

Seed biology of alkali barnyardgrass (*Echinochloa crus-galli* var. *zelayensis*) and junglerice (*Echinochloa colona*) for improved management in direct-seeded rice

Research Article

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Abstract

Alkali barnyardgrass [*Echinochloa crus-galli* var. *zelayensis* (Kunth) Hitchc] and junglerice [*Echinochloa colona* (L.) Link] are problematic annual weeds in direct-seeded rice (*Oryza sativa* L.) fields in China. The emergence ecology of the two weed species may differ in response to environmental factors. Laboratory and greenhouse experiments were conducted to evaluate the effects of light, burial depth, mulching with wheat (*Triticum aestivum* L.) residue, and time and depth of flooding on the emergence of the two weed species collected from Nanjing, China. Light strongly increased seed germination. Under dark conditions, *E. crus-galli* seed germination (85%) was higher than that of *E. colona* (70%). The seeds of both species exhibited the greatest germination (90% for *E. crus-galli* and 80% for *E. colona*) when sown on the soil surface, and emergence decreased with increasing soil burial depth. Burial depths of 2.2 and 1.4 cm reduced seedling emergence by 50% for *E. crus-galli* and *E. colona*, respectively. No emergence was found at a depth of 6 cm. The seedling emergence for *E. colona* was lower than for *E. crus-galli* at the same soil burial depth. Mulching with wheat residue considerably reduced the seedling emergence and aboveground biomass of both species. The inhibitory effect of mulching with wheat residue on *E. colona* was more notable than on *E. crus-galli*. Early and deep flooding significantly suppressed the emergence, height, and biomass of *E. crus-galli* and *E. colona*, especially *E. colona*. The results gained from this study could provide fundamental ecological knowledge for managing *Echinochloa* species in direct-seeded rice systems.

Introduction

Rice (*Oryza sativa* L.) is one of the most important food crops in the world for more than half of the global population (Qian et al. 2016; Shekhawat et al. 2020). Almost 90% of the world's rice is produced and consumed in Asia (Priya et al. 2019). The generally adopted method of rice planting in Asia is still manual transplanting; however, the main difficulties currently are the reduction of the rural labor force and increased wages for hired labor. Moreover, a significant irrigated rice area may suffer from a water shortage in Asia in the near future (Shivashenkaramurthy et al. 2020). Therefore, to deal with the increase in production costs and/or decrease in the availability of labor and water, there has been a shift from transplanting to direct-seeded rice (DSR) in recent years (Awan and Chauhan 2016).

China is the main producer of rice, contributing more than 28% of total global rice production (Liu et al. 2015). A change in the planting method from seedling-transplanted rice to DSR has occurred since the 1990s in China, with DSR mainly applied in the middle and lower reaches of the Yangtze River (Nie and Peng 2017). However, the application of DSR has unresolved problems. Weeds are a major constraint to DSR yield, as there is no standing water to suppress weed growth, and there is no seedling size advantage to suppress weeds during the rice establishment period (Chauhan and Johnson 2010a; Chauhan et al. 2012b).

Echinochloa species are the main problematic weeds in DSR fields (Awan et al. 2021; Chauhan and Johnson 2011). Among *Echinochloa* species, alkali barnyardgrass [*Echinochloa crus-galli* var. *zelayensis* (Kunth) Hitchc.], a variety of barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.], is widely distributed in rice fields in the middle-lower Yangtze Plain in China, significantly affecting rice production (Shi et al. 2021; Wang et al. 2004). Junglerice [*Echinochloa colona* (L.) Link.], widespread in the tropics and subtropics between 30°N and

30°S, is another *Echinochloa* species that has emerged as a problematic weed in DSR fields in China in recent years. These two species can mimic rice at the seedling stage, and by the time farmers can easily distinguish the weeds, grain yield loss of rice may already be unavoidable (Holm et al. 1991). Zhang et al. (2017) reported that both *E. crus-galli* and *E. colona* at a density of 6 plants m⁻² reduced rice yield by 22% to 55% and 2% to 12%, respectively, compared with the weed-free rice treatment. Prasad (2012) also reported that losses in rice grain yield increased from 48% to 86% as the density of *E. colona* increased from 50 to 400 plants m⁻². Ehsan et al. (2020) reported a decrease in yield ranging from 10% to 70% in DSR, with an increased density of *E. colona* from 22 to 88 plants m⁻². Chauhan and Johnson (2010b) also mentioned a significant decrease (93%) in yield when a single rice plant was surrounded by eight *E. colona* plants.

The use of herbicides is regarded as the most economic and effective option for farmers to manage weeds (Mahajan and Chauhan 2013), particularly in controlling high infestation of *Echinochloa* species in rice fields. However, herbicide resistance in *E. crus-galli* has evolved in China due to the intensive use of herbicides (Gao et al. 2021; Xu et al. 2013). *Echinochloa colona*, collected from rice fields in the middle-lower Yangtze Plain, also showed strong tolerance to metamifop and cyhalofop-butyl (Li et al. 2015).

The biological characteristics of weed seeds, such as germination and emergence, can be used to develop effective management practices through strategies of increasing emergence so that seedlings can be killed or suppressed (Chauhan 2012, 2020). Different environmental factors, such as light, seed burial depth, and soil moisture, exert an effect on the germination and emergence of weed seeds (Chauhan and Johnson 2010b; Chauhan and Johnson 2011; Mahajan et al. 2021). For germination, light may be an important ecological factor; if seeds need light to germinate, it is implied that seeds only germinate at or near the surface of the soil. However, little information is available concerning the effect of light on the germination of *E. crus-galli* and *E. colona* seeds from fields in China. Likewise, knowledge about the effect of soil burial depth on seedling emergence could help determine the best use of tillage measures to inhibit the emergence and growth of weeds.

Wheat (*Triticum aestivum* L.) or rice straw mulching practices have subsequently developed in rice production, especially in the Yangtze River basin in China, where rice–wheat rotations are the main cropping system (Fan et al. 2005; Huang et al. 2013). In addition to improving soil fertility and contributing to higher rice grain yields, crop residues left on the soil surface might also interfere with weed seedling emergence in some systems (Mhlanga 2016; Nikolić et al. 2021), and thus could be potential components for weed management in rice. However, relatively little detailed research is available on the effect of mulching with wheat straw on the seedling emergence of *E. crus-galli* and *E. colona* from China.

Flooding has long been considered an effective measure for controlling weeds in rice fields. The extent of weed control is governed by the time and depth of flooding (Chauhan and Johnson 2008; Chauhan and Johnson 2009a, 2009b; Ghosh et al. 2017; Shekhawat et al. 2020). Given that DSR cannot be irrigated immediately after sowing, irrigation is applied after crop emergence. Weeds may have already emerged when flooding occurs. Therefore, a better understanding of the effect of flooding time on weed growth could provide more effective ecological weed management decisions in DSR. We aimed to evaluate the effect of the abovementioned factors (i.e., light, soil burial depth, mulching

with wheat straw, and time and depth of flooding) on the germination and emergence behavior of the two weed species; understanding these factors could play a crucial role in developing a better weed management strategy in China. Such information will help to formulate cost-effective control measures for *E. crus-galli* and *E. colona* as well as for other weeds with similar emergence requirements in DSR.

