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ORIGINAL ARTICLE

Comparing the emergence of *Echinochloa crus-galli* populations in different locations. Part II: similarities and threshold parameters

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Abstract

The variability in the emergence process of different populations was confirmed for two *Echinochloa crus-galli* populations, one from Italy (IT) and the second from Norway (NO). Seeds were sown in 12 localities over Europe and the Middle East, and the emergence patterns of IT and NO were compared with those of several local populations at each location. Seeds of each population were sown in pots buried to the ground level. The base temperature (T_b) for emergence was estimated by (1) analysing logistic models applied to the field emergence of IT and NO, and (2) a germination assay set in winter 2020 at constant temperatures (8, 11, 14, 17, 20, 26, 29°C) with newly collected seeds in 2019 from the same fields where IT and NO had previously been harvested in 2015. The logistic models developed for IT and NO in each location showed that the emergence pattern of IT was similar to that of the local populations in

Poland, Italy, Spain, Turkey South and Iran, while NO fitted better to those in Sweden and Latvia. No germination was obtained for IT in a germination chamber, but the estimated T_b with the logistic model was 11.2°C. For NO, the estimated T_b was 8.8°C in the germination chamber and 8.1°C in the field. Results suggest that adaptation to local environmental conditions has led to inter-population differences in T_b and parameter estimates of thermal-time models to predict the emergence of *E. crus-galli* should only be used for populations with similar climatic and habitat conditions.

KEYWORDS

barnyard grass, climate change, emergence pattern, modelling, population variability

1 | INTRODUCTION

The behaviour of plant species is influenced not only by environmental conditions (Westoby et al., 2002) such as climatic and edaphic factors, but also by other factors among which, for weeds, the anthropic effect (field management) prevails over other factors, selecting weed populations which evolve to become adapted to disturbed environments (Neve et al., 2009). In the case of annual weed species, environmental conditions are especially relevant because the particular characteristics of each season may affect the whole life cycle of the populations. Each species shows different requirements for its development and, with specific reference to the sequence of processes regulating seedling emergence, the driving forces are mainly soil temperature and moisture (Baskin and Baskin, 2001). In this respect, base temperature (T_b) and base water potential for germination and emergence are two important parameters (Forcella et al., 2000), which can differ with species, and between seed populations and seasons (Finch-Savage and Leubner-Metzger, 2006). For example, intra-specific differences in these parameters have been found in two weed species, *Conyza bonariensis* (L.) Cronq. (Valencia-Gredilla et al., 2020) and *Abutilon theophrasti* Medik. (Loddo et al., 2019).

Echinochloa crus-galli (L.) P. Beauv. is considered among the worst weeds in the world (Holm et al., 1991), due to its abilities to infest a wide number of crops (Bajwa et al., 2015) and to develop herbicide resistance against many herbicide groups (Heap, 2020), making its control even more difficult. It is, originally, a tropical Asian C_4 species, although the rising temperature trend derived from climate changes is causing a northward movement of this and several other weed species (Peters and Gerowitt, 2015). As a consequence, *E. crus-galli* is gaining importance in higher latitude countries, such as Norway (VKM, 2016), which has motivated several research attempts to understand and model the emergence pattern of this weed species to optimise its management, as proposed by Forcella et al. (2000). All these emergence models work well, but their validity seems to be restricted to a limited area. For example, the models from Bagavatiannan et al. (2011) and Masin et al. (2014) have been found to be useful in Arkansas (USA) and Veneto (Italy), respectively, that is where they were developed. They may, however, need to be adjusted for other locations, as has happened in Croatia (Šoštarčić et al., 2021). *E. crus-galli* is clearly highly adaptable (Guo et al., 2017), for example the estimated T_b seedling emergence of different populations varied from 5°C (Sadeghloo et al., 2013) up to 13.3°C (Loddo et al., 2018), which results in large differences in thermal-time (TT) estimation.

With this background, the Working Group on Germination and Early Growth (WG-GEG) of the European Weed Research Society (EWRS) studied the emergence of two populations of *E. crus-galli*, one from Italy and the other from Norway, at 12 locations in Europe and the Middle East (Royo-Esnal et al., 2022). In that research, the population from Norway (NO) showed higher emergence at higher latitudes and lower emergence at lower latitudes, compared with the Italian population (IT). NO also generally emerged earlier and faster than IT, suggesting lower thermal threshold values, that is a lower T_b value and growing degree days requirement for 50% emergence (GDD_{50}). This study also suggested that the times of onset and termination of emergence depended on population characteristics, while the synchronicity of emergence was mainly under environmental control.

In this paper, the main objective was to compare the emergence patterns of the NO and IT populations (Royo-Esnal et al., 2022) with those of local seed populations collected in 12 locations. A further objective was to investigate whether the NO, IT and local populations could be grouped according to similarities in emergence characteristics. Additionally, and based on the differences reported by Royo-Esnal et al. (2022), T_b was estimated for the NO and IT populations.

2 | MATERIALS AND METHODS

2.1 | Field experiment

Experiments were set up at 12 different localities with different climatic characteristics (Table 1). At each locality, the study included the IT, NO and up to four additional populations, seeds of which were collected from infestations in different crops in the local area (Table 1). Seeds were collected during summer 2015 at maturity from several mother plants in the same population. After harvest and drying the

TABLE 1 Location and crop of origin for the common populations, locations of the experiment, sowing and disturbance dates, and crop of origin for the local populations of *E. crus-galli*: C, cotton; CB, common beans; G, garden; Gs, grass for seed production; M, maize; NC, non-cropped area; O, orchard; P, potato; R, rice; RB, red beet; SB, spring barley; SF, sunflower; T, tomato; WW, winter wheat

