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## 1 Core ideas

- 2 • Different ecotypes of barnyard grass have developed in southern and northern
- 3 populations
- 4 • In northern populations heading occurs earlier than in southern populations
- 5 • Vegetative development is similar in different populations

6

7 **Phenological development of barnyard grass plants originated from different geographical**  
 8 **locations**

9 Abbreviations: DAE, days after emergence; GDD, growing degree days

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**ABSTRACT**

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Barnyard grass (*Echinochloa crus-galli* (L.) Beauv) is a competitive C<sub>4</sub> weed species that is widely distributed throughout the world. While it originated in warm climatic conditions, currently it is found in Europe as far north as Norway. This study aimed to compare the phenological development of plants from different climatic conditions in varying environmental conditions. To represent the contrasting climatic conditions within Europe, seeds were collected in Norway and Italy and distributed to the study participants to be sown at 10 different sites as two common populations. In addition to that, seeds of two to three local populations were collected near each of the sites. The development of the plants was monitored in a pot experiment set up under field conditions. The time to reach heading in the first year of the experiment was 77.6% faster (on average, ranging from 45.9 to 98.3%) in the Norwegian than in the Italian population. However, in the leaf development stage, the difference between the common populations was smaller, on average 23.5% (0-46.7%) and mostly not significant. Our results indicate that different *E. crus-galli* ecotypes, characterized by differences in phenological development, evolved within the distribution area of this species in Europe. However, the early development of the plants progresses with negligible differences between populations. The findings reported here can be used to adapt existing models from one region to regions with different climatic conditions for use in decision support systems and for research of the plant population dynamics.

## 1. INTRODUCTION

61  
62 *Echinochloa crus-galli* (L.) P. Beauv. is a highly competitive summer annual C<sub>4</sub> weed globally  
63 spread across a wide climatic gradient. It has been reported in 61 countries in various crops (Maun  
64 & Barrett, 1986). Originating in warmer areas of Asia and Europe (Maun & Barrett, 1986), *E.*  
65 *crus-galli* spread to the northern parts of Europe and North America by the end of the 19<sup>th</sup> century,  
66 being discovered as far north as Norway in 1878 (Clements *et al.*, 2004; Brodal *et al.*, 2016). In  
67 Europe, countries, *E. crus-galli* occurs as a weed in spring cereal crops, potato (Brodal *et al.*, 2016)  
68 and maize (Pannwitt *et al.*, 2021), as well as rice (Bajwa *et al.*, 2015). Infestation results in yield  
69 loss and an additional threat is posed by herbicide resistance in this weed (Bajwa *et al.*, 2015;  
70 Heap, 2022). Phenological adaptations to the northern climate included a faster development to  
71 maturity that has involved biochemical adaptations of C<sub>4</sub> photosynthesis enzymes to colder  
72 conditions (Simon & Hatch, 1994) and differences in resource allocation between southern and  
73 northern populations (Potvin, 1986). Different ecotypes can exhibit various rates of biomass  
74 accumulation depending on temperature and photoperiod, and show diverse growth habits  
75 (prostrate or erect) and intensity of pigmentation (Rono, 1994). In addition, an interesting example  
76 of intraspecific variability between highland and lowland populations was described in the  
77 northwest Carpathians. This variability included differences in percentage germination, heading,  
78 and seed dispersal time, with plants from the highland location developing and dispersing seeds  
79 earlier compared to the lowland location (Martinkova *et al.*, 2021).

80 Differences in phenology between populations have also described for some other species  
81 which are distributed over a wide range of latitudes. For example, in *Ambrosia artemisiifolia* L.,  
82 the onset of flowering occurs earlier with increasing latitude (Stinson *et al.*, 2016). Co-variation  
83 between primary dormancy, vegetative growth rate, and flowering time along a latitudinal cline

84 was observed in *Arabidopsis thaliana* (L.) Heynh. genotypes. At higher latitudes, the vegetative  
85 growth rate was positively correlated with primary dormancy and negatively with flowering time,  
86 but the trend disappears at lower latitudes (Debieu *et al.*, 2013). Adaptation to shorter growing  
87 seasons in northern latitudes may have driven the selection of earlier flowering phenotypes.  
88 Agronomic pressures affecting weeds' life cycle, specifically seed yield, dispersal, or germination,  
89 can also become selection drivers. For example, a change in flowering time in response to harvest  
90 weed seed control was described in *Raphanus raphanistrum* L. (Ashworth *et al.*, 2016). In a C<sub>4</sub>  
91 grass *Miscanthus sacchariflorus* (Maxim.) Hack., flowering generally occurs earlier in plants  
92 originating from higher latitudes, whereas a higher accumulation of biomass tends to be associated  
93 with later flowering individuals, although factors other than latitude also influence flowering time  
94 (Jensen *et al.*, 2013).

95 Predicting the phenological development of weed species is of practical importance, as  
96 appropriate timing is essential for successful weed management. Both chemical and non-chemical  
97 control operations must be planned according to the weed's development stage, therefore, growth  
98 models based on phenological stages can be a useful basis for decision support systems (Parsons  
99 *et al.*, 2009). Predicting flowering time is also useful to reduce weed seed production, for example,  
100 planning hand weeding, and adapting harvest time to reduce weed seed rain, or selecting crop  
101 cultivars with the shorter life cycle, if necessary. These tactics can be important for implementing  
102 integrated weed management (IWM) approaches. Thermal time or growing degree days (GDD)  
103 has been successfully used to model the development of *E. crus-galli* plants (Swanton *et al.*, 2000;  
104 Shrestha & Swanton, 2007). However, weed populations must adapt to different climatic  
105 conditions and photoperiods to survive and reproduce. Therefore, a question arises whether a  
106 single growth model for *E. crus-galli* can describe the phenological development of plants of

107 different origin and/or plants of the same origin transported to non-native locations. As a step  
108 towards answering this question, growth of *E. crus-galli* plants of different geographic origins was  
109 compared in different countries under common garden conditions.

110 The study was carried out as a common experiment by the Germination and Early Growth  
111 Working Group of the European Weed Research Society. This experiment aimed to determine  
112 how plants originating from two contrasting climates developed at different geographical sites  
113 encompassing a range of climatic conditions. The main hypothesis was that the life cycle of *E.*  
114 *crus-galli* plants originating from the northern site would differ from that of the population derived  
115 from the southern site, when exposed to similar growing conditions in common gardens at multiple  
116 contrasting sites. Specifically, it was expected that the northern ecotype would complete its life  
117 cycle more rapidly.

