

WEEDY RICE: EVOLUTION, THREATS, AND MANAGEMENT

B. MARAMBE

Department of Crop Science, Faculty of Agriculture, University of Peradeniya,
Sri Lanka.

ABSTRACT

Weedy rice (*Oryza sativa* f. *spontanea*) is one of the most notorious weeds occurring in rice growing areas worldwide, and the problem is pervasive. The phylogenetic origin of the weedy forms of rice is closely related to that of the cultivated rice (*O. sativa*). The weedy rice has long been, and will continue to be a major problem throughout the world where rice crops are direct-seeded. Weedy rice, while sharing a number of characteristics with other successful weeds, possess unique characteristics such as phenological and morphological similarity to cultivated rice, belonging to the same species as cultivated rice, etc. Studies carried out in Sri Lanka have shown clear taxonomic differentiation of weedy rice from wild rice but a close relationship with cultivated rice. Evolution of weedy rice in Sri Lanka through de-domestication (becoming feral) cannot be excluded. Weedy rice is currently considered as one of the most troublesome, difficult-to-manage and economically damaging weed problems in Sri Lanka due to its impact on the main staple food crop. Development of a system for producing good-quality seed paddy free of weedy rice seeds is the essential first step in the implementation of control programmes for weedy rice, among many other options available. However, the impact will be limited unless all stakeholders in the rice industry are persuaded that control of weedy rice is possible and needed, and that the control measures have to be integrated and comprehensive.

KEY WORDS: Weedy rice, *Oryza sativa*, Sri Lanka

INTRODUCTION

Cultivated rice was domesticated in Asia during 8,000-15,000 BC (Zhao, 1998; OECD, 1999; Normile, 2004). Two species have emerged as the most popular cultivated rice, namely *Oryza sativa* and *O. glaberrima*, of which the former is more widely distributed and produced. From an early history in the Asian

WEEDY RICE IN SRI LANKA

region, rice has spread and is now grown on all continents except Antarctica. The progenitors of *O. sativa* are the Asian common wild rice species namely, *O. rufipogon* (perennial) and *O. nivara* (annual) (Vaughan and Morishima, 2003). Through domestication *O. sativa* has evolved into many different cultivars that are adapted to a wide range of conditions found in the rice growing regions of the world. In Asia the traits of the rice domestication syndrome are many but, due to the remarkable diversification of rice and introgression with wild rice, few traits are consistently different between wild and domesticated rice. Reduced shattering and reduced dormancy are the principal traits of domestication in rice. Vaughan et al. (2008) reported that the selection of the non-shattering sh4 allele resulted in rice becoming a species dependent on humans for survival.

The evolutionary history of rice is a complex process of selection by humans leading to the development of *O. sativa*. Genetic evidence suggests that rice was domesticated in regions that are suitable for growth of both wild and cultivated rice. The work of Sweeney and McCouch (2007) has shed light on the genetics of the transition from wild (*O. rufipogon* and *O. nivara*) to domesticated (*O. sativa*) rice. In the process of domestication there would have been multiple opportunities within local fields for rice to cross with its wild ancestor. *Oryza sativa* is predominantly autogamous, but does demonstrate low rates of out-crossing including hybridization with some wild rice species. The incidences of natural crossing in rice in other rice areas in Asia had been reported to be about 1% in Japan, 1.3-4% in Java, 2.4% in the Philippines and 0.07% in Sri Lanka (Delouche et al., 2007).

Weedy forms of rice (weedy rice) are one of the most persistent and noxious weeds found in rice-growing ecosystems worldwide (Cao et al., 2007). Being genetically close and having a similar physiological and life history to that of cultivated rice, has made weedy rice create an enormous challenge to farmers and scientists in the Asian region and worldwide in overcoming this biotic constraint to rice production. This paper provides an overview to the origin, threats and management of weedy rice under Asian context with special reference to Sri Lanka.

WILD RICE

Oryza is the only major genus that belongs to the Bambusoideae (Clayton and Renvoize, 1986), where other major cereals belong to Pooidae (barley, wheat

and oats) or Panicoideae (sorghum, and maize). Therefore, the characteristics of rice have been set apart from other cereals. Rice has a small genome, which is the best sequenced among cereals, and is a basic genome standard for comparison with the genomes of other cereals (Bennestzen, 2002).

The diversification of *O. sativa* complex has been primarily a result of the fluctuations of water level in their habitats. The effect of hydrological regime can be illustrated by variation in AA genome of wild rice (Vaughan et al., 2005). Wild AA genome *Oryza* species that grows in permanently deep water have perennial characteristics, while those in seasonally dry ponds have evolved annual characteristics. Vaughan et al. (2005) reported that the variations in hydrological regimes in Asia have resulted in the evolution of a perennial-annual continuum, which is characterized by changes in the breeding system from perennial out-crossing to annual inbreeding.

The AA genome of wild rice is common in Sri Lanka (Vaughan et al., 2005). As stated earlier in this paper, cultivated rice is predominantly self-fertilizing, due to its flower morphology and brief period of pollen viability. Wild rice species differ from cultivars by having a greater ability to out-crossing, longer styles, stigmas and anthers, and pollen that remains viable up to twice as long as in cultivated rice (Oka, 1988). Out of 20 wild rice species recorded worldwide (Vaughan, 1994; Siwakoti and Tiwari, 2007), five species are found in Sri Lanka, namely *O. nivara*, *O. rufipogon*, *O. eichingeri*, *O. granulate*, and *O. rhizomatis*. These usually come from abandoned reservoirs and rice fields, but none of these species have been reported as weedy forms being troublesome to farmers in cultivated rice fields.

