A model of the relationship between weedy rice seed-bank dynamics and rice-crop infestation and damage in Jiangsu Province, China

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A model of the relationship between weedy rice seed-bank dynamics and rice-crop infestation and damage in Jiangsu Province, China

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Abstract

BACKGROUND: A heavy infestation of weedy rice leading to no harvested rice has never been predicted in China due to a lack of knowledge about the weedy rice seed bank. We studied the seed-bank dynamics of weedy rice for three consecutive years and analyzed the relationship between seed-bank density and population density in order to predict future weedy rice infestations of direct-seeded rice at six sites along the Yangtze River in Jiangsu Province, China.

RESULTS: The seed-bank density of weedy rice in all six sites displayed an increasing trend with seasonal fluctuations. Weedy rice seeds found in the 0–10 cm soil layer contributed most to seedling emergence. An exponential curve expressed the relationship between cultivated rice yield loss and adult weedy rice density. Based on data collected during the weedy rice life-cycle, a semi-empirical mathematic model was developed that fits well with the experimental data in a way that could be used to predict seed-bank dynamics.

CONCLUSIONS: By integrating the semi-empirical model and the exponential curve, weedy rice infestation levels and crop losses can be predicted based on the seed-bank dynamics so that a practical control can be adopted before rice planting.

Keywords: weedy rice; damage; direct-seeded rice; seed bank; mathematic model; prediction

1 INTRODUCTION

Weedy rice (*Oryza sativa* L.) infests rice fields competing with the crop for nutrients, water and sunlight. Weedy rice generally grows taller and produces more tillers than cultivated rice and effectively reduces crop yield and affects quality.[1,2] Weedy rice seriously infests paddy fields and is widely distributed in rice-planting areas throughout the world, especially where direct seeding and intensive production prevail, particularly in Asia, South and North America, and southern Europe.[3–5] In recent years, weedy rice has become one of the most troublesome weeds in Chinese paddy fields, particularly in Liaoning, Heilongjiang, Jiangsu, Guangdong and Hainan provinces.[6–8]

As an important contaminant in rice seed, weedy rice seeds are hardly removed; therefore, contaminated rice seed ultimately contributes to the introduction of weedy rice into new and infested fields. Sowing rice seed contaminated with weedy rice is most likely a primary factor in weedy rice dissemination.[9,10] Contaminated rice seed may be the reason for the onset weedy rice infestations, but sustained high densities of the weed are likely to arise from a weedy rice seed bank built up of earlier seed shattering by limited weedy rice individuals.[11] Moreover, the shattered seeds can persist in the seed bank in a dormant condition, remaining viable for more than two years,[12] and some can survive for nine years or even more.[13] Many farmers ignore the importance of depleting the seeds in the soil seed bank.[14] Continued seed shattering by weedy rice would increase the size of its seed bank and result in higher population densities accompanying the crop, thus rendering weedy rice control more difficult.[15] Understanding the dynamics of the weedy rice seed bank would allow prediction of weedy rice infestations that could be used by farmers to implement effective control tactics before serious damage occurs.

Weedy rice is difficult to control under the direct-seeded cultivation system using single conventional weed-control methods such as chemical control because weedy rice is conspecific with cultivated rice.[16,17] Although a change from direct-seeded rice to transplanted rice is an effective alternative method to control weedy rice, farmers in Jiangsu Province, China increasingly prefer direct-seeding because it saves labor and costs. Some farmers take no action to remove weedy rice and ignore their associated yield losses in the beginning and continue with conventional cropping practices. However, devastating infestations of weedy rice can ultimately occur with the establishment of a gradually increasing weedy rice seed bank in dry direct-seeded rice fields.[18]

Therefore, cases of severe damage can be prevented if rice transplanting or rotations with upland crops are adopted in combination with herbicide applications before heavy weedy rice infestations occur. We consider that weedy rice infestations can be predicted provided there is a robust knowledge of the status of

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the weedy rice seed bank or the density of the mature weedy rice population in the previous season.

Seed banks play a prominent ecological and evolutionary role in linking past, present and future plant populations, as well as influencing the community structure and dynamics in a given habitat.[19–21] Agronomic research has focused primarily on the characteristics and management of weedy rice and thus limited information is available on its seed-bank dynamics. This is particularly the case for the dry direct-seeding system of rice which is becoming more prevalent in China. Therefore, we decided to build a semi-empirical model to explore the longer term trends in weedy rice seed-bank dynamics based on actual data obtained experimentally in dry direct-seeded rice fields.

The semi-empirical model is a mathematical representation that involves solving the relevant equation(s) of a system and describes complex processes and provides better understanding of real mechanism through some reasonable simplification. To determine the appropriate value of its parameters, a model should be tested experimentally and adjusted accordingly. There have been some semi-empirical models of different plant seed banks including *Brassica napus*, *Alopecurus myosuroides* and other weeds.[22–25]

These models were developed for different purposes, but all were derived from the annual life-cycle of the plants. Vidotto *et al*.[26] developed a semi-empirical model to study the population dynamics of weedy rice in relation to its seed bank. The model had relatively simple calculations and was easy to use. Using the model, they predicted the emergence of weedy rice under different tillage operations in a stale seedbed with flooded or saturated soil.

We report here our research on weedy rice and its seed bank in dry direct-seeded rice fields under no-till or shallow tillage conditions at four times during the cropping cycle to cover the most important growth stages of its life-cycle. We combined the seed bank and weedy rice population descriptors in the model and calculated the cultivated rice-yield loss caused by the weedy rice infestation based on the seed bank to gain further insight into the weedy rice problem and to better integrate weedy rice management practices.

Our objectives were to: (1) characterize weedy rice growth dynamics in Jiangsu Province, China; (2) determine the relationship between the weedy rice seed bank and seedling emergence in direct-seeded rice fields; and (3) build a simple deterministic mathematical model according to the life-cycle of weedy rice for predicting the seed bank reservoir, weedy rice occurrence and its possible damage to rice production.

2 MATERIALS AND METHODS

2.1 Sampling sites

This study was carried out from 2009 to 2011 in dry direct-seeded commercial rice fields in six counties (Yizheng, Yanghzou, Jingjiang, Changzhou, Haimen and Yixing) located in central and southern Jiangsu Province along the Yangtze River, where there is a long history of rice–wheat double cropping system with more than five years of direct-seeded rice cultivation and a previously recognized serious infestation of weedy rice.