## 118 2. MATERIALS AND METHODS

### 119 2.1 Seed collection and experimental setup

120 The seeds of two populations of *E. crus-galli* that were used in all sites (referred to as 'common  
121 populations') were collected from a maize field in Italy (IT, 45°20'N 11°58'E), and from a spring  
122 barley field in Norway (NO, 59°24' N 9°58'E) in August and September 2015, respectively. The  
123 fields were 0 and 54 km away from the sites where the experiment was carried out in Italy and  
124 Norway, respectively. Seeds were collected at maturity from at least 15 individuals, dried at 20-  
125 25 °C for one week, sieved to remove chaff, and stored at low temperature (3-5 °C) before sowing.  
126 The seeds of the two common populations were distributed to the participants by HerbiSeed Co.  
127 (UK) after obtaining phytosanitary certificates. In addition, seeds of two or three local populations  
128 were collected near to each study site using a similar protocol to the common population. These

129 additional populations, presumably adapted to the local environmental conditions, were used in  
130 the experiment to compare their phenology with that of the IT and NO populations. For  
131 convenience, the local populations were coded using the abbreviation of the site name (DK,  
132 Denmark, IT, Italy, IR, Iran, LV, Latvia, NO, Norway, PN, North Poland, PS, South Poland, SP,  
133 Spain, TN, North Turkey, TS, South Turkey) and the number of the population (L1, L2 and L3).

134 Pot experiments were set up under field conditions at 10 different sites belonging to  
135 different countries: Denmark, Iran, Italy, Latvia, Norway, two sites in Poland (North [Olsztyn] and  
136 South [Krakow]), Spain, and two sites in Turkey (North [Düzce] and South [Antakya]), obtaining  
137 a wide climatic gradient (Fig. 1, Table 1).

138

139 At each experimental site, seeds were sown in October-November 2015 (Table 1) and  
140 seedling emergence and plant development were monitored in 2016 and 2017 (Royo-Esnaol et al.,  
141 2022a), without allowing addition of any new seeds. Seeds were sown in 5 L plastic pots with an  
142 upper diameter of 25 cm. The pots were filled with typical agricultural soil from the local site and  
143 200 seeds were mixed in the upper 5 cm of soil in each pot. There were five replicate pots for each  
144 of the populations except in North Poland, where there were six.

145 The pots were dug into the ground so that only the upper 1 cm was above the soil layer and  
146 were covered with mesh (mesh size from 9 to 20 mm) to prevent seed predation. The pots were  
147 not irrigated except, if necessary, at sites where *E. crus-galli* development would otherwise be  
148 impossible and where crops are normally irrigated (Spain, Iran, South Turkey and, in 2017, Italy).  
149 The total amounts of water added as irrigation during the 2016 season were equivalent to 65 mm  
150 in Spain and 1127 mm in Iran. The amounts were not recorded in Italy and South Turkey. In spring



151 2016 and 2017, shallow soil disturbance was performed at the time when sowing or tillage would  
152 be performed in the local area. Either the upper 5 cm layer was removed, placed on a tray, mixed  
153 well, and replaced in the corresponding pot or the top 5 cm of soil was mixed with a garden  
154 cultivator (Latvia). NPK fertilizer was added at the time of spring disturbance, with a nitrogen rate  
155 of 50 kg ha<sup>-1</sup>.

## 156 **2.2 Assessments**

157 After the main flush of emergence in spring, determined as the date when highest number of newly-  
158 emerged seedlings was recorded (Royo-Esnal *et al.*, 2022a), seedlings were removed leaving three  
159 plants of similar age in each pot, which were preserved for monitoring development using the  
160 BBCH scale (Hack *et al.*, 1992). The BBCH stages used to characterize plant development are  
161 described in Table 2.

162

163 It was assumed that the competition among the plants would not influence their transition to  
164 different phenological stages (Swanton *et al.*, 2000 and references therein). The BBCH stage of  
165 each individual plant was recorded once or twice weekly during the period from emergence until  
166 tillering, at the sites where the plants were removed early (Denmark, North and South Poland,  
167 Spain, North Turkey), or until heading of the main tiller, that is, in Norway, Latvia, Italy, South  
168 Turkey, and Iran. The date of the emergence flush was set as the starting point for the accumulation  
169 of days after emergence (DAE). The time required to reach BBCH 12 and BBCH 41-59 was  
170 determined at each site for each plant. BBCH 12 is usually the stage from which postemergence  
171 chemical control should be applied. The duration of tillering was recorded as the period between  
172 BBCH 21 and 31, and the total number of tillers was recorded. The date when plants reached

173 BBCH stage exceeding 41 (BBCH 41-59) was recorded and was used as the starting date for  
174 heading. Only the plants reaching this stage were included in the analyses of the time of heading.

175 Growing degree days (GDD) were calculated for the same periods as DAE to allow  
176 comparison of sites with different climatic conditions. The base temperature ( $T_b$ ) for the  
177 accumulation of GDD during both leaf development and heading stages was considered to be 6.5  
178 °C (Shrestha & Swanton 2007). The GDD accumulation began the same date considered for DAE,  
179 when the main emergence flush was recorded in each population at each site. GDD was calculated  
180 following McMaster and Wilhelm (1997):

$$181 \quad \text{GDD} = \Sigma[(T_{\max} + T_{\min})/2] - T_b$$

182 where  $T_{\max}$  and  $T_{\min}$  are the daily maximum and daily minimum air temperatures and  $T_b$  is  
183 the base temperature. GDD was equal to 0 if  $(T_{\max} + T_{\min})/2$  was  $<T_b$ .

184 The weather data, including air temperature and precipitation, were obtained from  
185 meteorological stations nearest to each experimental site. The duration of the day in each site was  
186 calculated using the National Oceanic & Atmospheric Administration Solar Calculator online tool  
187 (<https://gml.noaa.gov/grad/solcalc/>).

188 In Denmark, only three plants per population (one pot) were observed and plants from the  
189 IT population did not survive beyond the tillering stage. The Danish data were, therefore, excluded  
190 from the analysis. Data from North and South Poland, Spain and North Turkey were included in  
191 the analysis of the time to BBCH 12, the duration of tiller formation (BBCH 21-31), and the  
192 number of tillers but not in the time to reach heading (BBCH 41-59) analysis.

### 193 **2.3 Statistical analyses**

194           Within each site, separate mixed linear models were used to analyse the data, Population  
195 (three to five populations, depending on the site) was included as a fixed factor, and the Pots were  
196 included as a random effect to account for subsampling (each pot contained up to three plants, that  
197 is, three observational units). In the sites where data was obtained for a second season, in the initial  
198 analysis Year was also included as a fixed factor, and Year \* Population as an interaction term.  
199 The dependent variable in each model was the time (DAE) required for each plant to reach BBCH  
200 12, the duration of tiller formation (BBCH 21-31), the number of tillers or DAE to reach heading  
201 (BBCH 41-59). All response variables were square-root transformed to ensure that the data  
202 conformed to the basic assumptions for the linear models. The transformation was selected after  
203 preliminary analyses based on the method outlined by Box and Cox (1964). The significance of  
204 fixed effects was tested using  $\chi^2$  likelihood ratio tests (Pinheiro & Bates, 2000). Multiple  
205 comparison testing was performed using a procedure based on multivariate t-distribution,  
206 controlling for the family-wise error rate (a generalized hypothesis testing procedure with  
207 multiplicity adjustment) (Bretz *et al.*, 2011). To compare the time (DAE) required to reach a  
208 particular stage of development between different populations, the difference between the mean  
209 DAE values was expressed as a percentage (%). To compare the two common populations:

$$210 \quad \text{Difference in DAE, \%} = (\text{DAE}_{IT} - \text{DAE}_{NO}) / \text{DAE}_{IT} * 100$$

211           An additional analysis was performed using mixed models to compare plant development  
212 in the two common populations between the sites. The interaction between the Site and Population  
213 (fixed effects), with Pot as a random effect and GDD to BBCH 12 and GDD accumulated before  
214 heading as dependent variables were tested.

