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Phenological development of barnyard grass plants originating from different geographical locations

Jevgenija Necajeva[1] | **Aritz Royo-Esnal**[2] | **Donato Loddo**[3] | **Peter Jensen**[4] | **Alireza Taab**[5] | **Agnieszka Synowiec**[6] | **Ahmet Uludag**[7,8] | **Ilhan Uremis**[9] | **Alistair Murdoch**[10] | **Anna Bochenek**[11] | **Andrea Onofri**[12] | **Kirsten Torresen**[13]

[1]Institute for Plant Protection Research 'Agrihorts', Latvia Univ. of Life Sciences and Technologies, Jelgava LV-3004, Latvia

[2]Dep. d'Hortofructicultura Botànica i Jardineria, l'Escola Tècnica Superior d'Enginyeria Agrària, Univ. of Lleida-Agrotecnio Center, Lleida 25198, Spain

[3]Institute for Sustainable Plant Protection, Consiglio Nazionale delle Ricerche, Legnaro, Padua 35020, Italy

[4]Dep. of Agroecology, Aarhus Univ., Slagelse 4200, Denmark

[5]Dep. of Agronomy and Plant Breeding, Faculty of Agriculture, Ilam Univ., Ilam 69391-7711, Iran

[6]Dep. of Agroecology and Crop Production, Univ. of Agriculture in Krakow, Krakow, Poland

[7]Faculty of Agriculture, Çanakkale Onsekiz Mart Univ., Çanakkale 17100, Turkey

[8]Faculty of Agriculture and Nature Sciences, Düzce Univ., Düzce 81620, Turkey

[9]Dep. of Plant Protection, Mustafa Kemal Univ., Antakya 31040, Turkey

[10]School of Agriculture, Policy and Development, Univ. of Reading, Reading, UK

[11]Dep. of Plant Physiology, Genetics and Biotechnology, Univ. of Warmia and Mazury, Olsztyn 10-71, Poland

[12]Dep. Agricultural, Food and Environmental Sciences, Univ. of Perugia, Perugia 74–06121, Italy

[13]Division for Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research, Ås NO-1433, Norway

Correspondence
Jevgenija Necajeva, Institute for Plant Protection Research 'Agrihorts', Latvia University of Life Sciences and Technologies, Jelgava, LV-3400, Latvia.
Email: jevgenija.necajeva@lu.lv

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Abstract

Barnyard grass [*Echinochloa crus-galli* (L.) Beauv] is a competitive C_4 weed species that is widely distributed throughout the world. Although 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 (ranging from 45.9 to 98.3% on average) in the Norwegian than in the Italian population. However, in the leaf development stage, the

Abbreviations: BBCH, Biologische Bundesanstalt, Bundessortenemt and Chemical industry; DAE, days after emergence; GDD, growing degree-days; IT, population originating from Italy; L1, L2, L3, first, second, and third local populations; LV, population originating from Latvia; NO, population originating from Norway; PCA, principal component analysis; PS, population originating from South Poland; TS, population originating from South Turkey.

difference between the common populations was smaller by, 23.5% on average (0–46.7%) and was mostly not significant. Our results indicate that different *E. crus-galli* ecotypes, characterized by differences in their phenological development, evolved within the distribution area of this species in Europe. However, the early development of the plants progressed 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 into plant population dynamics.

1 | INTRODUCTION

Barnyard grass [*Echinochloa crus-galli* (L.) P. Beauv.] is a highly competitive summer annual C_4 weed globally spread across a wide climatic gradient. It has been reported in 61 countries in various crops (Maun & Barrett, 1986). Originating in warmer areas of Asia and Europe (Maun & Barrett, 1986), *E. crus-galli* spread to the northern parts of Europe and North America by the end of the 19th century, being discovered as far north as Norway in 1878 (Clements et al., 2004; Brodal et al., 2016). In Europe, countries, *E. crus-galli* occurs as a weed in spring cereal crops, potato (*Solanum tuberosum* L.) (Brodal et al., 2016), and maize (*Zea mays* L.) (Pannwitt et al., 2021), as well as rice (*Oryza sativa* L.) (Bajwa et al., 2015). Infestation results in yield loss, and an additional threat is posed by herbicide resistance in this weed (Bajwa et al., 2015; Heap, 2022). Phenological adaptations to the northern climate included a faster development to maturity that has involved biochemical adaptations of C_4 photosynthesis enzymes to colder conditions (Simon & Hatch, 1994) and differences in resource allocation between southern and northern populations (Potvin, 1986). Different ecotypes can exhibit various rates of biomass accumulation, depending on the temperature and photoperiod, and show diverse growth habits (prostrate or erect) and pigmentation intensity (Rono, 1994). In addition, an interesting example of intraspecific variability between highland and lowland populations was described in the northwest Carpathians. This variability included differences in the percentage of germination, heading, and seed dispersal time, with plants from the highland location developing and dispersing seeds earlier than those from the lowland location (Martinkova et al., 2021).

Differences in phenology among populations have also been described for some other species that are distributed over a wide range of latitudes. For example, in *Ambrosia artemisiifolia* L., the onset of flowering occurs earlier with increasing latitude (Stinson et al., 2016). Covariation in the primary dormancy, vegetative growth rate, and flowering time along a latitudinal cline was observed in *Arabidopsis thaliana* (L.) Heynh. genotypes. At higher latitudes, the vegetative growth rate was positively correlated with primary dormancy and negatively with flowering time, but the trend disappeared at lower latitudes (Debieu et al., 2013). Adaptation to shorter growing seasons in northern latitudes may have driven the selection of early-flowering phenotypes. Agronomic pressures affecting weeds' life cycle, specifically seed yield, dispersal, or germination, can also become drivers of selection. For example, a change in flowering time in response to harvest weed seed control was described in *Raphanus raphanistrum* L. (Ashworth et al., 2016). In the C_4 grass *Miscanthus sacchariflorus* (Maxim.) Hack., flowering generally occurs earlier in plants originating from higher latitudes, whereas a higher accumulation of biomass tends to be associated with late-flowering individuals, although factors other than the latitude also influence the flowering time (Jensen et al., 2013).

