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REVIEW ARTICLE

Genetic approaches to impart brown leaf spot resistance in rice: A review

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Abstract

Brown leaf spot (BLS) of rice, caused by the fungal pathogen *Bipolaris oryzae*, is a widespread and economically significant disease affecting rice-growing regions worldwide. Historically known for contributing to the Bengal famine during the 1940s, the disease continues to impact both yield and grain quality, especially in rice grown in rainfed and nutrient-deficient ecologies. Despite its long-standing presence, Brown leaf spot remains as an under-researched disease compared to other major rice pathogens, limiting progress in resistance breeding. Climate change and widespread drought events have witnessed an increased incidence of this disease in the recent past. Therefore, developing stable and broad-spectrum resistance to multiple strains of *Bipolaris oryzae* across diverse agro-ecological zones is essential. This review provides insight into recent advances that are transforming BLS resistance breeding from the discovery of novel resistance donors in diverse germplasm to the deployment of high-resolution Quantitative Trait Loci (QTL) mapping, genome-wide association studies (GWAS) and Clustered Regularly Interspaced Short Palindromic Repeats associated protein 9 (CRISPR-Cas9) based functional gene validation. It highlights how combining conventional breeding with molecular tools like marker-assisted selection and gene pyramiding accelerates the development of rice lines with broad and durable BLS resistance. The review emphasizes recent advances that support more efficient and climate-resilient breeding strategies for sustainable rice production.

Keywords: *bipolaris oryzae*; breeding approaches; brown leaf spot; host plant resistance; resistance genes

Introduction

Rice (*Oryza sativa* L.) is a diploid species (2n = 24 chromosomes) belonging to the Poaceae family. It has a panicle-type inflorescence and produces a dry, one-seeded fruit known as a caryopsis, typical of grasses (1). Rice serves as a vital food crop in the developing world and a staple for over half of the global population. More than 3.5 billion people rely on rice for over 20 % of their daily caloric intake (2). Rising population and economic development continue to increase pressure on rice production systems (3). According to FAO's most recent projection, global cereal commerce in 2022-23 is estimated at 468 million tonnes, reflecting the growing global demand for staple crops like rice (4). However, yield-reducing diseases such as brown leaf spot (BLS) remains as a significant threat, particularly in low-input, rain-fed systems. BLS is responsible for average global yield losses of 4-5 % and in severe outbreaks, losses can rise to 45-52 % (5, 6). To maintain steady rice production, it is important to control these disease outbreaks and reduce losses from year to year. This requires knowing extent of damage that diseases cause and keeping track of new or changing disease problems, especially those linked to changes in farming practices and technology (7). Sustainable agricultural methods and broad-spectrum genetic resistance are complimentary approaches to disease management. Despite significant advancements in recent decades, further integration of these approaches is needed for tangible results in farmer's fields. Preventing losses from biotic and abiotic stresses provides a resource-neutral strategy to increase production in light of growing need for food. The ability to maintain or increase rice yields cost-effectively will depend on developing varieties that remain productive despite these challenges (8).

Although chemical, biological and cultural practices are widely used to manage BLS in rice, they are often costly, environmentally unsafe and provide only limited long-term effectiveness (9). In contrast, host plant resistance provides a sustainable and economically viable solution, especially when employing strategies such as gene pyramiding, multilines and partial resistance accumulation (10, 11). Advances in QTL mapping and rice genomics have equipped breeders with powerful tools to develop brown spot-resistant cultivars suited to diverse environment. Marker-assisted selection (MAS) now offers a faster, more efficient and reliable alternative to phenotypic selection, enabling early and accurate identification of resistance traits, even for complex characteristics that are challenging to breed through conventional methods. Considerable advances in QTL mapping, cloning of resistance genes and understanding of defence signalling pathways have significantly enhanced rice breeding, making MAS a powerful tool for developing brown spot-resistant cultivars with greater precision and in a shorter timeframe (12, 13). This review provides a comprehensive understanding of molecular defence mechanisms in rice, that are essential for accelerating breeding efforts towards long-lasting resistance against brown leaf spot. It also highlights recent advances and outlines future directions to manage disease outbreaks and enhance rice productivity.

Brown leaf spot

Rice is susceptible to 55 fungal diseases, of which 43 are seed-borne or seed-transmissible. Among these, three pathogens are particularly significant: *Pyricularia oryzae* (blast), *Bipolaris oryzae* (brown spot) and *Xanthomonas oryzae* (bacterial leaf blight) (14). Together, blast and brown spot diseases contribute to approximately 30 % of yield losses in rice (15). Brown spot, caused by the fungal pathogen *Bipolaris oryzae* Subr. and Jain, has been reported in Japan as early as 1900 (16). In India, brown leaf spot has been reported across all rice-growing states (17), since its first report by Sundararaman in 1919 from Madras. Historically famous for triggering the 1942-43 Bengal famine, which damaged 50-90 % of rice crop in Eastern India and caused two million deaths (18), BLS remains a global threat across Asia, Africa, the Americas and parts of Europe (16). The causal organism of brown leaf spot in rice has undergone multiple taxonomic reclassifications. Initially named *Helminthosporium oryzae* by Breda de Haan, it was later identified as *Ophiobolus miyabeanus* (perfect stage) and reclassified as *Cochliobolus miyabeanus* (19). The anamorph was renamed *Bipolaris oryzae* in 1955 due to its bipolar germination but was also referred to as *Drechslera oryzae* based on conidial features. *Bipolaris oryzae* produces well-branched mycelium and septate conidia of variable size (20). Optimal growth occurs at 27-30 °C, with conidial germination favoured at 25-30 °C and pH 6.8-7 (17). Genetic analysis of 288 isolates from Iran, Japan and the Philippines using 12 SSR markers revealed 278 haplotypes, indicating high genetic diversity and gene flow likely facilitated by seed exchange (21). This highlights the need for quantitative resistance breeding and diverse pathogen isolates in screening programs to ensure durable disease control.

