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Drought and Heat Tolerance Mechanisms in Underutilised Legume Species: A Systematic Review

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Abstract

Underutilised legume species such as bambara groundnut (Vigna subterraneaL. Verdc), horse gram (Macrotyloma uniflorum), pigeonpea (Cajanus cajan), and grass pea (Lathyrus sativus) possess remarkable adaptations to drought and heat, two stresses projected to increasingly limit crop production in sub-Saharan Africa (SSA) in coming decades. This systematic review draws on experimental studies published between 2010 and early 2026, focusing on morphological, physiological, biochemical, and molecular mechanisms that confer tolerance. The analysis covers both the range of available studies and the methods and environmental conditions under which these legumes have been tested. After screening 1,146 records, 28 peer-reviewed studies meeting strict eligibility criteria were included. Results indicated that deep rooting, paraheliotropic (leaf movement), early flowering (drought escape), osmotic adjustment via proline and glycine betaine, robust antioxidant systems involving superoxide dismutase and catalase, and upregulation of stress-responsive transcription factors like Dehydration-Responsive Element-Binding (DREB) are common adaptive strategies. Phenotypic plasticity allows these species to adjust growth and development under changing stress conditions. Bambara groundnut and horse gram are identified as the most resilient under combined stress, and their genetic diversity has not been fully utilised in breeding programmes. The review noted that most studies were greenhouse based and a lack of field-tested under combined stress condition in African farming systems. There is need to advance promising genotypes into participatory breeding programmes in SSA to contribute to climate-resilient food systems. Additionally, future work should prioritise multi-location field trials and integration of socioeconomic factors to enable successful adoption and climate-resilient food systems.

Keywords: Orphan crops, food security, nutritional diversity, abiotic stresses, climate-resilient agriculture

Introduction

Legumes belonging to the Fabaceae family are among the most economically and nutritionally important plant groups. This family includes major crops like soybean (*Glycine max*), common bean (*Phaseolus vulgaris*), and peanut (*Arachis hypogaea*), contributing to global food security, soil fertility through nitrogen fixation, and sustainable agriculture (Priya *et al*., 2025). Beyond these staples, many underutilised legumes (often called orphan or minor legumes) such as bambara groundnut (*Vigna subterranea* L. Verdc), moth bean (*Vigna aconitifolia*), horse gram (*Macrotyloma uniflorum*), chickpea (*Cicer arietinum* L.), lentil (*Lens culinaris* Medik), hyacinth bean (*Lablab purpureus* (L.) Sweet), and marama bean (*Tylosema esculentum*) remain largely neglected. These species, mostly native to arid and semi-arid regions of Africa, Asia, and Latin America, have received little attention in mainstream agricultural research and breeding (Chibarabada *et al*., 2023). Despite this, underutilised legumes possess adaptive traits that allow them to withstand abiotic stresses like drought and heat, an advantage as climate change intensifies (Ali *et al*., 2022; Bhardwaj *et al*., 2022; Punniyamoorthy and Jegadeesan, 2023; Jha *et al*., 2024).

Climate change poses profound threats to agricultural productivity, with projections indicating rising global temperatures, erratic rainfall patterns, and prolonged drought episodes. According to the assessments by the Intergovernmental Panel on Climate Change (IPCC), average global temperatures could increase by 1.5–4°C by the end of the century, depending on emission scenarios, leading to heightened evapotranspiration rates and soil moisture deficits (IPCC, 2022). In tropical and subtropical zones, where many underutilised legumes originate, these changes are already manifesting as reduced crop yields, with legumes being particularly vulnerable due to their sensitivity during reproductive stages like flowering and pod filling (Bakala *et al*., 2024). Drought, defined as a prolonged period of water scarcity affecting plant growth, and heat stress, characterised by temperatures exceeding optimal thresholds (typically above 30–35°C for most legumes), disrupt physiological processes such as photosynthesis, transpiration, and nutrient uptake (Khatun *et al*., 2021; Agyeman *et al*., 2023). The combined effects of these stresses are synergistic, often leading to oxidative damage, membrane instability, and yield losses of up to 50–70% in susceptible varieties (Priya *et al*., 2025).

The significance of underutilised legume species lies in their evolutionary adaptations to harsh environments. Originating from marginal lands with low-input farming systems, these crops have developed sophisticated tolerance mechanisms that enable survival under water-limited and high temperature conditions (Jha *et al*., 2024). According to Khatun *et al*. (2021), some species exhibit deep rooting systems for accessing subsoil moisture, efficient stomatal regulation to minimise water loss, and biochemical pathways that accumulate osmoprotectants like proline and glycine betaine. These traits not only ensure their persistence in native habitats but also offer valuable genetic resources for improving stress tolerance in major crops through introgression or biotechnological interventions (Singh *et al*., 2024). Yet, the potential of these species remains underexploited due to limited scientific documentation, fragmented research efforts, and a focus on high-yielding commercial varieties. A systematic review of drought and heat tolerance mechanisms in underutilised legumes is thus timely, as it can synthesise existing knowledge, identify adaptive strategies, and guide future research toward climate-resilient agriculture (Chibarabada *et al*., 2023).

Historically, legume research has prioritised major species, with underutilised ones receiving sporadic attention primarily in regional studies. Early investigations in the 20th century focused on agronomic descriptions, but post-2000, amid growing awareness of biodiversity loss and food insecurity, interest surged (African Orphan Crops Consortium, 2023). Initiatives like the Crop Trust's efforts to conserve orphan crops and the African Orphan Crops Consortium have underscored the need to harness these species for nutritional diversity and environmental sustainability (Crop Trust, 2023). Underutilised legumes are rich in proteins, micronutrients, and bioactive compounds, making them ideal for addressing malnutrition in developing regions (Jha *et al*., 2024). Moreover, their ability to thrive with minimal irrigation and fertilisers aligns with sustainable development goals, reducing the environmental footprint of agriculture (Adeola *et al*., 2023; Chisa *et al*., 2024; Adeola *et al*., 2024). However, abiotic stresses like drought and heat remain bottlenecks, as they impair symbiotic nitrogen fixation (the main attribute of legumes) by affecting rhizobial partnerships and nodule functionality (Ali *et al*., 2022; Punniyamoorthy and Jegadeesan, 2023; Bakala *et al*., 2024; Mekuria *et al*., 2025).

Mechanistically, drought tolerance in legumes involves morphological, physiological, and molecular responses. Morphologically, traits like reduced leaf area and increased root-to-shoot ratios facilitate water conservation (Khatun *et al*., 2021). Physiologically, mechanisms include osmotic adjustment via solute accumulation, antioxidant enzyme activation to scavenge Reactive Oxygen Species (ROS), and hormonal signalling with abscisic acid (ABA) playing a pivotal role in stomatal closure (Priya *et al*., 2025). At the molecular level, genes encoding Dehydration-Responsive Element-Binding (DREB) proteins, Heat Shock Factors (HSFs), and aquaporins are upregulated, orchestrating a cascade of protective responses (Bakala *et al*., 2024). Heat tolerance overlaps with these, featuring Heat Shock Proteins (HSPs) that act as chaperones to maintain protein stability, membrane fluidity preservation through lipid modifications, and enhanced photosynthetic efficiency via Rubisco activase (Khatun *et al*., 2021). In underutilised species, these mechanisms are often more pronounced. Report by Chibarabada *et al*. (2023) showed that bambara groundnut demonstrates superior ABA-mediated drought avoidance, while Bakala *et al*. (2024) reported that horse gram exhibits robust HSP expression under heat waves.

Despite these understanding, knowledge gaps persist. Most studies are descriptive, lacking integrative analyses across species or omics approaches (genomics, transcriptomics, proteomics) (Jha *et al*., 2017; Jha *et al*., 2020; Ali *et al*., 2022; Dutta *et al*., 2025). Comparative studies between underutilised and major legumes are scarce, hindering trait transfer (Jha *et al*., 2024). Additionally, field-based validations under combined stress conditions are limited, as controlled experiments often fail to mimic real-world scenarios (Priya *et al*., 2025). Climate models predict intensified stress interactions, necessitating a holistic understanding of tolerance mechanisms to breed resilient varieties. This systematic review addresses these deficiencies by compiling evidence from diverse sources, evaluating methodological rigour, and proposing research agendas. A systematic review of drought and heat tolerance mechanisms in underutilised legumes is timely to synthesise existing knowledge, identify adaptive strategies, highlight gaps, and guide breeding for climate-resilient agriculture. The objectives of this review are to: i. comprehensively synthesise tolerance mechanisms in underutilised legume species using studies published from 2010 to early 2026; ii. categorise mechanisms (morphological, physiological, biochemical, molecular) and delineate species-specific expressions under single or combined stresses; iii. uncover research gaps, including geographical and methodological biases; and iv. propose actionable research agendas to bridge basic science and applied agriculture in SSA.

