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Michigan State University, East Lansing, USA*e-mail: dukenbay@msu.edu**CURRENT STATE OF RESEARCH ON COMMON BEAN ANTHRACNOSE (*PHASEOLUS VULGARIS* L.): ETIOLOGY, GENETICS OF RESISTANCE, AND MANAGEMENT STRATEGIES**

Common bean (*Phaseolus vulgaris* L.) is one of the most important grain legume crops worldwide and a key source of plant protein. However, the stability of its production is significantly constrained by anthracnose, one of the most destructive and economically important diseases of common bean, widely distributed in regions with temperate and humid climates. The causal agent of the disease is the phytopathogenic fungus *Colletotrichum lindemuthianum*, which is characterized by high genetic and pathogenic variability as well as pronounced race differentiation. These features substantially complicate the breeding of resistant cultivars and effective disease control.

This review summarizes recent studies on the etiology of common bean anthracnose, the biology and life cycle of the pathogen, race diversity, and the genetic mechanisms underlying anthracnose resistance in *Phaseolus vulgaris*. The role of infected seeds as the primary source of infection and a major factor in transboundary disease spread is analyzed. Current approaches to the classification of *C. lindemuthianum* races are discussed, and the importance of continuous monitoring of the pathogen population structure is highlighted.

Special attention is given to the genetics of anthracnose resistance in common bean, including race-specific Co genes and quantitative trait loci (QTL) identified using genome-wide association study approaches. Prospects for gene pyramiding based on GWAS data and the application of genomic selection to achieve durable resistance are discussed. The situation in the United States, particularly in the state of Michigan, is used as an example to demonstrate the practical importance of monitoring the race composition of the pathogen. The review concludes that integrated anthracnose management strategies combining genetic resistance, agronomic practices, and phytosanitary control are essential for sustainable common bean production.

Keywords: *Phaseolus vulgaris*, anthracnose, *Colletotrichum lindemuthianum*, resistance, Co genes, QTL, race diversity, integrated plant protection.

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Ист-Лансинг, Мичиган штаты, АҚШ*e-mail: dukenbay@msu.edu**Кәдімгі үрме бұршақтың (*Phaseolus vulgaris* L.) антракнозын зерттеудің қазіргі жағдайы: этиологиясы, төзімділік генетикасы және басқару стратегиялары**

Кәдімгі асбұршақ (*Phaseolus vulgaris* L.) әлемдегі ең маңызды бұршақ тұқымдас дақылдардың бірі болып табылады және өсімдік тектес ақуыздың негізгі көздерінің қатарына жатады. Алайда оның тұрақты өндірісі қоңыр дақ ауруымен (антракнозбен) айтарлықтай шектеледі. Антракноз қоңыржай және ылғалды климат жағдайында кең таралған, экономикалық тұрғыдан аса зиянды аурулардың бірі болып саналады. Аурудың қоздырғышы фитопатогенді саңырауқұлақ *Colletotrichum lindemuthianum* болып табылады, ол жоғары генетикалық және патогендік өзгергіштігімен, сондай-ақ айқын нәсілдік дифференциациясымен ерекшеленеді, бұл төзімді сорттарды селекциялауды және ауруды бақылауды күрделендіреді.

Мақалада асбұршақ антракнозының этиологиясына, қоздырғыштың биологиясы мен тіршілік цикліне, патогеннің нәсілдік әртүрлілігіне, сондай-ақ *Phaseolus vulgaris* өсімдігінің антракнозға төзімділігінің генетикалық механизмдеріне арналған заманауи зерттеулерге шолу жасалған. Инфекцияланған тұқымдардың бастапқы инфекция көзі және аурудың трансшекаралық таралу факторы ретіндегі рөл талданған. *C. lindemuthianum* нәсілдерін жіктеудің заманауи тәсілдері

қарастырылып, патоген популяциясының құрылымын тұрақты мониторингтеудің маңыздылығы көрсетілген.

Антракнозға төзімділіктің генетикасына, соның ішінде нәсілге-арнайы Со-гендерге және genome-wide association study әдістері арқылы анықталған сандық төзімділік локустарына (QTL) ерекше назар аударылған. GWAS деректеріне негізделген гендерді пирамидациялау және геномдық селекцияны қолдану арқылы ұзақ мерзімді төзімділікті қалыптастыру перспективалары талқыланған. АҚШ пен Мичиган штаты мысалында қоздырғыштың нәсілдік құрамын мониторингтеудің практикалық маңыздылығы көрсетілген. Антракнозды басқарудың генетикалық төзімділікті, агротехникалық шараларды және фитосанитарлық бақылауды біріктіретін интеграцияланған стратегияларын қолдану қажеттілігі туралы қорытынды жасалған.

