# REVIEW

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# Rice virus disease in Indonesia: epidemiology and varietal resistance



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# Abstract

The geographical location of Indonesia in the tropical region, characterized by high temperatures and humidity, is favorable for the development of viral diseases in rice. Climate change and intensive rice production systems further exacerbate the detrimental effects of viral diseases on rice sustainability. Three major rice virus diseases in Indonesia—rice tungro disease (RTD), rice rugged stunt virus (RRSV), and rice grassy stunt virus (RGSV)—have affected more than 170,000 ha of rice from 2010 to 2022. Key factors contributing to viral disease epidemics in the country include the extensive planting of high-yielding varieties twice a year, intensive use of fertilizers, asynchronized planting, and erratic climatic conditions. Cultivating rice varieties that are resistant to both viruses and their vector insects is the most effective and efficient strategy for the integrated pest management of rice viral diseases. The development of RTD-resistant varieties. However, the development of RRSV and RGSV-resistant varieties remains challenging due to a lack of genetic resources for improving rice resistance. Progress has been achieved only by developing varieties resistant to brown planthoppers as vectors of these virus diseases. To address these challenges, the potential use of genetic technology to develop rice that is resistant to viral diseases is discussed.

Keywords Rice tungro disease, Dwarf viruses, Green leafhopper, Brown planthopper

# Background

Indonesia is an archipelago country located right of the equatorial line, where most of the region receives rainfall due to the influence of the Asian Monsoon and the Pacific Ocean (Loo et al. 2015). Paddy fields with natural

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volcanic soils and monsoon climatic influences suit rice growth. The rice area planted yearly is more than 10 million hectares of paddy fields consisting of different agroecosystems, including irrigated, rainfed, tidal swamp, and flood-prone areas (Rumanti et al. 2016; FAO 2024). Indonesia is currently the fourth largest rice-producing country in the world after China, India, and Bangladesh (FAO 2024). However, domestic rice demand continues to increase with population growth and relatively high per capita consumption. In 2022, rice per capita consumption was approximately 81 kg of milled rice per year (BPS-Statistics Indonesia 2023).

Under irrigated conditions, there are usually two rice planting seasons in Indonesia, which enable rice to grow throughout the year. The first season, or the wet season crop, is from October to December and is harvested from



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March to April. The second season or dry season crop starts from April to May and is harvested from August to September (Naylor et al. 2007). Uncertain climatic conditions occur because of the geographic position driven by the El Niño-Southern Oscillation (ENSO), which causes El Niño and La Niña cycles (Naylor et al. 2007). During El Niño events, Indonesia experienced drier conditions, whereas during La Niña events, the country experienced wetter conditions. These climatic anomalies significantly affect rice production in Indonesia (Iizumi et al. 2014). La Niña, a climate anomaly that causes a wet-dry season, strongly supports the expansion of rice cultivation in 2022; in contrast, low rainfall during the El Niño climate anomaly in 2023 significantly reduced rice production (Meylinah 2024). The impact of climate variability on rice production in Indonesia has also been linked to an increase in pest and disease infestations (Surmaini et al. 2024). Pest and disease may reduce food crops by up to 41% (Savary et al. 2000).

Viruses are among the most prominent infectious agents in rice (Qin et al. 2019). Various symptoms of viral disease in rice include stunted plants, yellow leaves, and other developmental abnormalities, such as ring spots, curled leaves, wilting, and necrosis (Mohamed et al. 2023). Seventeen rice diseases have been reported to be caused by viral infection in various regions (Qin et al. 2019). In Indonesia, three viral diseases are widespread and cause significant yield losses: rice tungro disease (RTD), rice ragged stunt virus (RRSV), and rice grassy stunt virus (RGSV) (Azzam and Chancellor 2002; Helina et al. 2023).

While the epidemics of RTD, RRSV, and RGSV are sporadic, these diseases cause significant losses worldwide. Rice tungro disease has spread to almost all major rice-growing areas, such as China, India, Indonesia, Bangladesh, Vietnam, and the Phillippines (Azzam and Chancellor 2002; Muralidharan et al. 2003; Dai and Beachy 2009; Nihad et al. 2021). The disease is estimated to cause annual rice yield losses of 5–10% in South and Southeast Asia (Dai and Beachy 2009). A high incidence of RRSV has been reported in Indonesia, the Philippines, Thailand, and Vietnam (Du et al. 2007; Cabauatan et al. 2009). High RGSV incidences have been reported in Indonesia, the Philippines, India, and Japan (Cabauatan et al. 2009; Wang et al. 2022).

