Risks of herbicide-resistant rice in India: A review

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Abstract

Herbicide-resistant (HR) rice has the potential to improve the efficiency of weed management and facilitate adoption of resource conservation technologies (RCTs) in India. However, several important risks associated with HR rice should be examined before its widespread adoption is encouraged. The greatest risk in the commercialization of HR crops is the potential for transfer of the gene conferring the HR trait to related wild and weedy relatives. This could lead to increased weediness or invasiveness. Gene transfer between cultivated and wild or weedy rice is known to occur and existing scientific literature confirms that HR genes can move from HR rice to wild and weedy relatives forming hybrids. The likelihood of such gene transfer is especially high in India, where cultivated rice and its relatives are sympatrically distributed and their flowering times overlap. Such gene flow can impact crop invasiveness, fitness of wild species, and the loss of native biodiversity. Additionally, HR rice may contribute to the problems of crop volunteers and evolution of herbicide resistance. Based on existing scientific literature, it appears that these risks are low, but that additional studies are needed to fully assess the potential adverse consequences of widespread adoption of HR rice in India.
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1. Introduction

Rice is the world's most important crop and is the staple food for more than half of the population (Khush, 2004). About 90% of rice production and consumption worldwide occurs in Asia (Gealy et al., 2003). In India, about 42 million hectares of rice are grown annually (FAO, 2004). The rice–wheat cropping system of the Indo-Gangetic Plains, occupying nearly 13.5 million hectares, is the most important cropping system for food security in the region. At present, sustainability of this cropping system is at risk as yields of both rice and wheat are static and total factor productivity is declining.

In India, rice is grown traditionally by transplanting rice seedlings into puddled soils. This method reduces weed competition and water percolation losses (Sanchez, 1973), but repeated puddling leads to degradation of soil physical

properties, contributes to formation of hard pans (Sharma and De Datta, 1985), and delays planting of the succeeding wheat crop (Hobbs and Morris, 1996). Labour and water scarcity, and soil health issues are factors stimulating the switch from transplanted to direct-seeded rice (DSR). In recent years, resource conservation technologies (RCTs) like zero tillage (ZT) and bed planting are being promoted in the rice–wheat cropping systems for both rice and wheat to reduce cultivation costs, energy consumption, and to improve soil health and profits. DSR eliminates puddling and does not require continuous submergence, which reduces water consumption. Research is underway to develop non-puddled, flat-surface or raised-bed and/or zero-till planting systems for DSR.

Weed control is a serious challenge in non-puddled DSR because the initial flush of weeds is no longer controlled by flooding (Baltazar and De Datta, 1992; Olofsdotter et al., 2000). Adoption of herbicide-resistant (HR) rice may overcome the problem of weed management in DSR and facilitate the adoption of RCTs (Malik et al., 2003; Kumar

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et al., in press). Three HR systems have been developed in rice: imidazolinone-, glufosinate-, and glyphosate-resistant varieties (Gealy et al., 2003). Glufosinate- and glyphosate-resistant rice were developed through transgenic technologies and convey resistance to these broad-spectrum, non-selective herbicides. Imidazolinone-resistant rice is not a transgene because it was developed through chemically induced seed mutagenesis and conventional breeding and conveys resistance to the imidazolinone group of herbicides (Gealy et al., 2003).

Despite the potential benefits of HR rice for promoting adoption of RCTs (Kumar et al., unpublished), there are several important risks associated with this technology. Cross-pollination between transgenic crops and sexually compatible wild and cultivated non-transgenic rice cultivars is the major pathway for gene escape (Lu et al., 2003; Scott and Burgos, 2004; Zhang et al., 2004). Cross-pollination can either increase or decrease the fitness of recipient species resulting in greater weediness or extinction (Ellstrand, 2003). The impacts of transgenic crops may be greater in the centres of origin of crops than elsewhere because wide arrays of wild progenitors, wild species, and land races are present there.