	Location	Latitude	Longitude	Climate[a]	Sowing (2015)	Disturbance (2016)	Common	L1[b]	L2[b]	L3[b]	L4[b]
IT	Padova	45°20′N	11°58′E				M				
NO	Svarstad	59°24′N	9°58′E				SB				
Sweden	Uppsala	59°49′N	17°39′E	Dfb	28/10	11/05		M	CB	WW	
Norway	Ås	59°40′N	10°46′E	Dfb	23/10	26/04		NC	Gs	RB	
Latvia	Carnikava	57°05′N	24°12′E	Dfb	27/10	13/04		SB	M		
Denmark	Aarhus	55°19′N	11°24′E	Cfb	11/11	03/05		M	G		
Poland	Kraków	50°05′N	19°52′E	Dfb	26/10	05/04		SB	WW	P	
Italy	Padova	45°20′N	11°58′E	Cfa	27/10	29/03		M	M	M	
Spain	Lleida	41°37′N	0°35′E	Csa	28/10	24/03		M	R	O	
Turkey (North)	Düzce	40°50′N	31°09′E	Cfb	23/10	12/04		M	M	T	M
Portugal	Oeiras	38°42′N	9°18′W	Csa	11/11	08/04		M	R		
Greece	Athens	37 °58′N	23°43′E	Csa				SF	C	R	
Turkey (South)	Antakya	36°16′N	36°14′E	Csa	23/11	05/03		M	M	M	
Iran	Ilam	33°39′N	46°23′E	Csa	15/11	20/04		T	R	R	

[a] Climate classification according to the updated Köppen–Geiger classification (Kottek et al., 2006): Cfa, temperate with no dry season, hot summer; Cfb, temperate with no dry season, warm summer; Csa, temperate with dry and hot summer (warm Mediterranean); Dfb, cold with no dry season and warm summer (continental). For specific climatic conditions of the experimental seasons (2015–16 and 2016–17), see Royo-Esnal et al. (2022).

[b] Locations of where local populations were collected and that differed from the experimental site: Norway, L1: 59°08′N/10°15′E, L2: 59°17′N/10°19′E, L3: 59°22′N/10°40′E. Latvia, L2: 56°29′N/22°58′E. Denmark, L1: 55°11N/12°08′E. L2: 55°00′N/12°00′E. Spain, L1: 41°34′N/0°30′E. L2: 40°41′N/0°43′E. L3: 41°16′N/01°59′E. Greece, L1:41°36′N/26°35′E. L2: 41°02′N/26°19′E. Iran, L2: 33°41′N/46°41′E. L3: 37°16′N/49°38′E. Turkey (North) L1: 40°43′N/30°22′E. L2: 40°41′N/30°35′E. L3: 39°53′N/26°16′E. L4: 40°07′N/26°28′E.

seeds at room temperature (20–25°C) for a week, IT and NO populations were sent to HerbiSeed in the UK to prepare phytosanitary certificates, while the local populations were stored in a refrigerator at 3–5°C until ready for use. The storage time from harvest to sowing varied between two and four months, depending on the location.

Seeds were sown during autumn 2015 in 25 cm diameter pots filled with local soil. The pots were buried in the ground, so that 1 cm of each pot extended above the ground. Sowing was carried out by removing the top 5-cm layer of soil, placing it in a tray and then mixing it by hand with 200 seeds. This mixture was then put back into the pot, so that seeds were distributed in the upper 5 cm of the soil. Pots were arranged in a randomised block design with five replicates, each block containing a control pot without any seeds in order to check for possible contamination of *E. crus-galli* seeds in the local soils. An extra pot without seeds was contained a temperature logger (HOBO Pendant®, Onset Computer Corporation), which was buried horizontally at 2.5 cm depth.

In spring 2016, the soil was disturbed at the time of the typical sowing date for the crops where *E. crus-galli* is found in each location. For the disturbance, the uppermost 5 cm of the soil in each pot was removed and mixed in a tray, where NPK fertiliser at a rate of 50 kg N ha^{-1} was added. Then, the soil was put back into the corresponding pot.

No water was applied to the pots during the experiment except Iran, Spain and Turkey South, where irrigation is a common practice and necessary for spring-sown crops, like maize. In these locations, 0.5 L/pot were added every two-three days, depending on the soil dryness. Additionally, daily maximum and minimum air temperature and precipitation were collected from the nearest weather station in each locality to estimate the soil temperature with the STM^2 program (Spokas and Forcella, 2009); in case, the datalogger did not work properly.

Non-destructive weekly counts were carried out until the spring soil disturbance. Counts were made every 2 days after soil disturbance and until the spring main emergence flush finished, and then weekly during summer. After the main emergence flush, seedlings were carefully removed to avoid shading that could affect ongoing emergence.

2.2 | Comparison of the emergence pattern of the IT and NO with the local populations

The emergence patterns (E_{pat}) shown by the common populations (IT and NO) in each locality were fitted to a Julian day-based log-logistic model (1) using the software SigmaPlot 11.0:

$$\overline{y}_{ct} = \frac{E}{1+\left(\frac{\mathrm{JD}_t}{\mathrm{JD}_{50}}\right)^{b}} \tag{1}$$

where $\overline{y}_{ct}$ is fitted percentage emergence for the common populations at time t expressed as a percentage of the annual total, E is the cumulative maximum annual emergence expressed as percentage, JD_t is the Julian day at time t, JD_{50} is the number of days required for 50% emergence, and b is the slope of the emergence progress curve at JD_{50}. To assess how well the predicted curves for the two common populations matched the patterns of emergence for each of the local populations, the root mean squared error of prediction (RMSEP) was calculated as follows (2):

$$\mathrm{RMSEP}_{cl} = \sqrt{\frac{1}{n}\sum_{t=1}^{n}\left(\overline{y}_{ct} - y_{lt}\right)^2} \tag{2}$$

where $\overline{y}_{ct}$ is the fitted percentage of emergence (model (1)) for the common population c at day t, y_{lt} is the observed percentage of emergence for the local population l at day t, and n is the number of observations. The lower the value of RMSEP, the higher the similarity of the E_{pat} of the common population to the local one, and thus, the better the predictive ability of a model using the parameters for the better-fitting common population.

