Print ISSN : 0972-8813
e-ISSN : 2582-2780

[Vol. 23(3) September-December 2025]

Pantnagar Journal of Research

(Formerly International Journal of Basic and
Applied Agricultural Research ISSN : 2349-8765)

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PANTNAGAR JOURNAL OF RESEARCH

Vol. 23(3) September-December, 2025

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Review

Frogeye leaf spot (*Cercospora sojina* K. Hara) in soybean: Emerging challenges, resistance genetics and sustainable management strategies

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ABSTRACT: Frogeye leaf spot (FLS), caused by the fungal pathogen *Cercospora sojina* K. Hara, is an economically important foliar disease of soybean (*Glycine max* L. Merr.) that threatens production in warm and humid growing regions worldwide. This review synthesizes current knowledge on the pathogen biology, disease epidemiology, economic impact, and management strategies, with a particular emphasis on research from India and international contexts. The pathogen exhibits high genetic diversity and race complexity, and the emergence of quinone outside inhibitor (QoI) fungicide resistance has complicated chemical control. Integrated disease management combining host resistance, cultural practices, and judicious fungicide use remains essential. Recent advances in genomics, molecular markers, and novel biocontrol agents offer promising tools for sustainable FLS management. This review highlights key research findings, identifies knowledge gaps, and discusses future directions for improving disease control in the face of evolving pathogen populations and changing climatic conditions.

Keywords: *Cercospora sojina*, frogeye leaf spot, fungicide resistance, host resistance, soybean diseases

Soybean (*Glycine max* L. Merr.) is one of the world's most important legume crops, providing protein, oil, and numerous industrial products. In 2024, soybean production in India was estimated at 13.36 million tonnes, harvested from about 12.93 million hectares, with an average productivity of 1,033 kg per hectare (Annual Report NSRI, 2024). Global soybean production has expanded dramatically over the past decades, but biotic stresses, particularly fungal diseases, continue to limit yield potential and quality. Among foliar diseases, frogeye leaf spot (FLS) has emerged as a significant threat in warm and humid soybean-growing regions worldwide (Barro *et al.*, 2023; Roth *et al.*, 2020). This disease causes yield losses to the tune of 66 per cent during epidemic years (Dogra 2015; Mittal, 2001 and Mian *et al.*, 1998).

Frogeye leaf spot, caused by the ascomycete fungus *Cercospora sojina* K. Hara, reduces photosynthetic area, accelerates defoliation, and decreases seed weight and quality (Barro *et al.*, 2023; Dashiell and Akem, 1991). The disease has been documented across major soybean production regions, including North and South America, Asia, and Africa, with particularly severe outbreaks reported in Argentina, the United States, and expanding incidence in other countries (Barro *et al.*, 2023; Dashiell and Akem, 1991; Mian *et al.*, 2008). In recent years, the disease has gained attention due to frequent outbreaks driven by susceptible cultivars, favorable weather, and continuous soybean cultivation (Barro *et al.*, 2023; Roth *et al.*, 2020).

In India, where soybean underpins food security and farmer livelihoods in central and northern regions, frogeye leaf spot has emerged as a growing constraint. Hotspot surveys report high disease pressure, prompting large-scale screening to identify resistant germplasm for breeding and near-term farmer deployment (Mishra *et al.*, 2021). This disease is commonly found in the northern plain zones of India viz., Almora, Palampur (Bhartiya *et al.*, 2023) referred as hotspots for the FLS disease, while reports from other parts of the country like Karnataka has also been done (Hugilol *et al.*, 2020).

The management of FLS has become increasingly challenging due to several factors: the pathogen's high genetic diversity and race structure, the emergence and spread of fungicide resistance (particularly to QoI fungicides), and the need for sustainable, integrated control strategies (Barro *et al.*, 2023; Zhang *et al.*, 2012; Standish *et al.*, 2015). This review includes Indian and global perspective on frogeye leaf spot, spanning pathogen biology, epidemiology, economic impact, management, resistance genetics, and recent technological advances.