Predicting the phenological development of weed species is of practical importance, as appropriate timing is essential for successful weed management. Both chemical and non-chemical control operations must be planned according to the weed's development stage; therefore, growth models based on phenological stages can be a useful basis for decision support systems (Parsons et al., 2009). Predicting flowering time is also useful for reducing the production of weed seed; for example, planning hand weeding and adapting the harvest time to reduce weed seed rain, or selecting crop cultivars with a shorter life cycle, if necessary. These tactics can be important for implementing integrated weed management approaches. Thermal time or growing degree-days (GDD) has been successfully used to model the development of *E. crus-galli* plants (Swanton et al., 2000; Shrestha & Swanton, 2007). However, weed populations must adapt to different climatic conditions and photoperiods to survive and reproduce. Therefore, the question arises whether a single growth model for *E. crus-galli* can describe the phenological development of plants from different origins and/or plants from the same origin transported to non-native locations. As a step towards answering this question, the growth of *E. crus-galli* plants of different geographic origins was compared in different countries under common garden conditions.

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

Core Ideas

- Different ecotypes of barnyard grass have developed in southern and northern populations.
- In northern populations heading occurs earlier than in southern populations.
- Vegetative development is similar in different populations.

2 | MATERIALS AND METHODS

2.1 | Seed collection and experimental setup

The seeds of two populations of *E. crus-galli* that were used in all sites (referred to as "common populations") were collected from a maize field in Italy (IT) (45˚20′ N 11˚58′ E), and from a spring barley (*Hordeum vulgare* L.) field in Norway (NO; 59˚24′ N, 9˚58′ E) in August and September 2015, respectively. The fields were 0 and 54 km away from the sites where the experiment was carried out in Italy and Norway, respectively. Seeds were collected at maturity from at least 15 individuals, dried at 20 to 25 ˚C for 1 wk, sieved to remove the chaff, and stored at a low temperature (3–5 ˚C) before sowing. The seeds of the two common populations were distributed to the participants by HerbiSeed Co. UK after obtaining phytosanitary certificates. In addition, seeds of two or three local populations were collected near to each study site via a similar protocol to the common population. These additional populations, presumably adapted to the local environmental conditions, were used in the experiment to compare their phenology with that of the IT and NO populations. For convenience, the local populations were coded with the abbreviation of the site name (IT, Italy; LV, Latvia; NO, Norway; PS, South Poland; TS, South Turkey) and the number of the population (L1, L2, and L3).

Pot experiments were set up under field conditions at 10 different sites belonging to different countries: Denmark, Iran, Italy, Latvia, Norway, two sites in Poland (North, Olsztyn; South, Krakow), Spain, and two sites in Turkey (North, Düzce; South, Antakya), achieving a wide climatic gradient (Figure 1; Table 1).

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

The pots were dug into the ground so that only the upper 1 cm was above the soil layer, and were covered with mesh (mesh sizes from 9 to 20 mm) to prevent seed predation. The pots were not irrigated except, if necessary, at sites where *E. crus-galli* development would otherwise be impossible and where crops are normally irrigated (Spain, Iran, South Turkey, and, in 2017, Italy). The total amounts of water added as irrigation during the 2016 season were equivalent to 65 mm in Spain and 1127 mm in Iran. The amounts were not recorded in Italy and South Turkey. In spring 2016 and 2017, shallow soil disturbance was performed at the time when sowing or tillage would be performed in the local area. Either the upper 5-cm layer was removed, placed on a tray, mixed well, and replaced in the corresponding pot, or the top 5 cm of soil was mixed with a garden cultivator (Latvia). Nitrogen–phosphorus–potassium fertilizer was added at the time of spring disturbance at a nitrogen rate of 50 kg ha^{-1}.

2.2 | Assessments

After the main flush of emergence in spring, determined as the date when highest number of newly emerged seedlings was recorded (Royo-Esnal, Onofri, Loddo, et al., 2022), seedlings were removed, leaving three plants of a similar age in each pot, which were preserved for monitoring their development on the Biologische Bundesanstalt, Bundessortenemt and Chemical industry (BBCH) scale (Hack et al., 1992). The BBCH stages used to characterize plant development are described in Table 2.

It was assumed that the competition among the plants would not influence their transition to different phenological stages (Swanton et al., 2000 and references therein). The BBCH stage of each individual plant was recorded once or twice weekly during the period from emergence until tillering at the sites where the plants were removed early (Denmark, North and South Poland, Spain, and North Turkey) or until heading of the main tiller (i.e., in Norway, Latvia, Italy, South