Several management practices are recommended to control viral diseases in rice, including monitoring the spread of the disease, simultaneously planting, controlling vectors, and planting resistant cultivars (Azzam and Chancellor 2002). Among these practices, the use of resistant cultivars is considered the most effective strategy when either virus- or insect-vector-resistant varieties are used. Therefore, improving the disease resistance of rice varieties is important for reducing yield losses caused by this disease. This paper reviews the epidemiology of rice viral diseases and the status of the development of virus-resistant rice in Indonesia.

# Epidemiology of rice virus diseases in Indonesia

The epidemic of viral diseases in Indonesia is triggered by several factors, including the extensive planting of highyielding varieties, intensive use of fertilizers (Suzuki et al. 1992; Azzam and Chancellor 2002), asynchronized planting (Sama et al. 1991; Aryawan et al. 1993), and erratic climatic conditions (Senoaji et al. 2023; Surmaini et al. 2024). The cultivation of superior rice varieties, such as Ciherang and Inpari 32, which cover more than 50% of the rice area in Indonesia (Sitaresmi et al. 2023a), is also vulnerable to the breakdown of varietal resistance to viral diseases and vector insects. From 2010 to 2022, a total of 178,554 ha of rice area was infected by RTD, RRSV, and RGSV, 15,766 ha of which were damaged by the disease (Directorate of Food Crop Protection 2023).

#### **Rice tungro disease**

Rice tungro disease (RTD) is caused by two viruses: rice tungro spherical virus (RTSV) and rice tungro bacilliform virus (RTBV) (Hibino et al. 1991). RTD is transmitted through the synergistic effect of RTBV and RTSV. RTBV is a pararetrovirus classified into the genus Tungrovirus and belongs to the Caulimoviridae family, which consists of a double-stranded DNA genome. The RTBV genome is a circular double-stranded DNA molecule of approximately 8 kbp, with two site-specific discontinuities resulting from the replication process by reverse transcription, and it has four open reading frames (ORFs), ORFs I-IV (Bao and Hull 1992; Laco and Beachy 1994; Marmey et al. 2005). The ORFs encode proteins P1 (24 kDa), P2 (12 kDa), P3 (196 kDa), and P4 (46 kDa) (Herzog et al. 2000). There is limited information on the functions of gene products from ORFs I, II, and IV. ORF-III encodes a large polyprotein, that contains a putative movement protein (MP), coat protein (CP), aspartate protease (AP), and replicase proteins (Hull 1996). The RTBV genomes from the Philippines, Thailand, India, and Malaysia have been reported, and they were grouped into two groups: South Asia and Southeast Asia (Nguyen et al. 2021).

Rice tungro spherical virus (RTSV), a picornavirus from the *Waikavirus* genus and the *Secoviridae* family, has a single-stranded RNA genome (Bousalem et al. 2008; Thompson et al. 2017). The RTSV genome is approximately 12 kb in length and has one large open reading frame (ORF) capable of encoding a viral polyprotein of approximately 390 kDa (Shen et al. 1993). The polyprotein is processed by a protease, resulting in three coat proteins (CPs) that are arranged adjacent to each other (CP1-3) (Shen et al. 1993). The complete genome sequence of RTSV has been reported for isolates collected from Mindanao, the Philippines (Isogai et al. 2000); Orissa and West Bengal, India (Verma and Dasgupta 2007); Andhra Pradesh, India (Sailaja et al. 2013) and Seberang Perai Malaysia (Kannan et al. 2020). Phylogenetic analysis based on the whole genomes classified the RTSV isolates into two groups, South Asia and Southeast Asia, indicating the influence of geographical region on virus genomic evolution (Kannan et al. 2020).

Rice tungro bacilliform virus (RTBV) is principally responsible for the development of symptoms that cause changes in plant growth, whereas RTSV encodes the proteins necessary for the transmission of viruses between individual plants. RTBV–RTSV interactions induce disease symptoms, including stunting and discoloration of diseased plants, reduced tillering, and sterile panicles (Cabauatan et al. 1999). The RTBV and RTSV are transmitted only by green leafhoppers and zigzag leafhoppers. Transmission efficiency differs between vector species. *Nephotettix virescens* is the most efficient green leafhopper species for transmitting both species of rice tungro virus, in addition to *N. nigropictus*, *N. malayanus*, and *N. parvus* (Widiarta 2014).