WEEDY RICE AND ITS ORIGIN

A central characteristic of weeds, which contributes to their success in agro-ecosystems, is the genetic variability and plasticity found within and among weed populations (Green et al., 2001). This enables weeds to infest a wide range of diverse habitats. Thus, a full understanding of the genetic diversity of weeds is a major prerequisite for their effective management. In addition, elucidating the origin and evolutionary processes of weeds is helpful for designing effective management strategies for weed control (Pys'ek and Prach, 2003). There are three principal processes for the origin of weeds (Baker, 1974; de Wet and Harlan, 1975),

WEEDY RICE IN SRI LANKA

namely (a) wild colonizing plants adapting to continuous habitat disturbances along with the domestication of crop species; (b) derivatives of hybrids between cultivated plants and their re productively compatible wild relatives; and (c) abandoned domesticates evolving towards a less intimate association with man. In addition, back-mutation and segregation of distant inter-varietal hybrids also play certain roles in the origin of weeds (Burger et al., 2006).

Generally, the term “Weedy rice” refers to populations of *Oryza* species that diminish farmers’ income both quantitatively through yield reduction and qualitatively through lowered commodity value at the harvest. Weedy rice of the family Poaceae is a weed accompanying cultivated rice and is widely distributed in rice growing areas all over the world, particularly in South and South-east Asia, South and North America, and southern Europe (Ferrero et al., 1999; Mortimer et al., 2000; Noldin, 2000). Weedy rice, although taxonomically classified as the same species as cultivated rice, is strongly characterized by its seed shattering and dormancy, which apparently increase the distribution of this species. Baltazar and Janiya (2000) reported that various weedy rice accessions shatter most of their seeds before cultivated rice is harvested, so the farmer loses rice yield while filling the soil seed bank with weeds.

Weedy con-specific rice and other *Oryza* spp. have also filled a vacuum and are much harder to deal within direct-seeded rice where the cultivated rice does not have a head start due to transplanting from nurseries (Noldin et al., 1999). Suh et al. (1997) reported that weedy rice has been classified into two groups corresponding to the indica and japonica sub species through genetic characterization of weedy rice accessions associated with *O. sativa*. Further, in both groups, two types with different propagating systems have been recognized; one is a crop mimic type that unconsciously seeds and is harvested by humans mixed with cultigens, and the other is naturally propagating type, which disperse its seeds, although the variation between the two types is continuous. Most weedy rice strains possess seeds with red pericarps; thus it is also referred to as red rice (Gealy et al., 2003) although some strains have white pericarps (Arrieta-Espinoza et al., 2005).

Weedy rice usually involves hybridization and/or selection of shattering types within primary gene pool of the two rice cultigens, namely *O. sativa* and *O. glaberrima* (Vaughan and Morishima, 2003) and their close relatives that share

AA genome. Apart from the AA genome *Oryza* species, only three other species (all in the *O. officinalis* complex) have been reported as weeds in rice fields, namely *O. latifolia* in Central America, *O. officinalis* in the Philippines, and *O. punctuata* in Africa (Vaughan et al., 2005). The appropriate taxonomic names for shattering weedy rice of the AA genome has not been established; however, a widely used name currently applied to weedy rice of the AA genome is *O. sativa* f. *spontanea*.

Weedy rice found in the regions where no wild rice occurs, is probably the derivatives of cultigens. They have naturally being selected for weediness either from cultigens or from progeny of natural hybridization between different cultivars. Such weedy plants may have been established for a long time at low frequency with higher adaptability than the improved cultivars when and where adverse conditions prevailed. Weedy rice found in areas where wild rice exists is probably a derivative of natural hybridization between the cultivar and the wild type grown in the close proximity. Gene flow is mainly from cultivated to wild forms, as the former is predominantly inbreeding where the latter is partially out-crossing. In cases where weedy rice is not related genetically with the associated cultigen, they are supposed to be relics of abandoned cultigens or introduced from outside through mixtures with rice seeds. Recently, Pratheeepha (2009) reported that weedy rice in Thailand might have originated from the introgression between cultivated rice and *O. rufipogon*, which often takes place in nature. This is mostly in a one-way process from cultivated rice to *O. rufipogon*. Akasaka et al. (2009) reported that weedy rice originated from cultivated rice varieties as an "off-type" caused by genetic mutation accompanied by the development of a strong shattering habit. Weedy rice derived from cultivated rice does not escape from the agricultural setting and remain confined to rice fields and their immediate ruderal surroundings (Vaughan et al., 2005), and has higher tolerance levels than the improved cultivars to various adverse environmental conditions such as drought, low temperature, and flooding (Suh et al., 1997).

WEEDY RICE THROUGH DE-DOMESTICATION OF RICE

"Feral", in the case of plants, is defined as plants that derive fully or in part from crop plants that have become partially or fully de-domesticated (Gressel, 2005). Marambe (2005) reported of the possibility of evolution of feral forms of rice by de-domestication of current species on its own (endo-ferality). The first

WEEDY RICE IN SRI LANKA

step-towards ferality may be to become a “volunteer weed”. Persistence of these volunteers in the same fields for extended periods would provide opportunities for selection of back mutations of various feral traits, and then for them to recombine (Al Ahmad et al., 2004). Weedy rice could represent partially de-domesticated forms arising from back mutation with indica characteristics, probably derived from old cultivars. Abandonment of old cultivars and landraces could continue generating locally adopted weedy rice populations, as a result of landraces becoming feral (Valverde, 2005).