In India, research on frogeye leaf spot of soybean is constrained by poor epidemiological data, limited understanding of pathogen diversity, and the lack of uniform screening protocols. Indian soybean cultivars have not been adequately evaluated under consistent disease pressure, restricting progress in resistance breeding. Key priorities include national disease surveillance, morpho-molecular characterization of the pathogen, and development of robust screening facilities. These efforts should be integrated with climate-linked forecasting and durable, biologically supported management strategies.

The Pathogen

Taxonomy and classification

Frogeye leaf spot is caused by *C.sojina* K. Hara, an ascomycete fungal pathogen belonging to the phylum Ascomycota, class Dothideomycetes, order Capnodiales, and family Mycosphaerellaceae (Barro *et al.*, 2023; Groenewald *et al.*, 2013). The fungus exists primarily as an anamorph (asexual stage), and although a teleomorph (sexual stage) has not been definitively observed in nature, molecular evidence suggests that cryptic sexual recombination may occur (Barro *et al.*, 2023; Shrestha *et al.*, 2017). Population genetic studies have revealed the presence of both mating-type alleles (MAT1-1 and MAT1-2) in field populations, indicating the potential for sexual reproduction that could contribute to genetic diversity and the emergence of new pathotypes (Shrestha *et al.*, 2017; Shrestha, 2017).

Morphology and identification

Cercospora sojina produces characteristic morphological structures that aid in identification. The pathogen forms geniculate (bent), fasciculate (clustered) conidiophores that emerge from stromata in infected leaf tissue (Dashiell and Akem, 1991; Chupp, 1953). Conidia are hyaline, elongate to fusiform, and septate, typically measuring 40-200 × 3-5 μm with multiple septa (Dashiell and Akem, 1991; Groenewald *et al.*, 2013; Chupp, 1953). These morphological features have been consistently described in outbreak reports and diagnostic isolations from various geographic regions (Dashiell and Akem, 1991; Chupp, 1953).

In culture, *C. sojina* colonies are typically slow-growing, grayish to olivaceous, with aerial mycelium (Groenewald *et al.*, 2013; Chupp, 1953).Standardization of growth media and temperature for rapid growth of *C. sojina* causing frogeye leaf spot of soybean were done and identifying Potato Cellulose Dextrose Agar (PCDA), Potato Dextrose Agar (PDA), Soybean Leaf Extract Agar (SLEA), and Flat Rice Agar (FRA) as the most suitable media, with optimum growth and sporulation at 25 °C (Sharma *et al.*, 2023).Cultural characteristics including colony color, growth rate, and sporulation patterns showed variation among isolates collected from Madhya Pradesh, Maharashtra, and Rajasthan (Agarwal *et al.*, 2013). However, morphological identification alone may be insufficient for accurate diagnosis, particularly when distinguishing *C. sojina* from other *Cercospora* species or related foliar pathogens. Therefore, molecular methods have become increasingly important for pathogen confirmation (Groenewald *et al.*, 2013; Goodwin *et al.*, 2001).

Molecular biology and genomics

Recent molecular advances have clarified the biology of *Cercospora sojina*. The ITS region of rDNA has been widely used for molecular identification and phylogenetic analysis, while whole-genome sequencing has provided deeper insight into pathogenicity mechanisms (Goodwin *et al.*, 2001; Groenewald *et al.*, 2013; Bluhm *et al.*, 2014; Luo *et al.*, 2018). The ~40.8 Mb genome encodes about 11,655 predicted genes and reveals a large secretome rich in candidate effector proteins, along with multiple secondary metabolite gene clusters, including those linked to cercosporin production (Bluhm *et al*., 2014; Luo *et al*., 2018). Transcriptomic studies further show strong induction of secreted proteins and secondary metabolism genes during early infection, underscoring their central role in disease establishment (Luo *et al*., 2018).