215           Data from three sites where complete data could be obtained (Norway, Latvia and Italy),  
216 were used for Principal Component Analysis (PCA). Variables that describe the phenological

217 development of the IT and NO plants were used in the PCA: DAE to reach BBCH 12, duration of  
218 the leaf stage, number of tillers, duration of the tillering stage, and DAE to reach heading (BBCH  
219 41-59). The first two principal components for row scores and column scores were displayed on a  
220 distance biplot. All analyses were performed using the R program version 4.1.1. (R Core Team  
221 2021) with the 'lme()' function in the 'nlme' package (Pinheiro & Bates, 2000), the 'glht()' function  
222 in the 'multcomp' package (Hothorn *et al.*, 2008) and the 'rda()' function in the 'vegan' package  
223 (Oksanen *et al.*, 2019).

### 224 3. RESULTS

#### 225 3.1 Climatic conditions at the experimental sites and seedling emergence

226 In 2016, mean air temperatures in spring and summer were higher in Spain, Iran, South  
227 Turkey and Italy (10.5-35.8 °C) than in North Turkey, Denmark, Latvia, South Poland and Norway  
228 (2.2-22.5 °C) (Fig. 2A). A temperature difference was generally apparent between the two groups  
229 of sites: the temperature was lower in the temperate or cold sites without a dry season (Köppen-  
230 Geiger Dfb, Cfb) and higher in the temperate regions with a dry season (Köppen-Geiger Csa, Cfa,  
231 warm Mediterranean). In North Turkey, the temperatures were higher than in other sites classified  
232 as temperate with no dry season (12.2-22.5 °C). The total amount of natural precipitation beginning  
233 from the time of soil disturbance in the spring (April) was highest in South Turkey and Norway  
234 (157 mm), and from May 2016 on, also in Italy (258 mm). In contrast, the amount of precipitation  
235 was lowest (40-68 mm) in Latvia, especially at the time of plant emergence and early development  
236 in April, in South Poland, and in Spain before the plants were irrigated more intensively starting  
237 in May (Fig. 2B). In Iran, plants were irrigated after the end of May. As a result, the combination  
238 of rainfall and irrigation provided a relatively high moisture level (Fig. 2B). In 2017, the  
239 meteorological conditions were not favourable for the development of *E. crus-galli*, probably due

240 to low precipitation, and plants did not develop in several sites. For this reason, only data from  
241 Norway, Italy, Latvia and South Turkey were analysed. No complete meteorological information  
242 was available for North Poland.

243

244 The daylength varied throughout the year and these differences in photoperiod between the  
245 sites were maximal at the end of June (Fig. 2C). During the period of emergence, the daylength  
246 exceeded 13 hours at all sites starting from South Poland and further to the north, considering the  
247 time of emergence in both years. The longest day was in Norway (17-18 hours, approaching 19)  
248 and the second longest in Latvia (17 hours, approaching 18), while in the southern sites (Italy,  
249 South and North Turkey, Iran), it ranged from 13 to 14 hours.

250 Seedling emergence did not start until Spring 2016 in most sites. An exception was North  
251 Turkey where a flush of emergence was observed before April 2016 (Royo-Esnal *et al.*, 2022a),  
252 but it was not considered in this study. The main flush of seedling emergence in 2016 occurred in  
253 mid-April in Spain and Italy and at the end of April and the beginning of May in North Turkey,  
254 South Turkey, and Iran (Table 1). In Iran, no emergence was recorded for NO and one of the local  
255 populations (IR\_L1). In North Poland and South Poland, the emergence dates differed between  
256 the populations and lasted throughout May. In Denmark, Latvia, and Norway, the main emergence  
257 flush was at the end of May. In 2017, the main emergence flush occurred later than in 2016 in  
258 Norway and Latvia (end of May-beginning of June), but earlier in Italy (beginning of April). In  
259 South Turkey, the emergence date was similar to 2016 (1 May and 2 May).

260 **3.2 Small differences in the early stage of phenological development between populations**  
261 **were observed**

262 In 2016, the median DAE to reach BBCH 12 in all populations at different sites was nine  
263 days (range: 2 to 20 days). Since growth conditions were not the same in each site, different  
264 populations were compared within each site. In the initial analysis performed to test whether the  
265 time (DAE) to reach BBCH 12 was similar in both years of the study, there was a significant  
266 interaction in Norway and Latvia, but not in Italy, so data for each year were analysed and  
267 presented separately. The number of monitored plants and mean values for each site in both years  
268 are given in the Supplementary Table. Only data for the sites with full results are shown in figures  
269 included the main text.

270 In Norway, in 2016, NO and NO\_L1 reached BBCH 12 significantly earlier than IT ( $p <$   
271  $0.0001$  and  $p = 0.0013$ , respectively). The NO population developed faster than two of the local  
272 populations (NO\_L2,  $p = 0.0285$  and NO\_L3,  $p = 0.0068$ ) (Fig. 3A). In 2017, the NO population  
273 reached BBCH 12 later than IT ( $p = 0.0038$ ) and local populations (NO\_L1,  $p = 0.0474$ , NO\_L2,  
274  $p = 0.0435$  and NO\_L3,  $p = 0.0416$ ) (Fig. 3B).

275 In Italy, in 2016, NO and IT reached BBCH 12 in a similar DAE, however, the NO  
276 population reached the same stage significantly earlier than the local populations (IT\_L1,  $p =$   
277  $0.002$ , IT\_L2,  $p = 0.012$ , IT\_L3,  $p = 0.02$ ) (Fig. 3A). There were no significant differences among  
278 the populations in 2017 (Fig. 3B).

279 In South Poland, IT plants developed faster ( $3.59 \pm 0.9$  DAE) than NO plants ( $6.78 \pm 1.1$   
280 DAE,  $p < 0.0001$ ). There were also significant differences between PS\_L1 and NO ( $p < 0.0001$ )  
281 and IT ( $p = 0.024$ ), and between local populations (PS\_L1 and PS\_L2,  $p < 0.0001$ ; PS\_L1 and  
282 PS\_L3,  $p < 0.0001$ ). In Spain, NO developed faster than each of the local populations ( $p = 0.0071$ ,  
283  $p = 0.0005$ ,  $p = 0.0004$ ). In North Turkey, the development of plants in all populations was rapid,



306 and there were no differences between local populations and the NO population. In Latvia, the  
307 tillering stage in the IT population was longer than in the LV\_L2 population ( $p = 0.0012$ ) (Fig.  
308 3A).

