

Revealing the challenges and prospects of Asian rice gall midge resistance in rice

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Abstract: The Asian rice gall midge (*Orseolia oryzae*) (Wood-Mason) is a major pest of rice, significantly reducing yields and challenging sustainable rice production. This review provides a comprehensive overview of the biology, lifecycle and geographical distribution of the rice gall midge, along with the damage symptoms it causes in rice crops. The interactions between rice and gall midge, the pest's infestation mechanism and the plant's defensive responses are also explored. Various management strategies are discussed in detail, including insecticides, cultural practices and resistant varieties. The review emphasises that breeding for resistance, especially through the pyramiding of resistance genes and integrated pest management approaches, shows the most promise for long-term control. Advances in crop improvement through breeding methods such as genotyping, phenotyping, field and greenhouse screening and the pyramiding of resistance genes are highlighted. The review emphasises the importance of monitoring virulence in gall midge populations to guide breeding efforts. The genetic basis of resistance is examined through studies of resistance genes, QTL mapping and marker-assisted breeding. Furthermore, molecular approaches, including metabolomic regulations, microarray analysis and biotechnological strategies, are reviewed for their potential in developing durable gall midge-resistant rice varieties. This article synthesises the current knowledge and highlights future research directions, such as identifying novel resistance genes, improving molecular breeding techniques, and developing integrated pest management strategies that combine genetic resistance with eco-friendly controls.

Keywords: *Orseolia oryzae*; rice pest management; resistance genes; host-plant resistance; marker-assisted selection; molecular breeding; integrated pest management

Rice (*Oryza sativa*) belongs to the Poaceae family of grasses and is thought to have originated eight thousand years ago in Asia, especially in China and India (Pasalu et al. 2004). It is one of the most important cereal grains, a staple diet for many of the global population, and a staple food in India. The world's population is increasing rapidly,

meaning that rice consumption will increase from 450 mil. t in 2011 to over 490 mil. t in 2020. To meet the demand for rice, an additional 40% of the output would be required by 2050 (Bentur et al. 2013). The rice gall midge (*Orseolia oryzae*), rice leaf folder (*Cnaphalocrocis medinalis* Guenee), brown hopper (*Nilaparvata lugens* Stal), yellow stem

borer (*Scirpophaga incertulas* Walker), green leafhopper (*Nephotettix virescens* Distant) and white backed planthopper (*Sogatella furcifera* Horvath) are among the most dangerous rice pests, leading to significant yield losses (Singh & Kumari 2020). Nevertheless, rice production is greatly affected by numerous unfavourable elements, including pests and illnesses. In this group of dangers, Asian rice gall midge (ARGM), *Orseolia oryzae* ranks third in damage, behind only borers and planthoppers (Singh & Kumari 2020).

Pest resistance in plants is a multifaceted phenomenon that depends on the efficacy of the plant's defensive mechanisms. Incompatible interactions between rice (*Oryza sativa*) and gall midge (*Orseolia oryzae*) can result in maggot mortality and potential local necrotic death of host tissue (Bentur et al. 2016), a hypersensitive response (HR+) or no death of host tissue (HR–) (Bentur & Kalode 1996). Genetic exchange between a virulence (avr-gene) gene of the pest and the resistance (R-gene) gene of the host determines whether rice plants are resistant to Asian GMs (Rawat et al. 2012a). This connection is similar to that between plants and pathogens. Eleven R-genes (*Gm1* through *Gm11*) resistant to gall midge (GM) have been identified in Indian rice germplasm (Suvendhu et al. 2014). All R genes except *gm3* are dominant, and they are being used to create GM-resistant rice varieties. However, new harmful GM biotypes have emerged due to the overuse of resistant rice species (Sama et al. 2014). This indicates that resistance and virulence in the GM are constantly coevolving mechanisms, and the R gene, which is responsible for gall midge resistance, should be improved.

Scientific studies and agricultural innovation have also been conducted to enhance yields, sustainability, and resistance to environmental difficulties (Cohen et al. 2004). Biological systems can be

better understood by conducting integrated transcriptomic and metabolomic data studies, which are collected from two different levels of the organism: the transcript and metabolite levels. A better understanding of molecular-level cellular complexity can be achieved through an integrated study of gene expression and metabolomics (Agarwal et al. 2016). When integrated 'omics' approaches have emerged, we have learned a great deal about the intricate pathway from gene expression to function in living systems subjected to different types of stress. Several recent studies have used microarray data combined with metabolomics data from gas chromatography mass spectrometry (GCMS) to investigate different areas of plant biology (Agarwal et al. 2016). Research on differences between root and border cells in Medicago (Makkar & Bentur, 2017), senescence in citrus fruits (Bentur et al. 2016), and triacylglycerol levels in red algae (Agarwal et al. 2016) has been conducted. The reaction of rice to bacterial blight pathogens has been studied (Himabindu et al. 2010). A few publications detail the interactions between insects and rice, and even fewer describe the process of analysing insect-plant interactions through the combined use of transcriptomics and metabolomics.

BIOLOGY AND ECOLOGY OF RICE GALL MIDGE

Asian rice gall midge is a member of the *Cecidomyiidae* family. The adult midges have dark-colored bodies and are small, mosquito-like insects that are 1–2 mm long (Figure 1). The legless, pale white larvae resemble maggots and are usually found inside the tissues of rice plants. Tubular gall formation at the base of the leaf nodes by the ARGM is also known as "onion leaves" or "silver shoots" (Nayak et

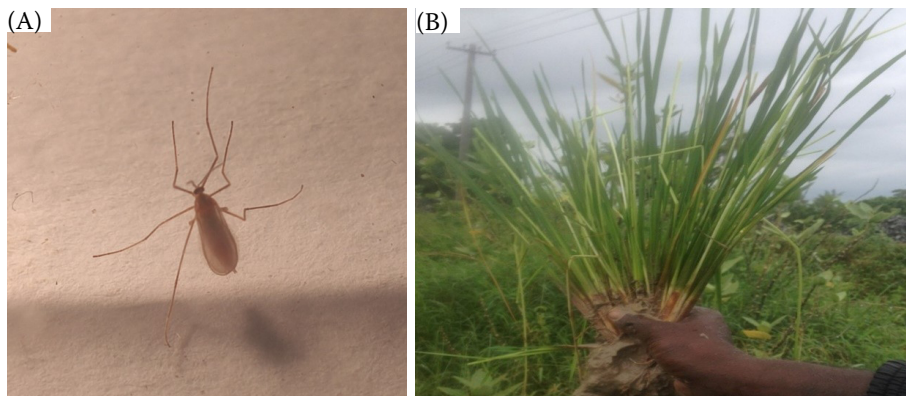


Figure 1. Adult Asian rice gall midge (A) and infested silver shoots (B)

al. 2023). In addition to rice, the gall midge has alternate hosts, including wild grasses like *Eleusine indica*, *Bothriochloa* sp., and *Paspalum* sp. These grasses allow the pest to survive even when rice is not in cultivation, contributing to its persistence in the ecosystem (Mardi et al. 2009).

Asian rice gall midge is a pest that attacks tillering rice crops in wetland rice fields, either irrigated or nourished by rain. Adults are most easily caught at night using light traps because of their nocturnal habits. The maggots stay in their pupal stage and are dormant throughout the dry season (Jagadeesha et al. 2010). They reawaken after the rains stop and the buds begin to expand. Cloudy or wet weather, growing high-tillering rice types, intense pest management, and minimal parasitisation all contribute to the density of the ARGM population (Basit & Bhattacharyya 2001).

The fly will lay its long, cylindrical, shiny eggs at the leaf bases singly or in clusters of two to six. The eggs might be white, red, and pinkish. After hatching, the maggot has a pointed front end and grows to a length of 1 mm. It seeps into the developing bud after sliding along the sheath. Around the feeding location, an oval chamber formed. Antennal horns assist the pupa as they vigour the tube to the tip of the silver shoot, which projects halfway out during emergence. The typical fly colour is a mosquito-like golden brown or orange (Rajamani et al. 2004).