Symptoms and economic impact

Bipolaris oryzae affects rice at both seedling and mature stages, damaging various plant parts including leaf blades, coleoptiles, sheaths, panicle branches, glumes and spikelets (22-24). Seedlings in nurseries often suffer severe damage (25). The disease is characterized by oval or circular leaf lesions with light grey centers, reddish-brown margins and yellow halos (17). It can also cause seedling blight, necrotic lesions, grain discoloration and dark spots on glumes, which may lead to shrivelled grains (26). Under favorable conditions, conidiophores and conidia form on infected tissues, giving a velvety appearance. In severe cases, the fungus penetrates glumes and endosperm, causing seed rotting, pre-emergence damping-off and reduced germination. Rarely, black lesions may also appear on young roots, though node and internode infections are uncommon (27-29). Fig. 1 shows the characteristic symptoms of brown leaf spot (BLS) on rice leaves.

BLS poses a widespread threat to rice production, resulting in considerable yield losses and economic damage (30-32). The disease causes both quantitative and qualitative losses in grain yield, as highlighted by (33). Currently, brown leaf spot is widespread across rice-growing regions, leading to significant yield losses, sec only to blast disease (34). Yield loss averages 10 % across lowland rice systems in South and Southeast Asia, with severely infected fields experiencing reductions of up to 45 % (33, 35). Table 1 summarizes the yield loss caused by brown leaf spot disease in rice in different regions. Besides quantitative yield losses, BLS reduces seed quality and germinability, further compounding its economic impact. The disease's severity is exacerbated by global warming, as the pathogen thrives in high-temperature conditions (36). Climate change and nutritional imbalances, especially deficiencies in nitrogen and potassium, are key factors driving its increased occurrence (37). Considering the substantial yield losses and reductions in grain quality, brown leaf spot remains an economic threat to rice production worldwide, necessitating urgent attention to mitigate its

Fig. 1. Shows the characteristic symptoms of brown leaf spot (BLS) on rice leaves.

Table 1. Yield loss due to brown leaf spot disease in rice

Region	Yield Loss (%)	Reference
South & Southeast Asia	10 % average, up to 45 % in severely infected fields	(33, 40)
Nigeria	12 %	(94)
North Sierra Leone	8-23 %	(95)
Florida, USA	16-40 %, with reduced milling quality	(96)
India (General)	19.2 % to 58.8 %	(97, 98)
India (West Bengal)	5.6-11.7 % in susceptible variety Tilakkachery, 2.2 % in moderately resistant Bhasamanik	(98)
Jammu Region, India	32.65 % to 74.51 % in 2018, 31.64 % to 75.83 % in 2019	(37)
Punjab, India	4.45 % to 34.38 %	(75)

financial burden on farmers and economies.

Environmental conditions

The development and spread of brown leaf spot (BLS) depend on three key factors: favorable climatic conditions, sufficient pathogen inoculum (from air, water, soil, or seeds) and a susceptible host plant. If any of these is absent, disease development will not occur (38). Optimal environmental conditions for BLS include temperatures between 23.6 °C and 34.2 °C, relative humidity of 80.7-85.8 %, 4.6-6.2 hrs of sunlight and wind speeds of 1.0-1.6 km/h (39). These factors promote pathogen growth, spore production and germination, with peak disease severity typically observed in the third week of September. The disease can affect rice from seedling to milk stage, with yield loss varying based on cultivar and time of infection (28). Deficiencies in potassium, manganese, magnesium, silicon, iron, or calcium intensify disease severity, which is why BLS is often referred to as the "poor farmer's disease". Its prevalence in low-input, rain-fed and upland systems underscores the need for better soil nutrient management to reduce its impact on smallholder farmers (40).

Agronomic practices and crop microclimate significantly influence BLS progression. Conventional planting methods result in higher disease incidence, while furrow planting and the System of Rice Intensification (SRI) help reduce severity by lowering humidity and increasing canopy temperature. High plant density and delayed transplanting worsen disease by creating a cooler, more humid microclimate. Meteorology-based regression models have shown high accuracy in predicting outbreaks, enabling timely interventions. Integrated approaches such as optimized planting geometry, reduced plant density and timely transplanting can effectively alter the microclimate, offering an eco-friendly strategy to manage BLS (41). Understanding these environmental and agronomic interactions is essential for developing predictive tools and location-specific management practices.

Pathogenesis

The pathogenesis of brown leaf spot (BLS) in rice begins with primary infections, which is mainly seed-borne (42, 43). *Bipolaris oryzae* is a necrotrophic pathogen that invades by killing host cells and feeding on the dead tissue. The disease cycle initiates when conidia (asexual spores) land on rice leaves and germinate, with germ tubes penetrating the cuticle directly or through stomata (17). The pathogen releases phytotoxins, such as ophiobolins, which disrupt cell membranes, leading to characteristic brown lesions with grey centres and reddish-brown margins (44). A key gene, BMK1, encoding a MAP kinase, is essential for fungal growth, conidiation and virulence. Its disruption reduces hyphal growth, impairs aerial hyphae, abolishes conidia production and renders the fungus non-pathogenic-paralleling MAPK roles in other fungal pathogens like *Cochliobolus heterostrophus* and *Magnaporthe grisea* (45). Targeting MAPK signalling may therefore offer novel disease control strategies (46).

