

Systematic Review

A Systematic Review of Bruchid Resistance in Common Bean: Genetic Mechanisms and Breeding Implications for Africa

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Abstract

Background: Bruchids (*Acanthoscelides obtectus* and *Zabrotes subfasciatus*) are responsible for severe post-harvest losses in common bean (*Phaseolus vulgaris* L.). Understanding the genetic mechanisms and molecular markers of resistance is critical for breeding durable cultivars, especially in Africa. **Methods:** This systematic review followed PRISMA guidelines. The protocol was registered on OSF before implementation. Ten databases and repositories were searched for peer-reviewed and gray literature evaluating cultivars, landraces, wild derivatives, or interspecific lines. Eligible studies reported genetic mechanisms, molecular markers, or breeding strategies for bruchid resistance. **Results:** Twenty-nine studies met inclusion criteria. Most identified resistance at the APA locus on chromosome Pv04, involving arcelins, phytohemagglutinin, and α -amylase inhibitors, which confer strong antibiosis. Additional loci on Pv03 and Pv07, together with seed-coat traits, contributed complementary non-APA resistance. Validated protein markers and SNPs linked to these loci were reported. Breeding approaches included backcrossing and interspecific introgression. **Conclusions:** Marker-assisted selection offers opportunities to pyramid multiple resistance genes into farmer-preferred germplasm. However, progress is constrained by limited germplasm diversity, inconsistent bioassays, and poor characterization of non-APA mechanisms. Greater emphasis on diverse African germplasm and standardized assays is needed to accelerate the breeding of resistant cultivars.

Keywords: *Phaseolus vulgaris*; *Acanthoscelides obtectus*; *Zabrotes subfasciatus*; APA locus; arcelin; antibiosis; seed coat traits; genome-wide association study (GWAS)



Academic Editor: Bin Liu

Received: 29 November 2025

Revised: 1 January 2026

Accepted: 18 January 2026

Published: 24 February 2026

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1. Introduction

The common bean (*Phaseolus vulgaris* L.) is a staple legume of major nutritional and economic importance throughout the developing world. It provides protein, energy, fiber, and important micronutrients—particularly iron and zinc—and is particularly central to smallholder diets in sub-Saharan Africa where per capita intake is one of the highest in the world [1,2]. With million-scale production and wide cultivation, the crop supports

household food security, income generation, and sustainable cropping systems through short growth cycles and biological nitrogen fixation [3,4]. These attributes make the improvement of bean productivity and post-harvest security a high priority for agriculture and nutrition programs throughout Africa.

A major constraint to bean value chains is post-harvest loss due to bruchid beetles, predominantly the bean bruchid *Acanthoscelides obtectus* (Say) and the Mexican bean weevil *Zabrotes subfasciatus* (Boheman) which cause seed damage in field and storage, resulting in loss of weight, market value, and viability of seed [5]. Reported dry weight losses under typical conditions range widely (10–39%), and reach catastrophic levels (49–70%) in cases of on-farm poor store management, immediately affecting household food availability, with distress sales being soon after harvest [6]. The two bruchids show some ecological differentiation, *Z. subfasciatus* is more common in warm, low-altitude tropical storage environments, and *A. obtectus* is more common in cooler, higher-altitude areas and can cause damage early in the field, making management approaches site-specific [7]. Current control measures—chemical disinfestation, botanical or ash treatments, vegetable oils, hermetic storage—have both strengths and significant limitations for African smallholders: the cost and availability of pesticides; environmental and health risks; labor intensity of traditional control methods; and the affordability of hermetic solutions [8–11].

These realities highlight the need for sustainable and farmer-friendly interventions. Host plant resistance (HPR) can provide a durable, low-cost, and environmentally benign approach to minimize bruchid damage. Resistance sources have been identified mostly in wild *Phaseolus* germplasm and related species (e.g., *P. acutifolius*), and many resistant phenotypes are linked to seed storage proteins encoded at the *arcelin-phytohemagglutinin-alpha amylase* (APA) locus on chromosome *Pv04* [5,12,13]. Arcelins—lectin-like seed proteins that are unique to some wild accessions—interfere with digestion and physiology in insects, along with phytohemagglutinins and alpha amylase inhibitors that further inhibit the growth and survival of insects [14,15]. Arcelin introgression has generated lines that show good resistance to *Z. subfasciatus* (e.g., RAZ lines), while resistance to *A. obtectus* is variable [16]. Importantly, some resistance factors have antinutritional implications for human consumption, that is, breeding needs to balance resistance in insects with food safety and acceptability [17].

Mechanistically, the APA locus on chromosome *Pv04* functions as a central biochemical defense hub in common bean. It encodes seed storage and defense proteins such as arcelins, phytohemagglutinins, and α -amylase inhibitors that act through antibiosis, impairing larval growth and survival after egg hatch. Arcelins, lectin-like proteins found in wild *Phaseolus* accessions and introgression lines, associate with reduced larval establishment, delayed development, and sharply lowered adult emergence [18,19]. In parallel, PHA and α AI disrupt gut physiology and digestive enzyme activity, limiting nutrient assimilation and weakening larval performance [20,21]. These proteins often operate additively or synergistically, which explains the strong resistance observed in arcelin-containing lines [22,23]. Resistance expression varies by bruchid species and genetic background. Strong effects against *Zabrotes subfasciatus* are frequently reported, while responses against *Acanthoscelides obtectus* are more variable [24,25]. This variability highlights the need to consider species-specific efficacy and to complement APA-mediated resistance with additional loci and seed-trait defenses for durable, broad-spectrum protection [26,27].

Beyond APA-encoded seed proteins, multiple non-APA resistance mechanisms have been documented in common bean and other legumes. This highlights that bruchid resistance is genetically and mechanistically diverse. Physical seed traits such as seed-coat thickness, hardness, seed size, and color influence oviposition preference, larval penetration, and survival, and have been associated with partial resistance in common bean and related

pulses [16,24,25]. Reduced starch content and altered seed polysaccharides can also impair larval development, pointing to carbohydrate-based defenses that act independently of APA proteins [12,13,15]. In African and Latin American landraces, resistance often occurs independently of classical APA profiles, pointing to novel seed proteins, bifunctional inhibitors, fatty acids, and diverse phytochemicals as additional defense factors [16,22,23]. Similar patterns of polygenic, quantitative resistance mediated by both morphological and biochemical traits are reported for bruchid resistance in mungbean, rice bean, cowpea, and other pulses, highlighting convergent but crop-specific solutions to storage pest pressure [6,7,28,29].

Although several reviews on bruchid management and resistance in pulses exist, most are cross-legume or focused on *Vigna unguiculata*. These syntheses emphasize APA-based mechanisms and rarely provide a systematic integration of molecular, biochemical, and quantitative genetic evidence for *P. vulgaris* [22–24]. Furthermore, evaluations of African common bean germplasm have focused mainly on the presence or introgression of known APA alleles. Only a small number of associated SNPs have been considered. In contrast, non-APA loci, locally evolved landrace resistance, and Africa-specific breeding materials have received limited attention [16,30]. Furthermore, evaluations of African common bean germplasm have focused mainly on the presence or introgression of known APA alleles. Only a small number of associated SNPs have been considered. In contrast, non-APA loci, locally evolved landrace resistance, and Africa-specific breeding materials have received limited attention [28,29]. Addressing these gaps is essential to strengthen the resistance toolbox beyond a single locus. It will also help capture under-used African diversity. Breeding strategies must be designed to withstand species-specific bruchid pressure and the varied storage environments found across the continent.

Recent genomic tools and breeding methods have increased the speed of bruchid resistance dissection and deployment. Quantitative trait locus (QTL) mapping, genome-wide association studies (GWASs), and transcriptomics identify candidate loci and markers from which to select markers for marker assistance selection (MAS), while interspecific introgression increases the base of alleles available to breeders [28,29]. Nevertheless, cultivated bean germplasm has a narrow genetic base in many cases, the inheritance of resistance can be complex, and useful marker sets suitable for African breeding programs are still limited. Moreover, to date, locally adapted landraces demonstrating promising resistance (e.g., Tanzania and Malawi landraces) need to be both genetically and mechanistically better characterized prior to their integration into national breeding pipelines [16,30].

This systematic review integrates existing knowledge on genetic, biochemical, and physiological mechanisms of bruchid resistance in common bean with a focus on applicability in African smallholder systems. The review has three linked aims: (1) to consolidate the evidence for the physiological and biochemical foundations of resistance—with particular reference to the role(s) of arcelins, phytohemagglutinins, and alpha amylase inhibitors; (2) to map the genetic discoveries (QTLs, GWAS hits, transcriptome responses) and assess the suitability of molecular markers for their use in MAS; and (3) to identify gaps in genomics resources and propose genomics-informed frameworks for breeding bruchid-resistant cultivars that are adapted for African agroecological and socio-economic contexts.

The central research questions were as follows: (1) What molecular and genetic mechanisms underlie resistance to *A. obtectus*, and *Z. subfasciatus* in the common bean germplasm, and (2) how can marker-assisted breeding be optimized to deliver durable, farmer-preferred resistant cultivars?

2. Materials and Methods

2.1. The Scope of the Systematic Review

The scope of this systematic review was defined by the PICOTS framework to extract a comprehensive picture of bruchids resistance in common bean from all domains. In this review, population referred to common bean (*Phaseolus vulgaris* L.) germplasm. The interventions encompassed genetic resistance mechanisms, molecular markers, and breeding approaches. Comparators included susceptible genotypes or alternative resistance sources where they were reported. Outcomes comprised measurable bruchid resistance responses and associated genetic or biochemical evidence. The study captured a full spectrum of the progress made in fortifying common bean against bruchids across time to date. This structured approach ensured the applicability of the study to all production systems where post-harvest losses due to bruchid infestations remain a persistent constraint.

2.2. Reporting Standards

This systematic review was conducted and reported in accordance with the PRISMA 2020 reporting guidelines. To enhance methodological transparency and reduce the risk of selective reporting, the review protocol was prospectively registered on the Open Science Framework (OSF) on 28 October 2025, Registration DOI:10.17605/OSF.IO/3JHFD. The objectives, eligibility criteria, and analytical approach were predefined prior to study selection and synthesis. Adherence to PRISMA standards and protocol registration ensured a transparent, reproducible, and structured review process, consistent with best practice for systematic evidence synthesis.

2.3. Eligibility

The criteria for inclusion in this systematic review were developed based on the PICOTS framework. The framework offers a rigorous basis to select studies leading to a better understanding of bruchid resistance in common bean. To overcome the effects of possible publication bias and in order to include a variety of perspectives, especially those produced by regional breeding programs, the criteria included both peer-reviewed publications and gray literature, such as theses, dissertations, institutional reports, conference proceedings, and technical documents from agricultural organizations. This inclusive approach ensured greater representativeness in synthesizing evidence, including practical insights from African contexts which may be underrepresented in formal journals.

