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Review Article

MOLECULAR MECHANISM FOR *SEPTORIA AVENAE* DISEASE RESISTANCE IN *AVENA SATIVA* L. (OAT)-A CRITICAL REVIEW

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ABSTRACT

Avena sativa L. (oat) is a cereal crop cultivated globally after wheat, rice, maize, and barley. In recent years, its cultivation has been affected by the *Septoria avenae* f. sp. *avenae,* commonly known as septoria leaf blotch disease. This article provides a comprehensive review of published data concerning the genomics underlying septoria leaf blotch disease resistance in oats. Weedy and wild species of *Avena* harbour precise genes that provide resistance to septoria leaf blotch, with discoveries made across 12 wild oat species. One potential breakthrough involves disrupting avenacinase activity that may halt the spread of septoria leaf blotch. Researchers are manipulating resistant wild oats species with cultivated oats species to harness these natural defenses. Notable efforts, including the transfer of resistance genes from weedy *Avena strigosa* and wild oat species (*Avena sterilis, Avena macrostachya,* and *Avena fatua*) into high-yielding oat varieties is also ongoing. There are some new sequencing techniques, including genomic selection (GS), quantitative trait loci (QTL) mapping, marker-assisted-selection (MAS), genome-wide association studies (GWAS), and CRISPR/Cas9 gene editing are helping to pinpoint and activate resistance genes. CRISPR/Cas9, in particular, allows precise modifications that can triggers plant's defence mechanisms. The path forward relies on integrating advanced genotyping, cutting edge sequencing and bioinformatics tools. Together, these innovations are paving the way for breeding oat cultivars that are not only high yielding but also resistant to *septoria* leaf blotch.

Keywords: Avena sativa, Septoria leaf blotch, Disease resistance genes, CRISPR/Cas9 gene editing, Genomic selection

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INTRODUCTION

Avena sativa L., commonly known as oat, is a member of the *Poaceae* family, which ranks sixth in global cereal production, following rice, wheat, sorghum, maize, and barley (Tomar and Singh, 2024). *A. sativa,* or the common oat, occupies around 10 million hectares of agricultural land worldwide (Singh *et al.,* 2025). It is primarily cultivated for its green fodder and grain production. Oats are rich in antioxidants (avenanthramides, α-tocopherol, and α-tocotrienol) and dietary fiber (Kaur and Goyal, 2017). It possesses high nutritional value, including high-quality protein, healthy fats, minerals, and have medicinal properties as well (Mao *et al*., 2022). Approximately 74% of livestock globally still depend on oat grain for feed (Chand *et al*., 2025). The highest production rate of oats is recorded in Russia i.e., 3.30 million tons, while in Canada is 2.64 million tons, Australia 9.60 thousand tons, the UK 8.30 thousand tons, the USA 8.28 thousand tons, while and Germany has the lowest production of 4.52 thousand tons in the year 2023. Further data is under consideration. Some of the key producers of oats and their production rates from 2004 to 2023 (Ritchie *et al*., 2023) are shown in Figure 1.

Notably, 20-40% of yield losses in agricultural products are due to pathogens, weeds, and animals (Kapoor and Singh, 2020). Microbial pathogens cause approximately 16% of global crop loss, with around 75% attributed to fungal pathogens (Lestari *et al*., 2023). Powdery mildew, smut, stem rust, crown rust, fusarium head blight, barley yellow dwarf virus (BYDV), and septoria leaf blotch are among the most critical diseases of oats and drastically reduce production (Shakeel *et al*., 2021). The fungus responsible for septoria disease in oats is *Septoria avenae* f. sp. *avenae* (Lashram, 2019), first described by Frank in Germany in 1895. This disease is also known by several common names, including septoria black stem, septoria leaf blotch, and speckled leaf blotch (Zeleneva *et al*., 2024). *S. avenae* also infects the other members of the genus Avena, including *A. byzantine*, *A. sterilis*, *A. fatua,* and *A. strigosa* (Sánchez-Martín *et al*., 2012; Gagkaeva *et al*., 2017).

