Weed Technology

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Research Article

Cite this article: Li T, Qian H, Yuan G, Fan J, Guo S (2023) Germination ecology and response to herbicides of *Ludwigia prostrata* and their implication for weed control in paddy fields. Weed Technol. **37**: 197–204. doi: 10.1017/wet.2023.34

Received: 24 January 2023
Revised: 27 April 2023
Accepted: 8 May 2023
First published online: 19 May 2023

Associate Editor:
Robert Nurse, Agriculture and Agri-Food Canada

Nomenclature:
Bentazon; butachlor; fluroxypyr; MCPA-Na; oxadiargyl; oxadiazon; prostrate water primrose; *Ludwigia prostrata* Roxb

Keywords:
Seed biology; integrated management; herbicide; dormancy; burial depth

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Germination ecology and response to herbicides of *Ludwigia prostrata* and their implication for weed control in paddy fields

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Abstract

Prostrate water primrose is a troublesome weed in rice paddy fields. A study was conducted to determine the influence of environmental and agronomic factors on its emergence. The efficacy of herbicides on this species was also examined. The germination percentage of mature seeds remained above 90% within 180 d after harvest, indicating a low primary dormancy of this species. Light stimulated seed germination. Seeds buried deeper than 0.5 cm did not form seedlings. These results suggest that stale seedbed practices and deep tillage operations can mitigate the occurrence of this species in paddy fields. The optimum temperature for germination varied from 25/15 C to 35/25 C. The osmotic potential and salt concentration needed to inhibit 50% of maximum germination were −0.4 MPa and 197 mM, respectively. Seeds were tolerant to flooding and did not germinate at pH 8 to 10. The preemergence herbicides oxadiazon, oxadiargyl, and butachlor had excellent control efficacy on prostrate water primrose, with a 95.4% to 100% reduction in seedling number and a 99.2% to 100% reduction in biomass, respectively. The postemergence herbicides MCPA-Na + bentazone, bentazone, MCPA-Na, and fluroxypyr applied at the 2- to 3-leaf stage of prostrate water primrose provided a 90.6% to 100% reduction in seedling number and a 99.3% to 100% reduction in biomass. The results of this study can help in developing sustainable and effective integrated weed management strategies for controlling prostrate water primrose in paddy fields.

Introduction

Rice is a principal source of food for more than half of the world's population (Chauhan 2012), but weeds are a major constraint to rice production (Parry and Shrestha 2018; Ranaivoson et al. 2018; Touré et al. 2011). Changes in rice cultivation, tillage systems, and long-term use of a single type of herbicide have caused shifts in weed populations and community structures (Chauhan and Johnson 2010; Singh et al. 2009), and many previously minor weeds have become troublesome in paddy fields in China. Among them is prostrate water primrose (Figure 1 A–C).

Prostrate water primrose is a troublesome weed that is causing increasing problems in paddy fields. It is native to central and southeast Asia (Barkley et al. 1980; Moody 1989; Reed 1977) and is commonly found in paddy fields, riverbanks, and other wet habitats. Prostrate water primrose is one of the most harmful weeds in rice cultivation, causing more than 30% yield reduction in rice in southern China (Zhang et al. 2000). It was listed as a "serious" and "principal" weed in Japan and Taiwan (China), respectively (Barkley et al. 1980). The weed also causes damage in both direct-seeded and transplanted rice fields in Korea (Kim et al. 1997; Kim and Pyon 1998) and poses a significant threat to rice production in subtropical regions.

Herbicides are popular in modern agriculture due to their high efficiency, economy, and labor savings. Preemergence (PRE) herbicides can prevent weed occurrence for a period of time, especially for seeds in the soil a few millimeters from the surface (McCullough et al. 2013). Postemergence (POST) herbicides can selectively kill emerged weed seedlings. Herbicides vary in their weed control spectrum. For example, bispyribac-sodium is effective against barnyard grass [*Echinochloa crus-galli* (L.) Beauv.] but poor against Chinese sprangletop [*Leptochloa chinensis* (L.) Nees] (Chauhan and Abugho 2012; Singh and Singh 2004). Another example is penoxsulam, which is effective against heartshape false pickerelweed [*Monochoria vaginalis* (Burm. F.) C. Presl ex Kunth], but poor against eared redstem (*Ammannia arenaria* Kunth) (Shiraishi 2005). Screening effective herbicides for a particular weed species is the key to identify effective management techniques.

Although the use of herbicides is considered the most economical and efficient method for weed control, it is unwise to rely too heavily on them. Intensive application of herbicides

Figure 1. Photographs of prostrate water primrose and the experiment. A) Damage to prostrate water primrose in a paddy field; B) prostrate water primrose plant; C) branch of prostrate water primrose; D) seeds of prostrate water primrose; E) seed germination test; F) herbicide screening test.

causes environmental pollution and results in the development of resistant weeds (Beckie and Harker 2017; Chauhan and Johnson 2010; Ruzmi et al. 2017). Additionally, any single method of weed control cannot efficiently and sustainably control them. Therefore, it is necessary to integrate multiple management methods to control weeds, including agronomic and herbicide strategies.