2.3.1. Inclusion Criteria

Studies were included for eligibility if they met all of the following numbered criteria: (1) Constituted of original research or gray literature, such as peer-reviewed journal articles, theses, dissertations, technical reports, or conference papers with primary data; (2) Primary research studies from any region; or (3) Reported on genetic dissection techniques (i.e., of QTGs, GWAs, transcriptomics), molecular markers amenable to marker-assisted selection (MAS) or breeding approaches (i.e., introgression or genomics-informed selection).

2.3.2. Exclusion Criteria

Conversely, studies that violated any of the following numbered criteria were excluded: (1) Based on non-original sources, e.g., narrative reviews, editorials, or secondary analyses without new empirical data; (2) Resistance mechanisms in legume species other than *P. vulgaris* or direct hybrids/admixture thereof, thus deviating from focal crop; or (3) Lack of reporting of objective resistance results, e.g., quantifiable resistance outcomes such as reduced larval survival, percent of seed damage, or validated genetic associations.

2.4. Information Sources

To comprehensively identify relevant studies for this systematic review, a multi-faceted search strategy was used. Ten bibliographic databases and gray literature repositories were searched to ensure a broad coverage of the agricultural, genetic, plant breeding, and entomological literature. The selected databases were the following: CAB Abstracts, PubMed, ScienceDirect, Google Scholar, AGRICOLA (via PubAg), AGRIS (FAO), ProQuest Dissertations & Theses Global and CGIAR Research Library. These sources were selected based on their high level of indexing open-access peer-reviewed articles, theses, institutional reports, and conference proceedings with relevance to common bean genetics and bruchid resistance mechanisms and breeding innovations [29,30]. This expanded approach lessened publication bias by including both formal publications and gray literature, such as published theses from African universities and technical reports from regional breeding programs.

2.5. Search Strategy

Searches were performed with a mix of controlled vocabulary terms (e.g., MeSH terms in PubMed) and free-text keywords, linked with Boolean operators (AND, OR, NOT) and truncation symbols (*) to capture terminology variations. To ensure reproducibility while accommodating differences in database syntax, the search strategy was adapted by platform. The reviewers maintained a consistent conceptual structure across sources. For platforms supporting advanced Boolean logic and/or controlled vocabulary, the following database-specific strings were used (adapted only for field tags and syntax). For platforms with more variable query parsing (e.g., Google Scholar) or interface constraints (e.g., query length and nesting), the core concepts were executed as a small set of targeted strings run iteratively.

2.5.1. Search Strings

To ensure reproducibility while accommodating differences in database syntax, the search strategy was adapted by platform while maintaining a consistent conceptual structure (crop × pest × resistance/breeding terms). Geographic relevance to Africa was addressed through a combination of keyword-based filtering at the search stage and explicit screening against predefined eligibility criteria. Where supported by database functionality, Africa-related terms were incorporated directly into the search strings; otherwise, geographic applicability was assessed during title/abstract and full-text screening.

1. PubMed (MeSH + free-text): ("*P. vulgaris*"[Title/Abstract] OR "common bean"[Title/Abstract]) AND (bruchid*[Title/Abstract] OR "*A. obtectus*"[Title/Abstract] OR "*Z. subfasciatus*"[Title/Abstract]) AND (resistan*[Title/Abstract] OR arcelin[Title/Abstract] OR "APA locus"[Title/Abstract] OR phytohemagglutinin[Title/Abstract] OR "alpha amylase inhibitor"[Title/Abstract] OR QTL[Title/Abstract] OR GWAS[Title/Abstract]) AND (Africa*[Title/Abstract] OR "sub-Saharan Africa"[Title/Abstract])
2. CAB Abstracts/AGRICOLA (via PubAg)/AGRIS (FAO)/CGIAR Research Library/ProQuest Dissertations & Theses (core Boolean string ("*P.vulgaris*" OR "common bean") AND (bruchid* OR "*A. obtectus*" OR "*Z. subfasciatus*" OR "bean weevil") AND (resistan* OR arcelin OR "APA locus" OR phytohemagglutinin OR "alpha amylase inhibitor" OR QTL OR GWAS OR marker* OR "marker-assisted selection" OR introgress*) AND (Africa* OR "sub-Saharan Africa"))
3. ScienceDirect: ("*P. vulgaris*" OR "common bean") AND ("*A. obtectus*" OR "*Z. subfasciatus*" OR bruchid*) AND (resistance OR arcelin OR "APA locus") AND Africa.
4. Google Scholar (iterative, concept-equivalent strings; run separately): ("*P. vulgaris*" OR "common bean") AND ("bruchid" OR "*A. obtectus*" OR "*Zabrotes subfasciatus*") AND

("arcelin" OR "APA locus" OR "QTL" OR "GWAS" OR "marker-assisted selection")
AND ("Africa ")

2.5.2. Filtering

No filters were applied for language and the date range was left open; this was chosen primarily to capture the depth of the search. No automation tools were utilized; instead, searches were performed manually by the lead reviewer, with duplicates removed using Mendley Desktop (version 1.17.13) reference management software. No language restrictions were applied, and non-English publications were screened and included where relevant. Translation was performed by Google Translator. This strengthened the representativeness of the review by incorporating studies beyond the English-language corpus. The final searches were executed between 19 and 28 December 2025, to incorporate emerging publications. Additionally, reference lists of included studies were hand-searched for supplemental citations (forward and backward snowballing).

2.6. Study Selection and Data Extraction

Initial screening and data extraction were manually performed by two reviewers using a standardized data extraction template created in Microsoft Excel. Resolutions to incongruities were achieved by discussion and a third opinion from another reviewer where necessary. The template was designed to capture key elements aligned to both the PICOTS framework and eligibility criteria, including the following: (1) bibliographic details (e.g., authors, year, publication type); (2) study characteristics (e.g., design, location, sample size for germplasm evaluated); (3) population specifics (e.g., *P. vulgaris* accessions tested, bruchid species; *A. obtectus* or *Z. subfasciatus* and infestation conditions); (4) intervention details (e.g., genetic mechanisms such as arcelin expression, molecular markers such as QTLs, or, for gray literature such as theses or reports, extraction was focused on practical breeding). For transparency, the full extraction template included structured fields for bibliographic details, study design, germplasm tested, bruchid species, infestation conditions, genetic mechanisms (e.g., arcelin expression, QTLs, GWAS hits), molecular markers, breeding approaches, and methodological limitations.

2.6.1. Incomplete Data

Where key variables were missing, unclear, or inconsistently reported, data extraction was limited to information that could be reliably interpreted from the primary source. No imputation or inference beyond what was explicitly reported by the study's authors was performed. Studies with partial reporting were retained only when core outcomes relevant to bruchid resistance mechanisms, markers, or breeding approaches could be clearly identified. As such, limitations were documented during extraction to avoid the over-interpretation of findings.

2.6.2. Geographic Representation and Evidence Balance

Variation in the geographic distribution of studies was addressed during extraction and synthesis. The approach used was to record the study location and contextual relevance. Although evidence was concentrated in a limited number of countries, studies were included only where findings were directly applicable regardless of national origin. Uneven geographic representation was therefore treated as a characteristic of the available evidence base rather than a source of analytical bias. Its implications were considered in the interpretation and limitations of the review.

2.7. Study Risk of Bias Assessment

To ensure that the methodological quality of the included studies was critically appraised, we used the Risk of Bias visualization tool RoBvis (Version 2) [31] to summarize and present the risk-of-bias judgements. Risk of bias was assessed across key domains relevant to experimental bruchid resistance research, including the following: (1) bias related to study design and replication/randomization, (2) bias related to infestation procedures and deviations from intended experimental conditions, (3) bias due to missing outcome data, (4) bias in outcome measurement, and (5) bias in selective reporting/statistical analysis. Each domain was rated as “low risk”, “moderate risk”, or “high risk” using a predefined domain rubric to support transparent and reproducible judgements.

The risk-of-bias assessment was conducted by two independent reviewers with expertise in plant breeding and bruchid resistance screening. Reviewers independently extracted the methodological information needed to support domain-level judgments for all included studies and recorded ratings in a structured Excel template to ensure consistency and traceability. Discrepancies were resolved through discussion, with arbitration by a third reviewer when consensus was not immediately reached. This approach was used to improve robustness and minimize subjectivity in the evaluation process. No automation tools were used; assessments were based on manual review of the full text and expert judgement.

2.8. Effect Measures

Quantitative effect measures were not calculated because outcomes across the included studies were not reported in a form amenable to statistical pooling. Bruchid resistance was quantified using heterogeneous and non-equivalent metrics under markedly different bioassays. In addition, several studies focused on mechanistic or marker-based evidence without reporting the summary statistics required to derive effect sizes with interpretable precision. Therefore, synthesis was conducted narratively. There was a pressing emphasis on the consistency, directionality, and biological plausibility of resistance mechanisms and breeding evidence rather than pooled quantitative effect estimates.

2.9. Study Synthesis Methods

The analysis relied on thematic coding and narrative synthesis. Statistical pooling was not possible because the studies varied in design, outcomes, and reporting. Instead, thematic analysis was employed to integrate findings systematically. Extracted data were coded into major themes (*APA*-mediated resistance, non-*APA* loci, breeding strategies) and sub-themes (species-specific efficacy, genotype $\times$ environment interactions, marker validation). This structured qualitative approach allowed systematic comparison across heterogeneous studies, highlighting convergences and divergences in methodology and outcomes. Extracted data were first arranged in a synthesis matrix, with studies grouped into three main themes: physiological and biochemical resistance linked to *APA* locus proteins, genetic findings from QTL mapping and GWAS, and breeding strategies involving marker-assisted selection in breeding pipelines.

Within each theme, sub-themes emerged through content analysis. These included comparisons of resistance against *Z. subfasciatus* and *A. obtectus*, as well as gaps in the use of local germplasm. This approach helped reveal points of agreement, contradictions, and the strength of evidence, such as the number of studies supporting arcelin-based resistance.

The synthesis was organized around two guiding questions: which molecular and genetic mechanisms drive resistance in African germplasm, and how marker-assisted breeding can be optimized. The summaries highlighted clear patterns, such as the dominance of arcelin-mediated resistance in wild introgressions [12]. They also noted important

limitations, including inconsistent field performance and limited sampling of highland-adapted landraces [30].

2.10. Certainty Assessment

Formal certainty grading using quantitative frameworks like GRADE was not applied. This follows the fact that the body of evidence did not support effect-size based synthesis or comparable outcome aggregation across studies. Confidence in the evidence was judged qualitatively by triangulating study rigor, consistency across investigations, biological plausibility, and convergence of phenotypic, biochemical, and molecular data. Greater certainty was attributed to resistance mechanisms and markers that were repeatedly validated across different germplasm backgrounds, bruchid species, and experimental settings. In the same sense, lower certainty was assigned to findings derived from single-location studies, limited sample sizes, or incomplete reporting. Consideration was also given to risk-of-bias assessments. This structured qualitative approach allowed transparent appraisal of confidence in the evidence while remaining consistent with the heterogeneous and mechanism-focused nature of the available literature.

