



Article

Competitiveness of Bensulfuron-Methyl-Susceptible and -Resistant Biotypes of *Ammannia auriculata* Willd. in Direct-Seeded Rice

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Abstract: *Ammannia auriculata* Willd. (eared redstem) has become one of the most troublesome weeds in paddy rice in China. Resistance to bensulfuron-methyl (BSM) has spread extensively in this species. Greenhouse and field experiments were conducted to determine how the eared redstem biotype and density affect competition against rice. In the greenhouse experiment, five treatments were tested: a BSM-susceptible biotype at low density (58 plants m⁻², SL), a BSM-susceptible biotype at high density (288 plants m⁻², SH), a BSM-resistant biotype at low density (RL), a BSM-resistant biotype at high density (RH), and a control without eared redstem (CK). Eared redstem grew slowly until 15 days after sowing (DAS); however, growth accelerated after 20 DAS, and the eared redstem plants were taller than the rice from 55 DAS on. The SH and RH treatments were associated with greater intraspecific competition: eared redstem plants in the SH and RH treatments had fewer branches, fewer capsules, and less shoot dry weight per individual plant relative to the SL and RL treatments. The SH and RH treatments also caused greater reductions in the rice yield. The dry weight of rice at 141 DAS was reduced by 73% in the SL treatment, 98% in the SH treatment, 51% in the RL treatment, and 82% in the RH treatment, all relative to the CK. At 141 DAS, BSM-resistant plants were smaller than BSM-susceptible plants, suggesting a fitness cost of herbicide resistance in the absence of a herbicide. In the field study, eared redstem densities as low as 5 plants m⁻² reduced the rice yield by 22%. A density of 50 eared redstem plants m⁻² reduced the rice yield by 70%. Overall, these findings demonstrate that eared redstem is a highly aggressive weed species and threatens the rice yield even at a low density. However, the findings also demonstrate that BSM-resistant populations are less competitive. There is an urgent need to develop integrated management programs for this aggressive weed, which may include tactics to shift competitive dynamics in favor of rice. Additionally, this research provides the theoretical basis for the damage level, resistance risk evaluation, and management strategy of eared redstem in rice cropping systems.

Keywords: *Ammannia auriculata* Willd.; direct-seeded rice; direct seeding; bensulfuron-methyl; herbicide resistance; competition; fitness cost



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1. Introduction

Rice (*Oryza sativa* L.) is one of the most important crops in the world. In China, rice is grown in every province except Qinghai, covering an area of 30.1 million hectares and

yielding 211.9 million tons [1]. Traditional methods of paddy farming in China include direct seeding, mechanical transplanting, throwing transplanting, or manual transplanting of rice seedlings. Direct seeding has rapidly increased in popularity because this method can reduce labor costs and increase sustainability relative to transplanting methods [2]. Direct seeding can improve the economic well-being of rice farmers in China as well as South Asia and Southeast Asia [3]. A disadvantage of direct seeding, relative to transplanting, is an increase in weed pressure [4]. Unlike traditional transplanted fields, direct-seeded rice fields are not flooded. Therefore, farmers who practice direct seeding cannot rely on standing water to inhibit weed germination and growth. Many farmers instead rely on chemical control. Bensulfuron-methyl (BSM), a herbicide in the sulfonylurea family of acetolactate synthase (ALS) inhibitors, is widely used for the control of broadleaf and sedge weeds in rice [5,6].

Although herbicides can provide effective weed control, over-reliance on chemical approaches has led to the evolution of herbicide resistance in 267 weed species worldwide [7]. Resistance to ALS inhibitors is the most common type of herbicide resistance, accounting for one-third of reported cases [7]. Weeds, such as *Ammannia auriculata* Willd. (eared redstem) [8], *Echinochloa crus-galli* (L.) P. Beauv. (barnyardgrass) [9], *Sagittaria trifolia* L. (arrowhead) [10], and *Cyperus difformis* L. (small-flowered nutsedge) [11], have developed resistance to commonly used ALS inhibitors. In China, herbicide resistance has been reported for 30 weed species and 47 herbicides with 11 modes of action [12]. Ten of these herbicide-resistant species (eight monocotyledons and two dicotyledons) are resistant to multiple herbicides. At least ten herbicide-resistant weed species occur in paddy rice fields in China [9]. As chemical control options become less effective, feeding China's 1.412 billion people [1] will increasingly require integrated weed management programs based on ecological principles. Such programs promote long-term sustainability and limit selection for herbicide resistance.