Environmental and agronomic factors are known to affect the seedling establishment of weeds (Ahmed et al. 2015). For example, photoblastic seeds can germinate only when they are located on or near the soil surface (Chung and Paek 2003). Temperature is closely related to seed germination speed and cumulative germination (Chauhan 2012). Several species can occur within a wide range of soil pH values, but others can germinate only within a specific pH range (Shaw et al. 1991; Singh and Achhireddy 1984). Flooding is also an important factor affecting weed emergence. Studies on seed germination ecology can facilitate the development of integrated weed management strategies (Bhowmik 1997; Chauhan 2012).

Few published studies exist on the germination ecology and management of prostrate water primrose. Ku et al. (1996) studied the dormant characteristics of this species in Korea and found that mature seeds germinated well within 30 d after harvest. However, we do not know the effects of environmental and agronomic factors on its emergence and which herbicides could be applied to control it. Thus, the objectives of this study were to 1) confirm whether prostrate water primrose seed has dormancy; 2) understand the influence of temperature, light, pH, osmotic potential, NaCl concentration, flooding, and burial depth on seed germination; and 3) screen effective herbicides for controlling it.

Materials and Methods

Seed Collection and Storage

The study was carried out in the laboratory and greenhouse of Shanghai Academy of Agricultural Sciences (SAAS; 30.950°N, 121.467°E), in Shanghai, China. Mature seeds of prostrate water primrose were collected from approximately 100 randomly selected plants growing as weeds in paddy fields at SAAS (Figure 1D). After harvest, seeds were cleaned manually, dried in shade, placed inside a self-sealing bag, and stored in a laboratory (20±5 C, 60% to 70% relative humidity) until use. Nearly 90% of the seeds were viable by the tetrazolium chloride test (França-Neto and Krzyzanowski 2019) before each experiment was carried out.

Seed Germination Test

Germination tests were performed in 10-cm-diam Petri dishes (Figure 1E) according to the following steps unless stated otherwise. In a Petri dish, 50 seeds were sown on three sheets of filter paper moistened with 5 ml of deionized water or test solution. To prevent moisture loss, Petri dishes were wrapped in plastic wrap and then placed in an environmental chamber (day/night temperature of 30/20 C, 12-h photoperiod). The 30/20 C temperature range was optimum for germination in the temperature and light test. The light intensity of 150 μmol m^{-2} s^{-1} was supplied by fluorescent lamps. The number of germinated seeds was recorded 21 d after sowing. Seeds with protruded radicles were considered germinated seeds (Tang et al. 2017). The germination percentage was calculated as the proportion of germinated seeds to the sown seeds in the Petri dish.

Dormancy Test

To evaluate whether prostrate water primrose seeds have dormancy, the germination percentage of seeds stored for 0, 30, 60, 90, 120, 150, and 180 d after harvest was examined. The test steps were the same as those described above.

Alternating Temperature and Light Test

To determine the influence of alternating temperature and light on seed germination, seeds were incubated at four alternating temperatures (20/10, 25/15, 30/20, and 35/25 C) in both light/dark and continuous darkness. The temperatures were set according to the actual conditions during the rice growing season in the region. In the dark treatment, each Petri dish was wrapped in three sheets of aluminum foil to prevent light from penetrating. The number of germinated seeds in the light/dark treatment was recorded daily for 21 d. In the continuous dark treatment, the number of germinated seeds was recorded only after 21 d. To verify whether continuous dark affected seed germination, we added another 5 ml of deionized water to Petri dishes with seeds that had not germinated, placed them under a 12-h light/dark schedule for another 21 d, and then recorded the number of germinated seeds.

Osmotic Stress Test

To evaluate the influence of osmotic stress on seed germination, seeds were sown in solutions with osmotic potentials of 0 (control), −0.1, −0.2, −0.4, −0.6, and −0.8 MPa. To prepare the solutions, appropriate amounts of polyethylene glycol 8000 were dissolved in deionized water according to the method proposed by Michel (1983).

Salt Stress Test

To assess the influence of salt stress on seed germination, seeds were sown in NaCl solutions of 0 (control), 25, 50, 100, 150, 200, and 250 mM. Solutions were prepared by dissolving NaCl in deionized water (Michel 1983).

pH Buffer Solution Test

The germination percentage of seeds in buffer solutions with pH 4, 5, 6, 8, 9, and 10 was determined, with deionized water (pH 7.05) serving as a control. The pH buffer solutions were prepared according to the method proposed by Chachalis and Reddy (2000).

