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## Unravelling critical climatic factors and phenological stages impacting spring barley yields across Europe

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## 12 **Abstract**

13 Yield is a complex trait reflecting the interaction between genotype, environment and farm  
14 management. The challenge of adapting spring crops to climate change involves unravelling the  
15 contribution of climatic factors that impact yield performance according to phenological stages. The  
16 aim of the present study was to identify the main Environmental Covariates (EC) – climatic variables  
17 calculated over phenological stages – driving spring barley yield levels. Five contrasting European  
18 agro-climatic (AC) regions were defined as follows: United Kingdom and Ireland (UK-IE), Denmark  
19 and Sweden (DK-SE), France (FR), Northeast Germany, Czech Republic and Poland (N. E. DE-CZ-  
20 PL) and South Germany and Austria (S. DE-AT). Yield data from 270 two-row spring barley  
21 accessions/varieties, grown in 125 environments between 2015 and 2021, were collected from a multi-  
22 environment trials network. Using the phenology-calibrated CERES-Barley model (DSSAT), 91 ECs  
23 were calculated in each environment based on collected weather data and simulated phenological  
24 stages. Partial Least Squares (PLS) regression analyses were carried out to sort out the main ECs  
25 impacting yield performance in each of the five AC regions. Results showed that elevated  
26 temperatures and solar radiation were the main yield-drivers in all AC regions. Associations between  
27 water availability and yield were detected in most AC regions. The strongest contrasts were observed  
28 for the critical phenological stages during pre-anthesis, which govern grain number per unit area. Cool  
29 temperatures (days with minimum temperature  $<0^{\circ}\text{C}$  or  $<7^{\circ}\text{C}$  and average temperature  $<15^{\circ}\text{C}$ ) during  
30 emergence and tillering, and solar radiation intensity between emergence and grain filling, were the  
31 most yield contributing ECs. This study showed the importance of considering climate during early  
32 stages to predict yields. The identification of major yields EC drivers suggests the need to adjust  
33 agricultural practices in spring barley production across Europe for climate adaptation. This study  
34 unraveled the complexity of yield ecophysiology affecting spring barley in Europe. In order to  
35 improve the adaptation of spring barley to climate change, the perspective is to examine the role of  
36 ECs on genotype x environment interactions for yield and develop stable cultivars that outperform  
37 existing germplasm.

## 38 **Keywords**



## 40 1. Introduction

41

42 Agriculture is subject to a major climatic transition which accelerated over the last 20 years. Global  
43 average temperature in the period 2011–2020 increased to 1.1°C above the pre-industrial level and is  
44 projected to reach +1.5°C in the near-term (2021–2040) (IPCC 2022). Future climate scenarios predict  
45 a decrease in agricultural production, mainly due to crop response to heat, drought episodes and  
46 extreme weather events (Trnka et al., 2014; Asseng et al., 2015; Xie et al., 2018). Global warming will  
47 putatively lead to redistribution of crop-growing regions and the need to adapt agricultural practices  
48 (e.g., modification of sowing dates and cultivar choices). Heat stress during spring, summer and  
49 meteorological extremes increased in most European regions making short-cycle spring crops highly  
50 sensitive to climate change (Deryng et al., 2014; Ray et al., 2015; Ceglár et al., 2019; Bras et al.,  
51 2021).

52 Future climate projections are expected to introduce uncertainty and an increase in yield variability  
53 (Trnka et al., 2011; Eitzinger et al., 2013; Rötter et al., 2013; Cammarano et al., 2019). To secure  
54 yields and optimize cultural practices, it is crucial to understand the impact of climate on crop yields.

55 Wheat

56 and maize have been frequently used as models to evaluate the influence of climatic factors on cereal  
57 yields. Heat and drought are considered to be the main yields-climatic drivers during the growing  
58 season (Lobell and Ortiz-Monasterio, 2007; Lobell and Field, 2007; Troy et al., 2015; Lesk et al.,  
59 2016; Zampieri et al. 2017; Webber et al., 2018; Vogel et al., 2019; Zeleke et al., 2023). Predictions  
60 indicate a decrease in maize yields, mostly due to hotter and drier conditions during the summer  
61 (Eitzinger et al., 2013). Anthesis and grain filling emerged as sensitive stages regarding heat and  
62 drought (Peltonen-Sainio et al., 2010; Kahiluoto et al., 2019). Lüttger and Feike (2018) have  
63 demonstrated that yield penalties can be observed when temperatures rise above 25°C during these  
64 stages. Temperature above 25°C could induce shorter crop development reducing incident radiation  
65 capture (Miralles et al., 2021). During the reproductive development, temperature above 30°C impact  
66 fertility (Abiko et al., 2005; Jacott and Boden, 2020; Callens et al., 2023).

67 Spring barley is a cereal crop that is suitable to explore the effect of climate on yield. It is distributed  
68 worldwide and cultivated under contrasting agro-climatic conditions, with a short cycle, lending  
69 vulnerability to climate change (Newton et al., 2011). Anthesis is known as a key stage in the crop's  
70 adaptation to the environment (Porker et al., 2020; Cammarano et al., 2021). Studies in other spring  
71 barley growing regions focused on specific growth stages and individual climatic variables related the  
72 period around anthesis as critical for radiation and temperature (Arisnabarreta et al., 2008a; García et  
73 al., 2015, García et al., 2018). Crop modeling combined with observed yields across a wide agro-  
74 climatic gradient revealed that pre-anthesis temperature and water stress influenced yields, with  
75 contrasting effects across different regions in Australia (Dreccer et al., 2018). European studies  
76 indicate yields decrease due to high temperatures throughout the crop cycle and water deficits during  
77 early growth stages (Peltonen-Sainio et al., 2010, 2011; Hakala et al., 2012). While these studies  
78 provide valuable knowledge, the complexity of yield determination involves several climatic factors,  
79 and their relative contribution is not defined. Studies focusing on the effects of climate on yields were  
80 based on pre-defined factors and evaluated their effect individually. To optimize production, there is a  
81 need to define and prioritize the main climatic drivers and decisive phenological stages of spring  
82 barley yields in Europe. This knowledge will be transposable to other growing areas with similar  
83 climatic conditions, supporting crop diversification in other regions. It will help anticipate and  
84 optimize agricultural practices to maximize yields under changing climate conditions. To the best of  
85 our knowledge, no study in the Northern Hemisphere has confronted spring barley yields grown in  
86 spring-summer season to a wide range of environmental covariates across the entire crop cycle using  
87 crop modeling over a broad agro-climatic gradient. Few studies focus on the very early growth stages,  
88 and key stages and variables are not clearly prioritized.

89 The major challenge in identifying the causes of yield variability, i.e., the main yield-drivers and key  
90 phenological stages, is to adequately characterize the crop environment. Crop models handle this  
91 challenge by simulating plant development time and growth, influenced by environmental factors, in  
92 daily steps. They can be used as tools to improve our knowledge of the environmental regulation of  
93 plant physiology and its effect on growth, development and yield (Chenu et al., 2017). Some studies

94 use modelling to project the impact of climate change on yields (Cammarano et al., 2019; Feng et al.,  
95 2019; Appiah et al., 2023). To understand yield ecophysiology and genotype x environment  
96 interaction (GEI), some approaches associate climatic factors with phenological stages simulated by  
97 crop models to obtain environmental covariates (EC) (Heslot et al., 2014; Dreccer et al., 2018; Rincent  
98 et al., 2019; Elmerich et al., 2023). ECs are climatic variables associated with critical developmental  
99 periods (phenophases). They precisely describe the impact of climatic conditions on the physiological  
100 processes that drive yields. Applying this method to spring barley, the ecophysiology of which has  
101 been poorly studied can be relevant to characterize climatic scenarios driving yields. Explaining the  
102 relationship between yields and climate on a large scale is difficult due to the heterogeneity of weather  
103 scenarios. Determining how climate influences yields within and across regions can provide a better  
104 perspective on the influence of climate change on barley production in Europe (Olesen et al., 2011;  
105 Trnka et al., 2011).

106 The aim of this study was to highlight the critical climatic variables and development stages – referred  
107 as environmental covariates (EC) – driving spring barley levels across Europe from multi-environment  
108 trials and crop model simulation.

109

## 110 **2. Materials and methods**

### 111 *2.1. Yield data and multi-environment trials*

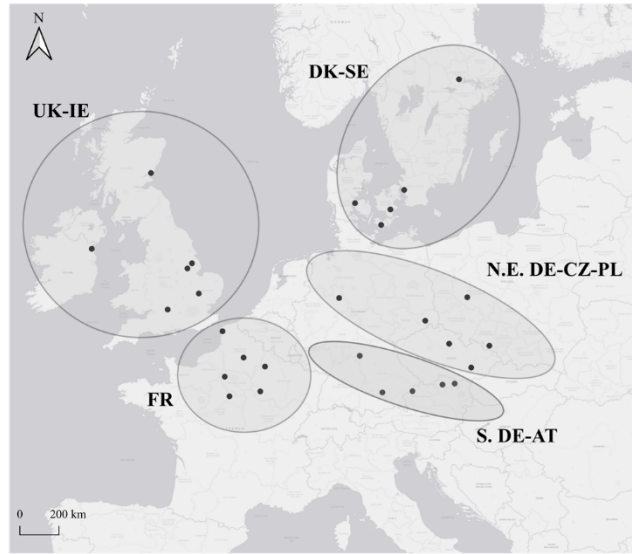
112

113 Grain yields of 161 two-row spring barley breeding lines and 109 reference cultivars, grown during  
114 the spring-summer season in 125 environments (location x year) from 2015 to 2021, were obtained  
115 from the multi-environment trial network of SECOBRA (<https://secobra.fr/en/accueil>). Sowing  
116 occurred in spring after the main cold period, with days lengthening from the time of sowing. The  
117 development cycle extended over five months from sowing to harvest. Trials were distributed across  
118 Western and Northern Europe including ten different countries: Austria, Czech Republic, Denmark,  
119 France, Germany, Ireland, Poland, Sweden and the United Kingdom (England and Scotland) (Table

120 S1, Table S3). The study focused on the European regional analysis of climatic factors affecting  
121 critical phenological stages for yield. Based on one-way ANOVAs, the database was subdivided into  
122 five agro-climatic regions that contrasted in monthly precipitation, temperature, and solar radiation on  
123 the historical period over three developmental phases. The first phase started at sowing (Z00) and  
124 ended at heading (Z55), the second one from heading to beginning grain filling (Z73) and the last one  
125 from beginning grain filling to physiological maturity (Z90). (Fig. 1). This subdivision represented the  
126 optimal grouping scenario, minimizing the error of Partial Least Squares regressions (PLS) while  
127 capturing the greatest climatic variability for yield. A linear regression was performed to characterize  
128 the tendency of annual yields in each agro-climatic region (Table S2).