2.3 | Estimation of the base temperature (T_b) of the common populations

The T_b for germination for the common populations was estimated using a twofold approach. First, a set of seeds from each common population was sent to the University of Reading to characterise its germination, but too few seeds germinated for unknown reasons. Therefore, in August 2019, seeds of *E. crus-galli* were newly collected from the same fields as in 2015. Seeds were sent to Lleida in September 2019 and were stored in the fridge at 4°C until their use in February 2020. Seeds of each population were put at constant 8, 11, 14, 17, 20, 23, 26 and 29°C, in 9-cm diameter Petri dishes lined with filter paper moistened with distilled water. For each temperature, four replicated dishes with 20 seeds each were used and the germination was counted daily for a maximum of 21 days. The cumulative germination percentage at each temperature was fitted to a non-linear log-logistic model, similar to (1), but replacing *JD* with the day from sowing (*D*). The reciprocal of the estimated period in days to reach 50% of germinated seeds (D_{50}) was used as an estimate of the germination rate ($1/D_{50}$). This parameter was regressed against germination temperature to estimate the T_b for the rate of germination, being the temperature at which the rate of germination was zero, that is where the regression line intersected the X-axis (Bradford, 2002).

The second attempt to estimate the T_b for the common populations was made by fitting a common thermal-time model based on soil temperature to emergence data from a group of locations, which were selected on the basis of the similarities for the common and local populations of first, their observed emergence patterns, and secondly, the climatic conditions of the localities (Sousa-Ortega et al., 2020). Consequently, data from Iran, Italy, Poland, Spain, Turkey North and Turkey South were used for the IT population, while data from Norway, Latvia and Sweden were used for the NO population. The thermal-time model was (3):

$$\overline{y}_{ct} = \frac{E}{1+\left(\frac{\mathrm{GDD}_t}{\mathrm{GDD}_{50}}\right)^b} \tag{3}$$

where $\overline{y}_{ct}$ is the cumulative percentage of emergence at time t, E is the maximum percentage of emergence (highest asymptote), GDD_t is the accumulated growing degree days at time t from spring disturbance, GDD_{50} is the growing degree days required for 50% of emergence, and b is the slope.

The GDD_t was defined as follows (4):

$$\mathrm{GDD}_t = \sum_{t=1}^{n}\left(T_t - T_b\right) \tag{4}$$

Overall, the above model (Equations (3) and (4)) had three parameters to be estimated (T_b, GDD_{50} and b) for each population. T_t is mean daily soil temperature (estimated or measured). Apparent differences between the emergence pattern of IT and NO in different locations prevented the use of the same set of parameters for each population in all locations. On the contrary, it was considered that T_b and GDD_{50} are confounded variables, as lower T_b implies higher GDD_{50}, and vice versa. Therefore, the values of T_b and b were allowed to vary between locations, as they represent the minimum temperature required for GDD accumulation and the emergence rhythm, respectively, whereas thermal time (GDD_{50}) was constrained to be constant. Parameter was estimated by minimising the residual sum of squares through the generalised reduced gradient method, as implemented in the Microsoft Excel solver (https://www.solver.com/excel-solver-algorithms-and-methods-used). A 'one-at-a-time' strategy was used for the optimisation, in an iterative manner, so that parameter values could be limited to a biologically reasonable range.

2.4 | Statistical analysis

The total emergence for each locality was split into three parts: seedlings emerging before spring soil disturbance and that would be killed by this disturbance; those emerging between spring disturbance and summer (defined as the end of July), which would compete with the crop (the main flush of emergence); and those emerging from summer to autumn, which would not compete with the crop. The first two emergence flushes are analysed here, that is from sowing to summer, because these may interfere with crop growth and development.

The total number of emerged plants (E_{tot}) was analysed separately for each locality because of the significant 'population by locality' interaction for the two common populations (Royo-Esnal et al., 2022) and because local populations were unique to each locality. One-way ANOVA and post hoc multiple comparison testing were performed based on Fisher's least significant difference. Data were arcsin-square root transformed, wherever necessary, to meet the basic assumptions of normality and homoscedasticity.

Transformed data were back-transformed to the original scales and reported in Tables.

3 | RESULTS

3.1 | Total emergence

At the first sight, when the total emergence of IT and NO is plotted together with the local populations, the emergence of the local populations generally fell between that of IT and NO in a given locality (Figure 1). Nevertheless, the diverse crops and habitats from which the 17 local populations were collected (Table 1), suggests that the local *E. crus-galli* populations should be analysed separately.

Between the two common populations, IT showed higher E_{tot} in southern latitudes (Greece, Iran, Italy and Spain), while NO emerged better in northern latitudes (Latvia, Norway, Poland, Sweden and Denmark) (Table 2). In each locality, the highest E_{tot} values were reached by NO in Turkey North, Poland, Sweden, Latvia, Portugal, Denmark (36.6%–87.5%) and by IT in Iran (42.9%), although not always significantly different from the local populations. In the other locations, local populations, mainly from maize fields, reached the highest E_{tot}, that is in Spain (54.4%), Turkey South (66.2%), Italy (24.8%) and Norway (59.4%), although in the last two locations, the local populations were not significantly different from IT and NO respectively (Table 2). On the contrary, the lowest E_{tot} until summer was for NO in Iran (0.8%), Italy (7.1%) and Spain (12.9%), and for IT in Latvia (25.5%) and Norway (25.2%). Local populations from rice fields also showed low E_{tot} values in Spain (17.2%) and Greece (2.3%), although these values were not significantly different from those obtained by NO. In Portugal, most of the NO seedlings (48%) emerged during autumn–winter, before the spring disturbance, and only an additional 2% emerged after this disturbance. By contrast, only 0.4% of the IT population emerged before soil disturbance compared to 12.8% afterwards.

In some localities (Spain, Turkey North and South), autumn emergence was also observed. Although in general there were very few seedlings (0.5% to 2.8% of sown seeds), 22.3% of L2 population from a rice field in Spain emerged in the autumn.

3.2 | Comparison of the E_{pat} for common and local populations

As a first approach, the E_{pat} of IT and NO in each location was fitted to a log-logistic function, except in the case of NO in Iran where its emergence was very low (Table 3). The goodness of fit of the models was generally very high ($R^2 > 0.91$) and only slightly lower for IT in Latvia and Denmark and for NO in Denmark ($R^2 = 0.87$, 0.76 and 0.87, respectively).