Tungro vectors and viruses have alternative hosts in addition to rice. Green leafhoppers live in rice seed-ling nurseries, ratoons, or volunteer rice. The most efficient tungro virus vector, *N. virescens*, thrives in rice. *N. nigropictus* thrives on rice and grasses and can transmit

the virus from grasses to rice plants. The virus was recovered from virus-infected weed host species, such as *Echinocloa colonum*, *E. crisgalli*, *Panicum repens*, *Cyperus rotundus*, *Paspalum dilatum*, *P. hydrophilum*, and *Leersia hexandra* (Patel et al. 2018). In South Sulawesi, RTBV has been found in the grasses *Panicum repens*, *Cyperus difformis*, *Echinochloa crusgalli*, *Fimbristilys miliacea*, and *Eleusine indica* (Rosida et al. 2023).

Although the population density of green leafhoppers in Indonesia is low, they play an essential role as transmitters of tungro virus. Insects can disperse, especially in areas with asynchronous rice cropping patterns (Widiarta 2014). The presence of viral inoculum sources in an area leads to a rapid transmission cycle, generating a tungro-endemic area. In rice-fallow and multi-crop planting systems, the spread of tungro disease is slow because of the low population density of the vectors (Widiarta et al. 1990; Aryawan et al. 1993; Widiarta et al. 1993).

Spherical viruses are detected earlier than bacilliform viruses in both rice plants and green leafhoppers, allowing vectors to acquire and transmit stem viruses (Cabauatan and Hibino 1984). The presence of both species of viruses in the early vegetative stage of rice plants causes severe symptoms of RTD in the form of stunted plants, reduced number of tillers, and yellow leaves from the tips, especially on the youngest leaves (Fig. 1). Plants infected only with spherical viruses generally do not show symptoms, whereas rice plants



Fig. 1 Symptoms of rice tungro disease include stunted plants and yellow leaves from the tips, particularly on the youngest leaves and the corresponding viral vector green leafhopper (*N. virescens*). Images source: IRRI Knowledge Bank (http://www.knowledgebank.irri.org/)

infected only with bacilliform viruses exhibit mild symptoms (Hibino et al. 1978).

The extent of RTD-affected areas in Indonesia increased during the La Niña climate anomaly in 2011 and 2012, with attack areas of 16,027 ha and 17,017 ha, respectively (Fig. 2). The lowest attacked area of the RTD was from 2018 to 2020. However, the loss from an affected area ranges from 1607 to 3717 ha per year, with a value of up to 1.2 million USD (Widiarta 2021). These losses are significant for farming households with

0.5 ha of cultivated land, the average landholding of farmers in Indonesia.

The RTD has spread to almost all provinces in Indonesia and has been previously found only in Java, Bali, and South Kalimantan (Azzam and Chancellor 2002; Widiarta 2021). During the 2022 planting season, four provinces had the highest number of affected areas: Central Kalimantan (8616 ha), South Kalimantan (4691 ha), West Java (309 ha), and Papua (171 ha) (Fig. 3).



Fig. 2 Rice areas in Indonesia were attacked by brown planthoppers (BPHs), rice tungro disease (RTD), rice ragged stunt virus (RRSV), and rice grassy stunt virus (RGSV) from 2010 to 2022. Source: Directorate of Food Crop Protection (2023)



Fig. 3 Rice tungro disease incidence in provinces of Indonesia during 2022 planting season. Source: (BBPOPT 2022)

#### **Rice dwarf virus diseases**

Brown planthoppers (Nilaparvata lugens) transmit two types of rice dwarf virus diseases, rice grassy stunt virus (RGSV) and rice ragged stunt virus (RRSV) (Fig. 4a, b). The rice ragged stunt virus belongs to the genus Oryzavirus within the family Reoviridae (Miyazaki et al. 2008). It infects plants of the Poaceae family, including rice plants. This virus was discovered in Indonesia and the Philippines in the 1970s (Palmer and Rao 1981). The rice ragged stunt virus contains an icosahedral particle approximately 65 nm in diameter and is composed of 10 double-stranded RNA segments (Yan et al. 1992). The nucleotide sequences of RRSV genome segments S5, S8, and S9 were determined. The genome segments S5 encodes ca 91 kDa minor structural protein (Li et al. 1996), S8 encodes a 67-kDa major structural protein (Upadhyaya et al. 1996), and S9 encodes a 38-kDa major structural protein (Upadhyaya et al. 1995). The RRSV isolates from Java-Indonesia had the closest affinity to AF486811-Philippines (Suprihanto et al. 2015).