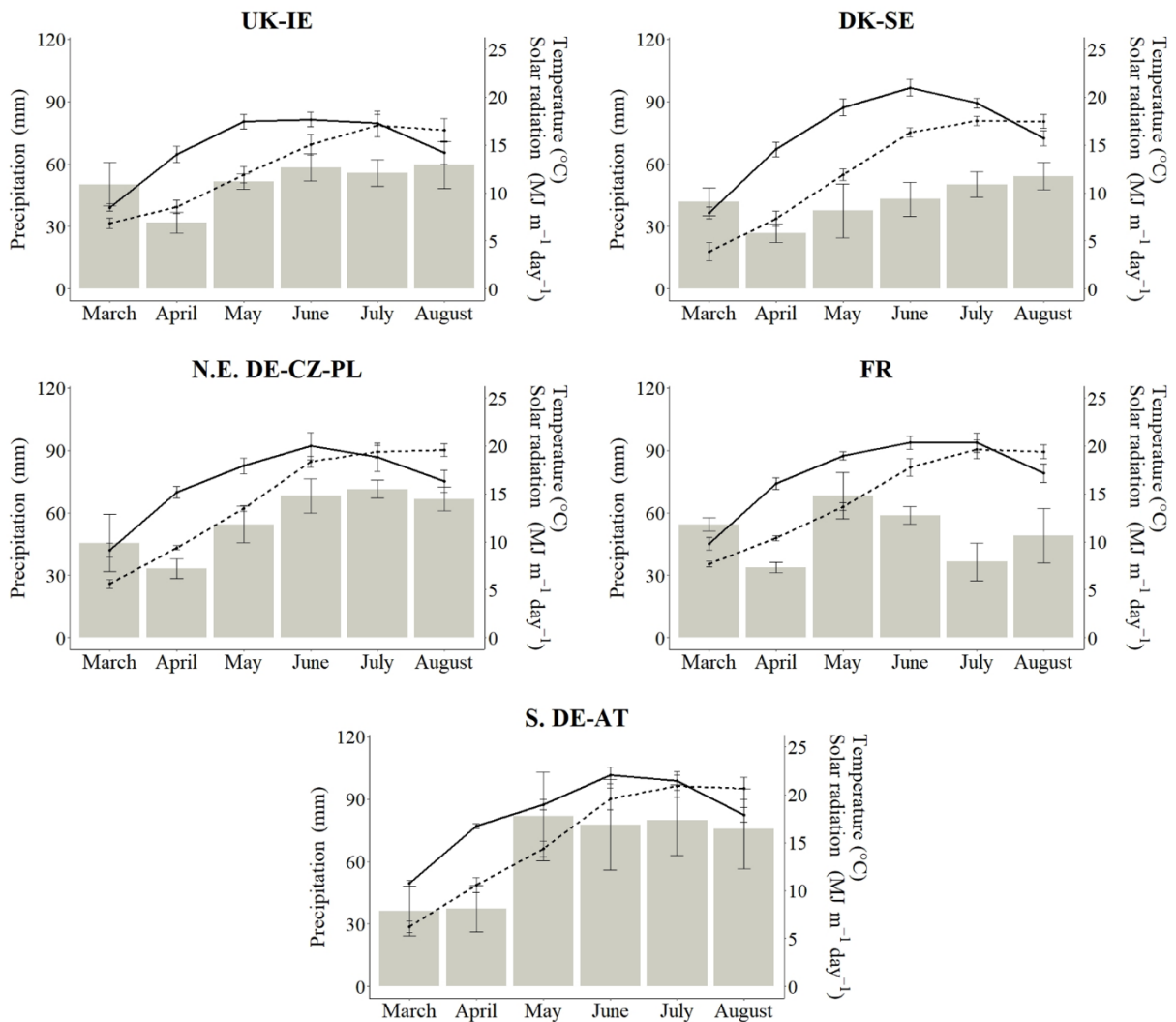


(a)



(b)

■ Cumulative precipitation (mm)    — Solar radiation ( $\text{MJ m}^{-1} \text{day}^{-1}$ )    - - Temperature ( $^{\circ}\text{C}$ )



130 **Fig. 1. Geographic distribution and meteorological characteristics of five European agro-**  
131 **climatic regions.** (a) Division of the seven-year MET locations across five European agro-climatic  
132 regions: United-Kingdom and Ireland (UK-IE), France (FR), Denmark and Sweden (DK-SE),  
133 Northeast Germany, Czech Republic and Poland (N.E. DE-CZ-PL), South Germany and Austria (S.  
134 DE-AT). Each point corresponds to a multi-year trial location. (b) Ombrothermic diagrams of the five  
135 agro-climatic regions combining monthly means of cumulative precipitations, temperature and solar  
136 radiation during the plant developmental cycle.

137

## 138 2.2. *Weather and soil data*

139

140 Daily weather data, interpolated on a grid of 25 km x 25 km, were extracted from the JRC-MARS  
141 meteorological database (<https://agri4cast.jrc.ec.europa.eu/>). It included minimum and maximum  
142 temperatures (°C), sum of precipitations (mm day<sup>-1</sup>) and total solar radiation (MJ mm<sup>-1</sup> day<sup>-1</sup>). For  
143 each location, the closest weather station was used (<13 km). Soil parameters at each location were  
144 obtained from the European Soil Database (ESDB) using a 1 km x 1 km grid  
145 (<https://esdac.jrc.ec.europa.eu/>). Data extracted were clay content (%), silt content (%), sand content  
146 (%), gravel content (%), bulk density (g cm<sup>-3</sup>) and rooting depth (cm) (Table S4)

147

## 148 2.3. *Crop modeling and environmental covariates calculation*

149

150 The CERES-Barley model – *Decision Support System for Agrotechnology Transfer* (DSSAT v4.8) –  
151 was used to simulate the phenology of two reference cultivars (cv. RGT Planet and cv. Laureate) that  
152 represented well the slight variations in phenology among the existing spring barley germplasm (Table  
153 S5, Table S6) (Jones et al., 2003; Hoogenboom et al., 2019). Field experiments (9 environments) were  
154 conducted in 2022 to calibrate the model for five critical growth stages: first leaf through coleoptile  
155 (Z11), head at 1 cm (Z30), half of head emerged – heading – (Z55), early milk (Z73) and physiological  
156 maturity (Z90) (Zadoks et al., 1974). Cultivar coefficients were manually adjusted to maximize the

157 Willmott index of agreement (d-stat) value (Willmott et al., 2012) and minimize the root-mean-square  
158 error (RMSE) (Willmott et al., 1985). Model validation was performed on the multi-environment trial  
159 network database (see Section 2.1), where phenology data were available (38 % of the dataset),  
160 providing a RMSE < 4 days for heading and physiological maturity dates.

161 The validated model was used to simulate the phenology of cv. '*RGT Planet*' and cv. '*Laureate*' in 125  
162 environments. Daily weather data, soil properties (see section 2.2.2) and management practices  
163 (sowing dates and irrigation scenarios) were used as minimum data input (Hunt and Boote, 1998). Due  
164 to low variations in simulated phenology between the two cultivars (< 3 days for heading and 4 days  
165 for physiological maturity in all AC), an average phenology (number of days after sowing) was  
166 considered to calculate a set of 138 environmental covariates (EC) in each environment.  
167 Environmental covariates are climatic variables calculated over specific phenophases (growth periods  
168 from the crop cycle) (Schoving et al., 2020; Elmerich et al., 2023). Herein, the crop cycle was divided  
169 into six phenophases: Sowing to Emergence (SO-EM), Emergence to Head at 1 cm (EM-1CM), Head  
170 at 1 cm to Heading (1CM-HD), Heading to Anthesis (HD-AN), Anthesis to beginning Grain Filling  
171 (AN-GF) and beginning Grain Filling to Physiological Maturity (GF-PM). For each phenophase, 18  
172 climatic variables related to daily precipitations, temperature, and solar radiation were calculated.  
173 Additionally, five ECs calculated by the model were considered: water stress factor, top layer soil  
174 moisture, potential evapotranspiration, soil humidity and soil temperature. Water stress factor  
175 calculation is based on the maximum root water uptake to atmospheric water demand ratio (Jones et  
176 al., 2003). Potential evapotranspiration is simulated by the default Priestley-Taylor method using the  
177 net daily solar radiation and temperature (Ritchie, 1998). The model uses soil and plant canopy albedo  
178 to compute daily soil evaporation and plant transpiration. From the 138 climatic variables, 91 were  
179 kept for the analysis to avoid strong autocorrelations.

