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REVIEW ARTICLE

Tracking sources and methods of gene transfer for emerging and tricky disease rice false smut (RFS)

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Abstract

Rice false smut (RFS), caused by *Ustilaginoidea virens*, is a destructive emerging fungal disease that significantly impacts rice production spots globally. The pathogen primarily infects rice at the flowering stage, leading to the development of greenish-brown smut balls on panicles, which significantly reduce grain yield, quality and seed health. Managing this disease has become increasingly difficult due to the pathogen's adaptability and resistance to commonly used fungicides. A major factor contributing to the persistence of *U. virens* is the horizontal transfer of resistance genes, allowing the pathogen to acquire genetic material from other microorganisms or environmental sources. This process enhances its virulence and complicates disease control. Understanding the molecular mechanisms behind gene transfer, such as backcrossing and marker-assisted selection, is crucial in developing effective strategies against false smut. Genetic diversity within *U. virens* populations further challenges disease management and influences the effectiveness of rice breeding programs. This article is compliance of the multidisciplinary approaches traditional, modern/integrated breeding techniques and crop protection strategies to combat this threat. Advanced research in pathogen genomics and resistant rice varieties can help better understand mechanisms, sources of resistance and mitigate the impact of false smut and sustain rice productivity. Strengthening disease surveillance and resistance breeding efforts will be key in reducing future outbreaks.

Keywords: gene transfer methods; prevention and cure; resilience mechanisms; rice false smut

Introduction

Rice is one of the important cereal crops, accounting for the majority of farmland. Rice is mainly cultivated in subtropical and tropical countries with India taking the first position with a production of 147.00 million tonnes. It is followed by China, Bangladesh, Indonesia and Vietnam with 145.28 million tonnes, 36.60 million tonnes, 34.60 million tonnes and 26.95 million tonnes, respectively (USDA, 2024-25) (1). Rice cultivation is prone to various types of stress both biotic and abiotic factors which include diseases and environmental problems (2). Among many diseases, newly discovered disease in recent times is false smut belongs to ascomycetous fungus that causes false smut sickness with high rainfall, high relative humidity (90 %) and low temperature ranging (25-30 °C) (3).

Rice false smut (RFS) is a disease that severely restricts rice production. The RFS pathogen, *Ustilaginoidea virens*, is a basidiomycetous fungus belonging to the smut fungus family. *U. virens* infects the flowering spikelets of rice and develops pseudo layered structures. Pseudo layered structures are composed of fungal hyphae, rice cells, gall cells and a spore coat with a series of masses rolled into a ball (4). In crossbred rice, false smut of rice causes a yield loss of 5 % to 20 % and, in some cases, even more (5). The spore ball in this disease is blue green, which is conformed to the spores contained in the spore ball matrix. The mature spore ball is smooth and greenish-black, becoming an eyesore. Chlamydospores germinate when the temperature, humidity and light are suitable, which transmits to damage new rice plants. The problem is common due to strong growth potential and high air-borne sporulating ability. At present, there are still some questions regarding the rice-stacking detailed classification of rice pathogen interaction, potential resistance genes detected and gradation of RFS resistance materials (6). RFS is significant rice disease and re-emerging as a serious problem in many growing areas. RFS usually infects at panicles emergence stage or at a very early flower stage. The natural infection by the virulent pathogen *U. virens* causes the development of deformed grains with false smut balls (7).

Overview of false smut disease in rice: Rice is the staple food for about half of the world's population. False smut of rice, caused by *Ustilaginoidea virens* (Cooke) Takam. & K.Hirata, affects the quality and yield of rice grains worldwide. It is one of the important diseases of rice, causing considerable economic loss in grains and energy loss in the brewing industry (8). False smut infected grains contain a large number of ascospores that favor multiplication and infectious grains by themselves are a source of inoculum. Hybrid rice is more enthusiastically promoted and bred and a number of hybrids have been rapidly expanded. However, at the expansion of hybrid rice, an outbreak of false smut was observed in southern China in 1994. Notably, it is seedborne disease, but no effective seed treatment control is reported (9). False smut does not have any predictable

signs and symptoms, so it stays undetected and directly appears at or just prior the critical stage maturity (10). Non availability of commercially acceptable level resistant cultivars makes rice farming and farmers in the disease prone areas more vulnerable.

Economic impact of false smut: In India, RFS was first reported in Tamil Nadu in 1878 forming black smoky appearance from very far distance over the infected area (11). Later came into notice in eastern Uttar Pradesh between 1984 and 1986, affecting during the flowering and booting stages of rice development with yield loss in India ranging from 0.2 % to as high as 49 % (12, 13). False smut outbreaks during the epidemic years with yield losses ranging from 0.01 % to 8.6 %, having the annual loss of 158.6 million kilograms in China during 2008-2016, the severity of false smut can affect the yield losses from 3 % to as high as 70 %, depends on the environmental condition (5). Since when agricultural practices started altering and hybrids rice varieties got promoted samples with mycotoxins have increased every season. The grain/food safety assurance and regulatory monitoring agencies have reported an upward trend in mycotoxin due to RFS. The false smut fungus produces two mycotoxins, namely ustiloxins and sorbicillinoids and ustilaginoidins, which are carcinogenic and thus a danger to human health and livestock (10).