Materials and Methods

Experimental Material and Site Description

Experiments were conducted in the laboratory and screenhouse facilities from May to September 2019 at the Jiangsu Academy of Agricultural Sciences, Jiangsu Province, China (32.3°N, 118.87°E). Seeds of *E. crus-galli* and *E. colona* used in this study were collected from 40 to 50 randomly selected plants in naturally infested rice fields (approximately 30 ha) around Nanjing in 2018. The seeds used in this study were collected from freshly harvested plants. The specific method of seed collection was to put a plastic box (32-cm long by 25-cm wide by 8-cm high) under mature weed plants, and then gently pat the plants to allow the mature seeds to fall into the plastic box. For long-term storage, these seeds were sun-dried and then processed by air flotation to remove trash and poorly filled seeds. The seeds were stored in a seed cabinet (Huruiming Instrument, Guangzhou, China) maintained at 4 °C with 40% relative humidity. The 1,000-seed weight was 1.7 g for *E. crus-galli* and 1.2 g for *E. colona*. *Echinochloa crus-galli* and *E. colona* seeds were taken out of the seed cabinet and sun-dried for several days to remove excess moisture and achieve uniform germination before the commencement of the experiments. The germination percentages of *E. crus-galli* and *E. colona* were 91% and 80%, respectively, indicating a high level of seed viability.

Seed Germination in Response to Light

Seed germination of *E. crus-galli* and *E. colona* was determined by placing 25 seeds of each species in a 9-cm-diameter petri dish (Devan Scientific, Wuxi, Jiangsu, China) with four replicates. Petri dishes contained two pieces of Whatman No.1 filter paper (Go On Chemical Co., Ltd., Shanghai, China) moistened with 5 ml of distilled water. To prevent any water loss, petri dishes were sealed with parafilm, and then incubated at 30/20 °C (day/night) under 12/12-h and 0/24-h light/dark regimes per 24-h cycle. To create completely dark conditions, petri dishes were wrapped with two layers of aluminum foil. Seed germination was recorded until 14 d because no further germination occurred after that time. The emergence of radicles was defined as seed germination (ISTA 1996).

Seedling Emergence in Response to Different Burial Depths

Seedling emergence in this study, expressed as a percentage of the number of seeds planted, was considered to be the appearance of seedlings above the soil and wheat straw mulch for seeds planted on or below the soil surface. Twenty-five seeds each of *E. crus-galli* and *E. colona* were buried in 9-cm-diameter plastic pots at depths of 0, 0.5, 1, 2, 4, and 6 cm in a randomized complete block design with four replicates. The soil (pH = 6.1) was composed of 42% clay, 32% silt, and 26% sand with 12.4 g kg⁻¹ organic matter, 115 mg kg⁻¹ alkali hydrolysable N, 45 mg kg⁻¹ Olsen-P, and 64.6 mg kg⁻¹ exchangeable K. Pots were watered initially with an overhead sprinkler and later subirrigated. Each treatment was replicated four times. Seedlings were counted daily, and the experiment was terminated at

21 d after sowing, by which time emergence had ceased (Chauhan and Johnson 2011).

Emergence and Biomass in Response to Different Amounts of Wheat Straw Mulch

The emergence and biomass of *E. crus-galli* and *E. colona* were evaluated in a screenhouse by placing 50 seeds of the same species on the soil surface in one 18-cm-diameter plastic pot for each replicate. The wheat straw used in this experiment was manually harvested. To be consistent with the length of mechanically harvested wheat straw, it was chopped to a length of about 5 cm. The air-dried finely chopped wheat straw from 'Yangmai 16' (a cultivar widely used in local production) was applied as mulch on the soil surface at rates of 0, 5.1, 10.2, 15.3, 20.3, and 25.4 g pot⁻¹, equivalent to 0, 2,000, 4,000, 6,000, 8,000, and 10,000 kg ha⁻¹. Emerged seedlings were counted daily until 21 d after sowing. Finally, the emerged seedlings (at 21 d after sowing) were harvested. The aboveground biomass was determined after oven-drying for 4 d at 70 C. This experiment was conducted in a randomized complete block design, and each treatment was replicated four times for a total of 48 pots for the two weed species. The soil used in the experiment was the same as that used in the soil burial depth experiment.

Emergence and Growth in Response to Flooding

Twenty seeds each of *E. crus-galli* and *E. colona* were sown on the soil surface in plastic pots (15-cm diameter, 15-cm height). Soil moisture in the pots was maintained at the field capacity level before flooding. Seedlings were thinned to 10 pot⁻¹ at 5 d after sowing. To flood seedlings at the same time, the sowing dates of the weeds were staggered. The plants were flooded at 5, 10, 15, and 20 d after sowing to 0- (saturated soil), 2-, 4-, and 6-cm water depths, respectively. On day 14 following the start of flooding, seedling survival was assessed by counting live plants, and plant heights were measured from the soil surface to the uppermost point of plant foliage, as described by Chauhan and Johnson (2011). Shoots (i.e., stem and leaf) and roots of seedlings were then washed to remove the soil particles, bagged separately, and oven-dried for 4 d at 70 C for biomass measurement. In this experiment, we observed that once *E. crus-galli* and *E. colona* seedlings emerged, flooding did not control them effectively. Therefore, another experiment was conducted to evaluate the effect of early flooding on seedling emergence, plant height, and seedling biomass of both species. Twenty seeds each of *E. crus-galli* and *E. colona* were sown on the surface of the soil in plastic pots. Treatments included five flooding times (0, 1, 2, 3, and 4 d after sowing), with each having four flooding depths (0, 2, 4, and 6 cm). The experiment was conducted in a randomized complete block design with four replicates. Seedling emergence, plant height, and biomass were determined at 14 d after completion of the flooding treatments.

Statistical Analysis

All experiments were conducted twice during the period May to September 2019. Data were pooled over the experimental runs, as no significant experimental run by treatment interaction was observed. Data were subjected to ANOVA by species using IBM SPSS v. 25.0 (SPSS, Chicago, IL, USA). Data variance was inspected by plotting residuals to confirm the homogeneity of variance before statistical analysis. Nonlinear regression was used for analysis where appropriate; otherwise, means were separated using the

LSD at the 5% level of significance. The emergence of *E. crus-galli* and *E. colona* in response to seed burial depths or straw residue amounts was described using a three-parameter sigmoid model. The model was:

$$E = E_{\max} / \{1 + \exp[-(x - T_{50})/E_{\text{rate}}]\} \quad [1]$$

In the model, E , E_{\max} , T_{50} , and E_{rate} represent the total seedling emergence (%) at time x , the maximum seedling emergence (%), the time to reach 50% of maximum seedling emergence, and the slope, respectively.

An exponential model described the relationship between seedling emergence (%) and burial depth. The model was:

$$E = E_{\max} * \exp(-E_{\text{rate}} * x) \quad [2]$$

In the model, E , E_{\max} , and E_{rate} indicate emergence (%) at burial depth x , maximum emergence, and slope, respectively.

Results and Discussion

Seed Germination in Response to Light

Light was not a requirement for seed germination of *E. crus-galli* and *E. colona*, but it increased the germination rate (Figure 1). Compared with dark conditions, the seed germination of *E. crus-galli* and *E. colona* exposed to the light/dark conditions was significantly increased by 9% and 18%, respectively. The seed germination of some weeds varies in response to light (Chauhan and Johnson 2010a). In our study, light was not a necessary factor for germination; however, it increased the germination of the two *Echinochloa* species compared with germination in complete darkness. Therefore, it is expected that a proportion of *E. crus-galli* and *E. colona* seeds will not germinate in the soil due to a lack of light to promote germination. However, a portion of seeds buried in the soil may be exposed to the soil surface by tillage, which may trigger seed germination (Milberg et al. 1996). Understanding that light stimulates the germination of *E. crus-galli* and *E. colona* could provide new strategies for weed control by using shade, such as straw mulching or burying seeds in the soil, which would likely affect emergence (Buhler et al. 1997; Forcella 1997; Manpreet et al. 2015).