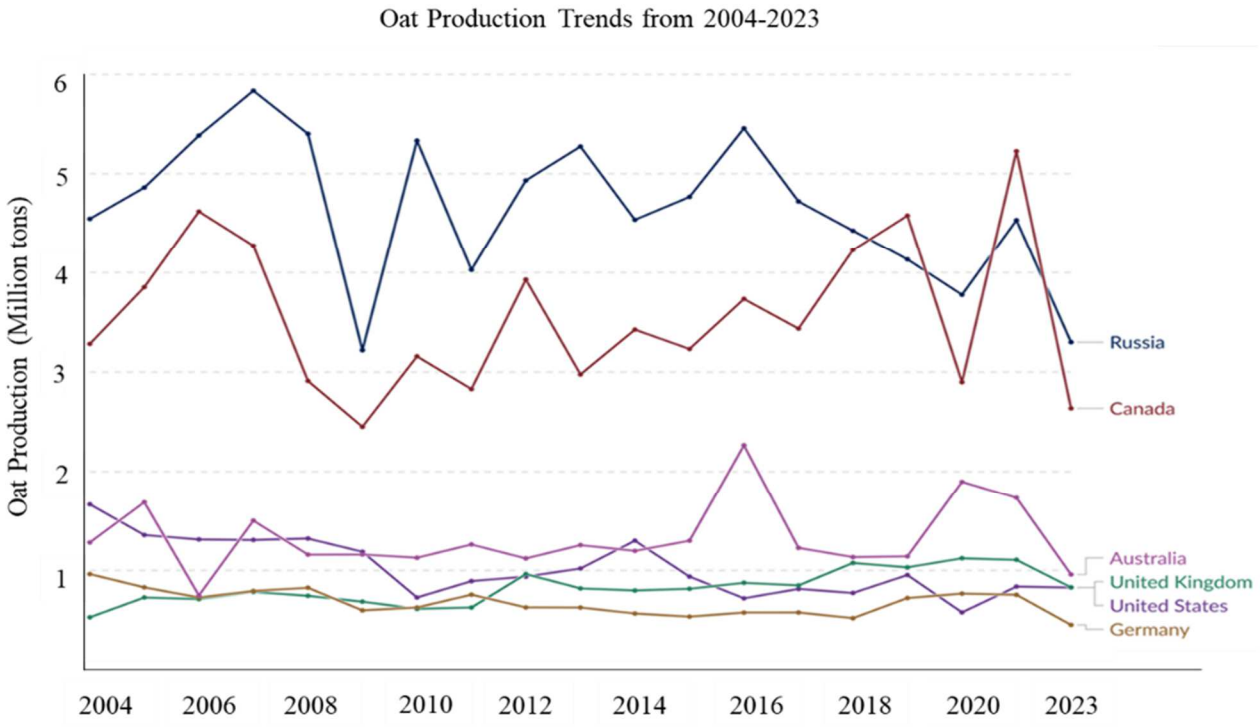

Fig. 1. Major oats producers in the world from 2004-2023

Decline in oat production-A growing concern: Globally, oat production has declined from about 26 million metric tons in 2003 to an estimated 23.16 million metric tons in 2018/2019 (USDA, 2025a; Kapoor and Singh, 2020). In Canada, research revealed that oat leaf pathogens were identified in 57% of oat crops, marking an increase from the previous year (29% in 2020). More than 15% loss in oats' yield was recorded across various states in Canada (Islam et al., 2022). Septoria leaf blotch reduces oat yields by up to 50% in Western Australia (Baxter *et al*., 2023; DPIRD, 2025). Abiotic factors such as soil condition, cold weather, low soil pH, and nutrient variation also contribute significantly to the decline in oat production (Wojtacki *et al*., 2025). Loss in yield of oats due to different diseases is demonstrated in Figure 2.