Understanding weed–crop interactions is a prerequisite for ecological weed management. Weed infestations reduce crop yield and quality while increasing expenses for farmers [13]. They often cause more economic damage than other crop pests, such as insects or fungi [14]. Crop yield losses are often driven by weed–crop competition for resources such as nutrients and light [15]. Factors influencing weed–crop competition include weed density, weed species, and weed biotype. Crop yield losses generally increase with increasing weed density, but this trend is not necessarily linear [15]. Some weed species are highly damaging in a given cropping system and environment, while others have little impact. Even within weed species, different biotypes can exhibit different competitiveness and cause different rates of crop yield loss [15]. This last factor is receiving increasing attention given the rapid proliferation of herbicide-resistant biotypes. The evolution of herbicide resistance sometimes incurs a fitness cost, i.e., resistant biotypes may achieve less growth and reproduction than susceptible biotypes when herbicides are not sprayed [16]. For example, glyphosate-susceptible lines of *Echinochloa colona* (L.) Link produced more biomass and more spikes than glyphosate-resistant lines in the absence of glyphosate [17].

Eared redstem is an annual herb in the Lythraceae family. This species occurs in tropical and subtropical regions worldwide, including parts of southeastern North America, Central and South America, Africa, Asia (including China), and Australia [18,19]. Plant height is often 15 to 40 cm but may reach 100 cm, exceeding the height of rice [18,20]. A single-eared redstem plant can produce approximately 50,000 seeds [20]. This species has become the third most dominant weed in main paddy fields in China, after barnyardgrass and *Leptochloa chinensis* (L.) Nees (Chinese sprangletop) and is increasingly harmful in direct-seeded rice in Zhejiang, Jiangsu, and Shanghai [20]. *Ammannia* spp. were reported to cause 39% rice yield loss at approximately 100 weeds m⁻² [21]. Eared redstem was estimated to cause a theoretical rice yield reduction of 58% at a density of 463 plants m⁻² [22]. Herbicide resistance is widespread in this genus and species. In California rice, BSM resistance was confirmed in *Ammannia* populations four years after this herbicide was

introduced [23]. Approximately 97% of eared redstem plants collected from the Ningshao and Hangjiahu plains within the Yangtze River Delta region of China were resistant to BSM [24].

This study evaluates how eared redstem density and biotype (BSM-resistant vs. BSM-susceptible) affect competitiveness against rice. We addressed this question through complementary greenhouse and field experiments.

2. Materials and Methods

2.1. Greenhouse Study

A greenhouse experiment was conducted at Huajiachi Campus, Zhejiang University (elevation 23 m, 30°16' N, 120°12' E) in Hangzhou, China. The temperature range in the greenhouse was 20 to 30 °C, humidity ranged from 50 to 90%, and 14 hr of natural light was provided. The soil used was a silty loam with a pH of 6.6, 1.35% organic matter content, and 0.14% total nitrogen. Compound fertilizer ($N + P_2O_5 + K_2O \geq 45\%$, 15-15-15, Jiangsu Zhongdong Fertilizer Co., Ltd., Changzhou, China) was applied at 525 kg ha⁻¹ before rice sowing.

The experiment was arranged in a completely randomized design with five treatments: low density of BSM-susceptible eared redstem (SL), low density of BSM-resistant eared redstem (RL), high density of BSM-susceptible eared redstem (SH), high density of BSM-resistant eared redstem (RH), and a control without eared redstem (CK). There were three replicates for treatment. The plot area was 0.87 m². Seeds of rice (cultivar Xiushui 123) were sourced from Hangzhou Seed Industry Group, Zhejiang, China. Seeds of the BSM-susceptible eared redstem biotype (HZ001) were collected from a farm ditch at Huajiachi Campus of Zhejiang University, which was rarely exposed to herbicides. Seeds of the BSM-resistant biotype (NB0143-05, resistance index 45.0) were collected from Ningbo (30°25' N, 120°21' E) rice fields in 2010. Previous studies have characterized the susceptibility or the resistance of these eared redstem populations to BSM [24]. These seeds were stored in a refrigerator (4 °C) until needed. Each biotype was grown in a low-density treatment and a high-density treatment. For the low-density treatment, seeds were sown at 200 seeds m⁻², and seedlings were thinned to 58 plants m⁻² at 30 days after sowing (DAS). For the high-density treatment, seeds were sown at 800 seeds m⁻² and thinned to 288 plants m⁻² at 30 DAS. These densities were based on the low and high ends of the range of eared redstem densities found in paddy fields in Zhejiang province. On the same day as eared redstem seeding, rice seeds were sown at 60 kg ha⁻¹ in all eared redstem treatments and the control (CK, artificial weeding). Water was added to keep the soil moist after sowing, and weeds other than eared redstem were removed by hand weeding. Urea ($N \geq 46.4\%$, Shandong Hualu-hengsheng Chemical Co., Ltd., Dezhou, China) was applied at 75 kg ha⁻¹ at 15 DAS and 30 DAS.