The fields, ranging in area between 760 and 1250 m^2, shared cropping patterns, tillage practices and soil types, but differed in their level of weedy rice infestations (Table 1). Every year, after wheat harvest, the fields were flattened by harrowing and then the rice seeds were sown manually onto the soil surface at a seedling rate of 60 kg ha^{-1}. The first irrigation was carried out after seeding (if there was no rain). After rice harvest, wheat seeds were sown directly onto the soil surface without tillage at a seeding rate of 150 kg ha^{-1}. The soil in these selected fields was classified as Magan soil, medium-loamy.

2.2 Seed bank and aboveground vegetation sampling

Soil samples were collected twice a year, in May and in October, from 2009 to 2011, for a total of six samples per site. Samples taken in May, before crop sowing and weedy rice germination allowed us to assess the persistent part of the weedy rice seed bank. Samples collected in October, right after crop harvest, were used to assess the contribution of weedy rice seed shattering to the seed bank.

Aboveground surveys of weedy rice emergence were conducted during July every year, about one month after the germination of direct-seeded rice. In Jiangsu Province, weedy rice usually has amaranthine leaf ring and auricle and brown basilar stalks, seedlings produce more tillers at greater angles and are taller but with a looser plant type than cultivated rice. Weedy rice densities were determined in September at crop maturity.

To systematically collect samples, each commercial field was divided into 25 uniform-size grid plots. Fifty soil cores of 2.5 cm diameter by 15 cm depth were randomly taken at each sampling date in each grid plot (for a total of 1250 cores per farm) and manually divided into three depth categories (0–5, 5–10 and 10–15 cm). The 50 subsamples of each soil depth were homogenized into a composite sample representing a total area of 0.025 m^2 (volume = 750 cm^3). Seeds were extracted from each composite subsample with running water over a wire sieve (2-mm

Table 1. The geographical coordinates, cultivated rice varieties, areas, cultivation histories and herbicide applications of the six sampling sites

Locations	Location	Rice cultivar	Sampling area (m^2)	Estimated weedy rice infestation[a]	Years of dry direct-seeding	Weedy rice control practice
Yizheng city (town of Xinji)	39° 19′ 33″ N, 119° 17′ 34″ E	Wuyunjin-7	760	3	7	Manual removal
Haimen city (Jiangxinsha farm)	31° 48′ 28″ N, 121° 05′ 32″ E	Wuyunjin-95	1250	2	6	Manual removal
Jingjiang city (town of Haiwei)	32° 04′ 03″ N, 120° 19′ 48″ E	Ningjing-3	910	4	6	Manual removal
Changzhou city (town of Menghe)	32° 00′ 48″ N, 119° 51′ 44″ E	Wuyunjin-95	800	3	7	Manual removal
Yixing city (town of Xinjie)	31° 21′ 59″ N, 119° 46′ 01″ E	Changyou-1	840	1	5	Manual removal
Yangzhou city (town of Chahe)	32° 20′ 23″ N, 119° 21′ 54″ E	Fengyouxiangzhan	750	5	8	None

[a] The level of weedy rice infestation is a visual estimate on a seven-class scale (synthesizing the abundance, height and coverage) at 30 days after planting.[27]

mesh). Once dried at ambient temperature, intact seeds were counted (broken ones were discarded). Long flat grains were weedy rice; those that were short and round were designated as cultivated rice seeds. Weedy rice density determinations at seedling stage and maturity were carried out in five 1-m^2 quadrats per grid plot (for a total of 125 quadrats per commercial field). Additionally, 50 weedy and cultivated rice plants each plot were selected during the survey of weedy rice density in September to determine tiller number, spikelet number per panicle, seed setting rate, and 1000-grain weight.

3 FIELD DATA ANALYSES

Data ($\log_{10}$ and square-root transformed if required) were analyzed using SPSS 16.0 software (SPSS Inc. Chicago, IL, USA).

Correlation analysis was used to determine the correlation coefficient between weedy rice seedling emergence and soil seed-bank density at different soil depths. Likewise, the relationship between weedy rice seedling emergence and soil seed-bank density was examined using linear regression. The relationship between weedy rice density and cultivated rice yield loss was assessed using an exponential function. A one-way analysis of variance (ANOVA) was used to distinguish between weedy rice seed-bank densities at different soil depths and at different times ($p \leq 0.05$). The theoretical cultivated rice yield was calculated from field data and its relation to weedy rice density at maturity was examined using nonlinear regression.

4 BUILDING A MODEL FOR WEEDY RICE SEED BANK DYNAMICS

Vidotto *et al.*[26] developed a model for weedy rice population dynamics in relation to its seed bank, but the results obtained had some discrepancies between the estimated and observed seedling emergence. In order to develop a model more applicable to our conditions, we synthesized information and modified models and parameters previously applied to study the population dynamics of weedy rice and other weeds.[22–26] The modified parameters such as the reproductive capacity were not considered to be fixed but density-dependent, the shattering rate and overwintering survival proportion was recalculated and the control efficacy was addressed based on local practices.

The proportion (g) of weedy rice seeds in the seed bank that germinated in any year was assumed to be the same. Only a proportion (d, for dormancy) of the seeds in both the seed bank and those newly produced in year t will survive to year $t+1$ (because of predation and decay) thus the seed-bank density in year $t+1$ is given by

$$S_{t+1} = d\,(1-g)\,S_t + dV_t \tag{1}$$

where S_t is the initial (May of year t) weedy rice density in the seed bank, d is the proportion of seeds developing dormancy in year t and successfully overwintering to year $t+1$, V_t is the number of newly shattered weedy rice seeds in year t, and g is the proportion of seeds in the soil seed bank that germinate in any year.

The density of newly shattered seeds from weedy rice is

$$V_t = M_t \cdot \mu \cdot Z_t \tag{2}$$

where M_t is the density of weedy rice in the population (plants m^{-2}), μ is the shattering rate of mature plants and Z_t is the number of seeds produced per plant (seeds $plant^{-1}$).

According to our study, only a proportion (p) of seedlings (E) may be expected to survive and become mature plants because of competition as expressed by

$$M_t = p \cdot E_t \tag{3}$$

$$E_t = g \cdot S_t \tag{4}$$

Seedlings compete for nutrients, light and water; therefore, the density of adult plants will be dependent on the seedling density.[28] The proportion that survives is assumed to be a function of seedling density, according to our own work (unpublished observations) and that of Watkinson[41] for *Agrostemma githago*, such that

$$p = \frac{1}{1+\alpha E_t} \tag{5}$$

where α is the reciprocal of the asymptotic value of E.

