covariates. The associations shown in Figure 2B further support this interpretation, with temperature-related covariates exhibiting the strongest associations with Factors 1–3, whereas global radiation contributed most strongly to Factor 4.

These findings illustrate the principal advantage of the IFA approach. By partitioning GEI into components associated with measured environmental covariates and latent factors orthogonal to those covariates (Tolhurst et al. 2022), the model allows part of the observed GEI to be related to specific environmental drivers, while retaining the ability to capture interaction patterns that cannot be explained by the available covariates. In contrast, models relying exclusively on measured environmental covariates may fail to capture important interaction patterns when relevant environmental drivers are unavailable or only incompletely characterized (Heslot et al. 2014; Jarquín et al. 2014). Although temperature and radiation emerged as the most influential covariates, the relatively small proportion of explained variance indicates that important drivers remained unmeasured. Potential contributors include developmental-stage-specific weather conditions, soil properties, disease pressure and management practices. Incorporating such variables into future IFA models may therefore improve the environmental characterization and interpretation of GEI, as well as the prediction of genotype responses across environments.

Breeding progress primarily increased overall performance

Across more than 50 years of European winter wheat breeding, genotypes varied substantially in overall performance and stability. No clear trade-off was observed, as several genotypes combined high overall performance with low RMSD. Other high-performing genotypes showed greater environmental sensitivity and may therefore be better suited to specific target environments (Smith et al. 2001; Smith and Cullis 2018). More recently released genotypes generally achieved higher overall performance, consistent with sustained genetic gain in European winter wheat (Voss-Fels et al. 2019), whereas RMSD showed no apparent relationship with release year (Figure 3). Using the same wheat panel, Voss-Fels et al. (2019) reported improved stability of modern cultivars based on the coefficient of variation and cultivar superiority index. Rather than being necessarily contradictory, these findings indicate that conclusions about breeding progress for stability depend on how stability is defined and quantified. These measures capture different aspects of genotype performance and stability than the FA-based RMSD. The coefficient of variation expresses phenotypic variation across environments relative to a genotype's mean yield and can therefore decrease simply because the mean yield increases, even if the absolute variation remains unchanged (Francis and Kannenberg 1978). The cultivar superiority index quantifies the squared deviation of a genotype from the highest-yielding cultivar in each environment (Lin and Binns 1988). Consequently, both indices are related to yield level as well as variation across environments, whereas RMSD quantifies deviations from the dominant genetic response pattern captured by the factor analytic model. Consequently, variation in genotype performance across environments did not decrease over the course of breeding. Instead, mean yield increased, making modern, higher-yielding genotypes appear more stable under scale-dependent metrics such as the coefficient of variation, even when their absolute variation across environments remained unchanged. Importantly, RMSD also provided no evidence for a deterioration of stability in more recently released cultivars (Figure 3).

The direction of stability therefore depends on its statistical definition. Calderini and Slafer (1998, 1999) observed similarly different trends when stability was expressed in absolute or relative terms and reported greater responsiveness of modern cultivars using Finlay-Wilkinson regression, which represents the response of each genotype by a single regression coefficient, such that a strong but systematic response to favourable environments is interpreted as lower stability. In contrast, the FA framework represents additive genetic covariance across environments through multiple latent factors. This enables the dominant performance pattern to be separated from higher-order differential responses, from which RMSD is derived. The absence of a clear relationship between RMSD and release year therefore does not imply that stability has not changed through breeding, but rather that modern cultivars did not show a consistent reduction in their deviations from the genetic response pattern captured by the FA model. Together, these findings suggest that breeding progress for stability cannot be described by a single metric and should be interpreted in relation to the specific stability concept applied. Nevertheless, the occurrence of genotypes combining high overall performance with low RMSD demonstrates that high performance and stability according to the FA-based definition are not mutually exclusive. Explicit consideration of both performance and environmental responsiveness may therefore be useful when selecting cultivars for broad adaptation (Waters et al. 2026).

Integrated factor analytic models predict additive GE effects across environments

The IFA4 model predicted additive GE effects in unseen environments with an overall prediction accuracy of 0.74 (Table 3). This exceeded the mean accuracies of 0.60 and 0.56 in cotton reported by Tolhurst et al. (2022) for an IFA4-3 model. In both studies, prediction accuracy differed considerably among environments. For example, the low prediction accuracy for KAL_2015 may reflect a specific GEI pattern that was not adequately represented by the remaining environments or model covariates (Supplementary Table S4). As the other KAL environments were predicted with moderate to high accuracy, this limitation appears specific to 2015. Therefore, this environment may not have been well aligned with the remaining environments (Cooper et al. 2023). Prediction may therefore be improved by including environments in the MET that better represent such extreme conditions.

