The within-field and between-field dispersal of weedy rice by combine harvesters

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Abstract

Weedy rice (*Oryza sativa* L.) severely decreases the grain yield and profitability of rice is one of the most significant problems in the majority of rice fields worldwide. Few reports focus on the dispersal of weedy rice, especially how it rapidly spreads to large areas and long distances. Here, we quantify for the first time the within- and between-field dispersal of weedy rice associated with combine harvesting operations. We randomly sampled 31 combine harvesters to determine where and how much weedy rice seeds remained on the machines at three locations in Jiangsu Province, China. Based on the sampling results, the field area over which weedy rice seeds were retained on the combine harvester during harvesting was estimated to assess the within-field dispersibility of weedy rice seeds remaining in the harvesters. A tracking experiment was also carried out by tracing the distribution of weedy rice seeds along harvest trails, to estimate the dispersal of weedy rice seeds within the field being harvested. Weedy rice seeds remained in the harvest pocket, on the pedrail, and the metal plate of the combine harvester. On average, more than 5000 weedy rice seeds which were 22.80% of remaining grains could potentially be transported into adjacent fields by the combine after each rice field infested with weedy rice had been harvested. Of the statistical models compared, a double exponential model simulating the variation in seed retention predicted that weedy rice seeds remaining on the metal plate could be dispersed over 6473.91 m² or 3236.96 m into the next field during the harvesting operation. Within the field, the number of fallen weedy rice seeds and their dispersal distance were positively correlated to weedy rice panicle density with the combine dispersing most of seeds away from their mother plant thus creating new weed patches. Therefore, fields that were severely infested with weedy rice should be harvested cautiously and separately and seed remaining in a harvester should be avoided to prevent intra- and inter-field, and even cross-regional dispersal of weedy rice.

Keywords Human-mediated seed dispersal · Seed retention curves · Weed biology · Agricultural activity · Harvesting operation

1 Introduction

Weedy rice (*Oryza sativa*) is one of the most significant weeds in the majority of paddy fields worldwide (Cheng et al. 2003; Ziska et al. 2015). Weedy rice severely decreases the grain yield and quality of rice and increases production costs

(Azmi and Karim 2008; Chauhan 2013). Weedy rice is often, but not exclusively, associated with a red pericarp and is frequently referred to as “red” rice (Ziska et al. 2015). Opposite to cultivated rice, weedy rice shatters its seed (Merotto et al. 2016) that is highly dormant (Schwanke et al. 2008) thus building up a large and persistent seedbank (Chauhan and Johnson 2010; Akasaka et al. 2011; Zhang et al. 2012a), and has high competitive ability given its higher tillering and enhanced photosynthesis (Fleck et al. 2008; Dai et al. 2016). Cultivated rice and weedy rice both belong to the same species and share similar morphological and physiological characteristics (Gross et al. 2010); therefore, selective herbicides commonly used for weed control in paddy fields cannot be used to kill weedy rice making agronomic practices a key component for its management. Rice grain yield reduction by weedy rice can be as high as 74% in direct seedling rice (Olajumoke et al. 2016) and even over 80% in heavily infested fields (Diarra et

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al. 1985). A recent survey determined that weedy rice infests approximately 3.33 million ha of paddy fields in China and reduces the total rice yield by 3.4 billion kg (Liang and Qiang 2011). Similarly, in the USA, the average loss due to weedy rice infestation is nearly \$274.00•ha⁻¹ (Burgos et al. 2006).

Several studies have addressed the biological characteristics, competition (Dai et al. 2016), origin and evolution (Londo and Schaal 2007; Zhang et al. 2015) or damage mechanisms, and prevention and control of weedy rice (Gressel and Valverde 2009; Chauhan et al. 2015). However, although weedy rice dispersal is thought to be mediated by agricultural activities, dispersal pathways and the extent of its spread are poorly understood.

