Weed Science

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Research Article

Cite this article: Chen Y, Masoom A, Huang Z, Xue J, Chen G (2025). Interspecific and intraspecific differences in seed germination response to different temperatures of three *Echinochloa* rice weeds: a case study with 327 populations. Weed Sci. **73**(e23), 1–9. doi: 10.1017/wsc.2024.104

Received: 4 August 2024
Revised: 27 November 2024
Accepted: 23 December 2024

Associate Editor:
Vipan Kumar, Cornell University

Keywords:
Echinochloa crus-galli var. *crus-galli* (L.) P. Beauv. (EC); *Echinochloa crus-galli* var. *mitis* (Pursh) Peterm. (ECM); *Echinochloa glabrescens* Munro ex Hook. f. (EG); seed germination

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Interspecific and intraspecific differences in seed germination response to different temperatures of three *Echinochloa* rice weeds: a case study with 327 populations

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Abstract

Echinochloa crus-galli var. *crus-galli* (L.) P. Beauv. (EC), *Echinochloa crus-galli* var. *mitis* (Pursh) Petermann (ECM), and *Echinochloa glabrescens* Munro ex Hook. f. (EG) are all serious rice (*Oryza sativa* L.) weeds that are usually treated as a single species in weed management practices. To determine interspecific and intraspecific differences in seed germination responding to different temperatures among the three *Echinochloa* weeds, we conducted field surveys and collected 66 EC, 141 ECM, and 120 EG populations from rice fields of East China in 2022; and tested their seed germination under 28/15 C (day/night), 30/20 C, and 35/25 C regimes, simulating temperatures of rice-planting periods for double-cropping early rice, single-cropping rice, and double-cropping late rice, respectively. In EC, ECM, and EG, seed percentage germination (cumulative percentage of germinated seed) and germination index (sum of the ratio of germinated seeds to the corresponding days) increased with increasing temperatures. At 28/15 C, the average percentage germination of EC populations (67.5%) was significantly ($P < 0.05$) higher compared with ECM (46.4%) and EG (43.7%); GD_{50} (duration for 50% total germination) for EC populations (5.2 d) was significantly shorter compared with ECM (5.9 d) and EG (5.8 d). At 35/25 C, the percentage germinations of EC (90.7%), ECM (80.5%), and EG (80.3%) were all significantly the highest among the three temperature treatments, respectively, and the GD_{50} values for EC (2.5 d), ECM (2.6 d), and EG (2.7 d) were all significantly the lowest. At 30/20 C and 35/25 C, the average germination percentages of populations collected from transplanted rice fields were significantly higher than those of populations collected from direct-seeded rice fields. Moreover, among EG populations, the longitudes and latitudes of collection locations were significantly correlated with seed percentage germination and germination indices. According to the interspecific differences and intraspecific variations of *Echinochloa* species, weed management strategies should also be customized according to the species and population characteristics in seed germination.

Introduction

The genus *Echinochloa* includes numerous problematic rice (*Oryza sativa* L.) weeds, such as *Echinochloa crus-galli* var. *crus-galli* (L.) P. Beauv. (EC) (Holm et al. 1979), *Echinochloa crus-galli* var. *mitis* (Pursh) Peterm. (ECM), and *Echinochloa glabrescens* Munro ex Hook f. (EG) (Chen et al. 2019) in rice-planting areas in Asia. EC, ECM, and EG are very similar in morphology and are usually treated as a single species in weed management practices. Spikelets of EC are 3 to 4 mm in length, and the lower lemma extends into an awn to 3 cm. Spikelets of ECM are about 3 mm in length and awnless or with awns shorter than 5 mm, while inflorescences of ECM are usually branched. The lower lemma of EG is convex, coriaceous, and shining; while the lower lemmas of EC and ECM are flat and herbaceous (Chen et al. 2019; Chen and Phillips 2006). Our previous studies found that the harmfulness of ECM and EG is not lower than that of EC and even higher in some regions. Zhang et al. (2014) found that 6 plants m^{-2} of EC and ECM resulted in 10.8% to 25.3% and 19.2% to 39.7% reduction in rice yield, respectively. Opena et al. (2014) found that EG may cause a yield loss of 7% to 87%.

EC, ECM, and EG propagate by seed (Chen et al. 2022; Li 1998). Therefore, knowledge on seed germination of these weed species is of key importance for their integrated management (Y Chen et al. 2023; Masin et al. 2014; Rezvani et al. 2021). Temperature is the primary factor influencing seed germination. EC did not germinate below 10 C, and its percentage germination increased with temperature increasing from 10 C to 24 C (Loddo et al. 2018). The optimal germination temperature for EC was around 25 to 30C (Kovach et al. 2010). EC buried in the autumn had a higher average percentage germination than seeds buried in the spring, and the optimal germination temperature for EC decreased with increasing seed age (Martinkova and Honek 2013; Martinkova et al. 2006). In the case of alternating light and dark, the percentage germination of EG populations at 25/15 C, 30/20 C, and 35/25 C were similar (Opena et al. 2014). The average percentage germination of ECM was 54.0% at 25 C and 0% at 17 C.

To date, research on *Echinochloa* species has been mainly on EC, and most studies on the seed biology of *Echinochloa* species were based on one to two populations. Yoshioka et al. (1998) confirmed soil CO_2 was responsible for causing intermittent flushes of germination by testing 50 EC populations. The differences in biological and ecological traits among these three species remain undefined. Considering the widespread distribution of the three *Echinochloa* species and the seriousness of their damage in rice fields, a comparative study of the variations between EC, ECM, and EG is necessary. It is the basis for differentiated and efficient integrated management.