Түйін сөздер: *Phaseolus vulgaris*, антракноз, *Colletotrichum lindemuthianum*, төзімділік, Со-гендер, QTL, нәсілдік әртүрлілік, өсімдіктерді интеграцияланған қорғау.

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Современное состояние исследований антракноза фасоли обыкновенной (*Phaseolus vulgaris* L.): этиология, генетика устойчивости и стратегии управления

Фасоль обыкновенная (*Phaseolus vulgaris* L.) является одной из важнейших зернобобовых культур мира и ключевым источником растительного белка. Однако стабильность ее производства существенно ограничивается антракнозом, одной из наиболее вредоносных и экономически значимых болезней фасоли, широко распространенной в регионах с умеренным и влажным климатом. Возбудителем заболевания является фитопатогенный грибок *Colletotrichum lindemuthianum*, характеризующийся высокой генетической и патогенной изменчивостью, а также выраженной расовой дифференциацией, что существенно осложняет селекцию устойчивых сортов и контроль заболевания.

В статье представлен обзор современных исследований, посвященных этиологии антракноза фасоли, биологии и жизненному циклу возбудителя, расовому разнообразию патогена, а также генетическим механизмам устойчивости *Phaseolus vulgaris*. Проанализированы данные о роли инфицированных семян как основного источника первичной инфекции и фактора трансграничного распространения заболевания. Рассмотрены современные подходы к классификации рас *C. lindemuthianum* и показано значение постоянного мониторинга популяционной структуры патогена.

Особое внимание уделено генетике устойчивости фасоли к антракнозу, включая расоспецифические Со-гены и количественные локусы устойчивости (QTL), выявленные с использованием методов genome-wide association study. Обсуждаются перспективы пирамидирования генов, основанное на GWAS и применения геномной селекции для формирования долговременной устойчивости. На примере ситуации в США и штате Мичиган продемонстрирована практическая значимость мониторинга расового состава возбудителя. Сделан вывод о необходимости интегрированных стратегий управления антракнозом, сочетающих генетическую устойчивость, агротехнические меры и фитосанитарный контроль.

Ключевые слова: *Phaseolus vulgaris*, антракноз, *Colletotrichum lindemuthianum*, устойчивость, Со-гены, QTL, расовое разнообразие, интегрированная защита растений.

Abbreviations and Notations

GWAS – genome-wide association study;
QTL – quantitative trait loci; MSU – Michigan State University; FAO – Food and Agriculture Organization

Introduction

Common bean (*Phaseolus vulgaris* L.) occupies a leading position among leguminous crops due

to its high nutritional value and ability to adapt to various agroclimatic conditions. The protein content of bean seeds averages 22–23%, making them an important component of the diet of more than 100 countries worldwide (FAO, 2019). According to the FAO, beans play a key role in ensuring food security and are one of the main sources of plant protein, especially for the populations of developing countries.

Despite their high economic value, the stability of bean production is significantly limited by diseases, including those transmitted by seeds. Among

them, anthracnose has remained one of the most economically significant and harmful diseases of common beans for decades (Pastor-Corrales & Tu, 1989). The disease is widespread in regions with temperate and humid climates and is characterised by a high degree of susceptibility, especially when infected seed material is used (Halvorson et al., 2021).

The causative agent of bean anthracnose is the fungus *Colletotrichum lindemuthianum*, which can infect all above-ground parts of the plant and, under favourable conditions, cause significant, even total, crop losses (Padder & Sharma, 2017). A significant difficulty in controlling the disease is the high genetic and pathogenic variability of the pathogen, which causes rapid overcoming of variety resistance (Balardin & Kelly, 1997). The particular danger of anthracnose is determined by the pronounced racial differentiation of the pathogen, which requires constant updating of the assortment and strategies for plant protection (Kelly & Vallejo, 2004).