Seedling Emergence in Response to Burial Depth

The emergence of both species was significantly affected when seeds were subjected to different burial depths. Seeds sown on the soil surface exhibited 90% emergence for *E. crus-galli* and 80% for *E. colona* (Figure 2). Seedling emergence decreased with increasing burial depth; 55% and 23% emergence rates were found at the 4-cm depth for *E. crus-galli* and *E. colona*, respectively. No seedling emergence was observed from 6 cm for either species, which may be due to failed germination resulting from the exhaustion of seed energy reserves (Benvenuti 2003). In addition, a depth-mediated secondary dormancy may be another reason for nongermination of these deeply buried seeds (Benvenuti and Pardossi 2017). According to the fitted model, the burial depth required for 50% inhibition of the maximum emergence was 2.2 cm for *E. crus-galli* and 1.4 cm for *E. colona* (Figure 3). When seeds were on the surface, the time for 50% seedling emergence (T_{50}) was 4.5 d for *E. crus-galli* and 4.2 d for *E. colona*, whereas increases in burial depth protracted emergence, causing the time for 50% emergence to increase (Table 1).

These two weed species produced the largest number of seedlings when their seeds were located on the soil surface, which is in

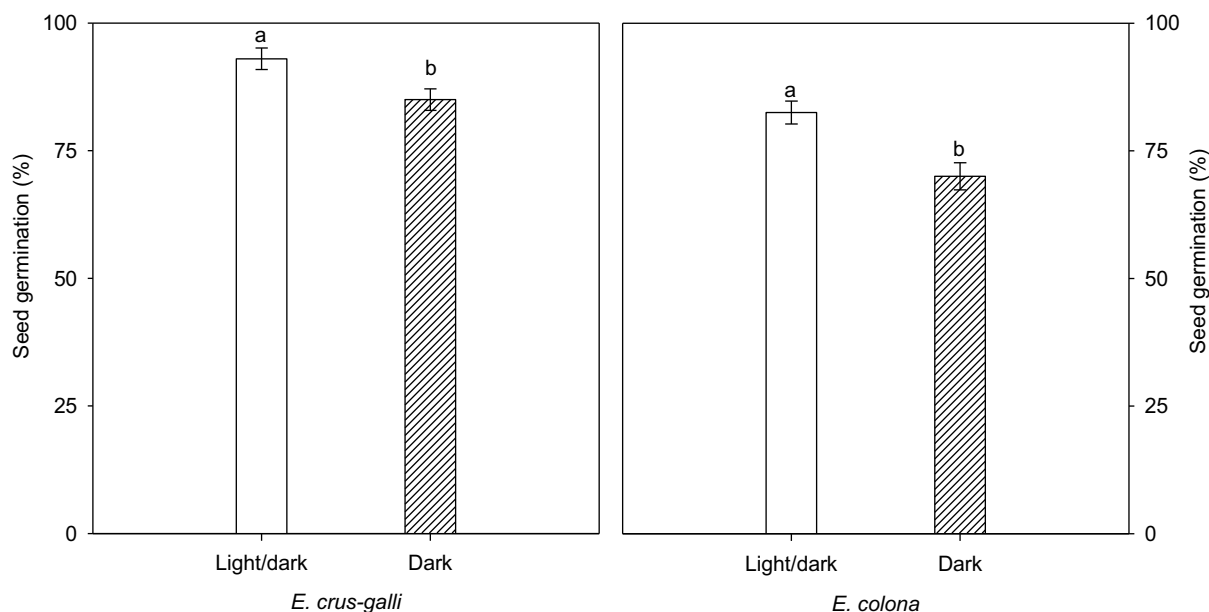


Figure 1. Seed germination of *Echinochloa crus-galli* and *Echinochloa colona* in response to light (light/dark [12 h/12 h] and dark [24 h]). Seeds were incubated for 14 d. For each species, different letters indicate a significant difference at the 0.05 probability level. Error bars denote \pm standard errors of the mean ($n = 8$).

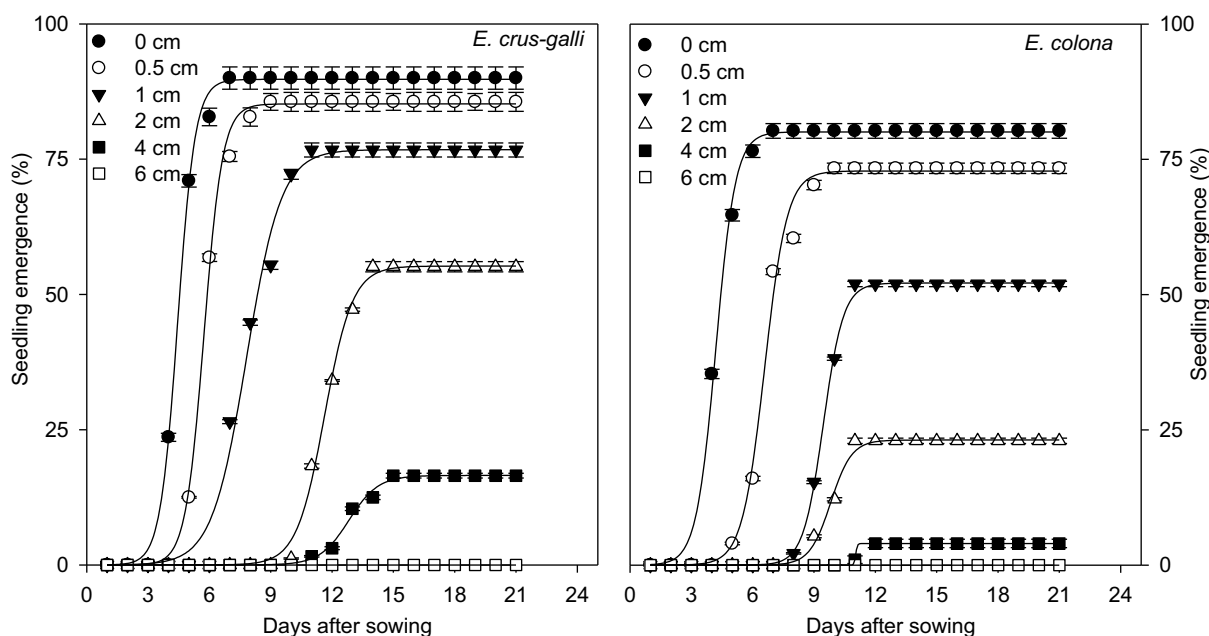


Figure 2. Emergence of *Echinochloa crus-galli* and *Echinochloa colona* seedlings in response to different burial depths (cm). Seedling emergence was assessed until 21 d after planting. Error bars denote \pm standard errors of the mean ($n = 8$).

line with the results illustrating that light stimulates seed germination (Chauhan and Johnson 2011). Light penetration limits germination of photosensitive seeds, because light can only be detected within the top few millimeters of the soil (Bablet et al. 2018). Apart from the need for light, previous studies have also shown that the partial removal of emergence inhibitors of buried seeds was facilitated by increased oxygen availability, suggesting that aeration of the surface soil facilitated seedling emergence (Benvenuti 2003; Benvenuti and Mazzoncini 2019). In addition, seed weight may also influence emergence, because larger seeds contain a greater amount of carbohydrate reserves than smaller seeds (Grundy et al. 2003). In this study, we also

demonstrated that the heavier *E. crus-galli* seeds (1.7 mg seed^{-1}) had higher emergence from deeper soil depths than the lighter seeds of *E. colona* (1.2 mg seed^{-1}). In DSR production, if the seedbank of these weed species is observed building up the soil surface, strategic tillage could be a useful option for the management of these weeds (Mahajan et al. 2021).

