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Envirotyping to Drive Spring Barley Adaptation in Northwestern Europe

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Abstract

Context: Cereal crops are highly vulnerable to extreme climatic events. Due to the restricted genetic diversity within the existing elite germplasm used in modern breeding, developing high-yielding and stable cultivars in the context of climate change requires deciphering genotype x environment interactions (GEI), commonly observed in multi-environment trials (METs).

Objectives: Our study on two-row spring barley, an economically important short-cycle crop, aimed to (i) highlight the main environmental covariates (EC) – climatic variables calculated over phenological stages – driving GEI for yield, and (ii)characterize genotypes' adaptation across the European spring malting barley production area.

Methods: Using data from 112elite genotypes across 121 environments (from 2015 to 2022), 91 EC were calculated for each environment using the calibrated CERES-Barley model and analyzed for their contribution to GEI. An environmental classification was conducted on the main GEI-drivers across1450environments, including tested and untested locations, within the production area.

Results: Elevated temperatures during barley stem elongation, as well as solar radiation intensity and water accessibility during grain filling, were identified as the major GEI-drivers. Thermal amplitude around anthesis also emerged as an influential factor. The analysis discriminated three environment types (ET) across the European Target Population of Environments (TPE), distributed according to clear spatial and repeatability variations. They contrasted mainly in terms of temperatures during vegetative growth, solar radiation intensity, and water availability during grain filling. Specific (suited to one ET) or broad adaptation (multi-ET) were identified for the tested genotypes, offering valuable information for characterizing germplasm performance and optimizing selection criteria.

Conclusion: We showed how controlling GEI-drivers through envirotyping enhanced year-to-year field trial predictability, selection intensity, and yield genetic gain and stability. Further advancements will need to integrate the genetic sensitivity to GEI-drivers into genomic selection methods toimprove accuracy in modern cereal breeding.

Keywords

Barley, Crop modeling, Ecophysiology, Genotype x environment interactions, Plant breeding, Target population of environments

1. Introduction

Adapting crops to the climate and climate instability is crucial to ensure food security. Global surface temperatures from 2011 to 2020 were 1.09◦C higher than in 1850–1900, and this warming has accelerated over the past two decades (IPCC, 2023). Extreme weather events, associated with year-to-year climatic variability, are challenging the production stability and quality of major crops, including cereals (Trnka et al., 2014; Webber et al., 2018; Xie et al., 2018; Vogel et al., 2019). Breeding efforts are being made to develop stable cultivars that outperform the existing germplasm under evolving biotic and abiotic stress conditions (Touzy et al., 2019; Snowdon, 2021; Raina et al., 2022; Cooper et al., 2023). However, genetic gain can be strongly compromised by genotype x environment interactions (GEI) effects observed in multi-environment trials (MET), which can have a stronger influence on total plant productivity than the genotype alone (Voltas et al., 2002; Mohamed, 2013; Solonechnyi et al., 2015; Katsenios et al., 2021; Fekadu et al., 2023). While breeding has been key for crop adaptation to changing climatic factors, the rapid evolution of these factors poses significant challenges. Understanding GEI is crucial to minimizing their impact in breeding programs and ensuring the success of future efforts in variable and unpredictable environments.

Crop models are powerful tools for exploring GEI in major crops such as wheat, maize, or soybean (Chenu et al., 2017; Messina et al., 2009; Schoving et al., 2020). These models can enhance our understanding of the environmental regulation of plant physiology and its impact on growth and development (Chapman, 2008). The strategy relies on simulating crop development in each tested environment across MET, calculating a large set of environmental covariates (EC) throughout the crop cycle from recorded weather data, and detecting the main GEI sources through multivariate analysis (Chenu et al., 2013; Heslot et al., 2014; Rincent et al., 2019; Costa-Neto et al., 2021; Bustos-Korts et al., 2022; Elmerich et al., 2023). This approach provides a detailed characterization of the environments in which cultivars develop and grow. Envirotyping involves characterizing the environmental conditions crops are exposed to for the definition of mega-environments, which can be established based on several indicators: geographic, stress indices, variations in yield and agronomic

traits, or a combination of these (Chapman et al., 2000; Windhausen et al., 2012; Crespo-Herrera et al., 2021; Bustos-Korts et al., 2022; Vitale et al., 2024; Corlouer et al., 2024). Envirotyping is necessary to define the Target Population of Environments (TPE), focusing on mapping out the mega-environments. Based on GEI-drivers, it would minimize GEI and help breeders select cultivars adapted to the European environment types (ET) (Cooper and Messina, 2021). Using such environmental classification, trials can be contextualized and weighted through the MET-TPE alignment to better evaluate cultivar performance across the TPE (Podlich et al., 1999) and guide future crosses.

For most crop species, cultivars are known to be either adapted to one prevalent climatic scenario (i.e., specific adaptation) or to a wide range of environments (i.e., broad adaptation). Deploying genotypes that match environmental patterns detected across the TPE is essential for optimizing crop adaptation. Spring crops are especially vulnerable to climate change due to their short growth cycles, which limit their ability to recover from the adverse effects of increasingly frequent extreme climatic events such as drought that can be counterbalanced in winter crop with a deeper root system (Olesen et al., 2011). It is imperative to explore their sensitivity to climate to improve their resilience and adaptation. Spring malting barley is a major spring crop, understudied in ecophysiology, widely cultivated worldwide under various pedoclimatic contexts. Modern spring malting barley shows limited genetic variability, making it important to identify the sources of GEI to enhance resilience against extreme climatic events (Laidig et al., 2017). The main drivers of relative yield performance for spring barley genotypes are not identified and prioritized. To the best of our knowledge, no envirotyping approach has been dedicated to malting spring barley in Europe where specific and/or broad adaptation patterns can be expected across this large production area.

The aim of this study is to improve our knowledge of two-row spring malting barley across the European production area, specifically to (i) highlight the main environmental covariates (EC) during each growth stage driving GEI for yield and (ii) characterize the nature and distribution of environment types (ET) to further explore adaptation zones and genotypic performance.

2. Materials and method

2.1. Multi-environment trials

Grain yield from 60 two-row malting spring barley breeding lines and 52 reference cultivars grown over the spring-summer season in 121 environments (location x year) from 2015 to 2022 were obtained from the multi-environment trials (MET) network of SECOBRA Recherches (https://secobra.fr/en/accueil). The trials were distributed across Northern and Western Europe, including seven countries: Czech Re- public, Denmark, France, Germany, Sweden, the United Kingdom (En- gland and Scotland) and Ireland (Table S1). For trials without replication information, the adjusted genotype means were used. When replication data was available, adjusted means were calculated by considering replication as a random effect.

