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RESEARCH PAPER

High level of variation among Sri Lankan weedy rice populations, as estimated by morphological characterization

DISNA RATNASEKERA[1], UDUGAHAPATTUWAGE I.P. PERERA[1], ZHUOXIAN HE[2], SENANAYAKAGE G.J.N. SENANAYAKE[1], GAMAGE A.W. WIJESEKARA[3], XIAO YANG[2] and BAORONG LU[2]*

[1]*Department of Agricultural Biology, Faculty of Agriculture, University of Ruhuna, Matara,* [3]*Department of Agriculture, Horticultural Crop Research and Development Institute, Peradeniya, Sri Lanka and* [2]*Ministry of Education Key Laboratory for Biodiversity and Ecological Engineering, Fudan University, Shanghai, China*

Weedy rice (*Oryza sativa* f. *spontanea*) is a notorious weed that infests paddy fields worldwide. Understanding the morphological variation pattern of this weed in a given rice-planting region will facilitate its effective management and use. Here, 29 populations, covering nearly all the rice-cultivation regions in Sri Lanka, were characterized in a common-garden cultivation experiment that was based on 13 morphological traits. The variation level of the weedy rice populations was considerably high, as estimated by the Simpson and Shannon–Weaver indices. An ANOVA revealed a higher level of among-population variation than within-population variation. Seed shattering was the most variable trait and the seed length and width were the least variable traits, as indicated by their coefficient of variation. The results of the principal component analysis, in which the first two principal components represented 57.5% of the total variation, indicated the important role of such traits as plant height, seed weight and number of tillers and panicles in the divergence of the weedy rice populations. However, the variation was not associated with their geographical locality. Knowledge of such a morphological variation pattern provides opportunities to design strategic management methods for weedy rice control in Sri Lanka, in addition to the proper use of it as a genetic resource for rice improvement.

Keywords: diversity, genetic resources, *Oryza sativa* f. *spontanea*, phenotype, weed.

Asian cultivated rice (*Oryza sativa* L.) is an important world staple food that is consumed by nearly one-half of the global population. Particularly in Asia, rice is considered as the most important crop for food and nutrition. The sustainable and efficient production of this crop is critical to ensure food security in this continent. Rice production is affected considerably by many pests. Among these, weedy rice (*Oryza sativa* f. *spontanea*) is considered as one of the three most noxious weeds (following *Echinochloa crus-galli* and *Leptochloa chinensis*; Yu *et al.* 2005; Song *et al.* 2009) infesting paddy fields worldwide, particularly in Asia, South and North America and southern Europe (Ferrero *et al.* 1999; Mortimer *et al.* 2000; Noldin 2000; Cao *et al.* 2006; Delouche *et al.* 2007). Weedy rice competes for resources, such as water, nutrients and sunlight, with its cultivated counterparts in rice fields, causing considerable yield losses of cultivated rice (Cao *et al.* 2006; 2007; Delouche *et al.* 2007). Weedy rice is characterized by strong seed shattering and seed dormancy, in addition to having red pericarps. These phenotypic characteristics can easily be used to distinguish weedy rice from cultivated rice, which usually has persistent and non-dormant

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**Correspondence to: Baorong Lu, Department of Ecology and Evolutionary Biology, Fudan University, #220 Handan Road, Shanghai 200433, China.*
Email: brlu@fudan.edu.cn

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seeds, as well as white pericarps. Weedy rice predominantly occurs in rice fields. This can distinguish weedy rice from wild rice, which usually is found in natural habitats (Delouche *et al.* 2007). These unique phenotypic characteristics promote the persistence of this weed in rice fields because of the potential populations in the soil seed banks (Delouche *et al.* 2007). When heavily infesting in rice fields, weedy rice can result in significant yield losses. For example, weedy rice has been reported to cause ≤88% of yield losses in the USA (Smith 1988), 74% in Malaysia (Karim *et al.* 2004), 100% in Thailand (Niruntrayakul *et al.* 2009) and 40–90% in Sri Lanka. In addition, weedy rice can reduce the commercial quality of the rice grains due to its red pericarp (Hoagland & Paul 1978; Delouche *et al.* 2007).