In the context of globalisation and active international seed trade, there is an increased risk of introducing new *Colletotrichum lindemuthianum* races, which reinforces the need for systematic monitoring of the pathogen and improvement of disease management methods (Halvorson et al., 2021). In this regard, a comprehensive analysis of current research on the aetiology of bean anthracnose, crop resistance genetics, and integrated control methods is relevant and in demand for both fundamental research and applied tasks in phytopathology and breeding. Additional field observations indicate that local foci can act as sources of further infection spread through inoculum dispersal and the movement of seed material, as demonstrated for white beans in Ontario, underscoring the importance of early detection of such foci (Tu, 1981).

Materials and methods

This work was carried out in the form of a review study. The literature analysis was conducted using the international scientific databases Web of Science, Scopus, PubMed, APS Journals, as well as specialised resources from FAO and MSU Extension (FAO, 2019; Halvorson et al., 2021). The review includes original and review articles published mainly between 2000 and 2024, devoted to the biology of *Colletotrichum lindemuthianum*, the

racial diversity of the pathogen, the genetic basis of bean resistance, and strategies for managing anthracnose (Kelly & Vallejo, 2004; Padder & Sharma, 2017). When selecting sources, priority was given to publications in peer-reviewed journals reflecting modern approaches to molecular genetics, genomics, and phenotyping, including studies using genome-wide association studies and mapping of quantitative resistance locus (Zuiderveen et al., 2016; Nunes et al., 2021). In addition, classic fundamental works that are key to understanding the bean–anthracnose pathosystem were used (Pastor-Corrales & Tu, 1989; Balardin & Kelly, 1997). For the comparison of genomic data and the interpretation of resistance loci, information on the common bean reference genome and evidence of its dual domestication were taken into account, as these are widely used as a basis for candidate gene annotation (Schmutz et al., 2014).

Results and discussion

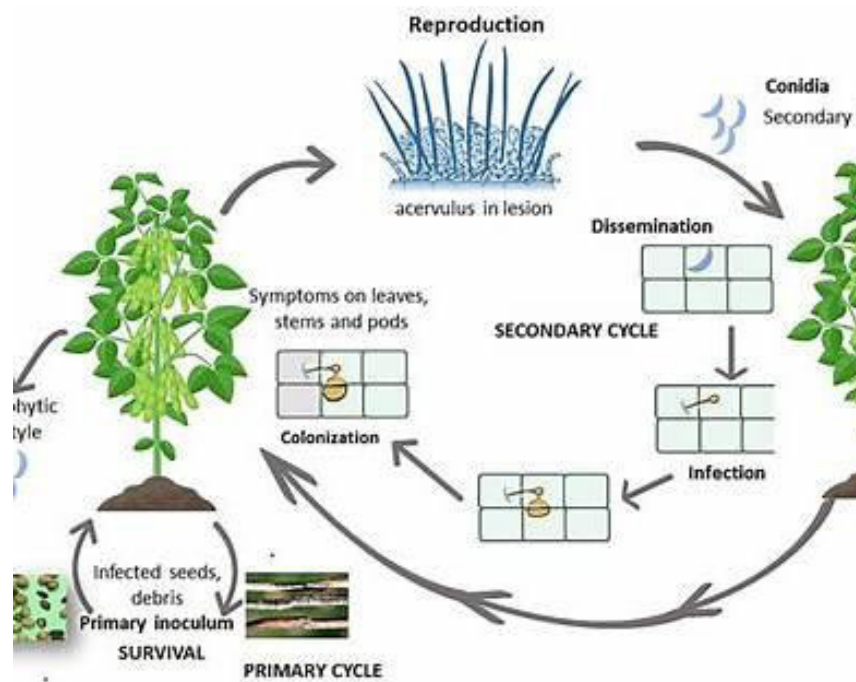
1. Etiology and life cycle of the pathogen

Colletotrichum lindemuthianum belongs to the hemibiotrophic phytopathogenic fungi and is characterised by a complex life cycle that includes biotrophic and necrotrophic phases (O’Connell et al., 2012). In the early stages of infection, the pathogen develops latently, which significantly complicates early diagnosis of the disease (Padder & Sharma, 2017). Subsequently, active destruction of plant tissues occurs, with the formation of characteristic necrotic lesions on leaves, stems, and beans (Pastor-Corrales & Tu, 1989). Genomic studies of pathogen isolates complement our understanding of mechanisms of pathogenicity and variability, including differences in gene repertoires associated with the infection process (de Queiroz et al., 2017).