Genetic diversity, races and pathogenic variability

Cercospora sojina populations exhibit high levels of genetic diversity, as demonstrated by studies using microsatellite markers, single nucleotide polymorphisms (SNPs), and genome-wide analyses (Shrestha *et al*., 2017; Shrestha, 2017; Mengistu *et al*., 2007). Morphological and molecular characterization studies of *C. sojina* isolates from different agro-ecological zones of India have revealed considerable variability in the pathogen population (Gupta *et al*., 2012). Population genetic studies in the United States have revealed significant genetic differentiation among geographic populations, with some evidence of clonal lineages associated with specific traits such as QoI fungicide resistance (Shrestha *et al*., 2017; Shrestha, 2017).The presence of both mating types in many populations indicates that sexual recombination, even if cryptic, may contribute to generating new genetic combinations and accelerating adaptation (Shrestha *et al*., 2017; Shrestha, 2017). The pathogen exhibits complex race structure, with multiple races identified based on differential reactions on sets of soybean genotypes carrying different resistance genes (Barro *et al*., 2023; Athow and Probst, 1952; Pham *et al*., 2015). However, race nomenclature and differential sets have not been standardized globally, leading to inconsistencies in race designations across different studies and regions (Barro *et al*., 2023; Pham *et al*., 2015). Some researchers have identified 5-6 races, while others have reported more than 15 races, reflecting differences in differential sets used and geographic variation in pathogen populations (Barro *et al*., 2023; Athow and Probst, 1952; Pham *et al*., 2015) (Table 1).The complexity of the race structure complicates breeding efforts and deployment of resistant cultivars. A pathogen population may contain multiple races simultaneously, and race composition can shift over time in response to selection pressure from widely deployed resistance genes (Barro *et al*., 2023; Athow and Probst, 1952).

Disease symptoms and diagnosis

Symptomatology

Frogeye leaf spot symptoms typically appear first on lower leaves and progress upward through the canopy as the season advances (Barro *et al*., 2023; Dashiell and Akem, 1991). The disease is characterized by distinctive leaf lesions that give the disease its common name. Initial symptoms appear as small, dark spots that expand into circular to angular lesions (Barro *et al*., 2023; Dashiell and Akem, 1991; Phillips, 1999). Mature lesions are typically 1-5 mm in diameter, with gray to tan centers surrounded by a characteristic reddish-brown to purple margin, resembling a frog's eye (Fig 1) (Barro *et al*., 2023; Dashiell and Akem, 1991; Phillips, 1999).

On susceptible cultivars under favorable conditions, lesions may coalesce, leading to extensive blighting of leaf tissue. Severely infected leaves often become chlorotic and drop prematurely, reducing the photosynthetic capacity of the plant and affecting pod fill and seed development (Barro *et al*., 2023; Dashiell and Akem, 1991; Phillips, 1999). The disease can also affect stems and pods, particularly

Table 1. Races of *Cercospora sojina* reported worldwide

Race	Location	Virulence / Key findings	Reference
Races 1–11	Southern USA	Captured major virulence diversity among 93 isolates; proposed standard race set	Mian *et al.* (2008)
Race 04	Brazil	Distinct differential reactions; Cristalina, Davis and Uberaba identified as resistance donors	Gravina *et al.* (2004)
Race 7	China	Partial resistance mapped; 15 QTNs identified, candidate genes on Chr 16	Li *et al.* (2023)
Race 15	USA (Tennessee)	Earliest documented race; foundation for historical race classification	Athow and Probst (1952)

during severe epidemics, with lesions on these organs appearing as elongated, reddish-brown streaks or spots (Dashiell and Akem, 1991; Phillips, 1999).

Disease epidemiology

Understanding the disease cycle of frogeye leaf spot is fundamental to developing effective management strategies. The primary source of inoculum for FLS epidemics is infected soybean residue from the previous crop (Barro *et al.*, 2023; Walters and Caviness, 1973; Wrather *et al.*, 1997). *Cercospora sojina* survives between growing seasons as mycelium and conidia in crop debris on or near the soil surface. The pathogen can persist on infested residue for extended periods, with survival documented for 12-24 months under field conditions (Barro *et al.*, 2023; Walters and Caviness, 1973).