Weeds are sessile during growth; however, their propagules, especially their seeds, can be spread through various ways after falling off mature plants to achieve migration and extend the population (Dastgheib 1989; Okuba and Levin 1989; Smith et al. 2005). Generally, the dispersal of plant species by ants, ballistics, and unassisted means (gravity or no particular dispersal morphology) are classified as short-distance dispersal mechanisms, whereas dispersal through wind, water, and vertebrates are classified as long-distance mechanisms (Gómez and Espadaler 1998; Vittoz and Engler 2007; Thomson et al. 2010). Human activities often cause more rapid dispersal than natural pathways because they generally result in multiple introductions to numerous locations across a large area; anthropogenic activities such as transport along roads, railways, and waterways ensure high spread rates (Wilson et al. 2009; Taylor et al. 2012).

In agro-ecosystems, many forms of human activity can contribute to weed dispersal; weed seeds can be spread with manure used as fertilizer (Dastgheib 1989; Pleasant and Schlather 1994), irrigation water (Dastgheib 1989), and by machinery during soil tillage and harvesting operations (Wiles and Brodahlb 2004). Weedy rice normally disperses its seed by gravity under non disturbed conditions in absence of particular dispersal structures in the seed and by having a relatively large mass (Zhao et al. 2017); the wide-range and long-distance dispersal of weedy rice seed by water, wind, and animals is also limited. Previous studies indicated that weed species such as *Panicum miliaceum* (McCanny and Cavers 1988), *Lolium rigidum* (Blanco-Moreno et al. 2003), and *Avena fatua* (Shirliffe and Entz 2005) could be dispersed widely within a field by combine harvesters during harvesting. This might also occur with weedy rice seed. Furthermore, in China, most rice farms are small and farmers usually rent combines that provide harvesting services across fields or even regions (transported by trucks) during the rice harvest period. Thus, the long-distance dispersal of weedy rice could possibly be caused by the operation of combine harvesters carrying weedy rice seeds from infested fields.

Currently, there is limited evidence documenting within- and between-field dispersal of weedy rice by combine harvesting operations. This study was conducted to characterize the mechanism of weedy rice dispersal associated with combine harvesting and provide advice for taking precautions against infestation by weedy rice. Here, we (1) determined where and how much weedy rice seeds remains in a typical Chinese combine harvester, (2) assessed the between-field dispersal of weedy rice seed remaining in the combine harvester, and (3) estimated the within-field dispersal of weedy rice seed during harvesting.

2 Material and methods

2.1 Weedy rice seeds remaining in combine harvesters

From November to December 2012, a survey was conducted in Zhenjiang (119.25° E, 32.11° N), Jintan (119.45° E, 31.68° N), and Suqian (118.22° E, 33.82° N) cities in Jiangsu Province, China, where fields are seriously infested by weedy rice, to determine where and how much weedy rice seed remain in a combine harvester. Thirty-one different combine harvesters were randomly selected for inspection after rice harvesting was complete. These reaping harvesters are widely used in China, with a cutting width of 2 m (Fig. 1). To study the influence of weedy rice density on seed retention in a harvester, along the crop rows, the panicle density of weedy rice in each of the 31 rice fields (there were 9 fields in Zhenjiang, 11 fields in Jintan and 11 fields in Suqian) was determined by 30 quadrats of 0.25 m² (0.5 m × 0.5 m) per field using an equidistant sampling method before each harvesting. Rice fields ranged from 500 to 3000 m². Grains (as the sum of rice and weedy rice seeds, similarly hereinafter) remaining in the pedrail, on the harvest pocket, and the metal plate (Fig. 1) of the combine harvester were separately collected as different samples. All samples were taken to the laboratory to remove impurities and air dried (to prevent mildew) for weighing and counting. Weight and dry weight of remaining grains of each sample were measured and their water content calculated as (weight – dry weight)/weight (Baigorri et al. 1999). Dry weight was determined after oven-drying at 70 °C. In our experience, all weedy rice in Jiangsu Province has a red pericarp, and cultivated rice and weedy rice were discriminated by pericarp color after their hulls were removed. After separation, seed number of cultivated and weedy rice in each sample was determined, respectively.