Weed-control practices, including hand removal, decrease the survival rate of seedlings, thus η is used to represent a decline in the proportion of seedlings that reach maturity.

Therefore, the expected number of mature weedy rice plants in year t is given by

$$M_t = \frac{E_t}{1+\alpha E_t} \cdot (1-\eta) \tag{6}$$

Because of intraspecific (weedy rice) competition, the fecundity per weedy rice plant (Z) is dependent on the number of surviving mature plants (M). Z at year t is described by the following relationship:

$$Z_t = \frac{Z_{\max}}{1+\beta \cdot M_t} \tag{7}$$

where $Z_{\max}$ is maximum seed production per weedy rice plant when grown in isolation, β is an approximate coefficient which represents the degree to which fecundity is reduced by the density dependent effects.

5 RESULTS

5.1 Seed-bank structure and dynamics

Seed-bank densities at a 0–5 cm soil depth were higher ($p \leq 0.05$) than those at 5–10 and 10–15 cm at most of the six sites and three years (Table 2). Seventy percent of the weedy rice seeds were in the top 0–10 cm soil layer; the 10–15 cm soil depth held only ~30% of the weedy rice seeds. In comparing the data from the three years, we found that the seed-bank density at the 0–5 cm soil depth in all six sites increased more rapidly than that at the other depths. The seed-bank density of weedy rice at the 10–15 cm changed only slightly over the three-year period. The seed-bank density in Haimen had the greatest increase over time; particularly at 0–5 cm depth with a more-than-five times increment compared with 5–10 cm in which the density doubled in those three years. Although the Yangzhou sample exhibited the highest initial seed-bank density of 414 seeds m^{-2} at 0–5 cm and 760 seeds m^{-2} at the end of the experiment (Table 2), its rate of increase was the lowest.

Table 2. Weedy rice seed-bank densities at three different soil depths in six surveyed locations over three years

		Weedy rice seed-bank densities (seeds m^{-2})					
Year	Soil depth (cm)	Yizheng	Haimen	Jingjiang	Changzhou	Yixing	Yangzhou
2009	0–5	139.2 a	89.6 ab	193.6 a	97.6 a	52.8 a	414.4 a
	5–10	80.0 b	104.0 a	169.6 a	83.2 a	41.6 ab	254.4 b
	10–15	57.6 b	68.8 b	54.4 b	91.2 a	33.6 b	225.6 b
2010	0–5	232.0 a	248.0 a	262.4 a	244.8 a	83.2 a	593.6 a
	5–10	107.2 b	142.4 b	177.6 b	172.8 b	52.8 b	305.6 b
	10–15	64.0 c	88.0 c	166.4 b	107.2 c	57.6 b	273.6 b
2011	0–5	380.8 a	558.4 a	627.2 a	464.0 a	280.0 a	760.0 a
	5–10	182.4 b	188.8 b	222.4 b	212.8 b	155.2 b	312.0 b
	10–15	132.8 c	91.2 c	171.2 c	161.6 c	86.4 c	217.6 c

Means within a location and year followed different lowercase letters are significantly difference at $p \leq 0.05$ among soil depths based on an F-LSD test.

The lowest seed-bank density at 0–10 cm soil depth was in Yixing with ∼ 100 seeds m^{-2} in May 2009 and 300 seeds m^{-2} in May 2011.

Total seed-bank densities (0–15 cm soil depth) underwent a 'rise–decline–rise–decline' process at all field sites (Fig. 1). The seed-bank density increased dramatically in October of each year because of the contribution of newly shattered weedy rice seed. The seed-bank density decreased significantly, as an average of three years, by >70% the next May in comparison with October of the previous year. However, the reservoir of weedy rice in the seed bank during May, before seed germination, displayed an annual upward trend. The greatest weedy rice seed-bank density in May, of ∼ 1072 seeds m^{-2}, was found in 2011 at the site in Yangzhou. Six months later, the seed-bank density decreased because some of the seeds were depleted through various factors not quantified in this work.

Rates of increase in the seed-bank density of weedy rice varied among locations (Fig. 1). These differences are probably related to differences in agricultural practices, particularly weedy rice control and biological aspects such as germination and shattering rates at different locations.

5.2 Seedling emergence as related to the seed bank

Based on a correlation analysis, it was determined that pooling the densities at 0–5 and 5–10 cm was more suitable for assessing the relationship between the seed bank and seedling recruitment than using the discrete depths (there was no correlation between the 10–15 cm soil depth and seedling emergence), and such a relationship was studied using the seed-bank densities at 0–10 cm.

We also consolidated the data on seedling emergence for the three years before performing a linear regression analysis. The results indicated that there was no significant difference in the slope of the line at the same site among different years when we used the data from three separate years to form the linear regression; therefore, germination probability could be treated as a constant.

There was a clear linear relationship ($p \leq 0.05$) between seed-bank density at 0–10 cm and weedy rice seedling emergence at all sampling sites, but with different slopes (Fig. 2). The fitted line was steepest in Yangzhou, which had the highest seedling emergence rate in the field investigation and the slope was shallowest in Yixing, which had the lowest seedling emergence rate.

5.3 Rice yield loss caused by weedy rice

We used the exponential function to fit the weedy rice density at maturity to the yield loss of cultivated rice (Fig. 3). As expected, crop-yield loss increased with increments in weedy rice density. Based on the established relationship, a weedy rice density of 6 plants m^{-2} would reduce rice crop yield by 20%, 30 plants m^{-2} by would reduce yield by 50%, and 80 plants m^{-2} would reduce yield by as much as 90%.

5.4 Model simulations

Based on its components (Eqns 1–7), the complete model formula for the weedy rice seed bank is:

$$S_{t+1} = d\,(1-g)\,S_t + d\mu\,(1-\eta)\,\frac{gS_t}{1+\alpha gS_t} * \frac{Z_{\max}}{1+\frac{\beta gS_t}{1+\alpha gS_t}\,(1-\eta)} \tag{8}$$

Density of mature plants (M_t) can be described by the following equation that is one of the components of the model:

$$M_t = \frac{gS_t}{1+\alpha gS_t}\cdot(1-\eta) \tag{9}$$

Solving Eqn (8) requires the specification of initial values, including S_t at time $t = 0$ (2009), and values for the seven parameters $d, g, \alpha, \beta, \mu, \eta$ and $Z_{\max}$.