Rice occupies 17.6% (0.7 million ha) of the total agricultural land in Sri Lanka, contributing to 14.2% of the total agricultural gross domestic product on the island (AGSTAT 2008; Census and Statistics 2009; Central Bank 2009). According to the spatial and regional distribution of rainfall, Sri Lanka is divided into three major climatic zones: (i) the wet zone (>2500 mm); (ii) the intermediate zone (1500–2500 mm); and (iii) the dry zone (<1500 mm) (Punyawardena *et al.* 2003). Of the total rice area, 31% is situated in the wet zone, 53% in the dry zone and 14% in the intermediate zone (Marambe & Amarasinghe 2000). Rice is cultivated in two distinct seasons that coincide with the monsoon rain and are known as "Maha" (December to February) and "Yala" (May to September). Weedy rice first was identified as a threat in the mid-1990s in the Ampara, Vavunia and Batticaloa districts and then was found throughout the eastern provinces of Sri Lanka (Marambe & Amarasinghe 2000; Marambe B., 2010, personal communication). Despite the heavy infestation and damage to rice production, very few studies have been conducted on weedy rice since it was first reported in Sri Lanka (Marambe & Amarasinghe 2000; Perera *et al.* 2010).

The lack of information concerning the morphological variation of weedy rice has led to confusion in identifying weedy rice from the endemic wild rice species in Sri Lanka. This has posed a serious problem to the endemic wild rice, a valuable genetic resource of cultivated rice, because farmers commonly attempt to eliminate the wild rice that is growing close to their paddy fields. It is important to generate baseline information about weedy rice in order to fill the knowledge gaps. In contrast, weedy rice might provide potential genetic resources for the improvement of cultivated rice. It is important to study the morphological variation pattern of the weedy rice populations that are occurring under diverse environmental conditions in Sri Lanka.

During the past few years, the authors have surveyed weedy rice populations and collected weedy rice samples from different agro-ecological zones in Sri Lanka. The objectives of this study were to: (i) determine the variation pattern of the weedy rice traits in Sri Lanka by a common-garden cultivation experiment; (ii) estimate the relationships of the weedy rice populations, based on morphological variation; and (iii) identify the major traits contributing to the variation. The generated knowledge will be very useful for designing and implementing effective management practices for weedy rice that occurs in paddy fields, in addition to the exploration of the germplasm of weedy rice for the genetic improvement of cultivated rice.

MATERIALS AND METHODS

Sampling of the weedy rice populations

A total of 29 weedy rice populations (Fig. 1) was sampled in the Yala (May–August) season in 2009. Seeds were collected from plants with an ~10 m spatial interval in all the weedy rice populations. Each weedy rice population was apart from the other by at least 5 km. The detailed identifying data, including the locality with the longitude and latitude at each site, were recorded with a global positioning system (eTrex vista; Garmin, Ltd, Southampton, United Kingdom) (data shown in Appendix S1).

Characterization of the weedy rice populations in a common-garden cultivation experiment

The common-garden cultivation experiment was designed and conducted in the Maha season (October 2009–March 2010) in the experimental field at the University of Ruhuna, Matara, Sri Lanka (6°3′21.07″N, 80°33′37.37″E). The 29 weedy rice populations (Fig. 1) that were collected from the rice fields were included for characterization.