The main source of primary infection is infected seeds, which makes anthracnose a particularly dangerous disease in seed production (Halvorson et al., 2021). The secondary cycle of infection is ensured by the mass formation of conidia, which are spread by rain splashes and mechanical contact between plants (Pastor-Corrales & Tu, 1989; Padder & Sharma, 2017). The polycyclic nature of the disease contributes to the rapid development of epiphytotics under favourable weather conditions (Balardin & Kelly, 1997).

Figure 1

Life cycle of anthracnose on common bean (*Phaseolus vulgaris* L.) caused by *Colletotrichum lindemuthianum*



Note: Adapted from Padder & Sharma (2017), based on Pastor-Corrales & Tu (1989)

In the figure, the disease cycle of common bean anthracnose caused by *Colletotrichum lindemuthianum* is shown, including primary infection originating from infected seeds and plant debris (primary inoculum), followed by infection, colonization, and symptom development on leaves, stems, and pods, as well as the secondary cycle involving acervulus formation in lesions, conidia production, dissemination, and repeated infections during the growing season.

Table 1
Pathogen and epidemiology of anthracnose of *Phaseolus vulgaris* L.

Parameter	Description
Pathogen	<i>Colletotrichum lindemuthianum</i>
Host	<i>Phaseolus vulgaris</i> L.
Source of infection	Infected seeds, plant debris
Ways of spreading	Rain splash, contact, seed
Type of epidemiology	Polycyclic

Table 1 presents basic information about the pathogen and epidemiological characteristics of bean anthracnose. The causative agent of the disease is the fungus *Colletotrichum lindemuthianum*, a specialised phytopathogen that mainly affects common beans (*Phaseolus vulgaris* L.), which determines its high degree of adaptation to this host (Pastor-Corrales & Tu, 1989; Padder & Sharma, 2017). The main source of infection is infected seeds, which play a key role in the initial infection of crops and contribute to the spread of the pathogen over long distances (Halvorson et al., 2021). An additional reservoir of infection is plant debris, in which the pathogen can persist during the inter-growing season (Balardin & Kelly, 1997).

The pathogen spreads during the growing season mainly through rain splashes and direct contact between plants, which is especially common in dense crops and high humidity conditions (Pastor-Corrales & Tu, 1989; Padder & Sharma, 2017). The seed route of transmission ensures long-term preservation and transboundary spread of the pathogen (Halvorson et al., 2021). The epidemiology of bean anthracnose is polycyclic, which means that mul-

multiple cycles of infection are possible during a single growing season. This leads to a rapid increase in infection under favourable weather conditions and explains the high pathogenicity of the disease (Balardin & Kelly, 1997).

2. Racial diversity and pathogenic variability of *Colletotrichum lindemuthianum*

One of the key problems in controlling bean anthracnose is the high racial and pathogenic variability of *Colletotrichum lindemuthianum* (Balardin & Kelly, 1997; Padder & Sharma, 2017). An international binary system based on the reaction of 12 differential bean lines of Andean and Mesoamerican origin is used to identify and classify pathogen races (Kelly & Vallejo, 2004). This system allows for the standardisation of race descriptions and the comparison of research results obtained in different regions of the world. The reactions of differential lines and the inheritance patterns of resistance in these lines have been characterized in detail, thereby improving the reproducibility of race diagnostics across different laboratories (Young & Kelly, 1996).

To date, approximately 298–300 races of *C. lindemuthianum* have been described worldwide, with their distribution varying significantly depending on the geographical region (Padder & Sharma, 2017; Sansala et al., 2024). The greatest racial diversity has been recorded in the countries of origin of beans, primarily in Brazil and Mexico, where the crop has been cultivated for a long historical period (Balardin & Kelly, 1997; Kelly & Vallejo, 2004). Reports on the emergence of new races and their interactions with germplasm, including cases documented in

Michigan, confirm the dynamic nature of pathogen populations and the risk of unexpected loss of resistance (Kelly et al., 1994).

The high racial diversity of the pathogen causes rapid loss of effectiveness of resistant varieties and significantly complicates the selection of beans for resistance (González et al., 2015). This necessitates constant monitoring of the population structure of *C. lindemuthianum*, especially in regions of intensive cultivation and active seed exchange (Halvorson et al., 2021). Regional reports on the detection of individual races, including those identified in Manitoba, demonstrate that phytosanitary surveillance must be sensitive to introductions in relatively new territories (del Río et al., 2003).