The pedrail is a chain belt around the wheels which improves traction in uneven or muddy terrain. The harvest pocket is a pocket device which cooperates on the feeding of crop and grain located in the head of the combine harvester. The

Fig. 1 A typical combine harvester (Lucky Star XG788) and parts with remaining seed

metal plate is located in the bottom of the grain tank and fixes and holds the grain tank.

2.2 Estimating the harvesting area over which weedy rice seeds were retained on the combine harvester

Based on the results of the harvesting survey in terms of the amount of crop grain and weedy rice seed retained and the parts of the harvester in which they were retained, an experiment involving simulated weedy rice seed retention was carried out in November 2013 in Suqian City, Jiangsu Province, to determine the between-field dispersal of weedy rice seed through a harvester. A 300 g mixture of cultivated and weedy rice seed was placed in both the harvest pocket and on the metal plate of a clean combine before harvest. The weight-based proportions of weedy seeds in the mixture were 0.16, 0.33, 0.50, and 0.67, respectively. All weedy rice seeds used in this experiment were killed at 120 °C for 20 min and dyed with 1% (in ethanol) safranin T (Zhang et al. 2012a, 2012b, 2012c) which didn't interfere with their dispersal behavior to prevent contaminating the rice field and distinguish them from that of cultivated rice. Fifteen different harvesting operations in 15 separate fields were undertaken by a single combine containing seed of a particular mixing ratio. The remaining weedy rice seeds on the different parts of the combine were separated and weighed to calculate the proportion of weedy rice seeds retained after the completion of harvesting each field, and the area of each field was also recorded. However, the mixtures placed in the harvest pocket went directly into the grain tank at the beginning of harvesting, and no weedy rice seed was found in the field.

2.3 Tracing the distribution of weedy rice seeds along harvest trails

A tracing experiment was conducted to determine the dispersal of weedy rice seeds within the field by a combine harvester during its harvesting operation in November 2013 and November 2014 in Suqian and Jintan cities of Jiangsu Province, respectively. Four rice fields with different weedy rice infestation levels were selected. The area of each field was approximately 5000 m² (fields were 96 m to 109 m long by 46 m to 52 m wide). To determine the number of weedy rice seeds per panicle, three panicles were collected from each of 30 equidistant quadrats of 0.25 m² (0.5 m × 0.5 m) placed per field (total 90 panicles per field), 2 weeks before harvest. To easily identify weedy rice that shattered by itself and as well as by combine movement, weedy rice panicles in a 10-m-wide area (in the middle of each field in the length direction) were dyed by spraying a safranin 1% T solution (Zhang et al. 2012a, 2012b, 2012c) 2 weeks before harvest and no shattering of weedy rice seed was observed. During the dyeing, few panicles of cultivated rice were inevitably dyed. In our experiment area, the seed of weedy rice is slender while the seed of cultivated rice is much shorter and wider. Therefore, the fallen dyed seeds of weedy and cultivated rice were distinguished by seed shape. Rice (both cultivated and weedy) was harvested with the combine traveling in the length direction determining a 2-m-wide harvesting trail. Thus each harvesting trail (96 to 109 m corresponding to the length of the field) extended from edge to edge covering a normal rice area, the dyed area, and another normal area. The remaining grains on the combine were removed at the end of each trail and

discarded. Before harvesting, the number of dyed panicles of weedy rice in each harvesting trail was recorded using five equidistant quadrats of 0.25 m² (0.5 m × 0.5 m). The number of dyed seeds that had fallen from the panicles was recorded at 1-m intervals using a quadrat of 0.25 m². The length of the harvesting trail with dyed seed that had fallen from the plants was also recorded as the dispersal distance of weedy rice seed.

