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Genetic Tolerance of Peanut (*Arachis hypogaea* L.) to Diverse Aspergillus flavus Strains and Its Implications for Fungal Colonization and Seed Quality in the Drylands of West Nusa Tenggara

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Abstract: Peanut (*Arachis hypogaea* L.) cultivated in tropical dryland agroecosystems faces a serious threat from Aspergillus flavus infection, which produces carcinogenic aflatoxins. This study aimed to synthesize host genetic tolerance mechanisms, pathogen strain diversity, and their interaction affecting fungal colonization and seed quality under dryland stress. A narrative review approach was applied to seventeen primary articles and seven supporting studies selected from PubMed, ProQuest, and ScienceDirect by adopting selected reporting elements of PRISMA 2020, then synthesized through four thematic clusters. The synthesis revealed that peanut tolerance is hierarchical and complementary across three defense levels, namely physical defense based on testa architecture, biochemical defense based on flavonoid accumulation (44.29% of total metabolites) and phenolic acids, and enzymatic-molecular defense through expression of eighteen hub genes and the candidate gene AhAftr1. Strain diversity of A. flavus at the morphotype, population structure, and pangenome levels (59% accessory genes) was closely associated with virulence and aflatoxin production variation. A study under semi-arid conditions reported that drought stress increased aflatoxin B1 contamination by up to 54.95%, with the pod-filling stage as the critical period. An integrated layered control strategy combining multi-trait breeding, atoxigenic biocontrol, and agronomic management is proposed as a site-specific direction for the drylands of West Nusa Tenggara, particularly Lombok Island, and still requires field validation.

Keywords: Aflatoxin; Dryland; Genetic tolerance; Plant breeding; Seed coat polyphenol

Introduction

Peanut (Arachis hypogaea L.) is an important oleaginous legume, the fourth global vegetable-oil crop, cultivated in more than one hundred countries (Akullo et al., 2025) and serving as a source of plant protein, energy, and essential fatty acids for developing countries across Asia and Africa (Pokhrel et al., 2024). In Indonesia, it is widely cultivated in dryland agroecosystems, including Lombok Island, West Nusa Tenggara, characterized by a long dry season and low rainfall and humidity, playing a strategic role for food security and farmer income in marginal regions.

The context of West Nusa Tenggara reinforces this urgency. Peanut productivity in the province is low, averaging about 1.2 tonnes per hectare, far below the seven to eight tonnes per hectare potential of superior varieties under optimal conditions (Dinas Pertanian dan Perkebunan, 2023), and it is generally grown as a secondary crop on rainfed land in southern Lombok. Part of the Nusa Tenggara drylands is semi-arid, with annual rainfall below 2,000 mm and five to ten dry months per year (Mulyani & Suwanda, 2019); the dry-season peak (August to November) frequently triggers drought, affecting about ten thousand hectares of provincial farmland in 2024 (BMKG, 2024). Water deficit during the pod-filling stage is the period most prone to pre-harvest aflatoxin contamination (Aminou et al., 2024; Pokhrel et al., 2024), so low productivity combined with drought places Lombok farmers at double risk.

The burden of aflatoxin contamination in Indonesia is not hypothetical: peanut contamination has been

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reported from 0.3 to 329.7 µg/kg, partly far exceeding the limit due to suboptimal post-harvest handling such as incomplete drying and humid storage (Broto, 2018; Safitri, Sarjan, et al., 2026). Globally, mycotoxin-producing fungi cause estimated losses above 932 million US dollars per year, while Africa loses over 670 million US dollars for failing European Union standards (Akullo et al., 2025). Standards have tightened: National Food Agency Regulation Number 10 of 2024 set maximum aflatoxin B1 at 10 µg/kg and total at 15 µg/kg, down from the previous 20 µg/kg (Badan Pangan Nasional, 2024). This demands tolerant local cultivars as a sustainable pre-harvest solution, especially since no synthesis has yet linked genetic tolerance and A. flavus diversity to the Indonesian dryland context.

The danger of A. flavus is twofold. At the plant level, this soil-borne fungus contaminates seeds directly because peanut pods form within the soil (geocarpy), which is the natural habitat of Aspergillus (Akullo et al., 2025; Pandey et al., 2019); a tropical environment of 28 to 31°C, humidity above 85%, and drought stress four to six weeks before harvest accelerates colonization and aflatoxin accumulation (Safitri, Sarjan, et al., 2026). At the consumer level, aflatoxin B1 (AFB1) is classified by the International Agency for Research on Cancer as a Group 1 carcinogen causing liver cancer, while chronic low-dose exposure is linked to immunosuppression, impaired child growth, and long-term health disorders (Ajmal et al., 2022; Pushkarna et al., 2025), strengthening the urgency of integrated control (X. Wang et al., 2019).

Aflatoxin contamination also causes substantial economic losses through export rejection, price reduction, and declining market quality (Gangurde et al., 2024). Control of A. flavus must therefore target the root problem, host resistance and pathogen diversity, rather than merely post-harvest symptoms. Understanding genetic tolerance mechanisms thus becomes the foundation for developing cultivars that suppress both colonization and aflatoxin accumulation.

Drylands aggravate A. flavus infection through abiotic stress and pathogen dynamics. Drought damages seed coat integrity lowers the plant immune response, and increases colonization susceptibility (Pokhrel et al., 2024). A study of fifty-five genotypes at the Sahelian Center showed AFB1 contamination rising with drought severity, with seed coat polyphenols negatively correlated with colonization incidence (Aminou et al., 2024). Because about three-quarters of world peanut production lies in arid and semi-arid regions (Pokhrel et al., 2024), studying host-pathogen interactions on drylands is crucial for site-specific control strategies such as those on Lombok Island.

Breeding tolerant cultivars is a main effort, and peanut defense against A. flavus has been studied at three levels. Physically, the seed coat (testa) structure and integrity form the primary barrier inhibiting hyphal penetration (Mendu et al., 2022). Biochemically, seed coat phenolics and flavonoids show antifungal and antioxidant activity, with the flavonoid cluster contributing 44.29% to the resistance response (Zhao et al., 2025). Molecularly, candidate gene AhAftr1 was identified within the effector-triggered immunity (ETI) pathway (Yu et al., 2024), while comparative transcriptomics revealed eighteen hub genes including PR10, MAPK kinase, and pattern recognition receptors playing key roles (Cui et al., 2022).