2.2. Weather and soil data

Daily weather data, interpolated on a grid of 25 km x 25 km, were extracted from the JRS-MARS Meteorological database (https://agri4cast.jrc.ec.europa.eu/), including minimum and maximum temperatures (°C), total precipitation (mm day^{-1}), and total global ra- diation (MJ m^2 day^{-1}). For each location, the closest weather station (< 13 km) was used. Soil parameters at each location were obtained from the European Soil Database (ESDB) using a 1 km x 1 km grid (https://esdac.jrc.ec.europa.eu/). Data extracted included clay (%), silt (%), and sand (%) content,gravel content (%), bulk density (g cm^{-3}), and rooting depth (cm).

2.3. Environmental covariates calculation and genotype x environment interactions analysis

The CERES-Barley model, part of the Decision Support System for Agrotechnology Transfer (DSSAT v4.8), was calibrated to simulate the phenology of two reference cultivars (cv. RGT Planet and cv. Laureate) that represented the variation in phenology among existing spring barley germplasm

(Table S2, Table S3) (Jones et al., 2003; Hoogenboom et al., 2019). Field experiments (nine environments) were conducted in 2022 to calibrate the model for five critical growth stages: first leaf through coleoptile (Z11), head at 1 cm (Z30), half of the head emerged – heading – (Z55), early milk (Z73), and physiological maturity (Z90) (Zadoks et al., 1974). Cultivar coefficients were manually adjusted to maximize the Willmott index of agreement (d-stat) (Willmott et al., 2012) and minimize the root-mean-square error (RMSE) (Willmott et al., 1985). Model validation was performed on the MET network database (see Section 2.1), where phenology data were available (38 % of the dataset), providing an RMSE <4 days for heading and physiological maturity dates. The validated model was then used to simulate the phenology of cv. RGT Planet and cv. Laureate in the 121 environments. Daily weather data, soil properties (see Section 2.2), and management practices (sowing dates and irrigation scenarios) were used as the minimum data input (Hunt and Boote, 1998). Due to the small variations in simulated phenology between the two cultivars (< three days for heading and four days for physiological maturity), the average simulated phenology (number of days after sowing) was used to calculate a set of 138 environmental covariates (EC) – climatic variables calculated over specific phenophases (growth periods between two stages in the crop cycle – in each environment. The crop cycle was divided into six phenophases: Sowing to Emergence (SO-EM), Emergence to Head at 1 cm (EM-1CM), Head at 1 cm to Heading (1CM-HD), Heading to Anthesis (HD-AN), Anthesis to beginning Grain Filling (AN-GF), and beginning of Grain Filling to Physiological Maturity (GF-PM). For each phenophase, 18 climatic variables related to daily precipitation, temperature, and solar radiation were calculated. Additionally, five EC calculated by the model were considered: water stress factor, top layer soil moisture, potential evapotranspiration (ETP), soil moisture, and soil temperature. The water stress factor calculation was based on the maximum root water uptake to atmospheric water demand ratio (Jones et al., 2003). The water stress ranges from 0 to 1, where 0 indicates no stress and 1 indicates maximum stress. Potential ETP was simulated using the default Priestley–Taylor method, which uses net daily solar radiation and temperature (Ritchie, 1998). The model used soil and plant canopy albedo to compute daily soil evaporation and plant transpiration. From the 138 EC, 91 were retained for the analysis to avoid strong autocorrelations.

Partial Least Squares (PLS) regressions were performed to detect the most relevant EC driving genotype x environment interactions (GEI) across the MET. PLS regression is a robust and commonly used statistical method to predict a response variable (Y-table) from a set of explanatory variables (X-matrix) in agronomy (Crossa et al., 2010). Orthogonal factors, called latent variables, with the best predictive values are extracted from the X-matrix. This method is suitable when the number of explanatory variables exceeds the number of observations in the Y-table and when multicollinearity is observed in the X-matrix (Abdi, 2010). Another advantage of this type of analysis over linear factor regression is the ability to evaluate several covariables, allowing for the integration of as many environmental variables as possible, thereby limiting a priori statements about which factors to include in the analysis. Variable se- lection methods were employed, accepting that the X-matrix can contain redundant or irrelevant variables without impacting the results (Mehmood et al., 2012). A total of 15 PLS analyses were performed: eight single-year PLS and seven double-year PLS (Table S4). For single-year analyses, only genotypes repeated across all environments of that year were used. For the two-year analyses, genotypes present in all environments across both years were included in the analysis (Table S4). The number of components was defined based on the Wold algorithm (Wold et al., 1984, 1987, 2001; Tenenhaus et al., 2005). The Variable Importance in Projection (VIP) scores were used to select variables driving GEI. Two VIP scores were calculated for each EC, based on the average VIPs from the single-year PLS analyses and the double-year PLS analyses. Variables with an average VIP score > 1 were considered.

2.4. Definition of the Target Population of Environments

Defining the Target Population of Environments (TPE) requires identifying, through a clustering method, a set of climatic scenarios at the MET scale, called environment types (ET) to classify each environ- ment (i.e., location x year) (Chapman et al., 2000; Crespo-Herrera et al., 2021; Elmerich et al., 2023). To cover the European malting spring barley cropping area, 120 locations were added to the initial MET database (Fig. 1). At each location, daily weather data from the period of 2013–2022, soil

properties extracted from the ESDB (see Section 2.2),and sowing dates were used as inputs to simulate spring barley phenology for cv. RGT Planet and cv. Laureate across the 1450 envi- ronments. An average phenology was used to calculate the 91 EC in each environment (see Section 2.3). For environments where the sowing date was not available, the nearest date was assigned based on the initial MET and national official trials.

Using the 35 yield GEI-drivers obtained from the method detailed in Section 2.3, combinations of 6–12 EC were tested for the best clustering model. This range of parameters appears reasonable for achieving a parsimonious model (Corlouer et al., 2019; Schoving et al., 2020; Elmerich et al., 2023).