3. Results

3.1. Study Selection

Records were identified through structured searches across major bibliographic databases and complementary sources. In total, 628 records were read. After exporting all results to Mendley Desktop (version 1.17.13), 46 duplicates were removed, leaving 582 unique records. Title/abstract screening was then conducted to exclude the literature which was not PICOTS-compliant. A total of 509 studies were excluded, resulting in 73 full-text articles assessed for eligibility. A total of 44 full-text articles were excluded; the main reasons were as follows: absence of a genetic/marker/breeding component relevant to bruchid resistance ($n = 14$); did not evaluate bruchid resistance in common bean germplasm or appropriate derived materials ($n = 9$); bruchid species/outcomes not aligned with resistance inference ($n = 8$); insufficient methodological detail or non-extractable outcomes to support synthesis ($n = 7$); and duplicate reporting/overlapping datasets where the most complete report was retained ($n = 6$). No exclusions were made based on language or geographic region, consistent with the global scope of the review and the emphasis on the transferability of genetic and marker evidence.

Following full-text assessment, 29 studies met the inclusion criteria and were included in the final synthesis. The PRISMA flow diagram (Figure 1) summarizes the process and its outcomes Table S1.

3.2. Excluded Studies

Several studies were highly relevant to bruchid management and resistance biology but were excluded because they did not conform to our preset PICOTS. A study conducted by [32] provided strong phenotypic evidence of resistance to *A. obtectus* in tepary bean (*Phaseolus acutifolius*). The study included antixenosis, antibiosis, and tolerance responses. However, it was excluded because the primary host species evaluated was tepary bean rather than *P. vulgaris*, making it outside the target crop scope despite its value as a donor source for introgression.

In another case, ref. [33] quantified seed physical and biochemical traits. The study tested susceptibility under no-choice and free-choice conditions against both *Z. subfasciatus* and *A. obtectus*. However, this study was excluded because it did not provide genetic loci, markers, or breeding-validation outputs, which limited direct integration into our genetics synthesis. Finally, ref. [34] was excluded, although it addressed both target bruchid species.

The study focus was on biological control in stored beans rather than host plant resistance, genetic mechanisms, or breeding strategies.

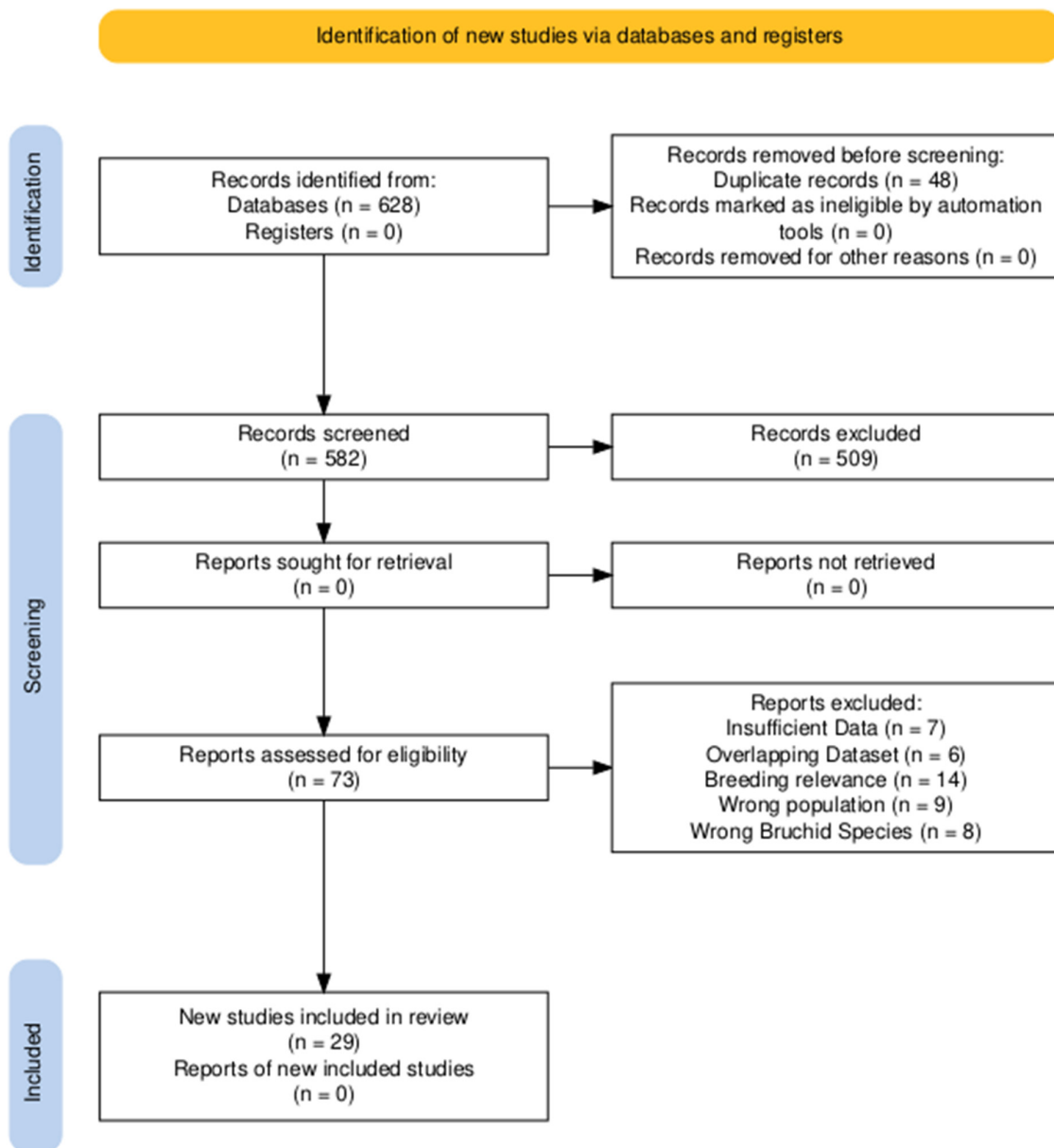


Figure 1. PRISMA flow diagram.

3.3. Study Characteristics

The included evidence base comprised 29 unique studies spanning Africa, the Americas, Europe, and Asia, and included peer-reviewed journal articles, graduate theses, and reports [6,7,13,14,16,22,24,25,27–29,35–53]. These studies reflected a progression from phenotypic screening and inheritance studies to marker-informed analyses (QTL/GWAS). Common themes included pre-breeding introgression pipelines targeting storage-bruchid resistance in common bean and closely related donor germplasm. Across studies, resistance was typically operationalized using laboratory infestation bioassays. There was also a smaller subset explicitly addressing genetic architecture (*APA/arcelin* region, QTL, and genome-wide associations) and deployment-oriented breeding. A comprehensive study-by-study summary is provided in Appendix A (Table A1).

3.4. Geographic Distribution of Included Studies

The 29 studies reflected a geographically broad but uneven research footprint [6,7,13,14,16,22,24,25,27–29,35–53]. Sustained activity was prevalent across Eastern and Southern Africa alongside mechanistic and genetics-heavy contributions from the Americas and Asia/Europe (Figure 2). Within Africa, the evidence base concentrated around national and regional breeding and storage protection priorities in Malawi, Zambia, Mozambique, Tanzania, Uganda, Ethiopia, and South Africa (Figure 2) [7,13,14,16,28,29,35–42,45]. In parallel, studies from Mexico, Brazil, Colombia, the United States, China, Japan, Spain, Switzerland, and Italy extend the evidence base through inheritance work, structured genetic studies, and locus/allele-focused mechanistic contributions [24,25,27,47,48,50–53]. Taken together, the distribution suggests that deployment-facing evidence is anchored in African target environments, whereas gene- and locus-level dissection is more frequently reported in a smaller set of globally distributed laboratories and breeding programs (Appendix A, Table A1).

Study Distribution

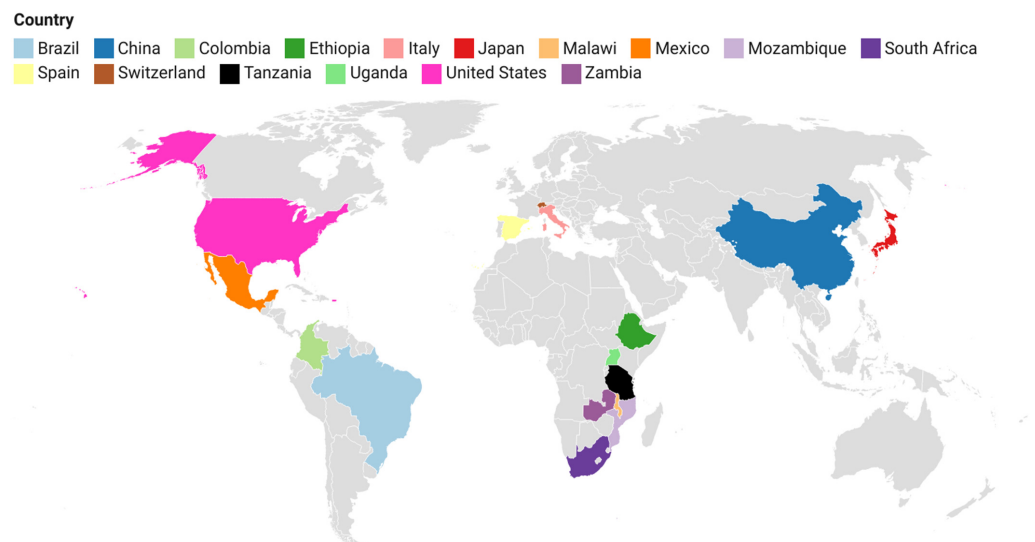


Figure 2. Countries with study contributions.

3.5. Resistance Phenotyping and Operationalization

Across the evidence base, bruchid resistance did not have the same methodological meaning. Studies operationalized resistance through bioassay-derived insect performance and seed damage outcomes. This created heterogeneity in what qualifies as a resistant response. Multiple studies prioritized direct storage-relevant metrics, thus classifying genotypes by susceptibility, damage, or resistance performance under infestation [6,25,27,39,41]. On the other hand, other studies framed resistance in terms of inheritance or genetic behavior in breeding material and populations [7,35,45,47]. A further subset emphasized that resistance can be context-dependent, highlighting genotype-by-environment considerations [51]. Several studies positioned their phenotyping as a bridge to breeding pipelines. This was to recover resistant segregants from arcelin-containing progenies or to support downstream deployment steps [14,16,36,37,44]. This pattern shows that, even before genetics enters the story, the literature distinguished resistance as either storage protection or insect suppression, and also as heritable improvement potential [13,38,40,43].