On the pathogen side, A. flavus strain diversity has been identified morphologically, genetically, and molecularly. The L-strain and S-strain morphotypes differ in sclerotia and aflatoxin production: the S-strain generally produces smaller but more numerous sclerotia and higher aflatoxin concentrations (Gilbert et al., 2018; Singh et al., 2020). Vegetative compatibility group (VCG) grouping characterizes population structure, while the AflaPan pangenome revealed previously undocumented gene clusters related to aflatoxin biosynthesis and secondary metabolites (Gangurde et al., 2024). This genetic variation implies differences in colonization ability and virulence among isolates, so linking pathogen strains to host responses is important for integrated control design.

Although research on host tolerance and pathogen diversity has developed rapidly over the past two decades, three main gaps remain. First, peanut genetic tolerance mechanisms have only been studied partially per defense level, without an integrative review synthesizing all three within one conceptual framework, particularly for drylands (Cui et al., 2022). Second, A. flavus strain diversity has been broadly characterized through morphology, VCG, and molecular techniques, but the specific relationship between strain variation and colonization ability and aflatoxin production has not been systematically reviewed across studies (Singh et al., 2020). Third, although drought aggravates infection, no narrative review has yet integrated host genetic tolerance, pathogen strain diversity, and dryland abiotic stress to explain colonization variation and its impact on seed quality (Aminou et al., 2024).

Based on these three gaps, this study aimed to synthesize host genetic tolerance mechanisms, pathogen strain diversity, and their interaction affecting fungal colonization and seed quality under dryland stress as an integrated narrative review. This builds a complete conceptual framework of host-pathogen-environment interactions on drylands while providing a basis for site-specific breeding strategies. The results are expected to form a foundation for screening A. flavus-tolerant germplasm in the drylands of Lombok Island, contributing to food safety, public health protection, and the economic resilience of West Nusa Tenggara farmers.

Method

Type and Approach of the Study

This study used a narrative review approach in accordance with contemporary guidelines (Sukhera, 2022), namely a knowledge synthesis rooted in the qualitative tradition that examines the literature in a deep, comprehensive, and interpretive manner. Unlike a systematic review, which requires a narrow question and quantitative meta-analysis, or a scoping review, which maps coverage, the narrative approach was chosen because the topic of peanut and *A. flavus* interaction on drylands is cross-disciplinary, spanning phytopathology, plant biochemistry, fungal genetics, and agroecology, thus requiring a flexible framework with high methodological rigour. For reporting transparency, the study adopted selected elements of the Preferred Reporting Items for Systematic Reviews and Meta-Analyzes (PRISMA) 2020 (Page et al., 2021), covering the description of databases, year range, keyword strategy, and explicit inclusion and exclusion criteria.

Data Sources and Search Strategy

The data sources consisted of primary and secondary literature from internationally indexed peer-reviewed journals, with a systematic search through three main databases, namely PubMed, ProQuest, and ScienceDirect, which were chosen for their broad coverage and relevance in agriculture, biology, and life sciences. Journal quartile classification followed the Scopus system (Q1 to Q4) to ensure source quality. Triangulation of the three databases was performed to maximise coverage and minimise selection bias (Pollock et al., 2021), and the search results were managed with Mendeley for systematic duplicate elimination.

The search strategy was developed from a combination of keywords reflecting three topic components, namely host, pathogen, and environment. These combinations were assembled using the Boolean operators AND and OR to construct effective search strings. The detailed keywords across databases are presented in Table 1.

Table 1. Keywords and Literature Search Strategy Across Databases

Cluster Component	Keywords Used
Host (peanut)	"Arachis hypogaea" OR "peanut" OR "groundnut"
Pathogen (*A. flavus*)	"Aspergillus flavus" OR "aflatoxin" OR "aflatoxigenic fungi"
Genetic tolerance	"genetic tolerance" OR "host resistance" OR "seed coat resistance" OR "polyphenol" OR "flavonoid"
Pathogen diversity	"strain diversity" OR "L-strain" OR "S-strain" OR "vegetative compatibility group" OR "VCG"
Dryland	"drought stress" OR "dryland" OR "semi-arid" OR "water deficit" OR "abiotic stress"
Main combination	("Arachis hypogaea" OR "peanut") AND ("Aspergillus flavus" OR "aflatoxin") AND ("drought" OR "dryland" OR "tolerance")

Source: Compiled from the research search strategy.

Selection Criteria and Literature Screening Stages

Literature selection followed four sequential stages adapting selected elements of PRISMA 2020 for transparency: identification, duplicate elimination, title and abstract screening, and eligibility determination through full-text reading (Page et al., 2021). It must be emphasized that this study is a narrative review, not a systematic literature review, so it only borrows the PRISMA reporting framework to keep the selection traceable without detailed counting at each stage or formal risk-of-bias assessment. Identification gathered the initial literature from the three databases; duplicate elimination used Mendeley; screening assessed the relevance of titles and abstracts; eligibility determination assessed suitability through full text. This process yielded seventeen primary articles for the four clusters and seven supporting studies. The inclusion criteria covered peer-reviewed articles indexed in Scopus (Q1 to Q4) with cross-verification against Web of Science (WoS) Q1 to Q4, published between 2020 and 2025 for empirical data and between 2015 and 2025 for theoretical and methodological references discussing peanut and *A. flavus* interaction in the context of drylands or abiotic stress; the exclusion criteria included articles before 2015 (except classic references), journals outside Scopus/WoS, articles without substantial empirical data, and studies of other *Aspergillus* species without comparative data. A summary of the criteria is presented in Table 2.

Table 2. Summary of Literature Inclusion and Exclusion Criteria

Aspect	Inclusion Criteria	Exclusion Criteria
Year of publication	Empirical data 2020–2025; theory/method 2015–2025	Before 2015, except classic references
Publication type	Research articles, peer-reviewed articles	Opinion, editorial, commentary without data
Journal reputation	Indexed in Scopus Q1–Q4	Outside the Scopus index (verified through Beall's List, Cabells Predatory Reports, and active Scopus/WoS indexing status)
Topic	*A. hypogaea* interaction with *A. flavus*, aflatoxin	Other *Aspergillus* species without comparative data
Environmental context	Dryland, semi-arid, drought stress	Controlled environment without dryland relevance
Language	English or Indonesian	Other languages without an official translation

Source: Compiled from the PRISMA 2020 guidelines (Page et al., 2021; Pollock et al., 2021).