Secondary infections arise from wind-dispersed conidia originating from infected residues like straw and stubble (17, 47). Soil and certain weed hosts also act as inoculum sources (48). Conidial production is highly responsive to environmental conditions, thriving at 21-26 °C and relative humidity above 92 %, peaking at 100 % RH (49). High humidity and intermittent rains during cooler months (October-December) favour spore dispersal and infection (50). Disease progression is most severe between flowering and dough stages, with flag leaf infection strongly correlating with kernel contamination. The pathogen can invade all parts of the kernel, especially the rachilla and sterile lemmas. As *B. oryzae* is seed-transmissible, it can cause coleoptile, root and first leaf infections in seedlings. Thus, flag leaf severity can serve as a predictor of seed infection, underscoring the importance of seed health testing and treatment in disease management. Fig. 2 shows the infection cycle of *Bipolaris oryzae*, the causal agent of brown leaf spot in rice.

Molecular mechanism and host-pathogen interaction

The infection process of *Bipolaris oryzae* in rice involves a series of intricate interactions between the pathogen and host, which are mediated by genetic and biochemical mechanisms. The pathogen employs various molecular strategies to invade host tissues, suppress plant defences and establish infection, ultimately determining the susceptibility or resistance of the host plant. The interaction between *Bipolaris oryzae* and its host is influenced by both the pathogen's virulence strategies and the host's defense mechanisms. In addition to rice, alternative hosts such as *Leersia hexandra*, a common weed in Indian rice fields and wild rice species have been reported to harbour the pathogen in nature (51, 52). Severe infections on *Zizania aquatica*, cultivated wild rice in the USA, demonstrate the broad host range of the pathogen (53). Collateral hosts could play a critical role in the pathogen's epidemiology, serving as reservoirs for inoculum and contributing to disease persistence in rice ecosystems.

The physiological and biochemical effects of *Bipolaris oryzae* infection are severe, especially in susceptible rice cultivars like 'Oochikara.' Infection triggers oxidative stress, increasing malondialdehyde (MDA) levels and electrolyte leakage (EL), which signal cell membrane damage. As the disease progresses, chlorophyll and other photosynthetic pigments decline due to ophiobolin toxins that damage

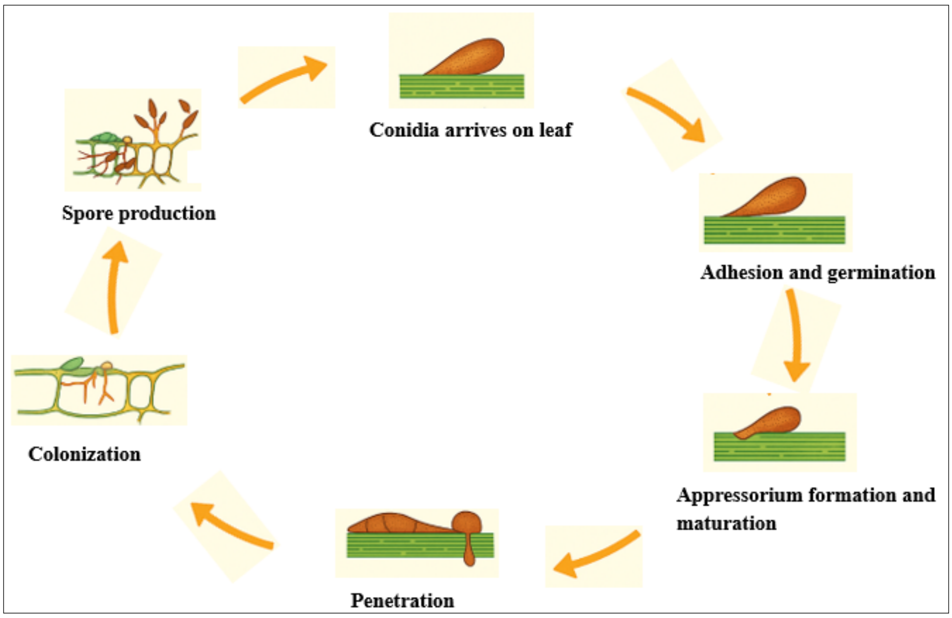

Fig. 2. Infection cycle of *Bipolaris oryzae*, the causal agent of brown leaf spot in rice.

chloroplasts and induce chlorosis. This leads to a 65 % reduction in net carbon assimilation, stomatal conductance and transpiration, resulting in significant loss of healthy leaf area and reduced plant vigour (54). Studies using rice cultivar MTL189 inoculated with two isolates of the pathogen, B5 (highly compatible) and K2 (less compatible), have shown that the severity of infection varies based on the host's defence mechanisms. The B5 isolate caused extensive tissue degradation and sporulation, whereas the K2 isolate led to limited hyphal growth and minimal damage due to the accumulation of hydrogen peroxide (H_2O_2) and polyphenolic compounds in the resistant plants. Structural defences such as callose deposition and fluorescent papillae further restricted pathogen development in resistant interactions, showing the role of early defence responses in limiting disease spread (55). The pathogen deploys toxins like ophiobolins that suppress rice's phenolic-based defences by significantly reducing phenolic content, peroxidase and phenylalanine-ammonia lyase activity that are key components of resistance. Although treatments that enhance phenolic metabolism (e.g., catechol, quinic acid, phenylalanine and Ethrel) delayed symptom development, the pathogen's toxins counteracted these responses, facilitating host colonization and disease progression (56).