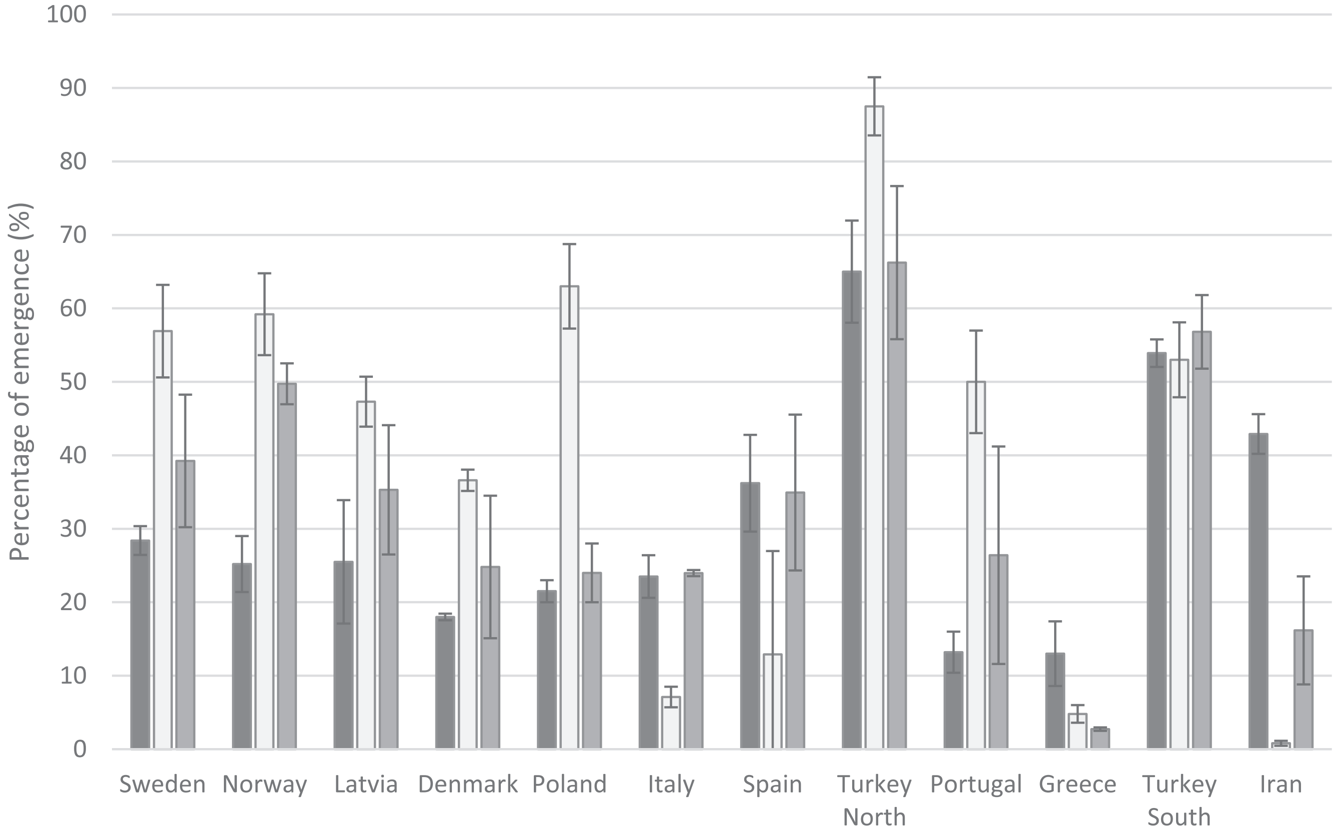

FIGURE 1 Average percentage of emergence ($E_{tot} \pm$ SE) of the common populations IT (dark grey bars) and NO (light grey bars) and of the pooled data for the local populations (medium grey bars) from sowing in autumn 2015 to summer 2016

TABLE 2 Average total percentage emergence (E_{tot}) of each population in each locality during the first season (2015/2016) until summer (end of July, above) and from summer to autumn (below) dashes

Country (part)	C1 IT[a]	C2 NO[a]	L1	L2	L3	L4
Sweden	28.4C	56.9A	52.9AB	42.6B	22.2C	
Norway	25.2B	53.4A	50.9A	59.3A	52.6A	
Latvia[b]	25.5B	47.3A	26.5AB	44.1AB		
Denmark[b]	18.0B	36.6A	34.5A	15.1B		
Poland	21.5BC	63.0A	16.0C	28.1B	27.9B	
Italy	23.5A	7.1B	23.6A	24.8A	23.5A	
Spain[b]	36.6B	12.9C	54.4A	17.2C	33.9B	
Turkey North	65.0B	87.5A	82.0A	38.2C	82.2A	62.5B
Portugal	13.2B	50.0A	11.6 B	41.2 A		
Greece[b]	13.0A	4.8B	2.8B	3.1B	2.3B	
Turkey South	53.9B	53.0B	66.2A	49.1B	55.1B	
Iran	42.9A	0.8D	2.5D	18.3C	27.7B	
Mean	**32.0a**	**39.4a**				
SE	**4.5**	**7.9**				
Spain	0.4	0.7	1.5	22.3	1.2	
Turkey North	2.1	3.4	1.3	1.6	2.7	2.8
Turkey South	1.0	1.1	1.5	2.0	0.5	
Mean (season)	**32.2**	**39.9**				
SE	**4.6**	**8.0**				

Note: Mean values for the emergence until summer and for the whole season (until summer + summer to autumn) are also provided. Lower case letters compare the mean E_{tot} of the common populations. Capital letters compare the E_{tot} between populations in each locality. Different letters denote significant differences at $p < 0.05$.

[a] Data already presented in Royo-Esnal et al. (2022). We repeat them just for the comparison with the local populations.

[b] Back transformed data after statistical analysis.