The debate about the environmental risks associated with transgenic organisms started with their first development. By the end of 1980s, a consensus developed that transgenic crops may pose environmental risks. Risk assessment is needed on a case-by-case basis, taking into account the transgene, recipient organism, intended release environment, and the frequency and scale of introduction (Andow et al., 1987; National Research Council (NRC), 1987; Tiedje et al., 1989; Andow and Zwahlen, 2006). Key categories of environmental risks associated with transgenic crops include (1) non-target and biodiversity risks; (2) gene flow and recombination; and (3) evolution of resistance in target organisms (Snow and Morán-Palma, 1997; Wolfenbarger and Phifer, 2000; NRC, 2002; Snow et al., 2005).

Non-target and biodiversity risks associated with HR rice are especially critical in India, one of the centres of biodiversity of wild rice. The foremost concern is the possibility of the transgene transfer conferring the resistant trait through gene flow to compatible weedy or wild *Oryza* species. Hancock (2003) suggested that the environmental risks of many transgenic crops can be assessed from already available information on the biology of the crop, the presence of compatible wild or weedy relatives, and the transgene phenotype. In this paper, we have attempted to summarize possible concerns of HR rice in India.

2. Wild and weedy relatives of rice in India

Centres of origin of crops are rich in biodiversity and contain land races with wide arrays of phenotypic diversity, wild progenitors, and wild species (Gepts and Papa, 2003). India has been identified as the centre of origin of rice (DeCandolle, 1886; Vavilov, 1926), and many wild and weedy relatives are present in rice-growing areas in India. Suh et al. (1997) classified weedy rice from different countries into two distinct groups corresponding to *indica* and *japonica* cultivars, each of which were further classified into forms resembling either cultivars or the wild type. Indian weedy rice belonged to group II (*indica* group similar to wild type) which means that these weedy rice strains may have originated from hybridization between wild and cultivated rice.

A critical first step in the assessment of gene flow and its consequences is identification of cultivated and wild or weedy relatives that can hybridize with HR rice in the region. There are more than 20 wild species in the genus *Oryza* (Brar and Khush, 1997; Khush, 1997). These are divided into four species complexes (*sativa*, *officinalis*, *ridleyi*, and *meyeriana*) (Aggarwal et al., 1999; Olofsdotter et al., 2000). These species with their genomes and distributions are listed in Table 1. Because *O. nivara and O. rufipogon* share the same genome AA as cultivated rice, HR rice crop can easily cross with them (Olofsdotter et al., 2000). In contrast, other wild species such as *O. malamphuzhaensis* (BBCC), *O. officinalis* (CC), and *Oryza granulata* (GG), present in India with genomes different from AA are difficult to cross with cultivated rice (Brar and Khush, 1997). The Western Ghats region of South India is rich in biodiversity of wild *Oryza* species including *O. rufipogon*, *O. nivara*, *O. granulata*, *O. malampuzhaensis*, and *O. officinalis* (Vaughan and Sitch, 1991; Thomas et al., 2001). The Bhoothathankettu, Parambikulam, and Kuralai forest reserves along the Western Ghats in Kerala have been identified for *in situ* conservation of these wild rice species by the International Rice Research Institute (Vaughan and Sitch, 1991). In India, *O. sativa* f. *spontanea* is considered a weedy species in cultivated rice.

In some northwestern states of India (e.g. Haryana and Punjab), wild and weedy relatives are not present, thus, there are very low risks of gene flow from HR rice to wild and weedy species except risks of gene flow from crop to crop. However, in eastern India (e.g. eastern Uttar Pradesh, Bihar, Orissa, Manipur, and West Bengal) and southern India, wild and weedy relatives are common and gene flow may occur from HR rice to these species.