Cluster Analysis and Synthesis Technique

The analysis used cluster synthesis following the six phases of reflexive thematic analysis (Braun & Clarke, 2024): data familiarisation, initial coding, cluster searching, reviewing, defining, and report writing. Reflexivity was maintained through open recording of the initial assumptions and the researcher's academic background in dryland agriculture. The literature was organized into four interrelated clusters that also served as the structure of the discussion (Table 3), with each article extracted using a consistent summary table covering author, year, location, method, and main findings, in accordance with recommendations for transparent data charting (Pollock et al., 2021).

Table 3. Four Synthesis Clusters and Their Relationship to the Research Objectives

Cluster	Focus of Discussion	Main Literature Sources	Addresses
Cluster 1	Genetic tolerance mechanisms of peanut (physical, biochemical, enzymatic)	Host physiology, biochemistry, transcriptomics studies	Objective 1
Cluster 2	Strain diversity and virulence of *A. flavus* (morphotype, VCG, pangenome)	Mycology, population genetics, pathogen genomics studies	Objective 2
Cluster 3	Host genotype × pathogen strain interaction under dryland stress	Semi-arid host-pathogen-environment interaction studies	Objective 3
Cluster 4	Seed quality implications and integrated management strategy	Breeding, biocontrol, agronomic management studies	Integration

Source: Compiled from the conceptual framework of the study.

Result and Discussion

Cluster-based synthesis covered seventeen peer-reviewed articles selected via selected PRISMA 2020 elements, addressing three objectives sequentially: host genetic tolerance mechanisms, pathogen strain diversity, and their interaction under dryland stress, then seed quality implications and the integrated management strategy.

The database characteristics are summarized in Table 4. Most articles (64.7%) were published from 2023 to 2025, peaking in 2023 and 2024 (four each); 82.4% were original research and three (17.6%) narrative reviews. Methodological approaches ranged from multi-omics (four articles), population genomics (three), QTL mapping, *in vitro*, and field experiments (two each), to Host-Induced Gene Silencing (one), a cross-level distribution prerequisite for evidence triangulation.

Table 4. Summary of the Synthesis Database Characteristics (n=17)

Characteristic	Dominant	Notes
Year of publication	2023–2025 (64.7%)	Eleven of seventeen articles
Study type	Original research (82.4%)	Narrative review, three articles (17.6%)
Main approach	Multi-omics, population genomics, QTL, field	Cross-level triangulation
Range period	2020–2025	Plus theoretical references 2015–2024

Source: Compiled from the extraction of seventeen selected articles.

The distribution among clusters was relatively balanced (Figure 1). Cluster 1 (host genetic tolerance mechanisms) was highest at 29.4% (five articles), while

Clusters 2, 3, and 4 each accounted for 23.5% (four articles), allowing an integrated synthesis without bias.

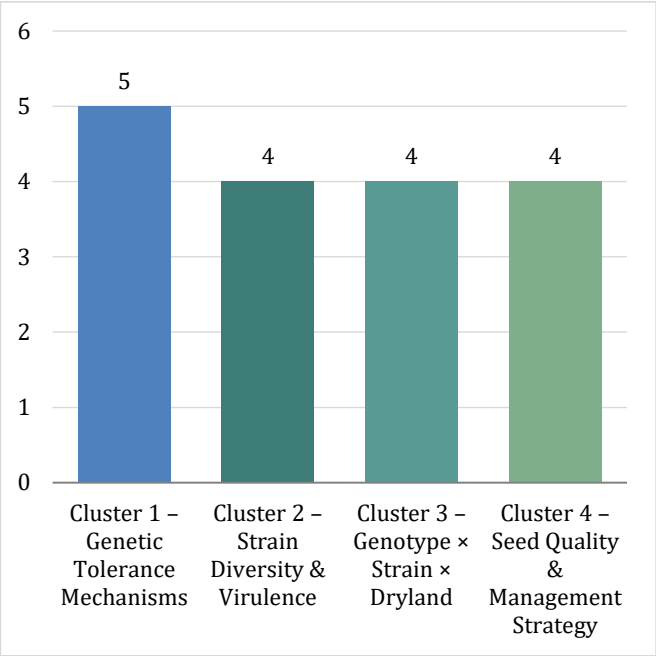

Figure 1. Distribution of Articles by Study Cluster (n=17)

Geographically, China (41.2%; seven articles) and the United States (29.4%; five articles) dominated, together contributing 70.6% of the database (Figure 2). Three articles (17.6%) were multi-country collaborations, one from Niger represented the Sahelian semi-arid region (Aminou et al., 2024), and one from Saudi Arabia examined temperature × water activity under arid conditions (Al-Zaban, 2023). The absence of Indonesian primary studies signals a local evidence gap, positioning this synthesis as a conceptual basis for follow-up research on Lombok Island.

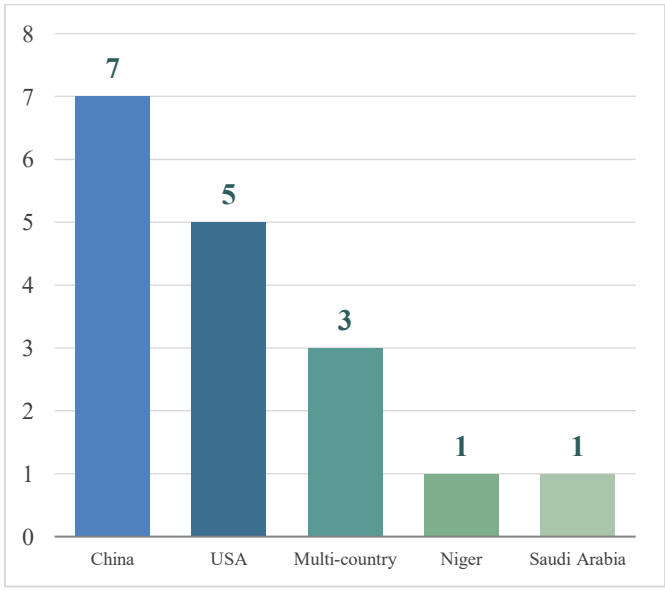

Figure 2. Distribution of Articles by Country of Study Origin (n=17)

Table 5 summarizes the seventeen articles by author, year, location, approach, and cluster for systematic cross-referencing.