RGSV is a member of the genus *Tenuivirus*, which consists of six members, including the rice stripe virus



Fig. 4 a Symptoms of rice grassy stunt virus (RGSV) include stunted plants and yellow-orange leaves. b Symptoms of rice ragged stunt virus (RRSV) include stunted plants, dark green short leaves, serrated or ragged leaves, twisting at the end, and impaired panicles. c Brown planthopper (*N. lugens*), the vector of RGSV and RRSV. Images source: IRRI Knowledge Bank (http://www.knowledgebank.irri.org/)

(RSV), which is the reference species (Cabauatan et al. 2009). The RGSV genome contains six single-stranded RNA segments that encode 12 proteins (Toriyama et al. 1998). The cumulative length of the RGSV genome is 25,142 nucleotides, and all six RNA segments have an ambisense coding arrangement (Toriyama et al. 1998). The RGSV isolates from Java–Indonesia had a closer affinity to GQ329710.1–Vietnam (Suprihanto et al. 2015).

The symptoms of RRSV include stunted plants, dark green short leaves, with serrated leaves and sometimes ragged leaves, which are twisted at the end; the ragged part is yellowish and brownish yellow; the leaf or stem veins sometimes swell; the leaf flag is twisted and short; and the flowers or panicles are impaired or partially exerted from the leafstalk and are usually empty (Suprihanto et al. 2015). In the 1980s, the symptoms of RGSV type II were found to resemble those of rice tungro disease, with yellow-orange leaves instead of the tips of young leaves, and the number of tillers was less than that of the grassy stunt (Suzuki et al. 1988).

The high population density of brown planthoppers (BPHs) increases the proportion of winged imago (Macroptera) populations that spread the virus along with migratory activities to new and more suitable hosts (Sawada et al. 1992). Rice dwarf virus is transmitted persistently; once the vector acquires the virus after the latent period, it becomes viruliferous. The recent increase in BPH attacks has led to an increase in the prevalence of RRSV and RGSV in Indonesia (Helina et al. 2020; Febrianto et al. 2023).

Brown planthoppers have transformed their status as major rice pests since the Green Revolution in the 1960s, when short-duration, semidwarf, and high-tillering rice types were widely adopted in Indonesia. These rice varieties allow multiple crops in a year and are highly responsive to fertilization. In contrast, plant architecture facilitates an increase in relative humidity under the canopy, which increases nymph survival (Isichaikul et al. 1994; Bottrell and Schoenly 2012; Sogawa 2015). The occurrence of El Niño and La Niña climate anomalies as an impact of climate change has induced BPH outbreaks, as fluctuations in population density are positively correlated with rainfall, air temperature, and relative humidity (Ali et al. 2014; Surmaini et al. 2024). In addition to the destruction of rice plants by insects, high infestation of the BPH has also led to the widespread spread of RRSV and RGSV diseases.

The outbreaks of dwarf virus disease in 2011 and 2017, which damaged 25,000 ha and 20,000 ha, respectively, coincided with the BPH outbreak (Fig. 2). Significant yield losses caused by RRSV have been reported in Indonesia's two most popular rice varieties, Inpari 32 and Ciherang (Kurniawati et al. 2023). These two varieties

have similar genetic backgrounds and are currently grown by more than 50% of rice farmers in Indonesia (Sitaresmi et al. 2023a). Therefore, the attack of these two varieties by the virus must be seriously anticipated.

The emergence of brown planthopper pests, followed by an explosion of RRSV and RGSV diseases in several regions of Indonesia, has also been suggested to be related to farming practices. Intensive rice cultivation throughout the year and the high use of synthetic pesticides have caused insecticide-induced resurgence of pests, particularly brown planthoppers (Thorburn 2015). High nitrogen fertilizer doses also trigger increasing the planthopper population (Gupta et al. 2017).

#### Other rice viral diseases

Other diseases caused by viruses in rice plants reported to date include yellow dwarf, rice stripe, and rice stripe necrosis viruses. Yellow dwarf disease was first identified in Indonesia in 1967 (Oka 1976). Yellow dwarf disease is transmitted by *N. virescens* and *N. nigropictus*. The disease remains minor and less important in Indonesia.

## Varietal resistance to viral diseases

Cultivating disease-resistant rice varieties is considered the most efficient strategy for controlling rice disease infestation (Leung et al. 2003; Shimizu et al. 2013). The availability of different virus-resistant varieties is an important resource for crop rotation as part of an integrated pest management strategy. This strategy is effective in controlling viral diseases in Indonesia. Integrating the rotation of RTD-resistant varieties and a uniform planting system in South Sulawesi, one of the tungro endemic areas in Indonesia, has lowered the incidence (Sama et al. 1991).