Rice defence against *B. oryzae* involves physiological and biochemical changes. Silicon (Si) induces resistance by disrupting the pathogen's manipulation of ethylene (ET) signalling, reducing ethylene production, phenolic compound accumulation and fungal spread, independent of salicylic acid (SA) or jasmonic acid (JA) pathways. Instead, it directly targets pathogen virulence factors (57). Abscisic acid (ABA) also enhances resistance by suppressing ET signalling via the OsMPK5 gene, involving hydrogen peroxide (H2O2) production at infection sites without relying on SA, JA, or callose responses (58). The interplay between ABA and ET signalling highlights the complexity of hormonal crosstalk in regulating host defense. The tryptophan (Trp) pathway is pivotal in rice defense against *Bipolaris oryzae*, with infection triggering increased anthranilate synthase (AS) activity, upregulated Trp biosynthetic genes (OASA2, OASB1, OASB2) and higher levels of Trp and intermediates like anthranilate and indole. Serotonin, produced via tryptophan decarboxylase (TDC), accumulates in infected tissues and integrates into cell walls through oxidative polymerization, forming a barrier that suppresses fungal growth. In serotonin-deficient mutant rice (sl), higher susceptibility occurs due to tryptamine accumulation, leading to lesion spread (59). Exogenous serotonin application restores cell wall defence and resistance, underscoring its role as a crucial secondary metabolite in rice defence.

Rice defence mechanisms differ against *Magnaporthe grisea* (rice blast) and *Cochliobolus miyabeanus* (brown leaf spot). Resistant varieties like Tetep show hypersensitive responses (HR) and localized cell death against both pathogens, while susceptible varieties (e.g., Nakdong) experience rapid cell death and uncontrolled fungal spread with *B. oryzae*. *B. oryzae* conidial germination fluid (CGF) triggers rapid cell death in both resistant and susceptible cultivars, indicating phytotoxins. Defence inducers like benzo (1,2,3)thiadiazole-7-carbothioic acid S-methyl ester (BTH) enhance resistance to *M. grisea* but not *B. oryzae*, suggesting pathogen-specific responses (60). Understanding *B. oryzae* infection strategies and rice defences highlights targets for breeding varieties with early, robust defence activation.

Approaches to improve BLS resistance

From chemical to biocontrol methods

Management of brown spot disease in rice has traditionally relied on chemical fungicides such as carbendazim and combinations like azoxystrobin + difenoconazole, which significantly reduce disease severity and improve yields. For instance, carbendazim, applied at 0.1 % concentration, significantly decreases disease intensity while improving plant health parameters and yield. Studies on the IRGA 424 rice cultivar in Paraguay revealed that a combination of azoxystrobin (20 %) and difenoconazole (12.5 %) applied at specific growth stages (R2, R3 and R4) reduced disease incidence from 90 % to 15.7 % and increased yields by 23 %. However, concerns over environmental impact, pathogen resistance and high costs limit their long-term use, especially for resource-poor farmers (61).

Botanical extracts have gained attention as sustainable alternatives that combine moderate disease control efficacy with environmental safety. Neem (*Azadirachta indica*) extracts, for example, have demonstrated significant reductions in disease intensity at a 10 % concentration. Besides disease suppression, neem also enhances plant health, contributing to increased root biomass and shoot vigour (62). Biocontrol agents have shown promise in managing brown spot disease. Under laboratory conditions, *Trichoderma harzianum* exhibited the highest inhibition of *B. oryzae* mycelial growth (65.33 %), followed by *Trichoderma viride* (57.76 %) and *Pseudomonas fluorescens* (32.68 %). Field trials with rice varieties Basmati-370, Jaya and PC-19 demonstrated that foliar applications of these biocontrol agents significantly reduced disease severity. *T. harzianum* provided the highest disease reduction (up to 64 %) and led to yield increases of 8-17 % depending on the variety. The efficacy of these biocontrol agents is attributed to the production of antifungal compounds and the induction of systemic resistance in plants (63). Similarly, the integration of *Trichoderma harzianum* with botanical extracts has shown promising results. Combined application of *Trichoderma harzianum* (0.1 %) with garlic bulb extract (10 %) reported a disease intensity of 33.06 %, markedly lower than the untreated control (45.20 %) (64). This treatment not only suppressed the disease and promoted plant growth but also proved economically feasible for farmers, as the Trichoderma and neem combination yielded the best cost-benefit ratio of 1:2.67. Utilizing biocontrol agents like *Trichoderma* spp. offers an eco-friendly alternative to chemical fungicides, mitigating issues related to pesticide resistance, environmental pollution and health hazards.

Phenolic antioxidants such as salicylic and benzoic acids have emerged as eco-friendly alternatives for managing brown spot disease. These compounds exhibit strong antifungal activity, with benzoic acid (20 mM) significantly reducing disease severity and improving yield components like grain filling and weight. Treated plants also show enhanced chlorophyll, carbohydrate and protein levels, offering both disease suppression and improved crop performance (65). While chemical fungicides remain effective for rapid control, their environmental and economic drawbacks highlight the need for integrated, sustainable solutions. Combining botanical extracts, *Trichoderma* formulations and phenolic compounds presents a cost-effective approach. Recent findings show that red light (550-650 nm) induces resistance in rice by activating the tryptophan and phenylpropanoid pathways, reducing lesion formation without directly affecting the pathogen. This light-induced defence, which strengthens with longer exposure, offers a novel, non-chemical strategy for brown spot management (66). Fig. 3 shows the integrated management strategies for brown leaf spot disease in rice.