The seeds from the weedy rice populations were placed in an oven (~55°C) for 5–7 days to break the seed dormancy before being presoaked in tap water for 24 h. The seeds then were sown directly into a nursery bed in the experimental field. Fourteen days after seed germination, the weedy rice seedlings were transplanted into field plots, each of which included 25 seedlings (5 × 5) from the same population. The seedlings were planted in a plot with 25 cm between the hills and rows. Three plots (replicates) for each weedy rice population were included in the experimental field, in which the cultivation plots were arranged following a complete randomized design for the plot layout (Fig. 2). All the

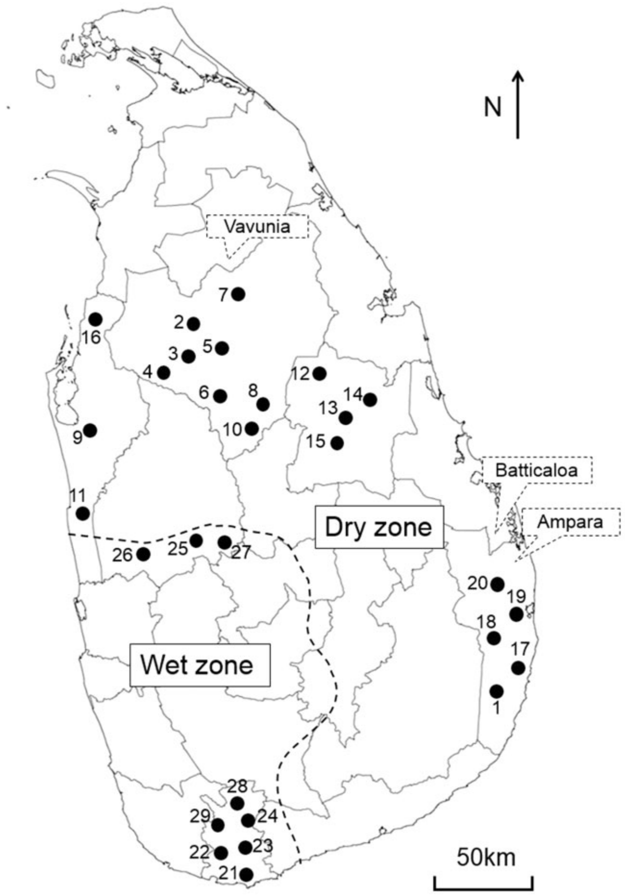

Fig. 1. Geographical locations of the 29 weedy rice populations that were collected in Sri Lanka. The numbers at each collection site represent the population codes (see Appendix S1). The country is divided into the dry zone and the wet zone by the "Sri Lankan Mahaweli Project" (http://iri.columbia.edu/~mahaweli/RiverBasinMahaweli/) and by Wikipedia (http://en.wikipedia.org/wiki/Geography_of_Sri_Lanka#Ecological_zones).

R1

6	15	17	3	26
14	27	22	11	7
4	21	1	24	13
18	29	10	16	28
8	20	9	2	23
19	5	12	25	

R2

5	27	11	21	7
19	23	2	8	16
13	17	26	10	24
28	22	6	14	3
25	1	29	18	12
15	9	20	4	

R3

11	17	9	27	13
21	4	19	16	1
26	15	29	6	22
2	23	7	28	12
10	18	14	25	3
24	5	20	8	

Fig. 2. Plot layout of the 29 weedy rice populations for each of the three replicates (R1, R2 and R3) in the common-garden cultivation experiment. The numbers in different squares (plots) represent the codes of the 29 weedy rice populations, arranged following a complete randomized design.

management practices, including fertilizer application and weed, insect and disease control, followed the recommendations of the Department of Agriculture, Sri Lanka.

Thirteen vegetative and reproductive traits were characterized for the weedy rice plants, as indicated in Table 1. The determination of the vegetative and reproductive traits followed the standard of Counce *et al.* (2000). The panicles of weedy rice were enclosed by nylon mesh bags before the seeds matured to avoid the loss of seeds due to seed shattering. To circumvent an edge effect, only the nine plants in the middle of each plot were characterized.