Burial Test

Fifty seeds were sown in each pot (10 × 10 × 8 cm height) filled with soil and then covered with soil to obtain corresponding burial depths of 0 (uncovered), 0.5, 1.0, 2.0, 3.0, and 4.0 cm. The soil was oven-dried at 180 C for 24 h and then sieved with a 0.3-cm screen mesh. The pots were irrigated regularly to keep the soil moist. Seedlings were judged to have emerged when cotyledons were visible. The number of seedlings that had grown was counted 21 d after sowing. The pots were placed in a chamber with a temperature of 25 to 30 C and a 12-h photoperiod. Emergence percentage was calculated as the proportion of the emerged seedlings to the sown seeds in the pot.

Flooding Test

Fifty seeds were sown in a single pot (as described above), which was placed into a larger tray (20 × 15 × 15 cm height). Water was retained and flooding depths were maintained at 0, 1, 2, 4, 6, and 8 cm. To avoid seed floating, these pots were kept moist for 6 h after sowing, allowing the seeds to absorb water. The desired flooding depth was introduced 12 h after sowing and was maintained for 21 d. The pot was then placed in a greenhouse at 20 to 25 C with natural illumination. The number of seedlings that emerged was counted 21 d after sowing, and the emergence percentage was calculated as the proportion of emerged seedlings to the sown seeds in the pot.

Herbicide Screening Test

The efficacy of PRE and POST herbicides against prostrate water primrose was evaluated by conducting two greenhouse experiments (Figure 1F). Twenty-five seeds were sown in each pot (as described above). Eight PRE herbicides and eight POST herbicides registered for use in rice paddies were tested (Table 1). The herbicides were applied by a research track sprayer. The sprayer was equipped with a fan nozzle operated at a pressure of 275 kPa delivering a spray volume of 450 L ha^{-1}. An untreated control was set for each experiment. PRE herbicides were sprayed 1 d after seeding. POST herbicides were sprayed at the 2- to 3-leaf seedling stage. In the POST herbicide screening experiment, five seedlings per pot were kept (some hypogenetic or runtish seedlings were removed; five well-developed seedlings were kept) before spraying. The number of surviving seedlings and the aboveground dry biomass were determined 21 d after herbicide application.

Statistical Analysis

All experiments were performed using a randomized complete block design with four replications. Each replication was arranged on a different shelf in a chamber or greenhouse and was considered a block. Except for the seed dormancy experiment, all experiments were repeated 15 d after termination of the first run.

The data were tested for normal distribution and homoscedasticity by the Kolmogorov-Smirnov test and Levene's test, respectively. If variances were not homogeneous, the data were arcsine square root–transformed before analysis. The data from the experimental repeats were pooled for analysis because of the absence of an experiment by treatment interaction. The data presented in the text and figures are means ± standard errors of two runs calculated using nontransformed data.

One-way ANOVA was performed to compare the differences in the data obtained from the dormancy test, pH test, burial test, and herbicide screening test separately using Fisher's protected LSD test. Two-way ANOVA with a general linear model was applied to reveal the independent and interactive effects of alternating day/light temperatures and light conditions on seed germination percentage. All statistical analyses were performed using SPSS software (version 20; SPSS, Chicago, IL). The significance level concerning the difference in relevant factors was set to 0.05.

Different functions were applied to reveal the relationships between seed germination or seedling emergence with different temperatures, osmotic potentials, salt concentrations, and flooding depths. The functions with a high coefficient of determination and low Akaike information criterion were selected. The relationship between seed germination percentage and temperature (Chauhan and Johnson 2008) was as follows:

$$G = G_{\max}/\{1 + \exp[-(T - T_{50})/G_{\rm rate}]\} \qquad [1]$$

where G, $G_{\max}$, T_{50}, and $G_{\rm rate}$ represent the cumulative germination percentage at time T, the maximum germination percentage, the

Table 1. Herbicides tested.[a]

Herbicide	Trade name	Formulation	Rate in active ingredient	Manufacturer
Pretilachlor	Saofute	EC	300 g L^{-1}	Syngenta Crop Protection Co., Ltd., Suzhou, China
Butachlor	Dingcaoan	EC	50%	Jiangsu Lvlilai Co., Ltd, Yancheng, China
Bensulfuron-methyl + pretilachlor	Zhiboning	WP	40%	Mefront Agricultural Chemicals Co., Ltd., Wenzhou, China
Pyrazosulfuron-ethyl	Caokexing	WP	10%	Nissan Chemical, Tianjing, China
Bensulfuron-methyl	Nongdeshi	WP	10%	DuPont, America
Oxadiazon	Nongsita	EC	12%	Bayer Crop Science, Zhejiang, China
Oxadiargyl	Daosida	WP	80%	Bayer Crop Science, Zhejiang, China
Pendimethalin	Shitianbu	EC	330 g L^{-1}	Jiangsu Rotam chemistry Co., Ltd, Kunshan, China
Penoxsulam	Daojie	OD	25 g L^{-1}	Dow AgroSciences Company, America
Florpyrauxifen-benzyl	Lingsike·Dan	EC	3%	Dow AgroSciences Company, America
MCPA-Na + bentazone	Guhuan	SL	460 g L^{-1}	BASF Plant Protection Co., Ltd. Jiangsu, China
Fluroxypyr	Shitalong	EC	20%	Jiangsu Zhongqi Crop Protection Co., Ltd., Jiangsu, China
MCPA-Na	Caojiang	AS	13%	Anhui Huaxing Chemical Co., Ltd., Maanshan, China
Bentazone	Paicaodan	SL	48%	BASF Plant Protection Co., Ltd. Jiangsu, China
Bispyribac-sodium	Shuangcaomi	SC	10%	Kumiai Chemical Industry Co., Ltd., Nanjing, China
Tefuryltrione + triafamone	Kenduo	SC	300 g L^{-1}	Bayer Crop Science, Zhejiang, China