In each plot, five points on the diagonal were selected. At each point, two rice plants and two eared redstem plants were selected for measurements. The height and number of tillers of selected rice plants were measured every 5 days from 10 to 80 DAS. The height and number of branches of selected eared redstem plants were measured on the same dates. At 141 DAS, the number of capsules and shoot dry weight was measured for eared redstem plants. At 141 DAS, the number of spikes and yield (dry weight) of rice were measured in three 25 by 25 cm sample squares on the diagonal line in each plot.

2.2. Field Study

The field experiment was conducted in a direct-seeded rice field in Shaoxing City, Zhejiang Province (elevation 9 m, 30°01' N, 120°68' E). The temperature range during the experiment was 20 to 32 °C with a 14 hr photoperiod. The soil was a yellow–purple clay with pH 6.7 and 2.8% organic matter. Compound fertilizer ($N + P_2O_5 + K_2O \geq 45\%$, 15-15-15) was applied at 525 kg ha⁻¹ before rice sowing. Rice (cultivar Xiushui 09) seeds

were sown at 63.75 kg ha^{-1} . Eared redstem plants in the paddy field were confirmed resistant to BSM with a resistance index of 55.1 [25]. The treatments comprised six densities (5, 10, 20, 30, 40, 50 plants m^{-2}) of this BSM-resistant eared redstem population, plus a control without weeds (CK, artificial weeding). Three replicate plots of each treatment were arranged in a randomized complete block design. The area of each plot was 7.5 m^2 . After rice sowing, weeds other than eared redstem were pulled out at 15 DAS, 30 DAS, and every 10 days thereafter. At 30 DAS, eared redstem seedlings were thinned or transplanted from outside the plots as necessary to reach the treatment densities. When thinning and transplanting, seedlings of similar age and height were selected. Urea ($\text{N} \geq 46.4\%$) was applied at 75 kg ha^{-1} at 15 and 30 DAS. All other agricultural operations, such as water and pest control, followed local management protocols. At rice harvest (136 DAS), the number of rice spikes was measured at 3 points (50 by 50 cm) on the diagonal line of each plot. Rice yield (dry weight) was measured at 3 points (100 by 100 cm) on the diagonal line of each plot.

2.3. Statistical Analysis

Data were analyzed using Fisher's analysis of variance (ANOVA). Eared redstem biotype, density, and days after seeding were considered fixed factors. Treatment means were compared using the least significant difference (LSD) test at $p < 0.05$. All statistical analyses were performed using SPSS® version 21.0 (SPSS, Chicago, IL, USA) and Microsoft Excel™ 2019 (Redmond, WA, USA).

3. Results

3.1. Greenhouse Experiment

3.1.1. Plant Height of Eared Redstem and Rice

The eared redstem initially grew slowly. In the low-density SL and RL treatments (eared redstem density of 58 plants m^{-2}), the eared redstem plants were significantly shorter than the rice plants for the first 45 DAS ($p < 0.05$) (Figure 1A). However, there was no significant difference in height between the two species at 50 DAS. Beginning at 55 DAS, the eared redstem was significantly taller than the rice ($p < 0.05$). A difference between the BSM-resistant biotype and the susceptible biotype also emerged over time. At 80 DAS, the BSM-resistant biotype was 15.8% shorter than the susceptible biotype (99.5 vs. 118.2 cm) ($p < 0.01$).

At low eared redstem density, the competition from the BSM-susceptible biotype did not reduce the rice plant height relative to the control without weeds (Figure 1A, SL vs. CK). However, competition from the BSM-resistant biotype did reduce rice plant height (6.35 to 9.54%) relative to the control treatment without weeds from 45 to 75 DAS ($p < 0.05$) (Figure 1A, RL vs. CK).

A high density of eared redstem (288 plants m^{-2}) had more impact on rice height compared with the low density (Figure 1B). The susceptible biotype (SH) reduced rice height relative to the control, beginning at 45 DAS. The resistant biotype (RH) reduced rice height relative to the control, beginning at 20 DAS. At 80 DAS, the eared redstem height was 114.2 cm in the SH treatment and 96.0 cm in the RH treatment. In contrast, the rice height in the CK treatment was 85.0 cm. The rice height was reduced by 16.2% in the SH treatment and 11.8% in the RH treatment compared with the CK ($p < 0.01$) (Figure 1B).