Emergence and Seedling Biomass in Response to Different Wheat Straw Mulch Amounts

Crop residues used as mulch are beneficial materials if left on cultivated land. Previous studies have demonstrated that crop residues

Table 1. Parameter estimates of three-parameter sigmoid model ($E = E_{\max}/\{1 + \exp[-(x - T_{50})/E_{\text{rate}}]\}$) fit to seedling emergence responses to seed burial depth (Figure 2).

Weed species	Seed burial depth	Parameter estimates ^a			
		E_{\max}	T_{50}	E_{rate}	R^2
<i>Echinochloa crus-galli</i>	cm		d		
	0.0	89.8 ± 1.6 a	4.5 ± 0.1 e	0.43 ± 0.12 b	0.99
	0.5	85.2 ± 1.2 b	5.7 ± 0.1 d	0.45 ± 0.15 b	0.99
	1	77.7 ± 2.3 c	7.8 ± 0.2 c	0.85 ± 0.21 a	0.99
	2	55.2 ± 1.2 d	11.6 ± 0.2 b	0.68 ± 0.11 a	0.99
	4	16.5 ± 0.5 e	12.8 ± 0.3 a	0.71 ± 0.08 a	0.99
<i>Echinochloa colona</i>	—	—	—	—	—
	0.0	80.1 ± 2.4 a	4.2 ± 0.1 d	0.47 ± 0.10 a	0.99
	0.5	72.8 ± 1.8 b	6.6 ± 0.2 c	0.55 ± 0.13 a	0.99
	1	52.1 ± 2.2 c	9.4 ± 0.3 b	0.49 ± 0.11 a	0.99
	2	23.1 ± 0.4 d	9.8 ± 0.2 b	0.51 ± 0.14 a	0.99
	4	4.0 ± 0.2 e	11.0 ± 0.3 a	0.04 ± 0.01 b	0.99
6	—	—	—	—	

^a E_{\max} , maximum emergence; T_{50} , time to reach 50% of maximum emergence; and E_{rate} , slope. A dash (—) indicates that no seedlings emerged when seeds were planted at 6-cm depth. Different letters in the same column indicate a statistical difference at $P < 0.05$ within the same weed species.

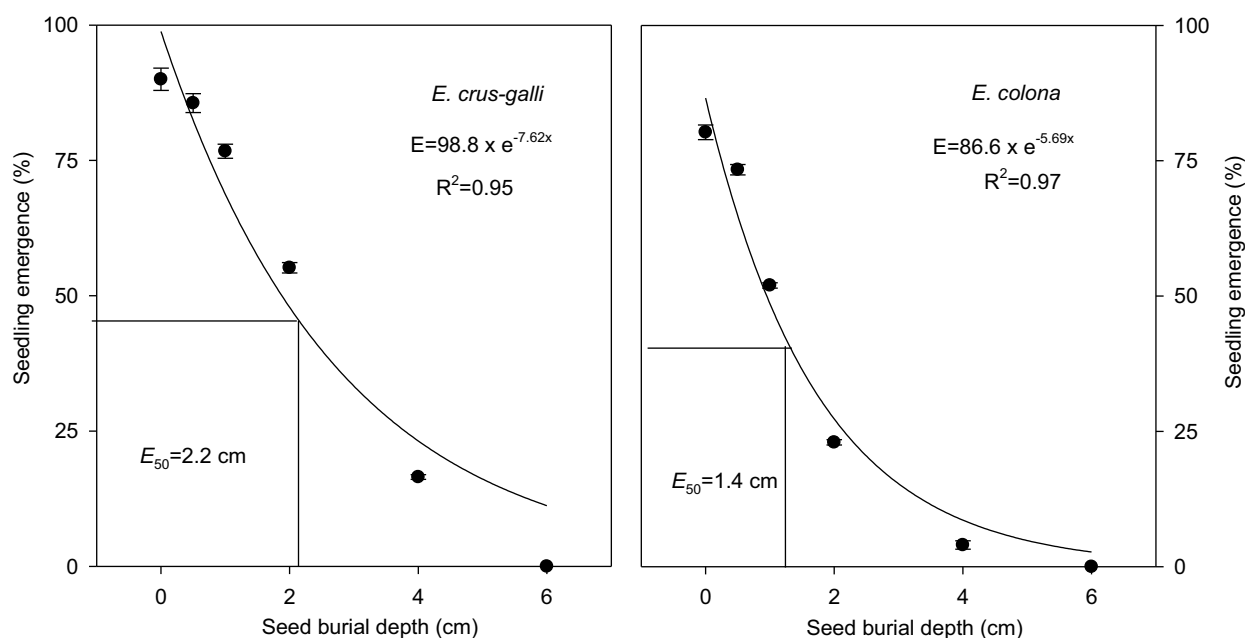


Figure 3. Effect of seed burial depth on seedling emergence of *Echinochloa crus-galli* and *Echinochloa colona*. The seed burial depth required to inhibit 50% of maximum emergence is 2.2 cm for *E. crus-galli* and 1.4 cm for *E. colona*. Vertical bars represent the standard errors of the mean ($n = 8$).

can act as an obstacle to light penetration and reduce soil temperatures by shading, which can cause a reduction or the complete absence of emergence of several weed species (Buhler et al. 1996; Chauhan and Abugho 2014; Chauhan et al. 2012a; Davis 2007; Ranaivoson et al. 2018). Our study showed that when no wheat straw was applied to the soil surface, seedling emergence of *E. crus-galli* and *E. colona* was 87% and 76%, respectively (Figure 4; Table 2). Compared with the control (no mulching with wheat residue cover), there was no influence on the emergence of *E. crus-galli*, but a greatly reduced emergence was observed for *E. colona* when wheat residue cover was 2,000 kg ha⁻¹. Seedling emergence decreased from 72% to 16% for *E. crus-galli* and from 42% to 13% for *E. colona* when wheat residue cover increased from 4,000 to 10,000 kg ha⁻¹.

Compared with the control, the biomass of *E. crus-galli* was not affected when the amount of wheat residue cover was 2,000 kg ha⁻¹, but it was significantly reduced when the addition of residues was up to 4,000 kg ha⁻¹ or more (Figure 5). *Echinochloa colona* produced a lower biomass when the wheat residue was more than 2,000 kg ha⁻¹. Seedling biomass was reduced by 19%, 43%, 68%, and 71% for *E. crus-galli* and 43%, 74%, 79%, and 84% for *E. colona* when the residue amount was 4,000, 6,000, 8,000, and 10,000 kg ha⁻¹, respectively, compared with the control. Previous studies have shown that with increasing amounts of residue, seedling emergence varies among different weed species; some species have decreased emergence with an increase in residue amount, while the emergence of other weeds increases at low rates of residue and then decreases at higher rates (María et al. 2018; Mohler

Table 2. Parameter estimates of three-parameter sigmoid model ($E = E_{\max}/\{1 + \exp[-(x - T_{50})/E_{\text{rate}}]\}$) fit to the seedling emergence responses to the quantity of wheat straw mulch (Figure 4).