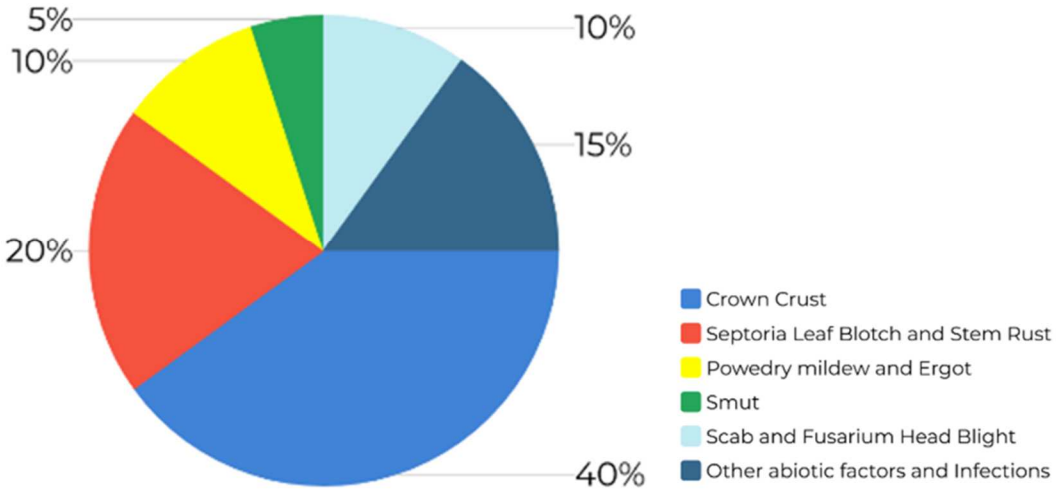

Fig. 2. The estimated oat yield losses due to Septoria leaf blotch (FAO, 2025) and crown rust infection (40%) (USDA, 2025b)

Life Cycle of *Septoria avenae*: The Septoria fungus first infects the lower leaves and then further spreads to the stem, ears, and upper leaves of oat. It produces chocolate brown to grey lesions on leaves (Vilvert et al., 2021).

Two types of spores (conidia and ascospores) are produced by the Septoria on oat leaves (McDonald, 2025). Pycnidia (asexual fruiting bodies) produce conidia of black colour on oat leaves during the summer season. In early spring and winter, ascospores are formed in perithecia (spore-bearing bodies) within the culm tissue and leaf sheath of oats (Mehta *et al*., 2014) (Figure 3). In the favourable condition, the lesions enlarge (chocolate brown or reddish brown), and the tissues of the leaf start to die (Shakeel et al., 2021). The spores of *S. avenae* are splashed by wind and rain onto other oat plants in the field (Madhushan *et al*., 2025). Animals and farm equipment also aid in spreading the spores to other plants or fields (Kayim *et al*., 2022). The life cycle of *S. avenae* is adapted from literature **(**https://ipm.illinois.edu/diseases/series100/rpd111/**).**