Studies carried out by Marambe (2005) indicated that rice plants in abandoned paddies have grown without human intervention, and this could lead to development of feral forms of rice. Abandoning of paddy fields has been common in irrigable areas under minor irrigation schemes (reservoirs with a command area less than 80 ha), and especially under village tank systems especially due to inadequate water storage or rainfall (Karunasena et al., 1997). Apart from scarcity of water for cultivation, a shift of labour from agriculture to industry and youth migrating to the cities for better employment have also resulted in abandoning of rice fields in the rural dry zone of Sri Lanka. Under these circumstances, it is important to ascertain whether the weedy forms have introgressed genes from or through de-domestication of cultivated rice. Haygood et al. (2003) suggested that wild relatives and landraces of crops are the most likely sources of genes for improving crops. This gene flow from wild types to cultivated species may enhance the possibility of evolution of feral forms (exo-ferality), leading to devastating results in the case of rice.

WEEDY RICE IN ASIA

Until recent past, weedy rice has not been among the more important weed problems in Asian rice production due to the dominance of the transplant rice culture (Delouche et al., 2007). Puddling of the soil with retention of a film of water on the surface destroys weed seedlings that have emerged and results in anaerobic conditions that are unfavourable for germination of weed seeds. In addition, the use of relatively well-developed seedlings for transplanting provides a competitive advantage to the rice crop and facilitates the identification of weedy rice and other weed seedlings that do emerge for removal during post-transplant weeding operations. The extensive adoption of direct-seeding technique in rice crop establishment has coincided with the increased occurrence of weedy rice

globally (Chin et al., 1999; Vaughan et al., 2005; Cao et al., 2007). In recent times, weedy rice has been increasingly reported as a major weed problem in Asian countries, such as Malaysia, Sri Lanka, Thailand, India, Republic of Korea, Philippines and Vietnam (Delouche, et al., 2007). The extent of the areas affected by weedy rice varies among the countries. In Thailand, more than 2 million ha are seriously affected by weedy rice, while more than 500,000 ha are also infested in the Mekong River Delta in Viet Nam. Malaysia, Sri Lanka and the Philippines also have substantial areas of paddy production infested with weedy rice.

WEEDY RICE IN SRI LANKA

The shifting agronomy to direct-seeded rice, necessitated by the unavailability of labour for transplanting, has exacerbated weed problems such as *Echinochloa* spp. (Marambe and Amarasinghe, 2002), the sedges (Marambe, 2006) and weedy rice (Marambe and Amarasinghe, 2000; Marambe, 2005). In mid 1990's, weedy rice was first identified in Sri Lanka as a threat from Vavunia, Ampara, and Batticaloa districts (Marambe and Amarasinghe, 2000). At present, the weedy rice has been spread to Puttalam, Anuradhapura, Polonnaruwa, Kurunegala and Matara districts. Ampara is a major rice growing region of the country covering about 67,000 ha of rice land and the district accounts for about 9-10% of the total rice cultivated in Sri Lanka (Marambe, 2005). Dry sowing is common in this district as the soil is non-calcic brown (Haplustalf) that can be easily ploughed under dry conditions. In addition, the scarcity and high cost of labour has forced farmers to dry sowing from transplanting. Direct seeding began supplanting transplanting about 20 years ago in the Ampara district, and has been the predominant practice for the last decade.

Subasinghe et al. (2007) attempted to identify the relationship of weedy forms of rice to cultivated and wild rice available in Sri Lanka using RAPD technique, and the morphological differences of weedy rice when compared to wild and domesticated rice. Six primers, which were used for the analysis of the rice accessions, have produced 38 reproducible polymorphic bands. These data were used to obtain the genetic distances between the five rice accessions as illustrated in the dendrogram (Figure 1). The UPGMA cluster diagram showed four major clusters as A, B, C and D corresponding to the different rice accessions. The Weedy Rice-2 was clustered together with two cultivated rice varieties suggesting a close relation among these three accessions. Bg 300, *Kaluheenati* and Weedy

WEEDY RICE IN SRI LANKA

Rice-2 separate into same cluster 'A' exhibiting exchange of genes between them. Cluster 'A' has divided into two sub clusters and two cultivated varieties were grouped together, which indicated close relationship between them.

From the Sri Lankan studies (Subasinghe et al., 2007), the smallest genetic distance was observed between Bg 300 (a 3 month old, improved variety) and *Kaluheeneti* (a traditional variety), which are the closely related cultivated rice varieties. The highest genetic distance was observed between *O. nivara* and Weedy Rice-2 followed by *O. nivara* and Weedy Rice-1 thus suggesting that these are distantly related rice accessions. Oka (1988) reported that weedy rice often has intermediate characteristics between wild and cultivated rice. However, more samples are required for a precise comparison of genotypes between weedy rice and cultivated rice varieties.

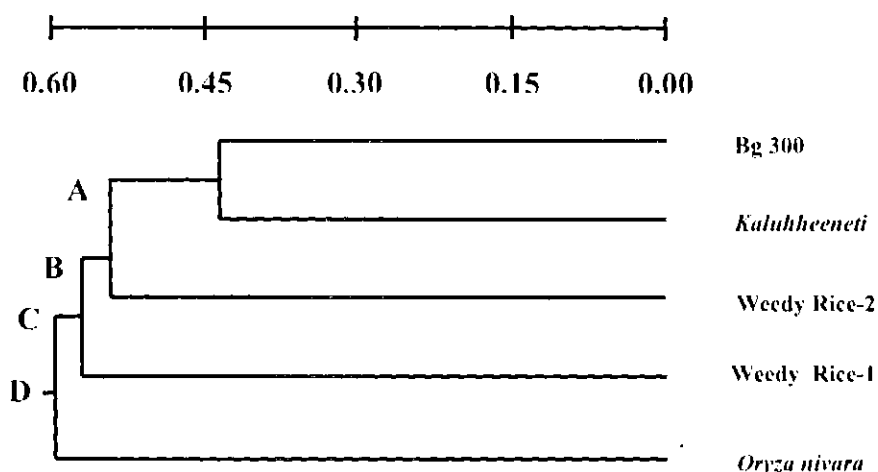


Figure 1. Dendrogram generated by OPF4, OPF16, OPF18, OPM10, OPM18 and OPY11 primers for five accessions tested; Bg 300 – new improved variety, *Kaluheeneti* – traditional variety, *Oryza nivara* – annual wild rice (Source: Subasinghe et al., 2007).