Symptoms and pathogenesis process: The color of false smut balls is one way to distinguish them from real smut symptoms. Unlike kernel smut, which typically shows symptoms only at harvest or during the later stages of maturity, the symptoms of false smut are more apparent outside of the rice kernels, in addition to their color (10). In false smut, round, soft spore balls composed of powdered chlamydospores are utilized instead of rice grains (13). It leads to produce unfilled grains, sterile spikelet's, deteriorated quantity and quality of grains with considerable amounts toxins in the essential plant parts (14). For the better understanding of the symptom's, an original photo of RFS infection incidents captured in between panicle initiation to booting, heading, flowering, milk grain, dough grain and mature grain are presented in Fig. 1.

Preventive methods: The infection process in general flows as depicted in Fig. 2. Once received optimum environment condition, *U. virens*, starts infecting rice flowers by colonizing interior floral organs with mycelial growth. It will lead to form interior organs (stamens, pistils) into false balls of smut filled and coated with powdery chlamydospores (15). The colour of RFS varies from yellowish orange to greenish brown (16). Sclerotia and chlamydospore both are considered as source of inoculum and it can hibernate for months in soil, seeds and other plant residuals. Apart from this it has wide range of infection and side hosts including weed species *Panicum tenellum*, *Panicum trypheron*, *Digitaria marginate*, *Echinochloa crusgalli* and *Imperata cylindrica* (13). When getting confronted to considerable day night temperature variation it produces sclerotia frequently (17). The severity of the disease

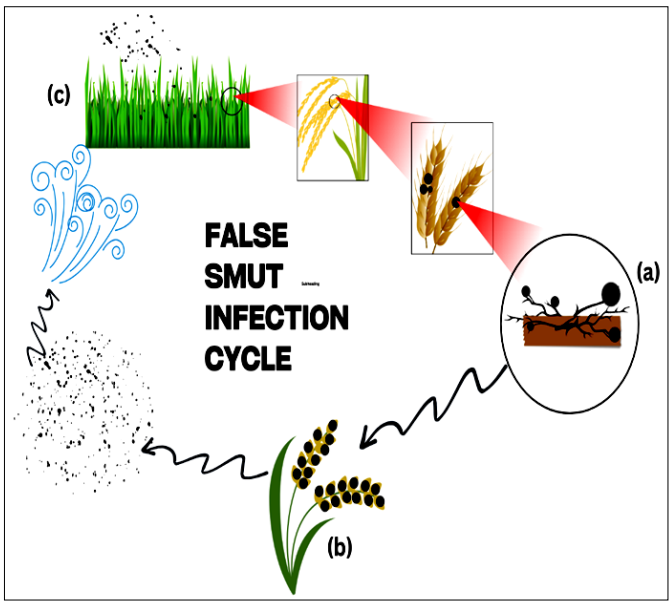

Fig. 2. Life cycle cum infection process of rice false smut (RFS). (a) Smut sori formation in the flowering structure; (b) Transmission of smut sori to other plants; (c) Transmission through wind.

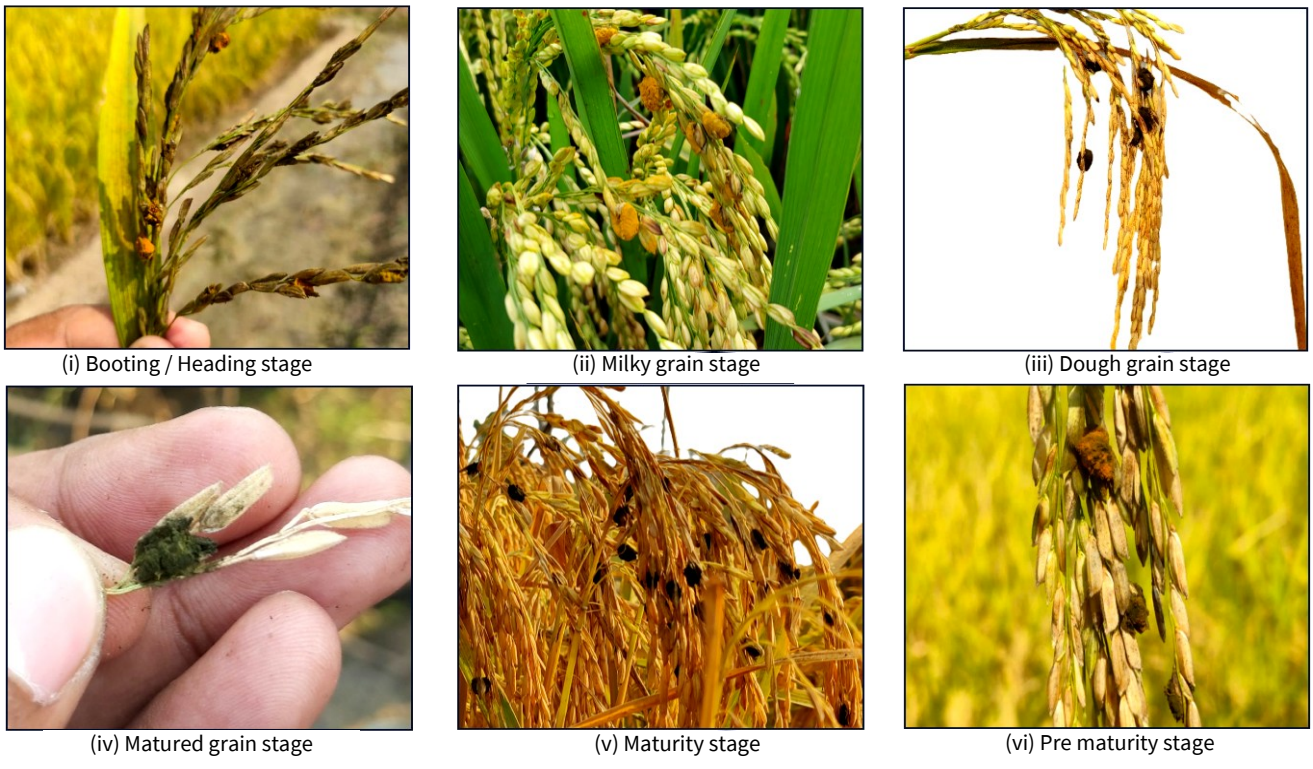

Fig. 1. An original caption of symptoms of rice false smut (RFS) recorded at an infection incident of reproductive stages.