Weed species	Residue amount	Parameter estimates ^a			
		E_{\max}	T_{50}	E_{rate}	R^2
<i>Echinochloa crus-galli</i>	kg ha ⁻¹	%	d		
	0	86.8 ± 1.6 a	5.1 ± 0.1 e	0.36 ± 0.12 b	0.99
	2,000	83.9 ± 1.5 b	5.2 ± 0.1 e	0.43 ± 0.13 ab	0.99
	4,000	71.4 ± 2.1 c	5.5 ± 0.1 d	0.42 ± 0.08 ab	0.99
	6,000	48.1 ± 1.3 d	6.1 ± 0.2 b	0.68 ± 0.14 a	0.99
	8,000	18.0 ± 0.8 e	5.9 ± 0.1 c	0.50 ± 0.17 a	0.99
<i>Echinochloa colona</i>	10,000	16.0 ± 0.6 d	6.7 ± 0.2 a	0.55 ± 0.12 a	0.99
	0	76.2 ± 1.5 a	5.2 ± 0.1 d	0.55 ± 0.11 b	0.99
	2,000	62.1 ± 1.4 b	5.2 ± 0.2 d	0.51 ± 0.09 b	0.99
	4,000	42.0 ± 1.1 c	5.8 ± 0.1 c	0.57 ± 0.13 b	0.99
	6,000	23.6 ± 0.8 d	6.4 ± 0.2 b	0.52 ± 0.10 b	0.99
	8,000	18.0 ± 0.5 e	6.7 ± 0.1 b	0.52 ± 0.09 b	0.99
10,000	12.4 ± 0.6 f	7.4 ± 0.2 a	0.70 ± 0.13 a	0.99	

^a E_{\max} , maximum emergence; T_{50} , time to reach 50% of maximum emergence; and E_{rate} , slope. Different letters in the same column indicate statistical difference at $P < 0.05$ within same weed species.

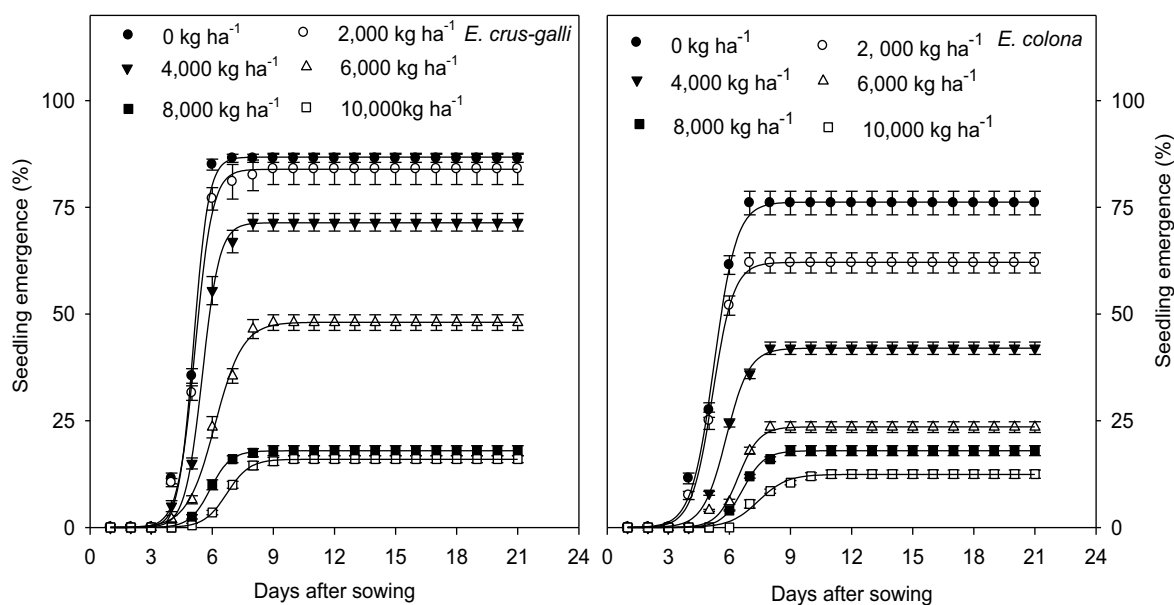


Figure 4. Seedling emergence of *Echinochloa crus-galli* and *Echinochloa colona* in response to wheat straw mulch (kg ha⁻¹) under screenhouse conditions for 21 d after sowing. Error bars denote ± standard errors of the mean ($n = 8$).

and Teasdale 1993). In our study, both seedling emergence and seedling biomass of *E. crus-galli* exhibited no difference between no-residue and 2,000 kg ha⁻¹ of residue treatments.

Our findings are in line with an earlier study conducted in the Philippines, in which the seedling emergence and biomass of *E. crus-galli* decreased with an increase in the rice residue amount (Chauhan and Johnson 2011). With an increase in the straw residue amount, the decrease in light transmittance and residue cover as a physical barrier could explain the reduction in weed emergence and growth. In addition, the reduction in the emergence and biomass of the two *Echinochloa* species can also be due to a complex physiological phenomenon known as allelopathy observed in some species (Macías et al. 2014; Sturm et al. 2018). However, until now, no literature has suggested that Yangmai 16, used in

our experiment, has allelopathic effects. Furthermore, it is unclear whether biochemical or physical factors of wheat straw mulching affected the seedling emergence and growth of *E. crus-galli* and *E. colona*.

Increased wheat residue mulching and deep burial depths not only suppressed but also retarded the emergence of *E. crus-galli* and *E. colona*. A delay in seedling emergence also has important significance for weed management. Seedlings that emerge later are usually less competitive with the crop for light, water, and nutrients, resulting in less biomass and seed production than early-emerging cohorts. Eventually, later-emerging seedlings may cause a lower loss of crop yield than early-emerging seedlings (Chauhan and Johnson 2010a). In addition, delayed-emerging seedlings can easily escape weed control because of the early application