In 2022, we collected 66, 141, and 120 populations of EC, ECM, and EG, respectively, from rice fields in East China. We compared the germination characteristics of these populations under different temperature regimes. It had been reported that there were significant intraspecific differences in the initial germination temperature of EC (Royo-Esnal et al. 2022). Nevertheless, the existence of intraspecific differences in ECM and EG had yet to be determined. With all 327 populations collected from rice fields in East China, the aims of this study were to (1) reveal intraspecific differences in seed germination of EC, ECM, and EG at different temperatures simulating different rice-planting periods; and (2) compare seed germination of EC, ECM, and EG at different temperatures.

Materials and Methods

Sampling and Investigation

In October 2022, we conducted field surveys on the occurrence of EC, ECM, and EG in rice fields of East China (Supplementary Table S1) and collected seeds from each rice field surveyed. A total of 250 independent rice fields (sites) where EC, ECM, or EG occurred were randomly surveyed, with an interval of >5 km for adjacent sites (Figure 1; Supplementary Table S1). Each site surveyed a rice field covering an area of about 0.1 to 0.2 ha. The identification of *Echinochloa* species was based on our previous work (Chen et al. 2019). A total of 327 *Echinochloa* populations were collected: 66 EC, 141 ECM, and 120 EG populations. Panicles with mature seeds were randomly collected from more than 100 individuals of each population with a pollen bag (100 mesh, 30 cm by 45 cm), and mature seeds were collected by hand. The relative dominance of *Echinochloa* species in rice fields was scored 0.1, 0.5, 1, 2, 3, 4, or 5 by visual inspection according to Qiang (2005) and our previous field surveys (Chen et al. 2013). Seeds were air-dried and stored in our lab at room temperature fluctuating from 15 C to 25 C. From March to June 2023, the 1,000-seed weight of each population was determined by weighing 5 replicates of 100 mature seeds.

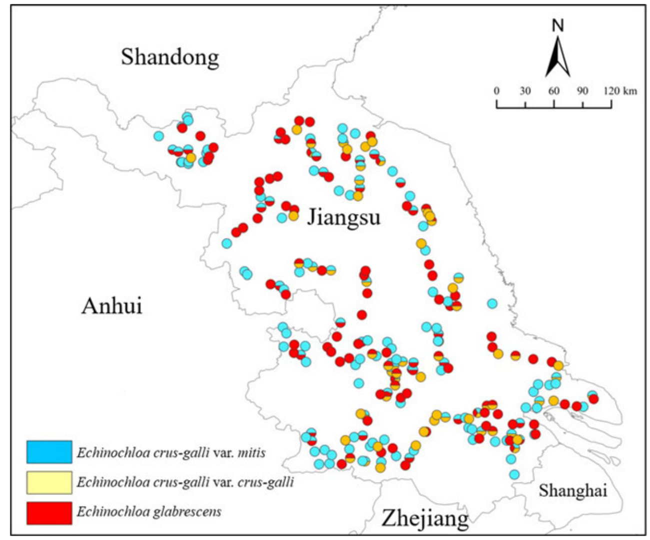

Figure 1. Collection sites of the three *Echinochloa* species populations in rice fields in China.

Experimental Design

To determine the adaptation of the three *Echinochloa* species to temperatures at the beginning of rice-planting season in East China, three temperature regimes were set responding to three different rice-cropping patterns in East China: single-cropping rice, double-cropping early rice, and double-cropping late rice. Single-cropping rice is mainly sown or transplanted around June 20, double-cropping early rice is usually transplanted around May 20, and double-cropping late rice is often transplanted around July 20. Therefore, seeds were incubated at alternating temperatures of 28/15 C (day/night), 30/20 C, and 35/25 C with a 12/12-h (light/dark) photoperiod to simulate the temperature of double-cropping early rice, single-cropping rice, and double-cropping late rice, respectively. From April to June 2023, about 7 mo after seed collection, seed germination for each population under the above three temperature regimes was determined in incubators (HBZ-400B, Changzhou Haibo Instrument Equipment, Changzhou, Jiangsu, China) with three replications. Fifty seeds from each population were placed into a 9-cm-diameter petri dish with two pieces of filter paper (Hangzhou Fuyang Beimu Pulp & Paper), which contained 6 ml of distilled water. The germinated seeds with a visible radicle were counted and removed (Rehman et al. 2011). Percentage germination of each petri dish was determined daily for 21 d. From May to June 2024, 20% of 327 *Echinochloa* populations were selected randomly for germination repeatedly.

Statistical Analysis

The percentage germination of each dish was determined by the percentage of germinated seeds out of the number of sown seeds (50). The germination index for each dish was determined using Equation 1 (Schmer et al. 2012):

$$GI = \sum (GT/DT) \quad [1]$$

where GT is the number of seed germinations per day; and DT is the germination day corresponding to GT. Coefficient of

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variations (CVs) for variables were determined using Equation 2 (Munthali et al. 2012):

$$CV = \sigma/\mu \times 100\% \quad [2]$$

where μ is the sample mean, and σ is the sample SD.

A three-parameter logistic function was fitted to test days and accumulated temperature required for germination (Equation 3), using the DRC add-on package in R v. 3.1.3 (Ritz et al. 2015):

$$Y = a/[1 + (x/e)^b] \quad [3]$$

where Y denotes the total germination (%) at day x of the germination or accumulated temperature x after sowing; a is the upper limit; b indicates the slope; e is the days required for 50% of total germination (GD_{50}) or the accumulated temperature required for 50% of total germination (TD_{50}). Accordingly, the days required for 90% of total germination (GD_{90}) and the accumulated temperature required for 90% of total germination (TD_{90}) were determined.

