UPEP
Unidad de Posgrados y Educación Permanente

FACULTAD DE AGRONOMÍA
UNIVERSIDAD DE LA REPÚBLICA

UNIVERSIDAD
DE LA REPÚBLICA
URUGUAY

# Mejora de la predicción genómica en trigo con modelos de regresión aleatoria con covariables ambientales

Guillermo Sniadower Silva

Maestría en Ciencias Agrarias
Opción Bioestadística

Marzo, 2026

# Mejora de la predicción genómica en trigo con modelos de regresión aleatoria para covariables ambientales

Guillermo Sniadower Silva

Maestría en Ciencias Agrarias
Opción Bioestadística

Marzo, 2026

Tesis aprobada por el tribunal integrado por Lic. Gene. (Dr.) Leonardo Vanzetti, Ing. Agr. (PhD.) Gustavo de los Campos y B.S. Statis. (PhD.) Inés Berro el (día) de (mes) de (año). Autor/a: Ing. Agr. Guillermo Sniadower. Director/a: Ing. Agr. (PhD) Pablo González Barrios. Codirector/a: Ing. Agr. (PhD) Lucía Gutiérrez.

## Agradecimientos

Mencionar a todos los que han sido parte, directa o indirectamente, de este gran y largo proyecto se torna una tarea imposible, sería injusto nombrar individualmente. Quisiera reconocer a todo el grupo del DBEC por su calidez y apoyo desde el comienzo. Qué fácil y grato han hecho todo.

A todo INIA y a su programa de mejoramiento de cultivares de trigo, por brindarse profesional y humanamente en distintas etapas de esta investigación. A la Dra. Lucía Gutiérrez, como cotutora, por su guía en este camino, y a todo su laboratorio en la Universidad de Wisconsin por aceptarme y acompañarme en mi pasantía y en este proyecto de investigación.

Especial mención a mi tutor, Dr. Pablo González, por confiar en mí, guiarme en todo este trayecto y haber mantenido una dinámica tan amena durante todos estos años. Finalmente, a mi familia, por apoyar todas mis decisiones, buenas y malas, que me han llevado a este momento de la vida tan gratificante.

# Tabla de contenido

# Resumen

El cultivo de trigo (*Triticum aestivum* L.), uno de los cereales más importantes para la seguridad alimentaria mundial, enfrenta crecientes desafíos debido al cambio climático, lo que exige variedades más resilientes. Este estudio evaluó estrategias para potenciar la selección genómica (GS) en trigo, incorporando covariables ambientales (EC) y modelos de regresión aleatoria (RRM) en ensayos multiambiente (MET). Se analizaron datos fenotípicos y genotípicos de 4.291 genotipos del Programa Nacional de Mejoramiento de Trigo (2010-2020) en 71 ambientes, utilizando 45 EC correspondientes a las fases vegetativa, reproductiva y de llenado de grano. A través de regresión por mínimos cuadrados parciales (PLS), se identificaron siete EC claves para modelar la interacción genotipo por ambiente (IGA) y probar su incorporación en diferentes escenarios de predicción genómica (CV0, CV1 y CV2). Se compararon los métodos GBLUP (*genomic best linear unbiased prediction*), análisis de factores (FA) y RRM en cuanto a su capacidad predictiva. El RRM, con tres o cuatro EC, superó a GBLUP en un 52-124 % de precisión en CV1 y CV2, aunque FA exhibió la mayor precisión general; notoriamente, el mejor RRM en CV1 igualó el rendimiento de FA. Además, el RRM mejoró las predicciones en más del 90 % de los ambientes para ambientes desconocidos (CV0) al probarse distintas combinaciones de EC. En resumen, integrar EC en RRM optimiza la predicción genómica al capturar eficientemente la IGA y reduce la sobreparametrización mediante la selección eficaz de covariables.

**Palabras clave**: cereales, selección genómica, cambio climático, interacción genotipo por ambiente

# Summary

## 2. Improving genomic prediction in wheat with random regression models for environmental covariates

Wheat (*Triticum aestivum* L.) cultivation, one of the most critical cereals for global food security, faces escalating challenges from climate change, necessitating more resilient varieties. This study evaluated strategies to enhance genomic selection (GS) in wheat by incorporating environmental covariates (ECs) and random regression models (RRM) in multi-environment trials (METs). Phenotypic and genotypic data from 4,291 genotypes in the National Wheat Breeding Program (2010–2020) were analyzed across 71 environments, incorporating 45 ECs related to vegetative, reproductive and grain-filling phases. Partial least squares regression (PLS) identified seven key EC for modeling genotype by environment (GEI) interactions and tested their integration into various genomic prediction scenarios (CV0, CV1 and CV2). Predictive performance was compared among genomic best linear unbiased prediction (GBLUP), factor analysis (FA) and RRM methods. RRM, using three or four ECs, outperformed GBLUP by 52–124% in accuracy for CV1 and CV2, though FA exhibited the highest overall accuracy; notably, the top RRM in CV1 matched FA's performance. Furthermore, RRM enhanced predictions in over 90% of environments for unseen conditions (CV0) across EC combinations. In summary, integrating ECs into RRM optimizes genomic predictions by efficiently capturing genotype by environment interaction, without overparameterization through a limited number of covariates.

**Keywords**: cereals, genomic selection, genotype by environment interaction, climate change

# 1. Introducción

El mejoramiento genético vegetal ha sido un pilar fundamental para garantizar la seguridad alimentaria global, que transforma especies silvestres en cultivos de alto rendimiento capaces de sostener una población mundial en constante crecimiento (Bernardo, 2010). Cultivos como el trigo (*Triticum aestivum* L.), el maíz (*Zea mays*) y el arroz (*Oryza sativa*), que aportan más del 50 % de las calorías consumidas globalmente, son fundamentales para la nutrición humana (Rawat et al., 2019; Shewry, 2009; Slafer et al., 2015). En particular, el trigo representa aproximadamente un quinto de las proteínas y calorías en la dieta mundial, con una producción que se triplicó entre 1981 y 2020, de 248 a 755 millones de toneladas, y un rendimiento promedio de 3,48 t/ha en la última década (Zakharova y Zakharov, 2024). Sin embargo, el cambio climático amenaza la productividad agrícola, debido a condiciones climáticas cada vez más extremas y frecuentes que afectan de forma negativa el rendimiento en cereales (IPCC, 2023; Thornton et al., 2014). El aumento gradual de temperaturas y la variabilidad de precipitaciones incrementan la intensidad y frecuencia de condiciones de estrés, como sequías y olas de calor, que han ralentizado el progreso en productividad agrícola en latitudes medias y bajas (IPCC, 2023). Estudios recientes advierten que el rendimiento global de trigo podría disminuir entre un 6 % y un 10 % por cada grado centígrado adicional durante la fase crítica de llenado de grano (Zhao et al., 2024). Aunque existen genotipos de alto rendimiento, su desempeño está cada vez más limitado por estos estreses bióticos y abióticos (Bohra et al., 2024; Dutta et al., 2023).

En este contexto desafiante, los programas de mejoramiento han aumentado la demanda de desarrollo de genotipos con mayores niveles de resiliencia a través de ambientes, o genotipos superiores en ambientes específicos, lo que exige herramientas modernas para abordar uno de los principales desafíos como lo es la interacción genotipo por ambiente (IGA) (Ceccarelli et al., 2010; Tester y Langridge, 2010). La IGA ocurre cuando el rendimiento relativo de los genotipos depende de las condiciones ambientales que se presenten (Malosetti et al., 2013). Por ejemplo, un genotipo puede tener un excelente desempeño bajo sequía, pero no destacarse en ambientes óptimos.

Esta variabilidad dificulta la selección de genotipos en diferentes ambientes por parte de los programas de mejoramiento, dado que un material con buena *performance* en determinadas condiciones ambientales puede fracasar en otras (Malosetti et al., 2013). Esta interacción causa cambios en el comportamiento y el orden relativo del desempeño de los genotipos en diferentes ambientes (Cooper y DeLacy, 1994; Falconer, 1952), que dificulta en muchos casos la selección en redes de ensayos multiambiente (MET) (Heslot et al., 2014; Jarquin et al., 2020). Para abordar la IGA, en principio es fundamental utilizar MET, evaluando los materiales en distintas localidades o años (Malosetti et al., 2013). En ese sentido, los genotipos ampliamente adaptados presentan un buen desempeño en la mayoría de los ambientes, mientras que los específicos se desempeñan bajo condiciones particulares. El concepto de *población objetivo de ambientes* (TPE, sigla en inglés) tiene como objetivo identificar los cultivares a seleccionar acorde a los ambientes donde se plantarán y maximizar su performance (Malosetti et al., 2013).

Existen distintas estrategias para abordar la IGA que incluyen ignorarla, cuando la IGA en nuestra población es baja; reducirla, mediante agrupación de ambientes similares, o explotarla mediante su inclusión en modelos de análisis estadísticos (Bernardo, 2010; Mumford et al., 2023). Esta última generalmente suele ser la más eficaz en la identificación de genotipos resilientes o con adaptación específica. Para abordar este problema metodológicamente, se han desarrollado aplicaciones mediante el uso de modelos lineales y bilineales como los AMMI (Gauch, 1992), GGE biplots (Lado et al., 2016), así como modelos mixtos con matrices de estructuras de correlación entre ambientes (Monteverde et al., 2019). Avances recientes en *enviromics* han potenciado estas estrategias al integrar covariables ambientales (EC) de alta dimensionalidad, tales como variables meteorológicas relevadas a través de sitios o información de atributos físico-químicos del suelo. Algunos trabajos recientes se han enfocado en modelar IGA, donde el ensamblaje de información genética con ambiental mediante enviromics ha reducido costos y aumentado la precisión en predicciones de plasticidad de rendimiento (Costa-Neto et al., 2021). Este enfoque no solo captura patrones de IGA en MET, sino que también permite predecir respuestas genotípicas en escenarios climáticos futuros, esencial para regiones con alta variabilidad climática. En resumen, existe un conjunto creciente de herramientas metodológicas que permiten mejorar la capacidad predictiva en contexto de evaluaciones multiambiente incorporando información ambiental. Sin embargo, es necesario incrementar el uso de estas en diversos contextos productivos y en particular en situaciones en donde se cuenta con altos volúmenes de información histórica en programas de mejoramiento vegetal.

## 1.1. Variabilidad ambiental en mejoramiento genético vegetal

La variabilidad ambiental ha sido un pilar central en el análisis de IGA desde los enfoques iniciales de estabilidad y adaptabilidad propuestos por Finlay y Wilkinson (1963), que evaluaban el rendimiento relativo de genotipos frente a condiciones medias ambientales para identificar patrones de adaptación general. Esta perspectiva se expandió con los modelos bilineales, como el análisis de efectos principales aditivos e interacción multiplicativa (AMMI) de Gauch (1992) y el GGE biplot (genotipo más genotipo por ambiente) de Yan et al. (2000), que descomponen la IGA en componentes aditivos y multiplicativos para visualizar megaambientes y cruces de genotipos ideales y facilitar la selección en MET. Por otro lado, los análisis factoriales, desarrollados por Crossa (1990) y extendidos por Vargas et al. (1999), incorporaron regresiones lineales y no lineales para modelar trayectorias de respuesta ambiental que permiten una descomposición más refinada de la variabilidad y la identificación de covariables que explican la heterogeneidad en el desempeño genotípico.

Con el auge de la selección genómica (SG), la IGA se integró en marcos predictivos, como en los trabajos de Lado et al. (2016), que adaptaron modelos paramétricos para capturar interacciones en trigo mediante marcadores genómicos integrando información de IGA y megaambientes. Esta tendencia se fortaleció con enfoques que incorporan covariables ambientales directamente en SG, como los modelos de regresión aleatoria de Jarquín et al. (2014) y los de Heslot et al. (2014), que mejoran la precisión predictiva al modelar efectos ambientales como la incorporación de EC. En contextos locales, estudios como los de Monteverde et al. (2019) y Rebollo et al. (2023) en arroz han aplicado estos principios para analizar G×E en MET y destacan la utilidad de datos ambientales de alta resolución para refinar predicciones en poblaciones de élite.

Estos avances culminan en el paradigma de enviromics, que fusiona genómica, fenómica y ambientalómica para un análisis holístico de la IGA (Resende et al., 2022). Por ejemplo, en trigo, el uso de enviromics ha permitido predecir rendimientos bajo escenarios climáticos variables mediante índices satelitales como el NDVI y optimizar la selección de genotipos resilientes en regiones con alta heterogeneidad, como el Cono Sur.

## 1.2. Avances en selección genómica y modelos de análisis

La SG ha revolucionado el mejoramiento vegetal al emplear marcadores moleculares de todo el genoma para predecir valores genéticos (GEBV, por sus siglas en inglés) y acelerar los ciclos de selección en diversos cultivos de interés comercial (Burgueño et al., 2012; Meuwissen et al., 2001). En trigo, la SG ha permitido predecir caracteres complejos como rendimiento, calidad del grano y tolerancia al estrés y reducir significativamente el tiempo necesario para desarrollar nuevas variedades (Bandeira et al., 2018; Montesinos-López et al., 2024). Modelos como el *genomic best linear unbiased prediction* (GBLUP) integran datos genómicos y fenotípicos en matrices de relación genómica, pero su precisión puede verse limitada por la variabilidad ambiental, que requiere modelos más flexibles (Heslot et al., 2014). Los RRM representan un avance significativo, ya que permiten modelar respuestas genotípicas específicas a gradientes ambientales mediante la integración de EC (Ly et al., 2018). Estos modelos han mejorado la precisión predictiva hasta en un 50 % en trigo, especialmente al predecir el desempeño en ambientes no evaluados (Montesinos-López et al., 2024; Tolhurst et al., 2022). Por ejemplo, al incorporar EC como temperatura durante el llenado de grano o precipitación en la fase vegetativa, los RRM capturan respuestas dinámicas en fases críticas del desarrollo del cultivo (Bustos-Korts et al., 2021). Desde una perspectiva bioestadística, los RRM destacan por su capacidad para manejar datos complejos, existiendo diversos paquetes estadísticos capaces de implementar este tipo de modelos mixtos avanzados (Butler, 2020). Otro abordaje complementario en SG ha sido la extensión de modelos factoriales y multicaracter, como los propuestos por Crossa et al. (2019), que incorporan análisis de factores para descomponer la IGA en componentes latentes, que mejoran la robustez en predicciones multicaracter y multiambiente. Por ejemplo, en maíz, estos enfoques factoriales han optimizado la selección de genotipos adaptados a megaambientes variables, un principio transferible a cultivos como el trigo para refinar el entendimiento y cuantificación de la heterogeneidad ambiental (Crossa et al., 2019). En ese sentido, la existencia de mayores volúmenes de información y la aparición de nuevas estrategias metodológicas generan constantes desafíos en trabajos con SG, como la selección de EC relevantes, ya que la multicolinealidad puede generar inestabilidad en los modelos (Lu et al., 2019). Varios trabajos han indicado que el uso de análisis como PLS permite reducir el conjunto de EC, seleccionando solo aquellas con alto poder predictivo, como se ha demostrado en estudios donde un reducido número de las EC iniciales son suficientes para predicciones robustas (Montesinos-López et al., 2023; Rebollo et al., 2023; Resende et al., 2022). Por otro lado, la integración de datos de alta resolución, como los derivados de sensores remotos, está comenzando a complementar estos enfoques, que ofrecen una caracterización más detallada de los ambientes de evaluación. Este panorama, que progresa desde modelos paramétricos básicos hacia integraciones multifactoriales, subraya la importancia de combinar fuentes diversas de información ambiental con marcadores genómicos y enfoques multicaracter para lograr una visión más integral del mejoramiento que capture la complejidad de la IGA y acelere la obtención de variedades adaptativas y resilientes.

## 1.3. Brechas de investigación y aportes al problema

A pesar de los avances en GS y RRM, persisten desafíos significativos en su implementación a gran escala, particularmente en cultivos como el trigo en regiones con alta variabilidad climática, como Uruguay. Uno de los principales obstáculos es la integración de datos multiómicos (genómicos, fenotípicos y ambientales) en tiempo real, que requiere métodos computacionales avanzados para procesar grandes volúmenes de datos sin comprometer la precisión (Millet et al., 2023). Por ejemplo, la modelización de redes multiambiente en donde interesa evaluar la IGA, que capturan relaciones complejas entre variables climáticas, edáficas y genotípicas, sigue siendo un área en constante desarrollo, con potencialidad para mejorar los niveles de predicción (Escamilla et al., 2025). Además, la incorporación de prácticas de manejo, como las fechas de siembra o el manejo de fertilizaciones, en modelos de GS permanece subdesarrollada, a pesar de su impacto en el rendimiento bajo condiciones variables (Mumford et al., 2023). Otro desafío es la escalabilidad de los RRM, ya que su complejidad computacional aumenta con el número de EC y genotipos evaluados, lo que limita su aplicación en programas de mejoramiento con recursos restringidos (Millet et al., 2023). En trigo, la evaluación de respuestas genotípicas en fases específicas del desarrollo (antesis, llenado de grano, entre otras) bajo estrés ambiental sigue siendo incipiente, especialmente en regiones donde la temperatura y la humedad modulan la evapotranspiración (Yue et al., 2025). La falta de bases de datos integradas que combinen información genómica, fenotípica y ambiental también dificulta la implementación de enfoques integrales a gran escala (Resende et al., 2024). Esta tesis aborda estas brechas al evaluar la integración de EC en RRM para optimizar la predicción genómica en trigo, con un enfoque en escenarios de validación cruzada que contemplan escenarios con condiciones climáticas diversas. Desde una perspectiva metodológica, el trabajo propone estrategias que combinan datos genómicos, fenotípicos y ambientales, utilizando herramientas como PLS y modelos mixtos para seleccionar EC relevantes y modelar respuestas genotípicas. Además, explora cómo las prácticas de manejo pueden integrarse en estos modelos y ofrecer estrategias para programas de mejoramiento adaptados al cambio climático.

## 1.4. Hipótesis y objetivos

### 1.4.1. Hipótesis general

La integración de EC seleccionadas mediante regresión por mínimos cuadrados parciales (PLS) en RRM mejora la precisión de la predicción genómica en trigo y captura de manera eficiente la IGA en ensayos provenientes de MET.

### 1.4.2. Objetivo general

Evaluar la integración de EC seleccionadas mediante análisis de PLS en modelos de regresión aleatoria para optimizar la precisión de la predicción genómica en trigo, con énfasis en la captura eficiente de la IGA en ensayos multiambiente basados en información histórica del Programa Nacional de Mejoramiento de Trigo de Uruguay (2010-2020).

### 1.4.3. Hipótesis especificas

H1: La selección de EC mediante PLS en RRM incrementa la precisión predictiva de los GEBV en comparación con GBLUP, al capturar respuestas dinámicas de la IGA en fases fenológicas clave (vegetativa, reproductiva y de llenado de grano) en los MET del Programa Nacional de Mejoramiento de Trigo.

H2: Un número reducido de EC optimiza los RRM al minimizar la multicolinealidad y sobreparametrización, y eleva la precisión en validaciones internas (CV1 y CV2) sin comprometer la estabilidad en los ambientes evaluados.

H3: Los RRM con EC integradas mejoran las predicciones en la mayoría de los ambientes no evaluados (CV0) y facilitan la extrapolación de la IGA a nuevos MET con heterogeneidad ambiental histórica.