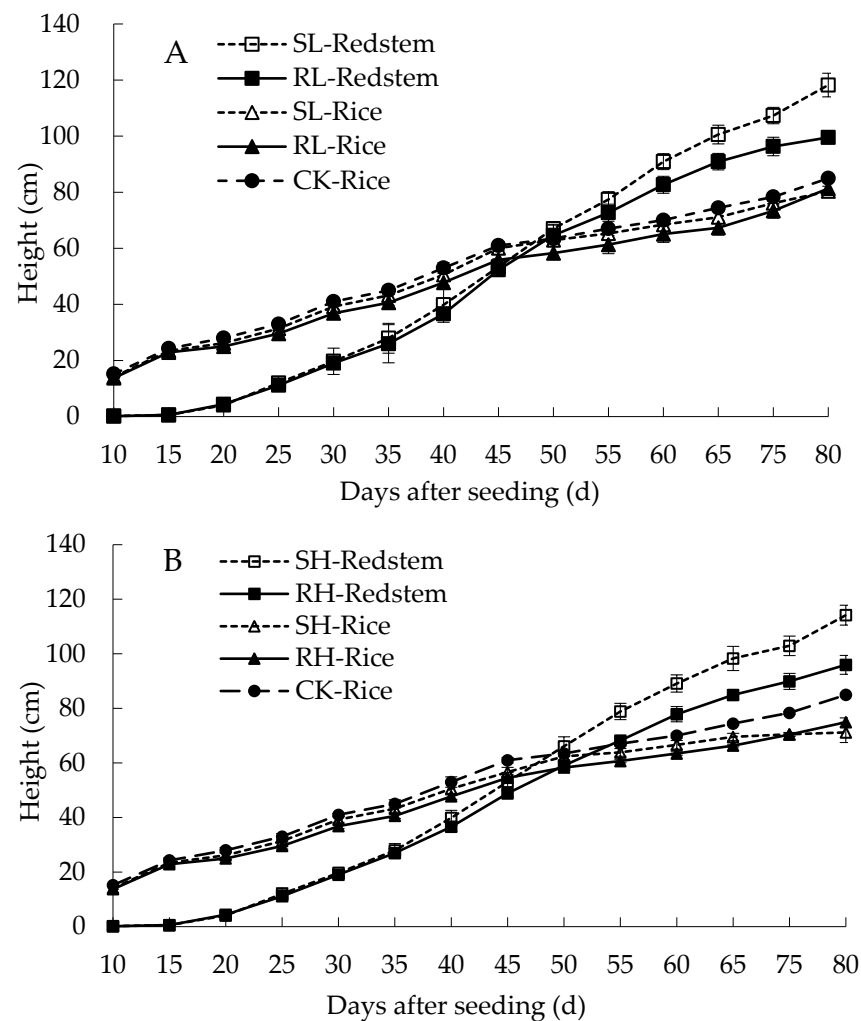


Figure 1. Height (mean $\pm$ standard error) of two eared redstem biotypes and paddy rice over time at (A) a low eared redstem density of 58 plants m^{-2} or (B) a high eared redstem density of 288 plants m^{-2} . The letters L and H refer to low and high densities, respectively. The letters S and R refer to BSM-susceptible and BSM-resistant biotypes, respectively. CK is the control in which only rice was planted. The rice seeding rate was 60 kg ha^{-1} in all treatments.

3.1.2. Branches, Capsules, and Dry Weight of Eared Redstem

Under low density, the number of branches on the susceptible eared redstem biotype (SL) increased rapidly after 55 DAS, reaching 29.9 branches per plant at 80 DAS (Figure 2A). The resistant biotype (RL) had significantly more branches than the susceptible biotype from 45 to 55 DAS ($p < 0.05$). At 55 DAS, RL plants had 63.9% more branches than SL plants ($p < 0.01$). However, the number of branches in the RL treatment then plateaued, so RL plants had 50.9% fewer branches than SL plants at 80 DAS ($p < 0.01$) (Figure 2A). Eared redstem had fewer branches when grown at high density relative to low density (Figure 2B). At high density, RH plants had 66.9% fewer branches than SH plants at 80 DAS ($p < 0.01$) (Figure 2B).

At low density, the average number of capsules per eared redstem plant was 1296.3 in the SL treatment and 48.2% lower in the RL treatment ($p < 0.05$) (Figure 3). At high density, the average number of capsules was 519.2 in the SH treatment and 48.9% lower in the RH treatment ($p < 0.05$). Similar patterns were observed for eared redstem shoot dry weight (Figure 4). At low density, shoot dry weight was 9.5 g in the SL treatment and 57.7% lower in the RL treatment ($p < 0.05$). At high density, shoot dry weight was 4.7 g in the SH treatment and 59.7% lower in the RH treatment ($p < 0.05$). The capsule number and shoot dry weight were both lower at high density relative to low density (Figures 3 and 4).