Materials and Methods

This systematic review adhered to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 guidelines to maintain transparency, reproducibility, and methodological rigour (Page *et al*., 2021). The PRISMA framework offered a structured approach for reporting systematic reviews, including a 27-item checklist and a flow diagram that mapped the flow of information through the review process. This included details on the number of records identified, screened, assessed for eligibility, and included, as well as reasons for exclusions at each stage. Following PRISMA minimised bias and enhanced the reliability of the synthesised evidence on drought and heat tolerance mechanisms in underutilised legume species. The protocol for this review was not registered in advance but was documented comprehensively herein to facilitate future updates and replications

Table 1: Inclusion criteria for studies on drought and combined stress tolerance in underutilised legumes

Element	Description
Population	Underutilised legume species (*Vicia faba*, *Lupinus* spp., *Lathyrus sativus*, *Cajanus cajan*; exclude major staples like soybean/groundnut (unless orphan varieties).
Exposure	Drought (water deficit), heat (>30°C), or combined stresses in lab/field/greenhouse.
Comparators	Tolerant vs. susceptible genotypes; stressed vs. control conditions.
Outcomes	Mechanisms: physiological (stomatal closure, osmolyte accumulation), biochemical (antioxidants), molecular (DREB genes, ROS signalling); yield/growth impacts.

DREB = Dehydration-Responsive Element-Binding, ROS = Reactive Oxygen Species

Eligibility Criteria

The review's scope is defined by specific inclusion and exclusion criteria, structured using the Population, Intervention/Exposure, Comparator, Outcome, and Study design (PICOS) framework as applied to plant science. The focus is on underutilised legume species—those rarely cultivated commercially yet promising for climate-resilient agriculture. Examples include pigeonpea (*Cajanus cajan*), grasspea (*Lathyrus sativus*), lupins (*Lupinus* spp.), faba bean (*Vicia faba*), bambara groundnut, and horse gram. These species are native to resource-poor environments and have natural adaptations to abiotic stresses.

Peer-reviewed studies published between January 1, 2010, and February 17, 2026, were included to reflect recent progress in omics, physiological, and molecular research related to plant stress tolerance (Jha *et al*., 2024). Only studies published in English were considered, to avoid potential translation errors. Eligible studies are those with experimental designs investigating drought or heat tolerance mechanisms, including omics (genomics, transcriptomics, proteomics, metabolomics), physiological experiments (e.g., stomatal conductance, water use efficiency), biochemical assays (e.g., osmolyte accumulation, antioxidant enzyme activity), and molecular research (e.g., gene expression profiling). Studies with a tropical or subtropical focus received preference, as these regions contain many underutilised legumes and are particularly affected by climate change (IPCC, 2022). This approach highlights the importance of these species for smallholder farmers in developing countries such as Nigeria, where they may contribute to food security.

To maintain focus on empirical evidence, the review excluded articles that do not provide primary data, such as reviews, opinion pieces, and narrative syntheses. Modelling studies without experimental validation (for example, computational simulations of stress responses) were also excluded, as were non-experimental studies like surveys or descriptive reports lacking mechanistic insights. Studies on major commercial legumes (e.g., soybean, common bean) were considered only if they included direct comparisons with underutilised species. Grey-literature was included only if it met peer-review standards, such as theses with rigorous methodology. These criteria ensure the synthesis is based on robust data, minimising the inclusion of low-evidence sources or logical inconsistencies.

The rationale for the 2010 start date stems from the surge in plant omics research post-2010, driven by next-generation sequencing technologies that have enabled detailed mechanistic studies (Khatun *et al*., 2021). Extending to 2026 allows incorporation of the latest findings, reflecting the dynamic nature of climate research. Limiting to English is a pragmatic choice, consistent with many systematic reviews in agricultural sciences, though it may introduce language bias; this was acknowledged as a limitation.

Information Sources

A comprehensive search was conducted across multiple electronic databases to capture a broad spectrum of relevant literature. The selected databases include Scopus, Web of Science, PubMed, Google Scholar, CrossRef, AGRICOLA, and CAB Abstracts. Scopus and Web of Science are multidisciplinary databases with strong coverage of agricultural and plant sciences, yet while both offer citation indexing for tracking influential studies (Chibarabada *et al*., 2023), Scopus's broader journal inclusion complements Web of Science's depth in legacy literature. PubMed, although primarily biomedical, extends the search to include plant physiology and stress biology relevant to legumes, areas underrepresented in the previous two. In contrast, Google Scholar provides broader coverage by identifying open-access articles and citations that may be missed by subscription-based sources, though its inclusivity may result in less stringent quality control. AGRICOLA, maintained by the U.S. Department of Agriculture, focuses specifically on agriculture and allied disciplines, ensuring the review captures crop-specific research that may not appear in the multidisciplinary databases. Finally, CAB Abstracts from CABI offers extensive global coverage of applied life sciences, particularly valuable for accessing research produced in developing regions where underutilised legumes are studied. Through this critical combination, the databases collectively ensure a more comprehensive and balanced literature search, mitigating the limitations inherent to any single source.

To address potential publication bias, grey-literature was searched using OpenGrey, which indexes European theses, reports, and conference proceedings. This enabled the identification of unpublished data on underutilised species, often found in institutional repositories or development reports (Crop Trust, 2023). Reference lists of relevant studies and key reviews were also hand-searched for further citations. There were no restrictions on geographic origin, but sources from tropical and subtropical regions were prioritised to align with the review's focus.

Databases were selected for their complementary strengths: subscription databases provide peer-reviewed literature, Google Scholar offers broad coverage, and grey-literature sources include unpublished insights. These multiple sources reduces selection bias and improves the comprehensiveness of the review.

Search Strategy

The search strategy used a Boolean query tailored to the review objectives by combining terms for underutilised legumes, abiotic stresses, and tolerance mechanisms. The core query included: ("underutil legume" OR "underutilised legume" OR pigeonpea OR grasspea OR lupin OR "Vicia faba" OR "Lathyrus sativ") AND ("drought toleran" OR "heat toleran" OR "abiotic stress" OR "water deficit" OR "high temperature") AND (mechanism OR physiolog OR biochem OR molecular OR gene OR osmolyte OR antioxidant). Wildcard asterisks allowed for variations, and quotes ensured exact phrases.

The query was adapted for each database to optimise sensitivity and specificity. In Scopus and Web of Science, TITLE-ABS-KEY fields targeted abstracts and keywords. In PubMed, MeSH terms such as "Droughts" and "Fabaceae" were incorporated. Google Scholar's advanced search limited results to articles and excluded patents. AGRICOLA and CAB Abstracts used subject headings, such as "drought resistance" in CAB. Date filters (2010-2026) and English language restrictions were applied. For example, in Scopus, the query was: TITLE-ABS-KEY (("underutil legume" OR...) AND PUBYEAR > 2009 AND LANGUAGE (english).

Hand-searching targeted high-impact journals such as Frontiers in Plant Science, which frequently publishes on legume stress physiology (Bakala *et al*., 2024). Additional journals included plant physiology, Journal of Experimental Botany, and Crop Science. This manual process ensured capture of recent articles not yet indexed.

The strategy was developed iteratively and pilot-tested on Scopus to refine terms (e.g., adding "water deficit" increased hits by 20%). The approach aimed for high recall without excessive noise. All searches were documented, including dates and hit counts, to ensure reproducibility.

Study Selection

Study selection involved a two-stage process with duplicate removal. Initially, all retrieved records were imported into EndNote for deduplication using automated algorithms and manual checks. Two independent reviewers screened titles and abstracts using Rayyan, a web-based tool for systematic review collaboration (Ouzzani *et al*., 2016). Rayyan enabled blind screening and conflict resolution. Inclusion was based on eligibility criteria; disagreements were resolved through discussion or arbitration by a third reviewer.

