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Weedy Rice: Competitive Ability, Evolution, and Diversity

Swati Shrestha, Shandrea Stallworth and Te-Ming Tseng

Abstract

Weedy rice is conspecific, the most troublesome weed of cultivated rice identified as a threat to global rice production. The weed has inherited high reproductive ability and high dormancy by outcrossing with modern rice cultivars and wild cultivars, respectively. Traits such as rapid growth, high tillering, enhanced ability to uptake fertilizers, asynchronous maturation, seed shattering, and long dormancy periods make weedy rice more competitive than cultivated rice. Weedy rice infesting rice fields are morphologically diverse with different hull color, awn length, plant height, and variable tiller number. Morphological diversity in weedy rice can be attributed to its high genetic diversity. Introgression of alleles from cultivated rice into weedy has resulted in high genetic and morphological diversity in weedy rice. Although variations among weedy rice populations make them difficult to control, on the brighter side, competitive nature of weedy rice could be considered as raw genetic materials for rice breeding program to develop vigorous rice plants able to tolerate high biotic and abiotic stresses.

Keywords: genetic diversity, phenotypic diversity, rice breeding, red rice, abiotic stress tolerance, biotic stress tolerance

1. Introduction

Weedy rice, also called as red rice because of its red pericarp, belongs to same genus and species as the cultivated rice, *Oryza sativa* L. It is one of the major weeds in rice field worldwide [1] and adulterates cultivated rice decreasing its productivity in the field and reducing crop quality due to seed contamination. Rice monocropping and direct-seeded rice system promote infestation of weedy rice, and severe infestation of weedy rice can cause up to 100% yield reduction in direct-seeded rice system [2]. Numerous weed control strategies are adopted by the farmers to control weedy rice in rice fields. Development of herbicide-tolerant rice was thought to solve the problem of weedy rice, but with the development of herbicide-resistant weeds, the value of this technology has become questionable. Management of weedy rice in rice fields is possible only through adoption of integrated weed management practice such as winter flooding, fallow tillage, and crop rotation [3].

The genus *Oryza* has 21 wild and two cultivated species. Two cultivated species include *O. sativa* the Asian rice and *O. glaberrima* the African rice, both with diploid AA genome. *O. sativa* has three major subspecies: *indica*, *japonica*, and *javanica*. Among the wild rice, nine are tetraploid (BBCC) (CCDD) and 12 are diploid [4]. Wild rice found in nature are those derived from *O. sativa*

(AA complex) and *O. Officinalis* complex (BB, CC, CCDD) [5]. *Oryza sativa* complex includes *O. rufipogon*, *O. barthii*, and *O. longistaminata*, while *O. officinalis* complex includes *O. punctata*, *O. latifolia*, and *O. officinalis*. However, weedy rice is distinct from wild rice and is believed to have been evolved through (i) hybridization among and within cultivated and wild rice, (ii) de-domestication of cultivated rice, and (iii) direct colonization of wild rice in agricultural rice fields [6].

The genus *Oryza* consists of numerous species, and studying the genetic structure of cultivated, wild, and weedy rice species is crucial for understanding the morphological and physiological characters of rice cultivars and the genes governing these characters. Proper understanding of numerous genes governing quantitative and qualitative traits in rice is essential for successful molecular breeding programs. Genetic diversity of *Oryza* can be utilized for crop improvement program by plant breeders in order to produce rice cultivars with higher yield that could meet the growing food demand.