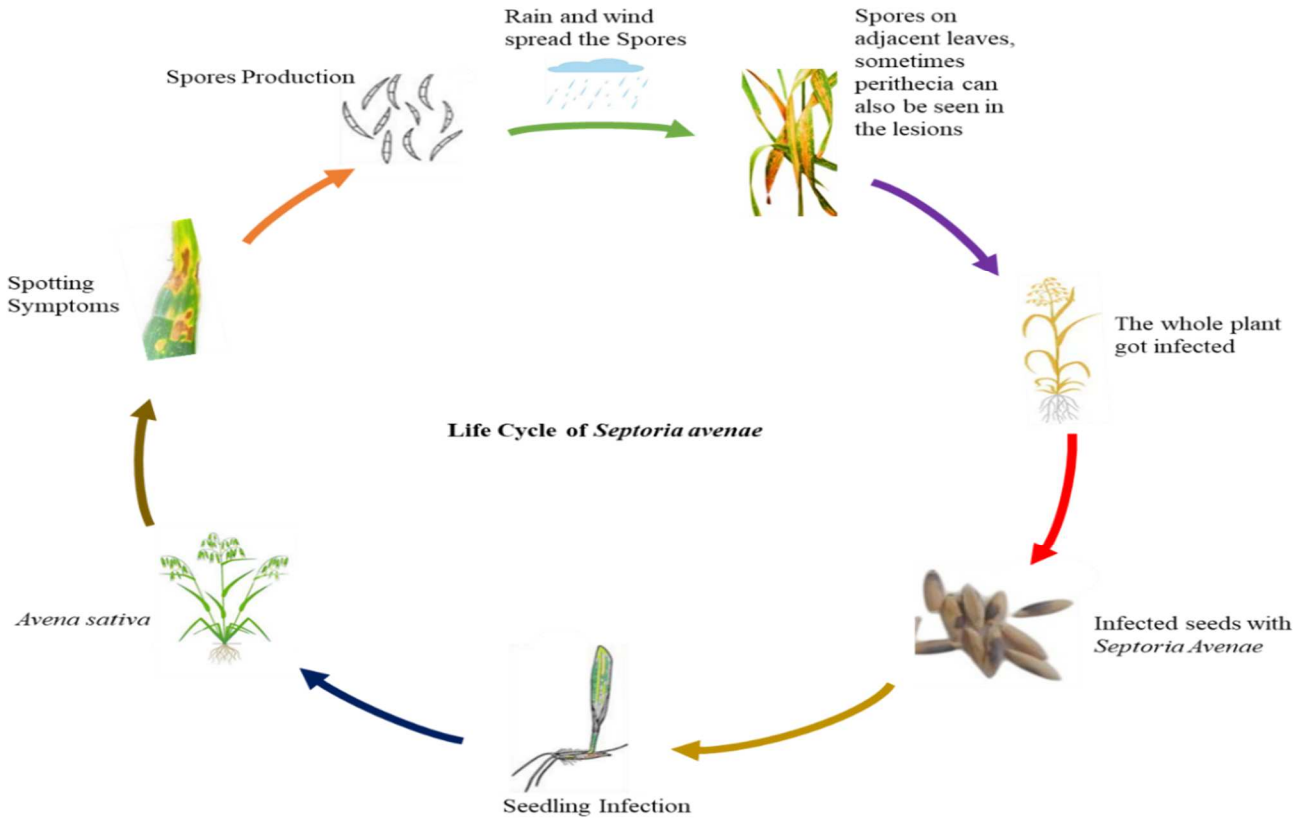

Fig. 3. Illustrates the *Septoria avenae* disease cycle in oat

Saponin-A naturally occurring antimicrobial glycoside in oat: Oat has the ability to accumulate antimicrobial triterpenoid saponins in its roots. Saponins are natural surfactants present in plant glycosides, including cultivated crops such as onions, soybeans, chilli, barley, spinach, oats, maize, quinoa, rice, tea trees, and some wild plant species (Zaynab *et al*., 2021; Hussain *et al*., 2019). Saponins act as antimicrobial agents by binding to and disrupting the integrity of cell membranes in pathogens. Within the cell membranes of these pathogens, saponins bind to sterols, compromising the integrity and functionality of the cells. Two types of saponin are found in oats: triterpenoid and steroidal (Kwon *et al*., 2024). Avenacins A_1, A_2, B_1, and B_2 are triterpenoid saponins described in the roots of oats (Hu and Sang, 2020). Steroidal saponins, avenacosides (A, B, C, and D), have been described in the aerial parts and grains of oats (Yang *et al*., 2016; Yokosuka *et al*., 2021; Woo *et al*., 2022). The oats' saponins, known as avenacins, have shown resistance against pathogens like take-all, which cause significant losses in wheat (Li *et al*., 2021). Research indicates that avenacins inhibit the infection of phytopathogens in plant hosts (Oliver, 2024).

***A. sativa* strategy against Avenacinase:** Avenacinase is an enzyme produced by specific pathogens that infect oats. It detoxifies the antimicrobial avenacin found in oats (Abdelrahman *et al*., 2020). Mutants lacking the genes responsible for producing avenacinase do not cause disease in oats. However, they retain the ability to remain pathogenic to other commercially important crops, such as barley and wheat (Derevnina *et al*., 2025). *A. longiglumis* (wild oat) does not produce the enzyme avenacin and is susceptible to *Gaeumannomyces graminis* var. *tritici*. Tomatine is another saponin compound that participates in resistance against *Botrytis cinerea* in the leaves of tomato (Li and Lue, 2025).