Data analysis

For the 13 measured traits, the following parameters were calculated to estimate the general variation of weedy rice in Sri Lanka: the coefficient of variation (CV, %), mean and standard deviation and maximum and minimum values. In order to estimate the variation of each population, Simpson diversity and Shannon–Weaver indices were calculated following the formula: $H = 1 - \Sigma P_i$ and $I = -\Sigma P_i \ln P_i$ (Shannon & Weaver 1949; Simpson 1949). An ANOVA was conducted in order to estimate the variation within and among populations, using SPSS v. 19.0 for Windows

Table 1. Selected traits for the morphological characterization of the weedy rice populations from Sri Lanka, with information on the methods for the measurement of each trait

Trait	Code	Method of trait measurement
Plant height at seedling stage (cm)	PH-S	Height from the base to the tip of the plants measured 32 days after seed germination
Plant height at booting stage (cm)	PH-B	Height from the base to the tip of the plants measured 56 days after seed germination
Number of tillers at seedling stage	T-S	Number of tillers per plant counted 32 days after seed germination
Number of tillers at booting stage	T-B	Number of tillers per plant counted 56 days after seed germination
Number of panicles per plant	PAN/P	Number of panicles per plant counted at maturity
Panicle length (cm)	PANL	Length of panicles from their base to the tip
Seed shattering (%)	SS	Ratio of shattered seeds against the total seeds per panicle after gentle presses by hand
Number of filled seeds per panicle	FS/PAN	Number of well-developed seeds per panicle counted at maturity
Number of spikelets per panicle	TS/PAN	Number of spikelets (including empty ones) per panicle counted at maturity
Number of spikelets per plant	TS/P	Number of spikelets (including empty ones) per plant counted at maturity
Seed length (mm)	SL	Average length of 10 well-developed seeds measured at maturity
Seed width (mm)	SW	Average width of 10 well-developed seeds measured at maturity
1000-seed weight (g)	S-WT	Weight of 1000 well-developed seeds dried to 13% moisture content

(IBM SPSS Statistics, Armonk, New York, USA). A principal component analysis (PCA) was used to determine the relationships of the 29 weedy rice populations, particularly those from the dry and wet zones, using the software Minitab v. 14.13.0 (Minitab 2008).

RESULTS

Variation pattern of the selected vegetative and reproductive traits

In general, a considerable variation pattern was observed according to the CV, ranging from 5.3% to 62.2% among the different traits (Table 2). The reproductive traits (i.e. PAN/P, PANL, SS, FS/PAN, TS/PAN, TS/P, SL, SW, S-WT) showed the highest and lowest variation, whereas the vegetative traits (i.e. PH-S, PH-B, T-S, T-B) showed intermediate variation. For example, the highest variable trait was seed shattering, followed by the number of spikelets per plant (CV = 39.2%) and the number of filled seeds per panicle (CV = 31.1%). The lowest variable traits were the seed length and seed width (CV = 5.3% and 6.0%, respectively). The traits with intermediate variation were the plant height at the seedling and booting stages and the number of tillers at the seedling and booting stages. In addition, the results from the ANOVA indicated a different proportion of variation among and within weedy rice populations for different traits. For example, some traits, such as the plant height at the seedling and booting stages, showed great among-population variation (>86%), compared to their within-population variation (<14%) across the country (Table 3). However, other traits, such as the number of spikelets per plant, showed moderate variation (62.50%) among the weedy rice populations (Table 3).

Morphological variation of the weedy rice populations

Based on morphological characterization, the overall level of variation in the weedy rice populations generally was high, as indicated by the overall values of the Simpson ($H = 0.843$) and the Shannon–Weaver ($I = 1.999$) indices (Table 4). However, the variation was not evenly distributed among the populations. The *H*-values varied from 0.615 to 0.833 and the *I*-values varied from 1.013 to 1.927 in the studied weedy rice populations (Table 4). The highest *I*-values and *H*-values were found in Population 2, Population 7 and Population 20, collected from the dry zone (Table 4, Fig. 1, Appendix S1). The lowest *I*-values and *H*-values were recorded in Population 29, collected from the wet

Table 2. Description of the variation in the 13 measured traits of the 29 weedy rice populations