Across the evidence base, several systematic sources of heterogeneity explain why resistance outcomes differ between studies. Assay design was a major factor: no-choice storage bioassays often intensified antibiosis signals by forcing larvae to establish on resis-

tant seed, whereas free-choice assays allowed beetles to avoid resistant seeds and therefore emphasized antixenosis and preference [6,25,27,39,41]. Pest ecology also contributed to variability. *Zabrotes subfasciatus*, which dominates warm low-altitude storage environments, consistently showed strong suppression in arcelin-containing lines, while *Acanthoscelides obtectus*, more common in cooler highland areas, produced variable results that were sensitive to temperature, humidity, and infestation duration [7,24,25,27–29,36,41–44]. Germplasm composition further shaped outcomes: Andean market classes often expressed partial resistance with background-dependent APA effects, while Mesoamerican and wild-derived sources displayed stronger antibiosis but sometimes carried linkage drag or end-use trade-offs [16,24,28,36,41,44]. Seed-coat traits such as testa thickness, hardness, and phenolic content also explained differences, with Tanzanian and Malawian landraces showing partial resistance attributable to these traits even when APA proteins were weakly expressed [16,33,35,38]. Infestation parameters, including egg density, exposure duration, and endpoint metrics, varied widely across studies, producing non-equivalent susceptibility indices and complicating direct comparison [6,28,29,36,41]. Finally, marker frameworks influenced interpretability: SSRs and protein banding provided practical tracking of APA proteins but limited fine-mapping, while SNP-based QTL and GWAS approaches identified small-effect loci that require validation across backgrounds [28,29,42,44,52,53]. Taken together, these methodological and biological differences clarify why APA-mediated resistance appears strongest and most reproducible against *Z. subfasciatus*, while resistance to *A. obtectus* is more quantitative, background-dependent, and sensitive to assay design. Harmonized bioassays, dual-axis phenotyping, and multi-marker validation are therefore essential to reduce heterogeneity and enable robust inference across African breeding pipelines [16,25,27–29,33,35–38,41–45,48–53].

3.6. Genetic and Marker Evidence

The genetic evidence base painted a clear continuum, as shown in Appendix B (Figure A1). Evidence spanned from classical inheritance and protein/locus-level mechanisms, through targeted locus mapping, to genome-wide association and QTL analyses. Several studies examined resistance at the APA/arcelin seed protein region by mapping markers around resistance loci, analyzing linkage disequilibrium, and defining resistant alleles in resistant genotypes and derived materials [24,48,50]. Other studies advanced to QTL mapping and genome-wide association to pinpoint regions and prioritize candidate genes or breeding markers [28,29,42,52,53].

The genetics layer connected to deployment, as introgression and stability studies translated resistance into market-class and regional backgrounds [16,36,44]. Backcross-focused studies frames arcelin transfer as a deliberate strategy to embed resistance in improved African cultivars [14]. The literature supported a synthesis in which resistance was simultaneously treated as a biologically grounded mechanism, often connected to seed protein/locus biology [24,50] and as a polygenic breeding target requiring mapping and validation across backgrounds and environments [28,29,42,52,53].

3.7. Genetic Sources and Germplasm Composition

According to the evidence base (Table A1, Appendix A), resistance inference was built on a deliberately mixed germplasm foundation spanning Andean, Mesoamerican, and combined gene pools. Multiple studies leveraged wild-derived arcelin sources and structured populations to separate the mechanism from background noise. Several studies drew on broad farmer and breeding germplasm, capturing realistic diversity for deployment-oriented screening [27,35,36,41–44]. In parallel, many studies leveraged structured populations like RILs, NILs/HIF lines, and backcross-derived arcelin introgressions. This

was performed to boost mapping power and attribute resistance to genomic regions or donor alleles rather than confounding population structures [16,28,37,38,45–48,50]. Notably, the literature incorporated interspecific validation through *P. acutifolius* introgressions and transgenic systems serving as mechanistic stress tests for candidate resistance factors [13,51]. Finally, high-throughput diversity panels and germplasm collections strengthened external validity and position evidence for genomics-enabled selection and regional breeding [29,41,52,53].

3.8. Validation and Deployment in Breeding Programs

Beyond locus discovery and association signals, a key subset of the evidence base addressed whether bruchid resistance can be moved into farmer- and market-relevant common bean backgrounds and remain effective (Tables 1 and A1). Deployment-oriented studies combined resistance phenotyping with introgression in adapted backgrounds. This proved that resistance can be embedded into Andean market classes and southern African breeding pipelines rather than confined to donor materials [36,41]. The work in Ethiopia demonstrated transfer of *Z. subfasciatus* resistance into targeted backgrounds using resistant donors and segregating families products [44]. This was a clear pathway from resistance sources to usable breeding. Complementary studies from Tanzania/Malawi connected resistant landraces and derived recombinant inbred populations to both *A. obtectus* and *Z. subfasciatus* resistance. That reinforced the standing point that deployable resistance can exist within locally relevant germplasm while also providing populations suitable for downstream selection [16,38].

Table 1. Summarizes validation and deployment of bruchid resistance in breeding programs.

Study (Author, Year)	Breeding Strategy	Validation Status	Major Limitation(s)
[16] Maro et al. (2022)	Landraces + RIL populations; links resistance to biochemical profiles (APA-related proteins)	Moderate: breeding-oriented populations + mechanistic support	Cross-study comparability limited by heterogeneity of assays/indices
[28] Kamfwa et al., (2018)	RIL-based QTL framework (Solwezi × AO line) for <i>A. obtectus</i> resistance → supports MAS in breeding	Strong for translation: mapping population aligned to breeding	QTL utility depends on validation across backgrounds/environments
[29] Mugovo et al., (2025)	Andean Diversity Panel + checks; GWAS for <i>A. obtectus</i> (novel loci) → genomic-enabled selection	Moderate–strong: panel + GWAS supports selection pipelines	GWAS loci require functional confirmation and independent validation
[35] Kananji (2007)	Screening of landraces + improved varieties (with checks) against <i>A. obtectus</i> and <i>Z. subfasciatus</i> (selection relevance)	Moderate: combines broad germplasm relevance with resistance phenotyping	Metric heterogeneity (indices/damage measures) complicates cross-study synthesis
[36] Chinji et al. (2024)	Introgression and stability testing in diverse market classes (advanced breeding lines; F5:7; parents) against <i>A. obtectus</i>	Strong: large breeding population; stability/introgression emphasis	Validation across seasons/storage systems not consistently standardized across studies

Table 1. Cont.

Study (Author, Year)	Breeding Strategy	Validation Status	Major Limitation(s)
[37] Kipato (2015)	Identification of resistant lines from arcelin-containing progenies derived from farmers' preferred varieties vs. <i>A. obtectus</i>	Moderate: farmer-preferred background + lab assays	Often limited multi-season/storage validation; sample size sometimes not fully specified
[38] Maro (2017)	Local landraces + RIL populations for dual-species resistance (<i>A. obtectus</i> , <i>Z. subfasciatus</i>) enabling selection	Moderate: population development supports breeding	Sample sizes/replication details commonly under-reported in theses
[41] Osorno et al. (2024)	Regional breeding pipeline evidence (improved lines + breeding populations + ADP) targeting <i>A. obtectus</i>	Strong breadth: multi-country program report; large n	"Project report" format may report less methodological detail than journal articles
[44] Tigist et al. (2021)	Introgression of <i>Z. subfasciatus</i> resistance into targeted background (families from resistant donor $\times$ adapted line)	Moderate–strong: breeding families + resistance evaluation	Extent of multi-environment/season confirmation may be limited/variable
[45] Beneke (2010)	Backcross breeding using SMARC/arcelin donor into commercial cultivars; derived lines screened vs. <i>A. obtectus</i>	Moderate: demonstrates translation into commercial types	Thesis reporting; limited external validation beyond tested set
[46] Nchimbi-Msolla et al. (2001)	Backcross breeding to introduce arcelin donor alleles into improved African cultivars (arcelin introgression)	Moderate: breeding translation intent clear	Often limited reporting of broad multi-location validation and harmonized metrics
[51] Li et al. (2022)	RIL population + association panel for <i>A. obtectus</i> (QTL/gene discovery)	Strong genetic inference; translation depends on validation	Transferability requires testing in African backgrounds and storage ecologies
[52] Li et al. (2023)	Large germplasm collection screened vs. <i>A. obtectus</i> (breeding resource)	Strong scale; translation depends on breeding integration	Same: needs validation in African breeding programs/environments

Earlier backcross-centered efforts explicitly framed arcelin transfer into improved African cultivars as a breeding strategy, which was a conversion of mechanistic resistance sources into agronomically acceptable lines [14]. Translation was strengthened when breeding materials were paired with genetic mapping (e.g., RIL-based QTL), enabling marker-assisted selection and reducing reliance on bioassays [28]. Across the dataset, deployability was constrained by incomplete multi-environment validation, non-standardized bioassays, and reliance on small mechanistic panels (Tables 1 and A1) [25,29,35,45,52,53].

3.9. Risk of Bias in Studies

In considering the methodological quality of the included studies, we observed domain-specific variation. Judgements clustered largely into low risk versus moderate

risk across the domains assessed, with none falling into the high risk category (Figure 3). Studies which delved into genetics and mapping as well as those which employed rigorous laboratory bioassays were rated low risk across domains [16,24,25,27–29,36,42–44,47,48,52]. By contrast, a subset of theses, earlier inheritance and breeding-focused work, and project-style outputs showed more moderate ratings. Even though the outcomes were generally objectives, most of these studies fell short in satisfying the requirements of a low risk assessment [7,13,14,35,37,38,40,41,45]. Domains tied to randomization and replication statements, infestation standardization, control of seed-related confounding, and completeness of statistical reporting detail were the most affected. Notably, several otherwise strong experimental studies were judged as moderate risk primarily because of confounding control domains, which affected the overall rating despite there being a low risk in most other categories [6,39,50,51]. Therefore, the evidence base supports a balanced interpretation. Many studies, particularly recent genomic and structured experimental papers, demonstrated consistently low risk of bias. However, a meaningful subset remained limited by unclear reporting in specific methodological domains.