180

#### 181 *2.4. Partial Least Squares regressions*

182

183 Partial Least Squares regression (PLS) is a robust and commonly used statistical method to predict a  
184 response variable (Y-table) from a set of explanatory variables (X-matrix) in agronomy (Crossa et al.,  
185 2010). Orthogonal factors, called (latent variables) with the best predictive values are extracted from  
186 the X-matrix. Such a method is suitable when the number of explanatory variables is higher than the  
187 number of observations in the Y-table and when multicollinearity is observed in the X-matrix (Abdi,  
188 2010). Another advantage of this type of analysis over linear factor regression is the possibility of  
189 evaluating several covariables, allowing the integration of as many environmental variables as  
190 possible, thereby limiting a priori statements on which factors to include in the analysis. Variable  
191 selection methods were used, accepting that the X-matrix can contain redundant or irrelevant variables  
192 without impacting the results (Mehmood et al., 2012). The response variable (Y-table) was the average  
193 spring barley yield at each of the 125 environments, and the explanatory variables (X-matrix) were the  
194 91 ECs. We used the filter method, taking Variable Importance in Projection (VIP) as a selection  
195 criterion (Elmerich et al., 2023). Variables with a VIP >1.5 were considered as being able to explain  
196 spring barley yields. The number of components was defined using the Wold algorithm (Wold et al.,  
197 1984, 1987, 2001; Tenenhaus et al., 2005). Five PLS models were performed: one for each AC region  
198 defined in Section 2.1. Analyses were performed using R software (v 4.0.5).

199

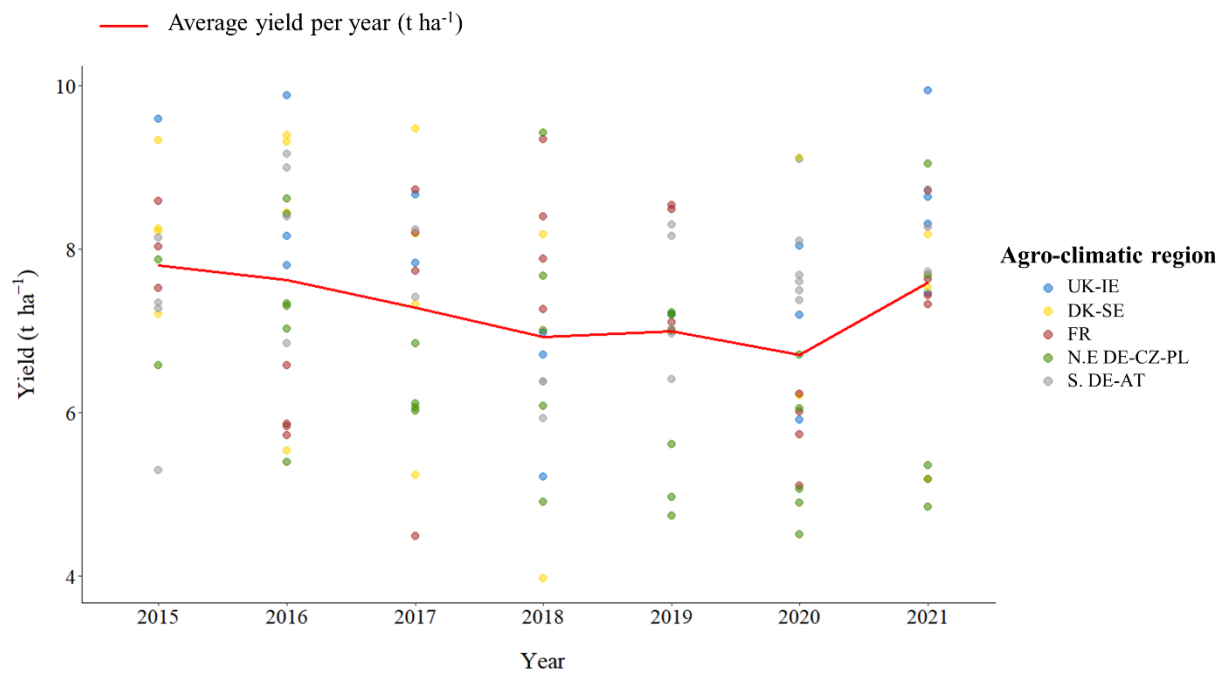
### 200 **3. Results**

#### 201 *3.1. Yield variations within the MET*

202

203 Yield data revealed low inter-annual and raised intra-annual variability (Fig. 2). The lowest average  
204 was observed in 2020 (6.7 t ha<sup>-1</sup>) and the highest in 2015 (7.8 t ha<sup>-1</sup>). Inter-annual variability ranged  
205 between 1 % (2015–2016) and 14 % (2010–2021). The average intraannual yield variability was 18 %.  
206 The lowest inter-location variability (14 %) occurred in 2015, while the figure rose to 22 % in 2018.  
207 No trend was identified within the five agro-climatic-regions throughout the years.

208



209  
 210 **Fig. 2. Average yields per year and yield variability in the Multi-Environment Trials (MET)**  
 211 **locations.** The red line represents the average yield calculated from MET locations from 2015 to 2021.  
 212 Annual yields of MET locations are represented by points distributed around the average. The colors  
 213 discriminate the yields of the agro-climatic region: blue for United-Kingdom and Ireland (UK-IE),  
 214 yellow for Denmark and Sweden (DK-SE), red for France (FR), green for Northeast Germany, Czech  
 215 Republic and Poland (N.E. DE-CZ-PL) and gray for South Germany and Austria (S. DE-AT).

216

### 217 3.2. Phenophases impacting yield levels

218 The critical phenophases for yield differed between agro-climatic regions (AC) (Table 1a). For  
 219 Denmark and Sweden (DK-SE), 60 % of the selected climatic variables were distributed over two  
 220 phenophases: Sowing to Emergence (SO-EM) and Emergence to Head at 1 cm (EM1CM). In United-  
 221 Kingdom and Ireland (UK-IE), the Head at 1 cm to Heading (1CM-HD) phenophase had the most  
 222 impact (56 %). For Northeast Germany, Czech Republic and Poland (N.E. DE-CZ-PL), 82 % of  
 223 selected climatic variables were distributed over two phenophases, from Heading (HD) to beginning  
 224 Grain Filling (GF). In South Germany and Austria (S.DE-AT), 75 % of the selected climatic variables  
 225 were included in the EM-1CM phenophase. In France (FR), climatic variables impacting yield were  
 226 spread over the whole plant cycle (except for the SO-EM phenophase), from Emergence (EM) to  
 227 Physiological Maturity (PM).

228 3.2. *Environmental covariates explaining yield levels*

229 Of the sixteen selected climatic variables, seven were related to temperature (Table 1b). In all AC  
230 regions except FR, elevated minimum temperature during almost all phenophases resulted in yield  
231 penalties. Most notably, this applied to DK-SE, for which yield was negatively impacted by this factor  
232 in four of the six phenophases (Table 1b). In UK-IE, DK-SE and S. DE-AT, high minimum, maximum  
233 and average temperature had a negative effect on yield during SO to HD phenophases (Table 1b). Fig.  
234 3 displays the linear relationship between yields and increasing minimum temperature during the EM-  
235 1CM phenophase ( $R^2 = 0.31$ ,  $P < 0.001$ ). Additionally, temperature thresholds during the EM-1CM  
236 phenophase emerged as ECs explaining the yield for these AC regions. Number of days with an  
237 average temperature below 15°C positively impacted yield for S. DE-AT and a minimum temperature  
238 below 0°C or 7°C had a positive impact on yield for S. DE-AT, DK-SE and UK-IE regions (Table 1b).  
239 Thermal amplitude during HD-AN phenophase was an EC driving yield, with a negative effect for FR  
240 and positive effect for N.E. DE-CZ-PL. Thermal amplitude was negatively related to yield during  
241 1CM-HD for UK-IE (Table 1b). During GF-PM, an average temperature threshold of 15°C had a  
242 negative effect on yield in FR and S.DE-AT (Table 1b).

243 Two solar radiation variables and the photothermal quotient (PTQ) – the ratio of radiation and average  
244 temperature – were selected for all AC regions but the phenophases involved were different. Yield was  
245 enhanced by high radiation during the EM-1CM phenophase in S. DE-AT, during the 1CM-HD and  
246 GF-PM phenophase in FR, during the HD-AN phenophase in UK-IE and during HD-GF phenophases  
247 in N.E. DE-CZ-PL (Table 1b). For these four regions, a high PTQ positively impacted yield during  
248 these phenophases. ECs linked to elevated level and cumul of radiation during HD-AN and AN-GF  
249 were identified to have a negative impact on yield in FR and DK-SE. No effect of radiation during  
250 GF-PM was detected (Fig. 3b).