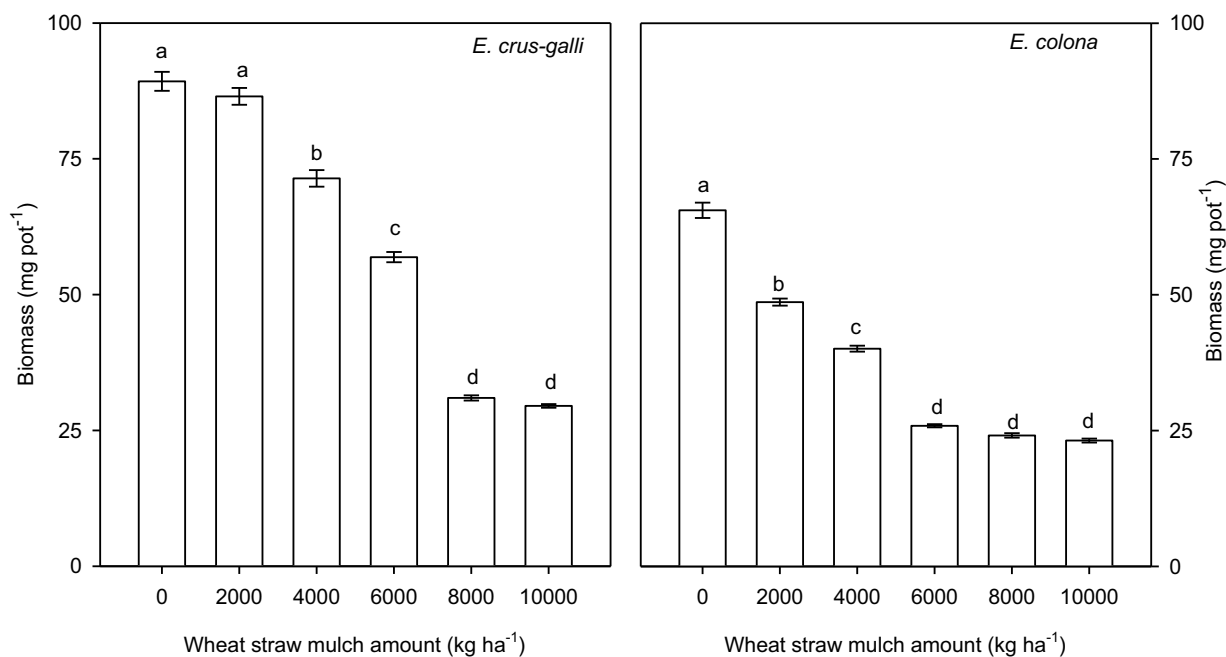


Figure 5. Seedling biomass (mg pot^{-1}) of *Echinochloa crus-galli* and *Echinochloa colona* in response to wheat straw mulch (kg ha^{-1}) at 21 d after sowing. Error bars denote \pm standard errors of the mean ($n=8$). Different letters indicate a significant difference at the 0.05 probability level.

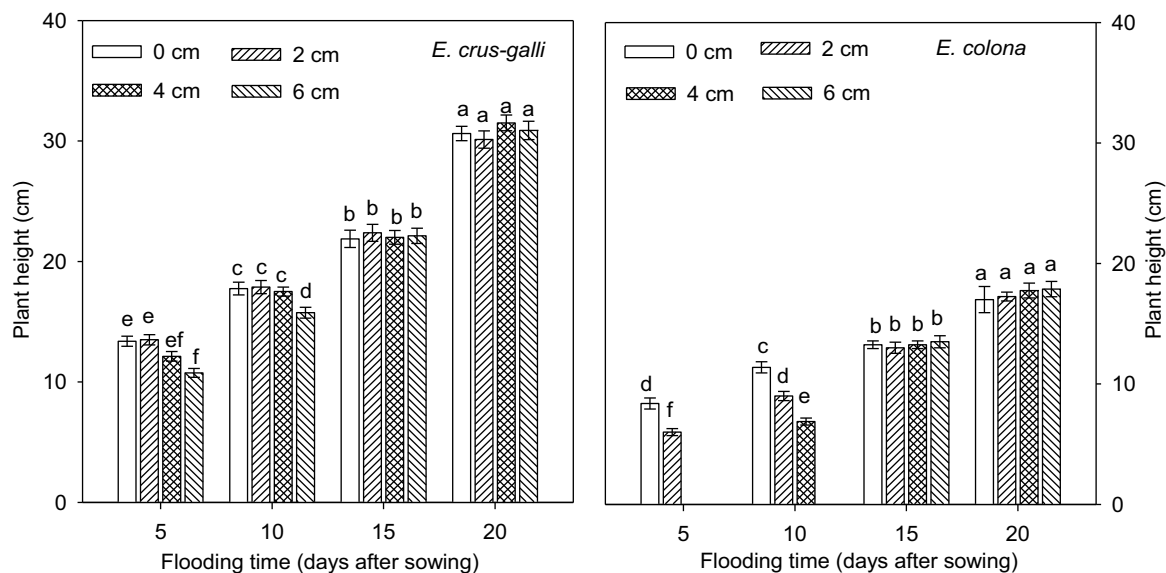


Figure 6. Plant height of *Echinochloa crus-galli* and *Echinochloa colona* in response to flooding depth (cm) and time when grown under screenhouse conditions at 14 d after the start of flooding. Error bars denote \pm standard errors of the mean ($n=8$). Different letters indicate a significant difference at the 0.05 probability level.

of postemergence herbicides. Although mulching with crop residue could effectively decrease weed seedling emergence and growth, a small number of weeds would still be present. Therefore, to successfully control weeds, additional control measures are still needed for DSR in China.

Growth in Response to Depth and Seedling Age at the Time of Flooding

The growth of several weed species can be inhibited by flooding; however, the extent of inhibition differs among species (Chauhan

2021; Chauhan and Johnson 2008; Chauhan and Johnson 2009a, 2009b; Driver et al. 2020). We observed that flooding did not kill *E. crus-galli* seedlings once they had emerged, but this was not the case for *E. colona* seedlings. *Echinochloa colona* seedlings could not survive a flooding depth of up to 6 cm at 10 d after sowing or more than 4 cm at 5 d after sowing, indicating that *E. colona* has poorer adaptability to flooding than *E. crus-galli*. This could be related to the growth environment of *E. colona*, which is mainly found in drylands in China (Chen et al. 2019).

The plant height, shoot biomass, and root biomass of both species were influenced by the timing and depth of flooding

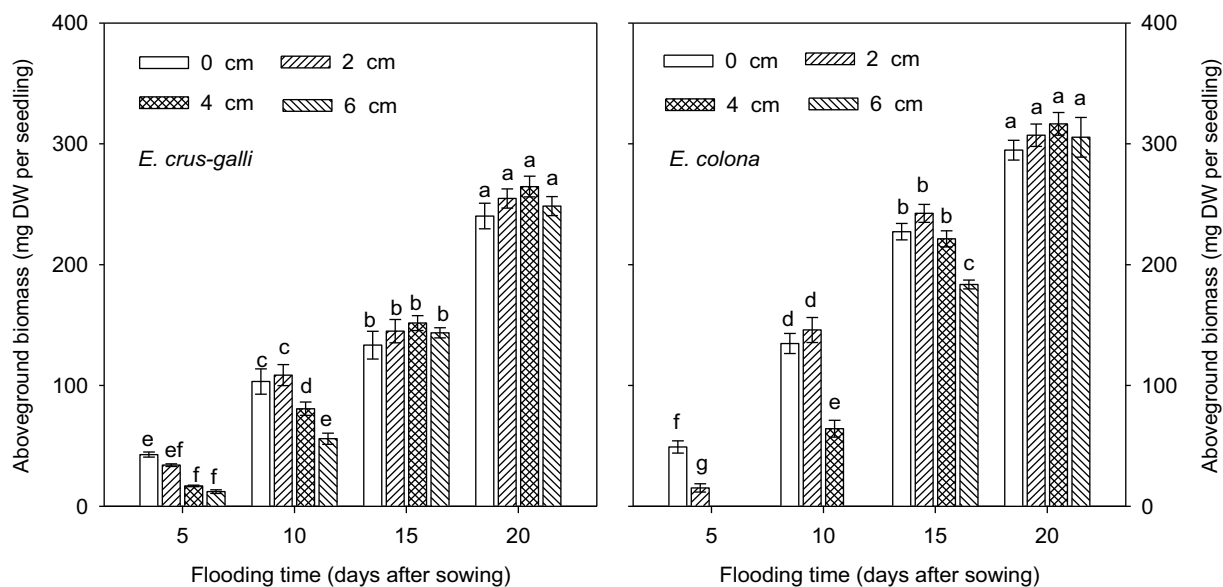


Figure 7. Aboveground biomass of *Echinochloa crus-galli* and *Echinochloa colona* in response to flooding depth (cm) and time when grown under screenhouse conditions at 14 d after the start of flooding. Error bars denote \pm standard errors of the mean ($n=8$). Different letters indicate a significant difference at the 0.05 probability level. DW, dry weight.