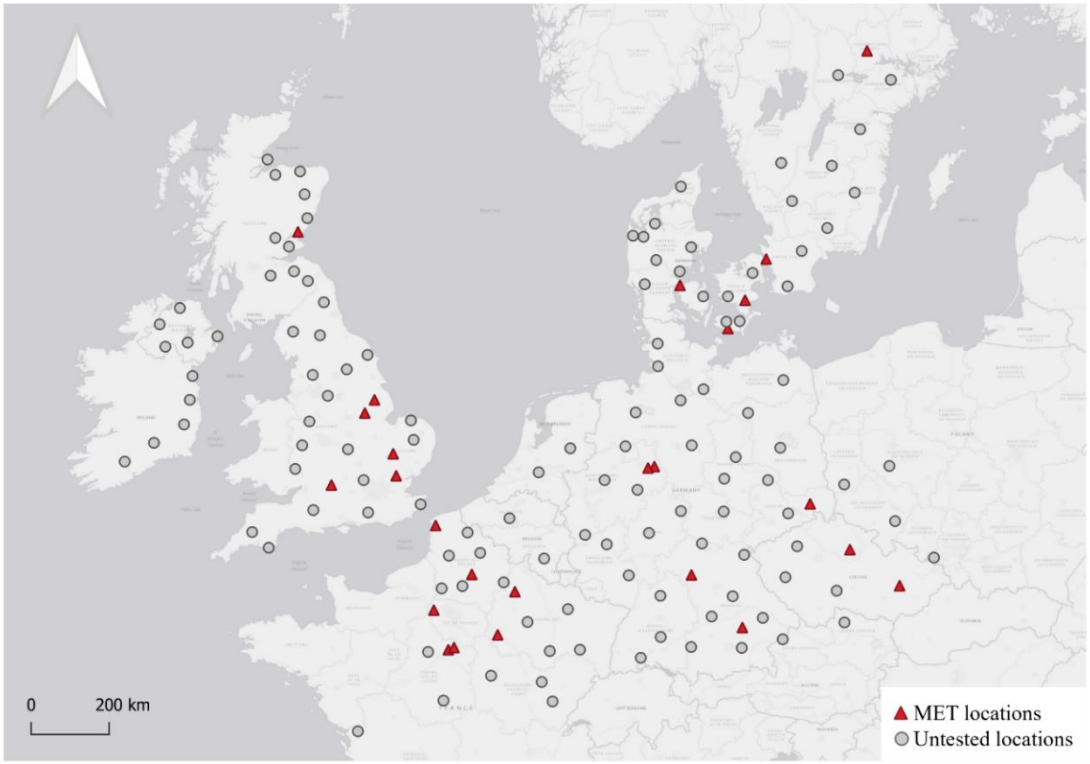
A hierarchical clustering was conducted based on the Euclidean distance using the hclust package (R software v4.2.1) to aggregate the 35 EC into n groups, where $n \in [6; 12]$ (Ward, 1963). All combinations of EC, encompassing one EC from each group, were tested, resulting in a total of 13,440 combinations of six EC, 26,880 of seven EC, 38,440 of eight EC, 46,080 of nine EC, 46,080 of 10 EC, 23,040 of 11 EC, and 15, 360 of 12 EC.

For each combination, a K-means clustering analysis was performed on the 1450 environments using the nbclust package (R software v4.2.1). The Euclidean distance and complete linkage method were employed to minimize within-cluster variance and ensure that the clusters formed were well separated. This process detected a set of ET encountered across the TPE for each model.

To choose the most parsimonious set of ET, each K-means model was fitted on observed yield data for the genotypes tested at least three times in each cluster. The performance of each clustering model was assessed using the method published by Elmerich et al. (2023). This method evaluates each clustering model based on: (i) the significance of the genotype x cluster interaction, which indicates variation in relative performance across ET; (ii) the percentage of significant genotype x cluster interactions (G×C), ensuring that the interaction involves multiple genotypes; and (iii) the ability to explain the genotype x cluster effect from the set of n EC.

After the envirotypes identification based on a subset of environ- mental covariates (ECs), a separate and independent analysis was per- formed to finely characterize each ET. For this, the full set of 91

ECs was used to test the effect of each EC on the ETs using an ANOVA. A Tukey test was conducted



to compare the means of ET when a significant effect was observed (p-value < 0.05).

Fig. 1. Distribution of the 145 selected locations used to define the Target Population of Environments (TPE) for two-row malting spring barley across Northern and Western Europe. The red triangles represent locations tested for yield, constituting the initial Multi-Environment Trials (MET). The gray dots represent untested locations for yield, added to create a continuum across the geographical area of two-row malting spring barley production.

2.5. *Genotype plus genotype by block of environments biplot*

The Genotype plus Genotype by Block of Environments (GGB) biplot graphically displays genotype performances and mega-environment identification in MET. It includes the two main principal components (PC1 and PC2) obtained from a Principal Component Analysis on a matrix centered on the environment, with genotype-by-environment data grouped by ET. The GGB biplot allows for the visualization of the genotype means in each block of environments. Genotype performances can be

analyzed by projecting a line from the biplot origin to the marker for the ET. Genotypes can then be ordered based on their projections on the ET axis, reflecting their performance in environments representative of this ET. In this study, the ET were defined as ET-1, ET-2, and ET-3. Herein, the GGB biplot was constructed based on the 2022 PLS analysis data including grain yield evaluated for 25 genotypes across 17 environments (Table S4) using the gge package in R software (v4.2.1) (Laffont et al., 2013).

2.6. Evaluation of envirotypes relevance in the Target Population of Environments

Two linear mixed models were used to analyze grain yield variance in the whole dataset and assess the relevance of the identified envirotypes in capturing GEI.

The first linear mixed model (Model 1) used as a baseline was defined as:

$$Y\,ij\; = \mu + G_i + E_j\; + e_{ij}\;\text{ with } G_i\; \sim \mathrm{N}(0, \mathrm{I}\sigma^2{}_G), E_j\; \sim \mathrm{N}(0, \mathrm{I}\sigma^2{}_E)\; and\; e_{ij} \sim N(0, \mathrm{I}\sigma^2{}_e)\;(1)$$

Where Y_{ij} is the observed yield for genotype i in environment j, μ is the overall mean, G_i is the random effect of genotype i, E_j is the random effect of environment j and e_{ij} is the residual error term.