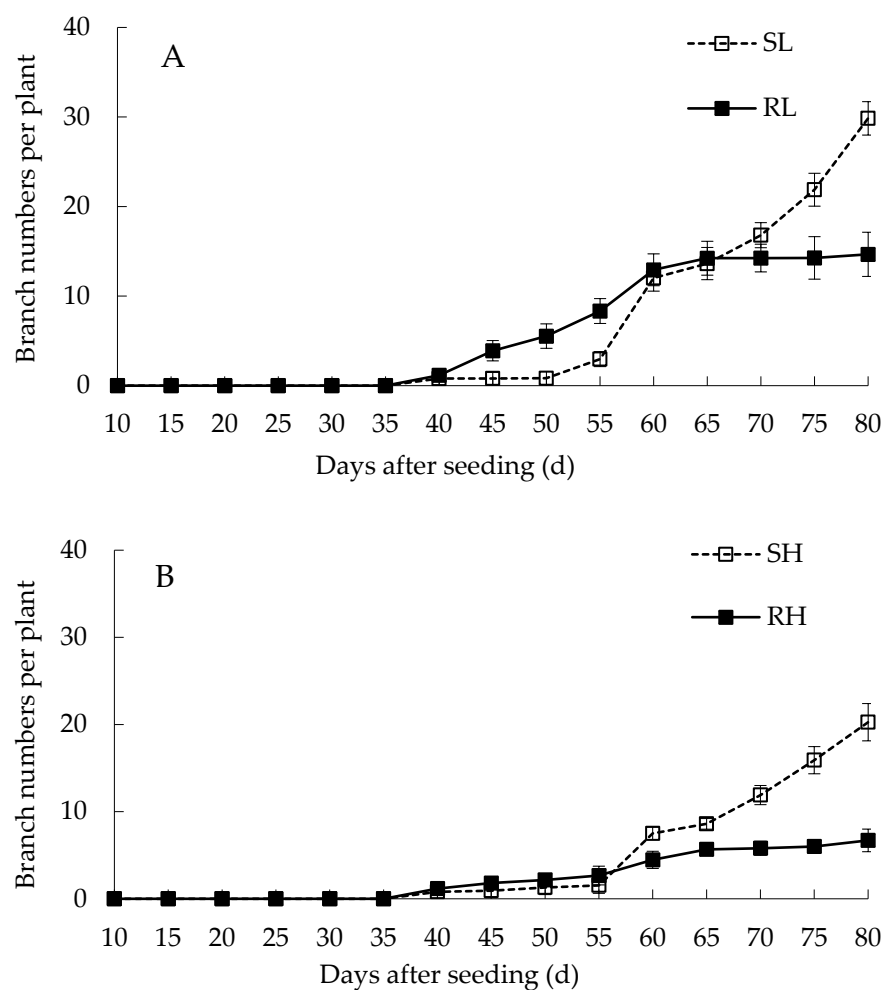


Figure 2. Number of branches (mean $\pm$ standard error) of two eared redstem biotypes over time at (A) a low eared redstem density of 58 plants m^{-2} or (B) a high eared redstem density of 288 plants m^{-2} . The letters L and H refer to low and high densities, respectively. The letters S and R refer to BSM-susceptible and BSM-resistant biotypes, respectively. The rice seeding rate was 60 kg ha^{-1} in all treatments.

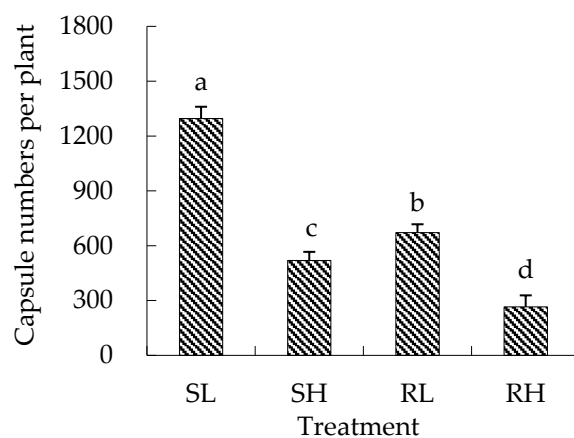


Figure 3. Number of capsules (mean $\pm$ standard error) per eared redstem plant at 141 DAS. The letters L and H refer to low and high eared redstem densities, respectively. The letters S and R refer to BSM-susceptible and BSM-resistant biotypes, respectively. Different letters above columns indicate significantly different means ($p < 0.05$).