Lifecycle of ARGM. The GM needs 22–28 °C and approximately 85–85% humidity to finish its life cycle, which takes 19–24 days (Figure 2). The pre-monsoon rains in India in May and June intensify pest activity in several hosts, including rice stubble. The last week of August through the first week of October is the most active stage of insects. Potential substitute hosts include *Graminaceous* plants such as *Leersia hexandra* and *Echinochloa crusgalli*, as well as wild types of rice such as *Oryza nivara*, *Oryza barthii*, and *Oryza rufipogon* (Seni & Naik 2019).

Egg: The translucent, shiny, light pink eggs of the gall midge were deposited in clusters on the underside of the rice leaves, close to their base, with an incubation period of 2 to 3 days (Figure 2). When the newly hatched maggots reach the apical or lateral buds, they travel between the leaf sheaths (Jagadeesha et al. 2010).

Larval: Rice leaf apical primordia are the first tissues larvae eat after they emerge from the eggs. They specifically attack growth sites, inflicting damage that results in the development of recognisable galls. The larvae are protected from these elements by these galls. Larvae feed and grow inside galls for multiple instars or periods between moults (Rajamani et al. 2004).

Pupal: After development, the larvae pupate inside the gall itself. The larva changes into an adult midge during the pupal, non-feeding stage. Pupae

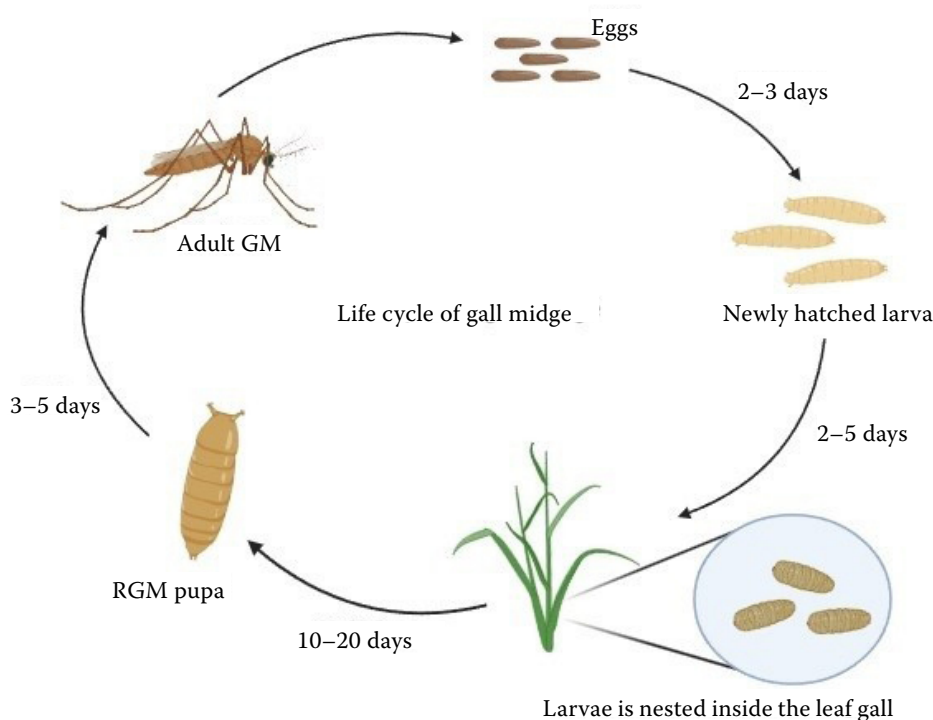


Figure 2. Asian rice gall midge life cycle of rice gall midge

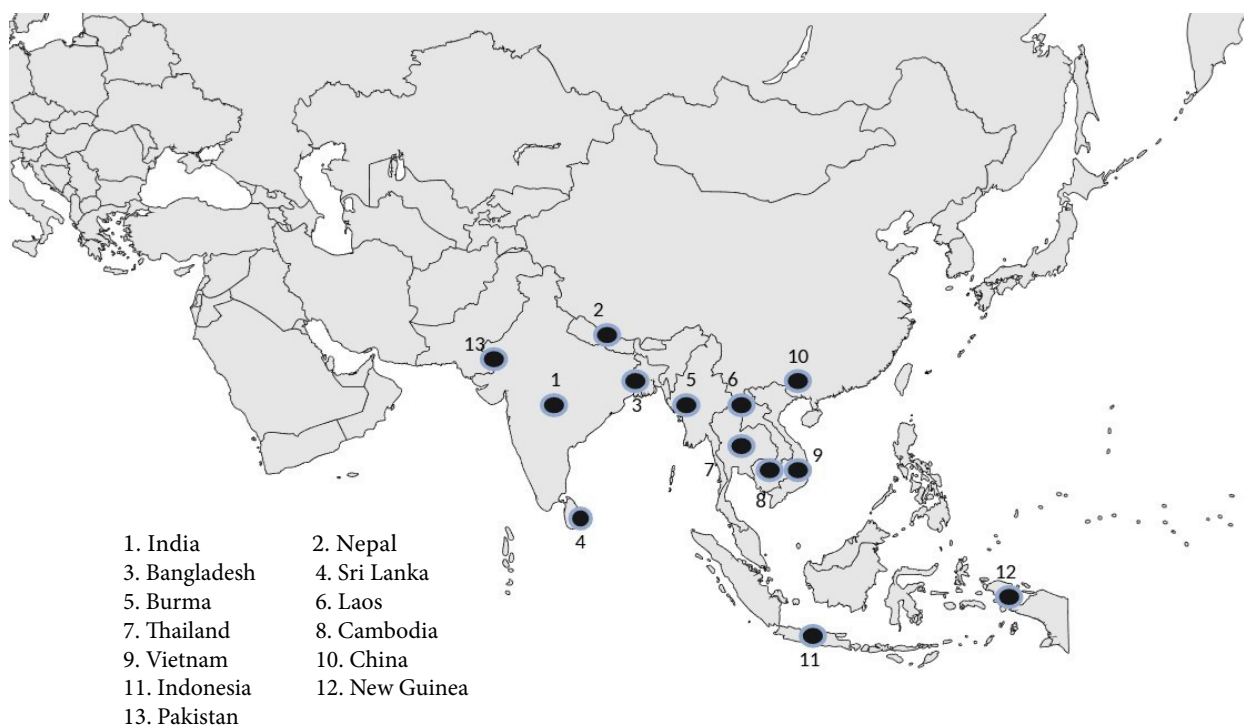


Figure 3. Distribution of ARGM in Asia

are frequently discovered in the soil close to or inside galls (Bhatt et al. 2018).

Adult: The pupae give rise to the adult rice gall midges. These tiny flies, typically measuring less than 2 mm long, have long antennae and delicate, slender bodies. Because they can fly, adult midges look for suitable rice plants to lay their eggs on, which restarts the cycle (Rajamani et al. 2004).

Silver shoots are tubular structures that develop when young plants feed on the shoot meristem while crops are tillering. The afflicted tillers do not produce the panicles (Bentur et al. 2016). ARGM attacks can cause a wide range of production losses; nevertheless, the crop can lose all its yield in the most severe instances. Estimates indicate that the yield loss in southern India is approximately 80 mil. USD or 0.8% of the overall yield (Ramasamy & Jatileksono 1996). Rather than insects' innate biotic capacity, abiotic variables are the primary determinants of insect pest abundance in agricultural ecosystems. To develop and execute a proactive and more long-term plan for site-specific pest control and management, it is crucial to have an effective early warning system that relies on a strong statistical model to forecast the accumulation of ARGM populations (Rathod et al. 2021).

The rice gall midge exhibits several biotypes, such as gall midge biotype (GMB) 1 to biotype 10,

which vary in their virulence and geographic distribution. These biotypes can overcome resistant rice varieties, making them a significant challenge for rice breeders and farmers. Biotypes 1–7 are mostly found in India (Devi et al. 2021) and South-east Asia (Figure 3). These regional biotypes have adapted to local environmental conditions and rice varieties. GMB1 is mostly found in Andhra Pradesh, Karnataka and Telangana (Kumari et al. 2020), GMB2 in Andhra Pradesh, Telangana and Karnataka (Vijaykumar et al. 2008), GMB3 in Uttar Pradesh, Andhra Pradesh, and Karnataka (Kumar et al. 2022), GMB4 in Gujarat and Maharashtra (Devi et al. 2021), GMB5 in West Bengal and Odisha (Vijaykumar et al. 2022), GMB6 in Assam, Tripura and Manipur, and GMB4M (GMB7) Warangal population in Andhra Pradesh (Bentur et al. 2009).