outbreak is often correlated with rice plants booting and heading phases coinciding with rainfalls (18). The pathogen may disrupt plants physiological process, hormonal balance, nutrient uptake, photosynthesis, etc. depending upon prevailing environment and variety under cultivation.

Transcription factors and effector triggered immunity (ETI) in plants (Fig. 3), produced by pathogens, are directly or indirectly in charge of controlling the growth and characteristics of the plant pathogen by regulating downstream gene expression. WRKY transcription factors are increasingly recognized as central regulators of rice immunity against *U. virens* and their coordinated activation offers clear opportunities for strengthening false smut resistance. Key members such as *OsWRKY45* and *OsWRKY13* enhance salicylic-acid signaling, while others modulate JA–ET pathways to re-establish hormonal balance disrupted by infection. Their regulatory influence on PR gene activation, ROS modulation and lignin-associated cell-wall reinforcement collectively restricts early pathogen establishment.

Broadly there are two methods to prevent and slow down disease infection on any crop plants. First one is cultural and crop management practices like sowing method, time, seed treatment, spraying chemicals, etc. followed to save crop yield and quality losses. Studies from the past showed dependence at large on heavy or combined foliar applications of fungicides such as propiconazole, azoxystrobin, copper oxychloride, cuproxat SC (cconcentrated suspension), difenoconazole, hexaconazole, prechloraz, simeconazole, tebuconazole, etc. were effective control of false smut (19, 20). Employing right cultural practice and right time can also reduce damage cause by RFS. Especially in the disease prone areas, proper management of cultural measures including sowing/ transplanting time, moisture, irrigation, nitrogen, weeds, crop rotation, plant spacing, land preparation and integrated use of different methods can effectively and economically help minimize losses due to diseases (21).

Some biocontrol agents such as *B. subtilis*, *Trichoderma viridae*, *T. koningii* and *Antennariella placitae* also found to be potentially effective, ecofriendly and sustainable solutions under protected environment. The commercialization of these bioagents stays unclear due to evolving nature of disease, diverse and changing environmental conditions (22). According to the *in vitro* study (14), the growth of *U. virens* can be completely controlled by using plant extracts derived from garlic bulb (*A. sativum*), turmeric rhizome (*C. longa*), lantana leaf (*L. camara*) and bael (*A. marmelos*), while the plant oils of lemon grass (*C. flexuous*), cinnamon (*C. zeylanicum*) and palmarosa (*C. martinii*).

Second method is the use of resistant varieties, hybrids, or released cultivars which could reduce yield loss of about 13 % (23, 24). The responses (genotypic and phenotypic) of cultivars vary from region-to-region. Certain cultivars showing lower infections against such disease can be utilized as resistant or sources of breeding new cultivars (25). Nine rice hybrids KRH-4, Hybrids VNR-211, 27P64, IRH-74, RH-10428, PRSH-9018, GK-5025, KPH-467 and HRI-140 shown complete resistance identified through artificial screening of total 125 genotypes (26).

Genetic basis of RFS disease resistance

RFS, which is caused by the fungus *Ustilaginoidea virens*, is an important disease affecting rice plants. *U. virens* infect the rice spikelet during the booting stage, hijack the normal development process of rice and then produce the false smut balls, Infections with this particular disease result not only in major reductions in the yield and quality of grains produced but also indirectly threaten human health and animal by producing mycotoxins that are damaging to health (27). As the pathogenic ascomycota fungus, *U. virens* has a complicated life cycle, which involves a sexual reproduction with a low infection rate and a vegetative propagation with a high infection