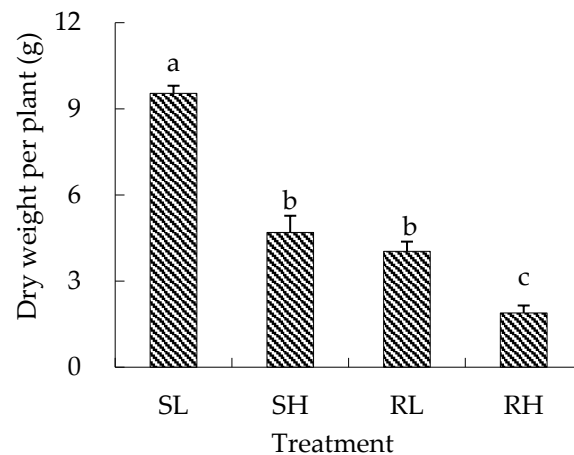


Figure 4. Shoot dry weight (mean $\pm$ standard error) per eared redstem plant at 141 DAS. The letters L and H refer to low and high eared redstem densities, respectively. The letters S and R refer to BSM-susceptible and BSM-resistant biotypes, respectively. Different letters above columns indicate significantly different means ($p < 0.05$).

3.1.3. Tillering and Yield of Rice

The rice produced tillers beginning at 25 DAS, and the number of tillers per plant increased quickly until 45 DAS. Rice plants in the SL treatment had fewer tillers than CK plants after 30 DAS ($p < 0.05$) (Figure 5A). At 80 DAS, CK plants had an average of 1 tiller per plant, and SL plants had 42.6% fewer tillers ($p < 0.01$). From 30 to 40 DAS, RL plants had fewer tillers than SL plants. For example, the number of tillers in the RL treatment was 40.3% lower than the SL treatment at 35 DAS ($p < 0.05$) (Figure 5A). Eared redstem caused greater reductions in rice tillering when grown at high density (Figure 5B). At 80 DAS, the number of rice tillers was 71.2% lower in the SH treatment than the CK and 59.5% lower in the RH treatment than the CK ($p < 0.01$) (Figure 5B). Plants in the RH treatment had fewer tillers than plants in the SH treatment from 30 to 50 DAS; however, from 55 to 80 DAS, there was no significant difference in tiller number between the two treatments.

The number of spikes and yield (dry weight) of rice were measured at 141 DAS (Table 1). In the SL and RL treatments, the number of rice spikes decreased by 41.2 and 40.1%, respectively, compared with the CK ($p < 0.05$). The rice yield decreased by 73.1 and 50.8%, respectively. These findings indicated that the lower density of the eared redstem plants had a significant impact on rice. The higher density of the eared redstem plants had a greater impact on rice. In the SH and RH treatments, the number of rice spikes decreased by 90.4 and 62.6%, respectively, compared with the CK ($p < 0.05$). The rice yield decreased by 98.3 and 81.8%, respectively. The susceptible biotype had greater negative effects on the rice spike number and yield than the resistant biotype (Table 1).

Table 1. Effects of two eared redstem biotypes on yield (mean $\pm$ standard error) of paddy rice in the greenhouse at 141 DAS. The letters L and H refer to low and high eared redstem densities, respectively. The letters S and R refer to BSM-susceptible and BSM-resistant eared redstem biotypes, respectively. CK is the control in which only rice was planted. Different letters within columns indicate significantly different means ($p < 0.05$).

Treatment	Spike Number Per 0.063 m ²	Reduction in Spike Number (%)	Dry Weight of Rice (kg ha ⁻¹)	Yield Reduction (%)
CK	18.7 $\pm$ 1.8 a		5275.5 $\pm$ 403.2 a	
SL	11.0 $\pm$ 1.5 b	41.2	1419.4 $\pm$ 157.7 c	73.1
SH	1.8 $\pm$ 0.7 d	90.4	88.4 $\pm$ 27.7 e	98.3
RL	11.2 $\pm$ 1.6 b	40.1	2596.9 $\pm$ 266.0 b	50.8
RH	7.0 $\pm$ 0.9 c	62.6	960.5 $\pm$ 91.8 d	81.8