Trait code	Coefficient of variation (%)	Mean (standard deviation)	Maximum value	Minimum value
SS	62.2	15.2 (9.8)	62.0	1.8
TS/P	39.2	838.7 (321.5)	2248.2	131.9
FS/PAN	31.1	80.5 (24.7)	167.7	13.5
TS/PAN	27.6	110.8 (29.8)	531.0	51.0
T-S	27.0	5.1 (1.4)	12.9	2.5
T-B	22.3	12.2 (2.7)	23.7	5.6
PAN/P	19.2	10.2 (1.9)	20.9	4.8
PH-B	16.0	90.5 (14.4)	127.4	54.6
PH-S	13.7	55.8 (7.7)	81.5	34.9
S-WT	9.5	25.8 (2.4)	32.3	14.5
PANL	7.9	22.0 (1.7)	26.9	16.4
SW	6.0	2.8 (0.2)	3.4	2.4
SL	5.3	8.0 (0.4)	9.5	5.7

Table 3. Variation of the 13 selected morphological traits among and within the 29 weedy rice populations, based on an ANOVA

Trait code	Proportion of variation		Mean square of variation		
	Among pops† (%)	Within pops (%)	Among pops (d.f. = 28)	Within pops (d.f. = 340)	Total (d.f. = 368)
PH-S	86.40	13.60	250.22	39.23	289.44
PH-B	86.10	13.90	878.56	141.70	1 020.26
S-WT	85.90	14.10	25.81	4.22	30.04
PANL	85.30	14.70	12.80	2.20	15.00
SW	82.90	17.10	0.11	0.02	0.13
SS	80.80	19.20	299.14	71.13	370.27
SL	80.40	19.60	0.56	0.14	0.70
T-S	77.50	22.50	5.59	1.62	7.21
T-B	75.60	24.40	19.18	6.18	25.36
FS/PAN	75.60	24.40	1 592.95	515.44	2 108.38
PAN/P	69.10	30.90	6.95	3.11	10.06
TS/PAN	67.10	32.90	1 784.57	876.35	2 660.92
TS/P	62.50	37.50	165 567.93	99 387.73	264 955.66
Average	78.10	21.90	–	–	–

† Pops, populations.

zone, and Population 5 and Population 13 (Table 4, Fig. 1, Appendix S1). Apparently, the north-central rice-planting area of Sri Lanka, especially in Anuradhapura district, showed a relatively high level of weedy rice diversity. The results of the ANOVA revealed an average of ~78% of the total variation among populations and ~22% of the total variation within populations, based on all the selected morphological characteristics (Table 3).

Relationships of the weedy rice populations, based on a principal component analysis

A scatter plot of the 29 populations, based on the first two principal components (representing 57.5% of the total variation) of the PCA, showed a largely divergent pattern of the selected populations that were not closely associated with their geographical locality (Fig. 3). There was no clear separation between the populations from

Table 4. The within-population diversity of the 29 weedy rice populations, calculated based on the 13 selected morphological traits

Population code	Simpson diversity index	Shannon–Wiener index
2	0.833 (0.025)†	1.927 (0.117)
7	0.829 (0.017)	1.914 (0.080)
20	0.818 (0.022)	1.854 (0.106)
21	0.808 (0.026)	1.810 (0.133)
3	0.807 (0.032)	1.778 (0.116)
23	0.806 (0.038)	1.805 (0.139)
1	0.805 (0.047)	1.809 (0.154)
24	0.802 (0.023)	1.764 (0.118)
28	0.799 (0.037)	1.789 (0.148)
12	0.797 (0.018)	1.674 (0.104)
9	0.795 (0.037)	1.713 (0.142)
10	0.794 (0.018)	1.741 (0.084)
15	0.787 (0.033)	1.725 (0.120)
4	0.783 (0.077)	1.696 (0.271)
17	0.779 (0.037)	1.600 (0.153)
6	0.776 (0.058)	1.634 (0.231)
25	0.763 (0.085)	1.613 (0.244)
19	0.759 (0.059)	1.586 (0.195)
16	0.752 (0.072)	1.524 (0.199)
14	0.748 (0.054)	1.458 (0.192)
18	0.740 (0.084)	1.492 (0.273)
8	0.739 (0.080)	1.445 (0.274)
22	0.739 (0.079)	1.509 (0.248)
27	0.722 (0.147)	1.430 (0.326)
11	0.722 (0.079)	1.396 (0.261)
26	0.714 (0.055)	1.338 (0.180)
13	0.644 (0.047)	1.093 (0.130)
5	0.625 (0.000)	1.040 (0.000)
29	0.615 (0.062)	1.013 (0.171)
Overall	0.843 (0.018)	1.999 (0.095)