Table 5. Summary of the seventeen articles analyzed in the synthesis

Author (Year)	Location	Main Approach	Cluster
Cui et al. (2022)	China	WGCNA, comparative transcriptome RNA-seq	1
Zhao et al. (2025)	China	Seed coat metabolomics–transcriptomics	1
Yu et al. (2024)	China	QTL mapping, fine-mapping, transgenic	1
Wang et al. (2023)	China	RNA-seq + seed metabolomics	1
Commey et al. (2021)	USA, India, Niger	IVSC + phenolic bioassay	1
Singh et al. (2020)	USA	Calmodulin & SSR phylogenetics	2
Drott et al. (2020)	USA	Population genomics; WGS	2
Gangurde et al. (2024)	USA, India	AflaPan pangenome; Pan-GWAS	2
Tumukunde et al. (2021)	China	Narrative review of regulatory genes	2
Aminou et al. (2024)	Niger	Field trial of 55 genotypes; polyphenol	3
Pokhrel et al. (2024)	USA	Review of physio-genetic drought mechanisms	3
Romero-Olivares et al. (2024)	USA	Metatranscriptomics of dryland soil fungi	3
Al-Zaban (2023)	Saudi Arabia	*In vitro* temperature × water activity	3
Jin et al. (2023)	China	QTL pyramiding; MAS	4
Prasad et al. (2023)	India, USA	Host-Induced Gene Silencing (HIGS)	4
Khadgi et al. (2025)	USA	Review of multi-omics precision breeding	4
Mamo et al. (2022)	China	Field trial of atoxigenic biocontrol	4

Source: Compiled from the data extraction of seventeen selected articles.

Genetic Tolerance Mechanisms of Peanut against Aspergillus flavus

Peanut tolerance was identified at three hierarchical, interrelated defense levels: physical defense based on seed coat (*testa*) architecture, biochemical defense based on phenolic and flavonoid secondary metabolites, and enzymatic-molecular defense through defense-gene expression (Commey et

al., 2021; Cui et al., 2022; Yu et al., 2024; Zhao et al., 2025). Figure 3 summarizes the dual barrier function of the seed coat, combining a physical barrier from multilayered *testa* architecture and a biochemical barrier from phenolic compounds, working synergistically to inhibit *A. flavus* infection and aflatoxin contamination pre- and post-harvest.

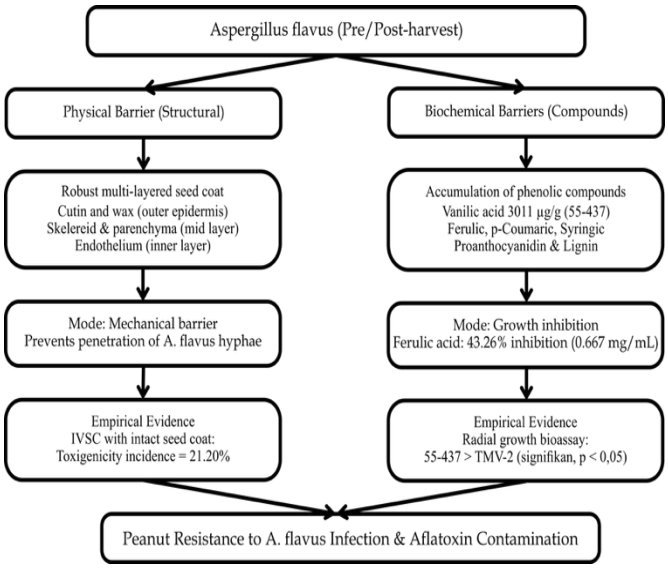

Figure 3. Conceptual framework of the dual barrier function of the peanut seed coat against *Aspergillus flavus* infection, comprising a physical barrier (left) and a biochemical barrier (right) that work synergistically. Conceptual synthesis from (Commey et al., 2021).

Physical defense is mainly mediated by the seed coat as a mechanical barrier and antifungal depot. The In Vitro Seed Colonization (IVSC) experiment showed a toxigenic-strain infection incidence of only 21.20% on intact-coated seeds, versus significantly higher infection in decoated seeds (Commey et al., 2021). Seed coat integrity depends on *testa* thickness, lignin density, and the endocarp and exocarp enveloping the embryo, inhibiting fungal cell-wall enzymes such as pectinase, cellulase, and cutinase (Mendu et al., 2022); mechanical *testa* damage from abiotic stress such as drought increases infection susceptibility.

Biochemical defense is mediated by antifungal and antioxidant secondary metabolites in the seed coat and cotyledons. Integrated metabolomics identified 1,314 metabolites in seed coats of five differently colored cultivars, with flavonoids contributing 44.29% of total metabolites and the anthocyanin *cyanidin-3-O-sophoroside* most strongly associated with resistance (Zhao et al., 2025). Its highest concentration was 10.83 mg/g dry weight in dark cultivars, with a minimum inhibitory concentration (MIC) of 50 µg/mL against *A. flavus*. Phenolic acids dominant in the resistant genotype 55-437, namely hydroxycinnamic and hydroxybenzoic acid derivatives, act as lignin precursors that strengthen the cell wall and inhibit fungal cell-wall enzymes (Commey et al., 2021).

Complementary transcriptomic and metabolomic studies revealed activation of the phenylpropanoid and linolenic acid pathways in the resistant genotype Zhonghua 6 after inoculation, with 5,768 differentially expressed genes and 349 differential metabolites, plus higher accumulation of *resveratrol*, cinnamic, coumaric, and ferulic acids, and 13S-HPODE (Y. Wang et al., 2023). Peroxidase, phenylalanine ammonia-lyase (PAL), lipoxygenase, and chitinase activities were also higher in the resistant genotype, indicating an active post-infection response besides the constitutive one. The findings converge on the phenylpropanoid pathway originating from L-phenylalanine (Figure 4).