The high overall prediction accuracy should nevertheless be interpreted cautiously. The overall prediction accuracy does not necessarily indicate that finer-scale or infrequent interactions were captured equally well. Rather the large proportion of variance explained by the first factor may indicate that the main effect explained most variation, which usually is easier to predict than other GEI effects. Other genomic prediction studies also reported moderate prediction accuracies for wheat grain yield. Burgueño et al. (2012) obtained correlations of 0.48 and 0.56 for models without and with GEI, respectively, while He et al. (2016) achieved 0.50 when using one year to predict the next. Weber et al. (2023) obtained similar accuracies based on haplotype blocks. More broadly, genomic prediction has become an integral component of modern wheat breeding. Using a panel of 191 European winter wheat cultivars evaluated across contrasting management intensities, Voss-Fels et al. (2019) demonstrated the potential of genome-wide haplotype information to characterize and exploit genetic variation for breeding. Although differences in models, datasets and validation designs limit direct comparisons, these studies show that genomic prediction can be effective beyond observed environments. Overall, IFA4 effectively predicted broadly repeatable genetic variation, whereas specific crossover GEI remained more difficult to predict.

Fungicide influences marker effects more than nitrogen fertilization

Genome-wide correlations of SNP marker effects were high across all management contrasts (r = 0.71–0.94; Figure 4), indicating that most additive genetic effects remained consistent across environments. However, marker effects were most similar between treatments differing only in nitrogen supply (r = 0.94), whereas contrasts involving fungicide application showed substantially lower correlations (r = 0.71–0.82). These results indicate that fungicide management induced larger changes in additive marker effects than nitrogen fertilization.

This pattern is consistent with previous analyses of the same MET, in which grain yield showed lower consistency under fungicide application than under untreated conditions, suggesting that plant protection increases GE interaction (Wang et al. 2025). Wang et al. (2025) proposed that fungicide application partially replaces the contribution of genetically controlled disease resistance by reducing disease pressure, thereby reducing the expression of genetic differences among cultivars for grain yield. Our results extend this interpretation by demonstrating that fungicide management was also associated with larger changes in marker effects than nitrogen fertilization, suggesting that disease control alters the relative contribution of genomic regions underlying yield performance across environments.

This interpretation is further supported by the localized reductions in marker-effect correlations observed across the genome. The strongest reduction occurred on chromosome 5A, with

additional pronounced fluctuations on chromosomes 1A, 2D, and 4D, while marker-effect correlations appeared more variable across the A and D subgenomes than across the comparatively stable B subgenome (Figure 4). These localized changes suggest that fungicide application altered the contribution of specific genomic regions to grain yield rather than uniformly affecting additive marker effects across the genome. In contrast, marker effects remained comparatively stable across nitrogen treatments, indicating that nitrogen availability primarily influenced the magnitude of genetic effects while having a smaller impact on their genomic distribution. This agrees with previous studies reporting genotype-dependent responses to nitrogen supply in wheat (Hirel et al. 2007; Cormier et al. 2013).

The pronounced reduction in marker-effect correlation observed on chromosome 5A are particularly noteworthy, as Voss-Fels et al. (2019), using the same underlying winter wheat panel, previously identified a resistance-associated LD block on chromosome 5A (5A_b000813) that showed genetic variance for grain yield only in the absence of fungicide application. This provides independent support for the hypothesis that genetic effects in this genomic region may depend on fungicide treatment and associated disease pressure. Although the local correlation patterns observed here cannot be directly attributed to the same LD block, the concordance between both analyses suggests that chromosome 5A may contain genetic variation whose contribution to grain yield changes with disease management. Likewise, the comparatively greater variability observed within the D subgenome may reflect its distinct genomic architecture. Moreover, Voss-Fels et al. (2019) identified large haplotype blocks associated with yield- and biomass-related traits within the wheat D subgenome, which may contribute to broader regional shifts in marker effects under changing environmental conditions. Furthermore, numerous QTL controlling agronomic performance, phenology, adaptation and disease resistance have been mapped across the wheat genome, including chromosomes 1A, 4D and 5D (Juliana et al. 2019; Tshikunde et al. 2019). These findings support the hypothesis that these genomic regions may contribute to environment-dependent changes in grain yield. However, the present analyses cannot identify the underlying causal loci, and the observed chromosome-specific patterns should therefore be regarded as exploratory. Future studies combining genome-wide association analyses or regional genomic prediction with disease phenotyping could determine whether these regions correspond to loci underlying fungicide-specific genotype responses.