[a]Abbreviations: AS, aqueous solution; EC, emulsifiable concentrate; OD, oil dispersion; SC, suspension concentrate; SL, soluble liquid; WP, wettable powder.

time required for 50% of maximum germination percentage, and the slope of the relationship, respectively. The model for the relationship between seed germination percentage and osmotic stress or salt concentration (Tang et al. 2017) was as follows:

$$G = G_{max}/\{1 + \exp[-(x - x_{50})/G_{rate}]\} \quad [2]$$

Where G, G_{max}, x_{50}, and G_{rate} represent the germination percentage at osmotic potential or salt concentration x, the maximum germination percentage, the osmotic potential or salt concentration for 50% inhibition of maximum germination, and the slope of the model, respectively. The relationship between seedling emergence inhibition percentage and flooding depth was modeled using the following function:

$$Gi = Gi_{max}/\{1 + \exp[-(x - x_{50})/Gi_{rate}]\} \quad [3]$$

where Gi represents the seedling emergence inhibition percentage at flooding depth x, Gi_{max} represents the maximum inhibition percentage, x_{50} represents the flooding depth for 50% of the maximum inhibition percentage, and Gi_{rate} represents the slope of the relationship. The seedling emergence inhibition percentage was calculated as follows:

$$Gi = (G_{max} - G_{min})/G_{max} * 100\% \quad [4]$$

where G_{max} is the number of emerged seedlings under the 0-cm flooding depth, whereas G_{min} is the number under the 8-cm flooding depth.

Results and Discussion

Seed Dormancy

One-way ANOVA demonstrated that the seed germination percentage of prostrate water primrose did not significantly differ within 180 d after harvest (P = 0.987). Approximately 90% of the newly collected seeds germinated immediately, indicating that prostrate water primrose seeds have a short period of primary dormancy, which is consistent with results previously reported by Ku et al. (1996; Figure 2). The results also suggested that stale seedbed practices prior to rice planting could mitigate the emergence of prostrate water primrose by depleting the seed bank of this species.

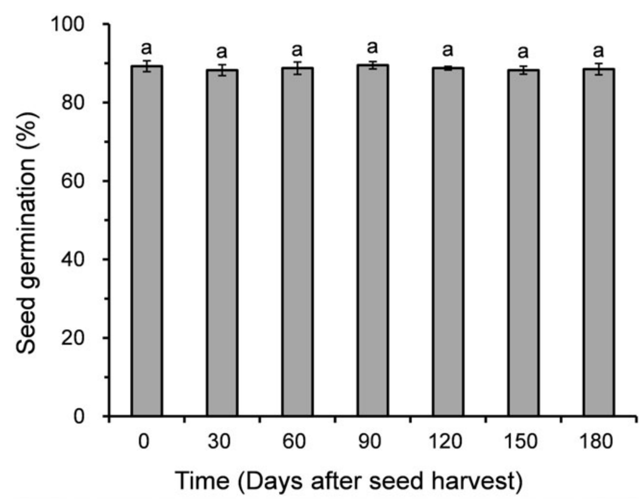

Figure 2. The germination percentage of prostrate water primrose seeds after harvest. Seeds were incubated at an alternating day/night temperature of 30/20 C with a 12-h photoperiod for 21 d. Vertical bars denote standard errors. Bars with the same letters are not significantly different (P < 0.05, n = 4).

Dormancy is an adaptation of seeds to adverse conditions that involves pausing growth and development (Jiang et al. 2016). Although low primary dormancy is detrimental to the continuation of prostrate water primrose populations, a combination of 1) seeds that are usually encased in capsules when mature and 2) seeds that fall to the soil surface often being covered by rice straw following rice harvest, would prevent the seeds from germinating rapidly and synchronously.

Alternating Temperature and Light

Two-way ANOVA showed that alternating day/light temperature, light condition, and the interaction of temperature and light all exerted significant effects on seed germination percentage (P < 0.001).

Light significantly stimulated the germination percentage of prostrate water primrose seeds. Under light/dark conditions, the seed germination of prostrate water primrose was greater than 60%. However, under continuous dark conditions, seed germination was less than 3% (Figure 3).