TABLE 3 Model parameters (Equation 1) for each of the two common populations in each location

		IT				NO			
Location of experiment		E	JD_{50}	b	R^2	E	JD_{50}	b	R^2
Sweden	Uppsala	100	153.2	−13.8	0.92	98.8	146.8	−19.0	0.96
Norway	Ås	92.6	150.7	−50.3	0.95	97.9	147.6	−122.4	0.99
Latvia	Carnikava	100	155.5	−14.5	0.90	93.0	143.4	−100.1	0.97
Denmark	Aarhus	93.4	136.7	−23.4	0.76	93.5	134.9	−24.8	0.87
Poland	Kraków	98.4	133.7	−20.4	0.95	100	127.1	−12.1	0.94
Italy	Padova	99.9	119.1	−14.1	0.98	98.8	108.1	−19.4	0.96
Spain	Lleida	93.5	108.7	−38.2	0.96	100	106.8	−35.3	0.96
Turkey N	Düzce	98.6	111.9	−62.8	0.99	98.5	112.5	−53.2	0.98
Portugal	Oeiras	100	155.5	−14.4	0.96	97.5	43.8	−16.1	0.96
Turkey S	Antakyia	100	130.5	−10.2	0.98	98.0	123.5	−14.2	0.95
Iran	Ilam	98.9	127.0	−80.1	0.98	NA			

Note: All regressions were significant ($p < 0.001$). E, maximum emergence (asymptote); JD_{50}, Julian days required for 50% of emergence; and b, slope. The R^2 of each model is also provided. NA: not fitted.

These models were evaluated for their ability to predict the E_{pat} for the local populations in each location (Table 4; Figure 2). The local models for IT provided a better description of E_{pat} for all local populations in Denmark, Poland, Italy, Spain, Turkey South and Iran, and for L3 in Norway and L1 in Portugal. On the contrary, the local models for NO provided a better description of E_{pat} for local populations in Sweden and in Latvia, and for L1 in Norway, L4 in Turkey North and L2 in Portugal. In Turkey North (Düzce), NO and

TABLE 4 Root mean square error predictor (RMSEP) for the day-based log-logistic models developed for each common population (IT and NO) with respect to the emergence pattern for local populations, in each locality

		L1		L2		L3		L4	
Location of experiment		**IT**	**NO**	**IT**	**NO**	**IT**	**NO**	**IT**	**NO**
Sweden	Uppsala	10.9 **G**	8.0 **VG**	17.5 **U**	10.1 **G**	9.4 **VG**	7.7 **VG**		
Norway	Ås	8.8 **VG**	7.9 **VG**	8.5 **VG**	9.0 **VG**	9.0 **VG**	14.0 **G**		
Latvia	Carnikava	23.1 **U**	8.7 **VG**	22.1 **U**	8.8 **VG**				
Denmark	Aarhus	16.5 **U**	20.5 **U**	25.6 **U**	29.7 **U**				
Poland	Kraków	8.4 **VG**	15.5 **U**	9.7 **VG**	14.8 **G**	10.1 **G**	18.3 **U**		
Italy	Padova	6.9 **VG**	17.8 **U**	12.6 **G**	26.8 **U**	7.2 **VG**	21.0 **U**		
Spain	Lleida	7.6 **VG**	9.9 **VG**	15.3 **U**	20.8 **U**	7.4 **VG**	13.3 **G**		
Turkey North	Düzce	2.5 **E**	2.76 **E**	4.73 **E**	4.20 **E**	4.2 **E**	3.4 **E**	5.3 **E**	3.4 **E**
Portugal	Oeiras	16.3 **U**	52.5 **U**	44.7 **U**	25.4 **U**				
Turkey South	Antakyia	7.2 **VG**	11.9 **G**	5.8 **VG**	9.2 **VG**	7.0 **VG**	7.7 **VG**		
Iran	Ilam	12.1 **G**	-	10.3 **G**	-	10.5 **G**	-		

Note: Shaded cells show the lowest RMSEP for each local population. Letters show the approximation based on Royo-Esnal et al. (2010): E, excellent (RMSEP < 5); VG, very good (5 < RMSEP < 10); G, good (10 < RMSEP < 15); U, unsuccessful (15 < RMSEP).

IT both behaved similarly (Figure 2), and, therefore, their fitted models provided similar descriptions of the E_{pat} for the local populations (Table 4); in Norway, the E_{pat} of L1 and L3 was similar to that of IT until 90% emergence, when they became more aligned to the E_{pat} of NO. In Portugal (Figure 3), all seedlings of NO, most of L2 and 20% of L1 emerged before the spring soil disturbance, so that these results are presented in days from sowing: Only IT and L1 showed similar E_{pat} from 40% emergence onward.

Considering the RMSEP, as proposed by Royo-Esnal et al. (2010), models based on common populations, either IT or NO, provided a very good description (RMSEP = 5–10) for the E_{pat} of 20 local populations, a good description (RMSEP = 10–15) for another eight. They were deemed unsuccessful for four local populations, that is L2 in Spain, and L1 and L2 in both Denmark and Portugal (RMSEP = 15.3, 16.5 and 25.6, and 16.3 and 25.4, respectively; Table 4). Noticeably, both IT and NO gave excellent descriptions (RMSEP < 5) for all local populations in Turkey North.

3.3 | Estimation of the base temperature in growth chambers

Results for germination assays in growth chambers differed for IT and NO. Only three seeds from the IT population germinated, while >90% of the NO seeds germinated. For this reason, T_b could only be estimated for the latter population. No germination was obtained at constant 8, and 11°C was the lowest temperature at which germination was observed. The rate of germination increased as temperature increased to 29°C (Figure 4 left). The logistic model fitted the germination progress curves at all temperatures where germination occurred ($R^2 > 0.99$). The regression line applied to the reciprocal of the time to 50% germination (D_{50}) of these models gave an estimated T_b for germination for NO of 8.77°C (±0.03°C; Figure 4 right).

3.4 | Estimation of the base temperature with field data

Based on the similarities of the emergence patterns of the common populations with the local ones (Table 4), two groups of localities were considered: Scandinavian-Baltic localities, comprising Norway, Sweden and Latvia to estimate the T_b for the emergence of NO, and all the other localities except Portugal and Denmark, to estimate the T_b for the emergence of IT (Table 5). Portugal was excluded because the emergence pattern differed from both common populations, and Denmark, because emergence in three out of five replicates of IT was affected by stagnant water.