Geographical distribution of Asian rice gall midge. Rice gall midge is a serious pest throughout Asia (Figure 4). While the Asian rice gall midge (ARGM) has over ten known biotypes (Behura et al. 1999; Katiyar & Bennett 2001), Perera and Fernando (1970) noted that the existence of these biotypes is evidenced by the different reactions observed in various rice varieties exposed to pest populations across different regions. The presence of rice GM biotype 1 in the surrounding region contributed to the expansion of the geographical

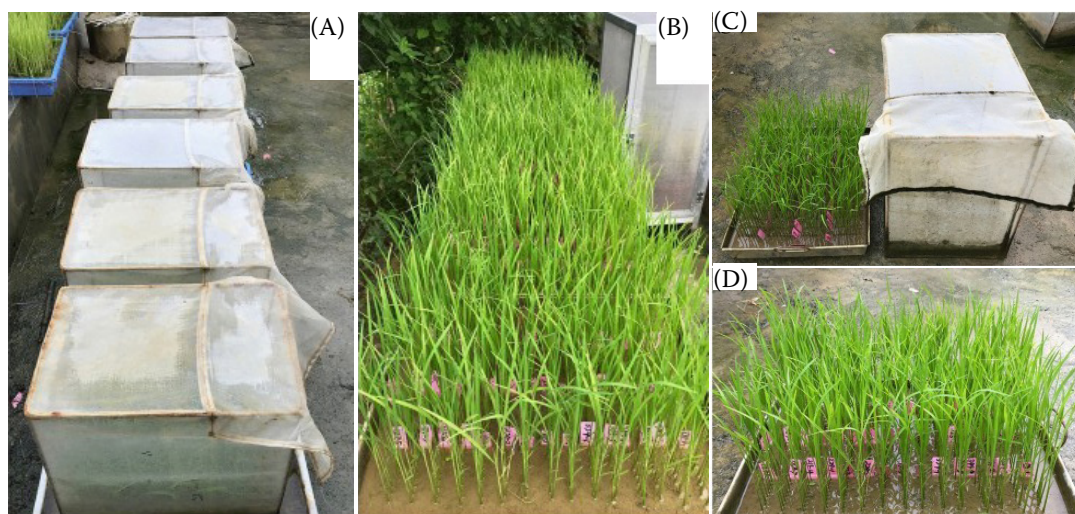


Figure 4. High-throughput phenotyping (HTPM) of gall midge in rice (Cheng et al. 2021)

A – seedling treated with RGM one day after infestation (DAI) and kept in a nested tray; B–D – seedlings treated with ARGV at 7 DAI

dispersion of the pest in the area. This occurred throughout the rainy and winter seasons.

ARGV has become more prevalent because of the widespread and continued cultivation of rice varieties susceptible to GM. These types include high-yielding, susceptible rice varieties and hybrids such as Jaya, Mangala, IR20, and IR64 (Lingaraj et al. 2008). Additionally, the climate conditions in all five locations, which are all located in the Cauvery River basin, are the same. Due to the widespread use of rice varieties that are resistant to insects, rice GM is no longer considered a nuisance in many regions (Hajjar et al. 2023). There was a 32.5% increase in the occurrence of GM in the delta area of the Krishna district in Andhra Pradesh after extensive adoption of brown planthopper-resistant genotypes, some of which were susceptible to GM (Begum et al. 2021). This was the result of the broad acceptance of these genotypes. The Kuttanad region of Kerala experienced a similar issue; the farmers in this region mainly relied on brown planthopper-tolerant genotypes, which resulted in a 90% decrease in production, equivalent to 1.8 mil. USD, because of ARGV (Lingaraj et al. 2008). ARGV biotypes were available in India before introducing resistant cultivars (Yadav et al. 2020). In addition, there are different reaction patterns in many GM-resistant donors and cultivars in two pest-endemic regions: Sambalpur in Orissa and Warangal in Andhra Pradesh (Kumar et al. 2020). Both regions are located in central India. The presence of two biotypes was further proven by the findings of testing programmes conducted on

rice cultivars at the national and international levels (Bentur et al. 2015). Therefore, in 1969, a state-wide initiative was taken to monitor the reactions of these standard rice gene differentials in various pest-endemic regions.

The results of the multilocation experiments conducted in India as part of the All-India Coordinated Rice Improvement Programme (AICRIP) also confirmed the existence of GM biotypes nationwide. A continuous biotype 1 distribution can be seen in South Karnataka, India (Seni et al. 2023). Given that the rice varieties that are now in use are susceptible to rice GM and that biotype 1 is in southern Karnataka, namely in the Cauvery River basin (Kumar et al. 2008), there is an immediate need to produce cultivars that are resistant to GM. As a result of this background information, it is suggested that the resistant genotypes (Abhaya, Aganni, ARC 6605, Phalgun and W1263) be used as parents in crop improvement initiatives (Makkar & Bentur 2017).

Rice infestation in India varies by region, with the highest severity in West Bengal, where severe infestations cause major yield losses. Assam and Bihar also experience high severity, significantly impacting crops in humid areas. Odisha faces moderate to high severity, while Tamil Nadu, Karnataka and Andhra Pradesh (Kumar et al. 2020) show moderate infestation levels. Manipur and Tripura have moderate to low severity, and Jharkhand experiences low to moderate impacts (Prasad et al. 2018a). Madhya Pradesh has the lowest severity with oc-

casional infestations. The most severe impacts are concentrated in Eastern India, decreasing towards central and southern regions (Rath et al. 2020).

Host plant interactions. The galls due to the infestation of midges cause a significant economic loss in food crops like rice and wheat because they make the tiller sterile. GM that have been extensively investigated are the Hessian fly (*Mayetiola destructor*) and the Asian rice GM (*Orseolia oryzae*), which infest wheat and rice, respectively (Sinha et al. 2012a). Asian GM is a member of the *Cecidomyiidae* family of *Diptera*. Although the larvae of the Hessian fly do not cause the development of a macroscopic gall-like structure, they are nonetheless considered GM because they produce nutritive tissue where they feed (Sinha et al. 2015).

After stem borers and planthoppers, ARGM is India's third most significant rice pest (Bentur et al. 2016). The ability to substantially manipulate one's host for survival is unique to ARGM. The last two groupings represent the species complex. Five distinct species of stem borers represent the Pyralidae and Noctuidae families. Few reports have mentioned plant defence against this pest (Sumathi & Manickam 2013).

While many landraces and cultivars of high-yielding rice are resistant to ARGM, most of these varieties are susceptible. Although maggots reach the apical meristem on resistant rice types (Lingaraj et al. 2015), they do not trigger gall formation or survive more than two to four days after hatching. Despite reports of ARGM resistance dating back more than a century, it was not until the late 1950s that modern rice breeding began, and the first hybrid variety of GM-resistant rice was released for cultivation in 1975 (Makkar & Bentur 2017). Over the past 20 years, new resistant cultivars have been developed based on resistance genes dis-

covered in local rice germplasm field evaluations (Bentur et al. 2013). Various GM biotypes (GMBs) are recognised as geographically separate populations because of the variable reactions of the same rice genotype to ARGM populations in different rice-growing areas, even during these early phases (Lu et al. 2013). The studies began to examine the genetic basis of resistance systematically, and it was not until the last two decades that they delved into the molecular basis of resistance and susceptibility, even though the studies revealed substantial manipulation of the host plant by the ARGM.