### 1.4.4. Objetivos específicos

OE1 (asociado a H1): Identificar y seleccionar EC relevantes mediante PLS para fases fenológicas críticas, incorporándolas en RRM y comparando su precisión predictiva con GBLUP y FA en datos fenotípicos/genotípicos de 4.291 genotipos de trigo en MET en más de 70 ambientes de evaluación.

OE2 (asociado a H2): Evaluar el impacto de combinaciones variables de EC (1 a 7) en la estabilidad de RRM, mediante validaciones CV1 y CV2, para determinar umbrales óptimos que reduzcan multicolinealidad en los ambientes y escenarios evaluados.

OE3 (asociado a H3): Validar el uso de RRM con EC en predicciones para ambientes desconocidos (CV0), cuantificando mejoras en precisión en diferentes escenarios, y vincular la relación de las EC con momento de siembra.

## 1.4. Estructura de la tesis

La tesis se estructura en cinco capítulos. El capítulo 1 es introductorio y proporciona un contexto general del mejoramiento vegetal y los avances en GS y estrategias para incorporar información ambiental modelando la IGA. El capítulo 2 presenta un artículo de investigación que aplica RRM con EC en red de evaluación histórica multiambiente del Programa Nacional de Mejoramiento de Trigo de Uruguay, ofreciendo un caso de estudio detallado. El capítulo 3 discute los resultados en un contexto más amplio, integrando los resultados de este trabajo con la literatura existente. El capítulo 4 ofrece conclusiones y recomendaciones, mientras que el capítulo 5 incluye la bibliografía y anexos.

# 2. Improving genomic prediction in wheat with random regression models for environmental covariates

Guillermo Sniadower[1], Rishap Dhakal[2], Paula Silva[3], Bettina Lado[2], Pablo Sandro[1], Inés Rebollo[4], Martin Quincke[1], Julie Dawson[1], Lucia Gutiérrez[1], Pablo González Barrios[2].

[1] Facultad de Agronomía, Universidad de la República, Av. Garzón, 780, Montevideo 12900, Uruguay.

[2] Department of Plant and Agroecosystem Sciences, University of Wisconsin-Madison, 1575 Linden Drive, Madison, WI 53706, USA

[3] Instituto Nacional de Investigación Agropecuaria (INIA), 70006, Colonia, Uruguay.

[4] Department of Agronomy and Plant Genetics, University of Minnesota, Saint Paul, USA.

Corresponding authors: gutierrezcha@wisc.edu; pablog@fagro.edu.uy

Abbreviations: BLUE, best linear unbiased estimation; PP, cumulative precipitation; CV, cross validation; DOL, location Dolores; EC, environmental covariate; ET, evapotranspiration; FA2, factor analytic of order 2; GBLUP, genomic best linear unbiased prediction; GEI, genotype by environment interaction; G, grain filling; FD, ground frost days; GS, genomic selection; GY, grain yield; INASE, national seed institute; INIA, National Institute of Agricultural Research; LE, location La Estanzuela; $T_{\overline{\text{max}}}$, mean maximum temperature; $T_{\overline{\text{min}}}$, mean minimum temperature; $T_{\overline{\text{mean}}}$, mean temperature; NWBP, national wheat breeding program; PA, predictive ability; PAm, median predictive ability; PLS, partial least squares; R, reproductive; R2, location Ruta 2; V, vegetative; YG, location Young.

## 2.1. Abstract

Wheat (*Triticum aestivum* L.), a crucial cereal crop for global food security, faces growing challenges from climate change, demanding resilient varieties. This study assessed strategies to enhance selection response through genomic selection (GS) in wheat by integrating environmental covariates (ECs) and random regression

(RRM) models in multi-environment trials (METs). We analyzed phenotypic and genotypic data from 4,291 genotypes of the National Wheat Breeding Program (2010-2020) across 71 environments, using 45 ECs derived from vegetative, reproductive, and grain-filling phases. Seven key ECs were selected via partial least squares (PLS) regression to model genotype by environment interactions (GEIs) and evaluate their integration in genomic prediction scenarios (CV0, CV1, and CV2). Genomic best linear unbiased prediction (GBLUP), Factor Analytic (FA), and RRM were compared for their predictive ability performance. RRM with three or four ECs outperformed GBLUP, achieving 52–124% higher accuracy in CV1 and CV2, although FA exhibited the highest accuracy overall. Notably, the best RRM in CV1 yielded an accuracy comparable to that of the FA. RRM improved predictions in more than 90% of environments for unknown environment scenarios when various EC combinations were tested. We conclude that integrating ECs into the RRM enhances genomic prediction by effectively capturing the GEI, with fewer covariates preventing overparameterization.

## 2.2. Introduction

Wheat (*Triticum aestivum* L.) provides approximately 20% of the calories in global diets, underscoring its crucial role in human nutrition (Shewry, 2009; Braun et al., 2010; Reynolds & Braun, 2022). However, significant changes in the global climate are expected to adversely affect cereal crop yields because increasingly frequent extreme weather conditions impact vital food sources such as cereals (Rezaei, 2023). Wheat performance is significantly affected by abiotic (heat, drought) and biotic stresses (diseases, insects) and is intensified by climate change (Dutta et al., 2023; Bhavani et al., 2022; He et al., 2022; Trethowan, 2022). In response, breeding programs are increasingly tasked with developing genotypes resilient to biotic and abiotic stressors, calling for advanced tools to address the complex interplay between genotypes and environments (Ceccarelli et al., 2010; Tester & Langridge, 2010).

Identifying superior genotypes with specific adaptations among diverse genetic materials has long been a challenge for plant breeders (Neyhart et al., 2021), largely because of genotype by environment interactions (GEI). GEI causes variations in genotype performance with complex crossover interactions, resulting in changes in the ranking of genotypes across the environment (Falconer, 1952; Cooper & DeLacy, 1994). This interaction is typically evaluated in multi-environment trials (METs; Jarquin et al., 2020; Neyhart, J. L., Silverstein, 2022); however, selecting top performers remains complex due to complex crossover interactions, which are not always predictable (Heslot et al., 2014).

Different strategies have been proposed to address the GEI: ignoring it when the overall GEI is low (DeLacy et al., 1996), reducing it by grouping more homogenous sets of environments or exploiting it to identify the top-performing genotypes for a specific environment or the more stable genotypes across conditions (Bernardo, 2010; Mumford et al., 2023).

Linear models such as the Finlay-Wilkinson model, the Eberhart and Russell model (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966), bilinear regression models such as AMMI (Gauch, 1992), GGE models (Yan et al., 2000; Lado et al., 2016), and mixed models with different correlation structures (Butler et al., 2023) have been proposed to characterize the GEI. Clustering environments into mega-environments (MEs; groups of environments that result in similar rankings of genotypes) further aids in identifying repeatable GEI patterns to optimize selection (Lado et al., 2016; González-Barrios et al., 2019; Sandro et al., 2024). With the availability of genomic data, models integrating genomic data and GEI have also been proposed (Burgueño et al., 2012).

Genomic selection (GS), proposed by Meuwissen et al. (2001), leverages whole-genome data to estimate genomic estimated breeding values (GEBV) for genotyped individuals, offering significant genetic gains over traditional methods in multi-environment trials (METs) (Burgueño et al., 2012; Malosetti et al., 2016). GS has been key in advancing wheat breeding because it enables early selection via markers (Resende et al., 2011; Berro et al., 2019). However, GS models incorporating GEI is necessary for complex traits such as yield to make the selection process reliable (Heslot et al., 2014). Mixed model with different variance covariance structure between the environment can be used for that purpose (Burgueño, 2012; Butler et al., 2023). Recent developments have further advanced GS by incorporating environmental covariates (ECs) into random regression models (RRMs; regressions of genotype-specific responses to each predictor factor) (Schaeffer., 2004). This approach enhances the ability to model the GEI and predict performance in new untested environments (Tolhurst et al., 2022; Rebollo et al., 2023; Tadese et al., 2024).

EC has long been used to interpret the GEI by incorporating it into regression models (Wood, 1976). Often termed 'enviromics', this environmental information characterizes environments through factors such as landscape and climatic variables that influence genotype growth and performance (Resende et al., 2024). Recent research has focused on integrating ECs into GS to improve prediction models, with studies demonstrating their value in capturing GEI dynamics (Monteverde et al., 2019; Jarquín et al., 2020; Costa-Neto et al., 2021; Neyhart, Gutierrez, 2022). Approaches to incorporating this information include a combination of modeling EC effects as fixed (Heslot et al., 2014) or random terms (Rebollo et al., 2023) or modeling the variance-covariance structure among environments created by the environmental covariates (Jarquín et al., 2014; Basnet et al., 2019). Because of existing collinearity between the ECs, it has been suggested that it may not be necessary to include all the ECs in the model, such as the RRM (Bustos-Korts et al., 2019). Concurrently, it also allows better model stability and inference (Dormann et al., 2013). Therefore, variable selection methods such as partial least squares (PLS) (Vargas et al., 1999), stepwise forward or backward procedures (Mumford et al., 2023), and feature selection methods (Montesinos-López et al., 2024) have been suggested for selecting variables to use as predictors in the RRM. Moreover, it has been proven to be beneficial for increasing the predictive ability of the RRM model (Rebello et al., 2023).

This study evaluated the performance of a wheat MET by selecting ECs to enhance genomic prediction through random regression and mixed model approaches. Specifically, the focus was on identifying their impact on grain yield prediction and their relationship with management practices. Our objectives were to (1) assess EC integration into the RRM to improve the predictive ability of a wheat MET and (2) evaluate the effects of ECs on grain yield by modeling the GEI across cross-validation scenarios. These findings provide a foundation for developing wheat breeding strategies that leverage environmental data to increase resilience and productivity.

## 2.3. Materials and Methods

### 2.3.1. Data

#### 2.3.1.1. Phenotypic Data

Yield data were collected from the MET across multiple years and locations as part of the National Institute of Agricultural Research (INIA) breeding program in Uruguay, as well as from the National Institute of Seeds (INASE) wheat evaluation program. A total of 4,291 inbred genotypes were evaluated, representing advanced inbred genotypes from INIA's program and the INASE evaluation program. These genotypes originated from preliminary, advanced, and elite yield trial phases. The trials were conducted under a randomized complete block design with three to four replications as well as a resolvable incomplete block design with two to four replications, where six to ten incomplete blocks were nested within each complete replication. The experimental setup aimed to account for environmental heterogeneity across trial sites and minimize experimental error.

Phenotypic data were collected from four locations in Uruguay: Dolores (DOL; 33°50' S, 58°14' W, 15 m.a.s.l.), La Estanzuela (LE; 34°20' S, 57°42' W, 81 m.a.s.l.), Young (YG; 32°59' S, 57°57' W, 85 m.a.s.l.) and Ruta 2 (R2; 33°45' S, 58°59' W, 95 m.a.s.l.). Within these locations, trials were further diversified by sowing date, as Uruguay´s optimal sowing window for wheat extends from May 15 to June 15 for most genotypes, depending on their maturity classes (Hoffman et al., 2012). Accordingly, three sowing periods were categorized for the trials: preoptimal (PreOpt), optimal (Opt), and postoptimal (PostOpt) periods. The PreOpt period included trials sown before May 15, the Opt period included trials sown between May 15 and June 15, and the PostOpt period included those sown after June 15.

Evaluations spanned eleven years (2010–2020), where environments were defined as year-by-site combinations, with sites defined as the interaction between management (sowing periods) and location. After each trial was categorized on the basis of the sowing period, all the trials that consisted of the same period were considered an environment, resulting in a total of 102 environments. However, owing to the very small number of genotypes and concurrent convergence issues when fitting models, environments with fewer than twenty-five genotypes were removed from the dataset, resulting in a total of 71 environments.

The phases were designed to progressively reduce the number of genotypes while increasing the confidence in their performance. Preliminary yield trials evaluated 300–1000 inbred genotypes per year at LE across different sowing periods, screening for agronomic potential and yield stability. Advanced yield trials narrowed the selection to 100–160 promising genotypes, which were evaluated in a MET across four to six sites to refine assessments of performance under more diverse environmental conditions. Finally, the elite yield trial phase tested forty elite genotypes across seven sites, identifying the top-performing genotypes for potential release.

The grain yield (GY) Best linear unbiased estimates (BLUEs) for all genotypes in each trial with a randomized complete block design were estimated using following model:

$$y_{ij} = \mu + g_i + r_j + \varepsilon_{ij} \tag{1}$$

where $y_{ij}$ is the GY of the *ith* genotype in the *jth* block, $\mu$ is the overall mean, $g_i$ is the fixed effect of the *ith* genotype, $r_j$ is the independent and identically distributed random variable of the *jth* block in the trial, with $r_j \sim N(0, \sigma_r^2)$, $\sigma_r^2$ is the block variance, and $\varepsilon_{ij}$ is an independent and identically distributed random variable, with $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$, where $\sigma_\varepsilon^2$ is the residual variance.

The GY best linear unbiased estimates (BLUEs) for all genotypes in each trial consisting of resolvable incomplete block designs were estimated using the following model:

$$y_{ijk} = \mu + g_i + r_j + \beta_{k(j)} + \varepsilon_{ijk} \tag{2}$$

where $y_{ijk}$ is the GY of the *ith* genotype *in the jth* replication for the *kth* incomplete block, $\mu$ is the overall mean, $g_i$ is the fixed effect of the *ith* genotype, $r_j$ is the independent and identically distributed random variable of the *kth* replication within the trial, with $r_j \sim N(0, \sigma_r^2)$, $\sigma_r^2$ is the replication variance, $\beta_{k(j)}$ is the independent and identically distributed random variable of the *k*th incomplete block nested within the *jth* replication within the trial, with $\beta_k \sim N(0, \sigma_\beta^2)$, $\sigma_\beta^2$ is the block variance, and $\varepsilon_{ijkl}$ is an independent and identically distributed random variable, with $\varepsilon_{ijk}$ ~N(0, $\sigma_{\varepsilon}^{2}$), where $\sigma_{\varepsilon}^{2}$ is the residual variance.

Additionally, Cullis's broad-sense heritability (Cullis et al., 2006) was estimated for each trial present in each environment, defined as $H^2 = \frac{1-\bar{v}_{\Delta}^{BLUP}}{2*\,\sigma_g^2}$, where $\sigma_g^2$ is the genotypic variance and where $\bar{v}_{\Delta}^{BLUP}$ is the average standard error of the genotypic BLUPs.

### 2.3.1.2. Genotypic Data

Genetic markers for 1,683 genotypes from the INIA wheat breeding program were obtained by genotyping-by-sequencing (GBS), as proposed by Elshire et al. (2011) and modified for wheat by Poland et al. (2012). The TASSEL GBSv2 pipeline (Glaubitz et al., 2014), which uses the cultivar Chinese Spring as the reference genome (IWGSC CS RefSeq v2.1) (Zhu et al., 2021), was used to identify 95,000 SNPs. Loci with a minor allele frequency of less than 5%, a heterozygosity level above 10%, and more than 80% missing values were discarded from the dataset. Missing data were imputed using BEAGLE 5.4 (Browning et al., 2018). The common genotypes across years and sites are illustrated in Figure 1.

### 2.3.1.3. Environmental Information

We retrieved daily environmental data for all locations across the entire time span of the dataset. This included unique values of variables related to radiation, temperature, wind, precipitation, humidity, and evapotranspiration (Supplemental Table 1). Consequently, each day within a given environment is associated with multiple environmental measurements of interest. This information was obtained using the *NASA Power* R package (Sparks, 2018). On the basis of this information, we constructed ECs for each genotype individually, using its specific location and growing season. ECs were derived from averages, cumulative sums, and other continuous and discrete variables to represent the environmental conditions experienced during each genotype's growing season. Initially, fifteen ECs were derived. The fifteen ECs corresponded to cumulative precipitation (PP), cloud coverage (CC), evapotranspiration (ET), frost days (F), maximum mean temperature

($T_{\overline{max}}$), mean temperature ($T_{\overline{mean}}$), temperature above 25°C ($T_{>25}$), minimum mean temperature ($T_{\overline{min}}$), minimum temperature below 15°C ($T_{<15}$), minimum temperature below 4°C ($T_{<4}$), photothermal quotient (Q), relative humidity (RH), solar radiation (SR), thermal amplitude (TA), and wind speed (WS).

Treating the wheat growing season as a homogeneous process may result in the loss of critical information about how ECs influence crop development. To address this, for each genotype, we defined three different growing phases. These time windows were established following Fischer's (1975) definition of the critical period in wheat as a 20-day pre-anthesis window and a 10-day post-anthesis window. The first window, referred to as the vegetative phase (V), spans from the planting date to the start of the reproductive phase (R). The second window, R, was defined as the critical period (i.e., 20 days before anthesis and 10 days after anthesis). Finally, the third window, defined as the grain-filling (G) phase, begins at the end of the R phase and lasts until the harvest date (used as a proxy for maturity). For each of these three phases, the same set of 15 ECs was calculated, resulting in a total of 45 ECs per genotype across the entire dataset.

### 2.3.2. Environmental covariate selection

We used partial least squares (PLS) to select the top ECs for yield prediction from 45 ECs constructed. PLS allows us to address the potential overparameterization and collinearity between ECs (Rebollo et al., 2023) and was performed using the *pls* package in R (Mevik & Wehrens, 2007). The response matrix for PLS represented the GY for each genotype in our dataset, which was the predictor matrix, our 45 ECs specific for each genotype growing cycle. From the 45 initial ECs, the top ones were included in our models following their variable importance in PLS projection (VIP) scores as described in Mehmood et al., 2020. The VIP score was computed using the *plsVarSel* package with the VIP function in R (Mehmood et al., 2012).

### 2.3.3. Characterization of GEI

For GEI characterization, we first estimated the variance components from our whole phenotypic dataset and then divided the environments into high-yielding and low-yielding years on the basis of yield data using the k-means method in R (R core team, 2024). Finally, those groups were characterized based on EC information.

### 2.3.3.1. Variance Components

Variance components were estimated by fitting the following model:

$$y_{ijkmno} = \mu + g_i + \tau_j + a_k + l_m + r_{n(j)} + \beta_{o(n)} + gl_{ij} + ga_{ik} + \varepsilon_{ijkmno} \qquad (3)$$

where $y_{ijkmno}$ is the GY, $\mu$ is the overall population mean, $g_i$ is the genotypic effect, being independent and identically distributed (IID) random variable, with $g_i$ ~N(0, $\sigma_g^2$), and $\sigma_g^2$ is the genotypic variance, $\tau_j$ is the trial effect, IID variable, with $\tau_j$ ~N(0, $\sigma_\tau^2$), and $\sigma_\tau^2$ is the trial variance, $a_k$ is the year effect, IID variable, with $a_k$ ~N(0, $\sigma_a^2$), and $\sigma_a^2$ is the year variance, $l_m$ is the site effect, IID variable , with $l_m$ ~N(0, $\sigma_m^2$), and $\sigma_l^2$ is the site variance, $r_{n(j)}$ is the replication effect, an IID variable, with $r_{n(j)}$ ~N(0, $\sigma_r^2$), and $\sigma_r^2$ is the replication variance, $\beta_{0(n)}$ is the block effect, an IID variable, with $\beta_{o(n)}$ ~N(0, $\sigma_\beta^2$), and $\sigma_\beta^2$ is the block variance, $gl_{ij}$ is and IID variable, with $gl_{ij}$~ N(0, $\sigma_{gl}^2$), and $\sigma_{gl}^2$ is the genotype by site variance, $ga_{ik}$ is an IID random variable, with $ga_{ik}$ ~ N (0, $\sigma_{ga}^2$), and $\sigma_{ga}^2$ is the genotype by year variance, and $\varepsilon_{ilkmno}$is the random residual variable, with $\varepsilon_{ilkmno}$ ~N(0, $\sigma_\varepsilon^2$), and $\sigma_\varepsilon^2$ is the residual variance.