When environmental conditions become favorable in the following growing season, conidia are produced on overwintered residue and dispersed by wind and rain splash to newly emerged soybean plants (Barro *et al.*, 2023; Walters and Caviness, 1973; Wrather *et al.*, 1997). Initial infections typically occur on lower leaves, and secondary inoculum produced on these lesions initiates polycyclic disease spread through the canopy (Barro *et al.*, 2023; Walters and Caviness, 1973). The polycyclic nature of FLS epidemics means that multiple infection cycles can occur within a single growing season, leading to exponential disease increase under favorable conditions (Barro *et al.*, 2023; Walters and Caviness, 1973).Seed transmission of *C. sojina* has been reported but appears to be of minor importance compared to residue-borne inoculum in most production systems. Long-distance dispersal of conidia by wind currents may also contribute to pathogen spread, particularly during severe regional epidemics (Barro *et al.*, 2023; Walters and Caviness, 1973).

Fig 1: Frogeye leaf symptoms of soybean

Environmental factors affecting disease development

Frogeye leaf spot development is strongly influenced by environmental conditions, particularly temperature, moisture, and leaf wetness duration (Barro *et al.*, 2023; Walters and Caviness, 1973; Melchers & Parker, 1922). The disease is particularly severe during the rainy season when high humidity and moderate temperatures (20-28°C) favor pathogen development and spore dispersal (Agarwal *et al.*, 2013). Moisture is critical for conidial germination, infection, and sporulation. Frequent rainfall, high relative humidity, and extended periods of leaf wetness create favorable conditions for disease development (Barro *et al.*, 2023; Walters and Caviness, 1973; Melchers and Parker, 1922). Controlled experiments have quantified the relationship between leaf wetness duration and infection success, showing that longer wetness periods result in higher infection rates and more severe disease (Walters and Caviness, 1973; Melchers and Parker, 1922). The combination of warm temperatures and abundant moisture during critical growth stages is particularly conducive to severe FLS epidemics (Barro *et al.*, 2023; Walters and Caviness, 1973; Melchers and Parker, 1922). Geographic regions with warm, humid climates during the soybean growing season, such as the southeastern United States, southern Brazil, Argentina, and parts of Asia including India, are at higher risk for FLS outbreaks (Barro *et al.*, 2023; Dashiell and Akem, 1991; Mishra *et al.*, 2021).

Economic impact of the disease in India

In India, soybean is a major kharif (monsoon season) crop grown primarily in the central and northern states, including Madhya Pradesh, Maharashtra, Rajasthan, and Uttarakhand (Mishra *et al*., 2021; Singh and Kapoor, 1999). Frogeye leaf spot has been identified as an emerging disease constraint in these regions, with hotspot surveys documenting substantial disease pressure in key growing areas (Mishra *et al*., 2021; Singh and Kapoor, 1999).

Indian researchers have conducted field surveys and screening trials in FLS hotspots, particularly in the hill regions of Uttarakhand, where the disease has been observed with high severity (Mishra *et al*., 2021). Survey studies conducted across major soybean-growing regions of India revealed widespread occurrence of FLS with disease incidence ranging from 15-45% and severity levels varying based on cultivar susceptibility and environmental conditions (Sharma *et al*., 2016). The identification of resistance sources is crucial for Indian soybean improvement programs, as deployment of resistant cultivars provides the most economical and sustainable approach to managing FLS (Mishra *et al*., 2021; Singh and Kapoor, 1999).While specific economic impact assessments of FLS in India are limited in the published literature, the disease's potential to cause significant yield losses, combined with the importance of soybean to Indian agriculture, underscores the need for continued research and management efforts (Mishra *et al*., 2021; Singh and Kapoor, 1999).

Disease Management Strategies

Effective management of frogeye leaf spot requires an integrated approach combining multiple tactics, including cultural practices, chemical control, biological control, and host resistance. No single management method provides complete control, and the emergence of fungicide resistance has made integrated strategies even more critical (Barro *et al*., 2023; Roth *et al*., 2020; Zhang *et al*., 2012; Standish *et al*., 2015).

