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Role of herbicide-tolerant (HT) rice in the weed management of direct seeded crop: Challenges and opportunities

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Abstract: Food insecurity which has been a global threat, forces researchers to develop crops with increased productivity even under varying climatic conditions. Rice, being a significant staple and strategic crop, helps ensure economic stability, food, and nutritional security globally. It meets 20% of the calorie requirement of people residing all over the world. Lately, rice cultivation and research have been facing hitherto unprecedented difficulties in the context of climate-induced water scarcity and dwindling resources of manpower, arable land, etc. In this regard, direct seeded rice (DSR) as a resource conservation technique is gaining popularity as a potential alternative to conventional transplanting with reduced input requirement, reduced methane and CO₂ emission, increased adaptability to climate change, and increased economic returns. The weed menace in DSR prevents it from reaching its fruitful attainment to a significant level. DSR highly depends on herbicide for weed control as manual weeding and other cultural practices are labour intensive which again meets a setback of crop injury (non-selective herbicide) and resistant weeds (selective herbicides). Herbicide-tolerant (HT) rice could be an effective and long-term solution for weed management in DSR. Three HT rice systems, viz., imidazolinones, glyphosate, and glufosinate, have already been developed in this context. This review gives an insight into the need for HT rice in DSR, its production system, limitations, and stewardship guidelines for proper weed management in rice.

Keywords: direct seeded rice; gene flow; herbicide; herbicide tolerance; weed menace

Rice is an integral part of the staple diet of more than 60% of the global population is cultivated throughout the world with approximately 90% of the global production from Asian countries (Fukagawa & Ziska 2019). Rice, popularly known for its paramount role in sustaining food and nutritional security, acts as a source of dietary intake for 20% of the world's population (Bin Rahman & Zhang 2023) and meets 43% of the calorie requirement of nearly two-thirds of the Indian population (Shankari et al. 2023). India being the second largest producer and consumer of rice next to China, produces 129.47 million tonnes of rice from 46.27 million hectares of area with a productivity of 2 798 kg/ha (INDIASTAT 2020–21; www.indiastat.com). By 2035, a whopping 114 million tonnes of milled rice should be produced additionally, which equates to a 26% boost in the upcoming 25 years (Dorairaj & Govender 2023). There isn't much scope for increasing the arable land under rice. In a bid to ensure long-term sustainability, this rising demand will need to be satiated by less water, less land, labour, and chemicals.

Among the facets of global warming, climate-induced water scarcity is one of the pressing issues affecting agriculture productivity (Sandhu et al. 2013), especially rice, which exploits nearly 50% of freshwater resources for field preparation and irrigation (Mythili et al. 2020). Rice, being a semi-aquatic crop, is cultivated in a broad spectrum of agro-ecosystems ranging from flooded wetland to rainfed dryland, namely flood-prone deep water, irrigated, rainfed lowland and rainfed upland. 75% of the rice production is predominately from irrigated rice system, which occupies 55% of the global rice area (Sandhu et al. 2021). As a crop with a high affinity for water, rice requires 3 000 L of water for the production of 1 kg of rice under puddled conditions (Anandan et al. 2022). In recent years, rice cultivation and research have been facing hitherto unprecedented difficulties owing to their water-sensitive nature, fluctuations in climatic conditions, diminishing arable lands, escalating labour, and water shortage, which necessities the search for alternative crop establishment methods with increased water productivity without impairing crop productivity in the slightest. In this regard, water and labour shortages in both rainfed and irrigated areas could be efficiently addressed by direct seeded rice (DSR) technology (Sagare et al. 2020).

DIRECT SEEDING RICE – A POTENTIAL ALTERNATIVE TO PUDDLED TRANSPLANTING RICE

Amidst the other crop establishment methods, puddled transplanting is predominantly employed for rice cultivation in the tropical regions of Asia as it provides competitive advantage to rice seedlings to suppress weed growth, increased nutrient availability, better establishment of seedlings, reduced seepage loss and elevated production. Contrary to the aforementioned benefits, transplanting is both water and labour intensive which are the most limiting factors in the present scenario as Asia is anticipated to experience a “physical water scarcity” by 2025 which affects around two million hectares of dry-season lowland rice and thirteen million hectares of wet-season lowland rice (Tuong & Bouman 2003) and agricultural labour forces are shrinking at a rate of 0.1–0.4% with 0.2% annually on average (Dawe 2005). Puddling alone accounts for 30% (1 300 to 1 500 mm) of the overall water requirement. Apart from that, the seasonal water utilization in the puddled transplanted rice (PTR) system varies from 660 to 5 280 mm regarding the growing season and transpirational loss (Sandhu et al. 2013). In terms of using groundwater for irrigation, India is at the top of the list, which resulted in a decline of available groundwater by 0.5 to 1.0 megalitres per year (Mythili et al. 2020). A 10% decrease in the amount of water used in irrigated rice will free up to 150 000 million m³, or around 25% of the total freshwater used for non-agricultural purposes globally (Meena et al. 2019). The other major cascade of setbacks limiting traditional PTR system are increased labour wages, depletion of soil fertility, a decline in resource use efficiency, negative impact on subsequent crop, greenhouse gas emission and environmental problems. The potential benefits of both PTR and DSR are compared in Figure 1.

Direct seeded rice, a resource conservation technique is gaining popularity as a potential alternative to conventional transplanting concerning reduced input requirement, methane and CO₂ emission, and increased economic returns (Nie & Peng 2017). DSR is an impending version of upland rice cultivation where rice is sown directly in the un-puddled soil and unsaturated soil. It is regarded as the best alternative crop establishment method with water productivity of 64 to 88%, less labour requirement (50% less), reduced methane and nitrous oxide emission, and

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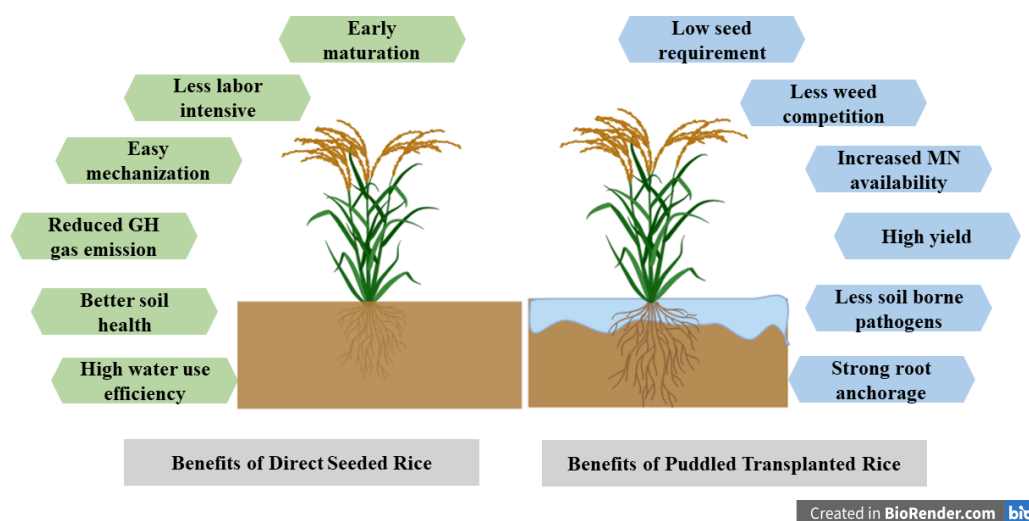


Figure 1. Comparison of potential benefits of puddled transplanted rice and direct seeded rice
GH – greenhouse; MN – micronutrient

adaptability to climate change. The predictions of depleting water resources under a varying climate and escalating labour scarcity have brought a paradigm swing from conventional transplanted rice to DSR in many countries namely, India, Malaysia, Sri Lanka, Vietnam (Rao et al. 2007) and United States, Latin America, Australia, West Africa and Europe (De Datta & Baltazar 1996). Coastal districts of Tamil Nadu *viz.*, Cuddalore, Thiruvavur, Nagapattinam, and Pudukkottai are witnessing an increased area under DSR due to the prevailing water scarcity (Robin et al. 2022).