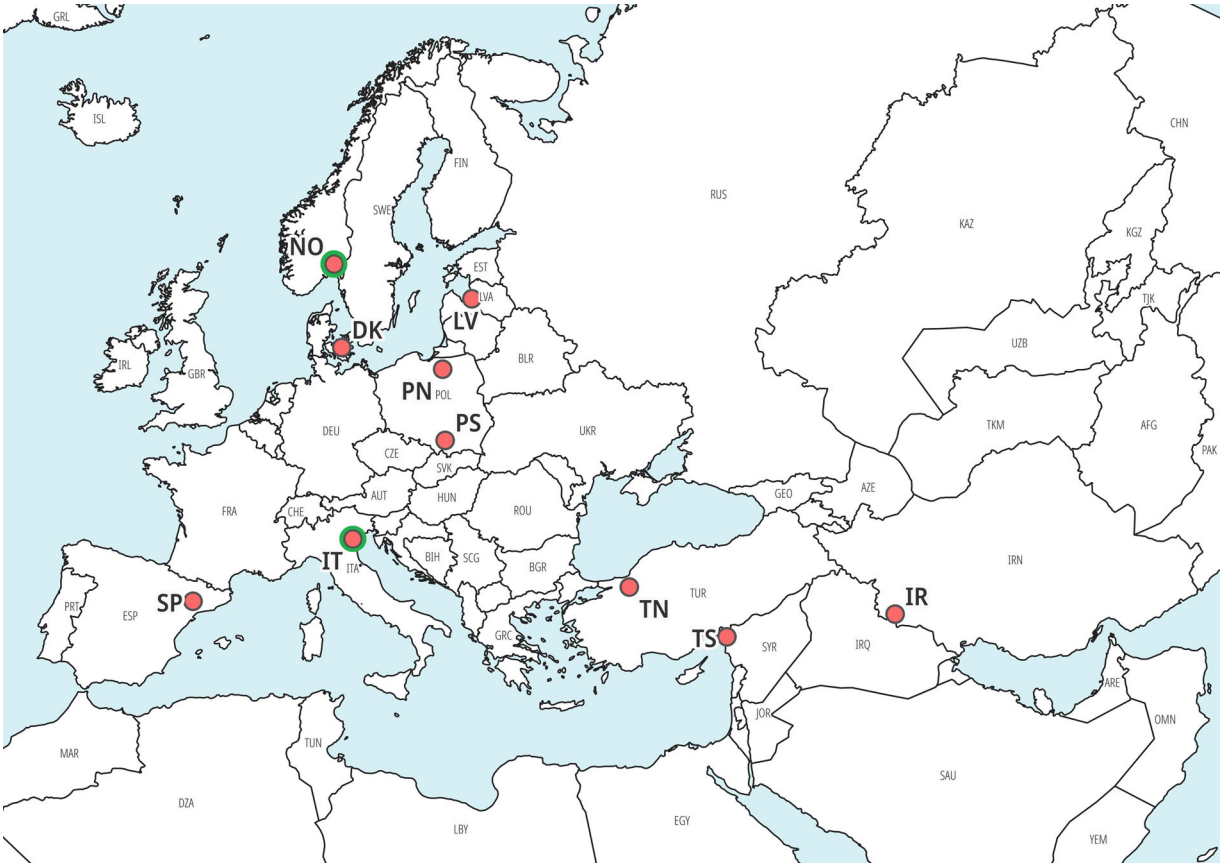

FIGURE 1 Map showing the geographic locations of the study sites. Seeds of the two common populations were collected in Norway (54 km from the NO site) and Italy (IT site). DK, Denmark; IR, Iran; IT, Italy; LV, Latvia; NO, Norway; PN, North Poland; PS, South Poland; SP, Spain; TN, North Turkey; TS, South Turkey

Turkey, and Iran). The date of the emergence flush was set as the starting point for the accumulation of days after emergence (DAE). The time required to reach BBCH 12 and BBCH 41 to 59 was determined at each site for each plant; BBCH 12 is usually the stage from which postemergence chemical control should be applied. The duration of tillering was recorded as the period between BBCH 21 and 31, and the total number of tillers was recorded. The date when plants reached BBCH stages exceeding 41 (BBCH 41–59) was recorded and was used as the starting date for heading. Only the plants reaching this stage were included in the analysis of the time of heading.

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

$$\text{GDD} = \Sigma\left(\frac{T_{\max} + T_{\min}}{2}\right) - T_b$$

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

The weather data, including air temperature and precipitation, were obtained from the meteorological stations nearest to each experimental site. The duration of the day in each site was calculated using the National Oceanic & Atmospheric Administration's online solar calculator tool (https://gml.noaa.gov/grad/solcalc/).

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

2.3 | Statistical analyses

Within each site, separate mixed linear models were used to analyze the data. Population (three to five populations,

TABLE 1 The geographic location of the experimental sites and growth conditions in 2016 and 2017

Site	Latitude and Longitude	Climate[a]	Sowing date	Year	Disturbance date	Emergence period	Date of emergence flush	Sand	Silt	Clay	OM	pH
								%				
Ås, Norway	59°40′ N, 10°46′ E	Dfb	23 Oct. 2015	2016	26 Apr.	13 May–23 Aug.	27 May	48.5	31.5	19.5	4.2	6.2
				2017	20 Apr.	18 May–5 Sept.	25 May–19 June					
Carnikava, Latvia	57°7′ N, 24°18′ E	Dfb	27 Oct. 2015	2016	13 Apr.	12 May–29 Aug.	24 May	52.0	35.0	13.0	2.4	5.8
				2017	12 Apr.	23 May–4 Aug.	31 May–4 July					
Flakkebjer, Denmark	55°19′ N, 11°24′ E	Cfb	11 Nov. 2015	2016	3 May	12 May–7 July	12 May–24 May	73.7	12.8	12.4	0.6	7.2
Olsztyn, Poland	53°46′ N, 20°29′ E	Dfb	29 Oct. 2015	2016	2 Apr.	Not recorded	6 May–2 June	–	–	–	–	–
Krakow, Poland	50°04′ N, 19°50′ E	Dfb	26 Oct. 2015	2016	5 Apr.	24 Apr.–27 June	24 Apr.–21 May	39.0	52.0	9.0	5.6	6.8
				2017	29 Mar.							
Padova, Italy	45°20′ N, 11°58′ E	Cfa	27 Oct. 2015	2016	29 Mar.	29 Mar.–29 June	19 Apr.	16.0	64.9	19.1	1.8	8.0
				2017	9 Mar.	23 Mar.–13 July	12 Apr.					
Lleida, Spain	41°37′ N, 0°35′ E	Csa	28 Nov. 2015	2016	24 Mar.	24 Mar.–16 June	18 Apr.	34.3	46.3	19.4	2.13	7.4
Düzce, Turkey	40°30′ N, 31°05′ E	Cfb	21 Oct. 2015	2016	12 Apr.	18 Apr.–22 July	22 Apr.	60.6	7.0	32.4	–	–
				2017	4 Oct.							
Antakya, Turkey	36°19′ N, 36°11′ E	Csa	23 Nov. 2015	2016	18 Apr.	18 Mar. –23 Sept.	2 May	38.3	20.4	41.2	0.6	7.4
				2017	10 Oct.	22 Mar.–25 Sept.	1 May					
Ilam, Iran	33°39′ N, 46°23′ E	Csa	15 Nov. 2015	2016	20 Apr.	20 Apr.–17 June	5 May	45.0	20.0	35.0	2.0	7.3
				2017	29 Apr.							

Note. OM, organic matter content.

[a]Climate classification according to the updated Köppen–Geiger classification (Kottek et al., 2006): Cfa, temperate with no dry season, hot summers; Cfb, temperate with no dry season, warm summers; Csa, temperate with dry and hot summers (warm Mediterranean); Dfb, cold with no dry season and warm summers (continental).

TABLE 2 BBCH growth stages used to characterize plant development (according to Hack et al., 1992)

BBCH stage	Plant development
12	Two fully extended leaves
18	Eight leaves on the main shoot fully unfolded
21	One tiller visible
29	Nine or more visible tillers
31	One 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

Note. BBCH, plant phenological development scale derived from the Zadoks scale.

depending on the site) was included as a fixed factor, and the pots were included as a random effect to account for subsampling (each pot contained up to three plants, that is, three observational units). In the sites where data were obtained for a second season, in the initial analysis, year was also included as a fixed factor and year × population was included as an interaction term. The dependent variable in each model was the time (DAE) required for each plant to reach BBCH 12, the duration of tiller formation (BBCH 21–31), and the number of tillers or DAE to reach heading (BBCH 41–59). All response variables were square-root transformed to ensure that the data conformed to the basic assumptions for the linear models. The transformation was selected after preliminary analyses based on the method outlined by Box and Cox (1964). The significance of the fixed effects was tested via χ^2 likelihood ratio tests (Pinheiro & Bates, 2000). Multiple comparison testing was performed according to a procedure based on multivariate *t*-distribution, controlling for the family-wise error rate (a generalized hypothesis testing procedure with multiplicity adjustment) (Bretz et al., 2011). To compare the time (DAE) required to reach a particular stage of development between different populations, the difference between the mean DAE values was expressed as a percentage (%). To compare the two common populations in terms of the difference in DAE (ΔDAE, as a percentage), the following formula was used:

$$\Delta\text{DAE} = (\text{DAE}_{\text{IT}} - \text{DAE}_{\text{NO}})/\text{DAE}_{\text{IT}} \times 100$$

where DAE_{IT} is the DAE for the IT population and DAE_{NO} is the DAE for the NO population.