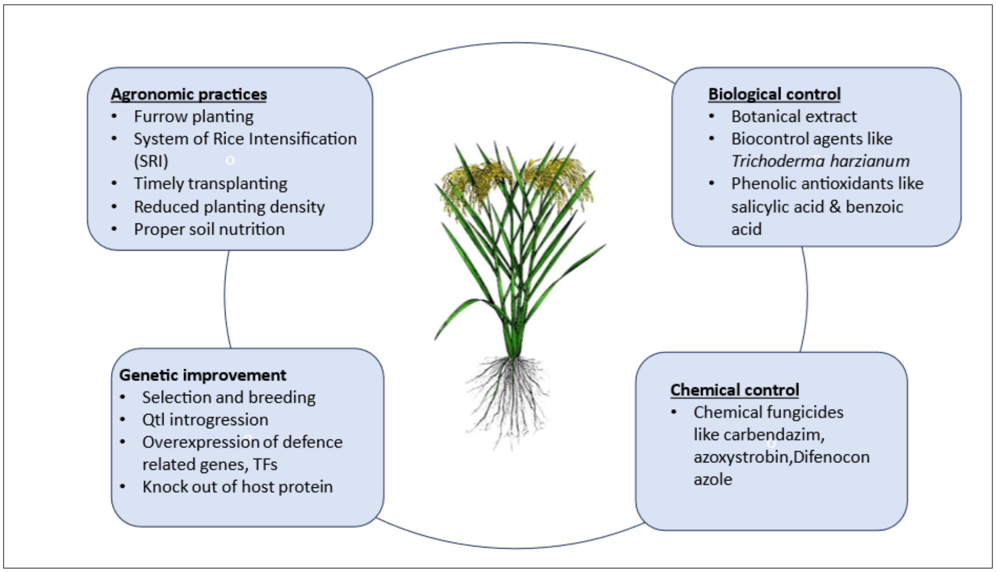

Fig. 3. Disease management approaches for brown leaf spot in rice.

Sources of resistance in breeding lines

Host resistance has been widely recognized as a sustainable method for managing brown leaf spot disease. Several studies have focused on identifying resistant genotypes across different regions. Asia and Africa have been notable sources of resistance, providing valuable genetic material for breeding programs aimed at developing resistant cultivars for farmers. The genetic variability of *Bipolaris oryzae* and the differential susceptibility of rice cultivars advocate the need to use host resistance to combat the disease effectively (67). The earliest recorded investigation of varietal resistance dates back to 1930, when the Korean cultivar ‘Kutto-urupe’ was reported as highly susceptible based on field observations without artificial inoculation (68). Subsequent studies in the United States identified the cultivar ‘Mubo-Aikoku’ as resistant through seedling inoculation tests (69). In Japan, Yoshii and Matsumoto employed spray inoculation across different growth stages, demonstrating that cultivars like ‘Tetep’ and ‘Ginnen’ were resistant, while others, including ‘Tadukan,’ showed moderate resistance (70). In Egypt, studies categorized ‘Pi1’ and ‘YNA282’ as resistant, contributing further to the pool of resistant germplasm (71).

Recent efforts have screened advanced breeding lines and commercial cultivars for BLS resistance. Table 2 shows the disease rating scale for screening rice varieties against Brown leaf spot. Among 29 advanced breeding lines and four check varieties (BR 11, BR 22, BR 25 and BRRI dhan 38), one accession showed resistance during the T. aman season, while the boro season revealed 29 moderately resistant cultivars (72). A field and laboratory assessment of 60 rice genotypes in Nepal identified significant variability in resistance levels, with only one genotype showing moderate resistance. However, most

Table 2. Disease rating scale for screening rice varieties against brown leaf spot

Rating	Affected leaf area	Host reaction
1	No incidence	Immune
2	Less than 1 %	Highly Resistant
3	1 - 3 %	Resistant
4	4 - 5 %	Resistant
5	11 - 15 %	Moderately Resistant
6	16 - 25 %	Moderately Resistant
7	26 - 50 %	Susceptible
8	51 - 75 %	Susceptible
9	76 - 100 %	Highly susceptible

genotypes, including landraces, exhibited high susceptibility, emphasizing the need for broader germplasm exploration (73). In Cameroon, field evaluations of four rice varieties (Nerica 3, Nerica 8, Kamkou and White Rice) during 2015-2016 found Nerica 8 and Nerica 3 to be highly tolerant, with disease severity at 110 DAS recorded at 2.05 % and 2.72 %, respectively. These varieties demonstrated superior resilience compared to Kamkou and White Rice, making them promising candidates for resistance breeding programs (74). Regional surveys in Punjab, India, highlighted its impact on local rice varieties. Commercial cultivars such as PR 116, PR 114 and PR 106 were highly susceptible, with PR 116 reaching up to 28.41 % severity. In contrast, the variety ‘Jaya’ consistently showed lower susceptibility, with a severity of only 3.23 % (75). These results underscore the importance of identifying and utilizing resistant genotypes, both traditional and modern, for managing brown spot disease. Enhanced screening efforts and the inclusion of diverse land races and wild relatives in breeding programs remain crucial for developing sustainable solutions to this persistent challenge.