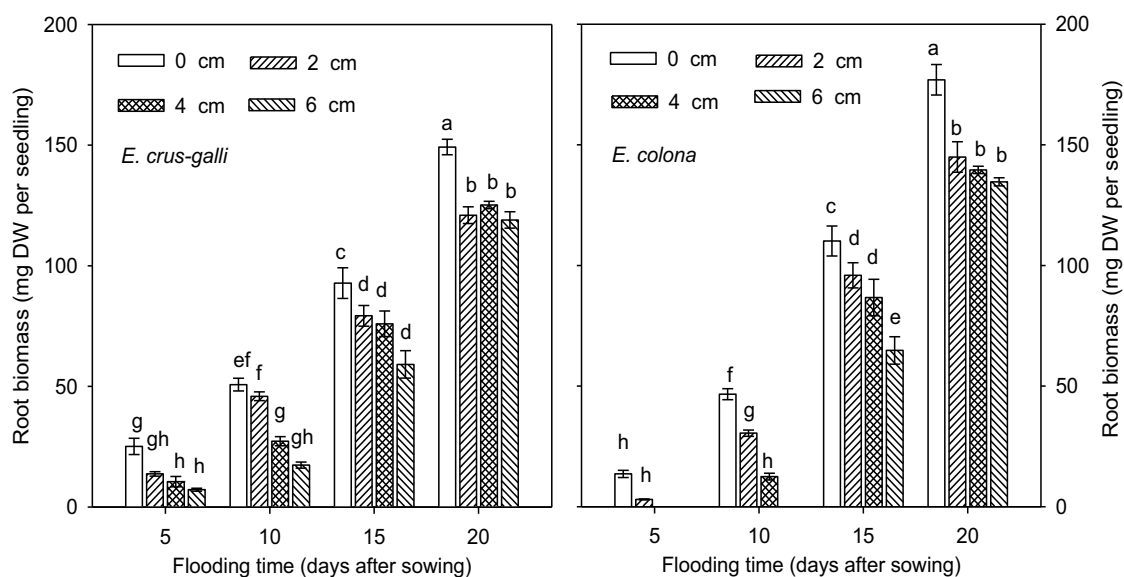


Figure 8. Root biomass of *Echinochloa crus-galli* and *Echinochloa colona* in response to flooding depth (cm) and time when grown under screenhouse conditions at 14 d after the start of flooding. Error bars denote \pm standard errors of the mean ($n=8$). Different letters indicate a significant difference at the 0.05 probability level. DW, dry weight.

(Figures 6–8). When flooding occurred at 15 d after sowing or later, there was no effect on plant height in either species. However, when flooding occurred at earlier stages, such as 10 d after sowing, plant height was reduced for *E. crus-galli* when the soil water was at the 6-cm depth only, but *E. colona* plant height decreased with all water depths compared with the 0-cm control (Figure 6). A similar response was also observed for shoot biomass (Figure 7). At 15 d after sowing or later, there was no difference in the aboveground biomass for *E. crus-galli* at the given flooding depth. However, aboveground biomass decreased with flooding

depths of 4 and 6 cm at 10 d after sowing or earlier. For *E. colona*, aboveground biomass showed no difference at the given flooding depth at 20 d after sowing, but it was significantly reduced when the soil was flooded at 4- and 6-cm depths at 15 and 10 d after sowing and at 2-, 4-, and 6-cm depths at 5 d after sowing (Figure 7). Root biomass of both species was reduced by flooding, and biomass decreased with the increase in flooding depth for the same time after sowing. We also found that the effect of earlier flooding on root biomass was greater than that of delayed flooding at equivalent flooding depths (Figure 8).

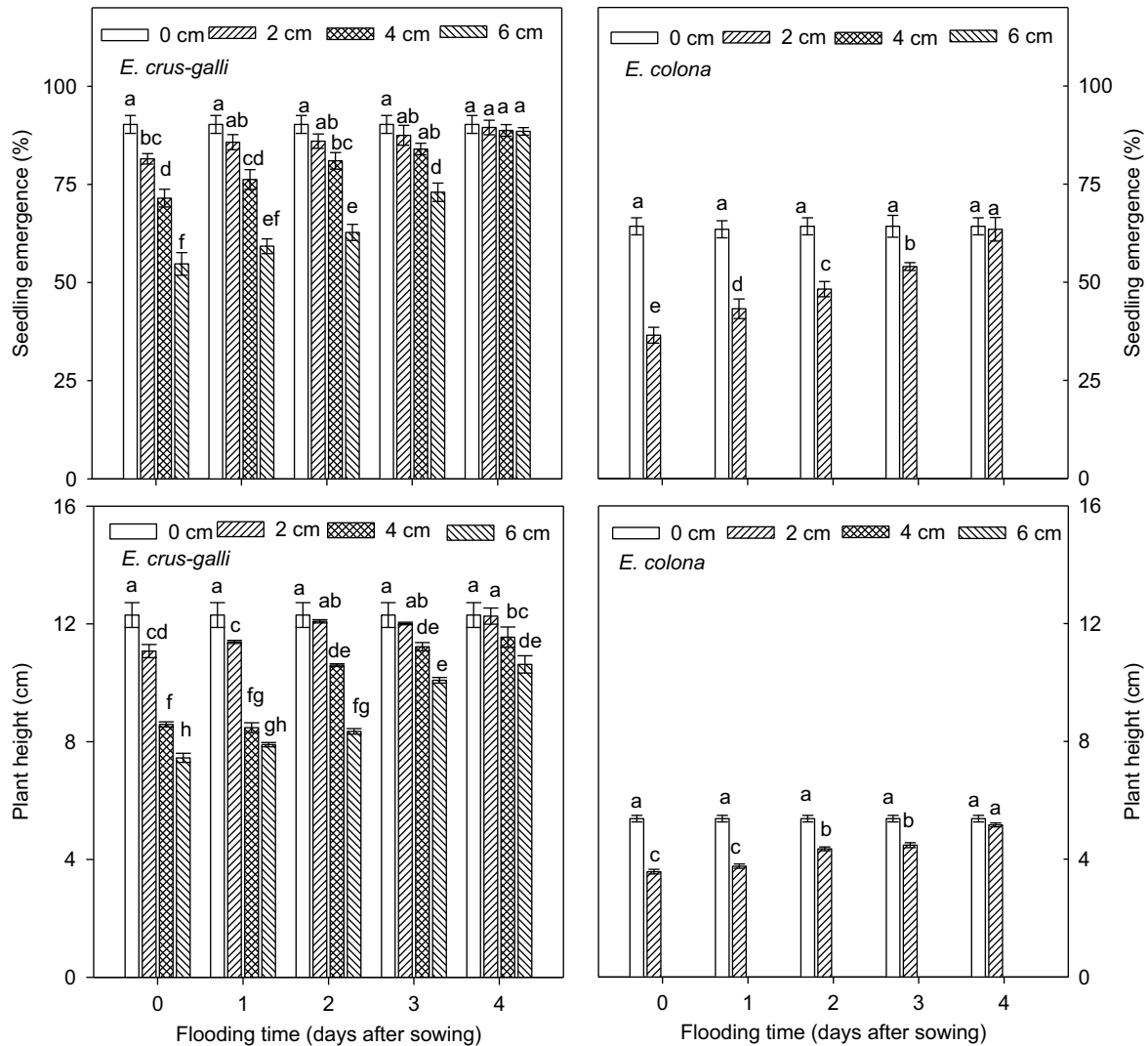


Figure 9. Seedling emergence and plant height of *Echinochloa crus-galli* and *Echinochloa colona* in response to flooding depth (cm) and time when grown under screenhouse conditions at 14 d after sowing. No seedlings of *E. colona* were observed at flooding depths of 4 and 6 cm. Error bars denote \pm standard errors of the mean ($n = 8$). Different letters indicate a significant difference at the 0.05 probability level.