2. Weedy rice: a troublesome weed

Weedy rice (*Oryza sativa* spp.) is currently distributed worldwide, and it is known to infest the areas in and around rice fields [7]. These weedy rice tend to have many undesirable traits when compared to cultivated rice such as the ability to germinate faster, reduce yields by 90%, and persist within the soil bed for up to 10 years [8]. Conventionally, in most of the developing countries, rice is transplanted into standing water, thus providing competitive advantage to the crop and enhancing crop productivity by suppressing weeds [9]. However, with the scarcity of labor and water, there has been a significant shift from puddled transplanting (PTR) to direct-seeded rice (DSR) system in Asian countries in the past two decades [2]. In the USA, all rice fields are cultivated through highly mechanized DSR system [10]. DSR involves rice stand establishment directly by sowing seeds in the fields and uses less water and labor and emits less methane than the PTR system [11]. Although DSR has numerous advantages over the PTR, sustainability of DSR with reference to control of weedy rice is becoming questionable. Currently, weedy rice has been reported in most of the rice-growing countries like China, India, the USA, Bangladesh, Bhutan, Brazil, Nepal, Thailand, Japan, the Philippines, Korea, Thailand, Sri Lanka, Vietnam, and Malaysia (**Figure 1**) [15]. Incidence of weedy rice has increased tremendously in Malaysia following the adoption of DSR in the 1980s [12]. In Vietnam, yield loss due to weedy rice has been reported from 15 to 70% [13]. Due to its ability to behave similarly to rice, management of these weedy species without causing damage to the crop itself has proven to be an issue [14].

According to Allston, the first weedy red rice was reported in the USA as early as 1800 as seed contaminants from Asia and since then has been affecting rice crop by limiting its yield [16]. Weedy rice share common gene pool with cultivated rice making them morphologically similar to cultivated rice but have high seed shattering and differential dormancy, making them difficult to control weeds in the rice fields. Some of the unfavorable traits possessed by weedy rice are long culm lengths, high tillering capacity, light leaf color, weak culms, red pericarp, highly shattering seeds, and high degree of seed dormancy [2, 17, 18]. It is difficult to control weedy rice because they mimic cultivated rice morphologically, biochemically, and physiologically. Physical weed management is difficult as weedy rice is morphologically similar to cultivated rice in early stages, and chemical weed management is limited as herbicides controlling weedy rice also kill rice plant [2]. In many places, farmers have altered their cropping pattern to non-rice system to manage this noxious weed [14]. Depending on the amount of infestation, weedy rice can cause yield losses