Cultural practices

Cultural practices form the foundation of integrated FLS management by reducing inoculum levels and creating less favorable conditions for disease development. Cultural management focuses on reducing inoculum and limiting favorable canopy conditions. Crop rotation away from soybean for at least two years with non-hosts such as corn or wheat allows infected residue to decompose and lowers primary inoculum, although effectiveness depends on pathogen survival on residue and environmental conditions (Barro *et al*., 2023; Walters and Caviness, 1973; Wrather *et al*., 1997). Residue management through tillage that accelerates decomposition or buries infected debris can further reduce surface inoculum and delay disease onset, but must be balanced with soil conservation and system sustainability (Walters and Caviness, 1973; Wrather *et al*., 1997). Optimizing planting date can help crops avoid peak inoculum or highly favorable weather, with early planting often reducing disease risk, though responses vary by region and season (Dashiell and Akem, 1991; Melchers and Parker, 1922). Adjusting plant density and row spacing to improve air circulation and reduce leaf wetness also suppresses disease development, provided yield are considered (Barro *et al*., 2023; Bradley *et al*., 2021).

Chemical control

Fungicides are widely used to manage frogeye leaf spot, especially under high disease pressure but their performance varies markedly among active ingredients and mixtures (Roth *et al*., 2020; Bradley *et al*., 2021; Grijalba and Palmucci, 2013; Barro *et al*., 2023b). Multi year trials and meta analyses show that mixtures with multiple modes of action, including DMI and SDHI combinations such as difenoconazole + pydiflumetofen, provide more consistent disease control and yield benefits than single-site products, with profitability highest when disease pressure is moderate to high (Grijalba and Palmucci, 2013; Barro *et al*., 2023b). Chemical control has been complicated by widespread QoI resistance in *Cercospora sojina*, caused by the G143A mutation in the *cytochrome b* gene, which confers high-level resistance and has spread across major soybean regions since about 2010 (Zhang *et al*., 2012; Standish *et al*., 2015; Neves *et al*., 2022). As a result, the efficacy of strobilurins alone has declined, necessitating greater reliance on fungicide mixtures and rotation of modes of action (Roth *et al*., 2020; Bradley *et al*., 2021; Barro *et al*., 2023b).

Biological control

Biological control and novel antimicrobial agents are emerging as useful complements to fungicides for managing frogeye leaf spot, particularly in the context of resistance and environmental concerns (Horváth *et al*., 2015). Plant derived antimicrobial peptides, such as a nodule specific cysteine rich peptide (NCR13) from chickpea, have shown activity against both QoI sensitive and QoI resistant *Cercospora sojina* isolates and reduced disease severity in greenhouse studies, with additive effects when combined with azoxystrobin (Horváth *et al*., 2015). Although dedicated biocontrol agents for FLS remain underexplored, antagonistic microorganisms hold promise, provided they are supported by robust field validation, effective delivery systems, and regulatory approval (Bradley *et al*., 2021; Horváth *et al*., 2015).

Biological agents tested against frogeye leaf spot include bacterial antagonists such as *Pseudomonas* and *Bacillus* strains, fungal antagonists notably *Trichoderma* spp., and broader plant growth-promoting rhizobacteria (PGPR) used to promote plant health and disease resistance (Lacey, 2018; Singh *et al*., 2024; Cassán*et al*., 2017). Research spans isolated foliar or seed/root applications and combined inoculations with rhizobia or chemical seed treatments to integrate disease suppression with agronomic benefits (Singh *et al*., 2024; Moreira *et al*., 2024). Bacterial antagonists including *Pseudomonas fluorescens* BNM297 and *Bacillus amyloliquefaciens* BNM340 and BNM122 have been evaluated specifically against *Cercospora sojina* in controlled assays, while *Bacillus* sp. CHEP5 has been identified as a native soybean biocontrol that induces systemic resistance against *C. sojina* (Lacey, 2018; Moreira *et al*., 2014). *Trichoderma* isolates such as *T. virens* and *T. hamatum* have been tested as root colonizers and foliar treatments for foliar diseases including frogeye leaf spot, and co-inoculation approaches combining *Bacillus*biocontrols with *Bradyrhizobium* have been explored to enhance disease reduction and plant performance (Lacey, 2018; Alori *et al*., 2020; Cassán*et al*., 2017).