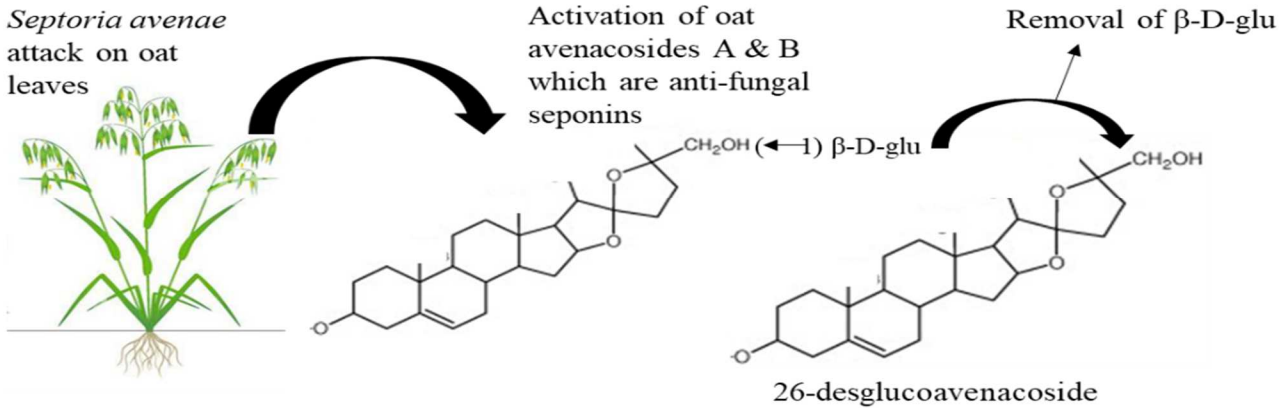

Fig. 4. Steroidal saponins enzyme avenacosides A & B activated when *S. avenae* attacks oat. Avenacosidase enzyme removes a glucose molecule (β-D-glu) and gives the enzyme 26-desglucoavenacosides A & B, which are antifungal (Inagaki *et al*., 2013; Abdelrahman *et al*., 2020).

Hybridization techniques to obtain resistance genes: Many significant disease-resistant genes, including BYDV, cereal cyst nematode, powdery mildew, stem rust, crown rust, and Septoria leaf blotch, have been identified in the oat gene pool in the above 31 wild oat species, out of which 12 showed significant resistance towards *A. sativa* (Loskutov and Rines, 2011). The wild oat *A. sterilis* exhibits multiple genes that confer resistance to various infections in oats. Notably, cultivars Victoria and Bond (cultivated *A. byzantina* K. Koch and *A. sativa*) contribute to the development of numerous disease-resistant cultivars. This has laid the groundwork for creating a variety of disease-resistant oat ecotypes suitable for diverse regions (Saini *et al*., 2019). Li *et al*. (2021) demonstrated that five genes (bAS1/Sad1, CYP51H10/Sad2, SCPL1/Sad7, MT1, and UGT74H5) are crucial for the biosynthesis of the avenacin compound in oats, and these genes are contiguous on a ~300 kb BAC contig (Mugford *et al*., 2013). Additionally, five other genes are genetically linked to this cluster, although the exact locations of these genes are unclear (Orme *et al*., 2019; Leveau *et al*., 2019). Li *et al*. (2021) showed that these genes found in the genome of *A. strigosa* (S75 genome) are located on scaffold AS02_289 (1.3 Mb) alongside three other characterised pathway genes (AAT1, UGT74H5, and CYP72A475/Sad6). These genes are present in the root tips of oats, which are the site of biosynthesis for the avenacin enzyme (Zhan *et al*., 2022).

Diploid wild oat species such as *A. damascena*-Ad, *A. canariensis*-Ac, *A. hirtula*-As, and *A. atlantica*-As contain variants of the A genome. Among the tetraploid wild species, resistance was evident in the perennial species of *A. macrostachya*. Medium level of susceptibility was demonstrated by *A. vaviloviana*-AB and *A. murphyi*-AC (Loskutov et al., 2021). Loskutov and Rines (2011) have reported 12 wild species of oat that showed resistance against Septoria leaf blotch (Table 1).

Table 1. Identification of 12 wild oat species that exhibited resistance against Septoria leaf blotch along their genome (Loskutov and Rines, 2011).

No.	Oat species	Genome
1	*A. damascena* Rajh. et Baum	Ad
2	*A. longiglumis* Durie.	Al
3	*A. canariensis* Baum	Ac
4	*A. wiestii* Steud.	As
5	*A. hirtula* Lagas.	As
7	*A. vaviloviana* (Malz.)Mord.	AB
8	*A. murphyi* Ladiz.	AC
9	*A. macrostachya* Balan.	CC
10	*A. fatua* L.	ACD
11	*A. ludoviciana* Durie.	ACD
12	*A. sterilis* L.	ACD

The genome of *A. sativa* contains 21 chromosome pairs (genome constitution of AACCDD), resulting from three distinct ancestral genomes (Loskutov *et al*., 2021). The first linkage map of oat was developed using 985-SNPs evaluated on 390 recombinant inbred lines (RILs), which were derived from six hexaploid oat biparental populations, along with SNP deletion analysis involving a set of monosomic stocks (Oliver *et al*., 2013). This linkage map demonstrated low error rates in scoring SNP markers and facilitated the joint mapping of markers assessed in parallel across multiple populations compared to the earlier map. Furthermore, advancements were achieved by incorporating high-density SNPs identified through genotype by sequencing (GBS) (Tinker *et al*., 2014).