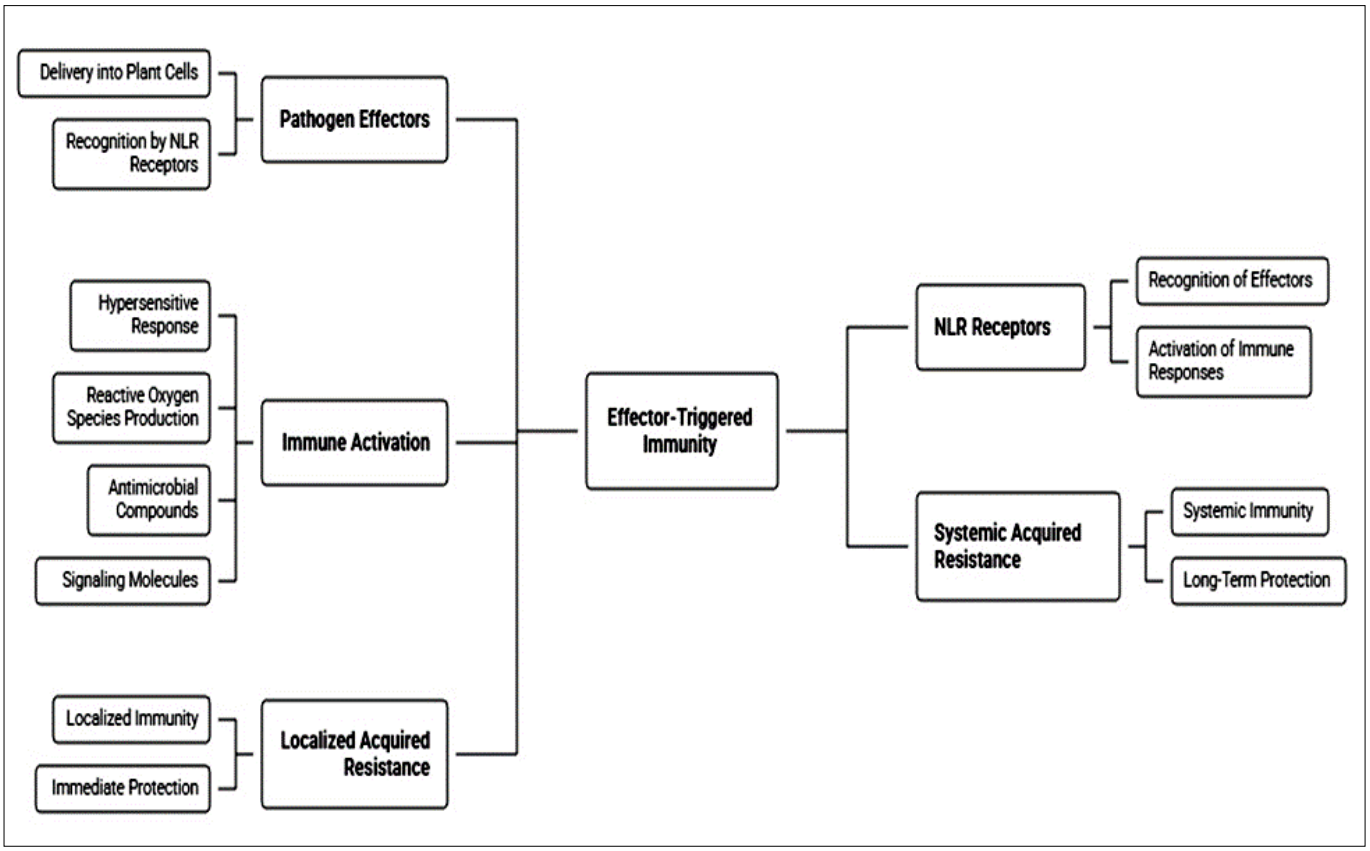

Fig. 3. Effector triggered immunity (ETI) in plants.

rate. During the infection process, rice cells generated a series of immune responses to counteract the fungal invasion, patter triggered immunity (PTI), the initial layer of plant immune defense, thus performs the role of pathogen-associated molecular pattern recognition that answers the challenges of a pathogen attack, is a nonspecific immune response, which can be elicited by most pathogens. In sensitive rice plants, effector proteins secreted by pathogenic bacteria could neutralize the PTI to facilitate the pathogen infection, some of the fungal effectors are recognized by the NLR proteins and such recognition results in ETI in resistant rice. Recent research indicates that PTI and ETI can complement each other to create a powerful disease resistance response (27).

Mechanisms and methods of resistance gene transfer in plants

Resistance genes in plants are crucial for enhancing their ability to withstand various biotic stresses, including pathogens and pests. The fungal pathogen of false smut is tricky and can manipulate defence system of rice plants to infect flowers. A control of this emerging disease depends on application of effective fungicides and mechanism of defence plant adopts. Generally, *U. virens* infects essential floral parts (androecium and gynoecium) *via* gap between lemma and palea (28). Yet there is limited known about how pathogen trick with the plant defence? and how flower defends itself from the attack. Therefore, it becomes essential to explore genetic resources and innovate existing breeding methods, respectively to develop fast, economic and stable sources of resistance from plant/field reservoirs and seed gene banks.

Traditionally, promising entries are introduced into new areas and after extensive testing in various environments, the best entries are selected for recommendation and use (4). Introduction, evaluation, selection and release of identified resistant cultivars had been the breeder's strategy of recent past. Apart from this, backcrossing is frequently being practiced for transferring one or more genes of interest from wild relatives, identified resistance sources to higher yielding rice varieties. Some released varieties through back cross breeding are listed in Table 1. Major gene/vertical gene transfer is easy to break and not durable as there is risk of disease evolving and breaking resistance. Natural gene transfer in plants occurs through recombination, mutations, or exchanges of genetic materials between plant cultivars and wild relative (29).