The second linear mixed model (Model 2) extended Model 1 by incorporating a fixed envirotype effect and a random genotypes * envirotypes effect:

$$Y\,ijk\; = \mu +\; ET_k +\; G_i + E_{j(k)} + (GxET)_{ik}\; + e_{ijk}\text{ with } G_i\; \sim \mathrm{N}(0, \mathrm{I}\sigma^2{}_G), E_j\; \sim \mathrm{N}(0, \mathrm{I}\sigma^2{}_E),$$

$$(GxET)_{ik} \sim \mathrm{N}(0, \mathrm{I}\sigma^2{}_{GxET})\; and\; e_{ijk} \sim N(0, \mathrm{I}\sigma^2{}_e)\;(2)$$

Where Y_{ijk} is the observed yield for genotype i in environment j and envirotype k, μ is the overall mean, ET_k is the fixed effect of envirotype k, G_i is the same as before, $\mathrm{E}_{j(k)}$ the random effect of environment j nested within ET k, $(Gx\mathrm{ET})_{ik}$ is the random interaction effect between genotype i and envirotype k, e_{ijk} is the residual error term.

The variance partitioning was obtained by ReML, and the Akaike Information Criterion (AIC) was obtained using maximum likelihood.

3. Results

3.1. Main environmental covariates explaining yield genotype x environment interactions

For genotype x location interactions (*i.e.*, single-year analysis), 81% of the selected climatic variables were distributed over two critical phenophases: Head at 1 cm to Heading (1CM-HD) and beginning Grain Filling to Physiological Maturity (GF-PM) (Table 1). Genotype x location x year interactions (i.e., double-year analysis) were explained by the phenophases from 1CM to PM, with a major contribution from the 1CM- HD and GF-PM phenophases, accounting for 33 % and 29 % of the selected climatic variables, respectively (Table 1).

During the 1CM-HD phenophase, temperature-related variables, such as daily average and maximum temperatures, were the most significant contributing factors to GEI. Thresholds of 15◦C for average temperature and 7◦C and 15◦C for minimum temperature impacted GEI during this phenophase. Temperature also emerged as a critical variable during the GF-PM phenophase, particularly maximum temperature, with the number of days exceeding 25◦C and 30◦C. This phenophase was also highly influenced by all solar radiation variables. In both analyses, water stress and ETP during GF-PM contributed to GEI. In double-year analyses, thermal amplitude emerged as the most explanatory variable during the HD to GF phases.

Table 1. Main environmental covariates (EC) impacting genotype x environment interactions for yield. (a) Frequency of phenological stage intervals and (b) distribution of the main variables. Fifteen variables were selected after PLS regression analysis, based on their average VIP score > 1 in single-year and double-year analyses. Single-year PLS revealed EC impacting genotype x location interactions, while double-year PLS revealed EC impacting genotype x location x year interactions. The six phenological intervals were: Sowing to Emergence (SO-EM), Emergence to Head at 1 cm (EM-1CM), Head at 1 cm to Heading (1CM-HD), Heading to Anthesis (HD-AN), Anthesis to beginning Grain Filling (AN-GF), beginning Grain Filling to Physiological Maturity (GF-PM).

		Sowing (SO)	Emergence (EM)	Head 1 cm (1CM)	Heading (HD)	Anthesis (AN)	Grain Filling (GF)	Physiological Maturity (PM)
	☐ Genotype x Location (1 year PLS analysis)	0%	14%	38%	5%	0%	43%	
	■ Genotype x Location x Year (2 years PLS analysis)	0%	0%	33%	24%	14%	29%	
DURATION	Duration			☐ ■				
TEMPERATURE	Average daily temperature			☐ ■	■		☐	
	Thermal amplitude		☐		■	■		
	Number of days below 15°C			☐ ■				
MINIMUM TEMPERATURE	Average minimum temperature				■		■	
	Number of days below 7°C			☐ ■				
	Number of days below 15°C			☐ ■			☐	
MAXIMUM TEMPERATURE	Average maximum temperature		☐	☐ ■	☐ ■	■	☐ ■	
	Number of days above 25°C			☐			☐	
	Number of days above 30°C						■	
RADIATION	Average daily solar radiation			☐			☐	
	Cumulative solar radiation						☐ ■	
	Photothermal quotient		☐	■	■		☐	
WATER	Cumulative potential evapotranspiration						☐ ■	
	Water stress factor					■	☐ ■	

3.2. Three main environment types for two-row malting spring barley in Northwestern Europe

A total of 209,280 clustering models were tested on observed grain yield. Each model used a unique combination of EC identified as major GEI drivers (Table 1). The best clustering model, constructed using 11 EC, was selected based on the criteria detailed in Section 2.4. It was fitted on 28 genotypes. In this model, 2 % of the yield variance was explained by the genotype, 2 % by the G×C effect, and the combination of EC used in this clustering model explained 25 % of the G×C effect.

Three clusters were defined according to the thermal amplitude from Emergence to Head at 1 cm (EM-1CM), the photothermal quotient during EM-1CM, the number of days above 25◦C from 1CM-HD, the number of days under 15◦C during 1CM-HD, the photothermal quotient from Heading to Anthesis (HD-AN), the average temperature from HD to AN, the thermal amplitude from Anthesis to beginning Grain Filling (AN-GF), the average daily solar radiation from GF-PM, the number of days under 15◦C during GF-PM, the water stress factor during AN-GF, and the minimum temperature during GF-PM (Fig. 2)

Environment types (ET) were characterized by the set of 91 EC if a significant difference was observed (p-value < 0.05) (Table 2). The first envirotype (ET-1), referred to as “maritime,” was characterized by the coolest temperatures throughout the crop cycle with long phenophases. No thermal amplitude was observed at early stages and at anthesis (AN) (below 7◦C and 8◦C, respectively). No heat stress was recorded from 1CM-HD and from GF-PM (number of days below 15◦C during 1CM-HD > 24 and above 25◦C during GF-PM < 3). ET-1 had the lowest solar radiation levels (e.g, 16 MJ m-² day during GF-PM). Elevated precipitation was recorded at early stages and post-AN, resulting in no water stress during EM-1CM and GF-PM (water stress factor < 0.1). The second envirotype (ET-2), referred to as “temperate,” had similarities with ET-1, with cool temperatures during pre-emergence and vegetative stages (number of days below 7◦C during SO-EM > 9). There was low thermal amplitude and no heat stress during 1CM-HD and GF-PM (number of days below 15◦C during 1CM-HD > 18 and above 25◦C during GF-PM < 9). ET-2 differed from ET-1 due to elevated temperatures during GF-PM and high solar radiation levels throughout the cycle (e.g., 19 MJ m-² day during GF-PM). Water stress was observed during EM-1CM and post-AN (water stress

factor > 0.4). The third envirotype (ET-3), referred to as "continental," emerged as the most stressed environment. It had elevated temperatures from sowing to physiological maturity, resulting in short phenophases. There was high thermal amplitude during early stages and at AN (above 11◦C and 12◦C, respectively). Heat stress was recorded during 1CM-HD and GF-PM (number of days below 15◦C during 1CM-HD < 12 and above 25◦C during GF-PM > 13). This was the ET with the highest solar radiation levels throughout the cycle (e.g., 21 MJ m^{-2} day during GF-PM). ET-3 had the lowest precipitation levels, resulting in water stress during the EM-1CM phenophase and post-AN stages (water stress > 0.4).