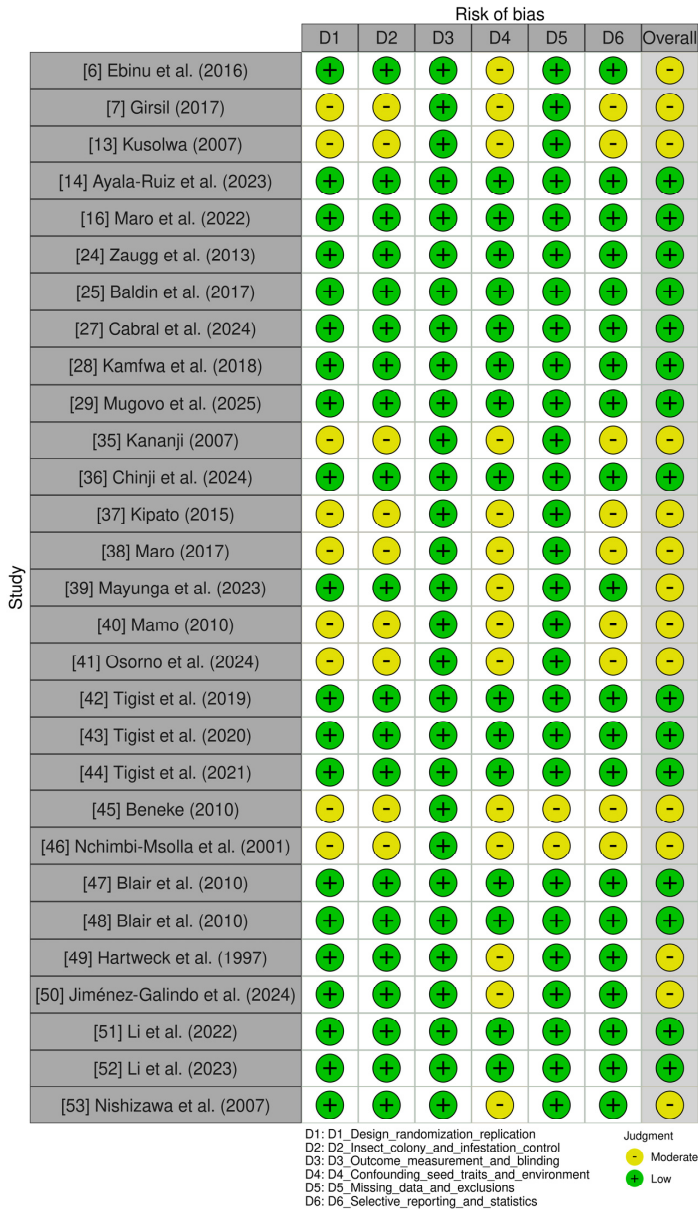


Figure 3. Risk-of-Bias traffic-light chart for the reported studies [6,7,13,14,16,22,25,27–29,35–53].

The evaluation of selective reporting similarly showed two broad patterns. Across a large proportion of the peer-reviewed genetics, mapping, and structured screening studies, reporting was judged low risk. This was consistent with clearer alignment between methods and presented results and more complete statistical reporting [6,16,24–29,36,39,42–44,47,48,50–52]. In contrast, several theses and older breeding and inheritance outputs were rated moderate risk for reporting bias. This was driven by unstandardized reporting conventions and, in some cases, ambiguous reporting of statistics and methods which hindered verification of all outcomes and analyses [7,13,14,35,37,38,40,41,45].

4. Synthesis of Results

Across the 29 included studies, the evidence base showed a coherent but heterogeneous pathway leading to deployment-oriented breeding and validation. The heterogeneity was generated by several adopted methodologies, germplasm types, and outcomes. This precluded a single pooled quantitative meta-analysis, so synthesis was conducted narratively with more consideration of risk-of-bias patterns (Figure 3). The synthesis nonetheless converged on two robust conclusions. Firstly, the APA-region biology (arcelin/ APA-family seed proteins) repeatedly appeared as a key resistance axis, especially for antibiosis against *Z. subfasciatus* and *A. obtectus* [6,7,13,14,16,24,35,38,42–44,48–50]. Secondly, recent genome-scale studies and large panels strengthened the mapping-to-deployment bridge, including the identification of non-APA loci and the evaluation in African breeding pipelines [28,29,36,41,52,53]. Additional experimental and observational studies contextualized resistance under diverse environments and pest pressures [25,27,39,47,51].

4.1. Sensitivity Analyses for Robustness

To assess the robustness of the synthesis against design and reporting variability, we conducted structured qualitative sensitivity checks by repeating the narrative conclusions under progressively stricter inclusion lenses.

When the synthesis was restricted to peer-reviewed journal articles, excluding theses, proceedings, project reports, the core interpretation remained stable. The APA/seed protein mechanisms and APA-proximal marker evidence continued to anchor mechanistic conclusions [24,48–50], while mapping/genomics studies still supported localization and marker utility for breeding [16,28,29,36,42–44,52,53]. The restriction of studies to African contexts preserved the deployment-relevant conclusions; thus, studies conducted in or explicitly targeting African breeding were utilized. Resistance sources and breeding materials with reported field relevance remained centered on *A. obtectus* and *Z. subfasciatus* control in the African germplasm [7,16,28,29,35–39,41]. Restricting the synthesis to studies with clear bruchid species attribution did not change the direction of inference. APA-linked evidence remained strongest for *Z. subfasciatus*-focused inheritance and protein studies, whereas large-panel and breeding pipeline studies reinforced *A. obtectus* relevance and pointed to additional loci beyond APA [28,29,36,41–44,48,49,52,53]. These sensitivity checks indicated that the principal synthesis conclusions were not driven by any single publication type, geography subset, or species-reporting subset, but are supported across strata of the literature.

4.2. Reporting Biases and Risk of Missing Results

Assessment of bias due to missing results was undertaken at the synthesis level. Because a meta-analysis was not conducted, funnel plot-based approaches were not applicable. Instead, the review evaluated reporting bias by checking the consistency between stated methods and reported outcomes, the completeness of outcome reporting across bruchid-response domains, and whether statistical reporting supported the conclusions

drawn. Across the dataset, more recent genomics and structured breeding pipeline studies tended to show stronger protections against selective outcome reporting. These studies provided clearer alignment between planned measurements, analytical steps, and reported outputs [25,27–29,36,47,51–53]. In contrast, theses, proceedings, and some older inheritance and breeding reports more often presented outcomes with limited reporting granularity. Commonly, there was incomplete specification of randomization and replication decisions, partial reporting across outcome domains, and limited statistical detail. This increased susceptibility to selective emphasis on significant and interpretable endpoints [7,13,14,35,37,38,40,41,45]. Importantly, these limitations primarily affected the strength-of-claim calibration rather than reversing conclusions. Even where reporting bias concerns were plausible, the direction of evidence in resistance present in specific materials, APA-linked antibiosis, and mapping signals in defined populations, remained broadly consistent with the wider literature [6,16,24,29,39,42–44,48–50].

4.3. Certainty of Evidence

Certainty in the body of evidence was judged qualitatively using a transparent, narrative rubric aligned to common certainty domains. These were explicitly informed by the domain-level risk-of-bias profile (Figure 3). In practical terms, bodies of evidence dominated by studies rated low risk across most domains (Figure 3) were interpreted with higher confidence. With the same measure, conclusions relying mainly on studies with more frequent unclear ratings, yielding a moderate risk judgment, were interpreted more cautiously and framed as priorities for further validation.

For APA/seed protein-linked resistance, the evidence reflected strong biological coherence as seed-mediated antibiosis aligned with APA/arcelin-related evidence. Protein assays, locus-linked genetics, and breeding trials all converged to reinforce the mechanism. Across these peer-reviewed studies, evidence consistently supported low risk outcomes (Figure 3) [16,24,42–44,48–50]. Where the evidence base included theses or proceedings with less explicit reporting on design or infestation control, these were treated as supportive rather than determinative sources. This did not materially change the direction of inference but moderated the certainty for some context-specific claims [7,13,14,35,37,38,40,45].

Non-APA loci and genome-scale mapping evidence was assessed as moderate certainty. GWAS and QTL analyses deliver strong locus-specific signals and transparent metrics, often reflected as low risk ratings (Figure 3). Yet, replication across populations and multi-environment validation in African storage and breeding contexts remain limited, constraining certainty for claims of broad transferability [28,29,42,52,53]. Accordingly, these loci were interpreted as high-priority targets for marker-assisted breeding and validation, rather than as universally confirmed resistance determinants across all market classes and agroecologies.

For breeding translation and deployment relevance, certainty was assessed as moderate. This domain benefited from multi-country screening and introgression with stability testing. Resistance evidence was directly aligned to breeding pipelines and market-class needs, thereby strengthening external validity [29,36,41,44]. Certainty was moderated where program and thesis-style outputs, though valuable for context and scale, lacked granular methodological detail. This limitation contributes to the moderate risk ratings in Figure 3 and reduced reproducibility for specific outcomes [14,35,37,38,45].

Ecology and seed-trait-dependent modifiers, such as seed physical traits, bruchid population variation, and environment or handling effects, were central to outcome variability. Certainty was judged moderate-to-low because these factors were often invoked but rarely measured with consistency or control. This methodological gap was reflected in “moderate” ratings for confounding-related domains (Figure 3). As a result, cross-study comparabil-

ity and the strength of causal attribution remain constrained [6,16,25,27,35,39,47,51]. The certainty profile supports high confidence in biologically plausible resistance mechanisms. Multiple validated resistance sources further reinforce this evidence base. However, transferability and durability of specific loci and trait combinations across African genetic backgrounds and storage ecologies remain the key priorities for systematic validation.

5. Discussion

5.1. Interpretation of the Findings

Across the included studies, bruchid resistance in common bean was supported by a multi-layered evidence chain. Mechanistic plausibility was established through seed-based antibiosis and defensive seed traits. Genetic localization and marker development further anchored resistance to specific loci; hence, introgression and validation in breeding-relevant materials confirmed applicability in practical contexts. Mechanistic and locus-focused studies consistently linked resistance to seed-expressed factors that suppress larval success and adult emergence [24,50]. On the other hand, large-panel phenotyping and mapping studies showed that resistance can also be quantitative, background-dependent, and detectable at genome scale [28,29,42,52,53]. Deployment-oriented studies showed that resistance was not confined to laboratory artifacts. It could be advanced through breeding pipelines and validated in market-class contexts relevant to African agriculture [36,41,44].

5.2. Geographic Distribution and Representativeness

The evidence base was geographically diverse but uneven, with stronger depth in specific national programs and breeding pipelines. Eastern and southern Africa contribute substantial African-context resistance phenotyping and breeding-oriented evidence [7,16,28,29,35–39,41–45]. Several influential mechanistic and mapping studies originated outside Africa but retained high relevance. Their focus on seed-based antibiosis, mapped loci, and marker development reflected resistance biology that is inherently transferable. These mechanisms have potential to be validated within African genetic backgrounds, ensuring applicability to regional breeding contexts [24,25,27,47–53]. This distribution pattern shaped interpretation, with conclusions strongest where mechanistic evidence, genetic localization, and breeding translation intersect. By contrast, evidence confined to a single layer proved weaker, limiting the robustness of inference across studies.

5.3. Germplasm Types and Gene Pools: Multiple Resistance Origins

The reviewed studies evaluated bruchid resistance in many germplasm types, including landraces, released varieties, breeding lines, and structured populations such as NILs, RILs, and HIFs. This breadth was critical because resistance expression was both gene pool- and background-dependent. African landraces remained central as reservoirs of resistance alleles that buttressed future breeding progress. Equally, farmer-preferred materials served as key deployment targets, ensuring that validated resistance was relevant to local production and market needs [7,16,35–38]. Structured populations strengthened causal inference and mapping resolution [28,47,52], while diversity panels enabled broader allelic sampling and highlighted variation that was likely to be encountered in breeding programs [29,36,42,43,53]. The practical implication was that a resistant line was not a universal solution unless its resistance was shown to persist across market classes, gene pools, and target environments [36,41,44].