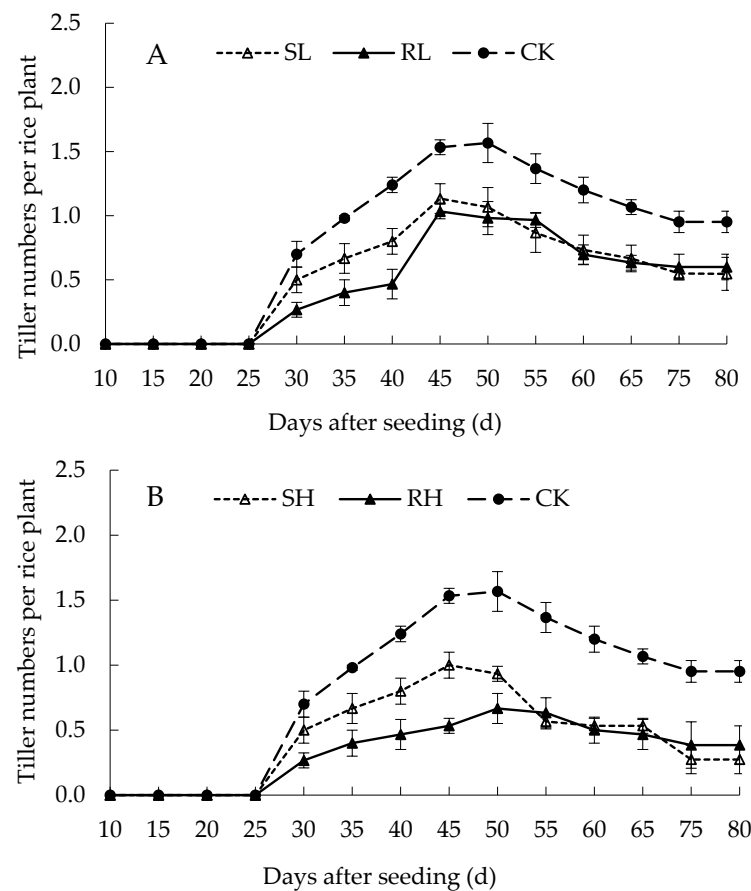


Figure 5. Number of tillers (mean $\pm$ standard error) of rice over time at (A) a low eared redstem density of 58 plants m^{-2} or (B) a high eared redstem density of 288 plants m^{-2} . The letters L and H refer to low and high densities, respectively. The letters S and R refer to BSM-susceptible and BSM-resistant biotypes, respectively. CK is the control in which only rice was planted. The rice seeding rate was 60 kg ha^{-1} in all treatments.

3.2. Field Experiment

Rice plants were grown in competition with eared redstem densities of 0 to 50 plants m^{-2} (Table 2). Even low densities of eared redstem had significant impacts on rice. A density of 5 plants m^{-2} reduced the rice spike number and yield by 18.7 and 22.2%, respectively, compared with the control (CK) treatment. Reductions in spike number and yield were magnified by increasing weed density. At a weed density of 50 plants m^{-2} , the rice spike number was reduced by 45.0% ($p < 0.05$), and the rice yield was reduced by 70.3% relative to the control (Table 2).

Table 2. Effects of eared redstem on yield (mean $\pm$ standard error) of paddy rice in the field at 136 DAS. Different letters within columns indicate significantly different means ($p < 0.05$).

Eared Redstem Density (Plants m^{-2})	Paddy Rice			
	Spike Number Per 0.25 m^2	Reduction in Spike Number (%)	Dry Weight of Rice (kg ha^{-1})	Yield Reduction (%)
0 (CK)	101.7 $\pm$ 1.2 a		8719.9 $\pm$ 889.3 a	
5	82.7 $\pm$ 3.5 b	18.7	6786.5 $\pm$ 398.3 b	22.2
10	80.0 $\pm$ 2.0 b	21.3	6034.2 $\pm$ 299.1 c	30.8
20	78.4 $\pm$ 3.1 bc	22.9	5129.7 $\pm$ 241.1 d	41.2
30	73.7 $\pm$ 3.6 cd	27.5	4069.6 $\pm$ 228.6 e	53.3
40	71.4 $\pm$ 4.3 d	29.8	3385.5 $\pm$ 195.2 e	61.2
50	55.9 $\pm$ 1.7 e	45.0	2586.9 $\pm$ 180.0 f	70.3

4. Discussion

Height measurements in the greenhouse experiment demonstrated that eared redstem grew very slowly before 15 DAS but later grew faster than rice. Beginning at 55 DAS, the eared redstem was significantly taller than rice. This finding is consistent with the height of eared redstem increasing slowly during the first two weeks after emergence, but plant height began to increase rapidly in the 3rd week after emergence, and height increased most rapidly between the 5th and 8th week of the study, with an average weekly height increase of 150 to 230 mm [26]. These results might indicate that eared redstem can tolerate and recover from prolonged shade. Consistent with this explanation, *A. coccinea* responds to shade through plasticity in morphological and physiological traits related to resource partitioning, leaf characteristics, and dark respiration [27]. *Ammannia* spp. respond to competition from rice through morphological changes that maximize height and light capture, even at the expense of nutrient capture or stability [21]. These shade avoidance responses reduce the likelihood that rice will suppress eared redstem and increase the likelihood that eared redstem will overtop rice. Based on previous studies and our results, it seems likely that eared redstem must be controlled prior to 50 DAS to prevent it from gaining a competitive advantage over direct-seeded rice.