Breeding for resistant cultivars which can sustain tricky disease like RFS, it needs to be stable and durable to be commercial acceptable. To develop durable resistance, breeders are exploring

Table 1. Rice varieties developed through back cross breeding

Rice variety	Breeding method	References
IR64	Backcross breeding	(23)
Nipponbare (with disease resistance traits)	Backcross breeding	(5)
Rasi	Backcross breeding	(23)
BRRI dhan49	Backcross breeding	(5)
Ranjeet	Backcross breeding	(3)

and inducing gene pyramiding, multiline varieties and horizontal (polygenic resistance) (14). Among these traditional methods, the introduction and acclimatization method are the most important method used in the development of resistant varieties. Rice genetic resources act as a reservoir of desirable resistances against various pests and diseases, different resistance genes, as well as numerous quantitative trait loci (QTLs) of rice diseases, have been identified in wild relatives and germplasm collections of rice (30). The varieties

Table 2. The variety, genes and their corresponding resistance levels to rice false smut (RFS)

Variety	Resistance level	Gene	References
Vaishak	Highly resistant	Pi-ta	(36)
Harsha	Highly resistant	Pi-ta, Fsm1	(36)
Makom	Resistant	Pi-b, Fsm1	(36)
Thekkancheera	Resistant	Pi-ta, Fsm1	(36)
Pavizham	Resistant	Pi-ta, Pi-b	(36)
Karthika	Resistant	Pi-ta, Fsm1	(36)
Kanakom	Moderately resistant	Pi-b	(36)
Revathi	Moderately resistant	Pi-b, Fsm1	(36)
Prathyasha	Moderately resistant	Pi-ta, Pi-b	(36)
IR96321-1447-521-B-2-1-2	Moderately resistant	Pi-ta, Fsm1	(10)
IR96321-1447-651-B-1-1-2	Moderately resistant	Pi-b, Fsm1	(10)
Swarna Shreya	Moderately resistant	Pi-ta, Fsm1	(10)
IR83294-66-2-2-3-2	Moderately resistant	Pi-ta, Fsm1	(10)
VNR211	Resistant	Pi-ta, Fsm1	(23)
GK-5025	Resistant	Pi-ta	(23)
HRI-140	Resistant	Pi-b	(23)
IRH-74	Resistant	Pi-ta, Fsm1	(23)
PRSH-9018	Resistant	Pi-b, Fsm1	(23)
KPH-467	Resistant	Pi-ta	(23)
RH10488	Resistant	Pi-ta	(23)
27P64	Resistant	Pi-b, Fsm1	(23)
KR4-4	Resistant	Pi-ta, Pi-b	(23)

carrying durable and substantial number of genes for resistance against false smut rice are presented in Table 2.

These approaches (Fig. 4) including pedigree method, backcross breeding (31), multiline breeding (32), pure line selection (33), recurrent selection (34) and mutation breeding (40). Each method has its own applicability, advantages and limitations depending upon mode of reproduction of a crop and disease (self, cross, often cross pollinated or asexual). Gene transfer via any method (oligo/polygene) is not as easy as it seems artistic in explanations. It has many complications; despite having identified sources of resistance yet breeders have to adapt to challenges like combining ability of source and parents; linkage drag with undesirable traits, physical and genetic barriers of hybridization etc. The development of elite cultivars has been made easy by following conventional breeding in combination with other intensive research efforts like at the International Rice Research Institute (IRRI) (35). Mutation breeding is broadly used to develop mutant rice varieties for resistance to various other plant diseases (36). The Genome-Wide Association Studies help in identifying genetic markers associated with specific traits, facilitating targeted breeding efforts (37).

Identification of sources through amplification of genetic materials

The DNA of *Ustilaginoidea virens* was detected from PCR amplification with the primers US1-5 (5′-CCGGAGGATACAACCAAAAAAACTCT-3′) and US3-3 (5′-GCTCCAAGTGCGAGGATAACTGAAT-3′) (38). The PCR amplification started with denaturation at 94 °C for 3 min. Denaturation took place at 94 °C for 30 sec, annealing at 58 °C for 30 sec and extension at 72 °C for 1 min for 30 cycles. A final extension of 7 min at 72 °C completed the process. In BOX-PCR, ERIC-PCR and REP-PCR techniques, specific primers were used to identify *U. virens* strains (7). Specific forward primers (5′-CTACGGCAAGGCGACGCTGACG-3′, 5′-

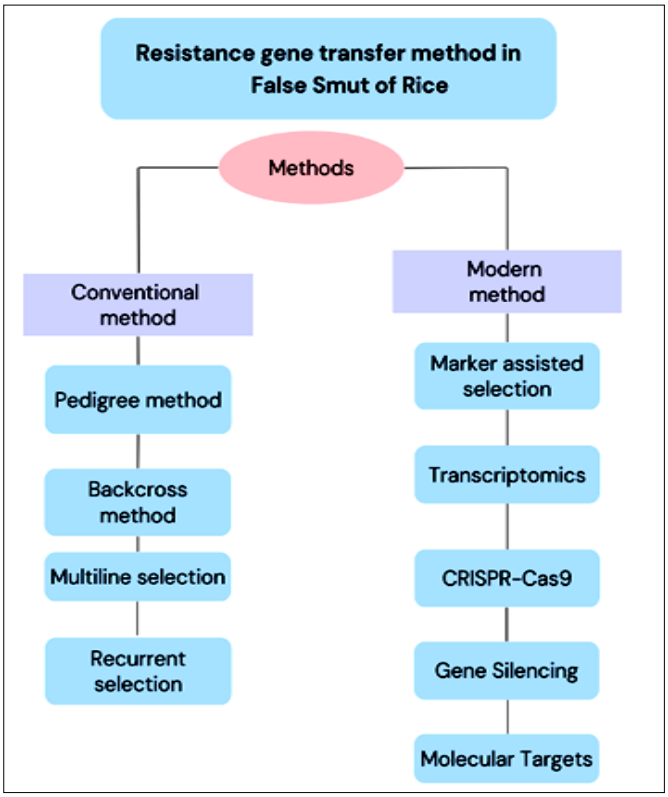

Fig. 4. Different methods of resistance genet transfer.