5.4. Bruchid Species and Resistance Comparability

Across the 29 studies, resistance was tested against *A. obtectus*, *Z. subfasciatus*, or both. This mattered because the same host genotype could express different resistance

levels depending on the pest species and infestation conditions. Dual-species studies strengthened claims of broad-spectrum resistance by demonstrating consistency across pest systems [6,14,16,24,35,38,50]. Meanwhile, several bodies of work focused largely on *Z. subfasciatus* in Ethiopian germplasm and breeding contexts [7,42–44]. On the other hand, southern African pipelines and large panels placed strong emphasis on *A. obtectus* [28,29,36,41]. Because of this heterogeneity, quantitative pooling was not suitable. Yet it offered a synthesis opportunity, since endpoints could be mapped to common biological constructs like antibiosis and damage suppression across differing assays.

5.5. APA Locus and Seed Protein Resistance

A substantial body of evidence pointed to seed-expressed antibiosis centering on the APA locus. Key proteins in this region, including arcelins and other APA-family components, were implicated. They plausibly disrupted larval digestion and development. The consequence has reduced adult emergence and diminished seed damage. This pathway was reinforced by classical assays and mechanistic studies. It was further validated by allele–phenotype associations in resistant genotypes. Marker and mapping analyses around the locus provided additional support [24,48–50]. African-focused studies reinforced this mechanism through evaluations of resistant donor lines and derived materials. These findings showed that the APA-linked axis was not a theoretical construct. Instead, it functioned as a practical breeding resource [7,16,37,44–47]. The breeding implication was clear. APA-linked resistance offered a high-confidence entry point for selection. Success depended on explicit testing of background effects and species-specific responses.

5.6. Polygenic Resistance and Seed-Trait Defenses

Several studies extended the resistance story beyond a single-locus view. Resistance involved additional loci and traits that altered its magnitude or stability, especially under variable storage conditions. Genome-scale mapping and large panels provided strong evidence for extra genomic regions and polygenic architecture [28,29,42,52,53]. Phenotyping and screening studies highlighted seed traits and cultivar differences not fully explained by one locus. This reinforced the likelihood of multi-factor resistance in practical systems [6,25,27,35]. Evidence for non-APA contributions did not negate the APA axis. Instead, it suggested that durable resistance benefited from stacking. A strong antibiosis pathway could be combined with complementary loci and seed-trait defenses. Together, these layers could buffer against background variation and environmental sensitivity.

5.7. Non-APA Mechanisms, Loci, and Breeding Potential

Beyond the APA locus, non-APA mechanisms also played a central role in bruchid resistance. These mechanisms deserved systematic integration into breeding strategies. Quantitative trait loci on *Pv03* and *Pv07* were repeatedly linked to seed-coat thickness, hardness, and phenolic content. Such traits reduced larval penetration and improved seed survival [29,42,52,53]. Ethiopian GWAS panels identified candidate SNPs on *Pv03* that were linked to testa integrity and phenolic accumulation. These associations correlated with reduced *Zabrotes subfasciatus* emergence [42,44]. Brazilian inheritance studies reported QTLs on *Pv07* that explained variation in seed-coat resistance independent of APA proteins [47,52]. Seed-coat traits themselves provide a robust axis of defense, thus thicker, harder, and more phenolic testae consistently correlated with lower adult emergence and reduced seed damage [33,35,38]. Tanzanian and Malawian landraces illustrated partial resistance that was attributable to seed-coat characteristics, even in the absence of strong APA expression [16,35,38].

Biochemical defenses also contributed, with tannins, flavonoids, and phenolic acids implicated in reduced larval success and oxidative stress responses under infestation [33,35,38].

Transcriptomic analyses further supported this, revealing upregulation of phenylpropanoid biosynthesis pathways in resistant landraces [29,42]. From a breeding perspective, non-*APA* loci broadened the genetic base, mitigated risks of pest adaptation, and avoided the antinutritional concerns linked to lectins [17,33]. These loci were often present in locally preferred germplasm, making them easier to integrate without severe linkage drag or trade-offs [16,35,38,42].

Priorities for African programs included functional validation of *Pv03/Pv07* loci, development of robust SNP/KASP markers, and pyramiding of *APA* and non-*APA* mechanisms to deliver durable, broad-spectrum resistance [28,29,42,44,52,53]. Therefore, non-*APA* mechanisms were not peripheral but central to sustainable bruchid resistance. They offered complementary layers of protection that stabilized performance, balanced insect suppression with nutritional safety, and enhanced farmer acceptance [16,24,25,28,29,33,35,38,41–45,52,53].

5.8. Marker Evidence from Loci to Genome-Wide

The literature included both targeted locus work and genome-scale approaches. Together, these created a continuum of marker evidence relevant for breeding. Targeted mapping around resistance loci provided practical marker resources. It also strengthened the biological grounding of resistance [24,48–50]. QTL and GWASs expanded this foundation by localizing multiple regions. They enabled candidate discovery and supported selection models that reflected quantitative inheritance [28,29,42,52,53]. Inheritance-focused and breeding-oriented studies added intermediate evidence. They showed segregation patterns and introgression performance even when molecular resolution was limited [13,14,35,37,38,40,45]. The combined implication was clear. Marker deployment needed to be guided by the strongest evidence bodies, while inheritance and breeding reports remained essential for real-world context and validation.

5.9. Resistance Translation in African Breeding Programs

A key strength of the evidence was the presence of studies that evaluated resistance in breeding-relevant populations and in multi-country African contexts. Large-scale pipeline and programmatic evaluations created a bridge between mechanistic genetics and farmer-relevant deployment [29,36,41]. Introgression and validation studies demonstrated how resistance sources were embedded into preferred genetic backgrounds [14,37,44,45]. Multi-location and regional context studies clarified performance under the realities of local storage pressures and bruchid population dynamics [6,16,35,39]. Studies outside Africa also contributed to the translation story. They supplied mapping, mechanistic, and germplasm insights that were validated and mobilized into African breeding programs [24,47,51–53]. Collectively, this body of work supported a deployment strategy in which validated resistance sources were prioritized, markers were used to accelerate introgression, and multi-environment validation was treated as a core requirement rather than a final optional step.

5.10. Food Safety and Nutritional Quality in Resistance Deployment

A frequent reviewer concern was whether seed proteins linked to resistance, such as lectin-like proteins and related components, posed risks to digestion or nutritional quality. The literature primarily treated these proteins in the context of insect antibiosis and resistance. It did not consistently quantify dietary risk. The breeding-relevant implication was that resistance needed to be deployed in ways that preserved consumer safety and acceptability. In practice, this meant prioritizing resistance sources that had been advanced into agronomically acceptable cultivars and market classes. It also meant ensuring compatibility with standard processing and cooking practices. Breeding and selection frameworks were used to avoid unintended trade-offs in end-use quality [14,36,37,41,44,45]. This evi-

dence further strengthened the case for stacking resistance mechanisms. A strong genetic resistance axis could be combined with complementary loci and seed-trait defenses. Feasible storage interventions added another layer, reducing the need to rely on the extreme expression of any single anti-insect factor [27,29,53].

5.11. Methodological Quality and Evidence Strength

The evidence base included both highly structured studies and those with less explicit reporting detail. Peer-reviewed mapping and panel studies dominated the structured category. Theses, proceedings, and project outputs more often lacked standardized reporting. This did not invalidate them; it meant conclusions had to be weighted toward evidence with clearer assay standardization, replication, and analytical transparency. Genomics and structured mapping studies provided stronger reproducibility scaffolding [28,29,42,52,53]. Breeding, introgression, and thesis studies added valuable context and applied insights but were constrained by inconsistent reporting granularity [7,13,14,35,37,38,40,41,45]. The most persuasive inferences emerged when independent study designs converged. Resistance appeared most robust when supported simultaneously by mechanistic plausibility, marker evidence, and breeding translation rather than by a single study type alone [24,36,44,48,49].

5.12. Pragmatic Pathways for Breeding Resistance

Taken together, the evidence supported a pragmatic breeding strategy. Well-supported resistance sources and markers were deployed, especially where locus evidence and repeated phenotyping converged, to accelerate routine selection [28,44,48,49]. Genome-scale evidence was incorporated to broaden the resistance base beyond single-locus reliance and to enable pyramiding for durability [29,42,52,53]. Multi-environment validation and market-class acceptability were treated as non-negotiable end-points, particularly in African programs where storage ecology, bruchid population structure, and farmer preferences shaped adoption [35,36,39,41]. Host resistance was integrated with feasible storage management and seed handling. This was performed because resistance expression in practice was a function of both genotype and the storage system.

6. Conclusions

This systematic review consolidated evidence that bruchid resistance in common bean was primarily mediated by *APA* locus proteins such as arcelins, phytohemagglutinins, and α -amylase inhibitors. Complementary non-*APA* loci and seed-coat traits also played important roles. Marker-assisted selection and interspecific introgression remained the most promising breeding strategies for African programs. Their success depended on how well resistance mechanisms were integrated into diverse agroecological and socio-economic contexts.

Sustainability of resistance required attention to durability, farmer adoption, and ecological safety. *APA*-mediated antibiosis was consistently strong against *Z. subfasciatus* but more variable against *A. obtectus*. This highlighted the need to pyramid *APA* with non-*APA* loci such as those mapped on *Pv03* and *Pv07*, together with seed-coat defenses, to stabilize effects across environments and genetic backgrounds. Farmer adoption depended on incorporating resistance into locally preferred germplasm without compromising yield, cooking quality, or market traits. Evidence from Tanzanian and Malawian landraces demonstrated that partial resistance could be enhanced while retaining farmer-valued characteristics.

Ecological safety was equally important. Host plant resistance reduced reliance on chemical pesticides and traditional storage treatments, thereby lowering environmental and health risks for smallholders. Food safety considerations also required attention. While arcelins and phytohemagglutinins conferred strong resistance, they posed antinutritional

risks when expressed at high levels. Breeding programs therefore needed to balance insect resistance with dietary safety, favoring alleles and loci that minimized adverse nutritional effects. Non-*APA* mechanisms, particularly seed-coat thickness and phenolic compounds, offered resistance without compromising nutritional quality. They represented a safer and more acceptable pathway for farmers and consumers.

Future research should prioritize functional validation of non-*APA* loci and their biochemical pathways. It should also focus on developing robust SNP and KASP markers for both *APA* and non-*APA* resistance, establishing harmonized bioassays for cross-study comparability, and advancing participatory breeding approaches that ensured resistant cultivars were acceptable to African smallholders. By integrating *APA* and non-*APA* mechanisms, balancing food safety, and focusing on farmer adoption, African breeding programs could deliver durable, sustainable, bruchid-resistant cultivars. These cultivars would strengthen food security and reduce post-harvest losses.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy16050491/s1>, PRISMA 2020 Checklist [54].

Author Contributions: T.E.C. and R.M.C. conceptualized the study, designed the methodology, and performed the literature search and data curation. W.N. participated in the design of the study, offered expert advice on data analysis, and helped with the interpretation of results. B.L.M. assisted in the data analysis and critical review of the manuscript. L.S. contributed to manuscript editing, scientific content refinement, and supervision throughout the study. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the World Bank, grant number E089-MZ.

Data Availability Statement: No data were generated in this study.