An additional analysis was performed with mixed models to compare the plants' development in the two common populations among the sites. The interaction between the site and population (fixed effects), with pot as a random effect were tested with GDD to BBCH 12 and GDD accumulated before heading as the dependent variables.

Data from three sites where complete data could be obtained (Norway, Latvia, and Italy), were used for principal component analysis (PCA). Variables that describe the phenological development of the IT and NO plants were used in the PCA: DAE to reach BBCH 12, duration of the leaf stage, number of tillers, duration of the tillering stage, and DAE to reach heading (BBCH 41–59). The first two principal components for row scores and column scores were displayed on a distance biplot. All analyses were performed using the R program version 4.1.1. (R Core Team, 2021) with the "lme()" function in the "nlme" package (Pinheiro & Bates, 2000), the "glht()" function in the "multcomp" package (Hothorn et al., 2008), and the "rda()" function in the "vegan" package (Oksanen et al., 2019).

3 | RESULTS

3.1 | Climatic conditions at the experimental sites and seedling emergence

In 2016, mean air temperatures in spring and summer were higher in Spain, Iran, South Turkey, and Italy (10.5–35.8 ˚C) than in North Turkey, Denmark, Latvia, South Poland, and Norway (2.2–22.5 ˚C) (Figure 2a). A temperature difference was generally apparent between the two groups of sites: the temperature was lower in the temperate or cold sites without a dry season (Köppen–Geiger Dfb and Cfb), and higher in the temperate regions with a dry season (Köppen–Geiger Csa, Cfa, and warm Mediterranean). In North Turkey, the temperatures were higher than in the other sites classified as temperate with no dry season (12.2–22.5 ˚C). The total amount of natural precipitation beginning from the time of soil disturbance in the spring (April) was highest in South Turkey and Norway (157 mm) and from May 2016 onwards, also in Italy (258 mm). In contrast, the amount of precipitation was lowest (40–68 mm) in Latvia, especially at the time of plant emergence and early development in April in South Poland, and in Spain before the plants were irrigated more intensively, starting in May (Figure 2b). In Iran, plants were irrigated after the end of May. As a result, the combination of rainfall and irrigation provided a relatively high moisture level (Figure 2b). In 2017, the meteorological conditions were not favorable for the development of *E. crus-galli*, probably because of low precipitation, and the plants did not develop in several sites. For this reason, only data from Norway, Italy, Latvia, and South Turkey were analyzed. No complete meteorological information was available for North Poland.

The daylength varied throughout the year, and these differences in photoperiod among the sites were maximal at the end of June (Figure 2c). During the period of emergence, the daylength exceeded 13 h at all sites, starting from South Poland and extending further to the north, considering the time of emergence in both years. The longest day was in Norway (17–18 h, approaching 19) and the second longest

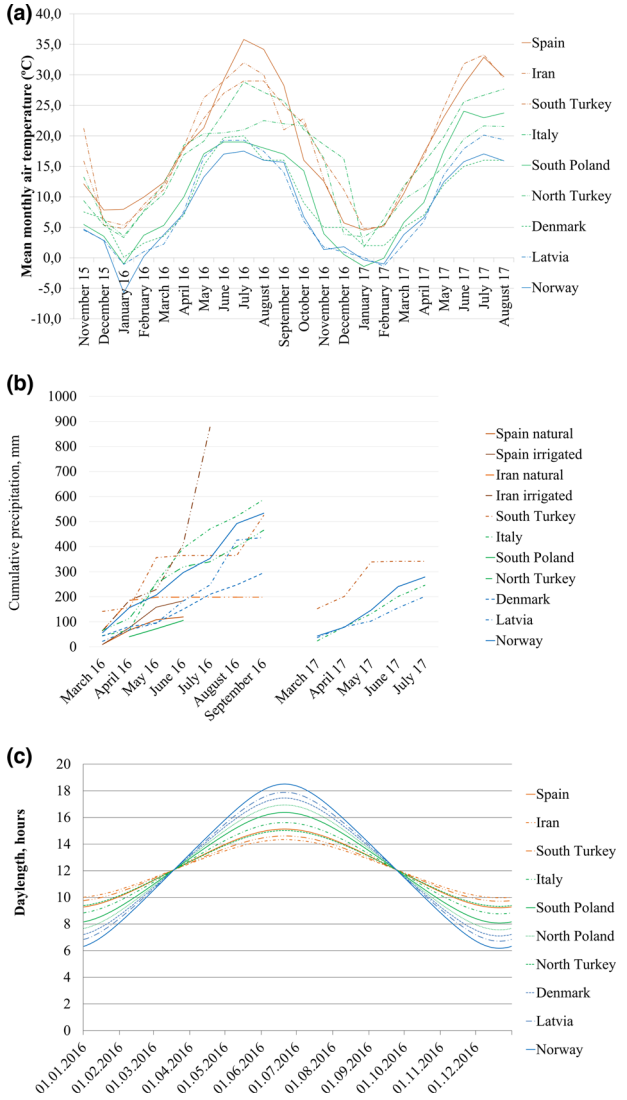

FIGURE 2 (a) Mean monthly air temperature in 2016–2017. (b) Cumulative precipitation and natural precipitation at the study sites in 2016 and 2017 from March until the last observation made at the site, including irrigation at the sites where it was applied (Iran, Spain). (c) Duration of the day in different months in 2016, assuming that the changes are similar in different years

was in Latvia (17 h, approaching 18), whereas in the southern sites (Italy, South and North Turkey, Iran), it ranged from 13 to 14 h.