IMPLICATIONS OF WEEDS ON DSR

Weed infestation is the major setback in DSR which holds accountable for the yield loss ranging from 15–20%, but in severe case, it may exceed 50% or even can cause complete failure (Sen et al. 2021) and the extent of loss yield caused by weeds in different establishment methods is depicted in Table 1.

In India, weed-triggered yield loss under DSR is in the range of 20–85% (Rao et al. 2007). Direct seeded rice is comparatively subjected to much higher weed pressure as it germinates together with weeds, eliminating the “head start” of transplanted seedlings. Weeds being a major threat in direct seeded rice, not only competes with rice for resources but also harbours pests and diseases, which ultimately hamper the productivity of rice. The weed-free environment should be maintained till 70 days after sowing (DAS) to achieve desirable productivity, although the crucial period of weed rice competition is till 41 DAS (Chauhan & Johnson 2011). Grover et al. (2020) advocate that with effective weed management, DSR yields are almost identical to those of transplanted rice. Weed control by manual weeding and cultural practices is restricted as they are labour-intensive and cumbersome in the context of labour scarcity. Thus, the application of broad-spectrum herbicides is an effective and economical way to control weeds under DSR and the development of herbicide-tolerant

Table 1. Extent of yield loss in various rice establishment methods

| Rice establishment methods | Yield reduction due to weeds (%) | References |
|------------------------------|----------------------------------|--------------------------|
| Upland rice | 97 | Singh et al. (2011) |
| Dry-seeded rice | 90 | Chauhan and Opeña (2012) |
| Upland direct seeded rice | 80 | Sharma et al. (2007) |
| Transplanted puddled rice | 57 | Mahajan et al. (2009) |
| Wet direct seeded rice | 85 | Singh et al. (2011) |
| Dry seeded rice zero tillage | 98 | Singh et al. (2011) |

rice varieties is one of the feasible and practical long-term solutions.

WEED FLORA AND THEIR DYNAMICS

Although the initial composition of weeds in DSR may not differ significantly from that of PTR, over time, a notable shift of weed flora towards more species-rich plants, particularly grassy weeds and sedges, was reported (Bhullar et al. 2018). In PTR, the predominant weed species reported by Ramachandra (2010) were *Echinochloa crus-galli*, *E. colona*, *Cyperus iria*, *C. rotundus*, *C. difformis*, *Ammania baccifera* and *Eclipta alba* while Reddy (2010) observed *Echinochloa crus-galli*, *C. difformis*, *Fimbristylis miliacea*, *Eclipta alba* and *Ammania baccifera* as the dominant weed species in DSR. Mythili et al. (2020) discerned the predominance of grassy weeds in DSR namely, *Echinochloa crus-galli*, *Cynodon dactylon*, *Chloris barbata*, and *Brachiaria reptans* followed by *Cyperus rotundus* (sedge) and broad-leaved weeds viz., *Basilicum polystachyon*, *Bergia ammannioides*, *Eclipta prostrata* and *Alternanthera paronychioides*. This was found to be following the previous report of weed spectrum found in DSR by Rao et al. (2007). Weed flora in rice is found to be regional-specific. In the USA, the weeds that are commonly found in rice field include red rice (*Oryza sativa*), *Echinochloa crus-galli*, *Sagittaria montevidensis*, *Echinochloa oryzicola*, *Cyperus iria* and *Ammania auriculata* (Heap 2014) while in Brazil, *Echinochloa crus-galli*, red rice (*Oryza sativa*) and *Leersia hexandra* under grasses, *Cyperus difformis*, *C. laetus*, *C. esculentus* and *C. ferax* under sedges, *Ipomoea* sp., *Hymenachne amplexicaulis*, *Alternanthera philoxeroides* and *Aeschynomene* sp. under broad-leaved weeds were

found to be the major weed flora in rice. Red rice and barnyard grass were found to be the omnipresent weeds causing major yield loss in most of the rice-growing countries viz., USA, Australia, Spain, etc. Some of the major weeds and their impact on rice yield are depicted in Table 2.

CHEMICAL CONTROL OF WEEDS IN RICE

Herbicide-based weed control is the most feasible option considering the non-availability of water and manpower. Herbicides suppress weed infestation by inhibiting/ interfering with the enzymatic pathway of branched-chain amino acids (acetolactate synthase (ALS) inhibitors), aromatic amino acids (glyphosate), photosynthetic activity (photosynthesis inhibitors), disrupting cell membrane, lipids (acetyl-CoA carboxylase (ACCase) inhibitors), etc., which ultimately results in the death of plants. The mode of action of these herbicides is pictorially represented in Figure 2. Rational and need-based application of herbicide plays a pivotal role in weed management in DSR. The list of pre- and post-emergence herbicides recommended for rice under DSR is listed in Table 3.

NEED FOR HERBICIDE RESISTANCE IN RICE

Weed Science and Society of America in 1998 defined herbicide tolerance as “the inherent ability of the crop species to survive and procreate after herbicide application without the influence of selection and genetic manipulation” while herbicide resistance is defined as “the inherited ability of a plant to survive and reproduce even after being exposed to a dosage

Table 2. Major weeds of rice and their impact on yield loss

| Weeds | Scientific name | Yield loss in rice (%) | Reference |
|-----------------------------|-------------------------------|------------------------|--------------------------|
| Red rice/weedy rice | <i>Oryza sativa</i> | 80 | Shivrain et al. (2010) |
| | | 90 | Ferrero (2003) |
| Barnyard grass | <i>Echinochloa crus-galli</i> | 7–50 | Shekhawat et al. (2020) |
| | | 13–55 | Zhang et al. (2017) |
| Nut grass | <i>Cyperus rotundus</i> | 20–90 | Peerzada (2017) |
| Flat sedge | <i>Cyperus iria</i> | 64 | Dhammu and Sandhu (2002) |
| Jungle rice | <i>Echinochloa colona</i> | 27–62 | Rao and Matsumoto (2017) |
| Small-flower umbrella plant | <i>Cyperus difformis</i> | 12–50 | Moody et al. (1984) |
| Hoorah grass | <i>Fimbristylis miliacea</i> | 42 | Hakim et al. (2011) |
| False daisy | <i>Eclipta prostrata</i> | 10 | Lee and Moody (1989) |

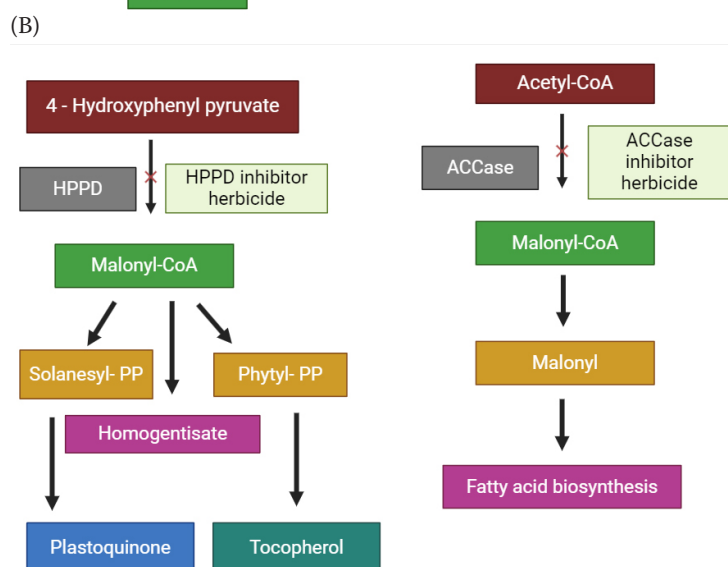


Figure 2. Amino-acid biosynthesis inhibitors *viz.*, AHAS inhibitors, glufosinate and glyphosate inhibiting the enzymatic biosynthesis of branched chain amino-acids, glutamine and aromatic amino-acids respectively (A); site of action of HPPD inhibitor and ACCase inhibitor herbicides and corresponding inhibition of biosynthesis of plastoquinone, tocopherol and fatty acid respectively (B)