309

310 In 2017, the duration of the tillering stage of the IT population differed significantly from  
311 all other populations in Norway ( $p < 0.0001$ ), but there were no significant differences in Italy  
312 (Fig. 3B). In Latvia, the tillering stage was longer in the IT population compared to the LVL1  
313 population ( $p = 0.0316$ ).

#### 314 **3.4 The transition to the heading stage was accelerated in the northern (NO) population.**

315 In 2016, in Italy, Latvia, Norway and South Turkey, where both common populations were  
316 present until heading stage (BBCH 41-59), NO plants headed earlier than IT plants ( $p < 0.0001$ )  
317 (Fig. 3A, Supplementary Table). The difference in DAE to heading between NO and IT ranged  
318 from eight days in South Turkey to 42 days in Italy and Norway and 60 days in Latvia. In Norway  
319 and Latvia, NO plants headed in July, while the IT plants did not head until September. In Italy,  
320 NO and IT plants headed in June and July, respectively. In Iran, the IT plants reached heading  $87$   
321  $\pm 2$  DAE but could not be compared to NO because none of its seedlings emerged. In North Turkey,  
322 the IT plants were cut at the late tillering stage (BBCH 29: 32 DAE), but 67% of the NO plants  
323 had already headed by this time – the final observation date. The average DAE until the heading  
324 stage of these plants was  $28 \pm 2$  days. On average, the NO population reached the heading growth  
325 stage 74% earlier than IT in DAE, from 46% earlier in South Turkey to 86% earlier in Italy.

326 In addition to the difference between the two common populations, in 2016, the local  
327 populations also differed from the common populations (Fig. 3A). In Italy, plants from the NO



328 population reached the heading stage earlier than the local populations ( $p < 0.0001$ ), while in  
329 Latvia, plants from the NO population headed slightly later than LV\_L1 ( $p = 0.008$ ). In Latvia and  
330 Norway, plants from the IT population headed more slowly than the local populations ( $p <$   
331  $0.0001$ ), whereas in South Turkey, both IT and NO headed earlier than the local populations ( $p <$   
332  $0.0001$ ). In South Turkey, there were also significant differences between TS\_L3 and the other  
333 local populations ( $p < 0.0001$ ), but not between TS\_L1 and TS\_L2. Plants from the NO population  
334 in Denmark reached heading 44 DAE, while those from the local populations were slower, not  
335 heading before 58 DAE (Supplementary Table).

336 In 2017, plants from the NO population tended to reach the heading stage earlier than those  
337 of the IT population, but there were no significant differences between the two populations, except  
338 in South Turkey ( $p = 0.0074$ ). In Norway, none of the IT plants reached the heading stage before  
339 the final observation on September 27, while all NO plants did (mean DAE to heading  $77.3 \pm 4$ ),  
340 so the DAE to reach heading could not be compared. In 2016, IT plants required 938 and 1429  
341 GDD to reach heading in Norway and Italy, respectively, while NO plants required only 502 and  
342 611 GDD. Possibly, in 2017 sufficient GDD was not accumulated before the termination of the IT  
343 plants. In Italy, the NO population reached heading before each of the local populations ( $p =$   
344  $0.0164$ ,  $p = 0.0001$ ,  $p < 0.0001$ ). There were no statistically significant differences between the  
345 populations in Latvia. Compared to 2016, the difference in DAE in reaching the heading between  
346 IT and NO was smaller – on average, 15% and ranging from 10% in Latvia to 18% in Italy).

347 Although it was not possible to use the photoperiod as a factor in the analysis, because the  
348 sites each had different photoperiods, in Norway and in Latvia, in 2016, very few (3 out of total  
349 22) IT plants headed if the daylength exceeded 14 hours. Interestingly, however, in 2017, more IT  
350 plants in Latvia reached heading at a 17 hours' daylength.

351 **3.5 Plants from the northern (NO) population reached heading at less GDD before heading**  
352 **than plants from the southern (IT) population**

353 Plants from NO and IT populations accumulated 46-238 GDD from the day of emergence  
354 until the BBCH 12 stage, depending on the site (median value, 99 GDD) (Fig. 6A). There was no  
355 significant interaction between Site and Population ( $p = 0.3737$ ), but significant differences  
356 between the two populations were found within both factors, Site and Population ( $p < 0.0001$ ,  $p =$   
357  $0.0047$ , respectively). The IT population accumulated a similar amount of GDD in Italy, Latvia,  
358 and Spain to reach BBCH 12. This value was higher in North Poland, but was not statistically  
359 different from Spain. In South Poland and Norway, the accumulated GDD was also similar and  
360 lower than in the previous site group. For the NO population, similar GDD values were recorded  
361 in Latvia and Italy, in South Poland and Norway, and in North Poland and Spain. In addition, the  
362 values in Spain were also similar to those in Italy and in Latvia to South Poland.

363 The NO population plants needed significantly lower accumulated GDD (291-772, median  
364 518) to reach the heading stage than IT plants (292-2497, median 1326) (Fig. 5B). The GDD values  
365 in different sites were variable, and moreover, there was a significant interaction between Site and  
366 Population factors ( $p < 0.0001$ ), indicating that both populations reacted differently to the factor  
367 Site. In Italy and Latvia, the value of the accumulated GDD for IT was similar (1404-1428) and  
368 significantly higher than in Norway (927) or South Turkey (442). In Iran, the GDD value was  
369 2034. This extremely high value could result from heat stress that results in a decrease in  
370 photosynthetic rate, an increase in respiration rate, and a slowed growth and development. The  
371 amount of GDD accumulated in the NO population was significantly different depending on the  
372 site.

373 **3.6 Comparison of plant development based on different phenological characteristics**  
374 **suggests two distinct ecotypes**

375 Data collected in 2016 from Norway, Latvia and Italy were analysed using an ordination  
376 method. The PCA analysis showed that PCA1 scores were different for IT and NO populations,  
377 the highest components being the duration of the tillering stage, the number of tillers and DAE  
378 that passed before the plants reached the heading stage (Fig. 6).

379

380 There was also a difference in PCA2 scores between the two populations in Norway.  
381 However, there was no clear distinction between the sites along PCA1 or PCA2, which combined  
382 accounted for 72.1% of the variance.