Host Resistance

Deployment of resistant cultivars is the most economical, effective, and environmentally sustainable strategy for managing frogeye leaf spot, as it reduces disease severity, safeguards yield, and limits dependence on fungicides (Athow and Probst, 1952; Mian *et al*., 1999; Pham *et al*., 2015; Roth *et al*., 2020; Bradley *et al*., 2021; Barro *et al*., 2023). Breeding for FLS resistance has been a priority in Indian soybean improvement programs coordinated through the All India Coordinated Research Project on Soybean (AICRP-Soybean) (Gupta *et al*., 2012). Screening of germplasm collections and breeding lines under natural epiphytotic conditions and artificial inoculation has identified several sources of resistance (Agarwal *et al*., 2013). Extensive screening of global soybean germplasm, including diverse plant introductions, has identified both major-gene and quantitative resistance to different races of *Cercospora sojina*, with Indian hotspot surveys also revealing locally adapted resistant genotypes suitable for breeding (Athow and Probst, 1952; Mian *et al*., 1999; Pham *et al*., 2012; Pham *et al*., 2015; Mishra *et al*., 2021; Singh and Kapoor, 1999).The Uttarakhand hotspot study explicitly names Indian genotypes found to be highly resistant and suggests them as donors; NRC 88; VS 2004–9; VS 2005–40; VS 2006–17; DSB 11; NRC 84; AMS MB 5 19; VLS 86; Himso 1685; MACS 1407; MACS 1442 as highly resistant entries (Mishra *et al*., 2021). Screening of soybean germplasm under field and greenhouse conditions identified Harder, JSM 285, CAT 195, and GP 465 as absolutely resistant to frogeye leaf spot, indicating their potential use as reliable resistance donors in breeding programs (Sharma *et al*., 2023). Field evaluation of indigenous and exotic soybean accessions identified 12 lines AGS 163B, AMS.MB 51-18, EC 251516, EC 383165, EC 457185, EC 456599, UPSL 470, JS 20-38, NRC 42, JS 89-24, RKS 52, and IMP 1 as highly resistant to frogeye leaf spot (Bhartiya *et al*., 2023). Several race-specific Rcs resistance genes, including Rcs3 and related loci, have been mapped, along with QTLs conferring partial or adult-plant resistance, notably on chromosome 13 (Mian *et al*., 1999; Pham *et al*., 2012; Pham *et al*., 2015; Li *et al*., 2023). Fine-mapping in accessions such as PI

594538A and PI 594650A has further narrowed these loci to small genomic regions containing candidate defense-related genes, strengthening prospects for marker-assisted breeding (Mian *et al.*, 1999; Pham *et al.*, 2015) (Table 2).

Breeding Strategies

Breeding for frogeye leaf spot resistance must account for the complex race structure of *Cercospora sojina* and the risk of resistance breakdown. Durable resistance is best achieved by pyramiding multiple resistance genes or QTLs, combining major-gene and quantitative resistance, diversifying resistance sources, and regularly aligning breeding targets with prevailing pathogen races (Athow and Probst, 1952; Mian *et al.*, 1999; Pham *et al.*, 2012; Pham *et al.*, 2015; Barro *et al.*, 2023). Marker-assisted selection strengthens these strategies by enabling efficient stacking of resistance loci using molecular markers. Tools such as KASP assays allow early, reliable identification of resistance alleles from diverse plant introductions, reducing dependence on field screening and accelerating breeding progress (Roth *et al.*, 2020; Pham *et al.*, 2012; Pham *et al.*, 2015).