AHAS – acetohydroxy acid synthase; HPPD – 4-hydroxyphenylpyruvate dioxygenase; ACCase – acetyl-CoA carboxylase; TCA – triacid cycle; GS – glutamine synthetase; PP – diphosphate; red cross indicates the inhibition of reaction

mutagenesis". Thus, herbicide tolerance is a natural ability while herbicide resistance is an acquired ability of plants to withstand the harmful effects of her-

Table 3. Recommended herbicides for rice cultivation

| Herbicide | Application time (DAS) | Dose (g a.i./ha) | Mode of action | Effective | Ineffective |
|-----------------------------|------------------------|------------------|--|---|--|
| Pendimethalin | 1–3 | 1 000 | microtubule assembly inhibitor | effective against grasses, some sedges and BLW | – |
| Oxadiargyl | 1–3 | 90 | protoporphyrinogen oxidase inhibitor | effective against broad spectrum of weeds | – |
| Pyrazosulfuron | 1–3 or 15–20 | 20 | ALS inhibitor | effective control of <i>Cyperus rotundus</i> , other sedges, grasses and BLW | ineffective against <i>L. chinensis</i> and <i>Dactyloctenium aegyptium</i> |
| Bispyribac-sodium | 15–25 | 25 | ALS inhibitor | efficient control of wide spectrum of weeds particularly <i>Echinochloa</i> sp. | poor on grasses namely, <i>L. chinensis</i> , <i>Dactyloctenium aegyptium</i> , <i>Eleusine indica</i> , and <i>Eragrostis</i> sp. |
| Penoxsulam | 15–20 | 22.5 | ALS inhibitor | wide-spectrum control of grasses, broad leaves weeds and sedges | poor on grasses namely, <i>L. chinensis</i> , <i>Dactyloctenium aegyptium</i> , <i>Eleusine indica</i> , and <i>Eragrostis</i> sp. |
| Fenoxaprop-ethyl | 25 | 60 | ACCase inhibitor | effective against grassy annual weeds | ineffective against BLW and sedges |
| Fenoxaprop-ethyl + safener | 15–20 | 60–90 | ACCase inhibitor | effective against grassy annual weeds | ineffective against BLW and sedges |
| Cyhalofop-butyl | 15–20 | 120 | ACCase inhibitor | effective against grassy annual weeds | ineffective against BLW and sedges |
| Propanil | 15–25 | 4 000 | photosynthesis at photosystem-II inhibitor | effective against wide range of weeds | – |
| Azimsulfuron | 15–20 | 17.5–35 | ALS inhibitor | effective against wide range of weeds especially <i>Cyperus rotundus</i> | ineffective control of <i>Echinochloa</i> sp. |
| Ethoxysulfuron | 15–20 | 18 | ALS inhibitor | effective on BLW and annual sedges | poor control on grasses and ineffective against perennial sedges like <i>Cyperus rotundus</i> |
| Triclopyr | 15–20 | 500 | synthetic auxins | effective on BLW | no effect on grassy weeds |
| 2,4-D ethyl ester | 15–25 | 500 | synthetic auxins | effective against BLW and annual sedges | – |
| Carfentrazone | 15–20 | 20 | protoporphyrinogen oxidase inhibitor | effective on BLW | no effect on grassy weeds |
| Chlorimuron + metsulfuron | 15–25 | 4 (2 + 2) | ALS inhibitor | effective against BLW and annual sedges | no effect on grassy weeds and ineffective against <i>C. rotundus</i> |
| Bispyribac + azimsulfuron | 15–25 | 25 + 17.5 | ALS inhibitor | effective against wide range of weeds including <i>C. rotundus</i> | poor control on grasses besides <i>Echinochloa</i> sp. |
| Fenoxaprop + ethoxysulfuron | 15–25 | 56 + 18 | ACCase and ALS | effective against grassy weeds viz., <i>L. chinensis</i> and <i>D. aegyptium</i> and other BLW and sedges | poor on perennial sedges such as <i>C. rotundus</i> |

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Table 3 to be continued

| Herbicide | Application time (DAS) | Dose (g a.i./ha) | Mode of action | Effective | Ineffective |
|--------------------------|------------------------|------------------|---|---------------------------------|---|
| Propanil + pendimethalin | 10–12 | 4 000 + 1 000 | photosynthesis and microtubule assembly inhibitor | controls wide spectrum of weeds | ineffective control on perennial sedges like <i>C. rotundus</i> |
| Propanil + triclopyr | 15–25 | 3 000 + 500 | photosynthesis and synthetic auxins | controls wide spectrum of weeds | ineffective control on perennial sedges like <i>C. rotundus</i> |

DAS – days after sowing; a.i. – active ingredient; ALS – acetolactate synthase; ACCase – acetyl-CoA carboxylase; BLW – broad-leaved weeds; adopted and modified from Kumar and Ladha (2011)

bicide. Repeated use of selective herbicides leads to the evolution of weeds with herbicide resistance, while the application of broad-spectrum herbicides is hampered by crop sensitivity, which limits their effective utilization in weed management. Red/ weedy rice (*Oryza sativa* f. *spontanea*) has become a notorious weed, causing a potential yield loss of 15 to 100% in the areas, which evidenced swift change from TPR to DSR (Kumar & Ladha 2011). Red rice management in DSR is extremely difficult due to their morphological and genetic synteny with rice which hinders their targeted control using selective herbicides without injuring the rice crop. It is the need of the hour to develop herbicide-tolerant rice varieties suitable for direct-seeded rice cultivation systems, which are reinforced by the factors. Namely, the availability of efficient novel herbicide molecule, increased cost of manual weeding, reduced herbicide cost, scarcity of labour and needs for mechanization. There are three herbicide-tolerant rice (HTR) systems viz., Liberty Link® (glufosinate tolerant), Roundup Ready® (glyphosate tolerant), and Clearfield® (imidazolinone tolerant) developed and commercialized by Bayer Crop Science, Monsanto and BASF (Duke 2005) respectively. Among these systems, Clearfield® rice is alone a non-transgenic developed through chemical mutagenesis while others were produced through transgenics. These three HT rice systems have been compared in Table 4. The herbicide-tolerant rice systems put forward numerous benefits viz., (i) effective management of a wide range of weed species using non-selective herbicides with little to no phytotoxic effect on rice; (ii) provides flexibility in selecting suitable crops for rotation as they do not have any residual effect; (iii) reduced crop injury; (iv) flexibility in the management practices as the herbicide can be sprayed at any stage of crop growth and (v) effective utilization of resources which results in enhanced productivity of rice. The imidazolinone group of herbicides are highly preferred over other herbicides for breeding herbicide-tolerant crops owing to their characteristics like controlling a wide range of weeds, effective at a low application rate, low mammalian toxicity and having a good environmental profile. Farmers were able to selectively control 95 to 100% of the weedy rice population by spraying imazethapyr (Avila et al. 2005) with the advent of imidazolinone resistant Clearfield® rice (Tan et al. 2005).