3. Likelihood of gene flow from HR rice

Gene flow is "the incorporation of genes into the gene pool of one population from one or more other populations" (Futuyma, 1998, p. 767). Gene flow is ubiquitous even in self-pollinated crops if compatible species present are sympatrically distributed and their flowering times overlap. These two conditions are pre-requisites for gene flow to occur.

Geographical distribution data suggest that transgene movement from cultivated rice to wild relatives may occur (Vaughan, 1994; Lu et al., 2003). Wild and cultivated rice are sympatrically distributed in large parts of India (Vaughan et al., 2005). Therefore, gene flow is likely to

Table 1
Genus *Oryza*: species with their genome and distribution

Species	Genome	Distribution
***Oryza sativa* complex**		
O. sativa L.	AA	Worldwide, cultivated
O. nivara Sharma et Shasty	AA	Tropical and subtropical Asia
O. rufipogon Griff. (= *O. perennis* Moench)	AA	Tropical and subtropical Asia, tropical Australia
O. glaberrima Steud.	AA	West Africa, cultivated
O. barthii A. Chev. (= *O. breviligulata* A. Chev. et Roehr)	AA	Africa
O. glumaepatula Steud.	AA	Central and South America
O. longistaminata A. Chev. et Roehr.	AA	Africa
O. meridionalis Ng	AA	Australia
***Oryza officinalis* complex**		
O. punctata Kotschy ex. Steud. (2n = 24)	BB	Africa
O. punctata Kotschy ex. Steud. (2n = 48)	BBCC	Africa
O. minuta J. S. Pesl. ex. C. B. Presl.	BBCC	Philippines and Papua New Guinea
O. malamphuzhaensis	BBCC	India
O. eichingeri A. Peter	BBCC	South Asia and East Africa
O. officinalis Wall. Ex. Watt	CC	Tropical and subtropical Asia, tropical Australia
O rhizomatis Vaughan	CC	Sri Lanka
O. alta Swallen	CCDD	Central and South America
O. grandiglumis (Doell) Prod.	CCDD	Central and South America
O. latifolia Desv.	CCDD	Central and South America
O. australiensis Domin.	EE	Tropical Australia
***Oryza meyeriana* complex**		
O. granulata Nees et Arn. ex. Watt	GG	South and Southeast Asia
O. meyeriana (Zoll. et Mor. ex Steud.) Baill.	GG	Southeast Asia
***Oryza ridleyi* complex**		
O. ridleyi Hook. f.	HHJJ	South Asia
O. longiglumis Jansen	HHJJ	Irian Java, Indonesia, Papua New Guinea
Species not included in any complex		
O. brachyantha A. Chev. et Roehr.	FF	Africa
O. schlechteri Pilger (2n = 48)	HHKK	Papua New Guinea
O. neocaledonica Morat (2n = 24)	??	New Caledonia

Classified according to species complexes. Reproduced with permission from Annals of Applied Biology, Blackwell Publishing Ltd., Oxford, UK. *Source*: Olofsdotter et al. (2000).

take place from HR rice in rice-producing areas of India where these wild and weedy relatives overlap.

The flowering time of wild rice varies significantly depending on geographical distribution (Lu et al., 2003). A study in China, showed that wild rice, *O. rufipogon*, and two cultivated rice cultivars viz. a late-maturing local variety and an improved variety (Minghui-63) had a significant overlap in their pollination and flowering timing (Lu et al., 2003). Wild rice usually has a protracted flowering period at each locality (Lu and Snow, 2005), which creates more favourable conditions for overlap of flowering with cultivated rice.

Gene flow from HR rice to wild and weedy relatives has been widely studied in the US, Europe, and China (Estorninos et al., 2002; Gealy et al., 2003; Song et al., 2003; Chen et al., 2004; Messeguer et al., 2004; Shivrain et al., 2006). In most of these studies, outcrossing rates were found to be less than 1%. Langevin et al. (1990) observed that the natural hybridization rate can range from 1% to 52%, depending on cultivar type. Outcrossing is

generally higher between Indica cultivars and wild species than with Japonica cultivars (Oka, 1988). Studies on gene flow from rice to weedy or wild rice are reviewed in Gealy et al. (2003), Lu and Snow (2005), and Lu et al. (2003).