Seedling emergence did not start until the spring of 2016 in most sites. An exception was North Turkey, where a flush of emergence was observed before April 2016 (Royo-Esnal, Onofri, Loddo, et al., 2022), but this was not considered in this study. The main flush of seedling emergence in 2016 occurred in mid-April in Spain and Italy, and at the end of April and the beginning of May in North Turkey, South Turkey, and Iran (Table 1). In Iran, no emergence was recorded for NO and one of the local populations (L1). In North Poland and South Poland, the emergence dates differed between the populations and lasted throughout May. In Denmark, Latvia, and Norway, the main emergence flush was at the end of May. In 2017, the main emergence flush occurred later than in 2016 in Norway and Latvia (end of May–beginning of June), but was earlier in Italy (beginning of April). In South Turkey, the emergence date was similar to 2016 (1 and 2 May).

3.2 | Small differences in the early stages of phenological development between populations were observed

In 2016, the median DAE to reach BBCH 12 in all populations at different sites was 9 d (range: 2–20 d). Because the growth conditions were not the same in each site, different populations were compared within each site. In the initial analysis performed to test whether the time (DAE) to reach BBCH 12 was similar in both years of the study, there was a significant interaction in Norway and Latvia, but not in Italy, so the data for each year were analyzed and are presented separately. The number of monitored plants and mean values for each site in both years are given in Supplementary Table S1. Only data for the sites with full results are shown in the figures included the main text.

In Norway in 2016, NO and NO_L1 reached BBCH 12 significantly earlier than IT ($p < .0001$ and $p = .0013$, respectively). The NO population developed faster than two of the local populations (NO_L2, $p = .0285$ and NO_L3, $p = .0068$) (Figure 3a). In 2017, the NO population reached BBCH 12 later than IT ($p = .0038$) and local populations (NO_L1, $p = .0474$; NO_L2, $p = .0435$; NO_L3, $p = .0416$) (Figure 3b).

In Italy, in 2016, NO and IT reached BBCH 12 in a similar DAE; however, the NO population reached the same stage significantly earlier than the local populations (IT_L1, $p = .002$; IT_L2, $p = .012$; IT_L3, $p = .02$) (Figure 3a). There were no significant differences among the populations in 2017 (Figure 3b).

In South Poland, IT plants developed faster (3.59 ± 0.9 DAE) than NO plants (6.78 ± 1.1 DAE, $p < .0001$). There were also significant differences between PS_L1 and both NO ($p < .0001$) and IT ($p = .024$), and between local populations (PS_L1 and PS_L2, $p < .0001$; PS_L1 and PS_L3, $p < .0001$). In Spain, NO developed faster than each of the local populations (SP_L1, $p = .0071$; SP_L2, $p = .0005$; SP_L3, $p = .0004$). In North Turkey, the development of plants in all populations was rapid, and more than 50% of the plants had reached the tillering stage at the first date when observations were recorded (11 DAE). There was no difference between the IT and NO populations in the early stages of development at this site.

There was no significant difference between IT and NO in Spain. All populations reached BBCH 12 at a similar DAE in Latvia (Figure 3a) and North Poland in 2016. In 2017, in

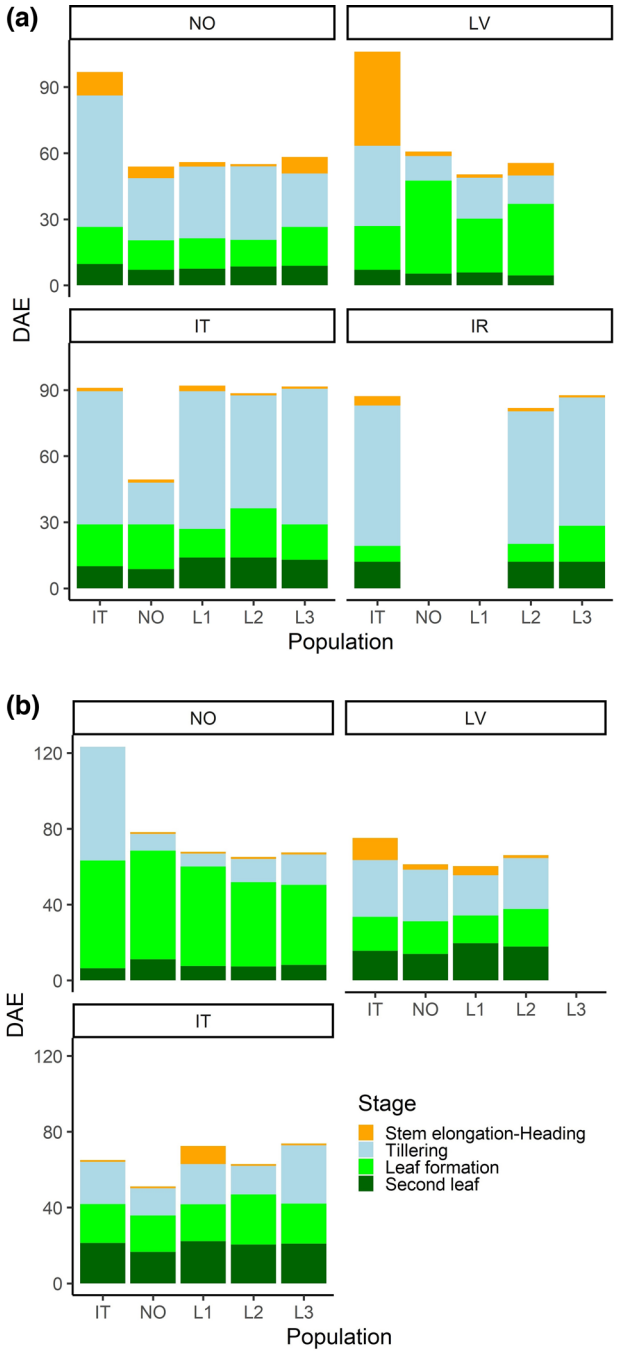

FIGURE 3 Days after emergence (DAE) elapsed before *Echinochloa crus-galli* plants from the two common populations [Italy (IT) and Norway (NO)] and the local populations (L1, L2, and L3) reached BBCH stage 12, the time of leaf development after developing the second leaf (BBCH 13–20), the duration of tillering (BBCH 21–13), and the time until heading (BBCH 41–59) in (a) 2016 and (b) 2017. Sites: IR, Iran; IT, Italy; LV, Latvia; NO, Norway. Mean values are shown for each population. BBCH, plant phenological development scale derived from the Zadoks scale

Latvia, NO plants reached BBCH 12 earlier than the plants of the local populations (LV_L1, $p = .0026$; LV_L2, $p = .0389$) (Figure 3b).