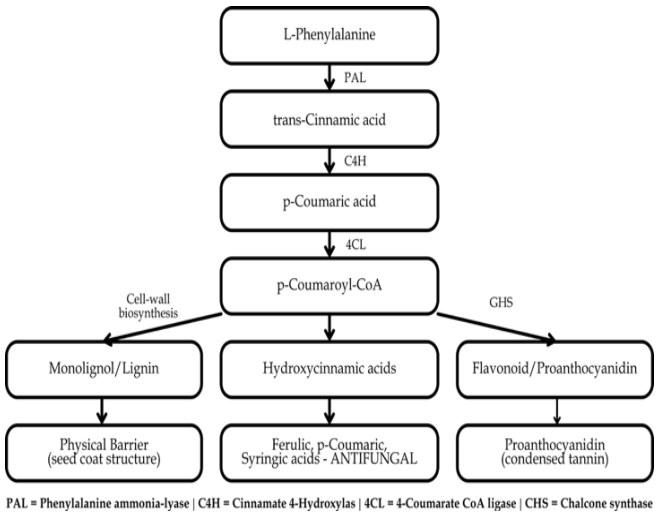

Figure 4. Scheme of the phenylpropanoid biosynthesis pathway in peanut, which is the source of three main groups of defense compounds: monolignol/lignin (left), hydroxycinnamic acids (center), and flavonoid/proanthocyanidin (right). Synthesis from Commey et al. (2021); Wang et al. (2023); Zhao et al. (2025).

Figure 4 shows why PAL is a crucial regulatory point: it catalyzes L-phenylalanine into trans-cinnamic acid, the universal precursor for all pathway branches. Selecting genotypes with constitutively high PAL and chalcone synthase expression could yield multi-mechanism resistance through a single upstream intervention. Table 6 summarizes key biochemical compounds with their pathways and mechanisms, confirming that biochemical defense relies on diverse complementary metabolites rather than a single compound.

Table 6. Key biochemical compounds in the defense of peanut seed against *Aspergillus flavus*

Compound Class	Specific Example	Antifungal Mechanism of Action	Source of Evidence
Anthocyanin	*Cyanidin-3-O-sophoroside* (MIC 50 μg/mL)	Inhibition of mycelial growth; antioxidant	Zhao et al. (2025)
Aurone & chalcone	Aureusidin; naringenin chalcone	Disruption of fungal cell membrane; radical scavenging	Zhao et al. (2025)
Hydroxycinnamic acid	Syringic, p-coumaric, ferulic acids	Lignin precursor; direct antifungal	Commey et al. (2021); Wang et al. (2023)
Hydroxybenzoic acid	Gallic, protocatechuic, vanillic acids	Inhibition of conidial germination	Commey et al. (2021)
Stilbenoid	*Resveratrol* and its derivatives	Phytoalexin; broad-spectrum antifungal	Wang et al. (2023)
Oxylipin	13S-HPODE from the LOX pathway	Defense signalling; jasmonic acid modulation	Wang et al. (2023)
Tannin	Condensed proanthocyanidin	Protein crosslinking; inhibition of fungal enzymes	Mendu et al. (2022)
Total polyphenol	Seed Coat Total Polyphenol (SCTPP)	Resistance biomarker; negative correlation with AFB1	Aminou et al. (2024)

Source: Compiled from the synthesis of Aminou et al. (2024); Commey et al. (2021); Mendu et al. (2022); Wang et al. (2023); Zhao et al. (2025).

A field study in Nigeria of fifty-five ICRISAT mini core genotypes under two water treatments confirmed a strong negative correlation between Seed Coat Total Polyphenol (SCTPP) and AFB1 (r^2 of 0.80 and 0.82) (Aminou et al., 2024). Five tolerant genotypes, ICG 2106, ICG 311, ICG 4684, ICG 4543, and ICG 1415, maintained high polyphenols with minimal AFB1 variation between well-watered and water-stressed conditions, positioning seed coat polyphenols as a resistance biomarker for field-based germplasm screening.

Enzymatic-molecular defense involves defense-gene expression, pathogenesis-related proteins, and signal transduction. WGCNA-based comparative transcriptomics identified eighteen hub genes encoding pathogenesis-related proteins (PR10), MAPK kinase, serine/threonine kinase, pattern recognition receptors, and cytochrome P450, with a faster transcriptional response in the resistant genotype J-11 than in the susceptible Zhonghua 12 (Cui et al., 2022). This priming is consistent with energetically efficient effector-triggered immunity (ETI). QTL mapping found the major QTL qAFTRA07.1 on chromosome A07 and the gene *AhAftr1* encoding an NB-LRR protein, with functional validation showing 57.3% aflatoxin reduction in transgenic plants overexpressing the resistant allele and over 77.67% in thirty-six lines carrying the AFTR.Del. A07 marker (Yu et al., 2024).

A summary of tolerant genotypes and their dominant mechanisms is presented in Table 7 as a reference for selecting donor parents. The Cluster 1 synthesis affirms that peanut tolerance against *A. flavus* is polygenic and multi-mechanism; the convergence of three defense levels in tolerant genotypes such as 55-437, Zhonghua 6, and J-11 forms the empirical basis for multi-trait breeding. The centrality of the phenylpropanoid pathway and PAL is reinforced by characterization of the AhPAL gene family across ten chromosomal genes (Chai et al., 2024), while coexpression network and miRNA analyses clarify host defense regulation (Jayaprakash et al., 2021; Joshi et al., 2025).

Table 7. Tolerant Peanut Genotypes and the Dominant Defense Mechanisms Identified

Genotype	Dominant Defense Level	Main Empirical Evidence	Source
55-437	Physical + biochemical	Inhibition of *A. flavus* by seed coat extract; high vanillic acid	Commey et al. (2021)
Dark-coated cultivar	Biochemical (flavonoid)	*Cyanidin-3-O-sophoroside* 10.83 mg/g; 44.29% of metabolites	Zhao et al. (2025)
Zhonghua 6	Biochemical + molecular	Phenylpropanoid activation; source of the *AhAftr1* allele	Wang et al. (2023); Yu et al. (2024)
J-11	Molecular (priming)	Rapid upregulation of 18 hub genes after infection	Cui et al. (2022)
ICG 2106 et al.	Biochemical (polyphenol)	High SCTPP; minimal AFB1 variation across water regimes	Aminou et al. (2024)

Source: Compiled from the synthesis of five main Cluster 1 studies.