In addition to gene flow from HR rice to its wild and weedy relatives, gene flow from HR rice to conventional rice cultivars is another risk in India. The contamination of Basmati rice (long grained aromatic rice) by gene flow is a major concern because India is one of the world's largest exporters. Information on gene flow from crop to crop is important especially if GM rice must be separated from non-GM rice for market acceptability. Messeguer et al. (2001) found 0.05–0.53% gene flow from HR rice to adjacent plants of non-HR rice counterparts. Rong et al. (2007) found that gene flow from crop to crop was dramatically reduced within a short distance from transgenic rice. For example, gene flow declined from 0.3% at 0.2 m to <0.01% at 6 m from transgenic rice. Gene flow from HR rice to non-HR-rice cultivars has the potential to increase the opportunities

of subsequent gene flow to wild or weedy relatives (Lu and Snow, 2005).

Information on the distance of pollen dispersal is essential for establishing an effective buffer zone to prevent gene escape to wild species and to avoid contamination of non-transgenic rice cultivars. The distance of gene flow is influenced by environmental factors especially wind speed and direction, ambient temperature, and relative humidity (Jackson and Lyford, 1999; Galan et al., 2000). Song et al. (2003) found gene flow from cultivated rice to *O. rufipogon* at a maximum distance of 43 m. Rice pollen flow has been detected up to 110 m (Song et al., 2004a).

Careful monitoring of HR rice is needed even in those areas where wild or weedy relatives are not present because with the adoption of DSR, problems of weedy rice would likely emerge. For example, weedy rice is becoming an acute problem in areas where transplanting is being replaced by DSR such as in Vietnam, Malaysia, SriLanka, Thailand, and Korea (Baki et al., 2000).

4. Effects of HR trait on crop invasiveness

Once a transgene is introduced into wild or weedy relatives, its long-term persistence in the environment depends on several factors, including whether the transgene confers a fitness benefit. The main potential harmful consequences of gene flow include: (1) increased fitness of wild relatives and hence evolution of increased weediness or invasiveness; (2) the loss of an effective tool (HR crops) to control closely related weeds; and (3) loss of biodiversity (e.g. increased likelihood of extinction of wild relatives) (Ellstrand et al., 1999; Gepts and Papa, 2003).

There are two main pathways by which a transgenic organism or its resistant gene could increase invasiveness in natural ecosystems: self-sustaining populations in the wild or introgression of genes (Wolfenbarger and Phifer, 2000). Crawley et al. (2001) conducted a 10-yr study on the performance of four transgenic crops (oilseed rape, potato, maize, and sugar beet) grown in 12 natural habitats. They found that these transgenic crops were no more invasive or persistent than their conventional counterparts in any of the habitats studied. The HR trait is unlikely to have any additional risks of increasing invasiveness in a natural setting, since most HR traits in crops are considered neutral in the natural environment (Duke and Cerdeira, 2005; Stewart et al., 2003). Current literature suggests that HR crops including rice are no more likely to be invasive in either agricultural or natural settings in the absence of the herbicide than their conventional counterparts (Lavigne et al., 1995; Hails et al., 1997; Snow et al., 1999; Oard et al., 2000; Zhang et al., 2003).

Another potential risk associated with the introduction of HR rice is the problem of HR-crop volunteers. A volunteer is a crop plant which grows in the subsequent crop or year in the same field from the seed loss from harvest of HR crops (Warwick and Stewart, 2005). Rice can be a volunteer weed in the next year's rice crop or any other subsequent crop. Glyphosate and glufosinate are currently used as burn-down herbicides before planting crops in ZT systems. Volunteer HR rice could limit the option of using these herbicides in ZT systems. The presence of HR volunteer rice would require use of other herbicides to control volunteers (Gealy, 2005). HR volunteer rice would also serve as a potential pollen source for dispersal of transgenes to weedy or wild relatives. Volunteer problems will be more challenging in ZT systems and also in Southern India where rice is grown multiple times a year.