On average, in 2016 the IT population took 23% more in DAE to reach BBCH 12 than NO, the difference ranging from zero in Denmark to 47% in South Poland.

3.3 | The northern (NO) population had a shorter tillering stage and fewer tillers compared with the southern (IT) population

In 2016, the duration of tillering (BBCH 21–31) was shorter in the NO population than in IT in Italy, Latvia, Norway, and North Poland ($p < .0001$), but longer in South Poland ($p < .0001$) (Figure 3a; Supplementary Table S1). On average, there were also fewer tillers per plant in NO than in IT, except in South Poland (Italy, $p = .0003$; Latvia, $p = .0077$; Norway, $p = .0001$; North Poland, $p = .0348$; Spain, $p = .0193$) (Figure 4).

The way in which the duration of tillering differed between both NO or IT and the local populations depended on the site. In Italy, tillering in the local populations continued for significantly longer than in the NO population ($p < .0001$), whereas the local and the IT populations behaved similarly. In South Poland, tillering in the NO population continued for longer than in local populations ($p < .0001$), although the difference was less pronounced. In contrast, in Norway, the tillering stage in the local populations was significantly shorter than for the IT population ($p < .0001$) and there were no differences between the local populations and the NO population. In Latvia, the tillering stage in the IT population was longer than in the LV_L2 population ($p = .0012$) (Figure 3a).

In 2017, the duration of the tillering stage of the IT population differed significantly from all other populations in Norway ($p < .0001$), but there were no significant differences in Italy (Figure 3b). In Latvia, the tillering stage was longer in the IT population than in the LV_L1 population ($p = .0316$).

3.4 | The transition to the heading stage was accelerated in the northern (NO) population

In 2016, in Italy, Latvia, Norway, and South Turkey, where both common populations were present until the heading stage (BBCH 41–59), NO plants headed earlier than IT plants ($p < 0.0001$) (Figure 3a; Supplementary Table S1). The difference in DAE to heading between NO and IT ranged from 8 d in South Turkey to 42 d in Italy and Norway, and 60 d

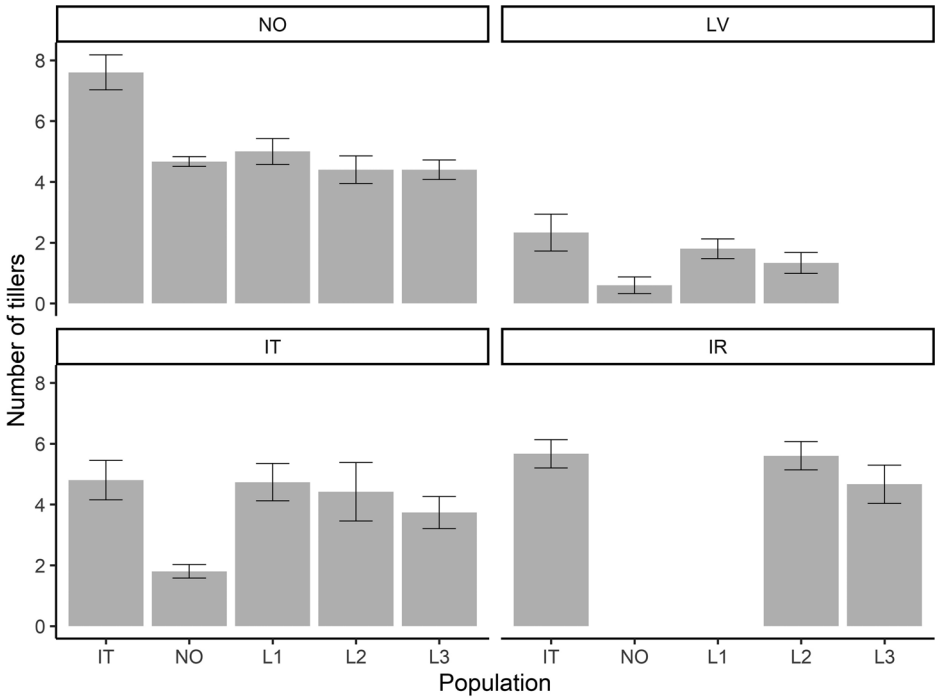

FIGURE 4 Number of tillers formed by plants from the two common populations from Italy (IT) and Norway (NO), and the local populations (L1, L2, and L3) in 2016. Sites: IR, Iran; IT, Italy; LV, Latvia; NO, Norway. Mean values are shown for each population; error bars indicate the SE. BBCH, Biologische Bundesanstalt, Bundessortenemt and Chemical industry; GDD, growing degree-days

in Latvia. In Norway and Latvia, NO plants headed in July, whereas the IT plants did not head until September. In Italy, NO and IT plants headed in June and July, respectively. In Iran, the IT plants reached heading at 87 ± 2 DAE but could not be compared with NO plants because none of the NO seedlings emerged. In North Turkey, the IT plants were cut at the late tillering stage (BBCH 29, 32 DAE) but 67% of the NO plants had already headed by this time (the final observation date). The average DAE until the heading stage of these plants was 28 ± 2 d. On average, the NO population reached the heading growth stage 74% earlier than IT in terms of DAE, from 46% earlier in South Turkey to 86% earlier in Italy.

In addition to the difference between the two common populations, in 2016, the local populations also differed from the common populations (Figure 3a). In Italy, plants from the NO population reached the heading stage earlier than the local populations ($p < .0001$), whereas in Latvia, plants from the NO population headed slightly later than LV_L1 ($p = .008$). In Latvia and Norway, plants from the IT population headed more slowly than the local populations ($p < .0001$), whereas in South Turkey, both IT and NO headed earlier than the local populations ($p < .0001$). In South Turkey, there were also significant differences between TS_L3 and the other local populations ($p < .0001$), but not between TS_L1 and TS_L2. Plants from the NO population in Denmark reached heading at 44 DAE, whereas those from the local populations were slower, not heading before 58 DAE (Supplementary Table S1).