Limitations of the study

Although the IFA model successfully separated predictable environmental effects from latent sources of GEI, several limitations remain. The environmental characterization was restricted primarily to routinely recorded weather variables, which are unlikely to capture the full complexity of the environments experienced by the crop. Incorporating additional descriptors such as soil physical and chemical properties, systematic measures of disease pressure across environments, and environmental conditions during critical developmental stages could improve the biological interpretation of the latent factors and increase the proportion of GEI explained by measured covariates. Furthermore, extending the analysis to a larger number of environments and years would provide a broader representation of the target population of environments and improve the robustness of genotype-specific environmental response estimates.

Conclusion

This study demonstrates that GEI in European winter wheat is shaped by both environmental conditions and crop management, with contrasts involving fungicide treatment showing larger changes in additive genetic effects than the nitrogen contrast evaluated without fungicide application. Although IFA models effectively interpreted and predicted additive GEI, measured environmental covariates explained only a small proportion of the additive genetic variance, highlighting that weather variables alone are insufficient to fully characterize breeding environments. Furthermore, more than 50 years of breeding improved overall performance, including under reduced nitrogen supply and without fungicide application, whereas no clear temporal trend was observed for the FA-based RMSD measure. The latter finding contrasted with previous stability assessments, showing that conclusions about breeding progress in yield stability depend on how stability is defined and quantified. Overall, combining measured environmental covariates with latent factors can help breeders better interpret and predict GEI in wheat.

Author contribution statement AU conceptualized the study, performed the formal analysis and investigation, and wrote the original draft. AF reviewed and edited the manuscript. SEW contributed to the conceptualization and supervision of the study, acquired funding, and reviewed and edited the manuscript. RJS supervised the study and reviewed and edited the manuscript. All authors read and approved the final manuscript.

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Data availability The dataset used in the study of Wang et al. (2025) has been published on Figshare (https://doi.org/10.6084/m9.figshare.27910269). The raw SNP marker data were published in the studies of Voss-Fels et al. (2019) (https://doi.org/10.1038/ s41477-019-0445-5) and Lichthardt et al. (2020) (https://doi.org/10.3389/fpls.2019.01771).

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Competing interests Author RJS is Editor-in-Chief of Theoretical and Applied Genetics.

References

Allard RW, Bradshaw AD (1964) Implications of Genotype-Environmental Interactions in Applied Plant Breeding[1]. Crop Sci 4:503–508. https://doi.org/10.2135/cropsci1964.0011183X000400050021x

Browning BL, Zhou Y, Browning SR (2018) A One-Penny Imputed Genome from Next-Generation Reference Panels. Am J Hum Genet 103:338–348. https://doi.org/10.1016/j.ajhg.2018.07.015

Browning SR, Browning BL (2007) Rapid and Accurate Haplotype Phasing and Missing-Data Inference for Whole-Genome Association Studies By Use of Localized Haplotype Clustering. Am J Hum Genet 81:1084–1097. https://doi.org/10.1086/521987

Burgueño J, Crossa J, Cornelius PL, Yang R (2008) Using Factor Analytic Models for Joining Environments and Genotypes without Crossover Genotype × Environment Interaction. Crop Sci 48:1291–1305. https://doi.org/10.2135/cropsci2007.11.0632

Burgueño J, De Los Campos G, Weigel K, Crossa J (2012) Genomic Prediction of Breeding Values when Modeling Genotype × Environment Interaction using Pedigree and Dense Molecular Markers. Crop Sci 52:707–719. https://doi.org/10.2135/cropsci2011.06.0299

Caldelas C, Rezzouk FZ, Aparicio Gutiérrez N, et al (2023) Interaction of genotype, water availability, and nitrogen fertilization on the mineral content of wheat grain. Food Chem 404:134565. https://doi.org/10.1016/j.foodchem.2022.134565

Calderini DF, Slafer GA (1998) Changes in yield and yield stability in wheat during the 20th century. Field Crops Res 57:335–347. https://doi.org/10.1016/S0378-4290(98)00080-X

Calderini DF, Slafer GA (1999) Has yield stability changed with genetic improvement of wheat yield? Euphytica 107:51–59. https://doi.org/10.1023/A:1003579715714