Genetics of FLS disease resistance

Genetic studies show that frogeye leaf spot resistance in soybean can be governed by either major genes or multiple QTLs, depending on the resistance source, pathogen race, and genetic background (Athow and Probst, 1952; Mian *et al.*, 1999; Pham *et al.*, 2012; Pham *et al.*, 2015). While some plant introductions display simple Mendelian, race-specific resistance controlled by single dominant genes, many sources exhibit complex, quantitative inheritance with additive and epistatic effects (Gravina *et al.*, 2004; Pham *et al.*, 2015). Combining ability studies indicate that additive effects predominate, supporting the use of recurrent selection and population improvement to enhance resistance durability (Gravina *et al.*, 2004).

Resistance genes, QTLs and molecular markers

Several major resistance genes conferring resistance to *C.sojina* have been identified and mapped in soybean, with Rcs3 and related loci consistently localized on chromosome 13 and fine-mapped to narrow genomic regions (Athow and Probst, 1952; Mian *et al.*, 1999; Pham *et al.*, 2012; Pham *et al.*, 2015). These regions harbor candidate genes encoding NBS-LRR proteins, receptor-like kinases, transcription factors, and other defense-related components, although functional validation is still required (Mian *et al.*, 1999; Pham *et al.*, 2015). Beyond major genes, numerous QTLs contributing to partial resistance have been identified through linkage mapping and GWAS, with a stable, major QTL on chromosome 13 repeatedly detected across populations, alongside additional loci on other chromosomes, including a notable QTL on chromosome 19 (Pham *et al.*, 2012; Pham *et al.*, 2015; Wen *et al.*, 2014; Li *et al.*, 2023). High-density SNP-based GWAS has further expanded the repertoire of resistance loci, highlighting the polygenic nature of FLS resistance (Wen *et al.*, 2014; Li *et al.*, 2023). Parallel efforts have produced tightly

Table 2: Summary of Genes, QTLs and GWAS Loci for Frogeye Leaf Spot Resistance in Soybean

Gene / QTL / Locus	Chromosome	Resistance Nature	Key References
Rcs3	13	Major gene; race-specific; complete	Athow and Probst (1952); Mian *et al.* (1999); Pham *et al.* (2015)
Major FLS locus (PI 594891)	13	Major gene; high-level; Rcs3-like	Pham *et al.* (2015)
Candidate genes (3 of 5)	13	Putative resistance genes	Pham *et al.* (2015)
QTL-Chr13	13	Quantitative resistance	McAllister *et al.* (2021)
QTL-Chr19 (novel)	19	Quantitative resistance	McAllister *et al.* (2021)
Race-7 GWAS loci (15 QTNs)	16 (major)	Partial resistance; polygenic	Li *et al.* (2023)
Validated genes (4)	16	Functionally confirmed resistance	Li *et al.* (2023)
Novel GWAS locus	11	Quantitative resistance	McDonald *et al.* (2023)
Additional minor QTLs	13, 16, 18, 19	Minor to moderate effects	Barro *et al.* (2023)
Rcs genes (historical set)	Multiple	Race-specific; complete	Mian *et al.* (2008); Barro *et al.* (2023)

linked SSR, SNP, and KASP markers for key resistance genes and QTLs, particularly on chromosome 13, enabling efficient marker-assisted selection, pyramiding of resistance loci, and rapid development of durable resistant cultivars (Athow and Probst, 1952; Pham *et al*., 2012; Pham *et al*., 2015; Roth *et al*., 2020) (Table 2).

Recent advances and emerging technologies

Several major Rcs genes conferring resistance to *Cercospora sojina* have been identified in soybean, with Rcs3 and related loci consistently mapped and fine-mapped to chromosome 13, where candidate genes encoding NBS-LRR proteins, receptor-like kinases, transcription factors, and other defence components reside (Athow and Probst, 1952; Mian *et al*., 1999; Pham *et al*., 2012; Pham *et al*., 2015). In addition to major genes, multiple QTLs governing partial resistance have been detected through linkage mapping and GWAS, including a stable, repeatedly detected QTL on chromosome 13 and additional loci on other chromosomes such as chromosome 19, underscoring the polygenic nature of FLS resistance (Pham *et al*., 2012; Pham *et al*., 2015; Wen *et al*., 2014; Li *et al*., 2023). Development of tightly linked SSR, SNP, and KASP markers for these loci has enabled efficient marker-assisted selection and pyramiding of resistance genes for durable cultivar development (Athow and Probst, 1952; Pham *et al*., 2012; Pham *et al*., 2015; Roth *et al*., 2020). Integration of multi-omics approaches, coupled with network analysis and machine learning, is further improving identification and prioritization of key resistance genes and pathways, accelerating functional validation and soybean improvement as sequencing costs decline (Luo *et al*., 2018; Pham *et al*., 2015; Wen *et al*., 2014).