251 Water variables influenced yield in most AC regions. Three ECs, of which two were simulated, were  
252 found to affect yield. High cumulative precipitations resulted in yield penalties during AN-GF in FR  
253 (Table 1b). In contrast, elevated precipitations and topsoil moisture during the SO-EM and 1CM-HD  
254 had a positive effect on yield in N.E. DE-CZ-PL and UK-IE respectively. Simulated

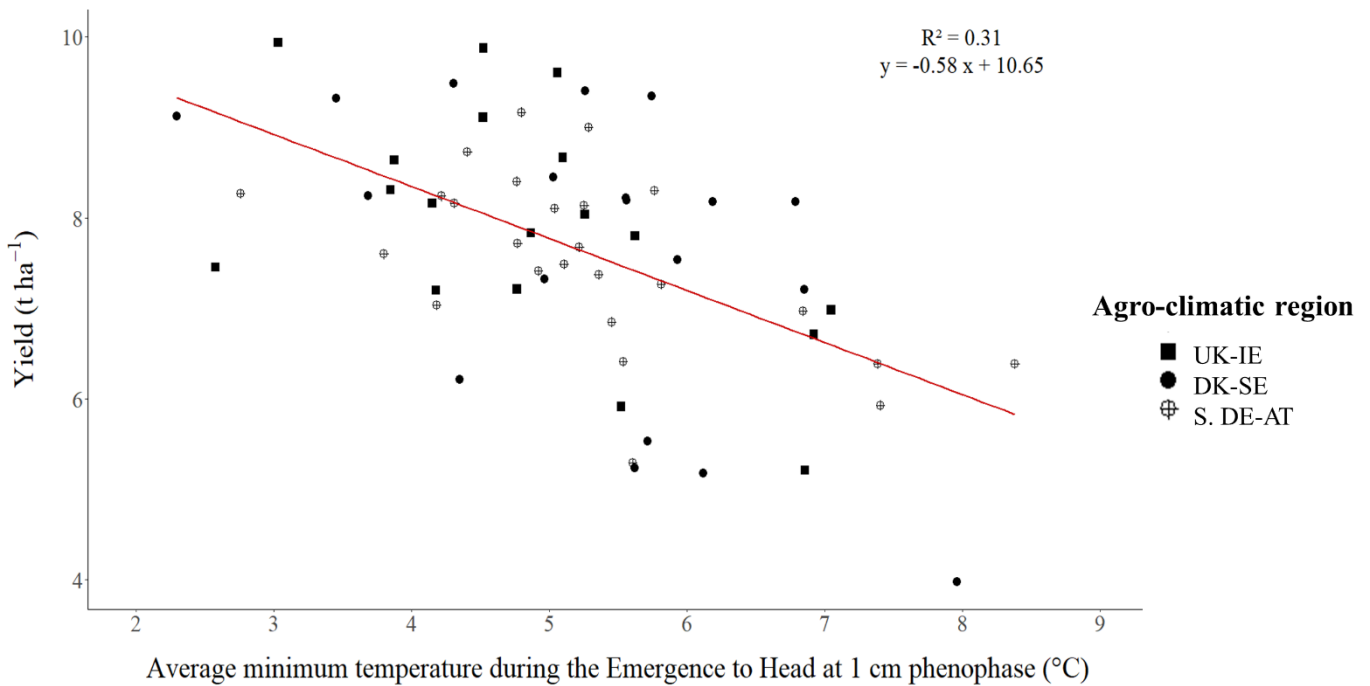
255 evapotranspiration (ETP) was detected as being positive for yield during HD-AN in N.E. DE-CZ-PL  
 256 and as being negative during HD-GF in DK-SE (Table 1b). A high crop model water stress factor  
 257 value resulted in yield losses during EM-1CM phenophase in FR and S. DE-AT (Table 1b). Soil  
 258 temperature, simulated by the crop model was selected as inducing yield losses in DE-SE region  
 259 during the SO-EM phenophase.

260 On the five PLS analyses, only one EC related to the GF-PM phenophase duration and negatively  
 261 impacting yield was selected for FR (Table 1b).

262

263 **Table 1. Main environmental covariates impacting spring barley yields across five European**  
 264 **agro-climatic regions.** (a) Frequency of phenological stages intervals and (b) distribution and effects  
 265 of the main climatic variables. 16 climatic variables were selected after Partial Least Squares (PLS)  
 266 regression analysis, based on their VIP-score > 1.5. The six phenological stages intervals were:  
 267 Sowing to Emergence (SO-EM), Emergence to Head at 1 cm (EM-1CM), Head at 1 cm to Heading  
 268 (1CM-HD), Heading to Anthesis (HD-AN), Anthesis to beginning Grain Filling (AN-GF), beginning  
 269 Grain Filling to Physiological Maturity (GF-PM). Green and red symbols represent positive and  
 270 negative effects, respectively (results of PLS  $\beta$ -regression coefficients). A total of 37 environmental  
 271 covariates (i.e., climatic variables calculated between two phenological stages) were identified for

		Sowing (SO)	Emergence (EM)	Head 1cm (1CM)	Heading (HD)	Anthesis (AN)	Grain Filling (GF)	Physiological Maturity (PM)
<b>(a)</b>								
■ United Kingdom and Ireland (UK-IE)		0%	33%	56%	11%	0%	0%	
● Denmark and Sweden (DK-SE)		40%	20%	0%	10%	20%	10%	
○ France (FR)		0%	10%	10%	30%	10%	40%	
△ North-East Germany, Czech Republic and Poland (N.E. DE-CZ-PL)		18%	0%	0%	55%	27%	0%	
<b>(b)</b>								
⊗ South Germany and Austria (S. DE-AT)		0%	75%	0%	0%	17%	8%	
DURATION								○
SOIL	Average humidity		△	■				
	Average temperature	●						
TEMPERATURE	Average daily temperature	●	■ ⊗	■		△ ⊗		
	Thermal amplitude			■	○ △			
	Number of days below 15°C			⊗				○ ⊗
MINIMUM TEMPERATURE	Average minimum temperature	●	● ■ ⊗		● △	△ ⊗	● ○	
	Number of days below 0°C		● ⊗					
	Number of days below 7°C		■ ⊗					
MAXIMUM TEMPERATURE	Average maximum temperature	●	⊗	■				
RADIATION	Average daily solar radiation				■ ○ △			○
	Cumulative solar radiation		⊗	○	△	●		
	Photothermal quotient		⊗		○ △	△		
WATER	Cumulative precipitation	△		■		○		
	Cumulative potential evapotranspiration				△	●		
	Water stress factor		○ ⊗					



272 their impact on yields (Table S7)

273

274 **Fig. 3. Relationship between observed grain yield and the average minimum temperature from**  
 275 **Emergence to Head at 1cm.** The environments are distributed across United Kingdom and Ireland  
 276 region (n = 21), Denmark and Sweden region (n = 19), South Germany and Austria region (n = 24).  
 277 Yields ranged from 4.0 to 9.9 t ha<sup>-1</sup>. For these three regions, the environmental covariates resulted in a  
 278 VIP score > 1.5 after Partial Least Squares (PLS) regressions performed on yield.

279

280

## 281 4. Discussion

### 282 4.1. Temperature and solar radiation were the main climatic yield-drivers in Europe

283 Large inter- and intra-annual variability in yields was observed within the Multi-Environment Trials  
 284 (MET) (Fig. 2). Results showed that high temperatures were major yield-drivers in Europe, in line  
 285 with Vogel et al. (2019) that also reported the importance of temperature factors in explaining yields  
 286 for several spring crops at large scale. The statistical approach, that strongly limits assumptions,  
 287 highlighted the factors associated with minimum temperature. As detected for several Euro pean  
 288 regions, the detrimental effect of night temperatures on yields, particularly during anthesis, was  
 289 already observed in spring barley in other production areas such as in Argentina, due to shorter



290 development resulted in low incident radiation capture (García et al. 2015; García et al. 2018). Lower  
291 minimum temperature proved to be associated with higher yields in Northern Australia (Dreccer et al.,  
292 2018). Ugarte et al. (2007) demonstrated that temperature can affect grain weight even before anthesis.  
293 The perspective would be to study the impact of temperature on yield components around this period.  
294 In United-Kingdom and Ireland (UK-IE), heat had a deleterious effect on yields during stem  
295 elongation by shortening the duration of the phase resulting in inadequate availability of assimilates  
296 (Barnabas et al., 2007; Ugarte et al., 2007). Herein, yield was highly influenced by temperature during  
297 vegetative stages. For UK-IE, DK-SE and S.DE-AT regions, positive effect of cool temperature on  
298 yield was observed from establishment to tillering. Few studies have been conducted on the  
299 relationship between tillering dynamics and temperature. del Moral and del Moral (1995)  
300 demonstrated that the temperature during tillering was inversely linked to the number of final shoots.  
301 In wheat, warm night proved to increase respiratory activity resulting in less assimilates for growth  
302 (Gimenez et al., 2021). Another study highlighted that high tillering could lead to an increase tiller  
303 mortality rate (Alzueta et al., 2012). In Europe, conditions regarding shading and temperature could be  
304 favorable for maintaining tillers and grains produced (García et al. 2015; Le Roux et al., 2024). A  
305 perspective would be to test under controlled conditions the effect of low temperatures on tillering and  
306 spike establishment in spring barley. Solar radiation and the combination of radiation and temperature  
307 – measured as photothermal quotient (PTQ) – were also essential yield drivers. Arisnabarreta and  
308 Miralles (2008b) established the critical period for barley grain number determination as being  
309 between 40- and 10-days pre-heading and affected by radiation. In other regions such as South  
310 America and Australia, shading at anthesis proved to be critical for yields (Fisher et al., 1995; Sadras,  
311 Dreccer 2015; Liu et al., 2020). In Northern Europe, studies also demonstrated that radiation was a  
312 major factor influencing yield. (Peltonen-Sainio et al., 2010; Trnka et al., 2011; Rötter et al., 2013).  
313 The results of our study are consistent since radiation had a positive effect on yields during active  
314 spike growth for FR and during heading and anthesis for UK-IE and Northeast Germany, Czech  
315 Republic and Poland (N.E. DE-CZ-PL). By affecting spike available assimilates, shading induced a  
316 reduction of fertile florets at anthesis (Arisnabarreta and Miralles, 2008a; Gonzalez ´ et al. 2011).  
317 Results demonstrated that the PTQ was a strong driver of yields for FR and N.E. DE-CZ-PL. They are