The seed bank of weedy rice in our experiments was divided into three layers: 0–5, 5–10 and 10–15 cm. Almost all weedy rice seedlings emerged from seeds at the 0–10 cm soil seed bank; therefore, we used the seed bank at the 0–10 cm soil depth as parameter S.

Because germination rates, survival proportions and shattering rates changed little among years at each specific site, we estimate that assumptions about the modified value of these parameters were credible. The average overwinter mortality of weedy rice seeds from 2009 to 2011 ranged from 79 to 89%, whereas the proportion of seed survival was ∼ 11–21%. Our experiments showed that only a few weedy rice seeds emerged, with the emergence rate ranging from 2.6 to 11.4% of the overwintering seed bank.

Control efficacy η can be calculated from the experimental data on weedy rice seedling and mature plant densities. Given the absence of selective herbicides to control weedy rice in rice and

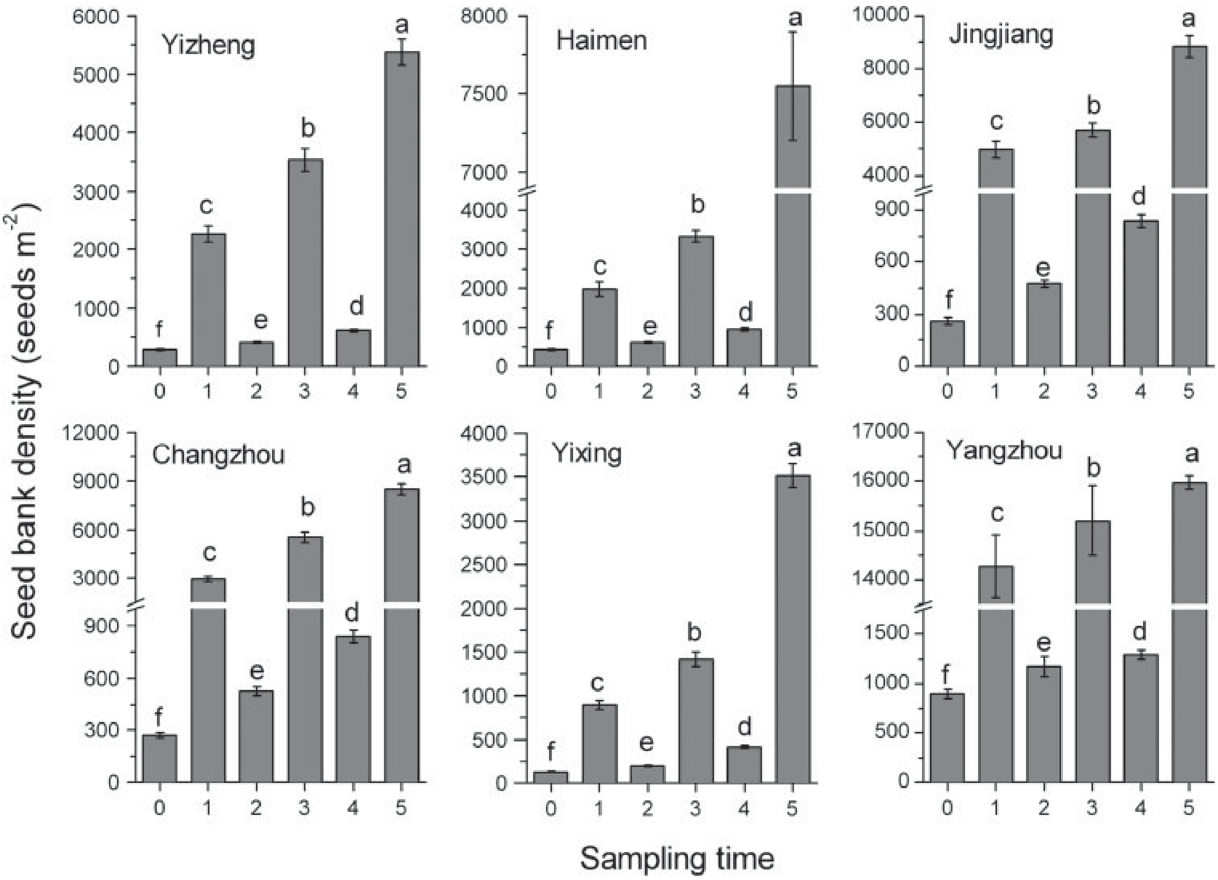

Figure 1. Seed-bank density (0–15 cm soil depth) of weedy rice at six different times and sampling sites. 0, 2 and 4 represent the densities in May 2009, 2010 and 2011, respectively; 1, 3 and 5 represent the densities in October 2009, 2010 and 2011, respectively. Bars indicate $\pm$1 SE ($n = 25$). Different lowercase letters indicate significantly different densities at $p \leq 0.05$ among the sampling dates based on F-LSD tests.

the limited efficacy of the few practices implemented by farmers, the value of parameter η is low, ranging from 0 to 0.29 in the six different sampling sites (Table 3).

Z_{max} represents the maximum seed production per weedy rice plant when grown in isolation, and its value was also derived from the experimental data. However, the fecundity of weedy rice showed changes due to fluctuations in the density of the species. High population density would lead to a reduction in weedy rice fecundity through intraspecific competition. So in the model, Z (seed production per plant) decreases as M (weedy rice density) increases. We used Eqn (7) to estimate Z. In Eqn (7), β is the approximate coefficient which represents the degree to which fecundity is reduced by density-dependent effects.

From the model above (Eqn 8), we found that the increase in seed survival contributed most to the rise in seed-bank density. The seed germination rate has a positive effect on the increase in seed-bank density at the end of the season. However, increasing the control efficacy leads to a decrease in seed-bank density. The initial value of the seed-bank density in year t (2009) is shown in Table 2.

The semi-empirical model predicted quite well the size of the seed bank in the succeeding two years (2010 and 2011) using the data from the first year (2009), although the regression function indicated a slight overestimation that we consider acceptable (Fig. 4).