MANAGEMENT OF ASIAN RICE GALL MIDGE

Chemical control of ARGM. Preventive control is highly advised for effectively reducing insect populations, with spraying insecticides being recommended. Farmers primarily rely on chemical insecticides to control rice pest populations, which shows active effects against this pest (Dutta et al. 2024). The insecticides available for this purpose include phosalone, carbosulfan, chlorpyrifos, fipronil, and thiamethoxam. The application of these insecticides is recommended at fourteen and twenty-eight days after transplanting. When the percentage of spoiled tillers exceeds the threshold of injuries, one kilogram of active ingredient per hectare is applied. Carbofuran (3%) and ekalux (5%) are recognised as effective insecticides. These insecticides should be systemic to eliminate larvae (Devi et al. 2023b) effectively. Once rice plants have formed panicle primordia, insect control becomes unnecessary. The significant decrease in the insect population occurs due to the absence of vegetative growing points. Implementing insecticide

Table 1. The effectiveness of modern insecticides against rice gall midge (*Orseolia oryzae* Wood-Mason) on rice

Sl. No.	Treatment	Concentration	Dose/acre	Average silver shoot infestation (%)
1	Chlorantraniliprole	18.5% SC	60 g	6.02
2	Eamectin benzoate	5% SG	80 g	5.53
3	Eamectin benzoate + thiamethoxam	3% + 12% WG	60 g	5.01
4	Flubendiamide	39.35% SC	60 mL	3.31
5	Novaluron + indoxacarb	5.25% + 4.5% SC	350 mL	5.52
6	Spinosad	45% SC	60 mL	2.41
7	Control	–	–	10.48

SC – suspension concentrate; WG – water dispersible granules; SG – soluble granules

control measures is crucial, especially in seedling beds where gall midges are endemic (Misra et al. 1981). Insecticide application in seedling beds is carried out 10 days before seedling removal, and the effectiveness of insecticide granules persists for 14 to 20 days post-application.

Among the various insecticides evaluated, thiamethoxam, chlorantraniliprole, spinosad, flubendiamide, emamectin benzoate, novaluron and indoxacarb, the application of spinosad is highly effective against rice gall midge, with a concentration of 45% SC of 150 mL per hectare (Kumar et al. 2020). As a pretreatment measure, the infestation levels ranged from approximately 7.7–9.4%. Fifteen days after the first spray, the infestation rate decreased significantly to 3.2% (Prasad et al. 2018b). A second spray, performed 15 days after the first, further reduced the infestation rate to 1.64% (Prasad et al. 2018c), subsequently increasing crop yield under the treated conditions (Table 1). In addition to spinosad, a combination of spinetoram and methoxyfenozide is effective against gall midge and other major pests (Kumari et al. 2020). Farmers often resort to the discriminating use of broad-spectrum pesticides to combat these pests. However, this practice carries several risks, including developing pesticide resistance, the emergence of secondary outbreaks, phytotoxicity, harm to beneficial organisms, and environmental pollution such as ground-water contamination and pesticide residues (Longkumer et al. 2024).

Cultural practice. Opting for early planting of rice crops and selecting fast-growing varieties is essential. ARGM infestations pose a significant threat during the wet season, while insect activity is notably reduced during the dry season. Early planting is advised in Indonesia's lowland paddy fields to mitigate insect damage. Early planting helps to minimise insect populations due to prolonged drought from September to November (Seni et al. 2023). Immediate ploughing of fields postharvest and removal of alternate hosts are recommended practices. Fertiliser application should be balanced, with an optimal amount of potash fertiliser suggested (Devi et al. 2023a). Additionally, the use of infrared light traps can effectively capture gall midges.

Natural enemies should be integrated with cultural practices in rice cultivation (Horgan 2017). In the highland regions of Indonesia, particularly West Java, rice is grown continuously throughout the year, with five crops cultivated over two years

(Horgan 2019). Local rice varieties that are not influenced by photoperiod are preferred. To enhance biological control, *Platygaster oryzae* -parasitised galls can be released at 1 per 10 m² in the field, 10 days after transplanting. It is important to conserve predatory spiders within the rice ecosystem, such as Tetragnatha and Argiope catenulata, and carabid beetles such as Ophionia indica. Gall midge infestations in rice plants tend to be minimal in areas where continuous planting is practised. This is due to the activity of parasites and predators in these regions (Iqbal 2020). Examples of these natural enemies include *Amblyseius imbricatus*, an egg predator; *Platygaster oryzae*, which parasitises egg larvae; and *Neanastathus oryzae*, a larval parasite. Maintaining a balance in the population between gall midges and natural enemies throughout the cropping period. Therefore, biological control is prioritised over insecticide-based control methods. During the wet season, insect damage is typically less than 5% (Way et al. 1991).

Use of resistant varieties. Developing resistant gall midge varieties is the most effective and cost-effective approach for maintaining grain yield stability (Bentur et al. 2011). Promising rice varieties resistant to gall midge have been identified and are encouraged for cultivation in paddy fields as a practical control measure. These resistant varieties include Shakti, R 650-1820, Orugallu, Kavya, Erra Mallelu, Shrakasha, Rajendran, Asha, Shamlei, Kunti, Phalguna, Lakshmi, Dhanaya, Kkatiya, IR 36, Sureka, Vikarm and MDU-3. W1263, Phalguna, ARC5984, Dukong 1, RP2333-156-8, Madhuri-L9, BG308, CR57-MR1523, RP2068, Abhaya and Aganni (Table 2) are some notable resistant varieties (Makkar & Bentur 2017). A sustained increase in yield growth is crucial to meet the projected demand for rice production by 2050. Therefore, developing high-yielding and multiple stress-tolerant rice varieties that can adapt to a wide range of environments is essential (Mohanavel et al. 2024).

CROP BREEDING METHODS

Genotyping for ARGM. Genotyping of Asian rice gall midge (*Orseolia oryzae*) is essential for comprehending population structure and evolutionary dynamics and developing effective control strategies. This involves collecting diverse samples from various geographical locations or rice fields and

Table 2. Gall midge resistant genes and their resistant varieties

Sl. No.	Genes	Varieties	Reference
1.	<i>Gm1</i>	Kavya	Rawat et al. (2012a)
2.	<i>Gm2</i>	Phalguna	Mohan et al. (1994)
3.	<i>gm3</i>	RP2068	Kumar et al. (1998b)
4.	<i>Gm4</i>	Abhaya	Shrivastava et al. (1993)
5.	<i>Gm5</i>	ARC5984	Kumar et al. (1998a)
6.	<i>Gm6</i>	Dukong 1	Tan et al. (1993)
7.	<i>Gm7</i>	RP2333-156-8	Kumar et al. (1999)
8.	<i>Gm8</i>	Aganni	Kumar at al. (2000)
9.	<i>Gm9</i>	Madhuri-L9	Shrivastava et al. (2003)
10.	<i>Gm10</i>	BG308	Kumar et al. (2005)
11.	<i>Gm11</i>	Suraksha	Bentur et al. (2008)
12.	<i>gm12</i>	MN62M	Leelagud et al. (2020)

isolating DNA using appropriate extraction protocols (Bentur et al. 2011). PCR amplification targets specific genomic regions associated with traits such as insecticide resistance or host preference. Selecting genetic markers, such as SNPs, SSRs, or RFLPs, is crucial for distinguishing genotypes. Genotyping assays, including RFLP analysis, AFLP, or HRM, are then performed (Table 3). Data analysis entails inferring genetic diversity and population structure and conducting association studies to correlate genetic variations with phenotypic traits (Randive et al. 2019). Marker-assisted selection guides breeding programs for developing ARGM-resistant rice varieties. The establishment of databases facilitates data storage and collaboration, while continuous

monitoring tracks genetic diversity changes, aiding in adapting control strategies to evolving pest populations and ensuring sustainable pest management in rice cultivation (Sahu et al. 2023a).

Phenotyping for evaluating resistance in rice against gall midge. The most essential and evident signal for evaluating resistance following infestation is the percentage of silver shoots (PSS). Due to the resemblance between galls and the leaf sheath, seedlings that develop galls are also known as onion emergence in China. Moreover, as per the International Rice Research Institute's (IRRI) Standard Evaluation System of the rice gall midge (RGM), seedlings with inflated shoots or many tillers are also deemed vulnerable.

Over the past few decades, studies on rice diseases and planthoppers have taken precedence over those on host plant resistance to ARGM. For instance, according to Sinha et al. (2011), four out of twelve ARGM resistance genes have been located on rice chromosome 4 alone: *Gm2*, *gm3*, *Gm6* and *Gm7* (Table 3). On the other hand, Divya et al. (2016) reported that 38 brown planthopper (BPH) resistance genes have been precisely mapped, with 9 of those genes having already been cloned. Due to their undetectability, it is impossible to employ ARGM resistance genes in marker-assisted selection for rice.