Cooper M, Powell O, Gho C, et al (2023) Extending the breeder's equation to take aim at the target population of environments. Front Plant Sci 14:1129591. https://doi.org/10.3389/fpls.2023.1129591

Cooper M, Voss-Fels KP, Messina CD, et al (2021) Tackling G × E × M interactions to close on-farm yield-gaps: creating novel pathways for crop improvement by predicting contributions of genetics and management to crop productivity. Theor Appl Genet 134:1625–1644. https://doi.org/10.1007/s00122-021-03812-3

Cormier F, Faure S, Dubreuil P, et al (2013) A multi-environmental study of recent breeding progress on nitrogen use efficiency in wheat (Triticum aestivum L.). Theor Appl Genet 126:3035–3048. https://doi.org/10.1007/s00122-013-2191-9

Falconer DS, Mackay T (2009) Introduction to quantitative genetics, 4. ed., [16. print.]. Pearson, Prentice Hall, Harlow

Finlay K, Wilkinson G (1963) The analysis of adaptation in a plant-breeding programme. Aust J Agric Res 14:742–754. https://doi.org/10.1071/AR9630742

Fradgley NS, Gerard GS, Govindan V, et al (2025) Prediction of Australian wheat genotype by environment interactions and mega-environments. Theor Appl Genet 138:241. https://doi.org/10.1007/s00122-025-05023-6

568 Francis TR, Kannenberg LW (1978) YIELD STABILITY STUDIES IN SHORT-SEASON MAIZE. I. A
569 DESCRIPTIVE METHOD FOR GROUPING GENOTYPES. Can J Plant Sci 58:1029–1034.
570 https://doi.org/10.4141/cjps78-157

571 Gilmour AR, Cullis BR, Verbyla AP, Verbyla AP (1997) Accounting for Natural and Extraneous
572 Variation in the Analysis of Field Experiments. J Agric Biol Environ Stat 2:269.
573 https://doi.org/10.2307/1400446

574 He S, Schulthess AW, Mirdita V, et al (2016) Genomic selection in a commercial winter wheat
575 population. Theor Appl Genet 129:641–651. https://doi.org/10.1007/s00122-015-2655-1

576 Heier T, Jain SK, Kogel K -H., Pons-Kühnemann J (2005) Influence of N-fertilization and Fungicide
577 Strategies on Fusarium Head Blight Severity and Mycotoxin Content in Winter Wheat. J
578 Phytopathol 153:551–557. https://doi.org/10.1111/j.1439-0434.2005.01021.x

579 Heslot N, Akdemir D, Sorrells ME, Jannink J-L (2014) Integrating environmental covariates and
580 crop modeling into the genomic selection framework to predict genotype by environment
581 interactions. Theor Appl Genet 127:463–480

582 Hirel B, Le Gouis J, Ney B, Gallais A (2007) The challenge of improving nitrogen use efficiency in
583 crop plants: towards a more central role for genetic variability and quantitative genetics
584 within integrated approaches. J Exp Bot 58:2369–2387.
585 https://doi.org/10.1093/jxb/erm097

586 Jarquín D, Crossa J, Lacaze X, et al (2014) A reaction norm model for genomic selection using high-
587 dimensional genomic and environmental data. Theor Appl Genet 127:595–607.
588 https://doi.org/10.1007/s00122-013-2243-1

589 Juliana P, Poland J, Huerta-Espino J, et al (2019) Improving grain yield, stress resilience and quality
590 of bread wheat using large-scale genomics. Nat Genet 51:1530–1539.
591 https://doi.org/10.1038/s41588-019-0496-6

592 Kelly AM, Smith AB, Eccleston JA, Cullis BR (2007) The Accuracy of Varietal Selection Using Factor
593 Analytic Models for Multi-Environment Plant Breeding Trials. Crop Sci 47:1063–1070.
594 https://doi.org/10.2135/cropsci2006.08.0540

595 Laird NM, Ware JH (1982) Random-Effects Models for Longitudinal Data. Biometrics 38:963.
596 https://doi.org/10.2307/2529876

597 Lichthardt C, Chen T-W, Stahl A, Stützel H (2020) Co-Evolution of Sink and Source in the Recent
598 Breeding History of Winter Wheat in Germany. Front Plant Sci 10:1771.
599 https://doi.org/10.3389/fpls.2019.01771

600 Lin CS, Binns MR (1988) A SUPERIORITY MEASURE OF CULTIVAR PERFORMANCE FOR CULTIVAR
601 × LOCATION DATA. Can J Plant Sci 68:193–198. https://doi.org/10.4141/cjps88-018