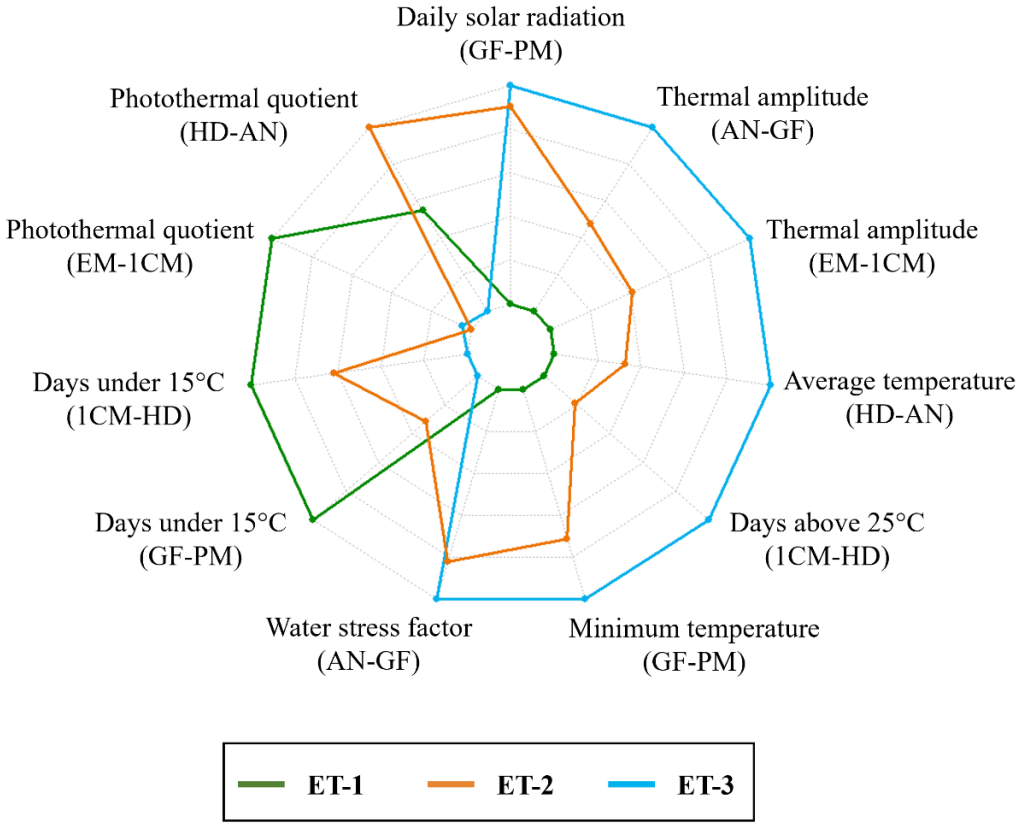


Fig. 2. Characterization of the three environment types (ET) by the 11 environmental covariates used for clustering. The phenophases are indicated in parentheses with the following stages: Sowing to Emergence (SO-EM), Emergence to Head at 1 cm (EM-1CM), Head at 1 cm to Heading (, 1CM-HD), Heading to Anthesis (HD-AN), Anthesis to beginning Grain Filling (AN-GF), beginning Grain Filling to Physiological Maturity (GF-PM). The inner and outer circles represent the minimum and maximum values for each eco-climatic factor, respectively. The colors indicate the envirotype: green for the first envirotype (ET-1), orange for the second envirotype (ET-2) and blue for the third envirotype (ET-3).

312 **Table 2. Description of the three environment types (ET) identified by clustering.** Yellow and blue shading correspond to the highest and lowest means of
313 environmental covariates (EC), respectively. The EC written in bold correspond to those used for the K-means clustering.

	Variables	SOWING EMERGENCE	EMERGENCE HEAD AT 1CM	HEAD AT 1CM HEADING	HEADING ANTHESIS	ANTHESIS GRAIN FILLING	GRAIN FILLING PHYSIOLOGICAL MATURITY	*Overview*
ET-1 ***MARITIME***	Duration						Long phase	*Cool temperatures during vegative stages, at anthesis and during grain filling. No thermal amplitude, no heat stress during stem elongation and grain filling. Low solar radiation. No water stress at emergence and grain filling.*
	Temperature min	Night temperature & TMIN < 7°C		TMIN < 7°C & **TMIN < 15°C**		Minimum temperature	Minimum temperature **TMIN < 15°C**	
	Temperature avg	Average tempertaure	TAVG < 15°C	TAVG < 15°C		**Average temperature**	Average temperature	
	Temperature max	Maximum temperature		**TMAX > 25°C**		Maximum temperature	Maximum temperature & TMAX > 25°C	
	Temperature ampl	Thermal amplitude	**Thermal amplitude**			**Thermal amplitude**		
	Radiation		Daily solar radiation	Daily solar radiation	Daily solar radiation	Daily solar radiation & **PTQ**	**Daily solar radiation**	
	Water	Precipitation	Water stress & ETP			Precipitation **Water stress**	Water stress	
	Soil	Soil temperature						
ET-2 ***TEMPERATE***	Duration	Long phase						*Cool temperatures during vegative stages, at anthesis but elevated during grain filling. No thermal amplitude, no heat stress during stem elongation. High solar radiation. Water stress at emergence and grain filling.*
	Temperature min	TMIN < 7°C					**Minimum temperature**	
	Temperature avg	Average temperature & TAVG < 7°C					Average temperature	
	Temperature max	Maximum temperature		**TMAX > 25°C**			Maximum temperature	
	Temperature ampl	Thermal amplitude				**Thermal amplitude**		
	Radiation		Daily solar radiation		PTQ	Daily solar radiation & **PTQ**	**Daily solar radiation**	
	Water	Precipitation	Water stress & ETP			**Water stress** & ETP	Water stress	
	Soil	Soil temperature						
ET-3 ***CONTINENTAL***	Duration	Short phase					Short phase	*Elevated temperatures during végative stages, at anthesis and during grain filling. Thermal amplitude, heat stress during stem elongation and grain filling. High solar radiation. High water stress at emergence and grain filling.*
	Temperature min	Night temperatures & TMIN < 7°C		TMIN < 7°C & **TMIN < 15°C**		Minimum temperature	Minimum temperature **TMIN < 15°C**	
	Temperature avg	Average temperature & TAVG < 7°C	TAVG < 15°C	TAVG < 15°C		**Average temperature**	Average temperature	
	Temperature max	Maximum temperature		**TMAX > 25°C**		Maximum temperature	Maximum temperature & TMAX > 25°C	
	Temperature ampl	Thermal amplitude	**Thermal amplitude**			**Thermal amplitude**		
	Radiation		Daily solar radiation	Daily solar radiation	Daily solar radiation PTQ	Daily solar radiation **PTQ**	**Daily solar radiation**	
	Water	Precipitation	Water stress & ETP			Precipitation **Water stress**	Water stress	
	Soil	Soil temperature						