The most likely explanation is that RGM was devalued globally because of its reputation as a secondary rice pest (Paramasiva et al. 2023). The development of current molecular biological approaches to bridge this gap could be facilitated by increased

Table 3. List of gall midge resistance genes and linkage DNA markers

Sl. No.	Gene	Marker	Ch. No.	Functional marker	Donor parent	Reference
1	<i>Gm2</i>	RFLP	4	RG329, RG476	Phalguna	Mohan et al. (1994)
2	<i>Gm6</i>	RFLP	4	RG214, RG476	Duo kang	Katiyar et al. (2001)
3	<i>Gm7</i>	AFLP	4	SA598	IR-BB21	Sardesai et al. (2001)
4	<i>Gm8</i>	AFLP	8	AR257, AS168	Jhitpiti	Jain et al. (2004)
5	<i>Gm1</i>	SSR	9	RM219, RM444	W1263	Biradar et al. (2004)
6	<i>Gm11</i>	SSR	12	RM28574, RM28706	CR57-MR1523	Himabindu et al. (2010)
7	<i>gm3</i>	SSR	4	RM17480, gm3SSR4	RP2068-18-3-5	Sama et al. (2014)
8	<i>Gm4</i>	SSR	8	RM22550, RM22551	Abhaya	Mohapatra et al. (2014)
9	<i>Gm5</i>	SSR	12	RM101, RM309	ARC5984, ARC5833	Dubey & Chandel (2010); Zhou et al. (2020)
10	<i>gm12</i>	SSR	2	RM6800, RM3340, RM110	MN62M	Leelagud et al. (2020)

RFLP – restriction fragment length polymorphism; AFLP – amplified fragment length polymorphism; SSR – simple sequence repeat; Ch. – Chromosome

research and a focus on ARGM as a significant agricultural concern. Studying plant-chewing insects can be aided by examining the rice-gall midge relationship. Research on host plant resistance to ARGM must therefore be expedited. In addition, the lack of accuracy of this method makes it incompatible with current molecular investigations. To research the interaction of rice-GM, it is necessary to conduct resistance evaluations of one or two rice lines (Sinha et al. 2012a). Investigations into resistance mechanism characterisation, gene quantitative trait locus (QTL) mapping and cloning, mutation screening, and resistance material identification usually necessitate precise phenotypic data (Cheng et al. 2021). To expedite research on host plant resistance to ARGM, it is crucial to establish an enhanced evaluation accuracy and a high-throughput phenotyping approach (HTPM).

Rice seeds enclosed in nylon bags were soaked in water in a bucket and incubated at 37 °C in darkness. The seeds were rinsed once or twice until germination occurred, and germination was expedited by keeping them in a humid environment for 24–36 h. Once the seeds had a 1 cm sprout, they were placed in trays, buckets, or cups per the experimental requirements (Figure 5). These containers were then transferred to a green room set at 30 °C and covered to maintain darkness for 3 days. Seven-day-old plants were subsequently exposed to a predetermined number of female RGM adults based on the experimental setup (Cheng et al. 2021).

Field phenotyping can involve various genotypes, including susceptible check TN1 and resistant check Abhya seeds, which are sown in a nursery area and transplanted after 21–25 days. The recommended spacing for sowing is 15 × 15 cm. Observations were made on gall midge damage or silver shoot formation 30 days after transplantation (DAT). The percentage of plant damage was computed utilising the following formula (Begum et al. 2018):

$$\text{Plant damage (\%)} = \frac{\text{Number of plants with silver shoot}}{\text{Total number of plants}} \times 100 \quad (1)$$

Following the plant damage percentage calculation using the formula above, the rice genotypes were evaluated based on the Standard Evaluation System for rice, as outlined by the IRRI in 2013. Subsequently, the plant reactions to the gall midge were recorded, and their interactions were classi-

fied as highly resistant, moderately resistant, resistant, susceptible, moderately susceptible, and highly susceptible (Sahu et al. 2022) (Table 4).

Field screening for gall midge resistance. To conduct field screening for Asian rice gall midge resistance, diverse locations where infestations are known or likely should be selected, encompassing various environmental conditions and rice cultivation methods. A diverse array of rice varieties, including both local and commercial varieties with varying susceptibilities to the pest, should be chosen for evaluation (Hari et al. 2022). Experimental plots should be established in selected locations using a randomised complete block design, with each variety replicated multiple times to account for environmental variability (Kumar et al. 2020). Depending on the availability of Asian rice gall midges, plots may be naturally infested or artificially inoculated to ensure consistent infestation levels. Regular monitoring of plots is essential for observing gall formation and other symptoms, with data recorded on infestation severity and plant health. The resistance levels of each variety were then assessed based on collected data (Seni & Naik 2017), utilising criteria such as gall incidence and plant vigour. Statistical analysis techniques such as ANOVA are employed to identify significant differences in resistance among varieties (Darro et al. 2023). Resistant varieties are selected based on screening results, offering recommendations for cultivation in areas threatened by Asian rice gall midges.

The GM population at Jagtial is categorised as GMB 3 (Lingaraj et al. 2015), while the population at Warangal is classified as Biotype 4M this is based on the field population's response to a standard set of host plant differentials (Seni et al. 2023; Kumar et al. 2022). Researchers from the Regional Agricultural Research Station (RARS) in Jagtial and Warangal assessed the efficacy of each test material against gall midge (GMB3) (Srinivas et al. 2016),

Table 4. ARGM infestation (%) and resistance categories

Damage to plants with silver shoot infestation	Observation
No damage	highly resistant
< 1%	resistant
1–5%	moderately resistant
6–10%	moderately susceptible
11–25%	susceptible
> 25%	highly susceptible

a pest that is particularly prevalent in humid environments, during the rainy seasons of 2014 and 2015 (Anusha et al. 2022). The seeds were dispersed in a grid pattern across elevated nursery beds in accordance with standard agronomic practices and timed to coincide with insect infestation (Thippeswamy et al. 2014). The germplasm lines were incorporated into the soil utilising a random block design (RBD) with 21-day-old rice seedlings. Two replicates contained twenty plants per replicate, and one seedling per hill, with each replicate separated by 20 × 10 cm. All cultural practices were implemented per standard agronomic procedures (Cheng et al. 2021). No application of insecticide spray occurred. Plant injury indicators were assessed on the test entries at both 30 days and 50 days following transplantation. The obtained data included the number of plants, the number of tillers per plant, the number of wounded plants with silver shoots, and the total number of damaged plants with silver shoots. The proportion of silver stems (SS) (%) and damaged plants (DP) (%) was ascertained as a percentage. The data were transformed and examined per repeated-measures ANOVA (Abhilash Kumar et al. 2017).

The test entries were considered resistant if they failed to cause any damage or injury to the plants, up to 20%, and susceptible otherwise (Pandey et al. 2018). Around forty-eight rice genotypes were identified at the National Rice Research Institute in Cuttack from 2014 to 2015 (Sai et al. 2023). In the districts of Andhra Pradesh and Telangana, which are endemic to gall midges, and in the northern coastal regions, 70% of the rice-growing areas are cultivated with gall midge-resistant varieties such as Surekha and Phalguna (Kumari & Prasad 2023). This resulted in an almost 45% increase in yield and substantially reduced insect incidence. This finding demonstrates the importance and impact of GM-resistant cultivars in reducing the incidence of ARGM. Six rice accessions were resistant to GM: IBT MRR 17, IBT MRR 19, IBT MRR 20, IBT MRR 21, IBT MRR 22, and IBT MRR 28. However, phenotypic screening of the IBT MRR 18, IBT MRR 23, and IBT MRR 24 revealed "Nil" GM damage. Singh et al. (2023) reported similar results.