BIOLOGICAL CHARACTERISTICS OF WEEDY RICE

A syndrome of characteristics is usually associated with weedy rice; they

are annual, most commonly found in direct seeded rice fields, generally mature before the crop, with variable degree of shattering and dormancy (Oka, 1988; Ferrero, 2003). Even the older literature in Asia (Graham, 1913; Roy, 1921; Chatterjee, 1947) has always emphasized the importance of shattering, shedding or deciduous nature of the spikelets in the persistence and spread of weedy rice. Weedy rice is frequently awned. On the basis of the awn length four different types of weedy rice has been reported in Sri Lanka (Marambe and Amarasinghe, 2000).

Weedy rice are generally taller, more heavily tillered, more open or spreading, have weaker culms, more susceptible to lodging, produce more straw, germinate and emerge a day or two earlier, emerge from greater depths, and exhibit more rapid seedling growth when compared to the cultivate rice that they infest (Sonnier, 1978; Fischer, 1999; Delouche et al., 2007). The duration of the dormancy varies according to the biotype and the storage conditions of the seeds after shattering, and could range from 1-3 years (Ferrero, 2003), and the longevity of weedy rice could be up to 12 years (Diarra et al., 1985). Seed age, burial depth, flooding conditions and heavy soil all have a negative influence on weed germination and emergence (Ferrero and Finassi, 1995). The germination of weedy rice seeds were reported to be low when compared to those of cultivated varieties (Marambe, 2005; Figure 2), however, it could still be significant in replenishing the soil seed bank aggravating the problem further.

Early seed shattering, which is a specific characteristic of weedy rice, is controlled by the gene *Sh*, which shows the shattering character in conditions of dominant homozygosity (*Sh Sh*) or heterozygosity (*sh Sh*) (Sastry and Seetharaman, 1973). Weedy rice samples collected from Sri Lanka have shown more than 80% shattering with less than 25% of filled grain (Marambe, 2005; Figure 3). Delouche et al. (2007) reported that the main flux of seed shattering in wild rice appears to be about the time the seeds attain physiological maturity and, thus, are fully capable of germination when dormancy is released. However, the seeds of some ecotypes begin to shatter considerably before they attain physiological maturity, even sooner than 10 days after anthesis.

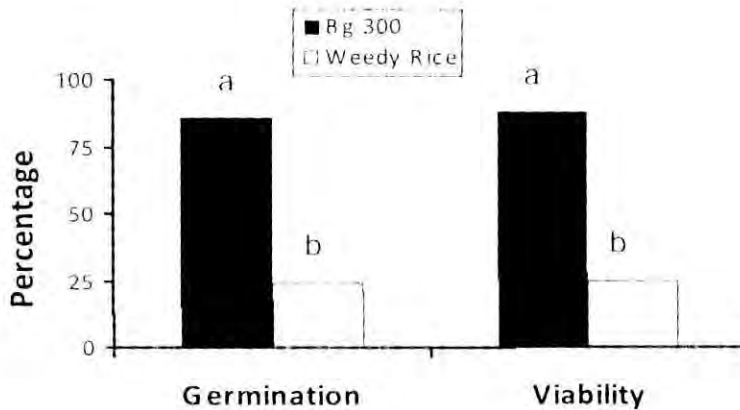


Figure 2. Germination and viability of weedy rice seeds in Sri Lanka compared to rice variety Bg 300 (Marambe, 2005). Within each parameter, bars represented by same letter are not significantly different by the t-test ($p=0.05$).

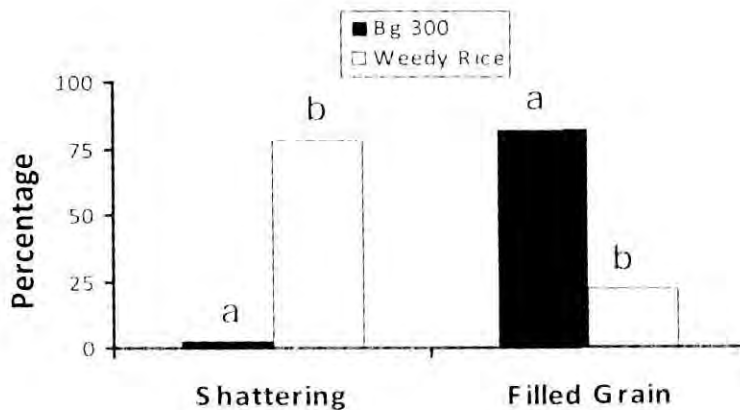


Figure 3. Shattering and filled grain percentage of weedy rice in Sri Lanka compared rice variety Bg 300 (Marambe, 2005). Within each parameter, bars represented by same letter are not significantly different by the t-test ($p=0.05$).

Cross-pollination in rice takes place to a certain extent, and the frequency largely depends on the climatic and varietal differences. Lord (1935) found the frequency of natural out-crossing between different rice varieties in Sri Lanka to range between 0.34 and 0.67 %. Weedy rice has been reported to have an out-crossing rate of 1-52% (Oka and Chang, 1959; Langevin *et al.*, 1996), which is higher than that of cultivated rice.

The morphological characterization of weedy rice collected from Puttalam district in the North Western Province of Sri Lanka indicated that the weedy rice accessions show intermediate characters between Bg 300 (a new improved variety) and *O. nivara*, as reported by Oka (1988). The average number of panicles per plant was significantly higher in weedy rice, but there were higher percentage of unfilled seeds (Subasinghe *et al.*, 2007). The colour of the leaf sheath in *O. nivara* and weedy rice was purple, while it was pale in Bg 300 and *Kaluheenati*, a traditional rice variety (Figure 4).