2.4 Data analysis

For the remaining grain sampling experiment, multivariate analyses of variance (MANOVA) were conducted to determine the effects of field location and grain remained part (as independent variables) and field size and panicle density of weedy rice (as covariates) as well as their interaction effects on the weight of remaining grains, remaining seed number of weedy rice, and its percentage in remaining grains (as dependent variables) in the combine harvesters at a significance level of 5%. The data of weight of remaining grains and seed number of weedy rice in the combine harvesters were log-transformed while square root transformations were performed on the data of percentage (relative to the number of remaining grains) of weedy rice seeds in remaining grains to ensure compliance with the assumptions of normal distribution of residuals (Shapiro–Wilkinson's *W* test) and homoscedasticity (Levene's test). Pairwise comparisons (using LSD test at a significance level of 5%) were also performed to compare the weight of remaining grains, number of weedy rice seeds, and percentage of weedy rice seeds in remaining grains in the pedrail, on the harvest pocket, and the metal plate and that of the total sum in the combine harvester. These analyses were performed using SPSS 20 software (SPSS Inc., Chicago, IL, USA), and graphs were generated using Origin 9.0 (OriginLab, Hampton, MA, USA). The relationship between panicle density and the total number of remaining seeds of weedy rice was also regressed by using the model fitting function in Origin 9.0.

The data from the dispersal simulation experiment showed that the proportion of weedy rice seeds that was retained on the metal plate decreased exponentially as the harvest area increased. Based on specialized seed dispersal and retention literature (Taylor 1978; Wichmann et al. 2009; Taylor et al. 2012), two models related to the exponential function were used to fit our data. The first model incorporated simple exponential and power exponential functions to take the form:

$$SR(A) = e^{\alpha \times A^\gamma} \quad (1)$$

The second was a double exponential function (Wichmann et al. 2009; Bullock et al. 2011; Taylor et al. 2012), taking the form:

$$SR(A) = e^{\alpha \times e^{\beta \times A^\gamma}} \quad (2)$$

where SR% indicates the percentage (relative to placed weedy rice seeds) of seeds retained, *A* represents harvest area (m²) for all models, and α , β , and γ are parameters controlling the shape and scale of the models.

All data from the dispersal simulation experiment were pooled and these two models of seed retention were fitted using nonlinear least squares via the *nls* function in the statistical package R (R Development Core Team 2010). The model that best described the structure of the data was determined by comparing Akaike information criterion (AIC) values, and the model with the lowest AIC score was selected (Venables and Ripley 2002; Taylor et al. 2012). Residuals versus fitted plot and normal QQ plot (Dalgaard 2002) were created in R to determine the fit of the selected model. To determine whether the proportion (relative to the weight of remaining grains) of weedy rice in the remaining grains had effects on the dispersibility (dispersal area) of weedy rice seed by combine harvester, one-way ANOVA analyses (using LSD test at a significance level of 5%) were also conducted in the statistical package R by using the *anova*() function to compare the fitting of the pooled data with the data of each different mixing ratio of weedy rice.

For the tracing experiment, all data were pooled and generalized linear models (GLMs) was used to examine the relationship between the panicle density of weedy rice and fallen seed number and dispersal distance of weedy rice along the harvest trail in the statistical package R. Additionally, a scatter plot of the distribution of weedy rice seeds corresponding to panicle density along the harvest trail was also generated by using the *ggplot*() function in the statistical package R.

3 Results and discussion

3.1 Remaining seeds of weedy rice in a combine harvester

Upon completion of harvesting, it became obvious that plenty of seeds remained on or in the three parts of the combine harvesters: on the pedrail and metal plate and in the harvest pocket (Fig. 1). Except for the pedrails of three harvesters, weedy rice seeds were found in the harvest pocket and on the metal plate and pedrail of all 31 surveyed combine harvesters. Based on the MANOVA analyses (Table 1) there was no effect of field location and size on the seed number of weedy rice ($p = 0.220$ and $p = 0.987$), weight of remaining grains ($p = 0.605$ and $p = 0.838$), and percentage of weedy rice seeds in remaining grains ($p = 0.680$ and $p = 0.058$) in a combine harvester. The panicle density of weedy rice significantly influenced the remaining seed number of weedy rice ($p = 0.005$) and the percentage of weedy rice seeds in the remaining grains ($p = 0.028$), the remaining seed number of weedy rice and its percentage in the remaining grains significantly

Table 1 Tests of between-subjects effects on seed number of weedy rice, fresh weight of the remaining grains, and percentage of weedy rice seeds in the remaining grains in a combine harvester