Understanding the mechanism by which rice plants respond to virus infection and the genetic mechanisms underlying plant resistance will aid in developing resistant varieties. An improvement in the resistance of rice varieties against viruses can be achieved by developing virus-resistant and vector insect-resistant varieties as single resistance strains or by bringing both virus and vector resistance strains into pyramiding. Significant research has been devoted to improving viral resistance in rice via classical and molecular breeding approaches. The challenge for these breeding programs is the identification and incorporation of elite genetic materials resistant to both vectors and viruses.

Different genetic regulations control the mechanism of rice plants in response to RTD and vary among different genetic sources. A dominant resistance gene to tungro spherical virus (RTSV) was found in the ARC11554 variety (Sebastian et al. 1996), whereas a recessive resistance gene was identified in the resistant varieties Utri Page 6 of 13

Merah and TKM6 (Azzam et al. 2001; Ebron et al. 1994; Lee et al. 2010). Evaluation of the genetic sources for tungro-resistant varieties, viz. Utri Merah, Utri Rajapan, Habiganj DW 8, Tjempo Kitjik, TKM 6, ARC 10312, and ARC 12596, against five tungro isolates from five different regions of Indonesia, indicated that Utri Merah was the most effective source (Table 1). This variety has been extensively used in breeding programs in Indonesia to develop tungro-resistant rice lines (Ladja et al. 2016).

The recessive gene *tsv1*, which controls RTSV resistance in Utri Merah, was mapped at chromosome 7, and the gene encoding the putative translation initiation factor 4G (*eIF4Gtsv1*) was found in the *tsv1* region (Lee et al. 2010). The *tsv1* allele of Utri Merah has been widely used in several breeding programs to improve rice resistance to RTSV (Simon et al. 2023). Markers for this gene have been developed based on SNPs of *eIF4G* through allelespecific PCR and used to select RTSV-resistant lines (Cho et al. 2018). For future breeding programs, other RTSV resistance genes with different virulence mechanisms are needed to anticipate the diversity of the virus. Further research is required to identify the sources of RTBV resistance.

Although intensive studies have identified genetic sources of resistance to RTD, limited information is available on the identification of resistance genes for RRSV and RGSV in natural varieties of rice (Shimizu et al. 2013; Sasaya et al. 2014; Lacombe et al. 2021). Several studies have shown that rice varieties and lines are resistant to these viruses. A dominant resistance gene for RGSV has been reported in O. nivara 101,508 (Nuque et al. 1982). A screen of 69 Indonesian rice germplasms revealed two rice accessions that were resistant to RRSV: MDK Karawang from West Java and Pulo Hitam from North Maluku (Roza et al. 2021). The study also identified one rice accession from East Java resistant to RGSV, viz. Ketik 1 (Roza et al. 2021). However, genetic information that controls resistance in these germplasms remains limited. Further genetic studies on these materials will be useful for improving the resistance of rice to dwarf virus disease. In addition, exploration of rice germplasm to identify other rice varieties or accessions that are resistant to these two viruses needs to be performed in anticipation of the diversity of the virulence mechanisms of these pathogenic viruses.

# Varietal resistance to vectors of virus diseases

Genetic studies on the resistance of rice to brown planthoppers and green leafhoppers as vectors of viral diseases have been conducted since 1970 (Fujita et al. 2013). Recently, at least 44 BPH resistance genes have been identified, many of which are located on the short arm of chromosome 4, namely, QBph4.1, QBph4.2,

Varieties	Country of origin	Bogor, West Ja	ava	Sidrap South S	ulawesi	Badung, Bali		Pesisir Selatan Sumatra	ı, West	West Papua, Pa	pua
		Disease incidence (%)	Response	Disease incidence (%)	Response	Disease incidence (%)	Response	Disease incidence (%)	Response	Disease incidence (%)	Response
Utri Merah	Indonesia	30	ш	45	×	30	×	20	Я	50	Z
Utri Rajapan	Indonesia	45	Z	45	M	55	S	30	M	25	M
Habiganj DW 8	Bangladesh	100	S	75	S	75	S	65	S	40	M
Tjempo Kitjik	Indonesia	55	S	50	S	60	S	40	M	47	M
TKM 6	India	95	S	100	S	56	S	41	M	100	S
ARC 10312	India	50	S	69	S	61	S	41	M	73	S
ARC 12596	India	95	S	70	S	100	S	60	S	58	S
Response: R = resist	tance, M = Moderate, S = S	usceptible									

Table 1 Resistance pattern of rice genetic sources for tungro resistance against five tungro isolates from Indonesia (Ladja et al. 2016)

*Bph12, Bph15, Bph17, Bph20(t), Bph30, Bph33,* and *Bph36* (Muduli et al. 2021). Among the BPH resistance genes, three genes, *Bph3, bph4,* and *Bph6,* were found to be resistant to most Southeast Asian BPH populations, including Indonesia (Horgan et al. 2015).