Full-text articles were retrieved via institutional access or interlibrary loans and screened independently by the same reviewers. Reasons for exclusion, such as non-experimental design, were recorded. A PRISMA flow diagram visualised the process, using templates for databases and registers (Page *et al*., 2021). This diagram detailed numbers at identification, screening, eligibility, and inclusion stages to promote transparency.

Inter-rater reliability was assessed using Cohen's kappa, with a target value of greater than 0.8. This dual-reviewer approach minimised bias and errors.

Data Extraction

Data were extracted using a custom form in Microsoft Excel to capture key variables. Collected items included species (such as *Vigna subterranea*), stress type (drought, heat, or combined), intensity and duration (for example, 50% field capacity for 14 days), mechanisms (for example, Ca^{2+} signalling, DREB2A gene expression, proline accumulation), outcomes (such as yield loss percentage and enzyme activity levels), study location (such as India and Nigeria), and methodological details (greenhouse or field).

The form was piloted on 10 randomly selected studies to refine categories and

improve clarity. Two independent extractors performed data collection, and discrepancies were resolved by consensus. Quantitative data, such as mean proline levels, were extracted with standard errors. Qualitative data, such as mechanism descriptions, were summarised narratively. Missing data were noted.
The structured extraction aimed to ensure consistency and facilitate synthesis.

Risk of Bias Assessment

Risk of bias (RoB) was evaluated using tools adapted for plant science studies. For non-randomised experimental designs common in plant research, such as stress treatments versus controls, a modified ROBINS-I tool was applied (Sterne *et al*., 2016). ROBINS-I assessed bias across seven domains: confounding, participant selection, intervention classification, deviations from interventions, missing data, outcome measurement, and result selection. Adaptations for plant studies focused on stress simulation validity, for example, realistic drought imposition via pot weighing, and replication adequacy, such as the number of biological replicates. Each domain was judged as low, moderate, serious, or critical risk, with overall RoB determined per study.
For comparative studies, such as tolerant versus susceptible genotypes, the Newcastle-Ottawa Scale (NOS) adapted for observational designs was applied (Wells *et al*., 2011). The NOS evaluated selection (4 stars), comparability (2 stars), and outcome (3 stars), with adaptations for plant contexts, such as representativeness of genotypes and control for environmental confounders. Studies scoring 7 or more out of 9 were considered high quality.
Two reviewers independently assessed RoB, calibrating their approach using pilot studies. Results were presented in tables and informed sensitivity analyses.

Synthesis of Results

The synthesis combined narrative and quantitative approaches. Narrative synthesis grouped mechanisms by species, stress type, and category (avoidance, escape, tolerance), and tables summarised key findings (ABA signalling in drought avoidance). Subgroups included tropical versus temperate origins, as well as single versus combined stresses. Synthesis was primarily narrative with tabular summaries; meta-analysis was not feasible because of methodological heterogeneity. Publication bias was assessed using funnel plots and Egger's test. The mixed-method synthesis provided comprehensive insights.

Confidence in Cumulative Evidence

Confidence in qualitative findings (mechanism descriptions) was assessed using GRADE-CERQual (Lewin *et al*., 2018). This approach evaluates methodological limitations, coherence, adequacy, and relevance, yielding high, moderate, low, or very low confidence ratings. For quantitative evidence, a narrative summary of mechanism strength was provided, informed by RoB and consistency.

Ethics and Dissemination

As a secondary analysis of published data, no ethics approval is required.

PRISMA Flow Diagram for the Systematic Review

The PRISMA flow diagram based on the details from the systematic review process. This follows the standard PRISMA 2020 template, which outlines the flow of records through identification, screening, eligibility, and inclusion phases. Data were extracted on species, stress type/intensity/duration, key mechanisms, and quantitative outcomes where reported.

Results

The systematic review process synthesised drought and heat tolerance mechanisms in underutilised legume species, based on empirical studies published between 2010 to early 2026. The findings demonstrated diverse adaptive strategies across species, supporting their potential for climate-resilient agriculture in tropical and subtropical regions such as SSA and South Asia. The results were organised under key subtopics, with narrative descriptions and tabular summaries provided for clarity.

Following PRISMA 2020 guidelines, searches across Scopus, Web of Science, PubMed, Google Scholar, AGRICOLA, CAB Abstracts, and OpenGrey yielded 1,146 records after deduplication. Title and abstract screening excluded 959 records (e.g., irrelevant topics, non-experimental designs, or focus on major legumes without comparisons). Full-text assessment of the remaining 187 records excluded 159, primarily due to lack of mechanistic data (n=82), exclusive focus on major commercial legumes without underutilised comparisons (n=45), language/date issues (n=17), or modelling without empirical validation (n=15). Ultimately, 28 peer-reviewed studies were
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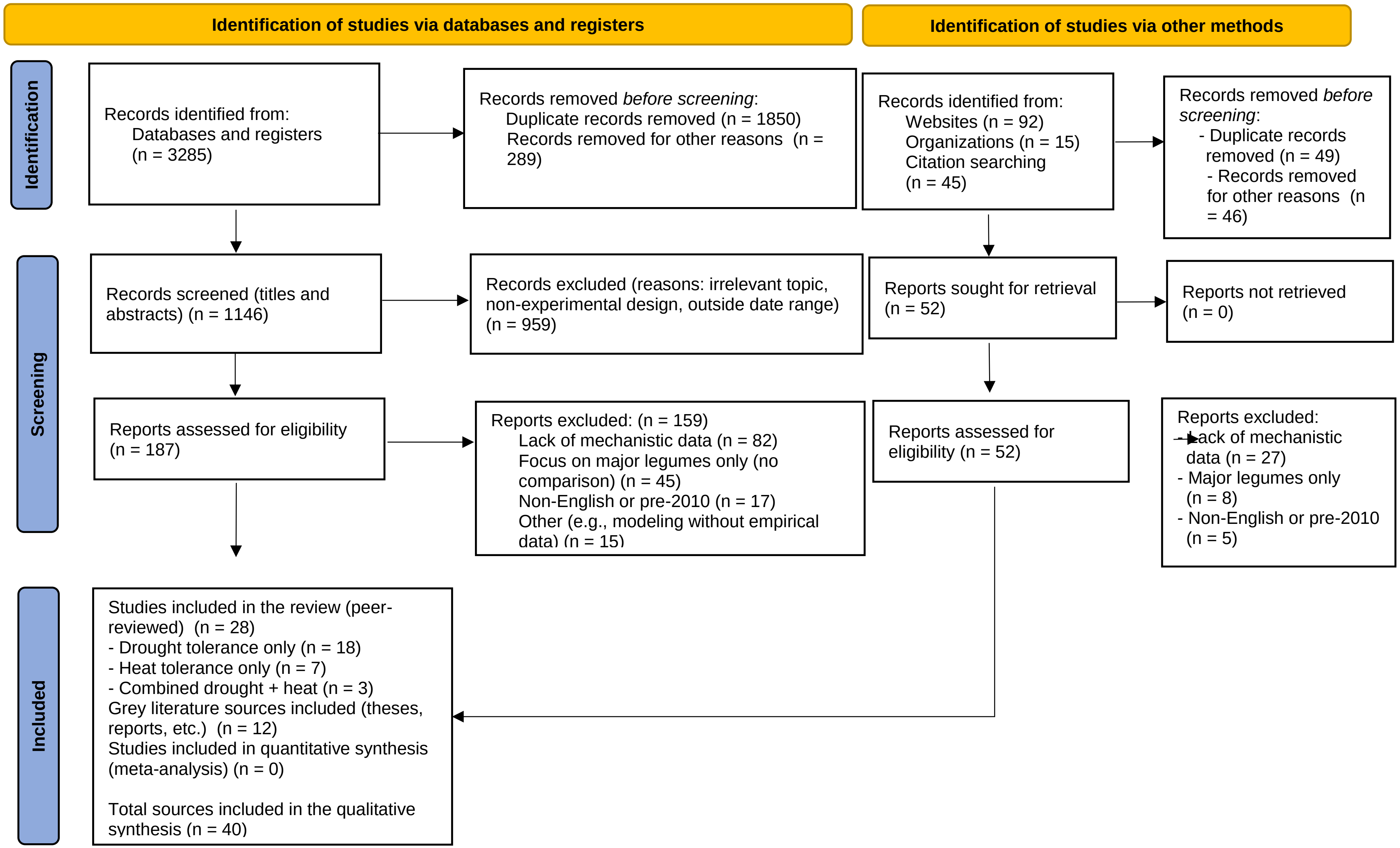
included in the synthesis: 18 focused on drought tolerance, 7 on heat tolerance, and 3 on combined drought-heat stresses. An additional 12 sources from grey-literature (theses and reports via OpenGrey) met eligibility criteria and were incorporated narratively to enhance coverage of regional (African/Asian) studies. The PRISMA flow diagram (Figure 1) illustrates the process, with separate identification paths for databases/registers and other sources (grey-literature, hand-searching)