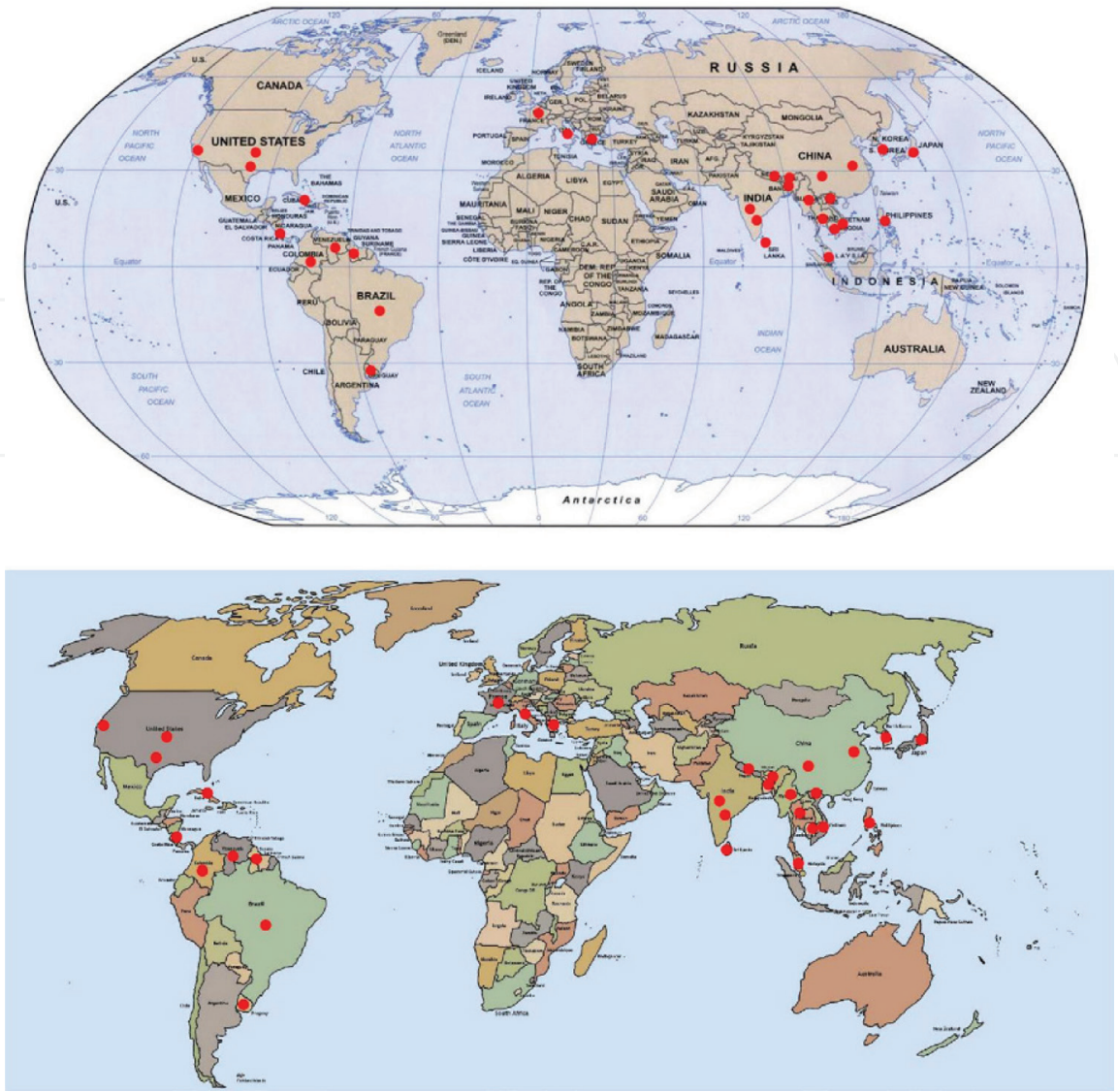


Figure 1.
Weedy rice distribution worldwide. Red dots represent regions where weedy rice infestation has been reported [15].

varying from 50 to 60% under moderate infestation to 70–80% under heavy infestation. In Arkansas, the highest rice-producing state in the USA, economic loss due to weedy rice has been estimated to be \$274/hectare [19]. The threshold for weedy rice infestation is one to three plants/m² in the USA; plant density higher than this can cause significant yield loss [20].

3. Competitive nature of weedy rice

Competition for limited resource is the drawing force for natural selection and shaping plant communities [21]. Weeds compete with crop for nutrients, space, and light, thus decreasing yield potential of crop. Traits of weedy rice such as taller growth habit, higher tillering, and higher nutrient use efficiency make it dominant and more competitive than the crop [22]. The success of weedy rice as weeds can be attributed to its high dormancy as they can remain viable in soil for a long period of time and emerge when conditions are favorable [23]. Noldin et al., in 2006, conducted an experiment to evaluate the dormancy and longevity of various weedy rice biotypes from four states in the USA [24]. The study found the differential level of dormancy among weedy rice ecotypes buried under the soil at different depths, and

all of them were more viable than commercial rice cultivar. Five weedy ecotypes had viable seeds even after 36 months of burial in the soil. The commercial rice seeds were nonviable after 5 months of burial in the soil. Weedy rice therefore has greater viability than cultivated rice under certain environmental conditions and can emerge from deeper soil surface, thus developing a robust soil seedbank [24].