THREATS AND MANAGEMENT OF WEEDY RICE

Rice farmers in Asia are already reeling from a host of problems, including less land, labour, and water to grow the region's most important crop, as well as the looming impact of climate change. With weedy rice in the rice fields, these farmers are facing perhaps the greatest threat ever faced by the direct-seeded rice crop, because of the close similarity between cultivated and weedy forms. Weedy rice phenotypes occur in more than 50 countries in Africa, Asia, and Latin America (Valverde, 2005). Weedy rice has been reported at damaging levels in Vietnam (Mai *et al.*, 2000), Malaysia (Azmi *et al.*, 2003), Philippines (Fajardo and Moody, 1995), Sri Lanka (Marambe and Amarasinghe, 2000; Marambe, 2005), Korea (Kim and Ha, 2005), and Thailand (Manecchote *et al.*, 2004). Morphologically, weedy rice appears to be an intermediate between wild and cultivated rice. Long-term sympatric distribution has led to similarities between weedy and cultivated rice through natural hybridization and introgression, making the control of weedy rice very difficult when compared with other weeds.

The yield losses from weedy rice have been estimated to vary from 10-100% due to their competitive ability (Marambe and Amarasinghe, 2000). Watanabe *et al.* (1997) reported a yield loss of 60-74% in direct-seeded rice within a 35% infestation level. Eleftherohorinos *et al.* (2002) stated that a density of 40 weedy

WEEDY RICE IN SRI LANKA

rice plants m^{-2} resulted in a yield reduction of 46 - 58 % in rice varieties. According to researches, weedy rice can result in as much as 60% losses when it comprises 35% of the crop or when there is 40 weedy rice plants/ m^2 of the field.

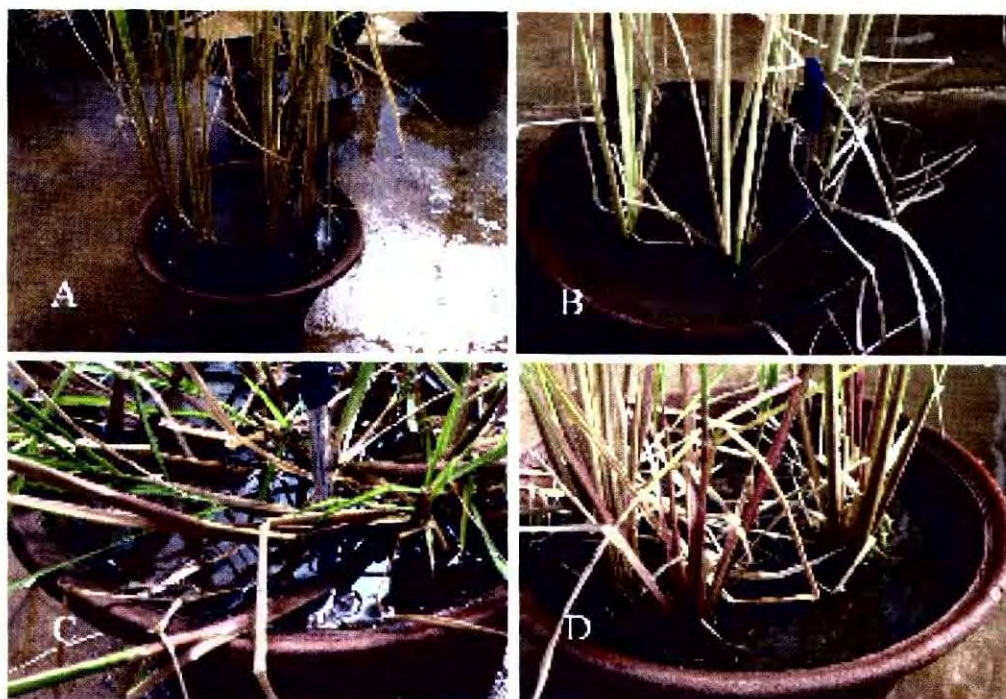


Figure 4. Colour of the leaf sheaths (A – Bg 300; B – Kaluheeneti; C – *Oryza nivara*; D – Weedy Rice)

Once farmers' rice fields are infested, the control costs for weedy rice are high. At present, no single management technique can effectively control the problem. Considering the complexities and multi-dimensional aspects of the diversity, phenology and ecology of weedy rice, the control measures are also complex, difficult, and multi-dimensional, and require exceptional discipline in crop management, patience and, perhaps most importantly, perseverance (Delouche et al., 2007). Ferrero (2003) recommended integrated approaches that combine preventive, cultural and chemical control methods to overcome the problems of these serious weeds (Table 1).

Table 1. Different strategies and methods to control weed rice.

Control Strategy	Control Method
Preventive	Certified seeds Cleaning of machinery Field Inspections
Cultural	Soil tillage (minimum tillage) Fallowing Burning of stubble and straw Stale seed bed preparation Water seeding Water management Rice variety Hand weeding Transplanting Crop rotation
Mechanical	Before rice planting After rice planting
Chemical	Pre-plant Post-plant
Genetic	Biotechnology: Herbicide-resistant rice varieties

Source: updated from Ferrero (2003)

Using clean, certified seeds from a known source and keeping machinery and canals free from weed seeds and infestations is an effective way of controlling weedy rice populations. Manual weeding and good land preparation can also reduce initial infestations of weedy rice. Transplanting had been the major method of weedy rice control (Gressel and Valverde, 2009). In Malaysia, water seeding and control strategies combining preventive and cultural measures have proven to be effective (Vijayanathan, 2006). Appropriate water management particularly on timing and depth of flooding are important factors for controlling weedy rice grown in rice ecosystem (Hamid et al., 2007).