Table 4. Comparison of three herbicide-tolerant rice systems with different mode of action

| Inhibitor | Imidazolinones | Glyphosate | Glufosinate |
|---|--|--|---|
| Herbicide | | | |
| Target enzyme | AHAS | EPSPS | GS |
| Target amino acid | valine, leucine and isoleucine | tryptophan, phenylalanine, and tyrosine | glutamine |
| Pathway involved | branched chain amino acid biosynthesis pathway | aromatic amino acid biosynthesis pathway | glutamine biosynthesis pathway |
| Nature of enzyme – substrate | uncompetitive | uncompetitive, competitive | competitive |
| Dosage (g a.i./ha) | 20–1 700 | 160–4 200 | 320–1 560 |
| Application method | foliar, soil | foliar | foliar |
| Time of application | pre-emergence, post-emergence | post-emergence | post-emergence |
| Residual effect | yes | no | no |
| Acute rat oral toxicity (LD ₅₀ g/kg) | > 5.0 | 5.6 | 1.91 |
| Herbicide-tolerant rice | | | |
| Commercialized crop name | Clear Field® | Roundup Ready® | Liberty Link® |
| Developed by | BASF | Monsanto | Bayer Crop Science |
| Mechanism of tolerance | tolerant AHAS | tolerant EPSPS, detoxification of glyphosate | detoxification of glufosinate |
| Method of development | mutagenesis | genetically engineered | genetically engineered |
| Foreign gene inserted | none | <i>gox</i> gene obtained from <i>Agrobacterium</i> sp. strain CP4, <i>Ochrobactrum anthropic</i> strain LBAA | <i>bar</i> or <i>pat</i> gene obtained from <i>Streptomyces hygroscopicus</i> , <i>S. viridochromogenes</i> |
| Modified or inserted target-site gene | variant AHAS gene | CP4-EPSPS or modified maize EPSPS gene | none |

AHAS – acetohydroxy acid synthase; EPSPS – 5-enolpyruvylshikimate-3-phosphate synthase; GS – glutamine synthetase; a.i. – active ingredient

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MECHANISM OF HERBICIDE TOLERANCE

Deciphering the molecular, physiological, and biochemical mechanisms behind the herbicide tolerance of genotypes is imperative to develop HT varieties suitable for DSR cultivation system. The mechanisms which are considered to confer resistance

to herbicides in crops are the exclusionary resistance mechanism, metabolic detoxification, differential resistance at the site of action, and overexpression of the target enzyme (Figure 3). The order of degree of herbicide resistance is primarily due to metabolic detoxification (Duke & Cerdeira 2010) followed by differential resistance at the site of action and

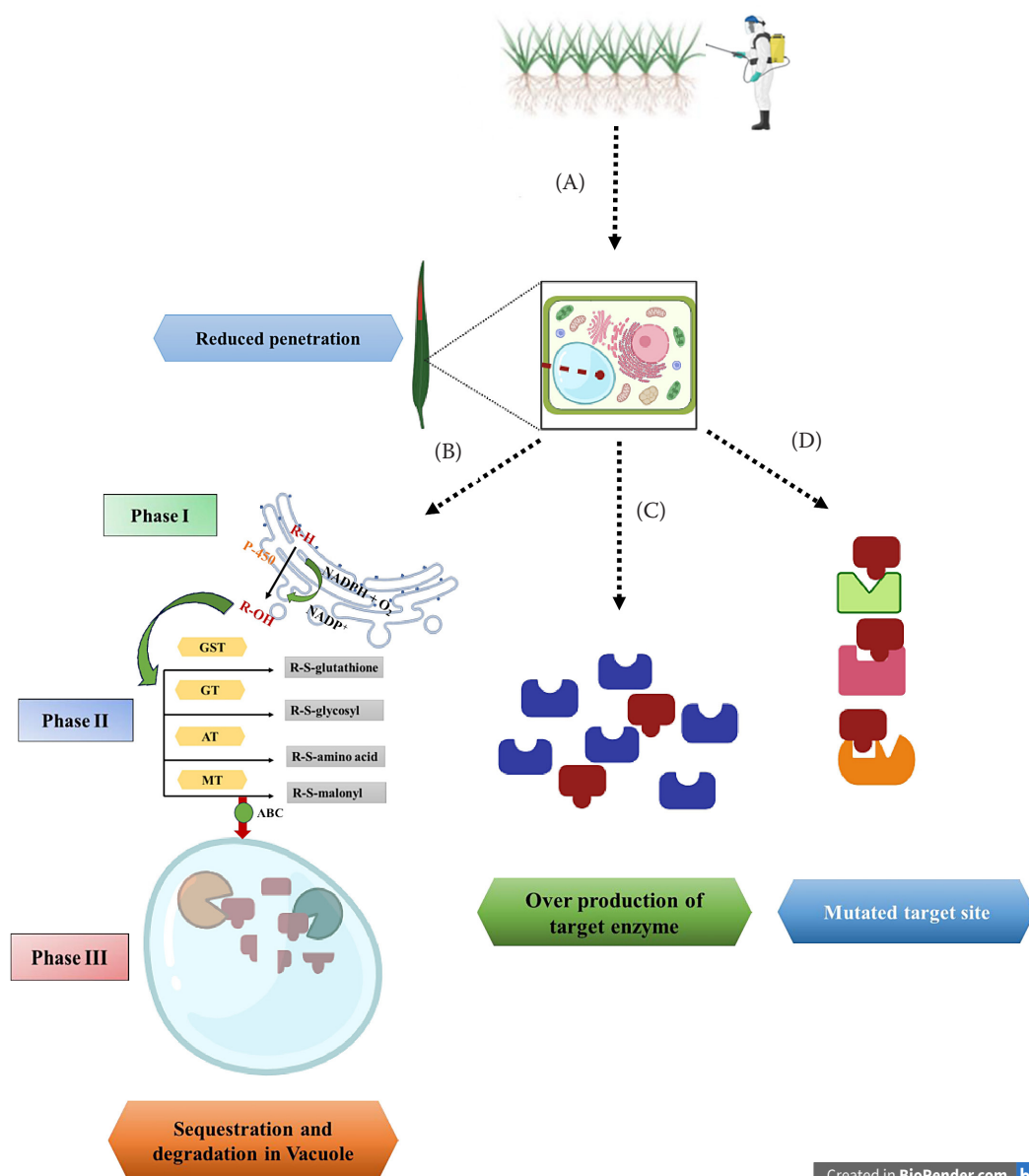


Figure 3. Mechanisms involved in the herbicide resistance in plants: reduced penetration of herbicide into plants (A); Phase I – functionalization of herbicide molecule, Phase II – hydroxylation and conjugation of herbicide, Phase III – sequestration/compartimentalization into vacuole and subsequent degradation of herbicide (B); overproduction of target site of action renders herbicide to be ineffective (C); mutation at the specific target site of action results in reduced affinity for herbicide binding (D)

R-H – alkane; R-OH – alcohol; P450 – cytochrome P450 monooxygenase; GST – glutathione-S-transferase; GT – glycosyl transferase; AT – amino acid transferase; MT – malonyl transferase; ABC – ATP-binding cassette

exclusionary resistance mechanism and with the advent of site-directed mutagenesis, overexpression of target enzyme is found to confer herbicide resistance in crops.

Exclusionary resistance mechanism. It is the physiological and morphological adaptations of the plants that prohibit the entry of the herbicide molecule into the target sites. Plants are bestowed with adaptive structures like cuticles, waxes, etc., which act as a first-level defence mechanism prohibiting the entry of herbicide molecules. Herbicide molecules are inactivated either through sequestration (binding) or translocated to metabolically inactive regions like cell walls and vacuoles (compartmentalization) by encasing them in vacuoles, dispersing them with exudates, and restricting their movement within plants thereby averting their detrimental effects. This mechanism is found in glyphosate-resistant plants which accumulate glyphosate molecules in the leaves, preventing their further movement within the plants. Ge et al. (2010) observed *Conyza canadensis* and *Lolium rigidum* compartmentalizing 85% of the glyphosate into the vacuoles.

Metabolic detoxification. One of the extensively employed mechanisms by plants against herbicides is the degradation or solubilization of toxins into non-toxic form by enhanced metabolism well before reaching the target site. Herbicides are detoxified through biochemical processes like oxidation, hydrolysis, reduction, and conjugation. The hydroxylation mechanism is commonly witnessed in plant resistant to cyanazine, bromoxynil, 2,4-D, and propanil. *HIS1* (4-hydroxyphenylpyruvate dioxygenase (HPPD) inhibitor sensitive 1) gene identified by Maeda et al. (2019) in rice encodes Fe^{2+/2-}-oxoglutarate-dependent oxygenase that confers resistance to β -triketone and benzobicyclon herbicides by detoxification through hydroxylation mechanism. Cytochrome P450 plays a significant role in the detoxification of numerous herbicides through hydroxylation or dealkylation of ALS-, PS II – and ACCase inhibitors in addition to their pivotal role in various metabolic processes of lipids, secondary metabolites and hormones making them indispensable in the plant (Yu & Powles 2014). As of now, in rice only one cytochrome P450 gene conferring tolerance to photosynthesis inhibiting herbicide, bentazone has been identified.