Acknowledgments: The authors would like to recognize the support from administrative and technical staff at Eduardo Mondlane University and the International Centre for Tropical Agriculture. The authors also wish to thank all institutions and libraries that facilitated access to the scientific literature used in this systematic review. During the preparation of this manuscript, the authors utilized GenAI tool (CHATGPT) to edit and improve the English grammar of the manuscript. The authors reviewed/edited all outputs and take full responsibility for the content of this publication. Above all, we would like to thank God.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

<i>APA</i>	Arcelin–Phytohemagglutinin–Alpha Amylase
GWAS	Genome-Wide Association Studies
MAS	Marker-Assisted Selection
PICOTS	Population, Intervention, Comparator, Outcomes, Timing, Setting
QTL	Quantitative Trait Locus

Appendix A

Table A1. Summary of studies included in the systematic review.

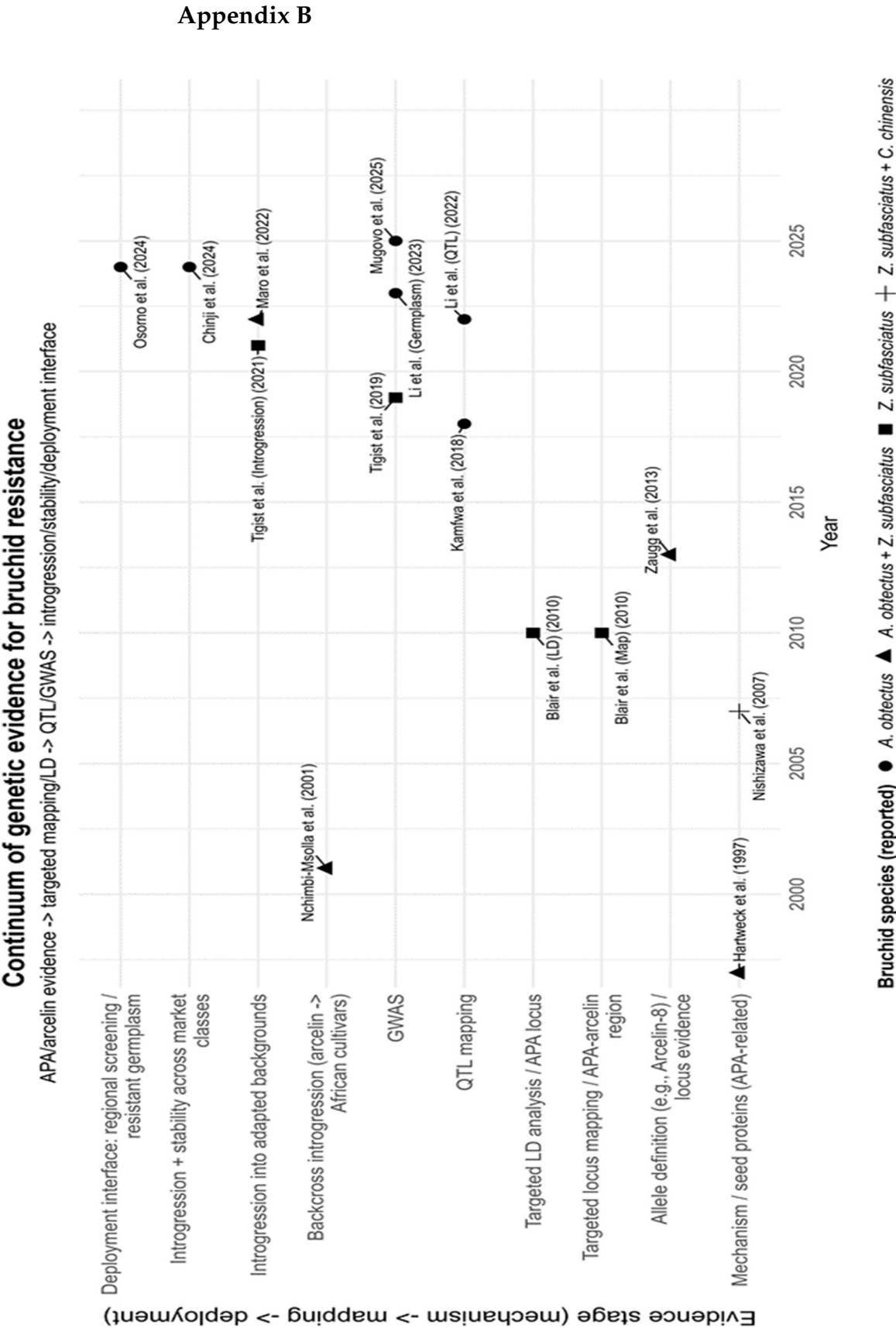
Author(s)	Country/Region	Publication Type	Species	Gene Pool	Germplasm Type	Sample Size (Genotypes)	Bruchid Species	Bioassay Type	Resistance Metric(s)	Resistance Mechanism	Locus/Chromosome	Marker Type	Mapping/Analysis Approach	Breeding Strategy	Validation Status	Transferability to Africa	Study Design Robustness	Major Limitation(s)
Kananji (2007). [35]	Malawi	PhD Thesis	<i>Phaseolus vulgaris</i> L.	Mesoamerican and Andean	Landraces and improved varieties	135	<i>Acanthoscelides obtectus</i> ; <i>Zabrotes subfasciatus</i>	Laboratory no-choice and field free-choice tests	Adult emergence; seed damage (%); weight loss; Dobie susceptibility index (DSI)	seed-coat-mediated resistance (non-arcelin)	NA	Phenotypic (no molecular markers)	Diallel mating design; segregation analysis; GCA/SCA	Conventional breeding using resistant landraces	Partially validated (laboratory and field)	High	High	No molecular mapping; resistance loci not identified
Ayala-Ruiz et al. (2023) [14].	Mexico	Journal Article	<i>Phaseolus vulgaris</i> L.	Mesoamerican	Landraces and NILs (HIF population)	148	<i>Acanthoscelides obtectus</i>	Free-choice long-term storage bioassay	Seed consumption; adult preference; 100-seed weight	Quantitative seed-based resistance (testa-related)	NA	None (phenotypic only)	HIF-based inheritance analysis; ANOVA; heritability estimation	Phenotypic selection using resistant NILs	Validated (replicated assays)	Moderate–High	High	No molecular markers or QTL validation
Baldin et al. (2017) [25].	Brazil	Journal Article	<i>Phaseolus vulgaris</i> L.	Mesoamerican and Andean	Improved lines and wild-derived arcelin lines	18	<i>Acanthoscelides obtectus</i>	Laboratory no-choice and greenhouse bioassays	Egg number; adult emergence; adult weight; grain damage (%)	Antibiosis and antixenosis (arcelin-mediated)	APA locus (Pr04; inferred)	Protein variants (arcelin types)	Phenotypic screening; ANOVA	Use of arcelin sources in breeding	Validated (lab and greenhouse)	Moderate–High	High	No molecular mapping or marker validation
Beneke, (2015) [45].	South Africa	MSc Thesis	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Commercial cultivars; RILs; NILs	NR	<i>Acanthoscelides obtectus</i>	Laboratory bioassays (no-choice)	Adult emergence; development time; seed damage	Antibiosis via arcelin seed proteins	APA locus (Pr04)	Protein-based assays (SDS-PAGE)	Backcross breeding and phenotypic screening	Introgression of arcelin into cultivars	Validated (multi-generation)	High	High	Limited molecular resolution; thesis-level evidence
Blair et al. (2017) [47].	Colombia	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean	Improved breeding lines	157	<i>Zabrotes subfasciatus</i>	Laboratory no-choice bioassay	Percentage adult emergence	Antibiosis via arcelin proteins	APA locus (Pr04)	SSR markers	Linkage mapping; QTL analysis	Marker-assisted selection for resistance	Validated (bioassay + mapping)	High	Very High	Reduced efficacy against <i>A. obtectus</i>
Blair et al. (2010) [48].	Colombia	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Wild accessions and breeding lines	105	<i>Zabrotes subfasciatus</i>	Laboratory no-choice bioassay	Adult emergence; egg counts	APA-mediated antibiosis	APA locus (Pr04)	SSR markers	Association mapping; LD analysis	Marker-assisted breeding	Validated (bioassay + marker)	High	Very High	Linkage disequilibrium limits fine mapping
Cabral et al. [27]. (2024).	Brazil	Journal Article	<i>Phaseolus vulgaris</i> L.	Mesoamerican and Andean	Elite cultivars and breeding lines	90	<i>Acanthoscelides obtectus</i>	Laboratory no-choice storage bioassay	Eggs laid; larval viability; adult emergence; seed damage	Antixenosis and antibiosis	NA	None (phenotypic only)	ANOVA; Scott–Knott grouping	Phenotypic selection	Validated (replicated)	Moderate–High	High	No genetic mapping or molecular validation
Chinji et al. (2024) [36].	Zambia; Malawi; Mozambique	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean	Advanced breeding lines (F5–F7)	571	<i>Acanthoscelides obtectus</i>	Laboratory no-choice (multi-location)	Seed perforation score; % damage	APA-mediated resistance with background effects	APA locus (Pr04)	APA-linked markers (reported)	Introgression breeding; mixed-model analysis	Validated across environments	Very High	Very High	Low recovery rate of resistance; linkage drag	
Ebinu et al. (2016) [6].	Uganda	Journal Article	<i>Phaseolus vulgaris</i> L.	Mesoamerican and Andean	Improved varieties and landraces	45	<i>Acanthoscelides obtectus</i> ; <i>Zabrotes subfasciatus</i>	Laboratory no-choice bioassay	Dobie susceptibility index; adult emergence; weight loss	No detectable resistance	NA	None (phenotypic only)	ANOVA; PCA; regression	None (diagnostic screening)	Validated	High	High	No resistant genotypes identified

Table A1. Cont.