The values of all parameters (d, g, α, β, μ, η and Z_{max}) at the six sampling sites were used in the means (Table 4), which can be considered to be representative of ordinary infestation conditions. The average seed-bank density of the six sampling sites at the first observation was assumed to be the initial value of the seed-bank density. The weedy rice seed-bank density before or after the initial year can be deduced using the model presented above (Eqn 8). The weedy rice occurrence (seedling emergence and adult plants) can be deduced when the seed bank reservoir is known. As a result, rice-yield losses were calculated using the exponential curve in Fig. 3.

An initial weedy rice density of 287 seeds m^{-2} would result in 10.8 individuals m^{-2}, responsible for a 28% crop-yield loss. Three years before, the seed-bank density could be deduced to have been only 12 seeds m^{-2}, and the few resulting weedy rice individuals that could cause damage to rice production would be negligible. One year before the seed bank reservoir would have reached 104 seeds m^{-2} and produced $\sim$4 plants m^{-2}, that would cause a 16% rice-yield loss. After three years, we predicted that the seed-bank density could have reached 2043 seeds m^{-2}, and $\sim$61 plants m^{-2} would grow and compete with cultivated rice, causing a yield loss of $\sim$80%. (Table 4)

6 DISCUSSION

6.1 The structure and dynamics of the weedy rice seed bank

Seed banks act as a reservoir for plant propagules and provide a constant source of weeds that enables their continuous appearance in the field.[29–31] The vertical distribution of the seed

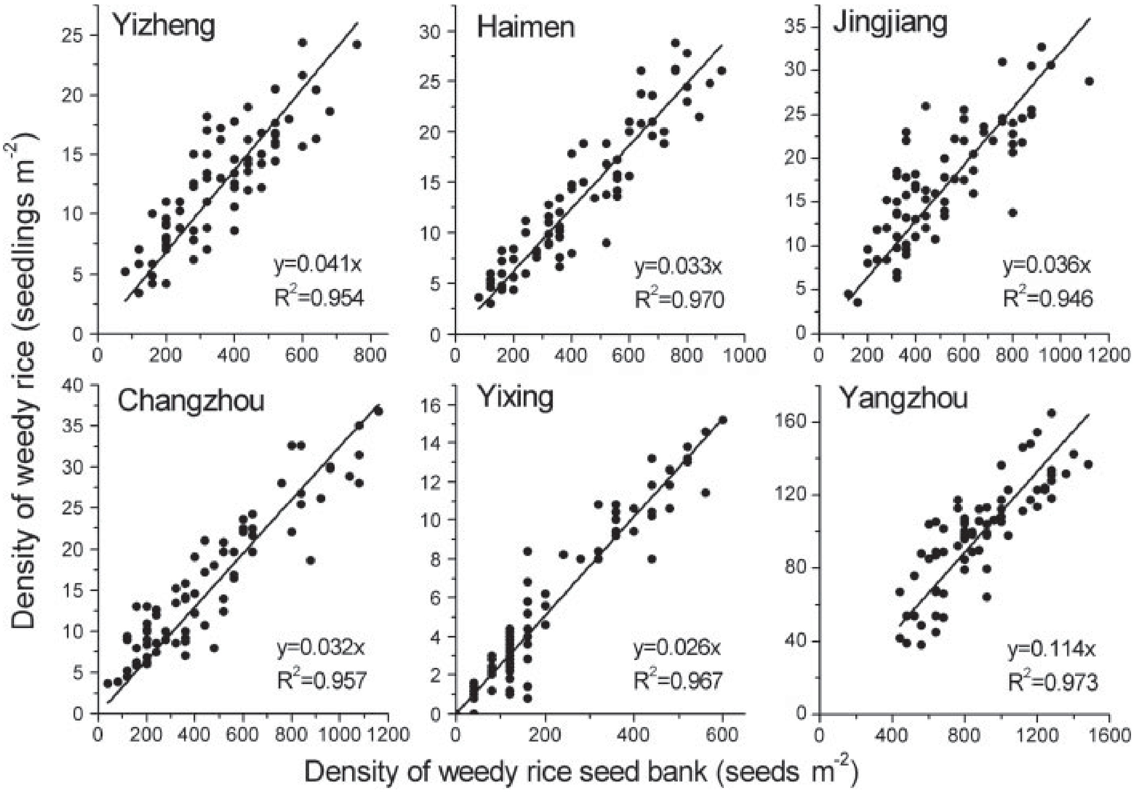

Figure 2. Relationship between soil seed bank of weedy rice (0–10 cm depth averaged over the three years of the study) and weedy rice seedling density at six sampling sites. Each symbol represents the average weedy rice density in one grid. R^2 is the adjusted R square. Seed bank data for 10–15 cm depth excluded from the analysis.

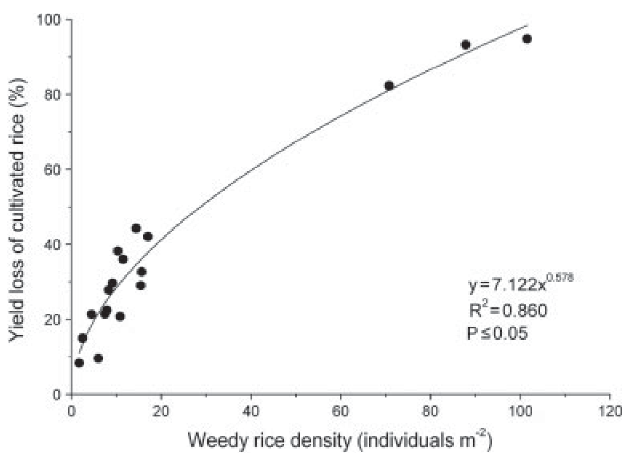

Figure 3. Relationship between weedy rice density at maturity and yield loss of cultivated rice. R^2 is the adjusted R square.

within the seed bank can be affected by cropping pattern, tillage practice and soil type.[32–34] In dry direct-seeded rice fields with rice–wheat rotation in Jiangsu Province, China, shallow tillage is generally conducted a few days after rice harvest but before wheat sowing; therefore, most of the newly shattered (>70%) weedy rice seeds could be buried in the upper soil layer enriching an active seed bank (0–10 cm) in which seeds could germinate during the next spring. These seeds contributes most to heavy weedy rice infestations, and a small part (∼ 30%; Fig. 1) was incorporated into the deeper soil layer (10–15 cm) and formed the potential seed bank where seeds remain dormant for future germination.