Advancements in hybrid rice breeding have identified promising parental lines and hybrids with significant resistance to brown spot (*Bipolaris oryzae*). A combined genetic analysis highlighted *Giza 178*, *Giza 179*, *HR195*, *Giza 181* and *Giza 182* as resistant parental lines suitable for developing hybrids with robust resistance to brown spot disease. Among cytoplasmic male sterile (CMS) lines, *K17A* exhibited strong general combining ability (GCA) for resistance-related traits, making it an effective contributor in hybrid breeding. The hybrid *K17A* × *Giza 182* demonstrated significantly enhanced resistance, with desirable reductions in disease severity and infected leaf percentages. These traits, alongside beneficial heterosis, highlight its potential for commercial deployment (76). The study emphasized the predominant role of additive gene action in conferring resistance, with *K17A*, *HR195* and *Giza 182* emerging as superior general combiners.

QTL mapping

Several cultivars that have been categorized as resistant did not show complete resistance (immunity) to Brown spot. Some varieties such as ‘*Tadukan*’ and ‘*Tetep*’ showed quantitative resistance to BLS (70-78). The first QTL analysis for resistance to BLS was conducted in 2008 using a set of recombinant inbred lines (RILs) derived from a cross between ‘*Tadukan*’ (resistant) and ‘*Hinohikari*’ (susceptible). Three QTLs for brown spot resistance were detected on chromosomes 2, 9 and 11, named qBS2, qBS9 and qBS11. The most significant QTL was qBS11, with the highest LOD score of 5.11 in composite interval mapping (CIM) and 2.82 in interval mapping (IM). This QTL accounted for 11.9 % to 15.3 % of the total phenotypic variation and reduced the disease score by 0.34 to 0.58. qBS9 was detected with a LOD score of 3.45 in CIM and 2.72 in IM, explaining 9.7 % to 12.9 % of the phenotypic variation. qBS2, identified only in CIM analysis, explained 11.1 % of the variation. The resistant alleles from the *Tadukan* variety reduced disease scores, confirming its effectiveness against brown spot and setting the stage for future map-based cloning to understand resistance mechanisms further (47). The previously found QTLs (qBS2, qBS9 and qBS11) were associated with brown spot resistance at the seedling stage in controlled conditions. Another research aimed to validate these QTLs under field conditions and introduce them into a regional rice variety, ‘*Koshihikari*’. This study identified three field resistance QTLs; qBSfR1 (chromosome 1), qBSfR4 (chromosome 4) and qBSfR11 (chromosome 11). The major QTL qBSfR11 aligns with the previously identified qBS11, demonstrating consistent effectiveness across conditions. Near-isogenic lines (NILs) containing qBSfR11 displayed significant field resistance, highlighting its potential utility for breeding programs. qBSfR1 showed no significant impact on resistance, suggesting limited practical value. The findings underscore qBSfR11 as a major QTL for developing brown spot-resistant rice varieties through marker-assisted selection (79).

The first practical brown spot (BS)-resistant rice variety named *Mienoyume BSL* was developed by incorporating the QTL qBSfR11 from the local resistant line ‘*Tadukan*’ into the background of the high-yielding yet susceptible cultivar ‘*Mienoyume*’. The resistance to BS is controlled by a single recessive gene, designated as *bsr1*, located within a 1.3-Mbp region on chromosome 11. This gene was introduced into *Mienoyume* through successive backcrossing. The resulting near-isogenic line (bsr1-NIL) showed significantly improved resistance to multiple strains of *Bipolaris oryzae*, yielding a BS disease score significantly lower than *Mienoyume* and achieving a 28.8 % higher yield in fields with severe BS incidence. The bsr1-NIL demonstrated stable agricultural performance, including larger grain width, comparable days to heading and improved grain filling, even under disease stress. The protein content was slightly lower in bsr1-NIL compared to *Mienoyume* (80). To verify the resistance conferred by the ‘*Tadukan*’ alleles at qBSfR1 and qBSfR11, near-isogenic lines (NILs) containing each of these QTL alleles from ‘*Tadukan*’ in the background of susceptible variety ‘*Koshihikari*’ were bred and evaluated under field conditions. A NIL containing the ‘*Tadukan*’ allele at qBSfR11 acquired significant BLS field resistance, but that with the ‘*Tadukan*’ allele at qBSfR1 did not. Besides ‘*Tadukan*’, ‘*Kasalath*’ was also identified as a resistant cultivar (36).

Quantitative trait loci (QTLs) for brown spot (BS) resistance in rice were discovered on chromosomes 2 (qBSR2-kc), 7(qBSR7-kc), 9(qBSR9-kc) and 11(qBSR11-kc) using backcrossed inbred lines (BILs) from a cross between the resistant indica variety ‘CH45’ and the susceptible japonica cultivar ‘*Koshihikari*’. qBSR11-kc was the major contributor to BLS resistance which explained 23.0 %-25.9 % of the phenotypic variation in disease resistance. qBSR9-kc and qBSR11-kc were consistently detected in both 2015 and 2016, while qBSR2-kc and qBSR7-kc were only identified in 2016, potentially due to variations in climate, such as higher temperatures and increased rainfall. The resistance alleles at qBSR2-kc, qBSR7-kc and qBSR11-kc originated from CH45, while the allele at qBSR9-kc came from *Koshihikari* (81). A recombinant inbred line (RIL) population from a cross between *Danteshwari* (moderately tolerant) and *Dagad deshi* (susceptible) was used to identify quantitative trait loci (*QTLs*) associated with brown spot tolerance. qBS1.1, qBS5.1 and qBS5.2 are the QTLs that were located on chromosomes 1 and 5. qBS1.1 (chromosome 1) exhibited a lower effect, explaining 9.15 % of phenotypic variance. qBS5.1 and qBS5.2 (chromosome 5) had high phenotypic variances of 55.35 % and 55.5 %, respectively, indicating major contributions to brown spot resistance. The negative additive effects suggested that the resistance alleles were inherited from the susceptible parent, Dagad deshi (82). Table 3 highlights Quantitative trait loci (QTLs) associated with resistance to Brown Leaf Spot (BLS) in rice.