602 Mathews KL, Trethowan R, Milgate AW, et al (2011) Indirect selection using reference and probe
603 genotype performance in multi-environment trials. Crop Pasture Sci 62:313–327.
604 https://doi.org/10.1071/CP10318

605 Oliveira ICM, Guilhen JHS, Ribeiro PCDO, et al (2020) Genotype-by-environment interaction and
606 yield stability analysis of biomass sorghum hybrids using factor analytic models and
607 environmental covariates. Field Crops Res 257:107929.
608 https://doi.org/10.1016/j.fcr.2020.107929

609 Patterson HD, Thompson R (1971) Recovery of inter-block information when block sizes are
610 unequal. Biometrika 58:545–554. https://doi.org/10.1093/biomet/58.3.545

611 Piepho HP (1997) Mixed models with multiplicative terms for cultivar trial data. In: Advances in
612 Biometrical Genetics. Proceedings of the Tenth Meeting of the EUCARPIA Section
613 Biometrics in Plant Breeding, eds P. Krajewski and Z. Kaczmarek (Poznan, Poland:
614 EUCARPIA). pp 215–220

615 R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for
616 Statistical Computing

617 Smith A, Cullis B, Thompson R (2001) Analyzing Variety by Environment Data Using Multiplicative
618 Mixed Models and Adjustments for Spatial Field Trend. Biometrics 57:1138–1147.
619 https://doi.org/10.1111/j.0006-341X.2001.01138.x

620 Smith A, Norman A, Kuchel H, Cullis B (2021) Plant Variety Selection Using Interaction Classes
621 Derived From Factor Analytic Linear Mixed Models: Models With Independent Variety
622 Effects. Front Plant Sci 12:737462. https://doi.org/10.3389/fpls.2021.737462

623 Smith AB, Cullis BR (2018) Plant breeding selection tools built on factor analytic mixed models for
624 multi-environment trial data. Euphytica 214:143. https://doi.org/10.1007/s10681-018-
625 2220-5

626 Snowdon RJ, Wittkop B, Chen T-W, Stahl A (2021) Crop adaptation to climate change as a
627 consequence of long-term breeding. Theor Appl Genet 134:1613–1623.
628 https://doi.org/10.1007/s00122-020-03729-3

629 The VSNi Team (2023) asreml: Fits Linear Mixed Models using REML

630 Tolhurst DJ, Gaynor RC, Gardunia B, et al (2022) Genomic selection using random regressions on
631 known and latent environmental covariates. Theor Appl Genet 135:3393–3415.
632 https://doi.org/10.1007/s00122-022-04186-w

633 Tolhurst DJ, Mathews KL, Smith AB, Cullis BR (2019) Genomic selection in multi-environment
634 plant breeding trials using a factor analytic linear mixed model. J Anim Breed Genet
635 136:279–300. https://doi.org/10.1111/jbg.12404

636 Tshikunde NM, Mashilo J, Shimelis H, Odindo A (2019) Agronomic and Physiological Traits, and
637 Associated Quantitative Trait Loci (QTL) Affecting Yield Response in Wheat (Triticum
638 aestivum L.): A Review. Front Plant Sci 10:1428. https://doi.org/10.3389/fpls.2019.01428

639 VanRaden PM (2008) Efficient Methods to Compute Genomic Predictions. J Dairy Sci 91:4414–
640 4423. https://doi.org/10.3168/jds.2007-0980

641 Voss-Fels KP, Stahl A, Wittkop B, et al (2019) Breeding improves wheat productivity under
642 contrasting agrochemical input levels. Nat Plants 5:706–714.
643 https://doi.org/10.1038/s41477-019-0445-5

644 Wang T-C, Rose T, Zetzsche H, et al (2025) Multi-environment field trials for wheat yield, stability
645 and breeding progress in Germany. Sci Data 12:64. https://doi.org/10.1038/s41597-024-
646 04332-7

647 Waters D, Finnegan C, Weber S, et al (2026) Designing high performing and stable genotypes
648 through complementary crossing schemes

649 Weber SE, Frisch M, Snowdon RJ, Voss-Fels KP (2023) Haplotype blocks for genomic prediction:
650 a comparative evaluation in multiple crop datasets. Front Plant Sci 14:1217589.
651 https://doi.org/10.3389/fpls.2023.1217589

652 Yates F, Cochran WG (1938) The analysis of groups of experiments. J Agric Sci 28:556–580.
653 https://doi.org/10.1017/S0021859600050978

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