Moreover, the identification of green leafhopper resistance genes has not progressed since 14 resistance genes for green leafhoppers were reported by Fujita et al. (2013), including *Glh1*, *Glh2*, *Glh3*, *glh4*, *Glh5*, *Glh6*, *Glh7*, *glh8*, *Glh9*, *glh10*, *Glh11*, *Glh12*, *Glh13*, and *Glh14*. We suggest that biological and chemical studies on the feeding of green leafhoppers are the same as those on brown planthoppers and that rice plants have acquired various forms of defense against planthoppers (Ling and Weilin 2016).

# Development of virus-resistant rice varieties in Indonesia

Since the beginning of the Green Revolution, rice improvement programs in Indonesia have released rice varieties with different characteristics to target various ecosystems and meet the demand for increasing national rice production. Over the past three decades, more than 200 rice varieties have been registered and released to meet specific ecosystems, such as irrigated lowlands, uplands, and swampy lands (Sitaresmi et al. 2023b). Some released rice varieties have been proposed to minimize the yield loss due to RTD (Table 2).

Most RTD-resistant rice varieties were introduced by the International Rice Research Institute (IRRI) or derived from parental lines from the IRRI. One IRRI variety, IR42, was released in 1980 and has become a popular rice variety for irrigated lowlands and tidal swamps. Between 1985 and 2009, IR42 covered 6.4 million hectares of rice area (Brennan and Malabayabas 2011). Several RTD-resistant varieties have been developed for specific regions where RTD is endemic, such as Bali (Azzam and Chancellor 2002). Tukad Petanu, Tukad Balian, and Tukad Unda are rice varieties recommended for cultivation in Bali and Nusa Tenggara Barat, whereas Celebes is recommended to be planted by farmers in South Sulawesi (Table 2). The RTD-resistant rice variety Inpara 9 Agritan was developed explicitly for tidal swamp areas where RTD has become a significant problem (Rumanti et al. 2016). Another variety, Inpari 32, is currently the most popular in Indonesia. In 2022, Inpari 32 occupied almost 25% of the total rice cultivation area in the country (Sitaresmi et al. 2023a). The variety was released in 2013 and developed from a cross between Ciherang and IRBB64.

Although numerous RTD-resistant varieties have been developed and deployed by farmers, progress in rice improvement for dwarf virus disease is still lacking Page 8 of 13

owing to the limited genetic source for resistance in natural alleles. Farmers have adopted rice varieties to control rice viral diseases by growing rice varieties resistant to N. lugens vectors. As the main insect in Indonesia, the variety release committee requires that the proposed elite lines have resistance to at least one of the biotypes of brown planthopper. Currently, there are three major brown planthopper biotypes in Indonesia. viz. biotype 1, 2, and 3. Some rice varieties are resistant to one or two biotypes, whereas others are resistant to all biotypes, such as IR66, Memberamo, Inpari 13, and Cakrabuana Agritan (Suprihatno et al. 2010; Sastro et al. 2022). However, this strategy only mitigates the destruction of rice crops because of the brown planthopper and not because of the virus incident, which potentially appears simultaneously during the explosion of the brown planthopper population or in successive seasons.

The cultivation of resistant rice varieties leads to several challenges that need to be addressed. The adoption of a high-yield-resistant variety in large areas, as in the case of Inpari 32 in Indonesia, would reduce genetic diversity and pose vulnerability to the breakdown of disease resistance (Leung et al. 2003). Breeding strategies to mitigate the potential reduction in genetic diversity and contribute to the sustainability of rice production include the sequential release of new resistant varieties over time and space, combining multiple resistant genes, and the development of multilines (Leung et al. 2003). Genetic heterogeneity would effectively suppress plant diseases when used over large areas, as evidenced in rice blast disease management (Zhu et al. 2000). The planting of hybrid rice carrying pyramided Bph14 and Bph15 together with susceptible hybrids significantly reduced the overall population of BPH in a large field area (Hu et al. 2016). Rotation of different group-resistant varieties has been implemented in South Sulawesi, Indonesia, to manage RTD (Sama et al. 1991).