5. Effect of HR trait on fitness of crop-wild hybrid

Most of the studies on fitness of crop-wild hybrids have compared fitness of conventional crop × wild hybrids to their parents. Such studies have been conducted on multiple crops including sorghum (Arriola and Ellstrand, 1997), sunflower (Snow et al., 1998), radish (Klinger and Ellstrand, 1994; Snow et al., 2001), rice (Langevin et al., 1990; Song et al., 2004b), canola (Jørgensen et al., 1996; Hauser et al., 1998a, b), and carrot (Hauser, 2002). In these studies, crop-wild hybrids demonstrated enhanced (e.g. Langevin et al., 1990; Klinger and Ellstrand, 1994), reduced (Jørgensen et al., 1996; Hauser et al., 1998b; Snow et al., 1998, 2001), or equal fitness (Arriola and Ellstrand, 1997; Song et al., 2004b) compared to wild controls.

To more fully evaluate the impact of HR transgenes on fitness of wild populations, the fitness of HR vs. non-HR crop × wild hybrids needs to be considered. Few studies have estimated the fitness of HR vs. non-HR crop × wild hybrids (rice, Oard et al., 2000; Zhang et al., 2003; sunflower, Massinga et al., 2005; and oilseed rape, Snow et al., 1999). Most of these studies found no direct positive or negative impact of the HR transgene on the fitness of crop × wild hybrids.

Different transgenes can have different impacts on fitness. Transgenes, which have the potential to release weedy or wild populations from constraints that restrict or limit their fitness, can exacerbate weediness and invasiveness (Lu and Snow, 2005). For example, Snow et al. (2003) demonstrated that the presence of an insect-resistant (*Bt*) transgene increased the fecundity of wild sunflower compared to its non-transgenic counterparts. Ecological theory suggests that HR traits have some costs associated with them in the absence of herbicide use (Bergelson and Purrington, 1996). These costs may be because of pleiotropy, insertion sites within the genome (linkage to deleterious alleles), and physiological costs of resistant traits (Bergelson et al., 1996). Fitness costs have been demonstrated for resistance to many herbicides including triazines (Bergelson et al., 1996; Holt and Thill, 1994; Gressel, 2002). However, HR traits are not always costly in the absence of herbicides and in some cases may even enhance fitness (Plowman et al., 1999). For example, no fitness cost was found to be associated with glufosinate-resistant genes in weedy *Brassica rapa* introgressed from

glufosinate-resistant oilseed rape (Snow et al., 1999). Plowman and Richards (1997) reported that susceptible (S) biotypes of *B.rapa* outperformed the resistant (R) biotypes at high light and medium temperatures, whereas at low light and high temperatures, R-biotypes out-competed S-biotypes.

If the resistance trait has a negative effect, wild relatives may be reduced in size (demographic swamping) (Levin et al., 1996; Wolfe et al., 2001), and can lead to extinction (Ellstrand and Elam, 1993; Levin et al., 1996). Alternatively if a resistance trait has a positive effect, the hybrid may become invasive (Tiedje et al., 1989). Pollen-mediated gene flow from crops to wild relatives is implicated in the evolution of weediness and extinction risk in several crops, including rice (Ellstrand et al., 1999).