318 in line with a previous study that reported a direct and positive relationship between this variable and  
319 grain number, 20 days before and 10 days after anthesis in Spain (Cossani et al., 2009). Critical  
320 developmental phase link seed number to temperature through the PTQ and growth rate during these  
321 periods, highlighted the need to adopt agronomic and breeding approaches to optimize crop yield  
322 under varying thermal and shading conditions (Sadras, Dreccer 2015). Drought is considered to be one  
323 of the main environmental factors that explain yield loss in spring crops (Trnka et al., 2011; Eitzinger  
324 et al., 2013; Troy et al., 2015; Cammarano et al., 2019). Associations between water variables and  
325 yield were detected for most regions although water stress was not identified as having the major  
326 influence on yield. The experimental stations studied are often located in soils with a high water-  
327 holding capacity (see section 2.2.2), reducing the water stress and explaining that it is not the main  
328 yield-driver in this multi-environment trials context. To consider a more accurate determination of  
329 water stress, an evaluation of soil water availability and vapor pressure deficit under contrasting soil  
330 properties may be considered. Our study demonstrates that water-simulated variables can be powerful  
331 yield-level indicators. Previous research shown that water variables simulated by crop modeling  
332 (drought-stress indices, crop transpiration) contribute to improved yield predictions (Feng et al., 2019;  
333 Shahhosseini et al., 2021). In the case of France (FR), the simulated water stress factor during  
334 emergence and tillering emerged as one of the main climatic factors to explain yields. This suggests  
335 that grain number is reduced due to the inhibition of tillering caused by drought (Lipiec et al., 2013;  
336 Rollins et al., 2013). Precipitation and soil water availability, also emerged as a key factor influencing  
337 yield in N.E. DE-AT-CZ-PL and UK-IE, underlying the importance of water for establishment and  
338 stem elongation. Unexpectedly, drought wasn't identified as a major yield-driver during the filling  
339 period. However, soil water availability remains an influential factor during this period, as it emerged  
340 with a VIP score > 1 for DK-SE, UK-IE and N.E DE-CZ-PL and (Table S7). While water may not be  
341 the most important factor, it remains essential for optimizing yields from sowing. The knowledge of  
342 key environmental factors and critical period for spring barley yields in the Western Europe can be  
343 transferred to other production areas and be useful if spring barley expand in northern re gions. These  
344 results will help anticipate climate changes. For instance, some French climates are expected to reflect  
345 future UK climate by 2040, enabling to prepare such evolution in Europe.

346

347

#### 348 *4.2. Crucial development period for yield were associated with population establishment*

349 Although the most important climatic factors influencing yield were largely the same among AC  
350 regions, there were strong regional contrasts in the critical phenological stages for yield. Our results  
351 identified that pre-anthesis stages are decisive and confirmed that yield is primarily explained by the  
352 grain number per unit area (Garcia del Moral et al. 2003; Peltonen-Sainio et al., 2007; Ferrante et al.  
353 2017, Kennedy et al., 2017). In the Southern Hemisphere, with autumn sowing, one critical period is  
354 observed around anthesis (Arisnabarreta et al., 2008; Sadras, Dreccer 2015). Herein, anthesis was one  
355 of the most sensitive periods, as previously demonstrated in different European field studies, and it  
356 explained a large part of the yield levels for N.E. DE-CZ-PL and FR (Hakala et al., 2012; Lüttger and  
357 Feike, 2018). Interestingly, our study highlighted the importance of the vegetative stages for final  
358 yield. Stem elongation has been recognized as being decisive and strongly correlated to grain number  
359 (Mirosavljevic et al. 2019) and was the most climate sensitive for UK-IE. The data revealed that yield  
360 levels were strongly associated with the maximum yield potential setting during emergence and  
361 tillering. Unexpectedly, grain filling was the period least affected by climatic factors. This period has  
362 been identified as being strongly associated with grain weight and sensitive to heat and drought  
363 (Peltonen-Sainio et al., 2010; Rajala et al., 2011; Hakala et al., 2012; Kahiluoto et al., 2019;  
364 Mirosavljevic et al. 2019). Our study did not identify grain filling as crucial in Europe, although this  
365 may change in the future. As a result of climate change, forecasts have indicated strong yield losses  
366 associated with heat and drought during the last phenological stages (Rotter et al., 2013; Trnka et al.,  
367 2014; Cammarano et al., 2019; Feng et al., 2019; Harkness et al., 2020). To adapt to climate change,  
368 several solutions can help maximize yields. Changing agro nomic practices can minimize the adverse  
369 impact of key environmental factors during critical periods and help breeders develop cultivars with  
370 phenological and tolerance characteristics suited to local agro-climatic conditions. In Europe, it will be  
371 necessary to consider whether to advance sowing, risking exposure to new limiting factors, or to  
372 switch to autumn sowing as observed in other production areas and Southern Europe and work on

373 genetics to adapt the germplasm to winter conditions and the higher diseases exposure. Cultural  
374 practices, including genotype selection, should be considered. Breeders are already focusing on  
375 anthesis phenology to adapt cultivar selection to conditions. In Australia, Liu et al. (2020) have shown  
376 that the optimal anthesis period depends on the combination of genotype, sowing date, and  
377 environment, suggesting the need to adapt breeding strategies and management to optimize yields  
378 according to location. There is a variability in genotypic response to environmental factors that also  
379 explains yield variations (Hakala et al., 2012). Explore this varietal gradient and genotype x  
380 environment interactions to optimize yields for specific locations can be a perspective (Cammarano et  
381 al., 2021; Appiah et al., 2023).

382

## 383 **5. Conclusion**

384 Climate change is expected to intensify variability and uncertainty in crop production. To secure yield  
385 and optimize agricultural practices, it is crucial to identify the main yield-drivers, i.e., climatic factors  
386 and critical phenological stages of crops. This study investigated spring barley yield ecophysiology  
387 across Western Europe using an original and unlimited assumption approach. Temperatures and  
388 radiation were the main climatic drivers influencing yields. Major differences were detected in the  
389 critical phenological stages across agro-climatic (AC) regions. In the United Kingdom and Ireland, the  
390 most sensitive period was stem elongation, influenced by average temperature. In Denmark and Swe  
391 den, high temperatures before emergence strongly reduced yield. For Northeast Germany and Eastern  
392 countries, anthesis was highly sensitive to solar radiation and temperature. In South Germany and  
393 Austria, plant establishment and tillering emerged as crucial stages, sensitive to temperature and solar  
394 radiation. In France, yield levels were influenced by precipitation during tillering, as well as  
395 temperature and radiation during anthesis. This study provided insight into improving yield  
396 predictions and optimizing management within different AC regions. Cultivar choice remains a key  
397 factor in compensating for the effect of climate change. Genetic sensitivity to environmental  
398 conditions causing Genotype x Environment interactions (GEIs) needs to be considered as it  
399 represents a significant source of yield variability. The next challenge will be to understand causes of

400 variation in the relative performance of genotypes-GEIs- using the same approach on a large multi-  
401 environment trials network, to help breeders to develop stable cultivars that outperform the existing  
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685 **Fig. 1. Geographic distribution and meteorological characteristics of five European agro-**  
686 **climatic regions.** (a) Division of the seven-year MET locations across five European agro-climatic  
687 regions: United-Kingdom and Ireland (UK-IE), France (FR), Denmark and Sweden (DK-SE),  
688 Northeast Germany, Czech Republic and Poland (N.E. DE-CZ-PL), South Germany and Austria (S.  
689 DE-AT). Each point corresponds to a multi-year trial location. (b) Ombrothermic diagrams of the five  
690 agro-climatic regions combining monthly means of cumulative precipitations, temperature and solar  
691 radiation during the plant developmental cycle.

692

693 **Fig. 2. Average yields per year and yield variability in the Multi-Environment Trials (MET)**  
694 **locations.** The red line represents the average yield calculated from MET locations from 2015 to 2021.  
695 Annual yields of MET locations are represented by points distributed around the average. The colors  
696 discriminate the yields of the agro-climatic region: blue for United-Kingdom and Ireland (UK-IE),  
697 yellow for Denmark and Sweden (DK-SE), red for France (FR), green for Northeast Germany, Czech  
698 Republic and Poland (N.E. DE-CZ-PL) and gray for South Germany and Austria (S. DE-AT).

699

700 **Table 1. Main environmental covariates impacting spring barley yields across five European**  
701 **agro-climatic regions.** (a) Frequency of phenological stages intervals and (b) distribution and effects  
702 of the main climatic variables. 16 climatic variables were selected after Partial Least Squares (PLS)  
703 regression analysis, based on their VIP-score > 1.5. The six phenological stages intervals were: Sowing  
704 to Emergence (SO-EM), Emergence to Head at 1 cm (EM-1CM), Head at 1 cm to Heading (1CM-  
705 HD), Heading to Anthesis (HD-AN), Anthesis to beginning Grain Filling (AN-GF), beginning Grain  
706 Filling to Physiological Maturity (GF-PM). Green and red symbols represent positive and negative  
707 effects, respectively (results of PLS  $\beta$ -regression coefficients). A total of 37 environmental covariates  
708 (i.e., climatic variables calculated between two phenological stages) were identified for their impact on  
709 yields (Table S7).

710 **Fig. 3. Relationship between observed grain yield and the average minimum temperature from**  
711 **Emergence to Head at 1cm.** The environments are distributed across United Kingdom and Ireland  
712 region (n = 21), Denmark and Sweden region (n = 19), South Germany and Austria region (n = 24).  
713 Yields ranged from 4.0 to 9.9 t ha<sup>-1</sup>. For these three regions, the environmental covariates resulted in a  
714 VIP score > 1.5 after Partial Least Squares (PLS) regressions performed on yield.