Author(s)	Country/ Region	Publication Type	Species	Gene Pool	Germplasm Type	Sample_ Size_ (Genotypes)	Bruchid_ Species	Bioassay_ Type	Resistance Metric(s)	Resistance_ Mechanism	Locus/ Chromosome	Marker_ Type	Mapping/ Analysis_ Approach	Breeding_ Strategy	Validation_ Status	Transferability_to_ Africa	Study_ Design_ Robustness	Major_ Limitation(s)
Girsil (2017) [7].	Ethiopia	PhD Thesis	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Landraces and breeding lines	300	<i>Zabrotes subfasciatus</i>	Laboratory and field screening	Adult emergence; seed weight loss; susceptibility index	Antibiosis via arcelin proteins	<i>Chr04; Chr07</i>	SNP (Illumina 6K)	GWAS; population structure analysis	Marker-assisted breeding	Validated (field and lab)	High	Very High	Resistance confined to exotic donor backgrounds
Hartweck et al. (1997) [49].	USA; Colombia	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean	Cultivated backcross lines and wild donor accessions	NR	<i>Acanthoscelides obtectus</i> ; <i>Zabrotes subfasciatus</i>	Laboratory artificial infestation bioassays	Adult emergence; days to adult emergence; susceptibility index	Antibiosis mediated by arcelin and seed protein composition	<i>APA</i> locus (<i>Pv04</i>)	Protein-based (arcelin variants; phaseolin-null background)	Backcross breeding; comparative bioassays; GLM analysis	Improvement of arcelin-based resistance in breeding lines	Validated phenotypically	Moderate	High	Resistance incomplete against <i>A. obtectus</i> ; no DNA marker resolution
Jiménez-Galindo et al. (2024) [50].	Mexico; Spain	Journal Article	<i>Phaseolus vulgaris</i> L.; <i>Phaseolus acutifolius</i>	Andean and Mesoamerican	Common bean cultivars and tepary bean accessions	10	<i>Acanthoscelides obtectus</i>	Laboratory no-choice storage bioassay	Number of eggs; larval mortality; adult emergence; grain weight loss	Antibiosis and antixenosis linked to seed-coat chemistry	NR	NR	GLM ANOVA; mean separation tests	Identification of resistance sources for breeding	Validated phenotypically across environments	Moderate	High	No molecular markers or genetic mapping
Kamfwa et al. (2018) [28].	Zambia; USA	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean	RIL population (F4:5)	210	<i>Acanthoscelides obtectus</i>	Laboratory artificial infestation (60 days)	Seed damage (%); perforation score; 100-seed weight	Quantitative resistance with <i>APA</i> involvement	<i>AO4.1SA</i> (<i>Pv04</i>); minor QTLs	SNP (Illumina BAR-CBean6K_3)	Linkage mapping; CIM; QTL analysis	Marker-assisted breeding using validated QTLs	Partially validated (mapping population only)	High	High	Low phenotypic variance explained by QTLs (~7–8%)
Kipato (2015) [37].	Tanzania	MSc Thesis	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Farmer-preferred varieties; introgression lines	NR	<i>Acanthoscelides obtectus</i>	Laboratory no-choice bioassay	Adult emergence; days to emergence; susceptibility index	Antibiosis via <i>APA</i> seed proteins	<i>APA</i> locus (<i>Pv04</i>)	NR	Phenotypic screening; ANOVA	Backcross introgression of resistance	Validated (laboratory assays)	High	High	No molecular markers used
Kusolwa (2007) [13].	USA; Tanzania	PhD Dissertation	<i>Phaseolus vulgaris</i> L. × <i>Phaseolus acutifolius</i>	Andean (recipient); tepary bean (donor)	Interspecific hybrids and BC populations	NR	<i>Acanthoscelides obtectus</i>	Laboratory feeding trials	Days to adult emergence; adult weight; seed weight loss	Antibiosis via arcelin-like proteins	<i>APA</i> locus (<i>arcelin-PHA-aAI</i> cluster)	PCR-based markers; protein profiling	Interspecific hybridization; backcross breeding	Validated (phenotypic + molecular)	Very High	Very High	Linkage drag; sterility issues; controlled-condition testing	
Li et al. (2022) [51].	China	Journal Article	<i>Phaseolus vulgaris</i> L.	NR	RIL population and natural diversity panel	157	<i>Acanthoscelides obtectus</i>	Indoor artificial infestation (netted cages)	% damaged seeds; perforation number	Quantitative resistance via candidate gene (α -amylase inhibitor family)	<i>qAO6.1</i> (<i>Chr06</i>)	SNPs; SSRs; bin mapping	QTL mapping; fine mapping; association analysis	Marker-assisted selection targeting <i>qAO6.1</i>	Validated in mapping population	Moderate	Very High	Functional gene validation lacking; geographic specificity
Li et al. (2023) [52].	China	Journal Article	<i>Phaseolus vulgaris</i> L.	NR	Germplasm collection (landraces + cultivars)	625	<i>Acanthoscelides obtectus</i>	Laboratory artificial infestation	Percentage damaged seeds; perforation counts	Quantitative resistance via <i>AAI</i> - and defense-related genes	Multiple loci (15 QTLs)	SNP (whole-genome resequencing)	GWAS (MLM); population structure analysis	Identification of resistant germplasm	Association-level validation only	Moderate	High	QTL effects small; no functional validation
Mamo et al. (2010) [40].	Ethiopia; Colombia	Doctoral Thesis	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Advanced breeding lines; landraces; cultivars	40	<i>Zabrotes subfasciatus</i>	Laboratory infestation bioassays	Egg number; adult emergence; seed damage	Antibiosis via arcelin proteins	<i>APA</i> locus (<i>Pv04</i>)	SSR markers; protein electrophoresis	Marker-assisted selection and phenotypic screening	Validated in breeding populations	High	High	Resistance mostly effective against <i>Z. subfasciatus</i>	
Maro (2017) [38].	Tanzania; Malawi	MSc Dissertation	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Landraces; RIL populations	NR	<i>Acanthoscelides obtectus</i> ; <i>Zabrotes subfasciatus</i>	Laboratory no-choice bioassays	Adult emergence; seed damage; susceptibility index	<i>APA</i> -mediated antibiosis plus minor non- <i>APA</i> loci	<i>Pv05; Pv09; APA</i> locus	SNP (GBS); protein profiling	QTL mapping; phenotypic analysis	Marker-informed breeding	Validated (phenotypic + QTL)	High	Very High	Environment-specific expression; limited validation

Table A1. Cont.

Author(s)	Country/Region	Publication Type	Species	Gene Pool	Germplasm Type	Sample Size (Genotypes)	Bruchid Species	Bioassay Type	Resistance Metric(s)	Resistance Mechanism	Locus/Chromosome	Marker Type	Mapping/Analysis Approach	Breeding Strategy	Validation Status	Transferability to Africa	Study Design Robustness	Major Limitation(s)
Maro. et al. (2022) [16].	Tanzania; Malawi	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean	Landraces; recombinant inbred populations	NR	<i>Acanthoscelides obtectus</i> ; <i>Zabrotes subfasciatus</i>	Laboratory no-choice storage bioassays	Adult emergence; seed damage; protein–resistance association	Antibiosis mediated by APA-related seed storage proteins	APA locus (Pt04)	Protein-based (SDS-PAGE; LC-MS/MS)	Biochemical characterization linked to phenotypic resistance	Identification of protein candidates	Validated phenotypically	High	High	No genetic mapping or breeding-marker validation
Mayunga. et al. (2023) [39].	Tanzania	Journal Article	<i>Acanthoscelides obtectus</i> ; <i>Zabrotes subfasciatus</i>	NR	Bruchid populations (no host germplasm)	NR	<i>Acanthoscelides obtectus</i> ; <i>Zabrotes subfasciatus</i>	Molecular taxonomy and phylogenetics	Sequence similarity; phylogenetic clustering	Insect population genetics (no host resistance)	NA	Mitochondrial DNA (12S rRNA; COI)	Sequence alignment; phylogenetic analysis	NA	Validated (mtDNA phylogeny)	NR	Low	Does not assess host plant resistance
Mugovo. et al. (2025) [29].	Zambia	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean	Landraces; breeding lines; varieties (Andean Diversity Panel)	476	<i>Acanthoscelides obtectus</i>	Laboratory no-choice storage bioassay (60 days)	Number of perforations; % damaged seed	Non-APA resistance involving regulatory and oxidative pathways	Pt03; Pt07	SNP (GBS)	GWAS (MLM); PCA; kinship; candidate-gene analysis	Use of novel loci with APA for durability	Association-level validation only	High	Very High	No functional validation; storage-only assays
Nchimbi-Msolla. et al. (2001) [46].	Tanzania	Journal Article/Proceedings	<i>Phaseolus vulgaris</i> L.	Andean	Improved cultivars; arcelin donor lines; backcross progenies	NR	<i>Acanthoscelides obtectus</i> ; <i>Zabrotes subfasciatus</i>	Laboratory storage bioassays; on-farm observation	Adult emergence; seed damage; resistance class	Antibiosis mediated by arcelin seed proteins	APA locus (Pt04)	NR	Backcross breeding; protein profiling; phenotypic screening	Introgression of arcelin alleles	Validated phenotypically	High	High	No molecular markers; incomplete resistance under mixed infestation
Nishizawa. et al. (2007) [53].	Japan	Journal Article	<i>Phaseolus vulgaris</i> L.; <i>Vigna angularis</i>	Mesoamerican (wild bean)	Wild accessions; NILs; transgenic lines	NR	<i>Zabrotes subfasciatus</i> ; <i>Callosobruchus chinensis</i>	Laboratory infestation; biochemical assays	Adult emergence; larval development; α -amylase inhibition	Antibiosis via α A1-2; multi-protein control required	APA locus (Pt04)	Protein-based; transgenic expression	NIL comparison; transgenic functional assays	Gene stacking concept for breeding	Validated (phenotypic + biochemical)	Moderate	Very High	α A1-2 alone insufficient; no breeding-level markers
Osomo. et al. (2024) [41].	Malawi; Mozambique; Zambia	Project Final Report	<i>Phaseolus vulgaris</i> L.	Andean	Improved breeding lines; large breeding populations	1148	<i>Acanthoscelides obtectus</i>	Laboratory no-choice storage bioassay	Perforation number; % damaged seed; resistance score	APA-mediated antibiosis	APA locus (Pt04)	InDel; SNP-KASP	Backcross breeding; marker validation; preliminary GWAS	Marker-assisted deployment in market classes	Validated (phenotype + marker accuracy)	Very High	Very High	Gray literature; GWAS preliminary
Tigist. et al. (2019) [42].	Ethiopia	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Landraces; varieties; breeding lines	297	<i>Zabrotes subfasciatus</i>	Laboratory no-choice storage bioassay	% adult emergence; % seed weight loss	APA-mediated antibiosis plus minor loci	Pt04; Pt07	SNP (Illumina BAR-CBean6K_3)	GWAS (MLM); population structure	Use of resistant lines for MAS	Association-level validation	High	Very High	Small SNP effects; limited multi-environment validation
Tigist. et al. (2020) [43].	Ethiopia	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Landraces; varieties; breeding lines	297	<i>Zabrotes subfasciatus</i>	Laboratory no-choice storage bioassay	Egg number; adult emergence; susceptibility indices	Phenotypic antibiosis inferred	NR	SNP (Illumina BAR-CBean6K_3)	Genetic diversity analyses (PCA; AMOVA)	Parental selection guidance	Phenotypic validation only	High	Moderate	Resistance loci not mapped; diversity-focused study
Tigist. et al. (2021) [44].	Ethiopia	Journal Article	<i>Phaseolus vulgaris</i> L.	Andean and Mesoamerican	Advanced breeding lines; F2:4 families	208	<i>Zabrotes subfasciatus</i>	Laboratory no-choice storage bioassay	Eggs; adult emergence; seed damage; weight loss	Antibiosis via arcelin proteins	APA locus (Pt04)	KASP SNP (BRU_00261)	Backcross introgression; marker validation	Marker-assisted introgression	Validated (phenotype + marker)	Very High	Very High	Single-population validation; no pyramiding



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