Differential resistance at the site of action. All herbicides have a specific site of action, which is either controlled by a single or few genes, any change or mutation in that site will prevent herbicide from

binding to them which confers resistance to the corresponding herbicides. This mechanism of altering the target site of action is the prime focus on developing resistance crops through site-directed mutagenesis. Most of the herbicide-resistant plants are found to have various target site specific mutations which make them resistant to various herbicides *viz.*, ALS, ACCase, 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) inhibiting herbicides. JD164, a rice variety with an altered site at S627N of the *AHAS* gene, conferred resistance to imazethapyr. Altered enzyme spatial conformation and reduced protein affinity for herbicides were the reasons behind the resistance towards ALS inhibitor herbicides caused by the mutation of amino acids in the ALS domain (Jin et al. 2022). Zhang et al. (2022) highlighted the cause of glufosinate resistance in *Eleusine indica* to be a naturally evolved point mutation involving Ser₅₉Gly substitution in *EiGS₁₋₁* and transformed rice calli with this mutant *EiGS₁₋₁* gene which showed resistance to glufosinate. OsGS1:1, a rice glutamine synthetase mutant harbouring Gly and Arg at positions 59 and 296 respectively showed elevated tolerance towards glufosinate (Deng et al. 2019).

Overexpression of the target enzyme. Herbicide resistance can also be achieved by over-production of the target molecular site of action *via* amplification of genes encoding target enzymes and their enhanced expression. As each herbicides target specific protein, their overproduction in plants makes the effect of herbicide to be negligible (Mulwa & Mwanza 2006). This mechanism is widely exploited in the commercialization of glyphosate-resistant transgenic crops. Hu (2014) observed that the over-expression of glutathione-S- transferase gene (*OsGSTL2*) in rice conferred enhance tolerance towards chlorsulfuran and glyphosate. Likewise, over-expression of cytochrome P450 genes in rice exhibited higher resistance against various herbicides with different mode of action through rapid degradation of herbicide molecules (Chen et al. 2009).

CONVENTIONAL BREEDING APPROACHES FOR HERBICIDE TOLERANCE

Screening of germplasm. Rice is considered the most highly diverse crop among the cereals. Rice germplasm exhibits variability for the traits *viz.*, plant height, grain quality, days from emergence to flowering, herbicide tolerance, yield, and other stress-related traits. The working collection of USDA-

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ARS rice germplasm containing 17 279 accessions was evaluated for 30 descriptors with herbicide tolerance as one among them and identified accessions conferring tolerance to non-selective herbicides *viz.*, glyphosate and sulfosate (Dilday et al. 1999). Kuk et al. (2008) unveiled the presence of the vast amount of genetic variability within the rice germplasm for various herbicides. The germplasm should be evaluated by screening under herbicide-sprayed conditions where germplasm lines are sprayed with varying doses of respective herbicides. The lines should be evaluated for the parameters namely, average plant stand, leaf damage score, days to flowering, days to maturity, floral development, photosynthetic ability, normalized difference vegetation index (NDVI) score, difference in yield between control and herbicide sprayed (treatment), harvest index, *etc.*, (Prakash et al. 2017). Further screening of the selected best lines should be carried out at multi locations for stability analysis of the herbicide tolerance. Superior lines identified can be either released as a variety or utilized as a donor in further breeding programme for the development of herbicide-tolerant variety.

Screening of wild relatives. Wild relatives of crops harbour desirable alleles for stress-resilient traits which were lost in the context of domestication. The phenomenon of superweeds led to the thought of utilizing wild relatives and volunteer weeds in developing herbicide tolerance in plants (Bain et al. 2017). Wild relatives of rice such as red rice (weedy rice) co-exist with rice as weeds in fields. Application of herbicide followed by selection pressure results in the development of herbicide in weeds (Prakash et al. 2020). Gene flow occurs frequently between wild relatives and crops and similarly among wild relatives themselves (Song et al. 2003). Shrestha et al. (2022) identified B2 weedy accession to be distinct from other 54 weedy accessions with elevated herbicide tolerance and allelopathic properties. Low breeding barrier between weedy rice and rice can be exploited for rice improvement programme as they are closely associated. Transfer of desirable herbicide tolerance/resistance alleles from weeds to cultivated rice can be achieved through hybridization and selection.

Induced mutagenesis. Genetic diversity in crops can be enhanced through induced mutagenesis using physical and chemical mutagens. Mutation serves to be an excellent source of herbicide tolerance even when there is no sufficient variability available in the germplasm (Bernasconi et al. 1995). Induced mutagenesis proves to be a reliable alternative for

developing rice varieties with resilience to various stresses as it has the potential to speed up the spontaneous mutation and expand the genetic pool of allelic variants useful for genetic improvement (Viana et al. 2019). Clearfield rice varieties *viz.*, CL121 and CL141 conferring tolerance against imazethapyr have been developed from 93AS3510 mutant (Ethyl Methane Sulfonate) by BASF (Sudianto et al. 2013). Argentine scholars carried out ethyl methane sulfonate (EMS) mutagenesis on the local variety IRGA417 and developed Puita' Intacl, a popular mutant variety harbouring mutation at the Ala122Thr region of *ALS* gene (Goulart et al. 2012). Likewise, IMINTA1 and IMINTA4 mutants were developed from IRGA417 using sodium azide. JD 164 is an imazethapyr tolerant japonica variety obtained by crossing Hudao55 (HD55) with a chemically mutated (EMS) indica variety 9311 containing single mutation (S627N) in *AHAS* conferring tolerance towards imidazolinone herbicides, including imazethapyr and imazamox (Piao et al. 2018). Correspondingly, using EMS, rice varieties showing resistance to ACCase-inhibitor and quizalofop-p-ethyl were developed (Camacho et al. 2019). Herbicide-tolerant mutant (HTM) Robin, an imazethapyr tolerant rice mutant was identified from an EMS mutagenized population an upland variety, Nagina 22 (N22) containing approximately 100 000 plants in M_2 generation (Shoba et al. 2017). Suitable donor parents for the future backcross breeding with adapted lines are listed in the Table 5.

Marker-assisted backcross breeding. Marker-assisted backcross breeding (MABB) provides an effective and precise means of trait introgression controlled by a single gene while retaining the core characteristics of the recurrent plant (Collard & Mackill 2008). It is found to be effective for genes or QTLs with major effects. This method utilizes molecular markers for identifying target loci, minimizing the linkage drag, and accelerating the recurrent parent genome recovery during back-crossing (Hospital 2001). Two imidazolinone-tolerant irrigated rice lines, CNA10756 (BRS Sinuelo CL) and CNA10757 were developed using BRS 7 Taim and BRS Pelota as recurrent parents and mutant line, 93AS3510 as a donor of the herbicide tolerance allele (Rangel et al. 2010). Grover et al. (2020) used MABB for transferring the mutant allele of acetohydroxy acid synthase (*AHAS*) gene, from the donor parent (DP) Robin into the genetic background of an elite popular Basmati rice variety, Pusa Basmati 1121 (PB 1121), for tolerance towards imidazolinone group of herbicides. The gene-linked