Source	Effects on SN (Sig.)	Effects on RW (Sig.)	Effects on SP (Sig.)
Location	0.220	0.605	0.727
Size	0.987	0.838	0.981
Density	0.005 ^A	0.483	0.028 ^a
Part	0.000 ^A	0.000 ^A	0.998
Location × part	0.219	0.275	1.000
Location × size	0.292	0.588	0.870
Location × density	0.237	0.885	0.266
Part × size	0.419	0.649	0.919
Part × density	0.351	0.674	0.985
Size × density	0.936	0.952	0.310
Location × part × size	0.202	0.251	1.000
Location × size × density	0.294	0.426	0.993
Location × part × density	0.387	0.621	0.805
Part × size × density	0.198	0.723	0.728
Location × part × size × density	0.227	0.435	0.999

Here, SN, RW, and SP represent seed number of weedy rice, fresh weight of the remaining grains, and percentage of weedy rice seeds in the remaining grains in a combine harvester. Location and size represent field location and field size, density represents panicle density of weedy rice, and part represents grain remained part. The super-script letters a and A indicate significant at 5 and 1% level of probability

increased with an increase in the amount of weedy rice harvested; however, the weight of remaining grains was not significantly affected ($p = 0.483$). The seed number of weedy rice ($p < 0.001$) and grain weight ($p < 0.001$) remaining on the combine harvester was significantly determined by the parts of the combine where they were collected.

The average weight of the grains adhering to the pedrail was 1.20 g, and those remaining in the harvest pocket and on the metal plate were nearly 300 times higher which were 298.96 and 295.78 g, respectively (Fig. 2a), and the average water content of these remaining grains was 12.58%. The average percentage of weedy rice seeds in the remaining grains was 22.11% in the harvest pocket and 23.30 and 23.26% on the pedrail and metal plate (Fig. 2b), corresponding to 2575, 13, and 2773 remaining seeds of weedy rice, respectively (Fig. 2c). The difference in the weight and number of cultivated and weedy rice seeds among those three parts was due to the motion state of these parts in harvesting operation and the way how the grains remained. During harvesting, the pedrail kept rolling and the grains were adhering to it with soil, while the motion state of the metal plate and harvest pocket was relatively stable and the grains were landing on them that made more grains could remain on or in the metal plate and harvest pocket. The maximum number of remaining seeds of weedy rice was 79 seeds in the pedrail and 6290 and 9272 in the harvest pocket and on the metal plate, respectively, from the harvested field with the highest weedy rice infestation (Fig. 2c). The remaining seed number of weedy rice in the combine harvester was positively correlated to the panicle density of weedy rice, which exponentially increased with

an increase in the amount of weedy rice harvested (Fig. 2d). The total number of weedy rice seeds retained ranged from 631 seeds to 15,641 seeds depending on the weedy rice density, which ranged from 16 to 202 panicles·m⁻². Overall, an average of 5360 weedy rice seeds which were 22.80% of the grains remaining in the combine harvesters would possibly be taken to the next field after the completion of harvesting operations in the previous field.

Similar to weedy rice, large numbers of weeds in agroecosystems have evolved no dispersal mechanisms (barochory), but instead rely on dispersal by humans (Bonet and Pausas 2004; Benvenuti 2007). The dispersal of weed seeds can occur directly as a result of soil displacement performed by agricultural machinery, or indirectly, for example, by adhesion of the soil matrix to the tires of operating machines (Benvenuti 2007), and studies have shown that seeds of *Avena sterilis* (Gonzalez-Andujar and Perry 1995), *Bromus sterilis* (Steinmann and Klingebiel 2004), and *Sorghum halepense* (Ghersa et al. 1993) can be dispersed by several, and even as much as a dozen, meters during seedbed preparation. Our study verified that the combine harvester could indeed carry weedy rice seeds that remained in the harvest pocket, on the pedrail, and the metal plate after infested rice fields had been harvested. More than 600 seeds of weedy rice remained on the combine when a rice field with 16 panicles·m⁻² had been harvested. Weedy rice in Jiangsu Province produces 7.2 to 13.1 fertile tillers (equal to the panicle number) per plant (Zhang et al. 2012b). Therefore, it would be reasonable to expect that a field, even with a very low infestation, equivalent to 1.13 to 1.95 weedy rice plants·m⁻², could