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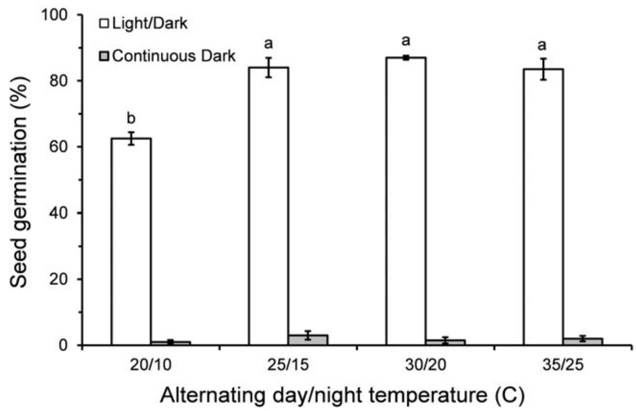

Figure 3. The germination percentage of prostrate water primrose seeds under alternating day/light temperatures and light. Vertical bars denote standard errors. Bars with different letters indicate significant differences of the seed germination percentage under different temperature treatments ($P < 0.05$). The differences of the seed germination percentage between light/dark and continuous dark are all significant at $P < 0.001$ ($n = 8$).

The influence of light on seed germination varies among species. Some species, such as Japanese brome (*Bromus japonicus* Thunb. ex Murr.), can germinate under light and dark conditions (Li et al. 2015). whereas other species, such as Chinese sprangletop, need light to stimulate seed germination (Teuton et al. 2004). In this study, prostrate water primrose exhibited low seed germination under continuous dark conditions regardless of temperature, indicating that light stimulates its germination. Weed species that need light to stimulate germination are more likely to cause infestations in no-tillage and less-tillage systems (Cousens et al. 1993). With the implementation of less tillage and shallow tillage regimes in paddy fields in southern China, the occurrence and damage caused by prostrate water primrose has increased. Straw mulching could be an efficient way to control seedling emergence of prostrate water primrose, and this practice also has important ecological significance for maintaining field fertility, reducing the use of chemical fertilizers, improving the carbon sink capacity of soil, and reducing or avoiding environmental pollution caused by burning. Moreover, we observed that the nongerminated seeds of prostrate water primrose (previously incubated in the dark) were able to germinate well (with a germination percentage of 85%) when they were transferred to light/dark conditions. Therefore, under field conditions, prostrate water primrose seeds previously buried under soil may be triggered to germinate when they are exposed to light.

Seed germination of prostrate water primrose was also affected by temperature. Under light/dark conditions, 84% germination was observed at 25/15 C, 87% at 30/20 C, and 83.5% at 35/25 C versus 62.5% at 20/10 C. As the temperature increased, seed germination accelerated, and the time to onset of germination at 20/10 C, 25/15 C, 30/20 C, and 35/25 C was 9, 4, 3, and 2 d, respectively. However, the total percentage of germination under the temperatures of 25/15 C, 30/20 C, and 35/25 C was similar (Figure 4).

Temperature has a critical effect on seed germination (Burke et al. 2003). Direct-seeded rice is planted in early May in southern China, when the mean temperature is close to 20 C. The seeds of prostrate water primrose germinated at all the tested temperature regimes, suggesting that seedlings of this species can emerge throughout the rice growing season in the region. A lower germination percentage was observed at 20/10 C, indicating that some seedlings would escape from the early use of PRE herbicides.

Osmotic Stress

As shown in Figure 5, the seed germination percentage of prostrate water primrose was greatly affected by osmotic stress. The maximum germination percentage (87.5%) was detected at an osmotic stress of 0 MPa. The germination percentage decreased from 87.5% to 0% with decreasing osmotic stress values from 0 to −0.8 MPa. The osmotic stress for 50% inhibition of maximum germination percentage was −0.4 MPa.