Table 5. Non- transgenic rice varieties developed through mutagenesis and hybridization

| Mutant | Wild type/donor parent | Amino acid substitution | Method | Herbicide | Gene | Reference |
|--------------------------|------------------------|-------------------------|--|---------------------------|------|--------------------------|
| 93-AS3510 | AS3510 | G654E | EMS | imidazolinone | ALS | Sudianto et al. (2013) |
| CL 121 & CL 141 | 93-AS3510 | – | hybridization with Cocodrie and Maybelle | imidazolinone | ALS | Wenefrida et al. (2007) |
| Puita-Inta-CL | IRGA 417 | A122T | EMS | imidazolinone | ALS | Livore et al. (2003) |
| PWC-16 | Cypress rice | S653A | EMS | imidazolinone | ALS | Wenefrida et al. (2004) |
| CL161 and Clearfield XL8 | PWC-16 | S653A | EMS | imidazolinone | ALS | Wenefrida et al. (2004) |
| SH Hyb | CL161 | S186P, K416E, L662P | spontaneous mutation | imazethapyr | ALS | Rajguru et al. (2005) |
| IMINTA1, IMINTA4 | IRGA417 | A122T | sodium azide | imidazolinone | ALS | Tan et al. (2006) |
| IRGA 422 CL | 93-AS3510 | G654E | EMS | imidazolinone | ALS | Roso et al. (2010) |
| MR220CL1 and MR220CL2 | CL1770 | – | hybridization with MR220 | imidazolinone | ALS | Sudianto et al. (2013) |
| HTM-N22 | N22 | S627D, G152E | EMS | imazethapyr | AHAS | Shoba et al. (2017) |
| JD164 | 9311 | S627N | EMS | imazethapyr | AHAS | Piao et al. (2018) |
| Sabbore (APPs resistant) | Sabbore | W2027C | gamma rays | aryloxyphenoxy propionate | ACC | de Andrade et al. (2018) |
| BRS A701 CL | Cypress CL | – | hybridization with BRS 7 Taim | imidazolinone | ALS | Rangel et al. (2018) |

EMS – ethyl methane sulfonate; ALS – acetolactate synthase; ACC – acetyl-CoA carboxylase; AHAS – acetohydroxy acid synthase

marker RM 6844 and 112 SSR markers were utilized for foreground and background selection, respectively. A set of 12 BC4F4 near-isogenic lines (NILs) with recurrent parent genome (RPG) recovery ranging from 98.66 to 99.55% were developed.

Mapping of herbicide tolerance trait. Following the identification of sources for herbicide tolerance, the next important step is deciphering the mechanism behind it and mapping the genomic location of the genes imparting herbicide tolerance in a precise manner. Identification of genes conferring resistance is empirical to develop functional markers which in turn helps in locating the precise genomic region containing genes associated with resistance. Shoba et al. (2017) carried out the genetic characterization of HTM Robin and analysed the inheritance herbicide tolerance in a cross between Pusa 1656- 10-61/HTM which showed that this trait is governed by a single dominant gene. Bulk segregant analysis (BSA) using microsatellite markers flanking the three putative candidate genes viz., an *acetolactate synthase* (ALS) on chromosome 6 and two *acetohydroxy acid synthase* (AHAS) genes, one on chromosomes 2 and another on chromosome 4 respectively were carried out to identify the causal gene. The marker, RM 6844 on chromosome 2, which is located 0.16 Mbp upstream of AHAS (LOC_Os02g30630), was found to be linked with herbicide tolerance.

BIOTECHNOLOGICAL APPROACHES FOR HERBICIDE TOLERANCE

Tissue culture and selection. Plant tissue culture is the simplest biotechnological approach which is purely based on the principle of “totipotency”. The discovery of heritable changes in the genome of plant cells known as soma-clonal variations, which can be triggered by applying selective pressure in vitro conditions (Hernández-Soto et al. 2021), paved the way for the selection of desirable traits like herbicide resistance from *in vitro* culture. Bae et al. (2002) isolated 3 HT rice lines viz., CHB1, CHB2 and CHB3 against cyhalofop butyl (CHB) from gamma-irradiated anther cell cultures. Ekanayaka et al. (2016) proved tissue culture could be a potential tool for developing HT rice calli by inducing glyphosate tolerance in a susceptible variety Bg250 variety via 0.2% EMS treatment on seed-derived calli. They also identified an amplified fragment length polymorphism (AFLP) marker, E11M32 specific to the HT trait in rice through which can further utilized to identify HT rice mutant.

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Genome editing. Genome editing harbours programmable nucleases for genetic manipulation of organisms by creating double-stranded breaks at desired locations in the genome. It utilizes the innate DNA repair mechanisms *viz.*, non-homologous end joining (NHEJ) and HR (homologous recombination), which allows highly specific and efficient manipulation of the genome through insertion, deletion, and substitution of target DNA (Romero & Gatica-Arias 2019). For developing herbicide-tolerant cultivars, genome editing *via* homologous recombination and substitution of herbicide-specific target domain of target enzyme with a mutated variant having reduced affinity for binding of herbicide molecule could be a reliable method. Li et al. (2016a) made use of CRISPR-Cas 9 mediated NHEJ mechanism to execute site-directed substitution of Thr₁₀₂Ile and Pro₁₀₆Ser (TIPS) bases of rice EPSPS gene with the corresponding TIPS mutations for glyphosate resistance. Lately, overexpression of this gene in rice led to enhanced yield and glyphosate tolerance at the field level (Achary et al. 2020). Cytosine base editor (CBE) was employed by Zhang et al. (2021) to generate a large number of missense mutations in the codons *viz.*, Pro₁₇₁ and Gly₆₂₈ of *ALS* gene in rice to exhibit tolerance against bispyribac sodium. Kuang et al. (2020) put forward a technique called the base-editing mediated gene evolution (BEMGE) method, which utilizes cytosine and adenine base editors in conjunction with an sgRNA library that encompasses the entire coding region of the target gene in order to efficiently induce a wide range of mutations within the target gene. The mutant with the highest bispyribac sodium resistance was Pro171Phe among the other mutants *viz.*, Pro171Leu, Arg190His, Pro171Ser, Ala154Thr and Ala152Thr which were obtained by editing the rice *ALS* gene using the BEMGE method. Ren et al. (2023) employed BEMGE method to evolve *OsGS1* gene endogenously and identified two novel and one previously reported glufosinate resistant alleles *viz.*, *OsGS1-AVPS*, *OsGS1-+AF* and *OsGS1-SGTA* respectively. Zafar et al. (2023) evolved bispyribac-sodium tolerant Super Basmati by introducing point mutation (W548L) *via* HDR mediated CRISPR-Cas9 system. The mutated herbicide resistance genes obtained by genome editing techniques are listed in Table 6.

Transgenic approach. In the context of functional genomics and genetic improvement of crops, genetic transformation is still the most sought-after technology especially for introgressing certain new traits and modifying or recombining already exist-

ing traits (Anjanappa & Gruissem 2021). Herbicide resistance *via* transgenesis can be achieved by the following four mechanisms which can be either used alone or in combination with others.

- Introgression of genes encoding herbicide degrading or detoxifying enzymes.
- Introgression of genes encoding herbicide insensitive form of the corresponding normal functioning enzyme or overexpression of genes encoding herbicide specific target enzyme in such a way that normal metabolism of plants remains unaltered.
- Modification of herbicide-specific target site of action rendering herbicide from binding to it.
- Engineering plants for active herbicide efflux.

Transgenic versions of IR64 plants containing CP4 EPSPS gene were found to be tolerant to 10 times the dosage of commercial recommendation of glyphosate (Chhapekar et al. 2015). Cui et al. (2016) identified a novel gene encoding glyphosate resistance labelled as *I. variabilis* EPSPS from *Isoptericola variabilis* and transformed it into a *japonica* variety, Zhonghua 11. Subsequently, highly resistant transgenic events were produced. Nevertheless, Yi et al. (2016) transformed *aroA* gene cloned from *Janibacter* sp. into Minghui 86 to generate high glyphosate-resistant transgenic plants. Fartyal et al. (2018) developed a transgenic rice event from Swarna (*indica* variety) having low herbicide residue in addition to high resistance towards glyphosate *via* transformation of two genes *viz.*, mutant *epsps* gene and *igrA* gene. (Cui et al. 2020) obtained three transgenic restorer line namely MY28, MY50 and MY51 by introgression of *I. variabilis* EPSPS gene into elite restorer line Minghui 86.

UNINTENDED CONSEQUENCES OF HTR TECHNOLOGY

The unintended consequences of herbicide tolerance in rice farming are multifaceted and require careful consideration. Some of the major consequences of herbicide-tolerant rice were discussed as follows.