383

#### 4. DISCUSSION

384 The results of this study demonstrate similarities and differences in the phenological  
385 behaviour of *E. crus-galli* populations originating from different climates when they were grown  
386 in common gardens. Differences between populations in early plant development were small or  
387 not significant. Similar results were obtained by another group of scientists in a greenhouse  
388 experiment involving two populations of *E. crus-galli*, from Germany and France. No significant  
389 growth rate difference was found during the leaf development stage between the populations  
390 (Bürger *et al.*, 2020). In contrast, in our study, the time to heading was variable in different  
391 populations within each site. Thus, the initial hypothesis was partly confirmed. In NO, the  
392 population originating from the northern site (Norway), the transition to heading was faster than  
393 in IT, originally from the southern site (Italy). Interestingly, the time to reach heading in plants  
394 from local populations in Norway and Latvia tended to be more similar to the NO ecotype, while

395 in local populations from Italy, Iran, and South Turkey, the times to heading were similar to the  
396 IT ecotype. This suggests that there are northern and southern ecotypes, with a considerable  
397 difference between them, and there are also possible intermediate ecotypes. Differences between  
398 plants from northern and southern locations are similar to those described on an altitudinal gradient  
399 by Martinkova *et al.* (2021). A shorter time to flowering could be an adaptation that facilitated the  
400 spread of this species to more northern areas the hypothesis that northern and southern populations  
401 differed such that they are adapted to local conditions can therefore be accepted.

402 Experiments in controlled or more standardized environments and the use of hydrothermal  
403 time would allow more precise comparisons of plant development between the sites. To calculate  
404 the GDD for modelling plant development, it would also be preferable in future studies to test the  
405 hypothesis that the base temperature for leaf, tiller, and flower development of plants from  
406 different populations are common as has been assumed in this paper. In the analysis of the  
407 emergence patterns of different populations of *E. crus-galli*, different  $T_b$  values for seedling  
408 emergence were suggested for two groups of countries: Scandinavian-Baltic (Norway, Sweden,  
409 Latvia) and other sites located in Poland, Italy, Spain, Turkey, and Iran (Royo-Esnal *et al.*, 2022b).

410 The different times taken to reach heading for the NO and IT populations could have been  
411 caused by different mechanisms. Sensitivity to the photoperiod was shown to influence flowering  
412 in *E. crus-galli* (Swanton *et al.*, 2000). The plants of two cultivated *Echinochloa* species, *E. utilis*  
413 Ohwi & Yabuno and *E. frumentacea* Link, had more and larger leaves during long photoperiods  
414 (16 h), but only *E. frumentacea* developed more tillers (Muldoon, 1985). Furthermore, different  
415 cultivars of these two species have different sensitivity to photoperiod, which helps to account for  
416 the plasticity of this trait. In another facultative short-day species, *Panicum virgatum* L., extended  
417 photoperiod increased the phyllochron (time elapsing between the development of consecutive

418 leaves), resulting in a longer development cycle (Esbroek *et al.*, 2003). As Norwegian plants  
419 generally developed faster in this study, it is likely that plants dispersed in northern locations  
420 adapted by losing sensitivity to photoperiod so that they were able to reproduce and produce seeds  
421 during a shorter vegetation season. Another possibility that could cause the observed differences  
422 in the time to reach heading between the plants from the NO and IT populations is the different  
423 reaction of the plants to drought, as no irrigation was applied at most of the sites in Central and  
424 Northern Europe. Drought stress under long day conditions caused delayed flowering in *E. crus-*  
425 *galli* var. *oryzicola* (Conover & Sovonick-Dunford, 1989). Moreover, heat stress has been shown  
426 to delay flower initiation in wheat (Ullah *et al.*, 2022) and in chrysanthemum, which is a short-day  
427 plant (Kazan & Lyons, 2016). Conversely, many plants react to drought by making a more rapid  
428 transition to flowering (Shavrukov *et al.*, 2017). As in the case of photoperiod sensitivity, the  
429 drought and heat sensitivity of different ecotypes should be tested in both controlled and field  
430 conditions, as they are related to the ongoing climate change.

431         In conclusion, the results presented suggest that a common model can be developed for the  
432 early stages of development of the *E. crus-galli* plants. Controlling weeds at an early stage is  
433 important both when using herbicides and / or mechanical control methods, as young plants are  
434 more susceptible. Because early plant development was similar in different populations, it is  
435 suggested that predictions may be valid regardless of the origin of the seeds. Nevertheless, there  
436 was considerable variation in plant development in different sites, caused by differences in  
437 environmental and soil factors. Therefore, a mechanistic model that considers various  
438 environmental factors that can influence plant development will be required to predict heading,  
439 depending on the growing conditions. Prediction of heading time can be used to prevent seed rain  
440 by adjusting harvest time, when possible, and to model the population dynamics of the weed in

441 different crops. The results imply that the origin of the seeds must be taken into account in models  
442 that predict flowering and that such models should be included in decision support systems that  
443 are used to plan crop rotation and weed control.

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#### 456 **CONFLICT OF INTEREST**

457 The authors declare no conflict of interest.

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551

552 Figure captions

553 **Figure 1.** Map showing the geographic location of the study sites. Seeds of the two common  
554 populations were collected in Norway (54 km from the NO site) and Italy (IT site).

555 **Figure 2.** (A) Mean monthly air temperature in 2016-2017, (B) cumulative precipitation and  
556 natural precipitation, including irrigation at the sites where it was applied (Iran, Spain), at the  
557 study sites in 2016 and 2017 from March until the last observation made at the site, and (C)  
558 duration of the day in different months in 2016, assuming that changes are similar in different  
559 years.

560 **Figure 3.** Days after emergence (DAE) elapsed before *Echinochloa crus-galli* plants from the  
561 two common populations – Italy (IT) and Norway (NO) – and the local populations (L1, L2, L3)  
562 reached BBCH stage 12, time of leaf development after developing the second leaf (BBCH 13-  
563 20), duration of tillering (BBCH 21-13), and time until heading (BBCH 41-59) in 2016 (A) and  
564 2017 (B). Sites: IR, Iran, IT, Italy, LV, Latvia, NO, Norway. Mean values are shown for each  
565 population.

566 **Figure 4.** Number of tillers formed by plants from the two common populations, Italy (IT) and  
567 Norway (NO), and the local populations (L1, L2, L3) in 2016. Sites: IR, Iran, IT, Italy, LV,  
568 Latvia, NO, Norway. Mean values are shown for each population; error bars indicate standard  
569 error.

570 **Figure 5.** Growing degree days (GDD) accumulated (A) before plants reached BBCH 12 and (B)  
571 before plants reached the heading stage (BBCH>41) in different sites in 2016. Data for the two  
572 common populations (IT and NO) are shown. Sites: IR – Iran, IT – Italy, LV – Latvia, NO –  
573 Norway, PN, PS – North Poland and South, SP – Spain, TS - South Turkey. Mean values are

574 shown for each population; error bars indicate standard error; different letters denote means that  
575 are significantly different within each site.

576 **Figure 6.** Biplot from Principal Component Analysis (PCA) where the parameters describing the  
577 phenological development of the *E. crus-galli* plants are analysed: DAE before reaching BBCH  
578 12 (DAE 12), DAE before heading (Heading), number of days after emergence before tillering  
579 stage (Leaf stage), number of tillers (Tillers) and duration of tillering stage (Tillering stage) in  
580 2016. Sites: ○ - Norway, □ - Latvia and △ - Italy; the two common populations are IT – Italy  
581 (filled symbols) and NO – Norway (empty symbols). Data from three sites where complete data  
582 could be obtained were used for analysis. BBCH 12=2 fully unfolded leaves on the main shoot,  
583 according to Hack *et al.* 1992.