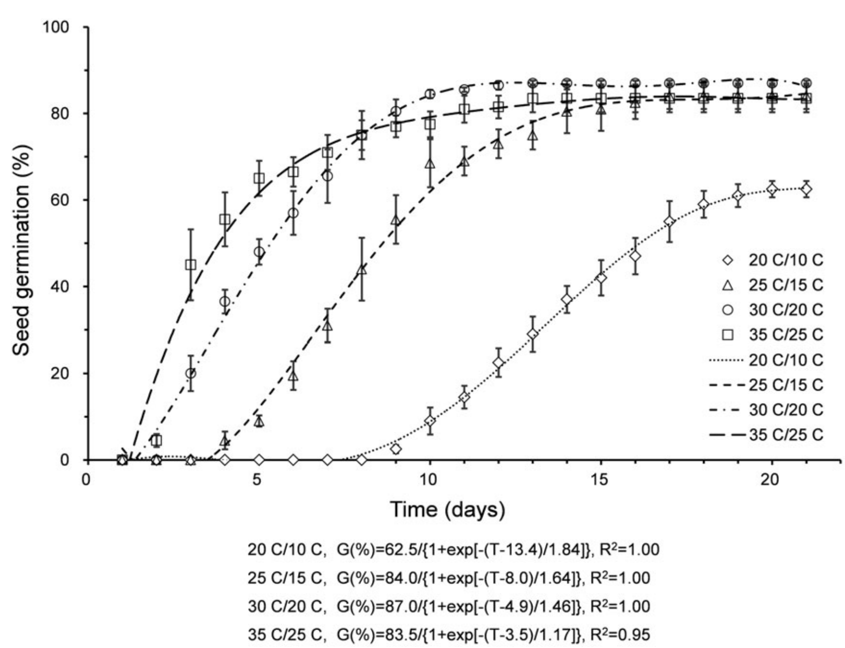

Figure 4. Influence of fluctuating day/night temperatures on seed germination of prostrate water primrose under light/dark conditions. Vertical bars denote standard errors ($n = 8$).

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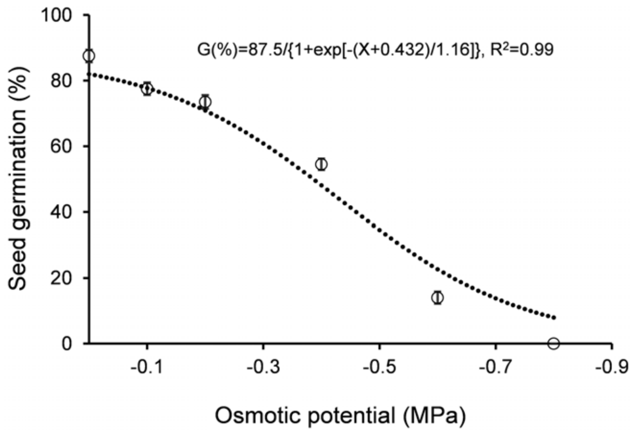

Figure 5. Influence of osmotic potential on seed germination of prostrate water primrose. Vertical bars denote standard errors (n = 8).

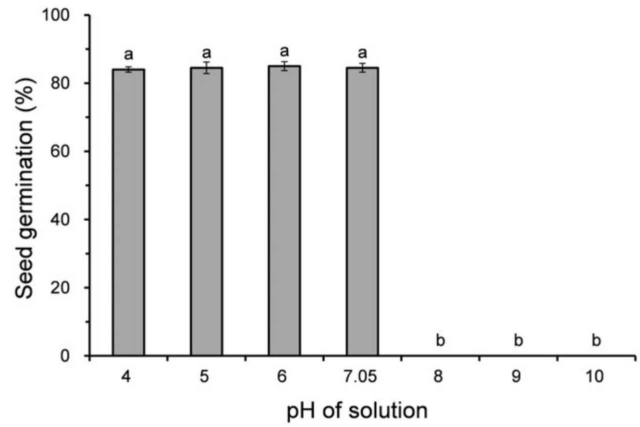

Figure 7. Influence of pH buffer solutions on seed germination of prostrate water primrose. Vertical bars denote standard errors. Bars with different letters indicate significant differences (P < 0.05, n = 8).

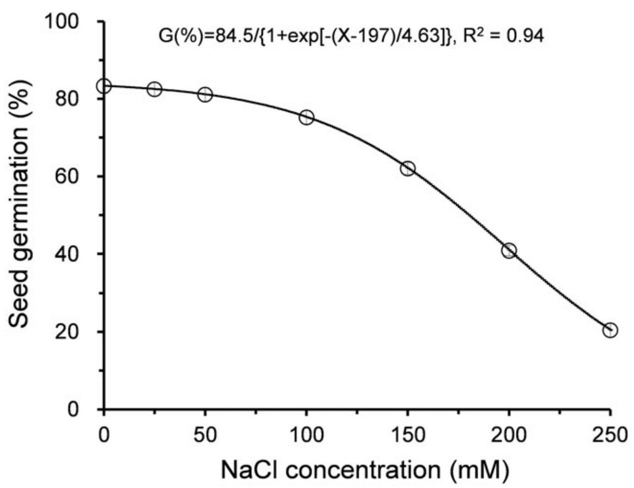

Figure 6. Influence of salt stress on seed germination of prostrate water primrose. Vertical bars denote standard errors (n = 8).

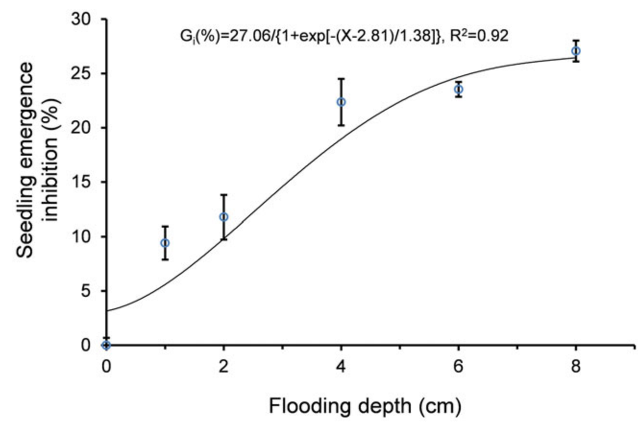

Figure 8. Influence of flooding on seedling emergence of prostrate water primrose. Vertical bars denote standard errors.