The relative fitness effects of HR traits depend at least in part on the mechanism of resistance. For target-site-based herbicide resistance, an associated decrease in plant fitness in the absence of herbicide is well documented for triazine herbicides (Holt and Thill, 1994; Gressel, 2002). This is because target-site mutation decreased the efficiency of photosynthetic electron flow through photosystem II, and consequently reduced fitness. In contrast to the triazines, resistance to ALS inhibiting herbicides does not consistently reduce plant fitness (Holt and Thill, 1994; Tranel and Wright, 2002). For example, Mallory-Smith et al. (1992) and Thompson and Thill (1992) found no evidence for decreased fitness in sulphonylurea-resistant (R) biotypes of *Kochia scoparia* compared to susceptible (S) biotypes originating from Kansas and North Dakota. Dyer et al. (1993) found that sulphonylurea R-biotypes from Montana germinated faster than S-biotypes but it is unclear what effect, if any, this has on relative fitness. Christoffoleti and Westra (1991) reported that ALS R-biotypes from Colorado appeared less competitive than S-biotypes. Potential fitness advantages (e.g. rapid germination under cool temperatures) in ALS R-biotypes have been demonstrated by many authors (Dyer et al., 1993; Thompson et al., 1994; Eberlein et al., 1999). However, Bergelson et al. (1996) demonstrated fitness costs associated with the ALS inhibitor resistance gene in *Arabidopsis thaliana*. For non-target-site-based resistance, costs may be associated with increased allocation of resources for production of novel detoxifying enzymes (Coley et al., 1985; Herms and Mattson, 1992). In this case, fitness costs depend on whether enzyme production is constitutive or induced by herbicide applications (Strauss et al., 2002). Because glyphosate- and glufosinate-resistant crops exploit the detoxification strategy (non target-based) (Tan et al., 2006), fitness costs may be associated with these traits. However, Snow et al. (1999) reported no fitness cost of the transgenic glufosinate-resistant trait introgressed from *Brassica napus* into weedy *B. rapa*. In contrast, glyphosate-tolerant *Ipomoea purpurea* biotypes from Georgia, USA, were less fit and produced 35% fewer seeds than S-biotypes in the absence of glyphosate (Baucom and Mauricio, 2004).

The effects of HR traits on the fitness of wild or weedy relatives of rice are summarized in Table 2. In all the fitness-related studies conducted so far on rice, the HR trait had no effect on hybrid fitness in the absence of herbicide. For example, glufosinate-resistant rice × red-rice hybrids and subsequent progeny were statistically similar to their susceptible counterparts in certain vegetative (plant vigour, plant density) and reproductive traits (dormancy and seed production) (Oard et al., 2000; Zhang et al., 2003). Cultivated rice (non HR) × wild rice (*O. rufipogon*) or red-rice hybrids were taller and had more tillers at the vegetative stage (Langevin et al., 1990; Song et al., 2004b) but had lower seed set and pollen viability than their wild parent (Song et al., 2004b).

6. Effect of the herbicide resistance trait on native biodiversity

Transgene flow can cause the erosion of genetic diversity in wild populations (Ellstrand, 2003). The possible impacts of transgenic HRCs on biodiversity may be caused by (1) leakage of resistant traits into related wild populations by hybridization; (2) acquisition of fitness traits by wild relatives through introgression with the HRC; and (3) impacts on non-target species (Thompson et al., 2003).

The possible effects of gene flow on the loss of biodiversity may occur through genetic assimilation, in which crop genes replace the genes in wild species through continuous hybridization or through demographic swamping, whereby hybrids are less fertile than their wild types and hence the population of wild plant shrinks in size (Levin et al., 1996; Wolfe et al., 2001). The populations which are small and rare are at higher risk and can be lost by swamping. Swamping has been implicated in the near extinction of *O. rufipogon* ssp. *formosana*, a wild relative of rice in Taiwan (Kiang et al., 1979 cited in Ellstrand et al., 1999). To our knowledge, no studies have been conducted on the long-term effects of HR traits on native biodiversity or effects on rare taxa.