In 2017, plants from the NO population tended to reach the heading stage earlier than those of the IT population, but there were no significant differences between the two populations, except in South Turkey ($p = .0074$). In Norway, none of the IT plants reached the heading stage before the final observation on 27 September, although all NO plants did (mean DAE to heading = 77.3 ± 4), so the DAE to reach heading could not be compared. In 2016, IT plants required 938 and 1,429 GDD to reach heading in Norway and Italy, respectively, whereas NO plants required only 502 and 611 GDD. Possibly, in 2017, sufficient GDD were not accumulated before the termination of the IT plants. In Italy, the NO population reached heading before each of the local populations ($p = .0164$, $p = .0001$, $p < .0001$ for IT_L1, IT_L2, and IT_L3, respectively). There were no statistically significant differences among the populations in Latvia. Compared with 2016, the difference in DAE in reaching the heading between IT and NO was smaller by 15% on average, ranging from 10% in Latvia to 18% in Italy.

It was not possible to use the photoperiod as a factor in the analysis because the sites each had different photoperiods. In Norway and in Latvia, in 2016, very few (3 out of 22 in total) IT plants headed if the daylength exceeded 14 h. Interestingly, however, in 2017, more IT plants in Latvia reached heading with a 17-h daylength.

3.5 | Plants from the northern (NO) population reached heading with fewer GDD than plants from the southern (IT) population

Plants from NO and IT populations accumulated 46 to 238 GDD from the day of emergence until the BBCH 12 stage, depending on the site (median value = 99 GDD) (Figure 5a). There was no significant site × population interaction (p = .3737) but significant differences between the two populations were found within both site and population (p < .0001 and p = .0047, respectively). The IT population accumulated a similar number of GDD in Italy, Latvia, and Spain before reaching BBCH 12. This value was higher in North Poland but was not statistically different from that in Spain. In South Poland and Norway, the total number of GDD accumulated was also similar and lower than in the other sites. For the NO population, similar GDD values were recorded in Latvia and Italy, in South Poland and Norway, and in North Poland and Spain. In addition, the values in Spain were also similar to those in Italy, and those in Latvia to those of South Poland.

The NO population plants needed significantly fewer GDD (291–772, median = 518) to reach the heading stage than IT plants (292–2,497, median = 1,326) (Figure 5b). The GDD values in different sites were variable; moreover, there was a significant site × population interaction (p < .0001), indicating that both populations reacted differently to the site factor. In Italy and Latvia, the number of GDD accumulated for IT was similar (1,404–1,428) and significantly higher than in Norway (927) or South Turkey (442). In Iran, the value was 2,034 GDD. This extremely high value could have resulted from heat stress, which produces in a decrease in the photosynthetic rate, an increase in the respiration rate, and slower growth and development. The number of GDD accumulated in the NO population was significantly different, depending on the site.

3.6 | A comparison of plant development based on different phenological characteristics suggests two distinct ecotypes

The data collected in 2016 from Norway, Latvia, and Italy were analyzed via an ordination method. The PCA showed that the scores of Principal Component 1 were different for the IT and NO populations, the highest components being the duration of the tillering stage, the number of tillers, and DAE before the plants reached the heading stage (Figure 6).

There was also a difference in the scores of Principal Component 2 scores between the two populations in Norway. However, there was no clear distinction between the sites along Principal Component 1 or Principal Component 2, which together accounted for 72.1% of the variance.

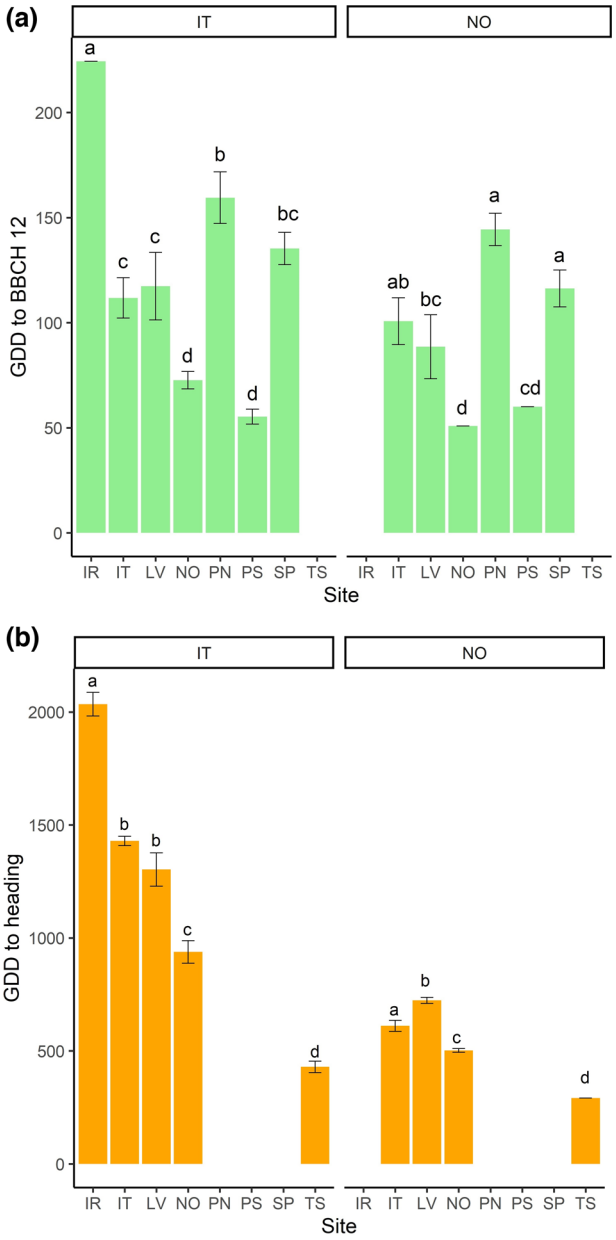

FIGURE 5 Growing degree-days (GDD) accumulated (a) before the plants reached BBCH 12 and (b) before the plants reached the heading stage (BBCH > 41) in different sites in 2016. Data for the two common populations (IT and NO) are shown. Sites: IR, Iran; IT, Italy; LV, Latvia; NO, Norway; PN and PS North and South Poland; SP, Spain, TS, South Turkey. Mean values are shown for each population, the error bars indicate the SE, and the different letters denote means that are significantly different within each site. BBCH, plant phenological development scale derived from the Zadoks scale

4 | DISCUSSION

The results of this study demonstrate similarities and differences in the phenological behavior of *E. crus-galli* populations originating from different climates when they were grown in common gardens. Differences between populations