3.3. Definition of the European Target Population of Environments for the two-row malting spring barley

Fig. 3 displays the frequencies in time and space of ET across the European two-row malting spring barley production area over the past ten years. The "continental" type (ET-3) was the most frequently recorded, accounting for 40 % of the encountered climatic scenarios. The "maritime" type (ET-1) was the least frequent, with a frequency of 25 %, while the "temperate" type (ET-2) appeared at 30 %. The distribution of these three environmental types differed across regions. There is a gradient in the ET distribution from Northwest to Southeast. In the Northwest, the "maritime" type was the most recorded (i.e., Scotland and Ireland), while the "continental" type was characteristic of the Southeast (i.e., Germany, Czech Republic, and Poland). Across the central geographic area, the "temperate" type was the most detected. Strong repeatability of the ET occurrences was observed in Ireland and Scotland, where ET-1 accounted for 90–100 % of the scenarios over the past 10 years. Some sites had an equal frequency between two ETs, as in Germany, where almost all locations were either ET-2 or ET-3. In contrast, low repeatability was observed in Northern France, where all ETs were recorded. Despite the proximity of some places, they exhibited different patterns, as seen in central Sweden. Conversely, some distant locations had similar patterns, such as between Germany and Northern Sweden or between Denmark and France.

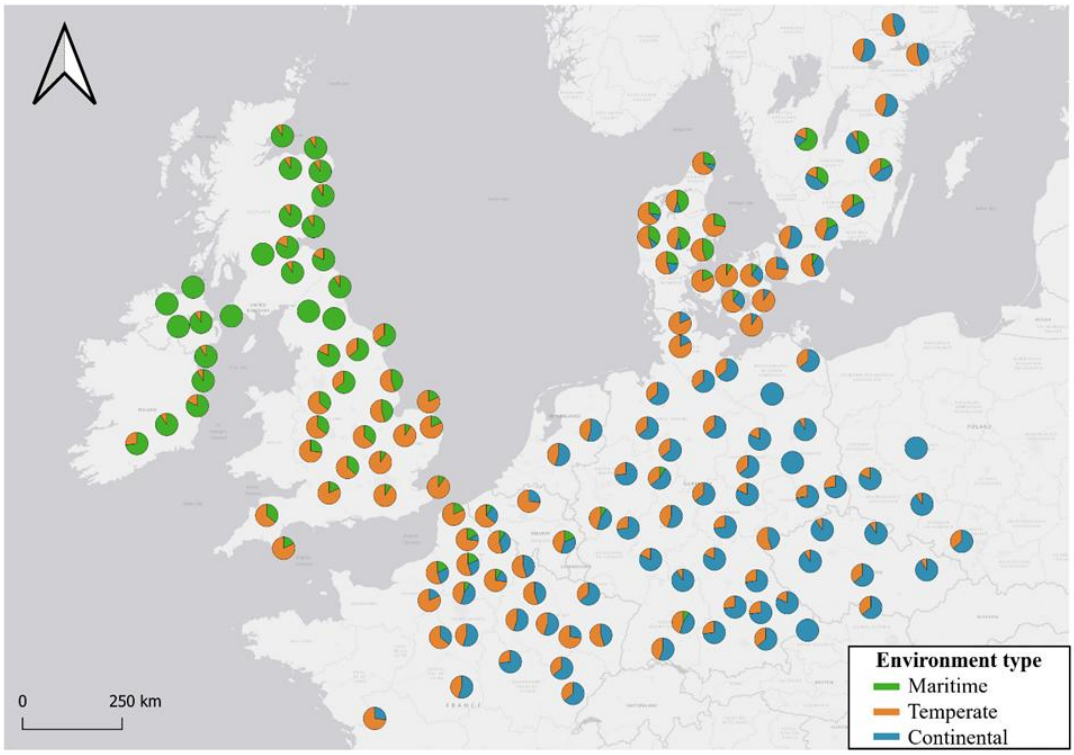


Fig. 3. European Target Population of Environments of the two-row malting spring barley. The environment types (ET) were defined using yield GEI-drivers. The 10- year ET frequency of occurrence was calculated and represented on the map using pie charts. The colors of each pie section indicate the envirotype: green for the first envirotype (ET-1), orange for the second envirotype (ET-2), and blue for the third envirotype (ET-3).

3.4. Genotypic performance variation across environment types

The evaluation of genotype adaptation to the three ET was achieved using a GGB biplot (Fig. 4). The MET was composed of 25 genotypes (GEN1 to GEN25) and 17 environments (e1 to e17) distributed across the three ETs: six environments were “maritime” (ET-1), two were “temperate” (ET-2), and nine were “continental” (ET-3). Some geno- types were strongly associated with a specific ET, such as GEN23, which was one of the highest-yielding genotypes in ET-2. Contrasts in perfor- mance between environments were observed for some genotypes; for example, GEN6 had good performances in ET-2 while low-yielding in ET-1. GEN17 was the most high-yielding genotypes across all ET. GEN15 was the least-yielding genotypes in this MET context.