Studies have focused on identifying resistant oat varieties and understanding the genetic diversity of pathogens. However, detailed mapping of Septoria isolates and a thorough investigation of oat genetic

responses are essential for developing effective management strategies (Brown, 2021). Saini *et al*. (2019) mentioned that specific genes providing resistance to Septoria leaf blotch in oats have not been broadly characterised or independently named, contrasting with some other disease resistance genes (*Pc* genes for crown rust). Numerous quantitative trait loci (QTLs) associated with Septoria leaf blotch resistance have been recognized (Zhou and Steffenson, 2013). Zhu *et al*. (2013) expressed two effective methods, RNA-seq and qPCR, for reviewing gene expression in response to pathogen infection. The molecular markers based on endosperm protein polymorphisms or DNA can identify the major genes responsible for conferring resistance to stem rust infection (Bakhshi *et al*., 2024).

Possible genomic approaches for detection of resistance genes: Genetic linkage maps have been developed using DNA markers from crossing populations of oats (Song *et al*., 2015). Canales *et al*. (2021) revealed that for marker-assisted breeding of oat varieties, DNA markers associated with trait loci are essential for identifying genes and QTLs. To identify the genes, DNA markers, and QTLs in oats that are linked to agronomically and nutritionally significant traits. Despite numerous scientists producing several linkage maps in oats with various mapping populations, only one consensus map (Chaffin *et al*., 2016) currently exists, illustrating the precise genetic locations of many disease-resistance genes.

Selecting desired traits, which are often challenging to assess phenotypically, and identifying various DNA markers streamlines plant breeding (Salgotra and Stewart, 2020). The Marker Assisted Selection (MAS) technique significantly aids plant selection based on these DNA markers. It can be applied to both qualitative and quantitative gene selection (Gao and Li, 2025). The MAS technique provides genetic gains superior to traditional phenotypic selection. The DNA marker system is not as advanced in oats compared to other crops such as rice, wheat, and maize. The restriction fragment length polymorphism (RFLP) (Ruwali *et al*., 2013), developed by Botstein *et al*. (1980), has been widely used to enhance mapping and relative linkage for detecting resistance genes for crown and stem rust in oats (Park *et al*., 2022). Yunus *et al*. (2025) comprehensively discussed the significant use of DNA molecular markers-assisted breeding techniques for studying agronomic traits and disease resistance in crops.

Researchers have created frequent linkage maps for oats using multiple mapping populations. Presently, only one consensus map exists that illustrates the genetic sites of some resistance genes in oat (Chaffin *et al*., 2016). A significant factor contributing to this gap is the absence of an oat genome sequence, which could provide insights into plant structure and the genomic relationships among different oat genomes (Fu and Yang, 2017). Deducing the complete oat sequence poses a challenge for scientists primarily due to the polyploid nature of oats. Reliable next-generation sequencing DNA markers, such as single-nucleotide polymorphisms (SNPs), commonly used in modern genomics, can assist in outlining the genome sequence of oats (Oliver *et al*., 2021).

Rapid marker-assisted breeding is the most effective practice, with advancements in new sequencing technologies for plant breeding aimed at disease resistance (Tiwari *et al*., 2023). It is beneficial to select the required individuals with the most important disease-resistance genes/QTLs. Nevertheless, minor genes/QTLs play a crucial role in disease resistance and contribute to producing more resilient oat varieties. As the genetic architecture of resistance evolves from single major R genes to a diverse range of minor genes, the best approach for molecular breeding will shift from marker-assisted selection to genomic selection (Sinha *et al*., 2025).