Weed shifts. A swift change in the spectrum of weeds predominantly towards non-native, invasive weeds and the evolution of herbicide-resistant weeds were the repercussions of monoculture of herbicide-tolerant rice and exclusive reliance on the corresponding herbicide. This shift in weed species includes a paradigm change in the diversity or density of weed flora as a result of existing weed control practices. In glyphosate resistant crops (GRCs), this weed species shifts were mainly due to highly

Table 6. Herbicide-resistant genes and corresponding mutations obtained by genome editing tools

| Gene | Position | Protein | Obtained mutation | Method | Herbicide | References |
|---|----------|--|-------------------------------------|---------------------------------|-------------------------------|--|
| <i>Acetohydroxy acid synthase</i> | Chr 2 | Q6K2E8 | W548 L or P171S | recombinant protein | imidazolinone | Kawai et al. (2008) |
| | | | W548, E549 | CRISPR-prime editing | | Xu et al. (2020) |
| | | | W548L, S627I | CRISPR | | Sun et al. (2016) |
| | | | W548L, P171S | CRISPR-prime editing | | Xu et al. (2020), Lin et al. (2020) |
| <i>Os02g0510200</i> | | | G628 W | CRISPR/Cas9 | | Wang et al. (2021) |
| <i>HPPD inhibitor sensitive 1 (HIS1) Os02g0280700</i> | | Fe (II)/2-oxoglutarate – dependent oxygenase | A96V (C287 T) | CRISPR/Cas9 base editor | imazamox | Shimatani et al. (2017) |
| <i>ACCase2</i> | | | 28-bp deletion allele (his1) | wild Nipponbare lacked deletion | β -triketone herbicides | Maeda et al. (2019) |
| | | | I1879V, W2125S | CRISPR/Cas9 base editor | | Liu et al. (2020) |
| <i>Os05g0295300</i> | Chr 5 | B9FK36 | D2176G, G2201A | CRISPR-prime editing | ACC inhibitor herbicides | Xu et al. (2020) |
| | | | C2186R | CRISPR-base editor | | Li et al. (2018) |
| | | | P1927 E, W2125C, S1866 F and A1884P | CRISPR-base editor | | Li et al. (2020b) |
| <i>OsEPSPS</i> | | | T169L, A170 V P173S | CRISPR-prime editing | glyphosate | Li et al. (2020a) |
| <i>Os06g0133900</i> | Chr 6 | A0A0N7K1H2 | T102I + P106S | CRISPR | | Li et al. (2016b) |
| <i>OsTubA2</i> | | | | | pendimethalin | |
| <i>Os11g0247300</i> | Chr 11 | Q53M51 | Q53M51 | CRISPR/Cas9 base editor | | Liu et al. (2021) |

HPPD – 4-hydroxyphenylpyruvate dioxygenase; ACC – acetyl-CoA carboxylase

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resistant biotypes or late blooming cohorts which avoids glyphosate effects. The emerging problematic weeds of GRCs are johnsongrass, Common lambsquarters, *Ambrosia* sp., Italian ryegrass, *Ipomoea* sp., *Amaranthus* sp., *Commelina*, *Cyperus* sp. and *Setaria* sp. Integrated weed management practices are of paramount importance in controlling/delaying weed shifts and sustaining HTR in the long run (Reddy et al. 2010).

HT rice as volunteer plants. It is becoming more common to find volunteer rice plants among the succeeding crop, especially in the tropics where there is no winterkill of seeds. The shattering ability of the cultivar, efficiency of previous crop harvest, and weed management between cropping seasons were some of the factors that highly influence the density of volunteer rice plants (Sudianto et al. 2013). Volunteer HT rice would be a major constraint when HT trait is the same in both volunteer and HT plants being cultivated in the same season. These volunteer plants act as an alternative host for pests and diseases preventing the crop from reaching its maximum productivity (Reddy & Nandula 2012). Hardke (2020) noticed that there was an abrupt increase in imidazolinone resistant *O. sativa* f. *spontanea* population due to the presence of HT hybrid volunteers and hybridization with weedy relatives. Volunteer plants from transgenic rice pose a serious threat because of potential gene flow from them to weedy rice which calls for effective and efficient weed management practices both in and out of season in the herbicide-tolerant rice system.

Potential gene flow. Futuyma (1979) defined gene flow as “the incorporation of genes into the gene pool of one population from the gene pool of other populations”. It is inevitable even in self-pollinating crops provided when compatible species exhibit synchronized flowering and are sympatrically distributed (Kumar et al. 2008). Several cases of gene

flow from HT rice to wild/weedy relatives of rice have been reported in USA, China and Europe (Shivrain et al. 2006). The rate of outcrossing in these cases was observed to be less than 1% and sometimes, it can vary from 1% to 52% based on cultivar type (Langevin et al. 1990) where *indica* cultivars are highly compatible with wild/weed species compared to *japonica* cultivars (Oka 2012). The cascade effects of gene flow include (a) evolution of weeds with increased invasiveness; (b) herbicide-tolerant crops with insignificant effect on weed management and (c) biodiversity loss (Kumar et al. 2008). The invasiveness of weeds can be enhanced either through the introgression of HT trait or selection pressure due to exclusive reliance on selective herbicide. Regulatory measures and careful management practices are essential to mitigate these risks.

Genetic erosion of wild species. Ellstrand (2003) indicated that there is a heightened probability of genetic erosion of wild species mainly attributed to the flow of transgene. Genetic assimilation in wild species wherein unique genes of wild plants were replaced by crop genes *via* demographic swamping or repeated hybridization which ultimately results in the shrinkage of biodiversity (Wolf et al. 2001). Inevitably, HT rice has a potential effect on the *in-situ* conservation of biodiversity of wild species, particularly when the transgenes pose any fitness penalty or advantage. However, the fitness effect of HT trait is comparatively negligible as the trait is considered to be neutral in the absence of herbicide application (Kumar et al. 2008).

Herbicide resistant weeds. The genetic evolution of weeds with herbicide resistance is primarily due to selection pressure exerted by extensive application of herbicide (Owen & Zelaya 2005) (Figure 4) and through gene flow from herbicide-resistant crops (Figure 5). As imidazolinone exerts a relatively high

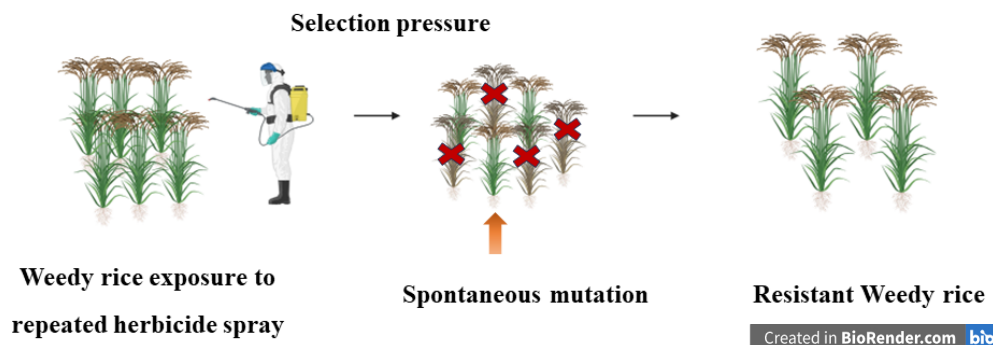


Figure 4. Evolution of herbicide-resistant weeds through spontaneous mutation

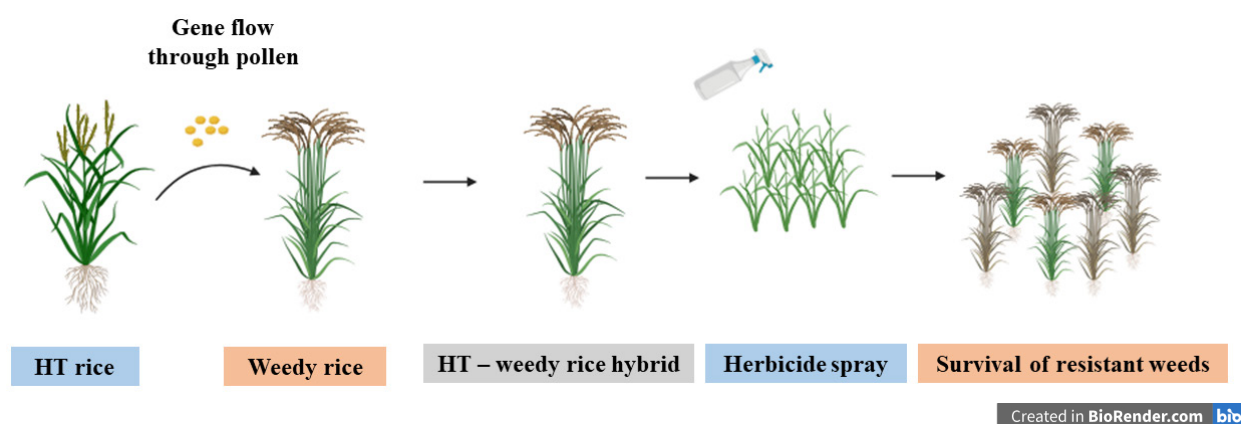


Figure 5. Evolution of herbicide-resistant weeds through gene flow from herbicide-tolerant (HT) rice