Monitoring changes in the weedy rice seed bank over a three-year period provided us with insight into the efficiency of applied measures to weed control and to predict its infestation in periods to come.

6.2 Analysis of the variables in the model

Vidotto *et al*.[26] developed a semi-empirical model based on the seed bank to describe the population dynamics of weedy rice. Their model was not intended to predict weedy rice dynamics under no-till conditions and because of its theoretical bases it was important to test it with actual data. Additionally, model estimations were not particularly reliable under no-till conditions; thus, the model was not as appropriate for dry direct-seeded rice fields. This motivated us to advance a semi-empirical mathematical model to study the seed-bank dynamics of weedy rice under no-tillage conditions over three years at fields in six locations. Furthermore, the present model can be used to predict weedy rice infestations and rice-yield losses based on the seed-bank dynamics of the previous year. The main input variables of our model included the shattering rate, seed overwinter survival proportion, germination rate, control efficacy and fecundity. Values of all parameters were obtained from the three-year survey in dry direct-seeded rice fields under no or shallow tillage.

The cumulative shattered weedy rice seeds and the newly shed seeds during rice harvest provided the greatest input of weedy rice into the seed bank and contributed to the build up of the seed bank. The shattering rate of weedy rice ranged from 0.34 to 0.55 and increased the seed bank in autumn to thousands of seeds per m^2. But only a small portion of newly shattered seeds persists in the seed bank to the following year to start a new generation.

Table 3. Parameter values and the initial conditions in year t ($t = 2009$)

Location	d	g	α	β	μ	η	Z_{max} (seeds plant^{-1})	S_t (seeds m^{-2})	E_t (plants m^{-2})	M_t (plants m^{-2})	Z_t (seeds plat^{-2})	V_t (plants m^{-2})
Yizheng	0.15	0.041	0.002	0.015	0.34	0.10	930	219.2	9.0	7.9	831	494
Haimen	0.13	0.033	0.004	0.018	0.48	0.27	1260	193.6	6.3	4.5	1165	725
Jingjiang	0.21	0.036	0.003	0.014	0.36	0.28	1290	363.2	13.2	9.2	1143	871
Changzhou	0.20	0.044	0.005	0.017	0.55	0.21	1040	180.8	7.9	6.0	944	626
Yixing	0.11	0.026	0.004	0.012	0.43	0.29	950	94.4	2.4	1.7	931	369
Yangzhou	0.15	0.114	0.001	0.016	0.34	0.00	1020	668.8	76.2	70.8	489	2028

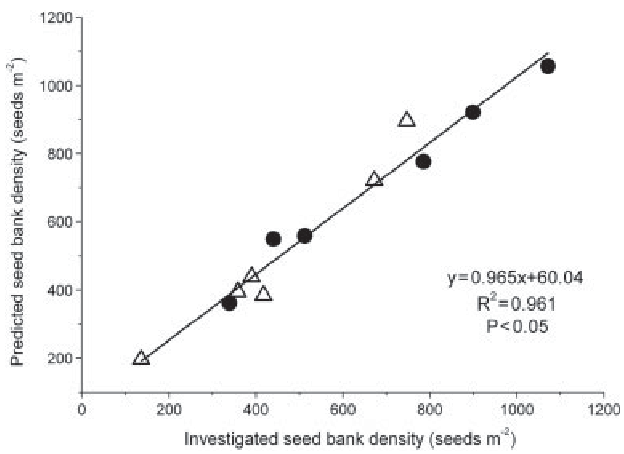

Figure 4. Size of the weedy rice seed bank as predicted by the model using initial data from 2009 vs. data collected during 2010 and 2011. •, data from 2011; △, data from 2010. The regression line represents a match between predicted and actual data from all six sampling sites.

The proportion of weedy rice seeds surviving over winter was 0.11–0.21 because the seeds must have been exposed to a number of mortality factors. Seed mortality is usually associated with ageing, predation by insects and vertebrates, bacterial and fungal decay, and physical damage by agricultural implements.[35] In addition, when the field is under no- or shallow tillage conditions, most seeds concentrate near the soil surface allowing for greater weed seedling emergence with corresponding seed bank depletion.[36]

The germination of seeds from the seed bank can significantly alter the dynamics of adult populations.[25] In laboratory tests, ~30% of the persisting full weedy rice seeds obtained in the soil cores germinated, and about half of the non-germinating seeds were alive according to the tetrazolium test (unpublished data). However, in the field, the germination rate of dormant seed was much lower. Although the total germination rate identified in our field experiments was low, ranging from 0.033 to 0.114, it was enough to cause serious weedy rice infestations when the seed bank (at 0–10 cm) density is not so low. Moreover, because no-tillage or only shallow tillage is conducted in direct-seeding fields before rice seed is broadcasted, most newly shattered seeds remain near the soil surface and are not buried deep in the soil profile constituting a large, but transient active, seed bank that that would be rapidly depleted by external factors as mentioned above.

Density dependence refers to the way in which growth, mortality and fecundity schedules change with fluctuations in the density of a species.[37] Over-compensating density dependence refers to a situation in which high population densities lead to reductions in growth, mortality or fecundity through intraspecific competition. The present results and those from other studies show that plant growth is affected by the density of seedlings because of a competition for resources,[38–40] which justifies inclusion of the density-dependent equation in the semi-empirical model to predict adult weedy rice density. The fecundity of weedy rice individuals was also density-dependent, as found in the present study and with the density increasing yearly, the seed set rate of each weedy rice individual decreased.

The control efficacy was negligible in all six sampling sites, ranging from 0 to 30%. Under a direct-seeded rice system, an efficient herbicide is not available to control weedy rice without injuring cultivated rice as a result of their similar physiological and morphological traits. Manual control was not effective because farmers could not distinguish weedy rice seedlings from those of the crop, as is the case elsewhere.[16]

With the adjusted parameter values, the model estimated the weedy rice seed bank reasonably well at different surveyed sites. Hence, we suggest that the model could be used with caution as a predictive tool. To improve it for use as a predictive tool, the model should be subjected to further evaluation with data from different environmental conditions and different years.