To determine differences in germination indices among three temperature regimes, data were subjected to ANOVA in SPSS software v. 26.0 (IBM, Armonk, NY, USA), using the one-way ANOVA procedure. Data were checked for normality and constant variance before analysis. Treatment means were separated using the LSD test at P = 0.05. The general linear model (GLM) in SPSS was used to test data of environmental factors and germination indices; *Echinochloa* species, planting methods, and collection cities were set as dependent variable; GD_{50}, GD_{90}, and percentage germination were set as fixed factors. Correlations among [1] the latitudes and longitudes of seed collection sites and germination indices; and [2] 1,000-seed weight and relative dominance, percentage germination, and GD_{50} were determined with SPSS using correlation analysis. The independent-sample *t*-test method in SPSS software was used to compare the differences in percentage germinations of *Echinochloa* species collected from direct-seeded rice fields and transplanted rice fields at different temperature regimes. The data presented are means ± SEs.

Results and Discussion

Distribution and 1,000-Seed Weight

Among the 250 collection sites (Figure 1), 2 *Echinochloa* species co-occurred in 68 collection sites, and 3 *Echinochloa* species co-occurred in 5 collection sites. ECM was the most frequent species (43.0%), followed by EG (36.6%) and EC (20.4%). Average values of relative dominance among seeds collected in rice fields were 2.5, 2.5, and 2.7 (Supplementary Figure S1), for EC, ECM, and EG populations, respectively, which did not show significant differences. *Echinochloa* species differed in their average 1,000-seed weights. EC were significantly the heaviest (average 1,000-seed weight of 2.92 g), followed by EG and ECM with 1,000-seed weights of 2.40 g and 2.26 g, respectively (Figure 2). Interestingly, the 1,000-seed weight of the 327 *Echinochloa* populations showed significant and positive correlations with relative dominance, percentage germination, and germination index (Figures 3 and 4).

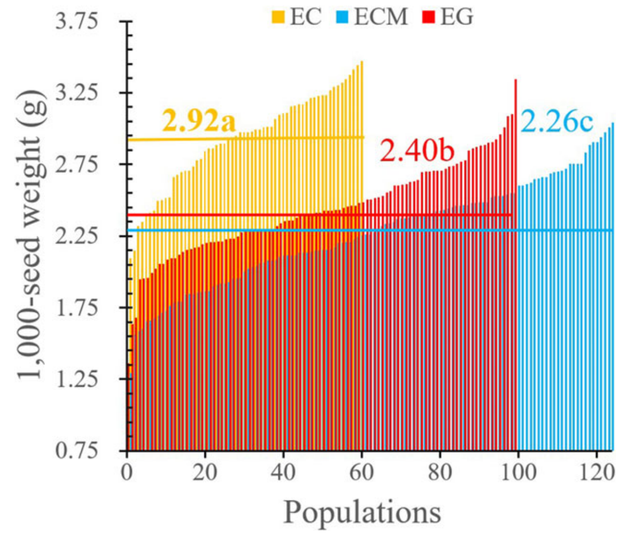

Figure 2. Thousand-seed weight of *Echinochloa crus-galli* var. *crus-galli* (EC), *Echinochloa crus-galli* var. *mitis* (ECM), and *Echinochloa glabrescens* (EG). The horizontal lines represent the average 1,000-seed weight of each of the three *Echinochloa* species. Different letters indicate significant differences among the three *Echinochloa* species.

Interspecific Differences

At 28/15 C, the average percentage germination of EC (67.5%) was significantly higher ($P < 0.05$) than that of ECM (46.4%) and EG (43.7%) (Figure 5), and the coefficients of variations (CVs) were 35.9, 43.2, and 44.2, respectively (Supplementary Table S2). The average percentage germinations of the three species at 30/20 C were like those of the same species at 28/15 C (Supplementary Table S3). Among the 120 EG populations, the latitude of population collection sites significantly and positively correlated with the percentage germination at 28/15 C and 30/20 C (Table 1); the longitudes of population collection sites significantly and negatively correlated with the percentage germination at 30/20 C. When temperature regime increased to 35/25 C, the average percentage germinations of EC, ECM, and EG were 90.7%, 80.5%, and 80.3%, and the coefficients of variation of EC, ECM, and EG decreased to 11.2, 17.5, and 17.8, respectively (Table 1; Supplementary Table S2).

The average germination indices of EC, ECM, and EG were 5.6, 3.8, and 3.6 at 28/15 C, respectively (Figure 6), and the coefficients of variation were 41.0, 55.7, and 52.2, respectively. At 35/25 C, the average germination indices of EC, ECM, and EG were also significantly highest among different temperature treatments, with 13.7, 9.8, and 9.7, respectively. The percentage germination and germination index of EC was higher than that of the other two species regardless of temperature regimes.

The percentage germination and germination process of EC were significantly higher and faster than those of ECM and EG at the same temperature treatments, which might be related to seed mass. Zhou et al. (2021) found that the smaller common ragweed (*Ambrosia artemisiifolia* L.) seeds germinated faster with a study of 26 populations. Here, the 1,000-seed of EC was heavier than those of ECM and EG by 29.2% and 21.7%, respectively (Figure 2). Meanwhile, species of *Echinochloa* and the city where the population was collected had significant influences on the GD_{50} and GD_{90} values and percentage germination (Table 2). Moreover, percentage germination at high temperatures was significantly