# Potential use of genome editing in developing virus-resistant rice varieties

Various gene technologies have been used to develop virus-resistant plants. RNA silencing and genome editing are two primary strategies for breeding plant antivirals (Zhao et al. 2020). RNA silencing or RNA interference methods have been used to improve rice resistance to viruses, including RTD (Tyagi et al. 2008; Sharma et al. 2018), RRSV (Lacombe et al. 2021), and rice stripe virus (RSV) (Ma et al. 2011; Shimizu et al. 2013). However, the commercial adoption of virus-resistant cultivars via RNA silencing has been hindered by complex regulatory processes as well as the social acceptance of genetically modified crops (Zhao et al. 2020). Genome editing

Varieties	Parentage	Year released	Maturity (days)	Yield average (t/ha)	Rice texture	Characteristic or resistance*	Target ecosystem
IR42	IR2042/CR94-13	1980	135–145	5.0	Hard	RTD, BPH, BLB	Irrigated lowland and tidal swampland
IR66	IR13240-108-2-2-3/ IR9129-209-2-2-2-1	1989	110-120	4.5	Hard	RTD, BPH, BLB, blast	Irrigated and rainfed lowland
Tukad Petanu	IR52256-84-2-3/ IR72//2*IR1561-228-3/ Utri Merah	2000	115–125	4.0	Medium	RTD, BPH, BLB	Irrigated lowland (mainly for Bali and West Nusa Teng- gara)
Tukad Balian	IR48613-54-3-3-1/ IR28239-94-2-3-6-2	2000	105–115	4.0	Soft	RTD, BPH, BLB	Irrigated lowland (mainly for Bali and West Nusa Teng- gara)
Tukad Unda	Balimau Putih /4*IR64	2000	100–123	4.0	Hard	RTD, BPH, BLB	Irrigated lowland (mainly for Bali and West Nusa Teng- gara)
Celebes	Tetep/IR2415-90-4-3- 2//IR19661-131-1-2	2000	105–110	5.0	Soft	RTD, BPH, blast	Irrigated lowland (mainly for the South Sulawesi region)
Kalimas	PSBRC2/IR39292-142- 3-2-3	2000	120-130	6.0	Soft	RTD, BPH	Irrigated lowland
Bondojudo	IR72/IR48525-100-1-2	2000	110-120	6.0	Soft	RTD, BPH	Irrigated lowland
Inpari 7 Lanrang	S3054-2D-12-2/Utri Merah-2	2009	110-115	6.2	Soft	RTD	Irrigated lowland
Inpari 8	IR65469-161-2-2-2-3-2- 2/ IR61979-136-1-3-2-2	2009	125	6.4	Soft	RTD	Irrigated lowland
Inpari 9 Elo	IR68064-18-1-1-2-2/ IR61979-136-1-3-2-2	2009	125	6.3	Soft	RTD	Irrigated lowland
Inpari 31	Pepe/BP342B-MR-1-3- KN-1-2-3-6-MR-3-BT-1	2013	119	6.0	Soft	RTD, BPH, BLB	Irrigated lowland
Inpari 32 HDB	Ciherang/IRBB64	2013	120	6.3	Medium	RTD, BLB, blas	Irrigated lowland
Inpari 36 Lanrang	IR58773-35-3-1-2/ IR65475-62-3-1-3-1-3-1	2014	114	6.7	Soft	RTD, blast	Irrigated lowland
Inpari 37 Lanrang	CT9162-12/Seratus Hari T36//Mem- beramo/Cibodas/// Cibodas/// IR66160- 121-4-5-3/Membramo	2015	114	6.3	Soft	RTD, blast	Irrigated lowland
Pamelen	IR64*2/O. rofipogon 102,186	2019	112	6.7	Soft	RTD, BPH, BLB, red rice	Irrigated lowland
Inpari IR Nutrizinc	R91153-AC 82/ IR05F102//IR68144- 2B-2-2-3-166///IRRI145	2019	115	6.2	Soft	RTD, BPH, BLB	Irrigated lowland
Inpara 9 Agritan	Mesir/IR60080-23	2014	114	4.2	Hard	RTD, BLB, tolerant to Fe toxicity	Tidal swampland

# Table 2 Rice tungro disease-resistant varieties released in Indonesia. Source: Sastro et al. (2022); Suprihatno et al. (2010)

\* *RTD*, rice tungro disease; *BPH*, brown planthopper; *BLB*, bacterial leaf blight

strategies have been developed to overcome the problems associated with genetic modification approaches.