6.3 Use of the model and control practices

Weedy rice reduces rice grain yield through interference with the growth of cultivated rice, with the degree of loss depending on the infestation level, duration of interference and crop management.[15] The model developed for the prevailing cropping system in Jiangsu province predicts that continuous dry direct-seeded rice cultivation without tillage or with shallow tillage before rice planting will cause a rapid and harmful increase of weedy rice density given that in-crop control measurements are practically ineffective. If the weedy rice infestation level can be predicted when infestation just begins and is not yet serious, farmers would be able to take effective measures to control the weedy rice and maintain profitability. The model we developed provides a predictive tool, with a simple output (similar to Table 4) can be alert farmers if potential yield loss when the seed-bank density or the weedy rice density is low enough to be manipulated.

Crop rotation can play an important role in weedy rice management. A change from direct-seeding to mechanical transplanting as a form of rotation while growing the same crop would allow the adoption and integration of alternative control measurements, including water suppression of weed growth. Maintenance of a 3–5 cm deep water table is required during transplanting, which can suppress weedy rice emergence from the seed bank.[41,42] It would be interesting to use the model to predict the impact of this rotations on the basis of actual data from

Table 4. Predicated weedy rice seed-bank densities and crop yield losses

Parameters value (mean value of the six samples)	Year before or after	Seed-bank density (seeds m^{-2})	Weed rice density at maturity (individuals m^{-2})	Yield loss (%)
$d = 0.150$,	−3	12	0.5	4.4
$g = 0.049$,	−2	36	1.4	8.4
$\alpha = 0.003$,	−1	104	4.0	15.6
$\beta = 0.015$,	0	287	10.8	28.0
$\mu = 0.430$,	1	692	24.7	45.4
$\eta = 0.192$,	2	1354	44.3	64.1
$Z_{max} = 1081$	3	2043	61.4	77.7
	4	2512	71.5	85.1
	5	2757	76.4	88.5

0, the initial year we assumed; −,year before the initial year.

commercial fields. In practice, the integration of chemical control and water suppression before rice transplanting can provide effective control of weedy rice.

We corroborated that the majority of weedy rice seedlings that emerge from the seed bank at 0–10 cm soil depth. The key to controlling weedy rice emergence is to deplete the weedy rice seed bank at a depth of 0–10 cm. Agricultural practices can play a major role in weedy rice control.[43] For example, tillage operations can have an impact on the distribution of weed seeds in the soil and on seed survival.[44] The emergence of weedy rice seedlings in relation to the 0–10 cm seed bank is highly influenced by the type of tillage.[45] Deep or moldboard plowing can be used before sowing rice to reduce the active seed-bank density near the soil surface (0–10 cm) as a temporary measure, which in turn reduces weedy rice emergence the growing season. However, the long-term effects of inverting the soil should be carefully considered as part of the integrated strategies to manage weedy rice.

For small-scale farming, manual removal of weedy rice plants at the booting to flowering stages is also an alternative to limit the contamination of rice grain with weedy rice seeds and reduces the number of seeds dropped into the soil seed bank.[42] Rotation rice with upland crops, as a good integrated method to control weedy rice, is also recommended,[46] making it easy to use chemical herbicides which can kill weedy rice in the rotation crop.

The model we developed can be used to increase the awareness of rice farmers about weedy rice problems and to provide them about the methods they could implement at appropriate times to ensure rice production, minimize economic losses and reduce labor intensity.

7 FINAL REMARKS

Early maturity and easy shattering of weedy rice seeds enrich the soil seed bank, which is the main source of weedy rice infestation in rice field the next season. Intense and prolonged dormancy maintains the seed viability of weedy rice during adverse climate conditions between harvest and the next planting season, even in the long term. The model we developed described the dynamics of the seed bank and estimated the damage caused by weedy rice after the slight initial infestation. Using this model, farmers would become aware about the potential damage caused by weedy rice at early stages of infestation in their field allowing them to adopt appropriate and effective measures to control it and prevent seed rain into the seed bank.

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REFERENCES

1 Diarra A, Smith RJ and Talbert RE, Growth and morphological characteristics of red rice (*Oryza sativa*) biotypes. *Weed Sci* **33**:310–314 (1985).
2 Ottis BV, Smith KL, Scott RC and Talbert RE, Rice yield and quality as affected by cultivar and red rice (*Oryza sativa*) density. *Weed Sci* **53**:499–504 (2005).
3 Ferrero A, Vidotto F, Balsari P and Airoldi G, Mechanical and chemical control of red rice (*Oryza sativa* L.var. sylvatica) in rice (*Oryza sativa* L.) pre-planting. *Crop Prot* **18**:245–251 (1999).
4 Noldin JA, Red rice status and management in Americas, in *Wild and Weedy Rice in Rice Ecosystems in Asia – a Review*, Limited Proceedings No. 2, ed. by Baki BB, Chin DV and Mortimer M. International Rice Research Institute, Los Baños, Philippines, pp. 21–24 (2000).
5 Bres-Patry C, Lorieux M, Clement G, Bangratz M and Ghesquiere A, Heredity and genetic mapping of domestication-related traits in a temperate japonica weedy rice. *Theor Appl Genet* **102**:118–126 (2001).
6 Yu GQ, Bao Y, Shi CH, Dong CQ and Ge S. Genetic diversity and population differentiation of Liaoning weedy rice detected by RAPD and SSR markers. *Biochem Genet* **43**:261–270 (2005).
7 Cao QJ, Lu BR, Xia H, Rong J, Sala F, Spada A and Grassi F, Genetic diversity and origin of weedy rice (*Oryza sativa* f. spontanea) populations found in north-eastern China revealed by simple sequence repeat (SSR) markers. *Ann Bot* **98**:1241–1252 (2006).
8 Liang DY, Qiang S, Zhang SM and Shen GH, Occurrence of weedy rice in paddy fields became more serious and threats to rice production. *China Plant Prot* **29**:38–39 (2009) (in Chinese).
9 Ma DR, Chen WF, Xu ZJ and Zhang WZ, Origin and control measurement of weedy rice in Liaoning. *Chin Agr Sci Bull* **21**:358–360 (2005) (in Chinese).
10 Valverde BE, The damage by weedy rice-can feral rice remain undetected?, in *Crop Ferality and Volunteerism*, ed. by Gresse IJ. CRC Press, Boca Raton, FL, pp. 279–294 (2005).
11 Diarra A, Smith RJ and Talbert RE, Interference of red rice (*Oryza sativa*) with rice (*O. sativa*). *Weed Sci* **33**:644–649 (1985).
12 Cohn MA and Hughes JA. Seed dormancy in red rice (*Oryza sativa*). *I. Effect of temperature on dry-after ripening*. *Weed Sci* **29**:402–404 (1981).
13 Smith RJ, Control of red rice (*Oryza sativa*) in water seeded rice (*O. sativa*). *Weed Sci* **29**:663–666 (1981).
14 Delouche JC, Burgos NR, Gealy DR, de San Martin GZ, Labrada R, Larinde M, et al, *Weedy Rices – Origin, Biology, Ecology and control*. FAO Plant Production and Protection Paper 188. FAO, Rome, 122 pp. (2007).
15 Mortimer M, Pandey S and Piggin C, Weedy rice in Sri Lanka, in *Wild and Weedy Rice in Rice Ecosystems in Asia – a Review*, Limited Proceedings No. 2, ed. by Baki BB, Chin DV and Mortimer M. International Rice Research Institute, Los Baños, Philippines, pp. 79–82 (2000).
16 Luis AA, Scott AS, Garry NM, James MC and John HO, Effect of flood timing on red rice (*Oryza* spp.) control with imazethapyr applied at different dry-seeded rice growth stages. *Weed Technol* **19**:476–480 (2005).
17 Gressel J and Valverde BE, A strategy to provide long-term control of weedy rice while mitigating herbicide resistance transgene flow, and its potential use for other crops with related weeds. *Pest Manag Sci* **65**:723–731 (2009).
18 Xie XD, Zhou YJ, Lu YL, Zhang H, Cheng LJ and Yu LQ, Survey of weedy rice with dark brown chaff in the soil seeds bank in Jiangdu, Jiangsu Province. *Weed Sci* **30**:34–36 (2012) (in Chinese).