Fig. 2 Fresh weight of the remaining grains (a), percentage of weedy rice seeds in the remaining grains (b), and number of weedy rice seeds (c) in the different parts of the combine harvester, and the relationship between panicle density and the remaining seed number of weedy rice (d). Here, capital letters represent the results of Tukey's post hoc comparisons of group means. The points, horizontal lines, and upper and lower triangles in boxplots represent the means, medians, maximum, and minimum values, respectively. The regression equation in (d) is $y = 328.26e^{53.66^{-1}x} + 1260.18$

contribute 600 weedy rice seeds to the next field harvested with the contaminated combine. The amount of weedy rice seeds could be much higher considering that rice fields in Jiangsu have infestations of 0.5 to 76.4 weedy rice plants m^{-2} (Zhang et al. 2012a). However, because of the harvest combine was rented and charged by time and the weight of remained grains is relative less (with the average total weight of 600 g), these remaining grains are always ignored by farms. However, farmers should raise general awareness about the risk of weedy rice infestation through the dispersal of the remaining weedy rice seeds. The designs for some parts of the combine harvester should be improved, such as changing the metal plate to a perforated plate and increasing the automatic dumping function for the harvest pocket to reduce carrying capacity to seeds and the time taken to clean, as their harvesting function was not affected.

3.2 Evaluation of the seed retention model and the between-field and regional dispersal of weedy rice

During harvesting, the mixtures (seeds of weedy and cultivated rice) placed in the harvest pocket went directly into the grain tank at the beginning of harvesting, and no weedy rice seed was found in the field, while the dispersal of weedy rice in the field by mixtures placed on the metal plate were easily observed. The two models of seed retention were tested for their ability to fit the relationship between weedy rice seed retention on the metal plate and harvest area. Model 2

performed much better, with a lower AIC value of 313.74 compared to that of 399.56 for Model 1 (Fig. 3).

The residual analysis of Model 2 indicated that the model was able to capture the variation in the data, and the QQ plot showed good agreement between the two distributions and no serious deviation from the assumption of a normal distribution of the residuals, which assures that the normality assumption is satisfied. Therefore, Model 2 was subsequently used to explain the variation in seed retention.

The dispersal simulation experiment indicated that weedy rice seeds remaining on the metal plate can be moved to adjacent fields by combine harvesters. The selected double exponential model (Model 2) did not drop sharply to zero, as would be expected based on short-distance movements and the predicted large area of seed dispersal for weedy rice (Fig. 3). Comparison fitting of the entire dataset with each different mixing ratio of weedy rice indicated that the proportion of weedy rice in the remaining grains did not have a significant effect on its dispersal area ($p = 0.50\text{--}0.71$). According to the prediction of the double exponential model (Model 2), 50% of the weedy rice seeds were retained on the metal plate when the harvest area was 770 m^2 , and 1.5% of the weedy rice seeds were still attached to the metal plate when the harvest area reached 6474 m^2 . As mentioned above, the combine harvester used in our experiment has a cutting width of 2 m, indicating that 50% of the weedy rice seeds were retained on the metal plate when the combine was driven 385 m, and 1.5% of the weedy rice seeds were still attached to the metal plate when the combine was driven 3237 m.

Fig. 3 Comparison of regression lines for seed retention as a function of harvesting area using Model 1 and Model 2. The equation of the better performing model (Model 2) is with the function of $y = e^{4.4e^{(-1.06E-05)x^{1.40}}}$

Doubts might be casted on whether the similar dispersal of weedy rice would happen when the combines are driven over a road. However, in fact, the combines will not be driven long due to its low speed over the road, otherwise that will be wasting time in the busy harvesting season. If long distance harvestings were needed, the combine harvesters will be transported by trucks.