716 **Table S1. Locations of the Multi-Environment Trials (MET).** Trials were distributed across  
 717 Western and Northern Europe over ten different countries in five agro-climatic (AC) regions: United  
 718 Kingdom and Ireland (UK-IE), Denmark and Sweden (DK-SE), France (FR), Northeast Germany,  
 719 Czech Republic and Poland (N.E. DE-CZ-PL) and South Germany and Austria (S. DE-AT).

Country	Site	Agro-climatic region	Latitude	Longitude
United-Kingdom	Angus	UK-IE	56.51	-2.74
United-Kingdom	Benniworth	UK-IE	53.31	-0.21
United-Kingdom	Boothby Graffoe	UK-IE	53.12	-0.49
United-Kingdom	Dunmow	UK-IE	51.88	0.40
United-Kingdom	Fulbourn	UK-IE	52.18	0.21
United-Kingdom	Wanborough	UK-IE	51.57	-1.71
Ireland	Cluide	UK-IE	53.84	-6.39
Denmark	Holleby	DK-SE	54.70	11.45
Denmark	Middelfart	DK-SE	55.47	9.84
Denmark	Rønnede	DK-SE	55.25	12.02
Sweden	Härslöv	DK-SE	55.93	12.87
Sweden	Kolbäck	DK-SE	59.57	16.25
France	Attray	FR	48.12	2.10
France	Barbèrey-Saint-Suplice	FR	48.32	4.00
France	Boynes	FR	48.13	2.36
France	Frapuy	FR	48.12	2.16
France	Heutrégiville	FR	49.33	4.29
France	Libermont	FR	49.69	2.97
France	Saint-Martin-Boulogne	FR	50.73	1.67
Germany	Bischoswerda	N.E. DE-CZ-PL	51.14	14.17
Germany	Lemgo	N.E. DE-CZ-PL	52.01	8.86
Czech Republic	Nechanice	N.E. DE-CZ-PL	50.24	15.64
Czech Republic	Smržice	N.E. DE-CZ-PL	49.29	17.00
Poland	Choryń	N.E. DE-CZ-PL	52.04	16.76
Poland	Modzurów	N.E. DE-CZ-PL	50.16	18.12
Germany	Buchbrunn	S. DE-AT	49.76	10.13
Germany	Feldkirchen	S. DE-AT	48.28	11.53
Austria	Großnondorf	S. DE-AT	48.64	15.98
Austria	Reichersberg	S. DE-AT	48.33	13.38
Austria	Edelhof	S. DE-AT	48.60	15.23

722 **Table S2: Characterization of yield evolution over time by agro-climatic region.** A linear  
723 regression was applied to assess the relationship between the yield and the year for each agro-climatic  
724 region. The estimate represents the average annual evolution in yield and p-value indicating the  
725 significance of this evolution.

726

Agro-climatic region	factor	estimate	Standard Error	statistic	p-value
UK-IE	YEAR	-0.078	0.158	-0.495	0.628
DK-SE	YEAR	-0.210	0.177	-1.189	0.251
FR	YEAR	0.031	0.123	0.253	0.802
N.E. DE-CZ-PL	YEAR	-0.241	0.119	-2.031	0.051
S. DE-AT	YEAR	0.055	0.093	0.593	0.559

727



728 **Table S3. Distribution of the 125 environments and 270 genotypes across 7 years and 5 agro-climatic regions.** This table summarizes the number of  
729 trials and distinct genotypes per agro-climatic region for each of the 7 years. The number of trials per region for a year ranged from 2 to 5 and the number of  
730 genotypes ranged from 18 to 52.

731

Agro-climatic region	2015		2016		2017		2018		2019		2020		2021		Total	
	Env.	Gen.	Env.	Gen.	Env.	Gen.	Env.	Gen.	Env.	Gen.	Env.	Gen.	Env.	Gen.	Env.	Gen.
<b>UK-IE</b>	2	30	3	29	3	18	3	30	2	25	4	26	4	43	<i>21</i>	<i>112</i>
<b>DK-SE</b>	3	27	4	30	3	25	2	25	2	22	2	24	3	42	<i>19</i>	<i>132</i>
<b>FR</b>	4	39	4	25	4	24	4	26	4	25	4	25	5	42	<i>29</i>	<i>161</i>
<b>N.E. DE-CZ-PL</b>	3	33	5	27	5	25	5	37	4	27	5	37	5	42	<i>32</i>	<i>205</i>
<b>S. DE-AT</b>	3	39	4	37	2	25	3	40	4	41	5	45	3	52	<i>24</i>	<i>133</i>
<b><i>Total</i></b>	<i>15</i>	<i>72</i>	<i>20</i>	<i>49</i>	<i>17</i>	<i>26</i>	<i>17</i>	<i>75</i>	<i>16</i>	<i>54</i>	<i>20</i>	<i>65</i>	<i>20</i>	<i>63</i>	<b><i>125</i></b>	<b><i>270</i></b>

732 **Table S4. Summary of soil texture and depth parameters from multi-environment trials distributed across the five agro-climatic regions.** The data  
 733 were collected using the Environmental Soil Database (ESDB) on the topsoil (0-30 cm) and subsoil (30 cm to depth).

Agro-climatic region	Clay content - Topsoil			Clay content - Subsoil			Silt content - Topsoil			Silt content - Subsoil			Depth		
	min	max	avg	min	max	avg	min	max	avg	min	max	avg	min	max	avg
<b>UK-IE</b>	20	51	34	21	32	28	13	52	26	14	34	21	50	>150	110
<b>DK-SE</b>	12	22	19	13	29	21	21	43	35	22	43	33	100	>150	140
<b>FR</b>	20	50	35	18	35	26	39	65	51	42	53	47	80	>150	140
<b>N.E. DE-CZ-PL</b>	19	37	28	25	45	37	29	47	38	34	47	39	100	>150	140
<b>S. DE-AT</b>	22	24	23	21	29	23	37	59	49	34	60	47	100	>150	140

734

735 **Table S5. Summary of heading dates recorded in 47 environments for 123 genotypes over the**  
736 **period 2015-2021 (Julian days).** The average per environment was calculated across a panel ranging  
737 from 17 to 51 genotypes. The minimum and maximum values correspond to heading dates of the  
738 earlier et later cultivar of the trial respectively. The difference between the two extremes was  
739 comprised between 4 to 8 days, with an average separation of 6 days.

Env.	Agro-climatic region	Average	Minimum	Maximum	Range
2015Attray	FR	152	149	154	5
2015 Feldkirchen	S.DE-AT	156	154	158	4
2015 Heutrégiville	FR	155	153	157	4
2015 Maule	FR	154	151	157	6
2016 Attray	FR	159	154	160	6
2016 Saint-Martin-Boulogne	FR	166	163	168	5
2016 Dunmow	UK-IE	163	159	165	6
2016 Feldkirchen	S.DE-AT	159	156	161	5
2016 Heutrégiville	FR	157	154	160	6
2016 Maule	FR	160	156	162	6
2017 Attray	FR	143	140	146	6
2017 Boothby Graffoe	UK-IE	156	152	158	6
2017 Dunmow	UK-IE	154	151	157	6
2017 Frapuy	FR	151	149	155	6
2017 Härslöv	DK-SE	171	168	174	6
2017 Heutrégiville	FR	148	144	150	6
2017 Maule	FR	148	145	150	5
2017 Smržice	N.E. DE-CZ-PL	154	151	155	4
2018 Attray	FR	147	145	151	6
2018 Lemgo	N.E. DE-CZ-PL	153	151	157	6
2018 Feldkirchen	S.DE-AT	154	152	157	5
2018 Frapuy	FR	146	144	150	6
2018 Heutrégiville	FR	147	145	151	6
2018 Maule	FR	148	146	151	5
2019 Attray	FR	155	153	158	5
2019 Feldkirchen	S.DE-AT	159	157	161	4
2019 Frapuy	FR	159	156	162	6
2019 Heutrégiville	FR	155	152	158	6
2019 Maule	FR	156	154	162	8
2020 Attray	FR	153	151	156	5
2020 Benniworth	UK-IE	165	162	168	6
2020 Boothby Graffoe	UK-IE	158	155	161	6
2020 Frapuy	FR	154	152	157	5
2020 Fulbourn	UK-IE	152	149	154	5
2020 Feldkirchen	S.DE-AT	161	159	164	5
2020 Heutrégiville	FR	149	146	152	6
2020 Maule	FR	149	145	151	6
2021Attray	FR	156	153	160	7
2021 Benniworth	UK-IE	172	171	177	6
2021 Boothby Graffoe	UK-IE	165	162	168	6
2021 Boynes	FR	158	155	160	5

2021 Feldkirchen	S.DE-AT	166	164	168	4
2021 Fulbourn	UK-IE	164	161	166	5
2021 Härslöv	DK-SE	168	165	172	7
2021 Heutrégiville	FR	155	154	160	6
2021 Maule	FR	155	152	159	7
					<i>Average range : 6</i>

740

741

742 **Table S6. Difference between the recorded heading dates of the two referenced cultivars and the**  
743 **average heading dates observed over the period 2015-2021.** The average per environment was  
744 calculated across a panel ranging from 17 to 51 genotypes. RGT Planet et Laureate were used for  
745 simulations as representative of early and late cultivars, respectively.