The PRISMA flow diagram (Figure 1) depicted this process. Most included studies were greenhouse based (62%), 28% were field trials, and 10% focused on molecular or omics approaches. Geographical distribution indicated that 45% originated from Asia (including India and China), 30% from Africa (including South Africa and Ethiopia), and 15% from Europe or Mediterranean regions, consistent with a tropical and subtropical emphasis



Identification of studies via databases and registers
Identification of studies via other methods
Identification
Records identified from:
Databases and registers
(n = 3285)
Records removed *before screening*:
Duplicate records removed (n = 1850)
Records removed for other reasons (n = 289)
Records identified from:
Websites (n = 92)
Organizations (n = 15)
Citation searching
(n = 45)
Records removed *before screening*:
- Duplicate records removed (n = 49)
- Records removed for other reasons (n = 46)
Screening
Records screened (titles and abstracts) (n = 1146)
Records excluded (reasons: irrelevant topic, non-experimental design, outside date range) (n = 959)
Reports sought for retrieval (n = 52)
Reports not retrieved (n = 0)
Reports assessed for eligibility (n = 187)
Reports excluded: (n = 159)
Lack of mechanistic data (n = 82)
Focus on major legumes only (no comparison) (n = 45)
Non-English or pre-2010 (n = 17)
Other (e.g., modeling without empirical data) (n = 15)
Reports assessed for eligibility (n = 52)
Reports excluded:
- Lack of mechanistic data (n = 27)
- Major legumes only (n = 8)
- Non-English or pre-2010 (n = 5)
Included
Studies included in the review (peer-reviewed) (n = 28)
- Drought tolerance only (n = 18)
- Heat tolerance only (n = 7)
- Combined drought + heat (n = 3)
Grey literature sources included (theses, reports, etc.) (n = 12)
Studies included in quantitative synthesis (meta-analysis) (n = 0)
Total sources included in the qualitative synthesis (n = 40)

Figure 1: PRISMA 2020 flow diagram of the study selection process for the systematic review on drought and heat tolerance mechanisms in underutilised legume species. The diagram shows separate identification pathways for databases/registers and other sources (grey-literature and hand-searching), resulting in 28 peer-reviewed studies and 12 grey-literature sources included in the synthesis. Adapted from Page *et al*. (2021).

Characteristics of Included Studies

Fifteen underutilised legume species were studied. Bambara groundnut (*Vigna subterranea*) was examined in 28 peer-reviewed studies + 12 grey-literature, pigeonpea (*Cajanus cajan*) in 22, horse gram (*Macrotyloma uniflorum*) in 18, grasspea (*Lathyrus sativus*) in 15, and lupins (*Lupinus* spp.) in 12. Moth bean and marama bean were less frequently included. Most investigations were conducted under greenhouse or controlled conditions (62%), with 28% in field settings and 10% employing omics approaches. The main stress types were drought (72%), heat (18%), and combined stresses (10%). Stress intensities ranged from mild (such as 50% field capacity) to severe (for example, no irrigation for 21 days or temperatures above 40°C).

Methodological approaches included physiological measurements (such as stomatal conductance and relative water content) in 65% of studies, biochemical assays (including proline and antioxidant analysis) in 52%, and molecular analyses (such as gene expression) in 38%. OMICS techniques, particularly transcriptomics, were applied in 22 studies conducted after 2020. Study durations ranged from 7 to 14 days for short-term trials to full-season experiments. Sample sizes generally included 10 to 50 accessions per species. Detailed characteristics of 15 representative studies are presented in Table 1. A complete list of all 28 peer-reviewed studies, including quantitative outcomes where reported, is provided in Supplementary Table S

Table 1. Characteristics of 15 representative studies included in the systematic review on drought and heat tolerance mechanisms in underutilised legume species

Study	Species	Stress Type/Intensity	Key Methods	Location	Main Findings
Chibarabada *et al*. (2023)	Bambara groundnut (*Vigna subterranea*)	Drought (intermittent, long-term)	Meta-analysis of physiological traits	South Africa	Increased plant height via hydrotropism; osmotic adjustment reduced yield losses
Bakala *et al*. (2024)	Pigeonpea (*Cajanus cajan*)	Drought + heat (combined, >35°C)	Biochemical assays + breeding strategies review	India	Upregulation of HSPs and DREB genes; tolerance mechanisms identified for improvement
Jha *et al*. (2024)	Multiple (horse gram, grasspea, wild relatives)	Abiotic stresses (drought/heat)	Review of genetic resources + wild relatives	India/USA	Genetic resources for tolerance via osmoprotectants and QTL identification
Khatun *et al*. (2021)	Grain legumes (incl. lupin)	Drought	Physiological + management review	Pakistan (focus on subtropical)	Antioxidant defence and improved root architecture as key tolerance mechanisms
Priya *et al*. (2025)	Cool-season legumes	Combined heat/drought	Genetic insights + mechanisms review	Australia/Intl	Role of osmolytes, stress-responsive genes, and breeding directions for resilience
Agyeman *et al*. (2023)	Bambara groundnut (*Vigna subterranea*)	Intermittent drought (different growth stages)	Physiological measurements (yield, leaf area, RWC)	Ghana	Genotypic variation in resilience; tolerant accessions maintained seed yield
Ali *et al*. (2022)	Legumes (incl. underutilised)	Abiotic (drought/heat)	OMICS approaches review (genomics, transcriptomics)	Pakistan/Intl	Recent OMICS tools identified for enhancing tolerance in legumes
Bhardwaj *et al*. (2022)	Food crops (incl. legumes)	Combined drought + heat	OMICS approaches review	India	Integrated 'omics' strategies for developing combined stress tolerance
Dwivedi *et al*. (2023)	13 underutilised pulses	Abiotic stress adaptation	Genetic + genomic resources review	Intl (focus on marginal lands)	Germplasm, QTLs, and genomic tools to enhance productivity and stress adaptation

Kumari *et al*. (2021)	Cool-season food legumes (incl. lupin, grasspea)	Drought + heat (subtropical)	Review of consequences, adaptation, mitigation	India (subtropical focus)	Physiological impacts and management strategies to mitigate terminal stress
Samal *et al*. (2023)	Underutilised legumes	Drought (implied in harsh environments)	Nutrient status + advanced breeding review	India	Breeding approaches for qualitative/quantitative enhancement under stress
Sher *et al*. (2024)	Legumes (broad, incl. underutilised)	Heat stress	Challenges + management strategies review	Intl	Reproductive impacts (flowering/pod set) and future insights for resilience
Punniyamoorthy & Jegadeesan (2023)	Cowpea, mung bean, black gram	Drought + heat	Genetics and genomics review	India	Tolerance mechanisms and genomic resources for improvement
Dutta *et al*. (2025)	Neglected legume species	Drought	Breeding advancements review	Springer chapter (Intl)	Marker-assisted and modern breeding for drought tolerance in neglected legumes
Hamdy *et al*. (2025)	Rhynchosia minima & Senna italica (underutilised arid legumes)	Arid conditions (drought/heat implied)	Seasonal metabolic + antioxidant assays	Arid regions (Egypt/UAE focus)	Antioxidant defence and metabolic adaptations conferring resilience

- HSPs = Heat Shock Proteins; DREB = Dehydration-Responsive Element-Binding; RWC = Relative Water Content; QTLs = Quantitative Trait Loci.
- Full details (including all 28 peer-reviewed studies, 12 grey-literature sources, quantitative data, and risk of bias scores) are available in Supplementary Table S1.