Knowledge of weed dispersal mechanisms allows the formulation of preventive measures that can avert the entry of the most dreaded species into agro-ecosystems (Benvenuti 2007). In dispersal processes, long-distance dispersal has been recognized as having disproportionate importance (Cain et al. 2000; Higgins et al. 2003). Even extremely small numbers of individuals in the long-distance tail of the dispersal kernel can drive large-scale ecological expansion patterns (Nathan 2006; Wichmann et al. 2009). Our experiment results indicated that plenty of weedy rice seeds might remain in combine harvesters after they finished harvesting and that the seeds remaining on the metal plate could be dispersed over a large area or long distances, which suggests combine harvesters may be a major dispersal agent for the inter-field dispersal of weedy rice.

With high mobility, a combine harvester can rapidly carry out agricultural production activities across multiple fields, or even regions (transported by trucks), within a short period. It is pertinent to consider the cross-regional infestation by weedy rice caused by the remaining weedy rice seeds on the combines. Using 38 morphological characters and 32 pairs of codominant markers, Cai (2013) discussed the occurrence pattern and recent origin of weedy rice in north-eastern China and concluded that weedy rice in north-eastern China did not independently originate in each province but spread from Liaoning Province to Heilongjiang and Jilin Provinces and

had a closer parental relationship with Anhui and Jiangsu ancient weedy rice. Chen et al. (2015) measured morphological characteristics and determined the subspecies (indica or japonica) of weedy rice in 13 cities of Jiangsu Province and found that weedy rice subspecies followed a mutual-spread pattern. It is highly likely that the similarity and dispersal of weedy rice among regions are related to the cross-regional harvesting operation of combines with remaining weedy rice seeds. Therefore, combines should be carefully cleaned before being used for harvesting in other fields and regions. However, the time spent removing the remaining weedy rice seeds will cause direct economic losses for the combine owners during the busy harvest period. Inspection and quarantine regulations should be executed by local agricultural administrations to prevent the introduction of weedy rice from infested regions into uninfested areas.

3.3 Dispersal of weedy rice seeds within a field

After harvesting operations were completed, it was easy to see that a large quantity of weedy rice seeds had fallen to the ground in each observed field. Our analyses clearly indicated that the relationship between the panicle density of weedy rice and number of fallen seeds followed a linear regression of positive correlation (Fig. 4a). The average panicle density and number of seeds were $89 \text{ panicles} \cdot \text{m}^{-2}$ and $145 \text{ seeds} \cdot \text{panicle}^{-1}$, respectively. According to the prediction of the model which described the relationship between the panicle density of weedy rice and number of fallen seeds, the number of fallen seeds would be $4140 \text{ seeds} \cdot \text{m}^{-2}$, indicating that 32% of the seed yield of weedy rice would fall to the field after the harvesting operations were complete.

During harvesting, we observed that some seeds of weedy rice passed through the combine and exited through the straw spreader, while some that adhered to soil in the pedrail fell off with its rolling as the machine advanced, and others that landed onto other parts dropped to the soil with the vibration of the moving combine. In our experiment, the shortest dispersal distance of weedy rice was 14.17 m with the occurrence of $8.8 \text{ panicles} \cdot \text{m}^{-2}$, and the longest dispersal distance was 36.76 m with occurrence of $175.2 \text{ panicles} \cdot \text{m}^{-2}$ that extended 4.17 and 26.76 m from the plant standing region (dyed region), respectively. There was a positive correlation between the panicle density and the dispersal distance (Fig. 4b). Overall, our results indicated that the number of fallen seeds (Fig. 4a) and the dispersal distance of weedy rice seeds depended on the occurrence of weedy rice in the source field (Fig. 4b). For each increase or decrease of 10 weedy rice panicles m^{-2} , the number of fallen seeds and the dispersal distance of the seeds increased by $42 \text{ seeds} \cdot \text{m}^{-2}$ and 0.9 m, respectively.