<b>Env.</b>	<b><i>RGT Planet</i></b>	<b><i>Laureate</i></b>	<b>Two cultivars average</b>	<b>Env. average</b>	<b>Absolute difference of means</b>
2015Attray	149	154	151	152	1
2015 Feldkirchen	154	157	156	156	1
2015 Heutrégiville	154	156	155	155	0
2015 Maule	152	155	154	154	1
2016 Attray	159	161	160	159	0
2016 Saint-Martin-Boulogne	165	168	167	166	0
2016 Dunmow	161	165	163	163	0
2016 Feldkirchen	158	159	159	159	0
2016 Heutrégiville	157	160	158	157	1
2016 Maule	159	162	160	160	0
2017 Attray	142	145	143	143	0
2017 Boothby Graffoe	155	156	156	156	1
2017 Dunmow	152	156	154	154	1
2017 Frapuy	151	153	152	151	1
2017 Härslöv	170	172	171	171	0
2017 Heutrégiville	148	150	149	148	1
2017 Maule	147	150	148	148	0
2017 Smržice	152	155	154	154	0
2018 Attray	146	148	147	147	0
2018 Lemgo	152	154	153	153	0
2018 Feldkirchen	152	155	154	154	1
2018 Frapuy	145	148	147	146	0
2018 Heutrégiville	146	148	147	147	0
2018 Maule	148	150	149	148	0
2019Attray	154	157	156	155	0
2019 Feldkirchen	157	160	159	159	0
2019 Frapuy	158	161	160	159	0
2019 Heutrégiville	153	157	155	155	0
2019 Maule	155	161	158	156	2
2020 Attray	152	155	154	153	0
2020 Benniworth	163	166	164	165	0
2020 Boothby Graffoe	157	159	158	158	0
2020 Frapuy	153	156	154	154	0
2020 Fulbourn	149	153	151	152	1
2020 Feldkirchen	160	163	162	161	0
2020 Heutrégiville	148	151	150	149	0
2020 Maule	147	150	149	149	0
2021Attray	155	158	157	156	1
2021 Benniworth	170	173	172	172	0

2021 Boothby Graffoe	163	166	165	165	0
2021 Boynes	157	160	158	158	0
2021 Feldkirchen	165	168	166	166	0
2021 Fulbourn	160	165	163	164	1
2021 Härslöv	167	172	169	168	1
2021 Heutrégiville	155	157	156	155	1
2021 Maule	155	157	156	155	1

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750 **Table S7. Environmental covariates with a VIP score > 1, sorted by descending VIP score.** (a)

751 UK-IE agro-climatic region, (b) DK-SE agro-climatic region, (c) FR agro-climatic region, (d) N.E.

752 DE-CZ-PL agro-climatic region and (e) S. DE-AT region.  $\beta$ -regression coefficients indicate whether

753 the considered variable has a positive or negative effect on yield.

754 (a)

Environmental covariates	Description	VIP	$\beta$ -coeff.
TMAX 1CM-HD	Average maximum temperature from Head at 1 cm to Heading	1.98	-0.08
TAMPL 1CM-HD	Average thermal amplitude from Head at 1 cm to Heading	1.87	-0.07
HUMsoil 1CM-HD	Average topsoil humidity from Head at 1 cm to Heading	1.71	0.07
RAINsum 1CM-HD	Sum of precipitation from Head at 1 cm to Heading	1.71	0.08
TAVG EM-1CM	Average temperature from Emergence to Head at 1 cm	1.68	-0.05
TMIN<7°C EM-1CM	Number of days with minimum temperature under 7°C from Emergence to Head at 1 cm	1.65	0.05
TMIN EM-1CM	Average minimum temperature from Emergence to Head at 1 cm	1.59	-0.05
SRADmean HD-AN	Average daily solar radiation from Heading to Anthesis	1.57	0.07
TAVG 1CM-HD	Average temperature from Head at 1 cm to Heading	1.54	-0.07
TAVG<15°C 1CM-HD	Number of days with average temperature under 15°C from Head at 1 cm to Heading	1.49	0.06
PTQ EM-1CM	Photothermal quotient from Emergence to Head at 1 cm	1.45	0.04
TMIN<15°C 1CM-HD	Number of days with minimum temperature under 15°C from Head at 1 cm to Heading	1.43	0.06
Duration AN-GF	Duration from Anthesis to beginning Grain Filling	1.43	0.06
TAMPL GF-PM	Average thermal amplitude from beginning Grain Filling to Physiological Maturity	1.41	-0.03
TMAX EM-1CM	Average maximum temperature from Emergence to Head at 1 cm	1.40	-0.04
TAVG<15°C EM-1CM	Number of days with average temperature under 15°C from Emergence to Head at 1 cm	1.39	0.04
SRADcumul EM-1CM	Cumulative solar radiation from Emergence to Head at 1 cm	1.32	0.04
TMIN AN-GF	Average minimum temperature from Anthesis to beginning Grain Filling	1.26	0.05

HUMsoil GF-PM	Average topsoil humidity from beginning Grain Filling to Physiological Maturity	1.24	0.04
Duration 1CM-HD	Duration from Head at 1 cm to Heading	1.24	0.05
Duration EM-1CM	Duration from Emergence to Head at 1 cm	1.23	0.03
TMIN<15°C EM-1CM	Number of days with minimum temperature under 15°C from Emergence to Head at 1 cm	1.23	0.03
ETPsum EM-1CM	Sum of evapotranspiration from Emergence to Head at 1 cm	1.21	-0.01
TMAX>25°C GF-PM	Number of days with maximum temperature above 25°C from beginning Grain Filling to Physiological Maturity	1.21	-0.03
PTQ HD-AN	Photothermal quotient from Heading to Anthesis	1.20	0.05
TAVG AN-GF	Average temperature from Anthesis to beginning Grain Filling	1.19	0.05
SRADmean GF-PM	Average daily solar radiation from beginning Grain Filling to Physiological Maturity	1.19	-0.01
ETPsum GF-PM	Sum of evapotranspiration from beginning Grain Filling to Physiological Maturity	1.19	0.03
SRADmean 1CM-HD	Average daily solar radiation from Head at 1 cm to Heading	1.17	-0.04
SRADCum GF-PM	Cumulative solar radiation from beginning Grain Filling to Physiological Maturity	1.15	-0.02
TMAX GF-PM		1.10	-0.02
ETPsum HD-AN	Sum of evapotranspiration from Heading to Anthesis	1.08	0.05
TMAX HD-AN	Average maximum temperature from Heading to Anthesis	1.08	0.04
		1.03	0.03
RAINsum GF-PM	Sum of precipitation from beginning Grain Filling to Physiological Maturity	1.02	0.01
PTQ GF-PM	Photothermal quotient from beginning Grain Filling to Physiological Maturity	1.00	-0.01

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756 (b)

<b>Environmental covariates</b>	<b>Description</b>	<b>VI P</b>	<b><math>\beta</math>-coeff.</b>
TAVGsoil SO-EM	Average soil temperature from Sowing to Emergence	1.88	-0.07
TAVG SO-EM	Average temperature from Sowing to Emergence	1.86	-0.08
TMIN SO-EM	Average minimum temperature from Sowing to Emergence	1.76	-0.07
TMIN HD-AN	Average minimum temperature from Heading to Anthesis	1.75	-0.09
TMIN GF-PM	Average minimum temperature from beginning Grain Filling to Physiological Maturity	1.75	-0.08
TMAX SO-EM	Average maximum temperature from Sowing to Emergence	1.73	-0.08
ETPsum AN-GF	Sum of evapotranspiration from Anthesis to beginning Grain Filling	1.68	-0.09
SRADCumul AN-GF	Cumulative solar radiation from Anthesis to beginning Grain Filling	1.58	-0.08
TMIN EM-1CM	Average minimum temperature from Emergence to Head at 1 cm	1.53	-0.06
TMIN<0°C EM-1CM	Number of days with maximum temperature under 0°C from Emergence to Head at 1 cm	1.52	0.06

SRADmean SO-EM	Average daily solar radiation from Sowing to Emergence	1.49	-0.07
RAINsum SO-EM	Sum of precipitation from Sowing to Emergence	1.48	0.08
TMIN<15°C GF-PM	Number of days with minimum temperature under 15°C from beginning Grain Filling to Physiological Maturity	1.44	0.07
TMIN<7°C 1CM-HD	Number of days with minimum temperature under 7°C from Head at 1 cm to Heading	1.43	0.06
Duration HD-AN	Duration from Heading to Anthesis	1.39	0.06
TAVG HD-AN	Average temperature from Heading to Anthesis	1.38	-0.07
SRADmean GF-PM	Average daily solar radiation from beginning Grain Filling to Physiological Maturity	1.36	-0.05
TAMPL EM-1CM	Average thermal amplitude from Emergence to Head at 1 cm	1.32	0.06
TMIN<7°C SO-EM	Number of days with minimum temperature under 7°C from Sowing to Emergence	1.30	0.05
Duration GF-PM	Duration from beginning Grain Filling to Physiological Maturity	1.24	0.05
TMAX HD-AN	Average maximum temperature from Heading to Anthesis	1.23	-0.06
TMIN 1CM-HD	Average minimum temperature from Head at 1 cm to Heading	1.18	-0.05
PTQ SO-EM	Photothermal quotient from Sowing to Emergence	1.16	0.05
TMIN AN-GF	Average minimum temperature from Anthesis to beginning Grain Filling	1.10	-0.05
TAVG GF-PM	Average temperature from beginning Grain Filling to Physiological Maturity	1.06	-0.04
SRADmean AN-GF	Average daily solar radiation from Anthesis to beginning Grain Filling	1.05	-0.05
PTQ EM-1CM	Photothermal quotient from Emergence to Head at 1 cm	1.05	0.03
HUMsoil GF-PM	Average topsoil humidity from beginning Grain Filling to Physiological Maturity	1.00	-0.06