Genome-Wide Association Studies (GWAS)

GWAS has become a powerful approach to identify genomic regions linked to complex traits such as disease resistance. While limited studies have focused specifically on BLS in rice, GWAS applied to related traits and species offers valuable insights. In switchgrass, a relative of rice, GWAS identified 27 SNPs associated with BLS resistance, many of which were linked to defense-related genes. This includes genes encoding nucleotide-binding site leucine-rich repeat (NBS-LRR) proteins, pentatricopeptide repeat (PPR) proteins and ABC transporters, all of which are involved in plant defense mechanisms (83). Although direct GWAS studies on *Bipolaris oryzae* resistance in rice are limited, significant progress has been made for analogous leaf spot diseases. For example, narrow brown leaf spot (caused by *Cercospora janseana*) was associated with a key locus, CRSP2.1, on chromosome 2. Fine mapping and functional characterization of these loci are being carried out to develop resistant rice cultivars. Moreover, GWAS on temperate-adapted japonica and indica rice identified 14 marker-trait associations (MTAs) for blast resistance. Several MTAs co-located with known blast resistance genes(Pi genes), while three (BRF10, BRF11-2, BRGC11-3) may represent novel resistance loci (84). Given that GWAS was successful in identifying the resistance loci for blast disease, a similar approach for brown leaf spot disease, could identify new resistance genes and quantitative trait loci QTLs that may provide a sound basis for breeding BLS-resistant varieties of rice. GWAS on other rice diseases, such as bacterial leaf blight, identified resistance loci and candidate genes, which increased our understanding of defense mechanisms in rice. Such studies reveal NBS-LRR proteins, crucial for the recognition of pathogens and activation of defense responses (85). In addition to the resistance genes, biocontrol agents like *Trichoderma harzianum* offer a complementary strategy. *Trichoderma harzianum* has demonstrated strong antifungal activity against *Bipolaris oryzae*, both *in vitro* and field studies. In vitro assays showed that *T. harzianum* overgrows *B. oryzae* and produces inhibitory metabolites, while foliar sprays (10^8 spores/mL) under field conditions significantly reduced disease severity and incidence and boosted grain yield, carbohydrate and protein content in rice leaves (86). Compelling research shows that genes from *Trichoderma* can be transferred into rice to enhance resistance. For example, the *ech42* gene (encoding an endochitinase) from *T. atroviride* was introduced into rice via transformation, leading to enhanced resistance not only against sheath blight but also against rice blast (87). This strategy could similarly enhance resistance to brown leaf spot by enabling rice to express antifungal genes effective against *Bipolaris oryzae*.

Omics approaches

Omics technologies have improved our understanding of complex traits such as disease resistance in rice. These approaches-genomics, transcriptomics, proteomics and metabolomics-offer insights into the host-pathogen interactions underlying Brown Leaf Spot (BLS). Transcriptomics is the most widely used omics tool for BLS studies. Techniques like RNA-Seq and qRT-PCR helps to unravel gene expression changes in rice upon pathogen infection. For instance, resistant cultivars upregulate defense genes such as *OsFBN6*, while susceptible ones show disrupted expression, revealing key candidates for breeding (88). Defense-related pathways, including the tryptophan pathway, phenylpropanoid metabolism and serotonin biosynthesis, are often differentially expressed. These contribute to early pathogen recognition and physical barrier

Table 3. QTLs identified for brown leaf spot resistance in rice

QTL	Chromosome	Flanking markers	Mapping population	Donor	% Phenotypic variance	Additive effect	Reference
qBS2	2	RM3515*-RM263	RILs (Tadukan × Hinohikari)	Tadukan	11.1	0.29	(47)
qBS9	9	RM3907-RM566* RM566*-RM257	RILs (Tadukan × Hinohikari)	Tadukan	9.7 12.9	-0.28 -0.62	(47)
qBS11	11	RM206-RM6449* RM6499*-RM6623	RILs (Tadukan × Hinohikari)	Tadukan	15.3 11.9	-0.34 -0.58	(47)
qBSfR 1	1	RM10604	RILs (Tadukan × Hinohikari) in Koshihikari background	Tadukan	12.3	-0.4	(79)
qBSfR 4	4	RM273	RILs (Tadukan × Hinohikari) in Koshihikari background	Tadukan	10.8	0.3	(79)
qBSfR 11	11	RM27096	RILs (Tadukan × Hinohikari) in Koshihikari background	Tadukan	19.2	-0.5	(79)
qBSR9-kc	9	RM3919*-RM6797	BILs (CH45 × Koshihikari)	Koshihikari	6.5	0.2	(81)
qBSR11-kc	11	RM6534*-RM4112	BILs (CH45 × Koshihikari)	CH 45	25.9	-0.5	(81)
qBSR2-kc	2	RM5578-RM5614	BILs (CH45 × Koshihikari)	CH 45	17.1	-0.6	(81)
qBSR7-kc	7	RM1353-1*-RM5672	BILs (CH45 × Koshihikari)	CH 45	7.8	-0.4	(81)

formation. Notably, serotonin-deficient mutants exhibit higher susceptibility, underscoring its role as a secary metabolite in rice defense (59) .