19 Thompson K and Grime JP, Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J Ecol* **67**:893–921 (1979).
20 Roberts HA, Seed banks in soils. *Adv App Biol* **6**:1–55 (1981).
21 Parker VT, Simpson RL and Leck MA, Pattern and process in the dynamics of seed banks, in *Ecology of Soil Seed Banks*, ed. By Leck MA, Parker VT and Simpson RL. Academic Press, San Diego, pp. 367–384 (1981).
22 Macdonald N, Models of an annual plant population with a seedbank. *J Theor Biol* **93**:643–553 (1981).
23 Doyle CJ, Cousens R and Moss SR, A model of the economics of controlling *Alopecurus myosuroides* Huds. in winter wheat. *Crop Prot* **5**:143–150 (1986).
24 Mistro DC, Rodrigues LAD and Schmid AB, A mathematical model for dispersal of an annual plant population with a seed bank. *Ecol Mod* **188**:52–61 (2005).
25 Pekrun C, Lane PW and Lutman PJW, Modelling seedbank dynamics of volunteer oilseed rape (*Brassica napus*). *Agr Syst* **84**:1–20 (2005).
26 Vidotto F, Ferrero A and Ducco G, A mathematical model to predict the population dynamics of *Oryza sativa* var. sylvatica. *Weed Res* **41**:407–420 (2001).
27 Qiang S, Multivariate analysis, description, and ecological interpretation of weed vegetation in the summer crop fields of Anhui Province, *China. J Integr Plant Biol* **47**:1193–1210 (2005).
28 Andersen M, Properties of some density-dependent integro-difference equation population models. *Math Biosci* **104**:135–157 (1991).
29 Boutsalis P and Powles SB, Seedbank characteristics of herbicide-resistant and susceptible *Sisymbrium orientale*. *Weed Res* **38**:389–395 (1998).
30 Sester M, Dürr C, Darmency H and Colbach N, Evolution of weed beet (*Beta vulgaris* L.) seed bank: quantification of seed survival, dormancy, germination and pre-emergence growth. *Eur J Agron* **24**:19–25 (2006).
31 Clemente AS, Rego FC and Correia OA. Seed bank dynamics of two obligate seeders, *Cistus monspeliensis* and *Rosmarinus officinalis*, in relation to time since fire. *Plant Ecol* **190**:175–188 (2007).
32 Staricka JA, Burford PM, Allmaras RR and Nelson WW, Tracing the vertical distribution of simulated shattered seeds as related to tillage. *Agron J* **82**:1131–1134 (1990).
33 Clements DR, Benoit DL, Murphy SD and Swanton CJ, Tillage effects on weed seed return and seedbank composition. *Weed Sci* **44**:314–322 (1996).
34 Vanasse A and Leroux GD, Floristic diversity, size, and vertical distribution of the weed seedbank in ridge and conventional tillage systems. *Weed Sci* **48**:454–460 (2000).
35 Wagner M and Mitschunas N, Fungal effects on seed bank persistence and potential applications in weed biocontrol a review. *Basic Appl Ecol* **9**:191–203 (2008).
36 Roberts HA and Feast PM, Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Res* **1**:316–324 (1972).
37 Buckley YM, Hinz HL, Matthies D and Rees M, Interactions between density-dependent processes, population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). *Ecol Lett* **4**:551–558 (2001).
38 Watkinson AR, Interference in pure and mixed populations of *Agrostemma githago*. *J Appl Ecol* **18**:967–976 (1981).
39 MacDonald N and Watkinson AR, Models of an annual plant population with a seedbank. *J Theor Biol* **93**:643–653 (1981).
40 Pacala SW, Neighborhood models of plant population dynamics. 4. Single-species and multispecies models of annuals with dorment seeds. *Am Nat* **128**:859–878 (1986).
41 Vidotto F and Ferrero A. Germination behaviour of red rice (*Oryza sativa* L.) seeds in field and laboratory conditions. *Agronomy* **20**:375–382 (2000).
42 Chin DV. Biology and management of barnyardgrass, red sprangletop and weedy rice. *Weed Biol Manag* **1**:37–41 (2001).
43 Olofsdotter M, Valverde BE and Madsen KH, Herbicide resistant rice (*Oryza sativa* L.): global implications for weedy rice and weed management. *Ann Appl Biol* **137**:279–295 (2000).
44 Cousens R and Moss SR, A model of the effects of cultivation on the vertical distribution of weed seeds with the soil. *Weed Res* **30**:61–70 (1990).
45 Ferrero A, Weedy rice, biological features and control, in *Weed Management for Developing Countries*, ed. by Labrada R. FAO, Rome, pp. 89–107 (2003).
46 Griffin JL and Harger TJ, Red rice (*Oryza sativa*) control options in soyabeans (*Glycine max*). *Weed Technol* **4**:35–38 (1990).