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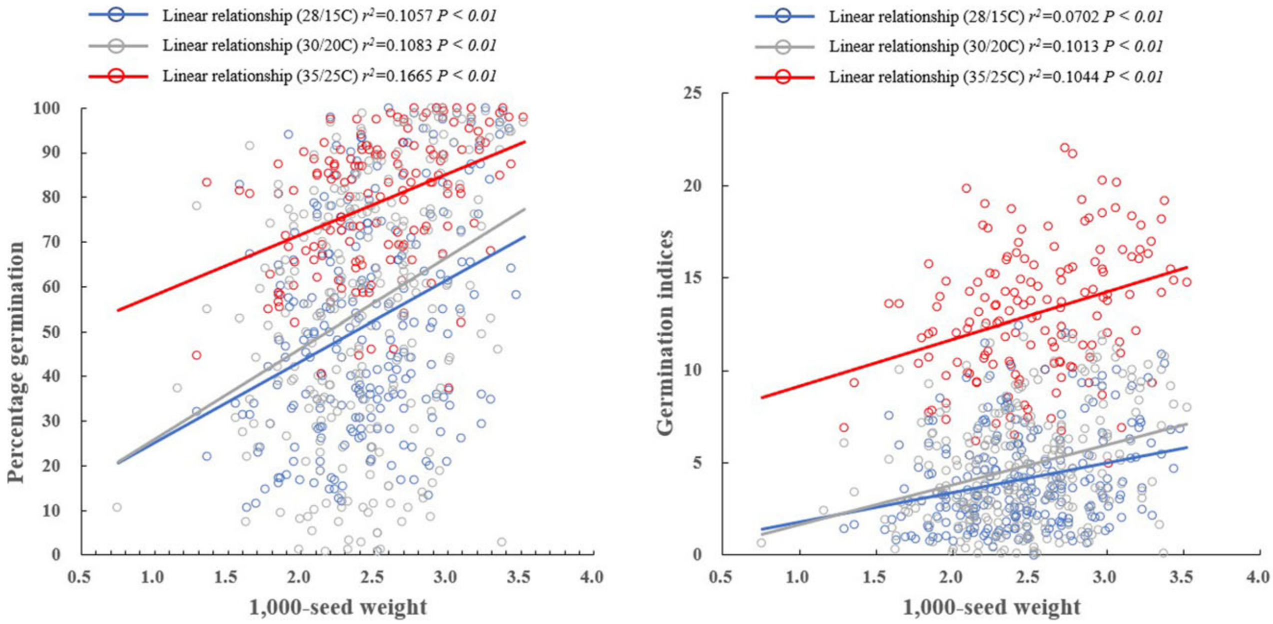

Figure 3. Correlations between 1,000-seed weight and percentage germination and germination index at different temperature regimes for the three *Echinochloa* species.

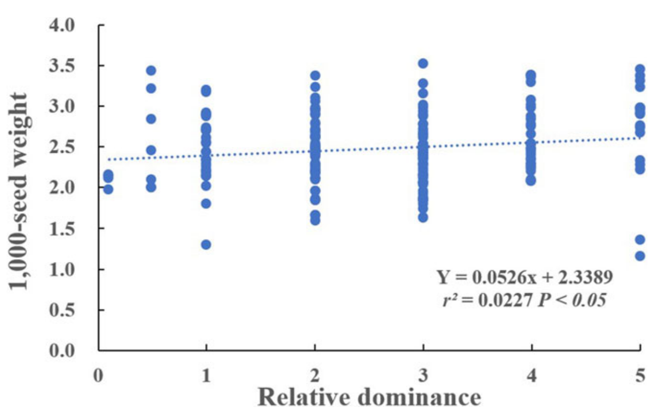

Figure 4. Correlations between 1,000-seed weight and relative dominance for the three *Echinochloa* species.

influenced by the planting method (direct seeding or transplanting) at the site where the seed was collected. Specifically, at 30/20 C, average germination percentage of overall populations collected from transplanted rice fields (62.9 ± 2.6%) were significantly higher than that of overall populations collected from direct-seeded rice fields (52.5 ± 2.1%), as well as the comparison at 35/25 C (85.9 ± 1.7% vs. 76.9 ± 1.5%) (Supplementary Table S4). The chemical control time window against *Echinochloa* species in rice fields is before planting or sowing to the rice bolting stage, which is about 10 d shorter in transplanted rice fields than in direct-seeded rice fields (Li et al. 2015; Sun et al. 2014). Thus, *Echinochloa* species populations escaping chemical control applications tended to have a longer growth period in transplanted rice fields than those in direct-seeded rice fields. This longer development time often results in higher-quality seeds (Chen et al. 2017), which could lead to a significantly high percentage germination of *Echinochloa* seeds collected from transplanted rice fields.

Compared with the average GD_{50} and GD_{90} values for ECM and EG, those of EC were significantly highest among the three temperature regimes (Figures 7 and 8). The GD_{50} values for *Echinochloa* species were significantly and positively correlated with the latitude of population collection sites and negatively correlated with the longitudes of population collection at 35/25 C, respectively. Considering the different climate zones in the world, accumulated temperature was more universal (Hou et al. 2014). At 28/15 C, the average accumulated temperatures of EC, ECM, and EG to 50% total germination were 111.0 C, 127.3 C, and 124.7 C, respectively (Table 3). At 35/25 C, the average accumulated temperatures of EC, ECM, and EG to 50% total germination were 74.3 C, 76.4 C, and 80.2 C, respectively. Six indices of ECM and EG seed germination showed no significant differences at the same temperature treatments, excluding GD_{90} and TD_{90} at 30/20 C and 35/25 C (Supplementary Table S5).

Interspecific differences were obvious among the three *Echinochloa* species, and seed germination could be affected by the latitudes and longitudes of the population collection sites (Zhou et al. 2021). Cheng et al. (2022) found that smooth cordgrass (*Spartina alterniflora* Loisel.) seeds germinated earlier at higher latitudes. In our results, germination indices of EG were also impacted by the latitudes and longitudes of collection sites (Table 1). EG seeds in the northwest region had a lighter 1,000-seed weight (Supplementary Table S6), the percentage germination tended to be higher, and the germination process tended to be slower. Furthermore, the city where the population was collected significantly affected the seed percentage germination and germination process of tested *Echinochloa* species populations (Table 2). This effect may be related to the influence of local rice cultivation, field management, climate, and other environmental factors (Li et al. 2009). Among these factors, previous crops were the most critical for weed impact, followed by tillage intensity and environmental parameters (Hanzlik and Gerowitt 2011). Additionally, geographic location and agricultural practices could affect the genetic variation of EC (Altop and Mennan 2011).