Gene flow poses problems in *in situ* conservation of wild biodiversity. Wild species and landraces are critical sources of genetic diversity for plant breeding (Braun and Bennett, 2001; Ellstrand, 2003). The forested hills of the Jeypore tract of Orrisa and Western Ghats region of South India are highly rich in native rice diversity (Vaughan and Sitch, 1991; Thomas et al., 2001). Other states where genetic diversity is rich and varied include: Uttar Pradesh, Bihar, West Bengal, Madha Pradesh, and many South Indian States. In Koraput district of Orrisa alone, scientists identified about 1500 rice land races (Richharia and Govindaswami, 1990). In Jeypore, native rice cultivars have fallen from 1750 to about 150 due to use of commercial cultivars. HR rice, therefore, has the potential to impact the *in situ* conservation of wild biodiversity, especially if transgenes confer any fitness advantage or penalty.

Table 2
Effect of transgenic HR traits on the relative fitness of rice-wild/weedy hybrid

Hybrid classification	Parents	Traits studied	Hybrid outcomes	Conclusion	Reference
F1 hybrid	Cultivated rice (non-HR) × red rice	Biomass production	Rice–red-rice hybrids demonstrated enhanced vegetative vigour, and hence to their total fitness	Hybrids more fit	Langevin et al. (1990)
F1 hybrid	Cultivated rice (non-HR) × wild rice (*O. rufipogon*)	Whole life history	1. Slightly inferior at sexual reproduction stage (lower seed set and pollen viability) 2. Superior (hybrid vigour) at vegetative stage (plant height and number of tillers) Overall performance similar to their wild parents	No fitness advantage	Song et al. (2004b)
F1 hybrid and F2 population	Cultivated rice [both transgenic HR (glufosinate-resistant) and non-HR] × red rice		Transgenic and non-transgenic-red-rice hybrids were tall compared to parental lines Seed fertility reduced in both transgenic and non-transgenic hybrids	HR trait (BAR gene) did not improve fitness or seed fecundity in F1 hybrid or subsequence progeny	Zhang et al. (2003)
F2 population	Cultivated rice [both transgenic HR (glufosinate-resistant) and non-HR] × red rice (four biotypes)	Vegetative and reproductive both	No significant difference seen in plant vigour, density, or seed dormancy Plant height and maturity: Louisiana (LA) populations derived from transgenic lines were significantly different from those developed from non-transgenic lines. Conversely, value for these traits was not greater than those found in red-rice biotypes Seed shattering: Arkansas (AR) populations derived from transgenic rice lines had higher shattering than population from non-transgenic rice lines but no significant difference was observed among LA population. However, seed shattering value was not greater than that found in red-rice biotypes	HR trait did not increase or decrease fitness value for reproductive success traits such as dormancy and seed production	Oard et al. (2000)

Lu and Snow (2005) proposed that gene flow from transgenic rice will not threaten the genetic diversity of wild relatives any more than gene flow from conventional varieties. Moreover, the fitness effects of the HR trait are likely to be small compared to other traits like disease, insect, or drought resistance, since the HR trait in HRCs is considered neutral in the absence of herbicide use.

7. Herbicide resistance in weeds

Another potential concern with HRCs is evolution of HR weeds due to increased reliance on herbicides for weed control (Owen and Zelaya, 2005). At present, about 310 resistant biotypes have evolved resistance to 19 different target-site chemistries (Heap, 2006). Evolution of herbicide resistance in weeds through selection pressure poses greater risks than development of resistance through gene flow in related species in those HRCs in which frequency of interspecific hybridization and subsequent introgression is often low (Beckie et al., 2001; Warwick et al., 2004). Development of resistance in weeds to glyphosate was considered unlikely because of its unique site of action. However, evolved glyphosate resistance was observed in *Conyza canadensis* 3 years after adoption of glyphosate-resistant soybean (VanGessel, 2001). Other weed species that also have evolved resistance to glyphosate include: *Lolium rigidum* in Australia (Powles et al., 1998), *Eleusine indica* in Malaysia (Lee and Ngim, 2000), and *L. multiflorum* in Chile (Perez and Kogan, 2003). Recently, glyphosate-resistant *Amaranthus palmeri* was confirmed in Georgia (Culpepper et al., 2006).