584 **Table 1.** The geographic location of the experimental sites and growth conditions in 2016 and  
 585 2017.

Site	Lat., Lon.	Clima te <sup>a</sup>	Sowi ng date	Year	Disturba nce date	Emerge nce period	Emerge nce flush, date	Sand , %	Silt, %	Clay , %	OM <sup>b</sup> %	pH
Norway Ås	59°4 0' N, 10°4 6' E	Dfb	23.10. 15	2016	26.04	13.05.- 23.08.	27.05	48.5	31.5	19.5	4.2	6.2
				2017	20.04	18.05.- 05.09.	25.05- 19.06					
Latvia, Carnika va	57°7' N, 24°1 8' E	Dfb	27.10. 15	2016	13.04	12.05.- 29.08.	24.05	52.0	35.0	13.0	2.4	5.8
				2017	12.04	23.05.- 04.08.	31.05- 04.07					
Denmar k, Flakkeb jerg	55°1 9' N, 11°2 4' E	Cfb	11.11. 15	2016	03.05	12.05.- 07.07.	12.05- 24.05	73.7	12.8	12.4	0.6	7.2
Poland, Olsztyn	53°4 6' N, 20°2 9' E	Dfb	29.10. 15	2016	02.04	Not recorde d	06.05- 02.06	-	-	-	-	-
Poland, Krakow	50°0 4' N, 19°5 0' E	Dfb	26.10. 15	2016	05.04	24.04- 27.06.	24.04- 21.05	39.0	52.0	9.0	5.6	6.8
				2017	29.03							
Italy, Padova	45° 20' N, 11° 58' E	Cfa	27.10. 15	2016	29.03	29.03.- 29.06.	19.04	16.0	64.9	19.1	1.8	8.0
				2017	09.03	23.03.- 13.07.	12.04					
Spain, Lleida	41°3 7' N, 0°35' E	Csa	28.11. 15	2016	24.03	24.03.- 16.06.	18.04					
Turkey, Düzce	40°3 0' N, 31°0 5' E	Cfb	21.10. 15	2016	12.04	18.04.- 22.07.	22.04	60.6	7.0	32.4	-	-
				2017	04.10							
Turkey, Antakya	36°1 9' N, 36°1 1' E	Csa	23.11. 15	2016	18.04	18.03.- 23.09.	02.05	38.3	20.4	41.2	0.6	7.4
				2017	10.10	22.03.- 25.09.	01.05					
Iran, Ilam	33°3 9' N, 46°2 3' E	Csa	15.11. 15	2016	20.04	20.04.- 17.06.	05.05	45.0	20.0	35.0	2.0	7.3
				2017	29.04							

586 a – Climate classification according to the updated Köppen-Geiger classification (Kottek *et al.*, 2006): Cfa, Temperate  
587 with no dry season, hot summer; Cfb, Temperate with no dry season, warm summer; Csa, Temperate with dry and hot  
588 summer (warm Mediterranean); Dfb, Cold with no dry season and warm summer (continental).  
589 b – OM, organic matter content

590 **Table 2.** BBCH growth stages used to characterize plant development (according to Hack *et al.*,  
 591 1992)

BBCH stage	Plant development
12	2 fully extended leaves
18	8 leaves on the main shoot fully unfolded
21	1 tiller visible
29	9 or more visible tillers
31	1 node detectable (beginning of stem elongation)
39	flag leaf fully emerged
41	flag leaf sheath extending (beginning of booting)
51	beginning of the heading stage
59	end of the heading stage

592

593

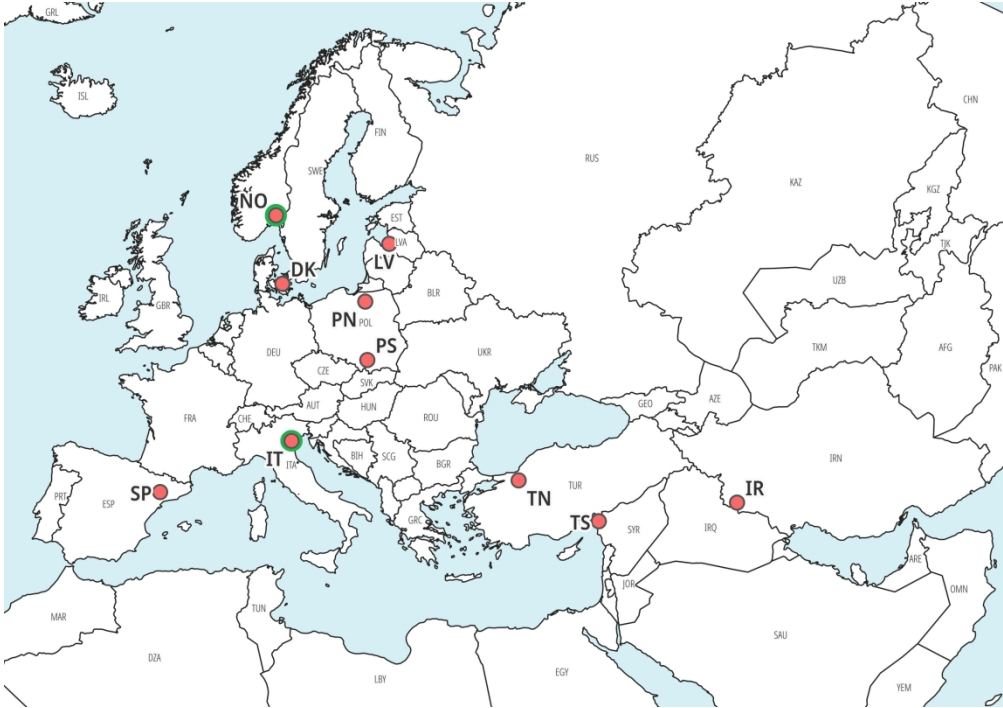


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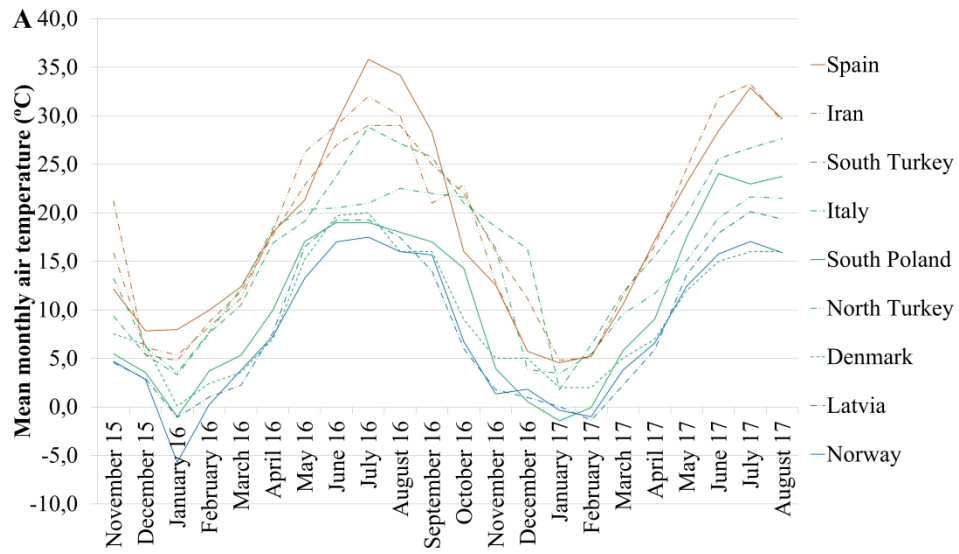
595 Supplementary Table