With respect to NO, when GDD_{50} was common for all populations, its estimated value was 156.9°C d, T_b varying from 5.9°C in Norway to 10.7°C in Latvia and the slope parameter, *b*, varying from 2.53 in Sweden to 13.09 in Norway. For IT, the common estimate of GDD_{50} was 201.5°C d, T_b ranging between 10.7 and 11.7°C (average of 11.2°C), except in Poland, where it was only 6.9°C (Table 5). The slope parameter *b* varied widely from 1.77 in Turkey South to 13.98 in Turkey North.

4 | DISCUSSION

In this experiment, the emergence patterns of Italian (IT) and Norwegian (NO) populations of *E. crus-galli* were compared with the emergence of local populations in 12 locations throughout Europe and the Middle East, and represent a previous necessary step for trying to study the applicability of different already developed emergence models or, in any case, further develop new ones. The results for total emergence (E_{tot}) and the emergence pattern (E_{pat}) demonstrated that IT and NO generally behaved similarly to the local ones, but one of them was always more suitable than the other

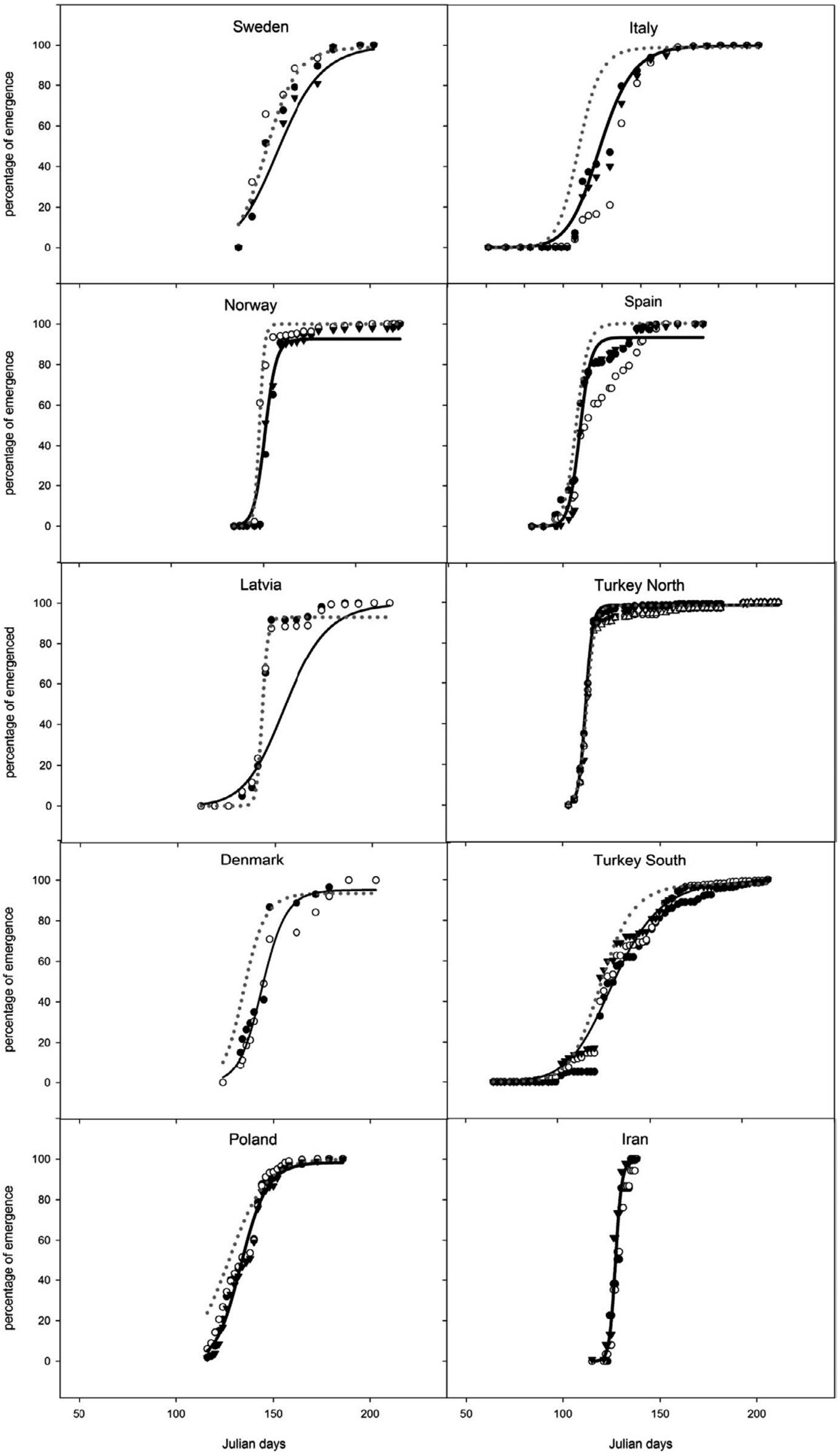

FIGURE 2 Comparison of the model developed for the IT (black line) and NO (grey dotted line) in each often locations with the local populations, based on Julian days. ●, local population 1 (L1); ○, local population 2 (L2); ▼, local population 3 (L3); ▲, local population 4 (L4). For clarity of the results, only the average percentage of the five replicates is shown

for describing the emergence of local populations at a given location. The 'better' model for any location was that where the E_{tot} and E_{pat} for either NO or IT coincided more closely with those of the local populations, and this was mainly achieved in Italy, Spain, and Poland. E_{tot} represents the capacity of a seed population to emerge, but it does not necessarily reflect E_{pat}, as has been demonstrated in temperature-specific germination experiments for weeds such as *Neslia paniculata* (L.) Desv. (Royo-Esnal et al., 2019). A change in the proportion of dormant/non-dormant seeds due to environmental conditions during maturation could explain wide variations in E_{tot}. For this reason and irrespective of the value of E_{tot}, it is argued that the more important criterion is the closeness of the fit of E_{pat} for the common and local populations, because this would allow the application of a common emergence model in those localities and, from