Strain Diversity and Virulence of Aspergillus flavus

Before strain diversity is discussed, the morphology of *A. flavus* on a microscopic preparation is presented in Figure 5 as a reference for morphotype classification. The structural characters, upright conidiophores with round vesicles bearing phialides and conidial chains, branched septate hyphae, and sclerotia as survival structures, form the basis of morphotype classification. Variation in sclerotia size is an early marker that field *A. flavus* populations are heterogeneous, comprising a mixture of morphotypes with different virulence implications.

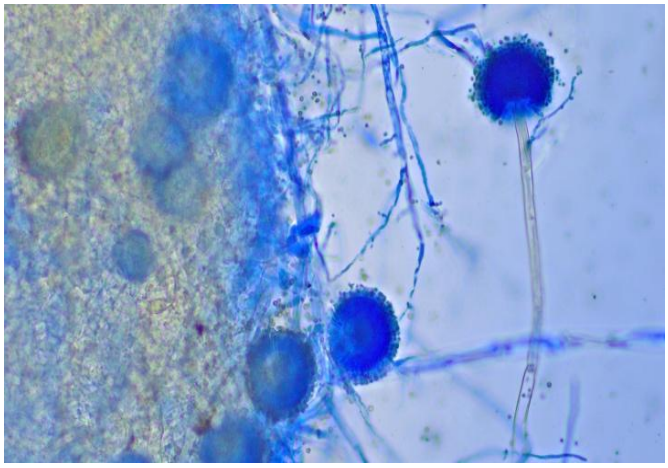

Figure 5. Morphology of *Aspergillus flavus* on a microscopic preparation showing upright conidiophores with large-diameter round vesicles densely covered by phialides and deep-blue conidial chains (top right and center), a network of branched septate hyphae (center and bottom right), and sclerotia as survival structures (left). The preparation was stained with lactophenol cotton blue at 40× objective magnification (Source: Author's personal documentation (Safitri, et al., 2026)).

The strain diversity of *A. flavus* was identified at three levels, morphotype, population structure, and pangenome composition, all related to colonization and aflatoxin production variation. A study of 494 S-morphology isolates in the United States revealed four phylogenetic clades: *A. flavus* S-morphotype (dominant, 89.7%), *Aspergillus agricola sp. nov.* (2.4%), *Aspergillus texensis* (2.2%), and *Aspergillus toxicus sp. nov.* (5.7%) (Singh et al., 2020). These two new taxa show that *A. flavus* diversity has been underestimated because morphology does not distinguish cryptic species. SSR genotyping of 443 isolates revealed 202 unique haplotypes, a very high intra-specific diversity that is a strong reason control strategies cannot be one-size-fits-all.

The L-strain and S-strain differ broadly in virulence, aflatoxin production, and thermal adaptation (Table 8). Of the four clades, only the *A. flavus* S-morphotype still produced aflatoxin at 40°C, while the others declined sharply (Singh et al., 2020). This is relevant to climate change, as rising temperatures may shift populations toward the more thermotolerant S-morphotype; for tropical drylands such as Lombok Island, where daytime temperatures frequently exceed 35°C, this potential dominance warrants attention in characterizing local populations.

Table 8. Comparison of the characteristics of L-strain and S-strain morphotypes of *Aspergillus flavus*

Characteristic	L-strain	S-strain	Source of Evidence
Sclerotia size	Large (>400 µm)	Small (<400 µm)	Singh et al. (2020); Gilbert et al. (2018)
Number of sclerotia	Few	Many	Singh et al. (2020)
Aflatoxin production	Variable, generally low	Consistently high (>1,000 µg/g)	Singh et al. (2020)
Thermotolerance (40°C)	Declines sharply	Continues to produce AFB1	Singh et al. (2020); Al-Zaban (2023)
Phylogenetic diversity	Relatively homogeneous	Divided into 4 clades including 2 new taxa	Singh et al. (2020)
Pre-harvest contamination	Moderate colonization	Severe AFB1 contamination	Singh et al. (2020)

Source: Compiled from (Al-Zaban, 2023; Gilbert et al., 2018; Singh et al., 2020; Tumukunde et al., 2021).

Population genomics based on whole-genome sequencing advanced understanding of *A. flavus* structure. Sequencing of 94 isolates from seven US states identified three differentiated populations: Population A (highest sexual frequency and recombination), Population B (sympatric, lower aflatoxin production from multiple gene deletions), and Population C (largely nonaflatoxigenic, closely related to *A. oryzae*) (Drott et al., 2020). Population C is a natural reservoir of biocontrol strains as competitive exclusion agents. The vegetative compatibility group (VCG) concept is operationally important because biocontrol strains from a locally dominant VCG displace toxigenic populations more effectively than foreign VCGs (Mamo et al., 2022). Population characteristics are presented in Table 9.

Table 9. Characteristics of the three differentiated populations of *Aspergillus flavus*

Population	Sexual Frequency & Recombination	Aflatoxin Production Capacity	Control Implication
Population A	Highest	High (intact biosynthesis cluster)	Main biocontrol target; resistance management
Population B	Moderate	Low (multiple gene deletions)	Reservoir of atoxigenic alleles; recent expansion
Population C	Low	Almost none (largely nonaflatoxigenic)	Candidate biocontrol strain; related to *A. oryzae*

Source: Compiled from (Drott et al., 2020).

The most recent milestone is the AflaPan pangenome from whole-genome sequencing of 346 isolates across various hosts and soils in ten US states (Gangurde et al., 2024). It produced 17,855 unique orthologous gene clusters, 41% (7,315) core and 59% (10,540) accessory, depicting a relatively open, highly adaptive pangenome. Pan-GWAS identified 391 pan-genes significantly associated with aflatoxin production, 369 (94%) from the accessory genome. This shifts the paradigm from the classic 70 kb gene cluster, affirming that aflatoxin regulation involves a complex network of *veA*, *aflR*, *aflS*, and *LaeA* (Tumukunde et al., 2021), with *aflR* as a master switch binding at least 540 genes (P. Wang et al., 2022).