selection pressure, the evolution of imidazolinone-resistant weeds has been considerably higher than that of glyphosate and other herbicides (Tranel & Wright 2002). HR weeds of rice field reported across the world are listed in Table 7 (Heap 2024).

Public perception and acceptance. Transgenic herbicide-tolerant rice had faced public scrutiny and scepticism for commercialization regarding the harmful effects of transgene on the environment and the associated use of herbicides (Reddy & Nandula 2012). Building public trust and ensuring transparency in the development and regulation of herbicide-tolerant rice technology is crucial. Momentarily, Bt cotton is the sole GM crop authorized for commercial production by the Genetic Engineering Appraisal Committee (GEAC) of Ministry of Environment, Forest and Climate Change (MoEF&CC) under the Government of India following a thorough assessment and fulfilment of all legal criteria. Strong opposition from environmentalists, consumers and farmers in India who are against the idea of commercialization of genetically modified (GM) food crop have resulted in an indefinite moratorium on Bt brinjal during 2010 and the approval of Dhara Mustard Hybrid-11 (DMH-11), a GM mustard have been withheld by the Indian Government (Singh et al. 2020). India had been reluctant to adopt GM food crops, but the current government, which is in favour of GMOs, has taken necessary steps to facilitate adequate field trials and regulatory measures.

MANOEUVRES TO OVERCOME THE NEGATIVE EFFECTS OF HTR

Meticulous stewardship guidelines are required for the effective utilization of HR rice in a long run. Lax fidelity to these guidelines results in the development

of herbicide resistance in weeds due to outcrossing between HTR and weedy rice (Sudianto et al. 2013). Necessary steps should be taken to prevent the escape of HT gene to weedy rice and to minimize the dispersal of weed seeds.

The following are the best weed control practices recommended for Clearfield® production system (Burgos et al. 2008):

- Utilization of authenticated seed.
- Implementation of herbicide program which includes herbicides with different modes of action available for rice cultivation in all possible combinations.
- Adoption of suitable management practices in which maximum efficacy of herbicide is ensured.
- Synchronization of flowering between weedy rice and HT rice should be minimized by adjusting the sowing dates.
- Prevention of remnant weeds from producing seeds.
- Adoption of crop rotation with imidazolinone tolerant crops (legumes, pastures, etc.) to prevent seed production of weedy or volunteer rice.
- Zero or minimum tillage can be practiced.
- Stale seedbed – to reduce the density of the weedy rice population which was allowed to germinate before rice planting and killed either using herbicide or by tillage.
- Weed-free fields should be harvested first followed by weed-infested fields.
- Rotation of Clearfield® with other crops to break the cycle of weedy rice.

CONCLUSION

Though DSR is gaining popularity as a resource conservation technique, its effective adaptation

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Table 7. List of globally identified herbicide-resistant weeds of rice (Heap 2024)

| Species | Common name | Country | First year | Site of action |
|--|-----------------------------|-----------|------------|--|
| <i>Cyperus difformis</i> | small flower umbrella sedge | Australia | 1994 | inhibition of acetolactate synthase |
| <i>Echinochloa crus-galli</i> var. <i>crus-galli</i> | barnyard grass | Brazil | 1999 | auxin mimics |
| <i>Cyperus difformis</i> | small flower umbrella sedge | Brazil | 2000 | inhibition of acetolactate synthase |
| <i>Cyperus difformis</i> | small flower umbrella sedge | Brazil | 2000 | inhibition of acetolactate synthase |
| <i>Fimbristylis miliacea</i> | globe fringer ush | Venezuela | 2010 | inhibition of acetolactate synthase |
| <i>Echinochloa colona</i> | jungle rice | Australia | 2010 | inhibition of enolpyruvyl shikimate phosphate synthase |
| <i>Cyperus iria</i> | rice flat sedge | Brazil | 2014 | inhibition of acetolactate synthase |
| <i>Echinochloa crus-galli</i> var. <i>crus-galli</i> | barnyard grass | Brazil | 2015 | multiple resistance: 3 sites of action inhibition of acetyl CoA carboxylase inhibition of acetolactate synthase inhibition of cellulose synthesis |
| <i>Echinochloa oryzoides</i> | early watergrass | Argentina | 2016 | inhibition of enolpyruvyl shikimate phosphate synthase |
| <i>Cyperus difformis</i> | small flower umbrella sedge | India | 2017 | inhibition of acetolactate synthase |
| <i>Echinochloa crus-galli</i> var. <i>crus-galli</i> | barnyard grass | India | 2017 | inhibition of acetolactate synthase |
| <i>Echinochloa crus-galli</i> var. <i>crus-galli</i> | barnyard grass | Brazil | 2018 | multiple resistance: 3 sites of action inhibition of acetolactate synthase inhibition of cellulose synthesis auxin mimics |
| <i>Oryza sativa</i> var. <i>sylvatica</i> | red rice | Colombia | 2018 | inhibition of acetolactate synthase |
| <i>Chloris radiata</i> | radiate fingergrass | Colombia | 2019 | multiple resistance: 2 sites of action inhibition of acetolactate synthase inhibition of enolpyruvyl shikimate phosphate synthase |
| <i>Oryza sativa</i> var. <i>sylvatica</i> | red rice | Turkey | 2020 | inhibition of acetolactate synthase |
| <i>Echinochloa crus-galli</i> var. <i>crus-galli</i> | barnyard grass | Australia | 2021 | inhibition of acetyl CoA carboxylase |
| <i>Digitaria ciliaris</i> | southern crabgrass | China | 2021 | inhibition of acetyl CoA carboxylase |
| <i>Ammannia multiflora</i> | many flowered ammannia | China | 2022 | inhibition of acetolactate synthase |
| <i>Echinochloa phyllopogon</i> | late watergrass | China | 2023 | inhibition of acetolactate synthase |
| <i>Leptochloa chinensis</i> | Chinese sprangle top | China | 2023 | inhibition of hydroxyphenyl pyruvate dioxygenase |

to meet the demand of the expanding population is restricted predominately due to weed menace. Chemical control of weeds utilizing broad-spectrum herbicides is found to be an effective and efficient option in the context of labour shortage, wage, and availability of low-cost herbicides. With the advent of HT rice varieties, chemical control can be exploited to the fullest as it allows for flexibility in the timely application of herbicide and controls a wide spectrum of weeds without injuring the rice and the subsequent crops in case of crop rotation. Introgression of herbicide tolerance trait into adapted drought or upland rice varieties could be a potential breakthrough in achieving higher yield under DSR conditions. While the debate on whether to approve GM rice or not for cultivation is a never-ending saga, non-transgenic HT rice could be a futuristic option for DSR provided with the dwelling natural resources and ever-changing climatic conditions. Framing effective stewardship guidelines for HTR utilization, creating awareness among farmers, crop rotation and integrating it with other weed management practices can help in realizing the fullest potential of HT rice varieties without any harmful effects on the environment and biodiversity.

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