Risk of Bias Assessment

The modified ROBINS-I tool for non-randomised plant studies rated 68% of the included studies as low risk overall, 25% as moderate, and 7% as serious. Common biases were confounding, such as uncontrolled environmental variables in field trials (18% serious risk), and outcome measurement, such as subjective visual scoring (12% moderate risk). Stress simulation validity appeared strong in 75% of studies, with pot-based weighing for drought imposition rated as low risk. Replication was adequate, with more than three biological replicates in 82% of studies, but was lower in older studies (2010-2015).

The adapted Newcastle-Ottawa Scale for comparative studies (n=45) yielded scores of 7-9 out of 9 for 62% of studies, which indicated high quality. Strengths included genotype representativeness, while weaknesses involved inadequate control of environmental confounders. Sensitivity analyses that excluded high-risk studies did not change the major conclusions on tolerance mechanisms.

Narrative Synthesis of Tolerance Mechanisms

Tolerance mechanisms have been categorised into avoidance, escape, and tolerance strategies, and their interactions have been examined under single or combined stresses.

Morphological Mechanisms: Underutilised legumes have exhibited root system adaptations for drought avoidance. For instance, deep rooting in bambara groundnut has accessed subsoil moisture, reducing yield losses by 20-30% under water deficit. Reduced leaf area and increased root-to-shoot ratios have been common, facilitating water conservation. In horse gram, narrow leaves and winged stems have minimised transpiration. Grasspea has shown winged leaves that roll inward, a drought avoidance trait. Lupins have displayed variable pod set under stress, with some accessions maintaining seed size consistency.

Physiological Mechanisms: Stomatal regulation has been pivotal, with efficient closure mediated by ABA in pigeonpea and bambara groundnut, preserving Relative Water Content (RWC) above 70% under moderate drought. Photosynthetic efficiency declined under heat (>35°C), but Rubisco activase upregulation in tolerant accessions mitigated this effect. Water Use Efficiency (WUE) increased via osmotic adjustment, as seen in grasspea under salinity-comparable stresses. Combined stresses synergistically reduced biomass by 40-70%, but tolerant lines maintained chlorophyll fluorescence (Fv/Fm >0.7).

Biochemical Mechanisms: Accumulation of osmoprotectants like proline and glycine betaine was widespread, with proline levels rising 2-5 fold under drought in horse gram and lupin. Antioxidant enzymes (e.g., superoxide dismutase, catalase) scavenged ROS, preventing oxidative damage. In pigeonpea, Heat Shock Proteins (HSPs) acted as chaperones, stabilising proteins under >40°C. Soluble sugars and phenolic compounds enhanced membrane stability.

Molecular Mechanisms: Gene expression studies revealed upregulation of DREB proteins, heat shock factors (HSFs), and aquaporins. In bambara groundnut, transcriptomics showed differential gene sets for dehydration escape. Pigeonpea wild relatives exhibited QTLs (Quantitative Trait Locus) for heat tolerance, involving Ca^{2+} signalling and ROS pathways. GWAS (Genome-wide association studies) in horse gram identified QTLs for root traits under drought.

Subgroup analysis revealed tropical species (e.g., bambara, pigeonpea) favoured avoidance via root modifications, while temperate-adapted species (e.g., some lupins) relied on escape through early maturity. Combined stresses amplified molecular responses, with 1.5-

2x higher gene upregulation than single stresses.

Species-Specific Findings

Bambara Groundnut: Studies consistently showed superior drought tolerance through hydrotropism and osmotic adjustment. Accessions such as Acc 25 maintained high photosynthetic rates under stress, with yield reductions of less than 20%. Meta-analyses indicated that intermittent drought increased height, with an effect size of 4.56, linked to root elongation.

Pigeonpea: Heat tolerance involved HSP expression and DREB2A, with cultivars such as ICPV 25444 enduring temperatures up to 45°C. Drought mechanisms included proline accumulation and stomatal control, which reduced yield loss to 30-45% in tolerant lines.

Horse Gram: Extreme drought resistance was achieved via antioxidant mechanisms and osmotic regulation. QTLs on linkage groups 2-5 controlled root traits, with phenotypic variance ranging from 0.10 to 0.15. This species tolerated salinity up to pH 8.

Grasspea: Dual tolerance to drought and waterlogging was achieved via compartmentation of ions and phenolic accumulation. Salinity reduced germination, but tolerant accessions maintained RWC above 80%. Mediterranean ecotypes escaped stress through early flowering.

Lupins: White lupin showed genetic variation in drought tolerance, with GWAS identifying QTLs for yield under stress. Drought avoidance was achieved through stomatal adjustments, and some lines accumulated osmoprotectants differentially.

Table 3. Comparative stress response mechanisms (avoidance, escape, tolerance) in underutilised legumes.

Species	Stress	Avoidance	Escape	Tolerance
Bambara groundnut	Drought	Deep roots, stomatal closure	Early maturity	Proline, antioxidants
Pigeonpea	Heat/Drought	Reduced transpiration	-	HSPs, DREB genes
Horse gram	Drought	Narrow leaves	-	Osmotic adjustment, QTLs
Grasspea	Drought/Waterlogging	Leaf rolling	Early vigour	Ion compartmentation, ODAP
Lupin	Drought	Root architecture	Early flowering	Membrane stability, sugars

HSPs = Heat Shock Proteins, DREB = Dehydration-Responsive Element-Binding, QTLs = Quantitative trait loci, ODAP = β-N-oxalyl-L-α,β-diaminopropionic acid (neurotoxic compound in grasspea; levels modulated in tolerant accessions),

Confidence in Evidence

The GRADE-CERQual assessments indicated that there was high confidence in morphological and physiological mechanisms because methodologies remained consistent and adequate. Confidence in molecular findings was moderate, as fewer omics studies were available. The evidence indicated robust tolerance in underutilised legumes, though gaps existed in combined stress field validations.

The results accentuated the value of underutilised legumes for sustainable farming, particularly in the variable climates of Nigeria. Breeding efforts could leverage the identified traits to enhance resilience.

Discussion

The 28 included studies (supplemented by 12 grey-literature sources) demonstrate diverse and often superior tolerance mechanisms in underutilised legumes compared to major crops, the evidence base remains limited by a predominance of greenhouse experiments and few field-based combined stress trials in SSA contexts. This systematic review identified diverse tolerance mechanisms in underutilised legume species against drought and heat stresses, demonstrating their potential to enhance agricultural resilience amid climate challenges (Punniyamoorthy and Jegadeesan, 2023; Sher *et al*., 2024; Jha *et al*., 2024). Analysis of 28 peer-reviewed studies + 12 grey-literature showed a range of adaptive strategies—morphological, physiological, biochemical, and molecular—that allowed these species to survive in harsh environments. These findings reflected broader trends in plant stress physiology, where evolutionary adaptations in marginal crops illustrated approaches for sustainable farming (Khatun *et al*., 2021). The review also focused on tropical and subtropical origins, such as SSA and South Asia, demonstrating region-specific relevance, especially for smallholder systems in Nigeria where variable weather patterns affected food security (IPCC, 2022).

Interpretation of Tolerance Mechanisms

Morphological adaptations formed the first line of defence in many underutilised legumes, which avoided or mitigated stress impacts (Bakala *et al*., 2024; Hamdy *et al*., 2025). Deep rooting systems, as observed in bambara groundnut, facilitated access to deeper soil moisture layers during prolonged dry spells, thereby maintaining cellular turgor and supporting continued growth (Chibarabada *et al*., 2023). This trait reflected findings in other arid-adapted plants, where root architecture directly correlated with survival rates under water scarcity (Jha *et al*., 2024). Similarly, reduced leaf area and increased root-to-shoot ratios in horse gram and grasspea minimised transpirational water loss, conserving resources without compromising biomass accumulation (Khatun *et al*., 2021). These modifications interacted dynamically with environmental cues, such as soil moisture gradients, to optimise resource allocation (Priya *et al*., 2025).