In the greenhouse experiment, eared redstem plants had fewer branches, fewer capsules, and less dry weight when grown at a higher density (288 plants m^{-2}) relative to a lower density (58 plants m^{-2}). The higher eared redstem density also increased the competitive effects of the weed on rice. Similarly, the field experiment showed that increasing densities of eared redstem had increasingly severe effects on rice. However, even a very low density of eared redstem (5 plants m^{-2}) reduced rice spike numbers and yield by approximately 20%. This finding suggests that the economic threshold for the control of eared redstem might not exceed 1–2 plants m^{-2} . Similarly, Tian et al. [28] reported that even the low densities of *E. crus-galli* (4 plants m^{-2}) and *C. difformis* (8 plants m^{-2}) decreased rice yield by 23.46 and 11.13%, respectively. Bajwa et al. [29] found that *Parthenium hysterophorus* L. should be controlled when weed densities reach 5 plants m^{-2} to avoid substantial yield losses (i.e., >15%) in direct-seeded rice. The control of weeds only when above the economic threshold level within the critical period is considered an effective strategy to prevent crop yield losses. From the perspective of long-term seed bank management, preventing any eared redstem plants from setting seed would reduce the risk of yield loss in future years.

We observed differences between the BSM-resistant and BSM-susceptible biotypes of eared redstem in the greenhouse experiment. Relatively early in the experiment, the resistant biotype exhibited increased growth. At low density, the resistant biotype had more branches than the susceptible biotype until approximately 55 DAS. Over a similar time period, rice plants had fewer tillers when grown in competition with the resistant biotype relative to the susceptible biotype. However, by the end of the experiment, plants of the susceptible biotype were larger than the resistant plants and had greater effects on rice growth. At final measurements, the resistant biotype was shorter and had fewer branches, fewer capsules, and less shoot dry biomass in both planting density treatments. The number of rice spikes and dry weight of rice were both lowest when rice was grown in competition with the susceptible biotype at high density. In previous research, some herbicide-resistant species were reported to be less fit than susceptible biotypes in the absence of the herbicide [30]. For example, the shoot dry weight of a *Brachypodium hybridum* atrazine-resistant biotype (0.82 g per plant) was significantly lower than that of the susceptible biotype (1.05 g per plant) [31]. Moreover, the imazamox-herbicide-resistant biotype of *Euphorbia heterophylla* L. produced 30% fewer leaves and 35% lower stem biomass than a susceptible biotype, respectively [32]. These findings are consistent with a fitness cost of herbicide resistance in eared redstem. Fitness costs have been reported in a wide array of herbicide-resistant species [16,33,34]. Fitness costs are widespread because both target-site resistance and non-target-site resistance can interfere with normal plant functions that were shaped by many generations of selection prior to the introduction of herbicides [34]. However, the link between the physiological performance and fitness of eared redstem at

the early stages of BSM resistance evolution has not been studied. Future research should focus on understanding the adaptive systems that BSM-resistant biotypes of eared redstem evolve during the process of BSM selection. We also need to understand how phenotypic variation across generations affects the fitness of eared redstem under recurrent herbicide selection pressure.

Overall, eared redstem is a most troublesome weed in rice cropping systems because it produces large quantities of seeds, exhibits rapid growth, and has a strong competitive ability. From a weed management perspective, it is important to avoid a rapid increase in the frequency of resistant biotypes in subsequent generations. In the future, multiple management practices need to be incorporated into an IWM system to effectively manage current BSM-resistant eared redstem populations in direct-seeded rice cropping systems. For example, the use of rape straw mulch is one promising option for controlling herbicide-resistant weeds and decreasing herbicide use in rice systems [35]. Other options for eared redstem control could include tillage or the flooding of rice fields [36], although the weed control benefits of these practices should be balanced against other considerations such as soil health. It is possible to take advantage of fitness costs in herbicide-resistant weeds to improve integrated weed management programs [33].

5. Conclusions

We performed greenhouse and field experiments to measure the competitive effects of BSM-susceptible and BSM-resistant eared redstem populations on rice. Our results demonstrate that even low densities of eared redstem pose a substantial threat to rice yield. The economic threshold for the control of eared redstem might not exceed 1–2 plants m⁻². Rice yield losses increased with increasing densities of eared redstem in both experiments. Our research also demonstrates that the evolution of BSM resistance may incur a fitness cost in eared redstem. We found that BSM-resistant eared redstem is less competitive against rice. To manage this resistant biotype, it may, therefore, be helpful to increase rice competitiveness through cultural approaches such as cultivar selection or increased planting density. Our study helps to develop more effective weed management strategies with less impact on the environment.

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