† Values in the parentheses are the standard deviation.

the dry zone and the wet zone, although the populations from the dry zone presented a slightly larger variation than those from the wet zone. The first component contributed 37.2% to the total variation, in which the plant height and seed weight played an important role in the divergence of the weedy rice populations (Table 5, Fig. 3). The second component contributed 20.3% to the total variation, in which the number of tillers at the booting and seedling stages played an important role (Table 5, Fig. 3). Noticeably, some populations, such as Population 1 and Population 19, showed distinct separation from all the other populations. Some populations, such as Population 7, Population 8 and Population 27, also showed some degree of divergence from the other populations (Fig. 3).

DISCUSSION

These results clearly showed that the morphological variation of weedy rice is not evenly distributed in the selected morphological traits. Seed shattering and the number of spikelets (grains) per plant are the most variable traits for weedy rice in Sri Lanka, which might explain the extent of the yield losses of cultivated rice, estimated to be >40% in Sri Lanka (Marambe & Amarasinghe 2000). However, according to recent unpublished data, weedy rice can cause >90% of rice yield loss in this country. In addition, the plant height at the two stages (PH-S, PH-B) varied considerably among the weedy rice populations (Table 3). The plant height is one of the traits that confers competitive advantage over cultivated rice and taller weedy rice plants are able to capture more light and shade their neighboring rice plants (Kwon *et al.* 1992; Shivrain *et al.* 2010). The results of this study probably indicate the impact of selection on plant height by farmers when they manually remove taller weedy rice plants in rice fields before their maturity (Gressel & Valverde 2009). In addition, the analysis suggests that the traits of the seeds had the least variability, indicating that these traits, such as grain shape, grain color and awn characteristics, can be used for the identification of weedy rice (Arrieta-Espinoza *et al.* 2005).

The results of this study also indicated a relatively high level of morphological diversity of the weedy rice populations in Sri Lanka, although the diversity of the weedy rice populations is not evenly distributed among regions. Even in the same region, some populations showed a relatively higher variation than other populations. It seems that the morphological variation of the weedy rice populations was not associated with the agro-ecological conditions; for example, the dry and the wet zone. This is probably caused by seed-mediated gene flow via farmers' frequent exchange of rice cultivar seeds or through other media, such as the machinery used for rice harvesting and water canals. If mixed in rice varieties, weedy rice seeds will be distributed throughout the country to the next season. This suggests that factors, such as the sources of rice varieties (with or without weedy rice contamination) received by farmers, rice-farming styles (e.g. transplanting or direct seeding) and weed management methods (weeding or non-weeding), play more important roles in the morphological differentiation of weedy rice than eco-geographical zones. Based on all these results, the authors recommend that