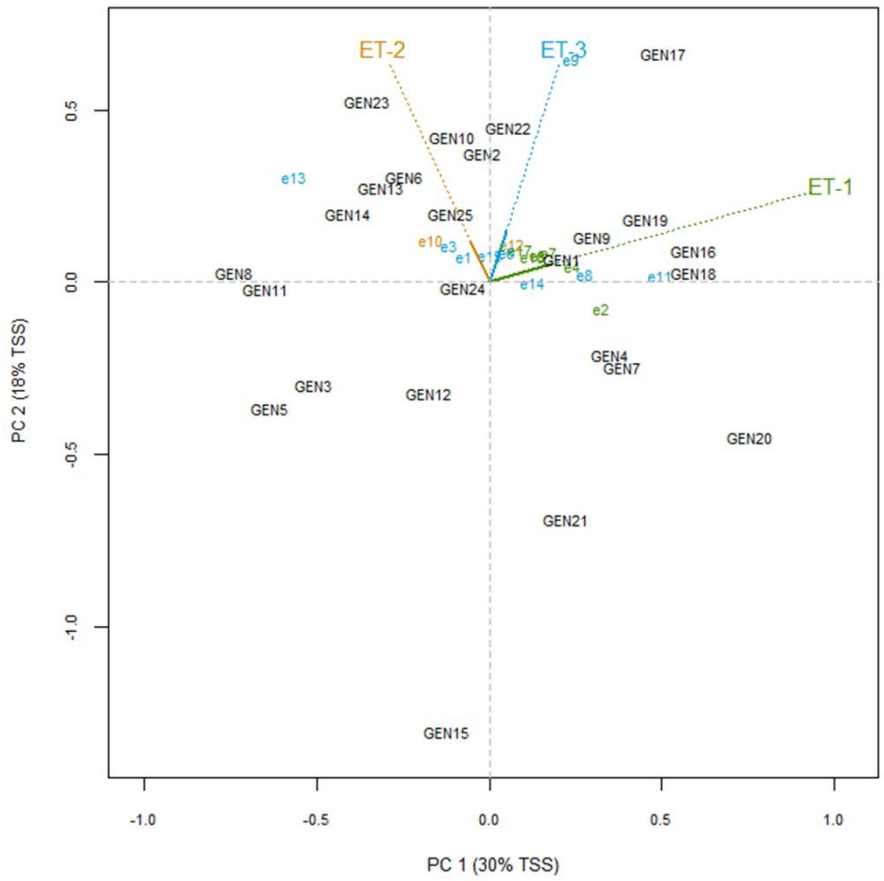


Fig. 4. Genotype plus Genotype by Block of environments biplot illustrating the contrasted performances of genotypes across environment types. The genotypes are annotated from GEN1 to GEN25 and the environments from e1 to e17. The environments are grouped into three ETs (ET-1, ET-2, and ET-3). The colors indicate the envirotype: green for the "maritime" (ET-1), orange for the "temperate" (ET-2) and blue for the "continental" (ET-3).

3.5. Evaluation of envirotypes relevance in the Target Population of Environments

Table 3. Results of the mixed linear models applied on the whole dataset to evaluate the impact of the envirotype and genotypes * envirotypes effects on variance partition and Akaike Information Criterion.

	% variance G	*% variance E*	*% variance GxET*	*% variance Ɛ*	*AIC*
Model 1	1.4	91.0		7.6	15225
Model 2	2.2	89.8	1. 3	6.7	15212

The whole dataset was used to estimate the variance contribution for grain yield of genotypes, environments, envirotypes and genotypes * envirotypes interactions (Table 3). Two linear mixed models were fitted to assess the relevance of the identified ET in capturing GEI. The first model revealed that most of the variance in grain yield was attributed to environments (91 %). The genotype effect accounted for 1.4 % of the total variance and 7.6 % was attributed to the residual error. In the second model incorporating interaction between genotypes and envirotypes, the environment effect remained dominant at 89.8 %, but the variance explained by genotypes increased to 2.2 %. The GxET interaction accounted for 1.3 % and the residual error was reduced to 6.7 % (Table 3). The fixed effect of envirotype in Model 2 was not statistically significant, with a p-value of 0.26. The Akaike Information Criterion (AIC) for Model 1 was 15225. It was slightly lower for Model 2, with a value of 15212.

4. Discussion

4.1. Environmental covariates driving yield genotype x environment interactions differed from those of yield levels

In the European spring barley germplasm, strong genotype x envi- ronment interactions (GEI) are observed despite the poor genetic di- versity (Tondelli et al., 2013). As with other spring crop species, yield variation attributed to GEI often surpasses the genetic effect, requiring the identification of the main yield GEI-drivers to assist breeding in crop adaptation and yield stability (Mwiinga et al., 2020; Katsenios et al., 2021). GxE studies are highly dependent on both the experimental design (MET) and the nature of the genetic material being studied. However, one of the main challenges in GxE analysis is the limited number of repeated genotypes across environments (Table S4) (Crossa et al., 2024). While our study is limited to a specific dataset, it still provides valuable insights that are reflective of what can typically be observed in Western Europe. This study identified 35 environmental covariates (EC) causing interactions for two-row malting spring barley across Western Europe (Table 1). Interestingly, the GEI-drivers contrasted with the yield drivers (Bicard et al., 2025). Yields were

largely determined at early stages, while the late crop cycle was the most sensitive for interactions. Our findings align with previous studies highlighting terminal heat (TMAX > 30◦C) and drought as factors affecting genotype performance during the grain filling period (Voltas et al., 1999; Hakala et al., 2012; Mahalingam, 2017). In Australia, Shirdelmoghanloo et al. (2022) detected differential genetic sensitivity to these factors for yield and the physical characteristics of the grain. Variability in relative yield can be attributed to different stay-green potential and Radiation Use Efficiency capacity, especially in shaded-prone environments (Kamal et al., 2019; Padovan et al., 2020; Shirdelmoghanloo et al., 2022). The detection of potential ETP during grain filling suggests various activity levels among cultivars under stress conditions, as previously observed in other species (Reynolds et al., 2002). The stem elongation period was key in understanding GEI and was influenced by temperature, similar to the impact on yields in some European regions (Bicard et al., 2025). Pre-heading minimum temperature and thermal time have already proven to be the main GEI-drivers for yield in wheat (Sanchez-Garcia et al., 2012). Elevated temperatures can lead to rapid spike growth, inadequate assimilate availability, and variability in cultivar yield (Barnaba´s et al., 2007; Ugarte et al., 2007). While AN was poorly detected in explaining yields in Europe, it was relevant for interactions and sensitive to temperature. At heading and AN, temperature proved to affect stomatal conductance, transpiration, respiration, and consequently photosynthetic activity, with different responses across cultivars (Hakala et al., 2012; Mahalingam and Bregitzer, 2019). Elevated temperatures can induce a shorter phase, reducing nutrient capture in cultivars. The identification of GEI-drivers provides more detailed knowledge of germplasm and its environmental response to guide initial breeding decisions and germplasm advancement. The perspective to assist breeding programs is to unravel the genetic architecture of traits involved in barley adaptation to climate (Corlouer et al., 2024). Our results confirm that breeding decision-making, if based solely on yield drivers, overlooks both cultivar stability and outperforming sources.