A similar conclusion was reported for nakedstem dewflower [*Murdannia nudiflora* (L.) Brenan], with an osmotic stress value of −0.4 MPa to achieve 50% suppression of maximum germination (Ahmed et al. 2015; Atkinson 2014). Additionally, we found that the nongerminated seeds of prostrate water primrose previously incubated at −0.8 MPa could germinate normally when they were incubated in deionized water. These results indicate that most prostrate water primrose seeds can germinate in wet habitats, but those in dry habitats cannot germinate until they become moist.

Salt Stress

The seed germination percentage of prostrate water primrose decreased as the salt concentration increased. Germination was greater than 80% at salt concentrations of less than 50 mM. As the salt concentration increased further, the seed germination percentage decreased sharply. Seed germination decreased from 84.5% to 23.7% with increasing salt concentration from 0 to 250 mM. The salt concentration for inhibition of 50% of maximum germination was 197 mM (Figure 6).

The response of seed germination to salt stress varied greatly among species. Nakedstem dewflower and Chinese sprangletop, as the dominant weeds in direct-seeded rice fields, were completely unable to germinate at a salt concentration of 150 mM (Ahmed et al. 2015; Chauhan and Johnson 2008). However, at the same salt concentration, prostrate water primrose seeds were able to germinate, with a germination percentage of over 60%. These results suggest that prostrate water primrose is more salt-tolerant than nakedstem dewflower and Chinese sprangletop.

pH Buffer Solution

One-way ANOVA showed that buffer solutions with various pH values significantly affected the seed germination percentage of prostrate water primrose (P < 0.001). Seeds germinated normally at pH 4 to 7.05, with a germination of approximately 85%. However, seeds did not germinate at all at pH 8 to 10 (Figure 7). These results indicate that prostrate water primrose cannot emerge under alkaline conditions, and this information could be used to predict where it might occur.

Burial Depth

One-way ANOVA showed that burial depth significantly affected the seed germination of prostrate water primrose (P < 0.001). Seeds sown on the soil surface showed maximum seedling emergence value (83.0%). Seeds buried deeper than 0.5 cm did not form seedlings. This

Table 2. Control efficacy of preemergence herbicides on prostrate water primrose seedlings applied 1 d after sowing.[a]

Herbicide	Rate	Reduction in seedling number	Reduction in biomass
	g ai ha^{-1}	%	
Oxadiazon	270	95.4 ± 2.6 a	99.2 ± 0.5 a
Oxadiargyl	72	100 ± 0 a	100 ± 0 a
Butachlor	1,125	96.5 ± 2.3 a	99.4 ± 0.4 a
Pretilachlor	450	76.2 ± 1.6 b	98.8 ± 0.1 a
Bensulfuron-methyl + pretilachlor	480	73.7 ± 1.9 b	98.9 ± 0.02 a
Pyrazosulfuron-ethyl	30	52.4 ± 1 c	95.2 ± 0.1 b
Bensulfuron-methyl	30	46.0 ± 4.4 c	93.5 ± 0.3 c
Pendimethalin	742.5	32.1 ± 3.4 d	79.6 ± 1.3 d

[a]The values are mean ± standard error. Different letters in the same column denote significant differences ($P < 0.05$, $n = 8$).

Table 3. Control efficacy of postemergence herbicides on prostrate water primrose seedlings applied at the 2- to 3-leaf stage.[a]

Herbicide	Rate	Reduction in seedling number	Reduction in biomass
	g ai ha^{-1}	%	
MCPA-Na + bentazone	1035	100 ± 0 a	100 ± 0 a
Bentazone	1080	100 ± 0 a	100 ± 0 a
Fluroxypyr	150	93.8 ± 3.6 ab	99.5 ± 0.3 a
MCPA-Na	487.5	90.6 ± 3.1 b	99.3 ± 0.2 a
Penoxsulam	22.5	31.3± 3.6 d	72.7 ± 1.4 b
Bispyribac-sodium	22.5	56.3 ± 3.6 c	73.4 ± 1.2 b
Tefuryltrione + triafamone	90	50.0 ± 5.1 c	67.1 ± 1.2 c
Florpyrauxifen-benzyl	36	56.1 ± 3.5 c	72.3 ± 2.1 b

[a]The values are mean ± standard error. Different letters in the same column denote significant differences ($P < 0.05$, $n = 8$).

is consistent with the observation that seed germination in this species is stimulated by light. Almost no light can be transmitted to soil deeper than 0.4 cm (Benvenuti 1995). Egley (1986) and Woolley and Stoller (1978) also reported that less than 1% of light could reach soil depths deeper than 0.2 cm. Insufficient light is probably the main factor for preventing the formation of seedlings from seeds buried below 0.5 cm. Therefore, deep tillage regimes may be a viable way to reduce the emergence of prostrate water primrose. Nevertheless, due to the shortage of rural labor in China, no-tillage and shallow tillage regimes are popular in agricultural production, which leads to the increasing yearly occurrence of this species.