Rice cultivars capable of germinating under anaerobic conditions may be widely grown in the future (Miro and Ismail 2013). Therefore, we explored the seedling emergence, plant height, and biomass of *E. crus-galli* and *E. colona* from China by flooding within 5 d, which represents the preemergence period after rice sowing. The seedling emergence of both species increased with the increase in flooding time under the same water depth, while it decreased with the increase in the flooding depth at 4 d after sowing or earlier (Figure 9).

Weed plant height showed similar trends as emergence for the two weed species, except at 4 d after sowing, when a significant decrease in plant height of *E. crus-galli* occurred with 4 and 6 cm of flooding effects but no change in seedling emergence was observed (Figure 9). Aboveground and root biomass were more effectively suppressed by early flooding than by delayed flooding, and both types of biomass declined as flooding depth increased (Figure 10).

Although flooding could considerably decrease the emergence and growth of the two *Echinochloa* species, water shortages may become an issue for many growers in China in the future (Yao

et al. 2020), and this may impose a constraint on the continuous use of flooding as a weed control measure.

When water for flooding is scarce, earlier flooding will provide weed suppression while conserving water. In DSR, early flooding could be practicable by integrating its use with rapidly emerging rice varieties and/or the use of pre-germinated seeds.

Ecological Recommendations for *Echinochloa* Management Strategies

Overall, both *E. crus-galli* and *E. colona* seeds under light/dark conditions had greater germination than under completely dark conditions, suggesting that light clearly increased the germination of the two weed species. In crop production, most weed seeds fall on the soil surface when they reach maturity. Therefore, in DSR fields, the use of light-limiting strategies (deep tilling and crop residue mulching) would be beneficial in reducing the germination and emergence of these weed species. In this study, no emergence of *E. crus-galli* or *E. colona* was observed from seeds buried at 6 cm. Similar to burial depth,

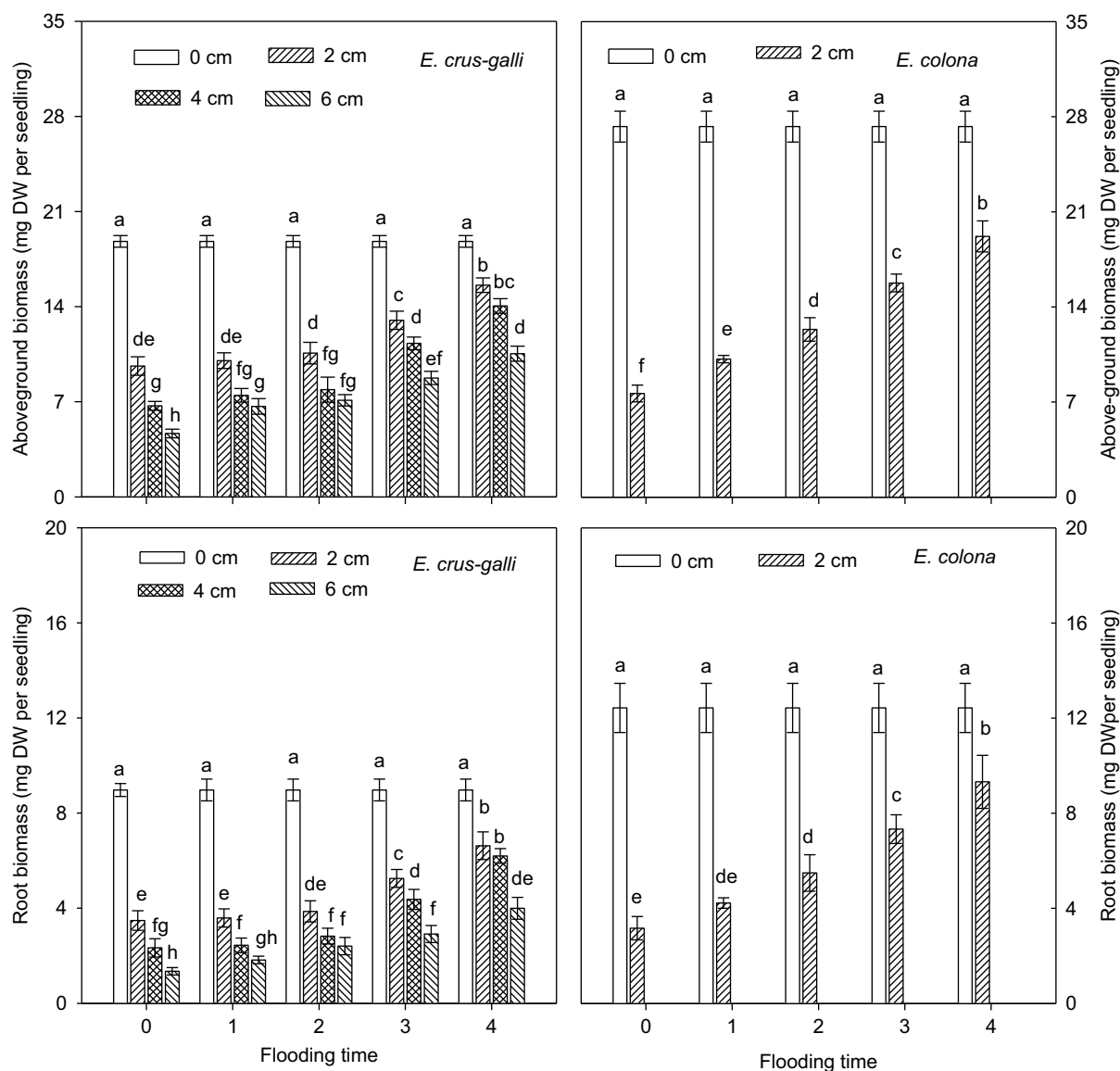


Figure 10. Effect of flooding depth (cm) and time on the biomass of *Echinochloa crus-galli* and *Echinochloa colona* when grown under screenhouse conditions at 14 d after sowing. Error bars denote \pm standard errors of the mean ($n=8$). Different letters indicate a significant difference at the 0.05 probability level. DW, dry weight.

mulching with wheat straw also significantly reduced the emergence and biomass of *E. crus-galli* and *E. colona*, especially for *E. colona*, when maximum suppression occurred with $\geq 6,000$ kg ha⁻¹ of wheat straw mulch. In addition, early flooding could inhibit seedling emergence and growth (plant height and biomass) of the two weed species. Although these practices are highly effective, they also have some limitations. First, a proportion of weed seeds buried in the soil may be exposed to the soil surface by tillage, which triggers seed germination. Second, mulching with wheat straw cannot completely suppress seed germination and seedling emergence of *E. crus-galli* and *E. colona*, even with the maximum amount used (10,000 kg ha⁻¹). Finally, growers may face water scarcity for DSR in the future. Therefore, in the DSR production system, physical and cultural management (deep plowing, mulching with wheat residue, and early flooding) combined with chemical herbicides may be highly effective for these two weed species. Information gathered from this study provides a better understanding of the effects of light, soil burial depth, mulch, and flooding on the germination and emergence of both *E. crus-galli*

and *E. colona*, which will aid in developing integrated weed management strategies for DSR in China.

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