### 2.3.3.2. Environment by Management

To further explore the relationship between the environment and management practices, we analyzed environment by management (E×M) interactions, with a particular focus on sowing dates.

We examined yield response patterns based on selected ECs, considering sowing dates as a key factor. This approach is complemented by a subsequent evaluation of E×M interactions stratified by material type, specifically categorized into short, intermediate, and long cycles, to capture specific yield variations associated with these combinations.

### 2.3.4. Genomic predictions

#### 2.3.4.1. Response variables for the genomic prediction model

Phenotypic data were first analyzed to obtain genotypic BLUEs for each genotype in each trial nested in an environment via Eq. 1 and Eq. 2, depending on the experimental design. These BLUEs were then used as inputs to estimate genotypic BLUPs within each trial nested in an environment, following the two-step approach described by Möhring & Piepho (2009). The resulting Best Linear Unbiased Predictor (BLUP), which represents the best estimate of the breeding values of genotypes in each trial environment, was subsequently used as the response variable in the genomic prediction models. We fitted the following model for predicting the BLUP per trial environment:

$$y_{ijk} = \mu + g_i + e_k + ge_{ik} + \tau_{j(k)} + g\tau e_{ji(k)} + \varepsilon_{ijk} \qquad (4)$$

where $y_{ijk}$ is the vector of the genotypic BLUEs for the *ith* genotype in the *jth* trial nested in the *kth* environment, $\mu$ is the overall mean, and $g_i$ is the random effect of the *ith* genotype, where $\mathbf{g} \sim \text{MVN}(0, \mathbf{\Sigma_g})$ and $\mathbf{\Sigma_g} = \mathbf{K}\sigma_g^2$. Here, $\sigma_g^2$ is the genotypic variance, and **K** is the realized genomic relationship matrix calculated using genotypic data following the VanRaden (2008) method in the *ASRgenomics* package (Gezan et al., 2022) in R. $e_k$ is the fixed effect of the environment, and $ge_{ik}$ is the random genotype by environment effect where $\mathbf{ge} \sim \text{MVN}(0, (\mathbf{\Sigma_E} \otimes \mathbf{\Sigma_g}))$. In this model, $\mathbf{\Sigma_E}$ was modeled by fitting a reduced rank factor analytic model with two-factor order (FA2) following Meyer (2009) and Burgueño et al. (2012). $\tau_{j(k)}$ represents the random trial-by-environment effect, $\tau_{j(k)} \sim \text{N}(0, \mathbf{I}\sigma_\tau^2)$, $\sigma_\tau^2$ represents the trial-by-environment variance, $g\tau e_{ji(k)}$ represents the random genotype-by-environment effect, $g\tau e_{ji(k)} \sim \text{N}(0, \mathbf{I}\sigma_{g\tau e}^2)$, and $\sigma_{g\tau e}^2$ represents the genotype-by-trial-by-environment variance. $\boldsymbol{\varepsilon}_{\mathbf{ijk}}$ is the model random residual where $\boldsymbol{\varepsilon}$ comes from a multivariate normal distribution with no free error variance. Here, the two-stage weighted approach is implemented where a parameterization of the first step BLUE error variance is used as an initial value to model the error variance in this model.

### 2.3.4.2. Model Selection

For the genomic prediction model, first, we fitted a baseline model (GBLUP). The following model was used:

$$y_{ijk} = \mu + g_i + e_k + ge_{ik} + \tau_{j(k)} + \varepsilon_{ijk} \qquad (5)$$

where $y_{ijk}$ is the vector of the genotypic BLUPs for the *ith* genotype in the *jth* trial nested in the *kth* environment, $\mu$ is the overall mean, $g_i$ is the random effect of the *ith* genotype with the same assumption as Eq. (4), $e_k$ is the fixed effect of the environment, $ge_{ik}$ is the random genotype-by-environment effect with the same assumption as Eq. (4), and $\tau_{j(k)}$ is the random trial-by-environment effect with the same assumption as Eq. (4). $\boldsymbol{\varepsilon}_{\mathbf{ijk}}$ is the model random residual where $\boldsymbol{\varepsilon}$ comes from a multivariate normal distribution with no free error variance. Here, the weighted approach is implemented where a parameterization of the first step BLUP error variance predicted via Eq. (4) is used as an initial value to model the error variance in the model.

Second, we fitted the $\text{GBLUP}_{\text{GxE}}$ factor analytic (FA) model with a reduced rank structure following Meyer (2009) and Burgeño et al. (2012). The following model was fitted:

$$y_{ijk} = \mu + g_i + e_k + ge_{ik} + \tau_{j(k)} + \varepsilon_{ij} \qquad (6)$$

where $y_{ijk}$ is the vector of the genotypic BLUPs for the *ith* genotype in the *jth* trial nested within the *kth* environment, $\mu$ is the overall mean, $g_i$ is the random effect of the *ith* genotype with the same assumption as in Eq. 4, $e_k$ is the fixed effect of the environment, $ge_{ik}$ is the random genotype-by-environment effect with the same assumption as Eq. 4, and $\tau_{j(k)}$ is the random trial-by-environment effect with the same assumption as Eq. 4. $\boldsymbol{\varepsilon}_{\mathbf{ijk}}$ is the model random residual where $\boldsymbol{\varepsilon}$ comes from a multivariate normal distribution with no free error variance. Here, the weighted approach is implemented where a parameterization of the first step BLUP error variance predicted via Eq. (4) is used as an initial value to model the error variance in the model.

Third, we fit the RRM using the ECs selected through PLS. We identified the ECs with better fit, and a forward stepwise selection method was used to incorporate the subsequent ECs until all the ECs were incorporated into the model. The model fitted for it:

$$y_{ijk} = \mu + ec_{ijk} + g_{oi} + g_{ni}ec_{nij} + ge_{ik} + \tau_{j(k)} + \varepsilon_{ijk} \qquad (7)$$

where $y_{ijk}$ is the vector of the genotypic BLUPs of GY for the *ith* genotype in the *jth* trial nested within the *kth* environment, $\mu$ is the overall mean, $ec_{ijk}$ is the fixed effect of the *e*nvironmental covariates for the *ith* genotype in the *jth* trial of the *kth* environment, $g_{oi}$ is the random intercept (i.e., random additive effect of the *ith* genotype), and $g_{ni}ec_{nij}$ is the random slope (i.e., deviation in the yield from $g_{oi}$ for the *ith* genotype for a unit change in $ec_{nij}$). Here, **g** and **gec** ~ MVN (0, **Σ).** As the number of ECs was increased, the $g_{ni}ec_{nij}$ effects and $\Sigma$ were expanded. For a single EC, $\Sigma = \boldsymbol{\Sigma}_g \otimes \begin{bmatrix} var(g_{oi}) & cov(g_{oi}, ec_1) \\ cov(ec_1, g_{oi}) & var(ec1) \end{bmatrix}$ where **Σg** is the same variance-covariance matrix explained for the previous Eq. 4, ⊗ is the Kronecker product. To make the model comparable with GBLUP and GBLUP$_{\mathrm{GxE}}$ reduced rank factor analysis (FA2), two terms were also added to the RRM model, where $\mathrm{ge}_{\mathrm{ik}}$ is the random genotype-by-environment effect with the same assumption as Eq. 4 and where $\tau_{j(k)}$ is the random trial-by-environment effect with the same assumption as Eq. 4. $\varepsilon_{ijk}$ is the model random residual where **ε** comes from a multivariate normal distribution with no free error variance. Here, the weighted approach is implemented where a parameterization of the first step BLUP error variance predicted via Eq. (4) is used as an initial value to model the error variance in the model. All the linear mixed models were fitted via *ASReml-R* (Butler, 2020).

2.3.4.3. Cross-validation strategies and predictive ability

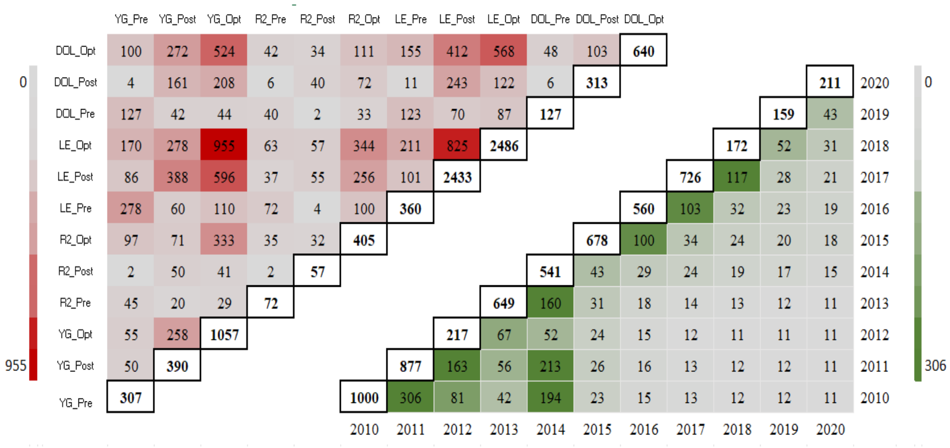
For GBLUP, GBLUP$_{\mathrm{GxE}}$ FA2, and RRM the models, we employed a 5-fold cross-validation method with 50 iterations to compare their predictive abilities (PA).

Alternative schemes were constructed simulating different scenarios a breeder might encounter, as described by Burgueño et al. (2012), Jarquín et al. (2017) and Bhatta et al. (2020). For cross validation 1 (CV1), where new or unphenotyped genotypes are predicted, we fitted the GBLUP, $\text{GBLUP}_{\text{GxE}}$ FA2, and RRM models. Cross validation 2 (CV2), where some genotypes are observed in some environments but need to be predicted in others (known genotypes in known environments), we again fitted the GBLUP, $\text{GBLUP}_{\text{GxE}}$ FA2, and RRM models. Finally, cross-validation 0 (CV0), where the tested genotypes are predicted in a completely new environment (unknown environments), was used to fit the GBLUP and RRM models.

After performing each iteration of cross validation, the Pearson's correlation between the predicted values of the masked data and the predicted genetic values was calculated via Eq. (4) for the *ith* genotype in the *jth* trial nested with the *kth* environment, i.e., the predictive ability (PA) was calculated. Centering was performed to reduce overestimation due to environmental effects for both the predicted values for the masked data and the predicted genetic values via Eq. (4) when $\text{GBLUP}_{\text{GxE}}$ FA2 was fitted. In CV0, the predictability ability (PA) difference was calculated as the deviation in the PA from that of the GBLUP model for each environment to report and visualize the gain in the PA when the RRM model with EC was used.

## 2.4. Results

This study includes phenotypic data from many genotypes evaluated within the framework of the National Wheat Breeding Program (NWBP) in a span of over eleven years across twelve testing sites, totaling 71 unique environments. Over the years, a significant reduction in the number of genotypes evaluated per year was observed, driven by changes in the program's design that resulted in fewer materials being tested annually. As shown in Figure 1, the distribution of genotypes across the dataset reveals a considerable imbalance, with a high degree of overlap between 2010 and 2014, which then decreased significantly from 2015-2020.



| | YG_Pre | YG_Post | YG_Opt | R2_Pre | R2_Post | R2_Opt | LE_Pre | LE_Post | LE_Opt | DOL_Pre | DOL_Post | DOL_Opt |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DOL_Opt | 100 | 272 | 524 | 42 | 34 | 111 | 155 | 412 | 568 | 48 | 103 | 640 |
| DOL_Post | 4 | 161 | 208 | 6 | 40 | 72 | 11 | 243 | 122 | 6 | 313 | |
| DOL_Pre | 127 | 42 | 44 | 40 | 2 | 33 | 123 | 70 | 87 | 127 | | |
| LE_Opt | 170 | 278 | 955 | 63 | 57 | 344 | 211 | 825 | 2486 | | | |
| LE_Post | 86 | 388 | 596 | 37 | 55 | 256 | 101 | 2433 | | | | |
| LE_Pre | 278 | 60 | 110 | 72 | 4 | 100 | 360 | | | | | |
| R2_Opt | 97 | 71 | 333 | 35 | 32 | 405 | | | | | | |
| R2_Post | 2 | 50 | 41 | 2 | 57 | | | | | | | |
| R2_Pre | 45 | 20 | 29 | 72 | | | | | | | | |
| YG_Opt | 55 | 258 | 1057 | | | | | | | | | |
| YG_Post | 50 | 390 | | | | | | | | | | |
| YG_Pre | 307 | | | | | | | | | | | |

| | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | 2020 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2020 | | | | | | | | | | | 211 |
| 2019 | | | | | | | | | | 159 | 43 |
| 2018 | | | | | | | | | 172 | 52 | 31 |
| 2017 | | | | | | | | 726 | 117 | 28 | 21 |
| 2016 | | | | | | | 560 | 103 | 32 | 23 | 19 |
| 2015 | | | | | | 678 | 100 | 34 | 24 | 20 | 18 |
| 2014 | | | | | 541 | 43 | 29 | 24 | 19 | 17 | 15 |
| 2013 | | | | 649 | 160 | 31 | 18 | 14 | 13 | 12 | 11 |
| 2012 | | | 217 | 67 | 52 | 24 | 15 | 12 | 11 | 11 | 11 |
| 2011 | | 877 | 163 | 56 | 213 | 26 | 16 | 13 | 12 | 12 | 11 |
| 2010 | 1000 | 306 | 81 | 42 | 194 | 23 | 15 | 13 | 12 | 12 | 11 |

**Figure 1**. Characterization of genotype distribution across sowing periods and years. The upper diagonal heatmap indicates the number of genotypes shared among pairs of sowing periods across all years, whereas the lower diagonal displays the number of genotypes evaluated that are shared among pairs of years across all sowing periods. The evaluated sowing periods include DOL_Opt, DOL_PostOpt, DOL_PreOpt, LE_Opt, LE_PostOpt, LE_PreOpt, R2_Opt, R2_PostOpt, R2_PreOpt, YG_Opt, YG_PostOpt and YG_PreOpt. The lower panel represents the number of genotypes evaluated per year along the main diagonal, with off-diagonal cells indicating the number of genotypes shared between pairs of years (2010–2020).

Figure 1 illustrates the connectivity of 1,683 wheat genotypes evaluated across 71 environments from 2010–2020, highlighting the distribution and overlap of genotypes across sites and sowing periods. The majority of genotypes were evaluated at the LE site, with comparable numbers at YG, R2, and DOL. Across all the sites, the optimal sowing windows (e.g., LE_Opt and YG_Opt) consistently accounted for the greatest number of genotypes, with LE_Opt and LE_PostOpt each evaluating more than 2,400 genotypes. The greatest connectivity was observed between LE_Opt, YG_Opt, and LE_PostOpt, indicating a significant overlap of genotypes in these combinations. A notable decline in the number of evaluated genotypes was observed over the years, particularly after 2014, driven by both a general reduction in trial size and the filtering of genotypes to include only those with complete phenotypic and genotypic data for this study. The highest connectivity levels were recorded between 2010 and 2014, reflecting the greater number of shared genotypes during this period.

Cullis broad-sense heritability ($H^2$) estimates were consistently high across years and sites (Supplemental Figure S1), with average $H^2$ values exceeding 0.8. The year 2012 presented particularly high heritability levels across trials, whereas 2010, 2015, 2018, and 2020 presented greater variability and lower average $H^2$ values. This reduction was driven not by specific trials with low estimates but rather by overall lower averages in these years, combined with increased environmental variability. Among the sites, DOL had the highest average $H^2$, suggesting more stable experimental conditions, whereas R2 tended to have slightly lower $H^2$ values. Nevertheless, all sites maintained heritability levels indicative of well-controlled trials. These results are particularly relevant considering that GY is typically regarded as a moderate- to low-heritability trait.

### 2.4.1. GEI characterization and EC selection

#### 2.4.1.1. Variance Components

The largest proportion of the total variance was attributed to year (27.1%) and site-by-year effects (13.3%), indicating high temporal variability within the MET (Supplemental Table 2). Genotype-by-environment interactions, including genotype-by-year (7.1%), genotype-by-site (0.7%), and three-way genotype-by-site-by-year interactions (3.4%), collectively accounted for a substantial portion of the total variance (11.2%). The genotype effect contributed 5.9% to the total variance, which was almost half of the GEI.

#### 2.4.1.2. EC selection

The top seven ECs selected on the basis of variable importance projection (VIP) PLS scores were cumulative precipitation during the reproductive phase (RPP), maximum mean temperature during the vegetative phase (VT$\overline{max}$), mean temperature during the vegetative phase (VT$\overline{mean}$), cumulative precipitation during the vegetative phase (VPP), minimum mean temperature during the vegetative phase (VT$\overline{min}$), evapotranspiration during the vegetative phase (VET), and frost days during the vegetative phase (VFD) (Figure 2A). The RPP EC had the highest VIP score, exceeding the other six selected ECs by approximately 20%, highlighting its strong association with yield variation. While RPP was the only variable linked to the reproductive phase, the remaining six ECs were related to the vegetative phase. Among the selected ECs, three ECs, VT$\overline{max}$, VT$\overline{mean}$ and VT$\overline{min}$ were correlated with each other (Supplementary Figure 3).