Greenhouse screening. This technique studies and quantifies the different qualities or characteristics of plants cultivated in controlled greenhouse environments. This is done to comprehend how plants react to various treatments, genetic vari-

ants, and environmental factors (Sinha et al. 2022). Greenhouse screening for resistance to Asian rice gall midge involves conducting controlled experiments to evaluate the susceptibility of various rice varieties. Initially, a diverse selection of rice varieties, including both local and commercial varieties with differing resistance levels, was chosen for assessment (Sain & Kalode 1994). The controlled environment of the greenhouse ensures consistent conditions, minimising external factors that could affect the results. Each rice plant is typically grown in individual pots or trays and replicated to ensure statistical reliability. Infestation with ARGM is introduced either through infested plant materials or direct introduction of the pests (Sarathchandra et al. 2021). Regular monitoring tracks the development of gall symptoms and other signs of infestation, with data recorded on gall quantity, size, and visible damage. Resistance was assessed by comparing the performance of different varieties under controlled infestation conditions, with lower gall formation and reduced damage indicating greater resistance (Anusha et al. 2017). Statistical analyses were then applied to identify significant differences in resistance levels among the tested varieties (Gorantla Nagamani et al. 2022). Based on screening outcomes, resistant varieties are pinpointed for further evaluation or recommended for cultivation in areas prone to Asian rice gall midge infestation (Bentur & Kalode 1996). Greenhouse screening is a controlled and effective method for gauging rice varieties' resistance to this pest, offering valuable insights for crop management and enhancement strategies.

Pyramiding of gall midge resistance genes. Incorporating resistance to GM, which is both broad-spectrum and long-lasting in rice, can be accomplished by pyramiding. To develop pyramid-resistant genes, more knowledge of resistance genetics, R gene mapping, allelic linkages, and linkage is needed (Himabindu et al. 2010). Resistance to GM is conferred by a monogenic gene that enables pyramiding to occur. To date, one of the most significant challenges that has impeded the long-term success of GM-resistant cultivars is the constant generation of new aggressive biotypes that counteract implanted resistance genes (Divya et al. 2018a). The different GM resistance genes are effective against different biotypes, and this varied reactivity offers the possibility of a technique for pyramiding resistance genes. Incorporating resistance genes into various types opens

the door to more effective and long-lasting resistance (Zhou et al. 2020); nevertheless, it is still necessary to research which gene combinations will provide the required level of durability. A robust agronomic framework is utilised in the suggested strategy, which entails the combination of genes with various resistance mechanisms. They mostly acquire resistance from the *Gm1*, *Gm2*, *Gm4*, and *Gm11* genes, which makes them less likely candidates for pyramiding (Sama et al. 2012).

The cultivars identified thus far that are resistant to gall midge are thus less likely to be pyramiding candidates. The *Gm2* and *Gm11* genes are susceptible to virulence at several different locations in India (Ray et al. 2022). The resistant variety known as Abhaya, which has the *Gm4* gene, demonstrated continued durability for over thirty years after it was first introduced, even though it was not commonly cultivated. Based on the information that has been gathered concerning the characteristics of resistance, the frequency of alleles that confer virulence against R genes (Bentur et al. 2016), the genetics of virulence, and the fitness cost associated with virulence, the optimal gene combination that has been proposed is either *Gm4* + *Gm8* or *gm3* + *Gm8* (Sarathchandra et al. 2021).

Virulence spectrum of ARGM population. The extensive planting of GM-resistant cultivars frequently produces more damaging biotypes, undermining the resistance of varieties with only one gene. This was a vicious cycle. Using gene pyramiding as a potential therapeutic technique is a promising strategy (Raina et al. 2023) that provides the possibility of developing resistant strains. In the process of gene pyramiding, using marker-assisted selection (MAS) and molecular markers derived from PCR has demonstrated encouraging results (Sahu et al. 2023a). PCR-based molecular indicators of eight of the eleven resistance genes were identified. The rice-GM relationship is a gene-for-gene relationship; hence, selecting suitable genes for pyramiding involves detailed research on the virulence composition of pest populations in the target area, plant resistance genetics, and insect virulence. This knowledge is necessary for selecting suitable genes for pyramiding. A modified F_2 screening approach was developed to monitor the pathogenicity of GM populations (Desta et al. 2023). This procedure was used to detect ARGM populations. According to nationwide studies using this methodology, the *Gm2* plant gene, which

is responsible for conferring resistance, is extremely hazardous. The rate of virulence development against *Gm1* was found to be lower in tests carried out at Warangal. On the other hand, the frequency of the virulence allele in GM that confers adaptation to *Gm2*, the plant resistance gene, increased at a high rate. Because the recessive gene *VGm2*, which is virulent to *Gm2* (Nanda et al. 2010), follows sex-linked inheritance, the resistance gene (*Gm2*) of the host plant does not remain active for as long as it is. This is because the virulence of this gene is fixed in the population at a faster rate than the virulence of the autosomally inherited virulence gene. The virulence against *Gm8* was very low, but the virulence against *Gm11* was very high (Sahithi et al. 2018).

Gall midge resistance genes in rice. The GM is an insect that feeds on the inside of plants and cannot be managed chemically. The most effective alternative strategy for managing the GM is to take advantage of the resilience of the host plant. Eleven gall midge resistance (R) genes have been discovered (Bentur et al. 2011), and seven corresponding biotypes have been identified (Nayak et al. 2023). These discoveries were made based on a set of host plant gene differentials. Management practices are not very effective for treating gall midge infestations. The best and most ideal approach to pest management is the cultivation of resistant cultivars. The Indian state of Telangana, which can be found at 17°7'23.46" N and 79°12' 31.77" E, has been where three of the seven different types of rice have been successfully recognised (Atray et al. 2015). Rice is grown throughout the state during both the dry and wet seasons. Researchers constantly look for strategies to develop new naturally resistant species because it is a prevalent and endemic pest throughout the vegetative phase.

Among eleven R-genes (anti-GM) identified in rice, only two, *Gm1* and *Gm8*, do not include HR (Leelagud et al. 2020), whereas the other nine R-genes do. Although GM resistance is most common in HR and leads to maggot death, HR is unnecessary for maggot mortality (Zhou et al. 2020). Phalgun, an HR+ rice variety that harbours *Gm2*, could withstand secondary infestation by virulent larvae without expressing HR because of its incompatible interaction with GM biotype 1 (Cheng et al. 2021). This shows that RP2068-18-3-5, an HR+ indica rice variety, exhibits HR in response to GM biotype 1 (GMB1) attack. As HR shows, the presence of *gm3*

in RP imparts resistance to five out of the seven gall midge biotype 1 strains identified in India. Currently, cloning, characterising, and functionally validating the *gm3* gene, which is located on rice chromosome 4, remains the sole recessive R-gene known to protect against GM (Rawat et al. 2010). The inability of maggot to survive on resistant hosts, the presence of a recessive gene, and the expression of HR all contribute to rice resistance against the gall midge biotype 1. Since there is very little research on the interaction between RP and GMB1, the *gm3* resistance mechanism can be elucidated by examining the molecular and biochemical reactions of the host to GMB1 attack (Kumar et al. 2012).

India is home to over seventy-five types of rice resistant to GM and now available for commercial production. Nevertheless, the evolution of more aggressive gall midge biotypes has led to a loss of resistance due to the widespread cultivation of varieties with a single resistance gene across a wide area (Bentur et al. 2003). Pyramiding two or more resistance (R) genes that have not been deployed previously is one strategy proposed for postponing the establishment of pathogenic biotypes (Li et al. 2020). Only *Gm1* and *Gm8* provide resistance without HR- type expression (Bentur & Kalode 1996). However, all other genes confer resistance linked to HR (Yao et al. 2016).

Genetic studies have provided detailed descriptions of the interaction between rice and GM. Three of the R genes, *Gm2* (Phalguna), *Gm6* (Dukong), and *Gm7* (RP2333-156-8), have been located on chromosome 4 (Sinha et al. 2017), (Oupkaew et al. 2011) and (Sahu et al. 2023b). Two studies linked *Gm2* and *Gm6* to the same RFLP marker, RG214 (Nanda et al. 2010). Additionally, the AFLP marker SA598 and the RAPD marker F8 were firmly associated and tagged with *Gm7* and *Gm2*, respectively (Bashir et al. 2012; Yasala et al. 2012). The mapping results for the *Gm2* and *Gm7* genes indicated they were likely allelic (Mohan 2015).