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758 (c)

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<b>Environmental covariates</b>	<b>Description</b>	<b>VIP</b>	<b><math>\beta</math>-coeff.</b>
TMIN<15°C GF-PM	Number of days with minimum temperature under 15°C from beginning Grain Filling to Physiological Maturity	2.65	-0.10
RAINsum AN-GF	Sum of precipitation from Anthesis to beginning Grain Filling	2.02	-0.08
SRADmean HD-AN	Average daily solar radiation from Heading to Anthesis	1.81	-0.06
WSF EM-1CM	Average water stress factor from Emergence to Head at 1 cm	1.70	-0.06
TAMPL HD-AN	Average thermal amplitude from Heading to Anthesis	1.66	-0.06
PTQ HD-AN	Photothermal quotient from Heading to Anthesis	1.60	-0.05
SRADcumul 1CM-HD	Average daily solar radiation from Head at 1 cm to Heading	1.53	0.06
Duration GF-PM	Duration from beginning Grain Filling to Physiological Maturity	1.52	-0.05
TMIN GF-PM	Average minimum temperature from beginning Grain Filling to Physiological Maturity	1.51	0.04



SRADmean GF-PM	Average daily solar radiation from beginning Grain Filling to Physiological Maturity	1.50	0.06
ETPsum HD-AN	Sum of evapotranspiration from Heading to Anthesis	1.46	-0.05
PTQ 1CM-HD	Photothermal quotient from Head at 1 cm to Heading	1.43	0.06
TAVG GF-PM	Average temperature from beginning Grain Filling to Physiological Maturity	1.39	0.05
TMAX HD-AN	Average maximum temperature from Heading to Anthesis	1.34	-0.05
SRADmean 1CM-HD	Average daily solar radiation from Head at 1 cm to Heading	1.31	0.05
WSF HD-AN	Average water stress factor from Heading to Anthesis	1.26	-0.04
SRADcumul HD-AN	Cumulative solar radiation from Heading to Anthesis	1.25	-0.04
HUMsoil HD-AN	Average topsoil humidity from Heading to Anthesis	1.23	0.03
ETPsum 1CM-HD	Sum of evapotranspiration from Head at 1 cm to Heading	1.20	0.05
SRADmean AN-GF	Average daily solar radiation from Anthesis to beginning Grain Filling	1.19	0.05
TMAX EM-1CM	Average maximum temperature from Emergence to Head at 1 cm	1.15	-0.02
Soilhum SO-EM	Average soil humidity from Sowing to Emergence	1.14	0.03
SRADmean EM-1CM	Average daily solar radiation from Emergence to Head at 1 cm	1.13	-0.03
TMAX SO-EM	Average maximum temperature from Sowing to Emergence	1.13	-0.04
TMAX>25°C GF-PM	Number of days with maximum temperature above 25°C from beginning Grain Filling to Physiological Maturity	1.11	0.04
SRADcumul GF-PM	Cumulative solar radiation from beginning Grain Filling to Physiological Maturity	1.10	0.05
SRADmean SO-EM	Average daily solar radiation from Sowing to Emergence	1.08	-0.03
TAVGsoil SO-EM	Average soil temperature from Sowing to Emergence	1.07	-0.04
RAINsum HD-AN	Sum of precipitation from Heading to Anthesis	1.07	0.03
Duration AN-GF	Duration from Anthesis to beginning Grain Filling	1.04	-0.04
RAINsum SO-EM	Sum of precipitation from Sowing to Emergence	1.00	0.03

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761 (d)

<b>Environmental covariates</b>	<b>Description</b>	<b>VIP</b>	<b><math>\beta</math>-coeff.</b>
TMIN AN-GF	Average minimum temperature from Anthesis to beginning Grain Filling	2.37	-0.15
Soilhum SO-EM	Average soil humidity from Sowing to Emergence	2.26	0.13
SRADmean HD-AN	Average daily solar radiation from Heading to Head at 1 cm	1.69	0.07
PTQ HD-AN	Photothermal quotient from Heading to Anthesis	1.68	0.07
TAMPL HD-AN	Average thermal amplitude from Heading to Anthesis	1.67	0.08
TAVG AN-GF	Average temperature from Anthesis to beginning Grain Filling	1.65	-0.10
ETPsum HD-AN	Sum of evapotranspiration from Heading to Anthesis	1.59	0.09
PTQ AN-GF	Photothermal quotient from Anthesis to beginning Grain Filling	1.58	0.08
TMIN HD-AN	Average minimum temperature from Heading to Anthesis	1.58	-0.09
SRADcumul HD-AN	Cumulative solar radiation from Heading to Anthesis	1.54	0.09
RAINsum SO-EM	Sum of precipitation from Sowing to Emergence	1.51	0.07
TAMPL 1CM-HD	Average thermal amplitude from Head at 1 cm to Heading	1.39	0.08
Duration AN-GF	Duration from Anthesis to beginning Grain Filling	1.38	0.07
TMIN<7°C EM-1CM	Number of days with minimum temperature under 7°C from Emergence to Head at 1 cm	1.33	-0.08
HUMsoil EM-1CM	Average topsoil humidity from Emergence to Head at 1 cm	1.32	0.08

TAVG>25°C GF-PM	Number of days with average temperature above 25°C from beginning Grain Filling to Physiological Maturity	1.27	-0.08
SRADcumul AN-GF	Cumulative solar radiation from Anthesis to beginning Grain Filling	1.26	0.04
TMIN GF-PM	Average minimum temperature from beginning Grain Filling to Physiological Maturity	1.24	-0.08
PTQ GF-PM	Photothermal quotient from beginning Grain Filling to Physiological Maturity	1.18	0.07
TMIN<7°C 1CM-HD	Number of days with minimum temperature under 7°C Head at 1 cm to Heading	1.16	0.08
RAINsum 1CM-HD	Sum of precipitation from Head at 1 cm to Heading	1.15	0.03
TMIN EM-1CM	Average minimum temperature from Emergence to Head at 1 cm	1.15	0.05
HUMsoil GF-PM	Average topsoil humidity from beginning Grain Filling to Physiological Maturity	1.14	0.06
PTQ EM-1CM	Photothermal quotient from Emergence to Head at 1 cm	1.12	-0.07
TMAX AN-GF	Average maximum temperature from Anthesis to beginning Grain Filling	1.11	-0.06
TMIN 1CM-HD	Average minimum temperature from Head at 1 cm to Heading	1.06	-0.07
TAVG EM-1CM	Average temperature from Emergence to Head at 1 cm	1.05	0.06
SRADmean 1CM-HD	Average daily solar radiation from Head at 1 cm to Heading	1.04	-0.06
WSF GF-PM	Average water stress factor from beginning Grain Filling to Physiological Maturity	1.02	-0.07
SRADmean SO-EM	Average daily solar radiation from Sowing to Emergence	1.02	-0.05

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763 (e)

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<b>Environmental covariates</b>	<b>Description</b>	<b>VIP</b>	<b>β-coeff.</b>
PTQ EM-1CM	Photothermal quotient from Emergence to Head at 1 cm	2.32	0.07
TMIN EM-1CM	Average minimum temperature from Emergence to Head at 1 cm	2.24	-0.07
TAVG EM-1CM	Average temperature from Emergence to Head at 1 cm	2.22	-0.07
TMAX EM-1CM	Average maximum temperature from Emergence to Head at 1 cm	2.08	-0.07
TAVG<15°C EM-1CM	Number of days with average temperature under 15°C from Emergence to Head at 1 cm	2.06	0.07
TMIN AN-GF	Average minimum temperature from Anthesis to beginning Grain Filling	2.02	-0.08
TMIN<7°C EM-1CM	Number of days with minimum temperature under 7°C from Emergence to Head at 1 cm	1.79	0.05
SRADcumul EM-1CM	Cumulative solar radiation from Emergence to Head at 1 cm	1.79	0.05
TAVG<15°C GF-PM	Number of days with average temperature under 15°C from beginning Grain Filling to Physiological Maturity	1.61	-0.07
TMIN<0°C EM-1CM	Number of days with maximum temperature under 0°C from Emergence to Head at 1 cm	1.59	0.05
TAVG AN-GF	Average temperature from Anthesis to beginning Grain Filling	1.56	-0.06
Duration AN-GF	Duration from Anthesis to beginning Grain Filling	1.54	0.06
WSF EM-1CM	Average water stress factor from Emergence to Head at 1 cm	1.51	-0.06

TMIN<15°C EM-1CM	Number of days with minimum temperature under 15°C from Emergence to Head at 1 cm	1.43	0.04
PRECcumSO_EM		1.43	-0.06
Duration EM-1CM	Duration from Emergence to Head at 1 cm	1.41	0.04
PTQ AN-GF	Photothermal quotient from Anthesis to beginning Grain Filling	1.41	0.06
ETPsum EM-1CM	Sum of evapotranspiration from Emergence to Head at 1 cm	1.37	0.03
RAINsum 1CM-HD	Sum of precipitation from Head at 1 cm to Heading	1.32	-0.06
TMAX AN-GF	Average maximum temperature from Anthesis to beginning Grain Filling	1.28	-0.04
TAMPL EM-1CM	Average thermal amplitude from Emergence to Head at 1 cm	1.26	-0.05
TAMPL HD-AN	Average thermal amplitude from Heading to Anthesis	1.15	-0.04
SRADCumul AN-GF	Cumulative solar radiation from Anthesis to beginning Grain Filling	1.14	0.05
SRADmean HD-AN	Average daily solar radiation from Heading to Anthesis	1.12	-0.04
PTQ HD-AN	Photothermal quotient from Heading to Anthesis	1.07	-0.04