Table 1. The correlation between the latitude (Lat.) and longitude (Long.) of the collection sites and the germination indices of three *Echinochloa* species populations. Values are correlation values and not GPS coordinates.

		Echinochloa crus-galli var. *crus-galli*	*Echinochloa crus-galli* var. *mitis*				*Echinochloa glabrescens*
Temperature	Index[a]	Long.	Lat.	Long.	Lat.	Long.	Lat.
28/15 C	GD_{50}	−0.12	−0.20	0.07	−0.11	−0.01	−0.03
	GD_{90}	−0.15	−0.09	0.03	−0.10	−0.07	0.04
	Percentage germination	−0.02	0.09	0.01	0.16	−0.12	**0.24***
30/20 C	GD_{50}	−0.13	−0.10	−0.07	−0.06	−0.05	0.06
	GD_{90}	−0.12	−0.04	−0.10	−0.04	−0.07	0.08
	Percentage germination	−0.08	0.19	0.06	0.09	**−0.18***	**0.24***
35/25 C	GD_{50}	−0.04	−0.19	−0.02	−0.02	**−0.47***	**0.36***
	GD_{90}	0.07	−0.24	0.02	−0.05	**−0.37***	**0.39***
	Percentage germination	−0.11	0.14	−0.08	0.09	0.15	−0.03

[a]GD_{50}, days required for 50% of total germination; GD_{90}, days required for 90% of total germination.
*Significant effect at $P < 0.05$. *NS* note was removed, because (1) *NS* does not need to be defined and (2) there are no entries with "*NS*" in Table 1.

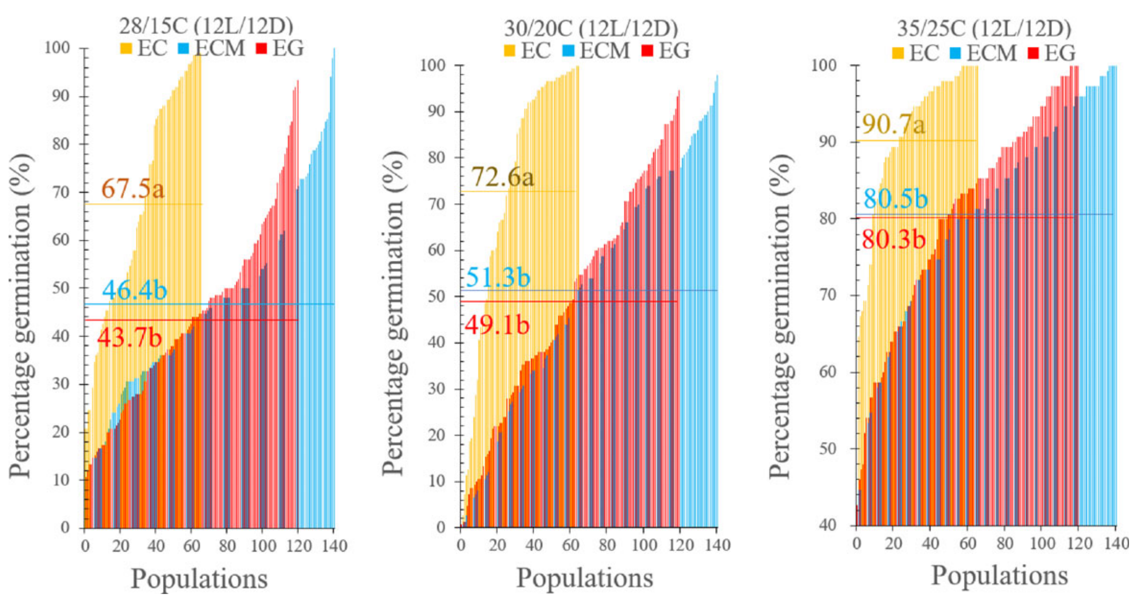

Figure 5. Percentage germination of *Echinochloa crus-galli* var. *crus-galli* (EC), *Echinochloa crus-galli* var. *mitis* (ECM), and *Echinochloa glabrescens* (EG) at 28/15 C, 30/20 C, and 35/25 C with a 12/12-h (light/dark) photoperiod (12L/12D). The horizontal lines represent the average percentage germinations of each of the three *Echinochloa* species. Different letters indicate significant differences among three *Echinochloa* species in the same figure.

Intraspecific Differences

Percentage germination and germination index of the three *Echinochloa* species increased with temperature increments, which were significant at 35/25 C. At 28/15 C, the average GD_{50} and GD_{90} values of EC (5.2 and 7.4), ECM (5.9 and 10.5), and EG (5.8 and 10.0) were significantly highest, followed by treatments at 30/20 C with EC (4.6 and 6.1), ECM (5.1 and 7.4), and EG (5.2 and 8.2). At 35/25 C, the GD_{50} and GD_{90} values for EC (2.5 and 3.4), ECM (2.6 and 3.8), and EG (2.7 and 4.0) were all significantly the lowest among different temperatures. The GD_{50} and GD_{90} values of EC were the lowest at the same temperature conditions, and the GD_{90}s of ECM and EG had significant differences at 35/25 C (Supplementary Tables S3 and S4).