Genome editing, such as transcriptional activator-like effector nucleases and clustered regularly interspaced short palindromic repeats (CRISPR)-associated endonuclease Cas9 (CRISPR/Cas9), have the potential to be used in the development of disease-resistant rice varieties (Mishra et al. 2021). The CRISPR/Cas9 system has been used to improve plant resistance against viruses in two ways: by targeting the viral genome and by targeting host susceptibility genes (Mushtaq et al. 2020; Zhao et al. 2020). A number of successful gene editing approaches for the development of virus-resistant crops have been reported. The CRISPR/Cas9 system has been used to develop resistant barley ((*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) against wheat dwarf virus, an insect-transmitted virus belonging to the *Geminiviridae* family (Kis et al. 2019; Yuan et al. 2024). Gene knockout in cucumber using the CRISPR/Cas9 system targeting the cucumber *eIF4E* gene has successfully generated mutant plants that exhibit resistance against viruses from the *Potyviridae* family (Chandrasekaran et al. 2016). CRISPR/Cas9-mediated genome editing targeting *eIF4E* in cassava improved the resistance of cassava against cassava brown streak disease caused by two species of positive-sense RNA viruses belonging to the family *Potyviridae* (Gomez et al. 2019).

The virus requires host factors such as eukaryotic initiation factors (*eIFs*) to progress infection. Rice resistance to RTSV has been identified as recessive and is regulated by *initiation factor 4 gamma* (*eIF4G*) (Lee et al. 2010). A CRISPR/Cas9 genome editing mutation in *eIF4G* has been obtained in RTSV-susceptible rice varieties to improve resistance to RTSV (Macovei et al. 2018). A similar strategy was used to induce site mutation in the *eIF4G* allele to improve rice resistance against the rice black-streaked dwarf virus (RBSDV) (Wang et al. 2021).

More recently, knockout mutants of rice vacuolar ATPase (*OsV-ATPase*) generated using the CRISPR/Cas9 system increased rice resistance to the southern rice black-streaked dwarf virus (SRBSDV) (Lu et al. 2023). This improved resistance is associated with jasmonate (JA) and abscisic acid (ABA) biosynthesis. A further challenge is to develop rice varieties resistant to RGSV and RRSV, where sources of resistance remain unavailable in natural variation.

#### **Conclusion and future perspectives**

The destructive effects of viral diseases on rice production must be anticipated to minimize yield losses and maintain production stability. Currently, farmers are highly dependent on synthetic pesticides to control virus vectors, which may potentially induce a resurgence of pests. An integrated pest management approach, in which resistant varieties are the main components for control, is required to manage the spread of RTD, RRSV, and RGSV. Breeding strategies should be directed to sequentially deploy new resistant varieties over time in different regions, combine multiple resistant genes, and develop multilines to maintain genetic diversity. Breeding rice to improve its resistance to RTD has been relatively successful in Indonesia, as demonstrated by the release and adoption of several resistant varieties. Current progress has been made in controlling dwarf virus disease by developing varieties resistant to brown planthoppers as vectors of dwarf virus disease. Successful genome editing application using the CRISPR/Cas9 system to improve viral resistance in different crops shows promise for its utilization in the development of virus-resistant rice, particularly for RSSV and RGSV diseases, in which the genetic sources for resistance in natural variations are limited.

# Abbreviations

ABA	Abscisic acid
AP	Aspartate protease
BLB	Bacterial leaf blight
BPH	Brown planthopper
CP	Coat protein
CRISPR	Clustered regularly interspaced short palindromic repeats
DNA	Deoxyribonucleic acid
elFs	Eukaryotic initiation factors
ENSO	El Niño–Southern Oscillation
IRRI	International Rice Research Institute
JA	Jasmonate
MP	Movement protein
ORF	Open reading frames
RBSDV	Rice black-streaked dwarf virus
RGSV	Rice grassy stunt virus
RNA	Ribonucleic acid
RRSV	Rice rugged stunt virus
RSV	Rice stripe virus
RTD	Rice tungro disease
	Southern rice black-streaked dwarf virus

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#### Author contributions

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#### Availability of data and materials

All the data is presented in the main text file.

#### Declarations

**Ethics approval and consent to participate** Not applicable.

#### **Consent for publication**

Not applicable.

#### Competing interests

The authors declare that they have no competing interests.

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