Evolution of resistance in weeds to ALS-inhibitor herbicides has been reported more frequently than any other herbicides. This is because they exert strong selection pressure as a result of high activity on susceptible biotypes as well as persistent soil residual activity (Tranel and Wright, 2002). It is estimated that mutation frequency for ALS-herbicide resistance in *O. sativa* could be 10^{-8}–10^{-9}

(Olofsdotter et al., 2000), much lower than normal mutation frequency for ALS inhibitors in other plants, which is estimated at about 10^{-6} (Chaleff and Day, 1984). Hence, resistance development to ALS-inhibiting herbicides (IMI-rice) in weedy rice through selection pressure might require more time than other species (Olofsdotter et al., 2000). Gene flow from IMI rice to weedy rice could, however, hasten resistance development in weedy rice.

The risks of development of herbicide resistance can be minimized with an integrated weed management approach. Long-term studies conducted by Powles et al. (1997) on the management of HR *L. rigidum* in Australia have confirmed that IWM can be very effective in management of HR weeds. IWM strategies include crop rotation, rotation of herbicides with different modes of action, herbicide mixtures, using the concept of critical period of weed control, adjusting cultural practices, use of HR rice, mechanical weeding, and use of stale seed bed practices. Beckie (2006) recently reviewed both herbicide (sequences and rotation, mixtures, application rate, site-specific application, and use of HRCs) and non-herbicide (crop rotation, cultural practices, and mechanical practices decision support system) tactics for the management of HR weeds. Integrating non-herbicide weed management practices with selective use of herbicides have mitigated the evolution and spread of HR weeds.

8. Conclusions and future research needs

The foremost concern associated with the commercialization of HR rice is transfer of the HR trait to wild and weedy relatives via gene flow. Gene flow from HR rice through crop-to-wild or weedy relatives is possible because in large parts of India many wild and weedy relatives of rice are sexually compatible, have sympatric range, and overlapping flowering times. However, the consequences of escaped HR transgenes are largely unknown. Resistant traits can potentially reduce the native biodiversity either by increased weediness (if the resistant trait confers a fitness benefit) or by increased likelihood of extinction of wild relatives (if the resistant trait confers fitness penalty). Based on currently published data, these potential risks are relatively low because the HR traits have not shown any fitness penalty or benefits to wild species in the absence of herbicide and HR trait in HRCs is considered neutral. There will be minimal risk in the northwestern Indian states of Punjab and Haryana as there are no wild or weedy relatives of rice present, but direct seeding in rice would potentially promote the problem of HR-weedy rice. The risks of gene flow and their consequences are higher in eastern and southern Indian states. Full assessment of the risks of HR rice would benefit from increased research in the following critical areas:

(1) Information on the current geographic distribution of cultivated rice and wild rice species and their time of flowering needs to be updated to predict the likelihood of gene escape from HR rice to wild and cultivated rice. There is a need for morphological and phenological characterization of the wild rice present in India.
(2) Further evaluation of hybridization rates between HR rice and its wild and weedy relatives present in India to determine the compatibility differences and heterosis potentials of hybrids between wild relatives and HR-rice cultivars.
(3) Information on the frequency and distance of outcrossing from HR rice to wild/weedy relatives and to conventional rice cultivars including basmati type under Indian conditions. This information will help in mitigating risks associated with gene flow by using spatial isolation between HR rice from wild relatives and conventional cultivars.
(4) More research on the consequences of gene flow to improve understanding of the effects of different HR traits on the fitness of wild relatives under Indian conditions.
(5) Research for the development of integrated management strategies to minimize the risk of development of herbicide resistance in weed populations in India. Regionally based agronomic research is needed to develop best management practices for weed control and resistance management (Gealy et al., 2003).

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