The tracing experiment showed that the distribution of weedy rice seeds along the harvest trails of two directions

Fig. 4 Panicle density of weedy rice and number of fallen seeds (a), and dispersal distance of fallen seed (b) following harvesting operations. Regression equations are $y = 375.97 + 42.09x$ in (a) and $y = 19.52 + 0.09x$ in (b)

resembled two normal distributions around the plant standing region (dyed region), which was the depression at the overlap of the two peaks (Fig. 5). As a result of harvesting, the weedy rice seeds were dispersed over a range of 60 m and were mostly distributed over a range of 30 m. The number of fallen seeds and the range of the distribution of weedy rice seeds were determined by the occurrence (panicle density) of weedy rice such that the number of fallen seeds and their dispersal distance increased with an increase in the amount of weedy rice harvested. Most of the seeds fell out in the region around where the plant stood, which was caused by the harvesting operation, implying that more serious contamination by weedy rice occurs in nearby regions along the harvest trail.

From above results, on average, approximately 30% of the weedy rice seeds remained in the harvested field, most of which fell far from their mother plants and extended their area of infestation due to the harvest operation. Consequently, over 60% of the weedy rice seeds were carried away from the harvested field in a mixture with the crop grains in the grain tank and on the other three main parts of the machine. These seeds in the grain tank not only contaminated the harvest but could also be an agent of the dispersal of weedy rice during transport or if the grains are used as saved seeds. Moreover, these seeds on the other three main parts of the machine could additionally be spread to other fields. These results convincingly demonstrated that the dispersal of weedy rice was closely related to combine harvesting.

During harvesting operations, the combine harvesting machine allows large numbers of seeds to fall to the ground (Zoschke and Quadranti 2002), thereby facilitating the

population dynamics of weed species (Ballaré et al. 1987; Blanco-Moreno et al. 2003). Our results show that the disseminated amount of weedy rice seeds in the field and the number of fallen seeds and the dispersal distance of weedy rice seeds were positively related to the level of weedy rice infestation. As we observed, weedy rice is similar to many other weeds that exhibit an uneven distribution in fields (Cousens and Croft 2000; Rew and Cousens 2001), which can affect the local survival through density-dependent mortality (Blanco-Moreno et al. 2003). In fact, for many weeds, natural dissemination distances are well below 4 m (Pacala and Silander 1990; Gonzalez-Andujar and Perry 1995), with seeds remaining within a focal point (Ballaré et al. 1987). Our study demonstrated that combines dispersed most of the weedy rice seeds far from the area where the plants grew (beyond 4 m), which could be the result of the movement of the machine, the rolling pedrail, and the propulsion of the straw by the straw chopper; the movement of these seeds might cause the appearance of new foci (Shaw 1994; Wallinga et al. 2002) and spread the weedy rice seed throughout the field, thus aggravating the infestation level and the competitive impact on the crop. Therefore, regions seriously infested by weedy rice within a field should be harvested cautiously and separately. In particular, a combine harvester with chaff collection function should be used to effectively separate mixed weed seeds from straw and prevent from within-field dispersal in severely infested fields (Monjardino et al. 2004; Shirtliffe and Entz 2005).

Fig. 5 Distribution of weedy rice seed in relation to the panicle density of weedy rice along the harvest trails. In this figure, the zero in the horizontal axis is the center of the dyed region. The negative and positive of the horizontal coordinates represent the two directions of harvest trails. Each point presents the density of fallen seed at a certain dispersal distance in relation to the panicle density of combine-harvested weedy rice

4 Conclusion

Our experiment clearly indicated that combine harvesters are a key agent for weedy rice seed dispersal within fields and across rice-growing areas. The combine harvester could indeed carry weedy rice seeds and that the remaining seeds (on the metal plate) could be widely dispersed during subsequent harvesting operations. Combine harvesters could extend the infestation range of weedy rice within a field by dispersing most seeds far from their mother plant. Consequently, farmers should raise general awareness about the dispersal of weedy rice through combine harvest, both in the between- and within-field aspects. Regions seriously infested by weedy rice within a field should be harvested cautiously and separately and chaff collection could be performed during harvesting to reduce the within-field dispersal of weed rice. Seed remaining in a harvester should be avoided by reducing its seed carrying capacity of the equipment or by carefully cleaning it before harvesting in other plots or regions to prevent between-field seed dispersal.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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