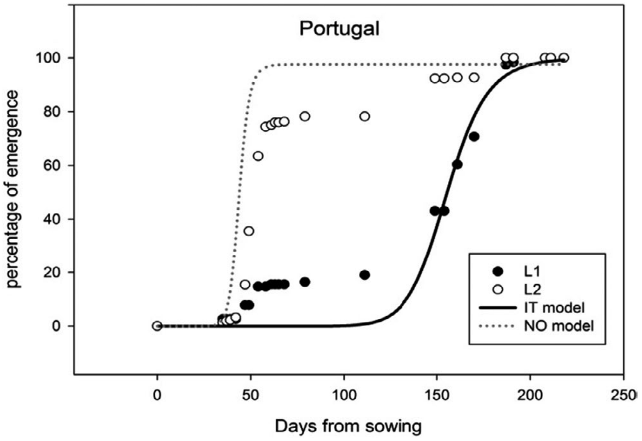

FIGURE 3 Comparison of the models fitted for IT (black line) and NO (grey dotted line) in Portugal with the local populations, based on days from sowing (11 November 2015). ●, local population 1 (L1); ○, local population 2 (L2). For clarity of the results, only the average percentage of the five replicates is shown

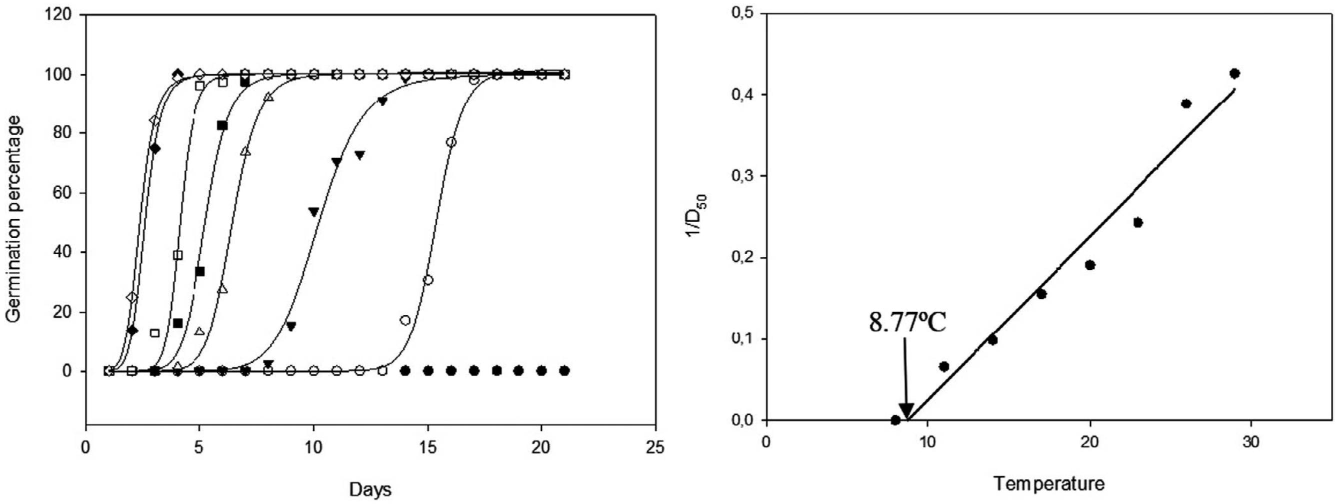

FIGURE 4 Left, cumulative germination percentage, standardised to 100%, of seeds of the Norwegian population (NO) at each constant temperature. ●, 8°C; ○, 11°C; ▼, 14°C;, 17°C; ■, 20°C; □, 23°C;, 26°C;, 29°C. Lines represent the log-logistic models fitted to each cumulative germination, all of them with a $R^2 > 0.99$. Right, the reciprocal of the D_{50} at each constant temperature and the fitted regression line ($R^2 = 0.96$); the point where the regression line intercepts the X-axis is the estimated T_b

TABLE 5 Base temperature (T_b) and parameter *b* of the log-logistic thermal-time model for seedling emergence of each common population (NO, Norwegian; IT, Italian), considering growing degree days for 50% emergence (GDD$_{50}$) as fixed variable

	NO			IT					
	Sweden	Norway	Latvia	Poland	Italy	Spain	Turkey North	Turkey South	Iran
T_b	7.6	5.9	10.7	6.9	10.7	11.4	11.7	10.9	11.2
b	2.53	13.09	3.17	3.60	3.57	5.47	13.98	1.77	9.64
RSS	2218.4			3263.6					

Note: The value of GDD$_{50}$ was 156.9°C for No and 201.5°C for IT. RSS, residual sum of squares of all considered functions.

a practical perspective, the potential use of the model in Decision Support Systems for the management of *E. crus-galli*.

On the contrary, the local populations were harvested in different crops, and thus perhaps, in different micro-climatic conditions. Environmental conditions during maturation affect the dormancy levels and germination requirements of seeds (Menegat et al., 2018), but it is unknown to what extent the crops in the fields where seeds were harvested might have affected these requirements, not even their effect on the initial seed viability, which was not studied in the present work. Apparently, and according to the results presented for the given localities (Table 5; Figure 2), the accompanying crop was not important except for rice. Most populations were obtained in crops that are typically grown in a rainfed crop rotation in temperate climates or in irrigated fields in Mediterranean climates. This can explain the better fit of the IT emergence to that of some local populations in Norway (L1) and Poland (L1–L3). In contrast, rice is a crop that usually does not enter rotation with other crops, and where soil is continuously flooded; *E. crus-galli* populations in this crop might have developed distinct emergence patterns (or dormancy levels) that could explain the observed results for L2 in Spain and Portugal. However, in Iran, local populations collected from rice behaved similarly to IT. For this reason, and considering there were only four populations from rice fields in the experiment, it is impossible to reach any certain conclusion without further research for these *E. crus-galli* populations.