In the USA, imidazolinone-tolerant (IT) rice cultivars have offered an opportunity for selective chemical control, however, rapid gene introgression

WEEDY RICE IN SRI LANKA

into rice has now constrained the utility of this germplasm (Rao et al., 2007). Experience with IT rice shows that gene flow to weedy rice is rapid, negating the utility of the technology. Transgenic technologies are available that can contain herbicide resistance within the crop (cleistogamy, male sterility, targeting to chloroplast genome, etc.).

Gressel and Valverde (2009) proposed to use glyphosate and glufosinate resistances separately as genes of choice, and glufosinate, glyphosate and bentazone susceptibilities as mitigating genes, with a six-season rotation where each stage kills transgenic crop volunteers and transgenic crop $\times$ weed hybrids from the previous season. Biotechnological developments and potentials are providing powerful incentives and resources for finally and fully understanding the eco-physiology of the weedy rice in the shorter rather than the longer term. Other reported chemical control methods application of pretilachlor with fenclorim during final land preparation, and higher seeding rates of more than 150 kg/ha.

CONCLUSIONS

Weedy rice is clearly pre-adapted to the habitat of direct-seeded rice, since it possesses many of the same life-history characteristics as the crop cultivar. The DNA fingerprinting has shown clear taxonomic differentiation of wild rice from weedy rice, which in turn was closely related to the prevailing cultivar. As indicated by Mortimer et al. (2000), there are three mechanisms to explain the occurrence of weedy rice, in the absence of introgression of genes conferring weedy traits from wild relatives to weedy rice; (a) immigration of weedy rice by seed dispersal, (b) cultivar breakdown due to high mutation rates at loci conferring weediness traits and subsequent selection of weedy forms, and (c) heterozygosity within cultivars used by farmers or conserved as on-farm seed. It is a known fact that there is a less chance for ferality when the certified seeds are cultivated. In Sri Lanka the production of certified rice seeds by the state and private sector accounts only to 15% of the total requirement, thus making provision for other un-registered suppliers to produce seeds without proper management practices and certification. Although self-production of seed by the farmers is encouraged, in many cases, successful results have not been achieved due to poor supervision or monitoring of the production process.

The poor knowledge of the genetics of weedy rice hinders the design of effective practical tools and methods for weedy rice management. The effective control of weedy rice cannot be based on one single practice, but should rely on complex management programme based on an appropriate combination of preventive, cultural, mechanical, chemical and genetic means. The potential for the occurrence of “volunteer weeds” in the case of rice to become feral rendering their control more difficult is a possibility. These could arise from de-domestication of volunteer rice that remain from previous seasons. Acquisition of the shattering habit would be the most important factor for the de-domestication of rice varieties. Levels of ferality in currently used and abandoned paddies in Sri Lanka, thus, should be ascertained to establish whether feral characteristics have evolved during de-domestication in paddies in the country.

REFERENCES

- Akasaka, M., J. Ushiki, H. Iwata, R. Ishikawa, and T. Ishii. 2009. Genetic relationships and diversity of weedy rice (*Oryza sativa* L.) and cultivated rice varieties in Okayama Prefecture, Japan. *Breeding Science*. 59: 401-409.
- Al-Ahmad, H., S. Galili and J. Gressel. 2004. Tandem constructs to mitigate transgene persistence: tobacco as a model. *Molecular Ecology*. 13: 697-710.
- Arrieta-Espinoza, G., E. Sa'nchez, S. Vargas, J. Lobo, T. Quesada and A.M. Espinoza. 2005. The weedy rice complex in Costa Rica. I. Morphological study of relationships between commercial rice varieties, wild *Oryza* relatives and weedy types. *Genetic Resources and Crop Evolution* 52: 575-587.
- Azmi, M., A. Sivapragasam, M.Z. Abdulla, and H. Muhamad. 2003. Weedy rice and its management through integration of cultural, physical and chemical interventions in direct-seeded rice. In *International Rice Conference*. (Ed: A. Sivapragasam). pp 1-19. Kedah, Malaysia.
- Baker, H.G. 1974. The evolution of weeds. *Annual Review of Ecology and Systematics* 5: 1-24.

WEEDY RICE IN SRI LANKA

- Baltazar, A.M. and J.D. Janiya. 2000. Weedy rice in the Philippines. In: Wild and Weedy Rice in Rice Ecosystems in Asia – A Review (Ed: B.B. Baki, D.V. Chin, and A.M. Mortimer,). pp 75-78. Limited Proceedings No 2, International Rice Research Institute.
- Bennetzen, J. 2002. Opening to the door to comparative plant biology. *Science* 296: 60-63.
- Burger, J.C., Lee, S., and Ellstrand, N.C. (2006): Origin and genetic structure of feral rye in the western United States. *Molecular Ecology* 15: 2527–2539.
- Cao, Q.J., B. Li, Z.P. Song, X.X. Cai, and B.R. Lu. 2007. Impact of weedy rice populations on the growth and yield of direct-seeded and transplanted rice. *Weed Biology and Management*. 7: 97-104.
- Chatterjee, D. 1947. Botany of the wild and cultivated rice. *Nature* 160: 234–237.
- Chin, V.C., Hach, C.V., Thanh, N.C., and Tai, N.T. 1999. Weedy rice situation in Vietnam. In *FAO. Global workshop on red rice control*, pp. 67–74. Report of Workshop, 30 August – 3 September 1999, Varadero, Cuba. Plant Production and Protection Division. Rome. 155 pp.
- Clayton, W.G. and S.A. Renvoize. 1986. *Genera Graminum*. London HMSO Publication. 387 pp.
- Diarra, A.R.J., R.J. Smith and R.E. Talbert. 1985. Growth and morphological characteristics of red rice (*Oryza sativa*) biotypes. *Weed Science* 33: 310–314.
- Delouche, J.C., N. Burgos, D. Gaely, G. Zorrilla and R. Labrada. 2007. Weedy rices—origin, biology, ecology and control, *FAO Plant Production and Protection Paper* 188, Rome, pp. 3–15.
- de Wet, J.M.J. J.R. and Harlan. 1975. Weeds and domesticates; evolution in man-made habitats. *Economic Botany* 29: 99–107.