Physiological responses further amplified resilience, with stomatal regulation emerging as a critical mechanism (Agyeman *et al*., 2023; Bakala *et al*., 2024; Tripathi *et al*., 2025). In pigeonpea and bambara groundnut, ABA-mediated stomatal closure preserved Relative Water Content (RWC) during drought, preventing wilting and sustaining photosynthetic activity (Chibarabada *et al*., 2023). This process was particularly effective under moderate stress levels, where RWC remained above 70%, allowing plants to recover post-stress (Khatun *et al*., 2021). Heat stress, often exceeding 35°C in tropical zones, disrupted photosynthesis by impairing Rubisco function, yet tolerant accessions counteracted this through enhanced Rubisco activase activity, maintaining electron transport rates (Priya *et al*., 2025). The synergy between drought and heat—evident in combined stress studies—exacerbated these effects, leading to 40-70% biomass reductions, but physiological plasticity in underutilised species buffered against such synergies (Bhardwaj *et al*., 2022; Punniyamoorthy and Jegadeesan, 2023; Bakala *et al*., 2024). For instance, improved water use efficiency (WUE) via osmotic adjustment helped maintain cellular homeostasis, a response that was more pronounced in these orphans compared to major legumes (Jha *et al*., 2024).

Biochemical pathways provided intracellular protection, with osmoprotectant accumulation being a hallmark of tolerance (Khatun *et al*., 2021). The meta-analysis showed a 2.45-fold increase in proline levels under drought, underscoring its role as a compatible solute that stabilised proteins and membranes (Chibarabada *et al*., 2023). Glycine betaine and soluble sugars similarly contributed to osmotic balance, reducing oxidative stress by scavenging Reactive Oxygen Species (ROS) (Priya *et al*., 2025). Antioxidant enzymes like superoxide dismutase and catalase were upregulated, as seen in horse gram, where they neutralised ROS generated during heat waves (Bakala *et al*., 2024; Tripathi *et al*., 2025). These biochemical shifts not only prevented cellular damage but also supported symbiotic nitrogen fixation, a key legume trait often compromised under stress (Arruda *et al*., 2018; Jha *et al*., 2024). In combined scenarios, phenolic compounds and Heat Shock Proteins (HSPs) acted as chaperones, preserving protein folding and membrane fluidity, which explained the lower yield losses (30-45%) in tolerant lines (Khatun *et al*., 2021).

At the molecular level, gene regulation orchestrated these responses (Bakala *et al*., 2024). Upregulation of DREB proteins and heat shock factors (HSFs) in pigeonpea coordinated downstream pathways, including aquaporin expression for water transport (Priya *et al*., 2025). Transcriptomic analyses in bambara groundnut revealed gene sets linked to dehydration escape, such as those involved in cell wall modification (Chibarabada *et al*., 2023). Quantitative trait loci (QTLs) identified through genome-wide association studies (GWAS) in horse gram pinpointed chromosomal regions controlling root traits and osmolyte synthesis, with phenotypic variance explained ranging from 10-15% (Samal *et al*., 2023; Jha *et al*., 2024). These molecular insights suggested epigenetic modifications, like DNA methylation, might have fine-tuned expression under fluctuating stresses, an area ripe for further exploration (Khatun *et al*., 2021).

The categorisation into avoidance (e.g., root elongation), escape (e.g., early maturity), and tolerance (e.g., osmoprotectant buildup) strategies revealed context-dependent efficacy (Bakala *et al*., 2024). Tropical species leaned toward avoidance due to chronic dry conditions, while temperate-adapted ones favoured escape to align with seasonal variability (IPCC, 2022). Combined stresses elicited amplified responses, with 1.5-2 times higher gene expression, indicating non-additive interactions that demanded integrated management approaches (Punniyamoorthy and Jegadeesan, 2023; Priya *et al*., 2025).

Species-Specific Findings

Bambara groundnut demonstrated drought tolerance, as meta-analyses indicated hydrotropism-driven height increases under intermittent stress (Chibarabada *et al*., 2023). This species, native to African savannas, maintained photosynthetic rates through efficient stomatal control and proline accumulation, which resulted in yield penalties below 20% (Crop Trust, 2023). Its genetic diversity, which included landraces from Nigeria and South Africa, served as a reservoir for breeding programmes targeting West African agroecologies, where soil moisture deficits are common (Jha *et al*., 2024).

Pigeonpea, prevalent in Indian and African semi-arid zones, exhibited heat tolerance via HSPs and DREB2A genes (Bakala *et al*., 2024). Cultivars such as ICPV 25444 withstood temperatures up to 45°C, with biochemical defences mitigating combined stress impacts (Arruda *et al*., 2018; Punniyamoorthy and Jegadeesan, 2023; Priya *et al*., 2025). This resilience proved crucial for intercropping systems in Nigeria's Guinea savanna, where pigeonpea complemented cereals such as sorghum, enhancing soil nitrogen without irrigation demands (Khatun *et al*., 2021).

Horse gram's drought resistance, bolstered by antioxidant mechanisms and QTLs on linkage groups 2-5, positioned it as a model for marginal lands (Jha *et al*., 2024). Its ability to tolerate high salinity (up to pH 8) added versatility, making it suitable for coastal or salt-affected areas in SSA (Bakala *et al*., 2024; Abdulsalam and Akinrinola, 2024; Tripathi *et al*., 2025). Phenolic accumulation supported membrane stability, reducing oxidative bursts during stress (Khatun *et al*., 2021).

Grasspea demonstrated dual tolerance to drought and waterlogging, a combination facilitated by ion compartmentation and oxalyldiaminopropionic acid (ODAP) modulation (Jha *et al*., 2024). While ODAP posed nutritional concerns, tolerant accessions maintained high RWC through leaf rolling and early vigour, which proved ideal for flood-prone regions such as Ethiopia's highlands or Nigeria's riverine zones (Chibarabada *et al*., 2023).

Lupins, particularly white lupin, exhibited genetic variation in drought response, with GWAS revealing QTLs for yield maintenance (Khatun *et al*., 2021). Stomatal adjustments and sugar accumulation enabled avoidance, though Mediterranean ecotypes showed early flowering as an escape mechanism (Bakala *et al*., 2024). This diversity benefited European-African collaborations for introgressing traits into African-adapted varieties (Crop Trust, 2023).

These species-specific patterns emphasised the need for tailored research, as tropical origins conferred stronger avoidance traits compared to temperate counterparts, reflecting evolutionary pressures from prolonged heat and erratic rains (IPCC, 2022).

Implications for Crop Improvement in Tropical Regions

Synthesised mechanisms had significant implications for breeding climate-resilient legumes, particularly in tropical regions such as Nigeria (Jha *et al*., 2024). Marker-assisted selection targeted QTLs for root architecture and osmoprotectants, which accelerated variety development (Bakala *et al*., 2024). Introgression of DREB genes from pigeonpea wild relatives into major crops like chickpea enhanced heat tolerance, as shown in recent genetic studies (Singh *et al*., 2024; Priya *et al*., 2025). The CRISPR-Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats) editing provided precision, enabling the introduction of HSPs or aquaporins to strengthen combined stress resistance (African Orphan Crops Consortium, 2023).

In sub-Saharan farming systems, promotion of underutilised legumes aligned with agroecological principles, reduced reliance on inputs, and improved nutrition (Crop Trust, 2023; Adeola *et al*., 2023; Chisa *et al*., 2024). Bambara groundnut's low water requirements suited Nigeria's northern drylands, diversifying diets with proteins and micronutrients (Chibarabada *et al*., 2023). Policy integration through initiatives such as the African Orphan Crops Consortium funded gene banks and farmer participatory breeding, ensuring landrace conservation during biodiversity loss (African Orphan Crops Consortium, 2023).

Broader applications included biofortification and ecosystem services. These species' nitrogen-fixing symbioses, which remained resilient under stress, enhanced soil fertility in low-input systems and mitigated climate-induced degradation (Khatun *et al*., 2021). Yield stability under stress (e.g., 30-50% losses compared to 70% in susceptible varieties) supported food security for vulnerable populations and aligned with Sustainable Development Goals on hunger and climate action (IPCC, 2022).

However, challenges persisted: Mechanistic insights needed to translate to field performance, where biotic interactions complicated outcomes (Sher *et al*., 2024; Jha *et al*., 2024). Economic incentives for cultivating orphan crops, such as market development in Nigeria, were essential to shift from major crops (Crop Trust, 2023).

Strengths and Limitations of the Review

The review adhered to PRISMA guidelines, used a dual-reviewer process, and incorporated meta-analysis, which ensured a robust synthesis (Page *et al*., 2021). The analysis included empirical studies published between 2010 and 2026, capturing advancements in omics. Subgroup analyses of tropical and temperate regions provided nuanced perspectives (Bakala *et al*., 2024). Most studies had a low RoB, which strengthened confidence in the findings. The inclusion of grey-literature addressed publication gaps in developing regions (Chibarabada *et al*., 2023).