3. Genetics of bean resistance to anthracnose

The genetic resistance of common beans to anthracnose is traditionally associated with Co genes located on different chromosomes and providing race-specific resistance of the “gene-on-gene” type (Kelly & Vallejo, 2004; González et al., 2015). Such resistance can be highly effective against individual races of the pathogen, but in most cases it proves to be short-lived due to the emergence of new pathotypes of *C. lindemuthianum* capable of overcoming the action of individual Co-genes (Balardin & Kelly, 1997). Allelic series within the Co-1 locus and their race specificity have been described for the Andean gene pool, which is important for the accurate selection of resistance donors (Melotto & Kelly, 2000). For Co-1, linked markers have also been proposed, facilitating the identification of resistance sources in breeding material (Mendoza et al., 2001).

Table 2

Conceptual map of resistance genetics

Component	What it means in the context of anthracnose	Practical conclusion
Vertical (race-specific) resistance	Effective against certain races, may «break down» when the population changes	Requires donor renewal and pyramiding
Horizontal (partial, quantitative) resistance	Reduces disease severity, usually more stable	Good basis for longevity, but rarely results in «zero» disease
Pyramiding	Combination of several resistance genes	Increases variety longevity, reduces risk of breakthrough
Epistasis and interactions	Genes can enhance or weaken each other's effects	Field and greenhouse testing of combinations is required
QTL/polygenic basis	Resistance is distributed across several loci	Suitable for genomic selection and resistance indices
GxE (genotype × environment)	Resistance effect varies depending on conditions	Multi-environment trials are needed

In this table are presented the main genetic components of resistance to anthracnose and the practical breeding conclusions that follow from each of them. The table contrasts vertical (race-specific) resistance, which can be highly effective but is vulnerable to breakdown when pathogen races shift, with horizontal (quantitative) resistance, which typically reduces disease severity more gradually yet tends to be more stable over time. It also highlights gene pyramiding as a strategy to combine multiple resistance genes to extend cultivar durability and lower the risk of resistance being overcome.

In addition, the table emphasizes that resistance outcomes are not always additive because of epistasis and gene interactions, meaning certain gene combinations may strengthen or weaken the overall response, so testing in both greenhouse and field conditions is essential. Finally, it summarizes how a QTL/polygenic basis supports the use of genomic selection and resistance indices, while genotype \times environment (G \times E) effects underline the need for multi-environment trials to confirm that resistance performance remains reliable under different climatic and production conditions.

Recent studies have shown that bean resistance to anthracnose has a complex genetic architecture and is determined not only by major genes but also by quantitative loci (QTL) (Zuiderveen et al., 2016). The use of genome-wide association study methods has made it possible to identify additional genome regions associated with anthracnose resistance and confirm the polygenic nature of this trait (Nunes et al., 2021). Clusters of resistance genes, including the B4 cluster, have been characterized with respect to allelic relationships and marker systems, supporting pyramiding strategies (Méndez-Vigo et al., 2005). The Co-4 locus has been localized on chromosome 3 and contains candidate resistance genes, while fine mapping has refined the boundaries of this region for further breeding applications (Melotto et al., 2004; Melotto & Kelly, 2001). Genetic dissection of resistance using sets of differential cultivars has shown that different combinations of loci confer resistance to multiple races, including analyses of the MDRK and TU lines (Campa et al., 2009). Additional reviews point to the presence of cluster-mediated resistance and emphasize the importance of considering their combined effects when selecting locus combinations (Campa et al., 2017).

The combination of race-specific Co-genes and quantitative resistance loci opens up prospects for genomic selection and gene pyramiding aimed at developing more long-term and sustainable protec-

tion of beans against anthracnose (Zuiderveen et al., 2016; González et al., 2015).

4. Situation in the United States and Michigan

In the USA, bean anthracnose is mainly localized, but under favorable weather conditions, especially when moderate temperatures are combined with high humidity, the disease can cause serious epiphytotic and lead to significant economic losses (Pastor-Corrales & Tu, 1989; Padder & Sharma, 2017). Outbreaks associated with the use of infected seed material, which is the main source of primary infection and contributes to the spread of the pathogen between regions, pose a particular danger (Halvorson et al., 2021).

A telling example is the situation in Michigan, one of the key dry bean producing regions in the United States. In 2017, race 109 *Colletotrichum lindemuthianum* was identified here, capable of overcoming the resistance of a number of commercial bean varieties previously considered resistant to anthracnose (Halvorson et al., 2021; Whyte, 2023). The discovery of this pathotype led to a review of recommendations on variety composition, strengthened phytosanitary monitoring measures, and an emphasis on the use of certified seed material.