Seed shattering, which distinguishes cultivated rice from its wild forms, is variable in weedy rice [25]. In weedy rice, the abscission layer degrades earlier as compared to cultivated rice, leading to earlier shattering and increasing its fitness for survival in the environment [26]. Shattering in weedy rice is controlled by unidentified regulatory genes distinct from wild rice, thus suggesting parallel evolution between weedy rice and wild rice [26]. Weedy rice is also generally taller than cultivated rice making them more efficient for light and space [27]. Weedy rice has higher nitrogen use efficiency causing greater yield loss in rice fields [28]. Thus, in fields infested with weedy rice, the application of nitrogen fertilizers may not lead to an eventual increase in rice yields; instead, the weedy rice plants grow bigger and compete more aggressively with rice resulting in rice plants with lower yield [28]. Nitrogen accumulation is higher in weedy rice than in cultivated rice in “nutrient-deficient” conditions, suggesting a more efficient nutrient uptake mechanism in weedy rice than cultivated rice [29]. In addition to higher nutrient response, weedy rice also has higher stress tolerance [30, 31]. Unlike commercial rice varieties, weedy rice can perform better in unfavorable environmental conditions such as higher carbon dioxide, lower nutrient supply, and high/low temperature, indicating that they have higher capability of enduring stress than cultivated rice and, therefore, thrive better in stressful environment. Weedy rice ecotypes have higher leaf area and root weight when grown at carbon dioxide level of $500 \mu\text{mol mol}^{-1}$ which is the projected CO_2 concentration in the middle and end of the twentieth century [30]. In saline conditions, growth and germination of most plant species are reduced; however, weedy rice accessions have higher germination index and seedling vigor than commercial rice at 16 dSm^{-1} (NaCl) salinity level [32]. A weed-crop competition modeled by Pantone and Baker showed that weedy rice is more dominant than cultivated rice and competitive ability of one weedy rice plant is equivalent to three plants of an old commercial rice variety “Mars” [33]. Ottis et al. studied the interference potential of weedy rice on five rice cultivars (CL161, Cocodrie, LaGrue, Lemont, and XL8) and demonstrated that yield reduction of rice cultivars ranged from 100 to 755 kg/ha for every weedy rice plant/ m^2 [34].

4. Evolution of weedy rice

There is immense diversity both among and within weedy rice populations and between weedy and cultivated rice [35–38]. Studying the differences in weedy rice populations in relation to phenological and morphological traits will help us better understand the evolution of weedy traits. There are a number of hypotheses that speak to the origination of weedy rice. These hypotheses include the following: weedy rice is a crop mimic of rice similar to a wild relative, it is a hybrid of natural crosses between wild and cultivated rice, and it is merely an evolved taxon from cultivated rice [39]. In areas inhabited by wild rice, De-Wet and Harlan believed that weedy rice arose from the selection of wild rice to agricultural habits for consumption [40]. While this may be true for areas with a prominent wild rice population, it does not address the prevalence of this weedy species in areas uninhabited by wild rice. Recent genetic studies point to specific examples of the evolutionary pathways of weedy rice.

Over the last 20 years, studies conducted on weedy rice have increased due to the increased infestation in rice fields. In 2006, Cao et al. noticed the resurgence of weedy rice and set out to conduct a molecular study utilizing 20 simple sequence repeat (SSR) markers and 30 different populations of weedy rice to identify the evolution of weeds in China's Liaoning province [41]. The weedy rice populations were compared to a wild rice relative, *O. rufipogon*, as well as cultivars to represent both indica and japonica biotypes. Cao et al. discovered, through genetic data, that the Liaoning cultivar, a japonica biotype, was very similar to that of weedy rice and clustered together to demonstrate this, while another Chinese japonica biotype did not follow the same clustering style. Through AMOVA analysis, the study found approximately 35% of the total genetic variation among regions, 18% within regions, and 46% within the populations. When the wild relative, *O. rufipogon*, and indica biotypes were compared to the weeds, they were further clustered from the weedy rice and Liaoning cultivar. Based on this data and the clusters presented, the authors concluded that weedy rice in the Liaoning province of China arose from the mutation and hybridization of Liaoning rice varieties [41]. This conclusion was challenged in 2010 by a paper from Ellstrand et al. stating "...if hybridization had occurred, it is likely that some *O. rufipogon* alleles would have been retained in the weedy lineages in the short time that they have been problematic" [38]. This could be true as Cao et al. found that there was a lack of heterozygosity within the weedy rice populations.