596 The number of monitored plants, average days after emergence (DAE) to the second leaf stage  
597 (BBCH 12), tillering (BBCH 21), average number of tillers and DAE to heading (BBCH 41-59)  
598 from the two common populations – Italy (IT) and Norway (NO) – and the local populations (L1,  
599 L2, L3) at each experimental site in 2016 and 2017. Standard deviation and standard error values  
600 are given. Sites: DK – Denmark, IR – Iran, IT – Italy, LV – Latvia, NO – Norway, PN = North  
601 Poland, PS – South Poland, SP – Spain, TN – North Turkey, TS – South Turkey.

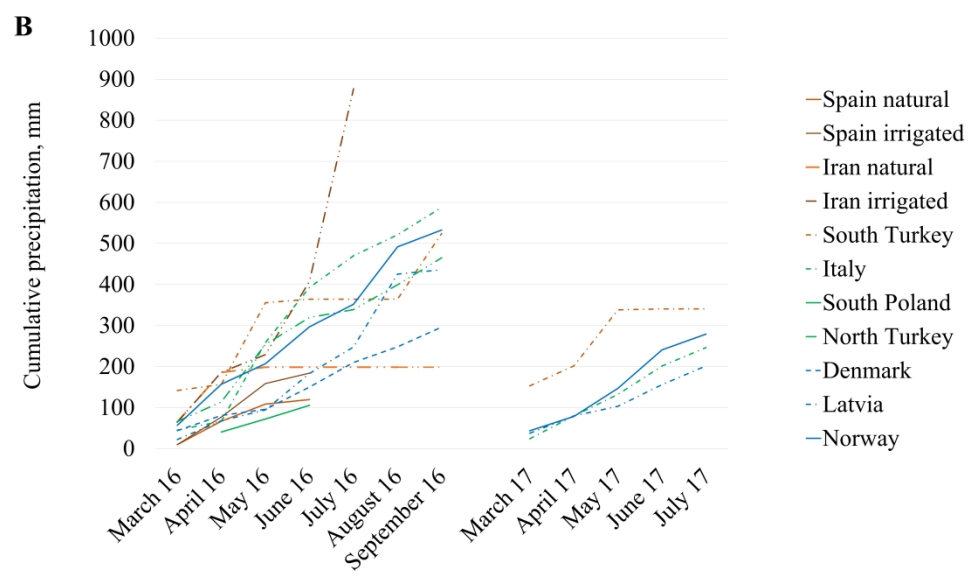
Year	Site	Population	Number of plants	Days after emergence (DAE)			Duration of tillering stage, days			Number of tillers			DAE to heading			
				to BBCH12	Standard deviation	SE	Standard deviation	SE	Standard deviation	SE	Standard deviation	SE	Standard deviation	SE		
2016	DK	C1	3	3.00	0.00	0.00	NA	NA	NA	3.00	0.00	0.00	NA	NA	NA	
2016	DK	C2	3	3.00	0.00	0.00		27.00	0.00	0.00	4.33	0.58	0.33	44.00	0.00	0.00
2016	DK	DKL1	3	3.00	0.00	0.00	NA	NA	NA	4.00	0.00	0.00	NA	NA	NA	
2016	DK	DKL2	3	3.00	0.00	0.00		41.00	0.00	0.00	6.33	1.15	0.67	58.00	0.00	0.00
2016	IR	C1	15	12.00	0.00	0.00		63.69	12.28	3.17	5.67	1.80	0.46	86.46	7.28	1.88
2016	IR	IRL2	15	12.00	0.00	0.00		60.08	8.78	2.27	5.60	1.80	0.47	79.92	10.64	2.75
2016	IR	IRL3	15	12.00	0.00	0.00		58.21	10.08	2.60	4.67	2.44	0.63	87.00	7.19	1.86
2016	IT	C1	15	10.00	4.00	1.03		60.47	17.37	4.49	4.80	2.51	0.65	89.93	3.69	0.95
2016	IT	C2	15	8.73	4.73	1.22		19.00	7.86	2.03	1.80	0.86	0.22	48.33	5.98	1.55
2016	IT	ITL1	15	14.00	0.00	0.00		62.47	4.37	1.13	4.73	2.37	0.61	91.00	0.00	0.00
2016	IT	ITL2	12	14.00	5.03	1.45		51.25	17.02	4.91	4.42	3.34	0.96	87.50	3.09	0.89
2016	IT	ITL3	15	13.00	3.46	0.89		61.67	2.77	0.71	3.73	2.05	0.53	90.60	1.55	0.40
2016	LV	C1	15	7.00	3.59	0.93		36.50	12.21	3.15	2.33	2.35	0.61	110.13	25.10	6.48
2016	LV	C2	15	5.33	3.42	0.88		11.14	15.63	4.04	0.60	1.06	0.27	60.00	4.15	1.07
2016	LV	LVL1	15	5.80	3.55	0.92		18.60	10.56	2.73	1.80	1.26	0.33	49.33	7.32	1.89
2016	LV	LVL2	15	4.50	2.98	0.77		12.93	13.29	3.43	1.33	1.35	0.35	53.33	5.79	1.49
2016	NO	C1	15	9.67	1.95	0.50		59.67	15.84	4.09	7.60	2.23	0.58	95.21	19.56	5.05
2016	NO	C2	15	7.00	0.00	0.00		28.20	5.71	1.47	4.67	0.62	0.16	52.93	2.81	0.73
2016	NO	NOL1	15	7.53	1.41	0.36		32.60	6.29	1.62	5.00	1.65	0.43	54.93	2.46	0.64
2016	NO	NOL2	15	8.60	2.03	0.52		33.40	6.29	1.62	4.40	1.76	0.46	54.00	0.00	0.00
2016	NO	NOL3	15	8.87	2.07	0.53		24.27	6.87	1.77	4.40	1.24	0.32	57.27	3.61	0.93
2016	PN	C1	18	10.33	4.70	1.11		25.25	8.30	1.96	7.50	1.15	0.27	NA	NA	NA
2016	PN	C2	18	11.67	3.45	0.81		15.33	3.60	0.85	6.33	1.75	0.41	NA	NA	NA
2016	PN	PNL1	18	10.33	3.83	0.90		20.00	6.64	1.57	7.67	1.85	0.44	NA	NA	NA
2016	PN	PNL2	18	9.50	3.60	0.85		22.40	7.37	1.74	7.00	1.46	0.34	NA	NA	NA
2016	PN	PNL3	18	10.33	3.65	0.86		16.83	4.69	1.11	7.83	1.25	0.29	NA	NA	NA
2016	PS	C1	15	3.20	1.66	0.43		12.53	2.50	0.65	5.27	1.87	0.48	NA	NA	NA
2016	PS	C2	15	6.00	0.00	0.00		17.57	1.95	0.50	5.93	1.67	0.43	NA	NA	NA
2016	PS	PSL1	12	3.00	1.81	0.52		13.75	2.26	0.65	5.33	2.02	0.58	NA	NA	NA
2016	PS	PSL2	15	6.00	2.62	0.68		13.53	2.88	0.74	5.20	1.47	0.38	NA	NA	NA
2016	PS	PSL3	15	5.20	3.76	0.97		11.60	2.67	0.69	4.40	1.80	0.47	NA	NA	NA
2016	SP	C1	15	9.80	2.81	0.73		18.67	5.51	1.42	5.20	1.74	0.45	NA	NA	NA
2016	SP	C2	15	8.00	2.98	0.77		18.33	5.90	1.52	3.73	1.75	0.45	NA	NA	NA
2016	SP	SPL1	15	10.71	2.70	0.70		18.85	3.36	0.87	5.29	1.94	0.50	NA	NA	NA
2016	SP	SPL2	15	11.40	2.95	0.76		17.73	3.71	0.96	4.67	1.76	0.45	NA	NA	NA
2016	SP	SPL3	15	11.53	3.34	0.86		17.07	3.31	0.85	5.00	1.60	0.41	NA	NA	NA
2016	TN	C1	15	NA	NA	NA		19.13	2.42	0.62	NA	NA	NA	NA	NA	NA
2016	TN	C2	15	NA	NA	NA		17.33	3.31	0.85	NA	NA	NA	NA	NA	NA
2016	TN	TNL1	15	NA	NA	NA		20.67	1.29	0.33	NA	NA	NA	NA	NA	NA
2016	TN	TNL2	15	NA	NA	NA		20.47	1.46	0.38	NA	NA	NA	NA	NA	NA
2016	TN	TNL3	7	NA	NA	NA		16.00	0.00	0.00	NA	NA	NA	NA	NA	NA
2016	TS	C1	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	26.27	5.69	1.47
2016	TS	C2	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	18.00	0.00	0.00
2016	TS	TSL1	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	42.93	8.72	2.25
2016	TS	TSL2	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	39.20	6.90	1.78
2016	TS	TSL3	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	53.67	8.64	2.23
2017	IT	C1	15	21.33	10.07	2.60		22.25	19.67	5.08	2.00	0.00	0.00	59.25	18.63	4.81
2017	IT	C2	15	16.53	8.88	2.29		14.36	6.96	1.80	1.71	1.20	0.31	48.47	6.94	1.79
2017	IT	ITL1	15	22.30	10.41	2.69		21.25	19.98	5.16	2.00	1.58	0.41	61.56	10.99	2.84
2017	IT	ITL2	15	20.53	8.51	2.20		15.07	14.91	3.85	1.71	1.68	0.43	65.29	13.01	3.36
2017	IT	ITL3	15	21.00	7.95	2.05		30.70	14.94	3.86	2.54	1.20	0.31	71.70	11.16	2.88
2017	LV	C1	15	15.62	4.39	1.13		30.00	7.50	1.94	4.14	2.54	0.66	65.80	25.01	6.46
2017	LV	C2	15	14.00	4.10	1.06		27.31	7.94	2.05	3.31	1.03	0.27	59.31	10.64	2.75
2017	LV	LVL1	13	19.67	6.15	1.71		21.27	8.84	2.45	2.82	1.72	0.48	53.50	13.02	3.61
2017	LV	LVL2	15	17.92	3.60	0.93		26.92	8.23	2.13	3.23	1.01	0.26	60.46	4.39	1.13
2017	NO	C1	9	6.44	2.60	0.87		60.00	17.04	5.68	2.00	2.10	0.70	NA	NA	NA
2017	NO	C2	12	11.08	2.71	0.78		8.83	12.15	3.51	0.75	0.97	0.28	77.25	12.64	3.65
2017	NO	NOL1	9	7.56	4.16	1.39		6.78	13.45	4.48	0.50	1.41	0.47	66.89	12.84	4.28
2017	NO	NOL2	8	7.38	3.78	1.34		12.25	13.54	4.79	0.88	0.99	0.35	64.13	10.48	3.71
2017	NO	NOL3	13	8.15	3.63	1.01		16.08	9.99	2.77	2.00	1.65	0.46	66.58	7.38	2.05
2017	TS	C1	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	35.93	6.41	1.65
2017	TS	C2	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	29.73	7.05	1.82
2017	TS	TSL1	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	39.67	3.42	0.88
2017	TS	TSL2	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	37.80	4.43	1.14
2017	TS	TSL3	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	48.53	8.56	2.21