Seed germination of the 66 EC populations at different temperatures simulating different rice-planting periods varied considerably, and intraspecific differences decreased significantly with increasing temperature (Supplementary Tables S2 and S3). Royo-Esnal et al. (2022) found that one EC population collected in Norway tended to emerge earlier than another population collected in Italy. Intraspecific variations in seed percentage germination and GD_{50} were also found in a study with 25 EC populations (Martinkova and Honek 1997). The 66 EC populations in the present study produced CVs of 35.9 and 24.3 in percentage germination and GD_{50} values at 28/15 C, while the CVs of both indices decreased dramatically at 35/25 C. Serra et al. (2018) found EC populations exhibited varying degrees of adaptability to environmental conditions during the seed germination stage. Intraspecific variations included population-level variations, between-individual variations, and within-individual variations, which were affected by the maternal plant (Albert et al. 2011). Our study was at the population-level, so these intraspecific variations would be affected by genotypic compositions of populations and a temporal variability in the environment. Intraspecific variations in the germination process and the percentage germination of EC were notable at low temperatures, and such variations narrowed with increasing temperatures. Increasing temperatures increased the percentage germination and accelerated the germination process (Bastiani et al. 2015; Derakhshan et al. 2018). Marambe and Amarasinghe (2002) found

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Table 2. The effects (*F*-values) of species, planting method, and city on three germination indices determined by generalized linear models.

Temperature	Index[a]	Species	Planting method	City
28/15 C	GD_{50}	4.50*	0.17^{NS}	3.95*
	GD_{90}	3.29*	0.16^{NS}	2.45*
	Percentage germination	22.78*	2.51^{NS}	3.94*
30/20 C	GD_{50}	2.18*	0.99^{NS}	2.06*
	GD_{90}	2.25*	0.27^{NS}	1.56^{NS}
	Percentage germination	16.13*	14.01*	4.32*
35/25 C	GD_{50}	2.95*	0.13^{NS}	2.56*
	GD_{90}	5.54*	2.65^{NS}	1.84*
	Percentage germination	17.06*	5.52*	1.84*

[a]GD_{50}, days required for 50% of total germination; GD_{90}, days required for 90% of total germination.
*Significant effect at $P < 0.05$.

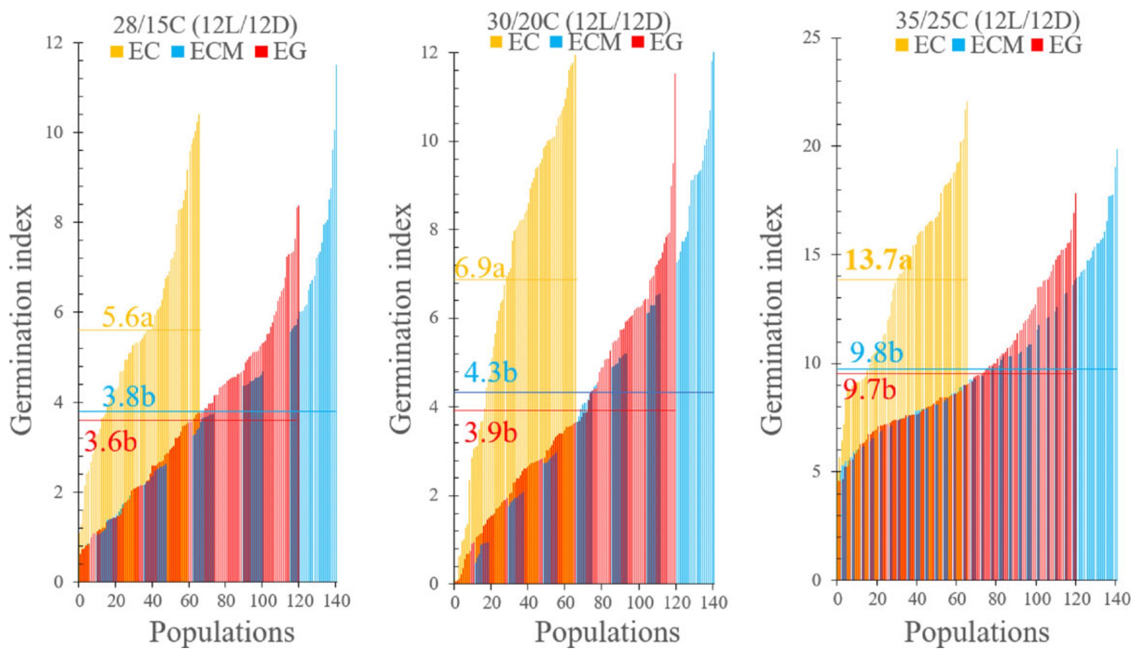

Figure 6. Germination index for *Echinochloa crus-galli* var. *crus-galli* (EC), *Echinochloa crus-galli* var. *mitis* (ECM), and *Echinochloa glabrescens* (EG) at 28/15 C, 30/20 C, and 35/25 C with a 12/12-h (light/dark) photoperiod (12L/12D). The horizontal lines represent the average germination indices of each of the three *Echinochloa* species. Different letters indicate significant differences among three *Echinochloa* species in the same figure.