Weedy rice can also be referred to as red rice due to the presence of a red pericarp not often witnessed within the cultivated rice. To determine if the presence of a red pericarp was a characteristic of weedy rice or cultivated rice, Gealy et al. used SSR markers to differentiate between weedy rice present in the Southeastern USA, cultivated rice, and hybrids [42]. In this study, 31 SSR markers were used to analyze 180 kinds of rice from the genus *Oryza* and 80 weedy rice and rice cultivars from the USA. The 31 SSR markers selected represented low to high polymorphism information content values to screen the population for genetic variation. Using AMOVA, the genetic variation of the 80 weedy rice and rice cultivars was 56% within populations and 44% among populations. When the study compared only the 38 weedy rice populations that were separated into three different weedy rice populations, the genetic variation was 47% within populations and 53% among populations. A large amount of genetic variability was explained by the considerable genetic variation within blackhull, awned red rice (BA+), and *Oryza sativa* with white bran (OSW). Gealy et al. also found that when comparing hull types among the red rice population, red rice with straw or blackhulls and awns were not molecularly different from one another. Gealy et al. found that many of the SSR markers used were able to differentiate between the OSW and the weedy rice. There were 12 SSR markers that produced alleles that were present in the cultivated rice with white bran that was absent in the weedy rice populations [42]. Through the study, they found that BA+ weedy rice had a greater genetic distance and more diversity than its strawhull, awnless counterparts with both varying genetically from the historic OSW population. To understand these differences, Gealy et al. also used principal component analysis to look at the clustering of populations based on genetic distance [43]. Through the analysis, they were able to find that hybrids were more closely associated with the weedy rice parent. This data was closely related to earlier studies completed by Gealy et al. [43]. Using structure analysis, genetic structure groupings were used to visualize the genetic backgrounds of weedy rice present in the USA. Six different groups were identified using STRUCTURE software by Pritchard et al. [44]. When analyzing the weedy rice population, the hybrid weedy rice fell in between strawhull,

awnless and blackhull, awned weedy rice. This outcome was expected given the data presented on genetic variation and principal component analysis. The same results were observed when all rice in the study were combined together suggesting that the selected SSR markers by Gealy et al. were able to capture enough genetic variability to differentiate the origination of sampled weedy rice present within the USA [42]. Gealy et al. went further and compared their findings to those of Cao et al. noting that US weedy rice was qualitatively different from those found in the Liaoning province of China. While US weedy rice was genetically different from historical rice grown in the USA, they were more closely related to *O. sativa*, *nivara*, or *rufipogon* species, but Liaoning weedy rice populations were related to rice grown in the area and *japonica* biotypes from other regions [42]. These findings could be related to the selection of SSR markers used in the study by Cao et al. lacking the ability to capture as much genetic variation present in their population [42]. While Gealy et al. used 31 SSR markers and Cao et al. used 20 SSR markers, the quality of markers may not have been to the same degree as Gealy et al.