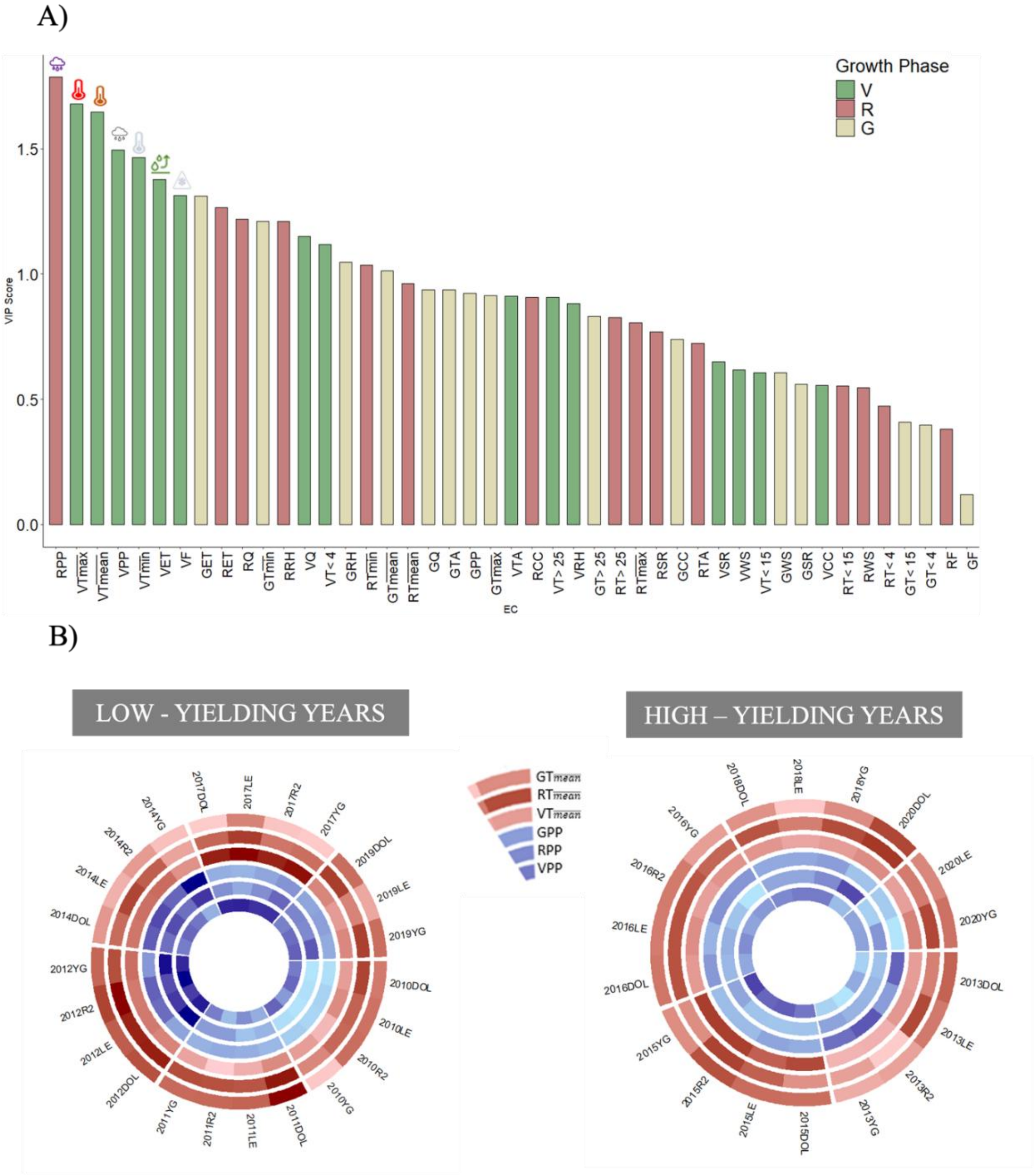


**Figure 2.** A) Variable importance in PLS projection (VIP) scores for partial least squares (PLS) analysis of ECs. The scores represent the importance of 45 ECs constructed for different crop growth phases (V: vegetative, R: productive, and G: grain filling). The seven most relevant covariates were selected for evaluation in the prediction models. B) Circus plot showing the behavior of the seven ECs selected across all the evaluation environments. The environments were grouped into two categories—high-yielding and low-yielding years based on the average productivity of each year. The ECs presented (from the outer to inner rings) are VT$_{\overline{max}}$, VT$_{\overline{mean}}$, VT$_{\overline{min}}$, RPP, VPP, VET, and VFD. The color intensity represents higher values of each EC in a given environment, with all ECs standardized using the entire dataset.

#### 2.4.1.3. Clustering of Environments

This classification provided a foundation for investigating the environmental factors underlying the observed yield differences between the two groups. The high-yielding group included the years 2013, 2015, 2016, 2018, and 2020, with an average yield of 5,667 kg ha$^{-1}$, whereas the low-yielding group included the years 2010, 2011, 2012, 2014, 2017, and 2019, with an average yield of 4,364 kg ha$^{-1}$.

High-yielding environments were generally associated with mild temperature and precipitation, whereas low-yielding environments, particularly those in 2012, 2014, and 2017, presented higher temperatures and precipitation. Notably, 2017 was characterized by high precipitation during the vegetative phase (Figure 2B).

### 2.4.2. Genomic predictions

#### 2.4.2.1. Model selection

All RRM models with EC presented greater PAs than did the GBLUP model for CV1 (new genotype), except when VFD was included alone in the model (Figure 3). VT$_{\overline{max}}$ was the RRM with one EC with the highest PAm (0.39), which was an 86% increase over the GBLUP model with PAm (0.21). The RRM model with two ECs, combining VT$_{\overline{max}}$ and RPP, yielded a PAm of 0.40, surpassing GBLUP by 90%. When three ECs were evaluated, adding VT$_{\overline{mean}}$ to VT$_{\overline{max}}$ and RPP improved the PAm (0.43) by 105% compared with GBLUP. The incorporation of a fourth EC, $VFD$, further increased the PAm to 0.47, a 124% improvement over GBLUP. The FA strategy resulted in a PAm of 0.51. For the CV1 scenario, the four-EC model achieves PA results comparable to those of the FA strategy, with only 0.04 points lower in terms of PAm.

RRM models outperformed the GBLUP model for CV2 (a known genotype in known environments), and a similar pattern was found for CV2 and CV1. VT$_{\overline{max}}$ or VT$_{\overline{min}}$ was the RRM with one EC with the highest PAm (0.41), which was 52% higher than that of the GBLUP with Pam (0.27). The RRM with two ECs with the highest PAm (0.45) included VT$_{\overline{max}}$ to RPP, which was 67% greater than that of the GBLUP model. Most of the RRM models with two ECs were better than the GBLUP model and those with one EC. The inclusion of a third EC consistently improved the PAs of the models evaluated with two ECs. However, the highest value was achieved with a specific combination utilizing the ECs VT$_{\overline{max}}$, RPP, VPP or VT$_{\overline{mean}}$ or VT$_{\overline{min}}$ or VFD. This model exhibited a PAm of 0.46, which was 70% greater than that of the GBLUP model. The RRM model with VT$_{\overline{max}}$, RPP, VT$_{\overline{mean}}$, and VFD EC was the model that resulted in the highest PA (0.51), which was 89% greater than that of the GBLUP model. Finally, the evaluation of the FA models yielded PAm values of 0.76, surpassing those obtained with the FA models in the CV1 scenarios. In this case, the gap between the best RRM model and the FA model was significantly larger, with a PAm difference of 0.25, representing a 33% decrease.

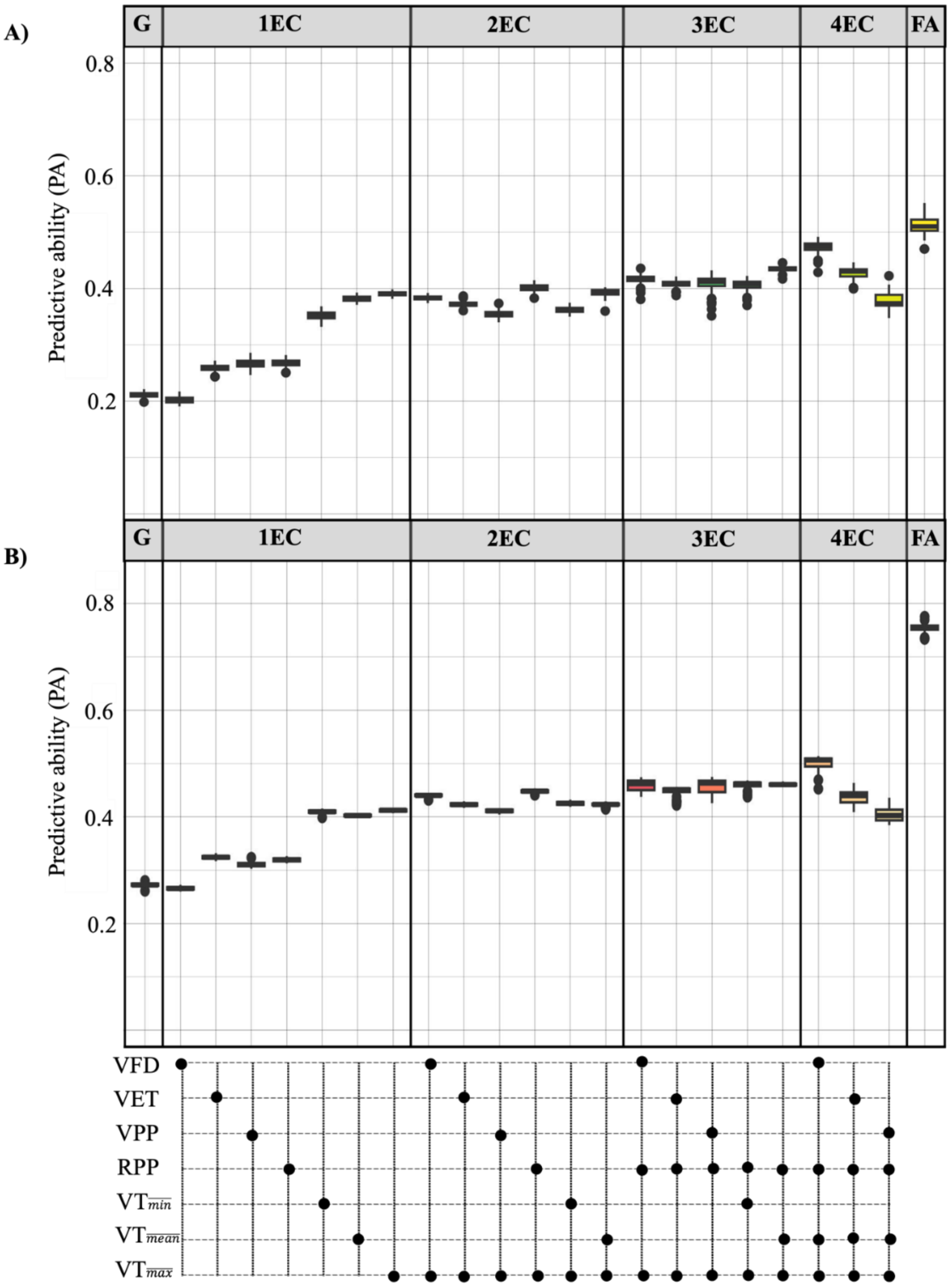


**Figure 3.** Predictive ability (PA) of different model strategies across increasing levels of environmental complexity under the CV1 and CV2 scenarios. A) Predictive ability (PA) of different model strategies across increasing levels of environmental complexity under the CV1 scenario. B) Predictive ability (PA) of different model strategies across increasing levels of environmental complexity under the CV2 scenario. Boxplots represent the distribution of PA values for each grouping: G

(GBLUP model), 1EC-4EC (models incorporating 1 to 4 ECs in an RRM framework), and FA (Factor Analytic variance-covariance structure). The lower panel represents the environmental variables included in each model strategy, categorized by Veg and Rep phases. The symbols indicate each EC: VFD, VET, VPP, RPP, VT$_{\overline{min}}$, VT$_{\overline{mean}}$, and VT$_{\overline{max}}$. The colors in the boxplots in Figure 3 (A) transition from dark blue (GBLUP) to yellow (FA), reflecting the increasing complexity of the models. The colors in the boxplots in Figure 3 (B) indicate the transition from dark blue (GBLUP) to light brown (FA), reflecting the increasing complexity of the models.

For predicting the unknown environment (CV0) across 71 environments, variability in PA was found via the GBLUP model (Figure 4). Environment 2012_DOL_preopt had the highest PA (0.78), whereas 2016_DOL_opt had the lowest PA (0.02) with PAm (0.43) across all environments (Figure 4; Table 1). The RRM model with VT$_{\overline{min}}$ as the single EC achieved the highest PA, improving the PA in 40 out of the 71 environments evaluated (Figure 4, Table 1). The addition of VT$_{\overline{min}}$ to the VT$_{\overline{max}}$ EC improved prediction compared with that of the GBLUP models in 44 environments, surpassing the performance of the models with a single EC in 4 environments. The highest prediction performance was achieved via three ECs, where RPP was added to two previously selected ECs, improving prediction in 44 environments compared with GBLUP models, with a median improvement of 0.02 in terms of PA. Surprisingly, adding VPP as the third EC reduced the prediction performance in the 71 evaluated environments, making this combination the least effective among all the combinations tested (Figure 4). The addition of a fourth EC did not increase the number of environments with improved prediction compared with GBLUP in any of the combinations tested (Table 1). Overall, most of the evaluated models improved the predictive PAs in 50–70% of the environments when various EC combinations were used. When assessed as a forward selection strategy for evaluating multiple variants, the results indicate that in more than 90% of the environments, it was possible to identify an RRM model with one or more ECs that enhanced PA compared with the GBLUP strategy.

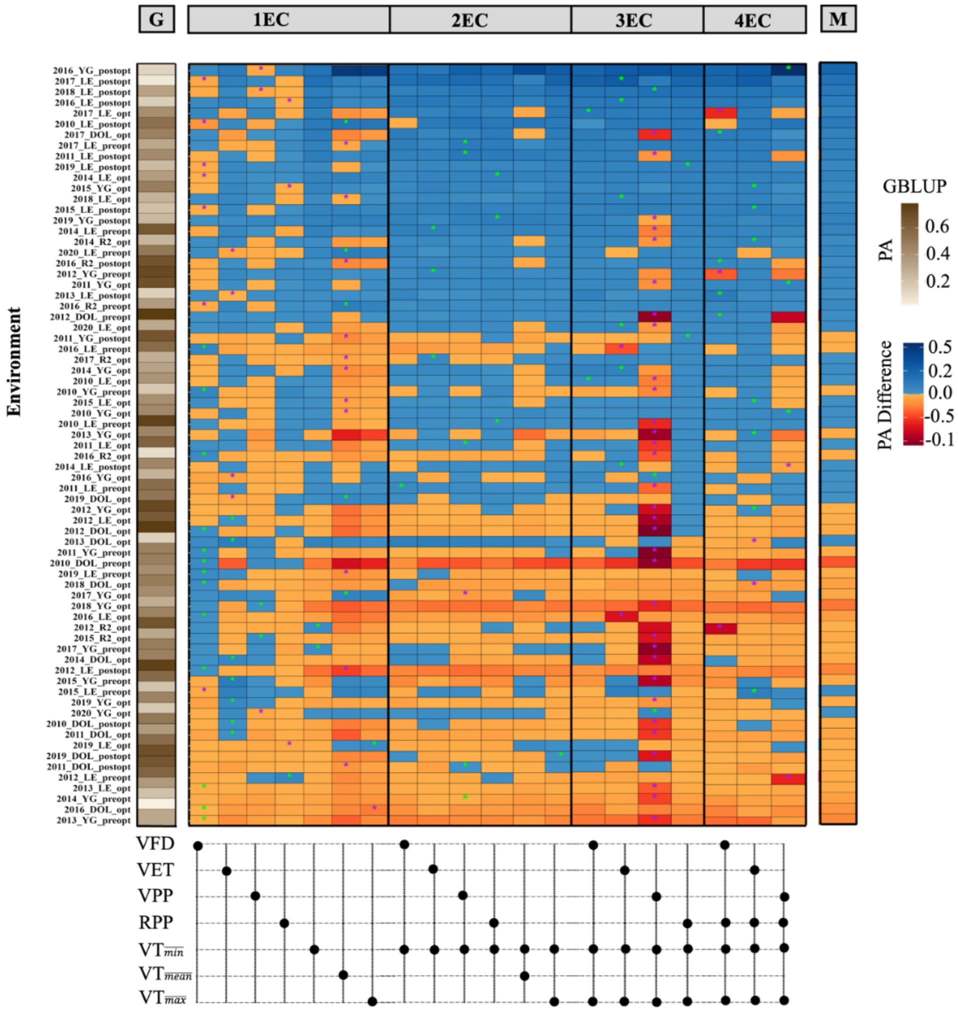


**Figure 4.** Median predictive ability (PA) and PA of GBLUP; median PA difference from GBLUP and PA difference from GBLUP for RRM models with EC across the environment and models under CV0 scenarios. The first panels (top left) show the median PA for the GBLUP model, the PA difference from GBLUP (top middle) for each RRM model and the median PA difference across environment models (top right). The heatmap below the top panels represents the PA of GBLUP for each environment (left); the PA difference from GBLUP for RRM models with EC across the environment (middle); and the median PA difference (M) across models (right). The lower panel represents the environmental variables included in each model

strategy, categorized by Veg and Rep phases. The symbols indicate each EC: VFD, VET, VPP, RPP, VT$\overline{min}$, VT$\overline{mean}$, VT$\overline{max}$. The colors in the heatmap transition from pink to white to brown for the GBLUP models indicating PAs for each environment from low to high PAs; on the other hand, the colors in the heatmap transition from red to light orange to light blue to dark blue for the RRM models indicating PA differences from low to high. The green and purple asterisks indicate the best and worst models, respectively, for each environment.

**Table 1.** The median for the GBLUP model and deviation from the GBLUP model for the RRM model were as follows: the number of environments in which the RRM was better than that in the GBLUP model; and the number of environments in which the RRM was the best and worst, with one, two, three, and four environmental covariates.

| | Median | >GBLUP | No of times best model | No of times worse model |
|---|---|---|---|---|
| GBLUP | 0.435 | | | |
| VFD | -0.001 | 32 | 13 | 7 |
| VET | 0.010 | 39 | 7 | 4 |
| VPP | -0.006 | 27 | 2 | 3 |
| RPP | -0.002 | 30 | 1 | 3 |
| VT$\overline{min}$ | 0.009 | 40 | 2 | 0 |
| VT$\overline{mean}$ | -0.075 | 23 | 5 | 11 |
| VT$\overline{max}$ | -0.046 | 30 | 1 | 1 |
| VT$\overline{min}$ + VFD | 0.007 | 39 | 1 | 0 |
| VT$\overline{min}$ + VET | 0.010 | 43 | 3 | 0 |
| VT$\overline{min}$ + VPP | 0.008 | 39 | 5 | 1 |
| VT$\overline{min}$ + RPP | 0.017 | 42 | 3 | 0 |
| VT$\overline{min}$ + VT$\overline{mean}$ | -0.004 | 33 | 0 | 0 |
| VT$\overline{min}$ + VT$\overline{max}$ | 0.017 | 44 | 1 | 0 |
| VT$\overline{min}$ + VT$\overline{max}$ + VFD | 0.008 | 42 | 2 | 0 |
| VT$\overline{min}$ + VT$\overline{max}$ + VET | 0.012 | 40 | 6 | 2 |
| VT$\overline{min}$ + VT$\overline{max}$ + VPP | -0.132 | 25 | 3 | 32 |
| VT$\overline{min}$ + VT$\overline{max}$ + RPP | 0.024 | 44 | 2 | 0 |
| VT$\overline{min}$ + VT$\overline{max}$ + RPP + VFD | -0.002 | 33 | 4 | 3 |
| VT$\overline{min}$ + VT$\overline{max}$ + RPP + VET | 0.024 | 43 | 7 | 2 |
| VT$\overline{min}$ + VT$\overline{max}$ + RPP + VPP | -0.023 | 30 | 3 | 2 |

### 2.4.3. Environment by Management

The environment-by-management (E×M) interaction was analyzed separately for short-cycle, long-cycle, and intermediate-cycle (Supplemental Figure S2) wheat materials, focusing on the impact of sowing date and key ECs on grain yield. The evaluation period spanned from day 0 (April 5) to day 125 (August 10), covering the sowing window relevant to wheat production in Uruguay. Key ECs included VT$\overline{min}$, VT$\overline{mean}$, VT$\overline{max}$, VPP, RPP, VFD, and VET. These were assessed in relation to sowing date to elucidate their influence on yield across cycle types.