High-throughput genotyping (HTG) is a rapid and large-scale approach to genetic analysis that is essential for identifying genomic selection (GS), genome-wide association studies (GWAS), the next-generation mutagenesis technique, and the newly developed genome editing platform CRISPR/Cas9 within a short timeframe (Bakala *et al*., 2020). In this context, sequencing the oat genome would be highly beneficial (Kamal *et al*., 2022). It will aid in the fine mapping and cloning of disease resistance genes, which pose a challenge for DNA marker technology aimed at achieving disease resistance. GWAS has been used to identify disease-resistance genes in various crops, primarily in maize, rice, and wheat. Furthermore, it has been employed to identify QTLs/loci associated with disease resistance (Rahmanzadeh *et al*., 2022). GWAS application is limited in oat because of genetic diversity in germplasm and the hexaploid genomic nature of oat that ultimately causes complexity in mapping and detection of specific traits (Wang *et al*., 2023). Correlation between SNPs and phenotypic variations, GWAS can identify the specific traits associated with resistance to *S. avenae* (Ayana, 2023).

Disease resistance features can be acquired from unrelated organisms, wild species, germplasm collections, mutations, or somaclonal variations (Pathania *et al*., 2021). Genes present in wild species have shown resistance against a wide range of pathogens and are super genes (Kapoor and Singh, 2020). The distinctive properties conferred to pathogens in wild relatives persist even when other resistance sources are present. Further studies on these resistant features rely on the relationship between wild and cultivated oat species. Fine mapping, gene identification, and functional validation are required to clarify the genetic mechanisms of resistance in oats (Argenta, 2023). Incorporating these findings into

breeding programmes will enhance the development of oat varieties with improved resistance characteristics to Septoria leaf blotch disease, thereby boosting sustainability and crop productivity.

Table 2. **Summary of molecular tools/techniques for identifying resistance genes in oat against *S. avenae*.**

Molecular Tool/Tech	Application in Oat	Findings
RFLP Argenta (2023)	Mapping of early stage resistance loci	Identified genetic linkage between Septoria resistance and chromosome 7C in *Avena sativa*
MAB Wight *et al*. (2020)	Selection based on known markers linked to resistance	Enables early, efficient selection of resistant genotypes using linked markers.
GS Crossa *et al*. (2017)	Genome-wide breeding	Predicts disease resistance using genome-wide breeding data
RAPD Penner *et al*. (1993)	Screening based on markers linked with resistance	Discovered polymorphic bands in resistant vs. susceptible oat lines
SSR-based QTLs Montilla-Bascón *et al*. (2013)	QTLs mapping for Septoria resistance	QTLs on chromosome of 1D, 4C, and 6A in *Avena sativa*
SNP-based GWAS Chaffin *et al*. (2016)	High-resolution mapping across diverse germplasm	SNPs linked to resistance on 5A and 7D
RNA-Seq Sanchez-Martin *et al*. (2017)	Gene expression during infection	Up-regulation of PR-1, PR-10, and NLR genes
CRISPR-Cas9 Morica *et al*. (2024)	Gene Editing/function via targeted mutagenesis	Knockout of suspected resistance Pm3-like NLR genes

RFLP: restriction fragment length polymorphism, MAB: molecular assisted breeding, GS: genomic selection, RAPD: random amplified polymorphic DNA, SSR: simple sequence repeat, SNP: single nucleotide polymorphism, GWAS: genome wide association studies, CRISPR-Cas9: clustered regularly interspaced short palindromic repeats/CRISPR-associated protein 9

Conclusion: This review outlines knowledge about the genetic response of oats to the pathogen *S. avenae*. It is concluded that by integrating detailed mapping of Septoria isolates, which can create effective genetic strategies for managing Septoria disease in oats. The genes involved in the biosynthesis of the avenacinase and avenacosidase enzymes in oats may help halt the spread. Crossbreeding with wild oat species can also play a significant role in minimizing the spread of *S. avenae*. This comprehensive approach combines advanced molecular tools and techniques such as QTLs, GWAS, MAB, GS, and CRISPR/Cas9 with traditional breeding methods to develop resilient oat varieties, ultimately enhancing crop productivity and sustainability. These findings directly contribute to the development of resistant oat varieties, ensuring sustainable oat production, but the hexaploid nature and absence of complete mapping of oat are the main key challenges that should be addressed.

Authors' Contributions: This work was carried out through the collective efforts of all authors involved. Authors AH developed the study's conceptual framework, conducted the necessary literature search, and wrote the initial draft of the manuscript. ZM and MNA edit this manuscript. The work was done under the supervision of UFA. All authors reviewed and approved the final manuscript.

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Conflict of Interests: The authors declare that there are no conflicts of interest related to this article.

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