5. Weedy rice diversity

5.1 Morphological diversity of weedy rice

Weedy rice exhibits high genetic and phenotypic diversity, and this diversity is dependent on the ecotype and habitat [45]. Weedy rice from different regions of Asia (Malaysia, the Philippines, Thailand, and Vietnam) varied in terms of grain characteristics and growth response under competition with cultivated rice [46]. The Philippines weedy rice produced the highest grain yield, while a higher growth potential was observed in weedy rice from Vietnam; weedy rice from Thailand was the shortest. Weedy rice from major rice-growing areas of Ampara District, Sri Lanka, were found to be morphologically diverse in terms of tiller number, plant height, and panicle number [47]. In Peninsular Malaysia, the weedy rice can be divided into four major clusters based on their morphological variation: (1) awned black and brownhull derived from wild *Oryza* population, (2) strawhull awnless weedy rice derived from rice cultivars with high shattering, (3) brownhull weedy rice, and (4) weedy rice of mixed weedy morphotype inferring multiple origin [48]. Similarly, weedy rice from major rice-cultivating areas of Italy can be awned, awnless, or mucronate. The highest variability was observed among awned weedy rice ecotypes than the awnless in terms of flag leaf length, 1000 seed weight, and germination rates [49]. In Arkansas, morphological characteristics varied among the two weedy rice ecotypes and within each ecotype (**Figure 2**) [45]. Blackhull weedy rice ecotype showed greater variation in traits than strawhull weedy rice. Plant height among blackhull accessions ranged from as short as 75 cm to as tall as 190 cm. The range of plant height in strawhull was greater (46–189 cm), but on an average, they were slightly shorter than blackhull weedy rice. Flag leaf lengths were longer in strawhull, 38 cm, than in blackhull weedy rice, 34 cm. Tillering capacity of blackhull weedy rice (mean = 105 tillers per plant) was higher than strawhull (mean = 95 tillers per plant). Also, weedy rice accessions from northeastern region of Arkansas flowered earlier than other regions in Arkansas. As the weedy rice is conspecific species of rice with AA genome, it has traits of both cultivated and wild rice. Weedy rice, being closely related to cultivated rice, has a tendency to pollinate with cultivated rice and produce progeny of different phenotypes [50]. Thus, weedy rice all over the world have

variable phenotype as they can readily exchange genetic information with nearby cultivated rice plants.

5.2 Genetic diversity of weedy rice and its gene flow potential

Morphological diversity in weedy rice can be attributed to its high genetic diversity. The genetic diversity of rice has been estimated using various markers like random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), and simple sequence repeats (SSR) [50–54]. Of these SSR markers are most commonly



Figure 2.
Weedy rice of different hull color and awn length collected from various rice fields of Arkansas, USA, in 2008–2009.

Species	Geographical location	Marker used	Genetic diversity	Reference
<i>Oryza sativa</i> f. <i>spontanea</i>	Northeastern China	SSR	Heterozygosity (H_e) = 0.313 Shannon's diversity index (I) = 0.572	Cao et al. [41]
<i>Oryza sativa</i> L.	Northeast Asia	SSR	H_e = 0.748 I = 0.434	Mao-bai et al. [51]
<i>Oryza sativa</i> L.	Liaoning province, China	SSR	H_e = 0.053	Yu et al. [52]
Awnless red rice	Arkansas, USA	SSR	Average genetic distance = 0.2	Gealy et al. [59]
Awned red rice	Arkansas, USA	SSR	Average genetic distance = 0.33	Gealy et al. [59]
<i>Oryza sativa</i>	Arkansas, USA	SSR	Nei's genetic distance (GD) = 0.7	Shivrain et al. [54]
<i>Oryza sativa</i> L.	Italy	SSR	H_e = 0.295	Grimm et al. [56]
Red rice	Uruguay	AFLP	Average of 25.6 bands per primer pair	Federici et al. [57]

Table 1.
*Genetic diversity of weedy rice (*Oryza sativa*) from different regions of the world as detected by molecular markers.*