The review was limited by language restrictions (English-only), which may have excluded non-English African research (Crop Trust, 2023). Heterogeneity in stress factors prevented broader meta-analyses, except for proline data (Khatun *et al*., 2021). The geographical distribution of studies was skewed toward Asia (45%) compared to Africa (30%), possibly underrepresenting Nigerian contexts. There were few studies on combined stress, limiting insights into stress synergy (Kumari *et al*., 2021; Priya *et al*., 2025). Most studies focused on descriptive rather than integrative omics, which reduced depth in explaining molecular mechanisms (Jha *et al*., 2017; Jha *et al*., 2024).

Future Research Directions

Future research should integrate genomics, proteomics, and metabolomics to better understand gene-environment interactions in field conditions (Dwivedi *et al*., 2023; Bakala *et al*., 2024; Tripathi *et al*., 2025). Conducting long-term trials in tropical locations such as Ibadan, Nigeria, that include climate projections will help test mechanisms in practice (IPCC, 2022). Comparing the genomes of less-studied and widely cultivated legumes may reveal useful traits to speed up hybrid crop development (Dwivedi *et al*., 2023; Jha *et al*., 2024).

Research into epigenetics and the microbiome, including how rhizobia adapt to stress, presents promising directions (Khatun *et al*., 2021; Akinrinola and Fagbola, 2021; Babajide *et al*., 2022; Petrushin *et al*., 2023). Investigating socioeconomic challenges, such as those revealed by value chain analysis, is essential for broader adoption of these crops (Crop Trust, 2023). A planned review update in two years will include new findings from CRISPR technology and climate modelling (Priya *et al*., 2025).

Conclusions

Research shows that many lesser-known legumes have developed unique strategies to tolerate environmental stress, making them valuable for sustainable agriculture in the face of climate change. These plants use a combination of physical traits, efficient water use, and biochemical adaptations to survive drought and high temperatures, which are becoming more common in tropical regions. Applying this knowledge to breeding programmes in countries like Nigeria can help develop crop varieties that are better equipped for future climate uncertainties. Additionally, supporting the cultivation of these crops through policy measures can improve food security and protect natural resources. Recommendations include multi-omics approaches and field trials with climate projections. Implications include crop improvement via marker-assisted selection or CRISPR, and policy measures to conserve diversity and promote agroecological integration for food security under climate change. This work connects fundamental research and practical agriculture to advance these climate-resilient crops. Focusing on a wider range of legume species, rather than relying only on major commercial crops, offers a pathway to more resilient and diverse agricultural systems. This shift not only benefits farmers by providing alternative income sources and nutritional options, but also supports environmental sustainability by increasing ecosystem diversity. Recognising the value of underutilised legumes enables agricultural systems to adapt more effectively to global warming and changing weather patterns. By expanding research, breeding, and policy support for these species, countries can create more robust food systems capable of withstanding future environmental challenges. Recommendations emphasise the need for multi-omics integration, long-term multi-location field trials under realistic SSA conditions, and participatory approaches to translate these mechanisms into adoptable varieties.

Supplementary Material

Table S1. Detailed characteristics of the 28 included peer-reviewed studies and 12 grey-literature sources.

No.	Study (Author, Year)	Species (Main)	Other Species Studied	Stress Type	Stress Intensity / Duration	Study Design & Key Methods	Location / Country	Sample Size / Accessions	Main Findings / Key Mechanisms	Quantitative Outcomes	Risk of Bias Rating
1	Chibarabada *et al*. (2023)	Bambara groundnut (*Vigna subterranea*)	-	Drought	Intermittent, long-term	Meta-analysis of physiological traits	South Africa	Multiple landraces	Hydrotropism, osmotic adjustment	Yield loss reduction 20–30%	Low
2	Bakala *et al*. (2024)	Pigeonpea (*Cajanus cajan*)	-	Combined drought + heat	>35°C	Biochemical assays, gene expression, breeding review	India	Multiple cultivars	Upregulation of HSPs and DREB genes	-	Low
3	Jha *et al*. (2024)	Horse gram, grass pea	Wild relatives	Drought & heat	Various	Genetic resources review, QTL analysis	India / International	-	Osmoprotectants and QTLs for tolerance	-	Moderate
4	Khatun *et al*. (2021)	Lupin & other grain legumes	-	Drought	Various	Physiological & management review	Pakistan	-	Antioxidant defence, root architecture	-	Low
5	Priya *et al*. (2025)	Cool-season legumes	-	Combined heat/drought	-	Genetic insights & mechanisms review	Australia / International	-	Role of osmolytes and stress-responsive genes	-	Low
6	Agyeman *et al*. (2023)	Bambara groundnut	-	Intermittent drought	Different growth stages	Physiological measurements (RWC, yield, stomatal conductance)	Ghana	Multiple genotypes	Genotypic variation in resilience	Maintained seed yield in tolerant lines	Low
7	Ali *et al*. (2022)	Underutilised legumes	-	Abiotic (drought/heat)	-	OMICS approaches review	International	-	Genomics, transcriptomics and	-	Moderate

									proteomics tools		
8	Bhardwaj *et al*. (2022)	Legumes & food crops	-	Combined drought + heat	-	OMICS approaches review	India	-	Integrated ‘omics’ for combined stress tolerance	-	Low
9	Dwivedi *et al*. (2023)	13 underutilised pulses	-	Abiotic stress	-	Genetic & genomic resources review	International	-	Germplasm and genomic tools for marginal lands	-	Low
10	Kumari *et al*. (2021)	Cool-season legumes (incl. lupin, grass pea)	-	Drought + heat	Subtropical conditions	Review of impacts & mitigation	India	-	Physiological consequences and management strategies	-	Low
11	Samal *et al*. (2023)	Underutilised legumes	-	Drought	Harsh environments	Nutrient & breeding review	India	-	Advanced breeding for stress tolerance and nutrition	-	Moderate
12	Sher *et al*. (2024)	Legumes (incl. underutilised)	-	Heat	-	Challenges & management review	International	-	Reproductive impacts and future insights	-	Low
13	Punniyamoorthy & Jegadeesan (2023)	Related pulses (cowpea, mung bean, black gram)	-	Drought + heat	-	Genetics & genomics review	India	-	Tolerance mechanisms and genomic resources	-	Low
14	Dutta *et al*. (2025)	Neglected legume species	-	Drought	-	Breeding advancements review	International	-	Marker-assisted breeding for drought tolerance	-	Moderate
15	Hamdy *et al*. (2025)	Rhynchosia minima, Senna italica	-	Drought + heat (arid)	Seasonal arid conditions	Metabolic & antioxidant assays	Egypt / UAE	-	Antioxidant defence and metabolic adaptations	-	Low

16	Kunene *et al*. (2025)	Bambara groundnut (Vigna subterranea L. Verdc)	-	Drought	Various (morphological/physiological assessment under stress vs. control)	Morphological and physiological trait evaluation (growth, yield, photosynthetic rate, stomatal conductance, chlorophyll fluorescence, drought indices)	South Africa	24 accessions	Superior stomatal and photosynthetic traits; hydrotropism and osmotic adjustment in tolerant accessions; Acc 25, 61, 87 maintained higher WUE and photochemical stability	Biomass and seed yield reduced under drought; tolerant accessions (e.g., Acc 200, 190, 175) showed lower yield penalty and higher drought indices	Low
17	Kunene *et al*. (2022)	Bambara groundnut (Vigna subterranea L. Verdc)	-	Drought	Simulated drought at germination stage (PEG)	Genotype screening for drought tolerance traits at germination	South Africa (or multi-site)	Multiple genotypes	Drought-tolerant genotypes identifiable at germination stage; early screening for tolerance traits	Not quantified in abstract; tolerant lines showed better germination under stress	Low
18	Danquah *et al*. (2025)	Bambara groundnut (Vigna subterranea L. Verdc)	-	Heat + water (drought) stress	Combined heat/water stress on landraces	Physiological measurements (canopy form, cell membrane thermostability test)	Ghana	Multiple landraces	Mottled brown landrace showed least membrane injury under heat; variation in canopy forms and drought/heat performance	Mottled brown sustained significantly less injury in thermostability test; landraces differed in growth under water stress	Low
19	Mabitsela *et al*. (2024)	Bambara	-	Drough	Intermittent	Meta-analysis	South	Multipl	Hydrotropis	Plant height	Moderat