Current challenges and future perspectives

Despite advances in frogeye leaf spot management, major challenges persist. High genetic diversity and rapid evolution of *Cercospora sojina*, coupled with widespread QoI fungicide resistance, have reduced chemical control options and demand continuous resistance monitoring and alternative strategies (Zhang *et al*., 2012; Standish *et al*., 2015; Neves *et al*., 2022; Barro *et al*., 2023). The complex race structure of the pathogen undermines durability of single-gene resistance, making pyramiding of major and quantitative resistance essential but operationally demanding (Athow and Probst, 1952; Pham *et al*., 2015; Roth *et al*., 2020). Progress is further constrained by inconsistent race nomenclature, which limits comparability across studies, and by knowledge gaps in India regarding pathogen race structure, resistance genes in local germplasm, and economic impacts (Pham *et al*., 2015; Mishra *et al*., 2021; Singh and Kapoor, 1999). Climate change adds uncertainty by altering disease distribution and epidemic dynamics, necessitating adaptive management strategies (Roth *et al*., 2020; Mahlein, 2016).

Future progress lies on functional validation of candidate resistance genes, development of durable gene combinations, and international standardization of race differentials and molecular typing systems (Pham *et al*., 2015; Barro *et al*., 2023; Luo *et al*., 2018). Expanding biocontrol options, refining integrated disease management packages, and adopting climate-smart forecasting tools will be critical (Horváth *et al*., 2015; Bradley *et al*., 2021; Mahlein, 2016). Breeding will remain central, with marker-assisted and genomic selection, and potentially genome editing, accelerating deployment of broad and durable resistance. Sustained investment, coordinated global collaboration, and effective technology transfer to farmers, particularly in emerging regions such as India, will ultimately determine the success of long-term, sustainable FLS management (Roth *et al*., 2020; Pham *et al*., 2015; Mishra *et al*., 2021).

Under climate change scenarios in India, frogeye leaf spot of soybean is expected to increase in severity and spatial distribution due to rising temperatures, prolonged leaf wetness, and higher relative humidity during the kharif season. Warm and humid conditions strongly favor infection, sporulation, and secondary spread of *C. sojina*, leading to earlier disease onset and more frequent epidemics (Dorrance *et al*., 2010; Wrather and Koenning, 2006). Future management will therefore require integration of durable quantitative resistance, climate-linked disease forecasting models, and greater reliance on biological control and PGPR-based strategies that enhance plant defense under combined biotic and abiotic stress conditions (Chakraborty *et al*., 2018; Singh *et al*., 2024).

CONCLUSION

Frogeye leaf spot, caused by *Cercospora sojina*, is a serious constraint to soybean production in warm, humid regions, including India, due to high yield losses, pathogen diversity, complex race structure, and widespread QoI fungicide resistance. Sustainable management relies on integrated strategies, with resistant cultivars as the cornerstone, supported by cultural practices and judicious fungicide use. While major advances have been made in identifying resistance genes, QTLs, and molecular markers, durable control requires pyramiding resistance loci and continuous pathogen monitoring. Genomic and biotechnological tools are accelerating breeding and improving disease understanding, yet challenges such as pathogen evolution, climate change, and regional knowledge gaps remain. Addressing these through coordinated research, standardized approaches, and effective technology transfer will be essential to ensure long-term protection of soybean yields.

ACKNOWLEDGEMENTS

We duly acknowledge ICAR and Director, ICAR-NSRI for the encouragement and the support.

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Received: December 17, 2025
Accepted: December 23, 2025