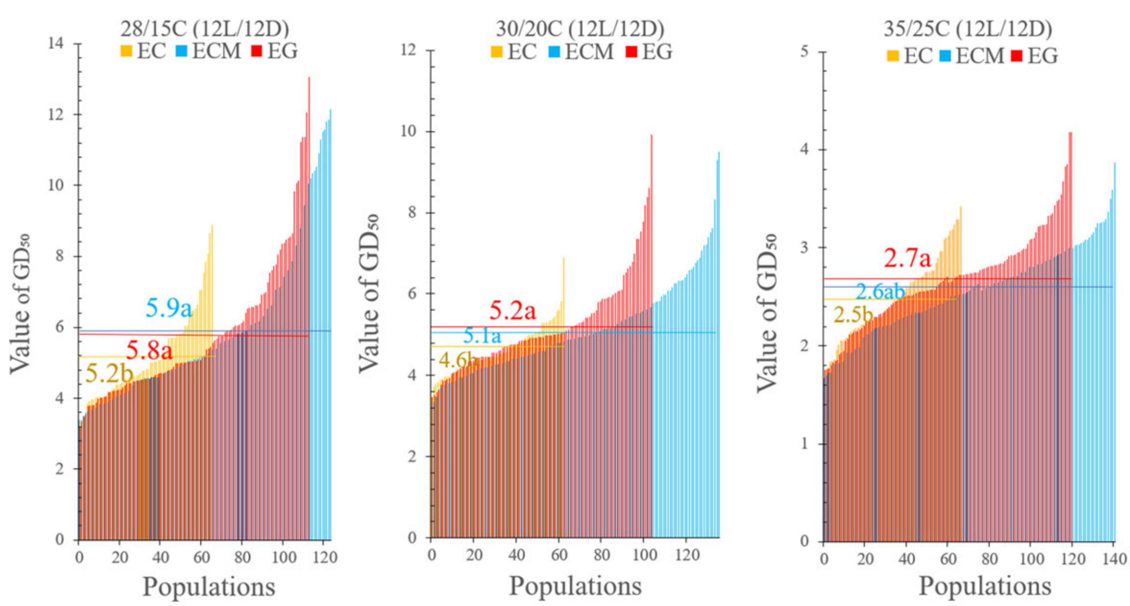

Figure 7. Number of days to 50% total germination rate (GD_{50}) of *Echinochloa crus-galli* var. *crus-galli* (EC), *Echinochloa crus-galli* var. *mitis* (ECM), and *Echinochloa glabrescens* (EG) at 28/15 C, 30/20 C and 35/25 C with a 12/12-h (light/dark) photoperiod (12L/12D). The horizontal lines represent the average GD_{50} values of each of the three *Echinochloa* species. Different letters indicate significant differences among three *Echinochloa* species in the same figure.

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Table 3. The accumulated temperature to 50% and 90% total germination (TD_{50} and TD_{90}) of *Echinochloa* species at different temperature regimes[a].

Temperature	*Echinochloa crus-galli* var. *crus-galli*		*Echinochloa crus-galli* var. *mitis*		*Echinochloa glabrescens*	
	TD_{50}	TD_{90}	TD_{50}	TD_{90}	TD_{50}	TD_{90}
28/15 C	111.01 ± 3.32a	159.21 ± 7.37a	127.26 ± 4.16a	225.17 ± 14.05a	124.70 ± 4.01a	214.97 ± 12.95a
30/20 C	116.08 ± 1.96a	153.02 ± 4.47a	128.02 ± 2.40a	184.11 ± 5.55b	130.28 ± 2.81a	205.24 ± 9.22a
35/25 C	74.25 ± 1.54b	103.37 ± 2.56b	76.41 ± 1.09b	111.47 ± 2.03c	80.16 ± 1.32b	120.78 ± 2.75b

[a]Different letters in the same column indicate significant differences among the three temperature regimes at $P < 0.05$.

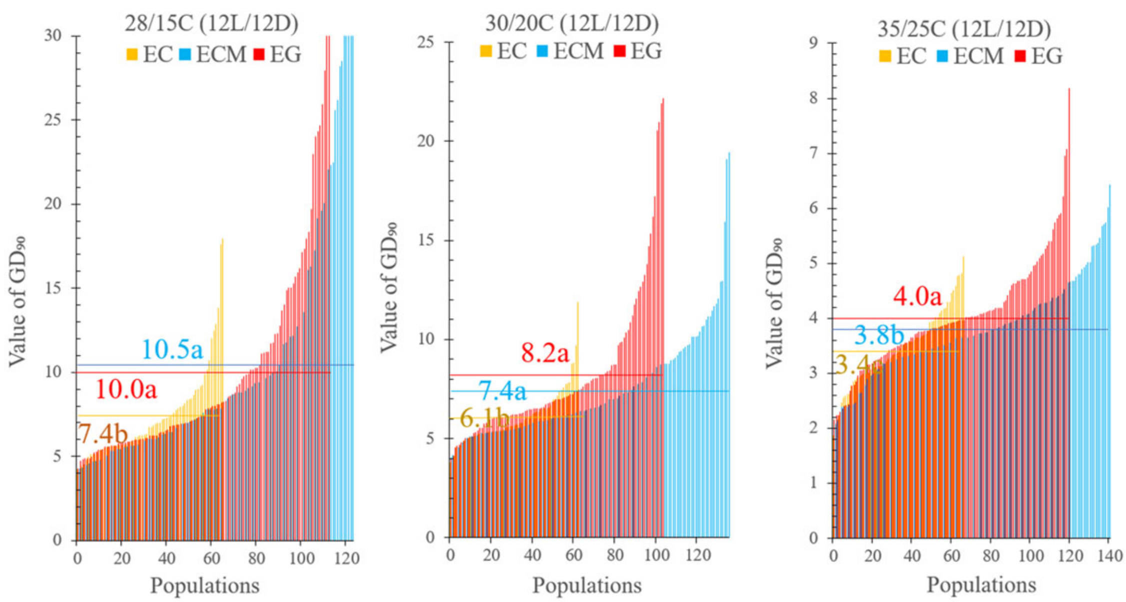

Figure 8. Number of days to 90% total germination rate (GD_{90}) for *Echinochloa crus-galli* var. *crus-galli* (EC), *Echinochloa crus-galli* var. *mitis* (ECM), and *Echinochloa glabrescens* (EG) at 28/15 C, 30/20 C and 35/25 C with a 12/12-h (light/dark) photoperiod (12L/12D). The horizontal lines represent the average GD_{90} values of each of the three *Echinochloa* species. Different letters indicate significant differences among three *Echinochloa* species in the same figure.