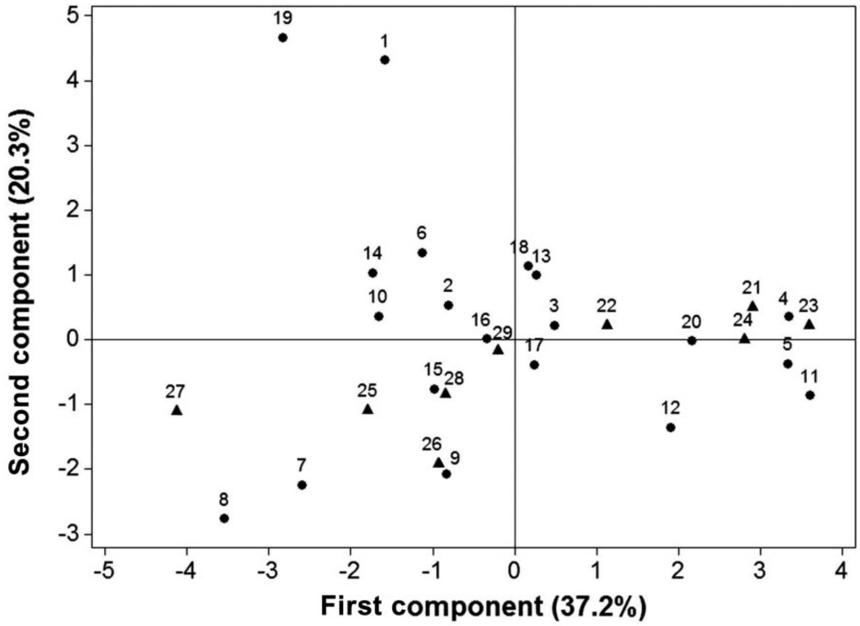

Fig. 3. Scatter plot of the first two principal components of morphological variation, showing the relationships of the 29 weedy rice populations. (●), The populations from the dry zone; (▲), the populations from the wet zone.

Table 5. Eigenvalues of the correlation matrix for the 13 characteristics of the 29 weedy rice populations

Trait code	PC-1 (37.2%)†	PC-2 (20.3%)
PH-B	0.419	−0.037
S-WT	0.395	0.122
PH-S	0.393	−0.064
FS/PAN	0.380	−0.116
SW	0.337	−0.030
TS/P	0.313	0.038
PANL	0.225	0.323
SS	0.198	0.170
SL	0.170	0.388
T-B	−0.137	0.526
TS/PAN	0.102	−0.096
T-S	−0.096	0.486
PAN/P	−0.025	0.398

† Values in the parentheses correspond to the proportion of total variation for the first two principal components (PCs).

strategic and integrated weedy rice management should be developed and applied to minimize the infestation and spread of weedy rice that increasingly is becoming a threat to the sustainable production of cultivated rice in Sri Lanka (Chauhan & Johnson 2010). Efforts should be made to maintain clean seed sources, without the contamination of weedy rice seeds. It is also important to eliminate or minimize the number of seeds in the soil seed banks by various management methods (Chauhan 2013) in order to reduce the population size of weedy rice in paddy fields and consequently to reduce infestation by weedy rice.

However, weedy rice could provide useful germplasm for the genetic improvement of cultivated rice, despite its negative impacts on rice production (Tang *et al.* 2011). The estimated high levels of morphological diversity of the Sri Lankan weedy rice populations in this study (e.g. the potential of more panicles and number of seeds) can be used in rice-improvement programs by determining the ideal genotypes from the weedy rice plants that are distributed in diverse ecological conditions. This should be useful for future rice breeding. Based on unpublished data from the authors' recent studies, a number of traits (plant height, number of tillers and number of filled seeds per plant, seed length and 1000-seed weight) has been identified from weedy rice that can be used in rice-breeding programs.

The rapid increase in infestation of Sri Lankan rice fields by weedy rice has become a serious challenge for rice production, which is probably true for many Asian countries. However, our understanding of basic scientific questions, such as the origin, dispersal, morphological and diversity pattern and seed physiology of weedy rice, still is very limited. Changes in agricultural styles, human activities and the global climate could promote the reemergence and spread of weedy rice in Sri Lanka, as well as other rice-planting counties, if no proper management method is adopted. Information concerning the morphological variation of weedy rice that has been generated from this study reflects an initial step in understanding its diversity and complexity in Sri Lanka. More studies are needed to investigate the genetic variation patterns, origin and evolutionary relationships of weedy rice populations in this country by using molecular tools.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1 The 29 weedy rice populations that were collected in different ecological zones and locations in Sri Lanka.