Integration with metabolomics helps to link gene expression to functional outputs such as higher phenolic compound accumulation in resistant lines. Combined omics approaches can detect novel resistance genes and metabolic signatures for use in marker-assisted selection (89). Recent transcriptomic studies in North-East Indian rice cultivars revealed a biphasic fungal infection strategy-early metabolic activation in the fungus followed by late effector expression in susceptible hosts. This suggests the need for early defense activation in breeding programs (90). Going forward, the fusion of omics datasets with machine learning could accelerate the discovery of candidate genes and biomarkers for BLS resistance. Integrative approaches will be essential for designing rice cultivars with durable, multi-layered defense.

Genome editing/CRISPR Cas9

Genome editing, particularly CRISPR/Cas9, has emerged as a revolutionary method for precise and efficient crop improvement. In rice, this technology has already been employed to develop resistance against major diseases such as blast and bacterial blight. Its application in managing Brown Leaf Spot (BLS) holds immense promise. CRISPR/Cas9 has demonstrated its potential by knocking out susceptibility genes, thereby enhancing disease resistance. For instance, editing the *OsERF922* gene significantly increased resistance to blast (91), while modifications in *SWEET* gene promoters disrupted effector-triggered susceptibility to bacterial blight (92). This precise technology shows great potential for targeting brown leaf spot (BLS). Possible uses include the knockout of susceptibility genes that allow for pathogen infection or the alteration of resistance-related genes to boost their effectiveness against BLS. Multiplex genome editing can enable the concurrent targeting of multiple genes, allowing for the combination of resistance traits and offering broad-spectrum and long-lasting resistance. CRISPR/Cas9-mediated editing of susceptibility genes (*Bsr-d1*, *Pi21* and *ERF922*) in rice revealed that *ERF922* mutants conferred strong blast resistance, while *Pi21* and *ERF922* knockouts also enhanced bacterial blight resistance via activation of salicylic acid (SA) and jasmonic acid (JA) pathways (93). This approach, which preserved key agronomic traits, suggests that targeting analogous genes in rice could similarly enhance BLS resistance via multiplex genome editing. By merging genome editing with molecular markers and genomic selection, this strategy could hasten the creation of BLS-resistant rice varieties, ensuring sustainable production in the face of evolving pathogen threats.

Challenges and Limitations

Breeding rice varieties resistant to brown leaf spot (BLS) presents several challenges due to the disease's complex epidemiology and the multifaceted interactions among the host plant, pathogen and environmental conditions.

- Slow disease initiation and progression, influenced by specific environmental conditions (e.g., optimal temperature and humidity), delay symptom expression and hinder early detection.
- Persistence of the pathogen is aided by continuous rice cultivation, favourable climate and survival on infected plant residues and seeds.
- High initial inoculum levels from contaminated seeds and crop debris lead to more severe disease outbreaks.
- Host susceptibility is affected by physical traits like leaf surface morphology and physiological stresses such as nutrient imbalance and water stress.
- Resistance evaluation is challenging due to environmental variability, difficulty in achieving reliable phenotyping and complex inheritance involving multiple QTLs.
- Pathogen variability and strong genotype × environment interactions complicate breeding for stable resistance.
- Marker-assisted selection (MAS) requires precise identification and mapping of QTLs, which is constrained by the polygenic nature of BLS resistance.
- Pyramiding multiple resistance QTLs is essential for durable resistance but may face compatibility and pleiotropy challenges.

Conclusion and Future Perspectives

Brown leaf spot (BLS) continues to pose a significant threat to global rice production, particularly in low-input, rain-fed systems. Its persistence is driven by complex interactions among the host, pathogen and environment, compounded by nutrient deficiencies and the pathogen's broad host range. While chemical and cultural controls offer temporary relief, host plant resistance remains the most sustainable and eco-friendly long-term solution. Considerable progress has been made in identifying QTLs, especially from landraces and wild *Oryza* species and incorporating them into elite lines using molecular tools such as marker-assisted selection (MAS). Advances in genome editing technologies like CRISPR/Cas9 further enable precise and efficient resistance breeding. To reduce the spread of BLS in the field, practical strategies such as the use of disease-free seed, crop rotation, residue management and balanced nutrition should be prioritized alongside genetic solutions.

To overcome the challenges posed by the polygenic nature of resistance and high pathogen variability, future breeding must focus on gene pyramiding, genomic selection and the development of multi-resistant cultivars. Additionally, continuous pathogen surveillance and the strategic deployment of resistance genes can help minimize selection pressure and prolong resistance durability. Future efforts must adopt a multidisciplinary approach, integrating host-pathogen interaction studies, pathogen genomics and systems biology to uncover novel resistance mechanisms. High-throughput phenotyping, environmental modelling and next-generation sequencing, supported by robust bioinformatics, will be crucial for breeding climate-resilient, broad-spectrum BLS-resistant cultivars. Collaboration across disciplines will accelerate the development of durable solutions, safeguarding rice yields in the face of evolving disease pressure and climate change.

Authors' contributions

ASMN wrote the main manuscript. RS, SM, CG and GS have reviewed the manuscript. BC did the final revision of manuscript. All authors read and approved the manuscript.

Compliance with ethical standards

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