For intermediate-cycle wheat, optimal yield outcomes were associated with sowing dates between days 60 and 80 (approximately June 4 to June 24), particularly in relation to temperature and frost-related ECs. Higher yields (upper yield quantile) were consistently linked to cooler temperatures during the vegetative phase, with optimal conditions at $VT_{\overline{min}} < 8°C$, $VT_{\overline{mean}} < 12°C$, and $VT_{\overline{max}} < 18°C$, aligning with wheat's preference for cooler early development to maximize resource accumulation. The pattern for VFD showed high variability, indicating a less consistent impact on yield across sowing dates. Precipitation patterns revealed that excessive water availability negatively affected yield, with VPP > 300 mm and RPP > 100 mm linked to lower yields, irrespective of sowing date. For VET, the highest yields were observed with values < 200 mm during the vegetative phase, suggesting an optimal water balance that supports canopy development without excessive water loss.

Long-cycle materials exhibited poorer yield performance when temperatures exceeded critical thresholds: $VT_{\overline{min}} > 8°C$, $VT_{\overline{mean}} > 12°C$, and $VT_{\overline{max}} > 18°C$. The pattern for VFD was diffuse, with no clear trend across sowing dates, suggesting that frost occurrence has a variable impact on yield. Notably, the highest yields were strongly concentrated around early sowing dates (days 0 to 40, approximately April 5 to May 15), associated with VPP < 300 mm. This indicates that early sowings, coupled with lower precipitation during the vegetative phase. For RPP, yields were maximized with values < 100 mm, reflecting sensitivity to excessive water during the reproductive phase.

Short-cycle materials, typically sown later (from day 50/60, approximately May 25 to June 4), showed diffuse patterns in yield response to temperature-related ECs ($VT_{\overline{min}}$, $VT_{\overline{mean}}$ , $VT_{\overline{max}}$), with no clear optima due to the shorter growth cycle and later sowing reducing temperature sensitivity. However, optimal yields were associated with RPP < 100 mm up to day 100 (July 14) and VPP < 300 mm, indicating that lower precipitation during both vegetative and reproductive phases favors yield by avoiding water-related stresses. The variability in temperature response suggests that short-cycle materials are less constrained by thermal conditions but are highly sensitive to water availability, consistent with their adaptation to later sowing windows.

Across all cycle types, a consistent pattern emerged: early sowing dates, lower temperatures ($\mathrm{VT}_{\overline{min}} < 8$°C, $\mathrm{VT}_{\overline{mean}} < 12$°C, $\mathrm{VT}_{\overline{max}} < 18$°C), and reduced precipitation (VPP < 300 mm, RPP < 100 mm) were associated with a higher probability of achieving above-average yields. This trend reflects the interplay of interannual variability, where cooler temperatures and lower precipitation during critical growth phases minimize stress and optimize resource allocation. Early sowings, particularly for long- and intermediate-cycle materials, align with Uruguay's climatic patterns, where cooler early-season conditions and moderate water availability enhance phenotypic stability. These findings underscore the importance of integrating management practices, such as sowing date optimization, with environmental data to improve genomic prediction and breeding outcomes under variable climatic conditions.

## 2.5. Discussion

This study demonstrated that it is possible to integrate EC and genomics to leverage wheat MET historical datasets to explore GEI and the use of EC to improve the predictive ability of genomic prediction models.

### 2.5.1. GEI characterization

This study characterized the GEI via a wheat historical MET dataset; the GEI overall accounted for 11.2% of the total variance (Table 1). A similar pattern was described in a similar population by Lado et al. (2016) and other studies where a 10–20% GEI was reported (Cooper & DeLacy, 1994; Monteverde et al., 2019).

### 2.5.2. EC Selection

Hundreds of ECs are available and can be included in GS models, with each one having an infinitesimal effect (Brancourt-Hulmel et al., 2000; Heslot et al., 2014). Researchers have used more than 50 ECs retrieved from weather databases to estimate the variance covariance between environments and incorporate them into the genomic prediction model (Jarquin et al., 2014). However, collinearity between ECs and the small amount of effect explained by each one may result in undesirable consequences for model inference and parameter estimation (Dormann et al., 2013). Variable selection methods are beneficial for selecting key variables that explain most of the effects of the dataset and use selected key variables as predictors in statistical models (James et al., 2013). Several variable selection methods are recommended in the literature: $R^2$ (Piepho, 2019), F tests (Buntaran, 2021), stepwise feature selection (Neyhart et al., 2021), forward and backward selection (Mumford et al., 2023), PLS (Vargas et al., 1999), and synthetic covariates (Tadese et al., 2024). Research on which method works best is still needed, and further research is needed. In our study, we used PLS, a method widely used to select between collinear variables.

Several alternative methods, such as the selective ratio (SR) and variable importance in projection (VIP), are available to select the key EC from PLS (Mehmood et al., 2020). We selected the ECs via the VIP score (Tadese et al., 2024). We identified 17 environmental covariates (ECs) with scores above one, which is the accepted threshold for variable selection (Mehmood et al., 2020). However, since VIP selection identified 17 ECs and the stepwise forward procedure requires running models for each combination, many models would need to be run. Therefore, to test the efficacy of environmental covariates in improving the predictive ability (PA) of the genomic prediction model, we selected only the top seven ECs values from the VIP score table to include in the RRM. The top seven covariates selected on the basis of VIP scores were RPP, VT$\overline{max}$, VT$\overline{mean}$, VPP, VT$\overline{min}$, VET, and VFD. In this set, we found few covariates (VT$\overline{max}$, VT$\overline{mean}$, VT$\overline{min}$) to be collinear, indicating that PLS-based variable selection can still include correlated variables. A possible explanation for this is that when many collinear predictors are chosen, PLS assigns high VIP scores to all as they contribute to the total sum of squares of the response variables. Therefore, correlation analysis is also required between the PLS-selected key ECs to avoid redundancy or multicollinearity problems in the RRM.

Our findings align with previously reported climate driven abiotic stresses and their impact on wheat grain yield. ECs related to temperature (Tmax, Tmean, Tmin), evapotranspiration (ET), precipitation (PP), and frost days (FD), were found significant (by PLS method) for grain yield. Abiotic stresses, particularly high temperatures, are major constraints on wheat yield worldwide, and their frequency and intensity are expected to rise in most wheat-growing regions (Trethowan, 2022).

Elevated temperatures during vegetative growth can suppress tillering and reduce the number of seed germination (Groli et al., 2024). Minimum temperatures above 13°C are associated with up to 30% reductions in yield (Rubio et al., 2017). High evapotranspiration with absence of sufficient precipitation may result in water stress and less biomass accumulation (Edmundo., 2002). Precipitation during vegetative and reproductive phases influences GY in a nonlinear pattern – limited rainfall declines both biomass and grain filling (Robertson & Giunta, 1994), whereas excessive moisture can induce disease pressures or disrupt grain development (De San Celedonio et al., 2014; Riella et al., 2025). In Uruguay, the highest yields were achieved with precipitations of the order of 30–120 mm and lowest ones were found to be associated with rainfalls over 150 mm (Rubio et al., 2017). Frost can cause damage to wheat during the vegetative phase, especially on early vegetative phases (Leske et al., 2022).

### 2.5.3. Prediction for new genotypes (CV1) and known genotypes in known environments (CV2)

Integrating seven ECs ($VT_{\overline{max}}$, $VT_{\overline{mean}}$, $VT_{\overline{min}}$, RPP, VPP, VET, and VFD) into RRM markedly improved PA compared with GBLUP for the CV1 (86–124%) and CV2 (52–89%) scenarios. This result coincides with the results of other studies, where models integrating EC had better PAs than did GBLUP models for both CV1 and CV2 (Malosetti et al., 2016; Jarquín et al., 2014; Rebollo et al., 2023; Hu et al., 2025; Kunwar et al., 2025; Crossa et al., 2025). This means that the RRM with ECs is able to capture both the environmental effect and the GEI. We also observed a similar pattern in PA increase between CV1 and CV2 when the same EC was incorporated individually or in combination following a stepwise forward procedure. A possible reason for this is that the selected ECs or its combination is able to capture the variance and GEI with the available EC information, thereby increasing the PA. However, in some RRM EC combinations, we found a decrease in the PA, which could have been caused by overparameterization of the model or an appropriate EC to capture the variance. On the other hand, the $GBLUP_{GxE}$ FA2 model had a higher PA for both CV1 and CV2, as expected since the model borrowed information between known environments (Smith et al., 2001; Smith et al., 2005). Although we also found that the

RRM EC model fitted with VT$_{\overline{max}}$, VT$_{\overline{mean}}$, RPP and VFD have PAs near FA2. Rebollo et al. (2023) fitted FA models with selected ECs; however, they reported no increase in PA when selected ECs were added to FA2; therefore, we decided not to run these models. For traits such as yield, which exhibit high GEIs, the best model for CV1 and CV2 would be a model with a FA variance covariance structure if yield data are available. Nevertheless, RRM with ECs is the best suited model if breeding programs lack yield data.

### 2.5.4. Prediction for unknown environments

Predicting a genotype's yield in new environments is one of the most challenging tasks because of the unknown characteristics of the new environment (Malosetti et al., 2016; Hu et al., 2025). The only viable options for prediction in new environments are either the use of GBLUP-predicted genomic estimated breeding value (GEBV) across environments or the incorporation of environmental covariates (ECs) to predict environment-specific GEBVs (Heslot et al., 2014; Piepho, 2022). Therefore, in this study, we tested this scenario (CV0) by masking one environment in a k-fold manner, hypothesizing that EC could improve the predictive ability compared with GBLUP.

For the GBLUP model, we also model the environmental effect, GEI effect, and trial effect for our training set, with the main genotypic effect accounting for the genomic relationship matrix. A study reported that modeling environmental effects and the GEI in the training population can improve predictive ability compared with the conventional GBLUP model, where only the main genotypic effect is modeled (Rebello et al., 2023). In addition, several factors are considered to influence the PA of the GBLUP model for new environment prediction. This includes the genetic relationship between the training and testing sets, the extent of the GEI, the type of environment set prediction and the number of genotypes in the testing population (Berro et al., 2019). With our GBLUP model, we were able to predict some environments with a PA of 0.78 and a PAm of 0.43. The reasoning for the higher PAs for some environments could be because of the contributions of all the factors mentioned above. Therefore, it becomes crucial to optimize the training population and testing set as well as include effects in the training set that capture some of the variance or noise to increase the PA of the GBLUP model for predicting a new environment.

By incorporating ECs in RRM, we were able to increase PA for more than 90% of the environment compared with GBLUP. This signifies the importance of the EC for modeling new environmental characteristics, the GEI and increased PA. With the stepwise forward procedure for ECs selection, we were able to increase the PA by fitting the ECs alone. For the RRM model with two to three combinations, we were able to increase the PA for more than 61% of the environments. For the other remaining environments, the other selected ECs combinations increased the PA. Integrating multiple ECs in the RRM allows modeling of the data in multidimensional space, allowing us to distinguish or complement ECs and thus the GEI pattern, therefore making more precise predictions (Mumford et al., 2023). However, for some environments, we were not able to increase the PA with the RRM-incorporated ECs. The possible explanation for this could be that the selected ECs was not able to model the pattern of those environments, which could be because those environments are off-types compared with other environments. Therefore, selecting ECs that can complement or distinguish them from each other is needed to make precise predictions.

## 2.6. Future remarks

In this study, using a linear RRM, we were still able to capture the GEI effect and increase the PA for different scenarios. This shows the potential of linear models. Modeling and predicting yield are complex phenomena, and the GEI makes them more cumbersome (Peng et al., 2020; Li & Gutierrez, 2023). Both statistical models (Jarquín et al., 2014; Malosetti et al., 2016; Millet et al., 2019; Lado et al., 2016; Hoefler et al., 2020; Rebollo et al., 2023; Sandro et al., 2024) and crop growth models (Chapman, 2008; Chenu et al., 2017) have been used to study and understand the GEI. Statistical models have focused primarily on genotype prediction via markers and environmental covariates for different genotype-environment combinations. However, they lack an in-depth understanding of genotype-specific physiology and response to external factors such as environmental covariates or management practices. While crop growth models have been able to dissect the effects of the environment and management, cultivar-specific responses are still lacking (Chenu et al., 2017); therefore, prediction for specific genotypes and environments is not yet possible.

For breeding programs, it is crucial to understand how genotypes perform in the target population of environments (Comstock, 1977). Therefore, a statistical approach such as linear RRM provides flexibility by allowing the prediction of genotype-specific responses to different environmental factors. The use of EC within RRM has emerged in recent years as a powerful strategy to increase its predictive ability across diverse crops, including rice (Rebollo et al., 2023), wheat (Ly et al., 2018), sorghum (Tadese et al., 2024), barley (Tadese et al., 2025), and cotton (Tolhurst et al., 2022). Notably, RRM might be a linear simplification of crop growth models, wherein reaction norms are primarily nonlinear; further studies using RRM for nonlinear fits, such as higher-degree polynomials or splines, are needed (Momen et al., 2019; Buntaran et al., 2019; Bustos-Korts et al., 2021). A much simpler approach could be dynamic modeling with simplistic models for better interpretation and making predictions in any given grid of genotype by environment (Voorn et al., 2023).

## 2.7. Conclusions

This study highlights the strong interannual variability in wheat yield, which is closely associated with fluctuating environmental conditions across years and evaluation sites. By integrating EC into genomic prediction models, we were able to better understand and predict the impact of these factors on yield performance. In particular, the mean maximum or minimum temperature during the vegetative period was the most influential EC, along with high precipitation during the reproductive period. Additionally, a set of variables associated with the vegetative phase, including precipitation, mean temperature, frost days and evapotranspiration, also influenced yield performance.

The use of EC in genomic prediction models, particularly through RRM, proved to be an effective strategy across all prediction scenarios (CV1, CV2, and CV0). Interestingly, the inclusion of one, two or three ECs consistently provided the best predictive ability for all the scenarios, whereas adding more selected covariates often led to an increase in the predictive accuracy for CV1 and CV2 but not for CV0. This suggests that a minimal yet well-selected set of ECs can capture the most relevant environmental information without introducing unnecessary complexity into the models.

In summary, this study demonstrates the relevance of incorporating environmental covariates into genomic prediction frameworks to improve the understanding and management of genotype-environment interactions. However, further research is needed to refine these strategies, particularly for predicting performance in untested environments and under increasingly extreme and frequent climatic conditions. Advancing these approaches will be critical for developing more resilient wheat genotypes and ensuring sustainable production in the face of climate change.

## 2.8. Supplemental Material

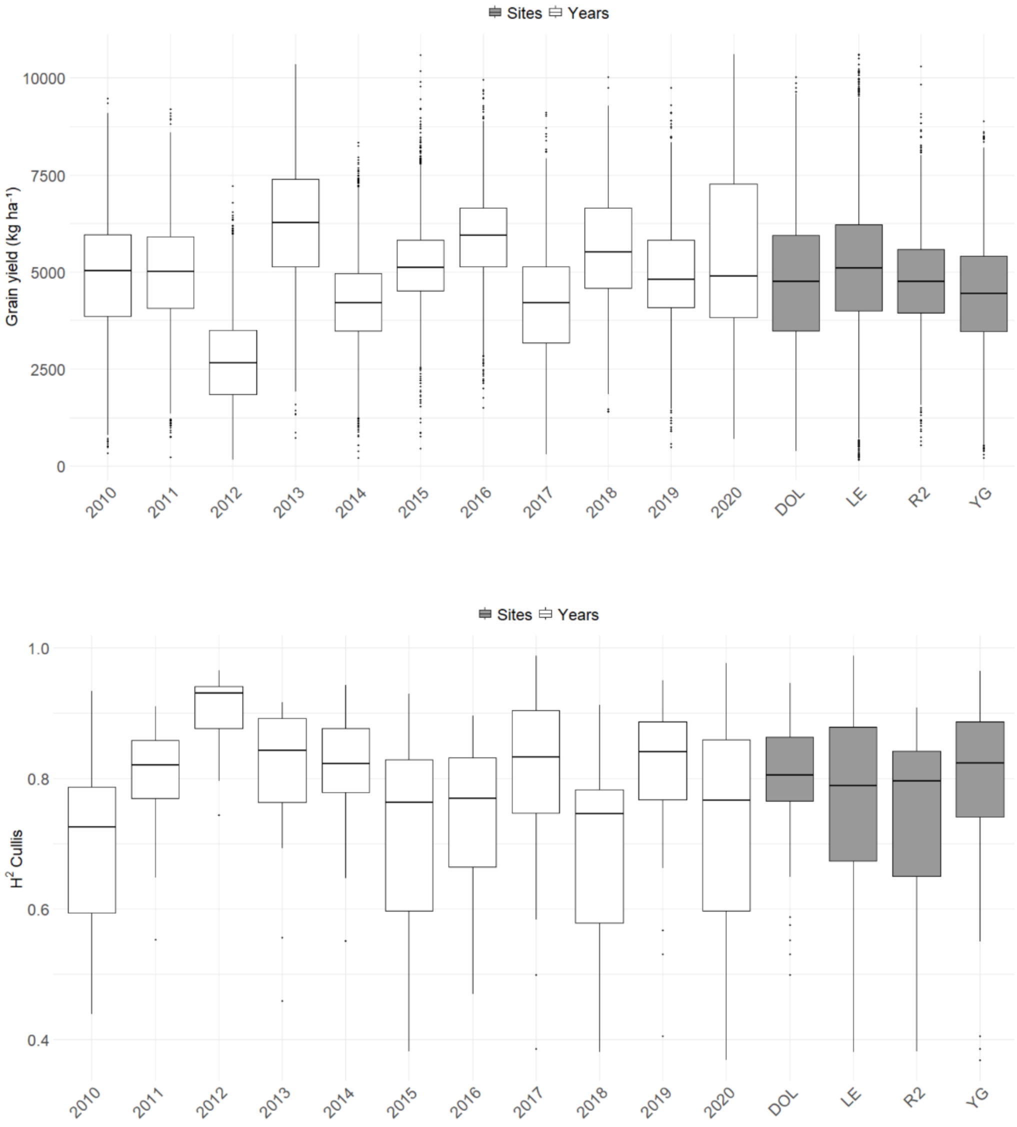
**Supplemental table T1.** Environmental Covariates employed.

| Climatic variable | Abbreviation | Unit | Description |
|---|---|---|---|
| Cumulative precipitation | PP | mm | Cumulative precipitation. |
| Cloud coverage | CC | % | The average percent of cloud amount during the temporal period. |
| Evapotranspiration | ET | MJ/$hr$ | The evapotranspiration energy flux at the surface of the earth. |
| Ground Frost | FD | _ | 1 if the temperature was below 0°C at 2 m above ground level and 0 if not. |
| Maximum mean temperature | $T_{\overline{max}}$ | °C | Maximum mean temperature. |
| Maximum temperature above 25°C | $T_{>25}$ | _ | 1 if temperature was above 25°C at 2 m above ground level and 0 if not. |
| Mean temperature | $T_{\overline{mean}}$ | °C | Mean temperature. |
| Minimum mean temperature | $T_{\overline{min}}$ | °C | Minimum mean temperature. |
| Minimum temperature below 15°C | $T_{<15}$ | _ | 1 if the temperature was below 15°C at 2 m above ground level and 0 if not. |
| Minimum temperature below 4°C | $T_{<4}$ | – | 1 if the temperature was below 4°C at 2 m above ground level and 0 if not. |
| Photothermal quotient | Q | MJ/$m^2/°C$ | Ratio of solar radiation to mean temperature (Base 0°C). |
| Relative Humidity | RH | % | Mean relative humidity. |
| Solar radiation | SR | $MJ/m^2$ $/día$ | Total solar irradiance incident at the surface of the earth under all sky conditions. |
| Thermal amplitude | TA | °C | Daily temperature range. |