ATGTAAGCTCCTGGGGATTCAC-3′ and IIIICGICGI-CATCIGGC-3′) and reverse primers (5′-CTACGGCAAGGCGACGCTGACG-3′, 5′-AAGTAAGTGACTGGGGTGAGCG-3′ and 5′-ICGICTTATCIGGCCTAC-3′) were used in BOX-PCR, ERIC-PCR and REP-PCR to amplify partial DNA sequences from 86 *U. virens* strains (39).

Identification of source through quantitative trait loci (QTL's)

The F_2 population developed from the resistant variety and the susceptible variety IR28 and HXZ to conduct QTL analysis, identifying two QTLs associated with resistance to RFS. Additionally, another study using 213 introgression lines (ILs) from the varieties Teqing and Lemont detected ten QTLs affecting the percentages of diseased hills, diseased panicles and diseased spikelet (40). Total seven QTLs linked to resistance were mapped on chromosome 2, 4, 5, 7 and 9 of rice, which were aligned with QTLs on chromosomes 2, 4 and 5 (41). QTLs on the chromosomes 7 and 9 were newly identified recently (42). These QTLs located on chromosome 5 are named qRFSr5.1 and qRFSr5.2 providing a minimal degree of resistance in qRFSr5.1 while providing a greater degree of resistance with qRFSr5.2 (34). Similarly, some more source populations developed along with genomic regions identified for RFS are furnished in Table 3.

The growth and virulence of *U. virens* are greatly facilitated by the enzyme UvCGBP1. Its deletion causes significant defects in both fungal growth and infectivity, leading to changed expression profiles of two major virulence factors, UvPmk1 and UvSlt2, mainly regulated by the MAPK signalling pathway. Fungal virulence is thus controlled by this pathway through UvCGBP1 (43). Host induced gene silencing is an important technique for inducing resistant to plant cultivars for controlling false smut. This method involves introducing small interfering RNAs into transgenic host plants to silence essential genes of the pathogen (44).

Genomic basis of RFS resistance

The preliminary genome of *U. virens* strain VU-8b was sequenced in 2014 and this is 39.4 Mb long with an estimated 8426 predicted genes, comprising approximately 25 % repetitive element (45). This fungus, closely related to entomopathogenic *Metarhizium* spp., exhibits a number of features that may contribute to its pathogenicity in rice:

Secretome: It contains a complex secretome comprised of around 628 proteins, which played a major role in the early stages of the infection.

Gene reductions: The genome contains fewer genes associated with polysaccharide degradation and G-protein receptors, transporters and the secondary metabolites than other ascomycetes, that may indicate its biotrophic lifestyle.

Protein-protein interaction network: A network based on genome sequences and gene expression profiles was constructed, providing insights into the molecular events that take place upon infection (46).

Mapping QTLs linked to resistance against RFS disease

There is progressive lead in the rice research internationally, some of RFS resistance and their genetic characteristics is depicted in Table 4. In F_2 hybrid of IR28 and HXZ, two QTLs associated with resistance to false smut were found and localized on chromosome 5. In the RIL population, five QTLs that cause false smut resistance were found. Of them, the most phenotypic diversity is indicated by qFsr8-1 within a short area on chromosome 8. These SSR markers, genetically linked to qFsr8-1, have been important for marker-assisted breeding aimed at enhancing the resistance of rice to false smut. DNMT2 (LOC_Os01g42630) was identified as the most important candidate gene of false smut resistance in Nanjing11 based on its transcriptional response to *U. virens* infection and observed sequence variations (47).

Total seven QTLs were mapped on the rice chromosomes. Two QTLs linked to the number of diseased panicles per plant were

Table 3. Summary of the QTLs identified with chromosome locations, flanking markers, cultivars and analysis

QTL for resistance	Chr. No.	Markers	Cultivars	Source of gene	Analysis	References
qRFS12.01	12	RM5341 & RM28195	IR77298-14-1-2 & IRGC117374-1	*Oryza sativa* Indica	Bulk segregant	(11)
FSR1	01	Indel15 & RM11334	Nanjing11	*Oryza sativa* Indica	Linkage mapping	(33)
LOC_Os01g15580	01	C1.8738751	315 core rice materials	-	Association mapping	(24)
QRFSr9.1	09	C9.8029326 & C9.9023440	RYT2668	*Oryza sativa* Indica	Linkage	(30)
qRFSr4.3	04	C4.31529767 & C4.31393008	RYT2668	*Oryza sativa* Indica	Linkage	(30)
qRFSr7.1a	07	C7.13373853 & C7.13369043	RYT2668	*Oryza sativa* Indica	Linkage	(30)
qFsr8-1	08	RM22507 & RM22540	MR183-2	*Oryza sativa* Indica	QTL	(15)
qFSR-3-9	03	RM16 & RM168	Lemont	*Oryza sativa Japonica*	Linkage	(27)
qFSR-11	11	RM229 & RM254	IR 28	*Oryza sativa* Indica	Segregation	(15)
qFSR-12	12	RM2771 & RM1246	IR 28	*Oryza sativa* Indica	Segregation	(27)

Table 4. Location and Mapping of QTLs for RFS from recombinant inbred lines

QTLs identified	Chromosome no	Mapping population	Resistant × Susceptible	References
2	5	F_2 176	IR28 × HXZ	(1)
5	2, 4, 8, 11	RILs	MR183–2 × 08R2394	(15)
8	2, 4, 5, 7, 9, 2, 10, 11	94 RILs	RYT2668 × PR116	(30)
49	1, 2, 3, 4, 6, 7, 8, 9, 10, 11, 12	315	GWAS	(24)
8	2, 3, 4, 6, 8, 9,11	125	GWAS	(18)
10	1, 3, 4, 6, 8, 10, 11, 12	150	GWAS	(8)
3	2, 10, 11	BC_1F_2 and F_2	Xiushui47 × FS159	(19)

identified, namely qRFSr5.3 and qRFSr7.1a. The QTL qRFsr9.1 was associated with the total number of smut balls per panicle, whereas four other QTLs namely qRFSr2.2, qRFSr4.3, qRFSr5.4 and qRFSr7.1b with disease severity score. These findings provide valuable insights into the genetics of resistance against false smut (48).