TROPICAL AGRICULTURIST, VOL. 157, 2008 & 2009

Eleftherohorinos, I.G., K.V. Dhima and I.B. Vasilakoglou. 2002. Interference of red rice in rice grown in Greece. *Weed Science*. 50: 167-172.

Fajardo, F.F. and K. Moody. 1995. Rice off-types in Central Luzon, Philippines. *International Rice Research Notes*. 20: 9-10.

Ferrero, A. 2003. Weedy rice, biological features and control. In *Weed Management for Developing Countries* FAO Plant Production and Protection Paper 120 Add. 1 (Ed: R. Labrada). UN-FAO, Rome.

Ferrero, A. and A. Finassi. 1995. Viability and soil distribution of red rice (*Oryza sativa* L. var. *sylvatica*) seeds. *Med. Fac. Landbouww., Rijksuniv. Gent*. pp. 205-211.

Fischer, A.J. 1999. Problems and opportunities for managing red rice in Latin America. In *FAO Global Workshop on Red Rice Control*, pp. 77-85. Plant Production and Protection Division. Rome.

Gealy, D.R., N.E. Saldain and R.E. Talbert. 2000. Emergence of red rice (*Oryza sativa*) ecotypes under dry-seeded rice (*Oryza sativa*) culture. *Weed Technology*. 14: 406-412.

Graham, R.J.D. 1913. Preliminary note on the classification of rice in the Central Provinces. *Mem. Dept. Agric. Ind. Bot., Series* 6(7).

Green, J.M., J.H.A. Barker, E.J.P. Marshall, R.J. Froud-Williams, N.C.B. Peters, and G.M. Arnold. 2001. Microsatellite analysis of the inbreeding grass weed Barren Brome (*Anisantha sterilis*) reveals genetic diversity at the within- and between-farm scales. *Molecular Ecology*. 10: 1035-1045.

Gressel, J. and B. Valverde. 2009. 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 Management Science*. 7: 723-731.

Hamid, Z.A.A., M. Mansor and M. Azmi. 2007. The effect of flooding on seed germination of weedy rice (*Oryza sativa* Complex, Locally Called Padi Angin) under plant house condition. *Journal of Bioscience*, 18: 23-33.

WEEDY RICE IN SRI LANKA

- Haygood, R., A.R. Ives, and D.A. Andow. 2003. Consequences of recurrent gene flow from crops to wild relatives. *Proceedings of the Royal Society of London*, 270: 1879-1886.
- Karunasena, K.G.J., B. Marambe, U.R. Sangakkara and P.B. Dharmasena. 1997. Productivity of rice and chilli under village tanks of Sri Lanka in *maha* season with respect to resource utilization. *Tropical Agriculture Research*. 9: 168-181.
- Kim, S.C. and W.G. Ha. 2005. Direct-seeding and weed management in Korea. In *Rice is Life -Scientific Perspectives for the 21st Century*. (Eds: K. Toriyama, K.I. Heong, and B. Hardy). pp 181-184. IRRI, Philippines, and JIRCAS, Japan.
- Langevin, S.A., K. Clay and J.B. Grace. 1990. The incidence and effects of hybridization between cultivated rice and its related weed red rice (*Oryza sativa* L.). *Evolution* 44: 1000-1009.
- Lord, L. 1935. The cultivation of rice in Ceylon. *Journal of Experimental Agriculture* 3: 119-128.
- Mai, V., H.V. Chien, A.V. Van, V. Thi, T. Suong and L.V. Thit. 2000. Rice seed contamination in Vietnam. In *Wild and Weedy Rice Ecosystems in Asia – A Review*. (Eds: B.B. Baki, D.V. Chin and A.M. Mortimer). pp 17-19. Limited Proceedings No 2. International Rice Research Institute, Philippines.
- Maneechote, C., S. Jamjod and B. Rerkasem. 2004. Controlling invasive wild rice with ACCase-inhibiting herbicides. *Proceedings of the 4th International Crop Science Congress*. p 7. Brisbane, Australia.
- Marambe, B. 2006. Control of sedges in Rice Cultivation of Sri Lanka. Chapter 2. In *Management of Sedge weeds in Rice* (Eds: Kil-Ung Kim and R. Labdrada), pp 13-21. Kyungpook National University, Korea.
- Marambe, B. 2005. Properties of rice growing in abandoned paddies in Sri Lanka.