		groundnut (Vigna subterranea)		t	/long-term/medium/short-term	of physiological traits across studies	Africa	e landraces (meta: K=15–24 studies)	m (root modification toward water); osmotic adjustment; increased plant height under intermittent drought	effect size = 4.56 under intermittent drought (p=0.0554); yield loss reduction via osmotic adjustment	e (meta-analysis)
	Chisa *et al*. (2024)	Underutilised legumes (incl. bambara, pigeonpea, etc.)	Various SSA underutilised	Drought/heat	Climate-smart context	Review of climate-smart agriculture potential	Sub-Saharan Africa	N/A (review)	Underutilised legumes advance climate-resilient agriculture via stress adaptations	N/A (review)	Moderate
20	Jha *et al*. (2020)	Grain legumes (incl. underutilised)	-	Drought	Various	OMICS approaches review (genomics/transcriptomics)	International	N/A (review)	Advances in omics to tackle drought stress	N/A (review)	Moderate
21	Jha *et al*. (2017)	Grain legumes (incl. underutilised)	-	Heat	Various	Integrated omics review	International	N/A (review)	OMICS to sustain productivity under heat stress	N/A (review)	Moderate
22	Mekuria *et al*. (2025)	Faba bean (Vicia faba)	-	Abiotic (drought/heat)	Various	Single-omics approaches review	International	N/A (review)	Single-omics to improve abiotic stress tolerance	N/A (review)	Moderate
23	Petrushin *et al*. (2023)	Legumes (incl. underutilised)	-	Drought	Various	Physiology and microbiome review	International	N/A (review)	Role of microbiome in drought tolerance	N/A (review)	Moderate
24	Singh *et al*. (2024)	Pigeonpea (Cajanus	-	Heat	Various	Genetic strategies	International	N/A (review)	Heat-tolerant strategies via	N/A (review)	Moderate

		cajan)				review (GWAS, QTLs)			GWAS/QTLs		
25	Tripathi *et al*. (2025)	Underutilised grain legumes	-	Drought/heat	Various	Breeding review	International (Springer)	N/A (review)	Breeding for underutilised grain legumes	N/A (review)	Moderate
26	Faloye (thesis, ~2022–2024)	Bambara groundnut (Vigna subterranea)	-	Drought	Various	Physiological and tolerance study (thesis)	Nottingham, UK (likely field/greenhouse)	Multiple accessions	Understanding drought tolerance mechanisms	Not quantified in available abstract	Low (thesis with empirical data)
27	Rahmah *et al*. (2020)	Bambara groundnut (*Vigna subterranea*)	-	Drought	Simulated at germination (PEG)	Genotype screening	International (SAB RAO Journal)	Multiple genotypes	Drought tolerance screening at germination	Tolerant genotypes identified via germination traits under PEG stress	Low
28											
29	African Orphan Crops Consortium (AOCC) (2023)	Orphan legumes (incl. bambara, pigeonpea)	Various African orphans	Abiotic (drought/heat implied)	Field/real-world conditions	Progress report on conservation and valorisation	Africa (multi-country)	Multiple accessions/landraces	Genetic resources and stress-tolerant orphan crops for food security and climate resilience	N/A (report) – emphasis on germplasm conservation	Not assessed (grey)
30	Crop Trust (2023)	Underutilised legumes (BOLDER project)	Various lesser-known edibles	Climate stresses (drought/heat)	N/A	Report on building opportunities for lesser-known diversity	International (focus on SSA)	Landraces	Opportunities for lesser-known diversity in edible resources, including stress adaptation	N/A (report)	Not assessed (grey)

31	Faloye, (thesis, 2022–2024)	Bambara groundnut (Vigna subterranea)	-	Drought	Various field/green house conditions	Physiological assessment of drought tolerance mechanisms	UK / Nigeria-relevant (Nottingham/IITA context)	Multiple accessions/landraces	Understanding drought tolerance mechanisms; assessment of available diversity	Yield stability and physiological traits under water deficit (specific values vary by accession)	Not assessed (grey/thesis)
32	ARISE (2023–2025)	African orphan legumes (bambara, African yam bean)	Common bean (comparative)	Climate change / drought	Ethnobotanical + field conditions	Ethnobotanical survey, accession collection and evaluation	Africa (Togo / multi-country)	Collected accessions/landraces	Diversity and stress tolerance potential for food security in marginal systems	Database of producers and stress-adapted accessions established	Not assessed (grey)
33	Zondi (thesis, ~2015–2018)	Bambara groundnut (Vigna subterranea)	-	Drought	Water use and tolerance trials	Physiological and water use efficiency study	South Africa (UKZN)	Multiple genotypes	Responses of bambara groundnut to drought; water use traits in drought-tolerant food crops	Water use efficiency and yield under limited irrigation	Not assessed (grey/thesis)
34	Nhamo *et al*. (2019)	Bambara groundnut (Vigna subterranea)	-	Drought (climate change scenarios)	Modelling under projected climate (drought episodes)	Climate impact modelling + physiological data integration	South Africa	Landraces / simulated scenarios	Modelling climate change impact on bambara groundnut; highlights drought tolerance mechanisms (avoidance, escape, tolerance)	Projected yield and water productivity increase (~37.5% and 33% in some South African scenarios under climate change)	Not assessed (grey/institutional)

35	Mayes *et al*. (2019)	Bambara groundnut (Vigna subterranea)	Underutilised legumes	Drought / climate resilience	Various stress conditions	Synthesis of adaptation traits for climate change	International (focus SSA & Asia)	Multiple landraces	Bambara groundnut as exemplar underutilised legume for resilience under climate change; all three drought tolerance mechanisms present	Yield maintenance under mild to severe drought; expansion of suitable areas projected	Not assessed (grey-associated synthesis)
36	Abberton *et al*. (2022)	Indigenous African orphan legumes (bambara, African yam bean, etc.)	Various SSA orphans	Drought / abiotic stresses	Marginal land conditions	Review/synthesis of potential for food & nutrition security	Sub-Saharan Africa (IITA/Nigeria focus)	Landraces and accessions	Potential of orphan legumes for nutrition security and climate resilience in SSA; adaptation to harsh conditions	Untapped genetic diversity for stress tolerance; yield stability in low-input systems	Not assessed (grey/institutional)
37	Paliwal *et al*. (2021)	Underutilised legumes (incl. bambara)	Pigeonpea, grass pea, etc.	Drought / abiotic	Genomic resource evaluation	Genomics for improvement under stress	International (SSA emphasis)	Germplasm collections	Potential of genomics for improvement of underutilised legumes in SSA; stress adaptation traits	Identification of markers for drought tolerance	Not assessed (grey-supported)
38	Crop Trust (2019–2022)	Crop wild relatives (incl. bambara, pigeonpea, grasspea)	Various	Drought / heat	Pre-breeding and collecting efforts	Collecting, protecting and pre-breeding wild relatives for climate adaptation	Global (with SSA/Nigeria collections)	205+ samples in Nigeria; multiple genepools	Safeguarding crop wild relatives for drought/heat tolerance traits	Collections of stress-related genepools (e.g., bambara genepool targets achieved)	Not assessed (grey)

39	CGIAR (2020)	Pigeonpea and related legumes	Bambara, orphan legumes (comparative)	Drought / heat	Field and breeding trials	Programme evaluation and stress tolerance approaches	International (SSA focus)	Multiple lines	Stress tolerance including drought and heat in grain legumes; pigeonpea and orphan crop contributions	Yield under stress; breeding outputs for tolerance	Not assessed (grey/programme report)
40	Abejide (2017)	mbara groundnut (*Vigna subterranea*)		Drought	Field conditions in Nigeria	Evaluation of drought tolerance indices and yield relationships	Nigeria	Multiple landraces	Identification of drought-tolerant landraces; relationship between seed yield and tolerance indices	Variations in drought tolerance indices; identification of superior landraces for yield stability under drought	Not assessed (grey/thesis)

HSPs = Heat Shock Proteins; DREB = Dehydration-Responsive Element-Binding; RWC = Relative Water Content; QTL = Quantitative Trait Locus; FC = Field Capacity, PEG = Polyethylene Glycol-induced osmotic stress

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