The RFS resistance genes

The rice genome contains genes closely linked to a diversity of resistance genes to fight certain diseases. The resistance genes (R genes) played a crucial role in plant disease resistance (27). These genes can activate various defence mechanisms to protect rice from the invasion of pathogens. In plants, resistance genes are mainly clustered within specific genomic regions. One of the important clusters of resistance genes is located on chromosome 12 on rice. *U. virens* is one among the important diseases of rice plants that caused false smut, decreased occurrence of false smut is the major objective of breeding of rice. It has been found that R genes, such as RLS1, RSR1 and RGH1, can impart defence against false smut in rice. The FGSC predicted gene models of *U. virens* consist of 136 putative effector proteins, which are predicted to contain the CFEM domain, List domain, Fg_BMH domain and C1-TPR domain. Among the 136 genes, 45 have CPGs with only one copy, 33 have 2-4 copies, 36 have 5-10 copies and 22 have more than 10 copies. A resistance of rice line IR77494-B-20-3-4 was discovered owing to the transfer of the Rfs3 locus from False smut resistant line IR77298-14-1-2: IRGC117374-1 on chromosome 12 (49).

Modern techniques

Breeders have been utilizing modern tools in combination to conventional breeding methods for quite some time now, some of the modern techniques trending in the rice research are presented in Table 5 with targeted results and outcomes. Molecular targets of the pathogen *U. virens* such as UvChs2 and UvChs5 have been identified as HIGS methods to reduce disease severity without affecting yield (50). Rice genetic materials can be analysed to reveal potential resistance to false smut based on studies performed in this species, for example. For example, 208486 SNPs that differentiated 25 diverse rice lines were identified across 10 subpopulations in India, indicating the genetic diversity available for breeding efforts to enhance resistance, similar study with 315 rice accessions in China found 271360 SNPs in 56 Subpopulations, indicating a larger genetic pool (51). Diverse accessions from a global rice diversity panel were tested for RFS in natural and artificial settings in which GWAS exhibited significant linkages for the diseased panicles per plant located on chromosomes 2, 3, 6, 9 and 11. Chromosomes 3 and 8 exhibited significant SNPs for the number of smut balls per plant, while the chromosomes 3, 4 and 11 revealed significant SNPs for the disease score (52).

Recent advances in pathogen pan-genome analyses have significantly enhanced our understanding of *U. virens*, by revealing the extensive genomic diversity underlying its pathogenicity and host adaptation. Importantly, pangenome-graph studies reveal both conserved core effectors and isolate-specific virulence determinants -a pattern that opens avenues for comparative functional genomics and targeted host-pathogen interaction assays. These insights underscore the importance of integrating multi-omics datasets (genomics, transcriptomics, metabolomics) and high-resolution

Table 5. Modern techniques for breeding rice false smut (RFS) resistance lines

Technique	Details of the results revealed	References
Molecular targets	Pathogen targets UvChs2 and UvChs5 identified as HIGS methods to reduce disease severity without affecting yield	(4)
	Genetic diversity studies: 208,486 SNPs in 25 diverse rice lines across 10 subpopulations in India. 271,360 SNPs in 315 accessions across 56 subpopulations in China	(13)
Transcriptomics	GWAS linkages for infected panicles and smut ball formation on chromosomes 2, 3, 6, 9, 11 (natural/artificial settings)	(18)
	The transcription factors are part of the WRKY in plant defense and have shown three members- OsWRKY53, OsWRKY69 and OsWRKY71-being up-regulated in RFS-resistant cultivar IR28 at *U. virens* infection	(42)
	Transcriptome analysis revealed that resistant/susceptible cultivars possess DEGs that encode peroxidases, receptor like kinases and WRKY transcription factors	(41)
	Identified 28 genes which encodes basic leucine zipper transcription factors in *U. virens* genome	(35)
CRISPR-Cas9	*SPR9 locus* influences resistance to RFS; CRISPR used to design highly specific gRNA targeting the first exon of SPR9 gene in Hui1586	(17)
	Editing *USTA* and *UvSLT2* genes in *U. virens* with CRISPR, resulting in reduced ustiloxin formation, increased cell wall disruption sensitivity and diminished fungal virulence	(40)
Gene silencing	RNA silencing using highly effective target genes (e.g., UvCom1 and UvPro1) essential for virulence and development	(6)
	Development of transgenic rice cultivars using UvCom1, UvPro1 and fungal-specific septin gene *UvAspE* for RFS resistance	(7)

pangenome frameworks to refine the evolutionary narrative of *U. virens* and to inform durable resistance breeding strategies in rice (53, 54).