The emergence of NO generally occurred earlier than IT, and it was only in Denmark and Turkey North that their emergence almost coincided. Accordingly, in most locations, local populations present a similar emergence pattern to one or other common population: the emergence of IT better described that of the local populations in Poland, Italy, Spain, Turkey South and Iran; and NO fitted better in Sweden and Latvia (Table 4; Figure 2). The case of Norway is, however, confusing, because L1 was better described by NO and L3 by IT, with similar results for L2. A possible explanation could be that the populations have adapted to different crop rotations and climatic conditions in the area where the populations were collected, but further research is needed to test this hypothesis. In Denmark, although IT better described the emergence of the local populations, the RMSEP values were high and three replicates of IT with stagnant water had to be discarded. In Turkey North, the E_{pat} of IT and NO were similar, and in Portugal, only IT compared with L1 (from a maize field) had an acceptable emergence similarity (RMSEP = 16.2), although still unsuccessful according to Royo-Esnal et al. (2010).

With these exceptions, the general similarities in the E_{pat} suggest that the developed emergence models could be widely applied for populations growing in similarly managed crops. As an example, models for *A. theophrasti*, *Chenopodium album* L. and *Sorghum halepense* (L.) Pers. developed for populations of these weeds in maize fields (Masin et al., 2012) were also applicable in soybean (Masin et al., 2014), and their use is probably feasible for other crops grown in rotation with maize. To achieve this purpose, basic threshold parameters must be established (Alvarado and Bradford, 2002) because the variation of the climatic conditions between locations and seasons affects the emergence pattern when it is based on Julian days, as in Figure 2. The difference in the temperature requirements of IT and NO reported by Royo-Esnal et al. (2022) has been confirmed here. The iterative analysis with the logistic model to match the emergence of IT and NO sown in different locations showed different temperature requirements, which have been expressed as differences in T_b. The T_b values for IT were estimated about 11.2°C, similar to the 11.7°C estimated by Masin et al. (2014) for *E. crus-galli* populations in the same region where IT was collected. Unfortunately, the lack of germination in the germination chamber experiment prevented us from confirming this. On the contrary, the T_b for NO estimated with the logistic model ranged from 5.9°C in Norway to 10.7°C in Latvia. This variability is quite high, and further research should be performed to explain it. Despite this, the average T_b value for NO considering the three locations (Latvia, Norway, Sweden) together was 8.1°C (±1.4°C), similar to that estimated by the germination assays performed in 2020 for seeds of this same population collected in August 2019, which was 8.77°C. Interestingly, the estimated T_b for NO in Carnikava (10.7°C), a Latvian location in the Baltic coast, was similar to that estimated by Bürger et al. (2020) in Rostock (10.0°C), a German location also on the Baltic coast. The lower T_b of NO explains the earlier onset of seedling emergence in NO and accounts for the adaptation of *E. crus-galli* populations to different environmental conditions and latitudes. As already reported for *Datura stramonium* L. and *Conyza canadensis* (L.) Cronq. (Loddo et al., 2014; Tozzi et al., 2014), populations such as IT coming from areas with milder winter temperatures (the average annual temperature is 13.9°C in Padua, Italy compared to 6.8°C in Svarstad, Norway) have a higher T_b and more primary dormancy which reduces germination during winter in unfavourable conditions for seedling growth. The higher primary dormancy could explain the limited germination observed for IT population during the germination assays in the growth chambers. On the contrary, populations such as NO coming from areas with lower winter temperatures have lower T_b and limited primary dormancy because winter temperatures are below T_b, so that no specific adaptation is required to avoid winter germination. The lower T_b and a limited primary dormancy instead allow those populations to germinate and emerge early enough in the spring or summer to complete their life cycle, which is clearly an important adaptation to the short growing season of northern European countries. Given their low T_b and limited primary dormancy, if seeds of these populations are exposed in the weeks after their dispersal to warm favourable conditions, autumn germination and seedling emergence can occur, as in the case of NO seeds sown in Portugal.

The variation in T_b values between years could be explained by the differences in the environmental conditions affecting the mother plant during seed development (Menegat et al., 2018). In this work, seeds of each population were collected in a single field and year, and the results suggest that differences in the stratification conditions (winter temperatures) can also affect the dormancy, germination and emergence requirements of the seeds, as observed by Taab and Andersson (2009) for *Solanum nigrum* and *S. physalifolium*. This is clearly seen with results obtained in Poland, a location classified as climatically cold (Dfs) by Kottek et al. (2006), where a very low T_b for IT was estimated with respect to all the other five locations, classified by these authors as temperate (Cfb or Csa; Table 1). Winter temperatures in Kraków were lower than in the other localities where IT showed a similar emergence pattern to the local populations, and the estimated T_b for this locality was much lower than in the other locations (6.9°C < 10.4 or 11.2°C), and more similar to that obtained by Guillemin et al. (2013) for a population from the Burgundy in France (6.2°C). Therefore, to consider the development of an emergence model, this location would need to be excluded. The effect of cold stratification on germination of weed seeds has been observed for several weed species, showing significant differences between populations for many of them (Milberg and Andersson, 1998); which can also suggest a limitation on the applicability of a hypothetical emergence model to those populations growing in locations with similar climatic conditions. This has been recently suggested for *Lolium rigidum* Gaud. (Sousa-Ortega et al., 2020), arguing that the emergence pattern becomes more unpredictable when the model is applied in climatic conditions for which it was not originally developed (Izquierdo et al., 2009).

5 | CONCLUSIONS

The emergence patterns of *E. crus-galli* populations were similar in different locations, and many populations from Europe and the Middle East could be described by a common emergence model, always considering the climatic similarity and original habitat (crop) conditions. Two population groups have been observed, those from Scandinavian-Baltic area, which could mostly be described by the emergence of the common NO population, with an average base temperature for emergence of 8.1°C, and those from Central Europe, the Mediterranean area and the Middle East, better described by the common IT population, with a higher base temperature for emergence of 11.2°C. Despite this, the effect of cold stratification on the temperature requirements for emergence restricts the application of a model, so that one developed for Mediterranean climates may not be applicable in Central Europe. Further research is needed to understand the variation in basic temperature thresholds such as base temperature. The results also highlight the need to develop a process-based mechanistic model to explain the dynamics of seed dormancy, germination and seedling emergence, as affected by environmental conditions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All the raw germination, emergence and climatic data are available for anyone who would like to consult them.

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