used as they are readily available, easy to use, highly polymorphic, and less expensive and give accurate results (**Table 1**). Genetic diversity of weedy rice populations from Liaoning province using SSR markers was found to be relatively high with H_e value of 0.313, and 35% of genetic variation was among regions [41]. Weedy rice from Northeast Asia are genetically diverse with high Shannon's information index of 0.748 and heterozygosity of 0.434 [51]. Among RAPD and SSR markers, SSR were superior to RAPD in detecting genetic diversity among weedy rice populations [52]. Weedy rice, weedy rice-cultivated rice hybrids, and rice cultivars can be distinguished using microsatellite SSR markers [53]. Molecular studies using SSR confirmed the differentiation of the two weedy rice ecotypes from Arkansas, USA [54]. Strawhull weedy rice were genetically distant compared to blackhull weedy rice. A higher genetic diversity within blackhull weedy rice ($D = 0.76$) was estimated compared to strawhull ($D = 0.68$). US weedy rice has high genetic diversity with nucleotide diversity (P_i) = 1.48 per Kb, thus indicating their higher potential to evolve [54]. Within weedy rice populations, the blackhull group showed higher nucleotide diversity ($P_i = 0.66$) than strawhull group ($P_i = 0.56$). Weedy rice was found to be closely related to *O. sativa* indica and *O. sativa* aus, instead of the commonly cultivated rice in the USA, *O. sativa* japonica [55]. Similar results were also observed by Londo and Schaal where most of the weedy rice clustered together with *O. sativa* aus. These results suggest that the US weedy rice evolved from *O. sativa* indica and aus rather than *O. sativa* japonica [38]. Genetic diversity of weedy rice from major rice-growing areas of Italy using 19 SSR markers was found to be relatively high with heterozygosity of 0.295 and average alleles of 3.368 [56]. Weedy rice from Uruguay is grouped into three distinct clusters based on their geographical location indicating similar characteristics of plants from similar location [57]. Great diversity in weedy rice accessions from different parts of the world supports the hypothesis that these are derived from natural hybridization among and within the cultivated and wild rice. It should be noted that not all blackhull, brownhull, and strawhull accessions are similar in terms of their genetic makeup or morphology. Their distinct characteristics can significantly affect management strategies that are adopted for controlling weedy rice making the control of weedy rice difficult.

Weedy rice and cultivated rice being closely related to each other have chances of exchanging genetic information. Gene flow from wild species to crop and vice versa has increasing practical implication with development of herbicide-resistant and genetically engineered crops. Transfer of genes conferring biotic and abiotic stress tolerance in crops to the wild species may pose great ecological threat. Thus, gene flow frequency between weedy rice and rice cultivars should be kept in mind while using weedy rice species for rice improvement programs. Studies have shown noticeable gene flow potential between weedy rice, wild rice, and cultivated rice. Gene flow frequency between weedy rice and cultivated rice ranged from 0.011 to 0.046% and between wild rice and cultivated rice ranged from 1.21 to 2.19% approximately [50]. Gene flow frequency from cultivated rice to wild rice (*O. rufipogon*) can be as high as 2.94% [58]. However, most of the gene flow studies have revealed outcrossing rate of up to 1% in *Oryza* species [59]. The variation in gene flow frequency in different studies reveals that the rate of gene flow between cultivated rice and their wild relatives depends upon various factors like weather conditions, density of infestation, and flowering synchrony. Studies have shown a possibility of crop-to-wild gene flow between *Oryza* species. As the infestation of weedy rice is increasing with change in rice production systems and climate change, the problem can become more severe in the future. Thus, steps should be taken to control weedy rice in the rice field, or it might have negative impacts on crop yield as well as the ecology of the area.

6. Conclusions

The research discussed above shows that weedy rice is one of the most successful weeds in rice due to key weedy traits including high seed dormancy and longevity, high seed shattering, high nutrient uptake and nitrogen use efficiency, more tillers, high panicle number and biomass, and tolerance to stresses including herbicides. For successful implementation of management strategies for weedy rice, the physiological and genetic basis of these competitive traits needs to be understood. Further, understanding the mechanism and genetic basis of these competitive traits may provide unique information for rice improvement owing to its close relationship with cultivated rice. However, numerous pros and cons associated with the use of the wild relatives for crop improvement program should be considered before using weedy rice as raw genetic material for developing robust rice cultivars.

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Conflict of interest

The authors declare that this work was presented in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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