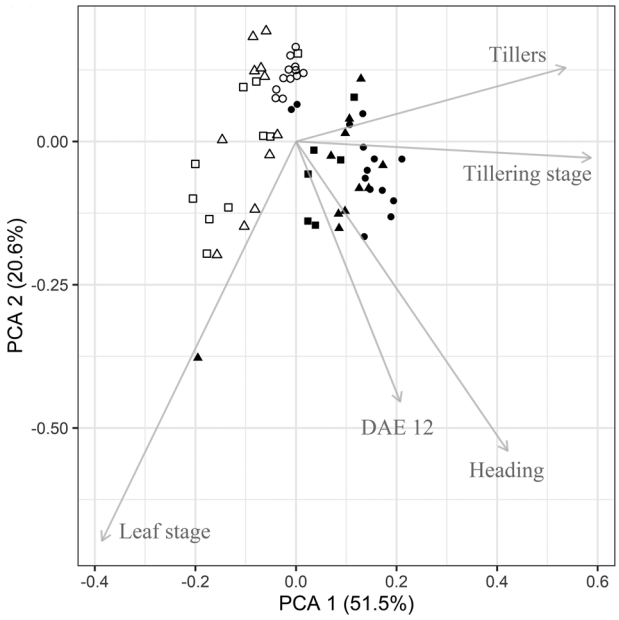

FIGURE 6 Biplot of the principal component analysis (PCA), where the parameters describing the phenological development of the *E. crus-galli* plants were analyzed: Days after emergence (DAE) before reaching Biologische Bundesanstalt, Bundessortenemt and Chemical industry (BBCH) 12 (DAE 12), DAE before heading (Heading), number of days after emergence before tillering stage (Leaf stage), number of tillers (Tillers), and duration of tillering stage (Tillering stage) in 2016. Sites: ○, Norway; □, Latvia; △, Italy. The two common populations were from Italy (IT, filled symbols) and Norway (NO, empty symbols). Data from three sites where complete data could be obtained were used for analysis. BBCH 12 = two fully unfolded leaves on the main shoot, according to Hack et al., 1992. BBCH, plant phenological development scale derived from the Zadoks scale

in early plant development were small or not significant. Similar results were obtained by another group of scientists in a greenhouse experiment involving two populations of *E. crus-galli* from Germany and France. No significant growth rate difference was found between the populations during the leaf development stage (Bürger et al., 2020). In contrast, in our study, the time to heading varied in different populations within each site. Thus, the initial hypothesis was partly confirmed. In NO, the population originating from the northern site (Norway), the transition to heading was faster than in IT, which was originally from the southern site (Italy). Interestingly, the time to reach heading in plants from local populations in Norway and Latvia tended to be more similar to the NO ecotype, whereas in local populations from Italy, Iran, and South Turkey, the times to heading were similar to those of the IT ecotype. This suggests that there are northern and southern ecotypes, with a considerable difference between them, and there are also possible intermediate ecotypes. The differences between plants from northern and southern locations are similar to those described along an altitudinal gradient by Martinkova et al. (2021). A shorter time to flowering could be an adaptation that has facilitated the spread of this species to more northern areas. The hypothesis that the northern and southern populations have differed so that they are adapted to local conditions can therefore be accepted.

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

The different times taken to reach heading for the NO and IT populations could have been caused by different mechanisms. Sensitivity to the photoperiod was shown to influence flowering in *E. crus-galli* (Swanton et al., 2000). The plants of two cultivated *Echinochloa* species (*Echinochloa utilis* Ohwi & Yabuno and *Echinochloa frumentacea* Link) had more and larger leaves during long photoperiods (16 h), but only *E. frumentacea* developed more tillers (Muldoon, 1985). Furthermore, different cultivars of these two species have different levels of sensitivity to photoperiod, which helps to account for the plasticity of this trait. In another facultative short-day species, *Panicum virgatum* L., an extended photoperiod increased the phyllochron (the time elapsing between the development of consecutive leaves), resulting in a longer development cycle (Esbroek et al., 2003). As Norwegian plants generally developed faster in this study, it is likely that plants dispersed in northern locations adapted by losing sensitivity to photoperiod so that they were able to reproduce and produce seeds during a shorter vegetation season. Another possibility that could cause the differences observed in the time to reach heading between plants from the NO and IT populations is the different reaction of the plants to drought, as no irrigation was applied at most of the sites in Central and Northern Europe. Drought stress under long-day conditions caused delayed flowering in *E. crus-galli* var. *oryzicola* (Conover & Sovonick-Dunford, 1989). Moreover, heat stress has been shown to delay flower initiation in wheat (*Triticum aestivum* L.) (Ullah et al., 2022) and in *Chrysanthemum*, which is a short-day plant (Kazan & Lyons, 2016). Conversely, many plants react to drought by making a more rapid transition to flowering (Shavrukov et al., 2017). As in the case of photoperiod sensitivity, the drought and heat sensitivity of different ecotypes should be tested in both controlled and field conditions, as they are related to the ongoing climate change.

In conclusion, the results presented here suggest that a common model can be developed for the early stages of development of *E. crus-galli* plants. Controlling weeds at an early stage is important both for herbicides and/or mechanical control methods, as young plants are more susceptible. Because early plant development was similar in different populations, it is suggested that predictions may be valid regardless of the origin of the seeds. Nevertheless, there was considerable variation in plant development in different sites, caused by differences in environmental and soil factors. Therefore, a mechanistic model that considers various environmental factors that can influence plant development will be required to predict heading, depending on the growing conditions. Predictions of heading time can be used to prevent seed rain by adjusting the harvest time, when possible, and to model the population dynamics of the weed in different crops. The results imply that the origin of the seeds must be taken into account in models that predict flowering, and that such models should be included in decision support systems that are used to plan crop rotation and weed control.

AUTHOR CONTRIBUTIONS

Jevgenija Necajeva: Investigation; Visualization; Writing-original draft; Writing-review & editing. Aritz Royo-Esnal: Conceptualization; Investigation; Methodology; Writing-review & editing. Alireza Taab: Investigation; Writing-review & editing. Donato Loddo: Investigation; Methodology; Writing-review & editing. Peter Jensen: Investigation; Writing-review & editing. Agnieszka. Synowiec: Investigation; Writing-review & editing. Ahmet Uludag: Investigation; Writing-review & editing. Ilhan Uremis: Investigation; Writing-review & editing. Alistair Murdoch: Methodology; Writing-review & editing. Anna Bochenek: Investigation. Andrea Onofri: Formal analysis; Writing-review & editing. Kirsten Torresen: Conceptualization; Investigation; Methodology; Writing-review & editing.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

ORCID

Jevgenija Necajeva https://orcid.org/0000-0002-0828-9721

Agnieszka Synowiec https://orcid.org/0000-0001-6585-7759

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