- Chapter 18. In Crop Fertility and Volunteerism (Ed. J Gressel). pp 295-303. Boca Raton, USA, CRC Press.
- Marambe, B. and L. Amarasinghe. 2002. Propanil-resistant barnyardgrass (*Echinochloa crus-galli* L. Beauv) in Sri Lanka: Seedling growth under different temperatures and control. *Weed Biology and Management*. 2: 194-199.
- Marambe, B. and L. Amarasinghe. 2000. Weedy rice in Sri Lanka. In *Wild and Weedy Rice in Rice Ecosystems in Asia – A Review* (Eds: B.B. Baki, D.V. Chin and A.M. Mortimer), pp 79-82. Limited Proceedings No 2. International Rice Research Institute, Philippines.
- Mortimer, M., S. Pandey and C. Piggin. 2000. Weedy rice: approaches to ecological appraisal and implications for research priorities. In *Wild and weedy rice in rice ecosystems in Asia – A Review* (Eds. B.B. Baki, D.V. Chin, A.M. Mortimer), pp 97-105. Limited Proceedings No 2, International Rice Research Institute, Philippines.
- Noldin, J.A. 2000. Red rice status and management in the Americas. In *Wild and weedy rice in rice ecosystems in Asia – A Review* (Eds. B.B. Baki, D.V. Chin, and A.M. Mortimer), pp 21-24. Limited Proceedings No 2, International Rice Research Institute, Philippines.
- Noldin, J.A., J.M. Chandler and G.N. McCauley. 1999. Red rice (*Oryza sativa*) biology. I. Characterization of red rice ecotypes. *Weed Technology*. 13:12-18.
- Normile, D. 2004. Yangtze seen as earliest rice site. *Science*. 275: 309.
- OECD. 1999. Consensus document on the biology *Oryza sativa* (rice). Report No. ENV/JM/MONO(99)26, OECD Environmental Health and Safety Publications, Paris.
- Oka, H.I. 1988. Origin of cultivated rice Japan Scientific Societies Press, Tokyo. 254 pp.

WEEDY RICE IN SRI LANKA

- Oka, H.I. and W.T. Chang 1959. The impact of cultivation on populations of wild rice, *Oryza sativa* f. *spontanea*. *Phyton*. 13: 105-117.
- Prathepha, P. 2009. Seed morphological traits and genotypic diversity of weedy rice (*Oryza sativa* f. *spontanea*) populations found in the Thai Hom Mali rice fields of north-eastern Thailand. *Weed Biology and Management*. 9: 1-9.
- Pys'ek, P. and K. Prach. 2003. Research into plant invasions in a crossroads region: history and focus. *Biological Invasions* 5: 337-348.
- Rao, A.N., D.E. Johnson, B. Sivaprasad, J.K. Ladha and A.M. Mortimer. 2007. Weed management in direct-seeded rice. *Advances in Agronomy*. 93: 153-255.
- Roy, S.C. 1921. A preliminary classification of the wild rices of the Central Provinces and Perar. *Agricultural Journal India*. 16: 365-380.
- Sastry, M.V.S. and R. Seetharaman. 1973. Inheritance of grain shattering and lazy habit and their interrelationship in rice. *Indian Journal of Genetics and Plant Breeding*. 38: 318-321.
- Siwakoti, M. and S. Tiwari. 2007. Emerging needs of wetlands protection for the conservation of wild rice biodiversity in Nepal: A case study from Lumbini area. *Scientific World*, Vol. 5: 95-99.
- Sonnier, E.A. 1978. Cultural control of red rice. In *Red Rice: Research and Control* (Ed. E.F. Eastin), pp. 10-15. Texas Agricultural Experiment Station Bulletin. B-1270.
- Subasinghe, S.A.C.C., A.M. Ranasinghe and B. Marambe. 2007. Molecular characterization of weedy rice in Sri Lanka. *Proceedings of the 21st Asian Pacific Weed Science Society Conference* (Eds: B. Marambe, U.R. Sangakkara, W.A.J.M. De Costa, and A.S.K. Abeysekara), 2-6 October 2007, Colombo, Sri Lanka. pp 469-476.

- Suh, S.H., Y.I. Sato and H. Morishima 1997. genetic characterization of weedy rice (*Oryza sativa* L.) based on morpho-physiology, isozymes and RAPD markers. *Theory of Applied Genetics*. 94: 316-321.
- Sweeney, M. and S. McCouch. 2007. The complex history of the domestication of rice. *Annals of Botany*: 1-7.
- Tang, L., H. Morishima and L.H. Tang. 1997. Genetic characterization of weedy rices and the interference on their origins. *Breeding Science*. 47: 153-160.
- Valverde, B.E., (2005). The damage by weedy rice—can feral rice remain undetected? Chapter 17. In: *Crop Fertility and Volunteerism* (Ed: J. Gressel). pp 279-294. CRC Press, Florida.
- Vaughan, D.A., L.U. Bao-Rong and N. Tomooka. 2008. The evolving story of rice evolution. *Plant Science*. 174: 394-408.
- Vaughan, D.A., P.L. Sanchez, J. Ushiki, A. Kago and N. Tomooka. 2005. Asian rice and weedy rice evolutionary perspectives. Chapter 16. In *Crop Fertility and Volunteerism* (Ed. J Gressel). pp. 257–277. Boca Raton, USA, CRC Press.
- Vaughan, D.A. and H. Morishima. 2003. Biosystematics of the Genus *Oryza*. In: *Rice - origin, history, technology and production* (Eds: W.C. Smith and R.H. Dilday). pp 27-65. Wiley Series in Crop Science, USA.
- Vaughan, D.A. 1994. *The Wild Relatives of Rice – A Genetic Handbook*. International Rice Research Institute, Manila.
- Vijayanathan, V.J. 2006. Control of Weedy Rice Infestation by Enhancing Rice Establishment in Anaerobic Direct Seeding. M.Sc. thesis, Universiti Putra Malaysia.
- Watanabe, H., M. Azimi, and I. Md Zuki. 1997. Emergence of major weeds and their population change in wet-seeded rice fields in the Muda area,

WEEDY RICE IN SRI LANKA

Peninsular Malaysia. Proceedings of the 16th Asian Pacific Weed Science Society. pp 246-250.

Zhao, Z. 1998. The middle Yangtze region in China is one place where rice was domesticated: phytolith evidence from Teh Diaotonghuan Cave, northern Jiangxi. *Antiquity*. 72: 885–897.