Transcriptomics

Functional studies further show that *U. virens* effectors suppress WRKY-mediated defense, highlighting the value of engineering effector-insensitive or defense-amplified WRKY alleles. Notably, resistant rice genotypes exhibit marked upregulation of WRKYs such as *OsWRKY53*, *OsWRKY69* and *OsWRKY71* following pathogen exposure, underscoring their role in mounting an effective defense response (55, 56). Comparative transcriptome analyses between resistant and susceptible cultivars also reveal substantial differences in WRKY activity alongside peroxidase- and receptor-like kinase-related gene expression, emphasizing the broader network in which WRKYs operate. Additionally, the presence of multiple pathogen-derived transcription factors and bZIP regulators in the *U. virens* genome suggests complex host–pathogen transcriptional interplay that WRKYs must counteract. Together, these insights position WRKY transcription factors as promising targets for genome editing and molecular breeding strategies aimed at developing durable resistance to RFS (57).

CRISPR CAS-9

The Spreading Panicle 9 (SPR9) locus, which governs a simple spreading panicle morphological change, has a strong influence the resilience of false smut of rice, The CRISPR-Plant database and website were used in the design of very specific gRNA spacer sequences, one of which targeted the first exon of the SPR9 gene in Hui1586 (58). The two genes involved in false smut in rice, USTA and UvSLT2, were used to edit by the CRISPR-Cas9 method. This led to a significant decrease in the amount of ustiloxin produced and heightened sensitivity to disruption of the cell wall, lowering the virulence in rice fungal pathogen.

Gene silencing

Selecting highly effective target genes is a crucial initial step of silencing RNA in HIGS. A few virulence genes are only reported in *U. virens* (13). The fungal-specific transcription factors UvCom1 and UvPro1 are essential for virulence and development. The transcriptional factors UvCom1 and UvPro1 are important for virulence and development (43). Using two genes, UvCom1 and UvPro1, as well as a novel fungal-specific septin gene designated as UvAspE (Uv8b_1773), the RFS resistance is developed in transgenic rice cultivars (44).

Identified practical breeding challenges for RFS resistance

Development of resistance to RFS remains challenging because of the gaps in translating knowledge into practical breeding. The disease is strongly influenced by genotype × environment making it difficult for accurate and consistent phenotyping. Most identified resistance genes and QTLs show small or unstable effects across locations and seasons. Only a few have been fully validated for practical use. The infection process itself is complex and occurs at the booting stage, making controlled screening labour-intensive and unreliable (59). Limited knowledge about host x pathogen interactions and pathogen diversity further limits the discovery of reliable resistance. Even when QTLs are known, they often bring linkage drag or behave differently in new genetic backgrounds, complicating their use in breeding programs. Additionally, gaps in functional validation, insufficient high-quality mapping populations and the slow adoption of genomics-assisted tools make it difficult to translate molecular findings into stable, reliable and high-yielding resistant cultivars.

Future perspective

The efficiency of identifying and characterizing resistance genes and quantitative trait loci for FS has improved with the different high-resolution genomic tools developed in recent years which includes genome wide association studies and next-generation sequencing. The tools enable researchers to successfully identify specific genes and regulatory elements that contribute to resistance, providing a pathway toward precision genetic improvement. Genomic selection (GS), in conjunction with marker-assisted selection, is anticipated to become an increasingly important means of transferring RFS resistance genes to elite cultivars in order to maximize yield. Moreover, the advent of genome editing technologies, especially CRISPR/Cas9, presents transformative approaches through targeted modifications to improve resistance. In addition, a knockout of susceptibility genes or the introduction of beneficial alleles using CRISPR/Cas9 can provide a basis for durable resistance to the causal agent of RFS, *Ustilaginoidea virens*. Not only is this method accurate but also can reduce the breeding cycle drastically than traditional methods. Further studies integrating omics technologies such as transcriptomics, proteomics and metabolomics, would provide a better insight into the host–pathogen interaction and identify potential novel resistance pathways. Combined with artificial intelligence and machine learning, these strategies can also optimize breeding by predicting gene-environment interactions and performance. Utilization of these advanced tools as synergistic partners with interdisciplinary approaches is the way forward for RFS resistance breeding and the development of resistance in disease, climate-resilient rice cultivar to secure food in an agro-climatic environment that is continuously evolving.

Conclusion

Based on the information tracked about RFS disease in the article, it can be concluded that it is one of the significantly affecting, evolving and tricky crop disease to the rice cultivating regions. It has limited sources of resistance. Existing resistance varieties, management and other preventive methods are not commercially durable, economical and sustainable for rice productions. The understandings of disease mechanism (plant-pathogen interaction) and genetics gene for gene hypothesis of RFS has provided the way forward to adopt right sources and methods for breeding resistant cultivars in the quick times. The achieved outcomes came through precise and targeted breeding methods traditional (introduction, backcrossing, gene pyramiding, mutation breeding) integrated with advanced breeding techniques like QTL's, MAS, CRISPR-Cas, genome editing, etc. Effective and efficient and innovations solutions have come along with the deeper understandings of molecular mechanisms. The complex and evolving nature of disease and changing global climatic condition are challenging obstacle for breeders apart from linkage drag and balance between other agronomic traits. The collaborative and emerging approaches along with the conventional will be essential to develop broad spectrum and durable RFS varieties of staple food crop.

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Authors' contributions

SG compiled reviews and wrote first draft of the article; CCP and identified topic, corrected, curated, concluded and prepared final article with added supporting references and pictures. NC overviewed compiled and suggested insights to the review. All authors read and approved the final manuscript.

Compliance with ethical standards

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