Gm6 protected rice GM populations from the Chinese biotype, which led to its classification as a novel gene (Rawat et al. 2013). This was determined without the use of allelism testing. Additionally, there was no evidence to support the claim that *Gm6* does not give resistance to the biotypes of the Indian gall midge population (Lingaraj et al. 2015). The recessive gene *gm3* in the RP2068-18-3-5 breeding line was discovered, and this line was not crossed with Phalguna to prove that the two genes

are separate. Perhaps this was not considered essential because *Gm2* was determined to be dominant in Phalguna, and *gm3* was recessive. GM biotypes 4 and 4 M were resistant to the *gm3* gene but not the *Gm2* gene (Divya et al. 2018b). According to several reports, resistance genes tend to cluster together (Divya et al. 2015).

Many plant-insect and pathogen associations have recessive genes, although most plant R genes are dominant. The rice-BB system has been extensively studied for recessive resistance genes (Sama et al. 2014). Nine of the forty-eight genes that confer resistance to BB are recessive. According to Agarwal et al. (2014), two of the twelve blast resistance genes, *Pi21* and *Pi55*, are recessive. On the other hand, the phenomena of recessive genes involved in plant-insect interactions are poorly understood (Sinha et al. 2012a). An ideal setting for studying such recessive genes is the rice-brown planthopper (BPH) interactions. Prasad et al. (2018d) state that the twenty-seven genes involved in BPH resistance are recessive. Recessive genes may work gene-for-gene and are better understood as variations in the dominant susceptibility alleles (Mohapatra et al. 2014). Ogah et al. (2012) reported that *Xa13*, another recessive gene, encodes a protein similar to MtN3, while Ojha et al. (2017) reported that *Xa5*, a gene conferring broad-spectrum BB resistance, encodes the small subunit of the transcription factor TFIIA. The protein encoded by the blast resistance gene *Pi21* has a proline domain at its C-terminus and a heavy metal transfer/detoxification domain at its N-terminus. The *Pi55* candidate gene encodes a protein that contains leucine-rich repeats (LRRs) (Kumar et al. 2020). The NBS-LRR class of resistance proteins is encoded by this gene, which is likely the sole one of its kind in rice. This study proves that the *gm3* recessive gene in RP2068-18-3-5 codes a resistance protein belonging to the NB-ARC class, which is genetically indistinguishable from the NB-LRR class (Li et al. 2020). Therefore, recessive resistance genes may likewise be involved in induced defence and be susceptible to natural selection as any other resistance. According to Sekhar (2020), there have been reports of virulence against *gm3* resistance in GMB5 and GMB6 populations. Although uncommon, *gm3* is still used in India to breed resistant rice varieties.

The emergence of new biotypes of rice GM that are more aggressive has resulted in the loss

of effectiveness for a significant number of the extensively farmed varieties that were previously resistant to this pest (Krishnakumar & Kumaravadivel 2018). There is the prospect of breeding enhanced cultivars by introducing novel R genes that function differently. The method of phenotyping germplasm accessions for ARGM resistance is a continuing procedure employed in this effort. According to Leelagud et al. (2019), the interactions between rice ARGM larvae and plants are deemed incompatible when the rice GM larvae cannot establish themselves via an R-mediated plant mechanism.

Genetic mapping and QTL identification for gall midge resistance in rice. Various studies have identified quantitative trait loci (QTLs) associated with resistance to gall midge (*Orseolia oryzae*), providing crucial insights into the genetic basis of resistance and aiding breeding programs for gall midge-resistant rice varieties. The QTLs *Gm1*, *Gm2*, and *Gm3* are linked to resistance to multiple biotypes of the Asian rice gall midge according to molecular markers and genetic mapping (Bentur et al. 2003). Using a mapping population derived from resistant and susceptible rice genotypes, resistance genes such as *Gm4* and *Gm8*, which confer resistance to specific gall midge biotypes, have been identified. Similarly, *Gm5* and *Gm6*, which are associated with resistance to specific biotypes, have been found through mapping populations from crosses between resistant and susceptible rice lines (Ramkumar et al. 2010). Additionally, *Gm7* has been detected in a mapping population from a cross between gall midge-resistant and susceptible rice genotypes (Bharathi et al. 2010). These QTLs represent genomic regions housing genes that contribute to resistance against specific gall midge biotypes. Leveraging marker-assisted selection based on these QTLs facilitates the development of gall midge-resistant rice varieties, promoting sustainable rice production practices.

GM is a significant insect that impacts rice production worldwide. Using SSR markers, QTL mapping of GM resistance in RILs resulting from a hybrid between the susceptible variety TN1 and the resistant variety RP2068-18-3-5 was performed (Sama et al. 2014). The expression of the flanking markers RM17480 and gm3SSR4 strongly correlated with the phenotype (Samal et al. 2021). The successful cloning of the sequence polymorphism gm3del3 using a marker-assisted selection (MAS) approach facilitated the integration of the *gm3* gene

into the elite bacterial blight-resistant cultivar improved samba mahsuri (B95-1) via the MAS technique. Mapping analysis revealed that within the $F_{2:3}$ population generated by crossing KDML105 and MN62M, the SNP markers S2-76222 and S2-419160 were used to characterise the *gm12* locus (Leelagud et al. 2020). This gene can precisely determine the ARGM biotypes in Southeast Asia and Thailand.

Mapping and marker-assisted breeding of gene alleles. One of the greatest advantages of contemporary agricultural improvement has been breeding gall midge-resistant varieties. Insecticides are no longer necessary to combat this significant pest because of the high level of resistance imparted by key genes. However, re-evaluating breeding strategies is necessary due to the rapid evolution of pathogenic biotypes in response to resistant rice varieties that carry a single main gene, which occurred in the 1980s and beyond (Devi et al. 2021): eleven known plant resistance genes (Vijaykumar et al. 2022) and seven pest biotypes. The resistance spectrum characterisation of these genes revealed that a combination of two or more genes is required to produce a wide range of resistance (Sinha et al. 2011). Two DNA pools of ten extremely resistant or susceptible lines were analysed using simple-sequence repeats and insertion-deletion markers across 12 rice chromosomes. Polymorphic markers found between the DNA pools and markers near the targeted region were examined to determine the genotypes of the F_3 population (Michelmore et al. 1991). A local genetic map was created using IciMapping (version 4.0) (Wang et al. 2015) to establish the logarithm of odds (LOD) threshold, and a permutation test with 1 000 iterations was conducted. The QTL IciMapping interval mapping method was then employed to analyse the genetic linkage maps and map the population phenotypes to identify resistance genes or QTLs associated with these traits (Cheng et al. 2021).

The investigations on monitoring virulence spectrum by Bentur et al. (2008) have shown that various genes impose distinct selection pressures on pest populations and that the resistance genes that have been deployed have variable durability rates. This is the first study on the mechanisms of resistance imparted by various genes involving two separate processes. Resistance is conferred by most of the genes in tandem with HR (HR+ type), in addition to two other genes, *Gm1* and *Gm8*, which transmit resistance independently

of HR (HR– type) (Makkar & Bentur 2017). New gene expression studies in the rice variety Suraksha with the *Gm11* gene that confers HR resistance imply the involvement of a typical pest-induced phenyl propanoid-mediated resistance pathway, in contrast to the unmodified genes in the variety Kavya with the *Gm1* gene that confers HR-type resistance (Rawat et al. 2012a). As a result, selecting genes for long-term GM resistance requires careful consideration. In contrast to the *Gm1* gene, which provides resistance to only one of the seven biotypes, the *Gm8* gene found in the landrace Jhitpiti (Paramasiva et al. 2023) confers resistance to five of the seven biotypes (Biradar et al. 2004). Unfortunately, neither the landrace nor the discovered markers were acceptable for MAS breeding.

The short-statured, profusely tillering, and medium-flowering cultivar Aganni is another good source of *Gm8* (Devi et al. 2021). The breeder's situation has improved by confirming the presence of *Gm8* and creating closely connected markers. This range was further expanded by the presence of this gene in nine additional germplasm accessions. Additional *Gm4*, *Gm11*, and *Gm8* gene sources were identified by molecular allelism testing (Suvendhu et al. 2014). Pyramiding is eminently possible with these genes' connected markers. Because *Gm4* gives HR type resistance, and *Gm8* provides HR– type resistance, these two factors make perfect sense. Since neither gene has been disseminated, the pest population will not have extensive exposure to them. The RP2068-18-3-5 breeding line has the potential for effective pyramiding of *gm3*.