percentage germinations of EC at 34/31 C were 27% to 29% higher compared with those at 28/24 C with two populations. In this study, the average percentage germination of the 66 EC populations at 35/25 C was 90.7%, which was significantly higher than those at 28/15 C and 30/20 C, respectively; the GD_{50} of the 66 EC populations at 35/25 C was 2.5 d, which was significantly lower than those at 28/15 C and 30/20 C. The CV of the average percentage germination among the 66 EC populations decreased from 40.7 to 11.2 as with treatment temperature increased from 30/20 C to 35/25 C, as did the germination index, GD_{50}, and TD_{50}.

Seed germination of the 141 ECM and the 120 EG populations also showed notable intraspecific variations, which also decreased significantly with increasing temperature. When the temperature increased to 35/25 C, the CVs of GD_{50} among the 141 ECM and 120 EG populations significantly decreased to 16.9 and 18.1, respectively, as well as percentage germination, germination index, and TD_{50}. The accumulated temperature could serve as a reference for the growth and development of wheat (*Triticum aestivum* L.), which required an accumulation of 70 to 80 C to produce each leaf on the main stem (Li et al. 2009). In contrast, the accumulated temperatures required for EC, ECM, and EG seed germination at high temperatures were significantly lower than those at low temperatures. This may be the less days that seed germination needed under high temperature regimes. Combined with data from experiment repetition in the second year (Supplementary Table S7), seed germination of the three *Echinochloa* species response to temperature had significant intraspecific variations.

Management Strategies

In management of rice weeds, different species of *Echinochloa* species are usually treated as a single species (Guo et al. 2017). Nevertheless, our results suggested interspecific differences among EC, ECM, and EG, as well as intraspecific variations among populations of the same species. Hence, management strategies against EC, ECM, and EG should also be customizable according to the target populations, especially when EC co-occurs with either ECM or EG in a rice field. The significant correlation between 1,000-seed weight, percentage germination, and relative dominance of *Echinochloa* weed populations is a warning to farmers to pay more attention to the rice fields with serious *Echinochloa* weed damage and formulate reasonable and effective control measures.

At the temperatures simulating the planting period of double-cropping early rice (28/15 C) and single-cropping rice (30/20 C), the percentage germinations of the three *Echinochloa* species ranged greatly, with a long duration. For long germination periods of the three *Echinochloa* species, onetime preemergence chemical control is not sufficient to control later-emerging seedlings. For double-cropping late rice (35/25 C), a majority of the 327 *Echinochloa* populations tested showed more than 90%

https://doi.org/10.1017/wsc.2024.104 Published online by Cambridge University Press

germination within 3 to 4 d. Therefore, preemergence chemical control at 4 d after rice seeding or transplanting could be highly effective (GQ Chen et al. 2023), as could stale seedbed strategies (Chen et al. 2022). When two or three *Echinochloa* species occurred in the same field at low temperatures (28/15 C and 30/25 C), species identification was crucial. At low temperatures, the same weed management can be applied to ECM and EG in view of their similar germination durations. However, the germination duration of EC was shorter compared with the other two species, making preemergence control should be applied within 5 to 6 d when EC occurrs in a rice field. Moreover, the longer germination periods of ECM and EG suggests they were more likely to partially evade preemergence herbicide treatment in rice fields. Consequently, management practices implemented too early may fail to completely control late-emerging seedlings, whereas management practices implemented too late will suffer from low efficacy (Marschner et al. 2024), and thus repeated application of preemergence herbicides will be necessary. Also, considering the significant influence of collection location on seed germination characteristics, weed management strategies employed in local or adjacent areas could be used as important references to improve the efficiency of integrated management against *Echinochloa* rice weeds in paddy fields (Boddy et al. 2012; Rezvani et al. 2021).

In summary, we collected 66 EC, 141 ECM, and 120 EG populations in 250 rice fields surveyed in East China, and average values of relative dominance of the three species did not show significant differences. The 1,000-seed weight of the 327 *Echinochloa* populations overall showed significant and positive correlations with relative dominance, percentage germination, and germination index. Significant interspecific and intraspecific variations in seed germination characteristics under different temperatures were identified. EC showed significantly the highest seed biomass and percentage germinations, which made EC damage more probable and timely EC control vital; EG and ECM showed similar germination patterns with each other under all temperature regimes treated (28/15 C, 30/20 C, and 35/25 C). Percentage germination of the three *Echinochloa* species increased with increasing treatment temperatures, with intraspecific variations narrowing with increasing temperatures. The city where the population was collected had significant influence on the germination of *Echinochloa* species. At 30/20 C and 35/25 C, average germination percentages of populations collected from transplanted rice fields were significantly higher than those of populations collected from direct-seeded rice fields. The accumulated temperatures required for EC, ECM, and EG seed germination at higher temperatures were also significantly lower. Together, the findings of this study suggest that management strategies against EC, ECM, and EG, such as stale seedbed and preemergence chemical control, should be customized according to the target populations, in particular when the temperatures are not high.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/wsc.2024.104

Acknowledgments. We thank Hongcheng Zhang (Agricultural College, Yangzhou University, Yangzhou, China) for his guidance in this study.

Funding statement. This study was funded by the National Key R&D Program Projects (2021YFD1700100), Jiangsu Key R&D Plan (BE2022338), Jiangsu Agricultural Science and Technology Independent Innovation Fund (CX (20)1012), and a project funded by the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD).

Competing interests. The authors declare no conflicts of interest.

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