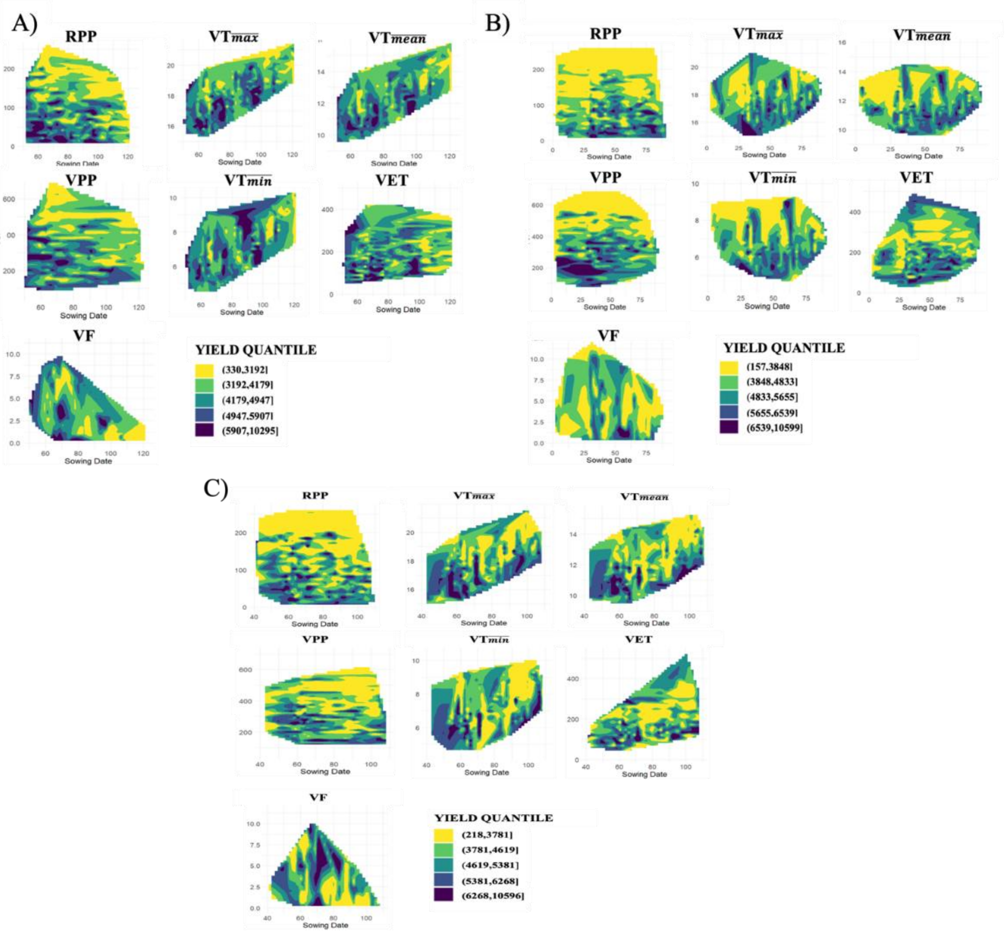
| | | | |
|---|---|---|---|
| Wind speed | WS | m/s | The maximum hourly wind speed at 2 meters above the surface of the earth. |

**Supplemental table T2.** Variance components for grain yield (kg ha$^{-1}$) using data from the complete network of the NWBP database. The variance components and their relative proportions for each source of variability are presented, integrating data from 300 trials across 59 environments from 2010-2020.

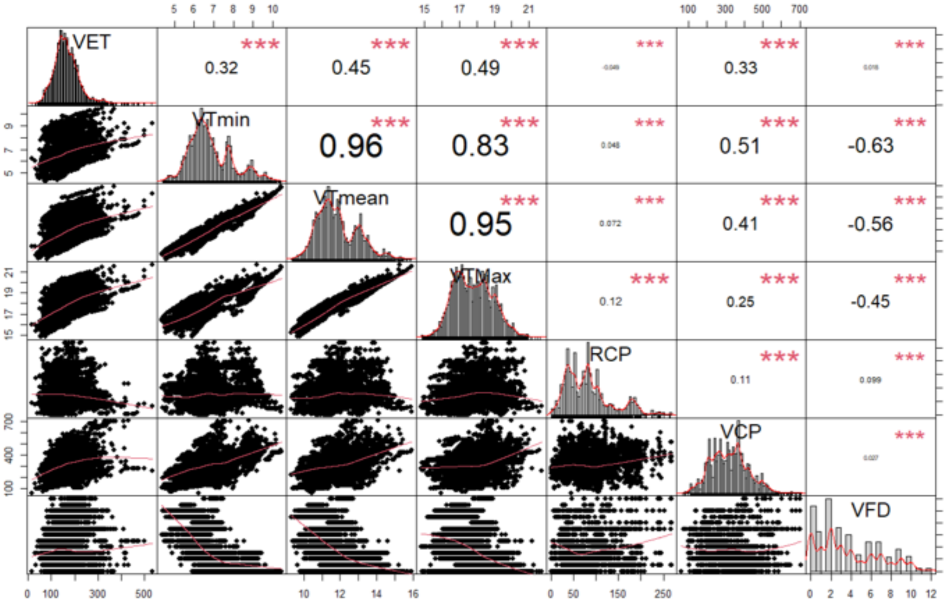
| **Variance** | **Proportion (%)** |
|---|---|
| Site | 3.1 |
| Year | 27.1 |
| Site by Year | 13.3 |
| Trial | 1.8 |
| Replication | 4.0 |
| Block | 1.3 |
| Site by Year | 19.3 |
| Genotype | 5.9 |
| Genotype by Year | 7.1 |
| Genotype by Site | 0.7 |
| Genotype by Site by | 3.4 |
| Residual | 13.0 |
| Total | 100.0 |



**Supplemental Figure S1.** Cullis broad-sense heritability (H²) estimates for grain yield (GY) across trials in the NWBP of Uruguay. Boxplots representing the distribution of H² values for each year (2010–2020) and location (DOL, LE, R2, YG) in Uruguay. Light-colored box plots correspond to individual years, whereas dark-colored box plots represent trial sites.



**Supplemental Figure S2**. Density maps illustrating the variation of the seven ECs selected by PLS as a function of the sowing date. A) Early cycle genotypes. B) Long cycle genotypes. C) Intermediate cycle genotypes. Colors represent grain yield quantiles (kg ha$^{-1}$), with dark blue indicating higher yields and yellow lower yields. Day 0 corresponds to the first sowing season sowing date (April 05), and day 60 corresponds to the late sowing season sowing date (June 04), standardized across years.



**Supplemental Figure S3.** Correlation between selected ECs from PLS.

## 2.9. References

Basnet, B. R., Crossa, J., Dreisigacker, S., Pérez-Rodríguez, P., Manes, Y., Singh, R. P., Rosyara, U. R., Camarillo-Castillo, F., & Murua, M. (2019). Hybrid Wheat Prediction Using Genomic, Pedigree, and Environmental Covariables Interaction Models. *The Plant Genome*, *12*(1). https://doi.org/10.3835/plantgenome2018.07.0051

Bernardo, R. (2010). *Breeding for quantitative traits in plants*. Stemma Press.

Berro, I., Lado, B., Nalin, R. S., Quincke, M., & Gutiérrez, L. (2019). Training Population Optimization for Genomic Selection. *The Plant Genome*, *12*(3), 190028. https://doi.org/10.3835/plantgenome2019.04.0028.

Bhavani, S., Singh, R.P., Hodson, D.P., Huerta-Espino, J., & Randhawa, M.S. (2022). Wheat Rusts: Current Status, Prospects of Genetic Control and Integrated Approaches to Enhance Resistance Durability. In: M.P. Reynolds, & H. J. Braun (Eds.), *Wheat Improvement* (pp. 125-141). Springer. https://doi.org/10.1007/978-3-030-90673-3_8

Brancourt-Hulmel, M., Denis, J. B., & Lecomte, C. (2000). Determining environmental covariates which explain genotype environment interaction in winter wheat through probe genotypes and biadditive factorial regression. *Theoretical and Applied Genetics*, *100*(2), 285–298. https://doi.org/10.1007/s001220050038

Braun, H.-J., Atlin, G., & Payne, T. (2010). Multi-location testing as a tool to identify plant response to global climate change. In *Climate change and crop production* (pp. 115–138). CABI Wallingford UK.

Browning, B. L., Zhou, Y., & Browning, S. R. (2018). A One-Penny Imputed Genome from Next-Generation Reference Panels. *American Journal of Human Genetics*, *103*(3), 338–348. https://doi.org/10.1016/j.ajhg.2018.07.015

Buntaran, H., Piepho, H.-P., Hagman, J., & Forkman, J. (2019). A cross-validation of statistical models for zoned-based prediction in cultivar testing. *Crop Science*, *59*, 1544–1553.

Buntaran, H. (2021). *Statistical methods for analysis of multienvironment trials in plant breeding: accuracy and precision* [Doctoral dissertation]. Universität Hohenheim.

Burgueño, J., G. de los Campos, K. Weigel, & Crossa, J. (2012). Genomic prediction of breeding values when modeling genotype x environment interaction using pedigree and dense molecular markers. *Crop Science*, *52*, 707–719. 10.2135/cropsci2011.06.0299.

Bustos-Korts, D., Boer, M. P., Malosetti, M., Chapman, S., Chenu, K., Zheng, B., & van Eeuwijk, F. A. (2019). Combining Crop Growth Modeling and Statistical Genetic Modeling to Evaluate Phenotyping Strategies. *Frontiers in Plant Science*, *10*. https://doi.org/10.3389/fpls.2019.01491

Bustos-Korts, D., Boer, M. P., Chenu, K., Zheng, B., Chapman, S., & Van Eeuwijk, F. A. (2021). Genotype-specific P-spline response surfaces assist interpretation of regional wheat adaptation to climate change. *In Silico Plants*, *3*(2), 1–23. https://doi.org/10.1093/insilicoplants/diab018

Butler, D. G. (2020). asreml:Fits the Linear Mixed Model. (R package version 4.2.0). http://vsni.co.uk/software/asreml-r

Butler, D. G., Cullis, B. R., Gilmour, A. R., Gogel, B. J., & Thompson, R. (2023). ASReml-R Reference Manual Version 4.2 ASReml estimates variance components under a general linear mixed model by residual maximum likelihood (REML). https://asreml.kb.vsni.co.uk/article-categories/asreml-r-resources/.

Chapman, S. C. (2008). Use of crop models to understand genotype by environment interactions for drought in real world and simulated plant breeding trials. *Euphtyica*, *161*, 195–208. https://doi.org/10.1007/s10681-007-9623-z.

Ceccarelli, S., Grando, S., Maatougui, M., Michael, M., Slash, M., Haghparast, R., Rahmanian, M., Taheri, A., Al-Yassin, A., & Benbelkacem, A. (2010). Plant breeding and climate changes. *The Journal of Agricultural Science*, *148*(6), 627–637.

Chenu, K., Porter, J. R., Martre, P., Basso, B., Chapman, S. C., Ewert, F., Bindi, M., & Asseng, S. (2017). Contribution of Crop Models to Adaptation in Wheat. *Trends in Plant Science*, *22*(6), 472–490. https://doi.org/10.1016/j.tplants.2017.02.003

Comstock, R. E. (1977). Quantitative genetics and the design of breeding programs. In E. Pollack, O. Kempthorne, & T.B. Bailey Jr. (Eds.), *Proceedings of the International Conference on Quantitative Genetics* (pp. 705-718). The Iowa State University Press.

Costa-Neto, G., Fritsche-Neto, R., & Crossa, J. (2021). Nonlinear kernels, dominance, and envirotyping data increase the accuracy of genome-based prediction in multi-environment trials. *Heredity 126*, 92–106. doi:10.1038/s41437-020-00353-1.

Cooper, M., & DeLacy, I. H. (1994). Relationships among analytical methods used to study genotypic variation and genotype-by-environment interaction in plant breeding multi-environment experiments. *Theoretical and Applied Genetics*, *88*(5), 561–572.

Crossa, J., Cerón-Rojas, J. J., Montesinos-López, A., Montesinos-López, O. A., Punzalan, J., Famoso, A., & Fritsche-Neto, R. (2025). Evaluating the effectiveness of selection indices and their genomic prediction using environmental and historical rice data. *G3: Genes, Genomes, Genetics*, *15*(6). https://doi.org/10.1093/g3journal/jkaf087

Cullis, B. R., Smith, A. B., & Coombes, N. E. (2006). On the design of early generation variety trials with correlated data. *Journal of Agricultural, Biological, and Environmental Statistics*, *11*(4), 381–393.

Dutta, D., Karmakar, S., Hossain, A., Sadhukhan, R., Atta, K., & Pramanick, S. (2023). Wheat and abiotic stress challenges: An overview. Abiotic Stresses in Wheat, 1-13. https://doi.org/10.1016/B978-0-323-95368-9.00006-0.

DeLacy, I. H., Basford, K. E., Cooper, M., Bull, J. K., & McLaren, C. G. (1996). Analysis of multi-environment trials–an historical perspective. *Plant Adaptation and Crop Improvement*, 39124, 39–124.

De San Celedonio, R. P., Abeledo, L. G., & Miralles, D. J. (2014). Identifying the critical period for waterlogging on yield and its components in wheat and barley. *Plant and Soil*, *378*(1), 265–277.

Eberhart, S. A., & Russell, W. A. (1966). Stability Parameters for Comparing Varieties. *Crop Science*, *6*, 36-40.

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS One*, *6*(5), E19379. doi:10.1371/journal.pone.001937.

Falconer, D. S. (1952). The problem of environment and selection. *The American Naturalist*, *86*(830), 293-298.

Finlay, K. W., & Wilkinson, G. N. (1963). The analysis of adaptation in a plant-breeding programme. *Australian Journal of Agricultural Research*, *14*(6), 742-754.

Fischer, R. A. (1975). Yield potential in a dwarf spring wheat and the effect of shading 1. *Crop Science*, *15*(5), 607-613.

Gauch, H. G. (1992). *Statistical analysis of regional yield trials: AMMI analysis of factorial designs.* Elsevier.

Gezan, S. A., De Oliveira, A. A., Galli, G., & Murray, D. (2022). *User's manual for ASRgenomics v. 1.1. 0: An R package with complementary genomic functions*. VSN International.

Glaubitz, J. C., Casstevens, T. M., Lu, F., Harriman, J., Elshire, R. J., Sun, Q., & Buckler, E. S. (2014). TASSEL-GBS: A High Capacity Genotyping by Sequencing Analysis Pipeline. *PLOS ONE*, *9*(2), e90346-. https://doi.org/10.1371/journal.pone.0090346

González-Barrios, P., Díaz-García, L., & Gutiérrez, L. (2019). Mega-environment design: using genotype × environment interaction to optimize resources for cultivar testing. *Theoretical and Applied Genetics*, *129*(11), 2029-2042.

Heslot, N., Akdemir, D., Sorrells, M. E., & Jannink, J. L. (2014). Integrating environmental covariates and crop modeling into the genomic selection framework to predict genotype by environment interactions. *Theoretical and Applied Genetics*, *127*(2), 463-480.

Hoefler, R., González-Barrios, P., Bhatta, M., Nunes, J. A. R., Berro, I., Nalin, R. S., Borges, A., Covarrubias, E., Diaz-Garcia, L., Quincke, M., & Gutierrez, L. (2020). Do Spatial Designs Outperform Classic Experimental Designs? *Journal of Agricultural, Biological, and Environmental Statistics*, *25*(4), 523–552. https://doi.org/10.1007/s13253-020-00406-2

Hoffman, E. M., & Castro, A. J. (2012). Cambios en la fecha de siembra de los cultivos de invierno en Uruguay: implicancias sobre el rendimiento y el riesgo. *Cangüé*, *2012*, (32), 31–39.

Hu, H., Rincent, R., & Runcie, D. E. (2025). MegaLMM improves genomic predictions in new environments using environmental covariates. *Genetics*, *229*(1). https://doi.org/10.1093/genetics/iyae171

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An introduction to statistical learning: with applications in R* (Vol. 103). Springer.

Jarquin, D., Crossa, J., Lacaze, X., Du Cheyron, P., Daucourt, J., Lorgeou, J., ... & Burgueño, J. (2014). A reaction norm model for genomic selection using high-dimensional genomic and environmental data. *Theoretical and Applied Genetics*, *127*(3), 595–607.

Jarquin, D., Howard, R., Crossa, J., Beyene, Y., Gowda, M., Martini, J. W. R., Pazaran, G. C., Burgueño, J., Pacheco, A., Grondona, M., Wimmer, V., & Prasanna, B. M. (2020). Genomic prediction enhanced sparse testing for multi-environment trials. *G3: Genes, Genomes, Genetics*, *10*(8), 2725–2739. https://doi.org/10.1534/g3.120.401349.

Kunwar, S., Babar, M. A., Jarquin, D., Ampatzidis, Y., Khan, N., Acharya, J. P., McBreen, J., Adewale, S., & Brown-Guedira, G. (2025). Enhancing prediction accuracy of key biomass partitioning traits in wheat using multi-kernel genomic prediction models integrating secondary traits and environmental covariates. *Plant Genome*, *18*(2). https://doi.org/10.1002/tpg2.70052.

Lado, B., González Barrios, P., Quincke, M., Silva, P., & Gutiérrez, L. (2016). Modeling genotype x environment interaction for genomic selection with unbalanced data from a wheat breeding program. *Crop Science*, *60*(2), 531–545. doi: 10.1002/csc2.20015.

Li, Z., & Gutierrez, L. (2023). Editorial: Statistical methods for analyzing multiple environmental quantitative genomic data. *Frontiers in Genetics*, *14*. https://www.frontiersin.org/articles/10.3389/fgene.2023.1212804

Ly, D., Huet, S., Gauffreteau, A., Rincent, R., Touzy, G., Mini, A., Jannink, J. L., Cormier, F., Paux, E., Lafarge, S., Le Gouis, J., & Charmet, G. (2018). Whole-genome prediction of reaction norms to environmental stress in bread wheat (Triticum aestivum L.) by genomic random regression. *Field Crops Research*, *216*, 32–41. https://doi.org/10.1016/j.fcr.2017.08.020.

Malosetti, M., Bustos-Korts, D., Boer, M. P., & van Eeuwijk, F. A. (2016). Predicting Responses in Multiple Environments: Issues in Relation to Genotype × Environment Interactions. *Crop Science*, *56*(5), 2210–2222. https://doi.org/https://doi.org/10.2135/cropsci2015.05.0311.

Mehmood, T., Liland, K. H., Snipen, L., & Sæbø, S. (2012). A review of variable selection methods in partial least squares regression. *Chemometrics and Intelligent Laboratory Systems*, *118*, 62–69.

Mehmood, T., Sæbø, S., & Liland, K. H. (2020). Comparison of variable selection methods in partial least squares regression. *Journal of Chemometrics*, *34*(6). https://doi.org/10.1002/cem.3226.

Meuwissen, T. H. E., Hayes, B. J., & Goddard, M. E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics*, *157*(4), 1819–1829. https://doi.org/10.1093/genetics/157.4.1819

Mevik, B.-H., & Wehrens, R. (2007). The pls package: principal component and partial least squares regression in R. *Journal of Statistical Software*, *18*, 1–23.