Flooding

The seedling emergence of prostrate water primrose was inhibited by flooding. The maximum seedling emergence was observed in saturated soil. As flooding increased from 0 to 8 cm, the inhibition of seedling emergence increased from 0% to 27.6% (Figure 8).

Flooding is an important method for weed control, and the tolerance of weed species to flooding varies. Ricefield flatsedge (*Cyperus iria* L.) cannot grow in flood conditions (Rsa and Moody 1979). The occurrence and growth of Chinese sprangletop were greatly reduced under shallow flooding (Chauhan and Johnson 2008). Other weeds such as heartshape false pickerelweed [*Monochoria vaginalis* (Burm. F.) C. Presl ex Kunth] prefer flooding for growth (Pons 1982). In this study, seedling emergence at a flooding depth of 8 cm was only reduced by 27.1% compared with germination without flooding. Therefore, prostrate water primrose is tolerant to flooding stress, which is likely why this species can cause damage in both direct-seeded and transplanted rice fields.

Efficacy of Herbicides

The efficacy of the tested PRE herbicides on prostrate water primrose varied greatly (Table 2). After application of oxadiazon, oxadiargyl, and butachlor, the seedling number and biomass of prostrate water primrose was reduced by 95.4% to 100% and by 99.2% to 100%, respectively. Pretilachlor, bensulfuron-methyl + pretilachlor, pyrazosulfuron-ethyl, and bensulfuron-methyl showed acceptable control efficacy on the biomass of prostrate water primrose, but the control efficacy on seedling number was relatively poor, with 93.5% to 98.9% reduction in biomass, and 46.0% to 76.2% reduction in seedling number, respectively.

Among the treatments with POST herbicide application, MCPA-Na + bentazone, bentazone, fluroxypyr, and MCPA-Na were highly effective against prostrate water primrose, and the seedling number and biomass were reduced by more than 90% and 99%, respectively. However, the efficacy of penoxsulam, bispyribac-sodium, tefuryltrione + triafamone, and florpyrauxifen-benzyl against this species was relatively poor, with a 31.3% to 56.3% reduction in seedling number and 67.1% to 73.4% reduction in biomass (Table 3).

Direct-seeded rice plays a dominant role in rice production in China. Weeds in rice fields are primarily controlled by herbicides. The most commonly used herbicides are bensulfuron-methyl + pretilachlor applied PRE and penoxsulam applied POST, which are recommended by government agencies and have been applied for more than 20 yr. However, the efficacy of bensulfuron-methyl + pretilachlor applied PRE and penoxsulam applied POST on prostrate water primrose was poor (Tables 2 and 3). This may be one of the reasons for the increasing damage caused by this species in paddy fields in China. When considering efficacy, safety, and rice cultivation regime, replacing the PRE herbicide bensulfuron-methyl + pretilachlor with oxadiazon or oxadiargyl and replacing the POST herbicide penoxsulam with bentazone or MCPA-Na + bentazone are potential optional schemes for alleviating the damage caused by prostrate water primrose in paddy fields. The results of this study will provide guidance for controlling prostrate water primrose in paddy fields.

Practical Implications

Shifts in weed flora and the development of resistant weeds pose a challenge to weed management in rice. Various weed management approaches need to be integrated to achieve effective, sustainable, and long-term weed control. And these management methods depend on a detailed understanding of seed germination ecology. According to the results of the present study, the following practices could be considered to control prostrate water primrose in paddy fields:

1) Because the seeds have a short primary dormancy, stale seedbed practices prior to rice planting likely will mitigate the occurrence of prostrate water primrose through depleting the seed bank of this species.
2) Light may stimulate and continuous dark may inhibit the germination of prostrate water primrose seeds. Therefore, straw mulching may be an efficient way to control seedling emergence of prostrate water primrose.
3) The seeds of prostrate water primrose buried deeper than 0.5 cm do not form seedlings. Therefore, deep tillage regimes may be a viable way of reducing the emergence of prostrate water primrose.
4) Seeds germinate normally at pH 4 to 7.05 but cannot germinate at pH 8 to 10. This information can be used to predict its potential distribution.
5) PRE herbicides such as oxadiazon, oxadiargyl, butachlor and POST herbicides such as MCPA-Na + bentazone, bentazone, and fluroxypyr may provide complete control of prostrate water primrose.

Acknowledgments. This work was funded by the SAAS Program for Excellent Research Team [hu nong ke zhuo (2022) 017, 009, 002]. There are no conflicts of interest to declare.

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