This case clearly demonstrates that even in regions with relatively low historical significance of anthracnose, there is a risk of new pathogen races emerging that could significantly affect the resistance of cultivated varieties. This highlights the need for regular monitoring of the racial composition of *C. lindemuthianum* and the prompt updating of breeding and phytosanitary strategies (Balardin & Kelly, 1997; Kelly & Vallejo, 2004).

5. Integrated strategies for managing bean anthracnose

Modern strategies for managing bean anthracnose are based on the principles of integrated plant protection and involve a combination of several complementary approaches aimed at reducing the infection background and limiting the development of the pathogen (Pastor-Corrales & Tu, 1989; Padder & Sharma, 2017). Key elements of such strategies include the use of healthy and certified seed material, the selection and introduction of resistant varieties, and agronomic practices aimed at reducing leaf moisture and conditions conducive to disease development.

If necessary, fungicides are used rationally, taking into account the epidemiological situation and the risk of pathogen resistance, especially in con-

ditions of intensive cultivation (Halvorson et al., 2021; Padder & Sharma, 2017). However, chemical protection is considered primarily as an auxiliary tool, the effectiveness of which increases significantly when combined with genetic resistance of plants. The effectiveness of seed treatment and the proper timing of foliar applications has been demonstrated in field studies and is considered a practical component of an integrated protection strategy (Gillard et al., 2012).

Of particular importance in the long term is the pyramiding of resistance genes and the use of genetically diverse source material, which reduces the likelihood of rapid resistance breakthrough by new races of *C. lindemuthianum* (Kelly & Vallejo, 2004; González et al., 2015; Zuiderveen et al., 2016). Combining genetic resistance with constant monitoring of the racial composition of the pathogen allows for timely adjustments to recommendations on variety composition and prevents the development of epiphytotics, ensuring the long-term sustainability of the bean protection system against anthracnose (Balardin & Kelly, 1997; Halvorson et al., 2021). The transition from classical breeding to marker-assisted selection and the pyramiding of resistance traits has been extensively discussed for common bean as a model crop (Miklas et al., 2006). Practical guidelines for disease identification and management are regularly updated in regional manuals and bulletins (MSU Extension, n.d.; APS, n.d.). Fundamental information on anthracnose diagnosis and control within seed production and crop management systems has been summarized in specialized common bean disease compendia (Schwartz et al., 2005).

Conclusion

Anthracnose of beans remains one of the key threats to global *Phaseolus vulgaris* production due to the high racial variability of *Colletotrichum lin-*

demuthianum and the seed-borne route of infection (Balardin & Kelly, 1997; Halvorson et al., 2021; Padder & Sharma, 2017). Modern genetic and genomic studies have significantly expanded our understanding of the mechanisms of bean resistance to anthracnose, including the role of race-specific Co-genes and quantitative resistance loci (Kelly & Vallejo, 2004; Zuiderveen et al., 2016; Nunes et al., 2021). At the same time, the pronounced race specificity of Co-genes and the high adaptability of the pathogen necessitate a transition to more complex breeding strategies based on gene pyramiding and the use of polygenic resistance (González et al., 2015; Zuiderveen et al., 2016).

The experience of the United States, particularly the state of Michigan, where new virulent races of *C. lindemuthianum* capable of overcoming the resistance of commercial bean varieties have been reported, highlights the importance of continuous monitoring of the pathogen and the application of integrated disease management measures (Halvorson et al., 2021; Whyte, 2023). This review justifies the need for further research aimed at creating bean varieties with long-term resistance to anthracnose, as well as the development of monitoring systems and integrated plant protection in the context of the changing population structure of the pathogen (Kelly & Vallejo, 2004; Padder & Sharma, 2017).

Thus, bean resistance to anthracnose should be considered as a dynamic property of the agroecosystem, formed by the interaction of genetic, phytosanitary and agrotechnological factors, which determines the priority of integrated and prognostically oriented approaches in plant breeding and protection. Effective long-term control of anthracnose is only possible through the close integration of breeding programmes, genomic methods, phytosanitary monitoring and production practices, which will make it possible to stay ahead of evolutionary changes in the pathogen rather than reacting to them after the fact.

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