Molecular approaches for the management of ARGM. There are a variety of responses to GM invasion in various rice species. Although only a small percentage of the variations can endure pest attacks, certain varieties can eliminate maggots within a few hours of feeding (Iqbal 2020). The variances can be broken down into two primary categories regarding resistance mechanisms. Generally, the resistant rice genotypes that cause tissue necrosis when maggots feed on them are termed HR+ types, representing human resistance plus. In contrast, certain genotypes are resistant to the substance that do not exhibit any hypersensitive reactions but exhibit maggot mortality (Bentur et al. 2016). These genotypes are referred to as HR–ve (HR–) types. The prevention of host-plant resistance is the most effective approach for managing this pest (Krishnakumar & Kumaravadivel 2018).

This is because resistance is inherently antimicrobial in the HR+ and HR– types.

More than three hundred primary sources of resistance were discovered after examining more than fifty thousand germplasm accessions in field and greenhouse environments (Lingaraj et al. 2015). Several studies on the rice gall midge resistance gene have frequently shown that it is a single recessive or dominant gene. Twelve genes are responsible for pest resistance, ten of which are dominant (*Gm1*–*Gm11*, except *gm3* and *gm12*) (Seni et al., 2023). Initial efforts to improve resistant varieties in India were founded on the hypothesis that GM biotypes were responsible for the problem. Seven distinct biotypes have been identified (Thippeswamy et al. 2014). These biotypes were characterised by their reaction pattern against five different rice cultures. Rice resistance genes (R genes) and GM biotypes interact with one another gene-for-gene, in a manner that is analogous to how illnesses interact with the plants that they infect (Wu Biqu et al. 2014). Because distinct R-genes impart resistance to different biotypes and different biotypes exhibit varying degrees of virulence against various R-genes, it may be deduced that neither the biotypes nor the R-genes confer resistance to every possible combination of biotypes. The range of different biotypes can be enhanced by combining multiple resistance genes through gene pyramiding.

Although it is widely acknowledged that resistance conferred by a single gene can rapidly deteriorate, the strategy of combining two or more genes with different resistance mechanisms (such as HR+ and HR–) has been proposed as a means of achieving long-term protection against the gall midge (Rawat et al. 2012b). This is because it is widely acknowledged that resistance conferred by a single gene can quickly deteriorate. Three genes confer resistance to gall midge have been successfully cloned and characterised. These genes are classified as *gm3*, *Gm4*, and *Gm8* (Abhilash Kumar et al. 2017). Furthermore, *Gm2* is allelic to one of the *gm3* genes. The *gm3* gene, which is recessive and HR+, encodes a protein with the NB-ARC (NBS-LRR) domain. *Gm4*, the dominant gene, is also HR+, but it encodes a protein containing leucine-rich repeats (LRRs). On the other hand, *Gm8*, a recessive gene, exhibits HR– and encodes a protein containing proline (Sama et al. 2012). As mentioned, using two or more genes that have not been utilised previously but have alternative resistance mechanisms is desirable. For example, the *Gm4* (HR+) and *Gm8* (HR–) genes can be utilised. Given that *gm3* is

an HR+ gene that is carried in a recessive manner and has not been utilised in any variety, it is possible that it could be another option for pyramiding. Applying marker-assisted breeding to pyramid-selected gene combinations in elite genetic backgrounds is easy. This is made possible by the availability of functional markers intimately related to all the important genes that confer resistance to the ARGM population (Divya et al. 2018c).

Metabolomic regulation for gall midge resistance. Studies explored the differential expression of genes and accumulation of metabolites in the host upon gall midge infestation, as well as the gene expression changes in the indica rice variety RP2068-18-5 after infestation by the avirulent gall midge biotype GMB1. Using a microarray, 57 381 probe sets were identified, with 43 738 passing quality checks (Agarwal et al. 2016). Among these, 7 598 probes showed significant differential expression (P -value ≤ 0.05). After applying a fold change threshold 2; 2 861 differentially expressed genes (DEGs) were identified, including 1 494 up-regulated and 1 367 down-regulated genes in infested tissues. Genes Ontology (GO) analysis revealed that the majority of DEGs were associated with biological processes (over 80%) and metabolomic processes (over 60%) (Agarwal et al. 2016). Carbon metabolism changes in the resistant rice variety RP2068-18-3-5 during infestation with gall midge biotype 1. It revealed that pathways like the TCA cycle, oxidative pentose pathway, fermentation and gluconeogenesis were up-regulated, while Calvin cycle and photosynthesis-related transcripts were down-regulated. There was a balanced regulation in glycolysis and one-carbon metabolism. Pyruvic acid and several organic acids generally decreased, except for certain acids like carbamic and glucuronic acids, which increased. Myristic acid initially decreased but later increased significantly, and azelaic acid, associated with stress response, also showed a similar pattern, corresponding with the host's hypersensitive response (HR) (Agarwal et al. 2016). In nitrogen metabolism, transcripts for polyamine and amino acid metabolism and nitrate reductase were up-regulated. Aspartic acid, glycine, and alanine levels decreased, while other amino acids, such as phenylalanine, tyrosine, and tryptophan, also showed elevated levels. There was up-regulation in transcripts involved in amino acid degradation pathways and increased nitrogenous metabolites like GABA and ornithine, while beta-alanine and urea levels decreased. The regulation of differential gene

expression, including several transcriptional factors and chromatin-related proteins, was down-regulated. However, specific transcriptional factors were up-regulated, such as EREBPs, bHLH, WRKY, NAC, several zinc finger families, and MYB-related, MADS box, HSE, bZIP, and others. This indicates a selective regulation of gene expression in response to the infestation (Agarwal et al. 2016).

Microarray analyses. Microarray analyses and studies used Affymetrix gene chip genome arrays for transcriptome analysis with three biological replicates. RNA quality was verified, and a labelled copy of RNA was prepared from 5 μ g of total RNA. Data processing and analysis were made using GCOS version 1.4 and Avadis version 4.3, with normalisation by the robust multichip average algorithm. Differentially expressed genes were identified using the Limma software (version 2010) (Rawat et al. 2012b), with a long fold change threshold of 1 and an adjusted P -value of 0.05. Functional analyses were conducted using MapMan software (Thimm et al. 2004). The microarray results were validated through real-time polymerase chain reaction (PCR) with RNA samples from the original and independent gall midge infestation at two time points (24 and 120 h post-infestation). Twenty-six genes with over two-fold changes were analysed using SYBR green chemistry on an applied biosystems 7 500 real-time PCR system. Rice ubiquitin genes (OsUbq) were used as the endogenous control. Real-time PCR reactions were highly efficient ($> 95\%$), and specificity was confirmed via melting curve analysis. The data was processed using 7 500 sequence detection software to calculate mRNA levels (Rawat et al. 2012b).

CONCLUSION

Asian rice gall midge (*Orseolia oryzae*) remains a significant challenge to rice production, with its ability to adapt and persist across environments. While substantial progress has been made in understanding the pest's biology, interaction with rice and the development of management strategies, the ongoing evolution of the gall midge population and the complexity of rice-pest interactions underscore continued research. Future efforts should focus on integrating advanced molecular tools and biotechnological approaches to enhance the durability of gall midge resistance in rice. The identification and pyramiding of multiple resistance genes, supported by precise genotyping and phenotyping, hold promise for devel-

oping cultivars with broad-spectrum resistance. Additionally, metabolomics regulation and microarray analyses can uncover new resistance mechanisms and potential targets for genetic improvement. Monitoring the virulence spectrum of gall midge populations is essential to guide breeding programs and ensure the longevity of resistance varieties. Furthermore, exploring ecological and cultural practices that can complement genetic resistance will contribute to a more sustainable approach to pest management. As climate change and agricultural practices continue to influence pest dynamics, an integrated pest management strategy that combines conventional and innovative methods will be crucial. The future of gall midge management lies in a multidisciplinary approach, where advances in genetics, molecular biology and regular field practices are harmonised to protect global rice production from this persistent pest. The effectiveness of marker-assisted selection (MAS) and gene pyramiding in developing resistant rice varieties against rice gall midge, combining multiple resistance genes, makes it a valuable genetic resource for future breeding programs. But still, traits such as a minimal percentage of silver shoot, representing gall midge incidence, should be given greater emphasis in future breeding programs to develop high-yielding, gall midge-resistant varieties.

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