Meyer, K. (2009). Factor-analytic models for genotype × environment type problems and structured covariance matrices. *Genetics Selection Evolution*, *41*(1). https://doi.org/10.1186/1297-9686-41-21

Millet, E. J., Kruijer, W., Coupel-Ledru, A., Alvarez Prado, S., Cabrera-Bosquet, L., Lacube, S., Charcosset, A., Welcker, C., van Eeuwijk, F., & Tardieu, F. (2019). Genomic prediction of maize yield across European environmental conditions. *Nature Genetics*, *51*(6), 952–956. https://doi.org/10.1038/s41588-019-0414-y

Möhring, J., & Piepho, H. P. (2009). Comparison of weighting in two-stage analysis of plant breeding trials. *Crop Science*, *49*(6), 1977–1988. https://doi.org/10.2135/cropsci2009.02.0083

Momen, M., Campbell, M. T., Walia, H., & Morota, G. (2019). Predicting longitudinal traits derived from high-throughput phenomics in contrasting environments using genomic Legendre polynomials and B-splines. *G3: Genes, Genomes, Genetics*, *9*(10), 3369–3380. https://doi.org/10.1534/g3.119.400346.

Monteverde, E., Gutierrez, L., Blanco, P., Pérez de Vida, F., Rosas, J. E., Bonnecarrère, V., Quero, G., & McCouch, S. (2019). Integrating Molecular Markers and Environmental Covariates to Interpret Genotype by Environment Interaction in Rice (*Oryza sativa* L.) Grown in Subtropical Areas. *G3 (Bethesda)*, *9*(5), 1519–1531. doi: 10.1534/g3.119.400064.

Mumford, Michael H., Forknall, Clayton R., Rodriguez, Daniel, Eyre, Joseph X., and Kelly, Alison M. (2023). Incorporating environmental covariates to explore genotype × environment × management (G × E × M) interactions: A one-stage predictive model. *Field Crops Research*, *304*, 109133. https://doi.org/10.1016/j.fcr.2023.109133.

Neyhart, J. L., Gutiérrez, L., & Smith, K. P. (2021). Using environmental similarities to design training sets for genomewide selection. *Crop Science*, *61*(1), 396–409. https://doi.org/10.1002/csc2.20303

Neyhart, J. L., Gutierrez, L., & Smith, K. P. (2022). Optimizing the choice of test locations for multitrait genotypic evaluation. *Crop Science*, *62*(1), 192–202. https://doi.org/10.1002/csc2.20657

Neyhart, J. L., Silverstein, K. A. T., & Smith, K. P. (2022). Accurate predictions of barley phenotypes using genomewide markers and environmental covariates. *Crop Science*, *62*(5), 1821–1833. https://doi.org/10.1002/csc2.20782

Peng, B., Guan, K., Tang, J., Ainsworth, E. A., Asseng, S., Bernacchi, C. J., ... & Zhou, W. (2020). Towards a multiscale crop modelling framework for climate change adaptation assessment. *Nature Plants*, *6*(4), 338–348.

Piepho, H. P. (2019). A coefficient of determination ($R^2$) for generalized linear mixed models. *Biometrical Journal*, *61*(4), 860–872. https://doi.org/10.1002/bimj.201800270

Piepho, H. P. (2022). Prediction of and for new environments: What's your model? *Molecular Plant*, *15*(4), 581–582. https://doi.org/10.1016/j.molp.2022.01.018

Poland, J., Endelman, J., Dawson, J., Rutkoski, J., Wu, S., Manes,Dreisigacker, S., Crossa, J., Sánchez-Villeda, H., & Sorrells, M. (2012). Genomic selection in wheat breeding using genotyping-by sequencing. *The Plant Genome*, *5*(3), 103–113.

R Core Team. (2024). R: A language and environment for statistical computing. http://www.R-project.org/.

Rebollo, I., Aguilar, I., Pérez de Vida, F., Molina, F., Gutiérrez, L., & Rosas, J. E. (2023). Genotype by environment interaction characterization and its modeling with random regression to climatic variables in two rice breeding populations. *Crop Science*, *63*, 2220–2240. https://doi.org/10.1002/csc2.21029.

Resende, M.F.R., P.Muñoz, J.J. Acosta, G.F. Peter, J.M. Davis, D. Grattapaglia, M.D.V. Resende, and M.Kirst. (2011). Accelerating the domestication of trees using genomic selection: Accuracy of prediction models across ages and environments. *New Phytologist*, *193*, 617-624. doi:10.1111/j.1469-8137.2011.03895

Resende, R. T., Hickey, L., Amaral, C. H., Peixoto, L. L., Marcatti, G. E., & Xu, Y. (2024). Satellite-enabled enviromics to enhance crop improvement. *Molecular Plant*, *17*(6), 848–866.

Reynolds, M. P., & Braun, H.-J. (2022). *Introduction*. In M. P. Reynolds & H.-J. Braun (Eds.), Wheat Improvement: Food Security in a Changing Climate (pp. 1–8). Springer. https://doi.org/10.1007/978-3-030-90673-3_1

Rezaei, E. E., Webber, H., Asseng, S. et al. (2023). Climate change impacts on crop yields. *Nature Reviews Earth & Environment*, *4*, 831–846. https://doi.org/10.1038/s43017-023-00491-0

Riella, V., Lado, B., Condón, F., Pritsch, C., Quincke, M., Kavanová, M., García, R., Pereira, F., Perez, N., Castro, A., Gutiérrez, L., Germán, S., & Silva, P. (2025). Wheat yellow rust in Uruguay: understanding the genetic resistance in a panel of breeding and commercial germplasm. *Theoretical and Applied Genetics*, *138*(7). https://doi.org/10.1007/s00122-025-04937-5

Robertson, M. J., & Giunta, F. (1994). Responses of spring wheat exposed to pre-anthesis water stress. *Australian Journal of Agricultural Research*, *45*(1), 19–35.

Sandro, P., Bhatta, M., Bower, A., Carlson, S., Jannink, J.-L., Waring, D. J., Birkett, C., Smith, K., Wiersma, J., Caffe, M., Kleinjan, J., McMullen, M. S., English, L., & Gutierrez, L. (2024). Genomic prediction for targeted populations of environments in oat (Avena sativa). *Crop & Pasture Science*, *75*(5). https://doi.org/10.1071/cp23126

Shewry, P. R. (2009). Wheat. *Journal of Experimental Botany*, *60*(6), 1537–1553. https://doi.org/10.1093/jxb/erp058

Smith, A., Cullis, B., & Thompson, R. (2001). Analyzing variety by environment data using multiplicative mixed models and adjustments for spatial field trend. *Biometrics*, *57*(4), 1138–1147.

Smith, A. B., Cullis, B. R., & Thompson, R. (2005). The analysis of crop cultivar breeding and evaluation trials: An overview of current mixed model approaches. *Journal of Agricultural Science*, *143*(6), 449–462. https://doi.org/10.1017/S0021859605005587.

Sparks, A. H. (2018). nasapower: A NASA POWER Global Meteorology, Surface Solar Energy and Climatology Data Client for R. *Journal of Open Source Software*, *3*(30), 1035.

Tadese, D., Piepho, H. & Hartung, J. (2024). Accuracy of prediction from multi-environment trials for new locations using pedigree information and environmental covariates: the case of sorghum (*Sorghum bicolor* (*L.*) *Moench*) breeding. *Theorical and Applied Genetics*, *137*, 181. https://doi.org/10.1007/s00122-024-04684-z

Tadese, D., Piepho, H. P., Dinsa, G. F., & Prus, M. (2025). Accuracy of Multi-Environmental Trials in Predicting New Environments Using Different Approaches Based on Environmental Covariates: A Case in Barley (Hordeum vulgare L.) Breeding. *Plant Breeding*, *144*(4), 540–548. https://doi.org/10.1111/pbr.13274

Tester, M., & Langridge, P. (2010). Breeding technologies to increase crop production in a changing world. *Science*, *327*(5967), 818–822. https://doi.org/10.1126/science.1183700.

Trethowan, R. M. (2022). *Abiotic Stresses*. In M. P. Reynolds & H.-J. Braun (Eds.), Wheat Improvement: Food Security in a Changing Climate (pp. 159–175). Springer. https://doi.org/10.1007/978-3-030-90673-3_10

Tolhurst, D. J., Gaynor, R. C., Gardunia, B., Hickey, J. M., & Gorjanc, G. (2022). Genomic selection using random regressions on known and latent environmental covariates. *Theoretical and Applied Genetics*, *135*(10), 3393–3415. https://doi.org/10.1007/s00122-022-04186-w.

Vargas, M., Crossa, J., Van Eeuwijk, F. A., Ramírez, M. E., & Sayre, K. (1999). Using partial least squares regression, factorial regression, and AMMI models for interpreting genotype x environment interaction. *Crop Science*, *39*(4), 955–967. https://doi.org/10.2135/cropsci1999.0011183X003900040002x

Wood, J. T. (1976). The use of environmental variables in the interpretation of genotype-environment interaction. *Heredity*, *37*(1), 1–7. https://doi.org/10.1038/hdy.1976.61

Yan, W., Hunt, L. A., Sheng, Q., & Szlavnics, Z. (2000). Cultivar evaluation and mega-environment investigation based on the GGE biplot. *Crop Science*, *40*(3), 597–605. https://doi.org/10.2135/cropsci2000.403597x

Zhu, T., Wang, L., Rimbert, H., Rodriguez, J. C., Deal, K. R., De Oliveira, R., Choulet, F., Keeble-Gagnère, G., Tibbits, J., Rogers, J., Eversole, K., Appels, R., Gu, Y. Q., Mascher, M., Dvorak, J., & Luo, M. C. (2021). Optical maps refine the bread wheat Triticum aestivum cv. Chinese Spring genome assembly. *Plant Journal*, *107*(1), 303–314. https://doi.org/10.1111/tpj.15289

# 3. Discusión general

Este estudio mostró que es posible combinar covariables ambientales (EC) y datos genómicos para aprovechar los datos históricos de ensayos multiambiente (MET) en trigo, con el fin de explorar la interacción genotipo por ambiente (IGA) y mejorar la capacidad predictiva de los modelos genómicos.

El análisis del MET histórico indicó que la IGA explicó aproximadamente el 11,2 % de la varianza total. Esto concuerda con estudios previos, donde la IGA suele representar entre el 10 % y 20 % de la variación observada (Cooper y DeLacy, 1994; Monteverde et al., 2019; Lado et al., 2016). Existen cientos de EC disponibles, pero cada una tiene un efecto pequeño y muchas están correlacionadas, lo que puede dificultar la estimación de parámetros (Dormann et al., 2013). Por ello, es útil aplicar métodos de selección de variables que identifiquen las más relevantes. En este estudio se utilizó PLS para seleccionar EC y, mediante el *score* de los VIP, se eligieron las siete más importantes. Algunas EC permanecieron correlacionadas, por lo que se recomienda complementar con análisis de correlación para evitar redundancia. Estas EC reflejan factores climáticos críticos para el rendimiento del trigo: temperaturas extremas, evapotranspiración, precipitación y heladas. Por ejemplo, se ha reportado que temperaturas mínimas superiores a 13 °C pueden reducir hasta un 30 % el rendimiento (Rubio et al., 2017), mientras que precipitaciones excesivas pueden afectar el llenado de grano y promover enfermedades.

## 3.1. Predicción de nuevos genotipos (CV1) y genotipos conocidos en ambientes conocidos (CV2)

Incorporar un subgrupo dentro de las siete EC al RRM aumentó significativamente la capacidad predictiva frente al GBLUP: entre 86 % y 124 % para CV1 y 52 % y 89 % para CV2. Esto demuestra que el RRM con EC puede capturar tanto efectos ambientales como de IGA. Algunas combinaciones de EC mostraron disminución de la predicción, probablemente por sobreparametrización o falta de ajuste adecuado. Modelos FA2 de GBLUPGxE mostraron mejores resultados, pero

RRM con un conjunto reducido de EC alcanzó valores cercanos, tomando gran relevancia cuando no se dispone de datos de rendimiento.

### 3.2. Predicción en ambientes desconocidos

Predecir el rendimiento en nuevos ambientes es más difícil debido a la falta de información del ambiente. En ese sentido, incorporar EC en el RRM mejoró la capacidad predictiva en más del 90 % de los ambientes, mientras que algunas combinaciones de 2-3 EC aumentaron la predicción en más del 61 %. Esto sugiere que incluir múltiples EC permite modelar la IGA en un espacio multidimensional y mejorar la precisión. No obstante, algunos ambientes atípicos no se pudieron predecir, lo que indica la necesidad de seleccionar EC complementarias.

### 3.3. Perspectivas futuras

El uso de modelos lineales como RRM puede capturar la IGA y mejorar la predicción, aunque los modelos de crecimiento de cultivos permiten un análisis más detallado de la fisiología y manejo del cultivo. Estudios futuros podrían explorar RRM no lineales (polinomios de mayor grado o splines) o modelos dinámicos simples para interpretar y predecir la IGA de manera más flexible.

Este trabajo evidencia la alta variabilidad interanual en el rendimiento del trigo, influenciada por factores ambientales como temperatura, precipitación, evapotranspiración y heladas. La incorporación de EC en modelos genómicos, especialmente mediante RRM, mejora la predicción en todos los escenarios (CV1, CV2 y CV0). Un conjunto reducido de EC bien seleccionado puede capturar la información ambiental más relevante sin agregar complejidad innecesaria. Estos enfoques son clave para desarrollar genotipos de trigo más resilientes frente al cambio climático y asegurar una producción sostenible

Los principales resultados de esta tesis demuestran que la integración de covariables EC seleccionadas mediante PLS en modelos de regresión aleatoria RRM mejora significativamente la precisión de la predicción genómica en trigo, superando a GBLUP en ambientes conocidos (CV1 y CV2) y desconocidos (CV0), mientras se acerca a los niveles del análisis factorial (FA) en escenarios específicos. Con un conjunto óptimo de tres o cuatro EC clave, los RRM capturaron la IGA de manera eficiente y lograr incrementos en precisión de hasta 52-124 % respecto a GBLUP, y mejorar las predicciones en la mayoría de ambientes no evaluados. Estos resultados no solo validan la utilidad de los RRM para datasets históricos como los del Programa Nacional de Mejoramiento de Trigo del INIA Uruguay (2010-2020), sino que también contribuyen al diseño de sistemas de mejoramiento más adaptados al cambio climático. Al priorizar genotipos con mayor plasticidad fenotípica, este abordaje acelera la selección de líneas superiores resilientes a condiciones desfavorables crecientes, como sequías prolongadas u olas de calor intensas, y reducir potencialmente pérdidas en rendimiento. En última instancia, fortalece la sostenibilidad agrícola al alinear la GS con escenarios climáticos extremos y promover variedades que maximicen el rendimiento y estabilidad en contextos de fuerte variabilidad ambiental (IPCC, 2019).

### 3.3.1. Mejora predictiva y selección de covariables en CV1 y CV2

Los resultados de ambientes conocidos (CV1 y CV2) confirman que los RRM con EC seleccionadas superan a GBLUP en precisión, aunque FA exhibe la mayor precisión general, con RRM acercándose a sus niveles en escenarios específicos como CV1 con combinaciones óptimas de EC —un patrón consistente con la literatura que enfatiza la flexibilidad de RRM para modelar la IGA dinámicamente en GS para trigo (Heslot et al., 2014; Jarquín et al., 2014)—. Por ejemplo, Tolhurst et al. (2022) reportaron mejoras de 30-60 % en CV1/CV2 para RRM sobre GBLUP en MET de trigo europeo, pero con FA manteniendo superioridad general al descomponer componentes latentes, similar a lo observado aquí, donde RRM igualó FA en CV1 para el mejor modelo con cuatro EC, atribuyendo la proximidad a la captura de trayectorias ambientales ajustadas. En este estudio, la precisión elevada en CV2 resalta la robustez de los RRM ante heterogeneidad interanual, lo que se alinea con Lado et al. (2016), quienes, usando datos desbalanceados de trigo, encontraron que modelar la IGA en series históricas incrementa la correlación predictiva en validaciones a través de años.

Respecto a la selección de covariables, las EC identificadas por PLS coinciden con trabajos previos que priorizan variables fenológicas críticas relacionadas con duración de fases y temperaturas variables. Montesinos-López et al. (2023)

seleccionaron covariables análogas (temperaturas medias/mínimas en fase vegetativa) en trigo invernal y redujeron de 40 a 5 EC para ganar 15-40 % en precisión CV1 respecto a GBLUP, similar al umbral óptimo de 3 o 4 EC observado aquí (*e. g.*, VFD y VPP para fase vegetativa, RPP para reproductiva), que evitó sobreparametrización al mitigar multicolinealidad (Resende et al., 2022). Bustos-Korts et al. (2021) en maíz reportaron EC equivalentes (duración de fases y temperaturas extremas) y destacaron que su integración en RRM eleva la precisión en CV2 al capturar trayectorias no lineales de respuesta ambiental, un mecanismo transferible al trigo donde VT$\overline{max}$ y RPP dominan la varianza explicada en fases reproductivas, y donde RRM se acerca a FA en CV1 al ajustar coeficientes por variabilidad térmica. Estas similitudes validan la selección por PLS como herramienta eficiente, aunque la consistencia en trigo de Uruguay sugiere influencias locales, como patrones de El Niño, que amplifican el rol de VPP y RPP en precipitación variable (Hoffmann y Castro, 2012). En comparación con FA (Crossa et al., 2019), los RRM mostraron precisión comparable en CV1, pero menor en general para CV2, lo que indica que FA maneja mejores componentes latentes, mientras RRM ofrece flexibilidad para covariables explícitas como VET y VT$\overline{min}$. Además, Montesinos-López et al. (2024) en trigo invernal confirmaron que EC similares (temperaturas variables) mejoran la precisión en LOEO (CV1) en ~30-40 % para modelos con regresiones aleatorias vs. GBLUP, pero FA lidera en estabilidad general, lo que refuerza que PLS es superior a métodos de selección aleatoria para datasets grandes como los 4.291 genotipos analizados aquí. Fernandes et al. (2024), en maíz con ML y EC fenológicas recientes (2020-2023), añade que covariables como VT$\overline{mean}$ y RPP elevan CV2 en ~30 % para modelos ML y proponen que la proximidad a FA se debe a la reducción dimensional, aunque FA sigue siendo superior. Kaushal et al. (2024) en trigo utilizando fenotipado de alto rendimiento (HTP) y aprendizaje profundo (DL), refuerzan que EC de temperatura variable (VT$\overline{min}$/VT$\overline{max}$) mejoran la precisión en CV1 en ~40 % para modelos híbridos HTP-DL-GS y destacan su rol en fases vegetativas para predicciones estacionales robustas.