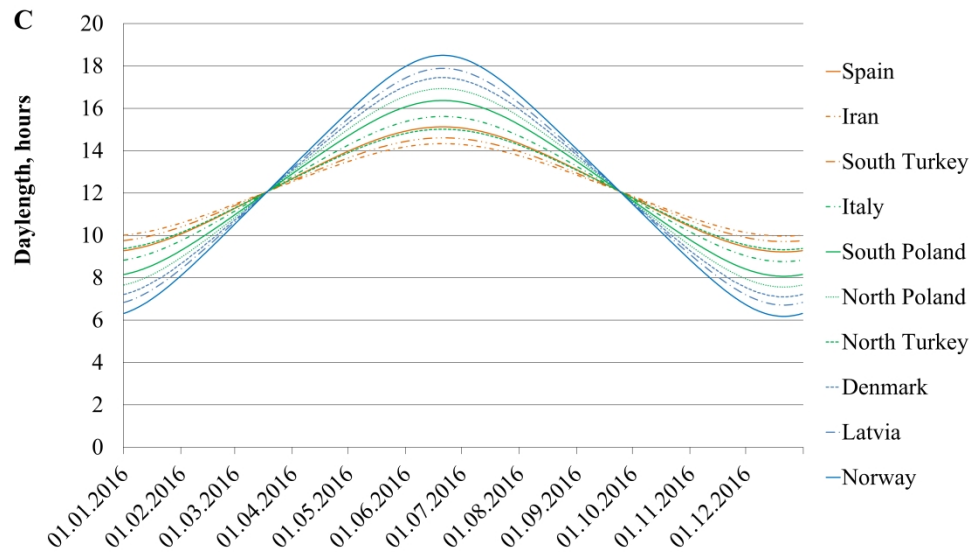
209x147mm (300 x 300 DPI)



636x397mm (300 x 300 DPI)



617x381mm (300 x 300 DPI)



638x392mm (300 x 300 DPI)