The Cluster 2 synthesis affirms that *A. flavus* strain diversity at morphotype, population, and genome levels is closely related to colonization and aflatoxin production variation. The large accessory genome and the 94% accessory-gene contribution to aflatoxin variation explain why site-specific population characterization is highly important (Gangurde et al., 2024). The *A. flavus* population on Lombok Island is presumed to differ in genetic composition and aflatoxin capacity from US, Chinese, or Nigerien populations, so local characterization is required before broad control is applied.

Host Genotype × Pathogen Strain Interaction under Dryland Stress

Drought stress shifts the host-pathogen balance to favor *A. flavus* through three simultaneous mechanisms: reduced seed coat integrity from osmotic pressure, reduced antifungal secondary metabolite accumulation from phenylpropanoid pathway disruption, and increased aflatoxin production from upregulated biosynthesis genes (Al-Zaban, 2023; Romero-Olivares et al., 2024). The strongest evidence comes from the ICRISAT Sahelian Center, Niger: drought reduced pod yield by 19.49%, seed yield by 27.24%, and haulm yield by 22.07%, while raising AFB1 by up to 54.95% and immature pods by up to 67.16% (Aminou et al., 2024). Contamination exceeding fifty percent in a single stress season affirms the urgency of cultivars maintaining biochemical defense under water deficit.

In vitro experiments on three *A. flavus* isolates across temperature and water activity combinations showed optimum AFB1 production at 34°C with water activity 0.95, whereas at 42°C the high-aflatoxin-producing isolate failed to produce AFB1 (Al-Zaban, 2023). Developmental regulatory gene mapping associated *laeA* with AFB1 production and *brlA* with colonization, both potential RNA interference targets to suppress colonization and aflatoxin production simultaneously. A metatranscriptomics study showed dryland soil fungi increased transcription of pathogenicity and stress genes under global change drivers, modulated by microsite characteristics (Romero-Olivares et al., 2024), confirmed by a supporting study on warming and rainfall reduction effects on dryland pathogenic fungi (Cuartero et al., 2024). Drought effects are summarized in Table 10.

Table 10. Effect of drought stress on agronomic parameters and aflatoxin contamination

Parameter	Direction of Change	Magnitude	Source
Pod yield	Decrease	−19.49% *[moderate]*	Aminou et al. (2024)
Seed yield	Decrease	−27.24% *[moderate]*	Aminou et al. (2024)
Haulm yield	Decrease	−22.07% *[moderate]*	Aminou et al. (2024)
AFB1 contamination	Increase	+54.95% *[moderate]*	Aminou et al. (2024)
Immature Pod Number	Increase	+67.16% *[moderate]*	Aminou et al. (2024)
In vitro AFB1 production (34°C/aw 0.95)	Optimal	Maximum production *[moderate]*	Al-Zaban (2023)
AFB1 production (42°C)	Failed in KSU114	0% in the high-aflatoxin-producing isolate *[extreme]*	Al-Zaban (2023)

Source: Compiled from (Al-Zaban, 2023; Aminou et al., 2024; Romero-Olivares et al., 2024).
Note: *[moderate]* = moderate stress condition (field stress from well-watered to water-stressed; (Aminou et al., 2024); and *in vitro* 34°C / aw 0.95, (Al-Zaban, 2023)); *[extreme]* = extreme temperature condition of 42°C *in vitro* (Al-Zaban, 2023).

Table 10 reveals an important paradox: moderate stress (34°C / aw 0.95) is optimum for aflatoxin production, whereas extreme stress (42°C) suppresses it to production failure. For tropical drylands, the pod-filling stage, generally under moderate stress, becomes the critical pre-harvest contamination period, so planting schedules avoiding this condition can be combined with tolerant-cultivar breeding. Peanut tolerance divides into broad-spectrum tolerance, effective against diverse strains via non-specific defense such as total polyphenols, and strain-specific tolerance via gene-for-gene interaction such as *AhAftr1* (Yu et al., 2024). The optimal strategy is pyramiding both types in the same cultivar, as in line QT 1059 (Jin et al., 2023).

Genotypes ICG 2106, ICG 311, ICG 4684, ICG 4543, and ICG 1415, maintaining high SCTPP, showed minimal AFB1 variation between well-watered and water-stressed conditions, indicating broad, stable polyphenol-based defense (Aminou et al., 2024). The Cluster 3 synthesis affirms that the host genotype × pathogen strain interaction on drylands is three-way and not reducible to two-way, because drought weakens host defense and modulates pathogen pathogenicity and aflatoxin biosynthesis gene expression. For Lombok Island, this requires multi-environment screening that tests broad tolerance against mixed local *A. flavus* strains under field conditions representative of dry-season stress (Pokhrel et al., 2024).

Implications for Seed Quality and Integrated Management Strategy

Seed quality under *A. flavus* infection is evaluated through two critical parameters: seed damage and aflatoxin concentration. Colonization damage includes cotyledon discoloration, reduced seed weight, reduced oil and protein content, and a musty odor lowering market value and seed viability (Mendu et al., 2022). Aflatoxin contamination is most critical, directly affecting food safety and market acceptability; National Food Agency Regulation Number 10 of 2024 sets aflatoxin B1 at 10 µg/kg and total at 15 µg/kg, while the European Union is stricter (4 to 10 µg/kg) (Badan Pangan Nasional, 2024). The AFB1 increase of up to 54.95% under intermittent drought (Aminou et al., 2024) illustrates the risk magnitude for tropical semi-arid farmers, affirming the need for both pre- and post-harvest intervention.

The integrative synthesis points to multi-trait breeding integrating at least five targets: broad polyphenol-based tolerance, strain-specific candidate-gene resistance, physiological drought tolerance, competitive seed weight, and site-specific adaptation. QTL pyramiding is feasible through line QT 1059, combining QTLs for aflatoxin production resistance, infected-seed percentage index, and hundred-seed weight, reducing aflatoxin by 34.77 to 47.67% while raising hundred-seed weight to 47.56 to 49.46 grams, refuting the resistance-yield trade-off assumption (Jin et al., 2023). A precision-breeding roadmap integrating phenotyping under stress, QTL/GWAS, multi-omics, CRISPR validation, and genomic selection offers a comprehensive framework for low-aflatoxin cultivars (Khadgi et al., 2025).