Our study revealed contrasted responses of genotypes despite the limited genetic pool (Tondelli et al., 2013) and provides a basis for a better understanding of crop adaptation and its implications in breeding. The identification of GEI-drivers demonstrated the importance of considering phenological

traits for the climate adaptation of crop species (Le Gouis et al., 2020; Le Roux et al., 2024). Herein, AN emerged as a key period to explain long-term stability in breeding and was confirmed to be a critical stage for barley's adaptation to various environments (Porker et al., 2020; Slafer and Savin, 2023). It is adjusted by the duration of stem elongation, which was highlighted as a major GEI-driver and can be strongly manipulated through breeding (Mirosavljevic et al., 2019). Flowering-time genes influence both the timing and duration of internode elongation (Huang, 2024). It has been demonstrated that Ppd-h1, a photoperiod response gene regulating environmental adaptation by adjusting flowering time, integrates environmental signals to modify developmental timing by influencing the number of spikelets initiated on the main shoot (Gol et al., 2021). Our study revealed that the relative performances of genotypes are influenced by a complexity of EC that can be used for environmental classification to guide selection strategies for yield stability and barley adaptation in the context of climate change.

4.2. Envirotyping to highlight contrasting spring barley adaptation zones

This first envirotyping approach in spring barley allowed for the identification of three contrasting envirotypes across Europe. The latter were mainly discriminated by 11 key GEI-drivers and presented distinct patterns of thermal, water, and light stress (Fig. 2). The definition of the TPE revealed heterogeneities in the distribution and occurrence of the different ETs, suggesting specific and broad adaptation zones (Bustos-Korts et al., 2022) (Fig. 3). In some regions, there is a predominance of one specific ET over the last 10 years. Such was the case in Scotland with the "maritime" envirotype. In contrast, in other European regions such as Denmark and France, the crop was exposed to a more complex pattern of climatic scenarios with low ET repeatability. Specific adaptation is characterized by high-yielding cultivars in a single ET. In contrast, broad adaptation results in high performance across all ETs and is stable in the TPE. One hypothesis could be the breeding history: programs based in regions with low ET repeatability advanced stable genetic material, while in regions with high ET repeatability, breeders designed genotypes with specific adaptations. Contrasts in ET occurrence across Europe suggest adjusting the breeding strategy and exploiting existing germplasm to adapt the crop to local climate conditions (Chenu et al., 2011; Elmerich et al., 2023). In regions with high

repeatability of one ET, developing high-yielding cultivars particularly adapted to this ET is crucial to maximize yield levels. By contrast, when heterogeneity in ET distribution is observed, there is a need to design cultivars with broad adaptation. Cultivars as GEN17 that suited to a multi-ET context appear to be very interesting for ensuring yield stability across the European spring barley TPE, especially in locations with significant year-to-year weather variation. The perspective is to design resilient ideotypes adapted to the ET (Martre et al., 2015).

Interestingly, the definition of the TPE can be used to generate a better design of the MET for yield evaluation. Our results showed that to develop material with specific adaptation for an ET such as the "maritime" or "continental" type, genotypes need to be tested in the UK or in Germany. To advance broadly adapted materials, yield must be assessed in regions such as Denmark or France. To achieve efficient selection for both specific and broad adaptation, the MET must be a representative sample of the TPE (Van Eeuwijk et al., 2016). The conventional and naive selection strategies evaluate a genotype based on average performances across the trial network, and when the MET diverges from the TPE, selection efficiency is reduced. MET-TPE alignment can be achieved by weighting trial results based on the ET frequencies within the targeted breeding area (Podlich et al., 1999; Costa-Neto et al., 2023). This method enables consistent germplasm selection aligned with the TPE, even in contrasted climatic years. Breeding will thus be directed toward the TPE. The envirotypes should remain stable as defined on the germplasm, but their distribution may evolve with climate change and consequently influence the definition of the TPE for breeding.

The presence of GEI is known to reduce yield heritability and limit genetic gain highlighting the importance of understanding the molecular basis of GEI and considering them in yield predictions (Touzy et al., 2019; Cooper and Messina, 2021; Crossa et al., 2021; Corlouer et al., 2024). The variance partition validates the efficiency of our clustering approach to capture GEI (Table 3).The introduction of a GxET interaction effect indeed resulted in the reduction of the residual variance of Model 1, that included GEI. Moreover, the introduction of GxET also increased the amount of genetic variance, highlighting the better relevance of Model 2, confirmed by its lower AIC. The difference of AIC between the two models was modest, probably because the environment effect already captured

around 90 % in both models. Nevertheless, the GxET interaction effect had a variance that was more than half of the main genetic effect, illustrating its relative importance. Note that the fixed ET effect was not significant, meaning that despite the presence of GxET interactions, the average yield was not different from one ET to another. Creating homogeneous groups with similar performances would increase yield heritability (Araújo et al., 2024). The ET definition offers the possibility to enhance genomic selection models by optimizing the training set by ET. This will be a major step toward the design of ideotypes that outperform the existing germplasm for specific or broad adaptation across the TPE (Semenov et al., 2014).

5. Conclusion

The climatic transition necessitates adapting crops to maintain pro- duction levels. Exploring genotype x environment interactions (GEI) at a large scale is a crucial step to develop high-yielding and stable cultivars under a changing climate. This study investigated the GEI ecophysiology of spring malting barley across Northwestern Europe using an original approach that limits assumptions. Temperature during stem elongation and drought during grain filling were the main GEI yield drivers. Defining the Target Population of Environment (TPE) revealed three contrasting environment types (ET) that minimize GEI in terms of temperature, drought, and radiation levels. Their frequency of occur- rence in time and space over the past 10 years showed significant het- erogeneity. Evaluating the performance of the existing germplasm across the TPE has improved knowledge on spring crop climate adap- tation by revealing malting spring barley cultivars with broad or specific adaptation. Defining the TPE will guide breeding strategies to design ideotypes and help breeders with cultivar positioning in the market. This method can be deployed for other species and other quantitative traits, such as quality traits. For further advancement in breeding, it is neces- sary to integrate the environmental covariates (EC) driving GEI into genomic selection models to improve data predictability.

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782 Data availability

783 The data that has been used is confidential.