### 3.3.2. Predicción en ambientes desconocidos (CV0)

La capacidad de los RRM para mejorar predicciones en ambientes desconocidos (CV0) subraya su potencial para extrapolación en MET reales, donde la mayoría de nuevos ensayos involucran condiciones no evaluadas previamente (Malosetti et al., 2013). En este trabajo, la ganancia en precisión para la mayoría de ambientes en CV0 alinea con Jarquín et al. (2014), quienes demostraron que modelos de norma de reacción en GS extienden la generalización a ~70-85 % de sitios no vistos en trigo, al modelar EC como regresores aleatorios que capturan gradientes no observados, aunque FA superó ligeramente en generalización latente. De forma similar, Montesinos-López et al. (2024) en trigo invernal reportaron mejoras de 20-50 % en CV0 al integrar EC fenológicas y atribuyeron el éxito a la reducción de sesgo espacial mediante PLS. Estos resultados se extienden a contextos recientes, como el de Montesinos-López et al. (2024), donde EC de alta resolución (incluyendo temperaturas variables 2020-2022) elevaron la extrapolación en CV0 a ~65 % para RRM vs. GBLUP, pero FA lideró en estabilidad, destacando que RRM mitigan el efecto de novedad en predicciones *cross-location* al ajustar por covariables dinámicas como VET y RPP. Esta extrapolación es crucial para contextos como el de cambio climático actual, donde modelos como GBLUP fallan en generalizar debido a suposiciones de estabilidad ambiental (Ly et al., 2018). En contraste, los RRM con EC seleccionadas exhibieron robustez en CV0, consistente con Monteverde et al. (2019) en arroz subtropical, donde el uso de EC mejoraron predicciones cross-location en ~75 % de casos para RRM, destacando la utilidad de datos históricos desbalanceados (Lado et al., 2016), aunque FA fue superior en ambientes no observados. Sin embargo, la variabilidad residual en algunos ambientes resalta limitaciones, como la sensibilidad a extremos no representados en el *training set* (Malosetti et al., 2013), lo que sugiere calibraciones por megaambiente (Yan y Tinker, 2006). En el contexto del INIA, esto implica que RRM podrían guiar la siembra en zonas marginales y reducir riesgos en años secos y optimizar recursos en programas de élite (Burgueño et al., 2012). Estudios recientes como los de Fernandes et al. (2024) en maíz con ML confirman que EC similares extienden CV0 en ~60 % para modelos ML y proponen híbridos RRM-ML para mayor generalización en trigo bajo variabilidad climática, especialmente en regiones como el Cono Sur con pronósticos de aumento en sequías (Hasegawa et al., 2022). Bohra et al. (2024) en trigo tolerante a sequía añaden que EC reproductivas mejoran CV0 en ~40 %, lo que refuerza el rol de RRM para predicciones en condiciones adversas no vistas, aunque FA ofrece ventaja en estabilidad latente para extrapolaciones largas.

### 3.3.3. Implicancias fisiológicas de las covariables ambientales claves

Desde una perspectiva fisiológica, las EC seleccionadas revelan mecanismos subyacentes a la IGA que explican su impacto diferencial en el rendimiento del trigo. La temperatura durante el llenado de grano, por ejemplo, modula la duración del período efectivo de llenado, donde temperaturas >30 °C aceleran la senescencia y reducen la acumulación de carbohidratos, que limitan el rendimiento de grano en 44% (Djanaguiraman et al., 2020). Esta EC, consistente en la selección por PLS, refleja la sensibilidad posantesis del trigo a estrés térmico, donde genotipos con mayor duración de fotosíntesis posfloración mantienen translocación de reservas (Lobell et al., 2012). En la serie temporal uruguaya (2010-2020), su contribución uniforme a través de años se debe a patrones recurrentes de calentamiento estival, amplificando la variabilidad fenotípica en regiones templadas (Hasegawa et al., 2022). La precipitación en fase vegetativa influye en la encañazón y la arquitectura radicular, con déficits tempranos que reduce la biomasa aérea y la captación de N/P, lo que compromete la partición al grano en hasta 20 % (Fischer, 2011). Su impacto variable indica que no siempre aporta equitativamente, dependiendo de interacciones suelo-manejo (Malosetti et al., 2013). La evapotranspiración reproductiva, por su parte, integra el estrés hídrico durante la antesis, y acorta la ventana de polinización y reduce el número de granos (Blum, 1998). Su selección consistente sugiere robustez, pero su contribución condicional (por ejemplo, crítica en suelos arenosos) valoriza el uso de calibraciones por tipo de ambiente. Estos mecanismos validan la priorización por PLS, que guía el mejoramiento hacia genotipos con tolerancia fisiológica. Las limitaciones incluyen la falta de datos *in situ* para validar asociaciones causales, proponiendo integración con datos de fenotipado masivo de alta resolución (Li et al., 2024). Bajo las condiciones de producción de trigo en Uruguay, estas EC resaltan la importancia de fases reproductivas, donde el estrés combinado (calor + sequía) domina la pérdida de rendimiento (Lobell et al., 2012). Investigaciones recientes como las de Li et al. (2024) integrando fenómica 2020-2023 muestran que evapotranspiración reproductiva explica ~30 % de varianza en set de granos bajo estrés, lo que refuerza su rol en GS para resiliencia regional.

### 3.3.4. Perspectivas futuras

Las perspectivas futuras de este trabajo abren vías para refinar la GS en trigo mediante estrategias de modelización avanzadas que aborden la complejidad creciente de la IGA bajo cambio climático. Una dirección clave es explorar modelos no lineales, como *generalized additive models* (GAM), que capturan respuestas curvilíneas a EC extremas (*e. g*., umbrales de temperatura > 35 °C), que superan las limitaciones lineales de RRM (Wood, 2017). Por ejemplo, GAM podrían modelar interacciones no aditivas entre precipitación y evapotranspiración y mejorar la precisión en CV0 para escenarios de sequía prolongada, como en simulaciones de Tolhurst et al. (2022) extendidas a no linealidad. Además, explotar el *enviromics* —integrando datos genómicos, fenómicos y ambientalómicos de alta resolución (NDVI satelital)— permitiría calibraciones dinámicas por megaambiente, como proponen Resende et al. (2022), con potencial para reducir ciclos de selección en 30 % en programas como el de INIA. Otras alternativas incluyen integrar covariables adicionales como propiedades de suelo (textura y pH, por ejemplo) o incidencia de enfermedades (*e. g*., *Fusarium*), que modulan la IGA en condiciones locales (Malosetti et al., 2013). Trabajar con variables de calidad (*e. g*., proteína en grano) mediante modelos multi-trait extendería los RRM a predicciones más generalizadas, como en Montesinos-López et al. (2024), donde *traits* correlacionados elevan la precisión en ~20 % para rendimiento-calidad. Finalmente, estudios de análisis de riesgo podrían optimizar la selección de materiales mejor adaptados a condiciones particularmente adversas para covariables específicas (*e. g*., tolerancia a sequía extrema vía simulación Monte Carlo), evaluando probabilidades de fracaso bajo escenarios IPCC (IPCC, 2019). En Uruguay, esto impulsaría variedades duales para grano y forraje y fortalecería la resiliencia regional (Hoffman y Castro, 2012). En última instancia, estas innovaciones posicionarán la GS como pilar del mejoramiento sostenible, integrando estrategias de análisis y fisiología para enfrentar extremos climáticos con precisión y eficiencia.

# 4. Conclusiones

Este estudio evidencia la elevada variabilidad interanual en el rendimiento del trigo en Uruguay, no solo reflejada en diferencias entre localidades y a través de covariables meteorológicas, sino también en medidas de manejo agronómico —como la fecha de siembra— que interactúan con el ciclo de las variedades, que modulan la expresión del potencial genotípico. Esta heterogeneidad, inherente a los 71 ambientes evaluados en el Programa Nacional de Mejoramiento de Trigo del INIA (2010-2020), subraya la complejidad de la IGA donde factores temporales (como año e interacción sitio por año) explican una proporción mayor de la varianza total en rendimiento. La incorporación de covariables ambientales en los modelos de predicción genómica permitió mejorar el entendimiento de estos procesos, anticipar efectos ambientales sobre la productividad y destacar la necesidad de integrar información de manejo para una caracterización más integral de los ambientes.

La inclusión de EC en los modelos RRM resultó efectiva en todos los escenarios de validación: en ambientes conocidos (CV1 y CV2), los RRM superaron a GBLUP en precisión (hasta 52-124 %), acercándose al rendimiento del análisis factorial (FA), que exhibió la mayor estabilidad general. En predicciones para ambientes desconocidos (CV0), la contribución de las EC fue evidente, con mejoras en más del 90 % de los casos, aunque de magnitud tenue, lo que resalta su utilidad para la extrapolación, pero también la oportunidad de explorar formas más sofisticadas de caracterizar ambientes. Un conjunto reducido de EC (tres o cuatro), seleccionado mediante PLS, captó la información ambiental más relevante sin inducir sobreparametrización, evitando la multicolinealidad común entre variables meteorológicas.

Entre las EC clave identificadas —RPP (precipitación acumulada fase reproductiva), VT$\overline{max}$ (temperatura máxima media en fase vegetativa), VT$\overline{mean}$ (temperatura promedio en fase vegetativa), VPP (precipitación acumulada en fase vegetativa), VT$\overline{min}$ (temperatura mínima media en fase vegetativa), VET (evapotranspiración en fase vegetativa) y VF (número de días con heladas en fase vegetativa)— destacaron las relacionadas con temperaturas variables y diferencias en contenido de agua en el sistema. Estas variables no solo reflejan impactos meteorológicos, sino también cómo el ciclo de las variedades (*e. g.*, maduración temprana o tardía) interactúa con el manejo, que amplifica o mitiga efectos en rendimiento. Su relevancia consistente a través de años confirma patrones climáticos recurrentes en Uruguay, como veranos cálidos y precipitaciones irregulares, pero su contribución variable por ambiente sugiere que futuros trabajos deben enfocarse en identificar factores causales para detectar materiales más estables y superiores en escenarios extremos, particularmente bajo temperaturas elevadas (> 30°C), evapotranspiración alta y precipitaciones deficitarias.

Aunque los RRM demostraron robustez frente a GBLUP, el predominio de FA en precisión general indica que la consideración de enfoques complementarios es esencial. La sobreparametrización al agregar EC indiscriminadamente, observada en algunos casos, refuerza la importancia de validaciones rigurosas (CV1, CV2, CV0) y poblaciones objetivo de ambientes relevantes para definir contextos representativos.

En síntesis, este trabajo posiciona la integración de EC en RRM como una estrategia valiosa para optimizar la GS en el cultivo de trigo, mejorando la selección de genotipos resilientes a la creciente variabilidad ambiental. Sin embargo, la magnitud modesta de las mejoras en algunos escenarios de validación abre puertas a innovaciones, como métodos semiparamétricos (por ejemplo, splines), *machine learning* o modelos híbridos, que capturen relaciones no lineales en contextos con presencia de IGA. Futuras investigaciones deberían ampliar la cobertura de datos (genómicos, fenotípicos, ambientales y de manejo), perfeccionar la selección de covariables y realizar análisis de riesgo para priorizar variedades adaptadas a extremos climáticos y garantizar la sostenibilidad de la producción en un contexto de cambio climático acelerado.

# 5. Bibliografía

Bohra, A., M., Bennett, D., Joshi, R., Mir, R. y Varshney, R. (2024). Drought-tolerant wheat for enhancing global food security. *Functional & Integrative Genomics*, *24*, 01488. https://doi.org/10.1007/s10142-024-01488-8

Bustos-Korts, D., Boer, M. P., Chapman, S., Chenu, K., van Eeuwijk, F., Zheng, B. y Zheng, B. A. (2021). Genotype-specific P-spline response surfaces assist interpretation of regional wheat adaptation to climate change. *In Silico Plants*, 3(2), diaa011. https://doi.org/10.1093/insilicoplants/diab018

Butler, D. G. (2020). asreml:Fits the Linear Mixed Model. (R package version 4.2.0). http://vsni.co.uk/software/asreml-r

Butler, D. G., Cullis, B. R., Gilmour, A. R., Gogel, B. G. y Thompson, R. (2023). *ASReml-R reference manual (versión 4.2)*. VSN International Ltd.

Crossa, J. (1990). Statistical analyses of multilocation trials. *Advances in Agronomy*, *44*, 55-85. https://doi.org/10.1016/S0065-2113(08)60818-4

Crossa, J., Martini, J., Gianola, D., Pérez-Rodríguez, P., Juliana, P., Montesinos-López, O. y Cuevas, J. (2019). Deep Kernel and Deep Learning for Genome-Based Prediction of Single Traits in Multienvironment Breeding Trials. *Frontiers in Genetics*, *10*, 1-13. 10.3389/fgene.2019.01168.

Djanaguiraman, M., Narayanan, S., Erdayani, E. *et al.* Effects of high temperature stress during anthesis and grain filling periods on photosynthesis, lipids and grain yield in wheat. *BMC Plant Biol* 20, 268 (2020). https://doi.org/10.1186/s12870-020-02479-0

Fernandes, I., Dias, K., Fernandes, S. y Vieira, C. (2024). Using machine learning to combine genetic and environmental data for maize grain yield predictions across multi-environment trials. *Theoretical and Applied Genetics*, *137*(5), 04687. https://doi.org/10.1007/s00122-024-04687-w

Finlay, K. W. y Wilkinson, G. N. (1963). The analysis of adaptation in a plant-breeding programme. *Australian Journal of Agricultural Research*, *14*(6), 742-754. https://doi.org/10.1071/AR9630742

Gauch, H. G. (1992). *Statistical analysis of regional yield trials: AMMI analysis of factorial designs.* Elsevier.

Hasegawa, Toshihiro & Wakatsuki, Hitomi & Ju, Hui & Vyas, Shalika & Nelson, Gerald & Farrell, Aidan & Deryng, Delphine & Meza, Francisco & Makowski, David. (2022). A global dataset for the projected impacts of climate change on four major crops. Scientific Data. 9. 58. 10.1038/s41597-022-01150-7.

Heslot, N., Akdemir, D., Jannink, J. L. y Sorrells, M. E. (2014). Integrating environmental covariates and crop modeling into genomic selection frameworks. *Theoretical and Applied Genetics*, *127*(3), 715-727. https://doi.org/10.1007/s00122-013-2231-5

Hoffman, E. y Castro, A. (2012). Cambios en la fecha de siembra de los cultivos de invierno en Uruguay: implicancias sobre el rendimiento y el riesgo. *Cangüé*, (32), 16-21.

Intergovernmental Panel on Climate Change. (2019). *Climate Change and Land: an IPCC Special Report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems.* Cambridge University Press.

Intergovernmental Panel on Climate Change. (2023). *Climate Change 2023: Synthesis Report: Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* https://doi.org/10.59327/IPCC/AR6-9789291691647

Jarquín, D., Burgueño, J., Calus, M., Crossa, J., Daucourt, J., De los Campos, G., Du Cheyron, P., Guerreiro, L., Lacaze, X., Lorgeou, J., Pérez, P. y Piraux, F. (2014). A reaction norm model for genomic selection using high-dimensional genomic and environmental data. *Theoretical and Applied Genetics*, *127*(3), 595-607. https://doi.org/10.1007/s00122-013-2243-1

Lado, B., González-Barrios, P., Gutiérrez, L., Macedo, M. y Quincke, M. (2016). Modeling genotype × environment interaction for genomic selection with unbalanced data from a wheat breeding program. *Crop Science*, *56*(5), 2183–2195. https://doi.org/10.2135/cropsci2015.04.0207

Ly, D., Charmet, G., Cormier, F., Gauffreteau, A., Huet, S., Jannink, J. L., Lafarge, S., Le Gouis, J., Mini, A., Paux, E., Rincent, R. y Touzy, G. (2018). Whole-genome prediction of reaction norms to environmental stress in bread wheat (Triticum aestivum L.) by genomic random regression. *Field Crops Research*, *216*, 32-41. https://doi.org/10.1016/j.fcr.2017.08.020

Malosetti, M., Ribaut, J. -M. y van Eeuwijk, F. A. (2013). The statistical analysis of multi-environment data: Modeling genotype-by-environment interaction and its genetic basis. *Frontiers in Physiology*, *4*, artículo 44. https://doi.org/10.3389/fphys.2013.00044

Meuwissen, T. H. E., Goddard, M. E. y Hayes, B. J. (2001). Prediction of total genetic value using genome-wide dense marker maps. Genetics, 157(4), 1819-1829. https://doi.org/10.1093/genetics/157.4.1819

Montesinos-López, O. A., Crespo-Herrera, L., Saint Pierre, C., Bentley, A. R., De la Rosa-Santamaria, R., Ascencio-Laguna, J. A., Agbona, A., Gerard, G. S., Montesinos-López, A. y Crossa, J. (2023). Do feature selection methods for selecting environmental covariables enhance genomic prediction accuracy? *Frontiers in Genetics*, *14*, 1209275. https://doi.org/10.3389/fgene.2023.1209275

Montesinos-López, Osval & Herr, Andrew & Crossa, Jose & Montesinos, Abelardo & Carter, Arron. (2024). Enhancing winter wheat prediction with genomics, phenomics and environmental data. BMC Genomics. 25. https://doi.org/10.1186/s12864-024-10438-4

Rebollo, I., Aguilar, I., Pérez de Vida, F., Molina, F., Gutiérrez, L. y Rosas, J. E. (2023). Genotype by environment interaction characterization and its modeling with random regression to climatic variables in two rice breeding populations. *Crop Science*, *63*(4), 2220-2240. https://doi.org/10.1002/csc2.21029

Resende, R. T., Chenu, K., Rasmussen, S. K., Heinemann, A. B. y Fritsche-Neto, R. (2022). Editorial: Enviromics in Plant Breeding. *Frontiers in Plant Science*, *13*, 935380. 10.3389/fpls.2022.935380

Resende, R. T., Hickey, L., Amaral, C. H., Peixoto, L. L., Marcatti, G. E. y Xu, Y. (2024). Satellite-enabled enviromics to enhance crop improvement. *Molecular Plant*, *17*(6), 848-866.

Tolhurst, D. J., Gardunia, B., Gaynor, R. C., Gorjanc, G. y Hickey, J. M. (2022). Genomic selection using random regressions on known and latent environmental covariates. *Theoretical and Applied Genetics*, *135*(10), 3393-3415. https://doi.org/10.1007/s00122-022-04186-w.

Vargas, M., Crossa, J., Ramírez, M. E., Sayre, K. y van Eeuwijk, F. A. (1999). Using Partial Least Squares Regression, Factorial Regression, and AMMI Models for Interpreting Genotype × Environment Interaction. *Crop Science*, *39*(4), 955-967. https://doi.org/10.2135/cropsci1999.0011183X003900040002x

Yan, W., Hunt, L. A., Sheng, Q. y Szlavnics, Z. (2000). Cultivar evaluation and mega-environment investigation based on the GGE biplot. *Crop Science*, *40*(3), 597-605. https://doi.org/10.2135/cropsci2000.403597x

Yan, W. y Tinker, N. A. (2006). Biplot analysis of multi-environment trial data: Principles and applications. *Canadian Journal of Plant Science*, 86(3), 623-645. https://doi.org/10.4141/P05-169

Zakharova, N. N. y Zakharov, N. G. (2024). Wheat grain production in the world and its dynamics. E3S Web of Conferences. 480. 10.1051/e3sconf/202448003001.

Zhao, C., Liu, B., Piao, S., Wang, X., Lobell, D., Huang, Y., Huang, M., Yao, Y., Bassu, S., Ciais, P., Durand, J. -L., Elliott, J., Ewert, F., Janssens, I., Li, T., Lin, E., Liu, Q., Martre, P., Müller, C. y Asseng, S. (2017). Temperature increase reduces global yields of major crops in four independent estimates. *Proceedings of the National Academy of Sciences*, *114*(35), 9326-9331 201701762.10.1073/pnas.1701762114.