A molecular strategy based on Host-Induced Gene Silencing (HIGS) is highly promising: a 4RNAi construct targeting four *A. flavus* genes (*nsdC*, *veA*, *aflR*, and *aflM*) reduced fungal biomass by 97% and 99% in transformed lines and aflatoxin below 20 ppb (Prasad et al., 2023). However, Indonesian implementation is constrained by genetically modified organism regulations and public acceptance, so non-transgenic strategies such as marker-assisted selection breeding and atoxigenic-strain biocontrol are more practical medium-term. Atoxigenic biocontrol as a competitive exclusion agent is consistently tested: three atoxigenic strains at 25 kg inoculum per hectare reduced aflatoxin by 82.8% to 87.2% without disturbing total soil fungal density (Mamo et al., 2022), confirmed by a supporting study reporting 74 to 99% reduction under co-inoculation (Rasheed et al., 2024).

Integrated control of aflatoxin contamination on drylands requires at least five complementary intervention components (Table 11), aligned with the integrated pest management framework prioritizing blended interventions over a single method. For Lombok Island, implementation should prioritize high-technology-readiness components without genetic modification: seed coat biochemical screening, marker-assisted selection, local atoxigenic-strain biocontrol, and post-harvest management.

Table 11. Components of the integrated control strategy for aflatoxin contamination in peanut on drylands

Intervention Component	Specific Approach	Reported Effect/Benefit in the Literature	Source
Multi-trait breeding	Pyramiding of resistance QTL + yield QTL	AFB1 reduction 34.77–47.67% + high weight	Jin et al. (2023)
Precision breeding	Integration of GWAS, multi-omics, genomic selection	Roadmap for low-aflatoxin-contamination cultivars	Khadgi et al. (2025)
Biochemical screening	Quantification of SCTPP as a biomarker	Identification of broadly tolerant genotypes	Aminou et al. (2024)

Intervention Component	Specific Approach	Reported Effect/Benefit in the Literature	Source
Marker-assisted selection	AFTR.Del. A07 marker for *AhAftr1*	Lines with AFB1 reduction >77.67%	Yu et al. (2024)
HIGS (if regulation permits)	4RNAi construct (*nsdC+veA+aflR+aflM*)	Fungal biomass reduction 97–99%	Prasad et al. (2023)
Atoxigenic biocontrol	Application of 25 kg/ha local atoxigenic strain	Aflatoxin reduction 82.8–87.2%	Mamo et al. (2022)
Water & planting management	Avoid stress during the pod-filling stage	Prevents optimum AFB1 conditions	Al-Zaban (2023)
Post-harvest management	Rapid drying to moisture content <8%	Prevents post-harvest colonization	Mendu et al. (2022)

Source: Compiled from the synthesis of seventeen articles across Cluster 1 to Cluster 4.

The convergence of the four clusters produces a layered integrated management framework: the first layer is multi-trait breeding combining tolerance and productivity QTLs, the second is direct molecular intervention via HIGS, and the third is field biocontrol with atoxigenic strains, all resting on local population characterization and agronomic management (Jin et al., 2023; Mamo et al., 2022; Prasad et al., 2023). Combining breeding with biocontrol theoretically suppresses contamination more effectively than a single intervention, although the additivity of this effect has not been empirically tested in a combined field trial, an important future research opportunity.

Overall, this cross-cluster synthesis provides a contribution unobtainable from partial studies: host tolerance, pathogen strain diversity, and dryland stress are not three separate factors but a single, mutually reinforcing three-way interaction system. Moderate drought stress simultaneously weakens host polyphenol defense and activates pathogen aflatoxin biosynthesis genes during the critical pod-filling period, so intervention against one factor is always weakened by the two unaddressed factors. Consequently, aflatoxin control on tropical drylands demands synergy of multi-trait breeding, local atoxigenic-strain biocontrol, and site-specific agronomic management, while gene editing remains a long-term option requiring regulatory readiness, facilities, and public acceptance. For Lombok Island, the most decisive priority is characterizing the local *A. flavus* population, because without local accessory-gene composition data, donor parent selection and biocontrol strain choice risk missing the target.

Evidence Limitations and Relevance to the Lombok Context

This synthesis has several limitations stated openly for proportional interpretation. First, most evidence comes from international studies, particularly China and the United States (a combined 70.6%), so transferability to Lombok drylands needs testing. Second, characterization data for local *A. flavus* strains on Lombok Island are unavailable to validate the pathogen diversity-contamination relationship locally. Third, as a narrative review adapting only selected PRISMA elements, the synthesis performs no quantitative meta-analysis or formal risk-of-bias assessment, so conclusions are interpretive and dependent on primary-study quality. The recommendations are therefore better positioned as a conceptual framework, applied hypotheses, and follow-up research directions requiring validation through genotype screening and local *A. flavus* strain characterization on Lombok Island.

Several practical considerations should accompany these recommendations. The most realistic genotypes for initial screening are materials easily accessible through national and international germplasm networks such as lines 55-437, J-11, and ICRISAT mini core accessions with documented tolerance, while the most economical campus-laboratory selection parameters are seed coat total polyphenol quantification and the *in vitro* seed colonization assay, which require no expensive genomic facilities. Local atoxigenic-strain biocontrol development can only begin after native Lombok *A. flavus* isolates are characterized, making local population characterization the indispensable first step before adopting other control strategies.

Conclusion

Peanut tolerance against *Aspergillus flavus* is polygenic across three complementary levels: physical, biochemical, and enzymatic-molecular, including the gene *AhAftr1*. Strain diversity at the morphotype, population, and pangenome levels drives site-specific control needs, while the host-pathogen-dryland interaction is three-way, with the pod-filling stage as the critical period. Aflatoxin control therefore requires integrated multi-trait breeding, atoxigenic biocontrol, and agronomic management. As the evidence is dominated by foreign studies without local isolate data, these recommendations remain hypotheses requiring validation on Lombok Island.

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